

**Inland Norway
University**

Faculty of Applied Ecology, Agricultural Sciences and Biotechnology

Jenny Valaker

Master thesis in Applied Ecology

Are bumblebees limited by floral resource availability due to cattle grazing in boreal forest pastures?

The effects of seasonality and cattle grazing on bumblebees in boreal forest pastures

Applied Ecology

2022

Preface

This thesis was written as the final part of a master's degree in Applied ecology at the Inland University (Faculty of Applied Ecology, Agricultural Sciences and Biotechnology).

Many long days in the field, in the lab and struggles behind a computer screen has gone into the process of this thesis. Throughout it all, my appreciation for nature has grown, leaving me even more in awe of the beauty and complexity of it all. The joy of being able to identify a bumblebee, landing on a flower in my garden will never become dull.

I would like to thank my supervisors Mélanie Spedener, Ander Nielsen and Marie Vestergaard Henriksen for helping, guiding, and enriching me with valuable knowledge. I consider myself extremely lucky to be your student. Additionally, to the whole CarniForeGraze team at Evenstad, a huge "thank you!", for creating a good working environment, filled with interesting people. Many great conversations with other students, fieldworkers, professors, and supervisors have shaped this study for the better and I will forever hold a great deal of gratitude for this.

Lastly, I would also like to thank my dear friends and family, for all your love and support throughout this process.

Jenny Valaker

Abstract

Boreal forests provides a wide range of ecosystem services and goods that serve the Norwegian community. For centuries humans have utilized this resource in commercial sectors through timber production and traditional forest pastures for livestock. However, these long traditions of keeping livestock in forest pastures has been subject to change as a result of re-establishing carnivore populations and agricultural intensification. The relationship between flowering plants and their pollinators plays a central role in securing a harmonious and healthy ecosystem in forest pastures. To ensure a viable population of wild pollinators in Norway, the Norwegian government aims to further increase knowledge on how to safeguard and provide suitable pollinator habitats. In line with the request for a more carnivore-compatible method for keeping livestock, the focus is directed to re-establish beef cattle (*Bos taurus*) in these forest pastures. These initiatives combined calls for effort to look at the effects of grazing on biodiversity, as there is a lack of previous research on the matter in boreal forest pastures.

This study investigates the effect of cattle grazing on bumblebees and their floral resources in the boreal forest, by comparing observations from areas with and without cattle grazing during the peak flowering season. The main objective is to study the effect of season on variation in floral resources, how cattle presence affects resource availability and how this in turn might affect the bumblebee diversity. The study shows that although there is less total abundance of floral resources in areas with cattle, there is no significantly negative relationship between cattle presence and the abundance and richness of bumblebees. The timing of flowering varied between different plant species, some reaching their peak earlier in the season and some later. These findings suggest that the bumblebees were not limited by less available resources because of cattle grazing. The consequences of cattle grazing in forest pastures may there for not pose a negative effect on bumblebees with a low intensity grazing pressure. However, further in-debt research about other plant-pollinator interactions in the area is needed to be able to give a more accurate inference of the effects of grazing.

Keywords: Boreal forest, grazing effects, phenology, resource availability, bumblebees, plant-pollinator interactions.

Sammendrag

Den boreale skogen gir et bredt utbytte av økosystemtjenester og varer som tjener det norske samfunn. I århundrer har mennesker utnyttet denne ressursen gjennom blant annet tømmerproduksjon og tradisjonelt skogsbeite for husdyr. Disse lange tradisjonene med å holde husdyr i skogsbeite har imidlertid vært utsatt for drastiske endringer, hovedsakelig som følge av reetablering av rovdyrbestander og intensivering av jordbruk. Forholdet mellom blomstrende planter og deres pollinatorer spiller en sentral rolle for å sikre et harmonisk og sunt økosystem i skogsbeite. For å sikre en levedyktig bestand av ville pollinatorer i Norge, har den norske regjeringen satt som mål å ytterligere øke kunnskapen om hvordan man kan best mulig sikre og sørge for egnede habitater for pollinatorer. I tråd med ønsket om en mer rovdyrkompatibel strategi for husdyrhold, rettes fokuset mot å reetablere kjøttfe (*Bos taurus*) i disse skogsbeitene. Disse initiativene til sammen oppfordrer til en innsats for å granske effektene av beiting på biologisk mangfold, da det finnes lite tidligere forskning på dette temaet i boreale skogsbeiter.

Dette studiet undersøker effekten av storfebeite på humler og deres blomsterressurser i norsk boreal skog, ved å sammenligne observasjoner fra områder med og uten storfebeite i toppblomstringssesongen. Hovedmålet er å studere årstidens effekt på variasjon i blomsterressurser, hvordan storfes tilstedeværelse påvirker ressurstilgjengeligheten og hvordan dette i sin tur kan påvirke artsmangfoldet til humlene. Studiet viser at selv om det er mindre total abundans av blomsterressurser i områder med storfe, er det ingen signifikant negativ sammenheng mellom storfes tilstedeværelse og abundans og artsrikdom til humlene. Tidspunktet for blomstringen varierte mellom ulike plantearter, der noen arter når blomstringstoppen tidligere i sesongen og noen senere. Disse funnene tyder på at humlene ikke var begrenset av mindre tilgjengelige ressurser på grunn av storfebeite. Konsekvensene av storfebeite trenger derfor ikke ha en negativ effekt på humler, ved et lavt beitetrykk. Det er imidlertid et behov for ytterligere forskning på andre plante-pollinator interaksjoner i området for å kunne gi en mer nøyaktig bilde på effektene av beiting.

Nøkkelord: Boreal skog, effekt av beite, fenologi, ressurstilgjengelighet, humler, plante-pollinator interaksjoner.

Contents

PREFACE	III
ABSTRACT	IV
SAMMENDRAG	V
LIST OF TABLES AND FIGURES	IX
1. INTRODUCTION	1
1.1 BUMBLEBEE ECOLOGY	2
1.2 PLANT-POLLINATOR INTERACTIONS – SEASONAL VARIATION IN FLOWERING	3
1.3 FORESTRY AND LIVESTOCK GRAZING IN THE BOREAL FOREST	4
1.3.1 GRAZING PREFERENCE	5
1.4 AIM OF STUDY	5
2. MATERIALS AND METHODS	7
2.1 STUDY AREA	7
2.2 STUDY ANIMALS	8
2.3 COLLECTION OF DATA	8
2.3.1 CAPTURING AND IDENTIFICATION OF BUMBLEBEES	9
2.3.2 PLANT SPECIES AND FLOWER COUNTS	9
2.4 ANALYSIS	10
3. RESULTS	12
3.1 THE FLOWERING OF DIFFERENT PLANT SPECIES THROUGHOUT THE SEASON	13
3.2 THE CHANGE IN ABUNDANCE OF ALL FLOWER SPECIES DURING THE FLOWERING SEASON	15
3.3 RELATIONSHIP BETWEEN THE AVAILABILITY OF FLOWER RESOURCES AND THE ABUNDANCE AND RICHNESS OF BUMBLEBEES	17

4. DISCUSSION	19
4.1 THE TIMING OF FLOWERING	19
4.2 THE EFFECT OF GRAZING ON THE ABUNDANCE AND RICHNESS OF FLORAL RESOURCES	21
4.3 ARE BUMBLEBEES LIMITED BY AVAILABLE FOOD RESOURCES?	22
5. CONCLUSION	24
REFERENCE LIST	25
APPENDENCIES	33

List of tables and figures

<i>Figure 1. Map of study area with sites.</i>	7
<i>Figure 2. Showing the nets used to catch bumblebees</i>	9
<i>Figure 3. A: Site design and grid</i>	9
<i>Figure 4 Mean number of flowers with visits, with and without cattle presence</i>	13
<i>Figure 5 Flowering in plant species with visits from Bumblebees, viewed separately.</i>	14
<i>Figure 6. The change in Flower abundance across the five sampling rounds</i>	15
<i>Figure 7. The abundance of bumblebees</i>	17
<i>Table 1. List of Observed bumblebee species</i>	12
<i>Table 2. Overview of the bumblebee visits on each flower species.</i>	12
<i>Table 3 Model fit (AICc)</i>	16
<i>Table 4. Coefficient estimates.</i>	18

1. Introduction

Grazing by large herbivores has a great impact on the function of ecosystems at a global scale (Austrheim et al., 2011). Moreover, changes in husbandry practices and intensification of agriculture in Norway has led to a decrease in grazing animals, such as cattle, in the Norwegian outfields (non-agricultural land), thus in forest pastures. In addition to this, the expansion of carnivore zones has restricted the practise of keeping livestock in the outfields, due to fear of predation from large carnivores, such as brown bear and wolf (Zimmermann et al., 2001).

The multifunctionality of the European forest developed what we now know as our cultural landscape (Vos & Meekes, 1999), and facilitated a mixed agricultural system combining practises, such as timber production and forest grazing for livestock. These traditional practises have created a cultural landscape that is the home for a diverse ecosystem that many species today depend on for surviving (Eriksson , 2018; Statsforvalteren i Innlandet, & Innlandet Fylkeskommune, 2021). To protect this important landscape for biodiversity, the Norwegian government (Norwegian Ministries, 2018) calls for a necessary effort to maintain traditional practices and new initiatives in the “National pollinator strategy”, to ensure viable populations of wild pollinators. With the aims to re-establish livestock populations in the outfields (Statsforvalteren i Innlandet, & Innlandet Fylkeskommune, 2021), cattle has been recommended as a more fitting animal to keep in carnivore-exposed areas (Zimmermann et al., 2003), due to a much lower documented depredation rate compared to sheep (about 100 times higher for sheep).

