Master's thesis

NTNU
Norwegian University of Science and Technology
NTNU University Museum
Department of Biology

Ranveig Straume

Spatiotemporal variation and flowering plant preferences of insect pollinators in grassland ecosystems

Master's thesis in Biology (Ecology, Behaviour, Evolution and Biosystematics)
Supervisor: Gunnar Austrheim
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Kunnskap for en bedre verden

Abstract

Pollinators are crucial members of most terrestrial ecosystems, and their current declines are of great concern. Large, natural fluctuations of insect pollinators among years make their trends difficult to study with short term surveys alone. Long term, continued research is therefore needed, along with increased knowledge on the spatiotemporal trends of these pollinators. The abandonment of semi-natural grasslands, an important habitat for many pollinators, results in the grasslands undergoing succession and becoming successional grasslands, a habitat type often considered less ideal for many pollinators. Increased knowledge on the pollinators in both semi-natural and successional grasslands and concrete data on the pollinators flowering plant preferences in these land-use systems may be important knowledge for future conservation efforts. In this study I examined: (1) spatiotemporal trends of bumblebees and butterflies in grasslands at a regional scale over a nine-year period, (2) pollinator abundance and species richness in semi-natural and successional grasslands over two years at a local scale, and (3) flowering plant preferences of pollinators, primarily bumblebees, in semi-natural and successional grasslands on a local scale. Surveys conducted at a regional (Trøndelag county, Norway) and local (Trondheim, a municipality in Trøndelag) scale was used in this study.

The bumblebee and butterfly abundance, species richness, and species composition were significantly different across the regional sites. This was likely caused by differences in habitat quality among the sites. Of the regional survey, the bumblebees had a stable trend over the years with a seemingly consistent species composition, while the butterflies had a positive trend with species such as *Aglais urticae* and *Pieris napi* becoming more abundant. No significant effect of land use was identified for the pollinators of the local survey, although the floral abundance and plant species richness were significantly higher in the semi-natural grasslands. The bumblebees of the local survey exhibited clear flowering plant preferences. They primarily visited *Knautia arvensis* in the semi-natural grasslands and *Epilobium angustifolium* in the successional grasslands and interacted with more flowering plant species in the semi-natural grasslands. The great pollinator declines that have been observed globally were not detected in this study. This may be due to the warming climate improving the conditions for butterflies in this region and past bumblebee declines causing present-day species compositions to consist of more generalist species resistant to change. Future long-term studies should incorporate more detailed climatic data when addressing the pollinator variations among years, and the dynamics of flower choice among pollinators should be studied further.

Sammendrag

Pollinatorer er viktige i de fleste terrestriske økosystemer og deres nåværende tilbakegang er av stor bekymring. De store, naturlige svingningene til insektpollinatorene mellom år gjør det vanskelig å studere trendene deres via korttidsstudier alene. Det er derfor et sterkt behov for flere langvarige og kontinuerlige studier, samt økt kunnskap om pollinatorenes romlige og temporale variasjon. Endt skjøtsel av semi-naturlige gressletter, et viktig habitat for mange pollinatorer, medfører suksesjon av gresslettene som slik blir til suksesjonsgressletter, et habitat ofte sett på som mindre ideelt for de fleste pollinatorer. Kunnskap om pollinatorene i semi-naturlige- og suksesjonsgressletter, samt konkret data på hvilke blomsterplanter pollinatorene foretrekker i de to habitattypene er nyttig kunnskap for fremtidig konserveringsarbeid. I dette studiet undersøkte jeg: (1) den romlige og temporale trenden for humler og dagsommerfugler i gressletter på en regional skala over ni år, (2) antallet pollinatorer samt pollinator artsrikdommen i semi-naturlige- og suksesjonsgressletter over to år på en lokal skala, og (3) blomsterplantepreferansen til pollinatorer, her primært humler, i semi-naturlige- og suksesjonsgressletter på en lokal skala. Data samlet inn på en regional (Trøndelag fylke, Norge) og en lokal (Trondheim, en kommune i Trøndelag) skala ble brukt i dette studiet.

Artsrikdommen, artssammensetningen og antallet individer observert for humler og dagsommerfugler var signifikant forskjellig mellom de regionale studieområdene. Dette er trolig på grunn av forskjeller i områdenes egnethet som habitater for pollinatorene. Humlene i det regionale studiet hadde en stabil trend over årene med en tilsynelatende uendret artssammensetning. Sommerfuglene hadde en positiv trend der enkelte arter, slik som *Aglais urticae* and *Pieris napi*, har blitt mer tallrike. Ingen signifikant forskjell mellom de to typene gressletter be funnet for pollinatorene i det lokale studiet selv om artsrikdommen til blomsterplantene og antallet blomsterplanter observert var signifikant høyere i de semi-naturlige gresslettene. Humlene i det lokale studiet viste tydelige preferanser for enkelte blomsterplantearter. De besøkte primært *Knautia arvensis* i de semi-naturlige gresslettene, og *Epilobium angustifolium* i suksesjonsgresslettene. De besøkte generelt flere plantearter i de semi-naturlige gresslettene. Den store nedgangen i pollinatorer observert globalt ble ikke funnet i dette studiet. Dette kan være grunnet klimaendringer som har ført til bedre forhold for dagsommerfuglene i denne regionen, og tidligere humle tap som har resultert i mest motstandsdyktige generalister i de gjenværende samfunnene. Fremtidige langtidsstudier bør inkludere detaljert værdata når pollinatorenes variasjon mellom år undersøkes. Dynamikken rundt pollinatorenes blomstervalg bør studeres videre.

Preface

The regional dataset used in this thesis was provided by the Norwegian Institute of Nature Research (NINA), and the local data from 2020 was collected by previous master students, Hildegunn Heggøy and Ajay Dhukuchhu.

Acknowledgements

I would like to thank my supervisors Gunnar Austrheim and Frode Ødegaard for their continued support, guidance, and insightful feedback throughout this thesis work. Thanks to James Speed for his useful inputs and suggestions on the data analyses. I'd like to thank the brave souls who accompanied me in the field, facing off horses, cows, and sunburns. And with that, another thanks to Gunnar Austrheim for finding my datasheet in the field, three weeks after I lost it. I'd like to thank my family and friends for their support and encouragement. And lastly, thanks to my fellow master students for the company throughout this memorable journey, for the long tea breaks, and for helping me keep track of the days with the consistency of Friday cake.

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1. Introduction

The mutualistic interaction of animal-mediated pollination is an essential part of most terrestrial ecosystems (Kearns et al., 1998; Potts et al., 2010; IPBES, 2016; Wagner, 2020). In their search for pollen and nectar, pollinators move pollen grains between the flowering plants they visit. This movement-allows for the sexual reproduction of many angiosperms to occur, as pollen is moved from the anther of one individual to the stigma of another (Buchmann & Nabhan, 1996; Willmer, 2011). As such, pollinators provide the crucial ecosystem service of pollinating most of the worlds' food crop species and wild flowering plants (Kearns et al., 1998; Potts et al., 2010). Around 75% of the world's food crop species and around 35% of the world's food crop production depend on animal-mediated pollination (Klein et al., 2007; IPBES, 2016). Similarly, estimates suggests around 90% of the world's wild plant species depend on animal-mediated pollination (Buchmann & Nabhan, 1996), with the majority, 80%, depending on insect-mediated pollination (Potts et al., 2010).

It is well established that the worlds pollinators are under increasing threat, and many species and populations have noticeably declined in recent decades (Buchmann & Nabhan, 1996; Potts et al., 2010; IPBES, 2016; Wagner, 2020). These declines are likely caused by increased anthropogenic activities leading to habitat loss, climate change and competition from introduced alien species (Kearns et al., 1998; Potts et al., 2010; Vanbergen & Insect Pollinators Initiativ, 2013; IPBES, 2016; Wagner, 2020). Fewer pollinators may lead to pollen limitation, a condition where flowering plants do not receive enough pollen, leading to reduced seed production of the flowering plants (Buchmann & Nabhan, 1996; Knight et al., 2005). The loss of the important ecosystem services provided by pollinators will likely have far-reaching consequences for both agricultural and natural ecosystems (Kearns et al., 1998; Potts et al., 2010; Vanbergen & Insect Pollinators Initiativ, 2013; IPBES, 2016).

Despite being well established, present pollinator declines are poorly understood, and year-to-year decadal data is sorely lacking (Wagner, 2020). Continued research on the spatiotemporal dynamics of pollinators at different geographical scales is needed, along with increased knowledge on pollinators flowering plant preferences and the potential changes in their species composition following their current declines.

1.1. Pollinators

Pollinating species are found among birds, mammals, and insects. Although some birds and mammals are significant pollinators, primarily in tropical regions, insects are by far the most important (Potts et al., 2010; Willmer, 2011). In northern ecosystems, insects are the only pollinators present and flowering plants are therefore especially dependent on them for their sexual reproduction in this region (Totland et al., 2013).

Insect abundance is known to fluctuate a lot among years. With their high reproductive ability and short generation time, most insects are able to respond quickly to favorable weather and resource conditions (Totland et al., 2013). Such fluctuations among years makes it difficult to study their overall trends from short term studies alone. Longer time scales are often needed in order to distinguish the natural fluctuations from the overall trends (Wagner, 2020).

A great decline of insects has been observed in recent decades (Wagner, 2020), with studies such as Hallmann et al. (2017) having found a 75% decrease in insect biomass over the last three decades in northwest Germany. Land use changes and agricultural intensification are considered primary drivers of these declines. As vast areas have been fragmented, abandoned, or transformed into monocultural landscapes, the habitat availability and floral resources of many pollinating insects have greatly been reduced (Kearns et al., 1998; Potts et al., 2010; IPBES, 2016; Wagner, 2020). Climate change is also a strong driver of these declines with increased precipitation and extreme weather events negatively impacting the insects and their floral resources (Wagner, 2020). In response to current climate change, altitudinal and longitudinal range shifts have been observed among multiple pollinator groups such as the bumblebees and butterflies (IPBES, 2016; Biella et al., 2017)

Of the worlds pollinating insects, the majority belongs to the orders Hymenoptera, Lepidoptera, Diptera and Coleoptera (Kearns et al., 1998; Totland et al., 2013). Bumblebees of the order Hymenoptera and butterflies of the order Lepidoptera are two of the most distinguishable and easily recognizable groups of pollinators.

1.1.1. Bees and bumblebees

Bees (Apoidea) are important and effective pollinators of the order Hymenoptera (Goulson, 2010; Willmer, 2011; Totland et al., 2013). Most bees are highly dependent on both pollen and nectar for their survival and are therefore frequent visitors of flowering plants (Willmer, 2011; Totland et al., 2013). They often have a dense hairy coat which makes them excellent pollen transporters (Totland et al., 2013). Bees are especially important pollinators in northern ecosystems where few other insects are as effective pollinators as them (Totland et al., 2013).

Bees may be sorted into two main categories: solitary bees and social bees. Although solitary bees are by far the most species rich, it is the social ones that are the most recognized (Goulson, 2010; Willmer, 2011). The social bees live in communities where the individual's behavior serves the community, while solitary bees live alone and serve themselves (Goulson, 2010; Totland et al., 2013). Solitary bees are often more specialized than the social ones, and they often rely on a shorter flight period that is synchronized with the flowering plants they are specialized to. The social bees, who are mainly generalist species, often have a longer flight period and rely on continuous access to flowering plants throughout the entire growing season (Totland et al., 2013).

Bumblebees (*Bombus*) are a particularly important and recognizable genus of the bees. Of the over 250 species of bumblebees found worldwide, 35 are found in Norway, 28 of which are social (Ødegaard et al., 2015). The social bumblebees follow an annual life cycle where the queens found nests in the spring and produce workers who provide for the colony until autumn where the workers, males and old queens die. Only fertilized females live until next summer where they found new nests (Goulson, 2010; Ødegaard et al., 2015).

Bumblebees are among the many pollinators that have been declining in recent decades (IPBES, 2016; Wagner, 2020). With current land use change, the bumblebees have lost suitable habitats and nesting areas along with the continuous supply of flowering plants they depend upon (Totland et al., 2013; Ødegaard et al., 2015). Climate change has also been found to negatively impact the bumblebees both directly, and indirectly through temporal changes in floral resource availability (Ogilvie et al., 2017; Soroye et al., 2020). Furthermore, changes in bumblebee species compositions have also been observed. The study by Bommarco et al. (2012) found a great decrease in bumblebee community evenness in Swedish red-clover fields over the last 70 years (Bommarco et al., 2012)

Negative trends of bumblebees have also been found in Norway with recent studies such as Fourcade et al. (2018) and Åström et al. (2021) having found evidence of bumblebee declines. Fourcade et al. (2018) found a negative trend for bumblebee species richness in low altitudinal sites in Norway. However, the overall trend was not negative, as the positive trend observed in the study's high altitudinal sites counteracted the negative trend found in the low altitudinal sites (Fourcade et al., 2018). Their findings are indicative of potential altitudinal range shift among bumblebees following current climate changes (Fourcade et al., 2018). Due to natural fluctuations of pollinator abundances among years, then-and-now comparisons, such as Fourcade et al. (2018), are subject to stochastic factors and long term continued research is therefore needed (Wagner, 2020). The ongoing survey on butterflies and bumblebees in Norway conducted by the Norwegian Institute for Nature Research (NINA) is one such continues study. In their most recent report, they found a slight negative trend for bumblebees in two out of three regions surveyed over the last 10 years (Åström et al., 2021).

1.1.2. Butterflies

Butterflies (Papilionoidea, Lepidoptera) are generally seen as poorer pollinators than bees and bumblebees (Totland et al., 2013). Butterflies do not depend on flowering plants for their survival in the same ways the bees do. As larvae they do not depend on either pollen or nectar as the bees, but instead feed upon the vegetative parts of the plants. Similarly, as adults the butterflies primarily feed on the nectar of the plants, and do not depend on pollen (Willmer, 2011; Totland et al., 2013). However, the butterflies still act as pollinators as pollen can sticks to their face and tongue as they visit different flowering plants (Willmer, 2011).

Great butterfly declines have been observed in many countries of Europe (IPBES, 2016; Wagner, 2020). A recent report on butterflies in Europe found grassland butterflies to have decreased in the last decades. Similarly, woodland butterflies were also found to have declined in the 1990's, but interestingly have increased again in the last decade (van Swaay et al., 2020). Similar inconsistencies are found in Norway, where the global trend of decreasing butterflies is not found. The recent report on the status of butterflies and bumblebees in Norway have found a positive trend of butterflies in the areas they've surveyed over the last 10 years (Åström et al., 2021).

1.1.3. Other pollinators

There is a multitude of other insects who visit flowering plants, some better pollinators than others. Some groups of flies (Diptera) and beetles (Coleoptera) are important and efficient pollinators, with some flowering plants relaying greatly on specific species of these groups (Willmer, 2011). Although beetles are important pollinators in some parts of the world, few species are considered important in Norway (Totland et al., 2013). Similarly, most flies in Norway are inefficient pollinators, however, some groups such as the hoverflies can be fairly important (Willmer, 2011; Totland et al., 2013). Other groups such as ants and stinging wasps, from the order Hymenoptera, are also not considered especially important pollinators. As such, most of these insects are inefficient pollinators who primarily visit plants with small open flowers with easily accessible nectar (Willmer, 2011; Totland et al., 2013). It is however worth noting that there are gaps in our knowledge on how most these groups function as pollinators, and some might be more important for pollination than what is currently known (Totland et al., 2013).

1.2. Plant-pollinator interactions

Pollinators rarely visit just one plant species, just as plants are rarely visited by just one pollinator species. This forms the basis of what can at times be quite complex networks of interactions. Most plant-pollinator interactions are generalized, meaning both plants and pollinators successfully interact with multiple species (Kearns et al., 1998; Potts et al., 2010; Totland et al., 2013). Despite this, there are some overarching trends of different pollinator groups preferring certain flowers over others. One example of this are the bumblebees. Although bumblebees are mostly generalists, they are found to mostly favour flowering plants with large flowers in the blue to purple and pink colour range, often with medium to long corolla tubes (Willmer, 2011).

The generalized interactions of plant-pollinator networks create redundancy within the networks. This may mitigate some of the consequences of current pollinator declines, as the loss of a few species would not be detrimental to the networks functionality (Potts et al., 2010). However, greater losses may result in networks that are more fragile and less resilient to further change (Burkle et al., 2013; Biella et al., 2020). Changes in pollinator species compositions are also found to alter the networks, and the loss of specialized species results in reduced redundancy within the networks (Burkle et al., 2013). Plant-pollinator networks, such as the plant-bee networks, can be very dynamic with seasonal shifts occurring throughout the year (Bendel et al., 2019), and current climate change can cause temporal mismatch among pollinators and the flowering plants they visit (Memmott et al., 2007; Hegland et al., 2009; Burkle et al., 2013).

In order to preserve the important ecosystem services provided by pollinators, and the many flowering plants they visit, management should focus on maintaining the stability and functionality of plant-pollinator networks. Efforts should be directed towards maintaining the species interactions, instead of protecting individual species (Kearns et al., 1998; Totland et al., 2013). Further knowledge on these interactions and the species within is therefore needed.

1.3. Semi-natural and successional grasslands

Semi-natural grasslands are mostly meadow like ecosystems, primarily formed through long-term low-intensity farming. The areas have often been cleared of its forest and used as pasture or hayfields, with little to no fertilizers having been applied to the soil (Hovstad et al., 2018). The grasslands are often species rich with a diverse flora that still rely on mowing or grazing by live stock in order to persist (Bullock et al., 2011; Hovstad et al., 2018). Similar to the pollinators, the flowering of these plants may vary among years in response to different weather conditions along with the natural variations in floral phenology (Willmer, 2011).

Semi-natural grasslands are often found to act as a source of pollinators to surrounding areas such as crop fields (Klein et al., 2007; Öckinger & Smith, 2007; Magrach et al., 2018). The species rich flora of the grasslands provides pollinators with a wide supply of resources throughout the growing season. The grasslands also provide suitable nest sites for nesting pollinators, such as bumblebees, and are generally seen as important habitats for many pollinators (Öckinger & Smith, 2007; Totland et al., 2013; Ødegaard et al., 2015; IPBES, 2016). Providing our crops with pollinators is one of the many ecosystem services provided by these grasslands, along with carbon storage, water cycling, education, and inspiration (Török et al., 2018; Nowak-Olejnik et al., 2020).

There has been a rapid loss of these grasslands in Europe over the last century, and the grasslands are classified as a vulnerable habitat type in Norway (Vessby et al., 2002; Johansson et al., 2008; Janišová et al., 2014; Hovstad et al., 2018; Török et al., 2018). Recent changes in landscape management and agricultural practices have led to many semi-natural grasslands being transformed into crop fields or forest plantations. Many have also been abandoned, and most of the remaining grasslands have been heavily fragmented (Johansson et al., 2011; Török et al., 2018).

