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Bumblebee resource dynamics: A review of foraging and nesting in the agricultural landscape

Resursdynamik hos humlor: En genomgång av födo- och boplatsresurser i det agrara landskapet

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Abstract

90 % of all plants on earth either benefits or entirely depends on pollination. There are pollinators among families of bees (*Apidea*), butterflies (*Lepidoptera*) and birds (*Aves*). Bees of genus *Bombus spp*., bumblebees, are especially important and provide pollination service for 80 % of the crops of Europe and many wild plant species. The bumblebee community both rise and fall within the same year with few exceptions. Only the newborn queen survives to the next year to form a new community. Since the intensification of agriculture many bumblebees species have been declining in numbers.

The purpose of this thesis was to review the drivers of bumblebees in the agricultural landscape, focusing on nesting and foraging. The aim was to understand what controls the quantity of bumblebees, which species were to be found and why them. This thesis consists of two parts: one reviewing foraging and nesting by a literature review and the other a field study of the effects of flower strips and honeybees. In the field study, I searched for bumblebee queens emerging in spring the year after an experiment with honeybees (*Apis mellifera*) and flower strips in fava beans (*Vicia faba*). I could not find a significant effect of flower strips nor honeybees in my field study. However, in my review several researches have come to the conclusion that both honeybees and flower strips can affect bumblebee density and thereby also potentially bumblebee dynamics. For instance, the impact of honeybees could be minimized by keeping the hives within the ecosystem the year around and not within areas with sensitive or endangered plant or bee species. Flower strips could potentially positively affect bumblebee population dynamics if the timing and floral quality meets the temporal need of the bumblebee populations, especially during critical events such as nest establishment and queen reproduction.

We need further testing of the impact of floral abundance in the agricultural landscape and presence of honeybees on bumblebee population dynamics, mainly during critical events such as nest establishment. Because this field study was first of its kind in Sweden, the method needs to be refined to better handle the impact of timing and changes in weather. Therefore several more studies during nest establishment are needed, studying the impact of overwintering survival and fitness of queens.

Preface

In the spring of 2019 I got the opportunity to be a part of an on going research project by the Swedish university of Agricultural Sciences (SLU) together with the Swedish Rural Economy and Agricultural Society. Working as an experiment technician I visited 17 different locations in Skåne, Sweden, counting emerging bumblebees, a study first of its kind in Sweden. I was rewarded by the opportunity to not just work in this project but also to use the data in my independent project within the Agricultural program – soil and plant science (300 credits) at SLU, in other words this very thesis.

My interest in agricultural entomology was founded in the year of 2015 when I wrote my thesis about bumblebees in red clover (*Trifolium pratense*) as a Higher degree diploma in Agricultural and Rural Management (120 credits) at SLU in Skåne. Since then I keep both agricultural entomology as well as plant science close to my hart.

I want to especially thank my supervisors Riccardo Bommarco at the SLU and Sandra Lindström at the Swedish Rural Economy and Agricultural Society. Thanks to you I got an opportunity to learn so much, expanding my knowledge within the subject as well as in scientific practises. I also want to thank Neal M. Williams at the University of California for sharing your knowledge, giving me a jump-start in both my fieldwork and my thesis. Last but not least I want to thank Veronica Hederström at SLU for your sharing your thoughts about researching bumblebees. Thank you!

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1 Introduction

Bumblebees are wild social bees belonging to the genus *Bombus* of the bee family (*Apidae*). They are living in communities of twenty to several hundred individuals (Benton 2006) and depend on the surrounding landscape to provide them habitats (areas providing food and nests). Habitat destruction and intensified agriculture are the main reason to bumblebee (*Bombus spp.*) decline in Europe, Asia and North America in the last decades (Persson & Smith 2013). Further more fertilizers and herbicides affect the occurrence and diversity of possible food plants (Goulson *et al.* 2005; Warren *et al.* 2007; Connor 2018). Most of the bumblebee species have declined in number since the 1950:s (Potts *et al.* 2010), but a few species seem to handle the altering agricultural landscape better than others (Westphal *et al.* 2009). We know little about what makes some colonies survive better than other, especially at a species level. Bumblebee colonies, with few exceptions, only survive the year of establishment (Benton 2006). Bumblebees need different habitats depending on stages of their life-cycle (Williams *et al.* 2012; Persson & Smith 2013; Rundlöf *et al.* 2014). The survival of the queen larvae, the overwintering of new born queens (gynes) and their nest establishment in spring are important factors for the population dynamic between years (Westphal *et al.* 2009; Goulson 2010; Rundlöf *et al.* 2014). All bumblebee species depend on social relations to each other forming communities with casts as queens, workers (always females) and males represented (Goulson 2010). Though some species, called cuckoo bumblebees, have evolved to depend entirely on other species to bring up their young. A cuckoo queen takes over a nest of another species, by tricking the workers and killing their queen. This essay will not discuss cuckoo bumblebees.

1.1 Purpose

The aim of this thesis is to review the drivers for bumblebees in the landscape, concentrating on foraging and nesting. The effects of adding flower strips as food resources and of competition with honeybees over floral and nesting resources are studied further in a field survey. A driver is a force that affects the spacing or timing of resources, affecting the abundance of bumblebees within their life cycle. For instance, habitat aggregation causing longer flying distances to reach floral resource within their flowering period (Williams *et al.* 2012). To investigate which and how drivers control the bumblebee abundance and species-richness, I focus on foraging and nesting in an agricultural landscape within a spatiotemporal context. The goal is to determine what we know and don't know about bumblebee population dynamic, to understand what makes the bumblebee population vary from one year to another. Other drivers such as predators and parasites are probably important but they are not subjects of this essay.

As much as I want to know what affects bumblebee dynamics, I also want to know how and why species react different on drivers. Because much research tell us that bumblebees do respond to change depending on their characteristics and behaviour (Benton 2006; Walther-Hellwig & Frankl 2000; Suzuki *et al.* 2009; Klumpers *et al.* 2019), we ought to review how behaviour and characteristics differs among bumblebee species to help to explain why species react differently to change. For instance, changes in land use and/or climate. There are several studies that points out potential drivers for bumblebee dynamics (Williams *et al.* 2012; Persson & Smith 2013; Rundlöf *et al.* 2014; Herbertsson *et al.* 2016; Lindström *et al.* 2016), but there are a lot of uncertainties in what way different bumblebee species are affected. Therefore I think it is important to review the different contexts (at an individual, social and habitat level), in which bumblebee foraging and nesting potentially affects the outcome of drivers. Contextualisation is used to handle complex matters as environmental issues were a lot of different aspects need to be viewed simultaneously (Nitsch 2000). Like the outcome of drivers of environmental issues depend on context, the effect of drivers on bumblebee population dynamics are depending on the characteristics and behaviour of the bumblebee species.

1.1.1 Field survey

I was given the opportunity to study the presence of overwintering bumblebee queens by a field survey in Skåne in southern Sweden. This was a part of a larger project called SpringQueen18 managed and run by the Swedish

University of Agriculture Sciences together with Swedish Rural Economy and Agricultural Society in Skåne. It was a crossed experiment to investigate if honeybees and flowerstrips in *Vicia faba* fields, independently or in combination, affect the bumblebee population. In my field survey I counted the number of overwintering bumblebees at the same location in the spring following harvest of legumes (*vicia faba*).

In the SpringQueen18 project seventeen organic *Vicia faba* fields were studied by adding “treatments” of honeybee hives and/or flower strips, to be compared to control sites without treatments. In my study I examined the potential effect of the honeybee hives and flower strips on emerging queens produced during last year growth season.

The hypotheses are that treatments of flower strips and honeybee hives do affect population dynamics by reducing the reproduction and/or fitness for survival during winter, measured by the amount of emerging queens in spring. The null hypothesis is that neither treatment affects the population dynamic.

1.2 Disposition

First I define population dynamics, followed by reviewing the importance of bumblebees to the reproduction of wild flowers and to economic value in crop production by pollination services. Then I review the agricultural landscape potential to provide bumblebee habitat. To further understand population dynamics, I have to learn about the bumblebee life-cycle, characteristics and behaviour through which they respond to change. Because honeybees (*Apis mellifera*) are often used as a compliment to pollination services (Herbertsson *et al.* 2016; Lindström *et al.* 2016; Henry & Rodet 2018), I also review how competition might cause diluting of bumblebee resources (Paini 2004) as well as the use of honeybees for pollination service. By reviewing food plant availability during colony growth and studying the potential competition of resources by honeybees, I am studying the prerequisites for queen production. To be able to measure if newborn queens successfully give birth to new colonies, I also have to study the nest establishment in spring. In the field survey the bumblebee reproduction and overwintering are studied in a field experiment were the abundance of floral resources and honeybees have been manipulated.

When writing the review I have studied literature written by researchers within the subject, located by database searching (for instance Science Direct and Scopus) as well as literature recommended to me by my supervisors and their colleagues. Even though I searched for scientific articles from all continents represented in the databases, a lot of the articles found are surveys made in Europe. Within the subject of bumblebees, I searched for information about pollination, population dynamics, foraging, flower strips, nesting, competition with honeybees and intensification of agriculture in general. The materials and methods of the field survey follow below.

2 Population dynamics

Population dynamic refers to how a population varies in size over time, often fluctuating in size in relative to its surrounding environment and other populations (Cain *et al.* 2014). Population dynamics in bumblebees are a function of the quantity of produced queens (gynes) and the probability of colony establishment and survival. Although female reproduction probably is the principal determinant of population dynamics, male reproduction is important to gene flow and in an evolutionary aspect. Parameters which affects this function is foraging (habitat abundance and foraging behaviour), nesting (habitat abundance and nesting behaviour), inter-species/intra-species competition, predation and parasites (Williams *et al.* 2012). Endo-parasitism, competition by honeybees and micro climate are other potentially important parameters driving population dynamics (Westphal *et al.* 2009).

Early studies have been measuring the amount of bumblebee workers in a single habitat as a way of deciding population size. Because bumblebees are able to search for suitable food plants up to several 1000 m for some species, bumblebee density might appear high as an aggregation effect. Recent studies compare the data of bumblebee abundance to the landscape context and the foraging range in order to get a more proper estimation of colony sizes. One way of doing this is to quantify the floral resources surrounding a colony during different time of the season, to be able to get the total amount of floral resource available to the colony (Williams *et al.* 2012). Furthermore by measuring the reproduction, instead of the amount of workers, the success of the bumblebee colony is measured by how many possibly new colonies they could father in the following years. At the same time misinterpretations depending on aggregation effects of taste and preferences in bumblebees are avoided (Williams *et al.* 2012). In a survey made by Persson and Smith (2013), there where a 30 times difference in bumblebee occurrence between landscape types but only three times difference between habitats (Persson & Smith 2013). I interpret this, as the overall landscape structure is as important as the presence of suitable habitats, because habitats have to be reached to be used.

Bumblebee dynamics is also affected by the dispersal abilities, specially coping with the fragmentation of nesting- and foraging habitats in agricultural landscapes. The critical threshold for loss of natural habitat depends on the aggregation as well as the dispersal ability of bumblebees. The effect of habitat loss depends on the dispersal ability of the bumblebee queens (Iles *et al.* 2018). Queens with short-distance dispersal were more likely to stay in the same habitat if the landscape where highly aggregated, even though the total of natural habitat were lowered their long-term growth rate were still positively affected by a higher aggregation. On contrast, a higher aggregation level negatively affected bumblebee queens with long-distance dispersal if the amount of natural habitat were low. But if the landscape were highly fragmented a similar quantity (35-40 % of the landscape) of natural habitats were needed for queens of both short- and long-distance dispersal. When studying a highly mobile organism we got to have in mind that there is no constancy in habitat-abundance in the landscape, because of dispersal effects and potential time lags (Iles *et al.* 2018).

3 The ecosystem service of pollination

Wild bees are the most important taxa that provide pollination services in many crops as well as wild flowers (Walther-Hellwig & Frankl 2000). About 90 % of all plants on earth need a pollinator to be able to breed (Goulson 2010b; Burkle et al. 2013). Even for self pollinating plants, and perennials, without pollination the viability of the progeny as a result of less variety in gene material, will decline. In the end many plant species runs a higher risk of going extinct. In an ever-changing world the plants need all the gene material they could get (Benton 2006).

From the human perspective pollination is not only a conservation concern, it is also a huge economical advantage having pollination as an ecosystem service. In Europe about 80 % of all crops depend on pollinators (Benton 2006). Pollinators set crop yield quality as well as quantity of important crops as for instance oil seed rape and legumes. The quality of oil seed rape is increased by pollination and thereby also the economic value (Bommarco et al. 2012). Legumes as Trifolium pratense L. (red clover) are not self-pollinated and pollination by insects is crucial to yield (Lankinen and Ölund 2013). The Vicia faba (fava bean), as well as Trifolium pratense L. (red clover), depends on long tongued bumblebee species to pollinate because of their deep corollas (nectar tubes) (Benton 2006).

