Insect Pollination of Oilseed Rape

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Cover: Oilseed rape buds, honey bee visiting an oilseed rape flower and swathered oilseed rape (photo: S. Lindström).

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Effects of Insect Pollination of Oilseed Rape

Abstract

Ecological intensification of agriculture is suggested as a way to reach higher crop yields without increasing inputs that may degrade the environment. Increased insect pollination in crops, such as oilseed rape, *Brassica napus*, has been suggested to increase yields, but is rarely integrated in crop management. To determine the value of enhanced crop pollination as a means of ecological intensification, reliable estimates of how yield is affected by insect pollination are needed. Further, little is known about interactions between insect pollination and other crop management factors such as cultivar, nitrogen fertilization, pest control, and irrigation. Finally, it needs to be assessed how increasing crop pollination by adding honey bees to crops impact the wild fauna of flower-visiting insects.

I addressed these issues in two sets of experiments. First, I performed a landscape-scale experiment with replicated whole fields of winter oilseed rape. I manipulated the pollinator community by adding honey bee hives or controlled the surroundings for absence of honey bees. I chose fields such that they were embedded in either intensively cropped landscapes or heterogeneous landscapes with more semi-natural pastures, expecting greater diversity of wild pollinators in the latter. In two cultivar types, I examined how honey bee addition affected crop yield and the wild pollinator community. Second, I performed two field plot experiments, in winter and in spring oilseed rape, to assess how insect pollination and the crop management factors cultivar, nitrogen fertilisation, pest control, and irrigation interactively shaped crop yield.

Insect pollination increased winter oilseed rape yield, but only in open-pollinated cultivars. Cultivars of open-pollinated type gave higher yields than cultivars of hybrid type. Thus, phasing out open-pollinated cultivars from the market emerges a missed opportunity for increased yields.

I show that the crop's access to water, nitrogen, and herbivory affect pollinator behaviour and potentially crop pollination. Interestingly, insect pollination tended to increase yields when no nitrogen was applied, indicating higher nutrient use efficiency in plants with access to insect pollination. Adding managed honey bee hives had negative effects on the densities of wild flying- and flower-visiting insects, with potential negative effects on crop pollination and biodiversity conservation. Overall, my thesis demonstrates the importance of including both agronomic and environmental perspectives when developing crop production systems that are productive and sustainable.

Keywords: Brassica napus, competition, pollination, yield, cultivar, ecological intensification, interactions, Apis, Bombus, pollen beetles

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Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Lindström, S.A.M., Herbertsson, L., Rundlöf, M., Smith, H.G., & Bommarco, R. (2016) Large-scale pollination experiment demonstrates the importance of insect pollination in winter oilseed rape. *Oecologia*, 180, 759-769. http://dx.doi.org/10.1007/s00442-015-3517-x

II Lindström, S.A.M., Herbertsson, L., Rundlöf, M., Bommarco, R., & Smith, H.G. (2016) Experimental evidence that honeybees depress wild insect densities in a flowering crop. *Proceedings of the Royal Society B*, 283: 20161641. http://dx.doi.org/10.1098/rspb.2016.1641

III Marini, L., Tamburini, G., Petrucco-Toffolo, E., Lindström, S.A.M., Mosca, G., Zanetti, F., & Bommarco, R. (2015) Crop management modifies the benefits of insect pollination in oilseed rape. *Agriculture, Ecosystems and Environment*, 207, 61–66. http://dx.doi.org/10.1016/j.agee.2015.03.027

IV Lindström, S.A.M., Klatt, B.K., Smith, H.G., & Bommarco, R. Pest control affects crop yield components and bee behaviour in oilseed rape. (submitted).

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The contribution of Sandra A.M. Lindström to the papers included in this thesis was as follows:

I Developed the research questions and experimental design together with MR, HGS, and RB. Lead and performed the field work. Did the statistical analyses, interpreted results, and wrote the paper with assistance from the co-authors.

II Planned the experiments together with MR, HGS and RB. Performed the experiments with help from LH in setting up the honey bee treatment in 2012. Analysed the data with help from HGS. Interpreted the results and wrote the manuscript with comments from all other authors.

III Developed the research questions and the experimental design together with LM and RB. Participated in interpreting results and writing the article which was led by LM.

IV Designed the experiment together with RB. Performed the experiments. BK helped with the behaviour observations. Analysed the data together with HGS. Interpreted results and wrote the manuscript with comments from all other authors.

1 Ecological intensification through insect pollination

1.1 Ecological intensification of agriculture

A growing and increasingly wealthy human population is expected to double the demands for food between 2005-2050 (Tilman *et al.*, 2011). Food production is also a central driver of global environmental change, contributing with negative effects on the climate, water resources, soils, and the rich biodiversity the world harbours (Foley *et al.*, 2005; Rockström *et al.*, 2009). Humanity stands in front of a great challenge to tackle these issues, and needs to develop the food production system as a part of the solution for a sustainable world (DeClerck *et al.*, 2016; Rockström *et al.*, 2017).

The future global food demand can be met by reducing food waste, changing diets, improving governance of food systems, and using resources more efficiently, but crop production also needs to increase (Foley *et al.*, 2011; Godfray & Garnett, 2014). Increased crop production has historically been achieved by agricultural expansion and intensification. Agricultural intensification was the main success factor behind the green revolution, where new cultivars and increased inputs such as mineral fertilizers and pesticides were important parts. However, these have had large negative consequences for the environment (Matson *et al.*, 1997; Foley *et al.*, 2005). A way to intensify agricultural production, without increasing or even by reducing inputs such as fertilizers or pesticides, is ecological intensification (Bommarco *et al.*, 2013; Wezel *et al.*, 2015).

Ecological intensification of agriculture implies management that augment ecological processes that improve agricultural production. However, successful implementation of ecological intensification requires careful quantification of the beneficial ecological processes (Garbach *et al.*, 2017), such as biological pest regulation, nutrient cycling, and insect pollination. This is a knowledge intensive solution that requires a thorough understanding of how ecological processes interact with the crop and crop management, and the mechanisms that lie behind them. In this way, agriculture can be the solution to the dual problem that humanity faces.

1.2 Insect pollination in crops

The loss of biodiversity caused by human activities is considered to exceed the thresholds for a stable environmental state on Earth (Rockström *et al.*, 2009). When species interact with their environment in an ecosystem, ecological processes occur. Some of these ecological processes provide services that benefit humans (Cardinale *et al.*, 2012), which are defined as ecosystem services (Daily, 1997; MEA, 2005). One often highlighted ecosystem service is insect pollination. The loss of biodiversity among pollinators has raised questions about whether the pollination services they provide are at risk (Garibaldi *et al.*, 2011). The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) was initiated in 2012 to provide governments and society with independent and scientifically based assessments of biodiversity and ecosystem services, corresponding to the Intergovernmental Panel on Climate Change (IPCC). IPBES has recently compiled a thorough review of the scientific literature and assessed the global status of pollinators, pollination and food production (IPBES, 2016), and concluded that pollinators and the pollination service they provide are threatened by land-use change, agricultural intensification, climate change, pesticide use, pathogens, genetically modified organisms, and invasive species (Dicks *et al.*, 2016; IPBES, 2016; Potts *et al.*, 2016).

Pollination is the sexual reproduction of plants, and includes the transfer of gametes from male to female flower parts. Gravity, wind, water, or animals are vectors that mediate this transfer. Pollination can occur between (cross-pollination) or within (self-pollination) plants. Self-pollination can take part within a single flower, autogamy, or between flowers on the same plant, geitonogamy. The extent of these ways of pollination varies among plant species and may even vary among varieties or cultivars within a species.

The bulk of global food production comes from crops that are self- or wind pollinated (Aizen *et al.*, 2009; Gallai *et al.*, 2009), but the majority of crops benefit from insect pollination. The yield increases in 87 of the 124 leading crops used for human consumption in the world (Klein *et al.*, 2007). In addition, insect pollination is required for the production of seeds for sowing in many crops, for example clover. In Europe, the pollination need is unknown for one third of the 264 crops grown, but insect pollination benefits yields in 84 % of the remaining crops (Williams, 1994). Insect pollination can also improve yield quality such as shelf life, fruit shape and colour of strawberries (Klatt *et al.*, 2014), fruit weight and size of apples (Garratt *et al.*, 2014), and seed germination, oil content and chlorophyll content of oilseed rape (Kevan & Eisikowitch, 1990; Bartomeus *et al.*, 2014). The economic market value of pollination in crop production globally is estimated to be $235 billion to $577 billion annually (Lautenbach *et al.*, 2012).

Insect pollination is important for global food nutrition (Chaplin-Kramer *et al.*, 2014). While calories mostly are produced by self- and wind pollinated crops, insect pollinated crops produce a large global share of micronutrients for human consumption. All Lycopene, 98% vitamin C, and 55% folate of the global production comes from crops that benefit from insect pollination (Eilers *et al.*, 2011). Also, vitamin A, antioxidants, lipids, carotenoids, and several minerals important for human health are produced by insect pollinated crops (Eilers *et al.*, 2011). Pollinators also provide cultural and societal values (IPBES, 2016), and contributes greatly to biodiversity conservation by pollinating the majority of Earth’s wild plant species (Ollerton *et al.*, 2011).

Benefits of insect pollination on crop yield are often studied in isolation, but effects can be modified by other crop management factors. Crop management can either have direct effects on pollinator behaviour and densities and thus pollination, or indirect effects by modifying the consequences of pollination within the crop when forming yield. Interactions between insect pollination and other crop management factors have recently been studied for some crops, but there is much left to discover (Lundin *et al.*, 2013; Klatt *et al.*, 2014; Klein *et al.*, 2015; St-Martin & Bommarco, 2016; Tamburini *et al.*, 2016).

Despite the large monetary values produced by pollinating insects, and the threats pollinators are exposed to, basic information is lacking on the extent to which pollinators contribute to yield quantity and quality. There is a need for enhanced understanding of the biological processes that underlie crop pollination and how it interacts with other crop management factors, for the development of ecological intensification of pollination dependent crops.

1.2.1 Pollinating insects in agricultural crops

Wild and managed flower-visiting insects pollinate crops. Managed western honey bees, *Apis mellifera*, are effective pollinators of many crops (Carreck & Williams, 1998). Addition of honey bee hives can drastically increase the number of pollinators in a flowering crop field, and they are therefore often used to increase crop pollination. Wild insects provide an added pollination benefit to crop pollination, irrespective of honey bee densities (Garibaldi *et al.*, 2013; Mallinger & Gratton, 2015). Depending on the crop flower traits, the community of flower-visiting insects and the effectiveness of different pollinators vary.

Honey bees are highly adapted to pollen- and nectar collection with branched hairs, and even hairy eyes that pollen grains stick to, pollen baskets, pollen combs and presses, and a communication system that allows them to transfer information on where to find floral resources (Abrol, 2007). They are highly social and live in colonies that host tens of thousands of individuals, which can be fed with sugar to survive periods with few flowering resources, and which can easily be transported to a crop field to increase the number of pollinators in a flowering field (vanEngelsdorp & Meixner, 2010). Honey bees are generalists, foraging in a wide range of plant species (Winston, 1991). There have been reports on honey bee losses from North America and parts of Europe the last years (vanEngelsdorp *et al.*, 2009; Potts *et al.*, 2010b). However, the number of managed honey bee hives in the world have increased by 50% since the 1960´s (Aizen & Harder, 2009; IPBES, 2016). The supply of managed honey bees is only enough to supply 64 % of the demand of crop pollination within Europe (Breeze *et al.*, 2014), and wild pollinator populations are declining in agricultural landscapes (Potts *et al.*, 2010a; Gill *et al.*, 2016). Along with an increased cultivation of insect pollinated crops (Aizen *et al.*, 2008), this have put the pollination service provided by pollinating insects at risk.

