

**Bumblebee communities in open and overgrown heathlands in
Nordhordland UNESCO Biosphere, Vestland, Norway**

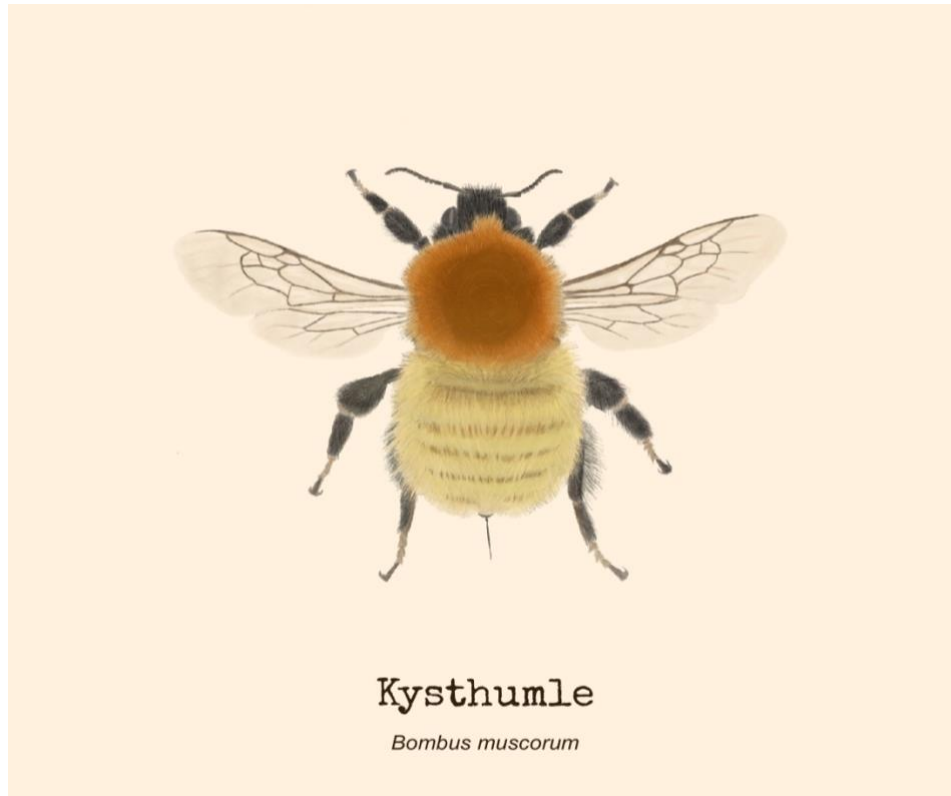


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Abstract

Insect pollinators such as bumblebees (*Bombus* spp.) play a vital role in the pollination of wild and cultivated plants and is therefore critical for ecosystem services and food security worldwide, especially in northern ecosystems. However, declines in pollinators have been reported due to anthropogenic drivers such as land use change and agricultural intensification. This study aims to investigate communities of *Bombus* species in open and overgrown heathlands in a UNESCO Biosphere Reserve in Vestland, Norway. Pan traps and insect aerial nets were used to effectively capture pollinators in six study sites during two distinct sampling periods: June and August. A total of nine *Bombus* species were identified, with the most abundant being *B. lucorum complex*, *B. jonellus*, and *B. pascuorum*, which accounted for 71% of the individuals. Species composition varied between the sites. The overgrown heathlands typically had a higher abundance of habitat generalists like *B. pratorum*, while the specialist and red-listed species *B. muscorum* were recorded exclusively in open heathlands. The sampling period was a significant predictor of *B. muscorum* abundance. *B. jonellus* however, was more abundant in overgrown sites despite being a specialist on Ericaceae, which may be due to the additional floral diversity and nesting sites found here. Further research should explore the potential impacts of landscape characteristics like fragmentation and management practices on the abundance of *Bombus* in heathlands. Habitat conservation is considered the most effective way to conserve insect pollinators and should be highlighted in policy-making decisions to maintain healthy populations.

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1. Introduction

1.1 The role of insect pollinators

Insects play a vital role in the seed production of both wild and cultivated plants. Around 70% of global crops consumed directly by humans depend on pollinators (Klein *et al.*, 2007). The ecosystem service provided by pollination has been valued at approximately 153 billion euros per year, illustrating the importance of pollinators for food production globally (Gallai *et al.*, 2009). In addition, many of the crops provide essential micronutrients, providing health benefits and preventing deficiencies in vitamin A, iron, and folate (IPBES, 2016). In wild plants, 87.5% of the species worldwide depend, to some degree, on pollination for sexual reproduction (IPBES, 2016). In Norway, up to 80% of wild plant species likely benefit from visitations by insect pollinators, which are also the only pollinators present in Northern ecosystems (Totland *et al.*, 2013). Some plants are pollinated by a small number of species, making them especially vulnerable to declines in insect populations (Totland *et al.*, 2013). Pollinators also directly impact various food webs, as many are eaten by predators, or indirectly, by aiding in the reproduction of plant species other species depend on (IPBES, 2016). The state of pollinator populations is relevant for several of the sustainable development goals (SDGs), but especially SDG 2: Zero hunger, and SDG 15: Life on land. As a consequence, declines in insect pollinator diversity and/or abundance are likely to have an array of negative impacts (IPBES, 2016). Any shifts or declines in pollinator communities and their drivers are thus important to monitor, and many are reporting declines (Kearns *et al.*, 1998; Goulson *et al.*, 2005; Wepprich *et al.*, 2019).

Providing evidence for declines in insect pollinators is difficult as we lack long-term data for many species, especially in areas outside Europe and North America (Wagner, 2020). Insect populations also fluctuate naturally from year to year, so separating this from long-term anthropogenic-induced declines may be challenging (Davies, 1988). This issue further illustrates the importance of historic data on pollinator species. Nonetheless, studies have reported declines in populations with land use change, pollution, pesticides, pathogens, and alien species being identified as direct anthropogenic drivers (NRC, 2007; Biesmeijer *et al.*, 2006; IPBES, 2016; Sánchez-Bayo and Wyckhuys, 2019). The International Union for Conservation of Nature (IUCN) estimated that about 9% of all bee species in Europe were threatened with extinction in 2014, while an additional 5% was considered near threatened

(Nieto *et al.*, 2014). However, more than half of the species were deficient in data, and thus their risk of extinction was not evaluated. When data-deficient species were excluded, an estimated 37% of bee populations in Europe were declining (IPBES, 2016). For Norway, the number of bees threatened with extinction has been predicted to be 17%, while almost 31% were listed on the Norwegian Red List in 2021, and 20 pollinator species were identified as being extinct (Artsdatabanken, 2021a). Even though many species are facing declines, some are also experiencing an increase in their relative abundance. A study in Britain showed that the species experiencing an increase in their relative abundance were the already common species, leading to a homogenization where mostly generalists dominated the community (Biesmeijer *et al.*, 2006). Species with narrow habitat requirements, those foraging on a small number of taxa, and/or long-tongued species showed larger declines. This was also true for species with slower development and lower mobility. In addition, they found that plants pollinated exclusively by bees were also in decline, confirming that specialist pollinators and the plants they pollinate are declining in tandem (Biesmeijer *et al.*, 2006). A study from Sweden found similar trends where the relative abundance of two short-tongued bumble bee (*Bombus*) species increased from 40% in the 1940s to 89% in 2010 (Bommarco *et al.*, 2011). This is alarming because changes in *Bombus* communities or decreases in species richness may impact pollinating services by reducing the magnitude and/or stability. The resilience of pollinating services is also reduced as species with potential differences in their response to changes, disappear from the systems (Bommarco *et al.*, 2011).

1.2 Bumble bees

Bumble bees (*Bombus*), from the superfamily Apoidea, are an important group of pollinators for many crops, with some examples being blueberry (*Vaccinium myrtillus*) and red clover (*Trifolium pratense*) (Holm, 1966; Campbell *et al.*, 2017). Because of their relatively large body size, dense fur, and thermoregulating abilities, they can fly when temperatures are cool, even as low as at 4°C (Bergman *et al.*, 1996). In addition, they can forage in low-light conditions, making them especially important pollinators at high elevations and in northern latitudes (Hatfield *et al.*, 2012). Worldwide, there are about 250 described species, mostly found in the temperate, alpine, and arctic parts of the Northern Hemisphere (Goulson *et al.*, 2008). In Norway, 35 species of *Bombus* have been registered, although one of them, *B. semenoviellus*, has only been found once (Ødegaard *et al.*, 2015). Of the established species,

five were listed on the Norwegian Red List in 2019, while six were listed in 2021 (Artsdatabanken 2021b; Bengtson and Røsok, 2019). Habitat loss and fragmentation, and agricultural intensification have been attributed as the main reasons for declines in *Bombus* species over the last 60 years (Kosier *et al.*, 2007; Goulson *et al.*, 2008). The decline of several species, including *B. subterraneus*, which was considered extinct in Norway in 2009, but has since been reestablished, is thought to be linked to agricultural changes (Goulson *et al.*, 2008; Artsdatabanken, 2014). More specifically, the reduction in leguminous crops, especially *T. pratense* previously used as fodder. In Europe, the increase in silage for cattle feed consequently reduced the abundance of Fabaceae-rich hay meadows. This switch is likely to have impacted the availability of floral resources for bumblebees (Goulson *et al.*, 2008). Habitat fragmentation often results in small and isolated populations, making them vulnerable to loss of genetic diversity through bottlenecks and drift (Keller and Waller, 2002). It is also believed that the impacts of habitat degradation and fragmentation are intensified by low effective population sizes, making *Bombus* species especially vulnerable to stochastic processes and inbreeding.

1.3 Coastal heathlands as a disappearing habitat

Coastal heathlands are one of the ecosystems that have suffered greatly from land use change and agricultural intensification (Gimingham, 1972). Being one of the oldest cultural landscapes in Europe, it started to develop more than 4000 years ago and had its maximal range during the 1800s (Parry, 2003). This semi-natural landscape was formed by human populations through their farming practices as an adaptation to the coastal climate with mild winters. Its range stretches along the coast of Europe from the south of Portugal, all the way to the north of Norway. In Norway, only 10% of the coastal heathlands remain, and here it is one of the most threatened vegetation types. For this reason, it was registered on the Norwegian Red List (EN) in 2018 and is also listed in NATURA 2000, making it protected in the EU countries (Kaland and Kvamme, 2013). Being considered a selected nature type in Norway, it is also under some protection here. In 2019, Nordhordland, an area on the west coast of Norway became designated as a UNESCO Biosphere Reserve. Here, it serves as a model area for sustainable development and one of the objectives is to conserve bio- and cultural diversity, including its coastal heathlands. Life in this region was traditionally based on farming and fishing, but many areas have become overgrown due to industrial

modernization (Kaland et al. 2018). The reduction of heathlands in Norway started around the 1950s when traditional farming methods were no longer profitable, and in 1980, these practices almost disappeared entirely. Since the 1800s, more than 80% of the heathlands in Europe have vanished (Kaland and Kvamme, 2013). The decline is caused by several factors like the absence of traditional farming practices, afforestation, invasion of Sitka spruce, intensified cultivation and fertilization, nitrogen deposits from rain (pollution), climate change, and land-use change related to infrastructure-, industry- and residential development. Being a semi-natural habitat, it requires management practices, like grazing, cutting, and burning to prevent it from becoming overgrown (Gimingham, 1972). Burning inhibits the establishment of shrubs and trees not grazed by livestock, like juniper (*Juniperus communis*) which can quickly dominate the area. Burning is also used to remove degenerate heather, and thereby increase the abundance of juvenile heather, grasses, and herbs, providing nutritious feed for livestock. The grazing quality is maintained by keeping a mosaic structure, with areas of heather in different stages and a variety of grasses and herbs. This structure is only maintained through regular burning which enables the livestock to graze all year (Måren 2009, Kaland and Kvamme, 2013).

