MANAGEMENT MATTERS: BEE COMMUNITIES IN OPEN AND DEGENERATE HEATHLANDS IN NORDHORDLAND UNESCO BIOSPHERE RESERVE

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Abstract—Land-use changes and agricultural intensification have been attributed as the main anthropogenic drivers of declines in insect pollinators. Anthropogenic coastal heathlands are one of the ecosystems that have suffered the most from these intensifications, as traditional management practices have discontinued and only 10% of last century´s coastal heathlands remain. We collected data during the field season of 2022 on pollinator communities with emphasis on bumblebees, in two different habitat types: open and degenerate heathlands in an UNESCO Biosphere Reserve in Western Norway. Here, we aim to get an insight into how pollinator communities may change as more heathlands are left without active management practices like prescribed burning and livestock grazing. Species composition varied between the two habitat types. Degenerate heathlands typically had a higher abundance of some relatively common species in Norway, like *B. pratorum*, while the red-listed species *B. muscorum* was recorded exclusively in open heathlands. *B. jonellus* was more abundant in degenerate sites despite being known to forage on Ericaceae. This may be due to an additional floral diversity and nesting/over-wintering sites here compared to the open sites. Further research should explore potential impacts of landscape characteristics like fragmentation and land-use change on the abundance and diversity of pollinators in heathlands.

Keywords—*Bombus* spp., *Calluna vulgaris*, coastal heathlands, secondary succession, cultural landscapes, degenerate heathlands

INTRODUCTION

Unfortunately, many studies have reported declines in pollinator populations with land-use change, pollution, pesticides, pathogens, and alien species being identified as direct anthropogenic drivers (NRC 2007; IPBES 2016; Koh et al. 2016; Sánchez-Bayo & Wyckhuys 2019; Grab et al. 2019; Dicks et al. 2021; Millard et al. 2021). Habitat loss and fragmentation, as well as agricultural intensification, have been attributed as the main reasons for declines in *Bombus* species over the last 60 years (Banaszak 1995; Goulson et al. 2008). Fragmentation often results in small and isolated populations, making them vulnerable to loss of genetic diversity through bottlenecks and drift (Keller & Waller 2002). This has been corroborated by Darvill and colleagues (2006) who discovered reduced genetic variation among certain bumblebee species, likely due to their small effective population sizes.

Although several pollinator species, including bumblebees, are facing declines (e.g., Soroye et al. 2020), some species have been reported to increase in their relative abundance (Herbertsson et al. 2021). Studies have found an increase in the relative number of records for some already common pollinator species like *B. terrestris* and *B. lapidarius*, leading to homogenization and generalist-dominated pollinator communities (Biesmeijer et al. 2006; Bommarco et al. 2011; Herbertsson et al. 2021). In contrast, significant declines have been reported for pollinator species with narrow habitat requirements, those foraging on a small number of plant species, and long-tongued species (Biesmeijer et al. 2006; Bommarco et al. 2011). This also holds true for species with slower development and lower mobility (Biesmeijer et al. 2006). These findings are alarming as changes in pollinator communities or decreases in species richness may impact pollination services by reducing the magnitude and/or stability (Balvanera et al. 2005).

Coastal heathlands are open, low vegetation ecosystems typically found along coastal regions of Europe. They are shaped by traditional management activities like livestock grazing, controlled burning, and turf cutting, which have maintained their open structure for centuries, and even millennia (Kaland 1986; Kaland & Kvamme 2013). In recent years, these ecosystems have been greatly affected by land-use change, in particular by agricultural intensification, forest plantations, infrastructure development, along with the discontinuation of traditional management practices (Gimingham 1972; Aerts & Heil 1993; Diemont 1996; Webb 1998; Prøsch-Danielsen 2000; Britton et al. 2001; Pakeman et al. 2003; Måren 2009; Fagundez 2012). These landscapes often have high biodiversity, supporting specialized flora and fauna, including pollinators, ground-nesting birds, and reptiles (Vandvik et al. 2005; Bargmann et al. 2015; Velle et al. 2023).

Due to societal development, many of these coastal landscapes are no longer viable in an economic perspective, and thus have either been converted by infrastructure development or afforestation. Afforestation may occur naturally, due to succession in the absence of traditional management (through natural encroachment of trees such as pine, spruce, birch, aspen, or rowan) or through intentional efforts to convert the land for commercial forestry or carbon sequestration (Måren 2009; Kaland & Kvamme 2013). As a result, heathlands have become one of the most threatened nature types in Norway as only 10% of their geographical extent remains (Kaland & Kvamme 2013; Hovstad et al. 2018, Artsdatabanken 2025). Much of Europe has seen the same decline (Fagundez 2012).

The heathland vegetation is dominated by dwarf shrubs (Ericaceae) with *Calluna vulgaris* (hereafter called *Calluna)* being the dominant species (Diemont et al. 2013). Other commonly occurring Ericaceous species in Norwegian coastal heathlands are *Erica tetralix, Erica cinerea, Empetrum nigrum, Vaccinium myrtillus, V. vitis-idaea* and *V. uliginosum* (Kaland & Kvamme 2013). If management intensity is too low (grazing pressure and/or prescribed burning), the heather enters the degenerate phase, where the canopy opens, gaps form, bryophytes and lichens reach maximum abundance, and later-successional species such as native and invasive bushes and trees colonize, resulting in natural afforestation. There is ample evidence of the ecological processes leading to degenerate heathlands, and eventually afforestation of former heathland areas (Watt 1947; Gimingham 1972; Miles 1979; Webb 1998; Måren 2009; Saure et al. 2013, 2014; Vikane et al. 2013).

Afforestation of heathlands can cause habitat fragmentation and loss of open-habitat species, while promoting forest-dwelling organisms. Afforestation alters the soil pH, nutrient dynamics, and light availability, which in turn leads to a shift in species composition and a decline in heathland specialists. Balancing afforestation goals (e.g., carbon sequestration and timber production) with biodiversity conservation presents significant challenges. During afforestation, the landscape transitions from open heathlands with patchy shrubs to densely vegetated areas dominated by young trees, and the mosaic structure of mixed vegetation types is replaced by more uniform forested areas over time (Saure et al. 2013, 2014; Vikane et al. 2013).