There is growing concerns that wild bees in agricultural landscapes decline in abundance and diversity, mainly due to habitat loss, loss of pollen- and nectar-producing flower resources, pesticide use, and pathogens (Goulson *et al.*, 2015; IPBES, 2016). The IUCN Red List has not assessed the global trends of pollinating insects, but in regional assessments often more than 40% of the species of pollinating insects are threatened by extinctions, and the population trends for alarmingly many bee species are unknown (IPBES, 2016). In Europe, 9.2 % of the 1965 bee species are threatened with extinction, but for 56.7% of the bee species, information to evaluate the threat status is missing (Nieto *et al.*, 2014). Only 244 of the 1965 bee species in Europe have stable population trends, and 13 species have increasing populations (Nieto *et al.*, 2014). The population status and trends of other wild pollinators such as flies are largely unknown (Goulson *et al.*, 2015; IPBES, 2016). Managed honey bees, wild bees (Hayter & Cresswell, 2006) and hover flies (Jauker & Wolters, 2008) are known to be pollen dispensers in oilseed rape, but it is not known which insects are visiting oilseed rape in Scandinavia, in particular not the winter cultivars that are flowering in early spring.

While honey bees contribute to crop pollination, they can also negatively affect wild bee communities. Honey bees can compete with wild bees in natural environments (Paini, 2004), but it is not known if competition also occurs when honey bees are added to mass-flowering crops, when foraging resources occur in superabundance and probably are less limiting. In plants pollinated by wild insects, competition by added honey bees could partially cancel positive effects on pollination.

1.2.2 Landscape effects on insect pollination

The agricultural landscape has gone through vast changes in quality and structure with enlargement of agricultural fields, removed and decreased semi-natural habitats and intensified agricultural management (Senapathi *et al.*, 2015; Potts *et al.*, 2016). These changes have led to loss of habitats for pollinating insects, such as semi-natural grasslands and field borders that are rich in flowering habitats (Rundlöf *et al.*, 2008; Öckinger *et al.*, 2009). This has in particular affected wild bees negatively. Heterogeneous agricultural landscapes that are rich in pollinator friendly habitat within flight distance have been shown to harbor higher abundances and richness of bees than homogenous intensively cropped landscapes (Öckinger & Smith, 2007; Holzschuh *et al.*, 2011; Kennedy *et al.*, 2013). Other flower-visiting insects, such as hover flies, marsh flies and other flies, are neither bound to return to a nest after a foraging trip nor dependent on floral resources at all life stages, and are therefore less dependent compared with bees on having semi-natural habitats within flight distance (Jauker & Wolters, 2008; Rader *et al.*, 2015; Power *et al.*, 2016). This might result in contrasting pollinator communities in crops within heterogeneous and homogenous landscapes (Földesi *et al.*, 2016), with potentially reduced pollination of agricultural crops in simplified landscapes (Ricketts *et al.*, 2008; Potts *et al.*, 2016).

The honey bee is native to Europe, and has thereby a long history of co-existence with wild insects. The transformed agricultural landscape might affect this coexistence. With decreased flowers within flight-range in the cropped landscape, there is a risk of increased competition for resources. Understanding of competition from honey bees is almost exclusively limited to impacts on wild bees in correlative studies in natural habitats or in cage experiments (Paini, 2004). It is not known if addition of managed honey bees to flowering crops affects the abundance of wild pollinating insects and displaces them from the focal crop.

1.3 Oilseed rape cultivation

Oilseed rape (*Brassica napus* ssp. *napus* L.) is the quantitatively most produced oil crop and the second most produced protein crop grown in Europe

(FAO, 2014). Its oil-rich seeds are used for human consumption, animal fodder, industrial purposes and bio-fuels.

Oilseed brassicas have been cultivated for thousands of years, but oilseed rape has only been a major crop since the mid-20th century (Snowdon *et al.*, 2007). In Europe, winter oilseed rape was cultivated to a minor extent in 1860-1880 for production of lamp oil (Meyer, 1997), but the cultivation almost ceased by the beginning of the 19th century (Rydberg *et al.*, 1914). After World War II, the cultivation increased rapidly for production of margarine (Snowdon *et al.*, 2007). In Sweden, production reached 176 000 ha by 1951 (Andersson & Granhall 1954 see Meyer 1997), has since then fluctuated, and in 2016 93 700 ha oilseed rape was grown (The Swedish Board of Agriculture, 2016c). China, India, Canada and the European union are the main producers of oilseed rape (Carré & Pouzet, 2014).

The mean yield across the globe has increased from 0.8 tonnes per hectare to 1.9 tonnes per hectare between 1970 and 2009 (Rondanini *et al.*, 2012) due to breeding, improved methods for crop establishment, plant nutrition management, and crop protection. Yields have stagnated in countries such as Germany, UK, and Australia since the mid-1980s (Berry & Spink, 2006), but in most countries yields are still increasing (Rondanini *et al.*, 2012).

Oilseed rape yield is formed by four important yield components: plants per area, number of siliques per plant, number of seeds per silique, and seed weight (Habekotté, 1993; Diepenbrock, 2000). Oilseed rape has a high plasticity and can combine these components in various ways to produce high number of seeds. Seed number per area is determined during flowering and is regarded as a main factor for increasing yield (Diepenbrock, 2000; Gomez & Miralles, 2011).

1.3.1 Management factors of oilseed rape

Oilseed rape production is associated with low production security in many parts of the world. It is highly attractive to a range of pest insects, frequently infected by pathogens, and autumn sown cultivars are sensitive to hard winters. Two key production factors are nitrogen management and a successful crop establishment that results in an even and competitive crop. Improvements of the genetic material through breeding and higher resource inputs has led to better winter hardiness and great increases of yield quantity, oil content, and quality (Meyer, 1997).

Oilseed rape can be of either spring or winter type. Winter types are sown in the autumn and require vernalisation to develop stem elongation and flowering, and flowers in the spring. Spring cultivars are sown in spring and flower about one month later than the winter type. An important distinction among cultivars of both winter and spring oilseed rape is that they are either of open-pollinated or hybrid type, based on method for plant breeding (Becker *et al.*, 1999). Open-pollinated cultivars are bred with traditional pedigree breeding, while hybrid cultivars are F1 hybrid seeds from mating of two inbred cultivars, a method that maximizes genetic heterosis effects. The hybrids have, due to the heterosis effect, been suggested to be more vital and tolerant against stressors (Léon, 1991), and have in the last years come to dominate the European market. Pollination properties of cultivars are not measured by plant breeders and information on the pollination traits and dependencies is lacking (Allen-Wardell *et al.*, 1998). It is, for instance, unknown whether the benefits of heterosis in hybrid cultivars can compensate for a lack of pollination, by, for example, increased pollen vigour, pollen productivity or increased self-compatibility, or *vice versa*, whether access to pollination changes the relative productivity of the cultivar.

Nutrient management is a key production factor and a main cost of production because oilseed rape requires high levels of nitrogen (Rathke *et al.*, 2006). Nitrogen is crucial for development of photosynthetic area, needed for the production of assimilates that fill the seeds. Nitrogen uptake from the soil is linked to water availability and soil characteristics (Rathke *et al.*, 2006). Water stress can occur in light soils, but due to high costs, oilseed rape is not commonly irrigated in northern Europe.

Several pest organisms attack oilseed rape throughout crop development, e.g. slugs, pigeons, nematodes, and insects (Alford *et al.*, 2003; Williams, 2010). Pollen beetles occur in both winter and spring oilseed rape, and can cause serious damages when they oviposit and feed on flower buds (Williams, 2010). Damages from pollen beetles are more severe in spring crops, which is in the bud stage at the same time as the peak migration of pollen beetles. In Sweden, spring oilseed rape crops are treated with insecticides every year against pollen beetles (The Swedish Board of Agriculture, 2016a).

1.4 Insect pollination in oilseed rape

Oilseed rape has a mixed pollination system, but is mainly self-fertile (Steffan-Dewenter, 2003). Considerable outcrossing has been observed (Olsson, 1960), and the degree has been shown to vary with environmental conditions and cultivars (Olsson, 1960; Becker *et al.*, 1992). Outcrossing can be mediated by wind, insects, or movements among plants, but their relative importance is unknown (Free, 1993).

Oilseed rape flowers are highly attractive to pollen and nectar feeding insects due to its bilateral, bright yellow flowers, that produces nectar from four nectary glands situated in the bottom of the flower (Abrol, 2007). The pollen grains are sticky and aggregated, which is typical for insect pollinated plants (Cresswell *et al.*, 2004). The flowers have a stigma surrounded by six stamens; two shorter that release pollen below the sigma, and four long stamens that first release pollen away from the stigma, but at the end of the flowering bend inward the flower. In this way, cross-pollination is favoured, but self-pollination can assure pollination at late flowering (Persson, 1953; Eisikowitch, 1981; Free, 1993; Abrol, 2007). The oilseed rape flower attracts a wide range of insect species (Stanley *et al.*, 2013).

Important quality parameters of oilseed rape are chlorophyll content and oil content that also affect the price to the farmer. Oil content have both been shown to increase with insect pollination (Bommarco *et al.*, 2012) and not (Adegas & Nogueira Couto, 1992).

Insect pollination benefits to yield are likely to be affected by resources and stressors on the plant, including access or not to water, nutrients, and biotic interactions that are either beneficial (e.g. pollination) or antagonistic (herbivory, pathogens). In wild plants, resource limitation has been shown to affect the outcome of pollination (Galen, 1985; Burkle & Irwin, 2009), and this has been hypothesised also in crops (Bos *et al.*, 2007). For example, resources such as water and nutrients, or damages caused by herbivores can limit yield formation through production of photosynthetic leaf area and assimilates needed for seed filling. Crop pollination studies rarely take agricultural management into consideration, or even measure agronomic covariates. Furthermore, effects of insect pollination on crop yield have often been examined in isolation, and until only recently have interactions with other crop management been considered.

Pollination in oilseed rape has mainly been studied in spring cultivars (Bartomeus *et al.*, 2014), whereas winter cultivars remain largely unexplored. Even if winter and spring oilseed rape is the same species, their pollination requirements might differ due to separation in flowering time, leading to differences in the availability and activity of pollinating insects and in weather conditions, which could affect pollen and stigma functioning (Hayter & Cresswell, 2006; Stanley *et al.*, 2013). Also, cultivars of both winter and spring oilseed rape could differ in their dependence on insect pollination. Differences among cultivars in pollination dependence are generally poorly understood for oilseed rape and most other crops (Klein *et al.*, 2007).

Influence on yield of oilseed rape from insect pollination is poorly understood, with large inconsistencies in the results (Free, 1993; Abrol, 2007), ranging from no yield benefits (Williams, 1985) to 50 % yield increases (Durán *et al.*, 2010). This may be explained by differences among cultivars (Williams *et* *al.*, 1987; Mesquida *et al.*, 1988), or by the use of widely different estimation methods.

1.4.1 Methods for estimation of insect pollination effects

To understand the value of insect pollination for society and farmers, there is a need to understand how insect pollination affects the agronomic yield (tonnes per hectare). However, influence of insect pollination on yields per unit area is rarely quantified directly. Seed set per plant, on a single branch of a plant, or even of single flowers are more commonly measured (Hayter & Cresswell, 2006; Bommarco *et al.*, 2012; Garibaldi *et al.*, 2013; Hudewenz *et al.*, 2013), but these are difficult or even impossible to translate to agronomic yields. The high plasticity of the oilseed rape plant makes intermediate measures of final yield problematic (Angadi *et al.*, 2003). Measurements on a flower, branch, or plant fail to account for the capacity of a crop to compensate. Crops are, to varying extent, able to allocate resources within the plant and compensate for resource limitations during the development of a yield component (e.g., plants per area or seeds per silique), by the increase of another yield component at a later stage (e.g., siliques per plant or seed weight) (Grosse *et al.*, 1992; Bos *et al.*, 2007). Variation in plant size and seed production among plants can therefore be high, especially for field crops with high compensation capacity such as oilseed rape (Tatchell *et al.*, 1983; McGregor, 1987).