Long traditions of keeping livestock in forested and mountainous areas have played a significant role for the establishment of many grasses, and other flowering plant species that need significant sunlight to grow (Wilson et al., 2012). Many of these species are also dependent on insect pollination for their reproduction. The intensification of agriculture has led to a drastic change of land use and is one of the main reasons for habitat loss. This loss of habitat has resulted in the decline in pollinators, including bumblebees, worldwide (Goulson et. Al., 2008). Pollination is a vital function in healthy ecosystem, as it positively affects the reproduction for ~89% of wild (Ollerton et al. 2011) and many cultivated plants (IPBES, 2016). A decline in pollinators can therefore lead to a dramatic change in our natural ecosystems as it can cause extinction in already vulnerable species of plants and animals (Kevan & Viana, 2003). Although many examples of birds, bats and other animals as pollinators exist throughout the world, pollination by animals in Norway is limited to only insects.

In line with the goals of the “National Pollinator strategy” (Norwegian Ministries, 2018), this thesis investigates trends in the local pollinator communities in the boreal forest of the Inlands. With the main objective being to obtain more knowledge on how forestry and food production from livestock in carnivore zones can coexist with maintaining and, hopefully, increasing the local biodiversity of plants and pollinators

1.1 Bumblebee ecology

Bees (*Apodidea*) in general, and bumblebees (*Bombus*) in particular, are important pollinators, as their mouthparts and bodies are well adapted for extracting nectar and carrying pollen (Kevan & Baker, 1983). These pollinators in turn depend on pollen and nectar as sources of protein and energy, and many species of bees also need it for feeding their larva, filling their wax-made nests with reserves of it (Goulson et al., 2010). Although often referred to as more of a primitive eusocial group compared to honeybees, bumblebees are of great importance for both natural and farmland ecosystems in the Northern hemisphere (Maebe et al., 2021). They are efficient pollinators in colder climates, partly due to their large body size compared to other bees (Goulson et al., 2010.) In addition their bodies are also well-insulated, covered with hairs and scales (Heinrich, 1974), and they are capable of endothermy (increasing their own body temperature above the actual temperature in the air, while in flight foraging). When brooding her young the queen also has the ability to thermoregulate by vibrating her chest-muscles to create a warm environment for her eggs when nursing them in her nest (Ødegaard et al., 2015). These adaptations make them more suited for colder climates where other pollinators are not present (Maebe et al., 2021) and the European bumblebee population is found to have larger species richness in subalpine zones, specifically in meadows with great diversity of flower resources (Goulson et al., 2010).

There are more than 250 known bumblebee species worldwide (Goulson et al., 2010) and 35 of these can be found in Norway. The majority of the species in Norway are social (28 species) which means that they live in colonies (Ødegaard et al., 2015). These colonies are annual and are created in early spring by an overwintered fertile queen. The queen lays her eggs and raises female bumblebees that will work to gather pollen and nectar for the colony and are therefore called workers. Male bumblebees are called drones and will be produced by the colony later in the summer, together with

fertile females (Ødegaard et al., 2015). At the end of the season, the females will copulate and search for a suitable shelter to hibernate over winter. The colony will then die out in the late summer, leaving only the new fertile females to live for another season (Maebe et al., 2021).

1.2 Plant-pollinator interactions – seasonal variation in flowering

There is great diversity within pollination systems for bees and the flowers they visit, due to the ability of bees to read complex systems for optimal foraging. Most of the flowers visited have developed features that align with the ecology of bees, which makes an intricate web of connections between flowers and bees (Kevan & Baker, 1983). However, each insect you can observe visiting a flower may not be a pollinator, as the visitor must be in contact with the flowers reproductive organs for so to transport the pollen to another flowering individual. In this way, all pollinators are flower-visitors but not all flower visitors are pollinators (Totland et al., 2013).

The beginning stage of a bumblebee colony is a vulnerable and detrimental time for the queen to secure the success of her colony, and the colony requires continuous access to floral resources to be able to sustain itself (Goulson et al., 2010). The available flower resources, climate, and other species-specific traits are important factors that affect the size of the colony (Goulson et al., 2010). The queen and the individual workers then act on behalf of the needs of the colony. The number of eggs the queen lays in the beginning of the season, together with the quality of the surrounding habitat, determines the size of the colony. The size of a bumblebee colony varies among species, with some species containing up to 350 individuals during their active season (Goulson et al., 2010).

Although the colony, as a whole, may forage on a variety of different flower species, the individual worker can have strong flower constancy, which means she will specialize on a particular species of flower for certain amount of time (Heinrich, 1976). This also helps build resilience for the colony and aids to protect it from disturbances that might influence the resource availability. Plant species flower at different times during the season, and the colony will benefit from a generalized foraging (Heinrich, 1976). However, the flowering of some plant species may be more important than others for certain amounts of time during the season. A lack of resources due to a sudden change in the flower resources may have fatal consequences for the colony.

1.3 Forestry and livestock grazing in the boreal forest

About 40% of Norway is covered by boreal forest (Framstad & Sverdrup-Thygeson, 2015) which is one of Norway's largest renewable resources (Bright et al., 2014). Most of the Norwegian boreal forest is therefore under active management for timber production. Although coniferous forests tend to be acidic and nutrient poor in the soil layer (Rekdal, 2006), the practice of clearcutting opens the canopy and allows for increased light influx on the ground vegetation. Increased light improves the growth conditions for a range of plant species, including herbs in the field layer that depend on insect pollination for their reproduction.

Clearcuttings and young forest stands can therefore have more diverse flower resources available for pollinators than old forests, which in turn can increase bee richness (Rubene et al., 2015). A diverse plant community, including a wide range of young deciduous trees, herbs and grasses, will then in turn create a temporarily available foraging habitat for wild ungulates and livestock (Tofastrud et al., 2019). Clearcuttings as patches of suitable foraging habitat will at some point become less accessible, as the growth of coniferous trees changes the landscape to a denser forest with less diversity of deciduous trees and other plants. Tofastrud, et al., (2019) found that cattle preferred young spruce forests (< 15 years) for grazing and resting.

Although damages to the young coniferous trees may occur in areas with cattle grazing, the damages posed on the trees are mainly caused by cattle when they are walking and laying down, not due to foraging (Hjeljord et al., 2014). Further, grazing can also accelerate the process of nutrient cycling because their feces and urine act as natural fertilizer, returning carbon and nutrients to the soil, and therefore also changing the available nutrients for the plants (Harrison & Bardgett, 2008). Positive effects of grazing can also be seen when plants respond with a compensatory growth, prohibiting growth of other later successional plants that may bring less nutrients when decomposing. These processes are, however, very complex and both positive and negative effects can occur depending on microbial activity in the soil and local composition of plant species (Harrison & Bardgett, 2008).

The Intermediate Disturbance Hypothesis is often used to predict how plant diversity peaks under moderate grazing (Gao & Carmel, 2020). Predicting that higher densities of livestock grazing lead to more negative effects on the biodiversity in plant communities, which in turn can affect other trophic levels in the ecosystem- such as insect pollinators (Franzén & Nilsson, 2008).

1.3.1 Grazing preference

Previous studies have demonstrated that cattle are opportunistic grazers that forage on not only green grass, but also forbs and shrubs and even browses the occasional tree if the preferred resources are scarce (Holechek et al., 1982). Wild ungulates, however, are mainly browsers and prefer foraging on forbs and the twigs and leaves of woody vegetation (Mathisen et al., 2010; Spitzer et al., 2020). A decrease in numbers of cattle livestock can partly enable wild ungulates to increase in abundance, especially moose (*Alces alces*) and roe deer (*Capreolus capreolus*) (Austrheim et al., 2011). Further, a shift from grazer dominance to browsing can lead to overgrowth in important habitats for other wildlife, and an increase in damage to commercial plants due to an increase in wild ungulates (Lorentzen Kolstad et al., 2018).

1.4 Aim of study

In this thesis, I look at how grazing affects the phenology and composition of plant-pollinator communities in clear cuts in a commercial forest dominated by spruce. Understanding the phenology and composition of species of flower visitors and the available floral resources is important when looking at the overall ecosystem biodiversity and the possible effects of grazing in boreal commercial forest. Although several studies have investigated the effects of grazing on pollinators and their flower resources in grasslands and temporal zones, little is known about these effects in boreal commercial forests (but see Nielsen and Totland 2014).

This thesis focuses on the consequences of grazing for bumblebees (*Bombus* spp), which are important pollinators in the boreal forest (Barrett & Helenurm, 1987). I ask the following questions: 1) How does the timing of flowering of different plant species vary throughout the peak flowering season in grazed and non-grazed areas? 2) How does the abundance and diversity of flower resources change during the peak flowering season in grazed and non-grazed clearcut areas? 3) Is there a

relationship between the availability of flower resources (measured as abundance and richness) and the diversity of pollinators and plant-pollinator interactions throughout the peak flowering season?

Due to differences in foraging preferences between wild ungulates and cattle, I expect flower resource availability to vary between plots with and without cattle. I also expect bumblebee abundance and richness to vary with flower resource availability. Lastly, I expect seasonal variation in the abundance and richness of flower resources and bumblebees due to species-specific differences in phenology.

2. Materials and methods

To compare seasonal change in abundance and richness of bumblebees and their flower resources, twelve plots were selected in young spruce plantations, with half of the plots inside a grazing area and half outside of it. Data was collected over a 5-week period during peak flowering (end of June until beginning of August).

