Ingvild Sandvin Groven

The Buzz on Grassland Management

Effects of management on pollinators and their flower resources in semi-natural grasslands

Photo: Martine A. Andersen Hennig

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Master's thesis in Natural Resource Management
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Abstract

Pollination of plants by pollinating animals, especially insects, provides monetary value and ecosystem services worldwide. There are global patterns of decline in biodiversity of pollinators, especially among wild species of pollinators. In Norway, one of the most pollinator friendly habitats are seminatural grasslands, however these habitats have become threatened by land use change in the form of agricultural intensification and abandonment.

The objective of this study was to investigate the impact of different management measures on plant-pollinator interactions in semi-natural grasslands. It aimed to understand how grazing and mowing as management practices influenced the richness and abundance of pollinator species, their flower resources, and plant-pollinator interactions throughout the growing season. During the summer of 2022, the richness and abundance of flowering plants and pollinators were recorded at six study sites with both grazed and mowed semi-natural grasslands in Trøndelag in Norway.

Both time of season and management type affected plant-pollinator interactions. The time of season affected the flowering plant richness and abundance, which in turn affected the pollinators. The richness of flowering plants also varied by study site, while flower abundance varied by management type. A diverse floral community positively correlated with higher pollinator richness and abundance. Mowing lands had higher pollinator abundance and more complex plant-pollinator networks compared to grazed lands. Among grazed lands, those with low grazing intensity and late onset grazing had the highest pollinator abundance.

While both mowing and grazing practices contributed to the preservation of pollinator diversity and ecosystem health, the results indicate that mowed semi-natural grasslands hold greater value as pollinator habitats. To ensure the availability of flower resources for pollinators throughout the season, mowed semi-natural grasslands should be promoted. To improve the value of semi-natural grasslands for pollinators, heterogeneous mowing practice should be encouraged in mowed sites, while late onset and low intensity grazing should be promoted in grazed sites.

Sammendrag

Pollinering av pollinerende dyr, spesielt av insekter, skaper økonomisk verdi og økosystemtjenester over hele verden. Pollinatorer opplever en global trend med nedgang i biodiversitet, spesielt blant ville pollinatorer. I Norge er seminaturlig eng blant de mest pollinatorvennlige habitatene, men disse er blitt truet av endringer i arealbruk i form av jordbruksintensivering og endt skjøtsel.

Denne studien undersøkte virkningen av ulike typer skjøtsel på interaksjoner mellom planter og pollinatorer i seminaturlige eng. Formålet var å forstå hvordan beiting og slått som forvaltningspraksis påvirker artsrikdom og antall av pollinatorer og deres blomsterressurser gjennom vekstsesongen. I sommeren 2022 ble artsrikdom og antallet av pollinatorer og blomstrende planter registrert på seks gårder med både beitemark og slåttemark i Trøndelag.

Både sesong og type skjøtsel påvirket interaksjonene mellom planter og pollinatorer. Sesongen påvirket mangfoldet og antallet av blomstrende planter, som igjen påvirket pollinatorene. Mangfoldet av blomstrende planter varierte også etter studieområde, mens blomsterantallet varierte etter skjøtsel. En mangfoldig blomstersammensetning hadde en positiv sammenheng med høyere artsrikdom og antall pollinatorer. Slåttemark hadde høyere antall pollinatorer og mer komplekse plante-pollinator-nettverk sammenlignet med beitede områder. Blant beitemark hadde områder med lav beiteintensitet og sen oppstart av beiting høyest antall pollinatorer.

Selv om både slått og beite bidrar til å bevare pollinatormangfoldet og økosystemets helse, indikerer resultatene at slåttemark har større verdi som pollinatorhabitat. For å sikre tilgjengeligheten av blomsterressurser for pollinatorer gjennom hele sesongen, bør slåttemark videre fremmes. For å forbedre verdien av seminaturlig eng for pollinatorer, bør heterogen slått oppmuntres på slåttemark, mens sen oppstart og lav intensitet av beiting bør fremmes på beitemark.

Acknowledgements

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My supervisors Gunnar Austrheim, Marie Vestergaard Henriksen, Frode Ødegaard and Dag-Inge Øien for their guidance, support, and expertise in everything from planning the fieldwork to completing the writing process. I would like to thank the farmers who generously allowed me access to their grasslands and the animals under their care. The animals themselves also provided excellent company and emotional support during fieldwork, especially Bajas at Storlia, Oreo and Karma at Fagerli and the two unnamed horses at Vennberg. I would like to extend a special thanks to Robert Brian O'Hara for his assistance with statistical analysis. And lastly, I would like to express my heartfelt gratitude to my fellow students, who kept me company and delayed my descent into madness during the long months of writing.

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1 Introduction

Pollinating animals affect the yield of many important crops that provide food, medicine, construction materials and biofuels for human use (IPBES, 2016). Most pollinating species are wild, such as wild bees, butterflies, flies, beetles, birds, or bats (IPBES, 2016). The diversity of pollinators encompasses the species richness and abundance, i.e., the number of distinct species and the their relative population sizes (Peet, 1974).

Considering the reliance on pollinators for food production, global pollinator decline has become a major concern worldwide (IPBES, 2016). Wild pollinators have experienced the most decline in species richness and abundances in the last decades (Wagner et al., 2021). The causes of pollinator decline are not yet completely understood, but it is strongly linked to factors such as land use change, pesticide use, pollution, invasive alien species, disease and climate change (IPBES, 2016).

In Norway, 25% of pollinating insects are red-listed, thus it is of increasing importance to maintain pollinator friendly habitats (Totland et al., 2013). Flower rich areas such as gardens or semi-natural grasslands are important for pollinators, however there is a knowledge gap in information about species distribution and population development of pollinating insects (Departementa, 2018). The impact of land use on plant-pollinator interactions in Norwegian grasslands is a topic of study in ecological research which is getting increasing attention.

Grazed and mowed semi-natural grasslands are part of the Norwegian cultural landscape, and the focus of this thesis. The current knowledge in this field of research indicates that land use practices can have profound effects on the composition and abundance of plant and pollinator communities (Ferreira et al., 2013; Hellerstein et al., 2017). It is well known that grazing and mowing positively influence vascular plant biodiversity in semi-natural grasslands (Norderhaug et al., 1999). Timing and intensity of management will affect flower abundance, which is often linked to pollinator richness (Nayak et al., 2015; Nilsson et al., 2013).

In grazed semi-natural grasslands, late-onset and low intensity grazing positively affect pollinator activity and abundance (Sjödin, 2007; Veen et al., 2009). In mowed semi-natural grasslands, also called hay meadows, the highest richness and abundance of pollinators are found with heterogenous mowing late in the summer (Valtonen et al., 2006).

Despite focus on this field, there is still limited data comparing how grazing and mowing as management measures impact richness and abundance of pollinators and their flower resources, as well as the variation in these variables throughout the growing season (Departementa, 2018).

1.1 Semi-natural grasslands

1.1.1 History and cultural value

Semi-natural grasslands are ecosystems dominated by herbaceous vegetation, where long term natural succession is stalled due to anthropogenic activity i.e., agricultural measures such as mowing and animal grazing (Van Andel et al., 1987). These grasslands mostly occur in Europe, where they are part of the cultural landscape due to traditional farming practices (Cousins & Eriksson, 2002). Regular disturbance, such as grazing and mowing, prevent competitive species from dominating. Thus, these grasslands support high biodiversity, especially of low-competitive herbs, flowers, and grasses, as well as pollinators (Cousins & Eriksson, 2002; Öckinger & Smith, 2006).

All Norwegian semi-natural grasslands are considered as vulnerable, and mowed grasslands ("slåttemark") are critically threatened (Hovstad, 2018). In the case of low productivity semi-natural grasslands, concerns for loss of biodiversity and cultural heritage are the main drivers for conservation (White et al., 2000). The biggest threat to semi-natural grasslands is land use change, in the form of abandonment. Climate change might also increase the speed of encroachment of trees and bushes in unmanaged grasslands. Loss of connectivity, agricultural intensification and development on agricultural land are also threats to semi-natural grasslands (Lindgaard & Henriksen, 2011).

1.1.2 Biodiversity and flower resources

Semi-natural grasslands have a high diversity of herbaceous plant species which flower at different times during the growing season (Bendel et al., 2019). This provides resources for pollinators in the form of pollen and nectar during their active period (Johansen et al., 2020). In Norway, almost 700 plant species are associated with semi-natural grasslands, and half are not found outside these habitats (Norderhaug et al., 1999). Without active agricultural or restorative management, these grasslands will over time be overgrown by tall grasses and woody plants. Species associated with semi-natural grasslands require much light and will disappear if bushes or trees shade the understory. Thus, to preserve plant biodiversity, semi-natural grasslands must remain open with low stature vegetation. Abandonment of traditional management practices in semi-natural grasslands is becoming increasingly widespread, often attributed to agricultural intensification and associated land abandonment (Vassilev et al., 2011).

The short Norwegian growing season narrows the activity period of pollinators, with most plant species flowering in June, July and August (Johansen et al., 2019). Semi-natural grasslands that have species with different flowering times will have flower resources available throughout the summer. This supports both season-long foragers such as bumblebees and short-season species like certain solitary bees (Ogilvie & Forrest, 2017). Seasonal variation in semi-natural grasslands is illustrated in Figure 1.

(a) Mowed site before mowing

(b) Mowed site after mowing

(c) Grazed site before grazing
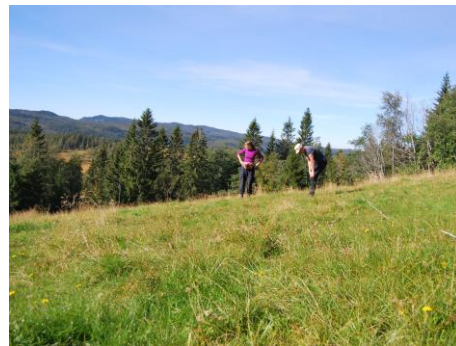
(d) Grazed site after grazing

Figure 1: Pictures from study site Beitlandet, Trøndelag illustrating seasonal variation in mowed and grazed semi-natural grasslands.

In mowed semi-natural grassland, the availability of flower resources will be impacted at the time of mowing. Mowing is often performed in mid- to late July every year, however less productive areas might only be mowed every other year (Elven & Bjureke, 2018). In mowed semi-natural grasslands, large parts of flower resources are removed in an important period of the summer for pollinators (Wehn et al., 2020). Mowing impacts plant-pollinator interactions by reducing floral abundance which disrupts pollinator foraging (Johansen et al., 2019). However, the predictable timing of mowing has allowed plants opportunities to adapt, selecting for shorter, rosetted plants with increased fruit production in areas with long term history of mowing (Lennartsson et al., 1998).

Grazing in semi-natural grasslands has more variable effects on species composition and plant-pollinator interactions than mowing. The effect depends on factors such as grazing intensity, timing, duration and herbivore species (Norderhaug et al., 1999). Disturbance in grazing lands is less predictable than in mowing lands, but is also more selective, which can decrease the availability of certain flower resources (Wissman, 2006). Grazed semi-natural grasslands in Europe have a slightly higher general plant diversity than mowed semi-natural grasslands, with certain exceptions, namely dry semi-natural grasslands, mountainous areas and areas grazed by sheep (Tälle et al., 2016). However, mowed semi-natural grasslands are associated with abundant flower resources, making them valuable habitats for wild pollinators

(Nicholls & Altieri, 2013). Late onset grazing and low intensity grazing can increase flower abundance, which has been shown to increase pollinator abundance (Wissman, 2006).

1.2 Pollinators

1.2.1 Value of pollinators

Without pollinators, 35% of crop volume would be impacted negatively and 5-8% of crop volume would be lost completely (IPBES, 2016). Although much of our caloric intake is from self-pollinating species, like rice or cereals, humans rely on pollinated crops for protein, vitamins and other micronutrients (Slaa et al., 2006). 75% of crop types - including high value crops like rapeseed, coffee and cocoa - would be negatively affected by lack of pollination services (Potts et al., 2016). The economic value of pollination services in Norway has not been calculated but accounted for at least 900 million NOK in 2017 through production of fruit, legumes and oil crops (Departementa, 2018).

Diversity in pollinators, especially wild pollinators, is a safeguard in case of decline of important pollinators for food production. It is important to maintain healthy ecosystems, which in turn can impact agriculture (Poppy et al., 2014).

Semi-natural grasslands have many flowering species, which support a high biodiversity of wild pollinators, strengthening the pollinator community. With global decline in pollinators, it is important to understand and protect habitats that pollinators depend on.

1.2.2 Pollinator groups

Different insect groups, such as bees, butterflies, flies, and beetles exhibit varying degrees of efficiency as pollinators. The more reliable pollinators are often those who are dependent on flowers for food, such as bees. Bees, both solitary and social, are often considered the most efficient pollinators (Kevan et al., 1990). Butterflies often have low pollination efficiency, yet many are regular pollinators and can be very specialized, dependent on the availability of specific plants (Totland et al., 2013). Flies are a diverse taxonomic group, but their importance as pollinators varies. Suborders, such as Syriphidae (hoverflies) or Bombyliidae (bee flies) are more important flower visitors compared to other flies (Abrol, 2012). Beetles are frequent flower visitors, but outside the tropics they are not considered as many, varied, or as important as other types of pollinators (Kevan & Baker, 1983).

