



**EFFECTS OF POLLINATOR ABUNDANCE AND DIVERSITY ON
CARAWAY (*CARUM CARVI* L.) YIELD**

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Tiivistelmä - Referat – Abstract <p>Pollinator abundance and diversity are declining at an alarming rate around the world, which poses a threat to ecosystem stability and human wellbeing. There are signs that growing pollination deficits are limiting agricultural yields in Finland and globally. More information is urgently needed on how changes in pollinator communities affect crop yields and how adequate pollination services could be achieved across a range of crops and locations. This study explores the effects of pollinator abundance and diversity on caraway (<i>Carum carvi</i> L.) pollination and yield. Caraway is partly wind-pollinated, but insect pollination has been shown to increase its yield. Flower visits of pollinating insects were monitored on 30 caraway fields in southern Finland in summer 2019. Yield samples were collected from open-pollinated plants and from control plants excluded from pollinators. Pollinator exclusion reduced caraway fruit set by 13.2% and seed yield by 39.6%. Fruit set, 100-seed weight and seed yield increased with increasing flower visitation. Pollinator species richness and Shannon index had no significant effect on the yield components, but evenness of the pollinator community had a negative effect on seed yield and the numbers of umbels and umbellets in the caraway plants. The most abundant pollinators visiting caraway were syrphid flies, non-syrphid Diptera and honeybees. Visits by syrphid flies and honeybees increased seed yield, while visits by non-syrphid Diptera, solitary bees and Lepidoptera had no significant effect on the yield components. Flower visits by beetles reduced 100-seed weight. The results show that syrphid flies provide an important pollinator service for caraway cultivation. It would be beneficial to study which syrphid fly species are the most effective pollinators for caraway and how to manage fields and farmland landscapes to increase their numbers. Relying only on managed honeybees to enhance caraway pollination may not be advisable due to their potential negative effects on wild pollinators. While increased pollinator diversity did not improve caraway pollination or yield in this one-season study, it may be important for the stability of pollinator services in long term.</p>		
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Tiivistelmä - Referat - Abstract <p>Pölyttäjien määrä ja monimuotoisuus vähenevät huolestuttavaa vauhtia eri puolilla maailmaa, mikä uhkaa ekosysteemien vakautta ja ihmisten hyvinvointia. On viitteitä siitä, että kasvava pölytysvaje rajoittaa maatalouden sadontuotantoa sekä Suomessa että maailmanlaajuisesti. Pölyttäjyhteisöissä tapahtuvien muutosten vaikutuksista satoihin sekä keinoista turvata riittävä pölytys eri viljelykasveilla ja alueilla kaivataan nopeasti lisää tietoa.</p> <p>Tämä tutkielma tarkastelee pölyttäjien määrän ja monimuotoisuuden vaikutuksia kuminan (<i>Carum carvi</i> L.) pölytykseen ja satoon. Kumina on osittain tuulipölytteinen, mutta hyönteispölytyksen on osoitettu nostavan sen satotaso. Pölyttäjyhteisten kukkakäyntejä tarkkailtiin 30 kuminapellolla Etelä-Suomessa kesällä 2019. Satonäytteet kerättiin vapaasti pölytetyistä kasveista sekä kontrollikasveista, joille pölyttäjien pääsy oli estetty.</p> <p>Hyönteispölytyksen esto vähensi kuminan siementen muodostumista 13,2 % ja siemensatoa 39,6 %. Kukkakäyntien kokonaismäärällä oli siementen muodostumista, sadan siemenen painoa ja siemensatoa lisäävä vaikutus. Pölyttäjien lajirikkaudella ja Shannonin monimuotoisuusindeksillä ei ollut merkitsevää vaikutusta satokomponentteihin, mutta pölyttäjyhteisön tasaisuuden (engl. evenness) kasvaessa siemensato sekä kerrannaissarjojen ja sarjojen lukumäärä kasveissa pienenivät. Runsaslukuisimmat pölyttäjyryhmät olivat kukkakärpäset, muut kaksisiipiset ja tarhamehiläiset. Kukkakärpästen ja tarhamehiläisten kukkakäynnit kasvattivat siemensatoa, kun taas muiden kaksisiipisten, erakkomehiläisten ja perhosten kukkakäynneillä ei ollut merkitsevää vaikutusta satokomponentteihin. Kovakuoriaisten kukkakäynnit vähensivät sadan siemenen painoa.</p> <p>Tulokset osoittavat, että kukkakärpästen tarjoamalla pölytyspalvelulla on tärkeä rooli kuminanviljelyssä. Olisi hyödyllistä selvittää, mitkä kukkakärpäslajit ovat tehokkaimpia kuminan pölyttäjiä ja miten maatalousmaita ja -maisemia tulisi hoitaa, jotta näiden yksilömäärä kasvaisi. Kuminan pölytyksen tehostaminen pelkästään tarhamehiläisten avulla ei välttämättä ole suositeltavaa niiden mahdollisten villipölyttäjille haitallisten vaikutusten vuoksi. Vaikka pölyttäjien monimuotoisuudella ei ollut kuminan pölytystä tai satoa parantavaa vaikutusta tässä yhden kasvukauden mittaisessa tutkimuksessa, se saattaa lisätä pölytyspalveluiden vakautta pitkällä aikavälillä.</p>		
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1 INTRODUCTION

Pollinator abundance and diversity are declining at an alarming rate around the world (IPBES 2016). This poses a major threat to ecosystem stability and human wellbeing (Potts et al. 2016), as around 90% of flowering plant species and 75% of globally important food crops are at least partly dependent on animal pollination (Klein et al. 2007, Ollerton et al. 2011). Apart from being economically important (Gallai et al. 2009), animal-pollinated crops, including fruits, vegetables, nuts and seeds, provide a significant proportion of micronutrients in human diets, making pollinators crucial for maintaining human health (Eilers et al. 2011, Smith et al. 2015). Agriculture has become increasingly pollinator-dependent over the last six decades (Aizen et al. 2019), and there are signs of growing pollination deficits; yields of crops with greater dependence on pollinators have grown at a lower rate and become more variable relative to less pollinator-dependent crops (Garibaldi et al. 2011). This trend seems to also occur in Finland, where cultivation area of insect-pollinated crops, such as caraway (*Carum carvi* L.) and broad bean (*Vicia faba* L.), has substantially increased in recent years (Natural Resources Institute Finland 2020). An analysis of Finnish agricultural statistics (Hokkanen et al. 2017) suggests that shortage of pollinators may limit yields at least in the most intensively cultivated parts of the country, where the yields of insect-pollinated crops have declined over the last 15 years.

Conventional agricultural intensification, with associated destruction of natural and semi-natural habitats, landscape homogenisation and pesticide use, has been identified as one of the main drivers of pollinator decline (Potts et al. 2016). Recent research had promoted ecological intensification as a strategy to support pollinators and pollination services (Dicks et al. 2016, IPBES 2016, Kovács-Hostyánszki et al. 2017, Kleijn et al. 2019). The concept is based on optimal management of the ecosystem services that enhance agricultural productivity, while reducing the use of external inputs such as agrochemicals (Bommarco et al. 2013). However, adoption of ecological intensification is constrained by lack of knowledge on the management practices that are required to achieve adequate pollination services across a range of crops, farming systems and locations (Bommarco et al. 2013, Kovács-Hostyánszki et al. 2017, Kleijn et al. 2019). In Finland, agriculture is practiced in unique conditions due to its northern location, which highlights the need for national studies on factors affecting the success of crop pollination. This far, this theme has received little attention. For example, recently published global syntheses on the contributions of insect pollinators to crop yields (Garibaldi et al. 2013, Garibaldi et al. 2015, Rader et al. 2016) contain no data from Finland.

Pollinator management in agriculture has mainly focused on increasing honeybee abundance, even though a diverse community of pollinators can provide more stable and effective pollination than any single species (Garibaldi et al. 2015). Furthermore, managed honeybees can be harmful to wild pollinator populations thereby reducing the pollination service provided by them (Lindström et al. 2016, Geldmann and González-Varo 2018, Valido et al. 2019). Besides managed and wild bees, less studied pollinators such as syrphid flies importantly contribute to crop yields (Rader et al. 2016). A recent review emphasised the need for more detailed information on how changes in pollinator communities affect crop yields (Kovács-Hostyánszki et al. 2017). What level of pollinator diversity and abundance is needed to achieve sufficient crop pollination and high yields? Can pollination and yields be better enhanced by supporting common generalist species (Kleijn et al. 2015) or species whose traits match those of the focal crop (Garibaldi et al. 2015)?

The purpose of this master's thesis is to study the effects of the abundance and diversity of pollinating insects on caraway (*Carum carvi* L.) yield. Caraway is an umbelliferous herb grown for its aromatic fruits (usually called seeds) which are mainly used as spice (Malhotra 2012). Caraway is pollinated by wind and insects, but the degree to which its pollination relies on insects is poorly known, with estimates ranging from around 15% (Bouwmeester and Smid 1995) to 50% (Saarinen 2016) yield reduction with pollinator exclusion compared to open pollination. Caraway is a domestically important crop with Finland being one of the largest producers in the world (Rahman et al. 2020), and its cultivation area in Finland grew nearly 85% between 2013 and 2018 (although, from 2018 to 2020 it decreased 26%; Natural Resources Institute Finland 2020). Regardless of its importance, there are very few studies on caraway pollination both in Finland and internationally – for instance, caraway is not included in recent global syntheses on crop pollination (Garibaldi et al. 2013, Garibaldi et al. 2015, Rader et al. 2016). This study aims to reduce this knowledge gap.

This master's thesis is part of a research project led by D.Sc. Marjaana Toivonen (Finnish Environment Institute) Crop pollination in Finland: effects of farming methods and landscape (funded by Maj and Tor Nessling Foundation and Oiva Kuusisto Foundation). It studies the effects of farming methods and landscape structure on pollinator communities and crop pollination services of turnip rape (Toivonen et al. 2019) and caraway.

2 POLLINATORS AND THEIR ROLE IN CROP PRODUCTION

2.1 Animal-mediated pollination

Pollination is the transfer of pollen from the anthers to the stigma of a flower, which is followed by pollen tube growth and fertilisation of the ovule. The process enables seed production and sexual reproduction in angiosperms (flowering plants; Willmer 2011, p. 55). Self-pollination occurs if pollen fertilises the same flower that produced it (autogamy) or a different flower of the same plant individual (geitonogamy), while cross-pollination (xenogamy) requires that a flower is fertilised by pollen from a different individual of the same species (*ibid*, p. 55, 83). To achieve cross-pollination, plants utilise mobile pollen vectors, namely wind, water and animals. It has been estimated that around 308 000 plant species, or 87.5% of all angiosperms, require transfer of pollen by insects and other animals (Ollerton et al. 2011). In this mutualistic relationship, animals typically visit flowers for nectar and/or pollen, and the plant benefits if the visit leads to pollination (Willmer 2011, p. 3–5).

Coevolution of angiosperms and animals has resulted in a wide diversity of flowers with many shapes, sizes and colours, and correspondingly, a range of pollinating animals with matching traits (Willmer 2011, p. 88–101). Flowers with easily accessible floral rewards are typically pollinated by a range of fairly generalist visitors, while flowers with often complex floral designs are pollinated by specialised visitors that match the shape and size of the flower (*ibid*, p. 54). Globally, nearly 300,000 animal species are known to be regular flower visitors and potential pollinators (Nabhan and Buchmann 1997). Apart from insects which constitute the majority of pollinators, birds and bats are important pollinators in tropical and subtropical regions, and some less well-known pollinators such as mice, squirrels and lizards have also been described (Willmer 2011, pp. 337–377, IPBES 2016, p. 8). However, apart from some exceptions in lower latitudes, only few food crops are pollinated by non-insects (e.g., feijoa is pollinated by birds and bananas by bats) (Klein et al. 2007, Willmer 2011, p. 363).

Not all anthophilous animals are significant pollinators. Sometimes visitors can be more detrimental than beneficial to the plant, such as when they feed on floral parts, or when they rob pollen or nectar without pollinating the flower. The pollination efficiency of an animal depends on many factors, including how well their body size and shape match the structure of the flower, how easily pollen gets attached to their surface structures, how much of that pollen is deposited to the stigma of the next flower, and their behaviour, such as their flower constancy and the way they move between plants.

In addition, environmental conditions such as temperature, cloudiness and wind affect the activity and flower visitation rates of pollinators (Kevan and Baker 1983, Willmer 2011, pp. 6–8).

2.1.1 Pollination by bees

Bees (Hymenoptera: Apoidea: Anthophila) are usually regarded as the most important pollinators both in abundance, efficiency and economic value (Klein et al. 2007, Willmer 2011, pp. 7-8, IPBES 2016, pp. 7–9, Rader et al. 2016). Bees collect both nectar and pollen, and they are obligate flower visitors, since they rely solely on flowers as a food source both as adults and as larvae (Willmer 2011, p. 378). Out of all insects, they are the best adapted to anthophily (Kevan and Baker 1983). Bees show high floral constancy and have hairy surfaces where pollen gets easily attached, making them excellent pollinators (Willmer 2011, p. 7, 378–417). Worldwide, there are over 20 000 known bee species (Ascher and Pickering 2015), and 785 species are known to visit crop flowers (Kleijn et al. 2015). According to Rader et al. (2016), 50–75% of visits to crop flowers are provided by bees.