2.1 Study area

Fieldwork was conducted in the Inlands of Norway, in commercial forest stands in Deset (Figure 1). Twelve sites were selected in clear cuts between the ages 5—15 years in spruce dominated forest. Sample sites were selected based on their proximity to forest roads for two main reasons: cattle use roads for travelling (Tofastrud et al., 2019) and because of efficiency when transporting materials in the field. Six sample sites were selected outside of the grazing area, six were selected within. At each site a quadrat of 20x20 meters were measured and marked with poles in each corner.

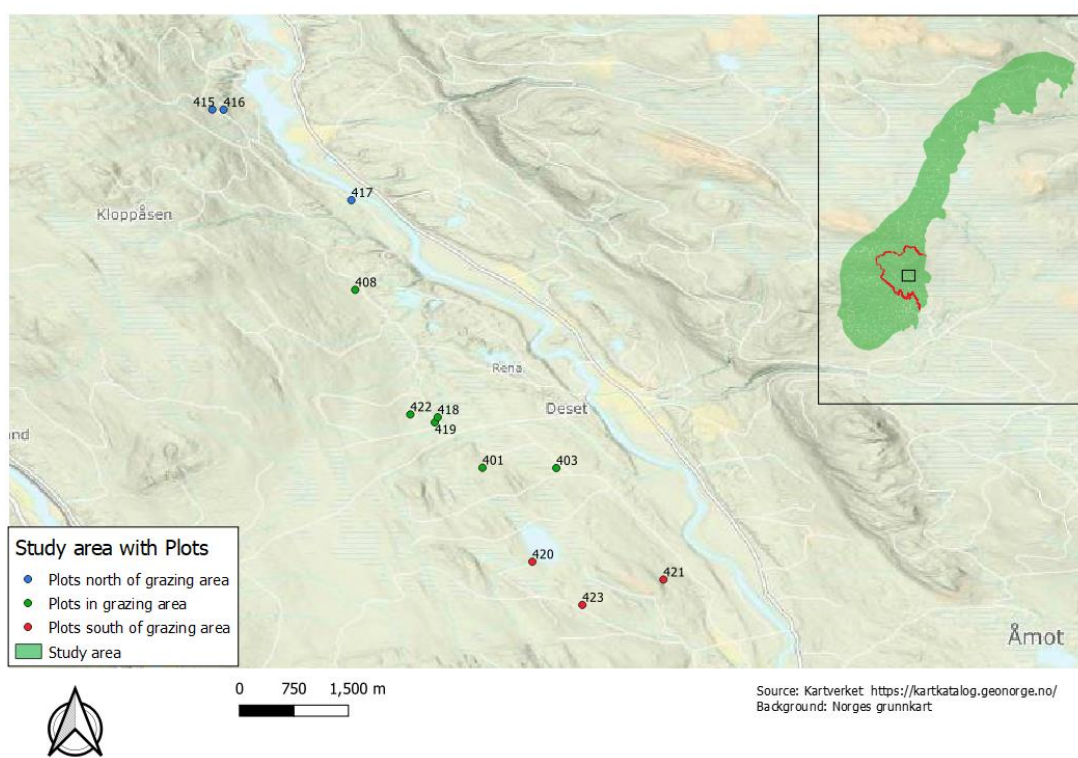


Figure 1. Map of study area with sites. Blue markers show the sites north of the grazing area, green markers show the sites within grazing area and red markers show the sites selected south of the grazing area.

A map was prepared beforehand to show all the potential clearcuts that had spruce dominated forest between the ages 5-15 years, because we knew that these areas were likely to be visited and grazed by the cattle (Tofastrud et al., 2019). Following this map, the sites were selected by going out and inspecting the areas in early spring. A physical inspection was important to be able to see if the clearcut was of the right age and forest type, if it would be big enough to place the quadrats in and how accessible they were for both cattle and field workers. A list of the coordinates for each selected site can be found in the Appendix (*Table 1*).

The study area covers a landscape at around 33 km² in total and is dominated by large areas with low productive pine Forest vegetation types, providing poor available food resource for livestock (Rekdal, 2006). In higher altitudes, however, you can find more productive spruce forest vegetation types, such as blueberry spruce forest, which is considered to have a better grazing value (Rekdal, 2006).

2.2 Study animals

The cattle grazing in the study area were Hereford beef Cattle (*Bos taurus*). In the year of the sampling period 20 suckler cows, each with one calf, were released onto the summer pastures in the forest. This number of cows and calf could be considered to be inflicting a low grazing pressure to the area, as the grazing capacity is 75-150 animals in the whole grazing area (Rekdal, 2006). The cattle (not calves) were equipped with Nofence collars (Nofence AS), a solar powered GPS-tracking device, giving the cows audio signals if they approached the edges of the grazing area. The boundaries of the grazing area can be created digitally and only if the cattle continued to cross said boundaries, could they receive electric pulses (Nofence AS). This means that the grazing area was not restricted with physical fences, and wild ungulates could move freely throughout the whole area.

2.3 Collection of data

Plants, bumblebees, and their interactions were observed once a week over five weeks during peak flowering in the summer 2021 (26.06.-04.08). When observations were made within the 20x 20 m quadrat at each sampling site, it was logged in a form (we used KoboToolbox, which is a collection of open-source tools for data collection: <http://www.kobotoolbox.org/>). We did the surveys during the day between 08.00 in the morning and 19.00 the evening and observations were made in good weather conditions (warm, sunny days with low wind). Pollinators, more specifically bee species, are

most active during the warmest hours of the day (Xu et al., 2021) so we were careful to rotate the time of day of which we did the surveys of the different plots, which means that we visited all the different plots in the morning, midday, and afternoon throughout the sampling period (overview in Appendix, *Table 2*). The methods for data collection for both pollinators and flower resources is explained in more detail in the following sections of this chapter.

2.3.1 Capturing and identification of bumblebees

Within each plot, we first did a 30 min random transect walk capture every bumblebee observed on a flower. Two fieldworkers, each equipped with their own insect net (Figure 2), carried out this method at the same time. The caught specimens were put in glass bottles (filled with 70% ethanol) marked with the plot identity, time, and the species of flowering plant they were visiting. The specimens died quickly when put in the alcohol. After the sampling was done, we sorted, pinned, and dried the bumblebees. Using a microscope and a bumble bee key (Løken, 1985) the bumble bees were identified to species level and the sex was determined.



Figure 2. Showing the nets used to catch bumblebees

2.3.2 Plant species and flower counts

In each quadrat we walked four transects, marking where we began so that we would start at the same side of the square each time we returned to the plot. The transect was lined up by a piece of rope by every 4th meter (see Figure 3a), this was used to navigate as we walked with the grid, keeping the rope in center. Each transect line was walked by one person, that looked through a 0,5x 0,5 m grid we held at hip height (Figure 3b-3c).

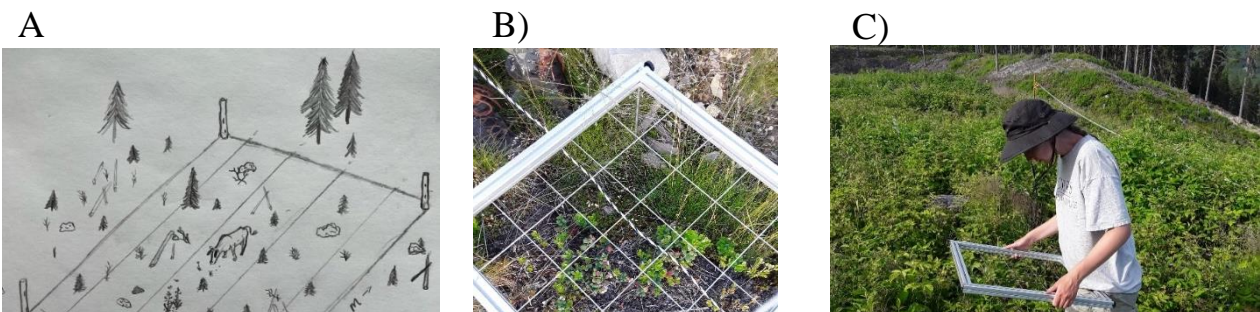


Figure 3. A: Illustration of the quadrat design in each site. The poles marking each corner and the lines showing the placement of the transects. B: Showing the 0,5X 0,5 m grid used for the transects. C: demonstration of how the transect was walked, while looking through the grid.

While walking, all the flowering plant species (within Angiospermae) that were observed were registered, and their flowers were counted. We counted every flower we could see through the grid as we walked the transect. Most flowers observed were easy to count one by one, but some had many flowers per inflorescence and was therefore counted by clusters or per stem (a table showing the clustered species in Appendix, *Table 3*). To identify the species of flowers in field, we used a combination of the citizen science Application Pl@ntNet (<https://plantnet.org/>) and the identification book *Gyldendals store nordiske flora* (Mossberg & Stenberg, 2016).

2.4 Analysis

To determine the relationship between flower resources and cattle presence and time of the season, generalised linear mixed models (GLMMs seen in *Table 3*) were fitted with flower abundance and flower richness as response variables and cattle presence and sampling week (Round) as predictors of both responses. I expected the effect of cattle on flower resources to vary with the sampling round and therefore included an interaction between the two predictors in the full models. Reduced models without this interaction term were also tested. Additionally, a null-model without predictor variables was also fitted. To test the relationship between bumblebee abundance and floral resources, models were fitted with the abundance and richness of flowering species in addition to sampling week (Round) as predictor variables. The same relationship was tested for when looking at bumblebee richness as a response.

