Pollinating bees in fruit orchards of Western Norway:

1. Where the Wild Bees Are: Exploring how the landscape context influences the abundance and diversity of wild bees visiting apple orchards

2. The foraging preference and behavior of managed and wild bees in apple and pear orchards

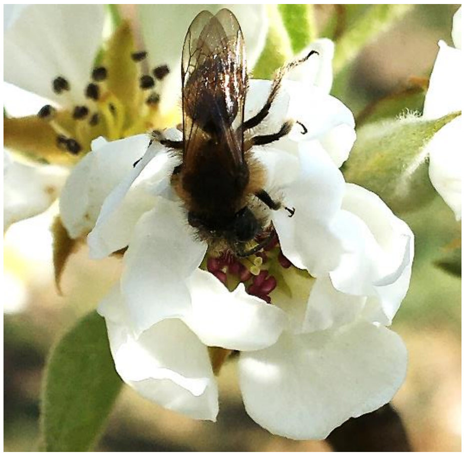

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Table of Contents

Background

The ongoing and well-known loss of biodiversity has been characterized as a human induced sixth mass extinction event (Ceballos et al., 2017; Dirzo & Raven, 2003; Thomas et al., 2004; Wake & Vredenburg, 2009). For insects, the situation is thought to be dire, leading to the phrase "The insect apocalypse", popularized in a New York Times article in 2018 (Jarvis). This was preceded by influential findings, showing dramatic losses in insect populations. Dirzo et al. (2014) reported a 45% decline in global insect populations in the last 40 years, while in Germany, an unexplained 75% decline in flying insect mass was recorded in protected areas (Hallmann et al., 2017). Three recent meta-analyses paint a more ambiguous picture, though. One showing that the abundance of terrestrial insects have been declining by ~1% per year, while aquatic insects were increasing by ~1% (van Klink et al., 2020b, 2020a). Another included 6000 marine, freshwater and terrestrial animal and plant taxa, where terrestrial insects showed the steepest decline (Pilotto et al., 2020), while the third showed no evidence of insect abundance decline (Crossley et al., 2020). However, these studies focused mostly on Europe and North America. In addition, study inclusion criteria in long-term monitoring data often exclude sites which have undergone serious changes, like those associated with agricultural conversion and habitat degradation. This means that estimates of insect decline might be conservative, especially since agricultural conversion and habitat degradation commonly is thought to be the main drivers of biodiversity and population declines (Diamond, 1989; Dirzo & Raven, 2003; Pereira et al., 2012; Sala et al., 2000; Sánchez-Bayo & Wyckhuys, 2019).

Biodiversity losses and population declines are particularly concerning due to potential cascade effects on ecosystem functioning. Reduced ecosystem functioning have severe consequence for human society, which is reliant on a host of ecosystem services (Cardinale et al., 2012; Isbell et al., 2017). Due to the large networks of species that interact to maintain ecosystems, species diversity is a major determinant of the quality and output of ecosystem services (Tilman et al., 2014). Pollination is an ecosystem service which will be profoundly affected by further losses of insect abundance and diversity. Most vascular plants (>90%) belong to the angiosperms (RBG Kew, 2016), of which almost 20% depend on bee (Hymenoptera: Apoidea) pollination (Ollerton, 2017), naming them the most important pollinator group, and the most effective for many plants (Földesi et al., 2021). This is even more clear in crop systems, even though the contribution of non-bee pollinators seems to have been undervalued (Rader et al., 2016). It has been estimated that around a third of global food production relies, directly or indirectly, on pollination, done mostly by bees (Klein et al., 2007; McGregor, 1976, pp. 1–4). Out of 108 investigated crops Klein et. al (2007) found that for 84% crop species pollination was beneficial, including 43 crops for which production decreased by minimum 40% when pollinators where excluded. In addition, pollination dependent crops account for a disproportionately high amount of micronutrients and economic value (Chaplin-Kramer et al., 2014; Eilers et al., 2011; IPBES, 2016, pp. 29–30).

There is a growing consensus that pollinators are declining in abundance and richness world-wide (Biesmeijer et al., 2006; Burkle et al., 2013; Dirzo et al., 2014; Koh et al., 2016; Ollerton et al., 2014; Pauw, 2007; Potts, Biesmeijer, et al., 2010). The most robust evidence comes from North America and Europe, especially for bumblebees (Bommarco et al., 2012; Cameron et al., 2011; Colla & Packer, 2008; Jacobson et al., 2018; Morales et al., 2013; Nieto et al., 2014; Rader et al., 2016) and honeybees (National Research Council, 2007, p. 40; Potts, Roberts, et al., 2010). Pollinator declines are concerning for several reasons, such as increased levels of pollen limitation and ultimately loss of pollinator reliant plants. In Britain and the Netherlands, declines in pollinators have been linked to parallel declines in insect pollinated plants (Biesmeijer et al., 2006), while Gomez et al. (2010) found a negative association between pollinator diversity and pollen limitation in the generalist plant *Erysimum mediohispanicum*. Even though lost pollinators can be successfully replaced by other effective groups in some systems (Hallett et al., 2017), the removal of a single pollinator species can affect the reproductive success of a host plant (Brosi & Briggs, 2013).

Of all pollinators, the western honeybee (*Apis mellifera)* is the most important pollinator for most crops (Garibaldi et al., 2013; Klein et al., 2007) (but see: Breeze et al., 2011) and in many natural habitats (Hung et al., 2018). The honeybee is uniquely useful as a managed pollinator because of a suit of attributes. Honeybees are described as a supergeneralist and can effectively pollinate a wide variety of crops (Földesi et al., 2021; Page & Nicholson et al., 2021). They form perennial colonies of 10,000-30,000 individuals which provides a large amount of pollinators when and where they are needed (National Research Council, 2007, p. 37). Furthermore, honeybees exhibit very high flower constancy (Free, 1963; Grüter et al., 2011), meaning that they rarely switch between plant species during a foraging trip. This promotes cross-pollination as fewer heterospecific pollen grains are deposited on the stigmas of flowers during their foraging trips, reducing stigma clogging. Managed honeybees are not reliant on proximity to natural and semi-natural habitats (Garibaldi et al., 2011; Ricketts, 2004; Ricketts et al., 2008; Steffan-Dewenter & Kuhn, 2003) and their hives can be placed where pollination services are needed. Honeybees can also travel long distances from their hive (Beekman & Ratnieks, 2000; Visscher & Seeley, 1982) and can recruit nestmates to flower resources using complex communication (Jha & Vandermeer, 2009; Willmer, 2011, pp. 415–416).

Between 1947 and 2005 there has been a honeybee colony loss of at least (only counting honey producing hives) 40% in the US (National Research Council, 2007, p. 40), while Europe has suffered a 16% loss between 1985-2005 (Potts, Roberts, et al., 2010). Declines also extend to feral colonies (Jaffé et al., 2009; Kraus & Page, 1995) and are largely attributable to the spread of invasive pests and pathogens (Genersch, 2010). Even though honeybees are increasing globally, the demand for pollination services is increasing at a much higher pace (Aizen & Harder, 2009; Breeze et al., 2014). The heavy reliance on honeybees is a potential risk for future food security (Winfree, Williams, et al., 2007), in part due to their susceptibility to invasive pests (Genersch, 2010) and predators (Alaniz et al., 2020; Monceau et al., 2014).

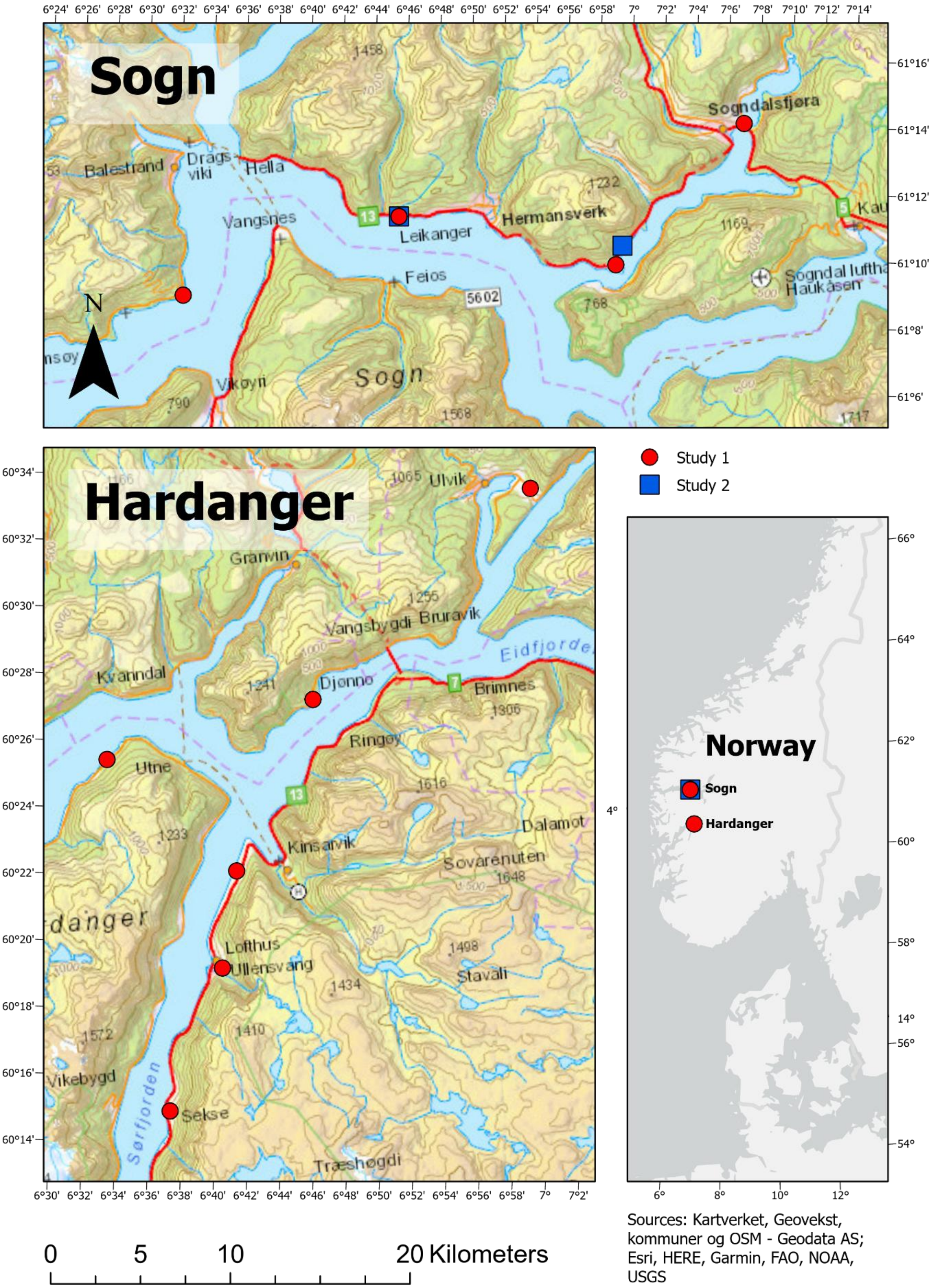
When honeybee colonies fail, a rich community of wild bees can act as pollination insurance for crops (Rader et al., 2012; Winfree, Williams, et al., 2007). Such systems are more stable in the face of disturbance (Bartomeus et al., 2013; Winfree & Kremen, 2009) and climate change (Nielsen et al., 2017). In addition, a meta-analysis of 41 crop systems has shown that the species richness of wild flower-visitors increase yield, regardless of honeybee abundance, suggesting that the positive effect of wild pollinator diversity is additive and they do not only act as insurance (Garibaldi et al., 2013). This has been illuminated in several studies which show that wild bees increase honeybee performance, by enhancing their visitation rate and movement between trees and rows, resulting in better pollination service (Brittain et al., 2013; Carvalheiro et al., 2011; Eeraerts et al., 2020 b; Greenleaf & Kremen, 2006). Honeybees, on the contrary, have been shown to exclude other potential crop pollinating bees through exploitative competition (Nielsen et al., 2017). Many studies have shown that wild bees often are more effective pollinators than honeybees (e.g. Földesi et al., 2021; Garibaldi et al., 2013; Willmer et al., 1994), including a meta-analysis of 168 studies and 240 plant species, which concluded that despite their high visitation frequency, honeybees are less effective than the average crop pollinating bee and rarely the most effective pollinator of a crop on a per visit basis (Page & Nicholson et al., 2021). It follows that crop systems that are visited by a diverse community of wild bees may be more likely to contain effective pollinators. Despite their effectiveness as pollinators, wild bees are unable to deliver sufficient crop pollination services without managed bees if their abundance and diversities are too low (Kremen et al., 2002). The ongoing abundance and diversity losses of wild pollinators are linked to landscape simplifications resulting from e.g. agricultural intensification (Dainese et al., 2019; Eeraerts et al., 2017; Kremen et al., 2002; Ollerton et al., 2014). Crop pollinating wild bees are reliant on proximity to natural and semi-natural landscapes containing quality habitats for nesting and abundant alternative food resources (Garibaldi et al., 2011; Kennedy et al., 2013; Ricketts et al., 2008).