Secondary succession impacts species that depend on open habitats (Banaszak & Ratyńska 2014; Kosior et al. 2008), including bumblebees, which typically prefer open, ruderal, and semi-natural spaces (Bąk-Badowska et al. 2021). Coastal heathlands serve as important habitats for *Bombus* spp. and other pollinators due to the floral resources and the succession of flowering periods (Descamps et al. 2015; Moquet et al. 2017). *Calluna* is especially important for pollinators towards the end of the season due to the high abundance of blooming heather in July-August. Furthermore, several pollinators are strongly associated with this habitat and its characteristic plants, such as *Colletes succinctus* and *B. muscorum.* Habitat and land-use changes alter the availability of floral resources accessible for pollinators, reducing the quantity and diversity of pollen and nectar (Biesmeijer et al. 2006; Kleijn & Raemakers 2008; Goulson et al., 2015). Fragmentation of heathlands can threaten pollinator species as gaps of floral resources increase and the continuity of flowering is affected (Moquet et al. 2017). Suitable nesting sites may also be disturbed or reduced by habitat changes in semi-natural habitats (Goulson et al. 2015). In addition, the presence of forest patches may act as a possible barrier for foraging individuals like *B. muscorum* (Kreyer et al. 2004). Bąk-Badowkska and colleagues (2021) compared *Bombus* communities in open and forested habitats, and found that forest sites harboured lower abundances, less richness, and lower diversity compared to open sites. Some *Bombus* species appear to be negatively impacted by encroachment as the presence of forest patches decreases their foraging area (Diaz Forero et al. 2011). However, it is important to note that the presence of forests may also be advantageous as they provide possible nesting and overwintering sites (Diaz Forero et al. 2011). Literature on insect communities in heathlands and their response to habitat management is limited, however one study in England showed that rarer species were associated with open conditions created by recently cut or burnt heathland (Usher 1992). Other studies show that maintaining a mosaic of *Calluna* in different successional stages benefits arthropod diversity (WallisDeVries et al. 2016; Hansen et al. 2020; Byriel et al. 2023)

In this study, we aim to explore bee communities in open and degenerate coastal heathlands, focusing on bumblebees in two distinct sampling periods: June 2022 and August 2022. Here, open heathland sites are defined as "heathland in building to mature phase" and degenerate heathland as "heathlands in late degenerate phase or already afforested by tall bushes and/or small trees" (Gimingham 1972). Studies on insects in Norway's coastal heathlands are limited (but see: Hatteland et al. 2005; Bargmann et al. 2015; Bargmann et al. 2016; Kerdoncuff et al. 2023), while vegetation dynamics are well documented (Kaland 1986; Måren 2009; Velle et al. 2023). This study aims to provide insights into potential future shifts in bee community composition as increasingly more heathlands are left unmanaged, resulting in reforestation and changing environments. Specifically, we wish to examine the abundance of heathland or heather-associated species like *B. muscorum* and *B. jonellus* in open and degenerate heathlands and compare the richness of *Bombus* in those habitats.

Based on the existing literature, we predict that bee abundances differ in open and degenerate habitats. Because of the strong association with coastal heathlands and the short foraging distance of *B. muscorum* (Walther-Hellwig & Frankl 2000; Bengtson & Røsok 2019), it is likely that this species is mostly found in open heathland sites. As *B. jonellus* is also associated with heaths and Ericaceae (Ødegaard et al. 2015), it is likely that the abundance of this species is higher in open heathlands compared to degenerate heathlands. Further, species richness may be higher in open heathlands, as *Bombus* species typically prefer open habitats (Bąk-Badowska et al. 2021). Since flowering *Calluna* were abundant only during our sampling period in August (Nagy et al. 2013), we predict that *Bombus* abundance is also higher for the open sites at this time, compared to *Bombus* abundance during the June sampling period. When *Calluna* is in bloom, the foraging distances between each flower are short, and thus individuals may benefit from foraging here by reducing their energetic costs related to flying (Heinrich 1979).

MATERIALS AND METHODS

STUDY AREA AND DESIGN

All study sites were located along the West-coast of Norway in Vestland County at 60 degrees north (Fig. 1) in Nordhordland UNESCO Biosphere Reserve. This area has an oceanic climate characterized by relatively high winter temperatures (annual mean: 0-4°C), relatively low summer temperatures (annual mean: 12-16°C), as well as high levels of precipitation (annual mean: 2000-2500 mm) and humidity (Moen 1998). The growing season is over 210 days, with the length of the growing season defined as "days with an average temperature over 5°C" (Moen 1998). In total, six study sites were categorized as either open heathlands (*N* = 3) or degenerate heathlands (*N* = 3) (Fig. 2 & 3). The open heathlands typically had a lower vegetation layer with a higher cover of *Calluna* and a lower tree and bush cover compared to the degenerate sites. The presence of species

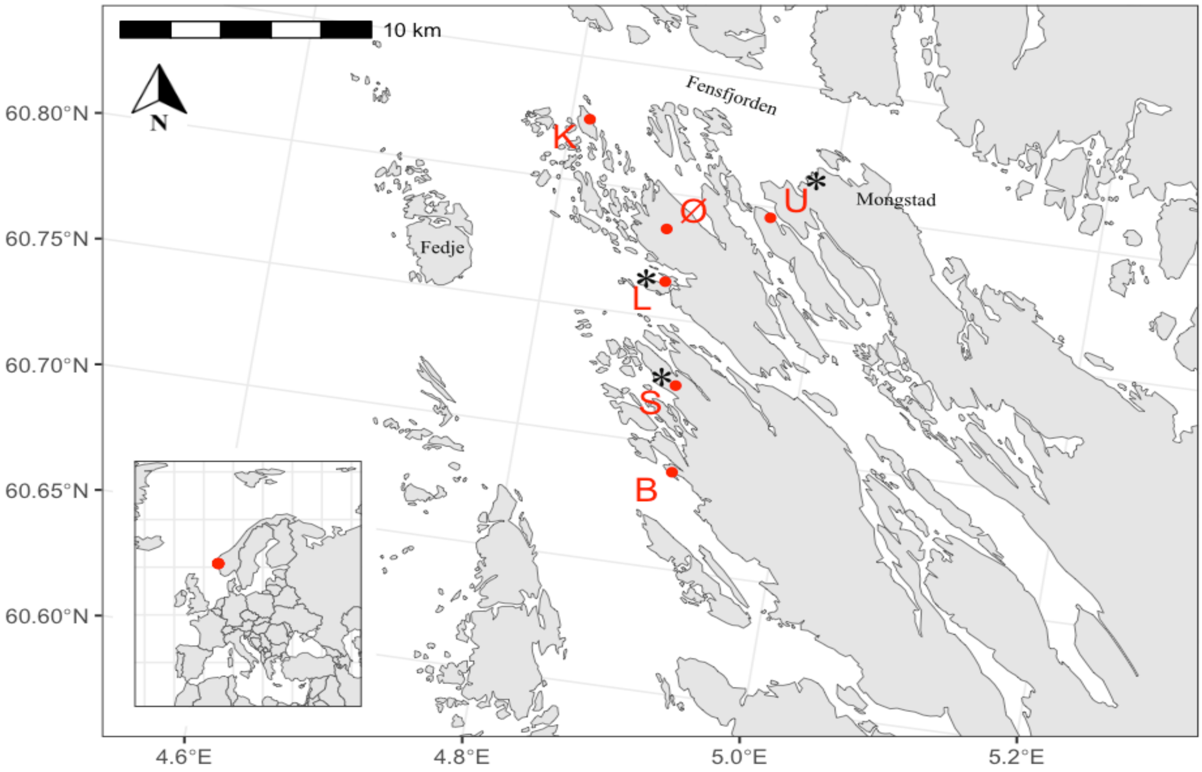

Figure 1: Distribution of the sampling sites in the outer parts of Nordhordland UNESCO Biosphere Reserve, Western Norway. Sites are marked with the first initial of the site name: K=Krossøy, Ø=Øksnes, U=Utkilen*, L=Lerøysundet*, S=Syltneset* and B=Byngja. Map source: GeoNorge. *degenerate heathland sites.