Honeybees are the most commercially used pollinator, however, other pollinators can be suited better for pollination of specific crops due to their morphology and behavior. Larger pollinators are often more efficient at transferring pollen, their size allowing them to carry more pollen grains and over longer distances (Jauker et al., 2016). Thus, big beetles and bumblebees are often good pollinators. Hairier pollinators have more surface area to pick up pollen grains as they move from flower to flower, positively impacting pollinator effectiveness

(Stavert et al., 2016). Other morphological traits, behavior, visit frequency and population size can also affects efficiency (Phillips et al., 2020).

Bumblebees and butterflies are used as indicator species in the monitoring of biodiversity in Norway due to their sensitivity to environmental changes and their ecological importance as pollinators (Jakobsson & Pedersen, 2020). There are 35 registered bumblebee species and about 100 butterfly species in Norway. These are charismatic and mostly easily recognizable species, making them popular choices for citizen science projects such as the "Bumblebee and butterfly monitoring project" run by The Norwegian Institute for Nature Research (Åström et al., 2015).

1.2.3 Community interactions

Pollination interactions are considered generalist or specialist depending on the number of species interacting with the other. Most pollinator species interact with many different plant species and most plants have many different pollinators interacting with them. Some species are specialized and only interact with a few other species, but obligate one-to-one mutualism is rare (Steffan-Dewenter et al., 2006). Pollination networks tend to be more generalized in its interactions, with a shift towards becoming more specialized towards the end of the season (Bendel et al., 2019; Waser et al., 1996).

Pollinator networks are often nested, meaning the specialist species interact with a subset of the species that the generalist species interact with. This leads to specialists often being dependent on the presence of generalist species, while generalists interact with both specialist and other generalist species (Bascompte et al., 2003). This creates some redundancy in the networks, protecting a species with overlapping interactions from the extinction of one of the interacting species (Potts et al., 2010). Plant communities are most negatively affected by the loss of pollinators with many links, e.g. a generalist pollinator, (Memmott et al., 2004). Specialist tend to be more vulnerable than generalists as they often have a patchier distribution and a higher risk of their niche disappearing (Henle et al., 2004). Parasitic species, such as parasitic bumblebees are more vulnerable than their hosts, needing sufficient habitat to support a healthy population of host species (Cagnolo et al., 2009).

For non-random interactions like pollination, ecosystem complexity enhances the network resilience (Huang et al., 2021). The presence of more species and more connections between them help maintain a stable and resilient community, while loss of species makes system more prone to collapse. Abundance also affects resilience; a plant-pollinator community with low species abundance becomes more likely to collapse, regardless of species richness and network complexity (Huang et al., 2021).

1.4 Objectives

The objective of this thesis was to investigate the effects of different management measures (grazing and mowing) on the flowering plants and plant-pollinator interactions in semi-natural grasslands. The study was conducted on six farms with both grazed and mowed semi-natural grasslands in Trøndelag, Norway. The objective was to examine the effects of (a) season and (b) management on flower and pollinator richness and abundance, as well as the effect on (c) plant-pollinator interactions networks. Data collection involved the observation of both richness and abundance of flowering plants and pollinators, as well as their interactions, throughout the summer of 2022.

I hypothesized the following:

a) There will be an increase in flower richness and abundance from June to July, with a peak in mid-summer, followed by a decrease in August as flowering tapers off towards the end of the growing season. Flower richness and pollinator richness is expected to have a positive relationship. Pollinator abundance will follow the flower abundance in each land management regime.

b) Both mowed and grazed grasslands will have high species richness of flowering plants early in the summer. Grazed grasslands will have lower flower abundance compared to mowing lands. Mowed grasslands will have little to no flower resources after mowing. Grazing lands will have higher flower abundance than mowing lands late in the season and can function as an alternative food source for pollinators that have foraged in mowed grasslands earlier in the season.

c) Flower visitation rate will show the flower preference of pollinators. The plant-pollinator network will be most complex in grasslands with high flowering plant species richness. Changes in the abundance of the flowering plant species will alter the interaction network.

I expect that this study will provide insights into the effects of different land management measures on plant-pollinator interactions in semi-natural grasslands. Specifically, I expect that the study will help to identify which management measure is more favorable for maintaining high levels of biodiversity of pollinators and floral resources as well as which flowering plants are preferred by pollinators. This can be used to suggest management measures to promote pollinators.

2 Methods

2.1 Area and study sites

Trøndelag county in Norway has a temperate maritime climate with mild summers and frequent precipitation throughout the year. The last 10 years, the average summer temperature in June, July and August, has been around 12°C, while the rainfall was around 300 mm (Klimaservicesenter, 2022).
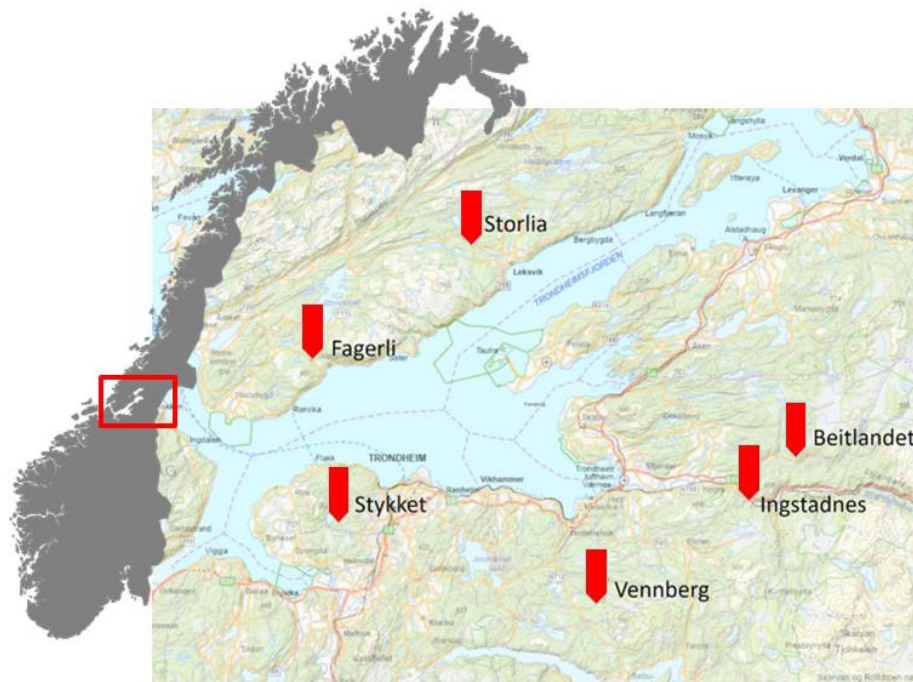
Figure 2: Map of study sites in Trødelag county.

The study sites were chosen among sites used by NIBIO in their report "Gode leveområder for pollinatorer i kulturlandskapet" (Johansen et al., 2020). These locations have some semi-natural grasslands scattered in the landscape, but the general land use is dominated by intensive agricultural production. The study sites were situated on six different farms with both grazed and mowed semi-natural grasslands in Trøndelag (Figure 2). Details about the grazing species and mowing times is shown in Table 1. More information about the study sites can be found in Appendix A.

Table 1: Management details for study sites

Site	Grazing species	Mowing time	Data collected
Fagerli	Sheep	Week 35	17.06.22, 12.07.22, 05.09.22
Storlia	Sheep/goat	Not mowed due to broken machine	17.06.22, 12.07.22, 05.09.22
Ingstadnes	Cattle	Week 34	19.06.22, 19.07.22, 07.09.22
Beitlandet	Cattle	Week 34/35	19.06.22, 19.07.22, 07.09.22
Vennberg	Horse	Week 32	20.06.22, 20.07.22, 21.08.22
Stykket	Sheep	Not mowed (municipality stopped responding)	24.06.22, 20.07.22, 21.08.22

2.2 Data collection

2.2.1 Sampling period and transects

Data was collected in three rounds from mid-June to early September 2022. In the first two rounds of data collection, all transects were visited within eight and nine days, respectively. The third round of data collection was done after mowing. Late mowing due to rainfall made the third round of data collection span over 18 days. While the last round spanned over both August and September, it is for simplicity's sake referred to as the "August"-round.

Figure 3: Dimension and position of transect lines.

At each site, pollinator and vegetation data were collected in three transects of 50 meters, spaced five meters apart (Figure 3). Transect locations for all sites can be found in Appendix A.

To ensure that pollinators were active, the data was collected on days without rain between 10:00 and 17:00, with a minimum temperature of 13°C. Cloud coverage, temperature and wind speed were noted at each site.

2.2.2 Pollinator data

Pollinator and plant visitation data was collected by recording activity 2.5 m on either side of the transect line while walking at a slow, steady pace (Figure 4). While walking, pollinator visits were recorded, both species of pollinator and species of plant they were visiting. A pollinator was only counted as a flower visitor when observed on the reproductive part of the flower.
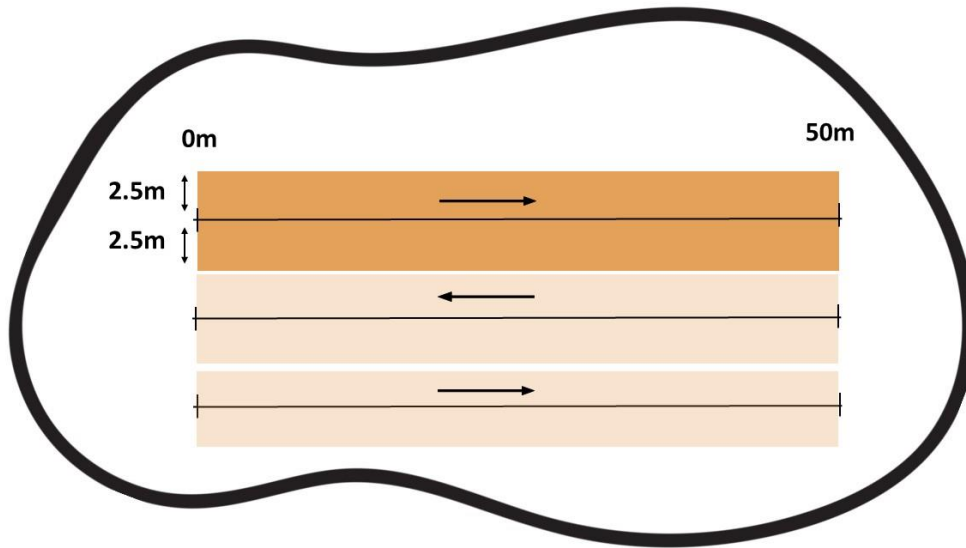
Figure 4: Transect for collection of pollinator and plant visitation data.

Bumblebees and butterflies were recorded to species level when possible, both when in flight and while visiting flowers. Individuals I was unable to identify immediately were captured with a net and placed in a glass to be identified later. Bumblebees flying across the transect line that I was unable to capture and identify, were noted as *Bombus* sp. Species identification was done with the help of "Humler i Norge" (Ødegaard et al., 2015) as well as photographs and descriptions from artsdatabanken.no.

Some bumblebees were only identified to morphologic group, due to the difficulty of separating these species in the field. This was done for parasitic bumblebees ("gjøkhumler") which consist of seven species, previously considered a separate genus from bumblebees, now a subgenus - *Psithyrus*. The same was done for the subgenus *Bombus* s. str. ("jordhumler") consisting of *Bombus lucorum*, *Bombus terrestris*, *Bombus cryptarum*, *Bombus magnus* and *Bombus sporadicus*. *Bombus sporadicus* can be identified in the field and was thus not included in in the *Bombus* s. str. category.

Species richness of bumblebees were used as indicators of total species richness of pollinating insects, following Åström et al. (2015).

Other important pollinators were only recorded when visiting a flower, and were identified to broad taxonomic groups: honeybees, wild bees, hoverflies, flies and beetles.

2.2.3 Flower data

Flower data was collected in 50 by 50 cm plots every 5 m along the transect line, giving 10 measurements per transect (Figure 5a). For each plot, a square frame divided into 16 squares was placed over the vegetation. In case of tall vegetation, the frame was laid down so that flowers with the base of the stem outside the plot was excluded. All currently flowering vascular plant species were noted in the plot, excluding grasses and sedges. To measure abundance, I used the number of squares within the frame in which a flowering species was found (Figure 5b). For each plot, all the flowering species had a value of 0-16, depending on how many squares in the frame the flower appeared in. Flowering species were identified to the lowest taxonomic level possible, using "Norsk Flora" (Lid, 2005). Additionally, the average vegetation height was estimated at each plot, using a yardstick. The different stages of data collection are summarized in Figure 6.
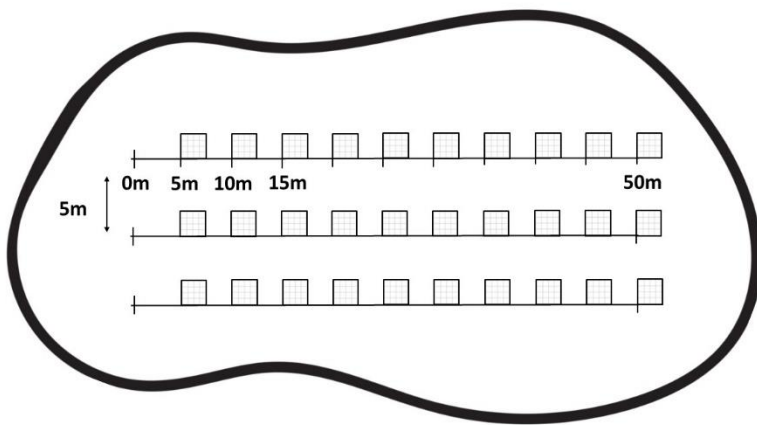
(a) Transect lines and plot location at site
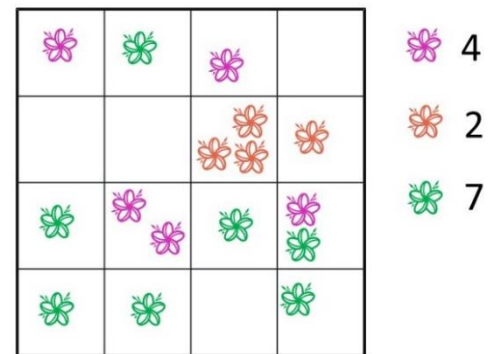
(b) Method for estimating flowering plant abundance

Figure 5: Details on collection of flower data

(a) Setting up transect line

(b) Observing pollinators in transect

(c) Admiring the wildlife

(d) Identifying bumblebee species

(e) Collecting floral data

(f) Measuring vegetation height

Figure 6: Data collection and species identification.