The abandoned grasslands are left to the effects of succession where new plant species outcompete the old. The shade-intolerant, low-growing species that originally constitute the flora of most semi-natural grasslands are outcompeted by taller more competitive species (Bohner et al., 2020). The new species alter the habitat and make it less suitable for the original flowering plants. As management seizes, the grasslands are slowly replaced by scrubs and secondary forest as woody plants establish, and the grasslands lose much of its former species rich flora (Johansson et al., 2011; Török et al., 2018; Bohner et al., 2020).

Multiple studies have found managed semi-natural grasslands to have a higher floral species richness than abandoned ones (Pykälä et al., 2005; Johansson et al., 2011; Johansen et al., 2019; Bohner et al., 2020). With a reduced floral species richness follows a reduction in the continuous and overlapping supply of floral resources many pollinators rely upon (Totland et al., 2013; Ødegaard et al., 2015). The current loss of semi-natural grasslands is an essential driver of the observed declines of many pollinator groups (IPBES, 2016; Walcher et al., 2017; van Swaay et al., 2020).

Loss of important habitats such as the semi-natural grasslands are of great conservational concern. The steady decline of this habitat, along with the important ecosystem services they provide, are worrisome. Research on the flora of these grasslands, along with the plant-pollinator interactions that occur in both managed and abandoned grasslands may be beneficial to further understand the effects and consequences abandonment may have on these important grasslands.

1.4. Aims and hypotheses

This study aims to examine the temporal and spatial trends of pollinator abundance, species richness and composition, as well as their flowering plant preferences. Primarily focusing on bumblebees and butterflies in grassland ecosystems, the objective of this thesis is to answer the research questions (1) How does pollinator abundance, species richness and species composition vary with space and time? (2) How does pollinator abundance and species richness differ between semi-natural and successional grasslands? And finally, (3) what flowering plants does the pollinators prefer?

Åström et al. (2021) have already identified a slight negative trend for bumblebees, and a positive trend for butterflies in Trøndelag, Norway. Their data was here used to further analyse these observed trends on a regional scale and identify potential effects of space on the pollinator's abundance and species richness (1). As some pollinators are more resilient to current habitat declines and climate change than others, pollinators species compositions may be changing (Potts et al., 2010; Bommarco et al., 2012; Fourcade et al., 2018). Here, the species composition of butterflies and bumblebees were analysed in more detail and potential factors affecting the compositions were explored (1).

Data from another survey conducted in Trondheim, a municipality in Trøndelag, was used to analyse pollinator abundance and species richness on a local scale. The effects of semi-natural and successional grasslands on the pollinators abundance and species richness were explored (2). Although it is well documented that some pollinators prefer certain flowering plants over others (Kearns et al., 1998; Willmer, 2011), detailed knowledge on what specific species the pollinators prefer is lacking. In this study we looked further into these preferences in an attempt to identify what flowering plants are especially favored by the pollinators in semi-natural and successional grasslands in Trondheim, and to get an overview of which flowering plants may be particularly important in these habitat types (3).

2. Methods

Two different datasets were used in this study. The first dataset, referred to as the regional data, consist of bumblebee and butterfly data sampled over nine years in 11 grasslands in Trøndelag county, Norway (Appendix A). The second dataset, referred to as the local data, consists of plant and pollinator data sampled over two years in 12 grasslands in Trondheim municipality, Trøndelag county (Appendix A).

2.1. The regional data

The regional data is a subsample of data collected by the Norwegian Institute of Nature Research (NINA). Using citizen scientists, NINA have collected butterfly and bumblebee data from multiple sites in non-alpine areas from three regions in Norway since 2009. This has been done as part of the national survey of butterflies and bumblebees in Norway, conducted by NINA on behalf of the Norwegian Environment Agency. In this study the data has been limited to grassland sites in Trøndelag county which have been consistently surveyed since 2012. The data was cleaned up and sorted using the R script provided by NINA (Åström & Åström, 2021).

The method of data collection used in the local survey is heavily inspired by the methods used by NINA, with the study design intended to be a replicate of their design. Despite this, there are some important differences between the two data sets. The primary difference is that the NINA data has been collected over three rounds each summer with 20 transects used per site, as compared to four rounds and five transects per site used in the local survey. Another relevant difference is the measure of flower cover in the regional dataset on a scale from 0 to 3, with 0 being no flower cover and 3 a high flower cover, as compared to the recorded flowering plant abundance and species identification in the local survey. Further details on the sites and methods used for local data sampling is given in the following subsections.

2.2. The local study sites

The local survey was conducted in Trondheim municipality in Trøndelag county, Norway (63°26′24″N 10°24′0″E). Trondheim is located in central Norway, close to the Norwegian Sea, and is classified as the fourth largest city in the country (Statistisk sentralbyrå, 2021). The municipality is primarily located in the Southern Boral Zone and is in the Slightly Oceanic Section (Moen, 1999).

The urban areas of the municipality consist of multiple grasslands of open firm ground and infield grazing, as classified in the Area Resource Map (AR5). These grasslands were further mapped and classified into different land-use categories by Kleppe (2019). Her categorizations and AR5 map was used by Heggøy (2021) and Dhukuchhu (2021) as the basis of their site selections. Using stratified random sampling, they selected 12 grasslands previously identified as either successional or semi-natural grasslands by Kleppe (2019). The criteria they used for sites were that the grasslands had to be large enough to encompass five transects at 50x5 meters with a five meters distance between them, including a 10 meters distance from the transects edge to the site edge. Heggøy (2021) and Dhukuchhu (2021) collected plant and pollinator data from the 12 field sites for their studies on pollinators in urban grasslands in the summer of 2020. Their sampling method was replicated the following year for this study.

Of the 12 sites, six are classified as successional grasslands and six as semi-natural grasslands (Kleppe, 2019). The size of the grasslands varied between 9 155-167 791 m^2 for the semi-natural grasslands and 18 218-47 494 m^2 for the successional grasslands (Heggøy, 2021). The grasslands studied are located throughout the urban and suburban areas of Trondheim (Figure 2.1). The surrounding landscape of these grasslands consists of built-up areas including roads and buildings, agricultural areas with fields as well as forest areas and other grasslands. As the municipality is primarily located in the Southern Boral Zone so are the majority of the sites, however two of the study sites identified as Lian Upper and Lian Lower are located at the border between the Southern Boreal Zone and the Middle Boreal Zone (Moen, 1999).

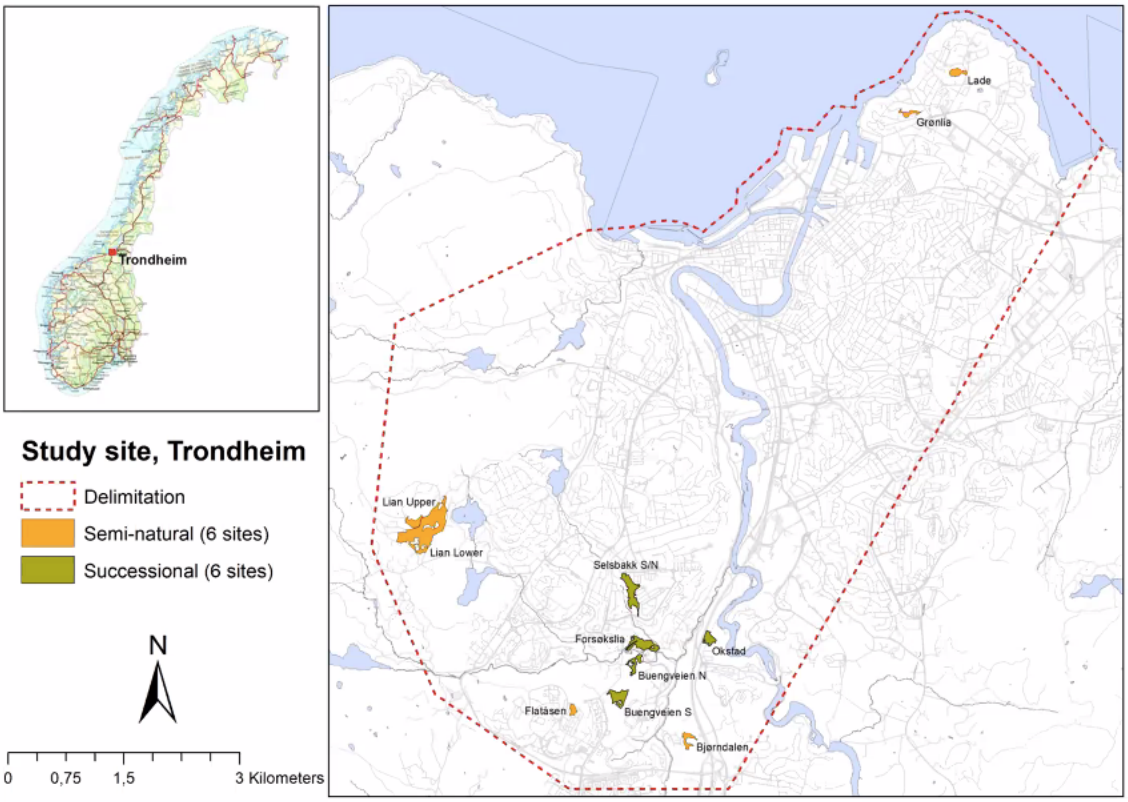

Figure 2.1: The selected semi-natural (yellow) and successional (green) grasslands of the local survey in Trondheim municipality, Norway. The delimitation line represents the border of the selected area in Kleppe (2019). (From: Heggøy (2021)).

2.3. The local fieldwork

The local fieldwork and data collection was conducted in the summer of 2020 and 2021. Five transects (50x5m) were established within each study site in 2020 by Heggøy (2021) and Dhukuchhu (2021). Using GPS coordinates for each transect, the same transects were visited in 2021 (Appendix A). Each year the data was collected by carrying out four replicates spanning the summer months from early to late summer. The first replicates were conducted in late May to early June, the seconds in late June to early July, the third in late July and the fourth and final in early August. All surveys were conducted on sunny to partly sunny days with a temperature no lower than 10˚C in May and 15˚C in the remaining summer months.

Data from each grassland was collected along the five established transects. Temperature and cloud cover was registered at the start of the data collection for each transect. Pollinators were recorded while walking along the transect, noting all pollinators observed at either side of the transect, 2.5 meters from the centerline. Herb species in bloom weas recorded when they occurred within a quadratic frame placed at every 10-meter interval of the transect (Figure 2.2).

Different fieldworkers conducted the data sampling in the summer of 2020 and 2021. To account for this, the fieldworkers of 2020 accompanied the fieldworkers of 2021 for the first survey of 2021 to demonstrate and conveyed methods of data collection and identification. Both years used the same standardized protocol and registration form to register plants and pollinators in the field (Appendix B).

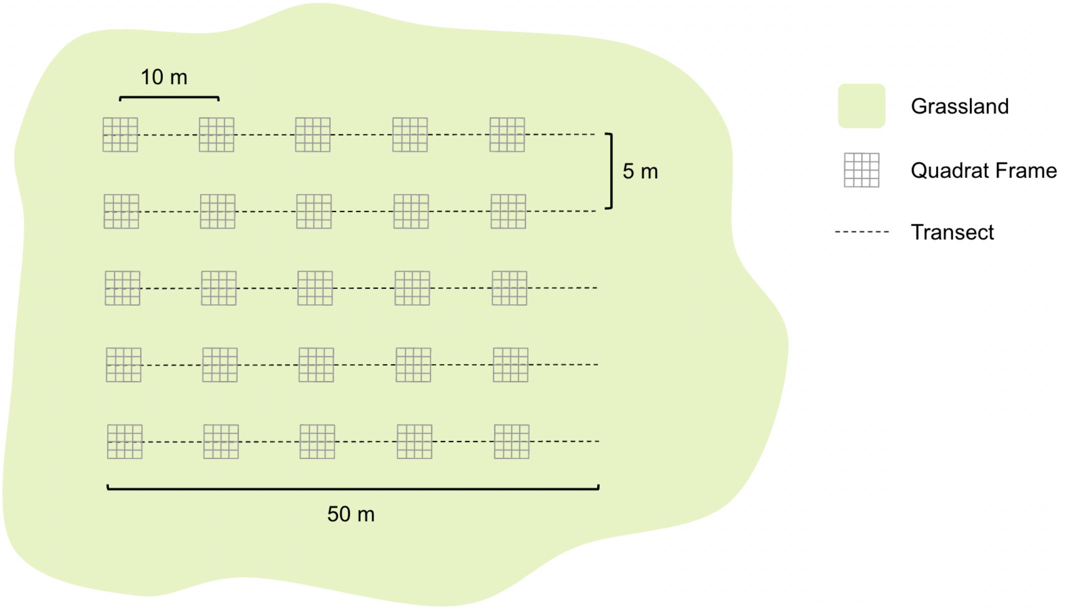

Figure 2.2: The study design of the local survey with the transects (dashed line) and quadratic frames (squares) in a grassland site.

2.3.1. Pollinator recordings

The pollinator data was acquired through registration of the pollinators observed when walking along each transects. The observations were limited to span 2.5 meters from either side of the mid-line of the transects. The time spent walking and recording along each transect was noted. Bumblebees and butterflies were identified to species level, with some exceptions. Bumblebee species that in general are hard to distinguish in the field such as *Bombus sensu stricto* and *Bombus* sg. *Psithyrus* were grouped in these higher orders and not identified to the species level. At times where bumblebees or butterflies passed by the transects too fast for identification to be done at the species level, they were recorded to the lowest possible taxonomic rank. Other taxa of pollinators such as stinging wasps, wild bees, honeybees, and hoverflies were only registered at this taxonomic level. Interactions between flowering plants and pollinators were also recorded with the pollinators and flowering plant species in question noted. Pollinators seen as more occasional and inefficient pollinators such as beetles and flies were only recorded when observed interacting with flowering plants.

A sweep net was used to capture any individuals difficult to identify. Bumblebees were placed in a glass vial for closer inspection (Figure 2.3). Pictures were taken of the individuals for later identification before they were released when identification was not possible in the field. Individuals especially difficult to identify were euthanized by freezing and identified in the lab. Only workers and male bumblebees were euthanized in this study.

Figure 2.3: Photo of a captured bumblebee placed in a glass vial for closer inspection and identification. Quadrat frame in the background. (Photo: R. Straume).

2.3.2. Flowering plant recordings

A quadratic frame, measuring 0.5x0.5 meters and containing 4x4 sub-quadrates, were used for the plant registration. The quadratic frame was placed at every 10-meter interval along the transects making up five subplots for every transect. Herb species in bloom occurring within the quadratic frames were identified and recorded. The flowering plants were counted as one observation for every subquadrate it occurred in. The flowering plants were identified to the species level with some exceptions where the individuals were identified to the genus level instead. All individuals belonging to the genus *Alchemilla* were noted as *Alchemilla vulgaris*. The vegetation height of every subplot was measured and recorded.

2.4. Statistical analyses

The statistical analysis of the data was performed using R, version 4.1.2 in R studio (R Core Team, 2021; RStudio, 2022). Base R and “ggplot2” was used to visualize the data (Wickham, 2016). Generalized linear models were used to analyse the effect of year and site on species richness and abundance for bumblebees and butterflies of the regional data (Venables & Ripley, 2002; R Core Team, 2021). Normal, Negative binomial and Poisson error distributions was used when appropriate, determined by the residual error distribution as well as the dispersion parameters. The package “MASS” was used with the function *glm.nb* for the models with negative binomial distribution (Venables. & Ripley. 2002). The corrected Akaike information criterion (AICc) was used to identify the model best fit for the data using the package “AICcmodavg” (Mazerolle, 2020). The same approach was used for the analysis of the local data. Here, the effect of year and land use system on pollinator abundances and species richness, as well as on floral species richness, Shannon diversity index and abundance were analysed. The Shannon diversity index was calculated using the “vegan” package (Oksanen et al., 2020).

The regional and local data was primarily analysed separately. However, a mean, Standard Error (SE) and Coefficient of Variance (CV) was calculated on transect level for both datasets. An asymptotic test for the equality of the CV of the two datasets were performed using the "cvequality" package, to determine if there were significant differences in the spread of the two data sets (Feltz and Miller, 1996; Marwick & Krishnamoorthy, 2019).

A non-metric multidimensional scaling (NMDS) was performed on the regional data of bumblebees and butterflies to investigate the differences in their species composition among sites and year. The ordination plots were constructed using the function *metaMDS* and *ordiplot* from the “vegan” package (Oksanen et al., 2020). Vectors visualising the effect of year, flower cover and temperature were constructed using *envifit*, and *adonis* was used to perform permutational multivariate analyses of variance (PERMANOVA) to identify the effect of these variables on the species composition. Both functions are from the “vegan” package (Oksanen et al., 2020).

Plant-pollinator interactions of the local data was visualized by ranking the flowering plants by their abundance and plotting the number of the observed plant-bumblebee interactions per species atop this. The plant-pollinator interactions of both bumblebee species alone as well as a higher taxonomic grouping of the pollinators was further visualized by constructing plant-pollinator networks using the function *plotweb* from the package "bipartite" (Dormann et al., 2008).

3. Results

3.1. Regional pollinator abundance and species richness

The mean abundance and species richness of bumblebees per site across all years and seasons were found to be 52.687 ± 4.719 and 5.253 ± 0.181 respectively, at the regional scale (Figure 3.1). Site was found to be of greater importance for both bumblebee abundance and species richness than year, with models containing site as the only explanatory variable being those best fit for the data (Appendix C). The models with year as an explanatory variable were not only a poorer fit for the data, but the effect of year was also not significant on either bumblebee abundance or species richness (1.000, $p = 0.993$; -0.053, $p = 0.381$, respectively).

The mean abundance and richness of butterflies per site across all years were found to be 13.535 ± 1.689 and 3.020 ± 0.246 respectively, for the regional data (Figure 3.1). Site and year were both found to have a significant effect on butterfly abundance and species richness. The models containing both year and site as explanatory variables had the lowest AIC and was therefore determined to be the best model for the data (Appendix C). A slight positive trend across the years was found for butterfly abundance and species richness (1.235, $p < 0.001$; 1.176, $p < 0.001$, respectively). This trend also remained when accounting for the potential effect of the immigrating species *Vanessa cardui* who invaded Norway in 2019. When the species was removed from the dataset the trend remained mostly the same (1.206, $p < 0.001$; 1.165, $p < 0.001$, respectively).

Mean abundance and species richness was calculated on the transect level for the local and regional data, and the standard error and Coefficient of Variance (CV) was further calculated (Table A.7, Appendix A). Through the asymptotic test the CV of the two datasets were found to be significantly different for bumblebee and butterfly species richness (D'AD = 4.432, $p = 0.035$; D'AD = 13.273, $p < 0.001$, respectively), but not for bumblebee or butterfly abundance (D'AD = 2.204, $p = 0.138$; D'AD = 2.606, $p = 0.106$, respectively).

Figure 3.1: Mean and standard error of the butterfly (red) and bumblebee (yellow) abundance (a) and species richness (b) observed in the regional sites during the nine years of the survey. The dashed lines represent the grand mean.