The bee fauna of Finland includes the western honeybee (*Apis mellifera*), bumblebees (*Bombus* spp.) and solitary bees. Honeybee is non-native, but beekeeping has a long history in Finland and today the species is widely managed for honey production and crop pollination (Söderman and Leinonen 2003). Several characteristics make honeybees efficient and convenient crop pollinators. They form large colonies (Willmer 2011, pp. 396, 414) and their movable hives allow easy management (IPBES 2016, pp. 82–83). Honeybees can forage over large areas and they have highly developed communication systems that enable workers to share information on floral resources (Willmer 2011, pp. 414–416).

Bumblebees have smaller colonies and less developed communication systems than honeybees, but they often move pollen between flowers faster and more efficiently, and with their tongue lengths ranging from short to very long they can forage on a broader range of flowers. Due to their furriness, relatively large size, and strong ability to thermoregulate, bumblebees are well adapted to colder climates and are therefore important pollinators in higher latitudes and altitudes (Willmer 2011, pp. 407–413). In Finland, there are 37 bumblebee species, out of which 8 are cuckoo bumblebees (subspecies *Psithyrus*) (Finnish Biodiversity Information Facility 2020). One species, *B. terrestris*, is used as a managed crop pollinator (Finnish Food Authority 2019).

Solitary bees are generally smaller in size, less abundant and forage over shorter distances than the eusocial honeybees and bumblebees (Söderman and Leinonen 2003, Willmer 2011, pp. 395–417),

but can nevertheless be important pollinators for some crops (Ricciardelli D'Albore 1986, Willmer 2011, pp. 609–613, Eeraerts et al. 2020). There are nearly 200 solitary bee species from 6 families in Finland (Finnish Biodiversity Information Facility 2020).

2.1.2 Pollination by non-bee insects

Besides bees, insect pollinators include species from various taxa, such as non-bee Hymenoptera (e.g., wasps and ants), butterflies and moths (Lepidoptera), flies (Diptera), beetles (Coleoptera) and thrips (Thysanoptera) (Kevan and Baker 1983). Flies are a diverse group of insects and frequent flower visitors, but their potential as crop pollinators is often overlooked (Inouye et al. 2015, Orford et al. 2015, Rader et al. 2016). While flies may not move pollen as efficiently on a single visit as bees, they can be significant pollinators due to their abundance (Inouye et al. 2015, Rader et al. 2016). The importance of flies as pollinators is particularly high in colder climates (Elberling and Olesen 1999). Syrphid flies (Syrphidae) are regarded as the most important group of pollinating flies (Kevan and Baker 1983, Willmer 2011, pp. 304–321). Adult syrphids feed on nectar and/or pollen, tend to show high floral constancy and have hairy surfaces that make them good pollen carriers. They are typically generalists but often prefer yellow and white flowers in Apiaceae, Asteraceae, Brassicaceae and Rosaceae families (Haarto and Kerpola 2007, p. 16–17, Willmer 2011, p. 311–315). In Finland, Diptera include over 4 200 species, out of which 370 are syrphid flies (Finnish Biodiversity Information Facility 2020).

Most butterflies and moths feed on nectar at their adult stage, and a few species also feed on pollen (Kevan and Baker 1983). Compared to bees, lepidopterans often fly longer distances between consecutive flower visits, thus carrying cross-pollen to stigmas and promoting outcrossing (Herrera 1987). However, they typically visit flowers less frequently, carry smaller pollen loads and may deposit less pollen per visit (Willmer 2011, p. 330, Winfree et al. 2011). Moths and butterflies are considered to have little importance in agriculture (Free 1970, p. 2) as very few commercial crops rely on or benefit from lepidopteran pollination (Klein et al. 2007).

In addition to Diptera and Lepidoptera, there are some other important pollinators among the non-bee insect groups mentioned above, such as beetles and wasps, but like Lepidoptera, these are rarely the main pollinators of crops (Klein et al. 2007, Willmer 2011, pp. 288–303, Rader et al. 2016). However, these groups may have more significance than currently is understood as they are often not included in pollination studies (Willmer 2011, pp. 288–303, Rader et al. 2016).

2.2 Pollination of crops as an ecosystem service

Pollination by animals has been defined as a regulating ecosystem service (following the definition by Millennium Ecosystem Assessment 2003, 2005; for other definitions see e.g., Haines-Young and Potschin 2018, Mace et al. 2011). Ecosystem services are benefits that people obtain from ecosystems (Millennium Ecosystem Assessment 2003, 2005), or in other words, “the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life” (Daily 1997). Regulating services refer to the benefits obtained from the regulation of ecosystem processes. These include for example climate regulation, water regulation and regulation of pests and diseases, in addition to pollination (Millennium Ecosystem Assessment 2005). The role of managed pollinators as ecosystem service providers is controversial. If ecosystem services are defined as benefits provided by natural ecosystems, managed pollinators may not fit under the description, as they can be seen as livestock or an agricultural input (IPBES 2016, Geldmann and González-Varo 2018). On the other hand, even agricultural systems, where managed pollinators provide services, are functioning ecosystems – agro-ecosystems – regardless of heavy management. Therefore, pollination by managed pollinators can be defined as an ecosystem service provided by agro-ecosystems (IPBES 2016, p. 210).

The ecosystem service provided by pollinators is important for the cultivation of several food crops. Klein et al. (2007) evaluated the reliance of global food production on animal pollination and found that 75% of world’s leading food crops rely, at least to some degree, on animal-mediated pollination for the quantity and/or quality of their yield. Measured in production volume (tonnes), these 87 crops account for around a third of global food production (Klein et al. 2007). The authors separately evaluated the pollinator dependence of 107 globally traded food crops that produce fruits or seeds directly consumed by humans (i.e., excluding crops for which seeds are only used (1) to produce vegetative parts that humans consume or (2) for breeding alone, when plants reproduce vegetatively and only vegetative parts are consumed). In total absence of pollinators, the production of 12% of the crops would decrease by more than 90%, 28% of the crops by 40–90%, and 45% of the crops by 1–40%, while 7% would not be affected (for 8% effects are unknown) (*ibid*). The above figures highlight the importance of pollinators for global food security. However, the direct contribution of pollinators to global food production may be less than 10% due to the large production volumes of pollinator-independent crops, such as cereals, and the great variation of pollinator dependency among crops (Klein et al. 2007, Aizen et al. 2009). Aizen et al. (2009) estimated the contribution at around 5% for developed world and 8 % for developing world, although, these shares may have grown over

the last decade, since the cultivation area of pollinator-dependent crops is increasing faster than that of nondependent crops (Aizen et al. 2019).

Although the direct contribution of pollinators to global food production volume may be relatively small, pollinators make an important contribution to global and local crop markets. Animal-pollinated crops include many valuable cash crops, such as coffee, cacao and almonds, that provide an income to numerous people (Klein et al. 2007). According to Gallai et al. (2009), the average price of pollinator-dependent crops is five times higher than that of non-dependent crops. Some estimates have been made for the total economic value of pollination services at a global scale, although there are significant uncertainties due to ecological and economic knowledge gaps (IPBES 2016, pp. 253–261). The Assessment Report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on Pollinators, Pollination and Food Production (IPBES 2016) reviews several studies conducted since 1990s and presents figures from Lautenbach et al. (2012) as the best estimate thus far. Using production prices and quantities from 2009, they valued the additional global crop production that can be directly attributed to animal-pollination at US\$235–577 billion (inflated to 2015 US\$) annually, which is approx. 10% of the total value of agriculture (Lautenbach et al. 2012). However, these benefits are not evenly distributed; loss of pollinators would lead to the largest economic losses in regions with widespread cultivation of pollinator-dependent crops and high market prices (particularly Mediterranean Europe, northern America, southern and eastern Asia), while poorer regions with high dependence on animal-pollinated crops would experience largest reductions in consumer and producer welfare (e.g. western, northern and central Africa) (Bauer and Wing 2016, Potts et al. 2016). In Finland, the contribution of pollinators on agricultural GDP is estimated between 2.6% and 5% (Lautenbach et al. 2012).

Besides economic losses, loss of pollinators could have many other negative consequences. First, while widely cultivated, pollinator-independent staple crops, such as cereals and sugar cane, form a large part of global food production volume, they are less rich in micronutrients than many animal-pollinated crops, such as vegetables, fruits, nuts and seeds (Klein et al. 2007, Smith et al. 2015). Based on a modelling analysis, Smith et al. (2015) conclude that pollinator declines can lead to significant global health burdens due to non-communicable diseases and micronutrient deficiencies. Second, lower yields due to insufficient pollination are often compensated by increasing cultivation area, which puts further pressure on natural ecosystems (Aizen et al. 2009, Garibaldi et al. 2011). Finally, pollinators provide various other benefits to humans in addition to pollination of food crops, such as honey and other beekeeping products, non-food crops including medicines, fibres and biofuels,

maintenance of biodiversity that supports ecosystem health and stability, and by supporting many cultural values (Potts et al. 2016).

2.3 Pollinator decline and pollination deficits

In recent years, declines in pollinator populations have been reported in several regions of the world. The observed changes include declines in species richness, evenness and abundance as well as range shifts (IPBES 2016, pp. 151–203). The International Union for the Conservation of Nature (IUCN) Red List provides assessments on the extinction risk status of species, with species rated as Least Concern, Near Threatened, Vulnerable, Endangered, Critically Endangered, Extinct in the Wild, and Extinct (IUCN 2012). Based on global assessments on bird and mammal pollinators, a total of 16.5% of vertebrate pollinators are threatened with global extinction (rated Near Threatened to Critically Endangered) (Aslan et al. 2013), and the status of most species is deteriorating rather than improving (Regan et al. 2015). While global level assessments are lacking for most insect pollinators, national and regional assessment indicate declining trends. In Europe, 9.2% of bees and 8.5% of butterflies are considered threatened (Vulnerable, Endangered or Critically Endangered) and a further 5.2% of bees and 10% of butterflies are rated as Near Threatened (Van Swaay et al. 2010, Nieto et al. 2014). In national assessments, these figures are often higher – for example, many European countries have listed over 50% of bees as threatened (IPBES 2016, p. 157). Population trends show that 35% of bee species and 31% of butterfly species in Europe are in decline (Van Swaay et al. 2010, Nieto et al. 2014).

In Finland, 17% of bees, 31.8% of butterflies and 17.1% of moths are threatened, but in syrphid flies, only 3.1% are threatened (The Red List 2019). Population trends for most pollinators in Finland are unknown due to lack of long-term monitoring programmes. Lepidopterans are an exception; monitoring of butterflies in Finnish agricultural landscapes since 1999 shows that more than half of the species are in decline (Heliölä and Kuussaari 2019), and the total abundance of moths has declined between 1993 and 2012 (Antão et al. 2020). Northward range shifts driven by global warming have been observed in both butterflies and moths (Pöyry et al. 2009, Antão et al. 2020). National programme for bumblebee monitoring was launched in 2019 (Finnish Environment Institute 2020).

The evaluations for species' extinction risk and population trends have significant uncertainties due to data gaps. For instance, the status of 56.7% of European bee species cannot be evaluated due to insufficient data, and for 79% of bee species, population trends are unknown (Nieto et al. 2014).

Many of the data deficient bee species are likely to be very rare or have very limited distribution (possibly endemic), which are typical traits for threatened species and could suggest that the percentages of threatened species are currently underestimated (IPBES 2016, p. 157). However, bees that pollinate crops are usually common rather than threatened species (Kleijn et al. 2015, IPBES 2016, p. 157). Most studies on insect pollinators have thus far focused on bees and covered a limited geographic area, namely Europe and North America. Therefore, a considerable amount of research is needed to assess the status and trends of different wild pollinator taxa at a global scale (IPBES 2016, p. 188).

The observed declines in pollinator populations are related to a global trend of diminishing biodiversity – a trend so severe it has been defined as the sixth mass extinction (Pimm et al. 2014, Ceballos et al. 2017, Sánchez-Bayo and Wyckhuys 2019). The main drivers of pollinator decline include land-use change and intensification, pesticide use, parasites and diseases, invasive alien species and climate change (Potts et al. 2016). Additionally, interactions between drivers may exacerbate the overall impact (Potts et al. 2010, Vanbergen and the Insect Pollinators Initiative 2013). The role of agriculture is significant, since over a third of global land area is in agricultural use (FAO 2020). Agricultural intensification has homogenised landscapes and caused destruction, degradation and fragmentation of natural and semi-natural habitats (Tscharntke et al. 2005, Potts et al. 2010), thus reducing floral and nesting resources vital to pollinators (Svensson et al. 2000, Gabriel and Tscharntke 2007, Holzschuh et al. 2008, Baude et al. 2016). Conventional agriculture is associated with high use of agrochemicals, including insecticides, which can have lethal and sub-lethal effects on pollinators (Godfray et al. 2014, 2015, Pisa et al. 2015), and herbicides and fertilisers, which can affect pollinators indirectly by reducing the abundance and diversity of floral resources (Gabriel and Tscharntke 2007, Holzschuh et al. 2008). In Finland, the area of semi-natural grasslands and wooded pastures, which are important habitats for many pollinators, has declined over 99% during the 20th century due to agricultural intensification and other land-use changes (Raatikainen 2018, Hyvärinen et al. 2019, pp. 90–98, Lehtomaa et al. 2019).

While pollinator populations are declining, agriculture has become increasingly dependent on pollinators as the cultivation area of pollinator-dependent crops has rapidly expanded over the past decades (Aizen et al. 2019). This has increased the risk of crop pollination deficits, i.e., quantitatively or qualitatively insufficient pollen receipt that decreases agricultural output (Vaissière et al. 2011). There are signs that reduced pollinator availability is affecting yields both globally and in Finland. Yield growth and stability of crops with high pollinator dependence have declined compared to less

pollinator-dependent crops (Garibaldi et al. 2011, Hokkanen et al. 2017). In the most intensively cultivated parts of Finland, yields of insect-pollinated crops (turnip rape, blackcurrant and caraway) have declined over the last 10–15 years, which may be explained by low pollinator availability caused by increased neonicotinoid use and reduced landscape complexity (Hokkanen et al. 2017).