2.3 Statistical analysis

Statistical analysis was performed using R version 4.3.0 (R Core Team, 2023). Figures were generated using the "ggplot2", "sciplot", and "bipartite" packages in R. Mean richness and abundance of flower and pollinator data were calculated at the site level for each sampling round.

Models were fitted for (1) flower richness (2) flower abundance, (3) bumblebee richness and (4) bumblebee abundance.

The model selection for flower (1) richness and (2) abundance included the explanatory variables season (i.e., month), management measure (i.e., grazing and mowing), temperature, and the random effect of site. Both flower richness and abundance were found to be non-normally distributed and overdispersed.

The relationship between (1) flower richness and the explanatory variables, was tested using a generalized linear mixed effect model with a negative binomial error distribution. Models were made with the "glm.nb" and "glmer.nb" functions in the "lme4" package.

To select the best predictor variables, the "dredge"-function from the "MuMIn" package was used. Non-significant variables were removed before model selection. Models with the different combinations of variables and interactions between them were made, then model selection was conducted using "model.sel" function from the "MuMIn" package. The Second-order Akaike Information Criterion (AICc) was used to determine the fit of the model. Models with a difference in AIC of less than 2 from the top model were tested for significant effect of the variables. The final model was selected based on the size and significance of the effect of the predictor variables.

The same was done for (2) flower abundance. Details on model selection for flower resources can be found in Appendix E.

Floral richness and abundance were highly correlated (0.72), so only floral richness was used as a predictor of bumblebee richness and abundance. Both variables significantly impacted the models, but floral richness had a bigger effect on bumblebee (3) richness and (4) abundance and was thus chosen.

The model selection for bumblebee (3) richness and (4) abundance, included the explanatory variables season, management measure, floral richness, temperature, cloud cover, wind and the random effect of site. Both bumblebee richness and abundance were found to be non-normally distributed and overdispersed.

The relationship between (3) bumblebee richness and the explanatory variables, was tested using a generalized linear mixed effect model with a negative binomial error distribution.

Selection of variables and model selection was done in the same manner as for flower richness. Details on model selection for bumblebees can be found in Appendix E.

The same was done for (4) bumblebee abundance.

The "plotweb" function from the "bipartite" package was used to make interaction networks of flowers and pollinators. For interactions between plants and bumblebees, data was grouped by management type and season, while for pollinator groups interactions were grouped only by season. The size of the boxes in the network indicates the proportion of interactions that included the species, while size of the lines between them indicates the proportion of interactions observed between which species.

3 Results

3.1 Flowering plant species richness and abundance

Mowed and grazed semi-natural grasslands, will onwards be named mowing lands and grazing lands. A total of 55 flowering plants species were recorded during the fieldwork, of these 41 were observed in mowing lands and 46 in grazing lands. As shown in Figure 7a, nine were exclusively found on mowing lands, 14 exclusively on grazing lands and 32 were found in both types.

a)

b)
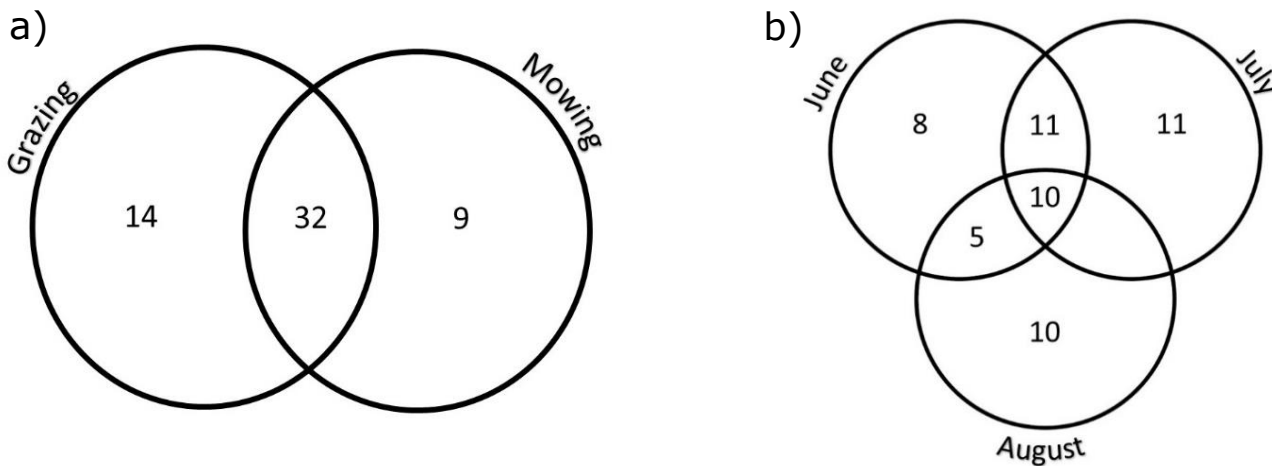
Figure 7: Species occurrence of currently flowering plants in a) grazing and mowing lands and b) different rounds of fieldwork.

The number of flowering plant species found in the different rounds of fieldwork is shown in Figure 7b. Only ten flowering plant species were found in both June, July and August. In June, a total of 29 flowering species were found, 24 in mowing lands and 20 in grazing lands. Eight of these were not found in the other rounds. The most flowering species were found in July, with 30 species in mowing lands and 30 in grazing lands, for a total of 37 flowering plant species. Eleven of these species were not found in the other rounds. The lowest number of flowering species was found in August, after mowing. A total of 25 flowering species were recorded, 16 in mowing lands and 20 in grazing lands. Ten species were only found in this last round.

The mean flower richness for all sites in the different rounds is shown in Figure 8. There was no significant difference between grazing and mowing lands. The best predictor of flower richness was season and the random effect of site. There was no interactions between the predictor variables. The richness of flowering species remained the same or increased from June to July and decreased from July to August. The highest richness of flowering species was found in Beitlandet. The lowest richness was found at Ingstadnes.
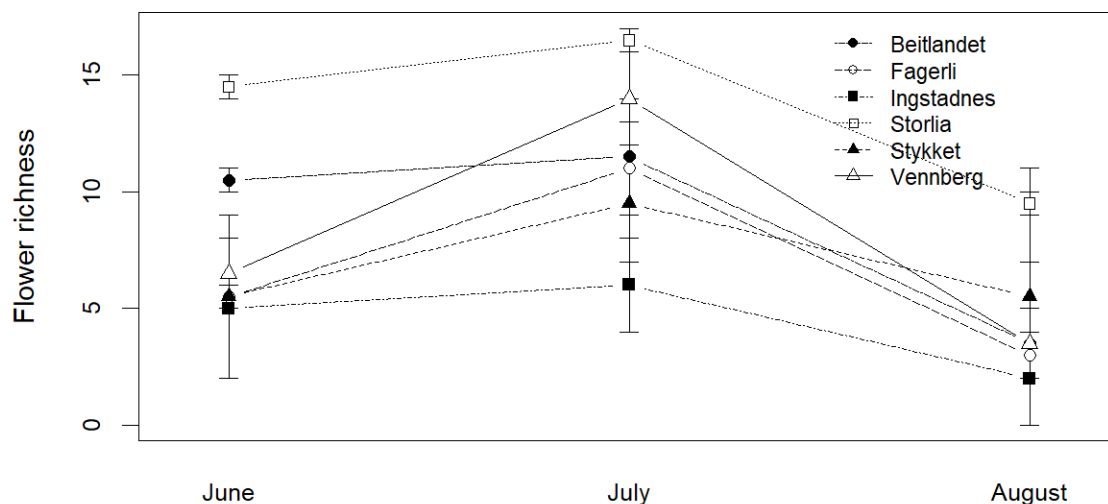
Figure 8: Flowering plant richness in June, July, and August at different study locations. Points show mean richness of currently flowering plants with standard error.

The flower abundance in the different rounds is shown in Figure 9. The best predictor of flower abundance was management measure and season, with no interaction between the predictor variables. Mowing lands had a higher flower abundance than grazing lands, except in August when the difference was non-significant. Season also had an effect, i.e., flower abundance was highest during June and July, and significantly lower in August. In grazing lands, the high abundance early in the summer may be due to late onset of grazing at sites Beitlandet and Storlia.
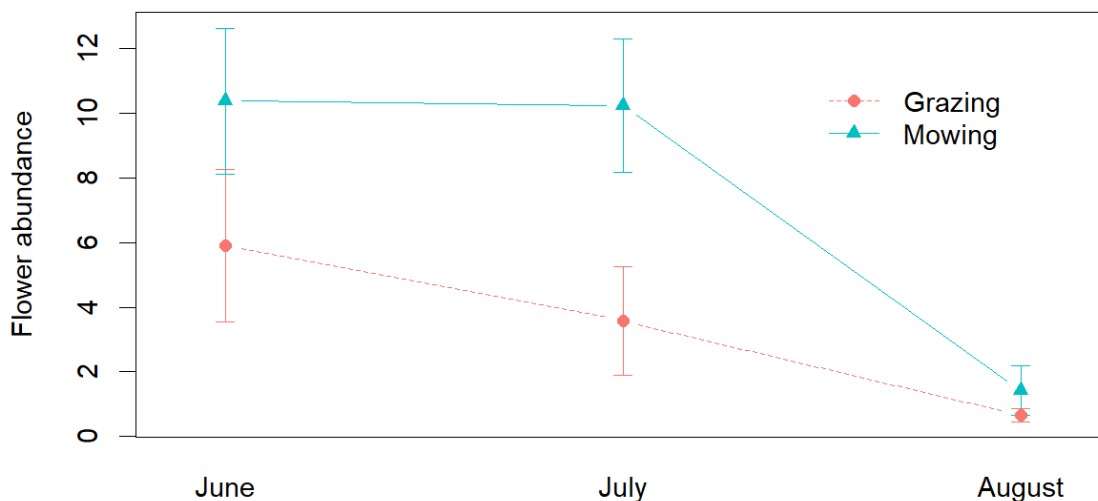
Figure 9: Flowering plant abundance in June, July, and August in mowed and grazed lands. Points show mean abundance of currently flowering plants with standard error

In mowing lands, the most abundant flowering species was *Potentilla erecta* in June, *Leucanthemum vulgare* in July and *Potentilla erecta* in August. The most abundant flowering species in grazing lands was *Ranunculus acris* in June, *Potentilla erecta* in July and August. Details about flower occurrence and abundance can be found in Appendix B.

3.2 Pollinator species and abundance

During the summer, a total of 2088 individual pollinators were recorded visiting flowers, of which 1085 were in mowing lands and 1003 in grazing lands. Six bumblebee species and two bumblebee subgenera were recorded, as well as eight unidentified bumblebee individuals. A total of 261 bumblebee individuals were recorded, 35 in flight and 226 while visiting a flower. 23 butterfly individuals from ten species were seen and recorded, 17 in flight and six visiting a flower.

Various beetles, flies, hoverflies, honeybees, solitary bees and spiders were also recorded, although only to higher taxonomic rank category.

Pollinator abundance was estimated as the number of pollinator individuals at each site (Figure 10a). The pollinator abundance was highest in June, then decreased in July and further in August. There was no significant effect of grazing and mowing on pollinator abundance.

In all rounds, flies were the most abundant in both grazed and mowed grasslands. The composition of pollinators in the different rounds, counted as number of flower visitors, are shown in Figure10b.
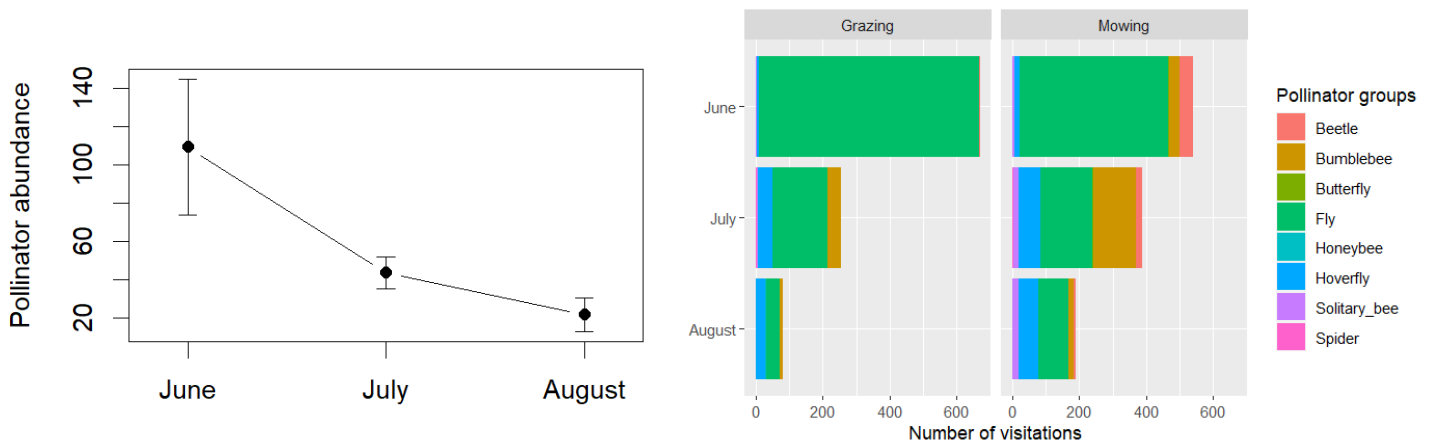
(a) Mean abundance with standard error of pollinators in June, July, and August.