Furthermore, experimental techniques often include netted cages to exclude or enclose pollinators (Adegas & Nogueira Couto, 1992; Koltowski, 2005; Durán *et al.*, 2010; Hudewenz *et al.*, 2013). Cages can be linked to several problems, both by altering pollinator behaviour and the growing conditions for the crop (Kearns & Inouye, 1993). Further, nets may lead to underestimation of wind pollination. Studies on the degree of outcrossing sometimes have not measured or taken account to potentially varying densities of pollinating insects (Olsson, 1952; Becker *et al.*, 1992). Another experimental technique comprises comparisons of yield at gradients of pollinators with increasing distance from honey bee hives (Fries & Stark, 1983; Aras *et al.*, 1996; Manning & Wallis, 2005; Sabbahi *et al.*, 2005), without proper controls. To get reliable estimates of the contribution of insect pollination to oilseed rape yield, there is a need to perform experiments with controls at landscape- or field scales which reflects the situation for commercial oilseed rape fields.

1.5 Aims

My aim with this thesis was to quantify the contribution of insect pollination to oilseed rape yield in a landscape-scale experiment with replicated whole fields of winter oilseed rape in controlled landscapes (paper I), to evaluate effects on wild insects of adding managed honey bees to flowering oilseed rape (paper II), and to explore interactions with landscape context (paper I and II). I also aimed to explore how insect pollination interacts with other crop management factors such as cultivar choice (paper I and III), nitrogen management (paper III), irrigation, and pest control (paper IV). The overall aim is to produce knowledge for the development of productive and sustainable crop production systems.

2 The contribution of insect pollination is modified by crop management

We conducted a large-scale landscape experiment with manipulated honey bee densities in farmers winter oilseed rape fields for two years in south Sweden (paper I and II), and two field plot experiments with cages to exclude pollinators, one with winter oilseed rape in northern Italy (paper III) and one with spring oilseed rape in south Sweden (paper IV).

2.1 Effects on yield of adding honey bees to flowering crops

We examined yield benefits from insect pollination in agronomically realistic settings in winter oilseed rape (paper I). In a large-scale landscape experiment, we collaborated with oilseed growers and honey bee keepers and added 624 honey bee hives to 23 fields of winter oilseed rape (figure 1), with two honey bee hives per hectare, over two years. We made sure that the areas around 21 other fields were free from honey bee hives (figure 2). The fields were sown with either of three hybrid cultivars (Excalibur, Compass, or Expower), or with one of three open-pollinated cultivars (Galileo, Epure, or Alpaga). We replicated the treatments in homogeneous and heterogeneous landscapes, with low versus high proportions of semi-natural grasslands and small *versus* large blocks of agricultural fields within 1 km around each field.

Figure 1. Experimental fields in 2011 and 2012 were either provided with honey bee hives (above), or controlled for the absence of honey bee hives in the surroundings and assigned as control fields (below).

Figure 2. Field locations in the region of Scania, southern Sweden, in 2011 (left) and 2012 (right). Honey bee treated fields (filled) and control fields (open), in heterogeneous (circles) and homogenous (triangles) landscapes.

Table 1. Number of fields of hybrid (H) or open pollinated (OP) cultivar type, in homogenous (Hom) or heterogeneous (Het) landscape types, in the two years and with added honey bee hives, and with surroundings controlled for absence of honey bee hives in control fields.

Honey bee treatment	Honey bee fields								Control fields							
Year	2011				2012				2011				2012			
Landscape type	Hom		Het		Hom		Het		Hom		Het		Hom		Het	
Cultivar type	H	OP	H	OP	H	OP	H	OP	H	OP	H	OP	H	OP	H	OP
Number of fields	3	3	2	4	3	3	3	2	3	3	2	2	3	3	3	2

We expected higher densities and differently composed pollinator communities in heterogeneous landscapes compares with homogeneous landscapes. To make sure that the added honey bee hives were equally strong, we measured their fluster activity during peak flowering (figure 3). We observed the flying and flower-visiting honey bees and wild insects in the fields during flowering (figure 4). The addition of honey bee hives successfully resulted in dramatic difference in abundance of honey bees; the mean model estimated abundance was 62.5 (95 % CI 41.4 – 94.4) per 200 m^2 transect and 20 minutes in honey bee treated fields compared with 2.6 (95 % CI 1.6 – 4.1) per 200 m^2 transect and 20 minutes in control fields. Once the crop was mature, we harvested areas of oilseed rape with small combine harvesters, reflecting the technique farmers use (figure 5).

Figure 3. Honey bee hive fluster activity, measured as the number of honey bees leaving the hive during two minutes, was measured for all honey bee hives in the landscape experiment.

Figure 4. During flowering, we observed flying and flower-visiting insects in the experimental fields. The most commonly observed insects were honey bees, bumble bees, solitary bees, hover flies, and other flies.

Figure 5. Harvest of an experimental field (photo: Lovisa Nilsson).

We found that adding honey bee hives to a crop field affected winter oilseed rape yield, but that the effect depended on cultivar type (paper I). Open-pollinated cultivars, but not hybrid cultivars, had 11% higher yields in fields with added honey bees than those grown in the control fields (figure 6). Yields were similar in homogeneous and heterogeneous landscape types, which probably can be explained by the low and similar numbers of wild flower-visiting insects in both landscape types. This is, to our knowledge, the first whole-field pollination experiment with proper control fields performed in replicated landscapes that combines a controlled honey bee treatment with a landscape treatment and where both agronomic factors and field conditions are considered. Realistic estimates of the yield-enhancing potential of ecological functions like insect pollination is necessary for the successful uptake among farmers (Cunningham, 2016).

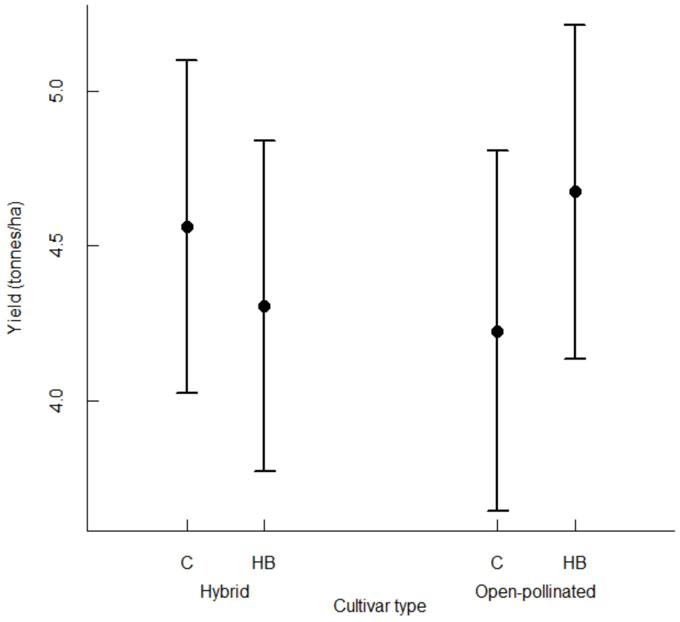

Figure 6. Model estimated mean yield per field for hybrid and open-pollinated cultivars of winter oilseed rape in fields treated with added honey bee hives (HB) and fields with surroundings controlled for absence of honey bee hives (C). The error bars denotes 95% confidence intervals.

2.1.1 Yield estimation in plot experiment

We studied interactions among insect pollination and crop management in winter oilseed rape. Yield benefits from pollination of different cultivars were estimated in a plot experiment (paper III), where pollinators had access to the flowers (open cages) differed to the yield when pollinators were excluded (closed cages) (similar to the cages in figure 9). Three cultivars were included in the experiment: one open-pollinated cultivar (Catalina) and two hybrid cultivars (Excalibur and PR45D01). The cultivars were grown in one long strip (75 × 15 m). Areas of the oilseed rape were harvested to estimate yield quantity in each plot.

We saw similar results in this plot experiment, performed in northern Italy (paper III), as in the landscape experiment in south Sweden (paper I). In the plot experiment, insect pollination increased yield by on average 19% in the open pollinated cultivar, but did not affect yield quantity in the hybrid cultivars (paper III, figure 7a).

There are a number of possible reasons to why yields only increased by 11% in the landscape experiment, compared to the 19 % yield increase in the plot-scale experiment. One could be that the three cultivars were grown in the same experiment in Italy, allowing cross-pollination among cultivars which potentially may lead to increased heterosis and crop yield. Another reason could be that different cultivars were included in the experiment. However, in the landscape-scale experiment effect size was estimated with considerable uncertainty, most likely because of unavoidable variation in growth conditions between fields.

In the plot experiment (paper III), we found a 6 % increase in oil content with insect pollination in the open-pollinated cultivar Catalina and in one of the hybrid cultivars, Excalibur. Impacts of insect pollination on yield quality are poorly studied, but increased oil content in spring oilseed rape has been shown (Bommarco *et al.*, 2012).

2.1.2 Cultivars

In two separate experiments, we found that insect pollination increased winter oilseed rape yields in the open-pollinated cultivars included, but not in the hybrid cultivars. Hybrid cultivars were introduced to Europe in the 1990s (Meyer, 1997), and have lately replaced the open-pollinated cultivars on the market due to higher yields (Sauermann and Finck 1998 see Diepenbrock 2000). Interestingly, we found that the open-pollinated cultivars in our experiments had on average 8.6 % *versus* 12.8 % higher yield than the hybrid cultivars in fields with added honey bees in the landscape experiment (paper I, figure 6), and in open cages in the plot experiment (paper III, figure 7), respectively. In the landscape experiment, we found no difference in yield between open-pollinated and hybrid cultivar types among the control fields (paper I). Even if the final yield of hybrids did not increase with insect pollination, yield components were affected in the plot experiment (paper III, figure 3). Insect pollinated plants of the hybrid cultivars had more, but lighter seed per silique, and produced fewer siliques per plant compared with plants from which pollinators were excluded (paper III). There are a number of potential mechanisms behind the observed patterns, e.g. differences between the cultivar types in pollinator attractiveness, benefit from cross-pollination, pollen quantity and quality, and yield formation components.

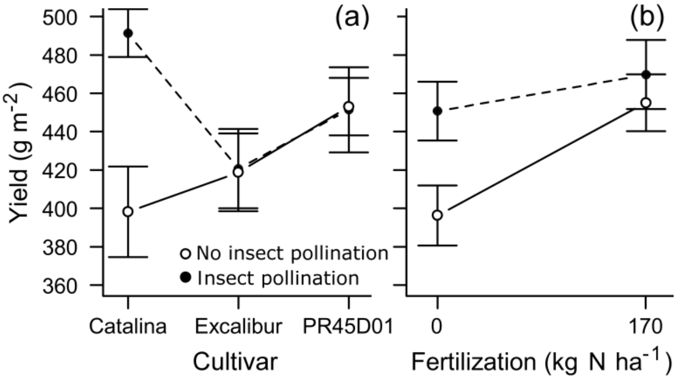

Figure 7. Mean winter oilseed rape yield per plot in open (filled circles) and closed cages (open circles) for a) hybrid and open-pollinated cultivars and for b) no nitrogen application and 170 kg N/ha. The error bars denotes standard error.

The cultivars in the plot trial received equally many pollinator visits, despite that the three cultivars were grown in the same experiment (paper III). In the landscape experiments, the open-pollinated cultivars received marginally more flower-visits from pollinators than the hybrid cultivars (paper I). There is limited knowledge on how cultivars differ in their over-all attractiveness to pollinators, but winter oilseed rape cultivars appear to differ in nectar secretion depending on breeding type, with 50 % higher nectar production in open-pollinated cultivars than hybrid cultivars (Bertazzini & Forlani, 2016).

The different yield response of insect pollination between the breeding types could also be caused by the higher genetic diversity within open-pollinated cultivars (Rai *et al.*, 2007), with a higher benefit of cross-pollination mediated by pollinators.

Pollen quantity and/or quality of pollen produced by the cultivar types might affect the need for insect pollination. Specific and effective pollen transfer from insect pollination compared to wind pollination, could benefit the pollination in cultivars with low pollen production or quality (Ramsay *et al.*, 2003; Hayter & Cresswell, 2006). In an *in vitro* experiment not included in this thesis, we examined how pollen fertility (figure 8) differed among seven winter oilseed rape cultivars (Lankinken, Å., Lindström, S.AM., & D’Hertefeldt, T., unpublished manuscript). We found that pollen tube germination differed among cultivars, but not between breeding types. For one hybrid cultivar (Compass) we measured the effect of pollen load on probability of silique production and seed quantity per flower, and found that seed production levelled off at relatively low number of pollen grains per stigma, indicating rather low dependence on cross-pollination. However, this should be tested for a larger number of cultivars of both breeding types.