Managed honeybees are frequently used as crop pollinators in areas where visitation by wild pollinators is insufficient for securing good yields. However, agricultural demand for pollinators has grown faster than the numbers of honeybee hives (Aizen and Harder 2009), and there are several reasons why farmers should utilise a more diverse pollinator fauna than just honeybees. Reliance on one species is a risky strategy, as has been highlighted by honeybee colony losses caused by multiple drivers such as parasites, pathogens, problematic bee management practices and pesticide exposure (Hristov et al. 2020). Recently, research has shown that wild pollinators, including non-bee insects, contribute to crop yields more than previously assumed (Garibaldi et al. 2013, Orford et al. 2015, Rader et al. 2016). In a global synthesis, Garibaldi et al. (2013) found that wild insects pollinated crops more effectively than honeybees and increased fruit set even when honeybees were present in high abundance, which shows that honeybees can only partially compensate for the pollination function of wild pollinators. It has also been demonstrated that increased pollinator diversity can enhance and stabilise crop pollination (Garibaldi et al. 2013, 2015). Moreover, there is growing evidence that managed honeybees can harm wild pollinator populations, especially in areas where honeybees are non-native, because they compete on the same resources and can spread diseases (Lindström et al. 2016, Geldmann and González-Varo 2018, Valido et al. 2019). Thus, there is increasing interest in developing ways to reduce the negative effects of honeybees (Sørensen et al. 2020) and to manage farmlands and landscapes to increase the numbers and crop visitation of wild pollinators (Kovács-Hostyánszki et al. 2017, Kleijn et al. 2019).

2.4 The importance of pollinator abundance and diversity for crop yields

Yields of animal-pollinated crops are affected by both the abundance and diversity of pollinators. Success of pollination is often measured by seed or fruit set, which is the proportion of flowers that develop into mature seeds or fruits (Garibaldi et al. 2013, Rader et al. 2016). High pollinator abundance increases the rate of flower visitation, which in turn increases pollen deposition on stigmas of crop flowers, therefore increasing seed/fruit set and yield (Garibaldi et al. 2013). When other resources are not limiting, yields should increase with increased pollinator abundance at a decelerating rate until pollen saturation is reached, i.e., until additional pollinator individuals do not

further improve seed/fruit set (Morris et al. 2010, Garibaldi et al. 2011). Very high pollinator abundance may even decrease yield if, for instance, excessive visitation causes damage to floral structures (Morris et al. 2010). Yield increase per pollinator, or per flower visit, also depends on the level of pollinator dependence of the crop (Klein et al. 2007, Garibaldi et al. 2011) and the pollinator species in question, as the efficiency of pollen transport and deposition differs among species (Rader et al. 2011, Orford et al. 2015, Rader et al. 2016).

Species diversity encompasses species richness, which is simply the number of species, and evenness, which refers to the relative abundance of species (Maurer and McGill 2011). Increase in pollinator species richness can enhance yields through several mechanisms. Species that are specialised and occupy different niches (niche complementarity) may contribute to the same ecological function, such as pollination, in differing ways (functional complementarity), in which case, these species may collectively contribute to the function more than any species alone (Blüthgen and Klein 2011). Thus, high species richness can enhance ecosystem functioning, and therefore ecosystem service provision. Pollinators can complement each other temporally (Blüthgen and Klein 2011); for example, different species may forage at different times of the day (Hoehn et al. 2008), or some species may be abundant early and others later in the growing season (Ellis et al. 2017). Temporal complementarity can be related to weather conditions such as wind, moisture, temperature and cloud cover (Blüthgen and Klein 2011, Ellis et al. 2017). For example, Brittain et al. (2013) found that wild bees were more tolerant to high winds than honeybees in almond orchards, while Ellis et al. (2017) found that flies visited strawberry and raspberry flowers in poorer weather than bumblebees and honeybees. Complementarity can also be spatial; different pollinator species may prefer to visit flowers in different parts of a plant or a field (Hoehn et al. 2008, Klein et al. 2009, Brittain et al. 2013), or they may deposit pollen at different parts of the same flower (Hoehn et al. 2008).

Species richness may also have a stabilising effect on yields due to functional redundancy, which occurs when species are generalised, or their functional niches otherwise overlap, and additional species do not enhance functional performance (Blüthgen and Klein 2011). According to the insurance hypothesis, ecosystem functioning is more stable in species-rich communities, because redundant species contributing to the same function offer an insurance against losses of other species (Yachi and Loreau 1999, Loreau et al. 2001). Species richness can stabilise productivity in a fluctuating environment in two ways: (1) by reducing the temporal variance, and (2) by increasing the temporal mean of productivity (Yachi and Loreau 1999). There are some underlying mechanisms through which functional redundancy can stabilise ecosystem functioning and these include: density

compensation, which occurs when a decrease in the abundance of one species results in increased abundance of another species; response diversity, i.e., one species responds negatively and another positively to the same environmental change; and cross-scale resilience, which means that different species respond to the same environmental variable at different spatial and/or temporal scales (Elmqvist et al. 2003, Winfree and Kremen 2009). These mechanisms are in fact examples of functional complementarity that occurs over longer periods of time, as species that once appeared redundant are such no longer after a change in environmental conditions (Loreau et al. 2001, Blüthgen and Klein 2011).

Pollinator species richness may also enhance pollination through functional facilitation, which occurs when one species positively affects the pollination function of another species (Greenleaf and Kremen 2006, Klein et al. 2009), or by increasing the likelihood that more efficient pollinator species are present, which is referred to as sampling effects (Tilman 1999). In addition, pollinator communities with high species richness often have higher aggregate abundance, which enhances pollination (Kremen and Chaplin-Kramer 2007). Pollinator richness is also beneficial for wild plant communities and when different crops are grown in the same area, as different plants are known to attract different flower-visiting species (Klein et al. 2009, Blüthgen and Klein 2011). On the other hand, high species richness may affect pollination negatively if less efficient pollinators compete for pollen with more efficient species, or if it reduces flower constancy, thus increasing the deposition of heterospecific pollen that clogs stigmas (Kremen and Chaplin-Kramer 2007).

Changes in species evenness (or its opposite, dominance) alter the distribution of traits in the community, which then affects species interactions and ecosystem processes (Hillebrand et al. 2008). Increase in pollinator evenness may enhance and stabilise pollination and yields via the complementarity mechanisms, facilitation and sampling effects reviewed above; however, it can have a negative effect if evenness results from the lack of an efficient species, such as honeybee (*ibid*). Evenness often reacts faster to environmental changes than species richness, which may show as altered ecosystem functioning long before species become rare or are driven to extinction (Chapin et al. 2000).

3 CARAWAY

3.1 Caraway cultivation in Finland

Caraway (*Carum Carvi* L.) is an umbelliferous herb in the family Apiaceae that is cultivated for its aromatic seeds (botanically fruits). Caraway seeds and essential oil extracted from them are mostly used as spice but also as an ingredient in cosmetics and medicinal products (Malhotra 2012). The odour and flavour of caraway essential oil is mainly attributed to volatile compounds carvone and limonene (*ibid*).

There are both annual and biannual forms of caraway. The cultivars grown in Finland are biannual, since the annual forms, grown for instance in southern and central Europe, do not succeed in the northern climate (Leppälä et al. 2007). In the sowing year, a biannual caraway plant grows a rosette and a long taproot that helps it overwinter. If the root has reached a thickness of more than 6 mm in the autumn, the plant will flower and produce seed in the following year (*ibid*). After flowering the plant dies. As some plants flower later than in the second year, caraway can be harvested for several years, usually 2–3 years (Leppälä et al. 2007, Keskitalo et al. 2014, p. 11, Arctic Taste 2018). In Finland, caraway usually flowers for 3–4 weeks in June, and harvest typically occurs in early August (Arctic Taste 2018).

Finland is among the largest producers of caraway in the world (Rahman et al. 2020). In 2019, the cultivation area of caraway in Finland was 18 600 ha and production 16 600 tons (Natural Resources Institute Finland 2020). Finnish caraway is considered high quality because, due to the long days of the northern growing season, it has a higher oil content – and hence a stronger aroma – than caraway grown in lower latitudes (Malhotra 2012, Niemi and Ahlstedt 2013, p. 20, 28). Oil content is also higher in the biannual than the annual forms (Keskitalo 2006, Bailer et al. 2001, Malhotra 2012).

3.2 Pollination of caraway

The inflorescence of caraway is a compound umbel, which comprises several umbellets that are formed of small white florets. As in other umbellifers, flowering is sequential with the central umbel at the top of the stem blooming first, followed by primary lateral umbels, then secondary lateral umbels and each umbel order successively. In addition, peripheral flowers within umbels and umbellets open before the more central flowers (Van Roon and Bleijenberg 1964, Koul et al. 1993, Willmer 2011, p. 29). Caraway exhibits andromonoecy, i.e., a single plant has both seed-producing

hermaphrodite flowers and male flowers that do not produce seed. The proportion of male flowers increases with umbel order, and it is higher in central than peripheral umbellets (Bouwmeester and Smid 1995). Bouwmeester and Smid (1995) demonstrated that the proportion of male flowers also increases with sowing density, but decreases if competing umbels are artificially removed, which suggests that resource availability regulates flower fertility. Caraway is self-compatible, but its flowers are protandrous, with pollen release occurring several days before stigmas become receptive, which promotes outcrossing. Self-pollination rarely occurs within an umbel, but geitonogamy is possible as pollen from later flowering, higher-order umbels can fertilise lower-order umbels with receptive stigmas (Van Roon and Bleijenberg 1964, Németh et al. 1999). Both protandry and andromonoecy are typical in Apiaceae (Webb 1981, Koul et al. 1993). The fruit produced by pollinated hermaphrodite flowers is a schizocarp, which at harvest splits into two achenes that are traded as caraway “seeds” (Van Roon and Bleijenberg 1964, Bouwmeester and Smid 1995).

Caraway flowers produce both pollen and nectar that attract pollinators (Langenberger and Davis 2002a). The compound inflorescence of Apiaceae provides a large, visually attractive landing platform, and the open disk-shaped florets with exposed nectaries are easily accessed by various types of insects (Koul et al. 1993, Willmer 2011, p. 25, 33). Umbellifers are therefore visited by a wide range of insect taxa, including Hymenoptera (bees, wasps, ants and sawflies), Diptera, Coleoptera and Lepidoptera (Bohart and Nye 1960, Lindsey 1984, Koul et al. 1993, Lamborn and Ollerton 2000, Willmer 2011, pp. 275–321). The size and shape of the florets favour small and short-tongued insects, such as flies, short-tongued bees, small wasps and beetles (Willmer 2011, pp. 275–321). Out of the wide range of visitors, only some species and groups are likely to be efficient pollinators (*ibid*, pp. 279–287).

It has been shown that successful pollination is needed to obtain high seed yield on caraway (Bouwmeester and Smid 1995, Saarinen 2016). Pollination of caraway is assisted by both wind and insects, but their relative importance is unclear. Gravity may also play a part in pollen transfer (Van Roon and Bleijenberg 1964, Bouwmeester and Smid 1995). Bouwmeester and Smid (1995) tested caraway pollination in Netherlands and found that pollinator exclusion with cages reduced the number of seeds per m² by 25%, while seed yield (g/m²) reduced 13% on biannual caraway and 20% on annual caraway. Besides the lack of insect visitation, the reduction in seed set and yield was likely also due to reduced wind pollination, as they found that caging reduced the amount of pollen moved by wind. The authors suggest that the roles of wind and insect pollination may depend on environmental conditions; in their experiment on biannual caraway, low number of insect visits was

compensated by efficient wind pollination, while on annual caraway later that year, there was less pollen transfer by wind but successful pollination was achieved due to a high number of insect visits. As additional hand pollination did not increase seed set in open-pollinated plants, Bouwmeester and Smid (1995) conclude that assimilate availability rather than pollination limits caraway seed yield. This contradicts Hokkanen et al. (2017), whose results suggest that caraway yields in some areas of Finland are limited by pollinator availability.

Saarinen (2016) tested the effects of insect pollination on caraway in southern Finland by comparing yields from open-pollinated plants, plants caged with honeybees and plants caged without insects. Honeybee hives had been placed on the field for the experiment. Seed yield from plants caged with honeybees (966 kg/ha) was slightly higher than from open-pollinated plants (953 kg/ha), while yield without pollinators was only around half of the yield from insect pollinated plants (500 kg/ha). Seed set was the highest in open pollinated plants (82%), second highest in plants caged with honeybees (60%), and lowest without insect pollination (42%). This shows that pollination was most successful when flowers were accessible to both honeybees and wild insects. The high seed yield regardless of lower seed set in plants caged with honeybees may be partly explained by seed filling that results from the plant having more available photosynthate per seed (Sihag 1986, Bouwmeester and Smid 1995). 1000-seed weight was indeed smallest in open-pollinated plants and largest in the plants excluded from pollinators. The result is aligned with Bouwmeester and Smid (1995) who also found that seed weight was increased by poor pollination. Another possible mechanism through which plants may compensate for pollen limitation is producing more flowers (Stanton et al. 1987, Zou et al. 2017).