The listed challenges associated with honeybees and the ongoing losses of pollinators pose threats to future food security. Because of the high pollinator potential of wild bees, it is necessary to have a broad and relevant knowledge of the environments which facilitate wild bee visits to crops, as well as a deeper understanding of the behavior and relative contributions of pollinators in these systems. Here, I explore aspects of these questions in two separate studies: In study 1, I explore the relationship between the surrounding landscapes of apple orchards and the abundance and richness of wild bees found in these systems. In study 2, I compare the visitation frequency and foraging behaviors of managed and wild bees in apple and pear orchards and discuss the implications of these behaviors for pollinator effectiveness.

Study area

The study areas for my projects were the Sogn and Hardanger regions of Vestland county, Western Norway. Both regions lie in a transitional climate zone between the oceanic climate on the west coast and the inland climate. This provides relatively high precipitation and mild climate, extending the growing season (Moen, 1998), making these areas ideal for fruit growing. Hardanger and Sogn are the most important fruit growing regions in Norway, being respectively the highest and second highest producers of apple and pear (County governor of Vestland, 2021). All study sites were situated in a varied fjord landscape, often with steep slopes leading to mountainous areas (e.g. figure 1). Forests in these landscapes are dominated by deciduous forests and pine trees, but there is also a high occurrence of planted spruce. In Sogn, the cropland predominantly consists of small fruit orchards at low densities, in addition to pastures for farm animals. Fruit production is dominated by apple and raspberry, but many farms grow multiple crops, including plum, cherry, strawberries, and pear (County governor of Vestland, 2021). In Hardanger, the farms are larger and occur at a higher density. Most fruit growing areas are focused on apples and plum (County governor of Vestland, 2021).

Figure 1 *Photo showcasing a typical study site (Ølmheim, Sogn). Orchards were situated at low altitudes (<100 m AMSL) along the fjords of a varied mountainous landscape. Photo: Jørund Johansen*



Sources: Kartverket, Geovekst, kommuner og OSM - Geodata AS; Esri, HERE, Garmin, FAO, NOAA, USGS

Figure 2*: Study regions and sites in Western Norway. Red circles indicate the ten sites sampled in study 1, while blue squares indicate the two sites in study 2.*

1. Where the Wild Bees Are: Exploring how the landscape context influences the abundance and diversity of wild bees visiting apple orchards

Abstract. Several studies have found that the presence of natural and semi-natural habitats is beneficial, particularly for wild bees visiting crops. These relatively undisturbed areas provide essential foraging and nesting opportunities for wild bees. However, the importance of these habitats seems to vary depending on the intensity of the agricultural activity in the area as well as the geographical and climactic regions being surveyed. In addition, the spatial scales at which different pollinator groups respond to the landscape context seems to be related to their respective foraging ranges. In Norway, the relationship between the landscape context and pollinator communities remains largely unexplored. Here, I provide evidence that semi-natural habitats increase the abundance and diversity of wild bees visiting apple orchards in Western Norway. Specifically, I found that the abundance and diversity solitary bees was related to the proportion of forest cover on the local scale (<500 m from orchards), while bumblebee abundance and richness was related to the proportion of pastures surrounding the orchards on scales from 500-2000 m. Even though my sample size was small, my findings indicate that natural and semi-natural habitats can enhance the wild bee abundance and richness in crop systems, even in the relatively heterogenous landscapes typically surrounding fruit orchards of Western Norway.

1.1 Introduction

Several studies have explored the relationship between the landscape context of crop systems and the abundance and richness of wild bees. When synthesized and meta-analyzed, these studies show that the species richness (Coutinho et al., 2018; Garibaldi et al., 2011; Ricketts et al., 2008), abundance (Coutinho et al., 2018) and visitation rate (Garibaldi et al., 2011; Ricketts et al., 2008) of wild bees is negatively associated with distance to natural habitats (Garibaldi et al., 2011; Ricketts et al., 2008) and proportion of crop area (Coutinho et al., 2018). Earlier studies have also found a positive impact of the proportion of semi-natural landscape on wild bee abundance and richness in grassy field margins and orchard meadows (Steffan-Dewenter, 2003; Steffan-Dewenter et al., 2002). However, a large European study did not find these effects when sampling crops (Carré et al., 2009). Instead, they found that the abundance and diversity of wild bees were influenced by different factors in different areas. In Central Europe (Sweden, Germany and Poland), wild bee abundance was positively associated with urban habitats and negatively associated with coniferous forests, while diversity was positively associated with broadleaf forest and woodland-shrub, as well as urban habitats and non-irrigated arable land. In the UK, abundance and diversity was positively associated with semi-natural habitats, while in France, only urban habitats were positively associated with abundance. These findings highlight the variation in wild bee responses to the landscape context in different geographic and climatic regions.

Most of these studies have been carried out in intensely driven, heavily disturbed and homogenous crop landscapes in Central Europe and North America. In Norway, the unique geographic and climatic conditions makes it hard to draw conclusions from work done in other countries (Totland et al., 2013, p. 59). Few studies have explored the landscape context in relation to wild bee abundance and species richness in Norway (but see: Rastad, 2021; Sydenham et al., 2014), and fewer still have associated the landscape context with wild bees in crop systems.

Sydenham et al. (2014) found no effect of the landscape context on the abundance and richness of bees sampled in cereal field edges in southeast Norway. Sydenham et al. (2014) pointed out that their study area was relatively heterogenous compared to study sites in Central Europe (e.g. Carré et al., 2009; Steffan-Dewenter, 2003; Steffan-Dewenter et al., 2002). In these systems, wild bees might not be limited by foraging and nesting resources to the same degree. This is even more true for many fruit orchards in Western Norway, which typically are small and relatively interspersed in a heterogenous landscape.

Here, I aim to identify the most important habitats for wild bee visitors to commercial apple orchards in Western Norway at different spatial scales. I examine the relationship between the proportion of land cover types and the abundance and species richness of wild bees sampled in apple orchards during bloom. Focusing on the most relevant land covers for bees, forest (deciduous, coniferous and mixed) and agricultural land (cultivated land and pastures) I ask the following questions:

1) Which land cover types influence the species richness and abundance of wild bees in apple orchards?
2) At which spatial scales are wild bees influenced by the surrounding landscape?

I made the following predictions:

1) Orchards with a higher proportion of natural and semi-natural habitats in the surrounding landscape will have higher abundance and richness of wild bees.
2) Due to differences in foraging distance, the relationship between the land cover and solitary bees will be stronger on smaller spatial scales, while bumblebees will respond on larger spatial scales.

1.2 Material and method

1.2.1 Study sites

A total of 6 apple orchards in Hardanger and 4 in Sogn (table 1 & figure 2) were selected as sites to represent variation in size, distance to fjord, location along fjord (north or south) and adjacent vegetation. The minimum distance between any two sites was 5,47 km measured between orchard centers. The distance between the northern- and southernmost sites was ~111 km. The distances between the study sites were significantly larger than the expected foraging distances of solitary bees and bumblebees (Reviewed in: Zurbuchen et al., 2010). Therefore, the spatial correlation of the study sites should have played a minor role, and each study site was considered an independent replicate.

Table 1 *Overview of sampling location, dates, effort and size.*

Region	Site	Coordinates	Elevation (AMSL)	Date(s) (2020)	# pantrap sessions	# net sessions	Orchard size (m²)
Sogn	Fosshagen	6.763193°E, 61.182544°N	19	May 20, 21, 22	2	3	2995
	Målsnes	6.543164°E, 61.139394°N	19	June 1, 2, 3	3	4	5798
	Nornes	6.988959°E, 61.161956°N	28	May 20, 21	2	4	8854
	Sogndal	7.117421°E, 61.234397°N	9	June 6	1	2	6810
Hardanger	Djønno	6.750213°E, 60.458129°N	61	May 28, 29, June 1	2	4	3871
	Lote	6.544342°E, 60.424482°N	5	June 2, 3	2	4	8405
	Opedal	6.668369°E, 60.322430°N	90	May 19, 20, 21	3	6	3616
	Sekse	6.620804°E, 60.250084°N	81	May 25, 26, 28	3	6	6271
	Ulvik	6.963327°E, 60.567082°N	57	May 29, 30, June 1	3	6	7987
	Urheim	6.679178°E, 60.371199°N	32	June 2, 3, 8	3	6	12601

1.2.2 Study design

Bee sampling

Bees were collected in May and June 2020 using two methods: aerial insect hand nets and pan traps. These sampling methods were chosen to complement each other, as the combination of the two is more likely to give an accurate representation of the bee community than each method alone (Roulston et al., 2007). Pan traps are commonly used to assess diversity and abundance of various pollinators in an area, such as solitary bees, but have lower success for bumblebees (Roulston et al., 2007). Nets, on the other hand, can measure the visitation to flowers, and hence may be more directly related to pollination, and is efficient for sampling larger pollinators such as bumblebees (Boyer et al., 2020).

Netting sessions were performed 2-6 times on each location: one session in the morning (ca. 9-10:30) and in the afternoon (ca. 13:30-15) each day for 1-3 days per site. Only one person recorded per site, but often sampled two orchards in the same day. Each session consisted of a transect walk along rows of apple trees which lasted 90 minutes (with two exceptions) to cover the whole orchard and give equal attention to each tree. The first new observed pollinator sighted inside a flower was caught. After netting, the individuals were transferred to a tube. After each session, the contents of the tube were gathered in a labeled container (date, time, orchard) and preserved in a freezer (-20ºC).

In every orchard 1-3 fluorescent pan trap-sessions were carried out. The traps were set out on ground-level in clusters of three, one of each of three colors (white and fluorescent yellow and blue), separated by ca. 3 meters. Every session included three clusters: two in opposing orchard corners and one in the middle. Each trap was filled with water and a droplet of odorless, transparent liquid soap to break the water surface. The sessions lasted between 4.5-13 hours, but most sessions were 7 hours (median = 7h ~ mean = 6:57). In some sessions, the traps operated through the night. In these cases, the “active period” of the traps were chosen to be between 08:00 and 21:00, assuming less activity outside this time frame. After sessions, the content of each pan was emptied into a container and labeled with date, time, orchard position and trap color. Later, the bees were rinsed, dried, and put in a freezer (-20ºC) for preservation.

All bumblebees were identified by Maren Kristine Halvorsen and Sandra Kaasen Vestheim, University of Bergen. *B. lucorum, B. magnus* and *B. cryptarum* are hard to distinguish without DNA-analysis, especially distinguishing between *B. lucorum* and *B. magnus* workers and errors might have occurred. Solitary bees were identified by Sandra Kaasen Vestheim and verified by Arnstein Staverløkk, Norwegian Institute for Nature Research (NINA).

Bee sampling was only done on days without precipitation and a minimum temperature of 12 ºC, when possible. This to avoid biased results because of weather.

Land cover data

For mapping landscapes around each orchard, the land resource map FKB-AR5 was used (NIBIO, 2017). This map is based on the most detailed geographical dataset of Norway (FKB) (Kartverket, 2022) and shows terrestrial resources on a scale of 1:5000, with special emphasis on agriculture and plant production. It uses the national land capability classification system AR5 which has 4 attributes: 1) surface type, based on vegetation and cultivation (primary), 2) forest site quality class, 3) forest cover type and, 4) soil conditions. The minimum mapping unit is 0.2 ha (Ahlstrøm et al., 2019).

Data on surface type and forest cover type was extracted from a buffer 3000m in radius around the center of each orchard. This contained the area for each of 11 land cover types inside the radius: 1) fully cultivated, 2) surface cultivated, 3) pastures, 4) forest: coniferous, deciduous and mixed, 5) bogland, 6) Misc. open areas (e.g., moors, quarries and sports facilities) 7) fresh water, 8) ocean, 9) glacier, 10) roads and railway and 11) buildings. Of these variables, I focused on forests and agricultural areas (cultivated land and pastures), as they are likely to be the most relevant for bee activity (e.g. Winfree, Griswold, et al., 2007).

Each 3000 m buffer was divided into 8 donut-shaped areas based on the distance from orchard centers: 1) 0-250m, 2) 250-500m, 3) 500-750m, 4) 750-1000m, 5) 1000-1500m, 6) 1500-2000m, 7) 2000-2500m and, 8) 2500-3000m. These sectors were chosen because they are likely to represent the foraging distances of most solitary bees and bumblebees (Steffan-Dewenter et al., 2002; Zurbuchen et al., 2010).

1.2.3 Data processing and statistical analysis

Abundance and species richness of bees were summarized for each sample. For netting, one session equaled one sample. For pan traps, each session was divided into 3 samples, including the pooled abundance/species richness of one triplet of white, yellow and blue traps in the same orchard position. Only 3 bumblebees were caught in pan traps (as opposed to 94 in nets). Since pan traps clearly did not give an accurate picture of bumblebee abundance, these were removed from the pan trap dataset.

To investigate whether there was a relationship between abundance and richness of wild bees and the landscape composition at various scales, I fitted a general linear mixed effects models using the glmmTMB package (Brooks et al., 2017) in R (R Core Team, 2021), with a Poisson error distribution. Because of different sampling methods, bumblebees (net) and solitary bees (pan trap) were analyzed separately. As there may be considerable correlation between the land cover types, I decided to run separate models for each fixed effect as well. Due to the high correlation between bee abundance and species richness (>0.8), species richness was only analyzed for fixed effects that had a statistically significant relationship with bee abundance. First, I tested the effect of the area of forests and agriculture on each spatial scale. If there seemed to be a relationship, I tested the constituent land cover types (table 2) to determine if more specific land cover types accounted for the relationship. Sampling effort was quantified as the number of sampling sessions (hand nets) and days (pan traps) and used as an offset variable. This to account for variation in effort between sites without the loss of statistical power associated with ratio conversion (Reitan & Nielsen, 2016). To account for clustering due to multiple samples at each site, Site-ID was used as a random effect.