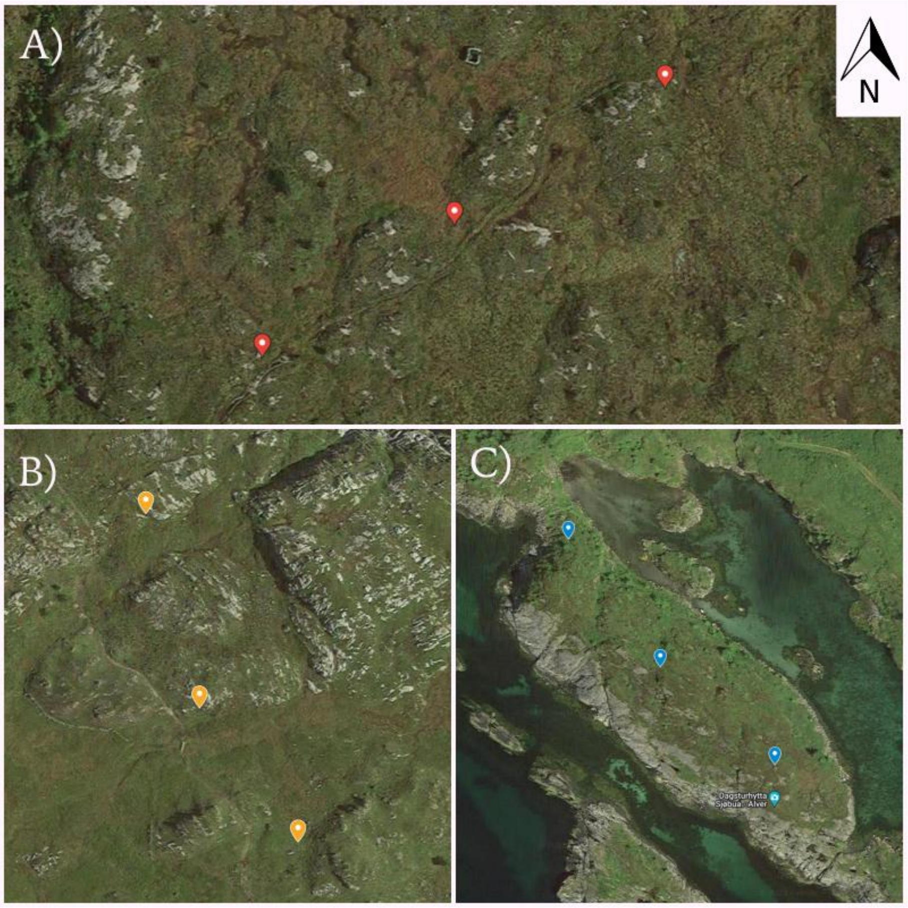

Figure 2: Satellite view of the open heathland sites and placement of pan traps. A) Øksnes B) Krossøy C) Byngja. The distance between pan trap 1 and pan trap 3 is 150 meters at all sites.

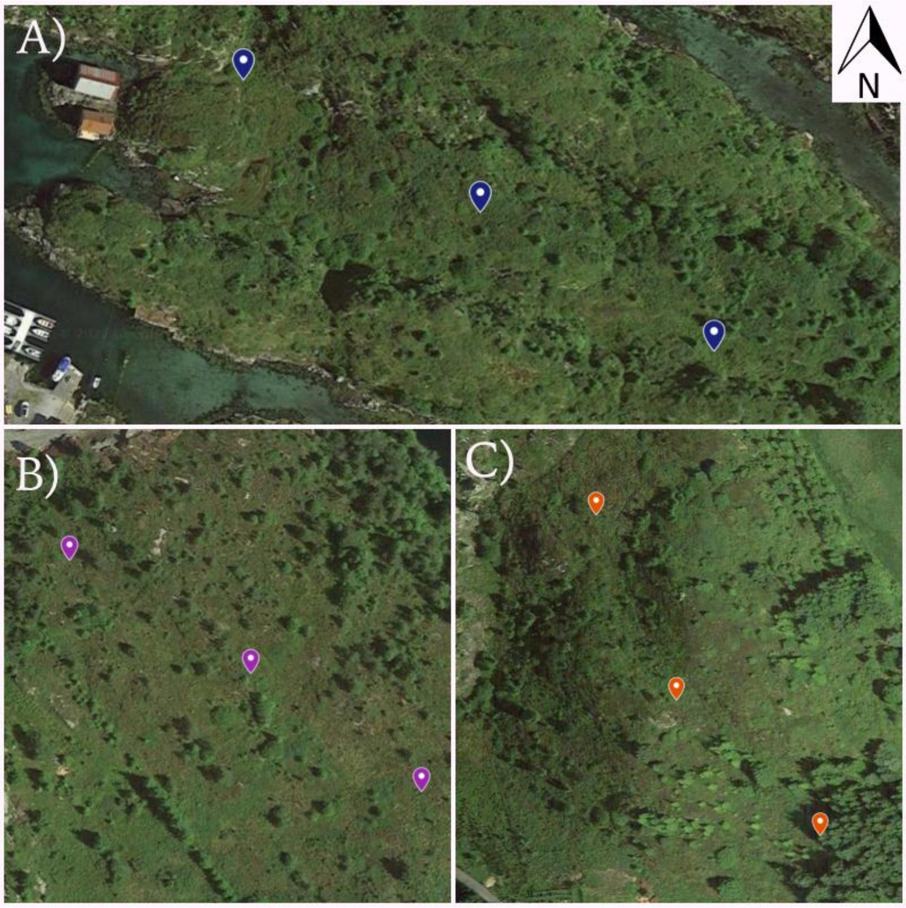

Figure 3: Satellite view of degenerate heathland sites and placement of pan traps. A: Lerøysundet, B: Utkilen, C: Syltneset The distance between pan trap 1 and pan trap 3 is 150 meters at all sites.

typical for heathlands in the degenerate phase, like *Juniperus communis, Betula pubescens, Sorbus aucuparia, Salix caprea, Pinus sylvestris,* and *Vaccinium uliginosum,* were more prevalent in the degenerate heathlands. Large scale planting of Sitka spruce (*Picea sitchensis*) over the past 100 years has resulted in self-seeding of the species into heathland areas in many parts of the coastal landscape, leading to habitat fragmentation and afforestation. Due to the possible long foraging distances of some bumblebee species (Walther-Hellwig & Frankl 2000), sampling sites were separated by at least 2 km in order to be considered independent.