The vegetation of heathlands is dominated by heather (Ericaceae) and other dwarf shrubs, with the wintergreen *Calluna vulgaris* (hereafter called *Calluna*) being the dominating plant (Diemont *et al.*, 2013). Its flowering period ranges from July to September, depending on the location (Gimingham, 1972). This is also the observed flowering time in Norway (Mossberg *et al.*, 2021). The flowers of *Calluna* have longitudinal splits which allow easy access for a large diversity of insects (Mahy *et al.*, 2011). Coastal heathlands serve as important habitats for *Bombus* species because of the floral resources (pollen and nectar) and the succession of flowering periods (Moquet *et al.*, 2017). They are often inhabited by specialist pollinator species subject to decline and provide refuge for many rare species (Descamps *et al.*, 2015; Moquet *et al.*, 2017). *Calluna* is especially important for pollinators during the end of the season due to the high abundance of blooming flowers in heathlands. Several insect orders are known to visit *Calluna*, but Mahy *et al.* (2011) identified bumblebees as being the most effective pollinators of this plant. In addition, *Erica cinerea* (NT), a heather species pollinated by *Bombus* species is found almost exclusively in these habitats (Waters *et al.*, 2011).

As heathlands are left unmanaged, tall shrubs and trees start colonizing the area, and the system gradually shifts towards woodland (Diemont *et al.*, 2013). Ecological succession will over time affect species depending on remaining open habitats (Banaszak and Ratyńska, 2014; Kosior *et al.*, 2008), and *Bombus* typically prefer open, ruderal, and semi-natural spaces (Bąk-Badowska *et al.*, 2021). Changes in habitats may alter the availability of floral resources accessible for *Bombus* species and the quantity and/or quality of pollen and nectar may be reduced (Kleijn and Raemakers, 2008; Moquet *et al.*, 2017; Goulson *et al.*, 2015; Bąk-Badowska *et al.*, 2021). Fragmentation of heathlands can threaten pollinators as temporal or spatial gaps of floral resources increase, as well as impact their lifecycles as the continuity of flowering is affected (Moquet *et al.*, 2017). Suitable nesting sites may also be disturbed and/or reduced, especially for species nesting on or just beneath the ground (Goulson *et al.*, 2015). In addition, the presence of forest patches could act as a possible barrier for foraging individuals like *B. muscorum* (Kreyer *et al.*, 2004). Bąk-Badowska and colleagues (2021), compared *Bombus* communities in open and forested habitats, and found that forest sites harbored lower abundances, less richness, and lower diversity compared to open sites. *Bombus* might be negatively impacted by encroachment as the presence of forest patches decreases their foraging area. However, it is important to note that the presence of trees may also be advantageous to some species as they provide possible nesting and overwintering sites (Diaz Forero *et al.*, 2011).

1.4 Aims and objectives

The aim of this study was to explore pollinator communities in coastal heathlands comparing findings from open sites with overgrown sites. Reviewing *Bombus* presence in overgrown sites can give us an insight into possible future changes in community compositions as more heathlands are left unmanaged. Abundance and species richness were examined at all sites. In addition, data on vegetation cover and weather conditions were also registered and their effects on abundance were reviewed. Studies on insects in Norway's coastal heathlands are scarce (but see: Hatteland *et al.*, 2005; Bargmann *et al.*, 2015; Bargmann *et al.*, 2016). Thus, this study will help fill knowledge gaps on pollinators in the heathlands of this region. This project is linked to and partially funded by the NFR project BIOSPHERE, which focuses on areas under pressure. Further, this thesis serves as a possible starting point for future

monitoring to document how communities change over time in Nordhordland UNESCO Biosphere Reserve.

Based on earlier studies, we can make some predictions of how *Bombus* communities differ in open and overgrown habitats. Because of the narrow habitat requirements and short foraging distance of *B. muscorum* (Walther-Hellwig and Frankl, 2000), it is likely that this species is mostly found in open heathland sites. As *B. jonellus* is a specialist on Ericaceae (Moquet *et al.*, 2017; Potapov and Kolosova, 2020), it is also likely that the abundance of this species is higher in open heathlands compared to overgrown heathlands. Further, species richness may be higher in open heathlands, as *Bombus* species typically prefer open and seminatural habitats (Bąk-Badowska *et al.*, 2021). Since the abundance of flowering *Calluna* is high during the last sampling period, *Bombus* abundance could also be higher for the open sites at this time. When *Calluna* is in bloom, the foraging distances between each flower are short, and individuals may benefit from foraging here by reducing their energetic costs related to flying (McCallum *et al.*, 2013). More specifically, I aim to investigate the following research questions to compare *Bombus* communities in the two different heathland habitats:

1. Is there higher abundances of the specialist species *B. muscorum* and *B. jonellus* in open coastal heathlands?
2. Is there a difference in *Bombus* richness between the habitat types?
3. Is there a difference in *Bombus* abundance for the two sampling periods related to the flowering period of *Calluna*?

2. Materials and methods

2.1 Study species

One of the red-listed species in Norway is the long-tongued moss carder bee (*Bombus muscorum*). This species has its range along the coast from Vest-Agder to Lofoten in Norway and is highly connected to coastal heathlands (Figure 1) (Bengtson and Røsok, 2019). *B. muscorum* was listed as near threatened (NT) on the Norwegian red list in 2010 and its status remained unchanged in 2019 (Bengtson and Røsok, 2019; Artsdatabanken, 2021b). On the European red list, it is classified as vulnerable (VU) (Nieto *et al.*, 2014). It prefers sandy meadows or fields, bogs, and heathlands as its habitat. Here, the queen usually forages on *Salix* spp. after emerging, and later on *Erica tetralix* and Fabaceae, while the workers feed on *Calluna* as well as several other plants (Bengtson and Røsok, 2019). *B. muscorum* is a late-emerging species, with males having been observed leaving the nest from the end of July (Ødegaard *et al.*, 2015). It nests on the ground and the group usually consists of less than 40 individuals (Ødegaard *et al.*, 2015). Another species strongly associated with *Calluna* is the heath bumble bee, *Bombus jonellus*. This species is found in several nature types but typically occurs in coastal heathlands, mountains, and dry forested areas (Figure 2). It prefers to forage on *Calluna* and other heath plants but also visits several other plants. This species emerges earlier than *B. muscorum*, with males in Norway having been registered flying from the beginning of June (Ødegaard *et al.*, 2015). It also differs from *B. muscorum* by being a short-tongued species (Goulson *et al.*, 2005). This species nests both above and below ground, and the colony can consist of anywhere from 50-120 individuals. *B. jonellus* is not listed on the Norwegian or European red list, however, some countries have reported declines for this species. Belgium, the Netherlands, Denmark, Germany, Switzerland, Austria, the Czech Republic, and Poland all listed this species as either endangered (EN), near threatened (NT), or vulnerable (VU) in 2001 (Celary *et al.*, 2007).

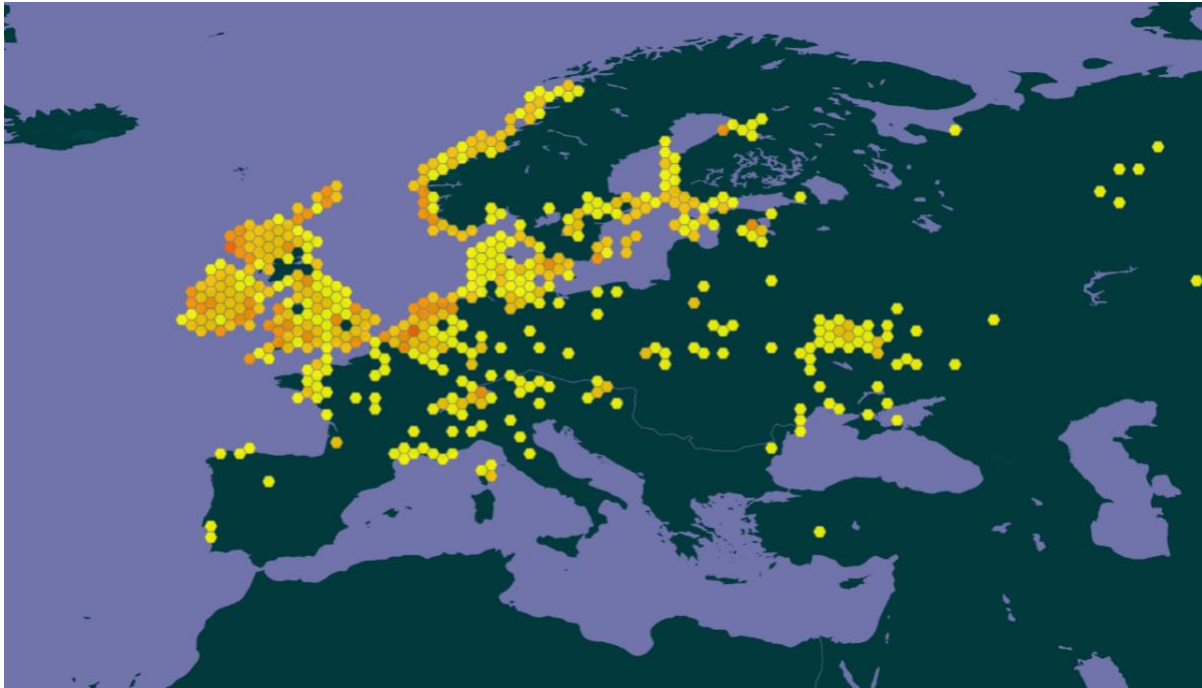


Figure 1: Distribution of *B. muscorum*. Darker colors indicate higher abundances. Generated by OpenStreetMap, OpenMapTilen, GBIF.

