Insect pollination of faba beans, *Vicia faba*

– The abundance and foraging behaviour of different pollinators and their effect on crop yield

Ylva Johansson

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Swedish University of Agricultural Sciences, SLU
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Agronomy – plant and soil science
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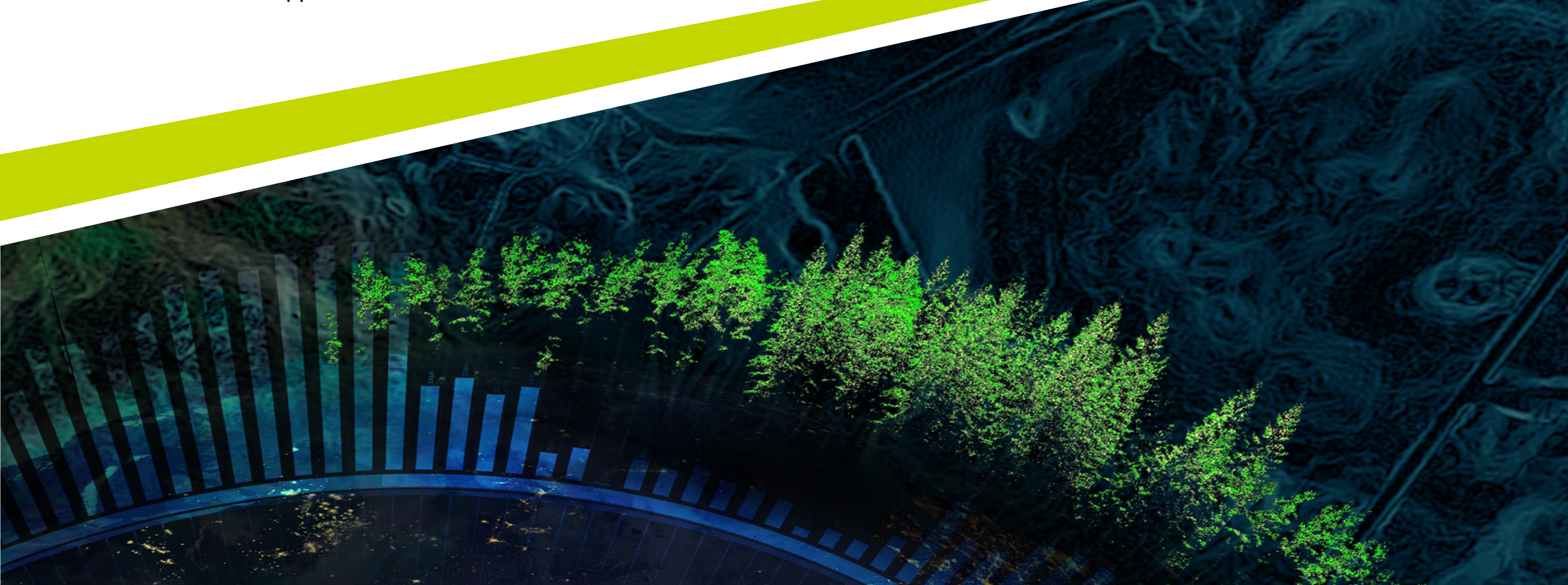

Insect pollination of faba beans, *Vicia faba*

– The abundance and foraging behaviour of different pollinators and their effect on crop yield

Ylva Johansson

Supervisor:	Ola Lundin, Swedish University of Agricultural Sciences, Department of Ecology
Assistant supervisor:	Chloë Raderschall, Swedish University of Agricultural Sciences, Department of Ecology
Examiner:	Erik Öckinger, Swedish University of Agricultural Sciences, Department of Ecology

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Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology

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Abstract

Faba beans, *Vicia faba* is known as a self-pollinating crop, however significant yield increases have been found in plants visited by honeybees and bumblebees. The bees either make positive visits, entering the flower and transferring pollen between different flowers resulting in cross-pollination, or negative visits, piercing the flower to “steal” nectar or collect nectar from extrafloral nectaries. Negative visits do not contribute to cross-pollination, however the movement on the flower facilitates self-pollination, suggesting both positive and negative visits are beneficial to some degree.

In this study the benefit of insect pollination was estimated by comparing the results from different experiments with pollination by honeybees and bumblebees or hand pollination. The mean benefit of insect pollination across a range of yield parameters was calculated by dividing the yield of cross-pollination treatments (insect pollination or hand pollination) with the yield of treatments without cross-pollination. The average benefit of cross-pollination was calculated as 42,6% (both insect- and hand pollination) and 51,8% (only insect pollination), however the range varied between -54% and 245%, due to differences in method, faba bean cultivar, climatic and agronomic factors such as soil conditions. Cross-pollination increased beans and pods per plant, beans per pod and pods per node and more beans reached maturity. However, in some experiments individual bean weight was greater in plants excluded from pollinators resulting in profitable bean yield despite inadequate pollination.

The most efficient pollinating species was found to be the long tongued *Bombus hortorum* due to a relatively large proportion of positive visits, high flower constancy and optimal bodyweight for tripping the flower. However, the honeybee, *Apis mellifera* was most abundant, suggesting it is the most important pollinator in faba bean cultivation despite their relatively lower tendency to make positive visits, making them less efficient on a per visit basis.

Keywords: honeybees, *Apis mellifera,* bumblebees, *Bombus,* faba beans, *Vicia faba,* pollination

Preface

I want to thank my supervisors Ola Lundin and Chloë Raderschall for their help and support during this work. I also want to thank my examiner Erik Öckinger and my opponent Emma Ryding for taking their time to read and review the thesis.

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1. Introduction

Faba bean, *Vicia faba* minor *L.* is one of the oldest crops grown and is used as a protein source for both humans and animals (Bishnoi *et al.* 2012). Faba bean cultivation has declined by 56% globally over the past 50 years (Jensen *et al.* 2010) due to yield insecurities associated with abiotic and biotic factors such as drought- and heat stress, weeds, diseases, pests and the absence of pollinating insects (Karkanis *et al.* 2018). Nonetheless, it is an important crop ensuring food and nutritional security (Bishnoi *et al.* 2012) by being a locally grown protein substitute for imported soybean (Stoltz *et al.* 2013). The local cultivation of faba beans reduce the need of soybean importation and thus reduce the greenhouse gas emissions and expenses from the importation. It also contribute to reduced deforestation of rainforests, which are often cut down to release cropland in soybean cultivation (Stoltz *et al.* 2013). Faba beans also fixate atmospheric nitrogen and make it available to the soil and future crops (Karkanis *et al.* 2018). Therefore faba bean is a valuable crop to include in a more diversified cropping system (Jensen *et al.* 2010). Due to increased awareness about the negative effects that soybean cultivation has on the climate, faba bean acreages has been increasing for the last ten years in many countries, including Sweden, as a locally grown protein-rich fodder (Holmberg 2013).