The sampling of pollinators was carried out during two periods: 6 – 17. June 2022 and 22. August – 2. September 2022, all days, excluding Saturdays and Sundays. This was done to obtain data in early summer as well as late summer during the main blooming of *Calluna.* These periods were chosen to assess if the presence of flowering *Calluna* attracted additional pollinators. Each sampling period consisted of 14 consecutive sampling days where pan traps were emptied twice a week (Mondays and Fridays), and sampling by insect net was conducted three days a week unless there was heavy rainfall (Tuesdays, Wednesdays, and Thursdays). The sampled individuals are housed at the University Museum of Bergen in their Natural History Collection.

STUDY SITES DESCRIPTIONS

The open heathlands varied greatly in their composition in vegetation (Fig. 2). At Øksnes, the *Calluna* was estimated to be in the mature phase. Grazing pressure was low, likely only grazed by deer, and management practices were not maintained. At Krossøy, the *Calluna* was estimated to be in the building phase. Grazing pressure from sheep was high, and the area had been burned within the last decade. This site was west facing and exposed to harsh weather. At Byngja, the *Calluna* was 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 recorded, and a field of Sitka spruce was located within 50 meters from the transect.

The degenerate sites were all clearly impacted by the absence of management practices like burning and grazing over a long period, at least the past 20 years (Fig. 3). The heath was 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 Sitka spruce were present.

SAMPLING METHODS

Pan traps (PTs) in blue, white, and yellow were placed at every site and used to collect a wide range of pollinators (Krahner et al. 2024). Traps were painted using a primer (white Motip® primer) and white and yellow Rocol® paints and fluorescent blue Liquitex® paint. One set of PTs contained three 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. All PTs from all locations were emptied on the same day to minimize differences caused by weather conditions.

To strengthen the sampling of bumblebees, we complemented pan traps with targeted netting, as this approach can mitigate potential underrepresentation during periods of high floral abundance (Westerberg et al. 2020). The netting was based on the locations of the PTs and was carried out by following the transect of 150 m and back again. Each way, 30 minutes were spent capturing bumblebees, guided by a timer, making a total of one hour netting at each location. The active sampling was only conducted between 09:00 and 17:00 on days with no precipitation. Temperatures ranged from 11.1 – 22.8°C and wind speed from 1.3 – 5.9 m/s. The order in which the sites were sampled varied to limit possible differences caused by temperature.

VEGETATION SURVEY

Vegetation was assessed by standard methods using quadrant analysis at each site (Vandvik et al. 2005; Måren & Vandvik 2009). Quadrants of 1x1 m were systematically placed at regular intervals along the transects used for the pollinator sampling. The first quadrant was placed about 7 meters from PT 1, and the next about every 14 meters along the whole length of the transect. In total, 10 quadrants were placed on each site. If quadrants landed on a body of water or barren rocks, they were moved to the nearest vegetation patch. The percentage of vegetation cover inside the quadrants was noted for functional groups; of moss, herbs, graminoids, heather, shrubs, and trees. 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.

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" (source: http://x.photoscape.org/). Here, trees were coloured 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 (hence, tree cover) was calculated.

SPECIES IDENTIFICATION

For bumblebees, Astrid Løken's "Norske Insekttabeller 9 Humler" (1985), and "Humler i Norge" by NINA (2015) were used to identify specimens morphologically to species level when possible. Some bumblebee species were grouped together to form the *Bombus lucorum* complex, as they are morphologically difficult to differentiate (Murray et al. 2008; Ødegaard et al. 2015). This group includes the four species *B. lucorum, B. terrestris, B. cryptarum,* and *B. magnus.* Additionally, solitary bee species were identified by examining morphological characteristics in conjunction with Falk (2015) key to bee species: "Field Guide to the Bees of Great Britain".

DATA ANALYSIS

The data analysis was performed using R version 4.2.2 and R-studio version 2022.12.0 (R Core Team 2022) using data pooled from both sampling methods. Rarefaction and species accumulation curves were generated to assess the effectiveness of sampling methods (package: vegan (Oksanen et al. 2022)). Here, the "rarefaction" method was chosen to find the mean species richness when accumulating individuals. A principal component analysis (PCA) was used to visualize dissimilarities of the sites based on species composition and their total abundance (package: vegan (Oksanen et al. 2022)). A PCA was chosen due to the short 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 (Oksanen et al. 2022)). Here, total abundance was used as the response variable, while period (sampling period), state (site category), and mean *Calluna* cover were the predictors. A log transformation of the species abundances was performed 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. Several models with different explanatory variables were tested during the model selection process, and the final models were selected based on correlations between environmental variables, AIC scores, ecological knowledge, and our research questions. A negative binomial distribution was used to account for overdispersion for all glms. For individuals captured with an insect net, the relationship between bumblebee abundance and wind and temperature was explored using ggplot (package: ggplot2 (Wickham 2016)) before fitting a negative binomial glm (package: MuMIn (Barton 2025). This was done to account for any effects on abundance caused by weather conditions. This analysis was not performed for individuals captured with pan traps, as all traps were emptied the same day, and thus weather conditions were not expected to drive differences in abundance. Unfortunately, the data set of solitary bees and hoverflies was limited, and individuals of hoverflies were not identified to species level, thus they were not included in the analyses.

RESULTS

In total, 443 bees were captured, of which 307 were bumblebees, 79 solitary bees, and 57 honeybees (*Apis mellifera*). For the bumblebees, a total of nine species were identified, including the *B. lucorum* complex group (Fig. 4). The most common bumblebees were *B. lucorum* complex, *B. jonellus,* and *B. pascuorum* (Fig. 4), constituting 71% of all the bumblebee individuals captured. Other species collected were *B. hortorum*, *B. muscorum*, *B. hypnorum*, *B. pratorum,* and the cuckoo species *B. campestris*. Both *B. hortorum* and *B. hypnorum* had less than five individuals. Targeted netting seemed to be the most effective sampling method for capturing bumblebees (Fig. S4). A total of 18 solitary bee species were collected, all captured using pan traps (Table S2). The most abundant species were *Lasioglossum albipes, Andrena lapponica, Lasioglossum calceatum, Andrena fucata, Andrena subopaca* and *Lasioglossum fulvicorne,* with the latter being the least abundant. These species constituted 70% of all solitary bee individuals captured. Other species collected were *Andrena ruficrus, Andrena scotica, Andrena semilaevis, Lasioglossum leucopus, Hylaeus hyalinatus, Lasioglossum fratellum, Andrena barbilabris, Andrena haemorroa, Colletes succinctus, Hylaeus brevicornis* and *Nomada marshamella*.