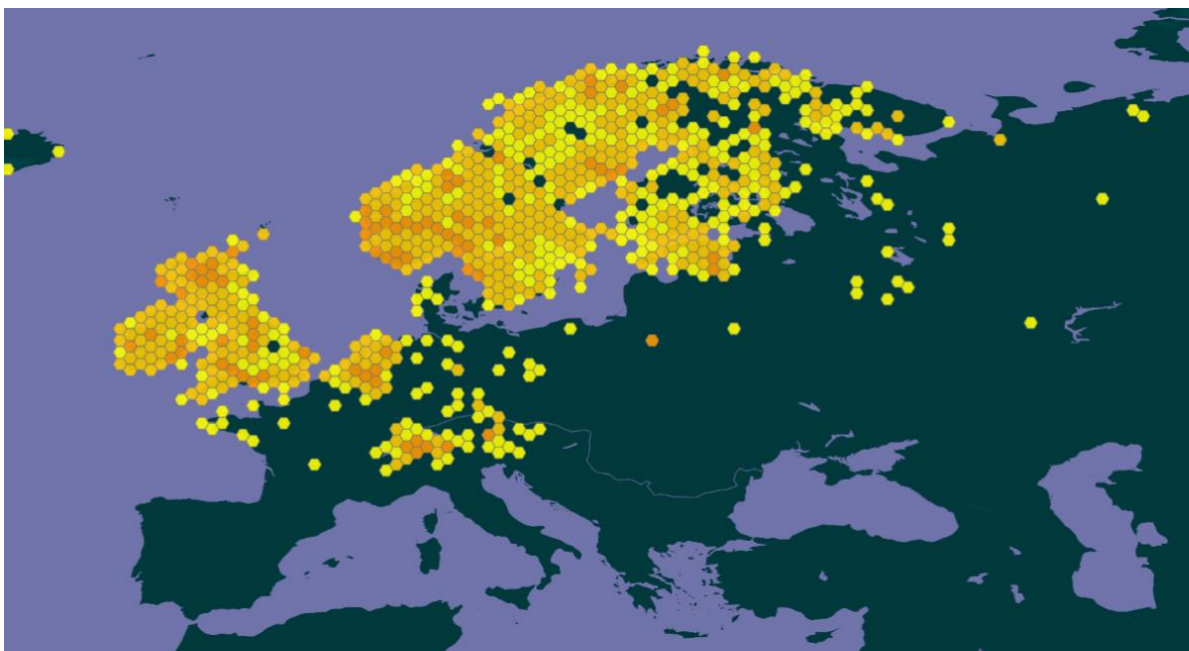


Figure 2: Table X: Distribution of *B. jonellus*. Darker colors indicate higher abundances. Generated by OpenStreetMap, OpenMapTilen, GBIF.

2.1 Study area and site criteria

All study sites chosen were located along the West-coast of Norway in Vestland County. Study sites were in the municipalities of Alver and Austrheim, at 60 degrees north (Figure 3). These areas have an oceanic climate with relatively mild temperatures and high precipitation. The mean annual temperature is 9 °C and the annual precipitation is 2258 mm. Winters are cold and rainy, with a mean temperature in January of 2 °C. Summers are cool with a mean temperature in July of 17 °C (data based on measurements from Flesland weather station 2005-2015, source: <https://www.timeanddate.no/vaer/@3157043/klima>). The growing season is relatively long with over 210 days, with the length of the growing season defined as “days with an average temperature over 5 °C” (Moen, 1998). All sites were in the outer parts of the Nordhordland UNESCO Biosphere Reserve.

The study sites chosen were categorized as either open heathlands (Figure 4) or overgrown heathlands (Figure 5). Six study sites were chosen in total, with three of each category. The open heathlands were characterized by having a higher cover of *Calluna* and a lower tree cover compared to the overgrown sites. The presence of several species typical for heathlands in the degenerate phase like *Empetrum nigrum*, *Betula pubescens*, *Sorbus aucuparia*, *Picea sitchensis*, *Pinus sylvestris*, and *Vaccinium uliginosum* were more prevalent in the overgrown heathlands. In addition, shrubs like *Juniperus communis* were taller and more abundant. Generally, the open heathland sites were in the building or mature phases, while the overgrown heathland sites were in the degenerate phase in the succession (Gimingham, 1972), as burning and/or grazing had not occurred for some time (Gimingham, 1972). Due to the possible long foraging distances of bumble bees (Walther-Hellwig and Frankl, 2000), each site was at least 2 km in flight distance apart to be considered independent.

2.2 Study sites descriptions

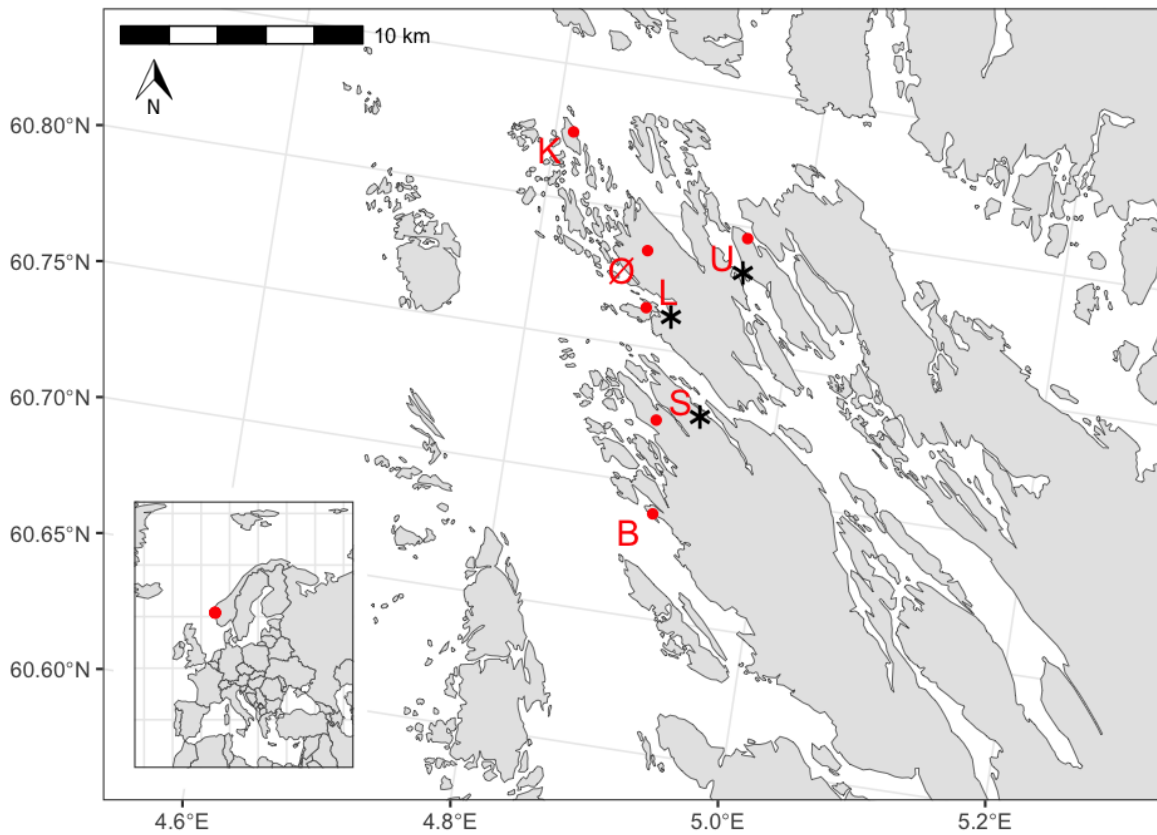


Figure 3: map containing all research sites marked with the initial of the site name. K=Krossøy, Ø=Øksnes, U=Utkilen*, L=Lerøysundet*, S=Syltneset* and B=Byngja. Map source: GeoNorge.

*Overgrown heathland sites.

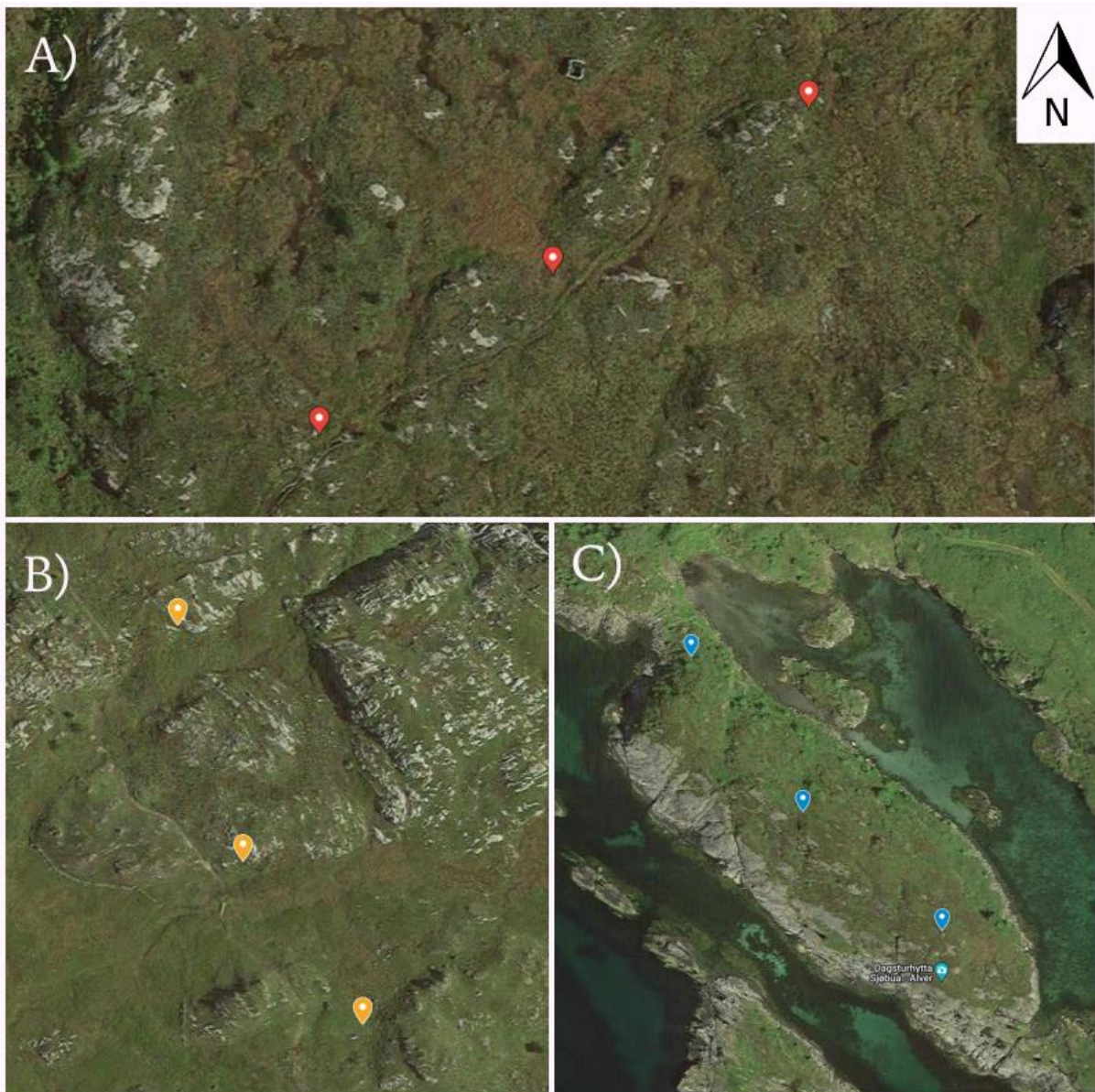


Figure 4. Satellite view of the open heathland sites and placement of pan traps. A: Øksnes – Calluna estimated to be in the mature phase. Grazing pressure was low, and likely only grazed by deer. Management practices were not maintained, and tree cover was higher compared to the other open sites. B: Krossøy - Calluna was estimated to be in the building phase. Grazing pressure from sheep was high and burning happened within the last decade. This site was west facing and exposed to strong weather. C: Byngja – Calluna estimated to be in the mature phase. The vegetation was partially managed by grazing goats and manual clearing of spruce seedlings. No signs of burning were detected, and a field of Sitka spruce was located 50 meters from the transect. The distance between pan trap (PT) 1 and PT 3 is 150 meters at all sites.