Table 2 *The Fixed effects analyzed, and the respective land cover types included in these.*

Fixed effect (proportion)	Land cover types included
Forest	Deciduous forest, coniferous forest and mixed forest
Deciduous forest	Deciduous forest
Coniferous forest	Coniferous forest
Agricultural areas	Fully cultivated land, surface cultivated land and pastures
Cultivated land	Fully cultivated land, surface cultivated land
Pastures	Pastures

1.3 Results

A total of 94 bumblebees were caught in hand nets (3 in pan traps), including 14 different species. The most common species (*B. pascuorum*, *B. lucorum* and *B. pratorum*) accounted for 67% of the individuals. The pan traps collected 183 (106 in hand nets) solitary bee species, representing 17 species. Five additional solitary species was caught using hand nets. Most solitary bee species belonged the genera *Lasioglossum spp.* and *Andrena spp*. The Hardanger region generally had higher abundance and species richness of both bee groups, compared to Sogn, but this was partly due to the higher sampling effort there (table 1). Nearly half of the solitary bee individuals collected in pan traps were from Djønno (Hardanger), while two sites (Ulvik and Sekse, Hardanger) represented 64% of the total bumblebee abundance.

The surrounding landscapes of the surveyed orchards were dominated by forests, on average accounting for 36% (range 25-54%) of the surface area in a 3000 m radius from orchard centers. Deciduous forests were slightly more common than coniferous forests (50 vs. 41% of the total forest cover, respectively). The mean proportion of agricultural land was 6.6% (range 2-15%), 74% of which was cultivated area, compared to 26% pastures.

1.3.1 Solitary bees

The proportion of forest cover (Pforest, henceforth) tended to influence the abundance of solitary bees on smaller spatial scales, but the predictive power of the models decreased as scale was increased (figure 3). Pforest had statistically significant effect on solitary bee abundance on the 0-250 m scale ($p < 0.05$, R-squared = 0.26), where more solitary bees were found on sites where the proportion of forest was higher (figure 4). The positive effect was also statistically significant for the species richness of solitary bees on the same scale ($p < 0.05$), but the model explained less of the variation between sites (R-squared = 0.13). A similar relationship was found between Pforest and solitary bee abundance on the 250-500 m scale, but the positive effect was not statistically significant (abundance: $p = 0.06$, R-squared = 0.20). Of deciduous and coniferous forests, only the proportion of coniferous forests (Pconiferous) showed a statistically significant positive relationship with solitary bee abundance on the 0-250 m scale ($p < 0.05$), but less of the variation was explained by the model (R-squared = 0.15), compared to Pforest on the same scale (R-squared = 0.26).

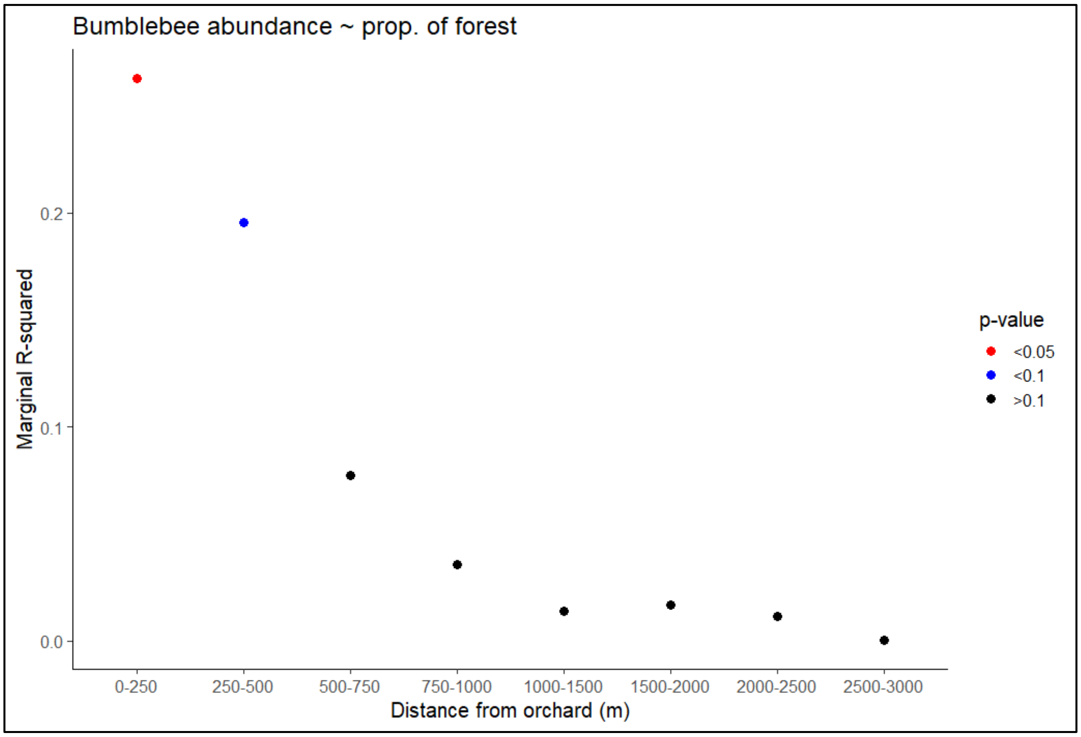


Figure 3 *Plotted marginal R-squared values for models where proportion of forests was the fixed effect. Marginal R-squared measures how much of the variation is explained by the fixed effect. Significant (p<0.05) scales are represented by red points, marginally significant (p<0.1) are shown in blue, while black dots represent scales where Pforest did not have a significant effect (p>0.1).*

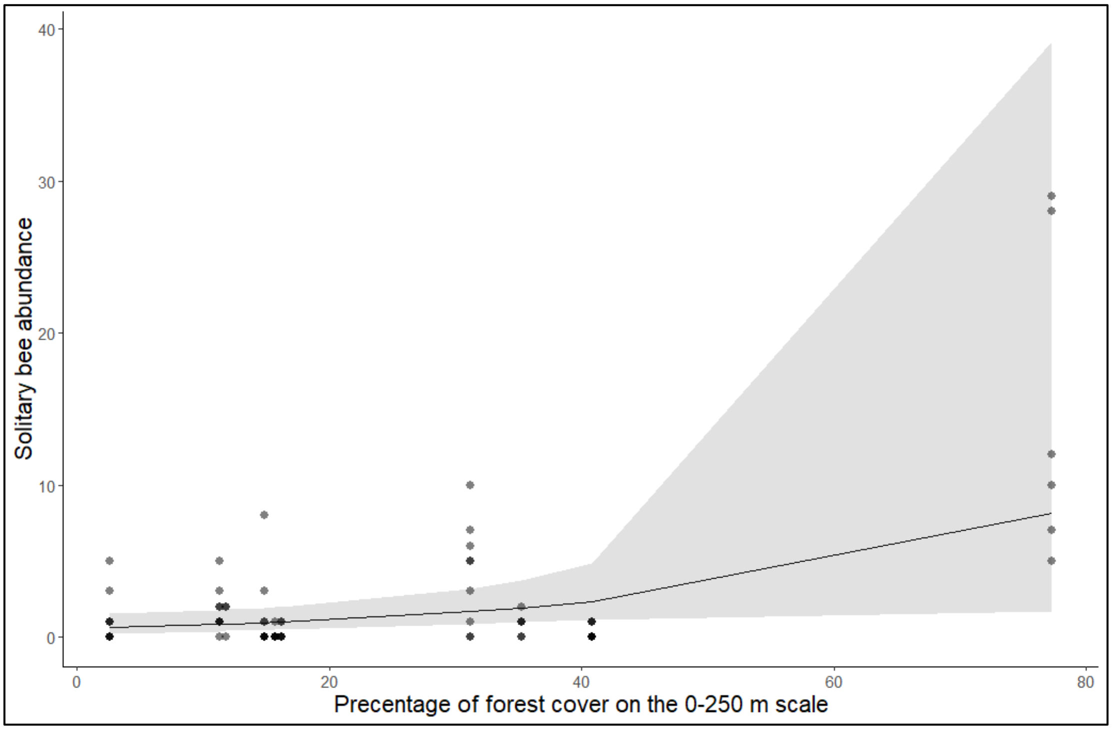


Figure 4 *Estimated solitary bee abundance as a function of the presentage of forests cover on the 0-250 m scale. The gray shaded area represents the 95% confidence interval. The observed abundances of solitary bees are represented by dots.*

Due to the negative correlation between the proportion of forest cover and agricultural land on the 0-250 scale (-0.73), the relationship between agricultural land and solitary bees was not analyzed.

1.3.2 Bumblebees

Pforest showed no relationship with the abundance of bumblebees on any scale ($p > 0.05$). However, the proportion of agricultural land (Pagriculture) tended to have a positive effect on scales above 500 m, which was statistically significant on the 1500-2000 m scale for bumblebee abundance ($p < 0.05$, R-squared = 0.25), but not for bumblebee species richness ($p > 0.05$, R-squared = 0.15).

Analyzing the proportion of cropland (Pcrop) and pastures (Ppasture) on the 1500-2000 m scale revealed that Ppastures ($p < 0.05$, R-squared = 0.39, estimate: figure 6), rather than Pcropland ($p > 0.05$, R-squared = 0.10), likely accounted for this effect. When I analyzed Ppastures on all scales I found a significant positive relationship with abundance on scales between 500-2000 m from orchards ($p < 0.05$, R-squared: figure 5). The 2000-2500 m scale also seemed to have an effect, but was not statistically significant ($p > 0.05$, R-squared = 0.21). The same relationship was found between Ppastures and bumblebee species richness, but the relationship was generally weaker, as fewer scales was (750-2000 m) had a statistically significant effect and the goodness of fit was lower on all scales (R-squared range: 0.005-0.27).

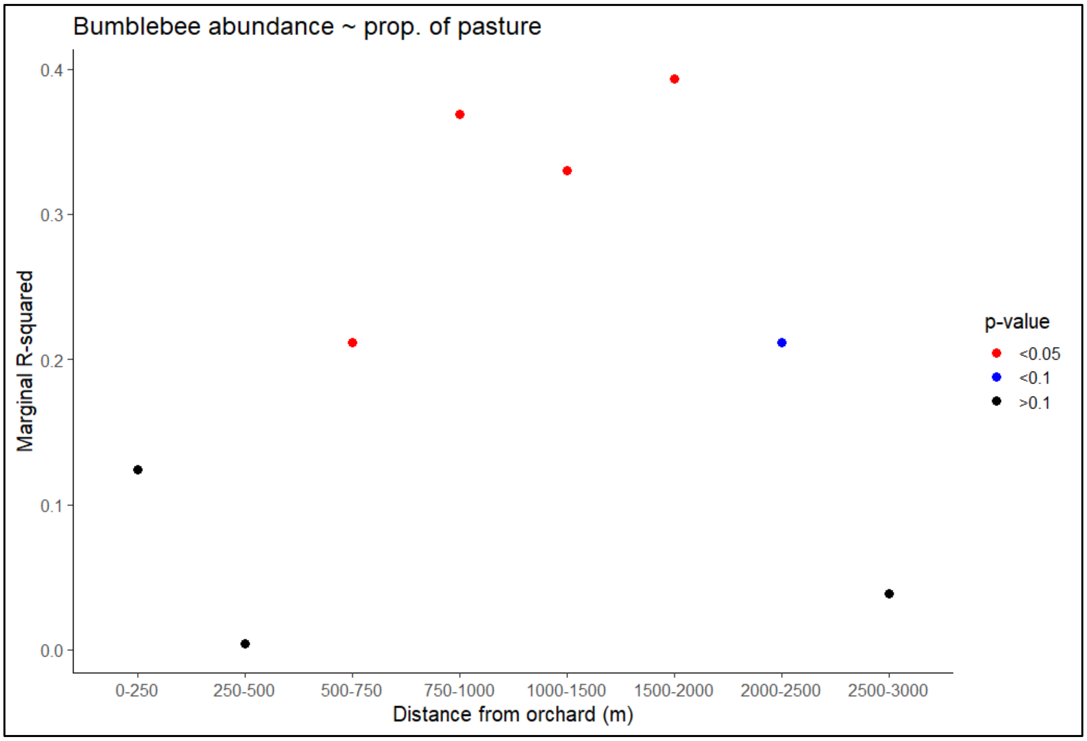


Figure 5 *Plotted marginal R-squared values for models where proportion of pastures was the fixed effect. Marginal R-squared measures how much of the variation is explained by the fixed effect. Significant (p<0.05) scales are represented by red points, marginally significant (p<0.1) are shown in blue, while black dots represent scales where Ppastures was not statistically significant (p>0.1).*