Faba bean is a self-pollinated crop, however, cross-pollination by insects have several yield benefits, though it varies greatly between cultivars (Bishnoi *et al.* 2012). Cross-pollination depends on insect pollinators, primarily bees and has been associated with increased bean yield; (Riedel & Wort 1960; Free 1966; Kendall & Smith 1975; Poulsen 1975) however, the benefit of insect pollination varies greatly between studies. Low frequency of pollinating insects has been reported by many authors as a major cause of the low and unstable yields, low ratios of pods per flower and beans per ovule, while others claim that yield instability and flower, pod, ovule, and bean abortion do not necessarily or exclusively result from inadequate cross-pollination by insects (Suso *et al.* 1996). Another factor might be differences in foraging behavior among pollinating species that make their pollination unequally efficient (Free 1993). Thus, some pollinating species might be more beneficial in faba bean cultivation than others (Free 1993). Visits by insects are referred to as positive and negative (Poulsen 1975). Positive visits are when pollinators enter the flower to collect pollen and nectar, thereby getting in contact with the male and female parts of the flowers leading to cross-pollination. Negative visits on the other hand, are when pollinators collect nectar by piercing the corolla tube, thus without getting in contact with the pollen and stigma of the flower and not facilitating cross-pollination (Poulsen 1975; Free 1993). There are also insects that collect nectar from extrafloral nectaries located on the base of the flower, thus without entering it and not facilitating cross-pollination either (Free 1962).

1.1. Purpose

The purpose of the essay is to assess the benefits of insect pollination in faba beans, *Vicia faba,* and study the differences in pollinator abundance, foraging behavior and -efficiency of different pollinating species.

2. Background

2.1. Characteristics of faba beans, *Vicia faba*

Faba bean, *Vicia faba,* belong to the family Fabaceae, and is a leguminous crop (Almquist *et al.* 2012). There are two varieties of *Vicia faba*, variety major (broad bean) and variety minor (faba bean) also called field bean. What differentiates them is that broad bean has larger beans and 2-9 ovules while faba bean has smaller beans and 2-4 ovules (Free 1993). In Sweden, faba bean is the most commonly grown variety of *Vicia faba,* mostly used as animal fodder (Holmberg 2013). Its acreage in Sweden has been increasing over the past decade with an increase of 82% between the years 2007 and 2018, as a result of recent interest in locally grown protein fodder and subsidies for a more varied crop rotation (Holmberg 2013; Jordbruksverket 2019).

A typical faba bean plant has between 50-80 flowers, though a large proportion of flowers and pods are shed during the season (Free 1993) partly due to inadequate cross-pollination (Suso *et al.* 1996; Bishnoi *et al.* 2012). The earliest flowers generally appear at the 6th node but the first pods usually do not appear until the 7th or 8th node (Soper 1959). Late flowers on the upper nodes generally do not produce pods (Soper 1959). Plants of the Fabaceae family has the characteristic "butterfly" looking flowers that consist of a rear seal, two lateral wings and a lower keel formed by the corolla, which consists of a standard, two wing petals and two lower petals united along their edges (Almquist *et al.* 2012). The sepals are combined in a five toothed calyx and the flowers have ten stamens, all or all except the upper e.g. the stamens of faba bean, combined into a sheath. Flowers of the family Fabaceae have one single ovary with a varied number of ovules (Almquist *et al.* 2012). The faba bean flowers produce a lot of high quality pollen, however their deep corollas only allow insects with long tongues to reach the nectar via positive visitation (Goulson & Darvill 2004). Under the stipules there are usually a pair of extrafloral nectaries with a scentless bead of nectar that maintain the interest of bees for the crop when no flowers are available (Stoddard & Bond 1987). When the faba bean flowers are ready to be pollinated, papillae on the stigma surface form an exudate which induces pollination (Free 1993). The style then brushes the pollen out of the keel onto the bees which bear the pollen to a different flower. The flowers reopen daily for 6-7 days after anthesis and 2-3 days after pollination. The flowers are fertilized 24 hours after pollination (Free 1993). Pollen is presented from 10.00 to 17.00 h with a peak period between 12.00-15.00 h where 91% is presented (Percival 1955). All new flower buds first open in the afternoon, 74% between 12.00 and 14.00 h (Percival 1965).

In a commercial crop of faba beans about one third of the population consist of hybrid and two thirds of inbred plants, however, the division varies a bit among fields (Kendall & Smith 1975). The hybrids are mostly self-fertile while inbreeds cannot set beans unless visited by insects, therefore about half of their progeny result from cross-pollination (Drayner 1959). This is because inbreeds contain some form of barrier to self-pollination that hybrid plants do not have (Free 1993). It has been suggested that self-pollination in hybrids is favored because of their dense pollen above the style that hinders foreign pollen from entering the stigma, thus insects that enter the flowers push the pollen plug closer to the stigma, favoring self-pollination rather than cross-pollination (Drayner 1959). Faba bean hybrids also produce beans more readily than inbreds, both during cross- and self-pollination (Bishop *et al.* 2020). Bean production in self-pollinating hybrids might result in a moderate harvest in years of poor pollination by insects, however the crops produced from their beans will be inbreds that depend on cross-pollination to set beans (Free 1993). Crops produced by cross-pollination are more vigorous and more susceptible to self-pollination than the progeny by self-pollination, they are also more frost resistant and able to survive the winter (Free 1993; Bishop *et al.* 2020). Cross-pollination gives the population flexibility while self-pollination ensures survival under periods of poor pollination or during fluctuations in the populations of pollinating species (Drayner 1959). However, self-pollination may also require bee visitation in order to cause a movement “tripping” of the flower that shake pollen to the stigma (Soper 1959; Suso *et al.* 1996).

2.2. Abundance of pollinators

Cross-pollination in faba beans depends on insect pollinators, mainly bees (Bishnoi *et al.* 2012). A variety of bumblebee (*Bombus spp.)* species are abundant and widespread in Europe, although *Bombus hortorum* are often low in numbers (Marzinzig *et al.* 2018). However, bumblebees are said to decline all over the world (Larsdotter 2015). The key pollen and nectar sources for bumblebees are plants of the Fabaceae family, thus the reduction of Fabaceae cultivation is the main reason for the radical change in the bumblebee species composition (Bommarco *et al.* 2012). The long tongued species have been more damaged by the cultivation change because they are specialized on flowers with deep corollas such as red clover and faba beans, while short-tongued species are generalists who are better adapted to exploit shallow open flowers (Bommarco *et al.* 2012). There is a correlation between the abundance of bumblebee species and their diet breadth when collecting pollen (Goulson & Darvill 2004). *B. lapidarius* and *B. terrestris agg.* (which include *B. terrestris, B. lucorum* and *B. cryptarum* since they cannot be distinguished under field conditions (Murray *et al.* 2008)) have a broad diet and long colony cycle which give them longer time to eat and develop, thus they are usually more abundant than *B. hortorum* which have a narrow diet and shorter colony cycle, due to later emergence from hibernation (Goulson & Darvill 2004). However, species common in central Europe are declining in Sweden, while species declining in central Europe do not seem to decline in Sweden (Larsdotter 2015). In Sweden the average proportion of *B. terrestris* has increased by 42% and B. *lapidarius* have increased by 7% in the last 70 years while the long tongued species *B. hortorum, B. pascuorum, B. distinguendus* and *B. sylvarum*, steadily have declined over the past 14 years, (Bommarco *et al.* 2012¸ Larsdotter 2015). Especially the five species *B. lucorum, B. magnus, B. cryptarum, B. terrestris* and *B. pascuorum* have declined significantly in Sweden and the species *B. hortorum* and *B. terrestris* have shifted towards the south (Larsdotter 2015).