The mean abundance of each species observed in the regional sites were calculated across all sites and years (Appendix A). The species composition of bumblebees and butterflies across the years was visualized by plotting the five most abundant species form each group (Figure 3.2). An NMDS ordination plot was constructed for the two pollinator groups (Figure 3.3). The ordination plot of the bumblebee species composition had a stress of 0.170, and the ordination plot of the butterfly species composition had a stress of 0.154 (Appendix D).

Site was found to have the greatest effect on bumblebee species composition ($F = 5.13$, $r^2 = 0.362$, $p = 0.001$), and flower cover was also found to have a significant effect ($F = 2.941$, $r^2 = 0.021$, $p = 0.006$). No significant effect of temperature on bumblebee species composition was found ($F = 0.905$, $r^2 = 0.01$, $p = 0.490$), and year had almost a significant effect ($F = 1.774$, $r^2 = 0.013$, $p = 0.066$). Both year and site were found to have a significant effect on the butterfly species composition ($F = 6.165$, $r^2 = 0.056$, $p = 0.001$; $F = 2.832$, $r^2 = 0.256$, $p = 0.001$, respectively). Flower cover was not found to significantly affect the butterfly species composition (F = 1.407, $r^2 = 0.013$, p = 0.169), while temperature almost had a significant effect (F = 1.816, $r^2 = 0.016$, p = 0.053).

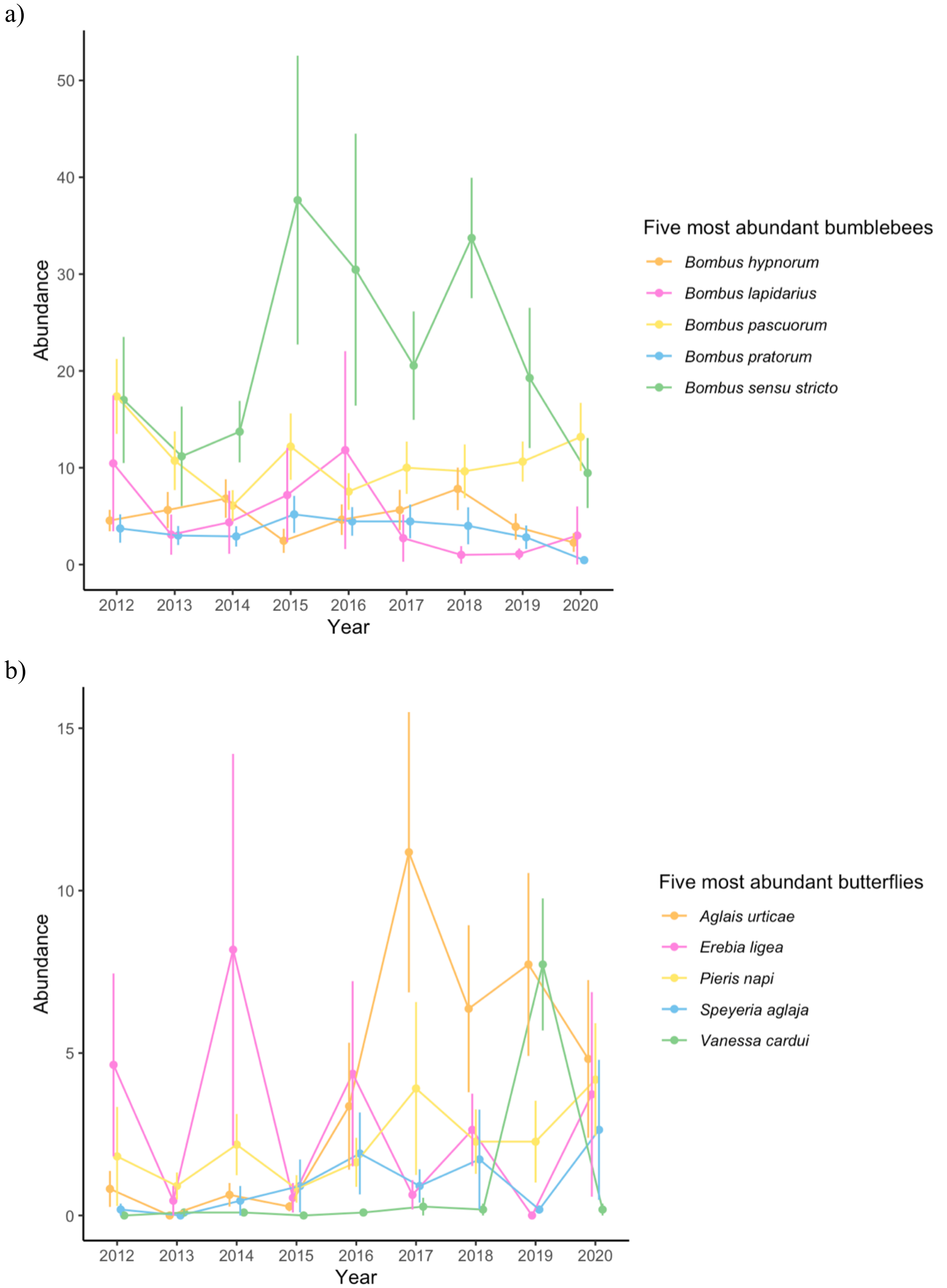

Figure 3.2: Mean abundance and standard error of the five most abundant bumblebee (a) and butterfly (b) species observed in the regional sites during the nine years of the survey.

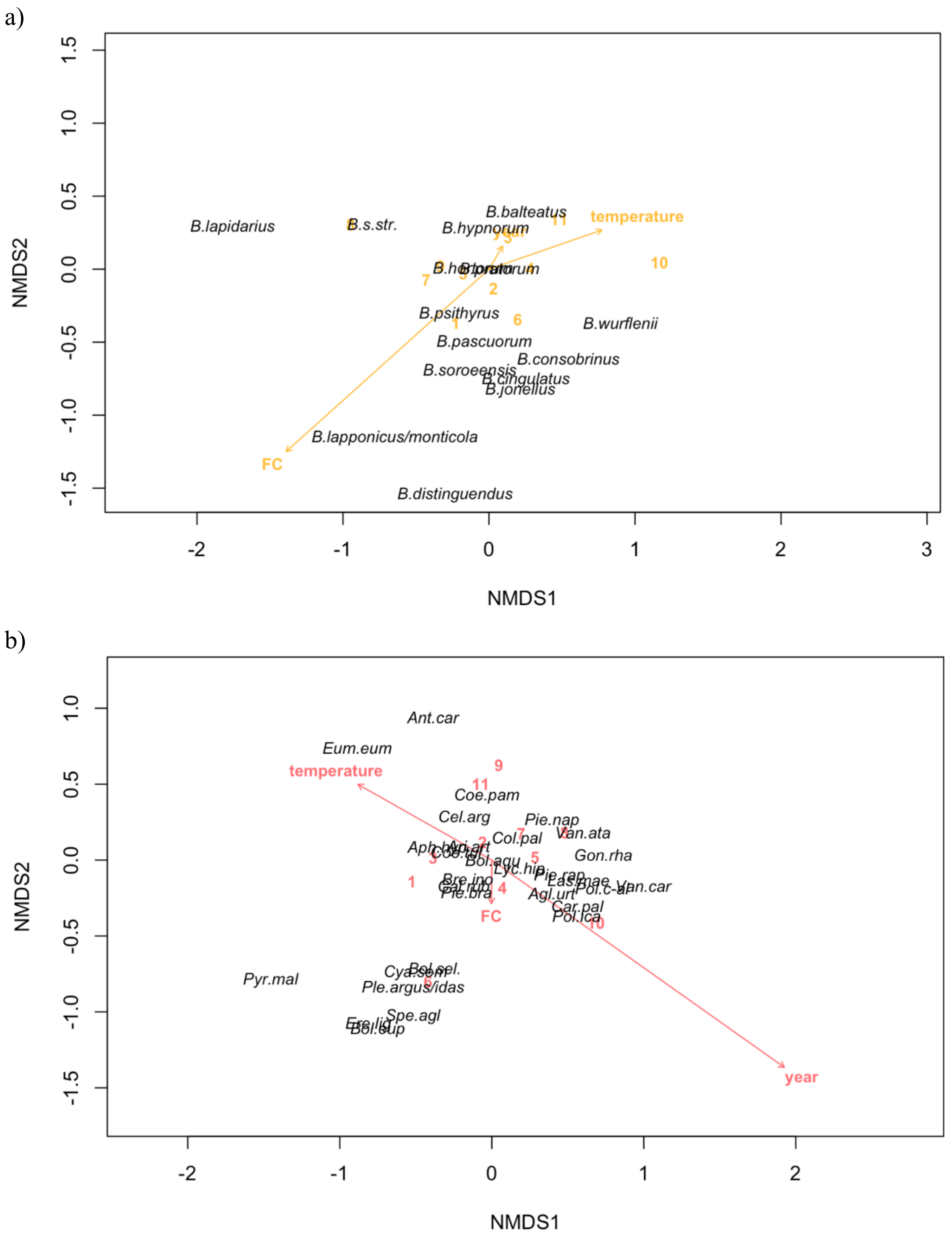

Figure 3.3: Ordination plot of the bumblebee (a) and butterfly (b) species composition in the regional sites along a non-metric multidimensional scaling (NMDS) with axis 1(MDS1) and 2 (MDS2). The vectors indicate the effect of the mean temperature (a: $r^2 = 0.030$; b: $r^2 = 0.037$), and flower cover (FC) (a: $r^2 = 0.155$; b: $r^2 = 0.003$) for each site each year as well as the effect of year on the species compositions (a: $r^2 = 0.002$; b: $r^2 = 0.202$). *B. pratorum* and *B. hortorum* overlapping in the centre (a). *Bol.eup, Ere.lig,* and *Bol.sel, Cya.sem* are overlapping bottom left (b). *Aph.hyp, Ari.art, Coe.tul, Pie.rap, Lyc.hip, Las.mae, Pol.c-al* and *Van.car* are overlapping in the centre (b). (The sites are 1: Agle, 2: Binde, 3: Lakketariusvollen, 4: Namdalseid, 5: Namsskogan, 6: Odden, 7: Rinnan, 8: Småland, 9: Sorgenfri, 10: Sparbu, 11: Vuku).

3.2. Local pollinator abundance and species richness

A total of 1447 bumblebees were observed in the local survey, 706 in 2020 and 741 in 2021. The mean abundance and species richness of bumblebees per site across the years and seasons were found to be 60.292 ± 12.024 and 5 ± 0.351, respectively (Figure 3.4 and 3.5). Bumblebee abundance was not found to be significantly affected by year or land use, with the best model being determined by the AIC to be the one without either as explanatory variables (Appendix C). Similarly, bumblebee species richness was not found to be significantly affected by year or land use. Although land use was included in the final model it was not found to significantly affect the species richness (-1.167, p = 0.097) (Appendix C).

106 butterflies were observed in the local survey, 44 in 2020 and 62 in 2021. The mean abundance and species richness of butterflies per site across the years and seasons were found to be 4.417 ± 0.944 and 1.792 ± 0.190, respectively (Figure 3.4 and 3.5). Butterfly species richness was not found to be significantly affected by land use or year, and the best models were also here determined to be those without either as explanatory variables (Appendix C). The best model for the butterfly abundance included land use as an explanatory variable but not year, and land use was not found to significantly affect the butterfly abundance (-0.514, p = 0.076) (Appendix C).

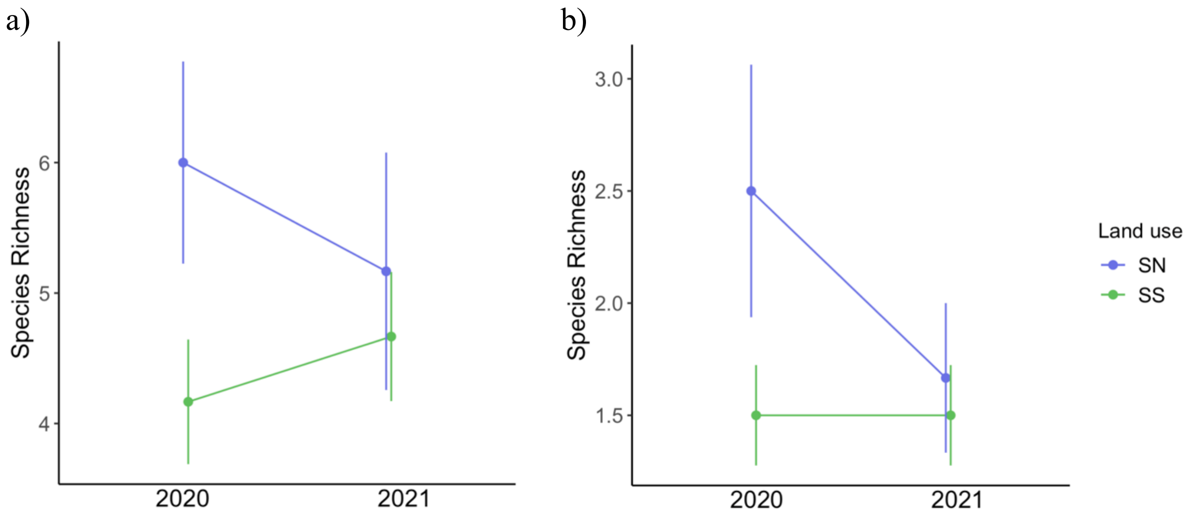

Figure 3.4. Mean and standard error of the bumblebee (a) and butterfly (b) species richness in the semi-natural (SN) and successional (SS) grasslands observed at the local sites in the two years of the survey.

Of the higher order pollinator groups recorded at the local sites, some groups had markedly different abundances in the two years (Figure 3.5). In 2020, 504 honeybees were observed, roughly three times more than the 185 observed in 2021. While there were a lot more honeybees observed in 2020 than 2021, the opposite was found for the flies. In 2020, 42 hoverflies were observed, this number was ten times higher in 2021 when 416 hoverflies were observed. Similarly, 128 flies grouped as “other flies” were observed in 2020 whilst 610 were observed in 2021, 5 times more than the year prior.

The models testing for the effect of land use and year on the higher order grouping of pollinators found no significant effect of land use. There was however a positive effect of year on the abundance (1.914, p = 0.020). Bumblebees and butterflies were excluded in the model, and the model determined to best fit the data was the one with only year as the explanatory variables (Appendix C).

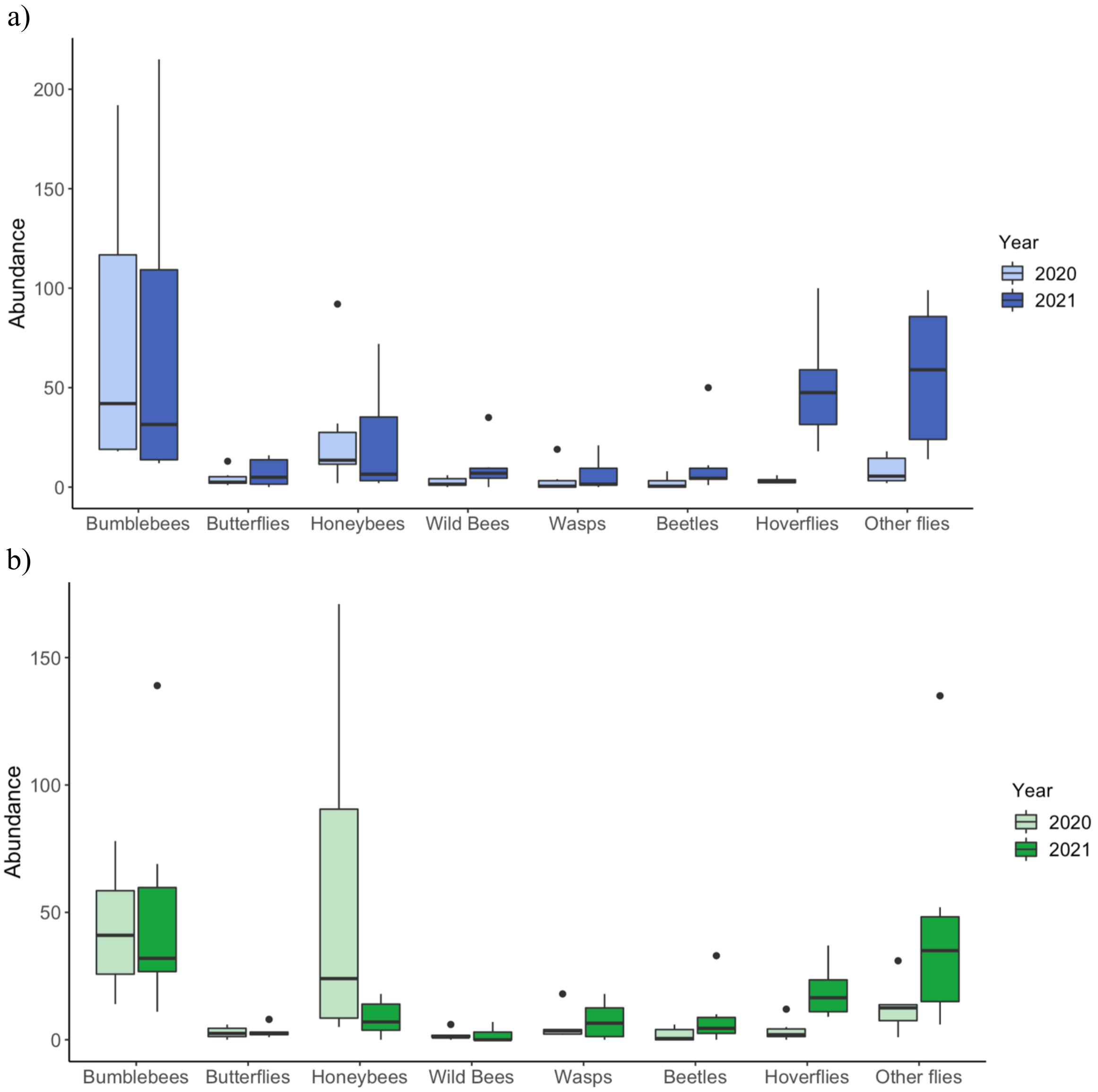

Figure 3.5: Abundance of the higher order pollinator groups in the semi-natural (a) and successional (b) grasslands observed at the local sites in the two years (2020 = lighter colours, 2021 = darker colours) of the survey. The horizontal lines represent the median, the boxes the upper and lower quartiles, and the whiskers the variability of the data.

3.3. Local plant-pollinator interactions

A total of 65 flowering plant species were observed in the local survey conducted in Trondheim overt the two years, 48 of these were observed interacting with pollinators (Appendix A). The AICc was used to determine the best models for flowering plant abundance, species richness and Shannon diversity index (Appendix C). The floral abundance, species richness and Shannon diversity index were all significantly higher in the semi-natural grasslands than in the successional ones (-266.17, $p < 0,001$; -8.500, $p < 0,001$; -0.4149, $p = 0.002$, respectively) (Figure 3.6). Year was found to have negative effect on both floral abundance and the Shannon diversity index (-266.17, $p = 0.015$; -0.2501, $p = 0.046$, respectively). The floral species richness was not found to be significantly different between the two years.