Bumblebee life-cycles are longer than those of wild solitary bees, and therefore they manage to pollinate throughout the whole season (Westphal et al. 2009). That´s why bumblebees, genus Bombus spp., are indeed very important pollinators in both crops and wild plants. There are 239 bumblebee species in the world, of which 40 exist in Sweden (Mossberg 2012), most of them live in the temperate areas due to their adaption to a cooler climate (Benton 2006).

3.1.1 Bumblebees vs. honeybees (*Apis mellifera*) pollination services

Even though honeybees could make up for some of the loss of bumblebees in some cases, there are many flowers that depend entirely on bumblebees. Bumblebees also have a better flower constancy, visiting the same species and therefore gives a higher amount of pollinated plants per individual than honeybees (Benton 2006). Compared to honeybees they are also able to forage in bad weather, such as drizzle and cold weather (Westphal et al. 2009). Bumblebees forage from a wide range of blossom types, some more specialised than others, and are able to learn and remember how to manage new flowers. They have a different foraging pattern than honeybees, which often gather around the first good source of flowers, while bumblebees often forage at a distance from the nest and appears to be spread out at low density. Even though plenty of food is located nearby the nest (Benton 2006).

Bumblebees are also able to buzz-forage. Buzz foraging is a way of retrieving pollen from inside poricidal stamens by vibrating causing pollen to release (De Luca *et al.* 2019). Honeybees cannot buzz forage. This makes bumblebees more efficient at foraging than honeybees. For instance domesticated Bombus terrestris forage more easily for pollen from tomatoes than honeybees does (Benton 2006).

The conclusion is that bumblebees play a key role for pollination in ecosystems and crops in northern hemisphere (Westphal *et al.* 2009; Williams *et al.* 2012). Williams *et al.* (2012) describes them as “the most efficient of multiple crop types”. Therefore, the bigger the colonies, the bigger the pollination effect and the better utilized are the big flowering fields of crops (food plants). But to be able to grow that big, there has to be plenty of food before the mass flowering event as well as after – so the reproduction ensures the possibility of bumble bee colonies following years (Williams *et al.* 2012).

4 Bumblebee life-cycle and habitats

The establishment of a bumblebee community starts in spring by one queen laying eggs, in time the eggs turns into workers, males or newborn queens (gynes). The additions of workers enable the community to keep growing by foraging for food and caring for the nest. At the mid- or end of summer the old queen dies along with her workers, and only the gynes survive to next year (Goulson 2010b; Benton 2006). Bumblebee queens need four different kinds of habitats in their life cycle: nesting, foraging, mating (not a subject in this assay) and hibernating (Benton 2006). These habitats differ in both look and usage, fulfilling different needs of the community. Although most colonies only survives the year of establishment (Goulson 2010b; Benton 2006), there are some few exceptions were whole communities last several years. One example is *Bombus terrestris* in New Zealand, were queens could live several years within the same community (Benton 2006). In some cases several cycles are possible during the same year, when the gynes lays new eggs instead of preparing for hibernation. This is true to some species with shorter cycles such as *Bombus pratorum* and *Bombus hortorum* (Benton 2006).

4.1.1 Nesting habitat

If we would look for bumblebees in the beginning of spring we will find early emerging queens. The year of the bumblebee community begins with one single queen wakes of from hibernation, a diapaus which has been taking place since sometime between July or October the year before (Makinson *et al.* 2019). She begins with foraging on early flowering plants from genus such as *Lamium* etc, altering with sun bathing and then begins her search for suitable nesting sites. This process is estimated to take between two to three weeks (Ouvrard *et al.* 2018; Makinson *et al.* 2019; Benton 2006). When a potential nesting place is found she starts by lying eggs which she incubates until they hatch in to larvae after three to four days. The total time from egg to fully grown individual is about four to five weeks, depending on temperature and food availability (Goulson 2010). The function and efficiency of the communication of work could be seen as drivers significant to the success of the nest. The queen dominates and controls the workers by being much bigger and, in some species, by realising pheromones that supresses the workers for as long as possible. Eventually the community inevitably still ends in conflict and the fall of the community. The success of community is measured in the quantity of queens and males produced (Goulson 2010).

Bumblebee species requires different kinds of nesting habitat (Goulson 2010). Some bumblebee species are nesting above ground, on the surface or inside bird nest in trees. This is true to *B. pascorum* which is an opportunist and uses natural as well as artificial nest. Others are nesting under ground in old rodent nests, for instance *B. terrestris* and *B. locorum*. The purpose of using old nest from other species is that nest-making materials are present. Bumblebee do not, with rare exceptions, collect nest material elsewhere to bring to the nest, but could drag some potential material if located nearby. The nest material are usually tussocky grass, dead leaf material, moss, hair or feathers from which the queen forms to ball shape with a cavity inside and one entrance (Goulson 2010; Lye *et al.* 2012).

The preferred nesting habitats in farmland are located in liner futures as hedge banks, woodland rides and fence lines (Osborne *et al.* 2008; Goulson 2010). It could also be located in undisturbed corners in park and gardens and open meadowland (Benton 2006). Habitats in open terrain are usually used by *B. terrestris*, *B, lapidarus, B. sylvarum* and *B. subterranius* (Svensson *et al.* 2000). Kells and Goulson (2003) also mention that *B. terrestris, B. ladidarius* and *B. locorum* prefer habitats that contain banks due to their underground nesting preferences (Kells & Goulson 2003). In a study by Svensson el tal (2000) *B. pascorum* and *B. lucorum* are often nesting close to forest edges (Svensson *et al.* 2000). Kells and Goulson (2003) have also found a strong relation between *B. pascorum, B. hortorum* and *B. ruderarius* and the use of tussocky vegetation (Kells & Goulson 2003).

The abundance of nest searching queens in different habitat types can be used as a measurement of habitat quality. If the quality as nesting habitat is good than a higher density of bumblebee queens could be expected. Although a high density could also mean that all good places are already occupied leading to a prolonged nest-searching phase (Svensson *et al.* 2000; Kells & Goulson 2003; Lye *et al.* 2012). O´conner *et al.* (2017) found a significant positive relation between the amount of nest searching queens and the number of nest later found at the same location (O’connor *et al.* 2017). On contrary they found that floral resource do not affect the amount of nest, confirming results from earlier studies (Svensson *et al.* 2000; Kells & Goulson 2003; Lye *et al.* 2012; O'connor *et al.* 2017). The only study where floral recourse positively affecting the amount of nest found, is in the early morning hours of *B. ardens* (Suzuki *et al.* 2009). Summarizing nest-searching queens as measurement of habitat quality could be used, though keeping in mind that it depends on species, time of day and year plus sink-source effects of aggregating bumblebees due to favoring or habitat deficiency (Iles *et al.* 2018). If spotting a nest searching queen we possibly located an high quality nesting area, while spotting a foraging bumblebee could be as a result of an aggregation effect. Additionally workers rarely forage closer than 100 m to the nests (Dramstad 1996; Dramstad *et al.* 2003; Greenleaf *et al.* 2007). To my knowledge there is no data about how queen forage.

4.1.2 Finding bumblebee nests

It is not easy locating nest of bumblebees. Several attempts have been made and we are getting closer and closer to an answer questions about where do bumblebees nest and how do they make their choice. The only way of knowing weather there is a nest for sure is to closely inspect the area hoping for workers or queens to give away it´s location by visiting or leaving the nest. The most recently, to my knowledge, used method is to count the amount of nest-searching queens (O'connor *et al.* 2017). The typically behaviour of a nest-searching queen is flying in zick-zack shaped pattern, sometimes landing for a quick estimation of the habitat quality (O'connor *et al.* 2017). O´conner et al. (2017) emphases that the number of nest found is probably lower than the actual number nest in the area. It is all about for how long the observation takes place and how big the search area is. For instance, the study made by Suzuki et al. (2009) a larger area were used and that might explained why they found correlation between habitat type and the number of nest per transect. If there is a lack of suitable nesting habitats, queens could try to take over already occupied nest and kill its inhabitants. Though this is the way of cuckoo bumblebees, this is not the ordinary way of other bumblebees species (Benton 2006).

We don't know much about what time of the day queens are most active in nest searching. Suzuki et al. (2009) proposes that in the morning when it is still cool that the species *Bombus ardens* are the most active in nest searching.

4.1.3 Foraging habitat

Today extensively managed semi-natural habitats, as field margins or fallows, together with crops make up for the majority of bumble bee food plants (Westphal *et al.* 2009). In the northern hemisphere, in a temperate climate, early flowers in spring appear in woodland, but in summer it is the grasslands and farmlands which got the most of the flowers (Williams et al, 2012). Bumblebees are central place foragers; the distance from the nest to an available food source limits them. It all depends on their ability to fly and carry food back and forth to the nest (Westphal et al 2006). Further more bumblebees do not store plenty of food in their nest, as honeybees do (Williams *et al.* 2012; Rundlöf *et al.* 2014). The, often, larger workers collecting nectar and pollen to retrieve to cover for the needs of the nest residents. Bumblebees are quite picky about which pollen to collect, and only a few plant species is good enough whereas nectar is collected from a great variety of species (Benton 2006). It appears that quality is as important as quantity and this affects which plants to visit. Bees prefer perennial plants to annuals or biennials. Although annuals are now dominating in our agricultural landscape which probably causing food plant quality to decline. Pastures, leys, road verges, field borders containing more perennials than annuals and biennials, which makes foraging habitats in these extensively managed areas especially important. In contrast to fallows that contains more annuals and biennials (Persson & Smith 2013).

Several early studies have focused on the quantity of flowers and knowingly discard the varying food plant quality when measuring the amount of available food for bees (family of bees in general). This has been recognised as a problem in recent studies (Williams *et al.* 2012). More studies have been made about the food plant quality and the needs for honey bees, whereas is has been concluded that low quality of pollen and low protein diversity in forage affects honeybee colony immune system negatively (Persson & Smith 2013). Even though there is yet much to learn about food plant quality for bees, Goulson *et al.* (2005) has found that especially pollen from Fabiaceae seems to be important for pollen quality for bumblebees (Goulson *et al.* 2005). A lot more research is needed in this area.

4.1.4 Hibernation habitat

Between July to October, the later for *Bombus terrestris* and *Bombus pascorum*, the gynes prepare themselves for hibernation. She dugs herself a few centimetres into the ground in north facing banks, woodland floor, loose soil in gardens, stone walls or into rotten tree stamps (Makinson *et al.* 2019; Benton 2006). When the queen has dug herself down into the soil she forms a compact chamber surrounding herself to protect for flooding. Sometimes queens hibernate together. Choosing a north-facing bank the bumblebee queen minimises her risk from awakening to soon by the warming spring sun (Makinson *et al.* 2019; Benton 2006).

We don't know much about the hibernation of bumblebee queens. Although finding a place to hibernate is surely a bottleneck, and the nest suitability will most likely affect the queen survival and thereby also the foundation in spring. The abundance of potential hibernation places as well as the behaviour of recognition and assessment of suitable places are most likely important traits acting on drivers for bumblebee population dynamics.

5 The agricultural landscape

It has been argued that the continuity of food plants and the amount of nesting habitats are the main drivers for population dynamics and especially reproduction (Williams *et al.* 2012; Persson & Smith 2013; Rundlöf *et al.* 2014). The composition of the agricultural landscape sets the potential to provide bumblebee habitat.

5.1 Intensification of agriculture

There has been a dramatically decline in pollinating insects in Europe, North America and Asia since the 1950:s (Potts *et al.* 2010). An intensification in agriculture has led to loss of natural habitat and towards monoculture of grown crops. The monoculture results in critical bottlenecks for foraging arthropods, where non food plants covers up the place once filled with flowering natural habitat and semi-natural habitat as field verges (Schellhorn *et al.* 2015). Important habitats in permanent, low input grasslands and legumes as fodder crops have declined in areal (Bommarco *et al.* 2012; Persson & Smith 2013). These semi-natural habitats provide both food plants and nesting habitats for many arthropods and the remains may still act as a source to the nearby landscape (Öckinger & Smith 2007).

Biodiversity is important in many ways. To have a large plant species pool increases the probability of food plants for bees throughout the colony lifecycle. The continuity and food security perennials offer might help to explain why bees prefer perennial plants to annuals or biennials. But annuals are now dominating our agricultural landscape which probably causing food plant quality for bees to decline (Persson & Smith 2013).