The honeybee, *Apis mellifera,* is used commercially for crop pollination, thus their abundance depends on beekeeping (Schlipalius *et al.* 2008). Honeybees are well spread all over the globe and most of the range expansion in Europe is a result of human transport (vanEngelsdorp & Meixner 2009). Populations are increasing globally, however, in parts of Europe and North America populations have declined due to diseases, parasites, pesticides, and environmental-, and socio-economic factors (vanEngelsdorp & Meixner 2009). Managed honeybees are the most economically valuable bee pollinators in agriculture globally, however, for some crops e.g faba beans, honeybees are not the most efficient pollinator on a per flower basis (Klein *et al.* 2007; Genersch 2010; Witter *et al.* 2014). This is due to their short tongues, making them more likely to visit the faba bean flowers negatively through holes already bitten by other insects, or collect nectar from extrafloral nectaries (Poulsen 1973)

2.3. Faba bean pollination by insects

The pollinators' different foraging behaviours affect the relative benefit they have for faba bean yield (Poulsen 1973; Tasei 1976). Bees collecting pollen contribute to cross-pollination (figure 1), however, only insects with long tongues can reach the nectar from the deep corolla tube of the bean flowers e.g. the bumblebees *B. pascuorum* and *B. hortorum* (figure 2) (Goulson & Darvill 2004). To obtain the nectar, short tongued bumblebees such as *B. terrestris agg.* bite holes near the base of the flowers to extract nectar from the outside (figure 3) (Stoddard & Bond 1987). This does not make any pollen stick to the insects and therefore these nectar thieves are not contributing to cross-pollination (Poulsen 1975). Only insects entering the corolla tube get in contact with the pollen and stigmas, and thus can contribute to cross-pollination (Free 1993). These types of visits are thus referred to as positive visits while negative visits are when bees collect nectar by corolla piercing, thus without coming into contact with the pollen and stigma of the flower (Poulsen 1973; Kendall & Smith 1975). However, negative visits might cause a movement of the flower, "tripping", which may shake pollen to the stigma, indirectly assisting in self-pollination (Soper 1959). Some species e.g. honeybees cannot bite holes themselves but can use already existing holes made by other insects with stronger mandibles (Free 1962). There are also insects that collect nectar from the extrafloral nectaries located on the underside of the stipules (figure 4), thus these species do not contribute to cross-pollination either (Free 1962).

Figure 1. Positive visit by the bumblebee Bombus terrestris.

Photo: Chloë Raderschall

Figure 2. Positive visit by the honeybee, Apis mellifera.

Photo: Chloë Raderschall

Figure 3. Negative visit by the bumblebee Bombus terrestris.

Photo: Chloë Raderschall

Figure 4. Nectar collection from extrafloral nectaries by the bumblebee Bombus terrestris.

Photo: Chloë Raderschall

3. Material and methods

A literature study was made to conclude the purpose of the thesis. Chapter 34 from the book “Insect pollination of crops” by Free (1993) was handed out by the supervisors and used as an entry point to finding relevant literature. Some of the references used in Free (1993) were then found in the database PubMed and studied more closely. Further articles and books were found using Google Scholar and PubMed using the keywords: “Faba beans”, “pollination of faba beans”, “faba bean Swedish climate”, “Faba bean future”, “Pollinators in faba beans”, “bumblebees”, “honeybees” and “pollinators decline”. Three references were also ordered from the SLU library since they were not available online.

4. Results and analysis

4.1. Abundance and efficiency of pollinating insects in faba beans

Six studies investigating the abundance and behavior of pollinators in faba beans are presented, three performed in England, one in Denmark, one in Germany, and one in France (Free 1962; Kendall & Smith 1975; Tasei 1976; Stoddard & Bond 1987; Bartomeus *et al.* 2014; Marzinzig *et al.* 2018).

4.1.1. Abundance of pollinating species visiting faba beans

The dominant pollinating species in faba beans grown in England were bumblebees (*Bombus spp.*), performing 54,4% of the visits, while in Denmark and Germany the honeybee, *Apis mellifera* were the most frequent, performing 90% and 56% of the visits respectively (Poulsen 1973; Bartomeus *et al.* 2014; Marzinzig *et al.* 2018). The most abundant bumblebee species in the three countries were the short tongued *Bombus terrestris agg* (Poulsen 1973; Bartomeus *et al.* 2014; Marzinzig *et al.* 2018). The other bumblebee species registered were the short tongued *B. lapidarius* and the long tongued *B. hortorum, B. pascuorum* and *B. distinguendus* (table 1) (Poulsen 1973; Bartomeus *et al.* 2014; Marzinzig *et al.* 2018). However, in England, all bumblebee visits were counted together instead of counting the different species separately (Bartomeus *et al.* 2014). In Germany, honeybees were most abundant in early flower stands of faba bean, while *B. lapidarius, B. pascuorum* and *B. hortorum* were more abundant in late flower stands. *B. terrestris agg.* were equally frequent in both flowering stands across the flowering season (Marzinzig *et al.* 2018). The long tongued bumblebee species were the most efficient cross-pollinators due to their relatively large proportion of positive visits. However, because of their low abundance, their overall pollination benefits were limited (Poulsen 1973; Bartomeus *et al.* 2014; Marzinzig *et al.* 2018).

Table 1.Percentage of visits by pollinating insect species in faba beans

Study	Region	Honeybees	Bumblebees total %	*B. terrestris agg*	*B. hortorum*	*B. lapidarius*	*B. pascuorum*	*B. distinguendus*	Solitary bees
(Bartomeus *et al.* 2014)	England	30,4	54,4	-	-	-	-	-	15,2
(Poulsen 1973)	Denmark	90,0	9,8	8,1	0,4	1,0	0,1	0,2	-
(Marzinzig *et al.* 2018)	Germany	56,0	44,0	37,0	4,0	1,7	1,3	0	-

4.1.2. Pollinating efficiency

The foraging behaviours of the pollinating insect species visiting faba beans were observed by supplying standardized transect walks that made notes of the species visiting the fields and their foraging behaviours. In Denmark positive visits by honeybees were 58% and 47% respectively for the years 1969 and 1970 while 21% and 38% of the bumblebee visits were positive (Poulsen 1973). However, the most frequent *Bombus* species, *B. terrestris* made the relatively fewest positive visits. In Germany *B. hortorum* was discovered as the most efficient pollinator since it only exhibited positive visits while the other species mostly made negative visits (Marzinzig *et al.* 2018). *B. hortorum* seemed to have the best morphology for pollen transfer in faba beans due to its long tongue and head easily reaching nectar and its weight for optimal tripping of the flower (Marzinzig *et al.* 2018). Due to high flower constancy *B. hortorum* also carried more intraspecific pollen compared to other bumblebee species, and thus induced higher cross-pollination and bean set (Marzinzig *et al.* 2018). *B. hortorum* was also the most efficient pollinator in a field of hybrid faba beans in France, because it only made positive visits, while almost all individuals of *B. lucorum* and *B. terrestris* made negative visits (Tasei 1976). Among the European bumblebees, other species than *B. hortorum* of the subgenus *Hortobombus* i.e *B. ruderatus,* and *B. pascuorum* usually make positive visits, due to their optimal bodyweight and long tongues (Stoddard & Bond 1987). In contrast, individuals of *B. terrestris agg* seem more likely to make negative visits by biting holes in the corolla base (Stoddard & Bond 1987). Although both *B. hortorum* and *B. pascuorum* have long tongues, *B. pascuorum* was equally efficient in cross-pollination as the short tongued species in Germany (Marzinzig *et al.* 2018).