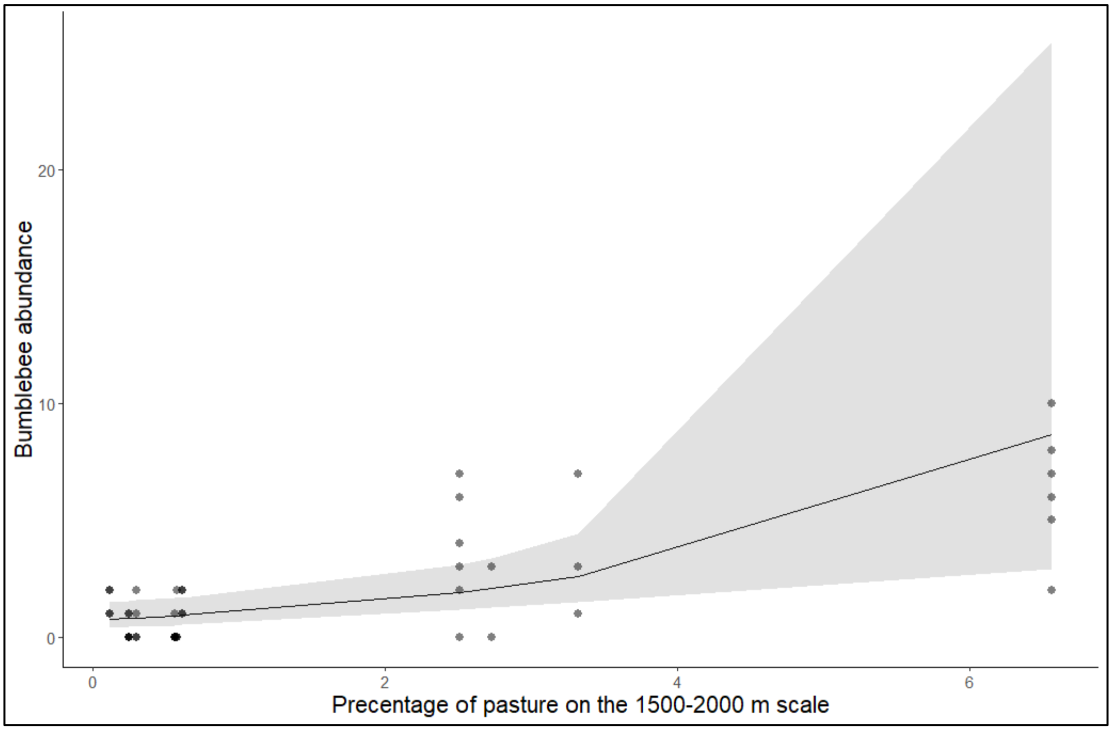


Figure 6 *Estimated bumblebee abundance as a function of the percentage of pastures on the 1500-2000 m scale. The gray shaded area represents the 95% confidence interval. The observed abundances of bumblebees are represented by dots.*

1.4 Discussion

Following my predictions, I found that 1) the area of natural and semi-natural habitats surrounding the apple orchards had a positive impact on the abundance and richness of wild bees, and 2) Solitary bees responded on the local scale (<500m), while bumblebees responded on the landscape scale (>500m).

Relating the abundance and richness of solitary bees to the area of forest and cropland revealed a positive effect of the area of forest. This tended to weaken further away from orchards and was only statistically significant on the innermost scale, 0-250m from orchards. The effect was significant for coniferous forest, but not for the area of deciduous forests. Still, the model including all forest types was the best predictor of solitary bee abundance and richness. In contrast, the abundance and richness of bumblebees was related to the area of cropland on larger spatial scales (>500m), being statistically significant at the 1500-2000m scale. Further analysis revealed that pastures, but not cultivated land, was important. The relationship between pastures and abundance of bumble bees was statistically significant at all scales between 500-2000m from orchards, and from 750-2000m for species richness.

The presented findings are supported by a growing body of literature, which recently have been synthesized. Ricketts et al. (2008) analyzed 23 studies of 16 different crops and found a strong negative effect of increased distance to natural and semi-natural habitats on pollinator richness and wild pollinator visitation frequency. They found a steep decline in visitation rates at distances over 0.6 km from natural habitats. This agrees with my finding that solitary bees visit orchards with a high proportion of natural and semi-natural forests in the vicinity, but contrast my finding that bumblebees respond to the area of semi-natural habitats (i.e. pastures) >500 m from orchards. However, Ricketts et al. (2008) surveyed studies including both solitary and social species in both temperate zones, where bumblebees are abundant, and tropical zones, where they are replaced by other social bees with shorter foraging ranges. In addition, a similar synthesis of 29 studies found that while the visitation rates of bumblebees in crops decreased in areas at larger distances from natural areas, this effect was weaker compared to other flower visitors (excluding honeybees) (Garibaldi et al., 2011). In general, bumblebees are known to have larger foraging ranges compared to many other smaller bees, including solitary bees (Greenleaf et al., 2007; Zurbuchen et al., 2010).

Contrary to my findings, Sydenham et al. (2014) found no relation between the abundance and richness of solitary bees and the surrounding landscape when sampling solitary bees in South Eastern Norway. Sydenham et al. (2014) reasoned that the landscape context is less important in the heterogenous landscapes they sampled, compared to the more homogenous crop landscapes studied in Central Europe (e.g. Carré et al., 2009; Steffan-Dewenter, 2003; Steffan-Dewenter et al., 2002). However, Sydenham et al. (2014) did not measure the effect of forest cover directly, but only as part of a landscape composition axis which correlated with forest cover. Moreover, they found that the field edges in landscapes with a high proportion of forest had more phenologically diverse species assemblages compared to less forested areas.

My finding that solitary bees are more present in forested landscapes is supported by earlier work. Martins et al. (2015) found that bee functional diversity was positively related to the area of meadows and forests surrounding apple orchards in a 680m radius. The same was shown by Watson & Wolf (2011), except that distances greater than 1000 m and 2000m from orchards were the best predictors of wild bee abundance and richness, respectively. Bennett et al. (2014) sampled bee visitation in native grassland plots in Canada and found that the proportion of forest cover in a 20 m radius increased the flower visitation of non-bumblebees (mostly small species, including solitary bees), but reduced visitation at the 10 m scale, suggesting proximity to forest edge, not forest cover, was the determining factor.

However, my finding that orchards surrounded by coniferous forests had more solitary bees is a little surprising. Especially considering that the sampled solitary bees in my study were dominated by a few ground nesting species (*Lasioglossum ssp.* and *Andrena ssp.)* which preferably nests in light soils in open, south facing slopes with sufficient solar radiation (Falk, 2015). Indeed, most bees are thought to prefer to forage in open, flower rich areas, rather than in the flower and light poor conditions of dense forests (Grundel et al., 2010; Odanaka & Rehan, 2020; Roberts et al., 2017). A possible explanation is that the area of forest was correlated with the access to edge habitats, which have been shown to hold more species than closed forests (Odanaka & Rehan, 2020; Sydenham et al., 2016). My study areas are, however, characterized by relatively open pine forests, which might be ideal habitats for bees.

Finally, it is important to note that the relationship between solitary bee abundance/species richness and forest cover was largely driven by one site, which represented half of the total solitary bee abundance caught in pan traps and included almost twice as many species as the second most species rich site. Removing this site from the model eliminated the relationship, suggesting that this could have been a statistical artefact. The relationship was also not significant for solitary bees caught in hand nets. A higher sample size is needed to establish the effect of land cover on wild bee abundance and richness in these regions.

Bumblebees, showed no relationship with the area of forest cover, although these bees can also be abundant along forest edges (Svensson et al., 2000; Willmer, 2011). Instead, the abundance and species richness of bumblebees were related to the area of pastures on the landscape scale (>500 m). This is similar to the findings of Morandin et al. (2007) which sampled canola fields in agriculturally intense areas in Canada. They measured the proportion of pastureland within 800 m from field edges and divided sites into categories with high a (>15%) or low (<6%) proportion of pastures. Areas in the high pastureland category had more wild bees than the low pastureland category, and the relationship was particularly strong for the abundance of bumblebees. However, these areas consisted mostly of annually tilled crops in addition to pasturelands, suggesting that pastures were the only suitable nesting areas for bumblebees. Watson & Wolf (2011) similarly found that the area of pastures surrounding apple orchards had a positive effect on wild bee abundance and richness sampled in these orchards. Other studies have shown variable effects of pastures on wild bees. Svensson et al. (2000) found more nest-seeking bumblebee queens in forest edges than in pastures. Considering landscape type, most queens were observed in relatively open areas, which were mostly surrounded by agricultural areas, including pastures. However, Svensson et al. (2000) found that the common bumblebee species in my study area (*B. lucorum* and *B. pascuorum*) were more prone to seek nests in forest edges. In a previous study (Kallioniemi et al., 2017) covering agricultural landscapes in Norway, the area of pastures had a weak negative effect on bumblebee density and richness, but the total length of pasture borders had a positive effect. Another complicating factor is that there seems to be some disagreement on which habitats should be included into the broader semi-natural category. Many studies count pastures as semi-natural habitat and find positive effects (Carré et al., 2009; Raderschall et al., 2021; Steffan-Dewenter et al., 2002), while Winfree et al. (2007) found a negative effect of forest cover on bee abundance and positive effect of agricultural areas, but included pastures in the latter. Other studies have found a negative association with agricultural area when including pastures (Connelly et al., 2015). In some studies, it is ambiguous whether or not agricultural land includes pastures (Ekroos et al., 2013). All in all, the evidence for pastures being important predictors of bumblebee abundance and richness seems variable and dependent on the context. It is, however, plausible that that these areas provide attractive open areas with alterative foraging resources when fruit crops are not in bloom. The most common bumblebee species found in my study area are ground nesters, typically exploiting abandoned rodent burrows (Falk, 2015), which very well could be abundant in and around pastures (Svensson et al., 2000).

Conclusion

In this study, I investigated the spatial effects of different land cover types on the abundance and species richness of wild bees visiting apple orchards. I found a positive association between the area of forest on the abundance and richness of solitary bees on the local scale, while the area of pastures influenced the occurrence of bumblebees on larger spatial scales. Even though my findings seem plausible considering the existing literature, the results should be interpreted with caution, mainly because of the small sample size of the study. Still, the findings could be used as a framework for future research, as the relationship between local and landscape features and the pollinator communities have received little attention in Norway.

2. The foraging preference and behavior of managed and wild bees in apple and pear orchards

Abstract. Effective pollinators are essential for the sexual reproduction of many important crops, especially for fruit crops that require cross-pollination with compatible cultivars to bear optimal fruit. To ensure pollination, managed honeybees hives are often placed in fruit orchards, as honeybees are flower constant generalists that can effectively pollinate a wide variety of crops. However, wild pollinators can act as pollination insurance if honeybee colonies fail. In addition, many wild pollinators are more effective pollinators on a per visit basis. In Norway, the relative importance of different pollinator groups has received little attention. In this study I compared the visitation frequency and foraging behavior between managed honeybees and wild bees in two fruit orchards producing apple and pear fruit. I found that honeybees likely are the most important pollinators of pear flowers in the study area, due to their superior visitation frequency compared to wild bees. However, bumblebees may be more important for apple pollination as they were similar to honeybees in their visitation frequency to apple flowers. In addition, I found that bumblebees are faster foragers, due to their lower handling times and search times, enabling them to visit more flowers per foraging trip than honeybees, potentially moving more compatible pollen between flowers.

2.1 Introduction

Pollination is the first phase of plant reproduction, where a pollen grain is transferred from a compatible stamen to a receptive stigma (Totland et al., 2013). To achieve successful pollination, many plants use animal flower visitors as vectors for their pollen (Willmer, 2011, p. 58). Not all flower visitors are effective pollinators, however. First, an effective pollinator needs to visit a plant during its effective pollination period (EPP), which is determined by stigma receptivity, pollen tube growth rate and ovule longevity (Sanzol & Herrero, 2001). In addition, visitors must carry enough conspecific pollen grains between receptive stigmas and have sufficient contact with the flower stigma to transfer the pollen on their bodies (Willmer, 2011, p. 280).

Pollinator effectiveness is normally measured as the visitation frequency (i.e. the number of visits a flower receives per unit time from a certain pollinator during its EPP) and single visit pollination effectiveness (the per visit contribution to pollination by a visitor) (Spears Jr., 1983; Vázquez et al., 2005). Even though the honeybee often is not the most effective pollinator on a per visit basis, it is the most frequent visitor in many crops systems where managed hives are used (Garibaldi et al., 2013; Nielsen et al., 2017; Rader et al., 2016). Some fruit crops, like pear, is thought to be less attractive to pollinators due to its low nectar content, and pear crops are therefore especially reliant on managed pollinators (Delaplane & Mayer, 2000, p. 240; Quinet & Jacquemart, 2017). In most systems, where a few pollinators are numerically dominant, visitation frequency is thought to be more important for plant reproduction than per visit effectiveness (Vázquez et al., 2012). A recent meta-analysis found a positive relationship between visitation frequency and single visit effectiveness, but interestingly, this was only true when honeybees where absent (Page & Nicholson et al., 2021). In any case, the relative importance of a pollinator is dependent on the crop in question as well as the other pollinators present in the system, which varies widely depending on the geographical region.