Before the discovery of artificial fertilizers, pesticides and the invention of combustion engines, agricultural landscapes where more heterogenic and provided plenty of different habitats (Goulson *et al.* 2005; Warren *et al.*

2007; Connor 2018). These inventions allow our human population to grow as the crop yield nearly tripled in just a century (Connor 2018). Some of the wild animals and arthropods also benefitted from large field with plenty of food provided by the crops, growing in large numbers outcompeting their competition. Our hasty make over of the agricultural landscape ecosystem through the inter-species interactions off balance (Warren *et al.* 2007). The thriving species are known as our pests or as the biological control by which humans tries to control the pests (Radosevich *et al.* 2007; Van Driesche 2008; Govorushko 2018).

The Convention of Biological Diversity (CBD), an international agreement from the summit of environment and sustainable development in Rio de Janerio 1992, explains the declining species richness due to land-use conversation, as the main driver, but also “overexploitation, intensification of agricultural production systems, excessive chemical and water use, nutrient loading, pollution and introduction of alien species” (https://www.cbd.int/). Bumblebees are affected by the declining amount of floral resource in the landscape (Williams *et al.* 2012), and this is correlating with the loss of natural habitat and the intensification of agriculture (Goulson *et al.* 2005; Bommarco *et al.* 2012). The use of artificial fertilizers together with the use of herbicides might indirectly affect bumblebees by affecting the abundance of weed as food plants. A study from Polen shows that using manure instead of fertilizers increase the amount of bumblebee visitations (Banaszak-Cibicka *et al.* 2019).

6 Floral resources in the agricultural landscape

There are two criteria for successful reproduction: the size of the colony and continuity of food plants (Westphal *et al.* 2009). Food resources are limiting the size of colonies, especially during critical events in the colony cycle, such as colony foundation in spring and reproduction in mid- to late summer. Available food plants is one crucial bottleneck (Goulson *et al.* 2005). But does it matter if the food comes from natural or domesticated sources? Several studies have been made to evaluate the effect of mass flowering crops on bumblebee abundance and species-richness. Walther and Frankle (2000) showed that crops could be used as temporal habitats of short tonged bumblebees whereas permanent foraging habitat showed more diversity in bumblebee species. They also acknowledge that the different species of bumblebees hade different foraging distances. To be able to forage from mass flowering crops, as *Brassica napus L.* or *Trifolium pratense L.*, bumblebees might have to fly long distances. For instance *Bombus terrestris* are able to fly longer distances than *Bombus moscorum* (Walther-Hellwig & Frankl 2000). Bumblebee flight distances are discussed further in chapter four.

6.1 Mass flowering crop as a driver

Several studies have come to the same conclusion that mass flowering crops bolsters the growth of bumblebee communities (Westphal *et al.* 2009; Rundlöf *et al.* 2014; Riedinger *et al.* 2015). Bigger colonies have a bigger chance of reproduction, regardless of food plant type, because the more workers the better they take care of the royal brood. Westphal et al. (2009) discovered that colonies showed different reproduction result depending on the weight of the colony: the heaviest colonies produces gynes, the medium colonies produces males and small ones did not have any successful reproduction phase (Westphal *et al.* 2009). Under natural condition bumblebees are thought to breed majority of males and a few gynes (Westphal et al. 2009). But the other criteria mentioned above, about continuity in available food plants, can not be forgotten. It has to be sufficient resources, in both quality and quantity, throughout the life-cycle of the queen brood as well as of the workers providing for her. The colonies grow until the switch to reproductive state, meaning the colony size is decided early in the season depending on early flowering plants. Whereas after the switch, the development of queen larvae is depending on sufficient food plants flowering mid- or late in the season (Westphal *et al.* 2009). Producing gynes (new queens) are a heavy investment. There is three times higher costs to produce a bumblebee queen than a male, and that's why bumblebees have a "strongly male-biased sex allocation" (Rundlöf *et al.* 2014). To sum up: it is a huge difference between when and where mass flowering crops are located and this affects its usage as a sufficient food source.

The differences in life-cycle between species also need to be taken under concern. All species have a similar life cycle but there is also some important differences. For instance some species, called early species (as *Bombus terrestris*) are active for many weeks before late species (as *Bombus hortorum*) awake from hibernation (Westphal *et al.* 2006). The length of the life cycle also varies among species. The food has to be available at the same time, and within foraging range, as it is needed by the bumblebee community. And the needs of the community differs throughout the life-cycle in both quantity and quality. Highly rewarding resources is extra important during nest establishment in spring, when only the queen or a few workers are foraging to meet the needs of the nest (Westphal *et al.* 2006). Early nesting species in the spring, will probably benefit more of early flowering crops than species which establishes nests later. The community also has to have the "man power" to successfully use the abundant flowering crops and the strength to fly back and forth to the nest (Riedinger *et al.* 2015). Nesting and early season population growth in homogenous landscapes are probably also supported by flowering trees and mass flowering crops as *Brassica napus L.* (canola) (Persson & Smith 2013). Early flowering mass flowering crops as *Brassica napus L.* is important to bumblebee colony growth by enhances the amount of food plants available for house-bees (workers assigned to nest maintenance and brood care) which abundance control the amount of queen larvae that the colony potentially can manage later in the season (Westphal *et al.* 2009). Later flowering mass flowering crops as *Trifoium partense* (red clover) are in fact bolstering communities to produce more queen larvae in contrast to earlier flowering crops which only bolsters worker and male amount (Rundlöf *et al.* 2014). A study in southern Sweden showed five times higher bumblebee queen abundance and 71 % higher male abundance in landscapes with *Trifolium pratense L.* making up for 0,2 % of the land cover type than landscapes without *Trifolium pratense L.* (Rundlöf *et al.* 2014). Although mass flowering crops could boost colony growth and sometimes even reproduction, only semi-natural habitat such as grassland and permanent field borders provide nesting and over-wintering sites (Rundlöf *et al.* 2014).

Though mass flowering crops could be very useful for bumble bees at a short term, providing extra food plants for a few weeks, at a long term mass flowering crops could generate a negative indirect impact on food resource. Mass flowering plants as *Brassica napus L.* causes dilution of pollinators in the surrounding habitats because of bumblebees preferring *Brassica napus L.* (Riedinger *et al.* 2015). The lack of pollinators is a huge problem for the survival and reproduction of wild plants, where crops could out-compete wild plants providing plenty of food for a short period – leaving the plants simultaneously flowering without pollinators and thereby at the long term potentially pollinators without food as a effect of declining plant populations (Riedinger *et al.* 2015). Westphal *et al.* (2009) showed in a study of *Brassica napus L.* that mass flowering crops could temporally boost the population growth rate during the its flowering period (Westphal *et al.* 2009). It was temporal because after the flowering period the colonies weighed similar, regardless of the previous access to *Brassica napus L.* (Westphal *et al.* 2009).

The mass flowering crops grown in huge fields gives plenty of food for those insects who manage to locate and reach the abundance. But insects, as bees *Apoidea*, do not only need food plants but also suitable habitats for nesting and hibernating (Westphal *et al.* 2009). The structures of forage habitat and nesting habitat often have different qualities, and can be hard to combine. Many bumblebee species prefer tussocky grass and/or moss as suitable materials for nesting, but places containing those materials often lack a lot of flowers (food plants) (Goulson 2010). Williams *et al.* (2012) argues that high – quality local habitat is most important for bees in degraded landscapes, even though flowering fields could make up for some of their foraging ground. Flowering crops are a temporal resource which could boost colony growth, and for early nesting species also boost reproduction. But it all depends on if the temporal floral resources meets the current need of the bees in quality as well as quantity, and if the other life-cycle stages are supported elsewhere (Westphal *et al.* 2009).

A conclusion is that wild bees are benefited of mass flowering crops as *Brassica napus L.* if they have a short life-cycle and their foraging need is coinciding with the flowering period of the crop. Their reproduction enhances from the temporally, but coinciding, increasing amount of flowers (Riedinger *et al.* 2015). Bees need prolonged flowering throughout the season. But the agricultural management has developed in a direction towards crops flowering at the same time and for a compressed period in order to get an easier harvest with lower spill and a higher yield (Boelt *et al.* 2015). In the case of *Triofium pratense,* a compressed flowering period is also a way of manage the pest beetles of *Apion spp.* in order to avoid the use of pesticides. The *Apion spp*. beetles, mostly *Apion apricans* and *Apion trifolii*, causes lower harvest by seed predation, a serious problem for seed-growing farmers (Lundin *et al.* 2016). In organic farming, where pesticide use is forbidden, this is the only way of managing these beetles. Yet another problem is that the seed growing of clover has declined by 90 % in Sweden since the 1940´s (Rundlöf *et al.* 2014).

6.2 Interspecies floral competition as a driver

Bumblebee species coexistences are mediated by different spatial resource patterns. For instance, it is more profitable for big bumblebee species to fly long distances to visit the flowers with the highest rewards while small species, as *B. pratorum*, fly shorter distances at a, probably, greater efficiency (Westphal *et al.* 2006). Smaller bumblebees as *B. pascorum* exploits more scarcely scattered food plants than *B. terrestris*. The *B. terrestris* having a bigger foraging need to cover for their larger body and colony size, foraging more effectively parting for better supply as soon as higher reward are detected. Thereby they could coexist by exploiting the floral resources in different ways, *B. pascorum* foraging of the leftover by the *B. terrestris*, both benefitting from mass flowering crops. (Westphal *et al.* 2006, 2009) Westphal *et al.* (2006) hypnotise that big species, as *B. terrestris*, reach their critical resource levels earlier because of their greater metabolic needs (Westphal *et al.* 2006).

There are several things that help coexistence of different bumblebee species. Westphal *et al.* (2006) mentions three: One is difference in proboscis (tongue) length affecting the foraging behaviour; long tonged bumblebee species always collects both pollen and nectar while short tonged species sometimes only forage for pollen which means visiting plants lacking nectar resource (Westphal *et al.* 2006). A second is the difference in the phenology of species lifecycle, where the length of lifespan and active period differs among species, making coexistence possible by utilizing resource at different time and space. The third example is in utilizing different sizes of floral patches, where short tonged are observed to use larger patches with copious supply of food plants while long tonged have been observed in smaller patches or in sparsely distributed food plants. This could be explained by a better communication (between individuals within a community) and recruitment system (when a forager be recruit other bees to start foraging) among short tonged species, finding rewarding patches more successfully than long tonged species (Westphal *et al.* 2006).

6.3 The landscape aggregation and floral composition

The distance between floral resource could act as a driver for bumblebee abundance. Persson´s and Smith´s (2013) survey of land-cover types of the agricultural landscape in southern Sweden shows a significant difference between the abundance in bumblebees by late July between simple and complex landscapes. Big homogenous fields, mainly crop production and few semi-natural habitats characterize simple landscapes. Complex landscapes are more heterogeneous with smaller fields, mixed farming and containing more semi-natural habitats as permanent grasslands for grazing. In the survey the two landscapes types initially contained similar amount of bumblebees, but by July the amount declined in simple landscapes but stayed the same or increased in the complex landscapes. Persson and Smith (2013) concludes that simple landscapes where limited in floral resources by midsummer. On the other hand, species-richness where a little higher in the complex landscapes but did not differ as much as the total amount of bumblebees between the landscape types. Many regionally rare species were noted in simple landscapes suggesting that rare species “survive in pockets of beneficial habitat” (Persson & Smith 2013) or that it might be an inflow of queens from nearby complex landscapes. For some species early nest establishment and shorter life-cycles could result in earlier reproduction state and thereby higher survival rate caused by simultaneously flowering period of mass flowering crops. Other less probable explanations to the relatively high amount of species in simple landscapes could be higher success in hibernation and nesting (Persson & Smith 2013). Complex landscapes contained 30 times more bumblebees and 30 times more floral resources than simple landscapes by the end of July. A Tukey´s test showed a significant higher species richness in complex landscapes as a result of richer border zones of complex landscapes than simple landscapes. This effect partly explained by the lacking of pastures in the simple landscapes. During the late July leys, pastures and total amount of flowering plants, potential nesting and foraging habitat, where positively related to the bumblebee amount (Persson & Smith 2013).

6.4 Flower strips as food plant resources

To handle de depletion of floral resource in the intensive managed agricultural landscape, a mixture of flowering plants called flower strips, are sown as a food source to pollinators (Haaland *et al.* 2011; Uyttenbroeck *et al.* 2016). For instance, flower strips has been used to enhance the affect of pollination and to control pest in olive cultivation in Greece (Karamaouna *et al.* 2019). Flower strips are tested to be used in intercropping systems as a way to control pests in agroforestry (Staton *et al.* 2019) and vineyards (Kratschmer *et al.* 2019). This way the amounts of flowering plants could be increased, as well as the flowering period are lengthened. Even though flower strips could boost some species population, it depends on the flower species quality as a food plant and the varying need of a bumblebee species (Haaland *et al.* 2011). In Belgium Ouvrard *et al.* (2018) noted an effect of flower strips, sown into an intensive managed landscape, on pollinator abundance in summer. But the poor floral resources in spring and autumn possibly reduced the positive effect. There is also a difference between homogenous and heterogeneous landscape. In a study made by Herbertsson *et al.* (2018) in Sweden shows that flower strips could enhance pollination in *Vicia faba* (Fava beans) and *Fragaria fresca* (woodland strawberries) in homogenous landscapes, but in heterogeneous landscapes the pollination could be reduced. An other Swedish study made by Rundlöf *et al.* (2018) suggest that an early sown flower strip could enhance the pollination effect in *Trifolium pratense L.* (red clover) but at the same time concludes that the seed set is mainly limited by pest as *Apion spp.* In summary, several studies indicates positive effects of flower strips, depending on the flower species and where and when the flower strips are used. As Scheper et al. (2015) argues it is needed more research to understand whether there is an effect at population-level.