Figure 8. Germination of oilseed rape pollen *in vitro* (left) and germinated oilseed rape pollen with a pollen tube (photo: Christopher Du Rietz) (right).

An alternative explanation of the cultivar type differences in yield responses of insect pollination is linked to how yield components are combined to form yield and their compensatory capacity. Hybrid cultivars are commonly, due to the increased vigour caused by heterosis, grown at a lower plant density than open-pollinated cultivars. Lower plant density leads to larger plants, which possibly are more prone to interplant collisions that move pollen from stamens to pistils through gravity and wind (Hoyle *et al.*, 2007), with a potentially reduced effect of insect pollination on yield. However, plant density did not affect yield in the landscape experiment (paper I) and plant density was controlled and equal among plots in the plot experiment (paper III). In open-pollinated cultivars with a lower compensation capacity, insect pollination leading to earlier pollination, shortened blooming period (Bell & Cresswell, 1998) and prolonged seed filling period (Sabbahi *et al.*, 2006) may be more important than for hybrid cultivars. Cultivars differ in how they combine yield components when yield is formed (Grosse *et al.*, 1992), and even if yields in the two hybrid cultivars in the plot experiment (paper III) were not affected by insect pollination, they did produce more flowers and pods in closed cages, potentially to compensate for poor pollination. The scale of our landscape experiment using a crop stand instead of isolated single plants did not allow us to investigate the mechanisms underpinning the cultivar type differences (paper I).

Previous studies have found no differences in yield benefits from insect pollination between the two breeding types of the cultivars (open-pollinated or hybrids (Koltowski, 2005; Hudewenz *et al.*, 2013). However, these experiments were performed in small plots or with potted plants, with several cultivars grown in the same experimental site. Under these conditions, cross-pollination can occur among cultivars and increase yields unrealistically compared with field conditions, where normally only one cultivar is grown in a large monoculture and the presence of cross-pollination among cultivars is very low. This can also be a problem in the cultivar testing, where several cultivars often are tested at the same place, which is rarely the case for commercially grown oilseed rape.

Since it was possible only to include a total of nine cultivars in our experiments, there is a possibility that our results depend on how specific cultivars respond to insect pollination rather being an effect of breeding type. However, we can with certainty say that different cultivars react differently to insect pollination. The clear differences in yield benefits of insect pollination among cultivars should be considered in crop management and breeding programs. No comprehensive information is currently available for pollination dependency of marketed cultivars. To understand if there are systematic differences between open-pollinated and hybrid cultivars there is a need of an extensive screening of insect pollination dependence in a larger number of both cultivar types. Trials comparing cultivars yield potential should include optimal management for all cultivars by providing pollinating insects, and to be performed with large areas of each cultivar to reduce cross-pollination among cultivars, reflecting the situation in commercial fields.

2.1.3 Nitrogen fertilization

It has been hypothesised that resource limitation can affect the outcome of pollination (Burkle & Irwin, 2010). However, interactions between pollination and fertilisation have not been detected in crops before, such as cucumber (Motzke *et al.*, 2015), alfalfa (Shebl *et al.*, 2009), almond (Klein *et al.*, 2015), or cacao (Groeneveld *et al.*, 2010).

We assessed whether access of nitrogen to the plant affected pollination benefits to yield in three cultivars of winter oilseed rape. In the plot experiment (paper III), each cultivar was treated with either no nitrogen fertilisation, or with 170 kg N per hectare in the spring, which is within the range of recommended doses (The Swedish Board of Agriculture, 2016b). We found a tendency that nitrogen fertilisation and insect pollination interactively affected crop yield. Yield increased by 15 % with insect pollination when no nitrogen was applied to the crop in the spring, for all cultivars (paper III, figure 7b). We saw no differences in yield between open and closed cages when the crop was provided with 170 kg N per hectare. In closed cages, we found more siliques per plant, but only when nitrogen was applied. A possible interpretation is that nitrogen fertilisation improves the compensatory capacity at pollination deficits. Yield increased with nitrogen fertilisation in closed cages where pollinators were excluded, but the effect of nitrogen fertilisation on yield was only marginal in open cages where pollinators had access to the flowering crop.

Our result gave the exciting indication that insect pollination can increase the nitrogen use efficiency in oilseed rape and inspires for future investigations. If confirmed, this would mean that the marginal value of nitrogen fertilisation is lower when insect pollination is enhanced. By strengthening insect pollination, this could lead to reduced use of nitrogen fertilisers, and to increased yields in parts of the world where availability of nitrogen is scarce. Leaching and aerial loss of nitrogen have large impact on terrestrial and aquatic environment, as well as on climate change (Billen *et al.*, 2013), and purchase of nitrogen fertilisers is a major crop production expense. The result can also have implications for organic oilseed rape production, where the steering of available nitrogen in spring is a challenge.

2.1.4 Combined effects of irrigation and crop protection

Pest attacks are a major limiting factor in oilseed rape production. Pollen beetles can, if not controlled, reduce seed yields by up to 70 % in spring oilseed rape (Nilsson, 1987). A recent study in winter oilseed rape showed that insect pollination and damage caused by pest insects interactively can affect crop yields (Sutter & Albrecht, 2016). It is not known if resource availability such as water availability can affect the plants responses to pest insect attacks and insect pollination (Bronstein *et al.*, 2007).

We examined how crop yield components were affected by insect pollination, irrigation and pest control of pollen beetles in an open-pollinated spring oilseed rape cultivar in a factorial cage experiment (figure 9) in south Sweden (paper IV). Yields were generally very low in open cages, which probably were caused by an infection of the fungi Sclerotinia outside the cages. Yields in closed cages were higher in plots with reduced pollen beetle densities, but only in the irrigated plots. The likely mechanism of the increased yield was that plants protected from pollen beetle attacks combined a higher number of seeds per silique with more siliques per main raceme (figure 10) and more water resources. Unfortunately, the Sclerotinia infection hindered us to evaluate interactive effects of pollination and the two other factors on yield.

Figure 9. Closed and open cages in the spring oilseed rape experiment in 2014.

Figure 10. Oilseed rape plants racemes (left), siliques (right above) and seeds (right below).

In the same experiment (paper IV), we also studied how irrigation and pest control modified the pollinator resources and the flower-visitation behaviour of honey bees and two species of bumble bees. We found that control of pollen beetles increased resources available for pollinators, by increasing both the number of flowers and the amount of nectar per flower (figure 11 and 12), but for nectar only when not irrigated. The pollen beetles could have damaged the nectaries, or fed on the nectar (Kirk *et al.*, 1995; Krupnick *et al.*, 1999), and irrigation can have helped plants to compensate in plots not treated against pollen beetles. We found higher pollinator densities, and that pollinating bees made more dips into the flowers when feeding on nectar, which implies higher pollination efficiency, when pollen beetles were controlled. More pollen beetles and larvae per plant during flowering, can have signalled reduced floral resources, or blocked the access to the nectaries (Kirk *et al.*, 1995), leading to pollinators avoiding plots with more pollen beetles. The reduction in nectar production and flower density could be a reason for the observed lower pollinator densities and thereby pollination (Bronstein *et al.*, 2007). However, we were not able to evaluate the effect on yield due to the Sclerotinia infection.

Figure 11. The oilseed rape flower has four nectary glands, visible in the picture (left) as green dots, at the base of the flower, from which we collected the nectar with capillary tubes from during peak flowering (right).

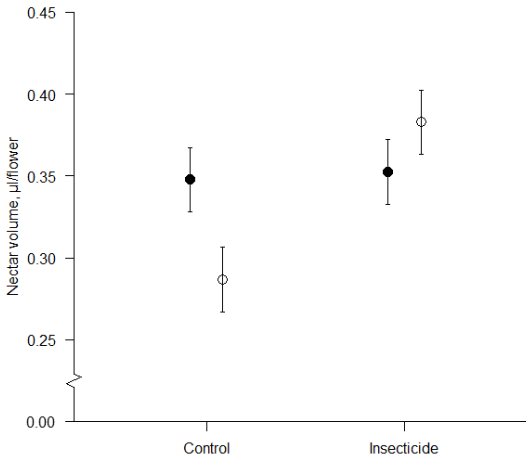

Figure 12. Model estimated mean nectar volume per flower in closed cages in control plots not treated against pollen beetles (Control) and in plots treated against pollen beetles (Insecticide), and irrigated (filled circles) and in non-irrigated (open circles) plots. The error bars denotes standard error.

Pest control can make the crop more attractive to pollinators and affect their behaviour potentially enhancing pollination. Therefore, yield losses due to pollen beetle attacks can have been fuelled by reduced pollinator densities and altered pollination behaviour. We found that there are complex interactions among resources and the crop that affect pollinator behaviour and potentially crop pollination.

2.2 Effects on wild insects of adding honey bees to flowering crops

We explored how honey bee addition affected wild flying and flower-visiting insects in flowering oilseed rape grown in landscapes with contrasting heterogeneity. In the landscape-scale field experiment (paper I and II), we studied fields in both homogeneous and heterogeneous landscape types, with expected low respectively high amounts of alternative pollen and nectar resources. Examining flower-visiting wild insects only, the total density was equal in the two landscape types (paper I). Honey bees were the main flower visitors and constituted 68 % of the flower-visitors, while flies other than hover flies and march flies made up 21 % of the flower-visitors. March flies, hover flies, bumble bees, solitary bees and other insects constituted 4% or less, each, of the flower-visiting insects. When analysing both flying and flower-visiting wild insects with values separated per insect group, we found an interaction between landscape type and insect group (paper II). Of all the flying and flower-visiting wild insects, 44 % were flies other than hover flies and march flies, 37 % were honey bees, and 6 % were march flies. Bumble bees constituted 5 % of all observed insects, while solitary bees, hover flies, and other insects made 3 % or less, each, of all observed insects.

Adding honey bee hives to flowering oilseed rape decreased the number of flying and flower-visiting insects in the crop (paper II), but the effect was more pronounced in large than in small fields (figure 13). We added two honey bee hives per hectare irrespective of field size, but even if we added them to a short side of each field, large fields did not have higher densities compared to small fields within 300 m distance from the field edge. A possible explanation is that the large fields had more alternative forage areas, where wild insects could forage away from the areas with the highest densities of honey bees.

Bumble bees and the flies except for hover flies and march flies, decreased in density with increasing distance from the field edge in fields without honey bees. When honey bees were added, their densities increased with distance from the field edge, suggesting that displacement was occurring.

Landscape type did not affect the influence of honey bees on wild insects, which possibly is explained by the early-season flowering of winter oilseed rape, when flowering resources in the landscape is scarce.

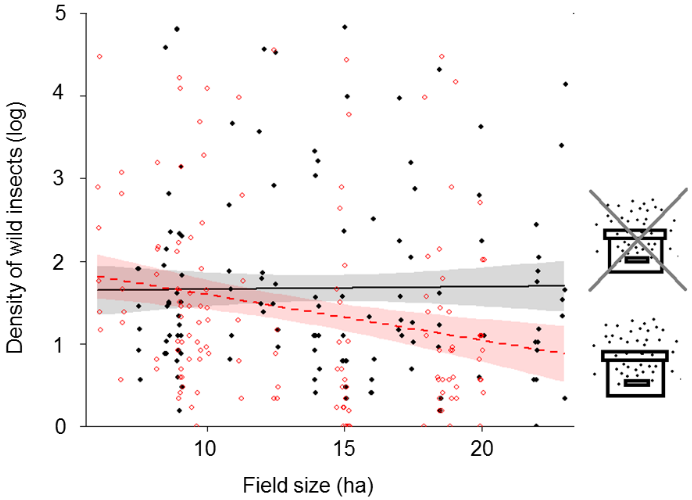

Figure 13. Model estimated density of wild flying and flower-visiting insects per field in relation to oilseed rape field size in honey bee treated fields (dashed line) and control fields (solid line). The error bars denotes 95% confidence intervals.