Foraging behaviour of honeybees and bumblebees in faba beans changes throughout the day and over the flowering season (Free 1962; Poulsen 1973; Kendall & Smith 1975). In Denmark, the percentage of positive bee visits increased later in the day due to changes in the *Bombus* species composition, shifting to more long-tongued species. In addition, *B. terrestris* foragers were more likely to make positive visits later in the day when younger flowers tend to open and new pollen is presented (Poulsen 1973). This indicates a positive relationship between pollen presentation of the flowers and pollen collection of the pollinators. This was also discovered in England, where honeybees visiting extrafloral nectaries tended to be most numerous at midday, before younger flowers had opened, while those making positive visits (especially pollen collectors), were most numerous between 14.00-16.00 at optimal pollen presentation (Free 1962). 86% of the honeybees employed one type of foraging behavior during a single foraging trip while 14% changed between negative visits or visits to extrafloral nectaries (Free 1962). In Denmark the percentage of honeybees collecting pollen decreased during the season while negative visits and gathering of nectar from extrafloral nectaries increased later in the flowering period (Poulsen 1973). However, the percentage of positive visits by *B. terrestris* increased. The increase of honeybees making negative visits was thought to be due to the increase in pierced flowers made by *B. terrestris.* Bumblebees making positive visits were more efficient than those made by honeybees in the fact that they visited more flowers per plant and flowers per minute. *B. distinguendus* was the most rapid visitor (15,3 flowers per minute) while *B. pascuorum* was the slowest (7,0 flowers per minute). *B. terrestris* made 8,6 and honeybees 4,3 positive visits per minute (Poulsen 1973). However, a study in England showed no difference in pollinating efficiency between honeybees and bumblebees when making positive visits to faba beans (Kendall & Smith 1975). One of the English studies showed that piercing of the corolla did not damage the sexual parts of the flower and therefore did not prevent pollination and pod set (Bartomeus *et al.* 2014). In England plants that had negative bee visits even set more pods than plants not visited at all (Kendall & Smith 1975).

4.2. The benefit of insect pollination

There are different ways in measuring the benefit of insect pollination. Studies compare different yield parameters between openly pollinated plants that are visited by the local pollinator community and plants that are enclosed in bags or cages with- or without insect pollinators (honeybee; *Apis mellifera* or the bumblebee species *Bombus terrestris*). In addition, hand-pollinated plants are used to simulate cross-pollination by insects and hand-tripped to simulate negative visits by insects simply by opening the flower facilitating self-pollination. Open pollination measure natural pollination conditions and hand pollination is used to simulate positive control by setting a 100% cross-pollination limit. Cages or bags excluding pollinators work as a negative control by excluding any type of insect pollination. Further, some studies have focused on the whole plant while others have focused on individual flowers when measuring the pollination benefit. Some studies are performed in the lab and some in the field at different locations.

4.2.1. Open pollination

Three studies compared open pollination with pollinator exclusion treatments (Kendall & Smith 1975; Svendsen & Brodsgaard 1997; Bartomeus *et al.* 2014). One of the studies was situated in Denmark where the two faba bean cultivars Alfred and Cargo were grown in open plots and in cages excluded from pollinators (Svendsen & Brodsgaard 1997). The other studies were performed in England where one study kept mesh cages over faba bean plots which were removed when weather was optimal so pollinators could access the plants (Kendall & Smith 1975). They then observed and marked the visited flowers and compared with unvisited flowers and flowers that were hand tripped. The other English study compared openly pollinated flowers with flowers enclosed in nylon bags, thus only exposed to wind and self-pollination (Bartomeus *et al.* 2014).

The Danish study showed that open plots had more beans per pod (ratio 113:100 for Alfred and 115:100 for Cargo) and pods per plant compared to cages excluded from pollinators (table 2). In contrast, plant height and weight per bean generally were higher in the cages. Dry matter content of the beans was similar for both open and caged plots (Svendsen & Brodsgaard 1997). One of the English studies showed great variation in the pod set of flowers not visited by bees, on average 34% pods were set in flowers not visited by bees (Kendall & Smith 1975). These unvisited flowers were able to set beans by self-pollination, thus one third of the plants were suggested to be hybrids (Kendall & Smith 1975). Flowers that had negative bee visits set more pods than plants not visited at all (49% compared to 34%), but less than plants with positive visits (table 2) (Kendall & Smith 1975). According to the other English study insect pollination had no impact on protein content (Bartomeus *et al.* 2014). However, the yield (gram beans per plant) increased by 40% in open pollinated plants compared to plants excluded from pollinators (table 2) (Bartomeus *et al.* 2014).

4.2.2. Honeybees

Five studies investigating the pollination benefit of honeybees in faba beans are brought up. Four of the studies compared open plots with cages with- and without honeybees (Riedel & Wort 1960; Free 1966, 1993; Poulsen 1975) and one tested the effect with honeybee hives placed at different distances from faba bean fields in Australia (Cunningham & Le Feuvre 2013). In one of the cage experiments the relative effect of honeybee-pollination on both broad beans and faba beans was investigated (Free 1966). Three of the studies were performed in England (Riedel & Wort 1960; Free 1966, 1993) and one in Denmark (Poulsen 1975).

In England, plots caged with honeybees set about 50% less beans than open plots but not significantly more than plots caged without honeybees (Riedel & Wort 1960). However, plants caged with bees set a greater percentage of pods on the lower nodes (9, 9 and 2 pods in the bottom, middle and top thirds of the stem) while plants caged without bees set a greater percentage of pods on the upper nodes (3, 5 and 4 pods in the equivalent positions.) This suggests that the concentration of pods on the lower stems are an important indicator of adequate cross-pollination. Plants in cages without bees compensated the inadequate cross-pollination on the lower inflorescences by setting a greater number of beans on the upper inflorescences, thus still gave a moderate yield (table 2) (Riedel & Wort 1960). Another English study found that plots caged with bees set fewer beans per pod than open plots although significantly more than those caged without bees (table 2). Significantly more beans matured, however weighed less, thus the total bean weight per plant was not significantly greater in plots caged with bees compared to plots caged without bees (Free 1993). Plants in plots without bees had a greater ovule abortion, thus produced fewer beans, which was compensated by making the beans larger (Free 1993). Open plots produced significantly more beans per pod than caged plots with bees and the individual bean weight was greater (table 2).

The Danish cage experiment showed that plants caged without bees gave 26% lower yield (beans per plant and m^2) than plants caged with bees and the result varied little between the years (20-30%) despite climatic differences (Poulsen 1975). Bee pollination increased pods per plant and beans per pod, however weight per bean was 5% higher in cages without bees. The increase in bean yield was concentrated on the lower inflorescences and bean set also initiated earlier in the bee pollinated plants independent of the position on the stem, the bee pollinated plants also ripened earlier. Plants kept without bees set a greater percentage of pods in higher inflorescences due to a smaller tripping requirement in late developed flowers (Poulsen 1975).

In Australia, pods per plant decreased with increasing distance from the honeybee hives (Cunningham & Le Feuvre 2013). There was also a significant negative effect of distance from hive on the number of early and mature pods (9.1 mature pods per plant at 0 m distance and 5.9 pods per plant at 550 m). Thus, vicinity to bees raised pod set 54%. The activity of the bees also decreased with increased distance from the honeybee hives (Cunningham & Le Feuvre 2013). In England, bee pollination did not greatly increase bean yield in faba beans but in broad beans it did (Free 1966). Plants enclosed with bees produced more beans per plant and pod for both faba and broad beans compared to plants excluded from bees (table 2). However, open plots had about twice as many pods, beans per plant and higher weight per bean than those caged with bees. Broad beans caged with bees also produced heavier beans and more mature pods at the first harvest than those caged without bees, but the total number of beans produced during both harvests were less in the caged plots than in the open due to a greater setting of early flowers of the open pollinated plants (Free 1966).