7 Bumblebee characteristics - defining characteristics responding to change

I have mentioned several different bumblebee responses to change; their flying abilities, foraging manner etc. This shows that bumblebees act on drivers through their characteristics. Therefore their characteristics limit their abilities to handle change. To be able to understand why bumblebee abundance differs, we need to find both the drivers and which bumblebee characteristics that sets the outcome of dealing with the driver.

7.1 The needs of a bumblebee

Bumblebees require pollen for protein and nectar for both energy and water balance. The foraging is made by the worker caste and the food is brought back to the nest, the worker uses only a minor part. They can carry up to 20 % of their body weight in protein and 90 % of their body weight in nectar (Benton 2006). The workers bumps up food from the honey stomach and mixes it with pollen, than they feed it to the larvae or place it in special vials called honey pots. From the honey pots both queen and the "house workers" feeds. Even though bumblebees get most of their water from nectar, some has been seen drinking from water drops. They get the right concentration by foraging in different hours of the day when the nectar still is diluted or by switching between flower species (Benton 2006). The qualities of the foraging product are equally important as the quantity of the product, the composition of nectar and pollen depends on the flower species and thereby affect the bumblebee demand. The larvae specially need protein to grow and develop in a healthy way. A foraging success can thereby only be validated if both quantity and quality are defined, and how well it fits the need of the community (Benton 2006). The food plants must cover all these needs, a food plant is not simply one kind of plant.

7.2 Bumblebee senses as defining characteristics

A bumblebee experience the world quite different than us humans. Their senses, even though they are similar, work a bit different which gives the bumblebees a distinctive experience of the world. Benton (2006) describes how a bumblebee perceive the world, here I recount for the most important characteristics. A bumblebee is only able to see colours of green and blue, but also ultra violet which we can not. Through hollow hair, called tricodier, covering their legs and body, bumblebees can detect tiny molecules in the air. Benton (2006) argues that this is how they know which flower to visit and who visited it before them, smelling and identifying species and places. This is thought to be how bumblebees manage to spread out throughout the landscape, keeping distance to another, unlike honeybees which forage closer to each other. Benton (2006) explains that a bumblebee is able to communicate abundance of food to others within her community, by making them follow her to the source. By running around, buzzing her wings and bumping in to other workers, she can get their attention and some will follow her scent to get to the rich location (Benton 2006). Though the hairs covering their body they feel touch, but they also detect vibrations in the air through a special organ in the antennas. Of course a bumblebee also experience taste, quite similar to humans. But then they also have another sense we don't know much about, pheromones. Pheromones are used to communicate with others within them same species and are very important in the understanding of how bumblebees manage their community and how they act on outside impressions. There are pheromones influences the behaviour for just a moment and those who has a long-term effect. For instance, the male marks a small patch with a pheromone to attract queens for mating, and it is only at those specific patches a male are able to recognise a queen. The queen on other hand has to emit a specific pheromone to be able to copulate. Pheromones are also used by queens of complex species to supress their workers. In foraging bumblebees uses pheromones to make sense of their surrounding: By making a trail of their own scent, putting their scent at each flower they visit, they are able to both navigate and tell whether a flower recently has been visited and by whom (Benton 2006). Pheromones (as well as other senses) are therefore important characteristics, which affect the behaviour of foraging and nesting and indirect the response to drivers in environments of habitats as well as landscape context. For instance, affecting the ability of handling fragmentation of landscape by navigation and communication of floral resource.

7.3 Bumblebee species differences

As discussed above differences within species affect their respond to change. Many bumblebee species that used to be common are nowadays rare. One of those are *Bombus distinguendus* in Sweden (Bommarco *et al.* 2012), but in Great Britain the same species are increasing in abundance while another, common species in Sweden, *Bombus subterraneus* has disappeared (Benton 2006). There is no single answer to why some species manage to survive at one place but not another, and why some species seem to thrive while others disappear. But a lot of research points out that although having lot in common, bumblebee differs at certain, sometimes life-saving, important traits.

7.3.1 Flying distances

Studies show that bumblebees rarely forage closer than 250 m to their nest, and often choose to fly longer distance even though suitable flower resources exists closer to the nest. Several attempts to explain this behaviour have been made. Benton (2006) discusses several theories: Bumblebees might be able to detect the density of foraging species and thereby choose to forage in areas with lower densities to avoid competition. Other explanations are to avoid competition within the community, risk management and as a result of an ecological adaption to coupe with evolutionary pressures not exciting today. But the theory doesn't explain how to manage competition and predation by other species (Benton 2006). Flight distances vary between different bumblebee species. *B. terrestris* is known to fly long distances up to 3000 m, and it could even be longer because one of the studies had their study area limit set to 3000 m. *B. lapidarous* is also known to fly long distances, up to 2750 m in several studies. While *B. pascorum* have a flight distance of a 1000 m and *B. pratorum* only 250 m (De Luca *et al.* 2019). Even though these numbers are based on estimated foraging ranges, there are related to both body and colony size. Big bumblebee species have larger wing-muscles and are therefore able to fly longer distances (Westphal *et al.* 2006). Westphal *et al.* (2006) emphases that this is an estimation based on data from their studies, it is hard to know the actual foraging ranges. It is also possible that other landscape types, with high amount of semi-natural habitat, show different foraging results (Westphal *et al.* 2006).

Williams *et al.* (2012) argue that the overall abundance of floral resources is a function of the density of flowers in habitats and the sum of habitats within reach of foragers. Large heterogeneity in the landscape makes room for many niches and thereby a lot of bumblebee species (Westphal *et al.*

2006). Flying abilities together with the landscape structure affects the bumblebee community in outcome of adaptation and survival.

7.3.2 The energy cost of foraging

As mentioned above, bumblebees are able to fly long distances to forage. Their main focus is theorized to be keeping a good rate of foraging rather than keeping a low flying distance (Oster and Wilson, 1979; Benton 2006). However the result of foraging is to cover both the energy need for flying back and forth to the nest as well as the needs of the housebees and larvae (Benton 2006). The bumblebee is thought to increase its fitness by focusing on keeping a high foraging rate, as well as specialising at few species of flowers at a time. Thereby the individual specialises at one flower type at a time, but as a species they are more or less generalists. This based on the *optimal foraging theory* (OFT) where the individual optimizes its chances by finding the better way of foraging – all based on Charles Darwin's theory *survival of the fittest*. Which can be used if foraging behaviour, biological traits as well as ecological relations of an organism are considered at the same time and if kept in mind that "learning and cognition plays a large part in shaping it" (Benton 2006; Oster and Wilson, 1978). Learning how to manage each flower species comes with a cost, but when they have acquired the technic needed it is often rewarded by a higher quantity of nectar. Keeping to these flowers will be profitable as long as they still flowers (Benton 2006). When the reward by other flowers are equal or greater than the ones visited, than there is room for reconsideration. A higher floral quality in added floral resources to enhance crop pollination could result in reduced pollination of the crops, if bees are preferring the added resources instead of the flowering crop (Nicholson *et al.* 2019). Some flowers have evolved to have a deep corollas (nectar tubes), by which long tonged bumblebees are able to reach and thereby more likely to be consistent to the same species – resulting in a higher degree of pollination (Benton 2006). Bumblebees are able to comprehend and copy other individuals' behaviour. By observing other bees they learn how to handle new flowers, and how to rob flowers if the corollas are to deep preventing them to reach the nectar (Goulson 2010b; Klumpers *et al.* 2019).

In the short run specialisation at some flower species occurs when handling costs are high and traveling costs are low, and when traveling costs are high but nectar reward is high or similar to other species. In a long-term perspective generalisation is favoured by the different timing and occurrence of flower species, and the covariance with pollinator activity (Benton 2006).

7.3.3 The minimum temperature threshold for activity

Bumblebees are forging during all hours of the day, but have been observed to be most active between 5 to 7 in the morning and 5 to 7 in the (Benton 2006). A bumblebee risks overheating if foraging in the middle of a sunny day, but are able to sustain drizzle. Also, because of the increased evaporation, the nectar becomes highly concentrated which is negative for the water balance of the bumblebee. Though foraging during cold weather costs extra energy, sometimes foraging early or late in the day is not the better option (Benton 2006).

7.3.4 Tongue length

Of all the parts of a bumblebee the tongue length, except for size, appears to be the one main thing that differs between species and also affects the handling of flowers (Goulson 2010; Klumpers *et al.* 2019). Bumblebees with short tongue prefer nectar of flowers with short corolla, while bumblebees with a longer tongue prefers flowers with deep corolla. That is because long-tongued bumblebees have difficulties managing flowers with short corolla plus they get a relatively low reward. So even though they are able to visit shallow flowers, they prefer deeper corollas with more nectar. Recent research have also shown that short tonged bumblebees can in fact handle long nectar tubes, but it takes more time to handle and therefore not favoured. The tongue length is not only determined by species but also by the very size of an individual bumblebee. Together they affect whether the bumblebee matches the flower, in amount of reward as well as in handling time (Klumpers *et al.* 2019). The tongue length thereby affects which flowers a bumblebee visit. For instance, a short-tongued bumblebee such as the common *Bombus terrestris* will not manage, and thereby probably not visit, the same species as the less common long-tongued *Bombus hortorum*. But tongue length does not only differ between species, difference in body size within species also affect tongue length, e. g. a *Bombus terrestris* queen are able to forage from the deep corolla of a *Trifolium pratense L.* (red clover) (Benton 2006).

8 Competition by honeybees

Honeybees (*Apis mellifera*) are used worldwide for their economic value of pollination services and honey (Henry & Rodet 2018). Up until the 1970s honeybees was viewed as a non-problematic, totally beneficial insect, than it was recognised as a potential invasive species (Thorp 1987). Following habitat loss, the next biggest threat to biodiversity is exotic species (Goulson 2003). Honeybees are often viewed as a beneficial insect, which gives us honey and pollination services, but in many cases honeybees are also an exotic bee that do not belong in the ecosystem put by beekeepers (Goulson, 2003). One single hive needs 10-60 kg of pollen/year and 20-150 kg of honey/year (Goulson 2003), competition over floral resources seems inevitable? Paini (2004) recognise six possibly negative effect of competition between honeybees and wild bees: "competition with native pollinators for floral resources; competition for nest sites; co-introduction of natural enemies; particularly pathogens that may infect native organisms; pollination of exotic weeds; an disruption of pollination of native plants".

Farmers in northern Europe are thought to have kept honeybees since the Neolithic age and feral communities existed until Varroa mites were introduced (Jaffé *et al.* 2010; Roffet-Salque *et al.* 2015; Lindström *et al.* 2016). Thereby honeybees and bumblebees have coexisted for a long time (Lindström *et al.* 2016). When both honeybees and bumblebees are native they are not likely to compete, because if they were sharing the same niche differentiation should have occurred (Herbertsson et al. 2016; Lindström *et al.* 2016; Paini 2004). However Herbertsson *et al.* (2016) accents that the conditions for coexistence has been undergoing a lot of change by the loss of semi-natural habitats and its floral resources. Because bumblebee species differ in foraging-related traits, so could the prerequisites of possible coexistence with honeybees (Herbertsson *et al.* 2016).

Interspecies competition does not necessarily affect the population dynamics of the dominated species (Goulson 2003). To be able to decide whether competition of honeybees reduces bumblebee fitness and survival, one must be able to see a significant difference in population size in the absence of the dominating honeybee (Goulson 2003) This not an easy task, bees are mobile by nature keeping apart the abundance of feral honeybees from managed ones are almost impossible (Goulson 2003). Feral honeybees could also be competing over nest resources if scarce (Goulson 2003).

Even though competition takes place, it does not necessarily mean that one species dominates and outcompetes another. It is when the floral resources are scarce, when the floral continuity is weak, that competition may impact at a population level (Goulson 2003). A lot of bumblebee species, as well as honey bees, have a polylectic diet (forage from several unrelated plants) but more specialised species could be at risk (Goulson *et al.* 2013; Mallinger *et al.* 2017). The hives of honeybees are often supplementary feed by humans, which heightened numbers that would not persist under natural conditions. (Goulson, 2003). This could further be altering the natural balance between species.