After looking at the distribution of the sampled data and considering that the response variables are count data, all models were fitted using either a Poisson error distribution (flower abundance and bumblebee abundance as response variables) or, when overdispersed, a negative binomial error distribution (flower richness and bumblebee richness as response variable). As a Poisson regression estimates the standard deviation based on the mean variance in the dataset, and a Negative binomial regression estimates the variance separately, which then accounts for a larger variance in the data (Bolker et al., 2022). The abundance and richness of both flowering plants and bumblebees were used as response variables, and the sampling rounds and presence of grazing was used as explanatory variables of both responses. Site was included in all models as a random effect to account for heterogeneity in the vegetation in the different locations. The continuous variables were scaled for a

better model fit, due to a skewed distribution. Best fitted models were identified using the relative ranking according to Second -order Akaike Information Criterion (AICc), instead of AIC, as this is recommended when dealing with a small sample size (Burnham & Anderson, 2002). This tool was used when comparing the full, alternative and null-models(see Table 1 in Results). Using the Car package(version 3.1-0), the variance inflation factors(vif) were calculated to rule out multicollinearity between the predictors. Finally, the function ggmmeans (ggeffects package version 1.1.3) was used to plot final models, to create a better data frame of marginal effects.

These analyses were done in R, version 4.2.1 (R Core Team, 2022) with an RStudio interface version 2022.07.1+554 (RStudio Team, 2022).

3. Results

In total, 35 species of flowering plants were observed during the sampling period across the study sites, where 9 of these (see Table 2) were found to have visits from bumblebees. The highest number recorded visits (204) were found on the plant *Chamerion angustifolium*, and the least amount of visits was found on the plant *Galeopsis tetrahit* with only 1 recorded visit.

Table 2. Overview of the bumblebee visits on each flower species.

Plant Species	Number of bumblebee visits
Aconitum lycoctonum	3
Chamerion angustifolium	204
Cirsium palustre	62
Filipendula ulmaria	4
Galeopsis tetrahit	1
Lactuca muralis	4
Melampyrum sp	17
Rubus idaeus	81
Solidago virgaurea	33

Table 1. List of Observed bumblebee species

Bumblebee species
B. pascuorum
B. cingulatus
B. pratorum
B. jonellus
B. hypnorum
B. sylvestris
B. hortorum
B. consobrinus

As for bumblebees, 8 different species (see Table 1) were collected and identified during the sampling period. All bumblebee species are listed as the conservation category “Least Concern” (LC) in the IUCN Red List (Artsdatabanken, 2022). Only one of the species observed (*B. sylvestris*) is a Cuckoo bumblebee, a member of the subgenus *Psithyrus* and acts as a parasite to the social species *B. pratorum*. The rest of the observed species are social bumblebees and belong to the genus *Bombus Latreille* (Artsdatabanken, 2022).

3.1 The flowering of different plant species throughout the season

The mean abundance of flowers on species visited by bumblebees varied between species in grazed and non-grazed study sites (Figure 4). Perhaps the most striking in this figure is the change in abundance of *Melampyrum* sp in areas without grazing compared with areas with grazing.

Melampyrum sp (*M. sylvaticum* and *M. pratense* grouped together) commonly known as Cow wheat peaks in flowering abundance in the first sampling rounds. These species have a noticeably difference in flower abundance in relation to presence of grazing, where the abundance overall is lower in the grazing area. When looking at the rest of the flowering species (with no observed visits from bumblebees), there was less of a visible pattern in the relationship between flower abundance and cattle presence (see appendix Figure 1 for plot and description)

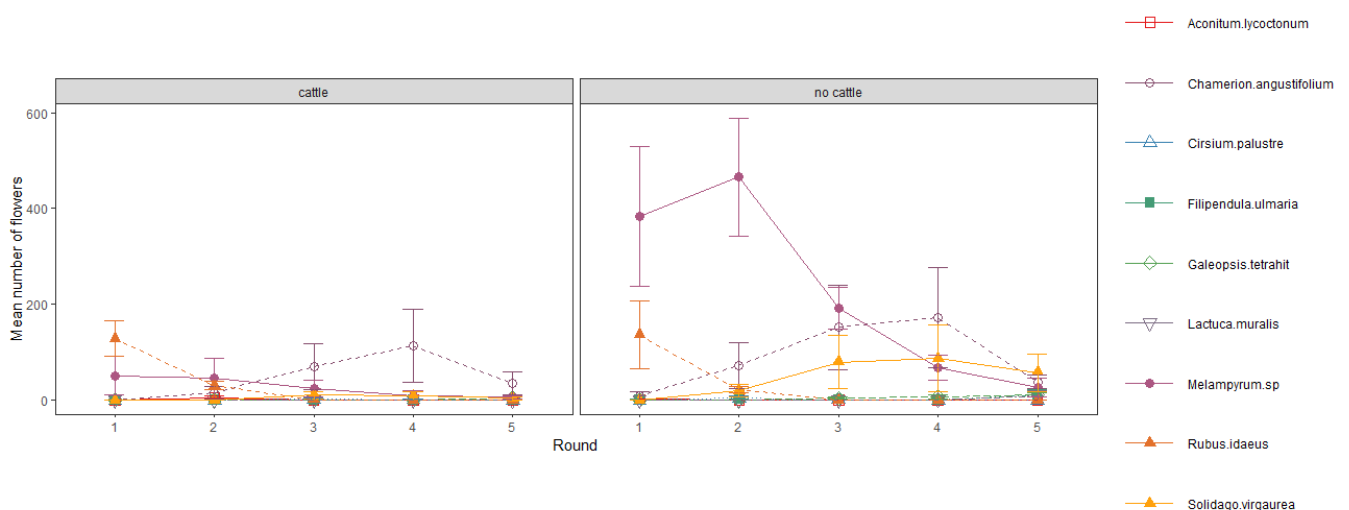


Figure 4 Mean number of flowers(+SE) for the different species that was visited by bumblebees across the sampling rounds, relative to each other, with and without cattle presence

To better see the variation between species in flowering abundance across the sampling rounds, another plot (see Figure 5) was formed using the same data (as seen in Figure 4) of only visited flowers. As seen more clearly in Figure 5, the raspberry flowers (*Rubus idaeus*) seem to decline in abundance rapidly after the first sampling week, and this decline seems to be very similar in areas

with grazing as areas without cattle grazing. The five species; *Chamerion angustifolium*, *Cirsium palustre*, *Melampyrum sp*, *Rubus Ideaus* and *Solidago virgaurea* were observed to have more than 10 visits, whereas the remaining four in this figure had less.

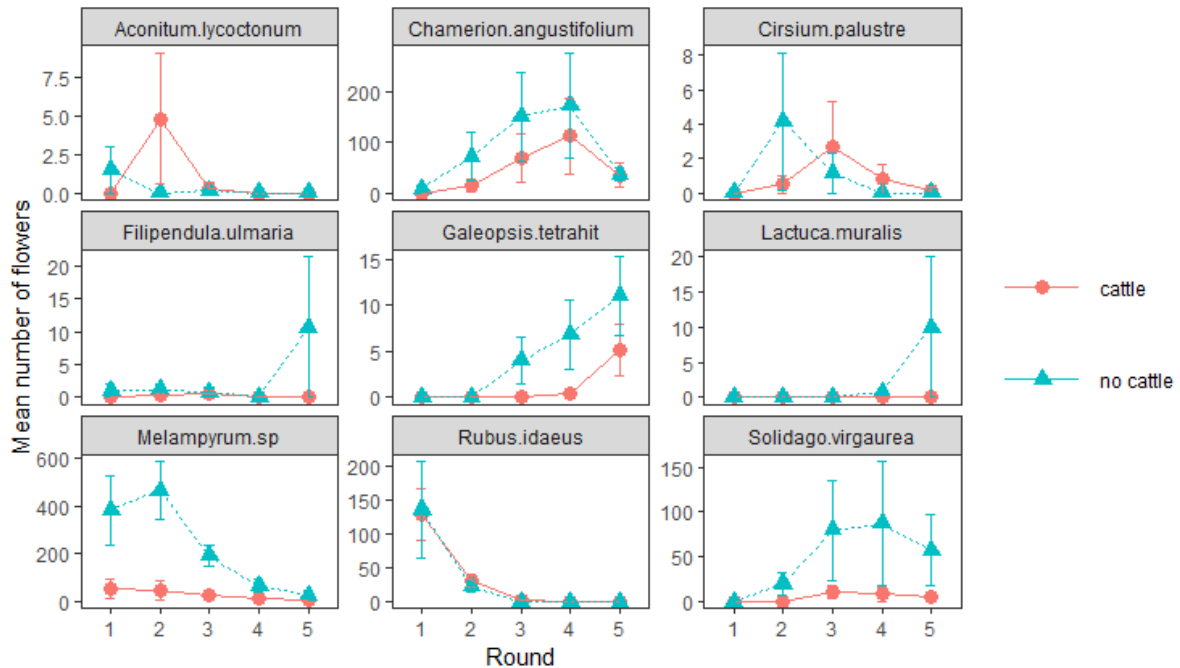


Figure 5 Flowering in plant species with visits from Bumblebees, viewed separately, across the 5 sampling rounds. The blue line shows the plants flowering inside the grazing area, and the red line outside the grazing area. The scale on the y-axis varies between flower species, some showing hundreds of flowers and other under twenty observations during the whole sampling period.

Fireweed (*Chamerion angustifolium*) and European goldenrod (*Solidago virgaurea*) seems to reach its peak of flowering later in the sampling period and both show signs to be of less abundance in the areas with cattle grazing. The Marsh thistle (*Cirsium palustre*) was found only in a few localities, with large variation between plots, which might help explain why there is no specific trend in flowering or pattern of relationship with cattle presence. There was also large variation in the flowering of Meadowsweet (*Filipendula ulmaria*), Wall lettuce (*Lactuca moralis*) and Wolf's-bane (*Aconitum lycoctonum*), also making it difficult to interpret any kind of pattern in relation to grazing presence. The Common Hemp Nettle (*Galeopsis tetrahit*), shows more of a pattern both in relation to grazing presence and sampling rounds, showing an increase in flowering towards the end of the sampling period and more abundant in areas without grazing.