When we analysed each group of wild insects separately, densities were negatively affected by honey bee addition for them all. The effect of honey bees depended on field size and/or distance from field edge. The bees (bumble bees and solitary bees), which are central place foragers, showed decreased densities in large compared to small fields with added honey bees. Non-central foragers (the three groups of flies and the other insects), were not affected by field size. Central place foragers are bound to a particular field close to their nest, and can respond to competition by displacement further away from the honey bee hives, but within the same field. Non-central place foragers, however, do not have a nest to return to and can thus more easily move to another field.

Displacement of wild insects caused by honey bee addition, which leads to reduced densities of wild pollinators in flowering crops, may have negative impacts on the pollination service they provide. Crop pollination by wild insects have been shown to increase seed set irrespective of honey bee densities (Garibaldi *et al.*, 2013; Button & Elle, 2014). Adding honey bee hives to insect pollinated crops might therefore offset the pollination benefit. However, given the low numbers of pollinating wild insects in the early flowering winter oilseed rape, potential effects on yield are probably small.

Our results indicate that winter oilseed rape in Scandinavia is mainly pollinated by managed honey bees. However, flies also occurred in high numbers, although not as many of them were visiting flowers as where observed flying. Our data of flower-visiting insects were included as one of 39 crop pollination studies world-wide in a synthesizing study showing that non-bees provide 25 - 50 % of flower-visits to crops, providing a comprehensive share of crop pollination (Rader *et al.*, 2015). Winter oilseed rape fields in homogeneous landscapes had higher densities of flies (hover flies and march flies excluded) compared to heterogeneous landscapes (Lindström et al. unpublished). Even if flies carry less pollen than bees, they carry pollen longer distances than bees (Rader *et al.*, 2011). Being less dependent on landscape heterogeneity than bees, flies could form an insurance of pollination services against bee population declines in homogenous landscapes (Rader *et al.*, 2015).

Other wild pollinating insects only constituted a small proportion of all pollinating insects in our study, suggesting that their importance for oilseed rape pollination is limited (paper I). However, and perhaps more importantly, they might provide resilience to the pollinator community and buffer negative impacts of environmental change (Brittain *et al.*, 2013; Rader *et al.*, 2013). There is a possibility that competition decreases resilience, and increases vulnerability of the cropping system.

Furthermore, competition early in the season, when winter oilseed rape is flowering, may have negative consequences for wild insects' populations throughout the season by delayed or reduced population growth. In that case, adding honey bees for bolstering pollination has the potential to increase the already heavy pressure on wild flower-visiting insects in agricultural landscapes. For bumble bees, mainly queens forage in winter oilseed rape. In a study using parts of the landscape-scale experiment in paper I and II, densities of bumble bees in field borders were lower nearby fields with added honey bee hives compared to nearby fields without honey bee hives weeks after the end of the winter oilseed rape flowering (Herbertsson *et al.*, 2016). Future studies are needed to find out if this observed displacement by honey bees also leads to lower fitness and population effects in agricultural landscapes.

3 Implications for ecological intensification

3.1 Integration of insect pollination in oilseed rape cultivation

We found that insect pollination modifies the influence of crop management factors such as cultivar choice (paper I and III) and nitrogen fertilisation (paper III) on winter oilseed rape yield, suggesting ways of ecological intensification of future oilseed rape cropping systems. Insect pollination substantially increased winter oilseed rape yield, but the effect depended on the choice of cultivar. With information on specific pollination requirements of different cultivars, oilseed rape growers could choose cultivars that suit their availability of pollinators. However, this information is currently not available. We suggest a screening of a broader range of commercially available cultivars, both to confirm the generality of the results we found in paper I and III, and to generate recommendations on pollination management and cultivar choice for oilseed rape growers.

In horticultural crops, development of cultivars that set fruit without fertilisation, parthenocarpy, has been suggested as a way to reduce pollinator dependency (Knapp *et al.*, 2016). In oilseed rape, the replacement of open-pollinated cultivars by hybrid cultivars on the seed market could be a path towards decreased pollinator dependency in oilseed rape. However, we found in two separate experiments that open-pollinated cultivars gave higher yields than hybrid cultivars in presence of pollinating insects. Phasing out open-pollinated cultivars from the market, could lead to a missed opportunity to increase yields. An alternative would be to keep open-pollinated cultivars and safeguard pollinators. We suggest that trials comparing cultivars yield potential should include optimal management for all cultivars by providing pollinating insects to the crop. To reflect the pollination environment in commercial fields, large areas of each cultivar should be grown in trials to reduce cross-pollination among cultivars. This would enable the highest potential yield for each cultivar to be correctly estimated.

We, further, show that complex interactions among resources and the crop can affect pollinator behaviour and potentially crop pollination. We found that pest control in spring oilseed rape makes the crop more attractive to pollinators and affect their behaviour, potentially leading to enhanced pollination. This should be taken into consideration when impacts of pests on crop yield are evaluated, since the effects can be mixed with lower pollination.

Wild flower-visiting insects were few in our landscape-scale experiment, suggesting that winter oilseed rape in Scandinavia is mainly pollinated by managed honey bees. Adding managed honey bees led to increased crop yield, but we also found negative consequences on the densities wild flying and flower-visiting insects. Hence, addition of managed honey bees as an attempt to mitigate low pollination due to decreased populations of wild pollinators can paradoxically aggravate the situation for wild pollinators, and potentially negatively affect the long-term resilience which may result in a more vulnerable cropping system.

3.2 Future research

Future studies aiming for realistic measures of agricultural yield should be performed on the whole-field scale, especially when cross-pollination is expected. There is need to reveal the mechanisms behind the contrasting responses of cultivars on insect pollination, regardless of whether it depends on breeding type or heritage. The interaction between insect pollination and nitrogen fertilisation needs to be confirmed. Future research should explore why insect pollination interacts with nitrogen fertilisation in oilseed rape, while other crops does not. Optimal honey bee hive stocking for oilseed rape pollination would also need to be estimated.

Flies constituted a large share of the insects found in flowering oilseed rape, and there is a need to understand their contribution to crop pollination, and what influence their population abundances. We need to know more about how species abundance and composition determines the stability of the crop pollination service over years. Future research also need to find out if displacement by honey bees leads to lower fitness and population effects in agricultural landscapes. There is a need to explore how competition from honey bees on wild insects could be mitigated, potentially by adding heterogeneity and flowering resources to agricultural landscapes.

Studies of ecological intensification need to integrate agronomic, conservation, and environmental perspectives to develop sustainable cropping systems.

References

Abrol, D. P. (2007). Honeybees and rapeseed: a pollinator-plant interaction. *Advances in Botanical Research*, 45, pp 337–367.

Adegas, J. E. B. & Nogueira Couto, R. H. (1992). Entomophilous pollination in rape. *Apidologie*, 23, pp 203–209.

Aizen, M. A., Garibaldi, L. A., Cunningham, S. A. & Klein, A. M. (2008). Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Current biology*, 18(20), pp 1572–5.

Aizen, M. A., Garibaldi, L. A., Cunningham, S. A. & Klein, A. M. (2009). How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Annals of Botany*, 103(9), pp 1579–1588.

Aizen, M. & Harder, L. (2009). The truth about honeybees. *New Scientist*, 204(2731), pp 26–27.

Alford, D. V., Nilsson, C. & Ulber, B. (2003). Insect pests of oilseed rape crops. In: Alford, D. V. (Ed) *Biocontrol of oilseed rape pests*. pp 9–42. Cornwall: Blackwell Publishing Ltd.

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Allen Cox, P., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G. P., Pavlik, B., Tepedino, V., Torchio, P. & Walker, S. (1998). The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*, 12(1), pp 8–17.

Angadi, S. V., Cutforth, H. W., McConkey, B. G. & Gan, Y. (2003). Yield adjustment by canola grown at different plant populations under semiarid conditions. *Crop Science*, 43, pp 1358–1366.

Aras, P., De Oliveira, D. & Savoie, L. (1996). Effect of a honey bee (Hymenoptera: Apidae) gradient on the pollination and yield of lowbush blueberry. *Journal of Economic Entomology*, 89(5), pp 1080–1083.

Bartomeus, I., Potts, S. G., Steffan-Dewenter, I., Vaissière, 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, p e328.

Becker, H. C., Damgaard, C. & Karlsson, B. (1992). Environmental variation for outcrossing rate in rapeseed (*Brassica napus*). *Theoretical and Applied Genetics*, 84(3), pp 303–306.

Becker, H. C., Löptien, H. & Röbbelen, G. (1999). Breeding: an overview. *Developments in Plant Genetics and Breeding*, 4, pp 413–460.

Bell, S. A. & Cresswell, J. E. (1998). The phenology of gender in homogamous flowers: temporal change in the residual sex function of flowers of oil-seed rape (*Brassica napus*). *Functional Ecology*, 12(2), pp 298–306.

Berry, P. M. & Spink, J. H. (2006). A physiological analysis of oilseed rape yields: Past and future. *The Journal of Agricultural Science*, 144(5), p 381.

Bertazzini, M. & Forlani, G. (2016). Intraspecific variability of floral nectar volume and composition in rapeseed (*Brassica napus* L. var. *oleifera*). *Frontiers in Plant Science*, 7, p 288.

Billen, G., Garnier, J. & Lassaletta, L. (2013). The nitrogen cascade from agricultural soils to the sea: modelling nitrogen transfers at regional watershed and global scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1621).

Bommarco, R., Kleijn, D. & Potts, S. G. (2013). Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, 28(4), pp 230–238.

Bommarco, R., Marini, L. & Vaissière, B. E. (2012). Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia*, 169(4), pp 1025–1032.

Bos, M. M., Veddeler, D., Bogdanski, A. K., Klein, A.-M., Tscharntke, T., Steffan-Dewenter, I. & Tylianakis, J. M. (2007). Caveats to quantifying ecosystem services: fruit abortion blurs benefits from crop pollination. *Ecological Applications*, 17(6), pp 1841–1849.

Breeze, T. D., Vaissière, B. E., Bommarco, R., Petanidou, T., Seraphides, N., Kozák, L., Scheper, J., Biesmeijer, J. C., Kleijn, D., Gyldenkærne, S., Moretti, M., Holzschuh, A., Steffan-Dewenter, I., Stout, J. C., Pärtel, M., Zobel, M. & Potts, S. G. (2014). Agricultural policies exacerbate honeybee pollination service supply-demand mismatches across Europe. *PLoS ONE*, 9(1), p e82996.

Brittain, C., Kremen, C. & Klein, A.-M. (2013). Biodiversity buffers pollination from changes in environmental conditions. *Global Change Biology*, 19(2), pp 540–547.

Bronstein, J. L., Huxman, Travis, E. & Davidowitz, G. (2007). Plant-mediated effects linking herbivory and pollination. In: Ohgushi, T., Craig, T. P., & Price, P. W. (Eds) *Ecological communities: plant mediation in indirect interaction webs*. 1st. ed, pp 75–103. Cambridge: Cambridge University Press.

Burkle, L. A. & Irwin, R. E. (2009). The effects of nutrient addition on floral characters and pollination in two subalpine plants, *Ipomopsis aggregata* and *Linum lewisii*. *Plant Ecology*, 203(1), pp 83–98.

Burkle, L. A. & Irwin, R. E. (2010). Beyond biomass: measuring the effects of community-level nitrogen enrichment on floral traits, pollinator visitation and plant reproduction. *Journal of Ecology*, 98(3), pp 705–717.

Button, L. & Elle, E. (2014). Wild bumble bees reduce pollination deficits in a crop mostly visited by managed honey bees. *Agriculture, Ecosystems & Environment*, 197, pp 255–263.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S. & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486(7401), pp 59–67.

Carré, P. & Pouzet, A. (2014). Rapeseed market, worldwide and in Europe. *OCL*, 21(1), p D102.