In a study of nectar and pollen foraging success in Rosemary in southern France, Henry and Rodet (2018) discovered that high-density beekeeping affects both wild bees as well as honeybees. Research made by Goulson *et al.*(2013) and Mallinger *et al.* (2017) shows similar results. Their results showed that, within 600-1.100 m around the apiaries, both the occurrence and nectar foraging success of wild bees declined by 55 % respectively 50 %, and for the honeybees the harvested nectar and pollen dropped by 44 % respectively 36 %. This affects might not just affect the fitness of wild bees, but also honey yields and the viability of the honeybee forager (Henry & Rodet 2018).

8.1 Assessing the affects of competition

Interspecies competitions are measured by both indirect, mainly, and direct methods. Several studies have focused on the indirect effect by studying the resource overlap between honeybees (*Apis mellifera)* and bumblebees (*Bombus spp*.), change in visitation rate of bumblebees and change in resource levels harvested from both honeybees and bumblebees (Paini 2004). Not as many have tested direct effects of competition by measuring the individual survival, fecundity and population records (Paini 2004). Paini (2003) explains how measuring the potential indirect effects could be misleading: If the native bee, within the same floral niche, changes its vitiating rate of a certain flower due to competition with honeybees it could be compensating by foraging for a longer period of time and comes up with an unchanged resource harvesting. And if there is a reduced visitation rate of that certain flower species, and a reduced resource harvesting of that same flower – the cause could still be simply by choosing another floral resource. Thereby adjusting its fitness rather than suffer from the competition by reduced survival or fecundity.

To assess the probability of causality by competition effects of survival of a highly mobile species, you ought to study their population dynamics both within as well as between years to see whether their fitness has been affected negatively (Goulson 2003). To be able to measure the affects the difference between years and seasons a lot of replicates would be needed, kilometres apart, for several years (Goulson 2003). For instance by introducing hives to areas with no apiaries present, and eliminating hives in areas with a lot of apiaries (Goulson 2003). A less difficult approach is to "correlate the patterns of diversity of native bees with abundance of exotic bees without manipulating their distribution" (Goulson 2003).

The foraging success of the bees could be measured by harvesting nectar from pollen crops and pollen sacs, as the method of Henry and Rodet (2018). Henry and Rodet (2018) emphases two ecological processes where massively introduced honeybees may compete with local wild be populations namely interference competition and exploitive competition. Interference competition, also called interspecific displacement, is described as when the superior competitor supresses other by physical interference. Exploitive competition is explained as the superior competitor alters other species fitness or abundance. For instance by monopolizing and depleting available resources. Although Henry and Rodet (2018) sees the exploitive competition as the main driver, they also recognise the shortage of studies that have been able to prove this due to the nectar and pollen resource availability has to be assed properly.

A systematic review made in 2017 by Mallinger *et al.* (2017) showed 53 % negative impact on wild bees by managed bees, 28 % no effects and 19 % mixed effects. The effect of managed bees on plant communities showed equal amount of positive and negative response, and the majority of all (70 %) reported potential negative effect of patogener transmission (Mallinger *et al.* 2017). The majority of all the reports reviewed measured the potential effects and not the direct effects (fitness, abundance and diversity) (Mallinger *et al.* 2017).

Further implication is to examine the effects of different agricultural management (Mallinger *et al.* 2017) and different climate and environment conditions in different continents where honeybees are kept (Paini 2004).

8.2 Characteristics of competition

Wild bees are hypnotized to be effected of honeybees *(Apis mellifera)* if they are in the same ecological niche, if there is a niche overlap and no further specialisations has occurred (Goulson 2003; Herbertsson *et al.* 2016; Lindström *et al.* 2016). The result could be either displacement, for instance finding an alternative floral resource or it will be effecting their survival (Goulson 2003; Herbertsson *et al.* 2016; Mallinger *et al.* 2017). Wild bees, for instance bumblebees, are often displaced to less profitable forage (Goulson 2003).

Both honeybees and bumblebees begin foraging earlier than other bees, even though smaller bumblebees might second because their size makes it more difficult to maintain body heat (Goulson 2003).

Wild bees with a large body size are more likely to outcompete honeybees, but instead they are found farther away from the apiaries. Henry and Rodet (2018) explain this by the bigger need of pollen than smaller ones, and that they are able to fly further distances. Smaller bees have been seen to bee physical disturbed by honeybees (Goulson 2003).

Wild bees with shorter foraging areas are hypothesed to be more affected by competition with honeybees, because they are not able to choose another foraging area. Though this is difficult to prove because they are often low in numbers (Herbertsson *et al.* 2016). The difference in body size and flying abilities, might partly explain why competition with honeybees is thought to effect solitary bee species more than social species. Solitary bees are traveling not more than a few hundred of meters and do not have the possibility of teamwork locating new resources quickly by communication (Goulson, 2003).

The lifespan of different bumblebee species might also affect the impact of competition. For instance *B. terrestris* as well as *A. mellifera* are both generalists and relatively long lived able to adept to a succession of different flower resources (Goulson, 2003).

8.2.1 Landscape structure

Homogenous landscapes are simplified, with decreasing floral resources, as a result of intensification of agriculture (Lindström *et al.* 2016). The impact is therefore expected to be larger in heterogeneous landscapes rich in floral resources than in homogenous landscapes with scarce floral resources (Lindström *et al.* 2016). In their study Herbertsson *et al.* (2016) discovered that adding honeybees to a homogenous landscape supressed bumblebee densities in field borders and road verges, but showed no effect in heterogeneous landscapes. The impact in homogenous landscapes are explained as a niche-overlap between honeybees and bumblebees (Herbertsson *et al.* 2016). In heterogeneous landscapes the density of bumblebee species with a shorter foraging range were lower, whereas in homogenous landscape one species with a long foraging range dominated regardless if honeybees were added. Herbertsson *et al.* (2016) proposes that that if apiaries are left in homogenous landscapes after the pollination service of crops, it could reduce the abundance of bumblebees.

Lindström et al. (2016) has found a negative effect of honeybees on bumblebees with increasing field size. This is explained to be an effect of displacement, where wild bees are avoiding areas with honeybees due to exploit competition or interference having the possibility choosing another foraging spot of the area (Lindström *et al.* 2016). The abundance of bumblebees also increased with the distance from the apiaries (Lindström *et al.* 2016).

Managed bees within their native range have less competitive effects than when they are exotic to the area, but they also have a potential greater effect of transmitting pathogens. To minimize the impact of honeybees is to evaluate the intended locations conditions, for instance if honeybees is native to the area, adjust the amount of hives to the floral resources, check for pathogens and parasites and verify if any rare bumblebee species are abundant in the area. And if possible place the apiaries in the middle of a field or as far away as possible from natural habitats (Mallinger *et al.* 2017).

Honeybees foraging behaviour could indirect affect the presence of floral resources by gathering rewards without pollinate due to mismatch. But the affect is hard to evaluate, *A. mellifera* being both effective pollinators for many flowers and floral parasites of some, and bumblebees for instance *B. terrestris* are also known to rob flowers (Goulson 2003). Mallinger *et al.* (2017) calls for additional research on direct long-term effect at population-level of manage bees.

9 Materials and methods

There are several ways of study bumblebee dynamics. One can measure colony growth rate per flower (E Crone & M Williams 2016) weighing the colonies and counting/estimating the flower abundance. Mark and recapture workers to learn about their flying distances or walk transects to survey edges and field borders, leys and permanent pasture (Persson & Smith 2013). It depends on what we want to learn and which method would help to answer the question asked. In the case of studying nest-searching queens walking a transect is the only way of doing it, that I know of, because there is no nest to study nor abundance of workers.

By counting the emerging bumblebee queens I am able to analyse if there has been a possible effect of flower strips and/or competition with honeybees. In the review several parameters have been noted to affect population dynamic through survival and reproduction, such as the availability of nesting habitats, foraging habitat and food plant consistency (Westphal *et al.* 2009; Williams *et al.* 2012; Cain *et al.* 2014). I have knowingly disregarded immigration and emigration affects on population dynamics, to be able to draw conclusions from data. If my hypotheses about flower strips and/or honeybees having an effect on bumblebee population dynamics are correct, the review might help to explain why.

Nest searching and flower visiting bumblebees were registered in transects within 500 m from last year bean field. Supported by Google maps potential areas which could by qualified as nesting places where identified in 500 m distance from the field. High quality nesting sites where predicted to contain tussocky grass, old leaf material and cavities made from rodents and therefore made up the criteria of potential transects. Ditches, stonewalls and road verges were selected as potential suitable nesting places. Habitats as gardens, semi natural grasslands as pastures and deciduous/boreal forest with a low amount of undergrowth would probably make up for the criteria and therefore be potential nesting sites, however these where not examined in this report do to time limitation. The transects were placed to represent the overall landscape within the landscape typ. For example transects placed on a roadside should not only contain flowers nor dryland if that's not the overall appearance of the landscape type. Places with thick undergrowth, steep hills and areas in danger of flooding were avoided due to inaccessibility. If possible, the transects were placed facing south to avoid shading from surrounding trees. The transects were divided into segments of 50 m, but differed in both width and minimum length. These nesting habitats could reach up to 6 m in width and had a minimum length of 50 m. Each transect were visited five times, with at least one week in between rounds.

The length and width of the transect were initially set at first visit but in almost every case the transects were lengthen by several more segments at the following visits. In some cases the width of already existing segments were widen further. The lengthening and widening of the transects were due to poor data quantity. Every adjustment was carefully noted in the field protocol. The length of the transects were measured by using a hand held GPS and the transects were always walked in the same direction, but the segments were not always walked in numerical order.

9.1 Skåne – the landscape scene

The location of the field study is Skåne county in southern Sweden. The field furthest to the east was located just outside Kristianstad close to the east coast, the one furthest to the west located on the peninsula Kullahalvön at the west coast. Skåne is known in Sweden for having good arable land with big fields, but actually this is only partly true. In the very south there is big fields of loam measuring several hundreds of hectares in a flat landscape, but to the north-east is dominated by a hilly landscape of sandy, silty loam making up smaller fields (Wastenson *et al.* 2002). To the north there is more of a woodland landscape dominated by mixed farming and smaller fields. In the middle there is a quite rocky woodland-grassland landscape with mixed farming as well as crop farming.

In the south and to the south-west the big fields had almost no field borders left due to drainage making fields larger in size, and therefore it was hard finding semi-natural habitats in these parts. Many garden owners were also observed mowing their lawn as well as the bordering road verges.

A common usage of field borders, regardless of location, adjacent to ditches called marginal zones, are usage for flower strips in combination with protection against the leaking of pesticides and fertilizers into the water. A lot of the road verges throughout Skåne were managed by cutting, scraping or contained tire tracks.

Summarizing, Skåne contains both simple landscape (homogenous big fields, crop farming) and complex landscapes (smaller fields, mixed farming) and therefore is an interesting area to investigate different agricultural landscape type effects on bumblebee communities.

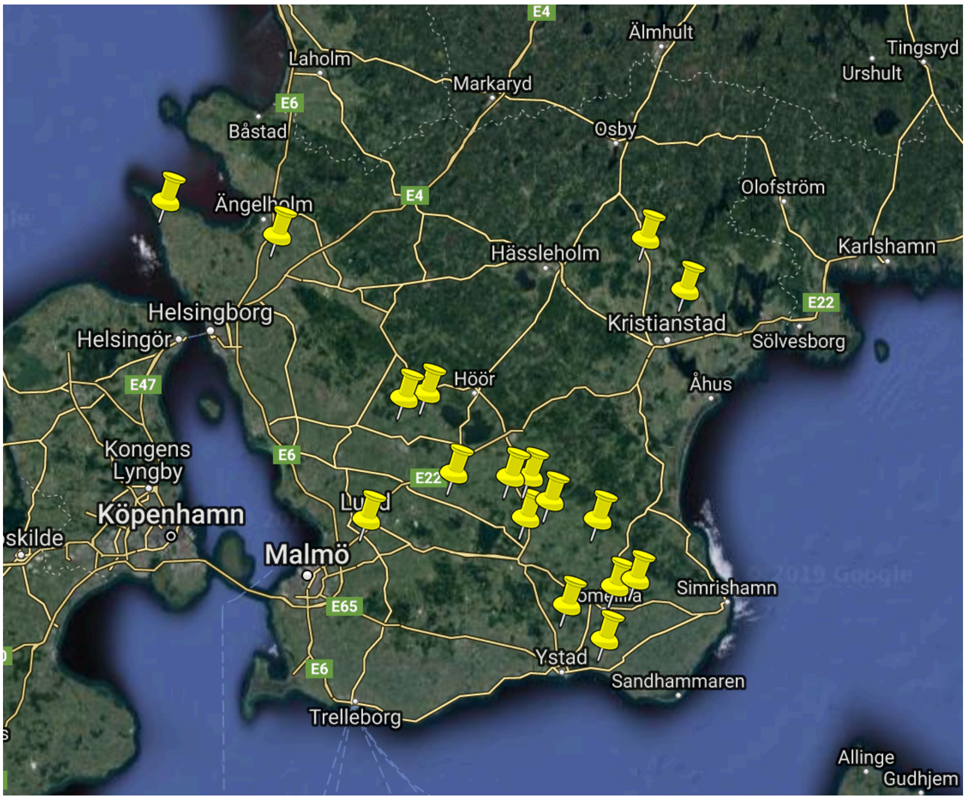

Figure 1 The region of Skåne and the location of the seventeen studied fava bean (Vicia faba) fields.