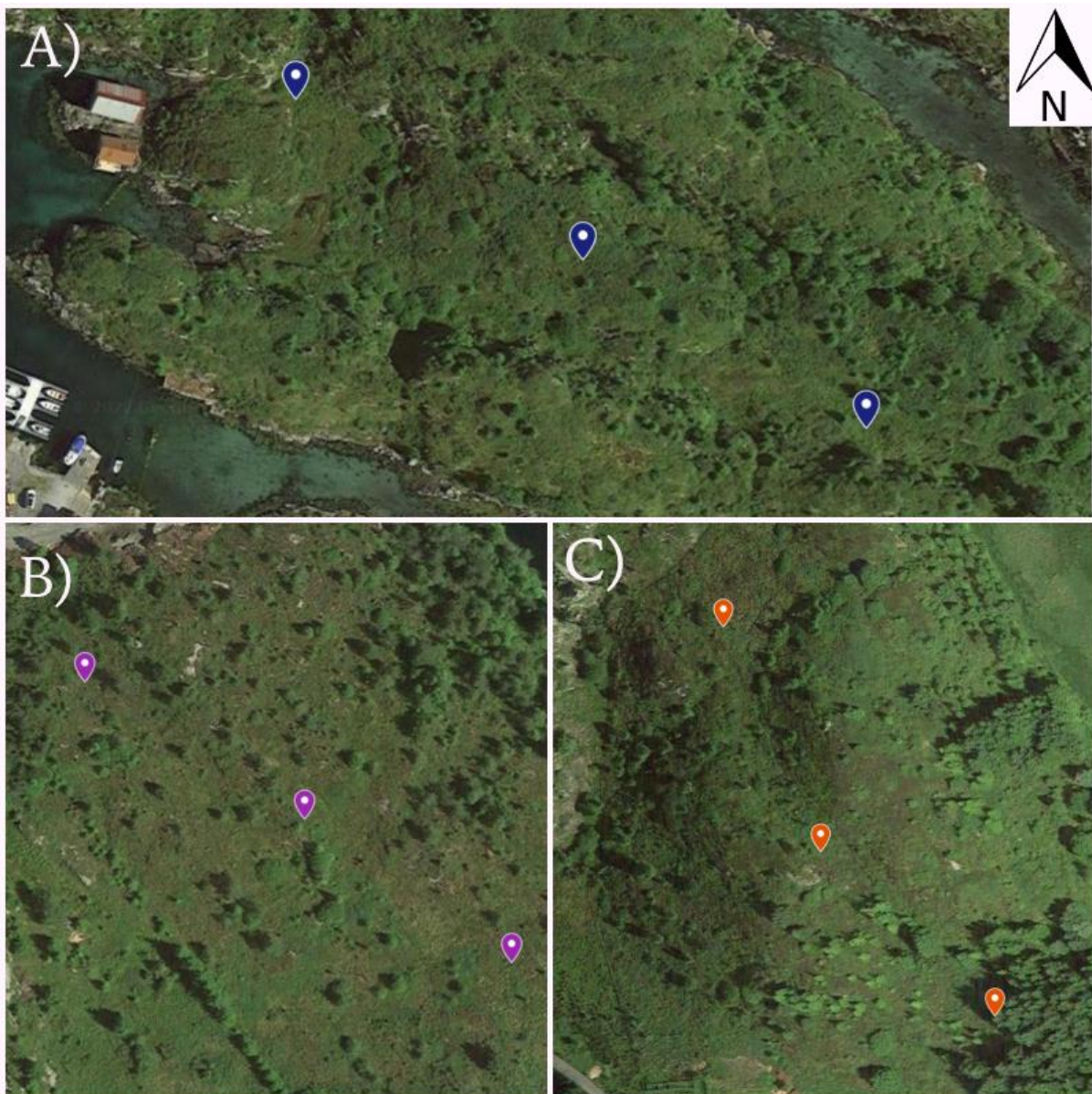


Figure 5: Satellite view of overgrown heathland sites and placement of pan traps. A: Lerøysundet, B: Utkilen, C: Syltneset. These sites were all clearly impacted by the absence of management practices like burning and grazing. The heaths were dominated by old *Calluna*, and shrubs like *Juniperus communis* were tall and widespread. The sites were also subject to tree encroachment and varying quantities of *Picea sitchensis* were present. The distance between pan trap (PT) 1 and PT 3 is 150 meters at all sites.

2.3 Study design

The sampling of pollinators was done over two periods of 14 sampling days each, with one period in June 2022 and one in August 2022. This way, I was able to obtain data in early summer as well as late summer during the blooming of *Calluna*. These periods were chosen to test if the presence of flowering *Calluna* attracted additional pollinators. Two sampling methods were used to capture pollinators; pan traps were used to capture bees, bumble bees, and hoverflies, and an insect aerial net was used specifically to capture bumble bees. Pan traps were emptied two days a week (Mondays and Fridays), and the sampling by insect net was completed three days a week unless heavy rainfall.

2.4 Sampling methods

2.4.1 Pan traps

Pan traps (PTs) in blue, white, and yellow were placed at every site and used to collect pollinators (Figure 6). Traps were painted using a primer (white Motip® primer) and white and yellow Rocol® paints and fluorescent blue Liquitex® paint. The traps were filled with soapy water to break the surface tension of the water, and trap and drown insects effectively. The soapy water contained 1 dl clear soap per L of water and each trap was filled about halfway. The chance of evaporation or heavy rainfall was considered when filling traps. One set of PTs contained 3 individual traps, one of each color. Three sets of traps were placed at every site, making a total of 54 individual traps. The traps were placed along a transect of 150 m, with one set of traps at 0 m, 75 m, and 150 m, named PT 1, PT 2, and PT 3 respectively (Figure 7).



Figure 6. Photo from the field showing one set of Pan traps in blue, white, and yellow.



Figure 7. Pan traps set-up for each site. One set of traps was placed at every 75 m inside the 150 m transect. Color of trap is placed in no particular pattern.

The collected individuals of interest (bumble bees, bees, and hoverflies) were placed in a tube with tags marked with the location ID, trap color, date, and capture time. The specimens were then transferred to a plastic bag for each sample, keeping samples from the different PT colors separated. The insects were rinsed and dried before being placed in the freezer for storage until identification. All PTs from all locations were emptied on the same day, to minimize differences caused by weather conditions.

2.4.2 Active sampling with insect net

Active sampling with insect aerial nets was used to catch *Bombus* individuals. After capturing, the individuals were transferred to a tube with tags on location, trap color, date, and capture time. On warm days, they were placed in a cooler bag to avoid overheating. The specimens were then placed in the freezer to be euthanized and stored.

The netting was based on the locations of the PTs, following the transect of 150 m. PTs and transects were placed in areas representative of the locations. I started at PT 1, walked past PT 2, and then stopped at PT 3. When PT 3 was reached, I walked back the same route (Figure 8). If I approached tall vegetation or steep hills difficult to walk past, I deviated slightly from the line of the transect. I spent 30 minutes each way capturing bumble bees, making a total of one hour netting at each location. A 30-minute timer was set each way to ensure that the correct amount of time was spent.

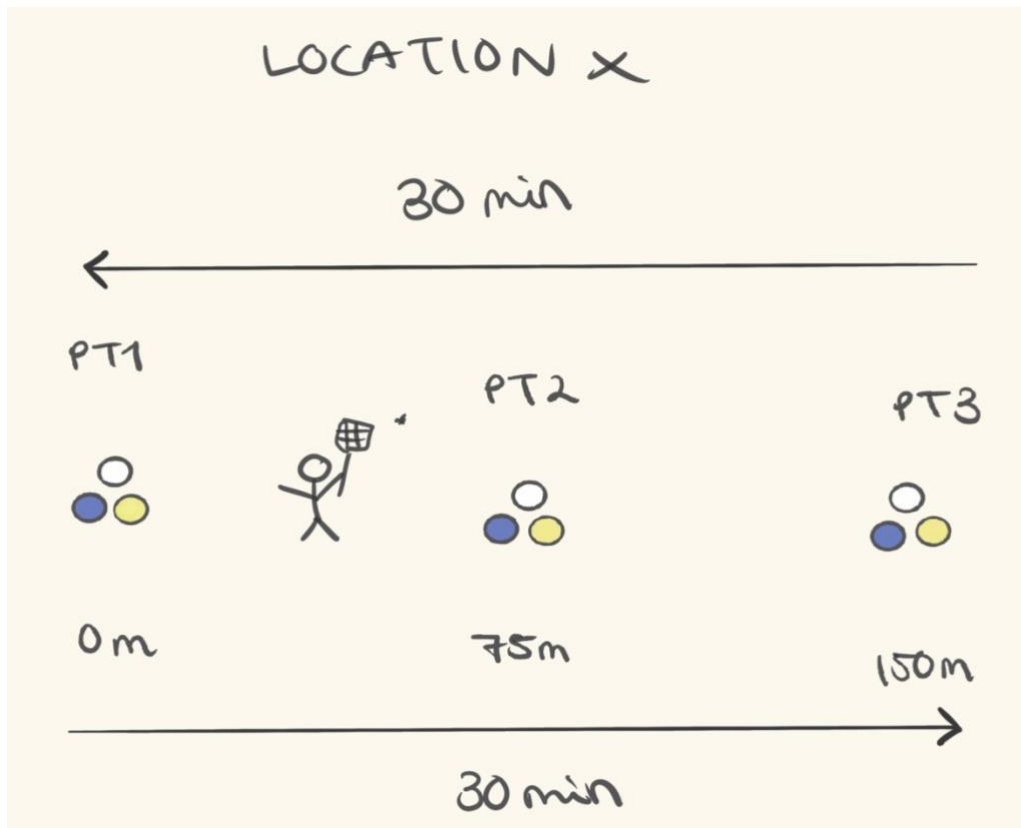


Figure 8: Sampler walking through the transect, capturing bumble bees with an insect net.

The active sampling was only conducted between 09:00 and 17:00 on days with no precipitation. The locations were split into two groups based on geographical proximity. Group A included Krossøy, Øksnes, and Utkilen, while Group B included Lerøysundet, Syltneset, and Byngja. Due to time constraints, only one group of sites was sampled each netting day. The order of the sampling within these groups varied to limit possible differences caused by temperature.

2.4.3 Vegetation plots

I conducted vegetation analysis at every site. Vegetation was assessed in plots; 1x1 meter quadrats, with plots placed at regular intervals along the transects used for the pollinator sampling. The first plot was placed about 7 meters from PT 1, and the next about every 14 meters along the length of the transect (Figure 9). If plots landed on a body of water or barren rocks, they were moved to the nearest vegetation patch.

The percentage of vegetation cover in the plots was noted for functional groups; of heather, herbs, shrubs, moss, trees, and graminoids. Identification to species level was conducted and noted in the field for all groups except for graminoids and some moss species, as it is mainly the cover of *Calluna* and flowering plants that is of interest to this study.