Up to 40% of the bumblebees were captured during the first sampling period, while 60% of the individuals were captured in the last period when *Calluna* was in bloom (Table S1). Species richness of *Bombus* found in open heathlands was similar to degenerate sites, representing eight and seven species, respectively. For solitary bees, 81% of the individuals were found during the first sampling period (Table S2). A higher species richness of solitary bees was found in degenerate heathlands compared to open heathlands, representing 15 and ten species respectively. The heathland specialist *Colletes succinctus* was recorded exclusively in only one of the open heathland sites.

Degenerate heathlands had a higher abundance of some bumblebee species regarded as common in Norway, like *B. pratorum*, while open heathlands had a higher abundance of the rarer, red-listed species *B. muscorum* (Fig. 4). Exceptionally, the *B. lucorum* complex was abundant at all sites, with a particularly high number of individuals found in the open heathland at Byngja. On the other hand, *B. muscorum* was exclusively recorded in open heathlands, of which a total of 26 individuals were found in the sites Krossøy and Øksnes. Furthermore, almost all specimens (92%) were

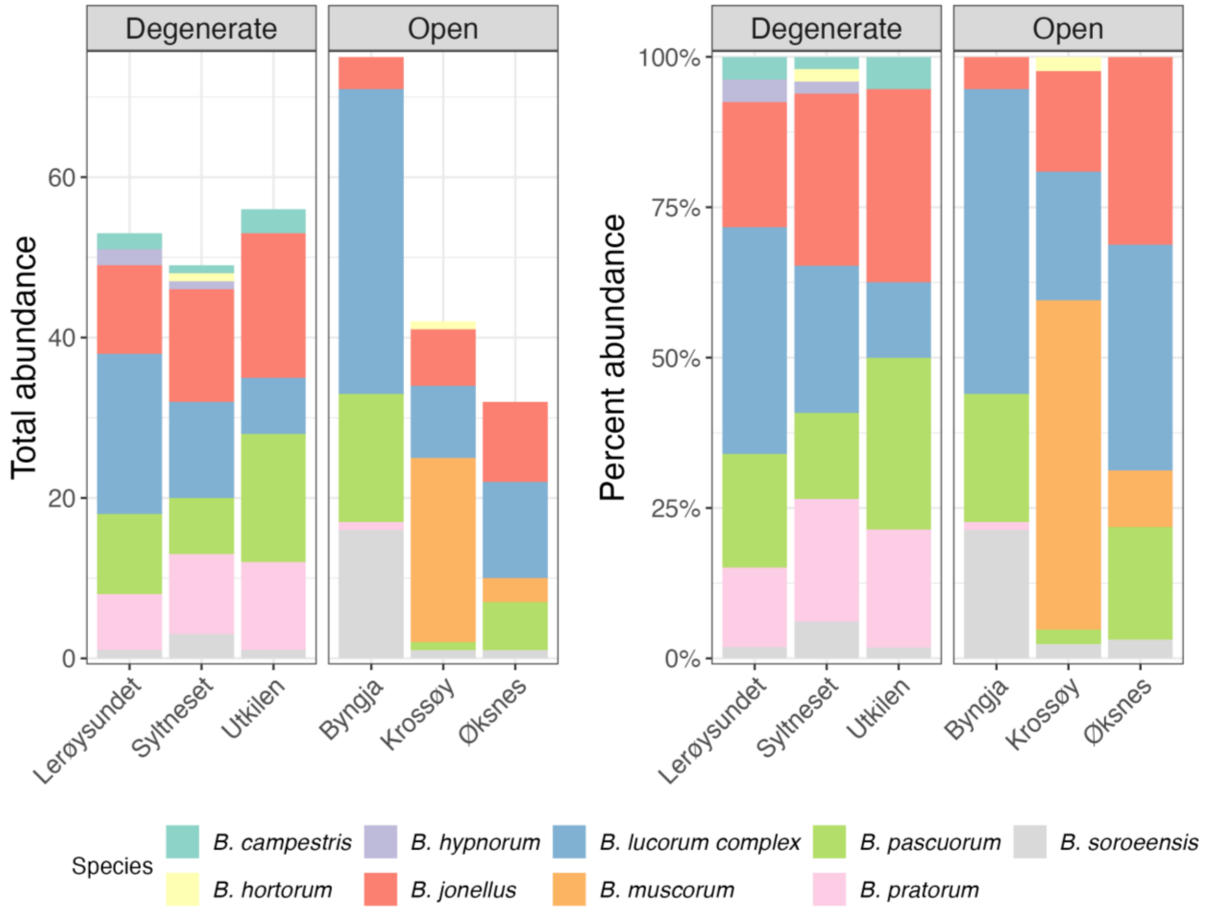

Figure 4: Total and relative abundance of Bombus species at the six study sites. Open facet shows sites in the category open heathland, while degenerate facet shows sites in the category degenerate heathland. *B. lucorum* complex is a group consisting of the species *B. lucorum*, *B. terrestris*, *B. cyptarum*, and *B. magnus*.

found in Krossøy, the largest and most well-managed of the heathlands sampled, and almost all individuals were found in late summer in the flowering period of *Calluna*. In the last sampling period, 67% of the captured individuals of *B. muscorum* were workers (Table S3). For *B. jonellus,* 64 individuals were found in total. This species was found in all sites, with 67% from the degenerate heathlands. Around 70% of the individuals of *B. jonellus* were found in the first period of sampling (Table S1). 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 full bloom (Table S1). Individuals from this group were abundant at all sites but were especially abundant at Byngja, an open heathland site. Byngja also had the highest abundance of hoverflies, although these were not identified to species level (Fig. S5).

The combined sampling by netting and pan traps was not successful in capturing all species at every site as shown by the rarefaction curve with the number of species sampled as a function of the total number of individuals (Fig. S1). Weather conditions (temperature and wind) during sampling did not seem to influence the number of individuals captured with targeted netting (Fig. S2 and S3). This was also confirmed by the negative binomial glm accounting for potential effects on bumblebee abundance caused by weather conditions (Table S4).

The percentage in mean cover of functional plant groups (Table 1) and flowering plants (Table S5) varied between sites. The open heathland sites had a higher cover of *Calluna* compared to the degenerate sites (Table S5). Byngja and Krossøy

Table 1: Mean cover (percentage) of plant functional groups and surrounding tree cover in open and degenerate heathland sites.