4.2.3. Bumblebees

Three experiments investigating the pollinating benefit of bumblebees for faba bean yield are presented. Two in Sweden (Käck *et al.* 2012; St-Martin & Bommarco 2016) and one in England (Bishop *et al.* 2015). All studies used the species *B.*

terrestris. One of the Swedish experiments kept faba beans in cages without pollinators, cages with colonies of *B. terrestris* and open pollinated plots (Käck *et al.* 2012). The other Swedish experiment kept faba bean plants, variety Fuego, in PCV tubes in a greenhouse together with a hive of *B. terrestris* (St-Martin & Bommarco 2016). The beans were sown in soil from two different crop rotation management types, (-barley monoculture versus ley-dominated six-year rotation). The inflorescences of half the plants were covered with a bag (2mm mesh size) to prevent bumblebee pollination while the other half was accessible for visits by *B. terrestris* (St-Martin & Bommarco 2016). The English experiment investigated the effect of heat stress on insect pollination in faba beans (Bishop *et al.* 2015). Faba bean plants were exposed to heat stress for 5 days during floral development and anthesis, some plants were pollinated by *B. terrestris* and some received no insect pollination (Bishop *et al.* 2015).

The study with cages in the field found that the yield was significantly greater in the open pollinated treatment and lowest in the cages without pollinating insects with a difference of 21%. Pods per plant, beans per pod and beans per plant increased with insect pollination (open- and cages with pollinators), the plants also reached maturity earlier, thus the water content at harvest was lower. The beans from the insect pollinated plants also had a higher germination rate and the weight per bean increased. However, insect pollination did not affect the protein content of the beans (Käck *et al.* 2012). The Swedish study performed in a greenhouse showed that plants pollinated by bumblebees had 38.1% higher bean yield (g/plant), produced 44.3% more beans per plant and had 33.4% more beans per pod than plants excluded from bumblebees (St-Martin & Bommarco 2016). There was a positive correlation between bean yield, beans per plant and pods per plant. There was an interaction between the bumblebee pollination benefit and the soil type. Plants excluded from bumblebees that were grown in soil from ley rotation had 32,4% lower bean weight and 40,8% fewer pods per plant, while there was no effect of bumblebee pollination on weight per bean or pods per plants in plants grown in soil from barley monoculture (St-Martin & Bommarco 2016). The heat stress experiment showed that pollinator benefit was 16% at control temperatures (18-26 degree Celsius) and extreme stress (34 degree Celsius) but 53% at intermediate stress at 30 degree Celsius (Bishop *et al.* 2015). At 30 degree Celsius plants without bumblebee pollination got a 15% yield loss (bean weight per plant) under heat stress, while plants pollinated by *B. terrestris* got a 2,5% yield loss (Bishop *et al.* 2015).

4.2.4. Hand pollination

Four experiments with hand pollination are presented. In one experiment- flowers in a field of faba beans in England were self- and cross-pollinated by hand and some were left some to be pollinated naturally (Free & Williams 1976). The other experiments were performed by Bishop *et al.* (2020) and tested the pollination requirements in different faba bean cultivars. The first two experiments were performed during 2017 and 2018 in a lab where five different faba bean cultivars Diana07, Fuego, Fury, Vertigo and Hedin/2 were grown in pots covered with mesh cages. Three treatments were used, cross pollination by hand, self-pollination by hand and natural self-pollination. The treatments should simulate cross-pollination by bees, tripping (opening of the flower facilitated by bees without cross-pollination) and auto fertility (self-pollination without the tripping by bees). The third experiment was performed in 2018 outside in the field on the three cultivars Fuego, Fury and Vertigo. The treatments were: undisturbed plants covered with mesh net, which simulated self-pollination (auto fertility without tripping by bees), self-pollination by hand (tripping) of plants covered with mesh net and open pollination outside the net (cross-pollination). Further, the economic value of insect pollination (average of cross- and self-pollination by hand) in the different cultivars was investigated based on the relative pollination dependence calculated as (mean yield of plants receiving pollination– mean yield of plants without pollination)/mean yield of plants receiving pollination. The economic value was estimated from the average total market value of UKs faba bean crop year 2015-2017 (values taken from the 2018 Agriculture in the UK report) that was £565.61/ha corresponding to 4604 SEK/ha per year 2018 (Dollartillsek.se 2018).

In one experiment hand pollination, both by self- and cross-pollination increased the number of pods per node and beans per plant compared to open plots (Free & Williams 1976). However there was no significant benefit with cross pollination over self-pollination (Free & Williams 1976). The benefit of hand pollination showed great variation among different faba bean cultivars. Bean weight varied between the cultivars from a 58% increase to 51% loss with self- and cross pollination. The bean weight also varied within the same cultivar depending on if the experiment was performed in a cage or open field, ranging between 10% loss and 37% increase, between the years it varied between 4-33% increase in one cultivar. The yield parameter measured also affected the estimate of pollination benefit ranging between -4% and 46% increase within the same cultivar and year. The difference in pollination benefit between the cultivars was partly due to different levels of self-pollinating ability (selfing). Self-pollination seemed to be heritable and more present in hybrids, which also typically gave a greater yield (Bishop *et al.* 2020). The pollinating benefit varied widely between the cultivars, year, whether the experiment was conducted in the laboratory or in the field, and which yield parameter was used. The economic value differed between −£55.6M corresponding to -452,6M SEK per year in 2018 (Dollartillsek.se 2018) (pod number in Hedin/2) and £76.4M corresponding to 621,9M SEK per year in 2018 (Dollartillsek.se 2018) (bean number in Diana07). The two experiments performed in the laboratory gave no significant difference in yield between self-pollination (including tripping) and cross-pollination within the same cultivar, however the effect of pollination treatment on yield parameters i.e. bean weight per plant, pods per plant and beans per pod varied significantly with cultivar (Bishop *et al.* 2020). There was a non-linear association between bean number and bean weight per plant indicating that more beans led to lower weight per bean (Bishop *et al.* 2020). The experiment in the field showed that the treatments had no significant effect on bean number or bean weight per plant within the cultivars but varied among cultivars. However, again more beans per plant led to reduced weight per bean (Bishop *et al.* 2020)

4.2.5. Compilation of studies

The results from the experiments presented in section 4.2 is discussed in this thesis and are presented in table 2. Table 2 is a compilation of some of the studies brought up in this thesis, with their relative results on the benefit of insect pollination. The yield difference is calculated by dividing the yield of cross-pollination treatments (insect pollination or hand pollination) with the yield of treatments without cross-pollination. The yield measurements included in the table are beans per pod, beans per plant, pods per plant, weight per bean and bean weight per plant. Figure 5 is a compilation of all values from table 2. An average yield parameter increase with cross pollination (all values included) is 42,6%. Among the studies the average value for beans per pod is 31,0% (10 studies), beans per plant 55,4% (9 studies), pods per plant 34,8% (6 studies), weight per bean 12,5% (2 studies) and bean weight per plant 89,9% (4 studies).