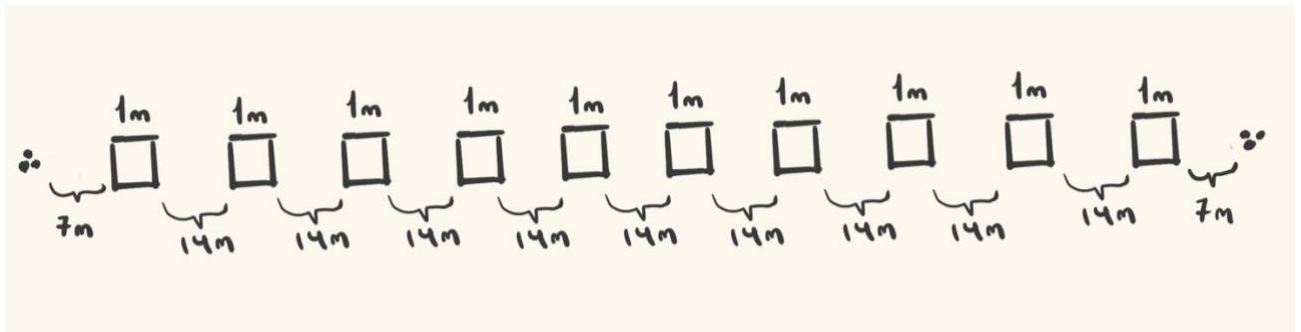


Figure 9: Set up for vegetation analysis along each transect. The three dots indicate the approximate placement of pan trap 1 and pan trap 3. Pan trap 2 is located in the middle of the transect.

2.4.4 Tree cover

For each site, the surrounding tree cover was calculated by marking a circle with a 1 km radius from PT 2 in Google Maps. The circle was imported to the photo editing program “PhotoScape X”. Here, trees were colored red, while other vegetation remained green, and bodies of water were removed digitally. The edited picture was later uploaded to “Geotests” (source: https://www.geotests.net/couleurs/frequences_en.html#), where the ratio of red and green pixels, and therefore tree cover, was found.

2.5 Insect species identification

For bumble bees, Astrid Løken's "Norske Insekttabeller 9 Humler" (1985), and "Humler i Norge" by NINA (2015) were used to identify individuals to species level where possible. Species of the *Bombus lucorum* complex were grouped together, as they are morphologically difficult to differentiate (Waters *et al.*, 2011; Ødegaard *et al.*, 2015). This group includes the four species *B. lucorum*, *B. terrestris*, *B. cyptarum*, and *B. magnus*.

Bees were identified to genus using the "Field Guide to the Bees of Great Britain and Ireland" by Steven Falk (2015), except honeybees (*Apis mellifera*), which were identified to species level. ZEISS SteREO Discovery.V8 was used in identification for all groups. Because of time restraints, hoverflies were not identified. However, all individuals were counted and added to the dataset.

2.6 Data processing

After species identifications, each individual was given a unique number associated with information about species name, sex, location, sampling method, cast, and additional comments. This information was plotted in Excel before being exported as a CSV and imported to R. Weather conditions were also included for the individuals collected with an insect net. Data on temperature and wind were found on seklima.met.no. The weather station at Flesland was used for all sites except Krossøy. Here, Fedje weather station was used as this site is more exposed to weather. Weather conditions were not included for individuals captured with pan traps as these were all collected on the same day. Data from the vegetation analysis and tree cover were also plotted in Excel before being imported to R as a CSV.

2.7 Data analysis

The data analysis was performed using R version 4.2.2 and R-studio version 2022.12.0.

Rarefaction and species accumulation curves were generated to assess the effectiveness of sampling methods (package: *vegan*). Here the “rarefaction” method was chosen to find the mean when accumulating individuals. A Principal component analysis (PCA) was used to visualize dissimilarities of the sites based on which species were present and their total abundance (package: *vegan*). A PCA was chosen due to the low axis length. To reduce the influence of the most frequent species, a log transformation on the abundance of *Bombus* species was performed. A redundancy analysis (RDA) was chosen to examine the effect of the sampling period, site category, and mean cover of *Calluna* on the total abundance of all *Bombus* species (package: *vegan*). Here, total abundance was used as the response variable, while period, state (site category), and mean *Calluna* cover were the predictors. A log transformation of the species abundances was done to reduce the effect of frequent species, while the vegetation data were already standardized to mean. For the specialist species *B. muscorum* and *B. jonellus*, and the generalist group *B. lucorum* complex, the effect of the sampling period and site category were tested using separate generalized linear models (GLM). Here, total abundance was used as the response, while period and state were used as predictor variables. Before analysis, correlations between response variables were examined. Several models with different response variables were tested, however, the final models were decided based on correlations between environmental variables, AIC scores, ecological knowledge, and research questions. A negative binomial distribution was used to account for overdispersion and additional variability often observed in count data. For the individuals captured with an insect net, the relationship between total abundance and wind and temperature was examined using *ggplot* (package: *ggplot2*).

2.8 Data availability

Data and scripts will be made available at Github:

https://github.com/sza009/Pollinator_diversity

3. Results

3.1 Bumblebee communities

In total 633 individuals of insect pollinators were captured, of which 307 were bumblebees, 91 solitary bees, 56 honeybees, and 179 hoverflies. For the bumblebees, a total of eight species were identified in addition to the *B. lucorum* complex group (Appendix A, Table 5). The most common bumblebees were *B. lucorum* complex, *B. jonellus*, and *B. pascuorum* (Figure 10). These combined consisted of 71% of all the individuals captured. Other species collected were *B. hortorum*, *B. muscorum*, *B. hypnorum*, *B. pratorum*, and the cuckoo species *B. campestris*. *B. hortorum* and *B. hypnorum* both had less than 5 individuals. About 75% of the bumblebees were captured with an aerial net, while the remaining 25% were captured in pan traps. Up to 40% of the individuals were captured during the first period, while 60% of the individuals were captured in the last period when *Calluna* was in bloom. A total of 149 individuals were captured in the sites categorized as open heathlands, which included seven species (including the *B. lucorum* complex). For the overgrown heathlands, 158 individuals were captured, with eight species (including the *B. lucorum* complex).

Generally, the overgrown heathlands had a higher abundance of some common bumblebee species, like *B. pratorum*, while open heathlands had a higher abundance of the rarer species *B. muscorum*. Exceptionally, the *B. lucorum* complex was abundant at all sites, with a particularly high number of individuals found in Byngja. Some common species in Norway, like *B. hypnorum*, *B. hortorum*, and *B. campestris* were rare across all study sites. Twenty-six individuals of *B. muscorum* were collected in total. These were found in the sites Krossøy and Øksnes, thus exclusively recorded in open heathlands. A total of 92% of these individuals were found in Krossøy, the largest and most well-managed of the heathlands. About 92% of the individuals of *B. muscorum* were found during the last sampling period. For *B. jonellus*, 64 individuals were found in total. This species was found in all sites, with 67% from the overgrown heathlands. Around 70% of the individuals of *B. jonellus* were found in the first period of sampling. For the sampling in August, 95% of the individuals were found in the open heathland sites. For the most common group, *B. lucorum* complex, 70% of the individuals were captured during the last period, when *Calluna* was in bloom. Individuals from this group were abundant at all sites but were especially abundant at Byngja. *B. pratorum* was collected at four sites and 97% of these individuals were collected from the

overgrown sites. All individuals of this species were collected during the first sampling period. No obvious connection between temperature or wind and the number of bumblebees collected with aerial nets was found (Appendix A, Figure 4 and 5).

A rarefaction curve with the number of species sampled as a function of the total number of individuals illustrates the effectiveness of the sampling effort (Figure 11). The figure shows that the sampling did not successfully capture all species at each site, however, the total number of individuals captured for the region was sufficient (Appendix A, Figure 6). Syltneset and Krossøy showed less success at sampling effort, whereas the rest of the sites were close to sufficiently sampled.

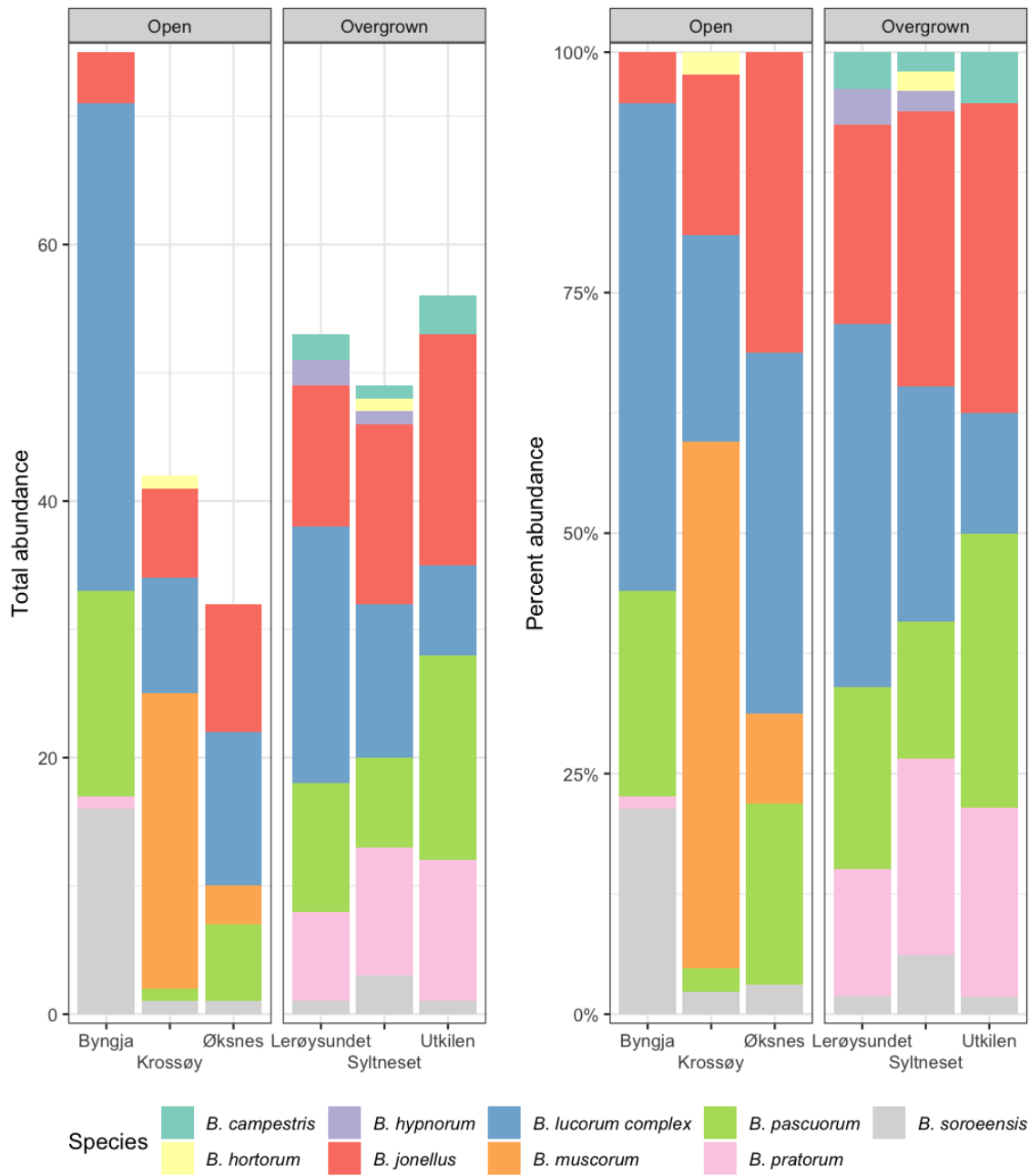


Figure 10: Total and relative abundance of *Bombus* species at the six different study sites. Open facet shows sites in the category open heathland, while overgrown facet shows sites in the category overgrown heathland. *B. lucorum complex* is a group consisting of the species *B. lucorum*, *B. terrestris*, *B. cyptarum*, and *B. magnus*.