3.2 The change in abundance of all flower species during the flowering season

There was a relationship between total flower abundance and cattle presence with higher abundance in non-grazed sites (Figure 6). There was however not clear relationship between the richness of all flowering species and cattle presence (Table 3). For both flower abundance and richness there was a decline towards the end of the sampling season, with the last sampling round showing the least amount and diversity of flowers observed.

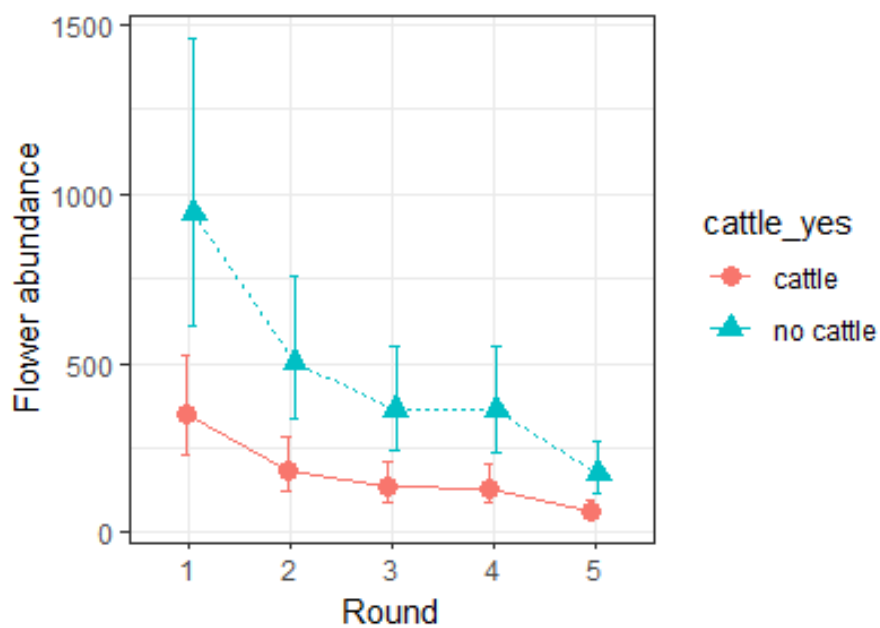


Figure 6. The change in Flower abundance across the five sampling rounds, and the difference in flower abundance with or without cattle presence at the sampling site.

Table 3 Model fit (AICc) for all tested models including full, reduced, and null models. Reduced models were fit to test for the inclusion of expected interactions between predictors. Plot ID is included as a random effect in all models. Best fit models (the most parsimonious model with the low est AICc and with $\Delta AICc > 2$) are shown in bold. Coefficient estimates for the best fit models are given in Table 4

Response	Model		df	AICc
Flower abundance	Full model	$y \sim \text{Round} * \text{cattle} + \text{Plot ID}$	12	785.76
	Reduced model	$y \sim \text{Round} + \text{cattle} + \text{Plot ID}$	8	779.98
	Null model	$y \sim 1 + \text{Plot ID}$	3	815.51
Flower richness	Full model	$y \sim \text{Round} * \text{cattle} + \text{Plot ID}$	11	290.99
	Reduced model	$y \sim \text{Round} + \text{cattle} + \text{Plot ID}$	7	281.2
	Null model	$y \sim 1 + \text{Plot ID}$	2	280.53
Bombus abundance	Full model	$y \sim \sqrt{(\text{flowers abundance}) * \text{Round} + \text{flower richness} * \text{Round} + \text{Plot ID}}$	17	375.7
	Reduced model 1	$y \sim \sqrt{(\text{flowers abundance}) + \text{flower richness} * \text{Round} + \text{Plot ID}}$	13	363.47
	Reduced model 2	$y \sim \sqrt{(\text{flowers abundance}) * \text{Round} + \text{flower richness} + \text{Plot ID}}$	13	361.96
	Reduced model 3	$y \sim \sqrt{(\text{flowers abundance}) + \text{flowers richness} + \text{Round} + \text{Plot ID}}$	9	351.68
	Null model	$\text{Bombus abundance} \sim 1 + \text{Plot ID}$	3	355.75
Bombus richness	Full model	$y \sim \sqrt{(\text{flower abundance}) * \text{Round} + \text{flower richness} * \text{Round} + \text{Plot ID}}$	16	260.43
	Reduced model 1	$y \sim \sqrt{(\text{flowers abundance}) + \text{flower richness} * \text{Round} + \text{Plot ID}}$	12	247.79
	Reduced model 2	$y \sim \sqrt{(\text{flower abundance}) * \text{Round} + \text{flower richness} + \text{Plot ID}}$	12	248.09
	Reduced model 3	$y \sim \sqrt{(\text{flower abundance}) + \text{flower richness} + \text{Round} + \text{Plot ID}}$	8	237.4
	Null model	$y \sim 1 + \text{Plot ID}$	2	233.02

3.3 Relationship between the availability of flower resources and the abundance and richness of bumblebees

The abundance of bumblebees (Figure 7) was related to the time of the season (Round), but not the abundance or richness of the flowers they visited. The highest abundance is to be found in round 3 and 4 and shows a decline the final sampling round. Even though it is not possible to prove statistically based on these data (Table 4), it is possible to see a slight increase in the bumblebee abundance as the flower abundance increases.

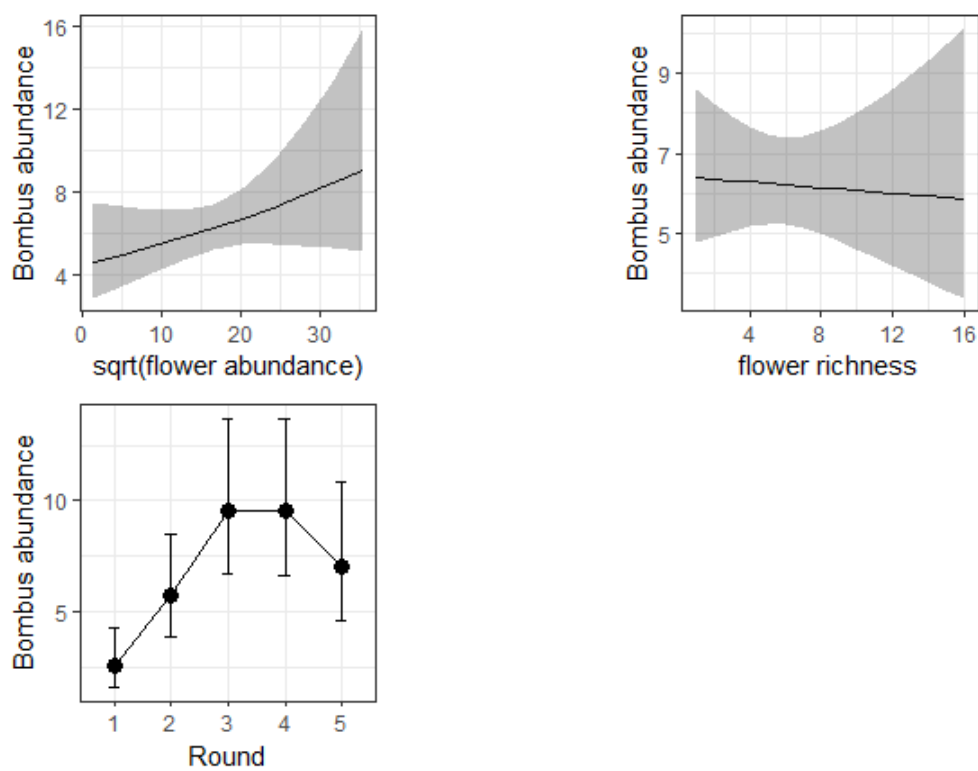


Figure 7. The abundance of bumblebees related to flower abundance, flower richness and across the five sampling rounds.

Table 4. Coefficient estimates (including 95% confidence intervals, CI) for best fit models. Significant effects (i.e. confidence intervals not overlapping zero) are shown in bold. Cattle is a binary variable scored as absence (reference level) and presence of cattle. Round is a categorical response variable with five levels with round 1 as the reference level. Results are not shown for responses (flower and *Bombus* richness) where the null model (with no predictors) was the best fit model.

Response	Coefficient	Estimate [95% CI]
Flower abundance	Round 2	-0.63 [-1.08, -0.13]
	Round 3	-0.95 [-1.42, -0.49]
	Round 4	-0.96 [-1.47, -0.49]
	Round 5	-1.68 [-2.13, -1.16]
	Cattle	1.00 [0.58, 1.42]
<i>Bombus</i> abundance	Round 2	0.80 [0.11, 1.40]
	Round 3	1.32 [0.68, 1.99]
	Round 4	1.31[0.66, 1.90]
	Round 5	1.01[0.27, 1.65]
	Flowers abundance	0.15 [-0.07, 0.35]
	Flower richness	-0.02[-0.20, 0.17]

4. Discussion

In short, the analysis indicated that there is a relationship between cattle presence and total flower abundance, but that this relationship varies between the different flowering species. These findings partly support my expectation that there is seasonal variation in floral resources. Contrary to my expectation, there was, however, no relationship between cattle presence and the richness of flowering species. Moreover, the abundance of bumblebees was related to the time of the season, but not the abundance or richness of the flowers they visited, suggesting that they were not limited by the available flower species in the sampling area, with or without grazing pressure. This confirms my prediction of seasonal variation in bumblebee abundances. The expected relationship with floral resources was however not found. There also was no relationship between bumblebee richness and either season or floral resources.