The foraging behaviors of pollinators are important aspects of pollination performance and many aspects must be combined to evaluate the usefulness of different pollinators (Willmer, 2011, p. 608). For example, many fruit crops like apple and pear require cross-fertilization with compatible cultivars (pollenizers). When these are grown commercially, pollenizers are often planted interspersed in the same row as the main cultivar or in separate rows adjacent to the main cultivar. This means that pollinators being more likely to change trees and/or rows are more likely to carry compatible pollen between the pollenizer and the main cultivar. Previous studies have shown mixed results when comparing managed honeybees to wild bees in their likelihood to change trees and/or rows while foraging in crops. Eeraerts et al. (2019) found that mason bees changed trees more often than honeybees, while bumblebees changed rows more often, in sweet cherry. Bumblebees have been shown to change trees and rows more often than the honeybee in raspberry (Willmer et al., 1994), while the same has been shown for the mason bee *Osmia cornuta* in almond (Bosch & Blas, 1994). Other studies have failed to detect differences in the frequency of row change between wild pollinators and honeybees in apple (Vicens & Bosch, 2000) and pear (Monzón et al., 2004; Quinet & Jacquemart, 2017) orchards.

The flower constancy of a pollinator can be used as a measure of how likely it is to visit the same plant species in consecutive flower visits (Willmer, 2011, p. 275). For cross pollination to happen, a pollen grain from a conspecific must be deposited on the stigma of the flower. The more loyal (i.e. higher flower constancy) a pollinator is to a plant species, the more likely it is to transfer pollen grains between two conspecific flowers (Waser, 1978). Honeybees are known to be extremely flower constant (Free, 1963; Grant, 1950), and while bumblebees also are considered to be highly flower constant (Heinrich, 1976; Rossi et al., 2015), they are often less constant than honeybees (Free, 1970; Grant, 1950; Willmer et al., 1994). The number of conspecific flowers a pollinator visits per time unit (flower visitation rate) is indicative of how well the pollinator handles the plant. In combination with high flower constancy, a high visitation rate means that the pollinator transfers pollen grains between many receptive flowers, and presumably does so before the pollen has dried out and the pollen has lost its ability to germinate (Willmer, 2011, p. 608). The foraging speed of a pollinator is the product of its handling time (the length of each visit) and its search time (the time elapsed between visits). Bumblebees have been shown to have lower handling times and/or higher visitation rate than honeybees in many crops, including apple (Martins et al., 2015; Ostevik et al., 2010; Thomson & Goodell, 2001), sweet cherry (Eeraerts et al., 2019) and raspberry (Willmer et al., 1994). However, only a few studies have compared the search time between pollinator groups in crops. Willmer et al. (1994) found that even though bumblebees have lower handling times and higher visitation rates in raspberry, the search time between flower visits and the proportion of search time during a foraging trip was lower for honeybees. Studies that compare all these characteristics between pollinators are lacking for many crop systems, this is especially true in Norway, where the geographical and climatic conditions makes it hard to draw conclusions from work done elsewhere (Totland et al., 2013, pp. 59–62).

Here, I compare the flower visitation frequency of honeybees and wild bees to flowers in commercial apple and pear orchards in Sogn, Western Norway. In addition, I compare the foraging behavior of honeybees and bumblebees in these systems. I ask the following question:

How does the foraging behavior of honeybees and wild bees differ in apple and pear orchards when considering the following attributes?

1) Flower visitation frequency
2) Flower constancy
3) Handling time
4) Search time between flower visits
5) Proportion of search time during foraging trips
6) Probability of tree and row changes

I predicted that:

1) Honeybees is the most frequent visitor, particularly to pear flowers.
2) Honeybees exhibit higher flower constancy than bumblebees
3) Bumblebees are faster foragers than honeybees, manifesting as lower handling and/or search time.
4) Bumblebees have a higher probability of changing trees and rows during their foraging trips

2.2 Material and method

2.2.1 Study sites

Two farms near Leikanger in Sogn (figure 2) were selected as study sites, based on the presence of apple and pear orchards with overlapping flowering periods. This allowed pollinator observations in both crops in the same sessions, enabling me to directly compare bee foraging behavior between them. Both locations have honeybee hives in their vicinity, which allowed observations of managed honeybees and wild bees in the same orchards. The orchards are reasonably close geographically (12.5 km apart) and therefore similar in terms of climate and plant and pollinator species assemblage.

Observations were done in *Summerred* apple cultivars and *Celina* pear cultivars during two days on each site. The cultivars are self-incompatible and need cross-pollination with compatible pollinizers to bear optimal fruit. A pollenizer tree was planted for every 10th tree in each row. One of the sites (May 14 and 19) is situated in Fosshagen, 2.5 km west of Leikanger (6.7622946°E, 61.1825526°N). The trees were separated by ~1 m and~4 m inside and between rows. The apple and pear orchard were situated adjacent to each other and could be part of the same transect walks. The studied area covered ~4000 m^2 and consisted of 5 rows of apple trees and 7 rows of pear trees. Two managed beehives were placed near one of the orchard corners.

The other site (20th and 21st of May) was situated in Ølmheim, 10 km east of Leikanger (6,9952655°E 61,1716274°N). The apple trees were separated by ~ 2 m and ~4.5 m inside and between rows, while the pear trees were separated by ~0.9m and 3.5m inside and between rows. There were no pollenizers in the apple orchard. The apple and pear orchards were separated by ca. 40 meters. The apple orchard was ~6000 m^2 but the observations were done in the southernmost part, predominantly in the lower part, measuring ~850 m^2. The pear orchard was ~2900 m^2. The farm had no beehives, but 6 hives were situated on a neighboring farm, ~40 meters from the edge of the pear orchard. Furthermore, 20-25 hives were installed in the larger area (2 km).

On both sites, the space between the rows of fruit trees was mowed the second day (May 18 and 21 respectively). Thus reduced the amount of alternative flower resources (dominated by

Taraxacum officinale aggr. (dandelion)) in the orchard. But these were still abundant under the trees. In Ølmheim, there were also a substantial amount of *Glechoma hederacea* (ground-ivy).

Observations took place between 09:00 and 18:00 only when conditions were ideal for bee activity (> 12º C, calm/no wind and no precipitation).

2.2.2 Study design and data treatment

To assess pollinator movement within and among flowers of my focal crops and wildflower patches within the orchards, I observed the foraging behavior of individual pollinators representing three groups of bees: honeybees, bumblebees and solitary bees. Two methods were used: 1) Flower visits to selections of flowers in apple and pear trees and in patches of wildflowers were done in 10-minute observation periods, 2) Individuals were tracked and timed during foraging trips. Both methods were exclusively done by the same person (except for one sample of flower visitation observations), to exclude observer bias. The methods are complementary, since the first method measures preferences and numerical importance of each bee group, while the second surveys important foraging behaviors influencing the per visit performance of each group.

Flower visitation frequency

The following method was used to measure the visitation frequency of each group (honeybees, bumblebees and solitary bees) in apple trees, pear trees and in wildflower patches.

All observations were done in apple or pear orchards. Specifically, the lower branches of apple and pear trees and ground floral patches inside the same orchards were observed. On the first sampling day (Fosshagen, May 14), only a few apple flowers were open, and observations were done in pear and floral patches only. On all other days, the observations were done on each of the plant species in alternated sequences between days. A branch or flower patch was first selected for observation. These varied in number of flowers, but flower patches were approximately 1 m^2 in size. Orchard name, date, time, observer, approximate position in the field (edge or middle) and number of flowers observed was noted before the observations started. Each observation period lasted 10 minutes and the pollinator group of each visitor and number of flowers visited by each group was noted. There was no discrimination between individuals inside a group, meaning that if a single honeybee individual visited 5 flowers on a branch, this was noted as 5 visits by honeybees. For each 10-minute observation, visitation frequency was calculated as the number of visits per flower per group.

Foraging behavior

Individual foraging bees were observed to determine a suit of indirect measures of per visit pollinator effectiveness. These were: 1) The frequency of changes between plant species: how often a flower visit was followed by a visit to different plant species, relative to the total number of observed visits (flower constancy), 2) The duration of each flower visit (handling time), 3) the time spent travelling between flower (search time), 4) The proportion of the observed foraging period that was spent travelling between flowers (proportion search time), and 5) how often individuals changed trees and rows relative to the total number of visits (probability of tree and row change)

Observation protocol

To observe the behavior of foraging pollinators, transect walks were done in each orchard. In the site where the apple and pear orchard were separated, about 30 minutes were spent in each. To note bee behavior, a cellphone voice recording app (standard application on iPhone 6S) and a handsfree headset (corded Apple EarPods) were used to report behavioral codes orally. A separate recording was used for each individual. At the start of each transect walk, a recording was started. When a foraging bee was spotted, the pollinator group and plant species was stated (e.g. “Bumblebee, apple”). When the bee sat in the first flower, the observer said “start”. When the bee left the flower, the observer said “stop”. Subsequent starting points of flower visits where stated in one of five ways: 1) “new flower”, if the bee landed on a flower in the same tree, 2) “new tree”, if the bee landed in a flower in a different tree of the same plant species, within the same row, 3) “new row”, if the bee landed in a new tree of the same species in a different row , 4) “new species” or the name of the plant species (e.g. “dandelion”), if the bee landed in the flower of a different species than the previous flower or 5) “same flower”, if the bee landed in the same flower again. The end of every flower visit was marked by stating “stop”. The bees were followed until they flew out of sight, or they had been followed for ~15 minutes, though the longest observation lasted 16 minutes and 46 seconds.

I tried to get an equal sample of each group in each crop species. Therefore, the selection of individuals was, to a certain degree, non-random, e.g., if many honeybees had been followed, the observer would actively look for bumblebees or solitary bees. Early on, it became clear that solitary bees were very hard to spot and even harder to track due to their size and swiftness. Because of this, I decided focus on honeybees and bumblebees. To be part of the comparison of variables other than flower constancy, three criteria had to be fulfilled: 1) the individual had to be a bumblebee or honeybee, foraging in apple or pear flowers, 2) the forager had to be followed for at least 3 flowers visits and, 3) all the observations for specific individuals had to be in the same plant species: There is evidence for plant exclusivity and specialization among individuals of social bees (Free, 1963; Grant, 1950; Heinrich, 1976). Changes between plant species were very rare, and these individuals were probably not representative for pear and apple foragers.

Dandelion and ground-ivy foragers were also observed, though these were not part of the comparison, and was sampled to a lesser extent. For ground-ivy, visits were ambiguous (starts and stops), due to there being many flowers densely situated on a small plant, in addition to many plants being submerged in the surrounding grass.

Visits that were too short to be recorded properly (>~0.5 seconds) were ignored, assuming that there was no contact with the stigma. This was also true for longer visits where there clearly was no contact with the stigma. In these cases, the bee was assumed to be resting/sunbathing. I was unable to determine whether or not the bees were nectar robbing (collecting nectar without coming into contact with the anthers) or distinguish between nectar and pollen foragers.

Data treatment

Voice recordings were processed using the sound editing software Audacity (Audacity Team, 2021). The voice recordings were stored in MPEG-filetype, which required the extension LAME (v3.100, October 2017). From the file metadata the following variables were extracted: 1) date (which informed which location the recording was from), 2) time when the recording was started, 3) identity of each recording (and thus the ID of each bee). Then every recording was listened through thoroughly. First, when an individual was identified, the group and plant was noted. If the individual foraged in two plant species, both were noted (e.g., apple/dandelion). Second, the start of the observation was noted, i.e., when the bee landed in the first flower, signified by the observer saying “start”. Then the end of the flower visit was identified (“stop”). These two points were noted (mm:ss), and the space between them (in the visual representation of the sound) was marked, which provided the time between "start" and "stop", i.e. the handling time (seconds). This was done for every subsequent flower visit in the recording, noting what kind of flower change had occurred. If the bee visited the same flower twice in a row, the visit length was added together and noted as one visit. The last "stop" before the individual was out of sight, was marked as the end of the observation. The total time of the observed foraging bout was calculated from the difference between the start of the first visit and end of the last visit. Then the number of flower visits were counted, and search time was calculated by subtracting the total handling time the total time of the observation. The proportion of search time was also calculated. Finally, the number of tree and row and plant species changes were summarized.

2.2.3 Statistical analysis

All statistical analyses were done using *R* (R Core Team, 2021). Five response variables were tested with the interaction between bee group and plant species as fixed factors (table 3). Response variables, including those measured as time, were treated as count data, with a poisson error distribution. General linear mixed effects models were fitted using the glmmTMB package (v. 1.1.2.3, Brooks et al., 2017). In the flower visitation frequency survey, only the site in Ølmheim was included in the analysis, due to low number of apple flowers that were open in Fosshagen. To account for clustered setup, plot-ID (branch or wildflower patch) or location-ID were used as a random effect (table 4). The DHARMa-package (v. 0.4.4, Hartig, 2021) was used to check for overdispersion (v. 0.4.4, Hartig, 2021). A negative binomial error distribution was used if overdispersion was discovered. Differences in number of flowers or flower visits observed were accounted for using offset variables (Reitan & Nielsen, 2016) (table 4). Multiple comparison of means was based on adjusted p-values (method: Tuckey) using the emmeans-package (Lenth, 2022).