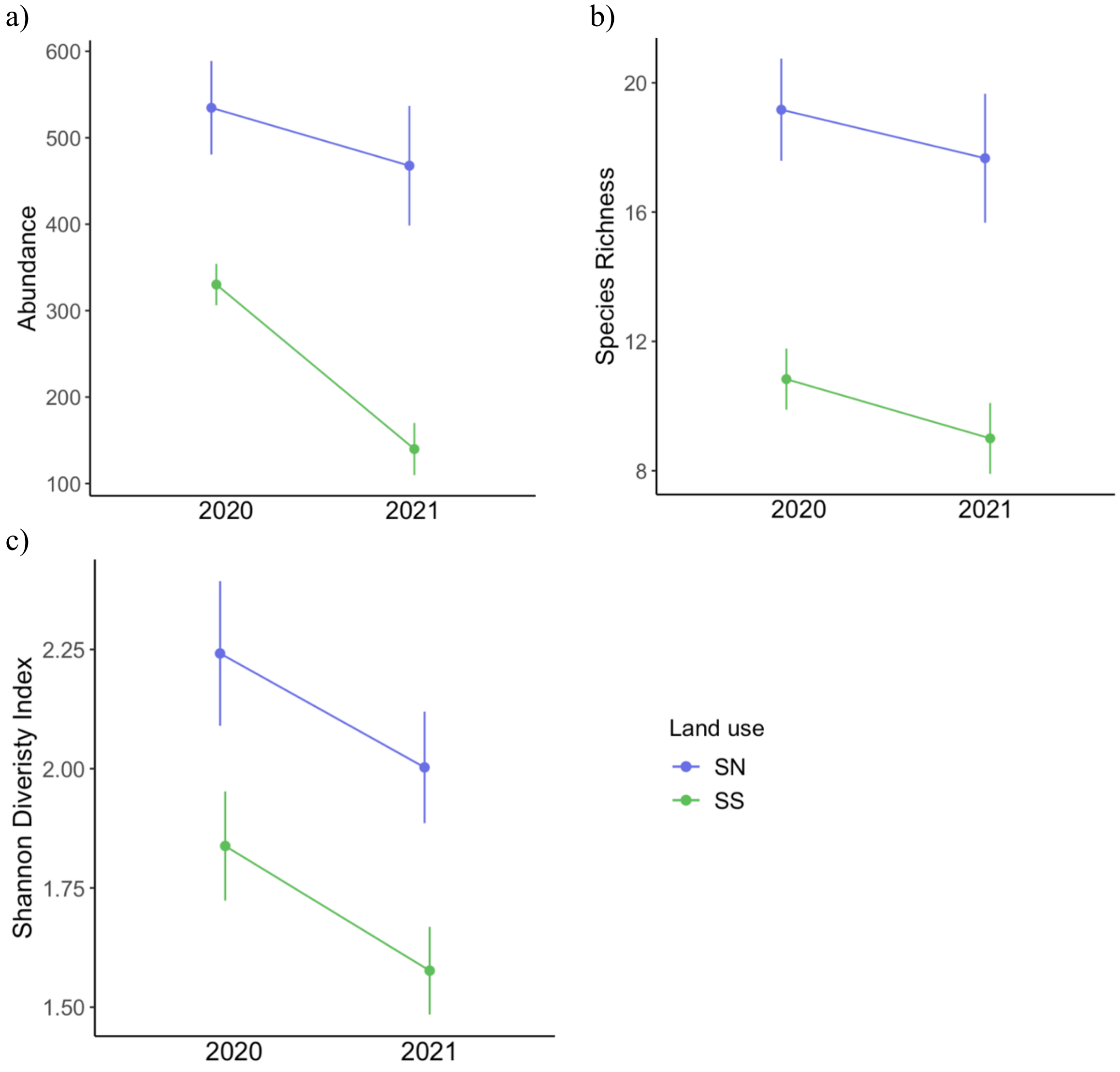

Figure 3.6 Mean and standard error of the flowering plant abundance (a), species richness (b) and Shannon diversity index (c) in the successional (SS) and semi-natural (SN) grasslands observed at the local sites in the two years of the survey

Of the 106 butterflies observed in the local study, only 13 were observed interacting with flowering plants, 4 in 2020 and 9 in 2021. Due to the low number of butterflies and plant-butterfly interactions observed, no further analyses were performed on the plant-butterfly interactions.

Of the 1447 bumblebees observed in the local study, 1263 were observed in interaction with flowering plants, 650 in 2020 and 613 in 2021. The bumblebee-flowering plant interactions from the two grassland systems were plotted with the flowering plant species ranked in order of their abundance (Figure 3.7 and 3.8). The percentage of bumblebee visits of each flowering plant from the total number of visits observed across both years for each land use system was calculated (Table A.6, Appendix A). The five most visited flowering plants in the semi-natural grasslands were *Knautia arvensis* (35.04%), *Campanula rotundifolia* (6.78%), *Epilobium angustifolium* (8.18%), *Trifolium pratense* (8.18%), and *Hieracium* sp. (9.21%), and the five most visited flowering plants in the successional grasslands were *Epilobium angustifolium* (67.98%), *Hieracium* sp. (9.15%), *Lathyrus pratensis* (7.07%), *Cirsium arvense* (6.86%), and *Trifolium pratense* (1.66%).

A full plant-pollinator network for the different bumblebee species were constructed for the different years and land use types (Appendix E). Of these, the networks in the semi-natural grasslands appeared to be more complex with more interacting species than what was observed in the successional grasslands. Similarly, a plant-pollinator network of the higher order grouping of the pollinators were also constructed (Appendix E), and these too appeared more complex in the semi-natural grasslands as compared to the successional grasslands.

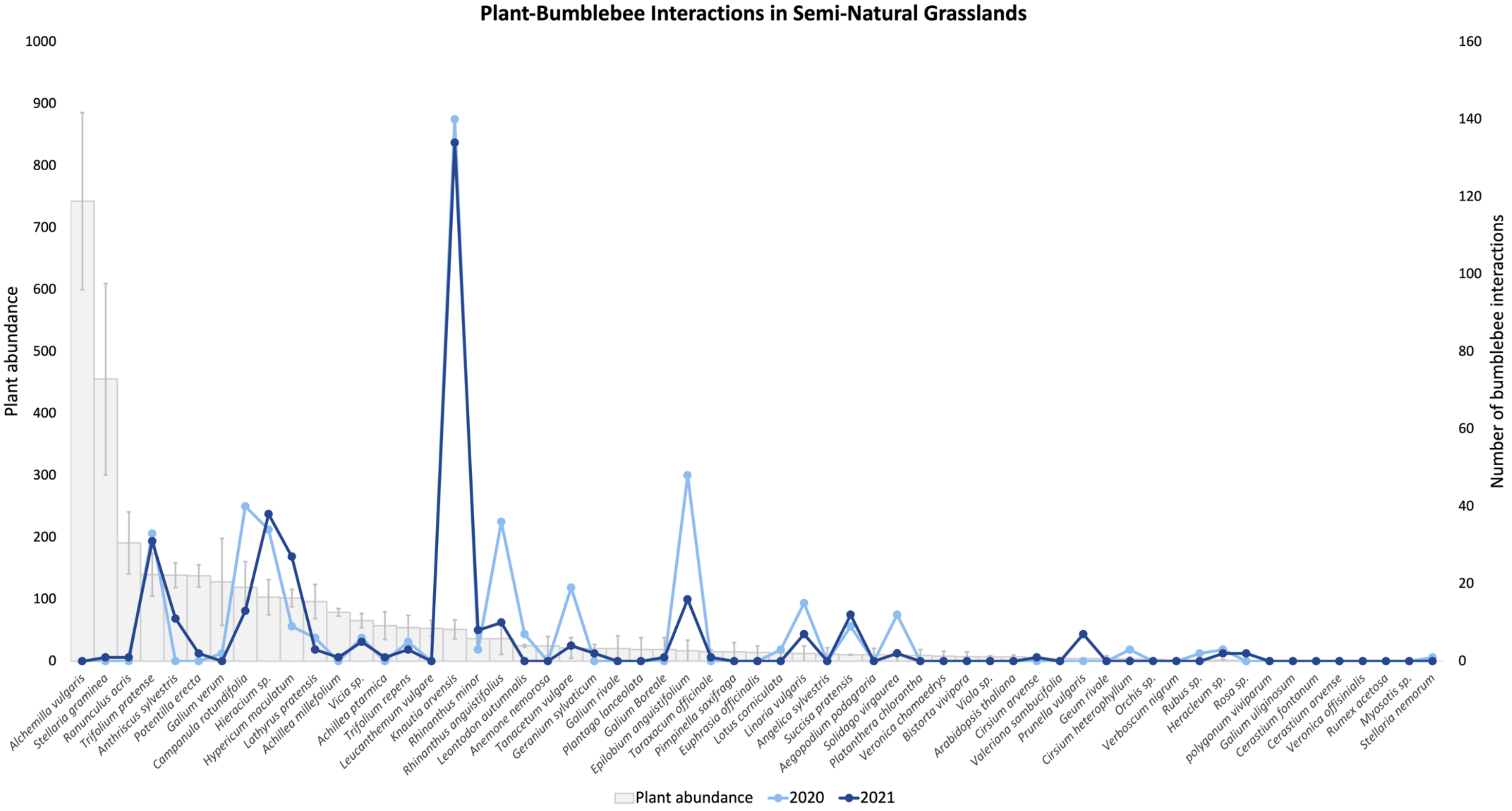

Figure 3.7: Plant-Bumblebee interactions in semi-natural grasslands. Mean and standard error of the total flowering plant abundance for the two year of the local survey is given for each flowering plant species present (grey bars), with the left y-axis denoting the plant abundance. The total number of observed bumblebee interactions per flowering plant species in 2020 (light blue) and 2021 (dark blue) is given with the right y-axis denoting the total number of interactions observed. The flowering plants are listed in order of abundance with the most abundant species being at the left end of the x-axis and the least abundant at the right end of the x-axis.

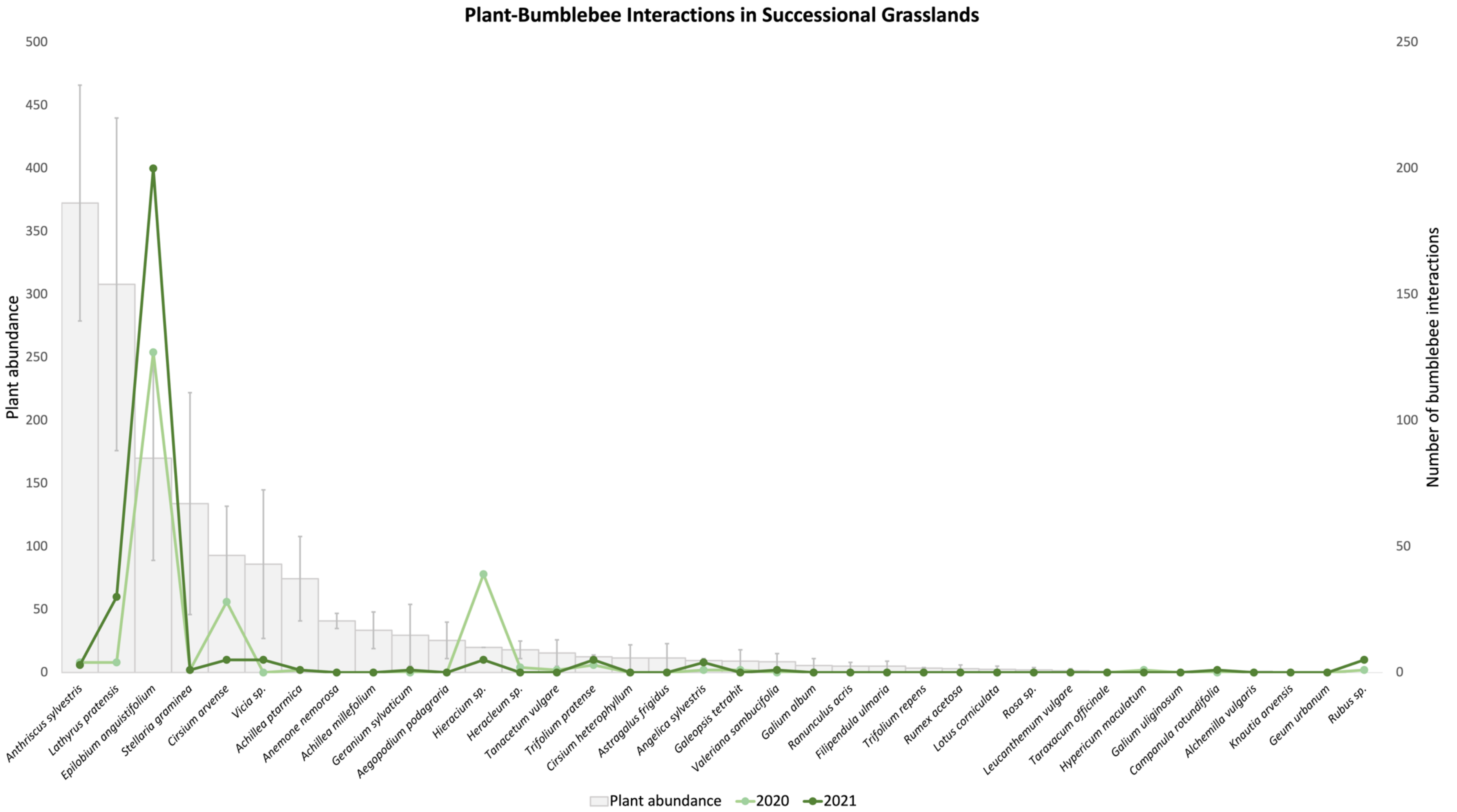

Figure 3.8: Plant-Bumblebee interactions in successional grasslands. Mean and standard error of the total flowering plant abundance for the two year of the local survey is given for each flowering plant species present (grey bars), with the left y-axis denoting the plant abundance. The total number of observed bumblebee interactions per flowering plant species in 2020 (light green) and 2021 (dark green) is given with the right y-axis denoting the total number of interactions observed. The flowering plants are listed in order of abundance with the most abundant species being at the left end of the x-axis and the least abundant at the right end of the x-axis.

4. Discussion

Pollinators, such as bumblebees and butterflies, are expected to vary across habitat and time. The primary aim of this study is to examine the spatiotemporal trends of pollinators abundance, species richness and species composition using local and regional pollinator data. Furthermore, the study aims at identifying flowering plant preferences of pollinators in two different land use systems, semi-natural and successional grasslands.

4.1. Regional pollinator abundance and species richness

4.1.1. Bumblebees

The analyses of the regional survey found no trend in bumblebee species richness or abundance over the years. Åström et al. (2021) did however find a slight negative trend in their analyses of the same data. This discrepancy may be a result of this study focusing on the grassland sites of the dataset, excluding data from the open woodland sites that were included in the analysis by Åström et al. (2021). Furthermore, Åström et al. (2021) have primarily used community indices in their analyses which may provide them with slightly different results than what was acquired here. Interestingly, the negative trend Åström et al. (2021) found was only reported in their 2020 report with previous reports, such as the 2019 report, not having found such trends (Åström et al., 2020; Åström et al., 2021).

The lack of a clear negative trend for bumblebees in this survey is in stark contrast to the many reviews, reports and studies that have found evidence of great bumblebee declines in Europe over the last few decades (Potts et al., 2010; Bommarco et al., 2012; IPBES, 2016; Soroye et al., 2020; Wagner, 2020). Most studies that have found negative trends for bumblebees, such as Bommarco et al. (2012), Fourcade et al. (2018) and Burkle et al. (2013), cover long timeseries with datasets dating back to the mid 1900's, often using then-and-now comparisons. As the regional survey only covers a nine yearlong period dating back to 2012, a longer time series might be needed in order to detect the potential trends. Furthermore, the results might suggest the greatest bumblebee declines may already have happened. The bumblebee species that disappeared or greatly declined in the study sites of Fourcade et al. (2018) and Bommarco et al. (2012), which were in Norway and Sweden respectively, from the mid 1900's to the early 2000's were primarily specialist species that are often more vulnerable to change. As such, these species may have already been lost in the mid to late 1900's, and what's remaining are stable populations of generalist species able to endure the current anthropogenic impacts. Finally, the observed patterns of pollinators undergoing range shifts to higher altitudes and latitudes with the warming climate (IPBES, 2016), may be another contributing factor of the stable trends observed in this study.

Bumblebee abundance and species richness of the regional data varied greatly among years. These variations are likely caused by weather conditions, such as precipitation and temperature, differing among the years. Extreme temperatures or precipitation alter floral resource availability and increase bumblebee mortality, affecting the bumblebee's overall abundance (Totland et al., 2013; Ogilvie et al., 2017; Woodard, 2017; Soroye et al., 2020). It is therefore likely the particularly bad years of bumblebee abundance and species richness observed in this study correlates with years of especially harsh weather conditions. Despite this, the mean temperature and precipitation of the four seasons of each year (Figure F.2, Appendix F) does not appear to correlate with neither the particularly good nor bad bumblebee years. More detailed climatic data, such as periods of drought and snow melt dates, could be beneficial for future studies to include, as such climatic variables may impact the observed bumblebee abundances (Ogilvie et al., 2017; Woodard, 2017).

The analysis of the regional data also found site to be an important factor for bumblebee abundance and species richness. This observed significance of site likely reflects the significance of habitat quality on bumblebee distributions. The regional survey have primarily defined the grassland sites as any open field outside of forests (Åström et al., 2021). Such a broad definition of grasslands with no further descriptions of the sites suggests there may be great variation among the sites. The sites may vary greatly in terms of their nest and resource availability, two factors deemed especially important for bumblebee distribution (Goulson, 2010; Totland et al., 2013; Ødegaard et al., 2015). Åström et al. (2021) highlighted the importance of flower cover on bumblebee species richness and abundance in their report, an element likely correlated with site. When the CV of the local and regional datasets were compared, the variation of the datasets was not significantly different for the bumblebee abundance, but was so for the species richness, with the regional data exhibiting greater variation than the local one (Table A.7, Appendix A). This difference may be due to the regional sites varying more in terms of habitat quality and geographical location than the local sites.

The ordination analyses of the site level bumblebee species composition found site and flower cover to significantly affect the bumblebee species compositions. As previously discussed, differences in the sites quality as habitats is likely the underlying cause of this significance. Along with differences in site resource availability, that may roughly be measured as flower cover, the regional sites also differ in location and proximity to one another (Table A.1. Appendix A). The regional sites vary in altitude and proximity to the ocean. Some sites are at 0 meters above sea level (m.a.s.l.) (Småland and Sorgenfri) while others are at higher altitudes, some above 400 m.a.s.l. (Lakketariusvollen and Odden) (Table A.1, Appendix A). As some bumblebee species are more adapted to specific habitats and climates (Ødegaard et al., 2015), the differences among the sites altitude and proximity to the ocean may be affecting the observed bumblebee species composition. Future studies could further assess the effect of such geographical variations among sites, and potentially include other site variables, such as past and present land-use systems of the sites and their surrounding areas, which may influence pollinator distributions (Öckinger & Smith, 2006; Walcher et al., 2017).