4.1 The timing of flowering

When looking at Figure 4 and 5, one can see a great deal of variation in the timing of flowering for different plant species. These results points to how differences in flowering phenology can provide continuous overlap in availability of different floral resources for pollinators in boreal forests. For example, *Melampyrum sp* decreased in numbers of flowers towards the end of the season and *Chamerion angustifolium* seems to peak later in the season.

A study from the boreal forest in North America (Helenurm & Barret, 1987) looked at the phenology of 12 boreal herbs(also mainly pollinated by bumblebees) and found similar overlap in flowering periods between species, with some reaching peak flowering earlier and some later. Further, this same study was able to spot a tendency in flowering where the species that flowered earlier in the season reached a higher flower abundance than the species reaching peak flowering later in the season. A similar pattern has not been found in this study. Other studies have found this same variation in timing of flowering of different plant species semi-natural grasslands (Bagella et al., 2013), providing a supply of nectar and pollen for honeybees during the summer season. Difference in flowering ensures that there are floral resources available for pollinators throughout the season. This is especially important for bumblebees that are bound to the area where their nest is located (Goulson et al., 2010) and therefore dependent on the local availability of resources throughout the season.

It is assumed that it is highly favorable for the plants reproduction that their pollinators have a certain fidelity, increasing the chance of seed dispersal within the same species (Goulson et al., 2010). However, in addition to this being a benefit for the plant, it can also be considered a constraint, as it may cause a dependency on specialized pollinators (Wilcock & Neiland, 2002). In such specialized relationships a loss of pollinators, causing a failure in pollination, might be fatal for the plant's reproduction. Moreover, the factors that play in to when a plant is flowering during the season is often separated into bottom-up and top-down effects (Elzinga et al., 2007). Bottom-up effects can be environmental cues, as a change in temperature or light conditions. The top-down selective forces, such as pollinators and antagonists, play an important role for the timing of the plant's reproduction.

A variety of choices in floral resources creates a security for bumblebees that can switch between different resources as flowering of different plants changes throughout the season. Compared to other bee species, bumblebees are more generalist (Heinrich, 1976) and use different plant species at different times during the season. The workers of the hive might show flower constancy to one or two flowers that gives a high reward, but at the same time "sample" flowers to see if there might be a higher reward elsewhere and then switch to that species (Goulson et al., 2010). As one flowering plant seems to give less reward in form of pollen and nectar, the bumblebees will then, in theory, work more efficiently by switching to another plant species. This generalist foraging behavior might in turn have less of an effect on the timing of flowering, as the precision of timing be of little consequence (Helgenurm & Barret, 1987). It is important to point out that the small sampling size also has an effect on the results, as patterns at a community level might be more difficult to detect within a small number of species (Helgenurm & Barret, 1987).

Although timing of flowering varied between the different flower species during the season, there was an overall lower abundance later in the season. An overall early peak in flowering may be of benefit to the plant, due to restrictions in abiotic factors such as temperature and light conditions. As a reaction to an increase in temperature due to global change in climate, several plant species have been found to respond (in the last 20-50 years) with advanced spring flowering (Fitter & Fitter, 2002; Hegland et al., 2009) with the same trends evident in the northern hemisphere (Sparks et al., 2000). In addition, studies have found that flowering plants may benefit from flowering earlier in the season, due through increased reproduction (Pardee et al., 2019)

4.2 The effect of grazing on the abundance and richness of floral resources

As expected, total flower abundance was lower in sites with than without cattle (Figure 6). The results of this study show a significant effect of cattle presence (Tabell 1), despite the number of cattle released in the study area being low compared to the grazing capacity estimated in the area (Rekdal, 2006). These results may enforce the narrative (Boles et al., 2019) of how livestock grazing is causing disturbance and damage to the vegetation. Previous studies have found negative effects due to overgrazing by cattle (Abril et al., 1999, 2005) and the term is often associated to grassland degradation in global located in tropical, dry regions (Yang et al., 2018).

Other studies have also found negative effects of herbivore foraging, causing a shift in the understory compositions due to high herbivore densities (Nuttle et al., 2014) and hindering the conservation efforts of threatened species (Mysterud & Østbye, 2004). The type of grazing animal and the frequency of their grazing are important components of both current and historical grazing. It is therefore important to consider the animals foraging behavior and densities of livestock when discussing the damages and/or benefits to the plant cover (Davies & Boyd, 2020).

“The legacy effect” is a term that can be used to explain the long-term effects of herbivory that can lead to epigenetic modifications of offspring plants for one or more generations (Yin et al., 2020). It is often explained in literature as an expression of negative effects of overgrazing by livestock in natural grasslands. However, the intensity and timing of livestock grazing are important factors to consider when looking at the long-term effects of grazing (Davies & Boyd, 2020). In addition to the long-term effects from previous years, it is also difficult to know what other aspects might cause a difference in vegetation within and outside the grazing area. As there are no physical fences in the area, wild ungulates are not restricted and can forage freely in the whole study area. All sites may therefore have been grazed at some point by wild ungulates.

Further, there was no significant effect of cattle on the species richness (Tabell 2) in the study area, even though the abundance of flowers were negatively affected. These findings may suggest that cattle grazing in this area is not endangering the overall diversity of the ecosystem, and that other aspects of cattle presence may even be of benefit to ensuring species richness. A study looking at effects of free-ranging cattle, found that cattle grazing stimulated a significant increase in species richness (Bokdam & Gleichman, 2000). Grazing can serve as a mitigating tool, as several species that

were previously dependent on natural disturbances, may benefit from traditional grazing and mowing (Pykälä, 2000). Prohibiting negative effects of overgrowth on biodiversity, and in this was facilitating for other species.

For some species there was a clear relationship between cattle presence and abundance (such as *Melampyrum sp.*, *Chamerion angustifolium* and *Solidago virgaurea*) but for many others it was inconsistent. These findings suggest that the grazing cattle preferred to forage on these species over others. A study of plant and vegetation preference of cattle in Norwegian semi-natural mountain pastures by Sæther et al. (2006) have found similar patterns of preference for the *Melampyrum sp.* (*M. pratense* and *M. Sylvaticum*). These findings, based on faeces samples analyzed for plant fragments, are confirming that these species are important grazing species for cattle. However, this study did not find the species *Chamerion angustifolium* and *Solidago virgaurea*, to be of the similar importance (Sæther et al. 2006). Moreover, they found raspberry (*Rubus idaeus*) to be of importance and preferred by cattle, which contradicts the findings of this thesis as there was no clear difference in abundance of this plant in areas with cattle presence (Figure 5). A study of cattle grazing in aspen forest (Fitzgerald et al., 1986) also found that wild raspberry (*Rubus strigosus*) was preferred over other species (although cattle preferred herbaceous species when present). These findings combined might suggest that the cattle in this study had other more preferred herbs to forage on, resulting in no relationship between cattle presence and raspberry abundance.

4.3 Are bumblebees limited by available food resources?

The abundance of bumblebees was related to the time of the season, but, contrary to my expectations, not the abundance or richness of the flowering plants (Figure 7). This suggests that bumblebees were not limited by the available floral resources in the sampling area, with or without grazing cattle. Contradicting these findings other studies have found bumblebees to be sensitive to grazing intensity (Kimoto et al., 2012; Xie et al., 2008) resulting in significantly lower abundance and diversity as their food sources were grazed upon. Several other studies (Heinrich, 1976; Kells & Goulson, 2003; Hatfield & LeBuhn, 2007) has found similar negative effects of intensive grazing on bumblebee community richness.

Despite the evidence of previous studies, indicating the negative effects on bumblebees, cattle presence in this study has not been found to significantly limit either bumblebee richness or

abundance (Tabell 2). This could be due to less intensity of grazing in the area, compared to that of the mentioned studies. However, the grazing pressure was high enough to have a significant effect on the availability of floral resources, suggesting that the bumblebee's dependency on those floral resources was not the limiting factor. However, the small sample size of this and limitations of data collection (not being able to collect every single bumblebee observed in field) limits this study. In other words, there might be a stronger relationship between cattle grazing and bumblebee diversity than what can be extracted from these results. A lack of statistically significant estimates does not mean that there might not be an ecologically significant relationship between the variables.

It is also possible that the bumblebees in the study area were able to move between sites and available resources and the small-scale availability of floral resources becomes less important. This can make them less vulnerable for local disturbances, than other habitat specialist pollinators (Winfree, 2010). The study sites inside and outside the cattle grazing areas were located between approx. 2 and 22km from each other. Bumblebees travel (up to several kilometers in distance to the nest) between patches in the landscape and can therefore move between areas that vary in available resources (Goulson et al., 2010).

In addition to travel distance enabling bumblebees to perhaps not be limited by local availability, other factors, such as suitable nesting sites can help to ensure abundance and diversity within the study area (Goulson et al. 2010). Suitable nest sites (suitability varies between species) may be found in areas with structures of stones, dense vegetation or even in old holes and burrows used by small mammals (Goulson et al., 2010). Clearcuts, such as the ones used as sampling sites in this study, fills these criteria quite well, as a result from disturbance from logging and animal activity. However, the disturbance caused by cattle trampling and laying down in these open areas might negatively affect the suitability of these areas for bumblebee nests (Kearns & Inouye, 1997; Kimoto et al., 2012).