9.2 Criteria of transects – placing and spacing

9.2.1 Stonewall nesting habitat

A total of 15 transects were studied, all together reaching 8 712 m^2 round 1, 7 638 m^2 round 2, 54 918 m^2 round 3, 68 105 m^2 round 4 and 62 475 m^2. The width of transects were determined by the actual width of the stonewall, but walking one side would potentially block the view of the other side by large stones. Because that was often the case and most of the transect begun at the middle of the stonewall reaching down just one side. From the "foot" (the edge of the stonewall) a further 0,5 m were added in order to get the marginal zone. The actual edge of the stonewall together with the marginal zone were marked by the end furrow made from plowing the field next to the stonewall. Every stonewall in this study bordered to either a field or a pasture, in one case also to a road. Which side of the stonewall to walk were decided by its accessibility and if it fulfilled the criteria mentioned above.

Figure 2 A stonewall transect

9.2.2 Ditch nesting habitat

A total of 15 transects were studied, covering 7 473 m^2 round 1, 5 586 m^2 round 2, 56 932 m^2 round 3, 88 757 m^2 round 4 and 82 044 m^2 at the last round. These transects were placed in either open ditches, half-covered ditches or edges of wetland/managed ponds. If possible big main drainage, the dewatering of entire areas of several estates to prevent flooding, were selected at first hand and smaller drainage, dewatering of single areas of fields, second. As far as possible at least 1 m of the transect width would cover the ditch side, however for short distances this was not possible without risking falling into the ditch while counting bumblebees. The total width were set by the outline of the adjacent

Figure 3 A ditch transect

field set by the marks of tire tracks or by the recent trimming of the field edges.

9.2.3 Road verge nesting habitat

16 transects were studied with a total of 2 208 m^2 round 1, 4 582 m^2 round 2, 29 960 m^2 round 3, 36 408 m^2 round 4 and 33 930 m^2 round 5. Transects placed on the side of the road had an additional slightly different criteria than the others. The goal was to find segments that contain at least 10 % tussocky grass (by an ocular estimate), but with the expansion of transects length, adding more segments to get more data, it was difficult to find segments by this criterion. Therefore some added segments only contained 5 % and a few 0 % tussocky grass. No short cut lawn-like road verge, no cultivated, no scraped nor recurrent used by traffic either. Further more they must measure a width of at least one meter, though this turned out to be a difficult criterion and some transect came slightly short of one meter.

Figure 4 A road verge transect

9.3 Protocol bumblebees

I walk through the transect while actively searching for bumblebee through its whole width. In mean I give each m^2 0,2 seconds of attention which means that a transect measuring 6x100 m will approximately take 2 minutes to walk through (with a velocity of 3 km/h). I alternate between looking on each side of the transect, in search for movement in the vegetation. A stopwatch is used to make sure that my pace is as constant as possible through the walk. When I spot a bumblebee it is identified to species, cast and behaviour noted in the field protocol. The behaviour is noted to “nest searching”, “nest visiting”, “in flight” or “flower visiting”. Nest searching is noted as a bumblebee is flying in a zick-zack pattern close to the ground investigating cavities. Nest visiting is noted as a bumblebee is walking to a cavity into the ground or vegetation, alternately flying into a cavity. A bumblebee which is just flying into or crossing a transect is noted as “in flight”. An “in flight” bumblebee flies higher, more obvious straight and direct, without any visible interest in flowers nor nests (Benton 2006; O’connor *et al.* 2017). Flower visiting bumblebees are noted as they carry pollen and visit flowers. The first observed activity is the one recorded in the protocol. If the behaviour is confusing the bumblebee is studied until one of the activities mentioned above is recognised. If there is risk of confusing one species to another the bumblebee is captured by net to be exanimated closely, using an identification key and sometimes photographed. All bumblebees are realised back to their habitat as soon as possible. As a bumblebee is caught, or further observed for behaviour, the stopwatch is paused until the identification is finished. If a bumblebee can not be identified to species, it is recorded as *Bombus spp*.

9.4 Weather condition and limitations

Each transect were visited sometime between 8.30-20.30 during the month of April and May. Each site either visited before or after noon, altering every visit to get visits from all places during different time of the day. All the sites in one direction were, if possible, not visited at once. In order to be time efficient sites within a quarter of an hour, or together in a remote place, where visited at the same time. The temperature had to be at least 7 °C, no more than moderate winds >8 m/s and the vegetation must be dry (no waterdrops on leaves). (O'connor *et al.* 2017) The weather was noted as a mean of the time during the survey, for example wind speed, temperature and cloudiness. To estimate the wind speed the Beaufort scale was used, even though it sometimes could be a bit difficult when no trees could be used as references. Moderate winds equals to Beaufort 4 which means that twigs and thin branches moves and dust swirls. Compared to Beaufort 5 when smaller trees starts to swing and waves on lakes start to form distinctive cams (O'connor *et al.* 2017).

9.5 Time consumption

A time consumption estimation of a transect spanning 100 m in length (two segments of 50 m each) and 6 m in width, walking with a pace of approximately 3 km/h, would take about 2 min to finish the survey. The estimation of flower resources (which results were not a subject of this thesis but in the larger project EcoBeans18) should take about the same time depending on the quantity of species. Each transect would then take about 5-15 min to do, including time for notes and identification. By these measures one could be able to make three or four transects each hour, if they where located close to each other. Though many of the transects had at least three or four segments (total of 150 m or 200 m), which meant that the actual time spent on each transect where in fact 30-45 min depending on the activity. Furthermore, they where often located more than half an hour apart from each other some up to 2,5 hours. For each replicate (round) more segments were added due to poor data quantity, first replicate took four days and the last replicate lasted seven days. Totally five visits per site were made possible.

10 Results field study

Of all 938 observations a total of 230 bumblebees were recorded, of which 117 were queens and 71 registered as unknown. A total of 13 different species were recorded, 11 of them representing queens. A quantile-quantile plot (see appendix) shows that the sample was slightly right skewed, which means that the sample is logarithmic normal distributed. In order to transform the sample to a normal distribution, the square root of each observation within the sample where used. A new quantile-quantile plot of the square root of the sample shows a normal distribution (see appendix). The ANOVA analyse were conducted on the 117 bumblebee queens and the overall bumblebee abundance (queens and workers) separately.

10.1 Effect of treatments on bumblebee queen density

To test the effect of the treatments honeybees and flower strips several ANOVA tests were conducted, on both queen density and the overall bumblebee density, but neither of them showed significance. The differences in numbers between fields with and without treatments were not big enough to minimize the chance factor, or the sampling quantity was too small. The F-value of the ANOVA-test of the synergy effect of honeybee and flower strip on the overall abundance was interestingly quite high (F-value: 2.98), although not significant (P-value: 0.149). Compared to the same ANOVA analyse but conducted on bumblebee queen abundance showed no interesting values (F-value: 0.2527 and P-value: 0.6214). However, a boxplot comparing all the treatments showed that flower strips could be having a positive effect on bumblebee queen density compared to fields without flower strips (figure 6). This could indicate that the effect of flower strips on bumblebee density might show significance with a greater data quantity.

Significance was noted in the effect of transect type (*) on the overall bumblebee abundance but no significance was noted on queen abundance (figure 7). The effect of treatments on the transect types (Stonewall, Road verge, Ditch) and the overall bumblebee density showed significance in the effect of honeybees (*).

The density of bumblebees varied between the 17 fields (figure 5). Ranging from 7.9 to 123.5 bumblebees per km^2 including all casts: queens, workers and unknowns (table in appendix).

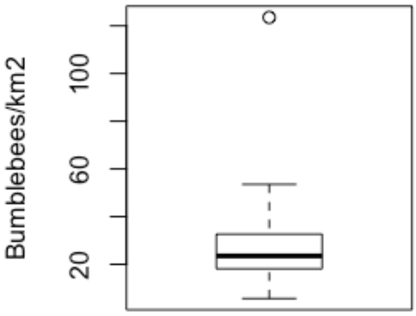

Figure 5 The density ranged from 7.9 to 223,5 bumblebees/km^2.

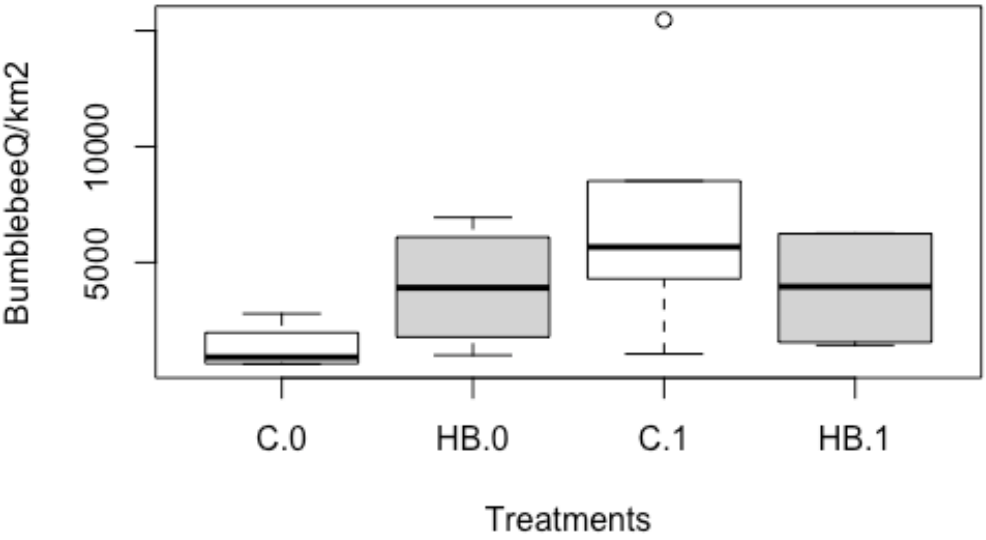

Figure 6 Density of bumblebee queens/km^2 in fields with neither honeybees nor flower strips (C.O), honeybees but no flower strips (HB.O), flower strips but no honeybees (C.1) and honeybees and flower strips (HB.1). The higher density of bumblebee queens in fields with flower strips might indicate a positive effect of flower strips on bumblebee reproduction.

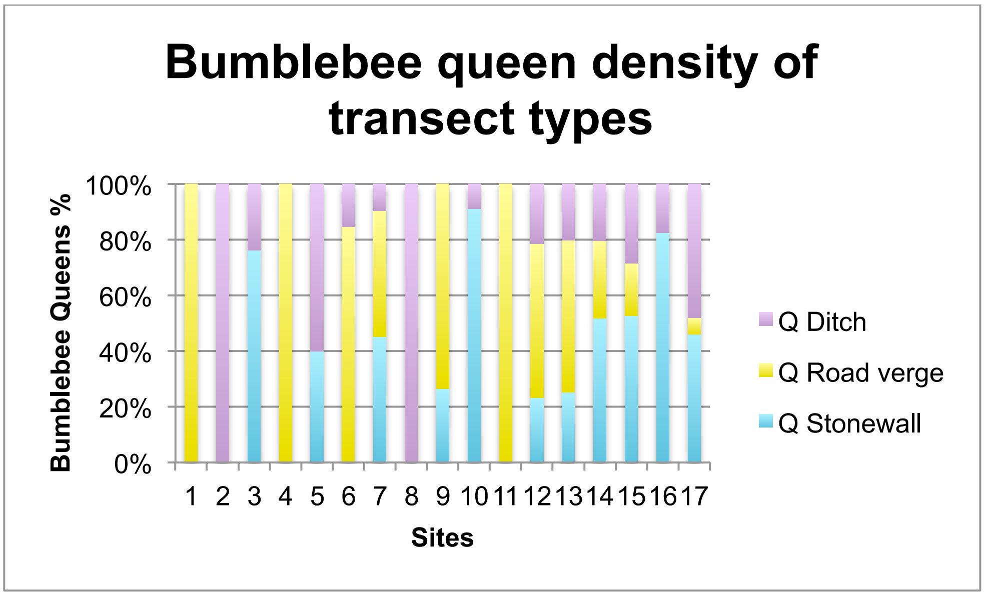

Figure 7 Bumblebee queen density of transect types in % per site.