Carreck, N. & Williams, I. (1998). The economic value of bees in the UK. *Bee World*, 79(3), pp 115–123.

Chaplin-Kramer, R., Dombeck, E., Gerber, J., Knuth, K. A., Mueller, N. D., Mueller, M., Ziv, G. & Klein, A.-M. (2014). Global malnutrition overlaps with pollinator-dependent micronutrient production. *Proceedings of the Royal Society B Biological Sciences*, 281(1794).

Cresswell, J. E., Davies, T. W., Patrick, M. A., Russell, F., Pennel, C., Vicot, M. & Lahoubi, M. (2004). Aerodynamics of wind pollination in a zoophilous flower, *Brassica napus*. *Functional Ecology*, 18(6), pp 861–866.

Cunningham, S. A. (2016). Human welfare and its connection to nature: What have we learned from crop pollination studies? *Austral Ecology*, 42(1), pp 2–8.

Daily, G. C. (1997). *Nature's services : societal dependence on natural ecosystems*.(Daily, G. C., Ed) Washington DC, USA: Island Press.

DeClerck, F., Jones, S., Attwood, S., Bossio, D., Girvetz, E., Chaplin-Kramer, B., Enfors, E., Fremier, A., Gordon, L., Kizito, F., Lopez Noriega, I., Matthews, N., McCartney, M., Meacham, M., Noble, A., Quintero, M., Remans, R., Soppe, R., Willemen, L., Wood, S. & Zhang, W. (2016). Agricultural ecosystems and their services: the vanguard of sustainability? *Current Opinion in Environmental Sustainability*, 23, pp 92–99.

Dicks, L. V., Viana, B., Bommarco, R., Brosi, B., Arizmendi, M. del C., Cunningham, S. A., Galetto, L., Hill, R., Lopes, A. V., Pires, C., Taki, H. & Potts, S. G. (2016). Ten policies for pollinators. *Science*, 354(6315), pp 975–976.

Diepenbrock, W. (2000). Yield analysis of winter oilseed rape (*Brassica napus* L .): a review. *Field Crops Research*, 67, pp 35–49.

Durán, X. A., Ulloa, R. B., Carrillo, J. A., Contreras, J. L. & Bastidas, M. T. (2010). Evaluation of yield component traits of honeybee pollinated (*Apis mellifera* L.) rapeseed canola (*Brassica napus* L.). *Chilean Journal of Agricultural Research*, 70(2), pp 309–314.

Eilers, E. J., Kremen, C., Smith Greenleaf, S., Garber, A. K. & Klein, A.-M. (2011). Contribution of pollinator-mediated crops to nutrients in the human food supply. *PLoS ONE*, 6(6), p e21363.

Eisikowitch, D. (1981). Some aspects of pollination of oil-seed rape (*Brassica napus* L.). *Journal of Agricultural Science, Cambridge*, 96, pp 321–326.

FAO. (2014) *FAOSTATS: Food and Agricultural Organization of the United Nations, Statistical division*. [online]. Available from: http://faostat.fao.org/. [2014-06-26].

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N. & Snyder, P. K. (2005). Global consequences of land use. *Science*, 309(5734).

Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O'Connell, C., Ray, D. K., West, P. C., Balzer, C., Bennett, E. M., Carpenter, S. R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D. & Zaks, D. P. M. (2011). Solutions for a cultivated planet. *Nature*, 478(7369), pp 337–342.

Free, J. B. (1993). *Insect pollination of crops*. 2nd. ed London: Academic Press.

Fries, I. & Stark, J. (1983). Measuring the importance of honeybees in rape seed production. *Journal of Apicultural Research*, 22(4), pp 272–276.

Földesi, R., Kovács-Hostyánszki, A., Kőrösi, Á., Somay, L., Elek, Z., Markó, V., Sárospataki, M., Bakos, R., Varga, Á., Nyisztor, K. & Báldi, A. (2016). Relationships between wild bees, hoverflies and pollination success in apple orchards with different landscape contexts. *Agricultural and Forest Entomology*, 18(1), pp 68–75.

Galen, C. (1985). Regulation of seed-set in *Polemonium viscosum*: floral scents, pollination, and resources. *Ecology*, 66(3), pp 792–797.

Gallai, N., Salles, J.-M., Settele, J. & Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, 68(3), pp 810–821.

Garbach, K., Milder, J. C., DeClerck, F. A. J., Montenegro de Wit, M., Driscoll, L. & Gemmill-Herren, B. (2017). Examining multi-functionality for crop yield and ecosystem services in five systems of agroecological intensification. *International Journal of Agricultural Sustainability*, 15(1), pp 11–28.

Garibaldi, L. A., Aizen, M. A., Klein, A. M., Cunningham, S. A. & Harder, L. D. (2011). Global growth and stability of agricultural yield decrease with pollinator dependence. *Proceedings of the National Academy of Sciences*, 108(14), pp 5909–14.

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., Hipólito, 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(6127), pp 1608–11.

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. *Biological Conservation*, 169, pp 128–135.

Gill, R. J., Baldock, K. C. R., Brown, M. J. F., Cresswell, J. E., Dicks, L. V., Fountain, M. T., Garratt, M. P. D., Gough, L. A., Heard, M. S., Holland, J. M., Ollerton, J., Stone, G. N., Tang, C. Q., Vanbergen, A. J., Vogler, A. P., Arce, A. N., Boatman, N. D., Brand-Hardy, R., Breeze, T. D., Green, M., Hartfield, C. M., O'Connor, R. S., Osborne, J. L., Phillips, J., Sutton, P. B. & Potts, S. G. (2016). Protecting an ecosystem service: approaches to understanding and mitigating threats to wild insect pollinators. *Advances in Ecological Research*. pp 135–206.

Godfray, H. C. J. & Garnett, T. (2014). Food security and sustainable intensification. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1639).

Gomez, N. V & Miralles, D. J. (2011). Factors that modify early and late reproductive phases in oilseed rape (*Brassica napus* L.): Its impact on seed yield and oil content. *Industrial Crops & Products*, 34, pp 1277–1285.

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(6229), p 1255957.

Groeneveld, J. H., Tscharntke, T., Moser, G. & Clough, Y. (2010). Experimental evidence for stronger cacao yield limitation by pollination than by plant resources. *Perspectives in Plant Ecology, Evolution and Systematics*, 12(3), pp 183–191.

Grosse, F., Leon, J. & Diepenbrock, W. (1992). Yield formation and yield structure of winter oilseed rape (*Brassica-napus* L.). 1. Genotypic variability. *Journal of Agronomy and Crop Science*, 169(1–2), pp 70–93.

Habekotté, B. (1993). Quantitative analysis of pod formation, seed set and seed filling in winter oilseed rape (*Brassica napus* L.) under field conditions. *Field Crops Research*, 35(1), pp 21–33.

Hayter, K. E. & Cresswell, J. E. (2006). The influence of pollinator abundance on the dynamics and efficiency of pollination in agricultural Brassica napus: implications for landscape-scale gene dispersal. *Journal of Applied Ecology*, 43(6), pp 1196–1202.

Herbertsson, L., Lindström, S. A. M., Rundlöf, M., Bommarco, R. & Smith, H. G. (2016). Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic and Applied Ecology*, 17(7), pp 609–616.

Holzschuh, A., Dormann, C. F., Tscharntke, T. & Steffan-Dewenter, I. (2011). Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society B Biological Sciences*, 278(1723), pp 3444–51.

Hoyle, M., Hayter, K. & Cresswell, J. E. (2007). Effect of pollinator abundance on self-fertilization and gene flow: application to GM canola. *Ecological Applications*, 17(7), pp 2123–2135.

Hudewenz, A., Pufal, G., Bögeholz, A.-L. & Klein, A.-M. (2013). Cross-pollination benefits differ among oilseed rape varieties. *The Journal of Agricultural Science*, pp 1–9.

IPBES (2016). *The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production*. Bonn, Germany: Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Jauker, F. & Wolters, V. (2008). Hover flies are efficient pollinators of oilseed rape. *Oecologia*, 156(4), pp 819–823.

Kearns, C. A. & Inouye, D. W. (1993). *Techniques for pollination biologists.* University Press of Colorado. ISBN 0-87081-279-3.

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. *Ecology letters*, 16(5), pp 584–99.

Kevan, P. G. & Eisikowitch, D. (1990). The effects of insect pollination on canola (*Brassica napus* L. cv. O.A.C. Triton) seed germination. *Euphytica*, 45(1), pp 39–41.

Kirk, W. D. J., Ali, M. & Breadmore, K. N. (1995). The effects of pollen beetles on the foraging behaviour of honey bees. *Journal of Apicultural Research*, 34(1), pp 15–22.

Klatt, B. K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E. & Tscharntke, T. (2014). Bee pollination improves crop quality, shelf life and commercial value. *Proceedings of the Royal Society B Biological Sciences*, 281(1775), p 20132440.

Klein, A.-M., Hendrix, S. D., Clough, Y., Scofield, A. & Kremen, C. (2015). Interacting effects of pollination, water and nutrients on fruit tree performance. *Plant Biology*, 17(1), pp 201–208.

Klein, A.-M., Vaissière, 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. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), pp 303–313.

Knapp, J. L., Bartlett, L. J. & Osborne, J. L. (2016). Re-evaluating strategies for pollinator-dependent crops: How useful is parthenocarpy? *Journal of Applied Ecology*.

Koltowski, Z. (2005). The effect of pollinating insects on the yield of winter rapeseed (*Brassica napus* L. var. *napus* f. *biennis*) cultivars. *Journal of Apicultural Science*, 49(2), pp 29–41.

Krupnick, G. A., Weis, A. E. & Campbell, D. R. (1999). The consequences of floral herbivory for pollinator service to *Isomeris arborea*. *Ecology*, 80(1), pp 125–134.

Lautenbach, S., Seppelt, R., Liebscher, J. & Dormann, C. F. (2012). Spatial and temporal trends of global pollination benefit. *PloS ONE*, 7(4), p e35954.

Léon, J. (1991). Heterosis and mixing effects in winter oilseed rape. *Crop Science*, 31(2), p 281.

Lundin, O., Smith, H. G., Rundlöf, M. & Bommarco, R. (2013). When ecosystem services interact: crop pollination benefits depend on the level of pest control. *Proceedings of the Royal Society B: Biological Sciences*, 280(1753), p 20122243.

Mallinger, R. E. & Gratton, C. (2015). Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop. *Journal of Applied Ecology*, 52(2), pp 323–330.

Manning, R. & Wallis, I. R. (2005). Seed yields in canola (*Brassica napus* cv. Karoo) depend on the distance of plants from honeybee apiaries. *Australian Journal of Experimental Agriculture*, 45, pp 1307–1313.

Matson, P. A., Parton, W. J., Power, A. G. & Swift, M. J. (1997). Agricultural intensification and ecosystem properties. *Science*, 277(5325).

McGregor, D. I. (1987). Effect of plant density on development and yield of rapeseed and its significance to recovery from hail injury. *Canadian Journal of Plant Science*, 67(1), pp 43–51.

MEA (2005). *Millennium Ecosystem Assessment. World Resources Institute*. Washington DC, USA.

Mesquida, J., Renard, M. & Pierre, J. S. (1988). Rapeseed (*Brassica napus* L) productivity - the effect of honeybees (*Apis mellifera* L) and different pollination conditions in cage and field tests. *Apidologie*, 19(1), pp 51–72.

Meyer, J. (1997). Olje- och spånadsväxter. In: Olsson, G. (Ed) *Den svenska växtförädlingens historia. [The history of Swedish plant breeding]*. pp 241–252. SHS Tryck och Tryck, Hållsta, Sweden: Kungliga Skogs- och Lantbruksakademien. Skogs- och lantbrukshistoriska meddelanden 20.

Motzke, I., Tscharntke, T., Wanger, T. C. & Klein, A.-M. (2015). Pollination mitigates cucumber yield gaps more than pesticide and fertilizer use in tropical smallholder gardens. *Journal of Applied Ecology*, 52, pp 261–269.