Table 3 *Specification for each of the five models.*

Response variable	Fixed effects	Random effect	Offset variable	Distribution
Visitation frequency	Group, plant, Group*plant	plot-ID	# flowers observed	Negative binomial
Handling time	Group*plant	Site-ID	# flower visits	Negative binomial
Search time	Group*plant	Site-ID	# flower visits	Negative binomial
Probability of tree change	Group*plant	Site-ID	# flower visits	Poisson
Probability of row change	Group*plant	Site-ID	# flower visits	Poisson

2.3 Results

In total, 168 foraging trips (> 3 flower visits) were observed (table 4), accounting for 2572 single flower visits. They included 82 foraging trips by bumblebees, 76 by honeybees while the remaining 10 were solitary bees.

***Table 4** Numbers of foraging trips tracked for more than 3 flower visits and the number of observations per bee group and plant species.*

Plant species	Bumblebee		Honeybee		Solitary bee		Total	
	Foragin trips	Visits	Foragin trips	Visits	Foragin trips	Visits	Foragin trips	Visits
Apple	34	580	34	493	0	0	68	1073
Pear	34	834	34	302	2	12	70	1136
Dandelion	3	63	8	130	8	27	19	220
Ground-ivy	3	N/A	0	N/A	0	N/A	3	N/A
Ground-ivy & pear	4	6	0	0	0	0	4	6
Ground-ivy & apple	2	3	0	0	0	0	2	3
Apple & pear	1	1	0	0	0	0	1	1
Dandelion & pear	1	1	0	0	0	0	1	1
Total plant species changes	8	11	0	0	0	0	8	11
Total	82	1582	76	925	10	39	168	2572

The 136 foraging trips which were included in the comparison were on average observed for 120 seconds, including 16 flower visits on average. Bumblebees were on average conducting more flower visits (21) than honeybees (12), but the average length of each observed foraging bout was longer for honeybees (135 sec vs. 105 sec).

2.3.1 Flower visitation frequency

Honeybees had the highest flower visitation frequency (FVF) to flowers in the orchards overall (1.19±0.25), which was more than twice as many visits per hour as the two other groups (table 6). The differences between honeybees and the wild bees were statistically significant ($p < 0.05$). The overall FVF was highest to apple flowers (0.77±0.17) and lowest to pear flowers (0.47±0.16), but the differences were not statistically significant between any of the plant species ($p> 0.05$, table 6).

Table 5: *Summary of mean±std.error visitation rate per hour between groups and between crops. Statistically significant differences in means (p < 0.05) are represented by different letters.*

Bee group	Visits per hour (mean±std.error)	Plant species	Visits per hour (mean±std.error)
Honeybees	1.19±0.25 A	Apple	0.77±0.23 A
Bumblebees	0.47±0.16 B	Pear	0.47±0.16 A
Solitary bees	0.29±0.08 B	Wildflowers	0.67±0.16 A

In apple flowers, the difference was small between honeybees (1.18±0.53) and bumblebees (0.96 ±0. 39), while the FVF of solitary bees (0.16±0.08) were considerably lower than the other two groups. The difference in mean FVF to apple was not statistically significant between groups (p > 0.5, figure 7). However, the FVF to pear by honeybees was significantly higher than the two other groups (p < 0.05). Honeybees had a similar FVF between plant species. Bumblebees visited apple flowers more often than pear, while solitary bees seemed to prefer wildflowers. Inside each group, only the difference in FVF between apple and pear for bumblebees was statistically significant (p < 0.05).

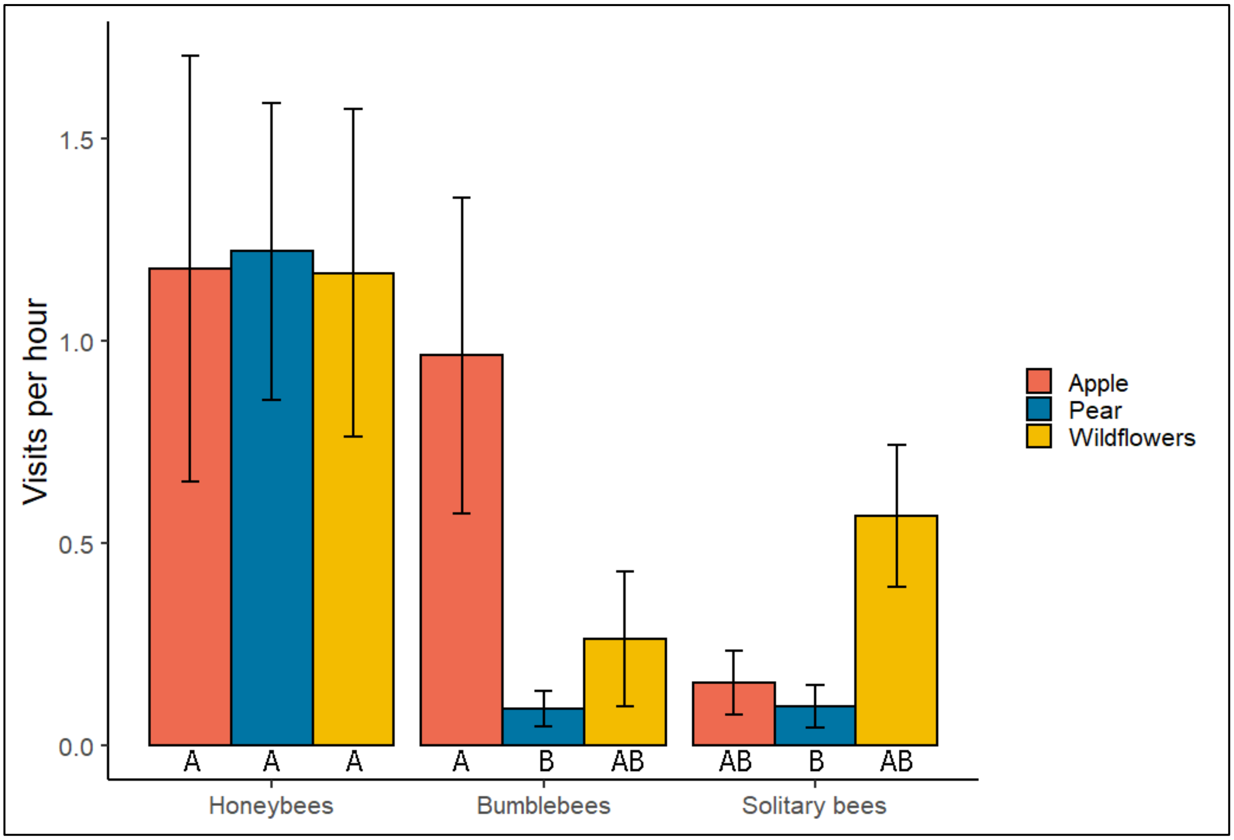


Figure 7 *The visitation frequency calculated as visits per hour for each bee group and plant species. Statistically significant differences in mean FVF (p < 0.05) are indicated by different letters underneath bars.*

2.3.2 Flower constancy

Among 168 recorded foraging trips and 2572 observed flower visits, only 11 changes between flower species were seen (table 5). All changes between plant species were observed during 8 foraging trips, all recording bumblebees. Of the 82 foraging trips by bumblebees, almost 10% included at least one change to a different plant species than the bumblebee was foraging on previously.

2.3.3 Handling time, search time and proportion search time

The average bumblebee had shorter handling times than honeybees (table 6), the difference between groups was statistically significant for both crops ($p < 0.05$, table 6), but was more pronounced in apple flowers, where honeybees had almost 3 times higher handling times on average, compared to bumblebees. Both groups had lower handling times in pear flowers, especially honeybees, which had half as long mean handling times in pear flowers. The difference was between crops for honeybees ($p < 0.05$), but not for bumblebees.

Table 6: *Summary of the means ± std. error for handling time, search time, proportion time and visitation rate between groups and species. Statistically significant differences in means (p < 0.05) are represented by different letters.*

		Foraging trips	Flower visits	Mean handling time per trip (sec)	Mean search time (sec)	Mean proportion search time	Visitation rate (flower visits/hour)
Apple	Bumblebees	34	580	3.65 ± 0.35 A	1.89 ± 0.12 A	0.33 ± 0.12	12.64 ± 0.70
	Honeybees	34	493	10.48 ± 0.69 B	3.60 ± 0.32 B	0.24 ± 0.11	5.06 ± 0.37
Pear	Bumblebees	34	834	2.78 ± 0.15 A	2.65 ± 0.25 C	0.44 ± 0.13	12.81 ± 0.69
	Honeybees	34	302	5.23 ± 0.39 C	3.47 ± 0.33 B	0.36 ± 0.15	8.19 ± 0.47

Considering search time, the result was similar, with bumblebees having shorter search times than honeybees in both fruit crops, and the difference being more pronounced between groups in apple flowers. The differences between groups were statistically significant ($p < 0.05$, table 6). The lower handling times and search times of bumblebees translated into a higher visitation rate overall (table 8), but bumblebees had similar visitation rates across crops, as they had higher handling time in apple (3.65±0.35 vs 2.78±0.15), but higher search time in pear (2.65±0.25 vs. 1.89±0.12, $p < 0.05$). Honeybees had higher visitation rate in pear, as their handling times were twice as low there, compared to apple, while the search time was similar between fruit crops and not significantly different ($p > 0.05$).

For both groups, the proportion of search time (PST) was lower than 0.5 in both crops (table 6), showing that the majority of the total foraging time was spent handling flowers, rather than travelling between them. PST was lower for honeybees compared to bumblebees in apple and pear. Both groups had a lower PST in apple flowers, compared to pear (figure 8).

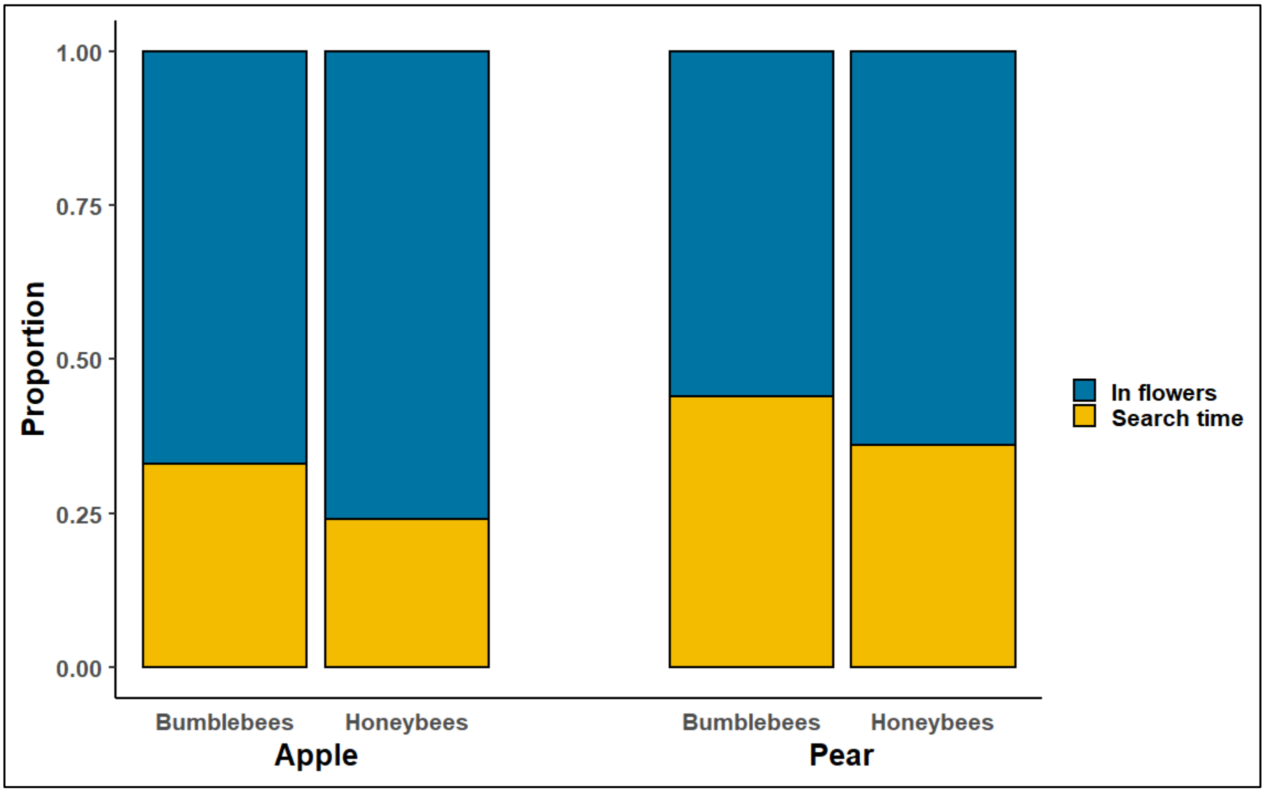


Figure 8 *Stacked barplot showing the average relative proportion of search time vs. handling time for honeybees and bumblebees in apple and pear flowers.*

2.3.4 Number of tree and row changes

The mean number of tree changes per flower visit for apple foraging bumblebees and honeybees was similar, showing no statistically significant difference ($p < 0.05$, table 7). In pear, however, there was a significant difference between groups, as honeybees changing trees more frequently (0.15±0.02 vs. 0.12±0.03, $p < 0.05$). The probability of row change was similar across groups and plants (0.01-0.03±0.01, table 11), and the means were not significantly different.