There was a significant relationship between bumblebee abundance and the sampling rounds (Tabell 3), with high bumblebee abundance in especially the third and fourth sampling rounds. This is expected due to the life cycle of the bumblebee colony, as the workers of the colony increase with abundance of resources (in peak flowering) (Goulson et al., 2010). However high numbers of workers might not necessarily give a reliable estimate of effective population size (Persson & Smith, 2013). The number of reproductive females is what determines the viability of the overwintering population (Winfree, 2010)

5. Conclusion

Keeping livestock in forest pastures has long rooted traditions in Norway and the re-establishments of such traditions calls for efforts to obtain more knowledge on the effect on biodiversity. By comparing observed abundance and richness of floral resources and bumblebees in areas with and without cattle presence, this study has shown that cattle effects abundance of the food resources of bumblebees. Moreover, the overall abundance of flowers was lower with cattle presence, but the effect of cattle varied between flower species. Some of these relationships were stronger than others, such as on *Melampyrum sp.*, a finding that concurs with previous studies on cattle grazing preference.

However, a significant effect on bumblebee abundance and richness was not found, suggesting that cattle presence is not limiting the population of bumblebees in this area. Based on other relevant studies on this topic, one can speculate that the effect of cattle in this study is small, partly due to the low intensity of grazing pressure. Another reason for this might be that bumblebees have a generalist foraging behavior and can travel long distances to find available resources, making them less vulnerable to local cattle disturbance. Finally, the main inference to this study is that; bumblebees are not limited by available resources due to cattle grazing, at least not in forest pastures in the boreal forest with a low grazing pressure.

The design of methods and data collected for this thesis is just part of the beginning of further studies made of the effects of cattle grazing on biodiversity in this area. Further studies should be expanded to different groups of pollinators to better advise for suitable management strategies on these forest pastures. Descriptive studies, such as this thesis can therefore be of use to help fill the knowledge gaps in the information available of boreal forest ecosystem.

Intensification of our land use has great negative consequences to the composition of species that depend on certain habitats. The continued efforts in research to provide improved knowledge on these matters are therefore necessary to ensure viable populations of not only pollinators, but for all parts of a healthy functioning ecosystem.

Reference list

- Abril, A., Barttfeld, P., & Bucher, E. H. (2005). The effect of fire and overgrazing disturberes on soil carbon balance in the Dry Chaco forest. *Forest Ecology and Management*, 206(1-3), 399-405.
- Artsdatabanken (2022, 12.10). Humler Bombus Latreille, 1802. Retrieved 19.10.22 from <https://www.artsdatabanken.no/arter-pa-nett/humler>
- Austrheim, G., Eriksson, O, (2008). Plant species diversity and grazing in the Scandinavian mountains - Patterns and processes at different spatial scales. *Ecography*. 24. 683 - 695. 10.1111/j.1600-0587.2001.tb00530.x.
- Austrheim, G., Solberg, E.J. and Mysterud, A. (2011), Spatio-temporal variation in large herbivore pressure in Norway during 1949-1999: has decreased grazing by livestock been countered by increased browsing by cervids?. *Wildlife Biology*, 17: 286-298. <https://doi.org/10.2981/10-038>
- Barrett, S. C., & Helenurm, K. (1987). The reproductive biology of boreal forest herbs. I. Breeding systems and pollination. *Canadian Journal of Botany*, 65(10), 2036-2046.
- Bagella, S., Satta, A., Floris, I., Caria, M. C., Rossetti, I., & Podani, J. (2013). Effects of plant community composition and flowering phenology on honeybee foraging in Mediterranean sylvo-pastoral systems. *Applied Vegetation Science*, 16(4), 689-697.
- Boles, O. J., Shoemaker, A., Courtney Mustaphi, C. J., Petek, N., Ekblom, A., & Lane, P. J. (2019). Historical ecologies of pastoralist overgrazing in Kenya: Long-term perspectives on cause and effect. *Human Ecology*, 47(3), 419-434.
- Bolker and others.(2022) GLMM FAQ <https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html#count-data>
- Bokdam, J. and Gleichman, J.M. (2000), Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland. *Journal of Applied Ecology*, 37: 415-431. <https://doi.org/10.1046/j.1365-2664.2000.00507.x>

-
- Bright, R. M., Antón-Fernández, C., Astrup, R., Cherubini, F., Kvalevåg, M., & Strømman, A. H. (2014). Climate change implications of shifting forest management strategy in a boreal forest ecosystem of Norway. *Global Change Biology*, 20(2), 607-621.
- Burnham, K. P. and Anderson, D. R. 2002 Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York, Springer-Verlag.
- Davies, K. W., & Boyd, C. S. (2020). Grazing is not binomial (ie, grazed or not grazed): a reply to Herman. *BioScience*, 70(1), 6-7.
- Elzinga, J. A., Atlan, A., Biere, A., Gigord, L., Weis, A. E., & Bernasconi, G. (2007). Time after time: flowering phenology and biotic interactions. *Trends in ecology & evolution*, 22(8), 432-439.
- Eriksson, O. (2018). What is biological cultural heritage and why should we care about it? An example from Swedish rural landscapes and forests. *Nature Conservation*. doi:10.3897/natureconservation.28.25067
- Fitter, A. H., & Fitter, R. S. R. (2002). Rapid changes in flowering time in British plants. *Science*, 296(5573), 1689-1691.
- Fitzgerald, R. D., Hudson, R. J., & Bailey, A. W. (1986). Grazing preferences of cattle in regenerating aspen forest. *Rangeland Ecology & Management/Journal of Range Management Archives*, 39(1), 13-18.
- Fourcade, Y., Åström, S. & Öckinger, E. Climate and land-cover change alter bumblebee species richness and community composition in subalpine areas. *Biodivers Conserv* 28, 639–653 (2019). <https://doi.org/10.1007/s10531-018-1680-1>
- Framstad, E. & Sverdrup-Thygeson, A. 2015. Økt hogst av skog i Norge – effekter på naturmangfold. – NINA Rapport 1149. 54 s.
- Franzén, M., & Nilsson, S. G. (2008). How can we preserve and restore species richness of pollinating insects on agricultural land?. *Ecography*, 31(6), 698-708.

-
- Gao, J., & Carmel, Y. (2020). Can the intermediate disturbance hypothesis explain grazing–diversity relations at a global scale?. *Oikos*, 129(4), 493-502.
- Goulson, D. (2010). *Bumblebees: behaviour, ecology, and conservation*. Oxford University Press on Demand.
- Goulson, D., Lye, G. C., & Darvill, B. (2008). Decline and conservation of bumble bees. *Annu. Rev. Entomol.*, 53, 191-208.
- Harrison, K. & Bardgett, R. D.(2008) The ecology of browsing and grazing *Ecological Studies* (eds Iain J Gordon & H.H.T Prins) Ch. 8, 201-2016. Springer
- Hatfield, R. G., & LeBuhn, G. (2007). Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp.(Hymenoptera: Apidae), in montane meadows. *Biological Conservation*, 139(1-2), 150-158.
- Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknæs, A.-L. and Totland, Ø. (2009), How does climate warming affect plant-pollinator interactions?. *Ecology Letters*, 12: 184-195. <https://doi.org/10.1111/j.1461-0248.2008.01269.x>
- Helenurm, K., & Barrett, S. C. (1987). The reproductive biology of boreal forest herbs. II. Phenology of flowering and fruiting. *Canadian Journal of Botany*, 65(10), 2047-2056.
- Heinrich, B. (1974). Thermoregulation in endothermic insects. *Science*, 185, 747–756. <https://doi.org/10.1126/science.185.4153.747>
- Heinrich, B. (1976). Bumblebee foraging and the economics of sociality: how have bumblebees evolved to use a large variety of flowers efficiently? Individual bees have specialized behavioral repertoires, and the colony, collectively, can harvest food from many different resources. *American Scientist*, 64(4), 384-395.
- Heinrich, B. (1976). Resource partitioning among some eusocial insects: bumblebees. *Ecology*, 57(5), 874-889.

-
- Holechek, J. L., Vavra, M., Skovlin, J., & Krueger, W. C. (1982). Cattle diets in the blue mountains of Oregon. II. Forests. *Rangeland Ecology & Management/Journal of Range Management Archives*, 35(2), 239-242.
- Hjeljord, O., Histøl, T. & Wam, H. K. Forest pasturing of livestock in Norway: effects on spruce regeneration. *Journal of Forestry Research* 25, 941-945 (2014).
- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, (2016) Assessment Report on Pollinators, Pollination and Food Production IPBES <https://zenodo.org/record/3402857#.YxjdTHZBw2w>
- Kevan, P. G., & Baker, H. G. (1983). Insects as Flower Visitors and Pollinators. *Annual Review of Entomology*, 28(1), 407–453. doi:10.1146/annurev.en.28.010183.002203
- Kevan, P. G., & Viana, B. F. (2003). The global decline of pollination services. *Biodiversity*, 4(4), 3-8. DOI: 10.1080/14888386.2003.9712703
- Kells, A. R., & Goulson, D. (2003). Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biological conservation*, 109(2), 165-174.
- Kearns, C. A., & Inouye, D. W. (1997). Pollinators, flowering plants, and conservation biology. *Bioscience*, 47(5), 297-307.
- Kimoto, C., DeBano, S. J., Thorp, R. W., Taylor, R. V., Schmalz, H., DelCurto, T., ... & Rao, S. (2012). Short-term responses of native bees to livestock and implications for managing ecosystem services in grasslands. *Ecosphere*, 3(10), 1-19.
- Lorentzen Kolstad, A., Austrheim, G., Solberg, E. J., De Vriendt, L., & Speed, J. D. (2018). Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species. *Ecosphere*, 9(10), e02458.
- Løken, A. (1985). Norske insekttabeller 9. Humler. Tabell til norske arter. – Norsk Entomologisk Forening, 39 s. (<http://www.entomologi.no/journals/tabell/tabell.htm>).