10.2 Effect of treatments on bumblebee species density

The most represented species of all casts were *Bombus terrestris-C*, followed by *Bombus ruderarius* and *Bombus hortorum* (figure 7). When the queens were examine separately, the same three species appeared but the last two in reversed order (figure 8). The species of queens were slightly more evenly distributed (see appendix). ANOVA analyses were only conducted on the overall density of bumblebees (workers and queens).

10.2.1 ANOVA analysis of species densities (queens and workers)

An ANOVA test suggested significant (***) difference between species at the different locations in the overall bumblebee abundance. Further ANOVA tests also showed possible effects of treatments (flower strip and honeybees) on the species density, a significance of ** for flower strips and a significance of *** on species density. But, due to the low quantity of observations and a warning message in ANOVA about “dropping rows” due to missing values, 9 rows for flower strips and 8 rows for honeybees (out of 938 rows), these analyses should be interpreted with care. For the analyse of the synergy effect of flower strip and honeybees on species density, 29 rows were dropped and the test showed significance (***).

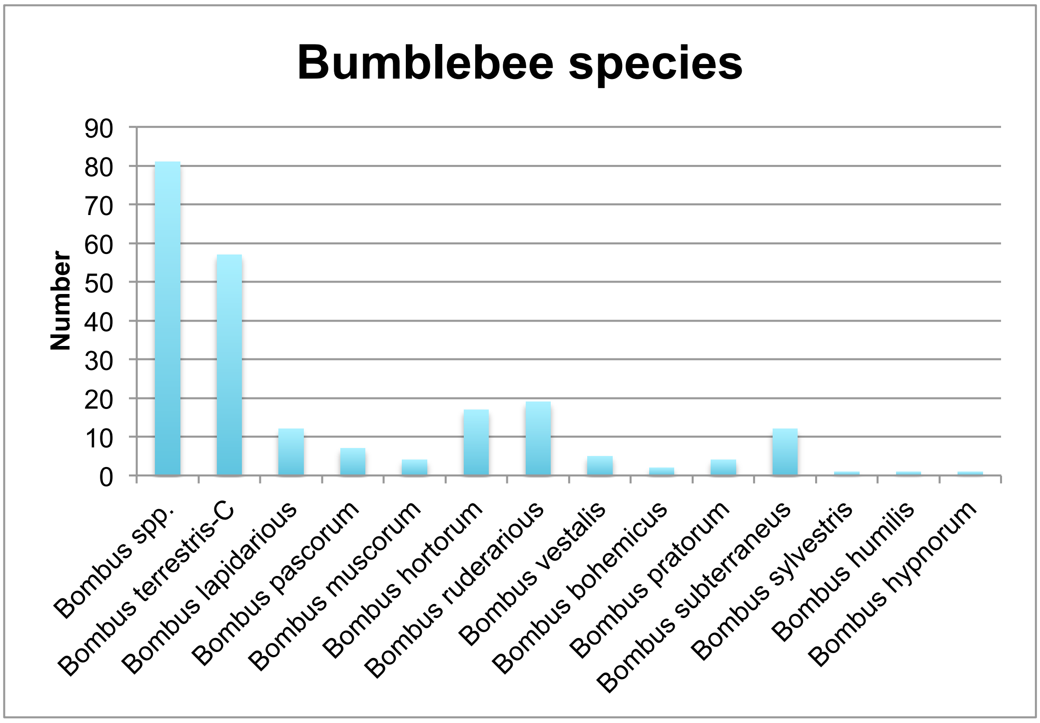

Figure 9 Species density at the different transects types and locations.

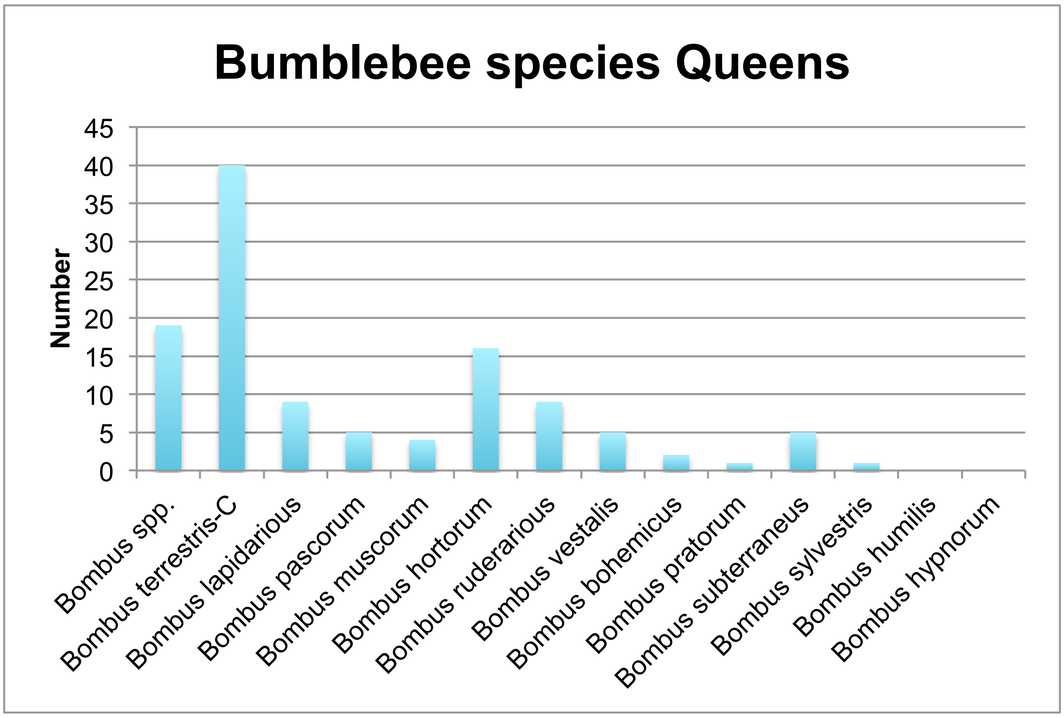

Figure 8 Species density at the different transects types and locations. Only queens.

10.3 Possible error sources

Because bumblebees were not collected, only identified by ocular inspection on site, some species that visually looks similar could be mistaken for each other. That is why bumblebees of the species *B. terrestris, B. cryptarum, B. magnus* and *B. locorum* were grouped together as *Bombus terrestris-C* in the analyse (Müller 2016). Both species and cast were sometimes impossible to identify due to bumblebees flying fast and irregular. For instance, of all 230 bumblebees only 117 were identified as queens. If a majority of the 71 bumblebees noted as unknown were in fact queens of rare species, the results might differ. Another possible error is within the handling of data, which could be effected in the process of the statistic analyse due to my inexperience handling R Studio. The differences between quantities of cast at a species level were not handled in the ANOVA analysis due to my inexperience in handling R Studio. Therefore, when analysing bumblebee species all cast were grouped together as one, even though only 117 of the 230 bumblebees were in fact queens.

The timing of the visits could also affect the outcome, as well as changes in weather conditions. It was difficult to find time to visit all the fields at different time of day: early morning, mid day and evening. The visit of a field either begun before or after 14:00, changing every other visit. Even though this made observations possible during different time of day, it was hard to find time to make the visits to really differ from each other. Would the sample differ further if the observations were made earlier or later during the day? Even though observations did not occur during rainy weather, could rainy weather still affect the foraging behaviour days after a heavy rain or after several very sunny days in a row? Another problem in the first two rounds was the morning temperature, it was below the minimum temperature criteria of 7°C and abled visits only later than 9:00. This effected not only the observations at the time, but also the later rounds due to the splitting of day set at 14:00.

11 Discussion

Reviewing the drivers for bumblebees of foraging and nesting in the agricultural landscape, I have been asking myself: Why do we care about bumblebee population dynamics? And how does drivers of foraging and nesting affect the population dynamics? I have found two main drivers of bumblebee foraging and nesting: 1. Floral resources and floral composition in the agricultural landscape 2. The landscape structure (level of aggregation). And one minor: Interspecies floral competition. Flower strips and competition with honeybees affects bumblebees through these drivers.

11.1 Why we care about bumblebee population dynamics

Bumblebees play a key role in pollination of plants within the northern hemisphere (Westphal *et al.* 2009; Bommarco et al. 2012) and pollination is important to both crops and wild plants, contributing to both quality and quantity of crop yields (Bommarco et al. 2012; Lankinen & Ölund 2013; Walther-Hellwig & Frankl 2000). Bumblebees: are better in pollinating flowers than other insects because they have higher flower constancy, are able to forage in bad weather condition, have a foraging pattern to keep low density potentially covering bigger areas, some species have longer flight distance and a longer lifespan than several other pollinating insects (Benton 2006; Westphal *et al.* 2009; De Luca *et al.* 2009). The bigger the colonies the better are the flowering crop field utilized (Williams *et al.* 2012). Therefore, it is also important in to find ways to support bumblebee colonies in order to reach ecological- and economical sustainability.

11.2 Drivers of bumblebee population dynamics

The bumblebee habitats are the arenas of which bumblebees act on and through which they respond to change. Bumblebee nesting habitat differs in appearance between species: some species nest above ground while others nest under ground, some prefer natural nesting sites whereas others could also use artificial (Osborne *et al.* 2008; Goulson 2010b; Svensson *et al.* 2000; Kells & Goulson 2003; Lye *et al.* 2012). This shows the importance in keeping a heterogeneous landscape when possible, making room for a lot of different nesting habitats. A good foraging habitat contains a lot of extensive managed parts as field margins (Westphal *et al.* 2009), depends on its spatiotemporal context (Williams *et al.* 2012) and is especially important in fragmented landscapes. The quantity as well as the quality has to be sufficient to the altering need of the bumblebees within its life-cycle (Williams *et al.* 2012). The continuity of food plants and food plant quality, especially pollen from fabiaceae (Goulson *et al.* 2005), are the main forage issues for colony survival and reproduction.

11.2.1 Floral resources and floral composition

Two criteria of successful reproduction of bumblebees have to be fulfilled: colony size and continuity of food plants (Westphal *et al.* 2009). Due to the drastic change of the agricultural landscape (Potts *et al.* 2010), a monoculture of crops and declining amount of extensively managed field verges (Schellhorn *et al.* 2015; Persson & Smith 2013), bottlenecks of and disruption of food continuity have negatively effected both bumblebees and plants depending on their pollination services. The interspecies competition has been thrown off balance (Warren *et al.* 2007). The decline in floral resource is correlated with the abundance of natural habitats and the intensification of agriculture (Goulson *et al.* 2005; Bommarco *et al.* 2012).

Short-tongued bumblebee species are supported at a higher level of artificial food sources as temporally flowering crops, but higher species diversity is found in permanent foraging habitat (Walther-Hellwig & Frankl 2000). Mass flowering crops could temporally bolster colony size (Rundlöf *et al.* 2014) and even reproduction (Westphal *et al.* 2009) depending on type of crop and the timing of flowering with the need of the colony. Crops flowering early in season could enhance reproduction whereas late flowering crops could boost colony size and indirectly possibly reproduction. It depends on: the timing of the Bumblebee species life-cycle with flowering period of crops (Westphal *et al.* 2006), differences in need of forage quality and quantity between sexes and life-stages (Rundlöf *et al.* 2014) and interspecies competition. Mass flowering crops could also result in negative impact by bumblebees choosing crops instead of wild flowers, eventually reduces the abundance of wild flowers by the loss of pollination (Reidinger *et al.* 2015). These artificial foraging habitats do only meet a temporal need of forage, and therefore other needs as nesting habitat, forage continuity and food quality are not supported (Westphal *et al.* 2009). The mass flowering is an event partly created by humans to enhance the yield (Boelt *et al.* 2015; Lundin *et al.* 2016) and thereby a conflicting objective to the needs of a bumblebee.

11.2.2 Interspecies floral competition

Different bumblebee species are able to coexist due to their different spatial resource patterns; were big species fly longer distances than smaller ones to meet their needs, usage of foraging habitat at different times and in different ways (Westphal *et al.* 2006, 2009).

11.2.3 The landscape structure (level of aggregation)

Simple landscape is limited in floral resources by midsummer, but species early in nest establishment and shorter life-cycles could still be supported. A significant difference in species-richness between simple and complex landscapes due to their richer border zones has been observed (Persson & Smith 2013). It seems to depend on the quantity of extensively managed parts of the complex landscapes.

The ability to fly long distances, learn how to handle new flower species, remembering flight paths, carrying capacity and their efficiency and flower constancy makes bumblebees even more important in a fragmented landscape, such as the agricultural (Benton 2006). It is all about the bee flight season, and flight distances, which set the limits to bee utilization of flowering plants (Williams *et al.* 2012).