(b) Composition of pollinators in grazed and mowed lands in June, July and August.

Figure 10: Seasonal variation in a) mean pollinator abundance and b) pollinator taxa composition.

When excluding flies, the most abundant pollinators were bumblebees, hoverflies, and beetles. Pollinator abundance then follows the pattern of flower richness, with an increase in July and a decrease in August. Bumblebees were most abundant in July, accounting for most of the visitations in mowed lands and almost half of visitations in grazed lands.

Due to few observations of butterflies, and most observations being in flight (Appendix D), butterflies were not suitable as indicators of species richness or community interactions. Bumblebee species richness was used as an indicator for total species richness for further analysis.

Bumblebee species richness and abundance were highly correlated (0.86) but were examined separately. The bumblebee richness is shown in Figure 11a and the bumblebee abundance is shown in Figure 11b.
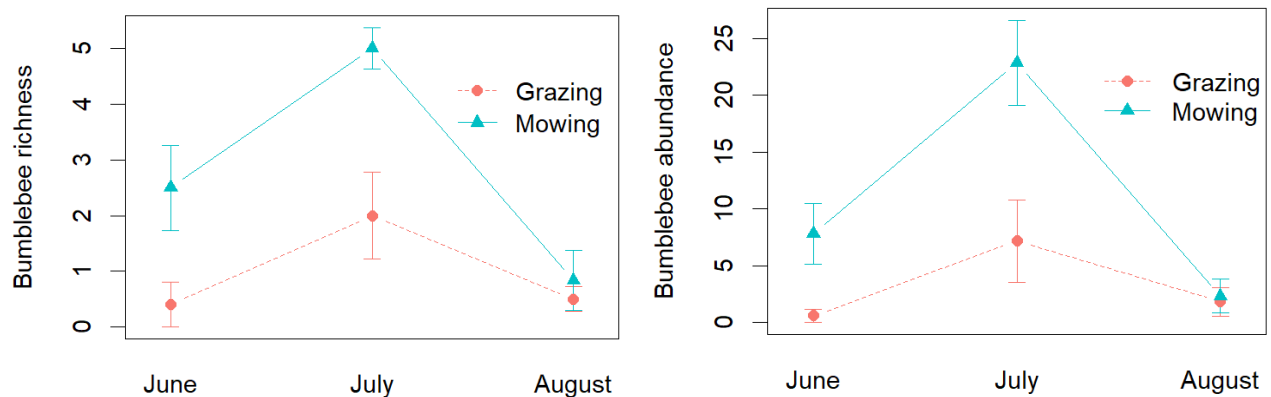
Figure 11: Seasonal variation in a) bumblebee species richness and b) bumblebee abundance

Bumblebee richness was affected by floral richness and management type. For bumblebee abundance, there was an effect of management type, floral richness and, with a small negative effect of cloud cover. Season was not a significant predictor for bumblebee occurrence; however, the effect might be nested within the effect of flower richness. The mean bumblebee richness and abundance was higher in mowed lands in June and July, but not in August, where there was no significant difference. The true number of bumblebee species is likely underrepresented, as morphologic groups are being used instead of species for the *Bombus s. str.* and *Psithyrus* subgenera.

The relationship between flower resources and bumblebee richness is shown in Figure 12. Increase in flowering plant richness was correlated with an increase in bumblebee species richness with a positive effect of mowing as a management type.
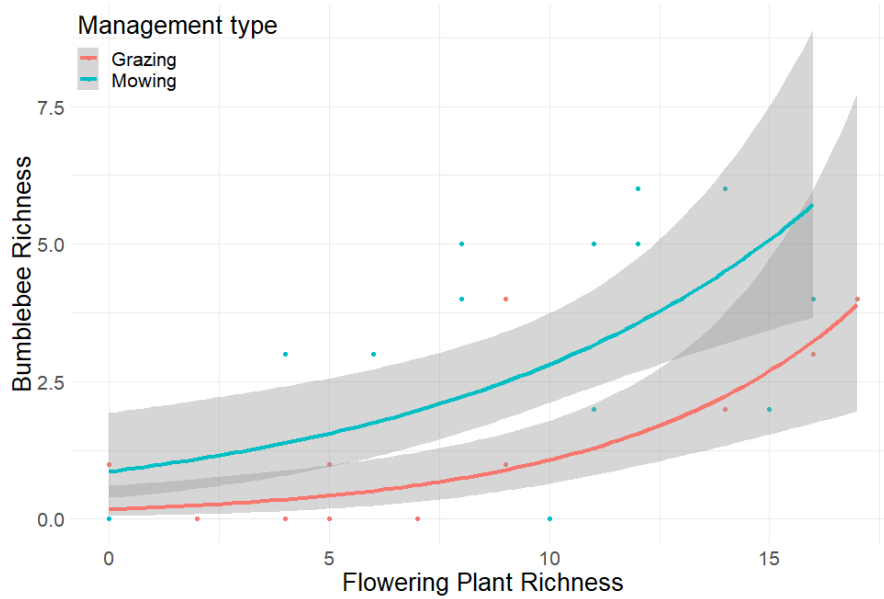
Figure 12: Plant-pollinator relationship between flowering plant richness and bumblebee richness in mowed and grazed grasslands. Standard error of the model is indicated with grey, shaded area.

The relationship between bumblebee abundance and floral richness is shown in Figure 13. Bumblebee abundance was also positively related to flowering plant richness, and there was a clearer difference between grazed and mowed sites. The model also showed cloud cover to a have a small negative effect on bumblebee abundance.
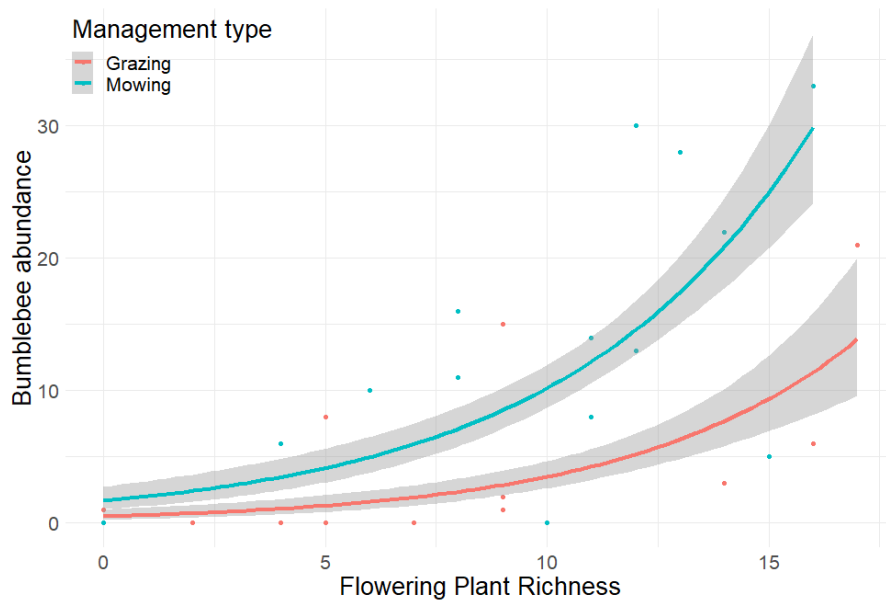
Figure 13: Plant-pollinator relationship between flowering plant richness bumblebee abundance in mowed and grazed grasslands. Standard error of the model is indicated with grey, shaded area.

3.3 Interaction network

Pollinator taxa

The most abundant flower visitor was flies, although the number decreased for each round. Flies preferred white and yellow flowers and were often seen on the most abundant flowers. In June the most visited flowers were *Ranunculus acris* which was among the most abundant flowers in that round. In July flies preferred *Leucanthemum vulgare*, as well as *Hieracium* sp and *Ranunculus acris*. In August flies were most seen on *Leontodon autumnalis* L*, Hypericum maculatum*, which were abundant in grazing lands.

Hoverflies had similar preferences to other flies, favoring white and yellow flowers. In June most interactions were with *Ranunculus acris,* while in July, they preferred *Galium sp* and *Leucanthemum vulgare*. Hoverflies were the only pollinator observed interacting with any *Galium* species. In August hoverflies preferred *Leontodon autumnalis* L and Hypericum maculatum.

Solitary bees and butterflies were mostly seen on the most abundant flower species in each round, *Ranunculus acris* in June, *Leucanthemum vulgare* in July and *Leontodon autumnalis* L in August*.*

Beetles were seen on *Potentilla erecta* in June, *Campanula rotundifolia* in July and *Achillea millefolium* in August.

All studied pollinator taxa except honeybees were observed in June, July, and August, while honeybees were only seen in August. Only three honeybee individuals were observed. The number of plant species in the network increased from June to July and decreased slightly from July to August.

Details about pollinator taxa and their interaction with plants can be found in Appendix C.

Bumblebees

The flower preferences of bumblebees are inferred from number of observed flower visitations. In mowing lands, the interactions for June, July and August are shown in Figure 14. From June to July there is an increase in the number of flowering species in the interaction network. In August there is a clear decrease in flowering species, only *Succisa pratensis* and *Campanula rotundifolia* had an observed interaction with a bumblebee.

The most common interactions were with flowers associated with bee pollination syndrome, e.g., blue, purple, white, and yellow flowers (Waser & Ollerton, 2006). Bumblebees were often seen on *Knautia arvensis*, *Trifolium pratense*, *Trifolium repens*, *Cirsium heterophyllum,* and *Rhinanthus minor* L. The flowers with most bumblebee interactions were usually highly

abundant in mowing lands. The exception is *Ranunculus acris*, which was among the most abundant species, but completely ignored by bumblebees in all rounds.

In grazing lands, there were comparatively less species and interactions than mowing lands in all rounds, as illustrated in Figure 15. The highest numbers of species and interactions were observed in July, with markedly fewer in June and August. The most visited species were *Veronica chamaedrys*, *Cirsium heterophyllum*, *Leontodon atumnalis* L, *Prunella vulgaris*) and *Trifolum repens*. In grazing lands there was a higher proportion of flower visits on less abundant species such as *Cirsium heterophyllum* and *Prunella vulgaris.*

For bumblebees, there were differences in the complexity of the interaction networks between the mowed and grazing lands (Figure 14). Mowing lands had more bumblebee species interacting with more flower species. In mowing lands, the most abundant species were favored by the bumblebees. In grazing lands, bumblebees showed a preference for many of the same species, even when they were less abundant.