However, a comparison including only pollination by insects change the average yield increase with insect pollination to 51,8%. The average of beans per pod changes to 31,5% (7 studies), beans per plant 56,5% (6 studies) and pods per plant 53,1% compared to cages with no insect pollinators (3 studies). A comparison between the experiments with insect pollination using cages in field i.e. Riedel & Wort (1960), Free (1993), Free (1966) Svendsen & Brodsgaard (1997) and Käck (2012) show an average yield increase in cages with bees 30,6% and open plots 81,6%. A comparison of the same yield measures change the average for beans per plant 35,7% (cage) (7 studies) and 90,0% (open) (5 studies), beans per pod 17,8% (cage) (5 studies), 48,0% (open) (5 studies), pods per plant 30,7% (cage), 82,9% (open) (2 studies) (figures 6 and 7).

Table 2. Compilation of results from different studies of the benefit of insect pollination in faba beans

Study	Treatments	Poll	Measure	Yield with insects		Yield without insects		Difference yield with insects/yield without insects (%)	
(Kendall & Smith 1975)	Visited flowers Open Hand tripped	HB and BB	Beans/ pod	**Average of pos and neg visits** 3,52		**Undisturbed** 3,21	**Hand tripped** 3,26	**Visited/undisturbed** 9,7	**Visited/hand tripped** 8,0
(Bartomeus *et al.* 2014)	Open Flowers in net	HB and BB	Bean w/ plant	-		-		40	
(Svendsen & Brodsgaard 1997)	Cage – Open	HB and BB	Beans/ pod	**Alfred** 3,43	**Cargo** 3,47	**Alfred** 3,00	**Cargo** 3,14	**Alfred** 14	**Cargo** 11
(Riedel & Wort 1960)	Cage + Cage - Open	HB	Beans/ plant	**Cage** 17,6	**Open** 28,3	13,1		**Cage** 34	**Open** 116
(Free 1966)	**Broad beans** Cage + Cage –	HB	Pods/ plant Beans/ pod Beans/ plant	**Cage** 12,6 5,95 23,9	**Open** 19,98 7,26 41,1	7,9 4,28 15,1		**Cage** 59 39 58	**Open** 153 70 172

	Open		Weight/ bean	3,23	3,44	2,54	27	35
			Bean w/ plant	36,7	65,9	19,3	90	241
(Free 1966)	**Faba beans**	HB		**Cage**	**Open**		**Cage**	**Open**
	Cage +		Pods/ plant	6,95	10,2	5,77	20	77
	Cage –		Beans/ pod	2,67	3,08	2,5	6,8	23
	Open		Beans/ plant	18,1	31,8	14,5	25	119
			Weight/ bean	0,63	0,665	0,689	-8,6	-3,5
			Bean w/plant	11,58	21,38	9,97	16	114
(Free 1993)	Cage +	HB		**Cage**	**Open**		**Cage**	**Open**
	Cage –		Beans/ pod	18,1	31,8	14,5	25	119
	Open							
(Poulsen 1975)	Cage +	HB		**Cage**	**Open**		**Cage**	**Open**
	Cage –		Beans/ pod	2,79	2,96	2,50	11,6	18,4
	Open		Pods/ plant	9,10	8,53	-	-	-
			Beans/ plant	10,84	10,80	9,17	18,2	18,0
(Cunningham & Le Feuvre 2013)	Beehives	HB	Beans/ plant	**Distance 0m**		**Distance 550m**		
				9,1		5,9	54	
(Käck *et al.* 2012)	Cage +	BB		**Cage**	**Open**		**Cage**	**Open**
	Cage –		Beans/ pod	3,3	3,4	3,1	6,5	9,7
	Open		Pods/ plant	13,9	14,6	12,3	13,0	18,7
			Beans/ plant	25,9	27,7	22,3	16,1	24,2

(St-Martin & Bommarco 2016)	[1]Closed bags Open	BB	Bean w/ plant	-					-					38,1				
			Beans/ plant	-					-					44,3				
(Bishop *et al.* 2020)	[1]Cage SP by hand (trip) Cage CP by hand Undisturbed plants	HP		[2]Diana	Fuego	Fury	Vertigo	Hedin	[3]Diana	Fuego	Fury	Vertigo	Hedin	Diana	Fuego	Fury	Vertigo	Hedin
			Beans/ plant	38	44	44,5	42	59	11	23	26	33	68	245	91	71	27	-13
			Pods/ plant	15	13,5	15	13,5	20	6	9	11	12	22	150	50	36	12	-9
			Beans/ pod	2,6	3,3	3	3,1	3,0	1,9	2,6	2,1	2,6	3	37	27	43	19	0
(Bishop *et al.* 2020)	[1]SP by hand (trip) Cage CP by hand Undisturbed plants	HP		[2]Diana	Fuego	Fury	Vertigo	Hedin	[3]Diana	Fuego	Fury	Vertigo	Hedin	Diana	Fuego	Fury	Vertigo	Hedin
			Beans/ plant	10	11,5	14	18	16	3	9	9	18	32	233	28	56	0	-50
			Pods/ plant	4,5	4,5	6	6	5,5	2	4	6	6	12	125	13	0	0	-54
			Beans/ pod.	2,2	2,8	2,5	2,7	5,9	1,2	2,5	1,4	2,6	2,7	83	12	79	4	119
(Bishop *et al.* 2020)	Cage - SP by hand (trip) Open (cross)	HP		[2]Fuego		Fury		Vertigo	[3]Fuego	Fury		Vertigo		Fuego		Fury	Vertigo	
			Beans/ plant	15		19,5		18	16	21		16		-6		-7	13	
			Pods/ plant	6		8,5		7	7	9		6		-14		-6	17	
			Beans/ pod	2,4		2,4		2,5	2,4	2,3		2,7		0		4	-7,4	

[1] Experiments in lab *[2] Mean trip and cross* *[3] Self-pollination* *SP=self-pollination* *CP=Cross-pollination* *HB=Honeybees* *BB=Bumblebees*
HP=Hand-pollination *Bean w=Bean weight* *Diana=Diana07* *Hedin=Hedin/2*