Saarinen (2016) also observed the amounts of honeybees, bumblebees, solitary bees, butterflies and syrphid flies on the study field and found that syrphid flies were the most abundant visitors initially, but honeybees dominated for most of the flowering period. The total number of pollinators observed was, however, very small during the whole study period which reduces the reliability of the results. Toikkanen (2017) studied pollinating insects on caraway fields in central Finland and found that syrphid flies visited caraway flowers nearly three times as often as bumblebees. Out of insects caught by pan traps, 84.6% were non-syrphid flies, 10.8% bumblebees, 2.2% other wild bees and 2.5% syrphid flies. The results suggest that flies may be significant pollinators of caraway in Finland.

In a study in Italy by Ricciardelli D'Albore (1986), wild insects, and particularly wild bees, had a major role in the pollination of caraway, while honeybees (*Apis mellifera ligustica*) only had a minor

role as they were attracted by other flowering plants near the crop. Of all pollinators visiting caraway 99% were wild insects, with *Andrella minutula* K. representing 61%, *Halictus maculatus* Smith 10%, Syrphidae 12% and other Diptera (Muscidae, Calliphoridae) 16% of pollinators present. In a Canadian study by Langenberger and Davis (2002a), honeybee was a frequent visitor on caraway during the first half of flowering, with numbers then sharply declining as bees were attracted by other food sources (canola and sweet clover) – similarly to Ricciardelli D'Albore (1986). Hymenoptera were the most frequent visitors with honeybee dominating and native bees and solitary wasps also visiting frequently. Diptera were the second most dominant group after Hymenoptera with Syrphidae, Muscidae and Calliphoridae observed most frequently. Studies on another umbellifer *Daucus carota*, which is visually similar to caraway, have recorded a wide range of insect visitors. Bees, wasps and flies are frequently reported as the most important pollinators, but their relative importance varies between locations and years (Bohart and Nye 1960, Koul et al. 1986, Lamborn and Ollerton 2000, Pérez-Bañón et al. 2007, Gaffney et al. 2018).

There is sufficient evidence to conclude that insect pollination can significantly increase caraway seed yield. Efficient pollination leads to better seed set, but the effect on seed yield may be less significant because caraway plants can compensate for poor pollination by growing larger seeds. Honeybees can be important pollinators of caraway depending on location and the presence of other floral resources attractive to the bees. In addition, smaller insects such as solitary bees, syrphid flies and other flies have been frequent visitors on caraway in earlier studies and are likely to be important for caraway yield. No studies were found on how pollinator diversity affects caraway pollination and yield, and apart from Saarinen (2016), the effects of insect pollination on caraway yield have not been previously studied in Finland.

4 RESEARCH OBJECTIVES

The aim of this study is to examine how the abundance and diversity of pollinating insects affect the success of caraway pollination and yield. My research questions are:

- 1) To what degree is caraway pollination dependent on pollinating insects?
- 2) What effect does the number of flower visits by pollinators have on caraway pollination and yield?
- 3) Is a diverse pollinator community beneficial to the pollination and yield of caraway?
- 4) Are some pollinator species or groups more important than others for caraway pollination?

I formulated three hypotheses for testing. Firstly, flower visits of pollinating insects have a positive effect on caraway pollination and yield. However, the effect on pollination success – measured as the proportion of flowers that develop fruit (fruit set) – may be larger than the effect on seed yield (g/plant) due to the plants' ability to compensate for unsuccessful pollination by growing larger seeds. Secondly, I predict that pollinator diversity affects pollination and yield positively. Finally, of all pollinator species and groups, visits of honeybees and smaller insects including solitary bees, syrphid flies and other Diptera have the largest effect on the pollination and yield.

5 MATERIALS AND METHODS

5.1 Field experiment

A field experiment on caraway was conducted in summer 2019 in the Uusimaa region in southern Finland (60°2'N–60°41'N, 24°23'E–25°56'E). The experiment followed the same study design, with small modifications, as an earlier turnip rape experiment conducted in 2017 as part of the same research project Crop pollination in Finland: effects of landscape and farming methods (see Toivonen et al. 2019). 30 caraway fields were selected for the experiment (Figure 1). To reduce the risk that the same pollinator individuals visit more than one study field, and thus to secure independent observations from each field, the study fields were located a minimum of 1 km apart. Although foraging distances of many pollinators can exceed 500 m, thus enabling them to visit two adjacent study fields, the distance was regarded as sufficient since pollinators usually forage on nearby resources when available (Couvillon et al. 2015, Redhead et al. 2016).

Information about farming methods (sowing year, cultivar, soil fertility, pesticide use, location of nearest beehives) was collected from farmers using questionnaires. The sowing years were 2016 on four study fields, 2017 on 18 fields and 2018 on eight fields. Caraway cultivars grown were Record (on 24 fields), Konzcewicki (2), Niededeutscher (2), Prochan (1) and Speeder (1). Soil fertility was rated as good (15 fields), satisfactory (14) and poor (1). According to information from the Finnish Food Authority, seven out of the 30 fields were organic. All apart from 9 fields (7 organic and 2 conventional) were sprayed against *Depressaria daucella* moth just before the onset of flowering. Herbicides were used on 13 fields. Five study fields had beehives within 500 m radius.

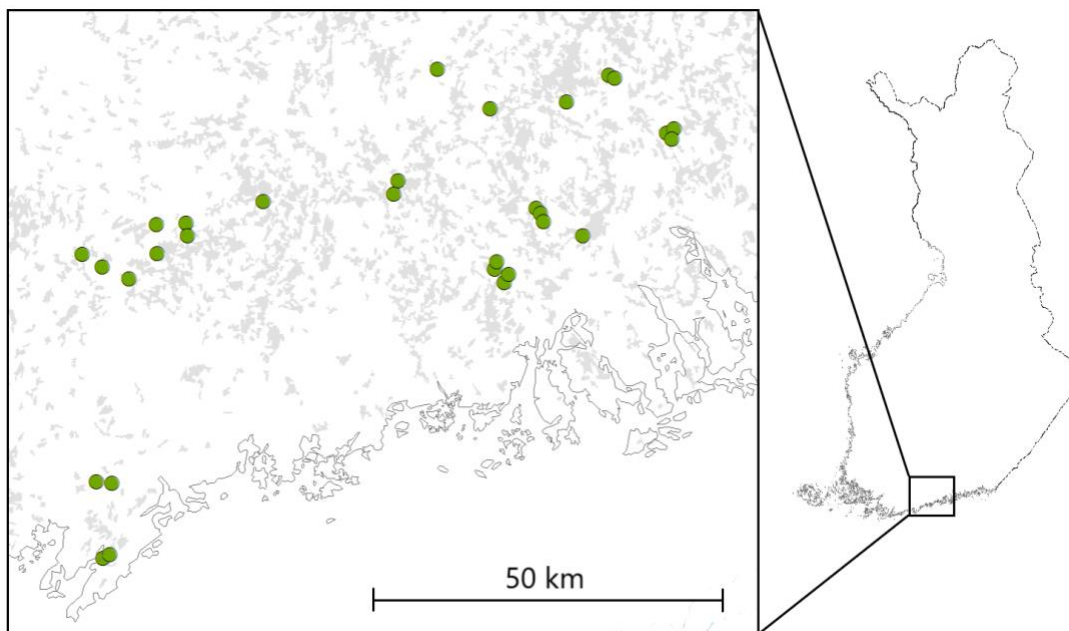


Figure 1. The locations of 30 study fields in southern Finland are shown in green. Grey colour on the map indicates arable land as derived from CORINE Land Cover 2018 database.

5.1.1 Flower visit monitoring

Pollinator visits on caraway flowers were monitored from 6th to 24th June 2019. Four 2 x 2 m square monitoring plots were established on the fields near an open field edge, i.e., field edge not bordered by forest. Two pairs of monitoring plots were placed 50 m apart along the field edge and at distances of 5 m and 20 m off the field edge (Figure 2). One corner of each plot was marked with a bamboo stick. Flower visits were monitored for 5 minutes at the time on each plot four times during flowering,

which totalled 80 minutes of monitoring per field. All insects visiting caraway flowers were recorded. A visit where an insect touched an umbellet of caraway was counted as one flower visit.

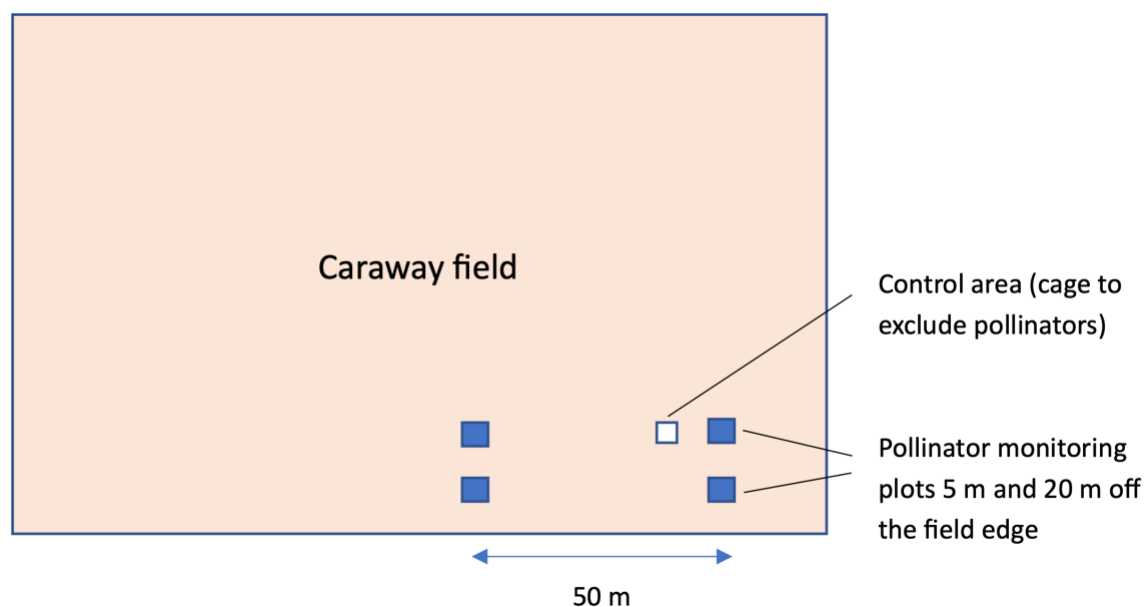


Figure 2. Locations of the pollinator monitoring plots and the control area with a cage to exclude pollinators during flowering.

Flower-visiting insects were identified to species or group: honeybees (*Apis mellifera*) and butterflies (Lepidoptera: Papilionoidea) to species; bumblebees to species, except for the *Bombus lucorum* group (*B. lucorum*, *B. terrestris*, *B. cryptarum* and *B. magnus*) which cannot be reliably identified to species on field; solitary bees as a group; syrphid flies to subfamilies (Syrphinae and Eristalinae); and all other flower-visiting insects at varied taxonomic levels.

Pollinator monitoring was done during the day at 9:00–17:00 and only in weather conditions when insects are active: below +15 °C – no monitoring; +15–17 °C – monitoring only if sunny and no wind; +17–20 °C – monitoring also in partly cloudy and slightly windy conditions; over 20 °C – monitoring also in cloudy and windy conditions. The weather conditions during monitoring were recorded. Local air temperature was checked from Foreca website (www.foreca.fi) via mobile phone. Beaufort wind force scale was used to estimate wind conditions, and pollinator monitoring was only done on levels 0–5 of the scale. The proportion of the monitoring done while the sun was shining (i.e., sun was not behind clouds) was estimated on a scale of 0–100%.

The number of open flowers (umbels and umbellets) per plot was estimated at each monitoring round. During the last monitoring round, the cover (percentage of the total area of the monitoring plot) of all caraway plants including non-flowering first-year plants, and the cover of flowering caraway plants were also estimated. In addition, the percentage of flowers damaged by the larvae of *Depressaria daucella* moth or by deer was estimated.

5.1.2 Control area

On each field, a control area was established 20 m off the field edge and 2 m off one of the monitoring plots (Figure 2). A 1 x 1 m wooden cage covered with white polyester netting (Quito, Eurokangas) was placed on the area to exclude pollinators during crop flowering (Figure 3). The control area allowed for the comparison of yields from open-pollinated plants and from plants that were not accessible to pollinators.

The mesh size of the netting was 1 mm, which was small enough to exclude the most important pollinators but allowed wind-pollination. Some flies and beetles appeared inside the cages during flowering, possibly because eggs had been laid on the site before the cage was put in place. However, their effect on the pollination of caraway was estimated to be very small. The netting was removed from the cages after flowering.



Figure 3. Pollinator exclusion cage.

5.1.3 Yield samples

Yield samples were collected in late July – early August once the crop had ripened. Two sample plants were collected next to the marking sticks of each pollinator monitoring plot, which made a total of eight open-pollinated plants per field. In addition, eight control plants were collected from inside the cages. Plants were selected randomly but avoiding plants with *D. daucella* damage. The central umbel of each plant was collected separately for more thorough examination. If the central umbel had severe *D. daucella* damage, the next highest umbel was collected.

On 13 out of the 30 fields, we were not able to collect the samples as planned. On seven fields, *D. daucella* larvae had damaged flowers inside the cages so that less than eight control plants (6 fields) or no control plants (1 field) could be collected. *D. daucella* damage was more severe in the control plants than in the open-pollinated plants because, in most of the study fields, the pollinator exclusion cages had been placed on the fields before insecticide application, preventing efficient application on the plants inside the cages. Four fields had been mowed before yield sample collection due to severe *D. daucella* damage or excessive weeds, and thus open-pollinated plants had to be collected from cut plants (1 field) or from around the cage where plants were intact (3 fields). On five fields samples had to be collected before the crop had ripened either because the farmer planned to mow the field or because of late flowering time. In addition, there was one field where a full number of samples was collected but the reliability of data may be reduced due to significant *D. daucella* damage in the sample plants. Thus, the quality of yield samples was compromised on a total of 14 fields (see Appendix 1 for details).