Nieto, A., Roberts, S. P. M., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M., Biesmeijer, J. C., Bogusch, P., Dathe, H. H., De la Rúa, P., De Meulemeester, T., Dehon, M., Dewulf, A., Ortiz-Sánchez, F. J., Lhomme, P., Pauly, A., Potts, S. G., Praz, C., Quaranta, M., Radchenko, V. G., Scheuchl, E., Smit, J., Straka, J., Terzo, M., Tomozii, B., Window, J. & Michez, D. (2014). *European red list of bees*. Luxembourg: Publication Office of the European Union.

Nilsson, C. (1987). Yield losses in summer rape caused by pollen beetles (*Meligethes* spp.). *Swedish Journal of Agricultural Research*, 17, pp 105–111.

Ollerton, J., Winfree, R. & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120(3), pp 321–326.

Olsson, G. (1952). Undersökning av graden av korsbefruktning hos vitsenap och raps. *Sveriges Utsädesförenings Tidskrift*, 62, pp 311–322.

Olsson, G. (1960). Self-incompatibility and outcrossing in rape and white mustard. *Hereditas*, 46(1–2), pp 241–252.

Paini, D. R. (2004). Impact of the introduced honey bee (*Apis mellifera*) (Hymenoptera: Apidae) on native bees: A review. *Austral Ecology*, 29(4), pp 399–407.

Persson, B. (1953). Undersökningar rörande insektspollinerade kulturväxter I, observationer rörande blommornas biologi hos raps (*Brassica napus* L.) med hänsyn till faran för bidöd vid behandling av rapsfält med insekticider. *Statens växtskyddsanstalt Meddelande*, 66.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W. E. (2010a). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25(6), pp 345–353.

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J. & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540(7632), pp 220–229.

Potts, S. G., Roberts, S., Dean, R., Marris, G., Brown, M., Jones, R., Neumann, P. & Settele, J. (2010b). Declines of managed honey bees and beekeepers in Europe. *Journal of Apicultural Research*, 49(1), p 15.

Power, E. F., Jackson, Z. & Stout, J. C. (2016). Organic farming and landscape factors affect abundance and richness of hoverflies (Diptera, Syrphidae) in grasslands. *Insect Conservation and Diversity*, 9, pp 244–253.

Rader, R., Bartomeus, I., Garibaldi, L. A., Garratt, M. P. D., Howlett, B. G., Winfree, R., Cunningham, S. A., Mayfield, M. M., Arthur, A. D., Andersson, G. K. S., Bommarco, R., Brittain, C., Carvalheiro, L. G., Chacoff, N. P., Entling, M. H., Foully, B., Freitas, B. M., Gemmill-Herren, B., Ghazoul, J., Griffin, S. R., Gross, C. L., Herbertsson, L., Herzog, F., Hipólito, J., Jaggar, S., Jauker, F., Klein, A.-M., Kleijn, D., Krishnan, S., Lemos, C. Q., Lindström, S. A. M., Mandelik, Y., Monteiro, V. M., Nelson, W., Nilsson, L., Pattemore, D. E., de O. Pereira, N., Pisanty, G., Potts, S. G., Reemer, M., Rundlöf, M., Sheffield, C. S., Scheper, J., Schüepp, C., Smith, H. G., Stanley, D. A., Stout, J. C., Szentgyörgyi, H., Taki, H., Vergara, C. H., Viana, B. F. & Woyciechowski, M. (2015). Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences*, 113(1), p 201517092.

Rader, R., Edwards, W., Westcott, D. A., Cunningham, S. A. & Howlett, B. G. (2011). Pollen transport differs among bees and flies in a human-modified landscape. *Diversity and Distributions*, 17(3), pp 519–529.

Rader, R., Reilly, J., Bartomeus, I. & Winfree, R. (2013). Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Global Change Biology*, 19(10), pp 3103–3110.

Rai, B., Gupta, S. K. & Pratap, A. (2007). Breeding methods. *Advances in Botanical Research*, 45, pp 21–48.

Ramsay, G., Thompson, C. & Squire, G. (2003). Quantifying landscape-scale gene flow in oilseed rape. Final Report of DEFRA Project RG0216: an experimental and mathematical study of the local and regional scale movement of an oilseed rape transgene. DEFRA.

Rathke, G., Behrens, T. & Diepenbrock, W. (2006). Integrated nitrogen management strategies to improve seed yield, oil content and nitrogen efficiency of winter oilseed rape (*Brassica napus* L.): a review. *Agriculture, Ecosystems & Environment*, 117(2–3), pp 80–108.

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., Viana, B. F., Steffan, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-herren, B., Greenleaf, S. S. & Alexandra, M. (2008). Landscape effects on crop pollination services: are there general patterns? *Ecology Letters*, 11(5), pp 499–515.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F. S., Lambin, E. F., Lenton, T. M., Scheffer, M., Folke, C., Schellnhuber, H. J., Nykvist, B., de Wit, C. A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P. K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R. W., Fabry, V. J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P. & Foley, J. A. (2009). A safe operating space for humanity. *Nature*, 461(7263), pp 472–475.

Rockström, J., Williams, J., Daily, G., Noble, A., Matthews, N., Gordon, L., Wetterstrand, H., DeClerck, F., Shah, M., Steduto, P., de Fraiture, C., Hatibu, N., Unver, O., Bird, J., Sibanda, L. & Smith, J. (2017). Sustainable intensification of agriculture for human prosperity and global sustainability. *Ambio*, 46(1), pp 4–17.

Rondanini, D. P., Gomez, N. V., Agosti, M. B. & Miralles, D. J. (2012). Global trends of rapeseed grain yield stability and rapeseed-to-wheat yield ratio in the last four decades. *European Journal of Agronomy*, 37(1), pp 56–65.

Rundlöf, M., Nilsson, H. & Smith, H. (2008). Interacting effects of farming practice and landscape context on bumble bees. *Biological Conservation*, 141, pp 417–426.

Rydberg, C., Kylberg, L. H., von Zwegbergk, G. & Ljung, E. W. (1914). *Jordbrukslära för skolor och självstudium.* 2nd. ed Stockholm: C. E. Fritzes Bokförlags Aktiebolag.

Sabbahi, R., De Oliveira, D. & Marceau, J. (2005). Influence of honey bee (Hymenoptera : Apidae) density on the production of canola (Crucifera : Brassicacae). *Journal of Economic Entomology*, 98(2), pp 367–372.

Sabbahi, R., De Oliveira, D. & Marceau, J. (2006). Does the honeybee (Hymenoptera: Apidae) reduce the blooming period of canola? *Journal of Agronomy and Crop Science*, 192(3), pp 233–237.

Senapathi, D., Carvalheiro, L. G., Biesmeijer, J. C., Dodson, C.-A., Evans, R. L., McKerchar, M., Morton, R. D., Moss, E. D., Roberts, S. P. M., Kunin, W. E. & Potts, S. G. (2015). The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proceedings of the Royal Society B Biological Sciences*, 282(1806), p 20150294.

Shebl, M. A., Kamel, S. M., Abu Hashesh, T. A. & Osman, M. A. (2009). The impact of using leafcutting bees (*Megachilidae hymenoptera*) with fertilization treatments on alfalfa seed production. *Revista de la ciencia del suelo y nutrición vegetal*, 9(2), pp 134–141.

Snowdon, R., Lühs, W. & Friedt, W. (2007). Oilseeds. In: Kole, C. (Ed) *Genome mapping and molecular breeding in plants - oilseeds*. pp 55–114. Berlin Heidelberg: Springer-Verlag.

St-Martin, A. & Bommarco, R. (2016). Soil compaction and insect pollination modify impacts of crop rotation on nitrogen fixation and yield. *Basic and Applied Ecology*, 17(7), pp 617–626.

Stanley, D. A., Gunning, D. & Stout, J. C. (2013). Pollinators and pollination of oilseed rape crops (Brassica napus L.) in Ireland: ecological and economic incentives for pollinator conservation. *Journal of Insect Conservation*, 17(1181).

Steffan-Dewenter, I. (2003). Seed set of male-sterile and male-fertile oilseed rape (*Brassica napus*) in relation to pollinator density. *Apidologie*, 34(3), pp 227–235.

Sutter, L. & Albrecht, M. (2016). Synergistic interactions of ecosystem services: florivorous pest control boosts crop yield increase through insect pollination. *Proceedings of the Royal Society B Biological Sciences*, 283(1824).

Tamburini, G., Berti, A., Morari, F. & Marini, L. (2016). Degradation of soil fertility can cancel pollination benefits in sunflower. *Oecologia*, 180(2), pp 581–587.

Tatchell, G. M., Adams, M. W., Gould, H. J., Harper, F. R., Berkenkamp, B., Sachs, T., Thimann, K. V., Thomas, T. H. & Winfield, A. L. (1983). Compensation in spring-sown oil-seed rape (*Brassica napus* L.) plants in response to injury to their flower buds and pods. *The Journal of Agricultural Science*, 101(3), p 565.

The Swedish Board of Agriculture (2016a). *Bekämpningsrekommendationer - svampar och insekter. BE17*. Jönköping.

The Swedish Board of Agriculture (2016b). *Rekommendationer för gödsling och kalkning 2017. Jordbruksinformation 24 - 2016*. Jönköping.

The Swedish Board of Agriculture (2016c). *Use of agricultural land in 2016, preliminary statistics. JO*

10 SM 1602. Jönköping.

Tilman, D., Balzer, C., Hill, J. & Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences of the United States of America*, 108(50), pp 20260–4.

vanEngelsdorp, D., Evans, J. D., Saegerman, C., Mullin, C., Haubruge, E., Nguyen, B. K., Frazier, M., Frazier, J., Cox-Foster, D., Chen, Y., Underwood, R., Tarpy, D. R. & Pettis, J. S. (2009). Colony collapse disorder: a descriptive study. *Plos One*, 4(8), p e648.

vanEngelsdorp, D. & Meixner, M. D. (2010). A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *Journal of Invertebrate Pathology*, 103, pp S80–S95.

Wezel, A., Soboksa, G., McClelland, S., Delespesse, F. & Boissau, A. (2015). The blurred boundaries of ecological, sustainable, and agroecological intensification: a review. *Agronomy for Sustainable Development*, 35(4), pp 1283–1295.

Williams, I. H. (1985). The pollination of swede rape (*Brassica napus* L). *Bee World*, 66(1), pp 16–22.

Williams, I. H. (1994). The dependence of crop production within the European Union on pollination by honey bees. *Agricultural Zoology Reviews*, pp 229–257.

Williams, I. H. (2010). The major insect pests of oilseed rape in Europe and their management: an overview. In: Williams, I. H. (Ed) *Biocontrol-based integrated management of oilseed rape pests*. pp 1–43. Springer Netherlands.

Williams, I. H., Martin, A. P. & White, R. P. (1987). The effect of insect pollination on plant development and seed production in winter oilseed rape (*Brassica napus* L.). *Journal of Agricultural Science, Cambridge*, 1987, pp 135–139.

Winston, M. L. (1991). *The biology of the honey bee*. London, England: Harvard University Press.

Öckinger, E., Franzen, M., Rundlof, M. & Smith, H. G. (2009). Mobility-dependent effects on species richness in fragmented landscapes. *Basic and Applied Ecology*, 10(6), pp 573–578.

Öckinger, E. & Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, 44(1), pp 50–59.

4 Populärvetenskaplig sammanfattning

Mänskligheten står inför en stor utmaning. Ökat välstånd och en växande befolkningen kräver ökad matproduktion, samtidigt behöver de negativa miljöeffekterna av matproduktionen minska. Under den gröna revolutionen lyckades man öka skördarna kraftigt, bland annat genom växtförädling och ökade insatser av mineralgödsel och växtskyddsmedel. Förändringarna inom jordbruket ledde dock till negativ påverkan på vattenkvaliteten, klimatet och den biologiska mångfalden. Den biologiska mångfalden i jordbrukslandskapet utför ekologiska processer som kan gynna matproduktionen, så kallade ekosystemtjänster. Genom att gynna ekologiska processer som till exempel biologisk reglering av skadegörare, omsättning av växtnäring och insektspollinering, kan man öka skörden utan att öka mängden insatsmedel. Detta sätt att intensifiera växtodlingen kallas för ekologisk intensifiering. För att förverkliga ekologisk intensifiering i praktisk växtodling, krävs det tillförlitliga skattningar av hur skörden påverkas av de ekologiska processerna.