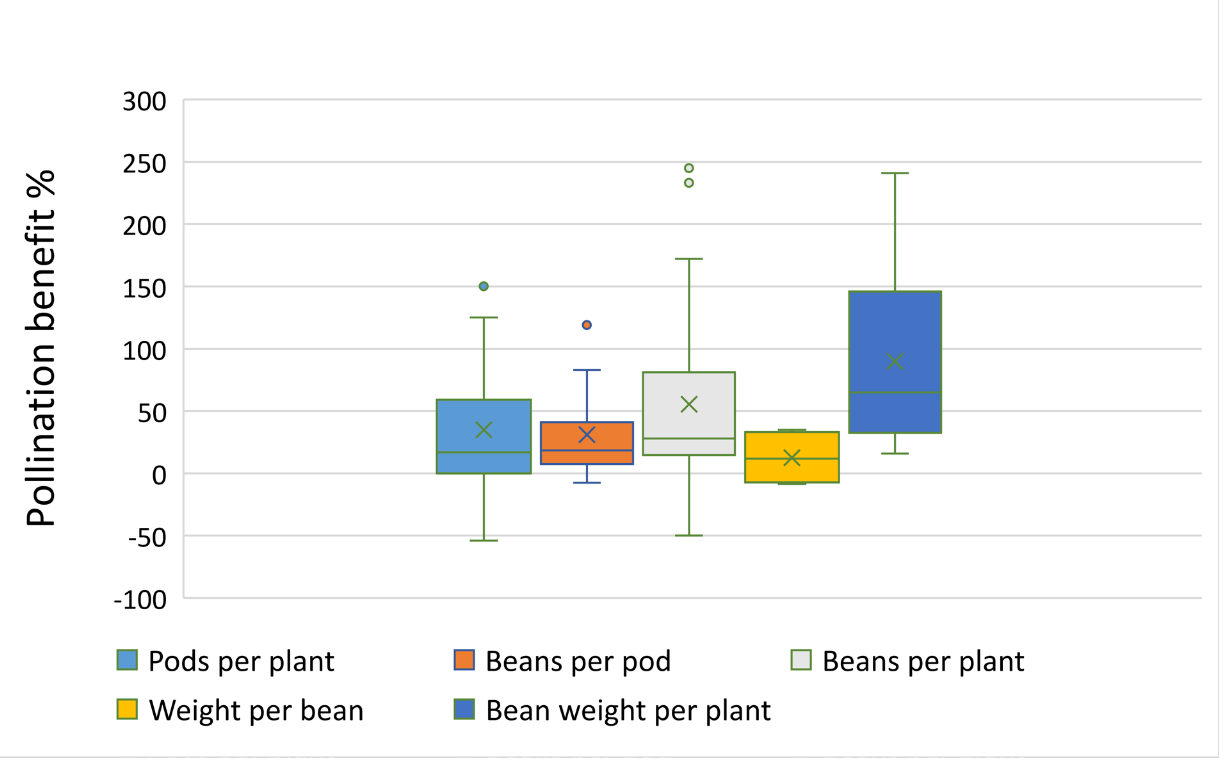

Figure 5. The difference in yield parameters between treatments with pollinators compared to treatments without pollinators. All studies included with the different yield measurements divided in separate stacks. The boxes mark the first and third quartile, x is the median and I mark the minimum and maximum values in the data set.

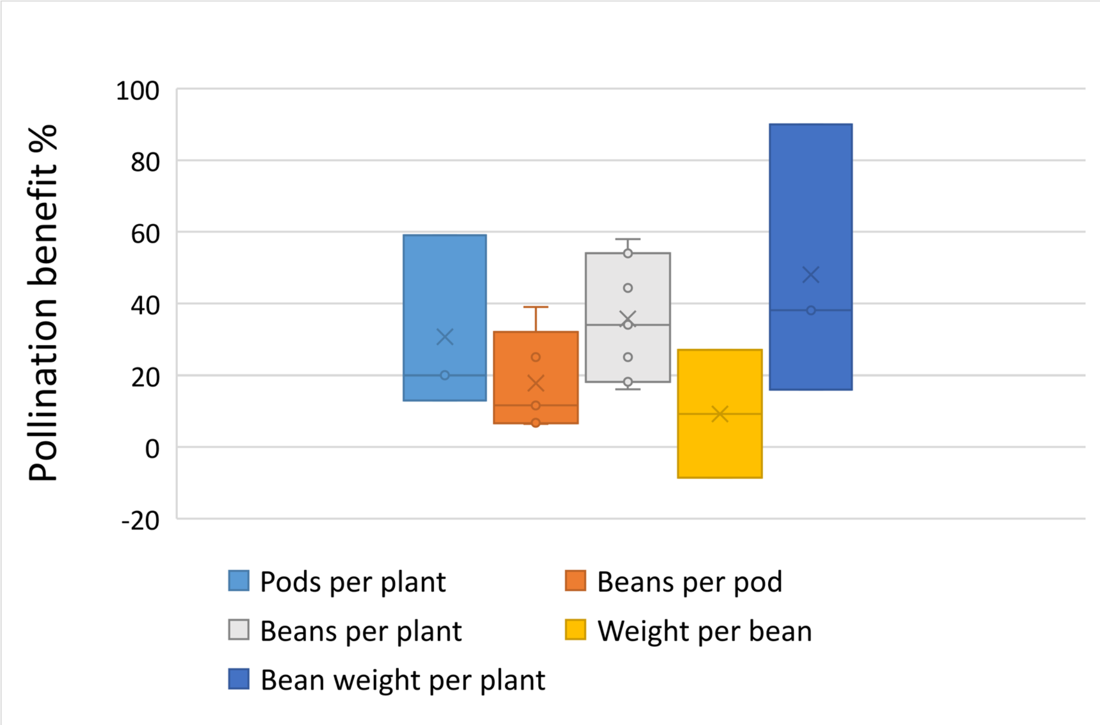

Figure 6. The difference in yield parameters between cages with pollinators compared to cages without pollinators. All studies using cages included with the different yield measurements divided in separate stacks. The boxes mark the first and third quartile, x is the median and I mark the minimum and maximum values in the data set.

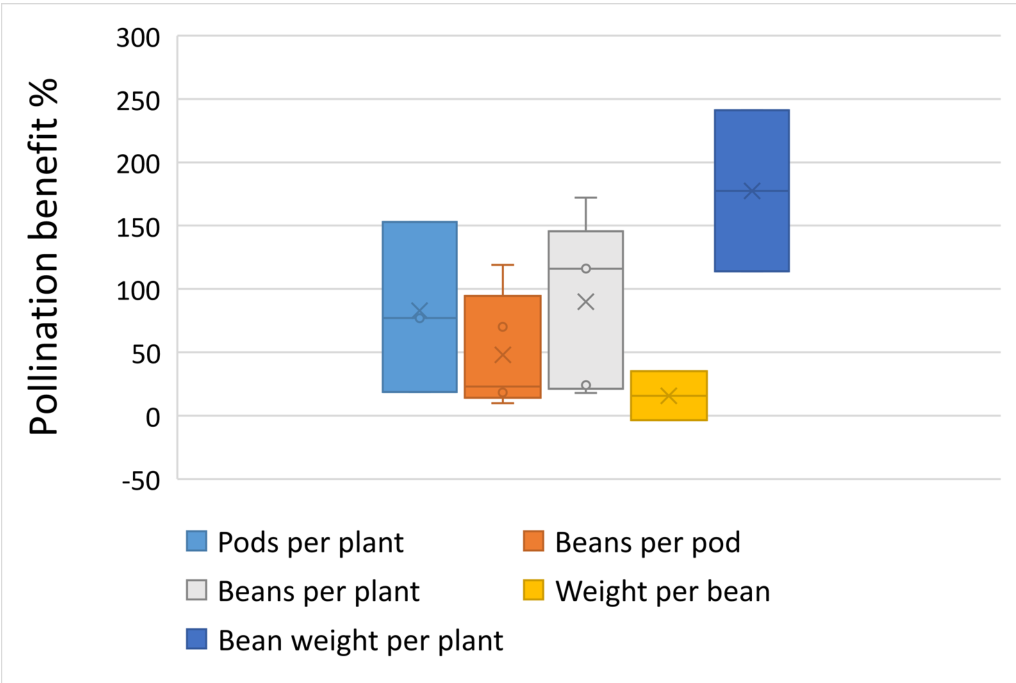

Figure 7. The difference in yield parameters between open pollination compared to cages without pollinators. All studies with open pollination included with the different yield measurements divided in separate stacks. The boxes mark the first and third quartile, x is the median and I mark the minimum and maximum values in the data set.

5. Discussion

Faba beans are considered self-pollinating, however cross-pollination by insects increases the yield. The benefit of insect pollination in faba beans varies greatly between studies, partly due to different experimental methods, genetic and climatic conditions, disturbing effects by cages and the relative proportions of inbred and hybrid plants (Kendall & Smith 1975; Poulsen 1975). The dependency on insect pollination varies tremendously among different cultivars of faba beans and also interacts with biological and agronomic factors e.g. climate and soil conditions (St-Martin & Bommarco 2016; Bishop *et al.* 2020). Further, studies measure yield in different ways and at different scales, i.e. within plant and at plot-level, complicating comparisons among them (Bishop *et al.* 2020). Therefore, to assess the pollination benefits in faba bean it is important to consider effects of different years, sites, methods, cultivars and yield parameters measured (Bishop *et al.* 2020).