The following yield components were measured: number of umbellets per central umbel; total number of florets, including those that developed fruit, per central umbel; number of fruits per central umbel; number of umbels per plant. Umbels and umbellets fully destroyed by *D. daucella* and fruits less than 3 mm long were not counted. The number of fruits per central umbel was doubled to calculate the number of seeds per central umbel, and fruit set (%) per central umbel was calculated by dividing the number of fruits with the number of florets. All umbels were dried in 35 °C for 24 hours, after which the seeds were harvested by hand and seed yield per central umbel (g) and seed yield per plant (g) were measured. To estimate 100-seed weight per central umbel, the total seed weight of each central umbel was divided by the number of seeds per central umbel and multiplied by 100.

5.2 Statistical analyses

The effects of pollinator exclusion, flower visitation and the diversity of pollinating insects on caraway pollination and yield were tested using statistical analyses with the following yield components as response variables: fruit set (i.e., the number of fruits per flower) per central umbel (%), 100-seed weight per central umbel (g), seed yield per plant (g), the number of umbellets per central umbel and the number of umbels per plant. All response variables were average values per field and had been calculated separately for open-pollinated plants and for the caged control plants. Seed yield per central umbel was not included in the analyses because it correlated strongly with both 100-seed weight per central umbel and seed yield per plant (Pearson's $R = 0.77$ for both).

The effects of pollinator exclusion were tested by running linear mixed-effects models (LME) with pollinator exclusion as a fixed factor and the study field as a random factor. Models were fitted using `lmer()` function from the `lme4` package (Bates et al. 2015) in R (R Core Team 2019). Plotting residuals against fitted values revealed slight heteroscedasticity. One study field was excluded from the analyses because no yield samples could be collected from inside the pollinator exclusion cage due to *D. daucella* damage.

The effects of pollinator abundance were analysed using the total number of flower visits per field (i.e., the sum of all flower visits on the four monitoring plots) as a predictor. The number of pollinator individuals had also been recorded, but since the number of individuals and the number of flower visits correlated strongly (Pearson's $R = 0.80$), only results for the effects of flower visitation are shown. Models to test the effects of flower visitation were first fitted using linear models (LM), but due to heteroscedasticity, generalized least square models (GLS) were used instead.

Initially, the plan was to relate the number of flower visits to the number of umbellets or the cover of flowering plants (%) per monitoring plot and use the calculated figure as a predictor. However, correlation tests showed that visits per umbellet and particularly visits per plant cover correlated negatively with seed yield and fruit set (Pearson's $R = -0.15 - -0.36$, and $-0.52 - -0.38$, respectively), while the number of visits correlated positively with the yield components (Pearson's $R = 0.42-0.51$). A possible explanation for this is that when several umbel orders bloom simultaneously, caraway flowers are situated in multiple layers, which makes it difficult to observe all flower visits especially when plant density is high. Thus, a larger proportion of flower visits may have gone unnoticed when the number of umbellets or the cover of flowering plants on the monitoring plot was high. Another

explanation could be that the abundance of flowers or flowering plants per plot do not correlate strongly with yield, because the proportion of male flowers is likely to increase with increased plant density (Bouwmeester and Smid 1995). However, the number of umbellets and the cover of flowering plants per plot showed moderate correlation with seed yield and fruit set (Pearson's $R = 0.42$ – 0.63 and 0.53 – 0.70 , respectively), which suggests that the first explanation may be more valid.

The effects of pollinator diversity were tested using linear models (LM) with Shannon index (H'), species richness (S) and species evenness (J') as predictors. Shannon index was calculated for each study field using the equation:

$$H' = -\sum p_i \ln p_i, \quad (1)$$

where p_i is the number of individuals of pollinator species/group i divided by the total number of individuals on the site (Shannon 1948). Species evenness was derived from H' by calculating:

$$J' = H' / \ln(S), \quad (2)$$

where $\ln(S)$ is the maximum value of diversity (Maurer and McGill 2011). The number of individuals per species was used in the calculations for those pollinators that were identified to species, and otherwise the number of individuals per pollinator group was used (see Appendix 2 for species and groups used in the calculations).

To compare the importance of different pollinator species and groups, GLS-models were conducted using the number of flower visits per field by honeybees, solitary bees, syrphid flies, non-syrphid Diptera, Lepidoptera and beetles as predictors. Due to low number of observations, no models for bumblebees and only two models for Lepidoptera could be formed. The effects on two response variables, the number of umbellets per central umbel and the number of umbels per plant, were not tested because in analyses conducted earlier, pollinator abundance (the total number of flower visits) had no statistically significant effect on those variables. Models for honeybees were also conducted without two study fields where the number of honeybee flower visits was exceptionally high, and models for syrphid flies were conducted without one study field with exceptionally high number of syrphid fly flower visits. The results of these additional analyses are shown in Appendix 3 and reported in the text if statistical significance differed from the analyses conducted with all fields.

As discussed in chapter 5.1.3, yield sample quality was compromised to varying degrees on 14 out of the 30 study fields. To test if these samples had a disproportionate effect on the results of the statistical analyses, some models were formulated with and without the fields with compromised sample quality. For the statistical analyses, the fields were divided into two categories: fields with slightly compromised sample quality and fields with severely compromised sample quality (Appendix 1). The analyses to test the effects of pollinator exclusion had more problematic fields than the other analyses because the data included samples from both caged control plants and open-pollinated plants, while in the other analyses, samples from inside the cages were not part of the data. The models to test the effects of pollinator exclusion were conducted excluding seven fields where sample quality was severely compromised, and then excluding 13 fields where sample quality was slightly or severely compromised (see Appendix 1 for details). To test the reliability of the dataset used in the other analyses, models testing the effects of pollinator abundance (the total number of flower visits) were conducted excluding four fields where sample quality was severely compromised, and then excluding ten fields where sample quality was slightly or severely compromised (see Appendix 1 for details). Exclusion of the fields did not markedly change model estimates. Some effects lost their statistical significance, but this can be expected when sample size is reduced. Thus, the yield sample data from all 30 fields can be considered sufficiently reliable. The results of the analyses conducted without the fields with compromised yield sample quality are shown in Appendix 3 and reported in the text if statistical significance differed from the analyses conducted with all fields.

To determine if any of the explanatory variables correlated significantly with each other, Pearson's correlation tests were performed using the function `cor.test()` of the R package `stats`. All LMs and GLS-models were run using functions `lm()` of the R package `stats` and `gls()` of the package `nlme` (Pinheiro et al. 2019). The residuals of LMs and GLS-models were tested for spatial autocorrelation with Moran's I tests, which were performed using the `moran.test()` function in the R package `spdep` (Bivand and Wong 2018). Spatial autocorrelation was only found in a small number of models which tested the effects of species richness, species evenness and flower visitation by certain pollinator groups. Therefore, no corrections were made to the models. All statistical analyses were run using R version 3.6.1. P-values less than 0.05 were considered statistically significant.

6 RESULTS

6.1 Pollinator taxa and flower visits

The pollinating insects visiting caraway flowers represented 23 species and groups (Table 1). The average number of flower visits per field was 109.4 (range 15–262). The most frequent visitors were syrphid flies, followed by honeybees and non-syrphid Diptera (Table 1). Due to the high number of fly (Diptera) individuals, the total number of fly flower visits over all fields was higher than that of all bees, even if bees made over twice as many flower visits per individual than flies (an average of 5.8 per bee and 2.4 per fly). Syrphid flies and other Diptera were present on all fields, beetles on 93%, honeybees on 83%, solitary bees on 63% and bumblebees on 20% of the fields.

Table 1. The total numbers of pollinator individuals and flower visits per pollinator species or group recorded on the four pollinator monitoring plots on 30 caraway fields.

	Individuals	% of all	Flower visits	% of all
All pollinators	1139	100.0	3283	100.0
All bees (Hymenoptera: Apoidea: Anthophila)	181	15.9	1058	32.2
Honeybees (<i>Apis mellifera</i>)	122	10.7	806	24.6
Bumblebees (<i>Bombus</i>)	10	0.9	66	2.0
<i>Bombus lucorum</i> group	8	0.7	62	1.9
<i>Bombus lapidarius</i>	1	0.1	1	0.0
<i>Bombus veteranus</i>	1	0.1	3	0.1
Solitary bees	49	4.3	186	5.7
Syrphid flies (Diptera: Syrphidae)	462	40.6	1179	35.9
Syrphinae	404	35.5	1058	32.2
Eristalinae	58	5.1	121	3.7
Non-syrphid flies (Diptera)	312	27.4	671	20.4
Non-syrphid Brachycera	287	25.2	619	18.9
Nematoceran flies	25	2.2	52	1.6
Butterflies and moths (Lepidoptera)	11	1.0	20	0.6
<i>Boloria selene</i>	1	0.1	1	0.0
<i>Nymphalis urticae</i>	3	0.3	3	0.1
<i>Vanessa cardui</i>	6	0.5	13	0.4
Moths	1	0.1	3	0.1
Beetles (Coleoptera)	128	11.2	253	7.7
Soldier beetles (Cantharidae)	72	6.3	157	4.8
Ladybird beetles (Coccinellidae)	38	3.3	59	1.8
Rose chafer (<i>Cetonia aurata</i>)	1	0.1	3	0.1
Other Coleoptera	17	1.5	34	1.0
Non-bee Hymenoptera	12	1.1	34	1.0
Ants (Formicidae)	5	0.4	14	0.4
Sphecidae	1	0.1	9	0.3
Other non-bee Hymenoptera	13	1.1	11	0.3
True bugs (Hemiptera: Heteroptera)	24	2.1	39	1.2
Green lacewings (Neuroptera: Chrysopidae)	8	0.7	20	0.6
Spiders (Araneae)	1	0.1	9	0.3

6.2 Effects of pollinator exclusion on the yield components

Pollinator exclusion had a statistically significant effect on fruit set per central umbel and seed yield per plant (Table 2). Fruit set was 13.2% smaller and yield per plant was 39.6% smaller in caged control plants compared to open-pollinated plants (Figure 4). Pollinator exclusion also reduced the number of umbellets per central umbel by 5.2% and the number of umbels per plant by 14.6%, but the differences were not statistically significant ($p = 0.132$ and 0.067 , respectively). 100-seed weight per central umbel was not affected, as pollinator exclusion increased 100-seed weight only by 0.6% and the effect was far from statistically significant ($p = 0.959$; Table 2). Running the models without the fields where the quality of yield samples was compromised did not alter statistical significance (Appendix 3, Table 1).

Table 2. The mean and standard deviation (SD) of the yield components in open-pollinated plants and caged control plants, and the effects of pollinator exclusion on the yield components.

Yield component	Open pollination		Pollinator exclusion		LME Estimate ^a	SE	<i>p</i>
	Mean	SD	Mean	SD			
Fruit set per central umbel (%)	67.39	13.68	58.47	16.25	-8.917	2.21	<0.001
100-seed weight per central umbel (g)	0.204	0.09	0.205	0.12	0.001	0.02	ns
Seed yield per plant (g)	2.11	1.55	1.27	1.14	-0.833	0.22	<0.001
Umbellets per central umbel	8.24	0.89	7.81	1.75	-0.427	0.28	ns
Umbels per plant	17.18	7.00	14.67	7.48	-2.505	1.32	ns

^aPollinator exclusion compared to open pollination

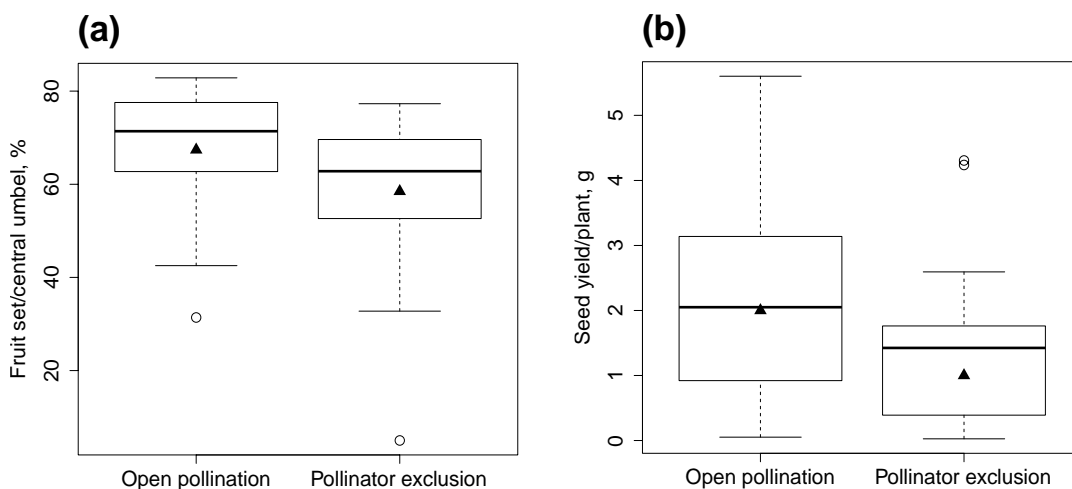


Figure 4. Yield components, (a) fruit set per central umbel (%) and (b) seed yield per plant (g) in open pollinated plants and in gaged control plants. Black triangle indicates mean.