a) June
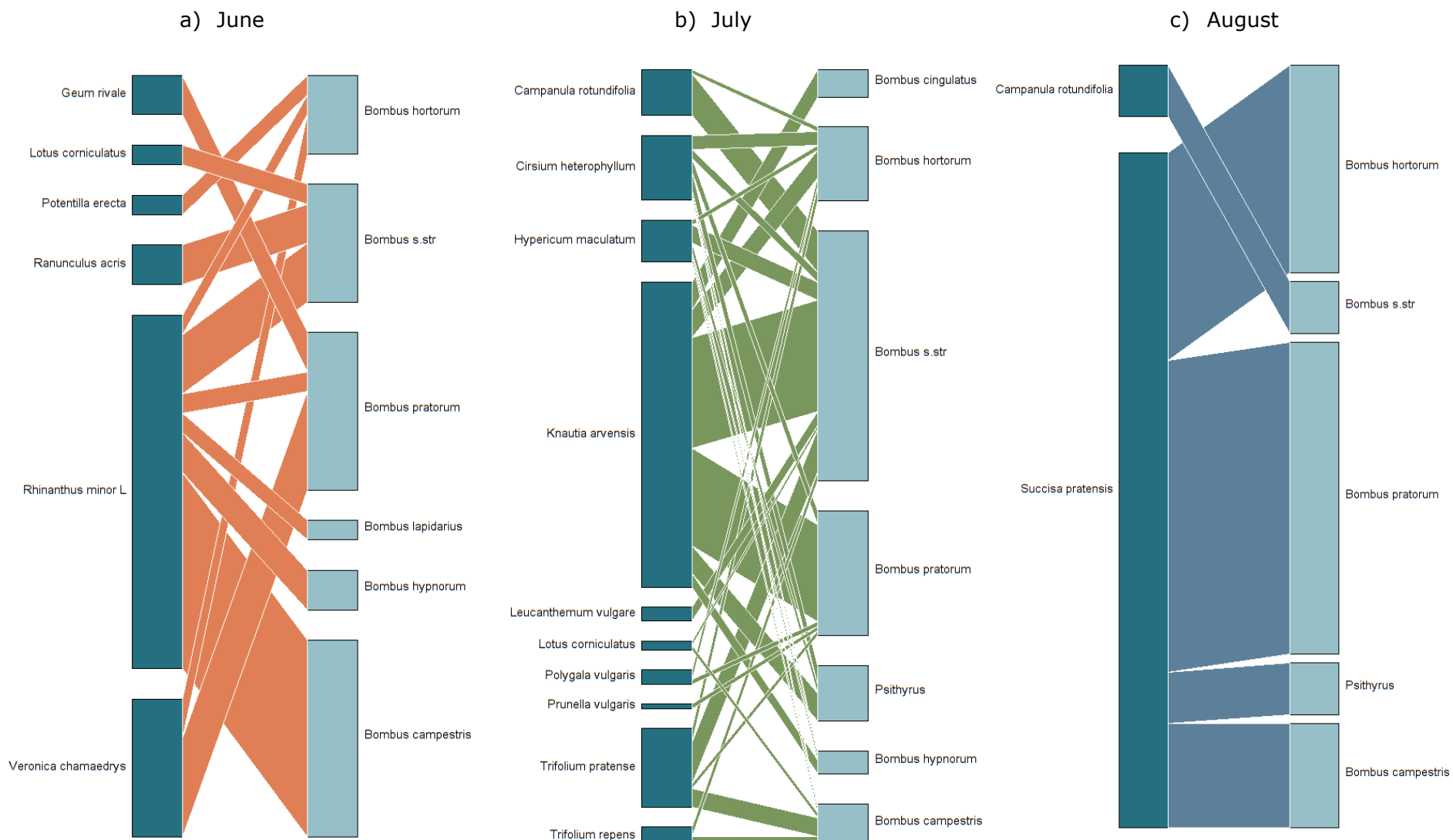
b) July

c) August

Figure 14: Plant pollinator interaction network in mowed grasslands in a) June, b) July and c) August. Size of each species is relative to proportion of observations. Size of connecting lines are relative to proportion of interaction with the connected species.
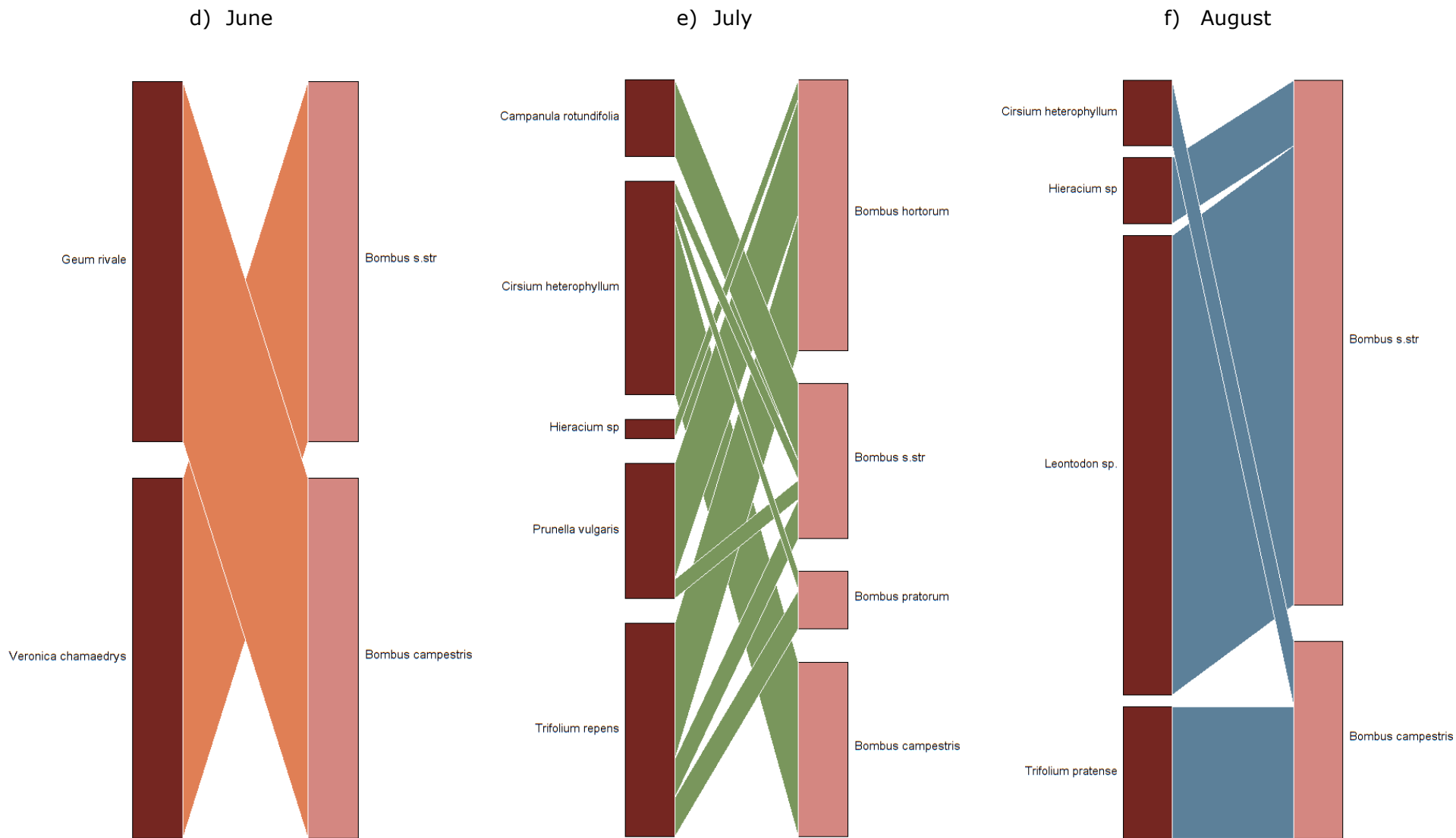
Figure 15: Plant pollinator interaction network in grazed grasslands in a) June, b) July and c) August. Size of each species is relative to proportion of observations. Size of connecting lines is relative to proportion of interaction with the connected species.

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4 Discussion

The objective of this study was to quantify the effects of different management types on plant-pollinator interactions in semi-natural grasslands. The richness and abundance of both flowering plants and pollinators were observed throughout the summer of 2022 in 6 mowed and 6 grazed semi-natural grasslands. The results suggest that plant-pollinator interactions in semi-natural grasslands are influenced by both management type and season. Study site was an important predictor for richness of flowering plants, which in turn was a strong predictor for pollinator richness and abundance. Mowing lands had more pollinators and a more complex plant-pollinator network than grazed lands.

Treatment effects

Flowering plants

Flowering plant richness was significantly affected by season and site, but not management type. The effect of site is likely a result of local variation in characteristics such as total grassland size, site condition, soil nutrients and land use history, which can impact vegetation composition, often more than present land use (Gilhaus et al., 2017). A long history of consistent management is considered beneficial to site quality, and studies have found that after abandonment of a site, 5 years of restoration did not restore the original species composition (Pöyry et al., 2005). The sites Storlia and Beitlandet had the highest flowering plant richness, perhaps due to the long history of management on these sites, spanning several hundred years (Lyngstad & Øien, 2006; Vesterbukt, 2017). It is worth noting that management was abandoned at Beitlandet between 1995 and 2005, but there had been 18 years of restorative efforts and active management by the time of data collection (Vesterbukt, 2017).

The grazing species can also affect the plant species composition. A study comparing the effect of grazing by sheep, cattle and horses found that compared to cattle, sheep had a more negative effect on several plant species, while horse grazing had a more positive effect (Milberg et al., 2020). This is due to sheep grazing more selectively, focusing more on herbs and legumes, compared to other grazers (Dumont et al., 2011). Due to the different grazing pressures and periods, it is difficult to compare the effect of grazing species in these sites. However, studies indicate that herb rich grasslands should preferably be grazed by cattle or horses rather than sheep to maintain high plant diversity (Nilsson et al., 2013). Storlia and Beitlandet are grazed by goat-sheep combination from late July and cattle from late June, respectively. Looking at these sites, with the highest floral species richness, we can infer that late onset of grazing and low grazing intensity positively affect floral richness, regardless of species of grazing animal.

Many flowering plant species appeared in both grazing and mowing lands (Figure 7), but 40% of flowering species were specific to management type. Management was not significantly

affecting the total number of flowering plant species, yet the species composition varied between management types. Mixed management creates different conditions, allowing for species with more varied environmental requirements to exist in proximity to each other (Bonari et al., 2017). Since all sites have both mowing and grazing lands, they are likely a valuable addition to the local landscape, allowing more species than in a homogenous landscape.

Flowering plant abundance was impacted by management type. This supports the hypothesis that the grazers eat the flower resources, as sites with late onset grazing (Storlia, Beitlandet) had ample flower abundance until grazing began. Grazing intensity is associated with less floral resources and lower plant recruitment, which matches what was observed in the field (Tadey, 2015; Wissman, 2006). At study site Ingstadnes, which was intensely grazed by cattle in June, there was almost no flowering plants the rest of the summer. This level of intense early grazing lowered the value for pollinators, however the effect on pollinators of the outfield grazing is also of interest. Studies indicate no negative effect of low intensity outfield grazing on bumblebee richness and abundance in forest areas, however this field of research is still expanding (INN, 2021; Valaker, 2022). The highest floral abundance in grazing lands was at Storlia, where grazing did not start until August. At Stykket, grazing intensity was very low, which seemed to have the opposite effect. It was overgrown by tall grasses and mown at the end of the season.

The small difference between grazed and mowed lands in August is not what was initially expected, however late or lacking mowing might explain some of the unexpected result. Lack of mowing in some sites let flower abundance be higher than normal, while late mowing coincided with low flowering in grazed grassland near the end of the flowering season. The difference in flower abundance after mowing might be larger in years with earlier mowing. Repeated surveys for a multi-year time series would be ideal to ensure a representative sample. However, when mowing occurs so late in the season, it does not appear that grazing lands are functional flower reservoirs for pollinators after mowing.

Pollinators

The bumblebee richness and abundance followed a similar pattern to the floral richness, with an increase in July and decrease in August. In other studies, wild bee abundance changes with flower richness, which matches what was seen (Bendel et al., 2019). This study showed a significant effect of both floral richness and abundance on bumblebee abundance. Since these variables are highly correlated, the effect of floral richness was chosen for the model, as the effect was larger.

A seasonal increase in bumblebee abundance is expected as the colony grows in size, as well as a decrease at the end of the flowering season (Persson & Smith, 2013). There was no effect of season in the model for bumblebee abundance. However, the effect of season is likely nested within floral richness, which already follows a seasonal trend.

The abundance of pollinator taxa in this study differed from similar studies of urban successional grasslands in 2020 (Dhukuchhu, 2021; Heggøy, 2021). Compared to the successional grasslands, the grazing and mowing lands had a higher proportion of flies, solitary bees and hoverflies, while honeybees and wasps were less abundant. In the same successional grasslands in 2021, the relative abundance of flies and hoverflies was higher, likely due to humid weather conditions (Straume, 2022). Conditions were similarly wet in 2022, possibly accounting for the high proportion of flies. The difference can also be attributed to the presence of grazing animals or agricultural areas nearby, the lack of nearby beekeepers and the distance from urban areas.

Composition of the surrounding areas was not included in this data analysis, but the surroundings are likely to plays a role in connectivity, available nesting habitat and alternative food sources for the observed pollinators.

Interaction webs

Before mowing, the plant-pollinator interactions webs were most complex in mowing lands. Due to lack of mowing, there were still some available flower resources in mowing lands in August at Storlia and Stykket. It was observed that even late in the season there was still bumblebee activity in these areas. This highlights the need for late-season floral resources close to mowing lands, such as grazing lands. In addition, other habitats such as forest edge vegetation or flower strips near mowing lands can have a positive effect on pollinators (Johansen et al., 2020).

Bumblebees showed preference for big, yellow, blue, or purple flowers. In mowing lands, bumblebee preference seemed to align with available flower resources, as flower visitation was common on the most abundant flowers . In grazing lands, bumblebees would visit many of the same flowering species, even when these species were not abundant. The observations indicate that a pollinator friendly habitat would have flowering of - among others - *Rhinanthus minor* in June, *Knautia arvensis*, *Cirsium heterophyllum*, *Trifolum pratens* and *Trifolum repens* in July, and *Succisa pratensis* and *Leontodon atumnalis* L in August.

Limitations & method

Originally, four rounds of data collection were planned, however due to temperature and rain conditions not being met, only three rounds were possible. An additional round was planned after mowing, to study if any flower resources would regrow after mowing. While this could not be examined, anecdotes from the farmers suggested that even with earlier mowing, mowing lands do not see more flowering after mowing.

In July and August 2022, Trøndelag experienced increased precipitation and weather that was colder and wetter than other years (Metrologisk-institutt, 2022a, 2022b). The weather is likely to have had an impact on the results from the fieldwork. Available foraging time for pollinators was likely decreased, as cooler temperatures and wet conditions make it difficult for

pollinators to locate and access flowers (Lawson & Rands, 2019). High soil moisture can also have increased the negative effect of trampling in grazed areas, causing damage to plant species (Renne & Tracy, 2007). The time of mowing was delayed due to the humid conditions, to avoid wet hay and disturbance of the soil when it is soft and muddy. At the time of mowing, there were few flower resources left in both management types. It is possible that in cases of earlier mowing, there might be a bigger difference in flower resources, allowing for grazing lands to serve as a food reserve for pollinators.

In case of repeated studies, this year will likely be an outlier, however it highlights the difficulty of observational studies and the reality of real-time adaptations in management. Long term monitoring is likely necessary to fully understand the effect of management on flower resources throughout the entire summer season.