Neither temperature nor year were found to significantly affect the bumblebee species composition. The temperature data was only records from fieldwork and did not include broader temperature trends for the sites or years. The effects of more detailed weather data, than simply what occurred during the field work, could be relevant for future studies to explore. As the species composition was not significantly altered over the years, this suggests the bumblebee species composition currently remains stable. This is further supported by the species in Figure 3.2a, where none of the five most abundant species appear to become more nor less abundant than the others over time.

4.1.2. Butterflies

In the regional survey, both butterfly abundance and species richness were found to increase over the years. This trend was also reported by Åström et al. (2021) in their analysis of the same data. Here, the analyses were further conducted with *Vanessa cardui* removed from the dataset. *Vanessa cardui* is a migrating butterfly species with a wide range (Shields, 1992). The species is mostly common in southern Europe but has been found to migrate further north to areas such as Scandinavia during more extreme migration events (Shields, 1992; Stefanescu et al., 2013). 2019 was likely a year with such an event as vast numbers of this species invaded Norway this year (Figure 3.4b) (Birkemoe, 2019). The potential effect of this invasion on the positive trend observed for butterfly species richness and abundance was tested for by the removal of this species from the dataset. The positive trend remained, indicating the migration event did not greatly promote the positive trends observed.

The observed variation in butterfly abundance and species richness among the years coincide partly with the patterns of the bicyclic species *Erebia ligea* (Figure 3.1 and 3.2b). Years with particularly low species richness and abundance, such as 2013 and 2015, coincide with years of *Erebia ligea* dormancy (Figure 3.2b). Butterflies are mostly associated with warmer summers (Willmer, 2011), and interestingly the two years with the highest mean species richness, 2018 and 2020, were both years with particularly dry and warm periods (Figure F.1, Appendix F) (Skaland et al., 2019; Grinde et al., 2020).

The positive trend is rather curious as it contradicts most of the findings in the rest of Europe (Nilsson et al., 2008; IPBES, 2016; van Swaay et al., 2020; Wagner, 2020). As discussed by Åström et al. (2021) the positive trend may, in part, be explained by the positive trend found for flower cover in the Trøndelag sites. The trend of pollinators undergoing range shifts to higher altitudes and latitudes with the warming climate (IPBES, 2016), may be contributing to the observed increase. As Europe is getting warmer (IPBES, 2016), southern regions are likely becoming less favourable for many pollinators, while northern regions may become more favourable. The latitudinal range shifts may therefore be more prevalent in pollinators, such as butterflies, with a more southern distribution (Kudrna et al., 2011, as cited in UFZ, 2011), than pollinators, such as bumblebees, who already have a quite northern distribution (Polce et al., 2018). This could potentially explain the positive trend of the butterflies and the stable to negative trend of the bumblebees observed in this study. There is, however, little research on this subject and the positive butterfly trends may simply be a result of the warming climate improving the conditions for butterflies in the study region, allowing the already present species to become more abundant as the summers are get warmer.

In the regional study, site was found to have a significant effect on butterfly species richness and abundance. As previously discussed for the bumblebees, this is likely due to the significance of habitat quality. Studies such as Öckinger and Smith (2006) have found habitat quality, in terms of floral abundance and vegetation height, as well as the size of the studied grasslands and their surrounding areas to be important factors for butterfly specie richness. Differences in floral availability and surrounding landscapes among the study sites may therefore be important factors contributing to the observed effect of site on butterfly species richness. When the CV of the local and regional datasets was compared the variation of the two was not significantly different for the butterfly abundance but was for the butterfly species richness. The same as was found for the bumblebees. Curiously, the butterfly species richness varied most in the local dataset, not the regional dataset as was the case for the bumblebee species richness (Table A.7, Appendix A). It is difficult to say why this is, but differences in the surrounding landscape among the regional and local sites, the seemingly low butterfly abundances observed in the local survey, and the noticably different weather conditions between the two years of the local survey may be contributing factors.

From the ordination analyses of the site level butterfly species composition, both year and site were found to significantly affect the species composition while no significant effect was found for the flower cover or temperature. The significance of site is likely caused by the same underlying elements as previously discussed. However, as flower cover was not found to significantly affect the butterfly species composition, differences in site location and surrounding areas may be the more essential factors for the butterfly species compositions. The curious clustering of species around site nr. 6 (Odden) in the NMDS plot (Figure 3.3b) may further support this notion given this site is at the highest altitude (450 m.a.s.l.) of all the regional sites (Table A.1, Appendix A), and most of the species found in this cluster are commonly found in higher altitudinal areas, like the *Boloria euphrosyne, Boloria selene, Plebejus idas* and *Speyeria aglaja* (Aarvik & Elven, 2014).

The significant effect of year on the butterfly species composition may suggests the species are not increasing equally in abundance over the years. As seen in Figure 3.2b species such as *Aglais urticae* and *Pieris napi* appear to become more abundant in the later years, while other species among the top five most abundant species appear to remain fairly stable. It is difficult to say why these species in particular are becoming more abundant in this study region, but the effect of climate change and increased summer temperatures may be at play. Addressing the Community Temperature Index (CTI) over these years could be an interesting next as studies such as Devictor et al. (2012) have already found evidence of rapid CTI changes in butterfly communities in Europe.

4.2. Local pollinator abundance and species richness

4.2.1. Bumblebees

In the local survey, land use was not found to significantly affect bumblebee species richness or abundance. These results are somewhat surprising as semi-natural grasslands are generally considered better habitats for bumblebees than successional ones (Totland et al., 2013; Walcher et al., 2017). Furthermore, as bumblebee species richness and abundance are closely linked to flower cover and plant species richness (Ogilvie et al., 2017; Walcher et al., 2017; Åström et al., 2021), their abundance and species richness would be expected to be higher in the semi-natural grasslands, as this was the case for the flowering plants (Appendix C). Curiously, Heggøy (2021) found bumblebee abundance and species richness to be significantly greater in the semi-natural grasslands than successional grasslands in her analysis of the 2020 data. As the data from 2020 and 2021 were analysed together in this study, it seems the bumblebee abundance and species richness of the two land use systems contrasted more in 2020 than in 2021. This is especially evident for the bumblebee species richness (Figure 3.4a). Despite this, neither year nor the interactions between year and site were found to be significant factors for the bumblebee species richness or abundance (Appendix C).

As pollinators may fluctuate a lot among years (Totland et al., 2013), the observed discrepancy may simply be a result of natural fluctuations caused by different weather conditions and floral availability among the two years. As the floral Shannon diversity index and abundance were significantly lower in 2021 than in 2020 (Appendix C), this differences in floral resources among the two years may have contributed to the bumblebee abundance and species richness of the two land use systems contrasting less in 2021 than in 2020.

It is worth noting the 2021 survey occurred 4 years after Kleppe (2019) did her survey and categorisation of the grasslands. The grasslands may have changed since then and species such as *Epilobium angustifolium*, a plant mostly associated with successional grasslands (Grindeland, 2022), have been observed in some of the semi-natural grasslands both in 2020 and 2021 (Figure 3.6). As such, continued succession of the unmanaged semi-natural grasslands (Bjørdalen, Flatåsen and Lade) may have contributed to the observed discrepancy. However, it is important to note these results only highlights the difference between the two years and do not indicate an overall trend.

4.2.2. Butterflies

Land use was not found to significantly affect butterfly species richness or abundance. Similarly to bumblebees, butterfly distribution is positively relate to flower cover (Åström et al., 2021). It is therefore surprising their abundance and species richness were not greater in the semi-natural grasslands, given these had a higher flowering plant species richness, Shannon diversity index and abundance than the successional grasslands. As discussed for the bumblebees, this discrepancy may be due to natural fluctuations of the pollinators and their floral resources among the two years. Just as with most other pollinators, the butterflies may fluctuate a lot among years (Totland et al., 2013; van Swaay et al., 2020) and the strikingly low species richness observed in the semi-natural grasslands in the second year of this survey (Figure 3.4b) may be a result of such fluctuations. Butterflies generally fair worse in years with cold and wet summers (van Swaay et al., 2020), and as the summer of 2021 did not have equally warm and dry periods as that of 2020 (Figure F.1., Appendix F), this may be a contributing factor to the observed drop in butterfly species richness this year.

4.2.3. Other pollinators

Other pollinator groups were also recorded in the local survey, and just as for the bumblebees and butterflies, land use had no significant effect on their abundance. This is likely due to the same factors as discussed earlier for butterflies and bumblebees such as natural fluctuations in both pollinators and their floral resources among the two years. The positive effect of year that was found is likely caused by natural variations and possibly heightened by the greater abundance of flies in the second year of this survey. Both hoverflies and flies were noticeably more abundant in 2021 than in 2020 (Figure 3.5). Many news outlets also reported on the strikingly high abundance of flies this year (e.g. Solås et al., 2021; Sverdrup-Thygeson, 2021). Like most other pollinators, large fluctuations in population size from one year to the next is not uncommon (Totland et al., 2013). The high abundance observed in 2021 is likely a result of favourable wet weather conditions this year, contrasting with rather dry period of June in 2020 that were likely less favourable.

The honeybee abundance varied greatly among the two years. Differences in beehive placements in relation to the study sites in the two years may explain this observed variation. In 2020, beehives were placed near two of the study sites, Forsøkslia and Selsbakk N (Heggøy, 2021), while in 2021 beehives were only placed near one, Flatåsen (Mattilsynet, 2022). These sites had the highest number of observed honeybees in their respective year of beehives being placed nearby. As such, the beehive placement is likely the main contributor to the observed variation of honeybees among the two years.

4.3. Local plant-pollinator interactions

As previously stated, the semi-natural grasslands were found to have significantly higher plant species richness, Shannon diversity index and abundance than the successional ones. Furthermore, the mean vegetation height was consistently higher in the successional grasslands than the semi-natural ones (Figure A.5, Appendix A). These findings are congruent with most other studies on grasslands (e.g. Pykälä et al., 2005; Johansen et al., 2019; Bohner et al., 2020). Interestingly, the flowering plant abundance and Shannon diversity index were significantly lower in 2021 than in 2020. These differences are likely caused by different weather conditions along with natural variations in floral phenology which can cause great fluctuations in floral supply among years (Willmer, 2011).

In the local survey, bumblebees appeared to prefer certain flowering plants over others. Although some bumblebee species are more specialised than others, most interact with multiple flowering plant species (Goulson, 2010; Willmer, 2011). There is a broad spectre of species visited by bumblebees, but most bumblebees appear to prefer larger flowers in the blue to purple and pink colour range, with medium to long corolla tubes (Willmer, 2011). Factors such as the abundance of the flowering plants, the rewards they are likely to provide, and the flowers shape and structure, determine what flowering plants the bumblebees visit (Goulson, 2010).

Despite being the most abundant flowering plant in the semi-natural grasslands, *Alchemilla vulgaris* was not visited by any bumblebees (Figure 3.6). Similarly, the most abundant flowering plant in the successional grasslands, *Anthriscus sylvestris*, was rarely visited (Figure 3.7). If the bumblebees had no preference in what flowering plants to visit, the most abundant flowering plants would likely have had the highest number of visitors. This was not the case, and certain flowering plants were highly visited despite their low abundance. This is congruent with most literature on the subject (Goulson, 2010; Willmer, 2011; Kaiser-Bunbury et al., 2014; Ødegaard et al., 2015).

In the semi-natural grasslands, the bumblebees primarily visited *Knautia arvensis* (Figure 3.6). All bumblebee species observed in this survey were found to interact with this flowering plant at least once (Figure E.1, Appendix E). As *K. arvensis* is considered an important flowering plant, highly preferred by many pollinators (Franzén & Nilsson, 2008; Goulson & Kristiansen, 2020), these results are not too surprising.

Campanula rotundifolia is another flowering plant that was frequently visited by bumblebees in the semi-natural grasslands (Figure 3.6). *C. rotundifolia* was primarily visited by *Bombus soroeensis* in 2020 (Figure E.1, Appendix E) (Dhukuchhu, 2021). This bumblebee species is considered a frequent visitor of *C. rotundifolia* (Ødegaard et al., 2015). The plant-bumblebee network for 2021 shows *C. rotundifolia* primarily being visited by *Bombus* s. str instead of *B. soroeensis* (Figure E.1, Appendix E). As *B. soroeensis* may easily be mistaken for one of the *Bombus* s. str. species (Ødegaard et al., 2015), it is highly likely such misidentification occurred in 2021. In the successional grasslands, where *C. rotundifolia* was rarely present, *B. soroeensis* primarily visited *E. angustifolium* (Figure E.2, Appendix E), a flowering plant this bumblebee species is also know to visit (Ødegaard et al., 2015).

Despite being most prominent in the successional grasslands, *E. angustifolium* was also observed in some of the semi-natural sites and was among the five most visited flowering plants in both land use systems. In the successional grasslands, *E. angustifolium* was the third most abundant flowering plant, and had the highest number of bumblebee visitors (Figure 3.7). Most bumblebee species observed in the successional grasslands interacted with this species (Figure E.2, Appendix E). Interestingly, *Bombus* s. str. was the primary visitor of the flowering plant in the semi-natural grasslands with few other species interacting with it (Figure E.1, Appendix E). The case of *E. angustifolium* may be similar to that of *Cirsium arvense.* In this survey *C. arvense* was among the five most visited flowering plants in the successional grasslands (Figure 3.7) and is found to be an important flowering plant for pollinators when others are not present (Haaland & Gyllin, 2009). It may be the case *E. angustifolium* too is especially preferred when there are few other alternatives.

Trifolium pratense and *Hieracium* sp. were among the five most visited flowering plants in both land use systems. *Trifolium pratense* is a known bumblebee flowering plant (Haaland & Gyllin, 2009; Willmer, 2011). From the network structures, it appears *Bombus pascuorum* is this species most prominent visitor (Figure E.1 and E.2 in Appendix E). *B. pascuorum* has a fairly long tongue with which it may access resources from flowering plants having long corolla tubes (Ødegaard et al., 2015), a trait typical for *T. pratense* (Lid & Lid, 2017). *B.*

pascuorum also appeared to be the most prominent visitor of *Lathyrus pratensis,* another highly visited flowering plants in the successional grasslands, also considered a typical bumblebee flowering plant (Willmer, 2011).

Both the bumblebee and higher order pollinator networks appear more complex in the semi-natural grasslands than in the successional grasslands (Appendix E). Further analyses on these network structures were not within the scope of this study, however, Dhukuchhu (2021) found the plant-pollinator networks to be more specialized in the semi-natural grasslands than the successional ones, in 2020. More complex networks in the semi-natural grasslands are expected as their higher floral richness likely allows for more interactions to occur. Interestingly, the great variation in both honeybees and flies observed in the two years is evident in the network structures (Appendix E). Although exploitative competition is known to occur among honeybees and bumblebees (Wignall et al., 2019), no such competition is evident in the plant-pollinator networks. It is however quite likely such competition did occur, especially in the sites with beehives placed nearby, and comparisons of the networks at site level might be needed to detect this.

Future research may further explore why certain flowering plants such as *K. arvensis* are preferred by the bumblebees, and how differences in plant and pollinator species compositions may affect these preferences. Identifying methods of applying this knowledge to the conservation of semi-natural grasslands and the many pollinators that rely on these habitats may be a useful next step.

5. Conclusion

From the regional survey, bumblebee abundance, species richness, and species composition remained stable over the years, although with some mixed results. The butterfly abundance and species richness increased over the years with species such as *Aglais urticae* and *Pieris napi* becoming more abundant. These trends may be caused by the warming climate having improved the conditions for butterflies in the study region and past bumblebee declines having caused the present-day species compositions to consist of generalist species resistant to change. Site had a significant effect on both bumblebee and butterfly abundance, species richness, and species composition. This is likely due to differences in habitat quality among the sites. Including more detailed information about the sites and their surrounding landscapes may be useful in future studies.

In the local survey, flowering plant species richness, Shannon diversity index and abundance were significantly higher in the semi-natural grasslands than in the successional ones. The floral abundance and Shannon diversity index were significantly lower in the second year of the survey. The pollinators abundances and species richness were not significantly different between the two land use systems. This is likely due to natural fluctuations of the pollinators and their floral resources among the two years. The bumblebees exhibited clear flowering plant preferences. They primarily visited *Knautia arvensis* in the semi-natural grasslands and *Epilobium angustifolium* in the successional ones and interacted with more flowering plant species in the semi-natural grasslands than in the successional ones, most of which are well known foraging sources for bumblebees. Future studies may further explore the dynamics of flower choice among pollinators and how differences in plant and pollinator species compositions affect such choices.

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Appendices

Appendix A: Supplementary tables

Table A.1: Site names, approximate meter above mean sea level (m.a.s.l.) and coordinates of the regional sites.

Site	m.a.s.l.	Latitude	Longitude
Agle	120	64.2605620006105	12.471614997934
Binde	100	64.085850000706	11.7449539982182
Lakketariusvollen	400	62.9046050005645	10.118255498098
Namdalseid	200	64.1973704755226	11.2782579959908
Namsskogan	200	64.9267710000035	13.1773950000563
Odden	450	62.9176650000035	10.4700734998178
Rinnan	40	63.7552495008959	11.4215255003948
Småland	0	63.5696310006266	10.7297909982274
Sorgenfri	0	63.4063155005788	10.387393997884
Sparbu	20	63.9185875008045	11.4113839986046
Vuku	150	63.7679685007953	11.7894435019627

Table A.2: Site names, land use, approximate meters above mean sea level (m.a.s.l.), and coordinates of the local sites.