6.3 Effects of pollinator abundance on the yield components

The total number of flower visits had a statistically significant, positive effect on fruit set per central umbel, 100-seed weight per central umbel and seed yield per plant, while the effects on the number of umbellets per central umbel and the number of umbels per plant were weakly positive but not statistically significant (Table 3, Figure 5). When the fields with compromised yield sample quality were excluded from the models, all effects lost their statistical significance (Appendix 3, Table 2). However, when four fields with severely compromised sample quality were excluded, the effects on fruit set and seed yield were still close to significant ($p = 0.057$ and 0.055 , respectively).

Table 3. The effects of pollinator abundance (the total number of flower visits) on the yield components.

Yield component	GLS Estimate	SE	<i>p</i>
Fruit set per central umbel (%)	0.0945	0.0281	<0.01
100-seed weight per central umbel (g)	0.0005	0.0002	<0.05
Seed yield per plant (g)	0.0133	0.0043	<0.01
Umbellets per central umbel	0.0033	0.0028	ns
Umbels per plant	0.0324	0.0179	ns

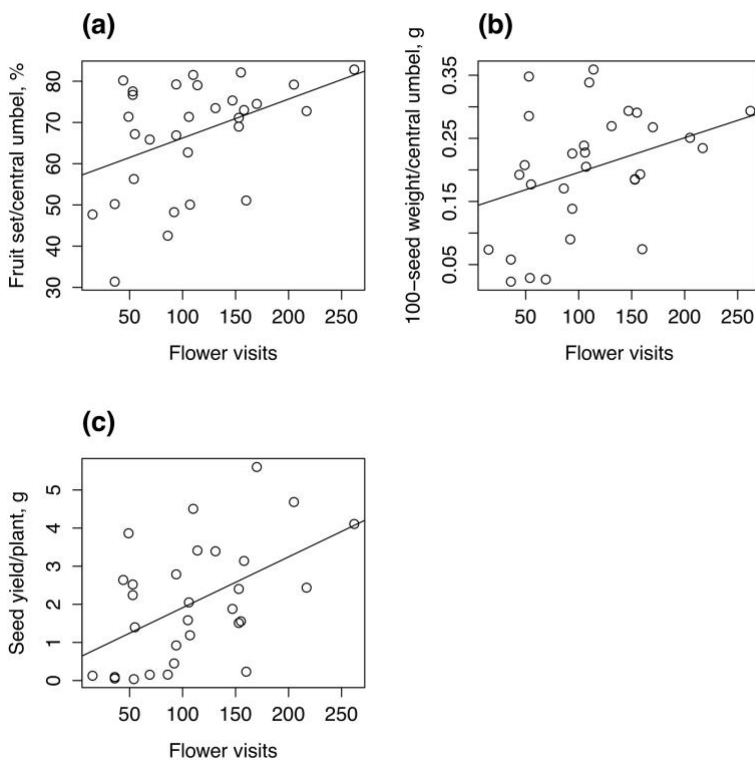


Figure 5. Yield components, (a) fruit set per central umbel (%), (b) 100-seed weight per central umbel (g) and (c) seed yield per plant (g) in relation to the total number of flower visits per field.

6.4 Effects of pollinator diversity on the yield components

Shannon index had a negative effect on all yield components, but none of the effects were statistically significant (Table 4). The effects of species richness were positive but again non-significant (Table 4). Species evenness affected the yield components negatively, and the effects on seed yield per plant, umbellets per central umbel and umbels per plant were statistically significant (Table 4, Figure 6). In addition, the effects on fruit set and 100-seed weight were close to statistical significance ($p = 0.086$ and 0.063 , respectively). Model residuals were positively spatially autocorrelated in a model that tested the effect of species richness on seed yield per plant and in a model that tested the effect of species evenness on the number of umbellets per central umbel.

Table 4. The effects of Shannon index, species richness and species evenness on the yield components.

Explanatory variable	Yield component	LM Estimate	SE	<i>p</i>
Shannon index	Fruit set per central umbel (%)	-4.671	9.133	ns
	100-seed weight per central umbel (g)	-0.077	0.064	ns
	Seed yield per plant (g)	-1.268	1.031	ns
	Umbellets per central umbel	-0.997	0.724	ns
	Umbels per plant	-4.023	4.850	ns
Species richness	Fruit set per central umbel (%)	1.325	1.425	ns
	100-seed weight per central umbel (g)	0.001	0.010	ns
	Seed yield per plant (g)	0.100	0.166	ns
	Umbellets per central umbel	0.020	0.118	ns
	Umbels per plant	0.611	0.766	ns
Species evenness	Fruit set per central umbel (%)	-41.360	23.220	ns
	100-seed weight per central umbel (g)	-0.319	0.165	ns
	Seed yield per plant (g)	-6.452	2.549	<0.05
	Umbellets per central umbel	-3.980	1.849	<0.05
	Umbels per plant	-27.138	12.063	<0.05

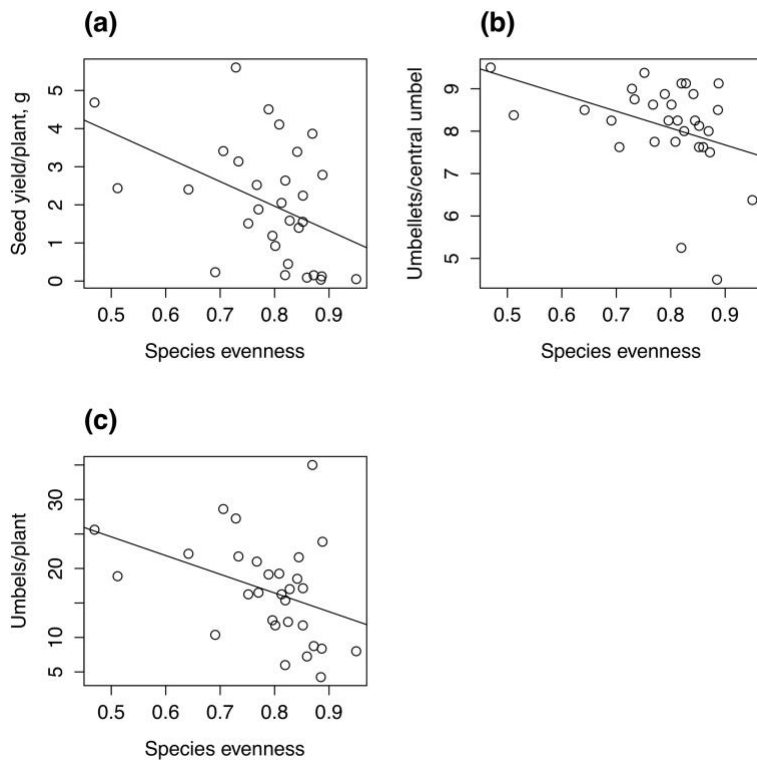


Figure 6. Yield components, (a) seed yield per plant (g), (b) the number of umbellets per central umbel and (c) the number of umbels per plant in relation to species evenness.

6.5 Effects of flower visitation by different pollinator groups

Flower visits by honeybees and syrphid flies both had a statistically significant, positive effect on seed yield per plant, while the effects on fruit set and 100-seed weight were also positive but not statistically significant (Table 5, Figure 7). A single visit by a honeybee had a slightly larger effect ($\beta = 0.034$) on seed yield than a single visit by a syrphid fly ($\beta = 0.024$). When two fields with exceptionally high number of honeybee visits were excluded from the analyses, the effect on 100-seed weight became statistically significant ($\beta = 0.0027$, $p = 0.015$, Appendix 3, Table 3). Exclusion of the field with exceptionally high number of syrphid fly visits did not markedly change the results (Appendix 3, Table 4). The effects of flower visits by solitary bees, non-syrphid Diptera and Lepidoptera were also positive but not statistically significant (Table 5).

Flower visits by beetles affected the yield components negatively. The effect on 100-seed weight was statistically significant (Table 5, Figure 7), while the effects on the other yield components were non-significant – although the effect on seed yield per plant was near significant ($p = 0.058$). Positive

spatial autocorrelation of model residuals was found in those solitary bee, syrphid fly and non-syrphid Diptera models where seed yield per plant was the response variable.

Table 5. The effects of the number of flowers visits by different pollinator species and groups on the yield components. Due to low number of observations, no models for bumblebees and only two models for Lepidoptera could be formed.

	Yield component	GLS Estimate	SE	<i>p</i>
Honeybees	Fruit set per central umbel (%)	0.0601	0.0373	ns
	100-seed weight per central umbel (g)	0.0006	0.0003	ns
	Seed yield per plant (g)	0.0339	0.0136	<0.05
Solitary bees	Fruit set per central umbel (%)	0.3468	0.2170	ns
	100-seed weight per central umbel (g)	0.0014	0.0021	ns
	Seed yield per plant (g)	0.0292	0.0383	ns
Syrphid flies	Fruit set per central umbel (%)	0.1114	0.0600	ns
	100-seed weight per central umbel (g)	0.0006	0.0003	ns
	Seed yield per plant (g)	0.0236	0.0088	<0.05
Non-syrphid Diptera	Fruit set per central umbel (%)	0.1387	0.1188	ns
	100-seed weight per central umbel (g)	0.0008	0.0009	ns
	Seed yield per plant (g)	0.0031	0.0124	ns
Lepidoptera	100-seed weight per central umbel (g)	0.0045	0.0137	ns
	Seed yield per plant (g)	0.1471	0.2844	ns
Beetles	Fruit set per central umbel (%)	-0.4812	0.3764	ns
	100-seed weight per central umbel (g)	-0.0045	0.0022	<0.05
	Seed yield per plant (g)	-0.0627	0.0316	ns

7 DISCUSSION

7.1 Relative abundances of the flower-visiting pollinator groups

The results confirm that caraway is mainly visited by honeybees and smaller wild pollinators, including flies, solitary bees and beetles, as has been shown in previous literature (Ricciardelli D'Albore 1986, Langenberger and Davis 2002a, Toikkanen 2017). Caraway appears to be particularly attractive to Syrphidae and other flies. The high abundance of Syrphidae is not surprising as they often forage on Apiaceae and on white flowers (Haarto and Kerpola 2007, pp. 16–17, Willmer 2011, pp. 311–313). The bumblebee numbers and their flower visits were very low, and the species recorded (*B. lucorum* group, *B. lapidarius* and *B. veteranus*) had either short or medium-length tongues (Pekkarinen and Teräs 1977, Pekkarinen 1979). This suggests that the small and shallow caraway florets are not very attractive to bumblebees, and especially the long-tongued species of bumblebees. Apart from the structure and colour of the flowers, caraway nectar and pollen may be more attractive to flies than to some other pollinators, such as long-tongued bees (Langenberger and Davis 2002b, Willmer 2011, pp. 161, 195–220), which could be explored in further studies.

The dominance of Syrphidae and other Diptera is aligned with Toikkanen (2017), who studied pollinator taxa visiting caraway fields in central Finland. However, bumblebees were more frequently observed by Toikkanen (2017); the number of bumblebee visits was slightly more than a third of syrphid fly visits, while in this study, syrphid flies made nearly 18 times more flower visits than bumblebees. The scarcity of bumblebees in this experiment could be potentially explained by low availability of bumblebees in the study area. However, in a pollination experiment conducted in the same region, Uusimaa, two years earlier on turnip rape (Toivonen et al. 2019), bumblebees were the most frequent wild pollinator visitors, which suggests that bumblebees are available in the area and visit crops if they are attractive enough to them. It is possible that bumblebee abundance was relatively low in 2019 when our experiment was conducted but we have no data to confirm this.

The relative abundances of the different pollinator groups also differed from Ricciardelli D'Albore (1986), where 71% of visits to caraway flowers were made by two solitary bee species, 12% by Syrphidae and 16% by other Diptera, and Langenberger and Davis (2002a), where honeybees and other Hymenoptera dominated. The significantly higher proportion of Diptera observed by us probably reflects the more northern location of our experiment, as the proportion of dipteran species out of all pollinator species increases with latitude (Elberling and Olesen 1999). Solitary bees were

absent on over third of the fields, but on some fields they were among the most abundant pollinator groups, suggesting that at least some solitary bee species are attracted by caraway, as in Ricciardelli D'Albore (1986), but on average their availability in the study region was not very high. Overall, the role of non-bee pollinators was significant. Rader et al. (2016), who synthesised data from 39 field studies globally, found that 25–50% of flower visits, or 39% on average, were performed by non-bees. The results obtained here go far above these figures as only 32% of the flower visits were made by bees and syrphid flies alone made 36% of the visits. Our results are more in line with an analysis of farmland habitats located mainly in the UK (Orford et al. 2015) where Diptera were found to represent 67% of all flower-visitors.

Honeybees were also attracted by caraway, but their abundance varied greatly between fields. Honeybee abundance is dependent on the amount of hives in the vicinity of the fields, but their visit frequency can also vary depending on the presence of other attractive floral resources in the area (Ricciardelli D'Albore 1986, Langenberger and Davis 2002a). It is possible that with high honeybee density, their flower visit frequency would equal or exceed that of syrphid flies. As wild insect populations fluctuate greatly from year to year (Herrera 1988, Price et al. 2005, Willmer 2011, pp. 438–440, 463–464), the relative abundances of pollinators are likely to vary between years and locations. Nevertheless, the results obtained here and by Toikkanen (2017) show that syrphid flies and other Diptera are more frequent visitors on caraway fields in Finland than any wild bee taxa.

7.2 Pollinator dependency of caraway

The results are in line with previous research (Bouwmeester and Smid 1995, Saarinen 2016) in showing that insect pollination is important for high caraway yields. The 13.2% reduction in fruit set due to pollinator exclusion shows that caged plants were mainly pollinated by wind, but also that more efficient pollination can be achieved in the presence of pollinators. In open pollination, both fruit set and seed yield increased with increasing flower visitation, which confirms the hypothesis that visits of pollinating insects can significantly enhance caraway pollination and yield.