Time spent in transects was a strong predictor of both bumblebee richness and abundance. It was excluded from the model selection as the relationship is backwards, as higher abundance of pollinators increased the time spent in a transect. To avoid this in future sampling rounds, a standard time of 10 minutes per transect should be followed.

This thesis did not account for the size of the farmlands or the habitats surrounding the area, which is likely to impact pollinator abundance through available nesting habitats and connectivity to other food sources (Rotchés-Ribalta et al., 2018). Further analysis could benefit from looking at the effects of landscape composition.

Management implications

Norway has implemented a national pollinator strategy aimed at promoting pollinator conservation and sustainable land management practices. The strategy recognizes the important role of pollinators in maintaining ecosystem health and biodiversity, as well as their economic and cultural significance (Departementa, 2018). It emphasizes the need for increased awareness, knowledge, and collaboration among stakeholders, to protect and promote pollinators and their habitats.

The national pollinator strategy includes measures such as promoting pollinator-friendly farming practices, reducing the use of pesticides, creating, and restoring pollinator habitats, and conducting research to better understand the status and trends of pollinators in Norway.

In Norway, there are subsidy schemes to aid management of threatened nature. There are subsidies available for selected cultural landscape areas, threatened species and nature types, as well as area improvements to aid wild pollinators (Miljødirektoratet, 2022). In mowed grasslands, farmers can also be given subsidies for once-a-year mowing of grasslands, after July 15th (Departementa, 2018). Farmers have stated that subsidies and concerns for biodiversity are motivators for otherwise cost-inefficient management (Naturvernforbundet, 2022).

Heterogenous mowing, e.g., partial mowing at different times, was practiced at Fagerli. This method allows flower resources to be available at larger parts of the season and is considered to be more beneficial to pollinators, although it takes more time and resources from the farmer (Johansen et al., 2020). To further improve mowed grasslands, mixed management like heterogeneous mowing should be encouraged. Due to the increased management cost, increasing subsidies for mowing might be beneficial.

Grazing lands can also be valuable as pollinator habitats. Depending on duration and intensity of grazing, grazing lands can have a high abundance of flower resources. The pollinator strategy should recognize the importance of - and encourage - late onset and low intensity grazing.

5 Conclusion

This study examined the effects of different management types on plant-pollinator interactions in semi-natural grasslands in Trøndelag, Norway. Both management type and time of season significantly impacted plant-pollinator interactions. Flowering plant richness differed between sites, while flowering plant abundance depended on management measures. A diverse floral community positively influenced pollinator richness and abundance. The plant species of grazing lands differed from mowing lands, emphasizing the value of mixed management approaches in promoting biodiversity in grasslands. Mowing lands exhibited higher pollinator abundance and more complex plant-pollinator networks compared to grazed lands. The grazed lands with the highest pollinator abundance were those with low grazing intensity and late onset grazing.

The results support the promotion of mowing lands as pollinator-friendly habitats, with an emphasis on heterogeneous mowing to provide flower resources throughout the season. It also emphasizes the value of late onset and low intensity grazing for maintaining flower abundance in grazed lands. The results suggest that both mowing and grazing practices contribute to the preservation of pollinator diversity and ecosystem health, but mowing lands are of greater value as pollinator habitats. Future studies should consider landscape composition and the long-term monitoring of management effects to gain a more comprehensive understanding of plant-pollinator interactions in grassland ecosystems.

6 References

Åström, S., Åström, J., Bøhn, K., Gjershaug, J. O., Staverløkk, A., & Ødegaard, F. (2015). Nasjonal overvåking av dagsommerfugler og humler i Norge. *Oppsummering av aktiviteten i*.

Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, *100*(16), 9383-9387.

Bendel, C. R., Kral-O'Brien, K. C., Hovick, T. J., Limb, R. F., & Harmon, J. P. (2019). Plant–pollinator networks in grassland working landscapes reveal seasonal shifts in network structure and composition. *Ecosphere*, *10*(1).

Bonari, G., Fajmon, K., Malenovský, I., Zelený, D., Holuša, J., Jongepierová, I., Kočárek, P., Konvička, O., Uřičář, J., & Chytrý, M. (2017). Management of semi-natural grasslands benefiting both plant and insect diversity: The importance of heterogeneity and tradition. *Agriculture, Ecosystems & Environment*, *246*, 243-252.

Cagnolo, L., Valladares, G., Salvo, A., Cabido, M., & Zak, M. (2009). Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Conservation biology*, *23*(5), 1167-1175.

Cousins, S. A. O., & Eriksson, O. (2002). The influence of management history and habitat on plant species richnessin a rural hemiboreal landscape, Sweden. *Landscape Ecology*, *17*(6), 517-529.

Departementa. (2018). *National Pollinator Strategy - A strategy for viable populations of wild bees and other pollinating insects*.

Dhukuchhu, A. (2021). *Effects of land use and season on flowering plants and plant-pollinator networks in urban grasslands* NTNU].

Dumont, B., Carrère, P., Ginane, C., Farruggia, A., Lanore, L., Tardif, A., Decuq, F., Darsonville, O., & Louault, F. (2011). Plant–herbivore interactions affect the initial direction of community changes in an ecosystem manipulation experiment. *Basic and Applied Ecology*, *12*(3), 187-194.

Elven, H., & Bjureke, K. (2018). Pollinatorvennlig skjøtsel av slåttemark og naturbeitemark. *Naturhistorisk museum, Universitetet i Oslo. Rapport*(77), 80.

Ferreira, P. A., Boscolo, D., & Viana, B. F. (2013). What do we know about the effects of landscape changes on plant–pollinator interaction networks? *Ecological Indicators*, *31*, 35-40.

Gilhaus, K., Boch, S., Fischer, M., Hölzel, N., Kleinebecker, T., Prati, D., Rupprecht, D., Schmitt, B., & Klaus, V. (2017). Grassland management in Germany: Effects on plant diversity and vegetation composition. *TUEXENIA*, *37*, 379-397.

Heggøy, H. (2021). *Effects of land-use on bumblebees and other pollinators in urban grasslands* NTNU].

Hellerstein, D., Hitaj, C., Smith, D., & Davis, A. (2017). *Land Use, Land Cover, and Pollinator Health: A Review and Trend Analysis*. U. S. D. o. A. (USDA).

Henle, K., Davies, K. F., Kleyer, M., Margules, C., & Settele, J. (2004). Predictors of species sensitivity to fragmentation. *Biodiversity & Conservation*, *13*, 207-251.

Hovstad, K. A., Johansen, L., Arnesen, G., Svalheim, E. og Velle, L. G. (2018). *Semi-naturlige naturtyper. Norsk rødliste for naturtyper 2018.* .

Huang, H., Tu, C., & D'Odorico, P. (2021). Ecosystem complexity enhances the resilience of plant-pollinator systems. *One Earth*, *4*(9), 1286-1296.

INN. (2021). *CarniForeGraze.* LARGE.

IPBES. (2016). *Summary for policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production.*: Zenodo Retrieved from

Jakobsson, S., & Pedersen, B. (2020). Naturindeks for Norge 2020 - Tilstand og utvikling for biologisk mangfold. *NINA Rapport*.

Jauker, F., Speckmann, M., & Wolters, V. (2016). Intra-specific body size determines pollination effectiveness. *Basic and Applied Ecology*, *17*(8), 714-719.

Johansen, L., Albertsen, E., Daugstad, K., Henriksen, M. V., Grenne, S., & Vesterbukt, P. (2020). Gode leveområder for pollinatorer i kulturlandskapet. *NIBIO Rapport*.

Johansen, L., Westin, A., Wehn, S., Iuga, A., Ivascu, C. M., Kallioniemi, E., & Lennartsson, T. (2019). Traditional semi-natural grassland management with heterogeneous mowing times enhances flower resources for pollinators in agricultural landscapes. *Global Ecology and Conservation*, *18*, e00619.

Kevan, P., & Baker, H. (1983). Insects as flower visitors and pollinators. *Annual review of entomology*, *28*(1), 407-453.

Kevan, P. G., Clark, E. A., & Thomas, V. G. (1990). Insect pollinators and sustainable agriculture. *American Journal of Alternative Agriculture*, *5*(1), 13-22.

Klimaservicesenter. (2022). *Klimaservicesenteret.no - Regionverdier*.

Lawson, D. A., & Rands, S. A. (2019). The effects of rainfall on plant–pollinator interactions. *Arthropod-Plant Interactions*, *13*(4), 561-569.

Lennartsson, T., Nilsson, P., & Tuomi, J. (1998). Induction of overcompensation in the field gentian, Gentianella campestris. *Ecology*, *79*(3), 1061-1072.

Lid, J. (2005). *Norsk Flora*. Det Norske Samlaget.

Lindgaard, A., & Henriksen, S. (2011). *Norwegian Red List for Ecosystems and Habitat Types 2011*.

Lyngstad, A., & Øien, D.-I. (2006). *Kulturlandskap i Storlia, Leksvik*.

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1557), 2605-2611.

Metrologisk-institutt. (2022a). *Været i Norge, Klimatologisk månedsoversikt, August 2022*.

Metrologisk-institutt. (2022b). *Været i Norge, Klimatologisk månedsoversikt, Juli 2022*.

Milberg, P., Bergman, K.-O., Glimskär, A., Nilsson, S., & Tälle, M. (2020). Site factors are more important than management for indicator species in semi-natural grasslands in southern Sweden. *Plant Ecology*, *221*(7), 577-594.

Miljødirektoratet. (2022). *Søke om tilskudd - tiltak for trua natur*. Norwegian Environment Agency.

Naturvernforbundet. (2022). *Miljøtilskudd til jordbruket - Slåttemark* [Video].

Nayak, G. K., Roberts, S. P. M., Garratt, M., Breeze, T. D., Tscheulin, T., Harrison-Cripps, J., Vogiatzakis, I. N., Stirpe, M. T., & Potts, S. G. (2015). Interactive effect of floral abundance and semi-natural habitats on pollinators in field beans (Vicia faba). *Agriculture, Ecosystems & Environment*, *199*, 58-66.

Nicholls, C. I., & Altieri, M. A. (2013). Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable development*, *33*, 257-274.

Nilsson, S. G., Franzén, M., & Pettersson, L. (2013). Land-use changes, farm management and the decline of butterflies associated with semi-natural grasslands in southern Sweden. *Nature Conservation*, *6*, 31-48.

Norderhaug, A., Austad, I., Hauge, L., & Kvamme, M. (1999). Skjøtselsboka for kulturlandskap og gamle norske kulturmarker. In (pp. 11-20, 75-84, 133-146).

Öckinger, E., & Smith, H. G. (2006). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, *44*(1), 50-59.

Ogilvie, J. E., & Forrest, J. R. K. (2017). Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science*, *21*, 75-82.

Peet, R. K. (1974). The measurement of species diversity. *Annual Review of Ecology and Systematics*, *5*(1), 285-307.

Persson, A. S., & Smith, H. G. (2013). Seasonal persistence of bumblebee populations is affected by landscape context. *Agriculture, Ecosystems & Environment*, *165*, 201-209.

Phillips, R. D., Peakall, R., van der Niet, T., & Johnson, S. D. (2020). Niche Perspectives on Plant–Pollinator Interactions. *Trends in Plant Science*, *25*(8), 779-793.

Poppy, G. M., Chiotha, S., Eigenbrod, F., Harvey, C. A., Honzák, M., Hudson, M. D., Jarvis, A., Madise, N. J., Schreckenberg, K., Shackleton, C. M., Villa, F., & Dawson, T. P. (2014). Food security in a perfect storm: using the ecosystem services framework to increase understanding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1639), 20120288.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345-353.

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220-229.

Pöyry, J., Lindgren, S., Salminen, J., & Kuussaari, M. (2005). Responses of butterfly and moth species to restored cattle grazing in semi-natural grasslands. *Biological Conservation*, *122*(3), 465-478.

Renne, I. J., & Tracy, B. F. (2007). Disturbance persistence in managed grasslands: shifts in aboveground community structure and the weed seed bank. *Plant Ecology*, *190*, 71-80.

Rotchés-Ribalta, R., Winsa, M., Roberts, S. P., & Öckinger, E. (2018). Associations between plant and pollinator communities under grassland restoration respond mainly to landscape connectivity. *Journal of Applied Ecology*, *55*(6), 2822-2833.

Sjödin, N. E. (2007). Pollinator behavioural responses to grazing intensity. *Biodiversity and Conservation*, *16*(7), 2103-2121.

Slaa, E. J., Sánchez Chaves, L. A., Malagodi-Braga, K. S., & Hofstede, F. E. (2006). Stingless bees in applied pollination: practice and perspectives. *Apidologie*, *37*(2), 293-315.

Stavert, J. R., Liñán-Cembrano, G., Beggs, J. R., Howlett, B. G., Pattemore, D. E., & Bartomeus, I. (2016). Hairiness: the missing link between pollinators and pollination. *PeerJ*, *4*, e2779.

Steffan-Dewenter, I., Klein, A.-M., Gaebele, V., Alfert, T., & Tscharntke, T. (2006). Bee diversity and plant-pollinator interactions in fragmented landscapes. *Specialization and generalization in plant-pollinator interactions*, 387-410.

Straume, R. (2022). *Spatiotemporal variation and flowering plant preferences of insect pollinators in grassland ecosystems* NTNU].

Tadey, M. (2015). Indirect effects of grazing intensity on pollinators and floral visitation. *Ecological Entomology*, *40*(4), 451-460.

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., & Milberg, P. (2016). Grazing vs. mowing: A meta-analysis of biodiversity benefits for grassland management. *Agriculture, Ecosystems & Environment*, *222*, 200-212.