Table 7 *means ± std. errors of the probability of tree and row changes between groups and plant species.*

		foraging trips	Flower visits	Probability of	
				Tree change	Row change
Apple	Bumblebees	34	580	0.11 ± 0.02 A	0.02 ± 0.01 A
	Honeybees	34	493	0.10 ± 0.02 A	0.03 ± 0.01 A
Pear	Bumblebees	34	834	0.12 ± 0.03 A	0.01 ± 0.01 A
	Honeybees	34	302	0.15 ± 0.02 B	0.02 ± 0.01 A

2.4 Discussion

The aim of this study was to compare the visitation frequency and a set of foraging characteristics between managed honeybees and wild bees visiting apple and pear orchards in Western Norway. Even though direct measurements of pollinator performance like flower visitation frequency and single visit contribution to pollination is essential for determining pollinator performance, a broader set of characteristics is useful to evaluate which pollinators are important. In Norway, this remains understudied, and my study provides insight to the relative contributions of common crop pollinators in Western Norway.

2.4.1 Flower visitation frequency

I expected honeybees to be the most frequent visitor to the apple and pear orchards in my study sites. The flower visitation survey confirmed my expectation; however, the bumblebees were similarly frequent to apple flowers, and the differences between groups was not statistically significant for apple flower visits. Furthermore, I expected pear flowers to receive fewer visits from wild bees compared to apple and wildflowers. This was what I found, as apple and wildflowers were visited more than twice as often as pear on average. This is consistent with previous work, which found lower pollinator visitation frequency to pear compared to apple flowers on the same farm (Quinet et al., 2016). However, no statistically significant difference was detected between plants for total bee visits, but this was driven by the high visitation by honeybees to pear. Honeybees visited pear flowers more than six times as frequently on average compared to the two wild bee groups combined. Honeybees showed no preference between plants, in contrast to the wild bees, which seemed to prefer apple (bumblebees) and wildflowers (solitary bees) over pear. The overall differences in visitation frequency between groups are likely explained in part by their relative abundances in the local area. Earlier surveys have indicated that honeybees, in fact, are very abundant compared to wild bees in or near these sites (Vestheim, unpublished dataset). But the lower visitation frequency to pear compared to apple and wildflowers by wild bees indicate that they prefer other plants.

The low attractiveness of pear is usually explained by the low nectar production in pear flowers and the low sugar concentration of pear nectar (Delaplane & Mayer, 2000). A recent study compared the nectar and pollen quality of five apple and four pear varieties (Quinet et al., 2016).

They found that the nectar volume per flower was higher in pear, while apple flowers produced twice the amount of pollen per anther. On the other hand, the nectar quality (sugar concentration) was higher in apple, while the pollen quality (polypeptide, amino-acid and phytosterol concentrations) was higher in pear. Thus, bees are assumed to often visit apple flowers to collect nectar, while visiting pear flowers to gather pollen (Díaz et al., 2013; Quinet et al., 2016). Even though the pear and apple orchards in this study largely overlapped in bloom, the pear flowers bloomed a couple of days before the apple flowers. It is possible that some pear flowers were largely depleted of pollen and were thus avoided by the pollinators, though the high visitation by honeybees makes this less likely. In addition, Willmer et al. (1994) found that bumblebees have a high preference for young flowers in raspberry orchards, while honeybees do not share this preference. If this preference persists in apple and pear flowers, this could explain why the bumblebees was more attracted to the apple orchard during the study period, as more young flowers were available there, while honeybees showed no preference between apple and pear flowers.

Earlier work has shown a positive relationship between visitation frequency and yield in apple and pear (Quinet et al., 2016; Stern et al., 2001, 2004, 2007). This underlines the importance of managed honeybees in these systems, and as essential for pear pollination, while bumblebees should be considered at least as important as honeybees for apple pollination. Given that there is a higher proportion of nectar foragers in apple, earlier work has suggested that honeybees are less effective apple pollinators, because they often work the flower from the side (‘sideworking’) when collecting nectar, without touching the stigma and anthers. Thomson & Goodell (2001) compared the pollen deposition and removal by honeybees and bumblebees in apple flowers and analyzed the effect of visitation type (pollen collectors, nectar collectors and sideworkers). They found that honeybees and bumblebees removed similar amounts of pollen, but pollen collecting bees removed more than nectar collectors and side-working honeybees removed less pollen than all other honeybees. Furthermore, bumblebees deposited more pollen grains per visit than honeybees, which was largely attributable to sideworking honeybees depositing less pollen than all other visitors. Similarly, Park et al. (2016) found that *Melandrena* and *Bombus* deposited more pollen per visit than honeybees and that nectar foragers that ‘top worked’ deposited more pollen than pollen foragers, while sideworking individuals deposited less pollen than topworkers. Furthermore, Park et al. (2016) found that higher pollen loads generally led to higher fruit and seed set, but due to the higher wild bee pollen deposition having a saturating effect on reproduction, the per visit effect on fruit and seed set was only slightly higher in *Malandrena*, while *Bombus* were similar to *Apis*. In another experiment, Kendall (1973) caught free foraging honeybees in apple orchards and brushed their bodies against virgin flower stigmas. The pollen from pollen foragers resulted in as many fertilized ovules as self-pollinated controls done by hand, while pollen from nectar foragers did not. This implies that the pollen deposition of honeybees, and possibly the single visit contribution to fruit and seed set, may depend on the proportion of nectar foraging individuals in the system, as well as the proportion of sideworking pollinators, which can vary among cultivars (Thomson & Goodell, 2001) and between years (Park et al., 2016). Whether bumblebees are gathering pollen or nectar does not seem to matter as much for their pollination performance (Thomson & Goodell, 2001). This could mean that if honeybees generally prefer to gather pollen from pear, their per visit performance could be enhanced in pear compared to apple. On farms, like my study sites, where both apple and pear trees are grown, the honeybee hives could get much of their pollen requirements met by foraging for high quality pollen in pear orchards, while turning to apple orchards mostly for nectar, possibly leading to lower per visit performance in apple orchards. The type of visit and the quality and quantity of rewards was not investigated here, and these dynamics needs further investigation in these systems.

Finally, the survey suggests that solitary bees are less important pollinators of the crops, at least locally, being much less frequent than honeybees in pear, and less frequent than both honeybees and bumblebees in apple flowers. As seen in study 1, they are more common further south in the Hardanger region, where they likely are important pollinators.

2.4.2 Flower constancy

When observing the flower constancy of honeybees and bumblebees during foraging trips, not a single occurrence of changes between plant species were observed for honeybees. Only 10% of the bumblebee trips included changes between plant species, which represented > 1% of the total flower visits by bumblebees. As predicted, both groups were highly constant during their foraging trips, and honeybees were more constant than bumblebees. Previous research has shown that individual honeybees often specialize on one species, and remains constant irrespective of flower color, reward quality, quantity or frequency (Wells & Wells, 1983) (but see Grüter et al., 2011). Naïve bumblebees tend to sample a variety of flowers before specializing on the most numerous flower with high nectar reward until it is exhausted, then they resample for better rewards (Heinrich, 1976, 1979). Earlier work has found higher numbers of intraspecific flower visits in both groups, but honeybees are generally more constant (Reviewed in Grant, 1950). A recent study analyzing pollen, found that bumblebees on average visit five flower species per foraging trip (Martínez-Bauer et al., 2021). However, the study was conducted in diverse flower meadows where many different flower species grew interspersed. In my study systems, the fruit trees of the same species were grown in rows where few other resources were available in a distance where it was possible to observe changes. The apple and pear orchards where adjacent on one of the sites (Fosshagen), and changes between apple and pear flowers were only possible to observe when tracking foragers in the area between the two orchards. The ground floral diversity was very low in all orchards, dominated almost entirely by *Taraxacum* in three orchards, and by *Taraxacum* and *Glechoma hederacea* in the pear orchard in Ølmheim. The meadow between the rows were mowed in all orchards during the study period, reducing the occurrence of wildflowers below the fruit trees, which is common practice to reduce the competition for pollinators between crops and wild plants. In addition, the observations only represented a subset of the total foraging trips and were biased towards individuals that moved less, as they were easier to follow for more than three flower visits. If some cue prompted the pollinator to look for different flower rewards, it is likely that they would have flown out of the orchard and be lost for further observation. Thus, individuals which were constant to one flower species were probably overrepresented. A more direct way to measure flower constancy is to analyze pollen loads, which have shown similar results in previous studies; honeybees being more constant than bumblebees (Free, 1963, 1970; Grant, 1950). Studying apple foragers, Russo et al. (2017) found that honeybees carried 70% apple pollen in their loads, compared to 61% in *Bombus impatiens*. Willmer et al. (1994) found higher pollen purity for both in raspberry, still with purer loads in honeybees (94-95% vs. 78-91% in bumblebees), but opposite has been shown in cranberries (Mackenzie, 1994).

Nonetheless, my findings suggest that both groups are highly constant, reliably transferring conspecific pollen between the flowers of apple and pear.

2.4.3 Handling time, search time and proportion search time

Measuring the speeds during foraging trips revealed that bumblebees spend less time handling and travelling between flowers than honeybees, in both apple and pear. The differences between groups were more pronounced in apple foragers. This translated into a higher visitation rate for bumblebees, in both crops, and especially in apple, where bumblebees visited over twice as many flowers per minute as honeybees. Bumblebees had similar visitation rates in apple and pear flowers, probably due to the search time being lower for bumblebees in apple orchards, while honeybees had higher visitation rates in pear orchards, as both their handling times and search times were significantly lower here. However, the proportion of foraging trips that were spent travelling between flowers were lower in honeybees in both orchards and both groups had a lower proportion of search time in apple orchards.

As predicted, the bumblebees were faster foragers than honeybees. This has been shown in a variety of other fruit crops, including sweet cherry (Eeraerts et al., 2019), cranberry (Mackenzie, 1994) and raspberry (Willmer et al., 1994). Several studies have compared the handling time and/or visitation rate of bumblebees and honeybees in apple. Martins et al. (2015), like me, found that bumblebees handled flowers on average about three times faster than honeybees, and visited over twice as many flowers per minute. Others have found that the type of visitation influences handling times; pollen foragers being faster than nectar foragers while sideworking honeybees are slower than other visitors (Free, 1960; Thomson & Goodell, 2001). Park et al. (2016) found that honeybees almost doubled their average handling times in apple flowers from the first study year, where 53% of honeybees were gathering nectar and 35% were sideworking, to the next year where 70% were nectar foraging and 61% were sideworking. My observations of apple foraging honeybees were more similar to the handling times in the high nectar/high sideworking year in Park et al. (2016) as well as the handling times of sideworking honeybees in Free (1960). This implies that many apple foraging honeybees were gathering nectar during my study period, and that a high percentage of these were sideworking. It might also explain why honeybees had twice as high handling times in apple compared to pear flowers, especially if the honeybees mainly visited the pear orchard to gather pollen, which previous work suggests (Díaz et al., 2013). Another explanation could be the higher nectar concentration in apple (Quinet et al., 2016), which has been linked to increased handling times in bumblebees (Thomson, 1986), as the bumblebees also had higher handling times in apple. It is also possible that these studies show the same thing, namely that higher nectar concentrations lead to a higher percentage of bees gathering nectar, and that gathering nectar is more time consuming than gathering pollen. Fewer comparisons have been done between bumblebees and honeybees foraging in pear flowers, but Quinet & Jacquemart (2017) did not find a significant difference in handling times between the groups. Quinet & Jacquemart (2017) reported higher handling times compared to my study, especially for bumblebees, where the average handling time was three times as high. Others, only focusing on honeybees, found similar handling times as me (Monzón et al., 2004) while Free's (1960) findings were similar to Quinet & Jacquemart (2017), showcasing that this can vary widely inside and across groups depending on some variables, like geographic location, weather conditions and the cultivar investigated.

The differences in search times and the proportion of search time between honeybees and bumblebees are also poorly documented. Experimental work showed that bumblebees make slower, but more accurate decisions when seeking rewards, while honeybees minimize search time, at the cost of accuracy (Morawetz & Spaethe, 2012). This is consistent with my finding that bumblebees spent a higher proportion searching for flowers compared to honeybees, but inconsistent with my finding that the search times of bumblebees were significantly lower in both fruit crops. Morawetz & Spaethe (2012) hypothesized that the search mode of bumblebees is optimized for rich floral meadows comprising of flowers with unequal reward levels, while honeybees have evolved in the tropics, with scarcer, but clustered food sources. Accuracy may be less advantageous in commercial fruit trees, where more or less identical rewards are clustered on each tree (Morawetz & Spaethe, 2012). It is possible that bumblebees change their behavior in response to this situation, discriminating less between flowers, thereby reducing search time. The only study I found which compared the search time and proportion of search time between honeybees and bumblebees also found that bumblebees spent a higher proportion of the foraging trip searching for flowers in raspberry orchards (Willmer et al., 1994). However, Wilmer et al. (1994) also observed higher search times in bumblebees than in honeybees, which was explained by the high preference for young flowers in bumblebees. It is unclear whether the preference for young flowers by bumblebees persists in apple, but during my study period, the apple orchards had bloomed more recently than the pear orchard, and likely contained more young flowers. The abundance of young flowers might have limited the need for discriminating between flowers, and thus lowered the search time there. Contrastingly, the bumblebees had significantly higher search time in pear, which may indicate that the rewards were more inconsistent here since the orchard was in full bloom and many flowers had probably been visited previously. This is, however, only speculation, and the dynamics of search time needs further research in these systems.