Like our results, earlier studies show a clear reduction in fruit set and yield in pollinator exclusion, but magnitudes vary between studies. The effect of caging on fruit set observed here (–13.2%) was smaller than the 25% reduction in Bouwmeester and Smid (1995) and the nearly 50% reduction in Saarinen (2016). The observed yield reduction (39.6%) falls between Saarinen (2016), where yield was 47.5% smaller in caged plants versus open-pollinated plants, and Bouwmeester and Smid (1995),

where yield reduction was 13% on biannual and 20% on annual caraway. Several factors can explain these varying results. The smaller effect on fruit set observed in this study could be explained by smaller density of pollinators visiting the open-pollinated plants. This seems possible, as the recorded number of flower visits was very low in some of the study fields, most likely limiting fruit set and yield. In Saarinen (2016), pollinator abundance may have been high as honeybee hives had been placed on the study field, and in Bouwmeester and Smid (1995), pollinator abundance was higher in the annual than the biannual crop. Another possible explanation is that wind pollination inside the cages was more successful in our experiment, for example due to larger mesh size of the netting or more favourable wind conditions. Also, Bouwmeester and Smid (1995) found that pollinator exclusion reduced fruit set particularly in secondary umbels which were not included in our results, while Bouwmeester and Smid (1995) calculated fruit set based on 1st, 2nd and 3rd order umbels. Bouwmeester and Smid (1995) also used shade treatments (i.e., cages covered with a cloth on the top but not on the sides) to assess how caging affected pollen transfer by wind and assimilate availability, and the results from closed cages were compared to those of shade treatments. A negative effect on pollen movement was detected, and decreased light intensity due to shading is likely to reduce photosynthetic rates, which limits assimilate availability and yield. Thus, the reduction in fruit set and yield observed by Bouwmeester and Smid (1995) may have been larger and closer to the figures in Saarinen (2016), had the results been compared to open-pollinated plants without shading.

As shown by Bouwmeester and Smid (1995), the negative effects on the yield components in pollinator exclusion were not only due to lack of insect pollination but also due to reduced assimilate availability and possibly reduced pollen transfer by wind. Reduced assimilate availability could explain the lower numbers of umbels and umbellets in the caged plants. In addition, it may have increased the proportion of aborted flowers and seeds, which would show as reduced fruit set (Bouwmeester and Smid 1995). Caging may have also altered moisture conditions. Furthermore, *D. daucella* damage was more severe inside the cages than in open-pollinated plants and was likely affecting the yields negatively. While it is not possible to quantify what proportion of the reduction in fruit set and yield can be attributed to lack of insect visitation, it was clearly less than the reductions we measured. On the other hand, with higher pollinator abundance, fruit set and yield in open pollination may have been higher, which would have resulted in a larger difference between the results of open pollination and pollinator exclusion.

Yield was more negatively affected (−39.6%) by pollinator exclusion than fruit set (−13.2%), which is contrary to my hypothesis that pollinator visitation would affect yield less than pollination success

because caraway can grow larger seeds to compensate for unsuccessful pollination. It is unclear whether yield compensation through seed filling occurred. Results of the caging experiment do not support this prediction as 100-seed weight per central umbel was not significantly increased by pollinator exclusion. However, in Bouwmeester and Smid (1995), pollinator exclusion only increased 1000-seed weight significantly in lower umbel orders and not in the central umbels of biannual caraway. As we only measured 100-seed weight of the central umbels, it is possible that some seed filling occurred in the lower order umbels. Saarinen (2016) also measured higher 1000-seed weight in caged plants compared to insect pollinated plants, but statistical significance was not tested. On the other hand, 100-seed weight in open pollination increased with increasing flower visitation, which is inconsistent with the finding that caging had no effect on 100-seed weight and indicates that seed filling in poorly pollinated plants did not occur. However, the correlation between 100-seed weight and the number of flower visits could potentially be explained by some variable that affects both seed weight and flower visitation but was not tested in this study. For example, highly fertile fields may grow healthy plants that both attract many pollinators and are able to grow large seeds. A similar factor may also partly explain the increase in seed yield with increased flower visitation. If we assume that 100-seed weight in all umbel orders was either increased or unaffected by pollen limitation, the yield reduction in pollinator exclusion must be explained by a decrease in the number of seeds, i.e., lower fruit set and lower number of flowers.

The plants were not compensating for pollen limitation by growing more flowers, since the numbers of umbels and umbellets were reduced by caging and slightly increased with increasing flower visitation. Although the effects were not statistically significant, pollinator visitation may have a slight positive effect on the number of flowers in caraway plants. On the other hand, the lower number of flowers in caged plants may have been due to reduced assimilate availability rather than insufficient pollination, and in open pollination, the correlation between the numbers of flowers and flower visits could be because a denser mass of flowers attracted more pollinators, instead of flower visitation having a positive effect on the number of flowers.

From the results of this study as well as previous literature, it can be concluded that pollinator dependency of caraway can vary according to the environment. Weather conditions and pollinator abundance vary in time and space (Herrera 1988, Price et al. 2005, Willmer 2011, pp. 438–440, 463–464), and weather affects pollinator activity (Kevan and Baker 1983) and possibly wind pollination (Bouwmeester and Smid 1995). When pollinator abundance is high, pollinators may take care of a larger proportion of the pollination, and vice versa, wind pollination may have a bigger role when

pollinators are scarce. Nevertheless, insect pollination is needed to secure high yields. It is also clear that yield compensation cannot be trusted to maintain good yield levels when pollination is insufficient.

Since fruit set and seed yield of open-pollinated plants increased with increasing flower visitation, the results do not support the conclusion of Bouwmeester and Smid (1995) that caraway yields are not limited by pollination. On the contrary, the results are aligned with Hokkanen et al. (2017) in suggesting that pollinator availability is a limiting factor for caraway yields at least in some parts of Finland. Increased flower visitation would have most likely increased yields in the fields where pollinator abundance was low, and it is possible that even the fields with the highest numbers of pollinator visits had not reached pollen saturation but would have benefited from higher density of pollinators.

7.3 Effects of pollinator diversity on caraway yield

Species richness and evenness of the pollinator community had contrasting effects on the yield components. The negative effects of evenness were notably larger than the positive effects of richness, and therefore the Shannon index, which is a combination of richness and evenness, also had negative, albeit not statistically significant, effects on the yield components. Evenness of the pollinator community had a significant negative effect on three of the yield components, and with a larger sample size, the effects on fruit set and 100-seed weight may have also been statistically significant. This means that when a community consisted of various insect groups with no single one being dominant, pollination was lower than when a community was dominated by one or few groups. The results contradict the hypothesis that pollinator diversity affects caraway pollination and yield positively. These results are not in line with recent global syntheses (Garibaldi et al. 2013, 2015) that found a positive relationship between fruit set and pollinator diversity. Garibaldi et al. (2015) who analysed data from 33 crop systems worldwide (but not including caraway) found that species richness affected fruit set more positively in fields with high evenness. In an earlier synthesis by Garibaldi et al. (2013), based on 41 crop systems that were partially the same as in Garibaldi et al. (2015), species evenness had no effect on fruit set. The results obtained here are, however, consistent with a turnip rape experiment by Toivonen et al. (2019), conducted in the same region in southern Finland, where species richness had no effect on yield components or total yield.

The number of flower visits correlated positively with species richness, which is in line with earlier studies where more diverse pollinator communities had higher aggregate abundances and visit

frequencies (Steffan-Dewenter and Tschardtke 1999, Larsen et al. 2005, Chacoff and Aizen 2006, Garibaldi et al. 2013). It is therefore possible that the weakly positive effects of species richness were not due to the number of species per se but rather due to higher pollinator abundance associated with high species richness, as was observed by Garibaldi et al. (2013) (contrary to Garibaldi et al. (2015) who found that richness increased fruit set independently of visitation rate). The positive correlation between flower visits and species richness suggests that a reduction in species richness can negatively affect the overall level of pollination services (Kremen and Chaplin-Kramer 2007). Species richness can also be beneficial for crop production by increasing the stability of yields over time (Yachi and Loreau 1999, Loreau et al. 2001, Blüthgen and Klein 2011). However, testing this assumption would require an experiment that spans over several years.

A likely explanation for the negative effects of species evenness is that the fields with higher evenness had a smaller abundance (i.e., less individuals) of efficient pollinators, such as honeybees, compared to fields where a few species and groups dominated. This explanation is supported by the correlation test showing that evenness correlated negatively with the total number of flower visits and with flower visits of honeybees and syrphid flies, which were the most frequently visiting groups and had the most effect on caraway yield. The total pollination effect of a species is a combination of their visit frequency and per-visit effectiveness, but it has been shown that visit frequency is generally a good predictor of the total pollination effect (Vázquez et al. 2005). An additional explanation may be that species evenness was higher on fields where some other factor apart from pollination was limiting plant growth and yield. For instance, an organic field with large amounts of weeds and no pesticide applications may support a pollinator community that has high species evenness but is also likely to have lower yielding crop plants than an intensively managed field. An analysis of the effects of farming methods on species evenness and the yield components could be used to test this hypothesis.

Spatial autocorrelation refers to a situation where values at nearby locations correlate with each other (Plant 2012, p. 59). Spatial autocorrelation is common in ecological and agricultural data and it is typically positive autocorrelation, meaning that nearby locations tend to have more similar values than locations that are further apart (*ibid*, p. 59). Some positive spatial autocorrelation of model residuals was found in the analyses testing the effects of pollinator diversity. However, this only occurred in two models with different explanatory and response variables and therefore does not cause significant bias in the results.

Only some pollinator groups were identified to species while most were identified to higher taxonomic levels. Therefore, the figures used in the analyses were an underestimation of the true species richness per field. At least the most frequently visiting insect groups, i.e., syrphid flies, other Diptera and solitary bees, in addition to honeybees, should be identified to species to get a better idea of the diversity of pollinators visiting caraway and to make more accurate analyses on the effects of pollinator diversity on caraway pollination and yield. Toikkanen (2017) recorded 104 syrphid fly species on caraway fields in central Finland. It would be interesting to study if the diversity of visiting syrphid flies is important for caraway pollination, or if pollination is mainly done by a few dominant species. It would also be interesting to test if trait diversity of pollinators predicts caraway yield better than species diversity (Garibaldi et al. 2015).

7.4 The relative importance of the different pollinator groups

The most important pollinators for caraway yield were honeybees and syrphid flies, which were also the most dominant pollinator groups with the largest shares of all flower visits. This result is consistent with studies showing that abundant species often contribute the most to the total pollination service (Morris 2003, Rader et al. 2009, Winfree et al. 2015, Kleijn et al. 2015). The third most frequently visiting group, non-syrphid Diptera, had no significant effect on the yield components, which suggests that, on average, the species in this group were not very efficient pollinators. Solitary bees had no significant effect either, which can be explained by their low numbers, and as expected, the role of Lepidoptera was not important.

Models for bumblebees could not be formed, but judging from their low visit frequency, their importance can be expected to be very low. However, had bumblebees visited caraway flowers more frequently, as was observed by Toikkanen (2017), a positive effect on the yield components may have been observed since bumblebees are considered to be effective pollinators (Willmer 2011, pp. 407–413). Nevertheless, the results support the hypothesis that honeybees and smaller wild insects have the largest effect on caraway pollination and yield. Although non-syrphid Diptera and solitary bees had less importance than expected, they may have an important supporting role in caraway pollination. Garibaldi et al. (2015) suggest that, in addition to enhancing pollinator abundance and diversity, crop pollination can be enhanced by supporting flower visitors whose traits match those of the focal crop. This seems to be true for caraway as the body size and mouthpart length of small insects may match the structure of caraway flowers better than those of larger insects (Willmer 2011, pp. 275–321). However, this cannot be confirmed since the effects of most pollinator groups were

statistically insignificant and as there is not sufficient information on which exact traits in pollinators are the most beneficial for caraway pollination.

The spatial autocorrelation of model residuals found in the three models where seed yield per plant was the response variable shows that yields on adjacent fields were more similar than they were on fields located further apart (Plant 2012, p. 59). This somewhat undermines the assumption of independence of the observations and may therefore reduce the reliability of the results (*ibid*, p. 7).

Interestingly, flower visits by beetles affected the yield components negatively. While the effect on 100-seed weight was significant and the effect on yield was close to significant, fruit set was not significantly affected, which suggests that beetles were harmful to seed growth but not to pollination. There are some fairly effective pollinators among beetles, such as soldier beetles (Cantharidae) and *Cetonia* beetles (Scarabeidae) (Willmer 2011, pp. 288–295), which were among the insects recorded. The majority of the recorded Coleoptera flower visits were by soldier beetles (157 of 253 visits) that typically feed on nectar and pollen on Apiaceae (Willmer 2011, pp. 288–289) and may move considerable amounts of pollen between flowers (Kwak and Bekker 2006, p. 375, Rhoades et al. 2011). Soldier beetles and Ladybird beetles (Coccinellidae), the second most abundant beetle group recorded, are also natural enemies of crop pests (Eitzinger and Traugott 2011, Michaud 2012, Fernandes et al. 2019), making them potentially useful for crop growth. On the other hand, many beetles cause damage to the flowers they feed on with their essentially chewing mouthparts (Willmer 2011, p. 289). This destructive feeding behaviour may explain the negative effects of beetle visitation on seed weight and yield. In addition, floral damage caused by herbivory or the presence of herbivores, such as beetles, can make inflorescences less attractive to pollinators (Kirk et al. 1995, Danderson and Molano-Flores 2010, Gaffney et al. 2020), which may have a further negative effect on seed development. No correlation was found between beetle visitation and the total number of flower visits, and therefore the effects of beetle visitation cannot be explained by lower flower visit frequency on fields with high number of beetle visits.