Site	Land use	m.a.s.l.	Latitude	Longitude
Bjørndalen	Semi-Natural	110	63.374679	10.374572
Flatåsen	Semi-Natural	180	63.378040	10.343790
Grønlia	Semi-Natural	45	63.446328	10.434083
Lade	Semi-Natural	60	63.451310	10.447930
Lian Lower	Semi-Natural	270	63.398327	10.305550
Lian Upper	Semi-Natural	300	63.400107	10.302423
Buengveien N	Successional	85	63.382230	10.358760
Buengveien S	Successional	100	63.379400	10.355470
Forsøkslia	Successional	70	63.384860	10.362340
Okstad	Successional	45	63.386145	10.378704
Selsbakk N	Successional	120	63.391903	10.359753
Selsbakk S	Successional	120	63.390898	10.359459

Table A.3: Mean abundance and standard error (SE) per bumblebee species across all sites and years in the regional survey

Species	**Mean**	**SE**
Bombus balteatus	0,020	0,020
Bombus bohemicus	2,091	0,598
Bombus campestris	0,051	0,026
Bombus cingulatus	0,020	0,014
Bombus consobrinus	0,051	0,026
Bombus distinguendus	0,020	0,014
Bombus flavidus	0,010	0,010
Bombus hortorum	2,424	0,553
Bombus hypnorum	4,859	0,557
Bombus jonellus	0,788	0,227
Bombus lapidarius	4,970	1,582
Bombus lapponicus/monticola	0,646	0,360
Bombus pascuorum	10,818	0,965
Bombus pratorum	3,444	0,473
Bombus sensu stricto	21,444	2,850
Bombus soroeensis	0,354	0,135
Bombus sylvestris/norvegicus	0,212	0,069
Bombus wurflenii	0,465	0,161

Table A.4: Mean abundance and standard error (SE) per butterfly species across all sites and years in the regional survey

Species	**Mean**	**SE**
Aglais urticae	3,909	0,794
Anthocharis cardamines	0,263	0,087
Aphantopus hyperantus	0,020	0,014
Aricia artaxerxes	0,051	0,030
Boloria aquilonaris	0,131	0,071
Boloria euphrosyne	0,071	0,061
Boloria selene	0,535	0,190
Brenthis ino	0,101	0,051
Callophrys rubi	0,051	0,026
Carterocephalus palaemon	0,020	0,014
Celastrina argiolus	0,020	0,014
Coenonympha pamphilus	0,020	0,014
Coenonympha tullia	0,010	0,010
Colias palaeno	0,081	0,034
Cyaniris semiargus	0,020	0,014
Erebia ligea	2,798	0,891
Eumedonia eumedon	0,010	0,010
Gonepteryx rhamni	0,030	0,017
Lasiommata maera	0,010	0,010
Lycaena hippothoe	0,111	0,040
Pieris brassicae	0,051	0,026
Pieris napi	2,222	0,450
Pieris rapae	0,222	0,105
Plebejus argus/idas	0,232	0,093
Polygonia c-album	0,081	0,034
Polyommatus icarus	0,131	0,055
Pyrgus malvae	0,020	0,020
Speyeria aglaja	0,990	0,344
Vanessa atalanta	0,364	0,088
Vanessa cardui	0,960	0,327

Table A.5: Mean and standard error vegetation height for each site across all seasons for each year of the local survey.

Site	**Land Use**	**Mean Vegetation Height (cm)**	
		2020	**2021**
Bjørndalen	Semi-Natural	60.53 ± 2.407	38.85 ± 1.89
Flatåsen	Semi-Natural	44.63 ± 2.77	36.96 ± 2.104
Grønlia	Semi-Natural	29.83 ± 1.279	18.95 ± 0.885
Lade	Semi-Natural	58.50 ± 2.729	33.90 ± 1.613
Lian Lower	Semi-Natural	20.36 ± 0.721	11.84 ± 0.449
Lian Upper	Semi-Natural	24.87 ± 1.311	17.50 ± 0.887
Buengveien N	Successional	84.25 ± 3.783	53.35 ± 2.455
Buengveien S	Successional	80.97 ± 3.188	63.40 ± 3.255
Forsøkslia	Successional	112.72 ± 9.756	71.59 ± 3.474
Okstad	Successional	108.63 ± 4.216	62.92 ± 4.011
Selsbakk N	Successional	98.85 ± 4.298	85.28 ± 4.562
Selsbakk S	Successional	99.35 ± 4.336	80.46 ± 4.145

Table A.6: Flowering plant abundance per species and number of observed visitations by bumblebees observed in semi-natural grasslands (SN) and successional grasslands (SS) over the two years (1 = 2020, 2 = 2021) in the local survey. % flower visits of the total number observed interactions of each land use system across both years

Flowering plants	**Plant abundance**				**Number observed flower visits**				**% Flower visits**	
	SN		**SS**		**SN**		**SS**		**SN**	**SS**
	1	**2**	**1**	**2**	**1**	**2**	**1**	**2**		
Achillea millefolium	73	85	48	19	0	1	0	0	0.128	0.000
Achillea ptarmica	80	35	108	41	0	1	1	1	0.128	0.416
Aegopodium podagraria	21	0	40	11	0	0	0	0	0.000	0.000
Alchemilla vulgaris	600	886	1	1	0	0	0	0	0.000	0.000
Anemone nemorosa	40	9	47	35	0	0	0	0	0.000	0.000
Angelica sylvestris	0	22	8	11	0	0	1	4	0.000	1.040
Anthriscus sylvestris	159	119	466	279	0	11	4	3	1.407	1.455
Arabidopsis thaliana	4	10	0	0	0	0	0	0	0.000	0.000
Astragalus frigidus	0	0	0	23	0	0	0	0	0.000	0.000
Bistorta vivipora	15	0	0	0	0	0	0	0	0.000	0.000
Campanula rotundifolia	161	78	0	2	40	13	0	1	6.777	0.208
Cerastium arvense	0	2	0	0	0	0	0	0	0.000	0.000
Cerastium fontanum	2	0	0	0	0	0	0	0	0.000	0.000
Cirsium arvense	9	1	132	54	0	1	28	5	0.128	6.861
Cirsium heterophyllum	7	0	22	1	3	0	0	0	0.384	0.000
Epilobium angustifolium	34	0	251	89	48	16	127	200	8.184	67.983
Euphrasia officinalis	3	25	0	0	0	0	0	0	0.000	0.000
Filipendula ulmaria	0	0	9	1	0	0	0	0	0.000	0.000
Galeopsis tetrahit	0	0	18	0	0	0	1	0	0.000	0.208
Galium album	0	0	0	11	0	0	0	0	0.000	0.000
Galium Boreale	0	38	0	0	0	1	0	0	0.128	0.000
Galium rivale	41	0	0	0	0	0	0	0	0.000	0.000
Galium uliginosum	2	0	2	0	0	0	0	0	0.000	0.000
Galium verum	198	58	0	0	2	0	0	0	0.256	0.000
Geranium sylvaticum	27	14	54	5	0	2	0	1	0.256	0.208
Geum rivale	0	9	0	0	0	0	0	0	0.000	0.000
Geum urbanum	0	0	0	1	0	0	0	0	0.000	0.000
Heracleum sp.	3	0	25	11	3	2	2	0	0.639	0.416
Hieracium sp.	75	132	20	20	34	38	39	5	9.207	9.148
Hypericum maculatum	88	116	2	0	9	27	1	0	4.604	0.208
Knautia arvensis	67	36	1	0	140	134	0	0	35.038	0.000
Lathyrus pratensis	124	69	440	176	6	3	4	30	1.151	7.069

Leontodon autumnalis	27	23	0	0	7	0	0	0	0.895	0.000
Leucanthemum vulgare	66	40	3	0	0	0	0	0	0.000	0.000
Linaria vulgaris	0	25	0	0	15	7	0	0	2.813	0.000
Lotus corniculata	23	4	5	0	3	0	0	0	0.384	0.000
Myosotis sp.	0	1	0	0	0	0	0	0	0.000	0.000
Orchis sp.	3	3	0	0	0	0	0	0	0.000	0.000
Pimpinella saxifraga	0	30	0	0	0	0	0	0	0.000	0.000
Plantago lanceolata	0	38	0	0	0	0	0	0	0.000	0.000
Platanthera chlorantha	19	0	0	0	0	0	0	0	0.000	0.000
polygonum viviparum	0	2	0	0	0	0	0	0	0.000	0.000
Potentilla erecta	120	156	0	0	0	2	0	0	0.256	0.000
Prunella vulgaris	5	4	0	0	0	7	0	0	0.895	0.000
Ranunculus acris	141	241	8	2	0	1	0	0	0.128	0.000
Rhinanthus anguistifolius	62	11	0	0	36	10	0	0	5.882	0.000
Rhinanthus minor	21	52	0	0	3	8	0	0	1.407	0.000
Rosa sp.	2	0	4	0	0	2	0	0	0.256	0.000
Rubus sp.	3	0	0	0	2	0	1	5	0.256	1.247
Rumex acetosa	0	1	0	6	0	0	0	0	0.000	0.000
Solidago virguarea	19	0	0	0	12	2	0	0	1.790	0.000
Stellaria graminea	610	301	222	46	0	1	1	1	0.128	0.416
Stellaria nemorum	0	0	0	0	1	0	0	0	0.128	0.000
Succisa pratensis	11	10	0	0	9	12	0	0	2.685	0.000
Tanacetum vulgare	38	5	26	5	19	4	1	0	2.941	0.208
Taraxacum officinale	19	12	0	2	0	1	0	0	0.128	0.000
Trifolium pratense	174	105	11	14	33	31	3	5	8.184	1.663
Trifolium repens	74	34	4	3	5	3	0	0	1.023	0.000
Valeriana sambucifolia	5	4	15	2	0	0	0	1	0.000	0.208
Verboscum nigrum	4	0	0	0	0	0	0	0	0.000	0.000
Veronica chamaedrys	0	16	0	0	0	0	0	0	0.000	0.000
Veronica offisinialis	0	1	0	0	0	0	0	0	0.000	0.000
Vicia sp.	77	54	145	27	6	5	0	5	1.407	1.040
Viola sp.	5	9	0	0	0	0	0	0	0.000	0.000

Table A.7. Mean, standard error (SE) and coefficient of variation (CV) for the bumblebees and butterflies observed along the 50m transects in the regional and local surveys.

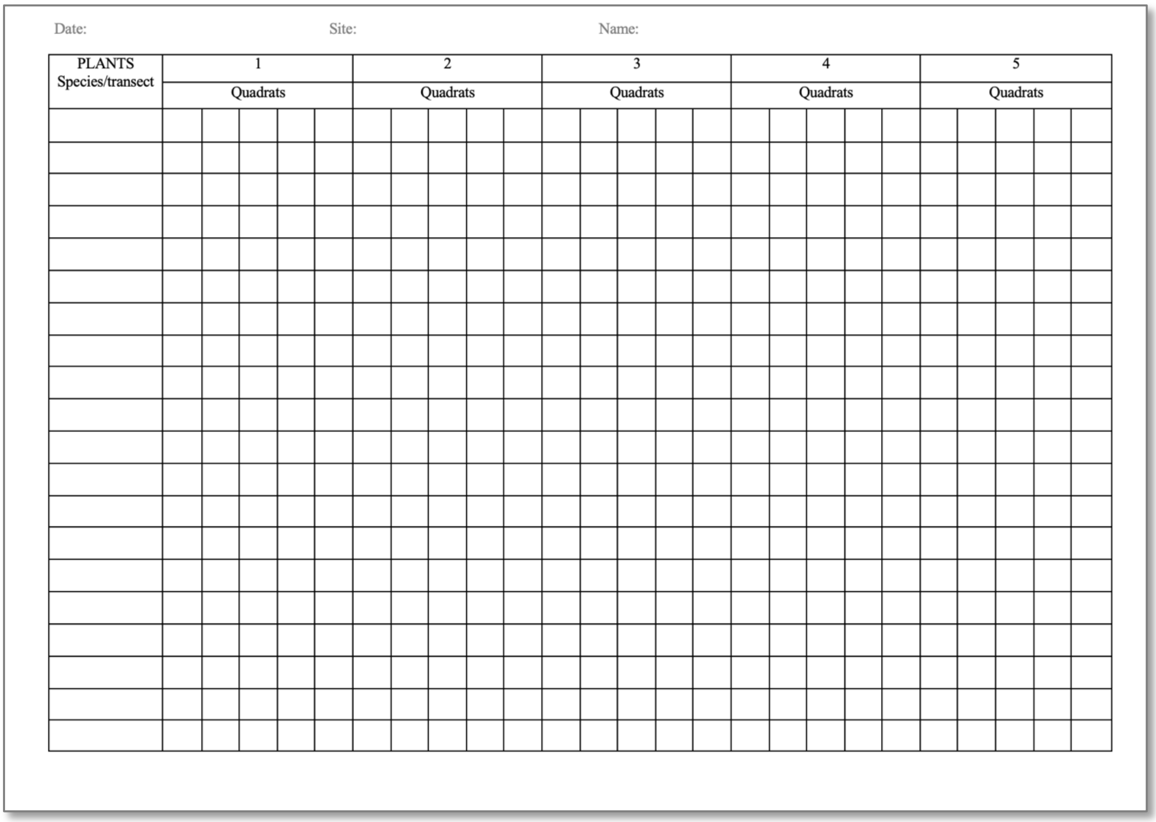
			Mean	SE	CV
Regional data					
	Bumblebees				
		Abundance	1.140	0.043	2.529
		Richness	0.572	0.014	1.663
	Butterflies				
		Abundance	0.294	0.014	3.224
		Richness	0.193	0.007	2.534
Local data					
	Bumblebees				
		Abundance	3.015	0.285	2.071
		Richness	0.963	0.060	1.369
	Butterflies				
		Abundance	0.221	0.025	2.436
		Richness	0.065	0.011	3.810

Appendix B: Registration forms used in the local survey

Standardized registration form for registration of pollinators and plants used in the local survey.

Date: Site: Name:

Time/cloud cover (%)/temperature (°C)															
POLLINATORS Species/transect	Interacting plant species			Interacting plant species			Interacting plant species			Interacting plant species			Interacting plant species		



Date: Site: Name:

PLANTS Species/transect	1					2					3					4					5				
	Quadrats					Quadrats					Quadrats					Quadrats					Quadrats				

Appendix C: Model selections and outputs

Regional pollinator data:

Model selection of models testing for the effect of site and year on bumblebee abundance (A), bumblebee richness (B), butterfly abundance (C) and butterfly richness (D). K = the number of parameters in the model. AICc = the corrected Akaike information criterion. ΔAICc = The difference in AICc of each model to the model with the lowest AICc. AICcWt = The AICc weight.

A: Model selection. Bumblebee abundance on a negative binomial distribution model.

Model	**K**	**AICc**	**ΔAICc**	**AICcWt**
Site	12	923.25	0.00	0.79
Site + Year	13	925.90	2.65	0.21
Site * Year	23	937.53	14.28	0.00
Constant	2	982.04	58.79	0.00
Year	3	983.22	59.97	0.00

B: Model selection. Bumblebee species richness on a linear model.

Model	**K**	**AICc**	**ΔAICc**	**AICcWt**
Site	12	383.02	0.00	0.71
Site + Year	13	384.80	1.78	0.29
Site * Year	23	399.96	16.94	0.00
Constant	2	400.81	17.79	0.00
Year	3	402.36	19.34	0.00

C: Model selection. Butterfly abundance on a negative binomial distribution model.

Model	**K**	**AICc**	**ΔAICc**	**AICcWt**
Site + Year	13	663.64	0.00	0.99
Site * Year	23	672.10	8.46	0.01
Site	12	690.20	26.56	0.00
Year	3	703.80	40.16	0.00
Constant	2	715.48	51.84	0.00

D: Model selection. Butterfly species richness on a Poisson distribution model.

Model	**K**	**AICc**	**ΔAICc**	**AICcWt**
Site + Year	12	377.62	0.00	0.99
Site * Year	22	387.37	9.75	0.01
Year	2	407.10	29.48	0.00
Site	11	424.71	47.09	0.00
Constant	1	454.70	77.08	0.00

Table C.1: Model output on the original log-scale of the selected model for the regional bumblebee abundance (A). Bumblebee abundance ~ Site.

	Bumblebee Abundance			
Predictors	*Estimate*	*SE*	*Z-value*	*P-value*
(intercept) [Agle]	4,005	0,191	20,958	< 0,001
Site [Binde]	-0,239	0,271	-0,881	0,378
Site [Lakketariusvollen]	-0,495	0,273	-1,817	0,069
Site [Namdalseid]	-0,705	0,274	-2,574	**0,010**
Site [Namsskogan]	0,074	0,270	0,274	0,784
Site [Odden]	-0,495	0,273	-1,817	0,069
Site [Rinnan]	0,508	0,269	1,890	0,059
Site [Småland]	0,867	0,268	3,235	**0,001**
Site [Sorgenfri]	0,201	0,270	0,746	0,456
Site [Sparbu]	-1,940	0,292	-6,649	**< 0,001**
Site [Vuku]	-0,557	0,273	-2,040	**0,041**
Observations	99			
R^2 Nagelkerke	0.792			

Table C.2: Model output of the selected model for the regional butterfly species richness (B). Bumblebee species richness ~ Site.

	Bumblebee Species Richness			
Predictors	*Estimate*	*SE*	*t-value*	*P-value*
(intercept) [Agle]	5,222	0,515	10,142	**< 0,001**
Site [Binde]	1,111	0,728	1,526	0,131
Site [Lakketariusvollen]	-0,889	0,728	-1,221	0,225
Site [Namdalseid]	-1,222	0,728	-1,678	0,097
Site [Namsskogan]	1,111	0,728	1,526	0,131
Site [Odden]	0,444	0,728	0,610	0,543
Site [Rinnan]	1,667	0,728	2,289	**0,024**
Site [Småland]	0,222	0,728	0,305	0,761
Site [Sorgenfri]	0,333	0,728	0,458	0,648
Site [Sparbu]	-2,000	0,728	-2,746	**0,007**
Site [Vuku]	-0,444	0,728	-0,610	0,543
Observations	99			
R^2 / R^2 adjusted	0.341 / 0.266			

Table C.3: Model output on the original log-scale of the selected model for the regional butterfly abundance (C). Butterfly abundance ~ Site + Year.

	Butterfly Abundance			
Predictors	*Estimate*	*SE*	*Z-value*	*P-value*
(intercept) [Agle]	0,858	0,349	2,461	**0,014**
Year	0,211	0,035	6,057	**< 0,001**
Site [Binde]	-0,135	0,422	-0,321	0,748
Site [Lakketariusvollen]	0,179	0,416	0,431	0,667
Site [Namdalseid]	0,435	0,412	1,057	0,291
Site [Namsskogan]	1,184	0,404	2,930	**0,003**
Site [Odden]	1,778	0,401	4,434	**< 0,001**
Site [Rinnan]	0,500	0,411	1,218	0,223
Site [Småland]	1,031	0,405	2,543	**0,011**
Site [Sorgenfri]	-0,114	0,421	-0,271	0,786
Site [Sparbu]	-0,813	0,443	-1,835	**0,066**
Site [Vuku]	-1,455	0,478	-3,046	**0,002**

Observations 99

R^2 Nagelkerke 0.780

Table C.4: Model output on the original log-scale of the selected model for the regional butterfly species richness (D). Richness ~ Site + Year.

	Butterfly Species Richness			
Predictors	*Estimate*	*SE*	*Z-value*	*P-value*
(intercept) [Agle]	0,433	0,223	1,940	0,052
Year	0,162	0,024	6,867	**< 0,001**
Site [Binde]	-0,348	0,267	-1,306	0,191
Site [Lakketariusvollen]	-0,693	0,297	-2,333	**0,020**
Site [Namdalseid]	-0,125	0,251	-0,500	0,617
Site [Namsskogan]	0,085	0,238	0,356	0,722
Site [Odden]	0,000	0,243	0,000	1,000
Site [Rinnan]	0,302	0,226	1,337	0,181
Site [Småland]	0,085	0,238	0,356	0,722
Site [Sorgenfri]	-0,693	0,297	-2,333	**0,020**
Site [Sparbu]	-1,128	0,347	-3,253	**0,001**
Site [Vuku]	-1,041	0,336	-3,102	**0,002**

Observations 99

R^2 Nagelkerke 0.747

Local pollinator data:

Model selection of generalised linear models of all pollinators with bumblebees, butterflies and other flies excluded (A), bumblebee abundance (B), bumblebee species richness (C), butterfly abundance (D), butterfly species richness (E). K = the number of parameters in the model. AICc = the corrected Akaike information criterion. ΔAICc = The difference in AICc of each model to the model with the lowest AICc. AICcWt = The AICc weight.