2.4.4 Tree and row change

Investigating the probability of tree and row changes revealed that apple foraging honeybees and bumblebees had a similar proportion of inter-tree visits, while honeybees had a significantly higher proportion of inter-tree visits than bumblebees when foraging in pear flowers. For probability of row change, no difference was detected between the two groups. These findings are contrary to my prediction that bumblebees have a higher probability of changing trees and rows. Similar studies have concluded that honeybees move less frequently between rows compared to bumblebees (Eeraerts et al., 2019; Willmer et al., 1994) or other wild pollinators (Bosch & Blas, 1994). However, I did not find any studies in apple or pear which report differences between honeybees and wild pollinators in their probability to change trees and/or rows. Vicens & Bosch (2000) recorded the number of inter-tree flights to different rows in honeybees and *O. cornuta* foraging in apple orchards. For honeybees the percentage of row changes was 18% vs. 21% in *O. cornuta*, but the difference was not statistically significant. These findings were in accordance with my results, where ~18% of the three changes in apple were row changes, for both groups. Quinet & Jacquemart (2017) recorded the number of pear foraging individuals that changed trees and rows during their foraging trips. They found that honeybees and bumblebees had similar percentages of tree changes (~60%) and row changes (~1%). This is equivalent to the percentages of trees changes found in my study (62-68%), but the percentages of individuals who changed rows were much higher. In the apple orchards 26% of individuals were observed changing rows at least once, in both groups, while in the pear orchards 21% of bumblebees and 18% of honeybees changed rows. Considering the higher foraging speed of bumblebees, the average bumblebee should visit a higher number of trees and rows than a honeybee during foraging trips of equal length, possibly contributing more to cross-pollination. This is especially true for apple, where the probability of tree and row changes were similar between groups, and the difference in foraging speed was more pronounced. The length of foraging trips was compared between bumblebees and honeybees in a recent study (Minahan

& Brunet, 2018). On average, the foraging trips of bumblebees were 10 minutes longer than for honeybees, but difference was not statistically significant. However, they found that bumblebees made significantly more trips per day and spent more total time foraging during a given day.

Previous research has also concluded that the presence of bumblebees leads to greater movement by honeybees through synergistic interactions inside the orchards. Sapir et al. (2017) found that adding bumblebees to apple orchards improved pollination compared to orchards with lower abundance of bumblebees. Sapir et al. (2017) attributed this not only to the increased number of pollinating insects, but also the increased movement of honeybees as well as an increased proportion of topworking honeybees, which are more efficient pollinators. Similar results have been found in pear, but the movement and proportion of topworking individuals were not analyzed (Zisovich et al., 2012). Bumblebee abundance and diversity has also been related to increased foraging rate and probability of row change in honeybees visiting sweet cherry (Eeraerts et al., 2020). Given these findings, one could expect the probability of row change and foraging rate of honeybees to increase in the apple orchards, given the higher bumblebee visitation there. This was not what I found, as the honeybees had a higher probability of row change and foraging rate when foraging in pear orchards. Honeybees have also been found to exchange pollen with nestmates by within-hive movements (Free & Williams, 1972; Paalhaar et al., 2008). This could lead to honeybees picking up compatible pollen inside the hive and disperse it to crop flowers on the next foraging trip. However, it might also lead to honeybees picking up pollen from other plant species than the crop they specialize on, decreasing pollen purity and increasing heterospecific pollen transfer to crops (Degrandi-Hoffman et al., 1986; Free & Williams, 1972).

As several other studies have pointed out (Free, 1960; Kron et al., 2001; Quinet & Jacquemart, 2017) the inter-tree and especially inter-row movements are very difficult to track, as bees are often lost out of sight when they change tree and especially rows. This was the case in my study as well, especially in the three orchards where irrigation systems were installed along the rows, making it difficult to move between rows when following bees. Thus, the observations were probably biased towards samples of foraging trips with little movement between rows, thereby underestimating the probability of row change overall.

2.4.5 Conclusion

In this study, I have shown that honeybees are frequent and constant visitors to apple and pear flowers in the investigated systems, making them essential for pollination, especially in pear crops, where the honeybees had higher probability of tree change, more equal foraging speed and superior visitation frequency, compared to wild pollinators. Bumblebees visited apple flowers as frequently as honeybees, possibly making them more important for apple pollination considering them being almost as constant during foraging trips and as probable to change trees and rows, while visiting many more flowers per minute, probably resulting in a higher contribution to cross-pollination per individual.

The observations were limited by the difficulty of tracking bees, especially when they moved between rows, biasing the samples towards individuals that were easier to follow. It is not clear how this affected the results, but the amount of movement between trees and rows was probably underestimated, while the flower constancy overestimated, as pollen was not analyzed. The method was also poor for evaluating the smaller solitary bees, which I was unable to track. Still, my findings provide important insight into bee behavior, especially the overlooked aspect of search time between flower visits, as well as the relative importance of different pollinators in fruit crops, which has received little attention in Norway. Future research should focus on replicating these findings in similar systems, as well as determining the single visit contribution of pollinators visiting fruit crops in Norway and their relative pollen purity, which was not measured here. Another unexplored topic is the relative pollen and nectar quality and quantity in the apple (*Summerred*) and pear (*Celina*) cultivars studied here, and how this relates to pollinator visitation and foraging behavior.

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Appendices

A. Model outputs study 1:

Summary outputs of the models where the fixed effect was significant ($p < 0.05$).

A.1 Solitary bees

Table I *GLMMs where a significant effect ($p < 0.05$) of Pforest or Pconiferous was found on the abundance/richness of solitary bees. All models (1-3) were fitted with a Poisson error distribution.*

Model 1: Solitary bee abundance~Pforest 0-250m

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
(Intercept)	-1.5236	0.5046	-3.02	0.0025	*
Pforest_0-250	17.6041	7.5506	2.343	0.0175	*
Random effects	variance	Std.Dev.			
location	0.9854	0.9927			

Model 2: Solitary bee species richness~Pforest 0-250m

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
(Intercept)	-1.5475	0.3831	-4.04	5.34E-05	*
Pforest_0-250	12.0932	5.4508	2.219	0.0265	*
Random effects	variance	Std.Dev.			
location	0.3916	0.6258			

Model 3: Solitary bee abundance~Pconiferous 0-250m

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
(Intercept)	-1.132	0.4005	-2.826	0.0047	*
Pconiferous_0-250	16.2984	7.1572	2.277	0.0228	*
Random effects	variance	Std.Dev.			
location	0.8638	0.9294			

A.2 Bumblebees

Table II *GLMMs where a significant effect (p < 0.5) of Pagriculture or Ppastures was found on the abundance/richness of bumblebees. All models (1-8) were fitted with a Poisson error distribution.*

Model 1: Bumblebee abundance~Pagriculture 1500-2000m

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
(Intercept)	-2.0623	0.4961	-4.157	3.23E-05	*
Pagriculture_1500-2000	2.7922	1.2297	2.271	0.0232	*
Random effects	variance	Std.Dev.			
location	1.29	1.136			

Model 2: Bumblebee abundance~Ppastures 500-750m

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
(Intercept)	-1.8285	0.4462	-4.098	4.17E-05	*
Ppastures_500-750	14.5378	7.2748	1.998	0.0457	*
Random effects	variance	Std.Dev.			
location	0.637	0.7982			

Model 3: Bumblebee abundance~Ppastures 750-1000m

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
(Intercept)	-1.8374	0.3595	-5.111	3.20E-07	*
Ppastures_750-1000	14.96	5.0227	2.978	0.0029	*
Random effects	variance	Std.Dev.			
location	0.4351	0.6596			

Model 4: Bumblebee richness~Ppastures 750-1000m

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
(Intercept)	-1.974	0.343	-5.757	8.58E-09	*
Ppastures_750-1000	12.753	4.635	2.752	0.00593	*
Random effects	variance	Std.Dev.			
location	0.3326	0.5767			

Model 5: Bumblebee abundance~Ppastures 1000-1500m

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
(Intercept)	-2.0207	0.3911	-5.167	2.38E-07	*
Ppastures_1000-1500m	8.7974	2.8435	3.094	0.00198	*
Random effects	variance	Std.Dev.			
location	0.3885	0.6233			

Model 6: Bumblebee richness~Ppastures 1000-1500m

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
(Intercept)	-2.1289	0.3776	-5.638	1.72E-08	*
Ppastures_1000-1500m	7.564	2.7053	2.796	0.00517	*
Random effects	variance	Std.Dev.			
location	0.3084	0.5554			

Model 7: Bumblebee abundance~Ppastures 1500-2000m

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
(Intercept)	-1.8708	0.3442	-5.435	5.48E-08	*
Ppastures_1500-2000m	6.756	2.0516	3.293	0.00099	*
Random effects	variance	Std.Dev.			
location	0.3626	0.6021			

Model 8: Bumblebee richness~Ppastures 1500-2000m

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
(Intercept)	-1.9929	0.3307	-6.027	1.67E-09	*
Ppastures_1500-2000m	5.6982	1.9108	2.982	0.00286	*
Random effects	variance	Std.Dev.			
location	0.2818	0.5309			

B. Model outputs study 2:

Summary outputs all models used in study 2.

B.1 Flower visitation frequency

Table III *GLMMs comparing flower visitation frequency between bee groups (1) and plant species (2) and the interaction between bee group and plant species (3). All models (1-3) were fitted with a negative binomial error distribution.*

Model 1: Flower visitation frequency: Bee group

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
groupbumblebees (intercept)	-2.578	0.3128	-8.242	<2e-16	*
grouphoneybees	0.9635	0.4315	2.233	0.0255	*
groupsolitary_bees	-0.464	0.4474	-1.037	0.2997	
Random effects	variance	Std.Dev.			
Plot-id	4.41E-09	6.64E-05			

Model 2: Flower visitation frequency: Plant species

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
plantApple (intercept)	-2.0473	0.3129	-6.543	6.02E-11	*
plantWildflowers	-0.1527	0.444	-0.344	0.731	
plantPear	-0.4968	0.4723	-1.052	0.293	
Random effects	variance	Std.Dev.			
Plot-ID	3.25E-09	5.70E-05			

Model 3: Flower visitation frequency: Plant species

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
Bumblebees, apple (intercept)	-1.8337	0.4507	-4.069	4.72E-05	*
grouphoneybees	0.2277	0.6307	0.361	0.71811	
groupsolitary_bees	-1.74	0.6891	-2.525	0.01157	*
plantwildflowers	-1.2962	0.667	-1.943	0.05197	.
plantPear	-2.3273	0.7326	-3.177	0.00149	*
grouphoneybees:plantWildflowers	1.2627	0.915	1.38	0.16759	
groupsolitary_bees:plantwildflowers	2.5124	0.9629	2.609	0.00908	*
grouphoneybees:plantwildflowers	2.3435	0.9889	2.37	0.0178	*
groupsolitary_bees:plantPear	1.7809	1.0677	1.668	0.09533	.
Random effects	variance	Std.Dev.			
location	4.33E-01	0.6583			

B.2 Handling time and search time

***Table IV** GLMMs comparing the handling times (1) and search times (2) across bee groups and plant species. All models (1-2) were fitted with a negative binomial error distribution.*

Model 2: Handling time					
Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
Bumblebees, apple (intercept)	1.25578	0.07199	17.443	< 2e-16	*
grouphoneybee	1.08016	0.10317	10.47	< 2e-16	*
plantpear	-0.23175	0.09772	-2.372	0.01771	*
grouphoneybee:plantpear	-0.44487	0.13602	-3.271	0.00107	*
Random effects	variance	Std.Dev.			
location	8.37E-04	2.89E-02			

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Model 3: Search time					
Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
Bumblebees, apple (intercept)	0.53463	0.18328	2.917	3.53E-03	*
grouphoneybee	0.79537	0.10354	7.682	1.57E-14	*
plantpear	0.26094	0.09621	2.712	0.006684	*
grouphoneybee:plantpear	-0.48282	0.138	-3.499	0.000467	*
Random effects	variance	Std.Dev.			
location	5.72E-02	0.2392			

B.3 Tree and row change

Table III *GLMMs comparing the probability of tree (1) and row (2) change across bee groups and plant species. All models (1-2) were fitted with a Poisson error distribution.*

Model 4: Tree change

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
Bumblebees, apple (intercept)	-2.0901	0.1534	-13.626	< 2e-16	***
grouphoneybee	-0.3231	0.2358	-1.37	1.71E-01	
plantpear	-0.3718	0.1635	-2.274	0.022951	*
grouphoneybee:plantpear	1.0757	0.2794	3.85	0.000118	***
Random effects	variance	Std.Dev.			
location	1.67E-02	0.1293			

Model 5: Row change

Fixed effects	Estimate	Standard error	z value	Pr(>|z|)	
Bumblebees, apple (intercept)	-3.5904	0.25	-14.362	<2e-16	***
grouphoneybee	-0.4128	0.4167	-0.991	3.22E-01	
plantpear	-0.9386	0.4167	-2.253	0.0243	*
grouphoneybee:plantpear	1.0232	0.6719	1.523	0.1278	
Random effects	variance	Std.Dev.			
location	5.12E-10	2.26E-05			