Per-visit effect on yield was slightly higher for honeybees than for syrphid flies, but this was compensated by the higher visit frequency of syrphid flies. The result aligns with the global synthesis by Rader et al. (2016) where non-bee pollinators were found to offer a comparable pollination service to bees regardless of their lower per-visit effectiveness. In another synthesis (Orford et al. 2015) based on data from 33 fields primarily in the UK, non-syrphid Diptera made around 80% of dipteran flower visits and carried nearly 85% of the dipteran pollen, suggesting that the typical practice of excluding

non-syrphid Diptera from pollination studies if unjustified. Here the role of non-syrphid Diptera was much smaller and more in line with the assumption that Syrphidae have more importance as pollinators than other pollinating flies (Kevan and Baker 1983, Willmer 2011, pp. 304–321). However, considering that non-syrphid flies were among the most abundant pollinator groups, it would be beneficial to further explore their contribution to the pollination of caraway and other crops. The importance of flies as crop pollinators may further increase if populations of other wild pollinators continue to decline. In Finland, a significantly smaller proportion of syrphid fly species (3.1%) are threatened with extinction compared to bees (17%), butterflies (31.8%) and moths (17.1%) (The Red List 2019). Flies can also be more tolerant of adverse weather than bees (Levesque and Burger 1982, Langenberger and Davis 2002a, Ellis et al. 2017), which may increase their importance in cold, rainy and windy summers. All in all, the results of this study along with earlier literature (Rader et al. 2016, Orford et al. 2015) highlight the importance of including non-bee insects, including non-syrphid Diptera, in future pollination studies to increase understanding on their role as pollinators in both natural and agricultural ecosystems.

As honeybees were shown to be efficient pollinators of caraway, adding honeybee hives to the vicinity of caraway fields may be advisable. There is a risk, however, that honeybees are more attracted by some other floral resources (Ricciardelli D'Albore 1986, Langenberger and Davis 2002a), although the competition with other mass-flowering crops, such as turnip rape, may be reduced by the earlier flowering time of caraway (Langenberger and Davis 2002a, Toivonen et al. 2019). Also, even in high numbers, honeybees may not be able to fully replace the pollination service of syrphid flies and other wild insects (Garibaldi et al. 2013). Furthermore, since honeybees can be harmful to wild pollinator populations (Lindström et al. 2016, Geldmann and González-Varo 2018, Valido et al. 2019), increasing honeybee abundance may reduce the pollination service of wild insects, making the investment to hives less profitable as well as it being harmful to ecosystems. Therefore, a better approach would be to manage farmlands and landscapes to enhance the numbers of wild pollinators, particularly syrphid flies.

Ecological intensification of agriculture, reduced pesticide use, diversified farming systems and increasing the amount of natural or semi-natural habitats in agricultural landscapes are among practices recommended for supporting pollinators (Potts et al. 2016). However, management strategies to ensure sufficient foraging and nesting resources may be somewhat different for bees and non-bee insects (Rader et al. 2016). For instance, Toikkanen (2017) found that land use types in the surrounding landscape had differing effects on pollinator groups visiting caraway. Syrphid fly

abundance and species richness increased with increasing area of mixed forest, while agricultural land had the opposite effect. Other flies were unaffected by the tested land use types, while bee abundance was positively affected by agricultural land and negatively by conifer forest. Studies conducted in Sweden (Sjödin et al. 2008) and Spain (Ricarte et al. 2011) also found that forest in the surrounding landscape had a positive effect on Syrphidae species richness.

The opposing effects on bees and syrphid flies can possibly be explained by their different resource requirements (Rader et al. 2016, Toikkanen 2017). While bees feed on floral resources both as adults and larvae (Willmer 2011, p. 378), Syrphidae larvae may, depending on the species, require for example aphids, plant matter, dead organic matter or dung (Haarto and Kerpolä 2007, p. 14). The diversity of resource needs should be taken into consideration when planning management actions to enhance crop pollination by wild pollinators. Studies conducted in different regions on the effects of landscape structure on syrphid flies and other pollinators (e.g., Steffan-Dewenter et al. 2002, Heard et al. 2007, Rundlöf et al. 2008, Meyer et al. 2009, Kennedy et al. 2013, Toikkanen 2017) have had partly contrasting results, which shows that more research on the topic is needed and that pollinator management measures should be tailored specifically to each location. It is also important to develop alternative methods to protect crops from pest damage which may increase as a result of reduced pesticide use and other pollinator management practices (Tscharncke et al. 2016, Toivonen et al. 2019).

8 CONCLUSIONS

This study clearly demonstrates that insect pollination plays an important role in caraway cultivation. Pollinator exclusion significantly reduced caraway fruit set and seed yield, and in open pollination, both fruit set and yield increased with increasing pollinator visitation. The relative importance of wind pollination and insect pollination varies according to the environmental conditions, but wind pollination alone is not sufficient for securing good yields. The results suggest that caraway yields in southern Finland would benefit from higher pollinator abundance.

The results for pollinator diversity were mixed, as species richness had no effect and species evenness had a negative effect on the measured yields components. The negative effects of evenness can be explained by lower relative abundance of efficient pollinator species on the fields with high evenness.

Although the results did not show a positive relationship between species diversity and caraway pollination and yield, pollinator diversity may have a stabilising effect on crop yields over time.

Syrphid flies and honeybees were the most important pollinators as their flower visits significantly increased caraway yield. The effects of other pollinators were not significant, but the mechanism is not understood. It would be beneficial to study which syrphid fly species are the most abundant and effective pollinators for caraway and how to enhance their numbers by management. The results of this study add to the growing body of evidence that emphasises the need to manage crops and farmland landscapes in ways that support wild pollinator populations and enhance the ecosystem service they provide for agriculture.

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APPENDICES

Appendix 1: Fields with compromised yield sample quality

Table 1. 14 study fields with compromised yield sample quality. For the statistical analyses testing the effects of pollinator exclusion, the fields were classed as: a = severely compromised (7 fields), b = slightly compromised (6 fields). Field number 3, where no samples could be collected from inside the cage, was excluded from the data for all analyses concerning pollinator exclusion. For the analyses testing the effects of pollinator abundance, the fields were classed as: c = severely compromised (4 fields), d = slightly compromised (6 fields).

Field	Description of the issue with yield sample collection	
1	Samples collected before the crop was ripe because farmer planned to mow the field due to severe <i>D. daucella</i> damage or excessive weeds.	b, d
2	Samples collected before the crop was ripe because farmer planned to mow the field due to severe <i>D. daucella</i> damage or excessive weeds.	b, d
3	Field mowed before sample collection. Open-pollinated samples collected from around the cage where plants were intact. No samples from inside the cage due to <i>D. daucella</i> damage.	c
4	Field mowed before sample collection. Open-pollinated samples collected from around the cage where plants were intact. Only seven samples from inside the cage due to <i>D. daucella</i> damage.	a, c
13	Only one sample from inside the cage due to <i>D. daucella</i> damage.	a
15	Only two samples from inside the cage due to <i>D. daucella</i> damage.	a
20	Only seven samples from inside the cage due to <i>D. daucella</i> damage.	b
24	Field mowed before sample collection. Open-pollinated samples collected from around the cage where plants were intact.	a, c
25	Severe <i>D. daucella</i> damage. Plants started to reflower in July after pressure from <i>D. daucella</i> larvae decreased, and samples were collected before the crop was ripe.	a, c
26	Samples collected before the crop was ripe because farmer planned to mow the field due to severe <i>D. daucella</i> damage or excessive weeds.	b, d
27	Samples collected before the crop was ripe because farmer planned to mow the field due to severe <i>D. daucella</i> damage or excessive weeds.	b, d
28	Only two samples from inside the cage due to <i>D. daucella</i> damage.	a
29	Plants damaged by <i>D. daucella</i> , but full number of samples collected.	b, d
30	Field partially mowed before sample collection. Open-pollinated samples from two monitoring plots collected from cut plants (4/8 open-pollinated sample plants). Only two samples from inside the cage due to <i>D. daucella</i> damage.	a, d

Appendix 2: Pollinator species and groups used in the calculations of diversity metrics

Table 1. Pollinator species and groups used in the calculations of the Shannon index (H'), species richness (S) and species evenness (J'). For pollinators identified to species, the number of individuals per species was used in the calculations. For pollinators identified at higher taxonomic levels, the number of individuals per group was used.

	Taxonomic groups used to calculate Shannon index, species richness and species evenness
Bees (Hymenoptera: Apoidea: Anthophila)	Honeybee (<i>Apis mellifera</i>) <i>Bombus lapidarius</i> <i>Bombus lucorum</i> group <i>Bombus veteranus</i> Solitary bees
Syrphid flies (Diptera: Syrphidae)	Syrphinae Eristalinae
Non-syrphid flies (Diptera)	Non-syrphid Brachycera Nematoceran flies
Butterflies and moths (Lepidoptera)	<i>Boloria selene</i> <i>Nymphalis urticae</i> <i>Vanessa cardui</i> Moths
Beetles (Coleoptera)	Soldier beetles (Cantharidae) Ladybird beetles (Coccinellidae) Rose chafer (<i>Cetonia aurata</i>) Other Coleoptera
Non-bee Hymenoptera	Ants (Formicidae) Other non-bee Hymenoptera
Other	True bugs (Hemiptera: Heteroptera)
	Green lacewings (Neuroptera: Chrysopidae)
	Spiders (Araneae)

Appendix 3: Results of statistical analyses conducted on a subset of study fields

Table 1. The mean and standard deviation (SD) of the yield components in open-pollinated plants and caged control plants, and the effects of pollinator exclusion on the yield components, when either 7 fields with severely compromised yield sample quality or 13 fields with slightly or severely compromised yield sample quality were excluded from the analyses. Exclusion of the fields did not alter the statistical significance of the results.

Analyses without 7 fields with severely compromised sample quality							
Yield component	Open pollination		Pollinator exclusion		LME Estimate ^a	SE	p
	Mean	SD	Mean	SD			
Fruit set per central umbel (%)	70.75	9.97	61.24	12.24	-9.505	1.91	<0.001
100-seed weight per central umbel (g)	0.220	0.09	0.221	0.10	0.0005	0.01	ns
Seed yield per plant (g)	2.51	1.49	1.60	1.11	-0.904	0.27	<0.01
Umbellets per central umbel	8.49	0.59	8.40	0.55	-0.088	0.10	ns
Umbels per plant	18.82	6.41	17.19	6.57	-1.631	1.52	ns
Analyses without 13 fields with slightly or severely compromised sample quality							
Yield component	Open pollination		Pollinator exclusion		LME Estimate ^a	SE	p
	Mean	SD	Mean	SD			
Fruit set per central umbel (%)	69.05	11.04	61.54	13.86	-7.504	2.21	<0.01
100-seed weight per central umbel (g)	0.208	0.09	0.216	0.09	0.008	0.01	ns
Seed yield per plant (g)	2.45	1.57	1.72	1.24	-0.725	0.34	<0.05
Umbellets per central umbel	8.52	0.59	8.38	0.47	-0.141	0.12	ns
Umbels per plant	17.88	5.61	17.26	6.74	-0.617	1.66	ns

^aPollinator exclusion compared to open pollination

Table 2. The effects of pollinator abundance (the total number of flower visits) on the yield components when either four fields with severely compromised yield sample quality or 10 fields with slightly or severely compromised yield sample quality were excluded from the analyses. The results are bolded if statistical significance differed from the analyses conducted with all fields.

Analyses without 4 fields with severely compromised sample quality			
Yield component	GLS Estimate	SE	<i>p</i>
Fruit set per central umbel (%)	0.0609	0.0304	ns
100-seed weight per central umbel (g)	0.0004	0.0002	ns
Seed yield per plant (g)	0.0097	0.0048	ns
Umbellets per central umbel	0.0021	0.0023	ns
Umbels per plant	0.0161	0.0186	ns
Analyses without 10 fields with slightly or severely compromised sample quality			
Yield component	GLS Estimate	SE	<i>p</i>
Fruit set per central umbel (%)	0.0522	0.0347	ns
100-seed weight per central umbel (g)	0.0004	0.0003	ns
Seed yield per plant (g)	0.0080	0.0053	ns
Umbellets per central umbel	-0.0004	0.0022	ns
Umbels per plant	0.0089	0.0180	ns

Table 3. The effects of honeybee flower visitation on the yield components when two fields with exceptionally high number of honeybee flower visits were excluded from the analyses. The results are bolded if statistical significance differed from the analyses conducted with all fields.

Yield component	GLS Estimate	SE	<i>p</i>
Fruit set per central umbel (%)	0.2039	0.1407	ns
100-seed weight per central umbel (g)	0.0027	0.0011	<0.05
Seed yield per plant (g)	0.0555	0.0186	<0.01

Table 4. The effects of syrphid fly flower visitation on the yield components when one field with exceptionally high number of syrphid fly flower visits was excluded from the analyses. Exclusion of the field did not alter the statistical significance of the results.

Yield component	GLS Estimate	SE	<i>p</i>
Fruit set per central umbel (%)	0.1269	0.1012	ns
100-seed weight per central umbel (g)	0.0011	0.0007	ns
Seed yield per plant (g)	0.0236	0.0112	<0.05