The nest searching behaviour in different species may act on drivers as an aggregation effect for the actual founding of a suitable nesting place. The bumblebee queen has to find and recognise a suitable nesting place, and this could be a bottleneck in todays rapidly changing landscape scene. The foundation all depends on her having the proper methods and biologic trait to be able to find a new potential nesting place. This might be one survival benefit of *B. pascorum* queens (Goulson 2010; Lye *et al.* 2012), as opportunists are able to recognise a potential even artificial nesting place in contrast to other less common species.

In my own observations after spotting a queen entering a potential nest, it could take several minutes before she could be spotted again and often I did not se her leaving at all. This might be as a result of queens returning from foraging to spend several days incubating eggs, after the three or four weeks of nest-searching. My conclusion is that I possibly unknowingly passed many nests of bumblebees, despite my constant effort to spot them. I had to be in luck to spot the very moment the queen decides to enter or leave the nest, whether she was trying them out or already had found one.

11.3 Flower strips and honeybees

Analysing the results of my field study, neither honeybees nor flower strips significantly effected queen survival. Therefore the null hypothesis can´t be disregarded. But the boxplot of all the treatments in comparison (figure 6) shows that a significant effect might be expected of flower strips on the density of bumblebee queens with a higher data quantity. The difference in species density, where a few dominate the overall abundance (figure 7 and 8), could also indicate that some species are much more sensitive to competition with honeybees and the availability of floral resources from flower strips than others. An ANOVA analyse of the effect on species would be very interesting, but this is too difficult for me to handle in R as well as the problem of an even lower data quantity at a species level. At total of 13 species were found (11 queen species) out of the 40 Swedish species (Mossberg 2012) existing in Sweden. The dominating species were the common ones as Bombus terrestris-C, a lot of the other species were poorly represented. This could be indicating that species richness is low in Skåne due to loss of habitats for mainly uncommon species. Because a survey of emerging queens has not been done before, there is no data for comparison. Thereby it is difficult to tell if the reproduction success of bumblebees is declining, both as a genus (*Bombus spp.*) and at a species level.

The overall bumblebee abundance (queens and workers) showed a significant difference between the transect types (road verge, ditch and stone wall) as well as transect type with a honeybee treatment. But no effect on the abundance on bumblebee queens was noted. This could indicate a higher amount of workers in some areas due to aggregation effects.

The review suggest that flower strips could make a difference for bumblebee population dynamics if the timing and floral quality corresponds to the need of the bumblebee populations (Haaland *et al.* 2011). The when and where of the flower strips location is crucial, as well as the floral quality. Flower strips are thought to enhance pollination in simple landscapes (Herbertsson *et al.* 2018) and when sown early in season (Rundlöf *et al.* 2018), to control pests as well as enhance the flowering period of possible food plants (Karamaouna *et al.* 2016; Staton *et al.* 2019; Kratschmer *at al.* 2019; Ouvrard *et al* 2018). But as Scheper *et al.* (2015) has argued more research is needed to investigate the effect at a population-level.

In the northern hemisphere honeybees located within the agro-ecosystem throughout the year makes them a natural component of the ecosystem (Paini 2004; Goulson 2003), as long as there are no sensitive and endangered species close by and that their density is proportional to the resource availability. For instance, smaller bumblebees are more sensitive to competition of floral resources (Henry & Rodet 2018) and feral colonies could compete over nesting sites (Goulson 2003). Due to their smaller size some bumblebee species are foraging second, have a shorter foraging range and a shorter lifespan (Goulson 2003). But because rare species are hard to find, how do we know if they do exist within an area?

Furthermore the ecosystems are already stressed due to great and fast alterations of the agricultural landscape the last century (Potts *et al.* 2010; Herbertsson *et al.* 2016). The heterogeneity of the landscape and field sizes was two important factors affecting bumblebee densities when competing with honeybees. Increasing field size and shorter distances to apiaries negatively affected bumblebee densities (Lindström *et al.* 2016). In homogenous landscapes bumblebee densities were supressed by added honeybees due to niche overlap and at heterogeneous landscapes the density of bumblebees with a shorter foraging range were lower (Herbertsson *et al.* 2016).

The fact that honeybees are supplementary fed (Goulson 2003) could potentially throw the interspecies balance off. The foraging activity of honeybees could be diminishing plant richness by foraging without successful pollination, in long term negatively affecting specialised bumblebee species by loss of floral resources (Paini 2004).

11.4 Proposed actions

Although my field analyse does not show a significant effect of flower strips nor honeybees on queen survival (and thereby population dynamics), several researchers in my review have proposed hands on practises to support bumblebee population dynamics. Westphal et al. (2009) suggest that it is during the critical phases, colony establishment and the reproductive phase in the second half of summer, that an enhance of floral resource would give the best conservation effect (Westphal *et al.* 2009). They also emphases that the sowing of wild seed mixtures should contain a wide variety of flowers which cover the preferred nectar and pollen for different bumblebee species. Persson and Smith (2013) proposes that it is especially in simple landscapes that the adding of wild flowers or mid/late flowering crops boost biodiversity in both plants and arthropods (Persson & Smith 2013).

When keeping honeybees for pollination services one is better to keep the hives in the agro-ecosystem the year around than just for the pollination of certain crops (Henry & Rodet 2018). Henry and Rodet (2018) also emphases to view the natural mass-flowering resources as shared by others. Further more they proclaim that it is also important not having apiaries in locations with sensitive or endangered plant or bee species. For instance, apiaries could be located in the middle of field away from important bumblebee habitat as field borders (Henry & Rodet 2018).

11.5 Further research questions

My initial research questions about bumblebee population dynamics are partially answered by my review and my field study: reviewing which and how drivers control the bumblebee abundance and species-richness when affecting foraging and nesting, the effects of flower strips and honeybees on floral resources, how and why species react different on drivers, what we know and don’t know about bumblebee population dynamics. A lot of questions still got no clear answer. The toughest question might be how do we protect rare species if we can´t find enough data to even statistically declare if they need protection – and what kind of protection do they need. Why do certain species prevail and others don´t in certain areas? Are they living at their biological limit or just in a place we don´t yet know about? Do landscapes with many semi-natural habitats contain more of the smaller bumblebee species? How do big forests pastures grazed by cows providing semi-open landscapes affect bumblebee species? Because mass flowering crops bolsters big bumblebee species, when the crop has stopped flowering do they outcompete small species by their enhanced larger colony size? Or have the life-cycle of smaller bumblebees already been fulfilled?

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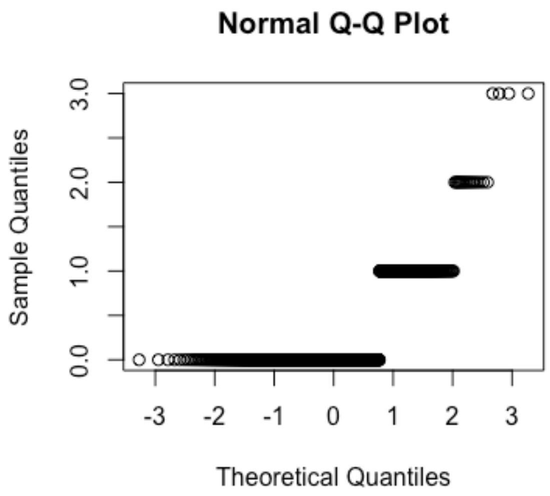
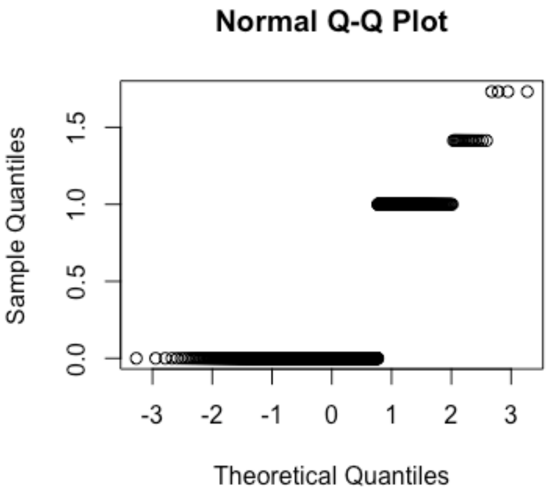
Appendix

A1 Quantile-quantile plots

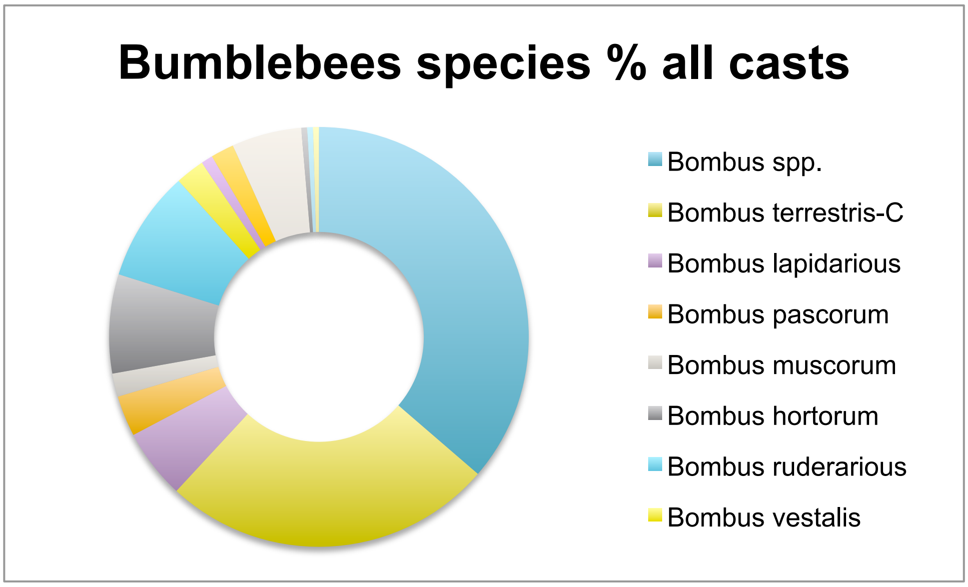


A quantile-quantile plot showing the distribution of the sample.

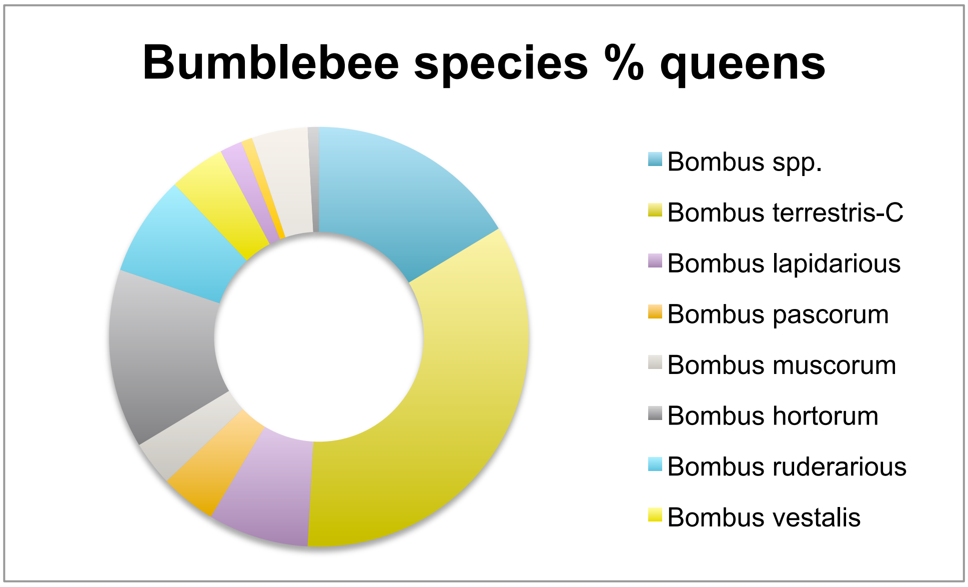


A quantile-quantile plot showing the distribution of the square root of the observations within the sample.

B1 Bumblebee species in percentage all casts



B2 Bumblebee species in percentage only queens



C1 Table mean bumblebee density at each location

The mean bumblebee density per square km at the different fields and the different treatments. Treatments of honeybees marked by C (control) and honeybees (HB). Treatments of flower strips marked by 1 (flower strip) and 0 (control).

Field	Bumblebees/km^2	Honeybees	Flower strip
CN	123.5	C	1
EP	18.1	C	0
HA	13.4	C	1
HN	39.4	C	1
HO	32.7	HB	0
JAA	23.5	HB	0
JE	20.5	C	1
JM	9.8	HB	1
JS	24.7	HB	0
MA	30.3	C	0
MH	24.6	HB	1
MM	5.7	HB	1
MP	22.6	C	1
NS	23.3	C	0
RN	53.5	HB	1
SV	7.9	C	0
VO	37.4	HB	0