Totland, Ø., Hovstad, K., Ødegaard, F., & Åström, J. (2013). Kunnskapsstatus for insektpollinering i Norge- Betydningen av det komplekse samspillet mellom planter og insekter. *Artsdatabanken, Norge*.

Valaker, J. (2022). *Are bumblebees limited by floral resource availability due to cattle grazing in boral forest pastures?: The effects of seasonality and cattle grazing on bumblebees in boral forest pastures* Høgskolen i Innlandet].

Valtonen, A., Saarinen, K., & Jantunen, J. (2006). Effect of different mowing regimes on butterflies and diurnal moths on road verges. *Animal Biodiversity and Conservation*, *29*(2), 133-148.

Van Andel, J., Bakker, J., & Snaydon, R. (1987). Disturbance in Grasslands Causes, effects and processes. *Geobotany*, *10*, 1-316.

Vassilev, K., Pedashenko, H., Nikolov, S. C., Apostolova, I., & Dengler, J. (2011). Effect of land abandonment on the vegetation of upland semi-natural grasslands in the Western Balkan Mts., Bulgaria. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, *145*(3), 654-665.

Veen, P., Jefferson, R., De Smidt, J., & Van der Straaten, J. (2009). *Grasslands in Europe: Of high nature value*. BRILL.

Vesterbukt, P. (2017). *Rekartlegging med skjøtselsplaner for slåttemark. Beitlandet, Stjørdal kommune. Nord-Trøndelag fylke*.

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences*, *118*(2), e2023989118.

Waser, N. M., Chittka, L., Price, M. V., Williams, N. M., & Ollerton, J. (1996). Generalization in pollination systems, and why it matters. *Ecology*, *77*(4), 1043-1060.

Wehn, S., Kallioniemi, E., Vesterbukt, P., Grenne, S., Can, J. M., & Johansen, L. (2020). Skjøtsel av semi-naturlig eng for å ivareta pollinatorer og deres blomsterressurser. *NIBIO Rapport*.

White, R. P., Murray, S., Rohweder, M., Prince, S., & Thompson, K. (2000). *Grassland ecosystems*. World Resources Institute Washington, DC, USA.

Wissman, J. (2006). *Grazing regimes and plant reproduction in semi-natural grasslands* (Vol. 2006).

Appendices

Appendix A: Site locations and management details

Figure A1: Location of transects at Fagerli

Figure A2: Location of transects at Storlia

Figure A3: Location of transects at Ingstadnes
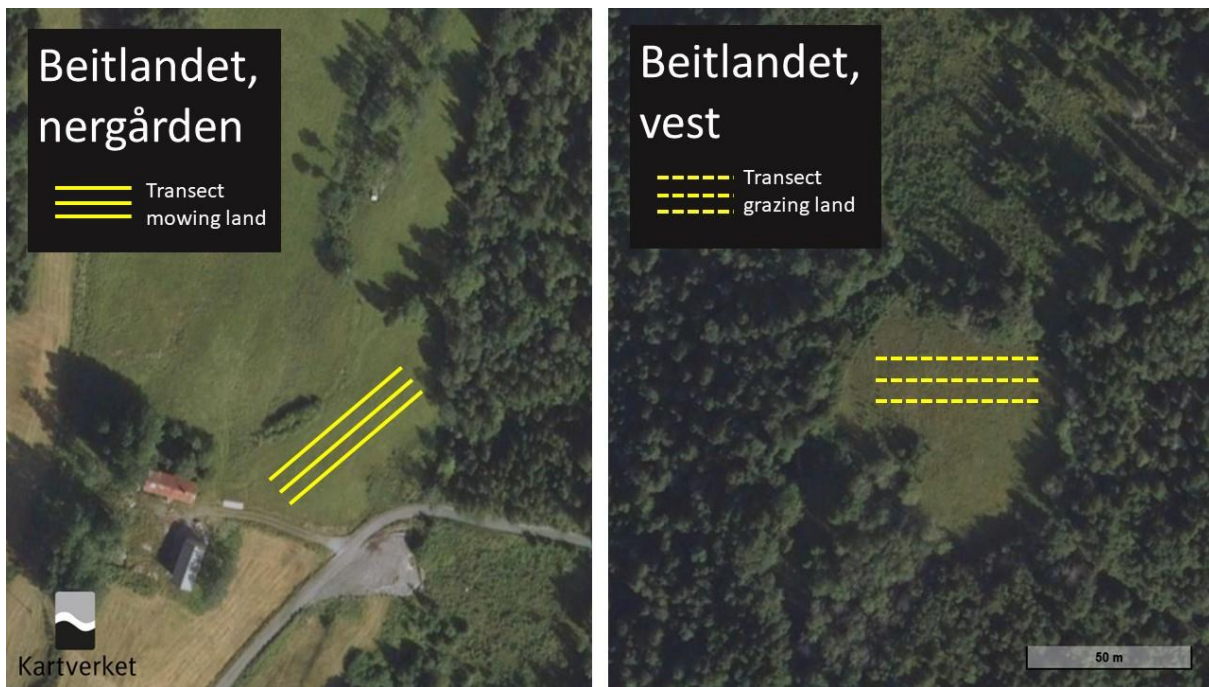
Figure A4: Location of transects at Beitlandet.

Figure A5: Location of transects at Vennberg
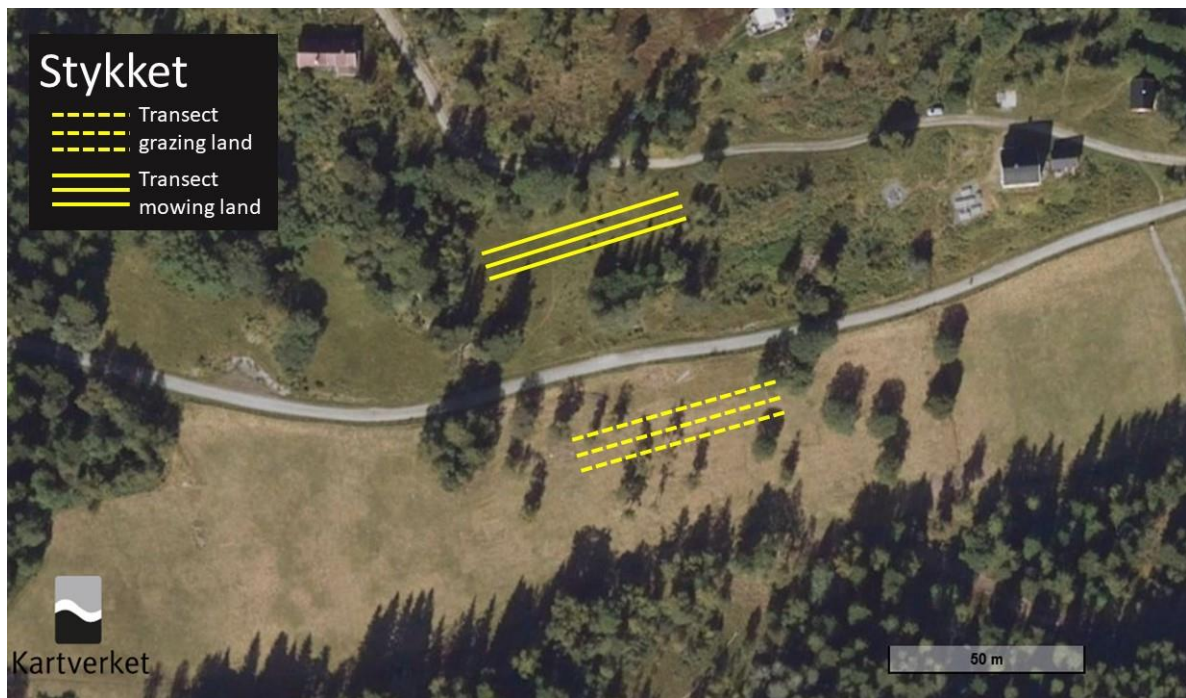
Figure A6: Location of transects at Stykket

Table A1: Site information, including grazer species, coordinates and elevation at main farm building, visitation dates and management status at each visit.

Site and main grazer	Location	Round 1 17-24th of June	Round 2 12-20th of July	Round 3 21st of august – 7th of september
Fagerli (sheep)	63.557838, 10.175305 Elevation: 200 m.a.s.l	17.06.22 Grazed: yes Mowed: no	12.07.22 Grazed: yes Mowed: no	05.09.22 Grazed: yes Mowed: yes (heterogenous)
Storlia (sheep/goat)	63.690592, 10.526148 Elevation: 168 m.a.s.l	17.06.22 Grazed: no Mowed: no (grazed by escapee goats)	12.07.22 Grazed: no Mowed: no	05.09.22 Grazed: yes Mowed: no (machine broken)
Ingstadnes (cattle)	63.444317, 11.203865 Elevation: 25 m.a.s.l	19.06.22 Grazed: yes (NA) Mowed: no	19.07.22 Grazed: no (no animals) Mowed: no	07.09.22 Grazed: no (no animals) Mowed: yes
Beitlandet (cattle)	63.495676, 11.311170 Elevation: 300 m.a.s.l	19.06.22 Grazed: no Mowed: no	19.07.22 Grazed: yes Mowed: no	07.09.22 Grazed: yes Mowed: yes
Vennberg (horse)	63.334089, 10.886530 Elevation: 327 m.a.s.l	20.06.22 Grazed: yes Mowed: no	20.07.22 Grazed: yes Mowed: no	21.08.22 Grazed: yes Mowed: yes
Stykket (sheep)	63.400772, 10.268615 Elevation: 270 m.a.s.l	24.06.22 Grazed: no Mowed: no	20.07.22 Grazed: no Mowed: no	21.08.22 Grazed: no (mowed) Mowed: no

Appendix B: Supplementary flowering plant data

Table B1: Average plant height with standard error for grazing and mowing lands in June, July and August

Treatment	Season	Plant Height (cm)	Standard Error
Grazing	June	18.61	2.49
Grazing	July	19.67	3.00
Grazing	August	13.57	1.39
Mowing	June	17.13	1.43
Mowing	July	27.43	2.54
Mowing	August	12.53	1.88

Table B2. Flower abundance per species observed in grazed semi-natural grasslands and mowed semi-natural successional grasslands in June, July and August

	Flowering plant abundance					
	Grazed			Mowed		
Flowering plant	**June**	**July**	**August**	**June**	**July**	**August**
Achillea millefolium		2	2		13	9
Achillea ptarmica		1	21		2	10
Ajuga pyramidalis				9		
Alchemilla sp.	84	11	2	165	50	3
Anthriscus sylvestris	21	21		14		
Arabidopsis sp	1					
Bistorta vivipara	3	9		15	40	
Campanula rotundifolia		24	1		156	29
Chrysosplenium alternifolium	4					
Cirsium heterophyllum		8			4	
Dactylorhiza sp				5	13	
Epilobium sp.		4		21	9	9
Euphrasia sp				14	84	55
Filipendula ulmaria		1				
Fragaria vesca	12				1	
Galium album						7
Galium aparine			1			

Galium boreale L.						1
Galium mollugo		1			9	
Galium sp.		21			8	
Geranium sylvaticum	5	1		7		
Geum rivale	10			3		
Hieracium sp		26		5	6	1
Hypericum maculatum		4	13		42	26
Knautia arvensis					26	
Lathyrus pratensis					2	
Leontodon atumnalis L			16			8
Lepidotheca suaveolens			3			
Leucanthemum vulgare		23	1	2	382	11
Lotus corniculatus	1			41	33	
Lysimachia europaea				0		
Melampyrum sylvaticum		1			10	
Mentha ×gentilis			0			
Myosotis sp	1					
Polygala vulgaris	3			30	87	5
Polygonum aviculare			1			
Potentilla erecta	91	173	25	547	274	61
Prunella vulgaris		28	1		2	
Ranunculus acris	370	51		212	5	
Ranunculus repens			3			
Ranunculus sp	1	4	6			
Rhinanthus minor L		15	1	318	140	
Rumex acetosa	51			30	1	
Solidago virgaurea		1				
Stellaria graminea		52	1	1	81	6
Stellaria media		19				
Succisa pratensis						4
Trifolium pratense	11	29	4	178	134	
Trifolium repens		41		1	83	
Veronica chamaedrys	129	10		130	2	
Veronica officinalis		29			19	
Veronica serpyllifolia subsp. serpyllifolia			2			
Vicia cracca	5	1		1	3	
Viola riviniana	1			1		
Viola sp.				4		
Sum	**804**	**611**	**104**	**1754**	**1721**	**245**

Appendix C: Supplementary pollinator data

Abundance of bumblebee species (orange), butterfly species (green), and other pollinators (blue) observed grazing and mowing lands in June July and August.