Site	Category	Dwarf shrubs (%)	Shrubs (%)	Herbs (%)	Graminoids (%)	Moss (%)	Surrounding tree cover (%)
Byngja	Open	65	8	5	7	16	26
Krossøy	Open	43	8	5	14	30	10
Øksnes	Open	45	7	11	26	11	26
Lerøysundet	Degenerate	58	21	6	6	9	38
Syltneset	Degenerate	61	24	3	7	7	32
Utkilen	Degenerate	44	1	6	13	33	37

had the highest cover of *Erica tetralix*, with 13 and 11%, respectively (Table S5). Øksnes had the highest cover of *Arctostaphylos uva-ursi* (8%), while Utkilen and Syltneset had the highest cover of *Vaccinium vitis-idaea (7%) (Table S5).* 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 also the only site containing *Erica cinerea* (Table S5). Moreover, sheep feces were only present in the vegetation analysis at this site, indicating a high presence of grazing animals. The tree cover analysis using aerial photos showed a higher tree cover surrounding the degenerate sites, ranging from 10–26% for open heathlands and 32–38% for degenerate heathlands (Table 1).

The open heathland sites showed somewhat greater within-category variation compared to the degenerate heathland sites (Fig. 5). PCA1 explained 62% of the total variance in the data, while PCA2 explained 27%, as shown by the eigenvalues (Table S6). In total, 90% of the total variation in the data is explained by the PCA (Table S6). We found some overlap between the open and degenerate categories, while Krossøy was found to be dissimilar to all other sites, regardless of category (Fig. 5). *B. muscorum* differentiated from the other bumblebee species and was closely connected to Krossøy.

The RDA indicated that the abundance of some bumblebee species seems to be connected to sampling period and/or habitat category (Fig. 6). A total of 67% of the variance between species composition and the explanatory variables; site category and sampling period was explained by RDA1, while 30% was explained by RDA2 (Table S7a) and together, 97% of the variance is explained by these two axes. The RDA model was found to be significant ($F = 2.31$, $P = 0.02$) (Table S7b), and a significant portion of the variance in *Bombus* abundance is explained by the predictor variable 'sampling period' ($F = 2.24$, $P < 0.01$) (Table S7c).

In our generalized linear model (glm), "last sampling period" significantly explained the abundance of *B. muscorum* ($Z = 3.17$, $P = 0.002$) (Table 2A). The glm did not, however, find any of the explanatory variables to be significant predictors for the abundance of *B. jonellus* or the lucorum complex (Table 2B & C). Examining the effect of the habitat category was not possible for *B. muscorum* in the glm due to a complete separation issue.

DISCUSSION

The relative abundance of the different bumblebees varied with the two different sampling periods in June and August. Not surprisingly, early emerging species like *B. pratorum* were more abundant during the first sampling period, while late-emerging species like *B. muscorum* were more abundant in August. Both habitat categories supported similar numbers of individuals and *Bombus* species, however the species compositions differed. Degenerate heathlands had higher abundances of common species like *B. pratorum*, while the red-listed *B. muscorum* was exclusively found in open heathlands. This was in accordance with our hypothesis, considering the documented distribution of the species in Norway. *Colletes succinctus,* a solitary bee associated with dry heathland feeding mostly on *Calluna* and *Erica* (Falk 2015), was also exclusively found in one of the open heathland sites. The highest number of individuals of *B. jonellus* were found in degenerate heathlands (67%), however, during the last

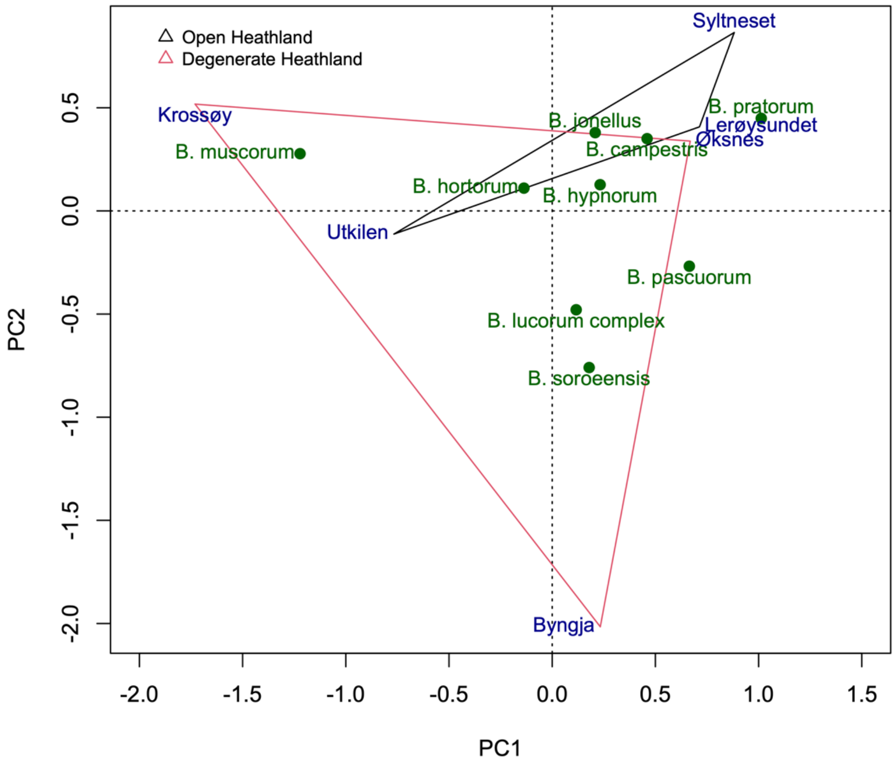

Figure 5: Principal component analysis (PCA) illustrating dissimilarities in sampled Bombus communities. Blue text depicts site names, while green text depicts abbreviated species names to avoid overlapping. Black triangle shows open heathland sites, while the red shows degenerate heathland sites.

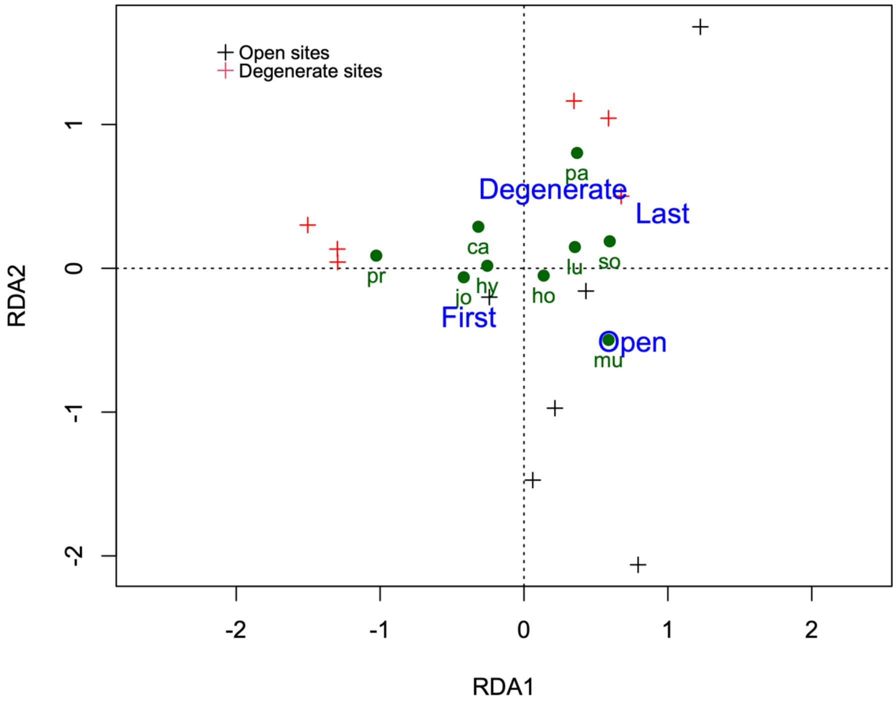

Figure 6: Redundancy analysis (RDA) of bumblebee abundance. Blue text depicts explanatory variables (first and last sampling period, open and degenerate heathland), while green text depicts species names. Species names are shortened to avoid overlapping, here *Bombus* is removed, and only the first two 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 degenerate heathland.