-
- Maebe, K., Hart, A. F., Marshall, L., Vandamme, P., Vereecken, N. J., Michez, D., & Smagghe, G. (2021). Bumblebee resilience to climate change, through plastic and adaptive responses. *Global change biology*, 27(18), 4223-4237.
- Mathisen, K. M., Buhtz, F., Danell, K., Bergström, R., Skarpe, C., Suominen, O., & Persson, I. L. (2010). Moose density and habitat productivity affects reproduction, growth and species composition in field layer vegetation. *Journal of vegetation science*, 21(4), 705-716.
- Mossberg, B., Stenberg, L., (2016). *Gyldendals store nordiske flora*. Gyldendal.
- Mysterud, A., & Østbye, E. (2004). Roe deer (*Capreolus capreolus*) browsing pressure affects yew (*Taxus baccata*) recruitment within nature reserves in Norway. *Biological Conservation*, 120(4), 545-548.
- Norwegian Ministries (2018) National pollinator strategy - A strategy for viable populations of wild bees and other pollinating insects. M-0750 E, Impression 200, Oslo: Norwegian Ministry of Agriculture and Food, Norwegian Ministry of Climate and Environment, Norwegian Ministry of Local Government and Modernisation, Norwegian Ministry of Transport and Communications, Norwegian Ministry of Defence, Norwegian Ministry of Education and Research, Norwegian Ministry of Petroleum and Energy.)
- Nofence AS. What is Nofence? Retrieved 25.10.2022, from <https://www.nofence.no/en/what-is-nofence>
- Nuttle, T., Ristau, T.E. and Royo, A.A. (2014), Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. *J Ecol*, 102: 221-228. <https://doi.org/10.1111/1365-2745.12175>
- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals?. *Oikos*, 120(3), 321-326.
- Ødegaard, F., Staverløkk, A., Gjershaug, J.O., Bengtson, R., Mjelde, A. (2015) *Humler i Norge. Kjennetegn, utbredelse og levesett.*- Norsk institutt for Naturforskning, Trondheim.

-
- Pardee, G. L., Jensen, I. O., Inouye, D. W., & Irwin, R. E. (2019). The individual and combined effects of snowmelt timing and frost exposure on the reproductive success of montane forbs. *Journal of Ecology*, 107(4), 1970-1981.
- Persson, A. S., & Smith, H. G. (2013). Seasonal persistence of bumblebee populations is affected by landscape context. *Agriculture, ecosystems & environment*, 165, 201-209.
- Pykälä, J. (2000). Mitigating human effects on European biodiversity through traditional animal husbandry. *Conservation Biology*, 14(3), 705-712.
- R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- RStudio Team (2022). RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL <http://www.rstudio.com/>.
- Rekdal, Y. (2006). Storfbeite i utmark for eiendommene Løsset, Deset og Rød: Åmot kommune (*Oppdragsrapport fra Skog og landskap 3/06*). Ås. Norsk institutt for skog og landskap.
- Rubene, D., Schroeder, M., & Ranius, T. (2015). Diversity patterns of wild bees and wasps in managed boreal forests: effects of spatial structure, local habitat and surrounding landscape. *Biological Conservation*, 184, 201-208.
- Sparks, T. H., Jeffree, E. P., & Jeffree, C. E. (2000). An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *International Journal of Biometeorology*, 44(2), 82-87.
- Spitzer, R., Felton, A., Landman, M., Singh, N. J., Widemo, F., & Cromsigt, J. P. (2020). Fifty years of European ungulate dietary studies: a synthesis. *Oikos*, 129(11), 1668-1680.
- Statsforvalteren i Innlandet, & Innlandet Fylkeskommune (Eds.). (2021). Tiltaksplan for jordbruket i Innlandet 2022-2024. Retrieved 25.10.2021, from <https://www.statsforvalteren.no/siteassets/fm-innlandet/07-landbrukog-mat/jordbruk/tiltaksplan-for-jordbruket-i-innlandet---horingsutkast--.pdf>

-
- Sæther, N. H., Sickel, H., Norderhaug, A., Sickel, M., & Vangen, O. (2006). Plant and vegetation preferences for a high and a moderate yielding Norwegian dairy cattle breed grazing semi-natural mountain pastures. *Animal Research*, 55(5), 367-387.
- Tofastrud, M., Devineau, O., & Zimmermann, B. (2019). Habitat selection of free-ranging cattle in productive coniferous forests of south-eastern Norway. *Forest Ecology and Management*, 437, 1-9.
- Totland, Ø. Hovstad, K. A. Ødegaard, F. Åstrøm, J. (2013) Kunnskapsstatus for insektpollinering i Norge - betydningen av det komplekse samspillet mellom planter og insekter.
- Vos, W., & Meekes, H. (1999). Trends in European cultural landscape development: perspectives for a sustainable future. *Landscape and urban planning*, 46(1-3), 3-14.
- Wilson, J. B., Peet, R. K., Dengler, J. & Pärtel, M.(2012) Plant species richness: the world records. *Journal of Vegetation Science* 23, 796-802, doi:10.1111/j.1654-1103.2012.01400.x .
- Wilcock, C., & Neiland, R. (2002). Pollination failure in plants: why it happens and when it matters. *Trends in plant science*, 7(6), 270-277.
- Winfrey, R. (2010). The conservation and restoration of wild bees. *Annals of the New York academy of sciences*, 1195(1), 169-197.
- Xie, Z., Williams, P. H., & Tang, Y. (2008). The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. *Journal of Insect Conservation*, 12(6), 695-703.
- Xu, X., Ren, Z. X., Trunschke, J., Kuppler, J., Zhao, Y. H., Knop, E., & Wang, H. (2021). Bimodal activity of diurnal flower visitation at high elevation. *Ecology and evolution*, 11(19), 13487-13500.
- Yang, X., Shen, Y., Liu, N., Wilson, G.W.T., Cobb, A.B. and Zhang, Y. (2018), Defoliation and arbuscular mycorrhizal fungi shape plant communities in overgrazed semiarid grasslands. *Ecology*, 99: 1847-1856. <https://doi.org/10.1002/ecy.2401>

Yin, J., Li, X., Guo, H., Zhang, J., Kong, L., & Ren, W. (2020). Legacy effects of historical grazing alter leaf stomatal characteristics in progeny plants. *PeerJ*, 8, e9266.

Zimmermann, B., Wabakken, P., & Dötterer, M. (2001). Human-carnivore interactions in Norway: How does the re-appearance of large carnivores affect people's attitudes and levels of fear. *Forest Snow and Landscape Research*, 76(1), 1-17.

Zimmermann, B., Wabakken, P. & Dötterer, M.(2003)Brown bear-livestock conflicts in a bear conservation zone in Norway: are cattle a good alternative to sheep? *Ursus*, 72-83.

Appendencies

Appendix A

List of study sites with Plot ID and their coordinates. The sites are ordered from north to south placements in study area.

Plot ID	Coordinates
415	61.3741024 11.3494863 405.70026492100703
416	61.3739058 11.353136 387.4830631881633
417	61.3475216 11.3891864 305.2247975993902
408	61.326693 11.3847014 366.2207567725123
422	61.295484 11.4033654 354.9227770321661
418	61.2957426 11.4079832 334.72075606140834
419	61.2933248 11.4075157 347.6251777852431
401	61.326693 11.3847014 366.2207567725123
403	61.2825111 11.4375284 345.58565998530406
420	61.2581537 11.4323569 375.73687935090743
423	61.2506665 11.4328841 387.00244637481114
421	61.2529128 11.4661695 344.7015273407105

Appendix B

Overview of sampling period and the rotation of plots between rounds

Plot-ID	Round 1	Time of day	Plot ID	Round 2	Time of day	Plot ID	Round 3	Time of day	Plot ID	Round 4	Time of day	Plot ID	Round 5	Time of day	
416	24.06.2021	mid day	419	02.07.2021	morning	408	12.07.2021	morning	408	19.07.2021	morning	419	26.07.2021	morning	
419	24.06.2021	evening	408	02.07.2021	mid day	419	12.07.2021	mid day	415	19.07.2021	mid day	418	26.07.2021	mid day	
403	25.06.2021	mid day	416	02.07.2021	evening	403	12.07.2021	after noon	419	19.07.2021	evening	403	26.07.2021	evening	
420	26.06.2021	mid day	420	03.07.2021	morning	416	13.07.2021	Morning	403	20.07.2021	morning	415	27.07.2021	morning	
418	27.06.2021	mid day	403	03.07.2021	mid day	415	13.07.2021	after noon	422	20.07.2021	mid day	408	30.07.2021	morning	
408	27.06.2021	evening	418	03.07.2021	evening	417	15.07.2021	morning	417	20.07.2021	evening	416	30.07.2021	mid day	
401	28.06.2021	morning	422	04.07.2021	morning	422	15.07.2021	mid day	418	22.07.2021	morning	420	30.07.2021	afternoon	
415	28.06.2021	mid day	415	05.07.2021	mid day	418	15.07.2021	evening	423	22.07.2021	mid day	401	03.08.2021	morning	
417	29.06.2021	morning	417	08.07.2021	Morning	420	17.07.2021	mid day	420	22.07.2021	after noon	417	03.08.2021	mid day	
422	29.06.2021	mid day	401	08.07.2021	mid day	423	18.07.2021	morning	421	23.07.2021	morning	422	03.08.2021	after noon	
423	01.07.2021	morning	423	09.07.2021	morning	421	18.07.2021	mid day	401	23.07.2021	mid day	421	04.08.2021	morning	
421	01.07.2021	mid day	421	09.07.2021	mid day	401	18.07.2021	evening	416	23.07.2021	evening	423	04.08.2021	mid day	
Days spent per round:	7			6			5			4			5		Sum of days spent
															27