Raps är världens tredje viktigaste oljegröda och näst viktigaste proteingröda, och därtill en viktig gröda i svensk växtodling. På grund av sitt stora behov av kväve och att den lockar flera skadedjur, är kvävegödsling och växtskydd viktiga odlingsfaktorer. Det odlas både höst- och vårformer av raps, och de kan förädlas med antingen linje- eller hybridteknik. Linjesorter förädlas med traditionella korsningsmetoder, medan hybridsorter tas fram genom korsning av två inavlade linjesorter för att maximera vitaliteten. Raps är delvis självpollinerad, men kan även pollineras via vind och insekter. Äldre studier som har undersökt insektspollineringens betydelse för rapsskördens storlek och kvalitet, har ofta utförts i burar eller växthus, eller fokuserat på effekter i enskilda plantor eller delar av plantor. Det saknas kunskap om hur insektspollinering påverkar skörden i hela fält, och om insektspollinering kan påverka effekten av andra odlingsfaktorer såsom sortval, kvävegödsling, skadedjursbekämpning och bevattning.

Både vilda insekter och tama honungsbin besöker och pollinerar raps. Tama honungsbin kan flyttas till blommande grödor för att snabbt öka mängden pollinatörer, men i vissa fall ger vilda pollinatörer en ökad pollinering oavsett om honungsbin också besöker grödan. Antalet honungsbisamhällen räcker dock inte till för att täcka behovet hos insektspollinerade grödor i Europa. Jordbrukslandskapet har förändrats kraftigt det senaste århundradet, vilket har lett till färre livsmiljöer och mindre föda för vilda bin. Varierade landskap med naturbetesmarker och blommande fältkanter har fler individer och större mångfald av vilda bin än intensivt odlade mer monotona landskap. Hur andra vilda pollinerande insekter, till exempel flugor, påverkas av landskapsförändringar är till stor del okänt. Skillnader i sammansättningen av pollinatörer i olika landskap kan leda till skiftande pollineringsbidrag i odlade grödor beroende på i vilket landskap de odlas.

Det finns spår av biodling i norra Europa sedan den yngre stenåldern. Honungsbin har alltså samexisterat med vilda blombesökande insekter under lång tid. Förändringar i jordbrukslandskapets utbud av blommande resurser kan ha ökat risken för konkurrens mellan vilda blombesökande insekter och tama honungsbin. Negativ påverkan av utsättning av tama honungsbin på vilda blombesökande insekter kan möjligtvis påverka pollinering av grödor negativt. Det är inte känt om honungsbin konkurrerar med vilda insekter i blommande grödor, och om effekten varierar beroende på hur varierat landskapet är.

I den här avhandlingen ville jag undersöka hur insektspollinering påverkar skörden i hela fält av höstraps, utvärdera hur utsättning av tama honungsbin påverkar förekomsten av vilda insekter, och ta reda på om effekterna varierade i olika landskapstyper. Jag ville också utforska hur insektspollinering interagerar med andra odlingsfaktorer så som sortval, kvävestrategi, bevattning och växtskydd. Det övergripande syftet med avhandlingen var att ta fram kunskap som kan utveckla produktiva och uthålliga odlingssystem.

Vi studerade dessa frågor med två typer av experiment. Vi gjorde dels storskaliga landskapsexperiment i höstraps med manipulerade förekomster av pollinatörer, och dels två rutförsök, ett i höstraps och ett i vårraps, för att ta reda på hur insektspollinering påverkade skördeeffekten av sortval, kvävegödsling, växtskydd och bevattning.

De storskaliga fältförsöken i höstraps utfördes i samarbete med biodlare och rapsodlare i Skåne. Sammansättningen av pollinatörer i fälten manipulerades, genom att vi satte ut 624 honungsbisamhällen till 23 fält, och såg till att området runt 21 andra fält saknade honungsbisamhällen. Hälften av fälten var sådda med linjesort och hälften med hybridsort. Lantbrukarna förság oss med uppgifter om bland annat såtid, etableringsteknik, gödsling och växtskydd. Fälten låg i antingen homogena, intensivt odlade landskap, eller i heterogena landskap med mer naturbetesmarker, där vi i de varierade landskapen förväntade oss fler vilda insekter än i de mer monotona intensivt odlade landskapen. Vi undersökte hur utsättning av honungsbin påverkade skörden och de vilda pollinatörerna i rapsfälten.

Höstrapsskörden ökade med 450 kg, motsvarande 11 %, när honungsbin var utplacerade vid fält under blomningen jämfört med fält utan honungsbin, men bara i fält sådda med linjesorter. Skörden i hybridsorter påverkades inte. Bland fälten som hade tillgång till honungsbin gav linjesorter 9 % högre skörd än fält sådda med hybridsorter. Fälten gav liknande skörd i de två landskapstyperna, vilket troligtvis berodde på de låga förekomsterna av vilda insekter jämfört med honungsbin. Detta är, så vitt vi vet, de första pollineringsexperiment med kontrollfält i upprepade landskap som kombinerar honungsbibehandling med en landskapsbehandling och där både odlingsfaktorer och fältförhållanden beaktas.

I rutförsöket som gjordes i höstraps odlade vi två hybridsorter och en linjesort under två kvävegödslingsnivåer, utan kvävegödsling på våren respektive 170 kg/ha mineralgödselkväve på våren, vilket är inom de rekommenderade givorna. Vi jämförde skörden i rutor utan tillgång till pollinerande insekter (stängda burar), och i rutor som besöktes av pollinerande insekter (öppna burar). Försöket utfördes i norra Italien. Vi såg samma mönster här som i de storskaliga fältförsöken som utfördes i Skåne. Insektspollinering ökade skörden med i genomsnitt 19 % i linjesorten. I hybridsorterna påverkades inte skörden, men plantor som hade tillgång till insektspollinering gav fler, men lättare, frön per skida och producerade färre skidor per planta jämfört med plantor som inte hade tillgång till pollinerande insekter.

I båda experimenten gav linjesorter 8,6 % respektive 12,8 %, högre skörd än hybridsorter när pollinerande insekter var närvarande. Resultaten är intressanta eftersom hybridsorter anses ge högre skörd än linjesorter. Utfasning av linjesorter från utsädesmarknaden skulle kunna minska behovet av insektspollinering, men innebär en förlorad möjlighet till ökade skördar genom odling av linjesorter och skydd av pollinerande insekter.

För korrekt skattning av olika sorters skördepotential ska dessa mätas under optimala, rättvisa förhållanden. Därför föreslår vi att pollinerande insekter ska finnas tillgängliga under blomningen i sortprovningsförsök. Tidigare studier har visat att skillnader i insektspollineringsbehov mellan rapssorter oberoende av förädlingstyp, men dessa har baserats på skördeuppskattningar i enskilda rapsplantor odlade i små rutor eller krukor. Under dessa förhållanden är sannolikheten stor att korspollinering sker mellan sorter, än under helfältsförhållanden eller försök med stora rutor av varje sort. Eftersom vi endast hade möjlighet att undersöka totalt nio höstrapssorter föreslår vi en screening av ett större urval kommersiellt odlade rapssorter. Denna behövs för att bekräfta våra resultat, och för att ta fram underlag om sorternas pollineringsbehov till förädlare och odlare.

I rutförsöket fann vi en tendens till att insektspollinering påverkade effekten av kvävegödsling. I led som inte fått kväve på våren ökade skörden med 15 % när insekter pollinerade rapsen, jämfört med när insekter stängdes ute, oavsett sort. I leden som gödslats med 170 kg N/ha såg vi ingen skillnad i skörd mellan öppna och stängda burar. En möjlig förklaring till den ökade skörden kan vara att kvävegödsling ökade rapsplantornas förmåga att kompensera för brist på pollinering. I öppna burar var skörden bara marginellt högre när kväve tillfördes, jämfört när det inte gjorde det. Det är ett intressant resultat, som indikerar att insektspollinering kan öka kväveeffektiviteten hos raps, och som inspirerar till uppföljande undersökningar.

I det andra rutförsöket, som utfördes i Skepparslöv, Skåne, studerade vi hur insektspollinering, bevattning och växtskydd påverkade skörd och födosöksbeteenden hos bin i vårraps. Vi mätte förekomsten av rapsbaggar under knoppstadiet, och behandlade hälften av rutorna med insekticider medan den andra hälften av rutorna lämnades obehandlade. Vi bevattnade hälften av rutorna (både insekticidbehandlade och icke-insekticidbehandlade rutor), två gånger strax innan blomning och en gång strax efter blomning, medan hälften av rutorna inte bevattnades. Rutorna försågs med öppna och stängda burar för att tillåta blombesökande insekter respektive stänga dem ute. Dessvärre drabbades experimentet av bomullsmögel, främst i de öppna burarna, med kraftigt sänkt skörd som följd. Våra resultat visade att behandling mot rapsbaggar under knoppstadiet ökade antalet blommor och tätheten av blombesökande insekter under blomningen. Vi hittade fler blommor med rapsbaggelarver i rutor som inte behandlats mot rapsbaggar under knoppstadiet. Mängden nektar ökade i rutor som behandlats mot rapsbaggar, men endast i obevattnade led. I bevattnade led var nektarproduktionen oförändrad, vilket kan bero på att bevattning tillät plantorna att kompensera för skador av rapsbaggelarver på nektarierna. Honungsbin och humlor besökte blommor för att dricka nektar oftare i rutor behandlade mot rapsbaggar än i obehandlade rutor. Resultaten i min avhandling visar att reglering av rapsbaggar leder till en mer attraktiv gröda för pollinerande insekter och påverkar deras beteende, vilket möjligtvis kan förbättra pollineringen. Detta bör man ta hänsyn till när man undersöker rapsbaggars effekt på rapsskörden, eftersom effekter av rapsbaggar kan vara förenade med minskad insektspollinering.

Slutligen undersökte vi vilka insekter som besökte höstrapsen i de storskaliga landskapsexperimenten, och om utsättning av honungsbin påverkade de vilda insekterna. Tama honungsbin utgjorde den största delen av de blombesökande insekterna, men även flugor (exklusive blomflugor och hårmyggor) utgjorde en stor del av insekterna i blommande höstraps. Vår undersökning ingick som en av 39 pollineringsstudier från hela världen i en syntes som visade att icke-bin bidrar med 25-50 % av blombesök i grödor, och därmed troligen en betydande del av pollineringen. Flugors bidrag till insektspollinering är dåligt känt, och behöver undersökas vidare. Våra resultat visade också att det fanns färre flygande och blombesökande vilda insekter i fält till vilka vi satt ut honungsbisamhällen, och att effekten var större i stora fält. I stora fält finns det mer alternativ födosöksplats, längre bort ifrån honungsbisamhällena, än i små fält. Effekten påverkades inte av den omgivande landskapstypen, vilket kan bero på att höstraps är den största blomresursen i båda landskapstyperna tidigt på säsongen. Eftersom vilda insekter har visats ge en pollineringseffekt oavsett honungsbin, kan utsättning av honungsbin delvis försämra pollineringen genom att vilda insekter undviker grödan där honungsbina är. I höstraps är denna effekt troligen liten, eftersom de vilda insekterna var få jämfört med honungsbina. Givet den negativa utvecklingen för vilda bin i odlingslandskapet, är det viktigt att insatser för att gynna insektspollinering inte ytterligare ökar hoten mot de vilda pollinerande insekterna. Framtida forskning behöver undersöka om konkurrens leder att populationerna av vilda insekter faktiskt minskar, och ta fram åtgärder som kan mildra effekterna av konkurrens. En möjlighet är att öka mängden blommor i jordbrukslandskapet. Resultaten i min avhandling belyser vikten av att inkludera både agronomiska och miljömässiga perspektiv när nya odlingssystem utvecklas.

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