The PCA visualizes the similarity between study sites based on the community data (Figure 12). It also shows similarities between the *Bombus* species based on which sites they were sampled and their abundance. Here, we find that *B. muscorum* differentiated from the other species, as it is placed furthest away on the x-axis. From the site values, we find that Krossøy shows dissimilarities from the other overgrown sites. In addition, there was some overlap between the site categories, open and overgrown heathland. The eigenvalues show that PC1 explained 62.04% of the total variance in the data, while PC2 explained 27.01% (Appendix A, Table 1). Therefore, most of the variation explained is captured along the x-axis, while PC2 captures less of the variation. In total, the plot explains 89.05% of the total variation in the data. The RDA illustrates the relationship between species composition and the environmental variables; site category and sampling period (Figure 13). A total of 67.49% of the variance was explained by RDA1, while RDA2 explained 29.73%. These two axes in the RDA plot together explain 97.21% of the variance. The model was found to be significant ($F = 2.31$, $P = 0.02$) (Appendix A, Table 3), and the predictor variable sampling period, explains a significant portion of the variance in *Bombus* abundance ($F = 2.24$, $P < 0.01$) (Appendix A, Table 4).

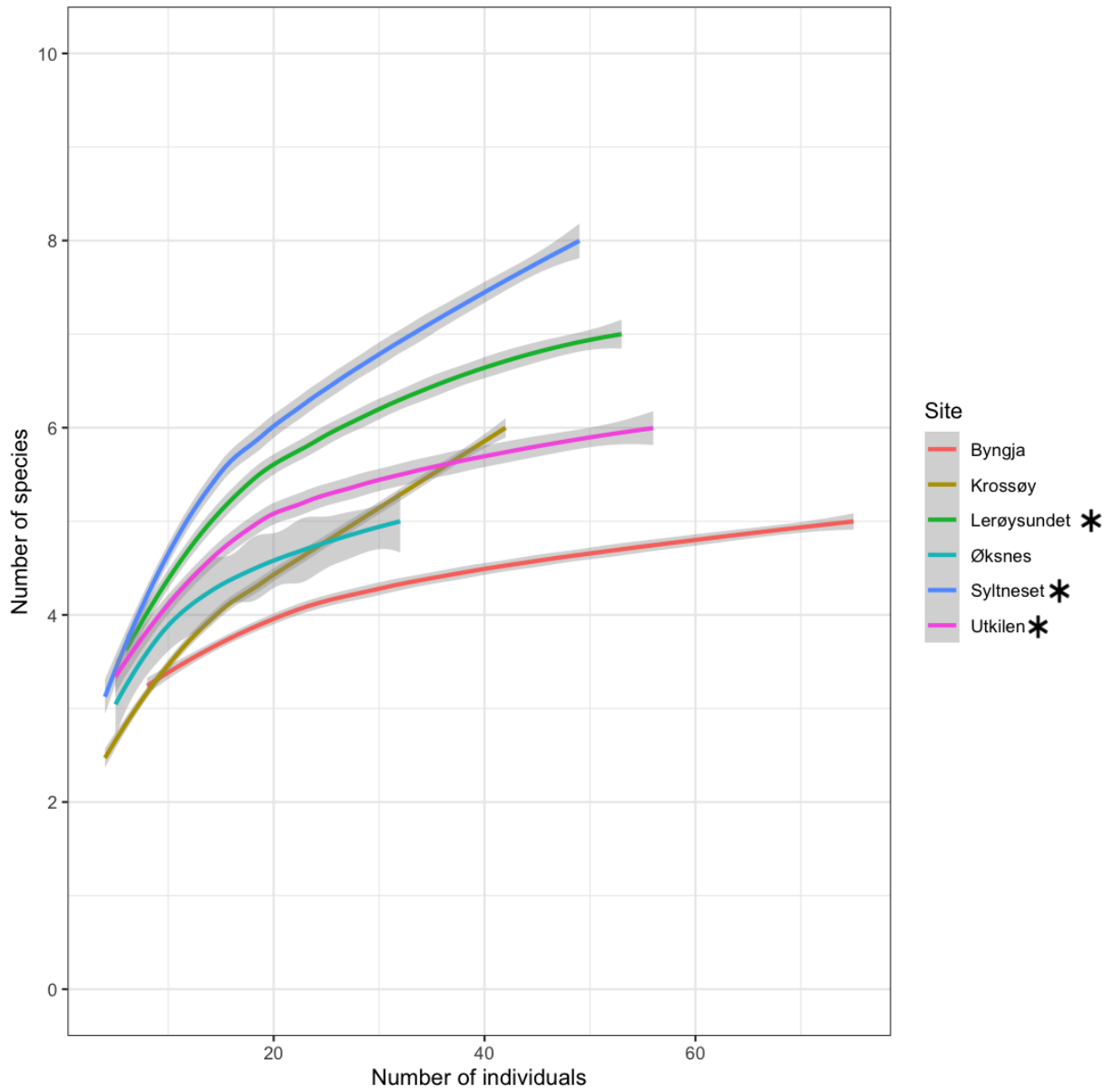


Figure 11: Rarefaction curves for *Bombus* communities at the six different study sites. Grey line depicts the standard deviation.

*Overgrown heathland sites.

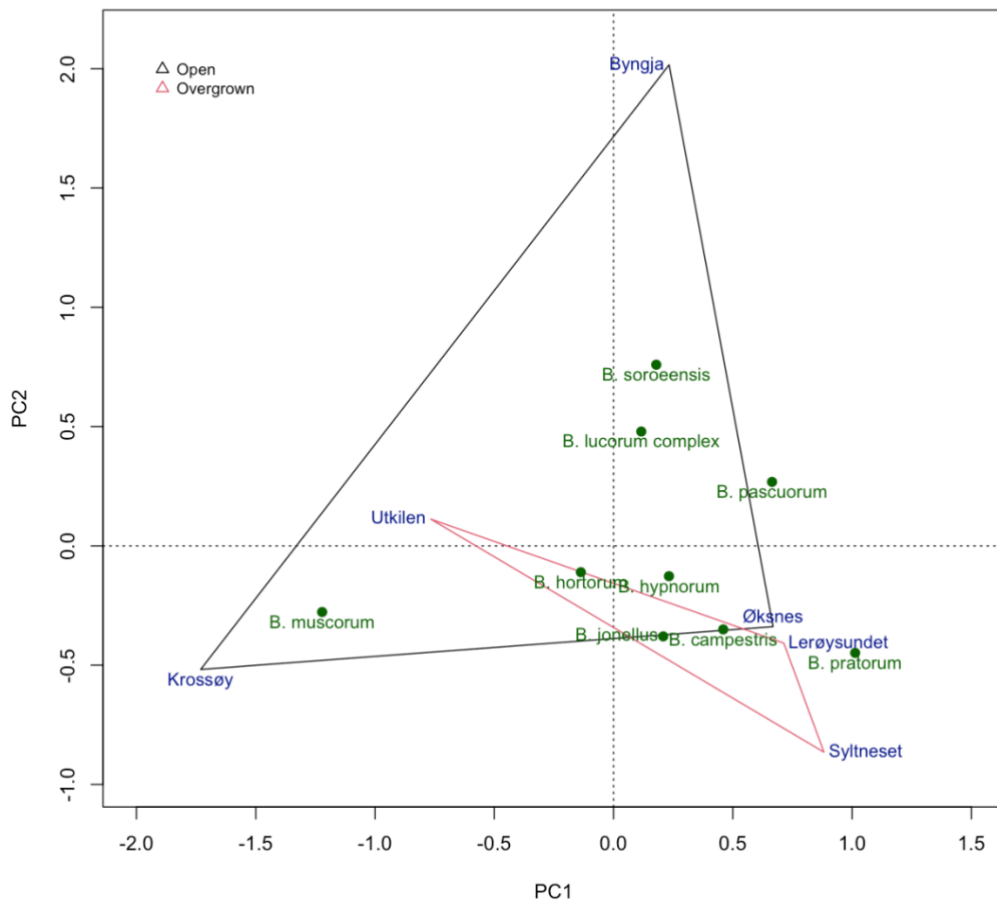


Figure 12: Principal component analysis (PCA) illustrating dissimilarities in *Bombus* communities. Blue text depicts site names, while green text depicts abbreviated species names to avoid overlapping. Here “*Bombus*” is removed, and only the first three letters are displayed. Black triangle shows sites in the category open heathlands, while the red triangle shows sites in the category overgrown heathlands.

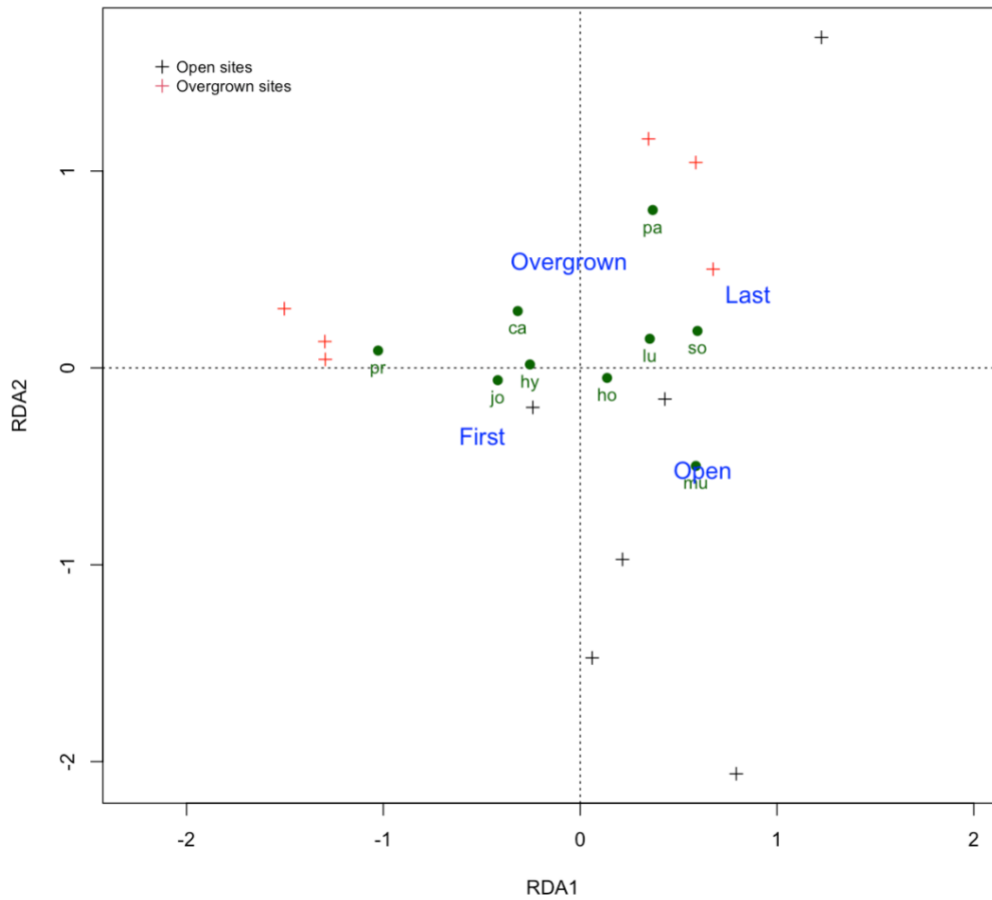


Figure 13: Redundancy analysis (RDA) of bumblebee abundance. Blue text depicts explanatory variables, while green text depicts species names. Species names are shortened to avoid overlapping, here *Bombus* is removed, and only the first two letters are displayed. Sites are doubled to include scores for both sampling periods. Black cross depicts sites in the category open heathland, while red cross shows sites in the category overgrown heathland.