sampling period in August, 94% of *B. jonellus* individuals were found in open habitats. *Calluna* blooms relatively late, when other flowers may be scarce (Mahy et al. 2011), thus serving as an important food source for several pollinator species towards the end of summer. The generalist group *B. lucorum* complex was abundant at all sites, and especially at Byngja. This was expected as *B. lucorum* complex is a generalist group able to forage on a range of different plant species. Not surprisingly, the last sampling period also revealed a higher abundance of *B. muscorum*, due to the lifecycle of the species, as workers and males emerge later in the season (Ødegaard et al. 2015).

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

	Estimate	Std. Error	Z value	Pr(>|z|)
A) *B. muscorum*				
(Intercept)	-1.099e+00	7.071e-01	-1.554	0.12026
State: Degenerate	-3.691e+01	1.955e+07	0.000	1.00000
Period: Last	2.331e+00	7.360e-01	3.167	0.00154
B) *B. jonellus*				
(Intercept)	0.44579	0.84368	0.528	0.597
State: Degenerate	1.01120	0.98513	1.026	0.305
Periode: Last	0.04122	0.98183	0.042	0.967
C) *B. lucorum* complex				
(Intercept)	0.85745	0.64300	1.334	0.182
State: Degenerate	0.04611	0.75165	0.061	0.951
Period: Last	0.96353	0.74487	1.294	0.196

In accordance with our expectations, *B. muscorum* was exclusively found in open heathlands. The species was especially abundant at Krossøy, the largest and most well-managed of the open heathland sites This might be explained by its strong association with open coastal habitats like the coastal heathlands (Bengtson & Røsok 2019). However, *B. muscorum* may visit a range of open habitats, including moorland and dunes (Goulson et al. 2005), in addition to the heather dominated areas. It is regarded as a polylectic species visiting a number of different plant species beside *Calluna* (Walther-Hellwig & Frankl 2003) and may thus take advantage of heterogenous habitats. Queens typically forage on *Salix spp.*, *Erica tetralix* and flowers in the pea family (Bengtson & Røsok 2019). In Norway, this species has only been documented along the coastline (with one exception), in contrast to its distribution in other European countries (Source: https://www.gbif.org/species/1340286). It should be noted that, in our study, 24 of the 26 individuals of *B. muscorum* were collected at a single site, Hence the observed association between this species and open heathlands may reflect site-specific conditions or other unmeasured factors rather than a general habitat preference. Further studies with greater spatial replication would be needed to determine whether this pattern is consistent across other heathland systems. The relatively late emergence of *B. muscorum* (Ødegaard et al. 2015) makes it well suited to heathlands as many of its workers fly during the flowering period of *Calluna*. This timing ensures that the workers have access to an abundant food source close to the nest, which may be especially important as *B. muscorum* has a short foraging range (Walther-Hellwig & Frankl 2000). It is therefore not surprising that the August sampling period coincided with high *B. muscorum* abundance.

Contrary to our hypothesis and despite being associated with *Calluna* and other dwarf shrubs, *B. jonellus* was more abundant in degenerate sites. Previous studies on *B. jonellus* appear to support our finding, indicating that this species may be found in a variety of habitats. A study from Russia found that the species tended 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 & Kolosova 2020). Additionally, Goulson et al. (2006) recorded *B. jonellus* in three different habitats: gardens, lowland heathland, and calcareous grassland, also indicating this species to be less restricted to specific habitats. Interestingly, in the August 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 *Calluna* flowering period. As managed heathland vegetation tends to be relatively homogenous (Kaland & Kvamme 2013), degenerate sites might have 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* (Ødegaard et al. 2015) and might consequently have a weaker dependence on *Calluna* or other late-flowering Ericaceous species. Instead, other Ericaceous species like *V. vitis-idaea* and *V. uliginosum* may be important, which were both more abundant at the degenerate sites. This is also supported in our study since most of the individuals were captured during the first sampling period. The distribution of *B. jonellus* is not solely limited to coastal regions, as it can also be abundant at higher elevations (Ødegaard et al. 2015). Therefore, the abundance of *B. jonellus* is not exclusively dependent on coastal heathlands.

For heathland-associated solitary bees, only one species with one individual was found, namely *C. succinctus*. This individual was captured at Krossøy. It should also be noted that *Andrena fuscipes*, another solitary bee associated with *Calluna*, was not found in this study (Exeler et al. 2010). However, the species has previously been registered in one of the open heathland sites, Øksnes, through "Artskart" (2018) (source https://www.artsobservasjoner.no/Sighting/31279680). The other species collected may be considered generalists, and thus not strongly connected to heathlands or *Calluna*. We found an overall higher diversity of solitary bees in degenerate sites and higher abundance in the first sampling period, which may be explained by higher floral resources in these sites during spring and early summer.

We found no significant difference in *Bombus* richness between open and degenerate heathland sites. 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 a mixed forest cover. Since *Bombus* typically prefer open and semi-natural habitats (Bąk-Badowska et al. 2021), our results were somewhat surprising. However, sites with closed-canopy forests are not included in our study, which may explain the small difference in richness between heathland types. These habitats are expected to have fewer species, especially in dense forests like plantations. It is possible that the preference for open habitats was counterbalanced by the additional floral diversity and nesting sites in degenerate habitats. Further research is required to validate this assumption. Furthermore, 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, as well as it only being registered along the coastline in Norway.

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 connection between sampling period and *Bombus* abundance may be explained by the distinct lifecycles of species rather than the presence of flowering *Calluna*. Lifecycles may also explain why most of the solitary bees were found during the first sampling period. One of the most abundant species, *A. lapponica*, emerges relatively early in the season and feeds heavily on bilberries (Falk 2015). This is also true for many *Andrena* species (Herrera et al. 2023) like *A. fucata* (Banaszak & Szefer 2014) and *A. haemorroa* (Olsen & Sunesen 2004). *A. fucata* is associated with Rosaceae, while *A. haemorroa* commonly visits spring flowers like Taraxacum and *Tussilago farfara*. Other species, like *L. alpibes* and *L. calceatum*, are thought to fly into September and October, (Falk 2015). However, as most of our individuals were females, these may have been overwintering and thus explain why they were sampled earlier.