Species	Grazing			Mowing		
	June	July	August	June	July	August
B. campestris	2	14	3	18	11	3
B. cingulatus	0	0	0	0	6	0
B. hortorum	0	17	0	4	19	4
B. hypnorum	0	0	0	4	5	0
B. lapidarius	0	0	0	1	0	0
B. pratorum	0	3	0	12	29	6
B. s.str	1	9	8	8	57	1
B. sp	1	2	0	1	3	1
Psithyrus	0	0	0	0	10	0

Species	Grazing			Mowing		
	June	July	August	June	July	August
Anthocharis cardamines	0	0	0	0	1	0
Argynnis aglaja	0	0	1	0	0	3
Boloria selene	0	0	0	0	3	0
Callophrys rubi	0	0	0	1	0	0
Camptogramma bilineata	0	0	0	0	1	0
Cyaniris semiargus	0	0	0	0	1	0
Erebia ligea	0	1	0	0	3	1
Pieris napi	1	0	0	0	0	0
Vanessa atalanta	0	0	1	0	0	1
Vanessa cardui	0	0	0	0	0	2

Species	Grazing			Mowing		
	June	July	August	June	July	August
Beetle	2	1	0	40	17	6
Fly	667	166	40	444	155	89
Honeybee	0	0	1	0	0	2
Hoverfly	5	43	29	13	66	59
Solitary bee	3	4	1	7	15	16
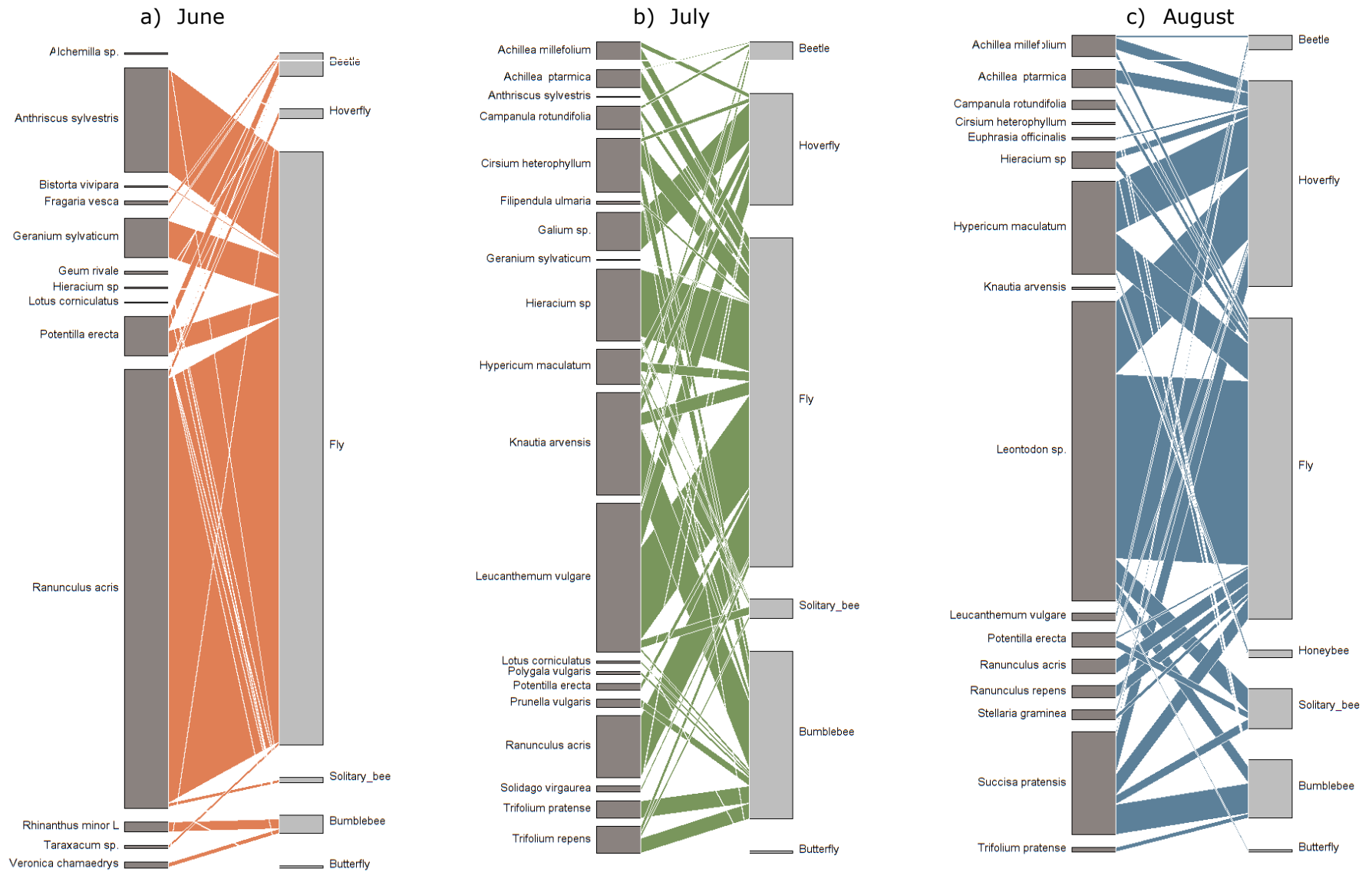
Figure C1: Plant-pollinator interaction network of pollinator taxa a) June, b) July and c) August. Size of each species is relative to proportion of observations. Size of connecting lines are relative to proportion of interaction

Appendix D: Field survey forms

Date: ……………………………….   Site: ……………………………….   Name: ……………………………….

PLANTS Species/ transect	1 Quadrats					2 Quadrats					3 Quadrats					4 Quadrats					5 Quadrats					6 Quadrats				
Plant height																														

Date: ……………………………….   Site: ……………………………….   Name: ……………………………….

Time/cloud cover % / temperature °C /wind B.No												
POLLINATORS Species/transect	Interacting plant species				Interacting plant species				Interacting plant species			

Appendix E: Supplementary model selection information

Figure E1: Correlation matrix for continuous predictor variables. "humle_abund" = bumblebee abundance, "humle_rich" = bumblebee richness, "veg_rich"= flowering plant richness, "veg_abund_tot" =flowering plant abundance, "cloud_cover" = cloud cover, "temperature" = temperature, "time"= time spent in transect.

Model selection

The following tables show the model selection for species richness of flowering plant (Table E1), abundance of flowering plants (Table E2), species richness of bumblebees (Table E3) and abundance of bumblebees (Table E4):

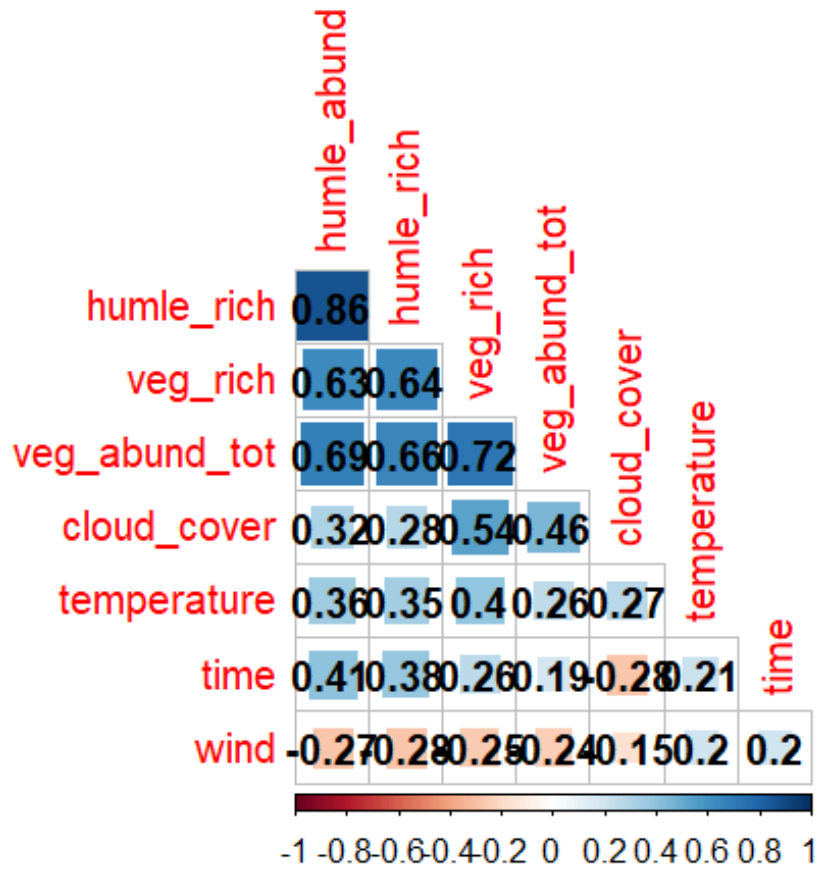*Table E1. Model selection for flower richness. Predictor variables are season (ssn) and management measure (typ). Interactions are indicated by a colon ":". Models are fitted with a generalized linear mixed effect model with a negative binomial error distribution.*

Model	ssn	typ	ssn:typ	df	AICc	ΔAICc	weight
mod_r5	**+**			**5**	**204.6**	**0.00**	**0.481**
mod_r7	**+**	**+**		**6**	**205.2**	**0.57**	**0.362**
mod_r1	+			4	207.8	3.20	0.097
mod_r6	+	+		5	209.9	5.29	0.034
mod_r9	+	+	+	8	211.0	6.38	0.020
mod_r10				2	215.6	10.97	0.002
mod_r8	+	+	+	7	215.8	11.12	0.002
mod_r3				3	217.4	12.80	0.001
mod_r2		+		3	217.5	12.88	0.001
mod_r4		+		4	219.3	14.63	0.000

Table E2. Model selection for flower abundance. Predictor variables are season (ssn), management measure (typ) and temperature (tmp). Interactions are indicated by a colon ":". Models are fitted with a generalized linear mixed effect model with a negative binomial error distribution.

Model	ssn	typ	tmp	ssn: tmp	ssn: typ	tm: typ	ssn: tmp: typ	df	AICc	ΔAICc	weight
mod_a5	+	+						5	409.2	0.00	0.598
mod_a1	+							4	411.4	2.16	0.203
mod_a6	+	+	-0.032					6	412.0	2.81	0.147
mod_a8	+	+					+	7	415.0	5.75	0.034
mod_a7	+	+	-0.148	+				8	417.6	8.41	0.009
mod_a9	+	+	-0.029		+			8	418.3	9.06	0.006
mod_a2		+						3	421.4	12.19	0.001
mod_a11								2	422.4	13.15	0.001
mod_a4		+	0.073					4	423.3	14.04	0.001
mod_a3			0.082					3	423.9	14.68	0.000
mod_a10	+	+	-0.272	+	+	+	+	13	436.2	26.95	0.000

Table E3. Model selection for bumblebee richness. Predictor variables are season (ssn), management measure (typ) and flower richness (veg_r). Interactions are indicated by a colon ":". Models are fitted with a generalized linear mixed effect model with a negative binomial error distribution.
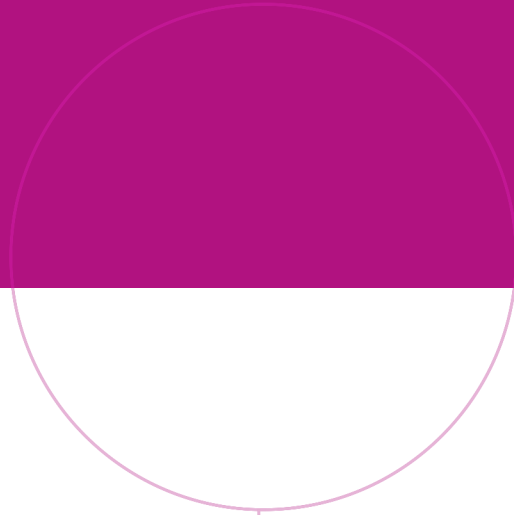
Model	ssn	typ	veg_r	ssn:typ	typ:veg_r	ssn:veg_r	ssn:typ:veg_r	df	AICc	ΔAICc	weight
mod_rb6	+	+	0.089					6	115.5	0.00	0.342
mod_rb7		+	0.148					4	116.2	0.72	0.238
mod_rb12	+	+	0.138			+		7	116.7	1.23	0.185
mod_rb9		+	0.185			+		5	118.1	2.57	0.094
mod_rb4	+	+						5	118.7	3.25	0.067
mod_rb11	+	+	0.088				+	8	120.2	4.71	0.032
mod_rb13	+	+	0.112			+		8	121.8	6.34	0.014
mod_rb3			0.162					3	122.2	6.68	0.012
mod_rb8	+	+					+	7	122.8	7.36	0.009
mod_rb5	+		0.110					5	123.9	8.46	0.005
mod_rb1	+							4	128.6	13.11	0.000
mod_rb10	+		0.133			+		7	129.9	14.39	0.000
mod_rb2		+						3	131.9	16.46	0.000
mod_rb14	+	+	4.494	+	+	+	+	13	134.6	19.13	0.000
mod_rb15								2	135.6	20.07	0.000

Table E4. Model selection for bumblebee abundance. Predictor variables are flower richness (veg_r), cloud cover (cc) and management measure (typ). Interactions are indicated by a colon ":". Models are fitted with a generalized linear mixed effect model with a negative binomial error distribution.

Model	veg_r	cc	typ	cc:veg_r	typ:veg_r	cc:typ	cc:typ:veg_r	df	AICc	ΔAICc	weight
mod_ab8	0.3450	-0.018	+					5	185.8	0.00	0.400
mod_ab5	0.3936	-0.020						4	186.7	0.93	0.252
mod_ab6	0.2214		+					4	187.7	1.89	0.155
mod_ab9	0.3315	-0.029		0.001				5	189.1	3.31	0.076
mod_ab1	0.2474				+			3	189.2	3.42	0.073
mod_ab10	0.2017		+					5	190.3	4.49	0.042
mod_ab3			+					3	199.3	13.55	0.000
mod_ab7		0.011	+					4	199.6	13.85	0.000
mod_ab4								2	200.8	14.99	0.000
mod_ab11		0.010	+			+		5	202.4	16.58	0.000
mod_ab12	0.4545	-0.068	+	0.006	+	+	+	9	252.3	66.53	0.000
mod_ab2									260.3	74.53	0.000