3.2 Vegetation

Generally, I found differences in some of the vegetation characteristics between the site categories, while for others, no clear distinctions were found. The open heathland category had a higher cover of *Calluna* compared to the overgrown sites (Figure 14). In addition, the surrounding tree cover was found to be lower in the open sites (Figure 15). For vegetation groups, there was more variation between sites. The mean cover of functional groups for each site is presented in Table 1.

For flowering plants, there was also considerable variation between sites, particularly in their percentage of cover. Byngja and Krossøy had the highest measure of *Erica tetralix*, with a cover of 13 and 11% respectively. Øksnes had the highest cover of *Arctostaphylos uva-ursi* (8%), while Utkilen and Syltneset had the highest cover of *Vaccinium vitis-idaea* (7%). The presence of *Cornus suecica* was highest in Lerøysundet (4%) and Byngja (4%). *Potentilla erecta* was present at all sites, while *Lotus corniculatus* was only found at Krossøy. Krossøy was the only site containing *Erica cinerea*. It was also the only site where sheep feces were present in the vegetation plots, indicating a high presence of grazing animals.

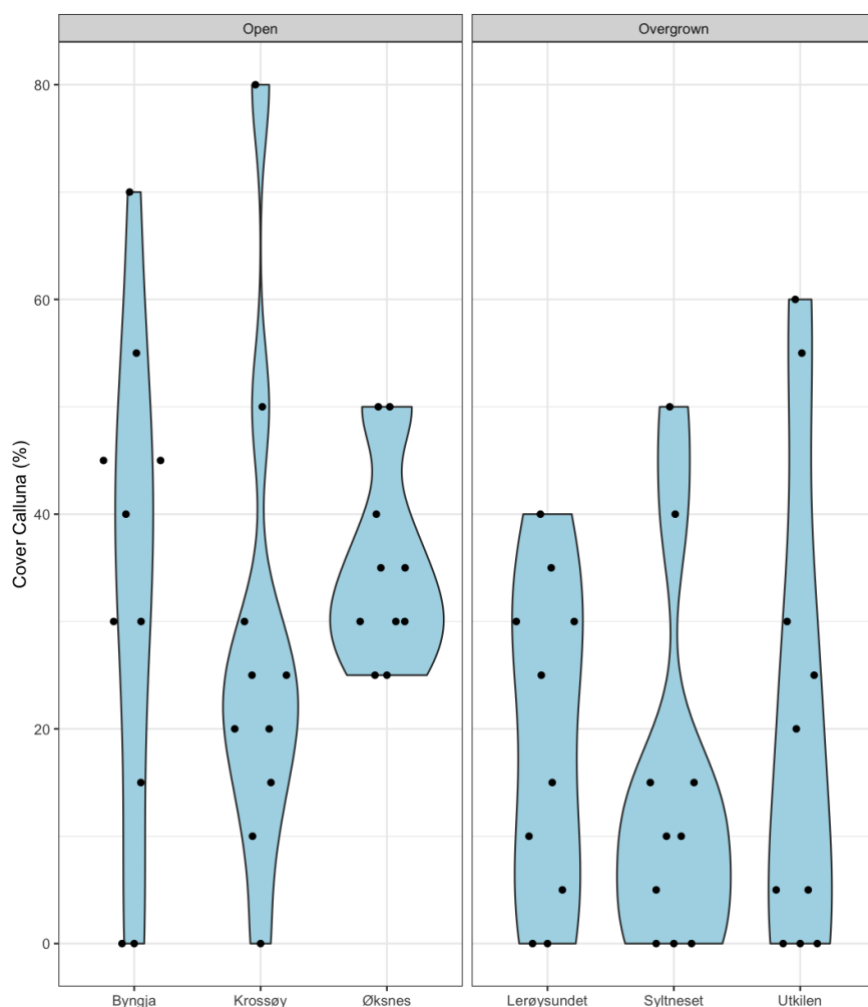


Figure 14: Violin plot showing the cover of *Calluna vulgaris* for all plots at all 6 sites. Open facet shows sites in the category open heathland, while overgrown facet shows sites in the category overgrown heathland.

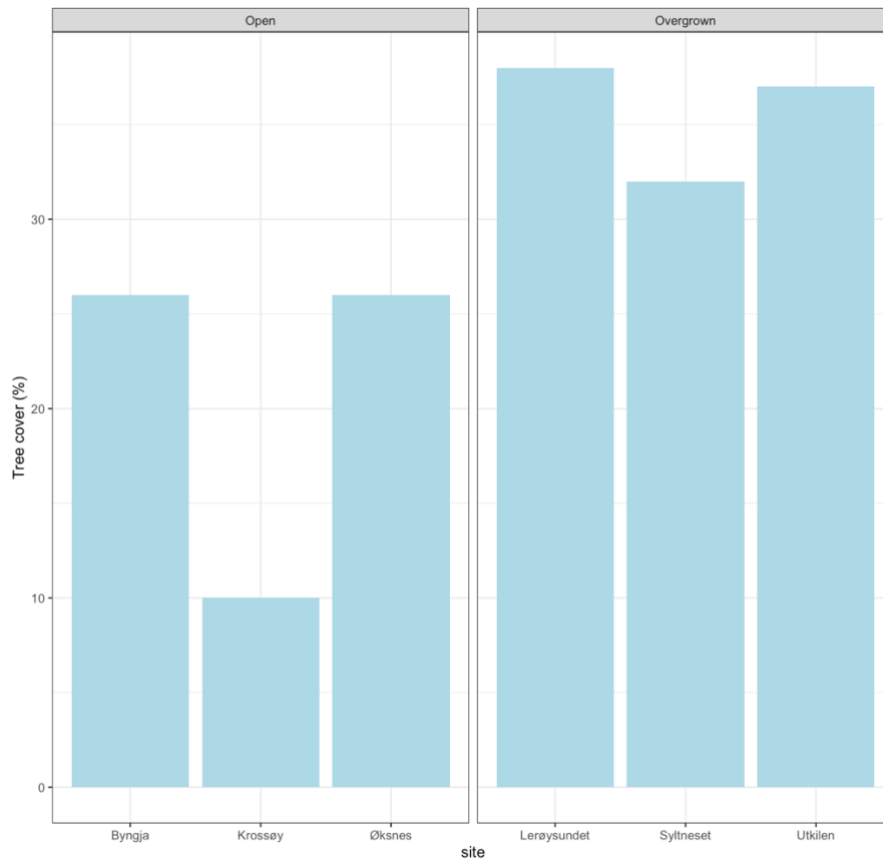


Figure 15: Cover of trees surrounding study sites, with a 1 km radius from traps, in open and overgrown heathland sites.

Table 1: Mean cover in the percentage of plant functional groups across open and overgrown heathland sites.

Site	Category	Heather (%)	Shrubs (%)	Herbs (%)	Gramnioids (%)	Moss (%)
Byngja	Open	65	8,0	5,0	6,5	16
Krossøy	Open	43	8,0	5,0	14	30
Øksnes	Open	45	6,5	11	26	11
Lerøysundet	Overgrown	58	21	6,0	6,0	9,0
Syltneset	Overgrown	61	24	2,5	5,5	7,0
Utkilen	Overgrown	44	1,0	5,5	13	33

3.3 Effects on abundance

A generalized linear model (glm) was used to further examine the effect of the environmental variables on the abundance of the specialist species *B. jonellus* and *B. muscorum*, and the generalist group *B. lucorum* complex. For *B. jonellus*, none of the predictor variables in the negative binomial model were statistically significant (Table 2a). This was also the case for the group *lucorum* complex (Table 2c). For *B. muscorum* however, the predictor “last sampling period” were found to be significant for its abundance ($Z = 3.17$, $P = 0.002$) (Table 2b). The effect on the habitat category (state) was not successfully examined due to complete separation in the glm.

Table 2: Coefficients for the negative binomial generalized linear model (GLM)

a) *B. jonellus*

	Estimate	Std. Error	Z value	Pr(> z)
(Intercept)	0.44579	0.84368	0.528	0.597
stateovergrown	1.01120	0.98513	1.026	0.305
periodelast	0.04122	0.98183	0.042	0.967

b) *B. muscorum*

	Estimate	Std. Error	Z value	Pr(> z)
(Intercept)	-1.099e+00	7.071e-01	-1.554	0.12026
stateovergrown	-3.691e+01	1.955e+07	0.000	1.00000
periodlast	2.331e+00	7.360e-01	3.167	0.00154

b) *B. lucorum* complex

	Estimate	Std. Error	Z value	Pr(> z)
(Intercept)	0.85745	0.64300	1.334	0.182
stateovergrown	0.04611	0.75165	0.061	0.951
periodlast	0.96353	0.74487	1.294	0.196

4. Discussion

This study identified a total of nine *Bombus* species, including *B. lucorum complex*. This group, together with *B. jonellus* and *B. pascuorum*, accounted for 71% of all individuals. Furthermore, the relative abundance of the different bumble bees varied during the two different sampling periods in June and August. Early-emerging species like *B. pratorum* were more prominent during the first sampling period while late-emerging species like *B. muscorum* were more abundant in August. This was expected considering the distinct lifecycles of *Bombus* species. Most of the individuals (60%) were captured in the last period when *Calluna* was flowering, while the remaining 40% were caught in the first period. Both habitat categories had similar numbers of individuals and species, but species composition differed. Overgrown habitats showed higher abundances of common species like *B. pratorum*, while the coastal heathland specialist *B. muscorum* was exclusively found in open heathlands. This was in accordance with my hypothesis, considering the documented distribution of the species. Most individuals of *B. jonellus* were found in overgrown habitats (67%), but during the last sampling period, 94% of individuals were found in open habitats. The generalist group *B. lucorum complex* was abundant at all sites, especially at Byngja. This was also expected as it is a generalist group able to forage in a range of different habitats. *B. muscorum* differed the most from the other species also according to the PCA ordination, and this was also the case for the site Krossøy. Moreover, the sampling period was a significant predictor of the abundance of *B. muscorum*, which also relates to its lifecycle.