Both pan traps and netting were used as a sampling method for bumblebees in this study, as each Sitka spruce method has inherent biases but may complement one another in representing pollinator communities (O'Connor et al. 2019; Graham et al. 2023). Bumblebees were mainly captured using netting in all six sites, while solitary bees were only sampled using pan traps.

The *B. lucorum* complex was chosen as a study species, as this species within this group are common throughout the season (Ødegaard et al. 2015). During the August sampling period, 58% of the *B. lucorum* complex individuals were caught. The abundance was similar for both habitats during the June sampling, however, in the August sampling, 67% of the individuals were from the open habitats. This indicates that late-flowering species like *Calluna* may be especially important for pollinators at the end of the season. Interestingly, Byngja (the most fragmented of the open habitats with an area of Sitka spruce 50 meters from the pan traps) had a particularly high abundance of this group, with 55% of all individuals. In contrast, Krossøy, another open heathland, only inhabited 13% of the individuals. Byngja also had the highest abundance of *B. soroeensis,* with 70% of all individuals (Table S1), and the highest abundance of hoverflies. This could indicate that the *Calluna* in Byngja provided an abundant food source in a region that is otherwise heavily forested with low floral abundance and therefore attracts many foraging individuals. No relationship between the abundance of *B. lucorum* complex and the sampling period was indicated. This may be caused by the restricted number of sites and sampling, or because it is a group of generalist species like *B. terrestris* with a wide diet (Somme et al. 2015) and can thrive without foraging on *Calluna*. Some species, like *B. terrestris,* may travel up to 1750 m to forage (Walther-Hellwig & Frankl 2000). Thus, it is likely this species visits floral resources across different habitats, depending on the habitat size and connectivity. *B. lucorum* may therefore not be as dependent on the abundance of *Calluna* in heathlands as species with a shorter foraging range, like *B. muscorum (*Walther-Hellwig & Frankl 2000*)*.

Bombus species may benefit from foraging on *Calluna* in heathlands because of the short distances between each flower, thereby limiting their energetic costs related to flying (Heinrich 1979). 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. This could also be influenced by the nesting habits of different species. *B. hypnorum,* for instance, typically nests in trees and may struggle to find suitable nesting sites in open heathlands. For fragmented habitats, forest patches may also serve as physical barriers for some species.

Large and continuous habitats are favourable in the conservation of *Bombus* which may be susceptible to inbreeding and stochastic events (Goulson et al. 2008). Consequently, it would be beneficial to know whether there exists a specific minimum habitat size required to sustain different pollinator species. For instance, a study of pollination failure in an orchid species *Ptegodium 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 peringeuyi* (Pauw 2007). Finding the exact habitat size needed to host stable populations of specific species like *B. muscorum* requires more research and is likely to depend on a combination of 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; Dicks et al. 2021). In addition, fragmented habitats with limited floral resources may increase competition between pollinators. In coastal heathlands, *B. muscorum* may compete with managed honeybees (Nielsen et al. 2024), as well as other bumblebee species (Plowright et al. 1997). For these reasons, the best way to conserve vulnerable pollinator species, like those with narrow habitat ranges, is likely by preserving their habitats for floral resources, nesting sites as well as overwintering sites. Habitat size, connectivity, and management practices may also explain why Krossøy was the only site with a higher number of *B. muscorum* individuals. Here, grazing animals (sheep) were present, 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 currently managed.

FURTHER RESEARCH

This study provides important insights, considering the limited number of studies on pollinating insects in northern coastal heathlands. However, further research should be conducted to better understand the status of pollinators in these ecosystems, especially considering our limited sampling period. Insect populations are subject to natural fluctuations; consequently, studies of insects can benefit from being conducted across multiple seasons. Sampling in two discrete periods instead of continuously may also overlook seasonal variations and broader ecological trends. By collecting data on bee communities in sites of a later successional stage such as young forests, we could observe how communities may change further as heathlands are left unmanaged. Additional studies could investigate potential impacts of landscape characteristics such as fragmentation, management, and surrounding land use on *Bombus* diversity and abundance. Further research is needed to determine minimum heathland management levels for maintaining healthy populations of *B. musorum* and *C. succinctus* in heathland ecosystems, as well as clarify how excessive grazing pressure or overly frequent burning may affect bees in heathland ecosystems. As *B. muscorum* is vulnerable to inbreeding due to fragmented habitats (Darvill et al. 2006), genetic studies could be used to investigate genetic diversity as well as gene flow between populations. Comparing individuals from present populations to earlier sampled specimens could give us key insights into how genetic diversity has changed through time.

CONCLUSIONS

The results from our study indicate that open heathlands, opposed to degenerate heathlands, are preferred by the red-listed species *B. muscorum*, which was exclusively found in open habitats. This appears to be the case for *C. succinctus* as well. In addition, the open heathland sites harboured more bumblebees later in the season, including generalist species. This indicates that heathlands and *Calluna* may be important for many species during this time, as the abundance of other flowering plants are limited.

The August sampling period was strongly associated with *B. muscorum* abundance, confirming its association with *Calluna*. *B. jonellus* however, was more abundant in degenerate habitats, which might be due to the additional availability of floral diversity or nesting/overwintering sites here. The degenerate heathland sites also had a higher number of other common bee species. Overall, this study provides valuable information to support the conservation of bumblebees like *B. muscorum*, by also managing the coastal heathlands as a cultural landscape with its multitude of ecosystem services, including pollination services and biodiversity conservation.

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AUTHOR CONTRIBUTION

Susanne Zazzera: Conceptualization, Data curation, Formal Analysis, Investigation, Software, Writing – original draft.
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DISCLOSURE STATEMENT

All authors declare that they have no conflicts of interest.

GENERATIVE AI DISCLOSURE STATEMENT

ChatGPT (Free Version) was used to suggest a concise abstract for the article. The finished abstract was edited by the author to ensure accuracy.

DATA AVAILABILITY STATEMENT

The data used in this study is available through Zenodo: https://zenodo.org/records/13913579.

APPENDICES

Additional supporting information may be found in the online version of this article:

Figure S1: Rarefaction curves for *Bombus* communities.

Figure S2: Relationship between *Bombus* abundance and temperature.

Figure S3: Relationship between *Bombus* abundance and wind.

Figure S4: Sampling methods for all individuals.

Figure S5: Abundance of hoverflies.

Table S1: Total abundance of *Bombus.*

Table S2: Total abundance of solitary bees.

Table S3: Sites for *B. muscorum.*

Table S4: Coefficients for the negative binomial GLM.

Table S5: Mean cover of various flowering plant species.

Table S6: Importance of components in PCA.

Table S7: Importance of components in RDA.

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