A: Model selection. Pollinator abundance on a negative binomial distribution model

Model	K	AICc	ΔAICc	AICcWt
Year	3	264.96	0.00	0.49
Year * Land use	5	267.00	2.04	0.18
Constant	2	267.18	2.22	0.16
Year + Land use	4	267.87	2.90	0.12
Land use	3	269.49	4.53	0.05

B: Model selection. Bumblebee abundance on negative binomial distribution model

Model	K	AICc	ΔAICc	AICcWt
Constant	2	248.45	0.00	0.49
Land use	3	249.49	1.05	0.29
Year	3	251.06	2.61	0.13
Year + Land use	4	252.36	3.91	0.07
Year * Land use	5	255.50	7.05	0.01

C: Model selection. Bumblebee species richness on a linear model

Model	K	AICc	ΔAICc	AICcWt
Land use	3	97.23	0.00	0.43
Constant	2	97.68	0.44	0.34
Year + Land use	4	100.07	2.84	0.10
Year	3	100.25	3.01	0.09
Year * Land use	5	102.20	4.97	0.04

D: Model selection. Butterfly abundance on a negative binomial distribution model

Model	K	AICc	ΔAICc	AICcWt
Land use	3	127.68	0.00	0.39
Constant	2	128.01	0.33	0.33
Year	3	129.87	2.19	0.13
Year + Land use	4	129.91	2.23	0.13
Year * Land use	5	132.91	5.23	0.03

E: Model selection. Butterfly species richness on a linear model

Model	K	AICc	ΔAICc	AICcWt
Constant	2	68.25	0.00	0.32
Land use	3	68.29	0.04	0.31
Year	3	69.60	1.34	0.16
Year + Land use	4	69.76	1.51	0.15
Year * Land use	5	71.46	3.21	0.06

Table C.5: Model output on the original log-scale of the selected model for the local pollinator abundance (A). Pollinator abundance ~ Year

	Pollinator abundance			
Predictors	*Estimate*	*SE*	*Z-value*	*P-value*
(intercept) [SN]	3.528	0.443	7.966	**< 0,001**
Year	0.649	0.280	2.321	**0.020**
Observations	24			
R^2 Nagelkerke	0.273			

Table C.6: Model output of the selected model for the local bumblebee species richness (C). Bumblebee species richness ~ Land use.

	Bumblebee Species Richness			
Predictors	*Estimate*	*SE*	*t-value*	*P-value*
(intercept) [SN]	5.583	0.476	11.728	**< 0,001**
Land use [SS]	-1.167	0.673	-1.733	0.097
Observations	24			
R^2 / R^2 adjusted	0.120 / 0.080			

Table C.7: Model output on the original log-scale of the selected model for the local butterfly abundance (D) Butterfly abundance ~ Land use.

	Butterfly Abundance			
Predictors	*Estimate*	*SE*	*Z-value*	*P-value*
(intercept) [SN]	1.764	0.252	7.008	**< 0,001**
Land use [SS]	-0.665	0.374	-1.776	0.076
Observations	24			
R^2 Nagelkerke	0.177			

Local flowering plant data:

Model selection of linear mixed effect models testing for the effect of land use and year on flowering plant abundance (A), species richness (B) and Shannon diversity index (C). K = the number of parameters in the model. AICc = the corrected Akaike information criterion. ΔAICc = The difference in AICc of each model to the model with the lowest AICc. AICcWt = The AICc weight.

A: Model selection. Plant Abundance on a linear model

Model	K	AICc	ΔAICc	AICcWt
Year + Land use	4	304.54	0.00	0.60
Year * Land use	5	305.86	1.32	0.31
Land use	3	308.51	3.98	0.08
Year	3	322.86	18.32	0.00
Constant	2	323.31	18.78	0.00

B: Model selection. Plant Richness on a linear model.

Model	K	AICc	ΔAICc	AICcWt
Land use	3	133.74	0.00	0.63
Year + Land use	4	135.13	1.40	0.31
Year * Land use	5	138.35	4.61	0.06
Constant	2	153.88	20.15	0.00
Year	3	155.94	22.20	0.00

C: Model selection. Shannon diversity index on a linear model.

Model	K	AICc	ΔAICc	AICcWt
Year + Land use	4	15.32	0.00	0.61
Land use	3	17.08	1.77	0.25
Year * Land use	5	18.53	3.22	0.12
Year	3	23.56	8.25	0.01
Constant	2	23.98	8.66	0.01

Table B.8: Model output of the selected model for the local flowering plant abundance (A)
Abundance ~ Year + Land use

	Flowering Plant Abundance			
Predictors	*Estimate*	*SE*	*t-value*	*P-value*
(intercept) [SN]	694.17	80.78	8.593	**< 0,001**
Year	-128.67	48.71	-2.641	0.015
Land use [SS]	-266.17	48.71	-5.464	**< 0,001**
Observations	24			
R^2 / R^2 Adjusted	0.637 / 0.602			

Table B.9: Model output of the selected model for the local flowering plant species richness (B)
Species richness ~ Land use

	Flowering Plant Species Richness			
Predictors	*Estimate*	*SE*	*t-value*	*P-value*
(intercept) [SN]	18.417	1.018	18.083	**< 0,001**
Land use [SS]	-8.500	1.440	-5.902	**< 0,001**
Observations	24			
R^2 / R^2 Adjusted	0.613 / 0.595			

Table B.10: Model output of the selected model for the local plant Shannon diversity index (C).
Shannon Diversity Index ~ Year + Land use

	Shannon Diversity Index			
Predictors	*Estimate*	*SE*	*t-value*	*P-value*
(intercept) [SN]	2.4974	0.1952	12.793	**< 0,001**
Year	-0.2501	0.1177	-2.125	**0.046**
Land use [SS]	-0.4149	0.1177	-3.524	**0.002**
Observations	24			
R^2 / R^2 Adjusted	0.446 / 0.394			

Appendix D: NMDS ordination stress plots

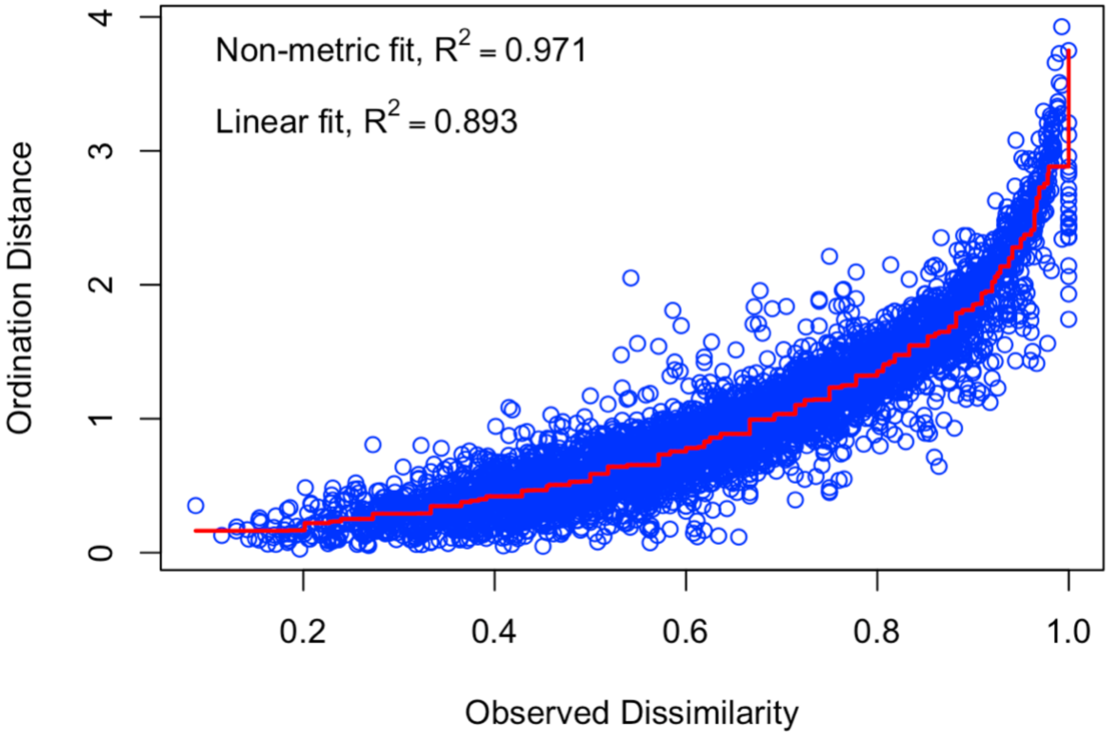


Figure D.1: Stress plot of the ordination for bumblebee species composition in the regional sites.

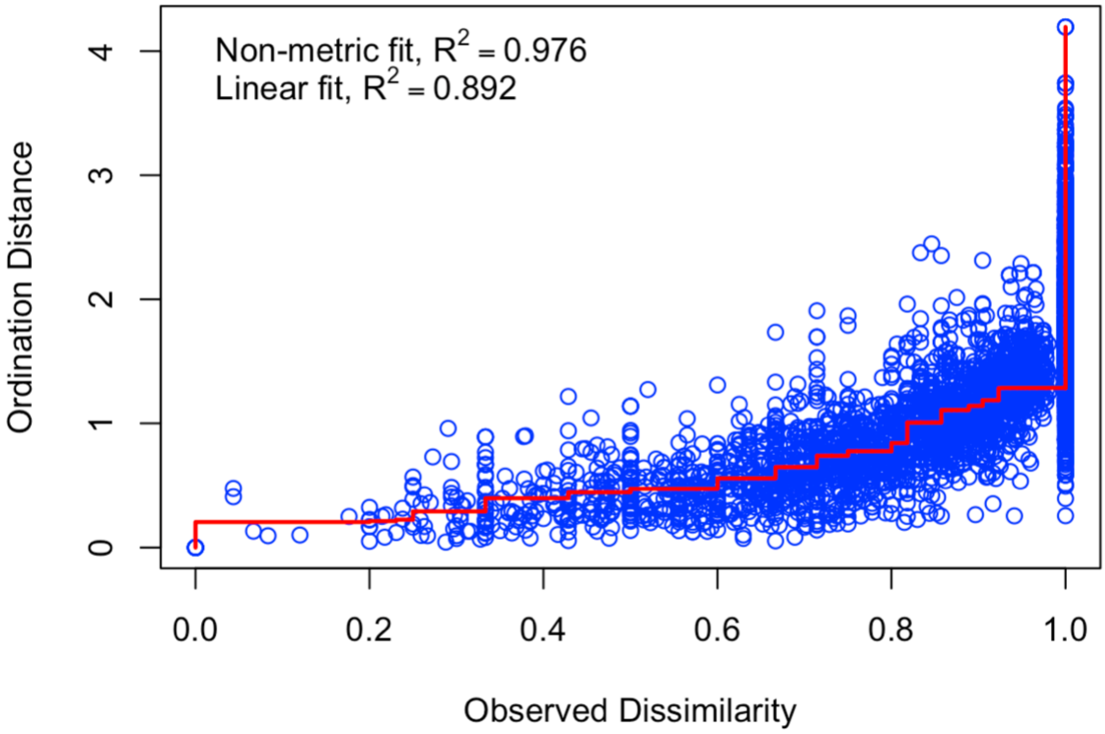


Figure D.1: Stress plot of the ordination for butterfly species composition in the regional sites.

Appendix E: Plant-pollinator networks

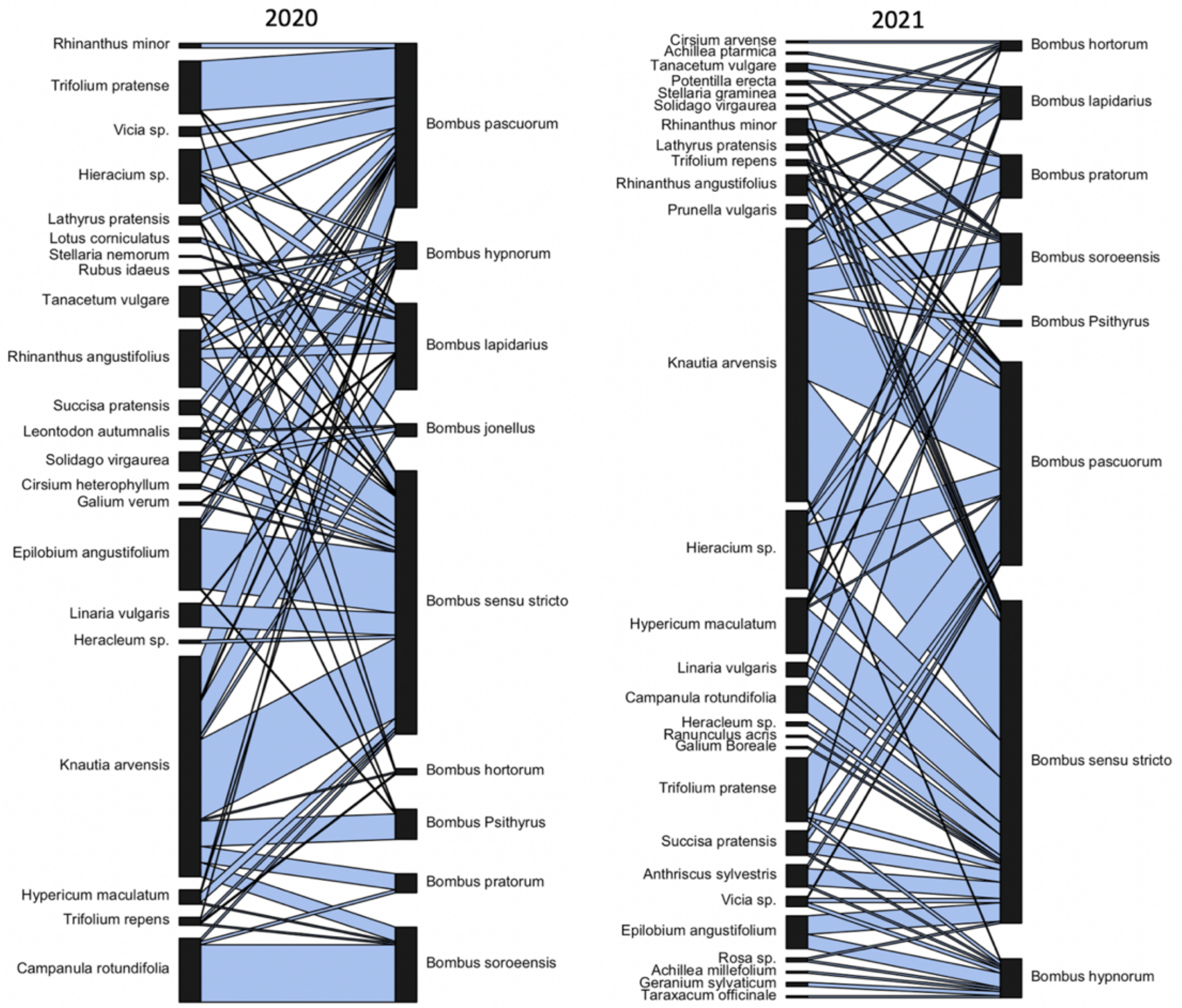


Figure E.1: Plant-pollinator network constructed for plant-bumblebee interactions observed in semi-natural grasslands in Trondheim, the local survey, in 2020 and 2021.

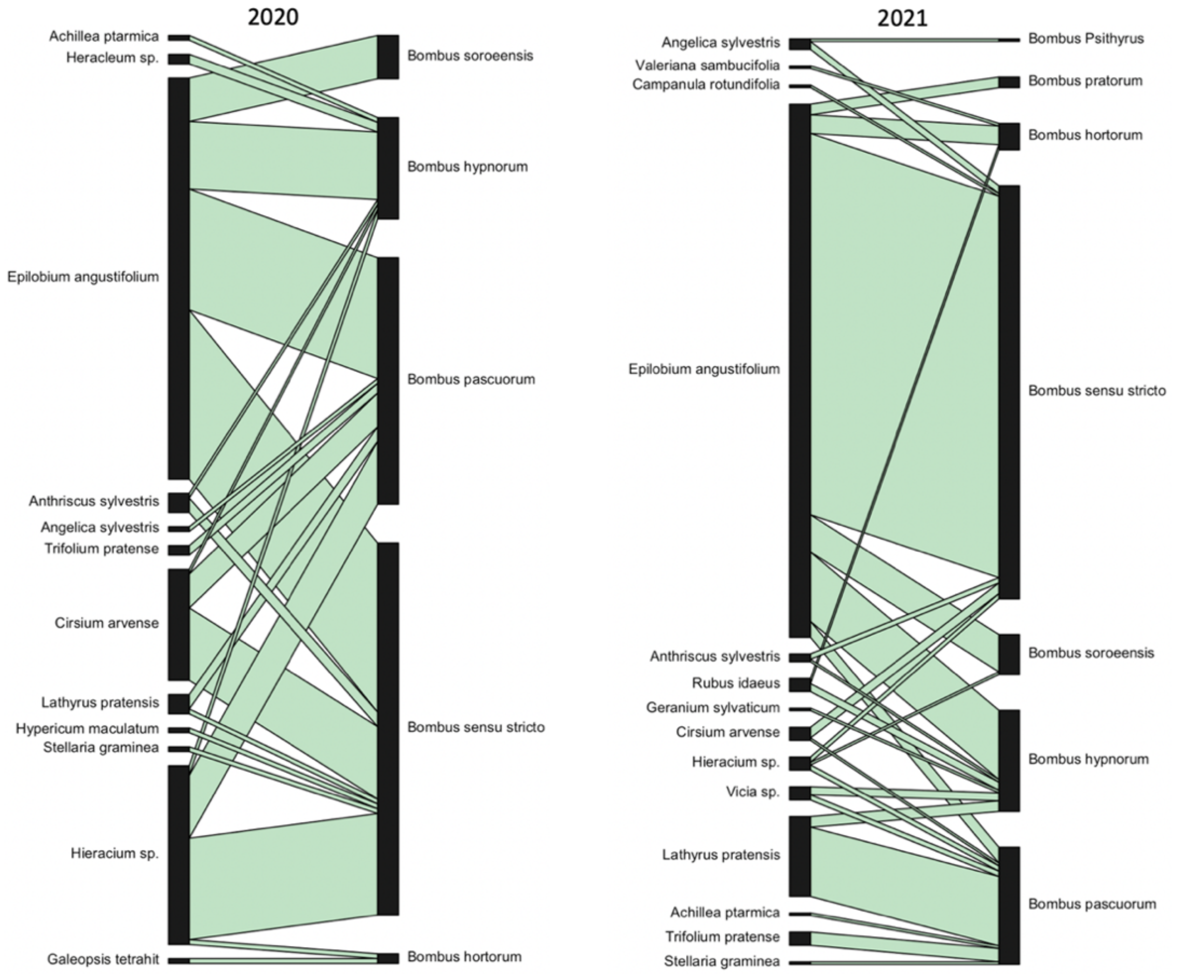


Figure E.2: Plant-pollinator network constructed for plant-bumblebee interactions observed in successional grasslands in Trondheim, the local survey, in 2020 and 2021.