4.1 Specialist species

In accordance with my expectations for the first research question, *B. muscorum* was exclusively found in open habitats. The species was especially abundant at Krossøy, the largest and most well-managed of the open heathland sites, which seem to be hosting a stable population. As shown in other studies, this might be explained by its strong association with coastal heathlands and the plants found here (Bengtson and Røsok, 2019). The late emergence of *B. muscorum* makes it particularly suited to heathlands due to the synchronized emergence of its workers and the flowering of *Calluna* (Mahy *et al.*, 2011; Bengtson and Røsok, 2019). This timing ensures that the workers have access to an abundant food source close to the nest, which is especially important as *B. muscorum* has a short foraging range (Walther-Hellwig and Frankl, 2000). It is therefore not surprising that the sampling period

was a significant predictor of *B. muscorum* abundance. Contrary to my hypothesis and despite being a specialist on Ericaceae, *B. jonellus* was more abundant in overgrown sites. Previous research shows that *B. jonellus* can be found in various habitats. A study from Russia found that the species had a tendency to forage in open habitats in the northern part of the study area, however, further south it was numerous in various types of forests (Potapov and Kolosova, 2020). Goulson *et al.* (2006) also found that in the UK, *B. jonellus* was recorded in three different habitats: gardens, lowland heath, and calcareous grassland. Interestingly, in the final sampling period, 94% of individuals were found in open habitats. This suggests that sites with a high abundance of *Calluna* are preferable for *B. jonellus* during the flowering period. As overgrown sites tend to be more heterogeneous (Prévosto *et al.*, 2011), it might be that these sites offered a greater abundance of floral resources during the initial sampling period and were therefore preferable at this time. In addition, this species has an earlier emergence than *B. muscorum* and might consequently have a weaker dependence on *Calluna* or other late-flowering Ericaceous species (Ødegaard *et al.*, 2015). Instead, other Ericaceous species like *Vaccinium vitis-idaea* and *Vaccinium uliginosum* may be important, which were both more abundant at the overgrown sites (Appendix A, Figures 7 and 8). My results also confirm this as most of the individuals were captured during the first sampling period. Its distribution is not solely limited to coastal regions, as it can also be abundant at higher elevations (Figure 2). Therefore, the abundance of *B. jonellus* is likely not dependent on coastal heathlands as a habitat.

4.2 *Bombus* richness

No significant difference in *Bombus* richness between the habitat types was recorded. This differed from the results of Bąk-Badowska *et al.* (2021) who found that sites with the highest abundance, richness, and diversity were open ruderal-segetal habitats. They also found that species diversity was negatively correlated with mixed forest cover. Since *Bombus* typically prefer open and semi-natural habitats (Bąk-Badowska *et al.*, 2021), my results were somewhat surprising. However, sites with closed-canopy forests are not included in my study, which may explain the small difference in richness. These habitats are expected to have fewer species, especially in dense forests like Sitka plantations. It is possible that the preference for open habitats was counterbalanced by the additional floral diversity and nesting sites in overgrown habitats. However, further research is required to validate this

assumption. Also, species with long colony cycles and large foraging ranges may exceed the habitat boundaries defined in this study, as colony success is likely to depend on access to multiple habitats (Novotny *et al.*, 2021). Goulson *et al.* (2006) found that the *Bombus* species they studied were often found in a broad range of biotopes and thus concluded that most species are not habitat specialists. This may clarify why species richness and abundance from both habitat categories in this study were similar. In contrast, Williams (2005) argued that some species prefer particular habitats, which also supports our findings of *B. muscorum* exclusively present in open heathlands.

4.3 Sampling period

Because of the distinctive life cycles of different species, the effect of the sampling period associated with the flowering of *Calluna* on *Bombus* abundance was challenging to assess. The redundancy analysis showed that the sampling period was a significant predictor variable of *Bombus* abundance ($F = 3.83$, $P < 0.01$) (Appendix A, Table 4). However, this is likely due to the distinct lifecycles rather than the presence of flowering *Calluna*. The *B. lucorum* complex was chosen as a model species, as this species group is common throughout the season (Ødegaard *et al.*, 2015). During the final sampling period, 58% of the *B. lucorum* complex individuals were caught. The abundance was similar for both habitats during the first sampling, however, in the last, 67% of the individuals were from the open habitats. Interestingly, Byngja (open heath) had a particularly high abundance of this group, with 55% of all individuals. Byngja is the most fragmented of the open habitats with a field of Sitka spruce 50 meters from the pan traps. Krossøy in contrast, only habituated 13% of the individuals. Byngja also had the highest abundance of *B. soroeensis*, with 70% of all individuals. This could signify that the *Calluna* in Byngja provides an abundant food source in a region that is otherwise heavily forested with low floral abundance, and therefore attracts many foraging individuals. No significant relationship between the abundance of *B. lucorum* complex and the sampling period was found (glm). This may be caused by the very restricted number of sites and sampling, or because it is a group of generalist species with a wide diet and thus can thrive without foraging on *Calluna* (Moerman *et al.*, 2016). The bumblebee's potentially large foraging range (Walther-Hellwig and Frankl, 2000) also makes it likely for the group to visit floral resources in different habitats and it is thus not directly dependent on the high abundance of *Calluna* in heathlands. *Bombus* species may benefit from foraging on

Calluna in heathlands because of the short distances between each flower, thus limiting their energetic costs related to flying (Balfour *et al.*, 2021). However, if their nest is located far from the *Calluna* patches, the energetic costs related to foraging here may consequently not be energetically beneficial regardless.

4.4 Habitat size and conservation

Large and continuous areas are favorable in the conservation of *Bombus* as they are susceptible to inbreeding and stochastic events (Goulson *et al.*, 2008). This brings us to the question of whether there exists a certain habitat size necessary to sustain pollinator species. A study of pollination failure in an orchid species *Pterodidium catholicum*, suggested that a habitat of about 385 ha when separated by an urban matrix, was too small to sustain populations of the bee *Rediviva peringueyi* (Pauw, 2007). Finding the exact size needed to host stable populations of specific species like the red-listed *B. muscorum* requires more research and is likely to depend on local factors like floral diversity, nesting sites, and microhabitats. Still, habitat fragmentation and degradation are thought to affect pollinators negatively through the loss of floral and nesting resources, as well as possible introductions to insecticides (Potts *et al.*, 2010). For these reasons, the best way to conserve vulnerable *Bombus* species, like those with narrow habitat ranges, is likely by preserving their surroundings. Habitat size, connectivity, and management practices may also explain why Krossøy was the only site with a seemingly stable population of *B. muscorum*. Here, grazing pressure was high and burning happened within the last decade. Øksnes was also a large and continuous open heathland, however, there were no signs of active management, and only three individuals were recorded here. Lastly, Byngja had no individuals of *B. muscorum* and was neither continuous nor managed.

4.4 Reflections on methodology

The initial objective of this thesis was to study bumblebees, bees, and hoverflies. Therefore, the methods were chosen to capture a wide range of pollinating insects. However, *Bombus* was selected as the study species because of time restraints, as this was the most abundant group. To capture *Bombus* effectively, other methods may be more beneficial. For instance, using blue vane traps instead of pan traps could increase the number of sampled individuals

(Hall, 2018), and thus return more robust results. These traps could also be used to examine the abundance of bumblebees for woodland and/or afforested sites. Still, the species accumulation curves suggest that most of the species were likely captured, thus the sampling method can be considered sufficient for the region. Krossøy in contrast, had a steep rarefaction curve and may therefore habituate more species than observed in this study. One possible explanation for this could be the typically higher wind speed of this site, which may cause some species to stay in their nest or seek other places to forage (Uthoff and Ruxton, 2022). However, no relationship between temperature and/or wind speed was detected for *Bombus* abundance. This is possibly because sampling with insect net was only performed on days with temperatures ranging from 11.1 – 22.8°C, and wind speed from 1.3 – 5.9 m/s, thus inside the range of when *Bombus* is active (Uthoff and Ruxton, 2022). Consequently, it is difficult to suggest an explanation for the steep curve in Krossøy, but more sampling would be expected to clarify this. The number of sites in this study is low, as the sampling process is time-consuming, given the timeframe of this study. For this reason, it is also challenging to draw conclusions across habitat types, especially as there were differences within site categories. For example, all the open habitats had different levels of management, ranging from high grazing pressure with prescribed burning to no active management. Other things to consider are the size and connectivity of the habitats. This varied greatly, especially when comparing the heathlands at Krossøy, which were large and continuous, to Byngja, which were small and fragmented. The glm failed to provide an appropriate estimate of the *B. muscorum* abundance related to the different habitat states: open or overgrown heathland. This was due to a complete separation issue as there were no observations of this species in overgrown heathlands. A higher number of samples is expected to solve this, alternatively, other models could be explored like quasi-likelihood models. No effort to make a quasi-likelihood model was done in this study as the result would be difficult to compare with the other negative binomial models. In summary, having more similar study sites within each category, and a higher number of sites and sampled individuals would greatly improve the robustness of my findings.

4.5 Further research

This study provides important insights into *Bombus* community composition and species abundance in open and overgrown heathlands in Vestland, Norway. However, there are several areas where further research should be conducted. First, additional studies should investigate the potential impacts of landscape characteristics such as fragmentation, management, and surrounding land use on *Bombus* diversity and abundance. Additional information about the floral and nesting preferences of different *Bombus* species could also help in understanding their habitat requirements and inform conservation efforts. Moreover, further research is needed to determine the optimal heathland management practices for maintaining healthy and diverse *Bombus* populations in heathland ecosystems. Investigating *Bombus* communities in heathlands across the south-north gradient in Norway and Europe would also be valuable to expand our knowledge about insects in heathlands and possibly in understanding the effects of climate change. As *B. muscorum* is vulnerable to inbreeding (Darvill *et al.*, 2006), genetic tests could be used to examine the health of the existing population in Krossøy. Comparing individuals from present populations to earlier data would give us key insights into how genetic diversity has changed through time. Also, genetic studies could be used to successfully identify all species of *B. lucorum complex* and thus expand our knowledge of these species and their possible habitat preferences. This would be especially interesting for *B. magnus*, as previous research has suggested that this species may also be a heathland species strongly associated with feeding on *Calluna* (Waters *et al.*, 2011). Further research could also investigate the pollination webs of flowering species in heathlands, including potential different impacts of generalist species like *B. lucorum complex* and specialists like *B. muscorum*. This is especially important considering the potential timing mismatch between pollinator activity and flowering periods for effective pollination. Lastly, it is encouraged that the methods of this study be repeated every five years or so to detect any possible declines and/or shifts in community composition. Sampled individuals should also continue to be registered in *Artskart.no*, to help fill in data gaps on pollinators in Norway.

4.6 Conclusions

The importance of insect pollinators in seed production for both wild and cultivated plants makes monitoring their populations increasingly important. Insect pollinators are facing many threats, with some of the most prominent being land-use changes and agricultural intensification. An increasing number of coastal heathlands are being lost due to the absence of traditional management, which will eventually shift the system to woodland. The succession is likely to affect species depending on open habitats. This study showed that open heathlands were preferred by the coastal heathland specialist and red-listed species *B. muscorum*, which was exclusively found in open habitats. The sampling period was a significant predictor of *B. muscorum* abundance, confirming its strong association with the flowering of *Calluna*. *B. jonellus* however, was more abundant in overgrown habitats, which might be due to the additional availability of floral diversity or nesting sites here. Overall, this study provides valuable information for the conservation of *B. muscorum*, however further research is needed to develop appropriate management strategies to support *Bombus* populations. Such research is crucial for maintaining the sustainability of the ecosystem services provided by pollinators.

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