5.1. The relative benefit of different bee species

The relative benefit of different pollinating species is in need of further investigation. While no difference in pollinating efficiency between positive visits by honeybees and bumblebees was seen in England (Kendall & Smith 1975), positive visits by bumblebees in Denmark were more efficient because they visited more flowers per plant and flowers per minute (Poulsen 1973). Among bumblebees the species in the subgenus *Hortobombus* seem to be the most efficient since they are more likely to make positive visits, with *B. hortorum* being the most efficient (Tasei 1976; Stoddard & Bond 1987; Marzinzig *et al.* 2018). However, *B. hortorum* is rare in European regions (Marzinzig *et al.* 2018), suggesting they might not be the most important bumblebee species in faba bean pollination. Even though pollinating behavior influence the efficiency of pollination, several authors have proven negative visits to be positive for yield increase in faba beans by assisting in self-pollination when tripping the flower (Soper 1959; Kendall & Smith 1975; Marzinzig *et al.* 2018). Insects that collect nectar from extrafloral nectaries do not contribute to either cross- or self-pollination during that particular visit, however, the interest of the faba bean plant is maintained until new flowers go through anthesis (Stoddard & Bond 1987). This suggests any pollinating species in faba beans should be positive for yield increase, thus the most abundant pollinating insect might be more important than the most efficient for yield increase. Therefore, despite a possibly lower pollinating efficiency, honeybees might be the most important pollinator in regions where bumblebees are less abundant e.g. Denmark and Germany. The fact that bumblebees are declining all over the world also speaks for a greater importance of honeybees in future faba bean cultivation.

It seems like positive visits by both honeybees and bumblebees increase later in the day at the time of maximal pollen presentation (Free 1962; Poulsen 1973). However, negative visits by honeybees increase later in the flowering period, due to more holes in the corolla which make nectar robbing possible (Poulsen 1973). This indicates that pollination of honeybees might be more important early in the season while bumblebees might be more important later, especially *B. terrestris* which usually have a greater abundance and increase their positive visits later in the flowering season (Poulsen 1973). The benefit of honeybees might also lower in regions where bumblebee species that pierce the corolla i.e *B. terrestris agg* are more abundant, making them more likely to switch to negative visits.

5.2. The pollination benefit based on study method

The benefit of insect pollination differs greatly among studies both within and between different yield measures (table 2). However, all cage experiments with insect pollination showed a positive relationship for every yield parameter, except individual weight per bean in four studies (Free 1966, 1993; Poulsen 1975; Svendsen & Brodsgaard 1997). The increase in weight per bean in cages excluded from pollinators has been suggested to be a compensation mechanism for inadequate cross-pollination. By increasing the weight per bean the plant compensates for the fewer beans per pod and pods per plant, resulting in a profitable total bean yield despite inadequate cross-pollination (Poulsen 1975). Open pollination did always result in a greater yield than cages with bees, suggesting a negative effect from the cages themselves. The cages might have a disturbing effect on plant growth or influence the behavior of the pollinators. Increased plant height in cages with- and without bees, might be a compensation mechanism for inadequate cross pollination, just like the increased weight per bean. However, in Denmark, caged plants received 20% less sunshine than open plots so the greater plant height was thought to be a compensation mechanism for inadequate light (Svendsen & Brodsgaard 1997). Thus, the disturbing effects of cages do not make cage experiments a flawless method to examine the benefit of insect pollination under field conditions.

Experiments using hand-pollination give a better control on which flowers are being pollinated and if the fertilization is by self- or cross-pollination. Hand-pollination makes it possible to set a 100% limit on maximal yield with optimal cross-pollination. However, hand pollination does not consider the relative effect from different pollinating species and is a bad indicator for cross-pollination potential under natural conditions. In two studies hand pollination even resulted in lower yield than in plants that were left undisturbed (self-pollinated) (Free & Williams 1976; Bishop *et al.* 2020) suggesting that hand pollination can have disturbing effects through human impact on the plants. However, there have been few experiments where bees have been supplemented to faba bean fields without the use of cages to investigate the pollinating benefit. Only one study was found, situated in Australia, where honeybee hives were placed at different distances from fields of faba beans, (Cunningham & Le Feuvre 2013) thus there is a need for further investigation. Experiments supplementing honeybee hives to fields best simulate natural conditions without interfering with abiotic- and biotic factors, and thus should give more accurate results of the benefit of insect pollination. Open pollination treatments also best simulate natural conditions; however, if the open pollination treatment is compared to a cage without pollinators the benefits of cross-pollination might be overestimated due to the negative effects of the cages, or underestimated due to external factors like insect-pests or drought. Therefore, the best way to investigate the benefits of cross-pollination should be to include open pollination treatments as well as cages with- and without pollinators.

The average benefit of cross-pollination across a range of yield parameters in the investigated studies (insect- and hand pollination included) was a 42,6% increase. However, the negative results of the hand-pollination treatments affected the average value quite a bit, thus, an average of the studies with insect pollination were also calculated. This changed the yield benefit of insect pollination to 51,8%. This suggests that insect pollination is profitable for faba bean cultivation. Insect pollination also results in a more simultaneous ripening which facilitates drying and harvesting (Free 1993). In cold and wet seasons, faba beans might not mature early enough and thus risk destroyed harvests (Alghamdi *et al.* 2012). Insect pollination might speed up the ripening and is thus important for safe harvests in cold and wet regions. The relative protein content is independent of insect pollination (Käck *et al.* 2012; Bartomeus *et al.* 2014). Further, the benefit of insect pollination is affected by climatic and soil conditions. For example, during heat stress, yield loss is reduced with cross-pollination by bees compared to self-pollination with a greater benefit of cross-pollination at 30 degrees Celsius than at 18-26 and 34 degrees Celsius (Bishop *et al.* 2015). This suggests that insect pollination might gain further importance under future climatic conditions, where extreme weather events, like heat waves, might become more frequent. The benefit of cross-pollination also varies depending on the soil type the plants are grown in. Plants grown in soil from ley rotation have a greater yield benefit from cross-pollination than plants grown in soil from barley monoculture (St-Martin & Bommarco 2016). This might be because soil from ley rotation contain about 50% less potassium than soil from barley monoculture, which limit flower production (St-Martin & Bommarco 2016). These interactions between pollination benefit, soil type and climate, show that the pollination benefit is context dependent.

6. Conclusions

Pollination by honeybees and bumblebees contribute to higher and more stable yields in faba beans trough a more adequate flower fertilization both directly through cross-pollination in positive visits and indirectly through self-pollination in negative visits by tripping the flower. Positive visits by insects are most valuable for yield increase, however negative visits are better than no visits at all. It seems like the bumblebee species *B. hortorum* is the most efficient pollinator, however the most frequent seems to be the honeybee, *Apis mellifera.* The average benefit of insect pollination across a range of yield parameters was calculated as 42,6% (insect- and hand pollination treatments), and 51,8% (only insect pollination). However, there is great variation in pollination benefit among studies, with values ranging between -54% and 245%, due to differences in experimental method, faba bean cultivar, and climatic and agronomic factors such as soil conditions. Thus, the value of insect pollination in faba beans needs further investigation.

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