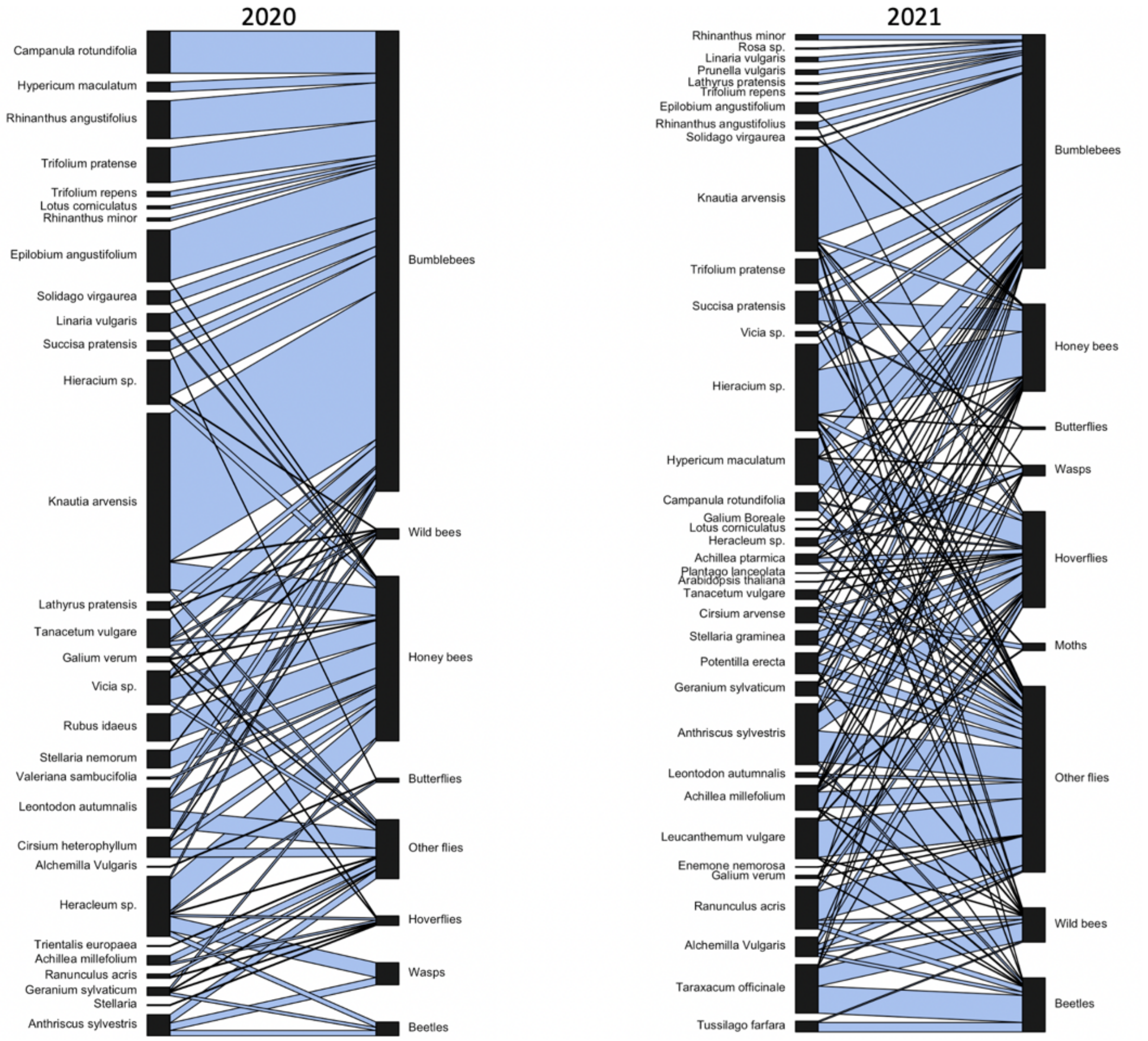


Figure E.3: Plant-pollinator network constructed for higher order groups of pollinators and their interactions with flowering plants observed in semi-natural grasslands in Trondheim, the local survey, in 2020 and 2021.

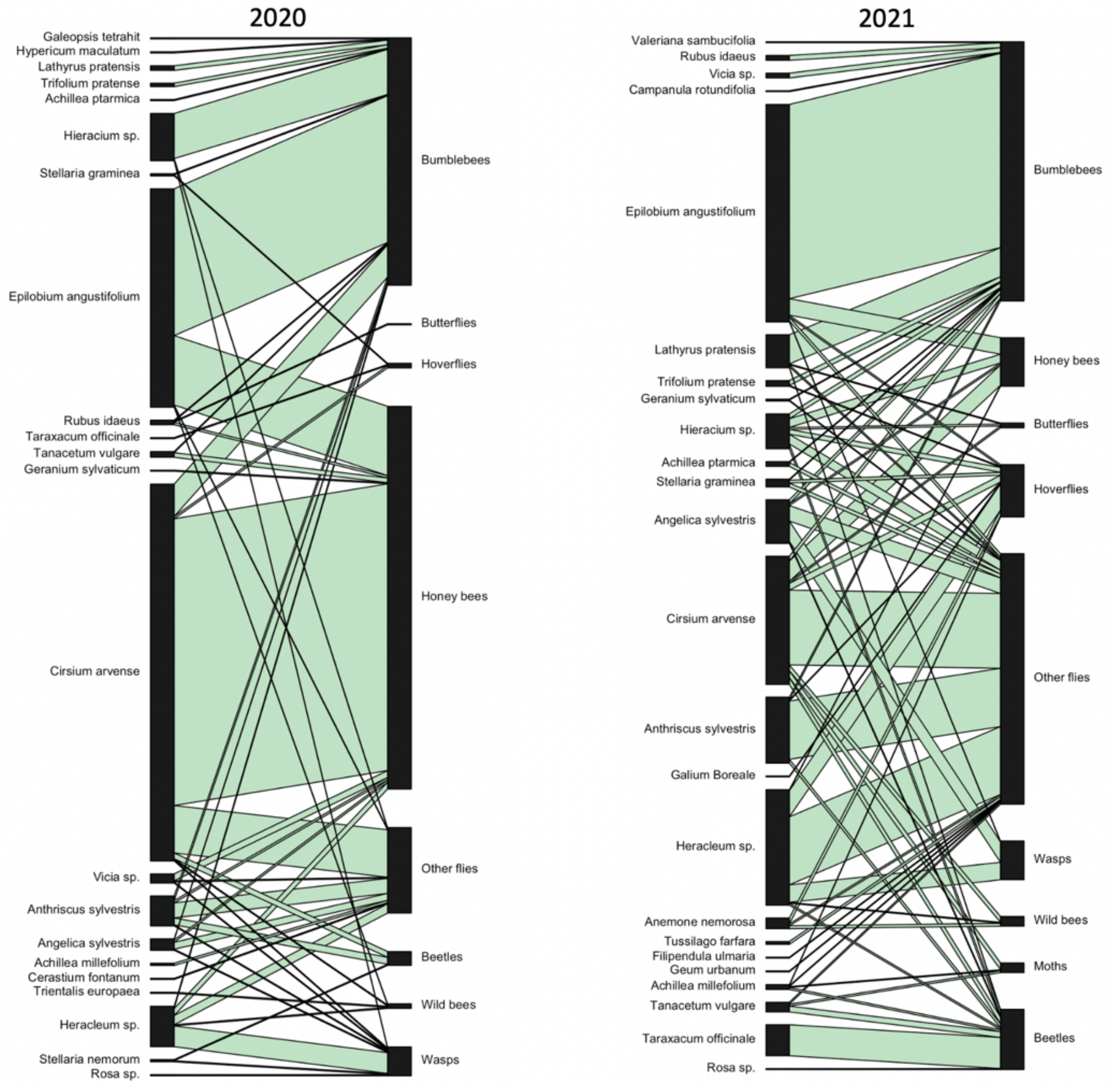
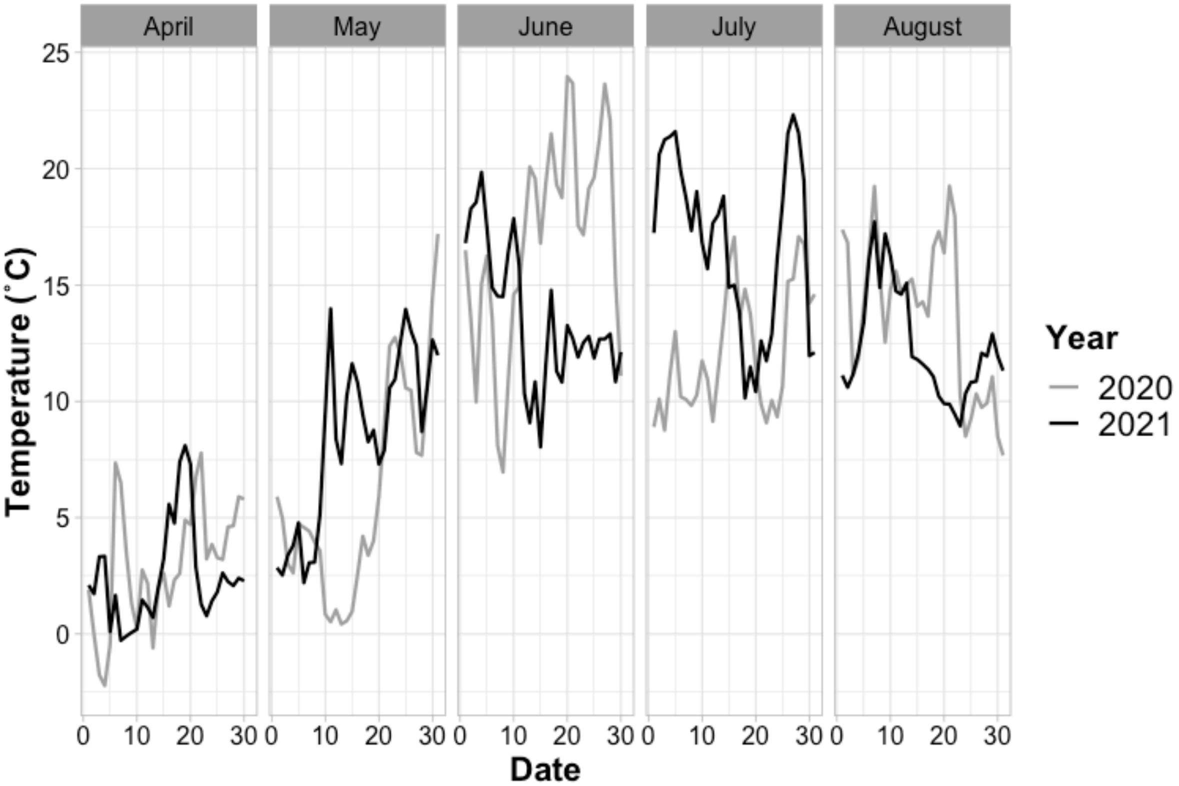


Figure E.4: Plant-pollinator network constructed for higher order groups of pollinators and their interactions with flowering plants observed in successional grasslands in Trondheim, the local survey, in 2020 and 2021,

Appendix F: Weather data for the regional and local areas

a)



b)

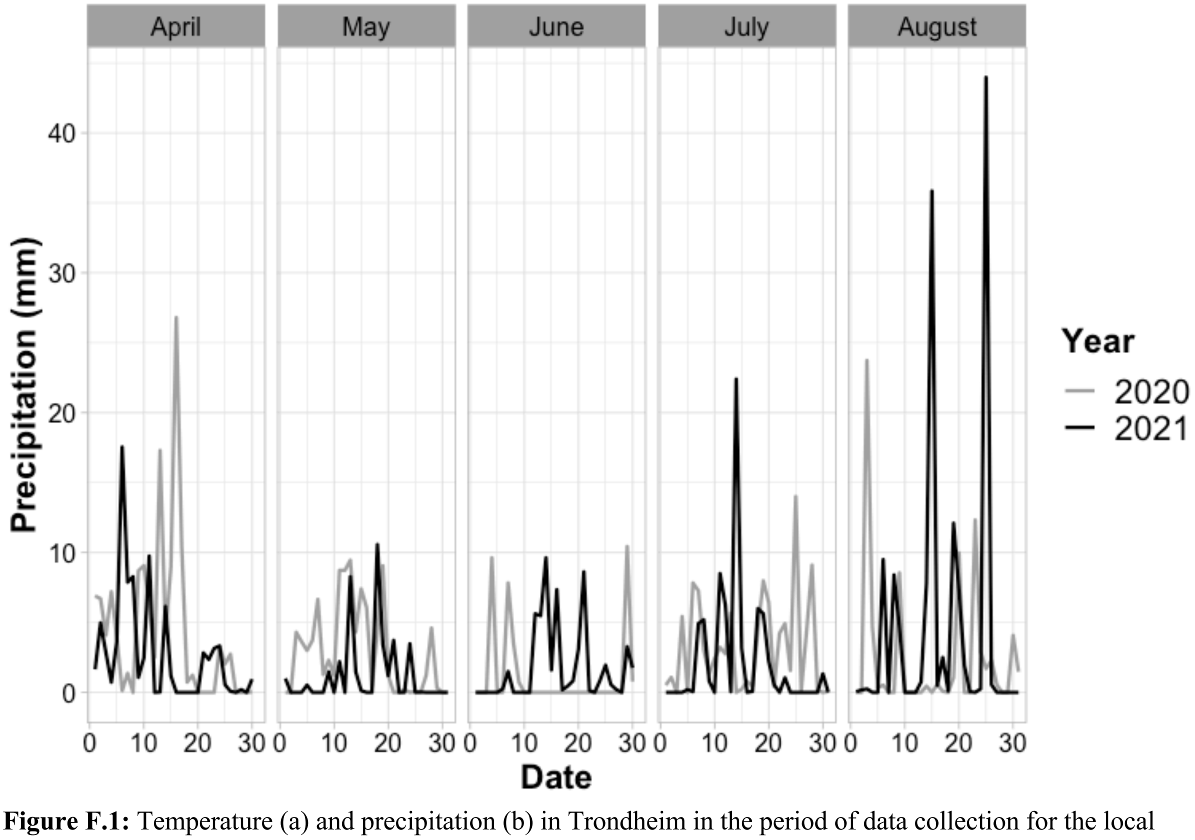


Figure F.1: Temperature (a) and precipitation (b) in Trondheim in the period of data collection for the local survey for each year, 2020 (grey) and 2021 (black). The weather data is from Norsk Klimaservice senter, Seklima.met.no.

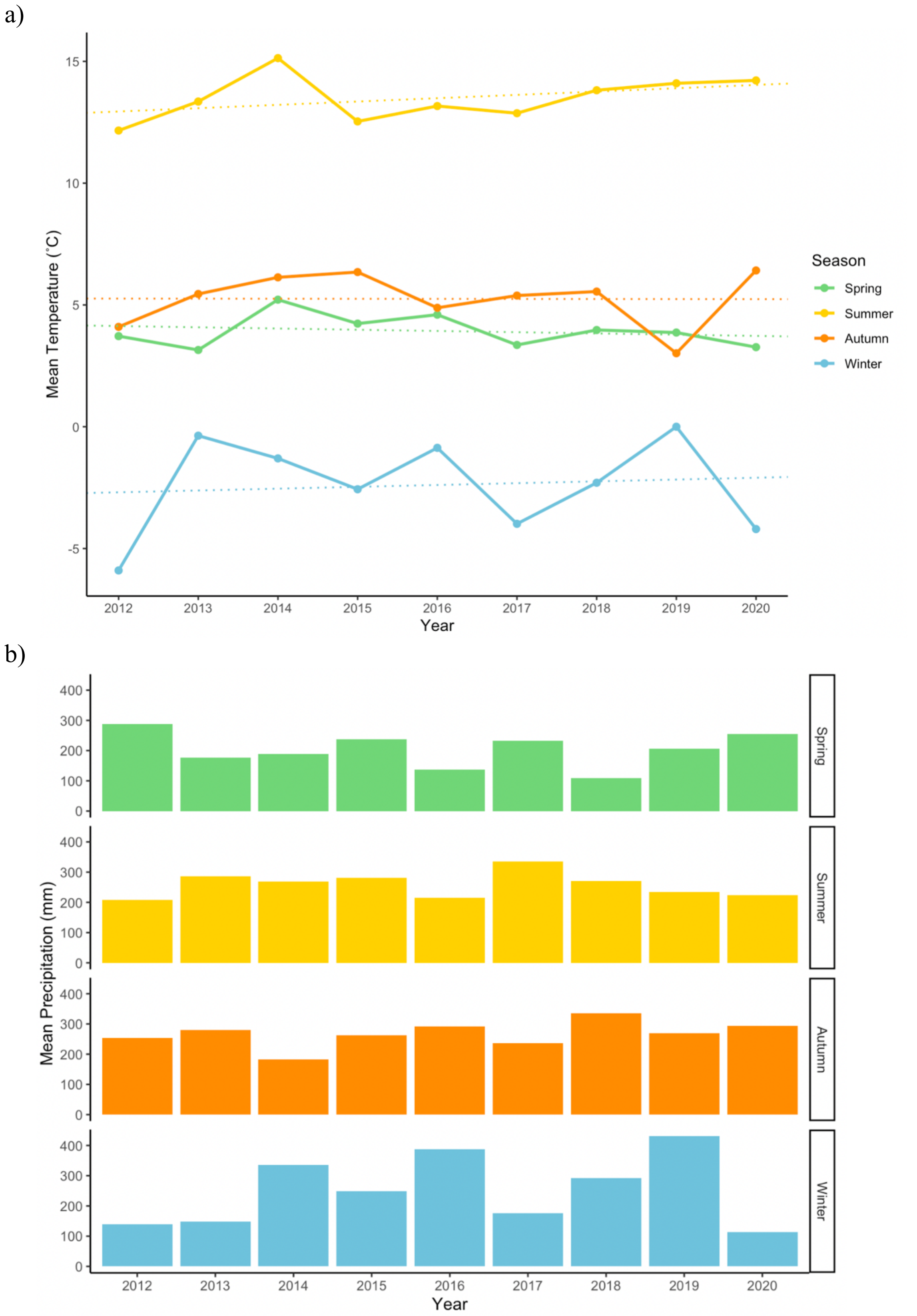


Figure F.2: Mean seasonal temperature (a) and precipitation (b) across weather stations near the regional sites. Each season encompass the mean over three months, spring (March, April and May), summer (June, July and August), Autumn (September, October and November) and Winter (December, January and February). The weather data is from Norsk Klimaservice senter, Seklima.met.no.

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