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## **PREFACE**

This thesis is written as part of the Master of Science in Biology with a specialization in Ecology, Behaviour, Evolution, and Biosystematics. The research was performed at the Norwegian University of Science and Technology University (NTNU) Museum, Trondheim. I have written this thesis while studying at NTNU, where I got a chance to explore many new things and most parts of the Trondheim municipality during my research period.

Finding a master thesis's topic was challenging and exciting too. At the beginning of the master's program, I was given a wide range of topics and research ongoing in my faculty. Looking over those topics finally, I decided to choose the topic related to the plant-pollinator relationship, which fits with my background too. This study has investigated the effects of land-use changes and season on the flowering plant species and plant-pollinator interaction networks across urban grasslands in Trondheim.

Although it has been hard during the fieldwork, I am glad to say that it has been a memorable experience in my life to learn new skills and techniques. I want to express my deep sense of gratitude and sincere appreciation to my supervisor Frode Ødegaard and co-supervisor Gunnar Austrheim for their technical and deliberate guidance, supervision, and valuable suggestions throughout the research and preparation of this manuscript. I would also like to acknowledge Sandra Åstrom for her guidance on sampling methods. Finally, I would like to acknowledge all my friends and family who helped me directly or indirectly during this research period.



## ABSTRACT

Plant-pollinator ecological relationship is crucial interaction in global biodiversity as it maintains pollination services and balances biotic communities in the ecosystem. Land-use changes in urban grasslands may affect the plant-pollinator interaction by changing the plant-pollinator composition and their relationship. In addition, seasonal changes will also affect the interaction networks by influencing the phenology of flowering plant species and determining the resource availability for pollinators. Pollination services in urban habitats are considered to be threatened, but few studies have examined plants and pollinators regarding the pollination interactions in Norway. This study has examined the effects of land-use changes and season on flowering plant species and plant-pollinator interaction by mapping pollination networks in two land-use types along with seasonal shifts in grasslands in Trondheim municipality. This study focused on the change in flowering plant richness and abundance with their impact on bumblebee richness and interactions network at the species level of bumblebee and different pollinator groups in different seasons. Floral richness, floral abundance, pollinator abundance, and bumblebee richness were found higher in semi-natural grasslands than in successional grasslands. These results show that changes in land use will affect plant and pollinator community composition. Furthermore, network indices like links per species, Shannon diversity, and Specialization Index ( $H2'$ ) were calculated. These network indices showed that with the increasing number of links per species and species diversity, networks were more specialized in semi-natural grasslands than in successional grasslands for both bumblebee species and pollinator group networks as determined by the specialization index. With the change in season, the diversity and links per species varied, and the network specialization of respective grasslands. The results suggest that plant-pollinator networks will change throughout the growing season due to resource availability in existing land-use types, determined by the changes in land use. Therefore, conservation and land-use management practices should be promoted to enhance the pollination services and maintain the plant and pollinator biodiversity in the existing urban grasslands.

**Keywords:** Urban grasslands, land use, season, species richness, bumblebees, interaction, plant-pollinator network.





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# **1. INTRODUCTION**

In an ecological community, numerous species exist and are obligated to each other by a network of interactions. Species interaction is the foundation for many ecosystem services like food webs, nutrient cycling, and pollination service (Agrawal et al., 2007). Pollination is thus an ecological service that supports the plant biodiversity and productivity of agricultural systems worldwide. Pollination is the transfer of pollen from anther to the stigma of the same or another flower, leading to the fertilization of ovules and sexual reproduction in the plants. It supports both plant reproduction and food production for humans and animals by developing fruits and seeds. Plants can be self-pollinating, where the plant can fertilize itself, or cross-pollinating, in which the plant needs a pollinator for pollination. A pollinator can be anything that helps transferring pollen to the stigma of the same or different flower. Wind and water are abiotic pollinators, whereas birds, insects, bats, and other animals that visit flowers are biotic pollinators. Since this study focuses on animal pollinators, the term "pollinator" will only refer to animal pollinators. Paleontological studies reveal that plant-pollinator mutualisms date back to the Cretaceous period when pollinators began to collect food from floral resources. Flowering plants achieve higher reproductive success through pollen movement pollinators (Kearns & Inouye, 1997). Natural and semi-natural habitats support a wide range of plant and pollinator communities, ecological functions, and associated ecosystem services. With intensive management practices or land-use change activities, the ecosystem degrades, which lead to the loss of habitat and the world's biodiversity by threatening the provision of pollination services and food security which it supports (Kearns et al., 1998; Potts et al., 2010)

## **1.1 Land-use and seasonal changes**

Landscape characteristics and land use have an essential role in maintaining diverse pollinator communities in several ways. Many studies and assessment (Aguirre-Gutiérrez et al., 2015; IPBES, 2016; Kennedy et al., 2013; Tschardt et al., 2005) showed that land-use changes could alter the distribution and diversity of pollinating resources by affecting individual behaviour, community composition, and population dynamics of both floral and pollinator species. Decreasing heterogeneity of landscapes results in pollinator decline (Andersson et al., 2013), and reduces patch size, connectivity, and loss of habitat area, further declining species richness (Marini et al., 2014). Urban areas, the most extensively changed landscapes, are increasing worldwide, leading to more habitat fragmentation and loss of natural habitat, thus

affecting plant-pollinator composition and relationship (Harrison & Winfree, 2015). Plant communities exist in small fragmented or isolated patches in urban areas relying on limited pollinator populations available there, which are vulnerable to population fragmentation. (Alberti, 2005; Angold et al., 2006; Kearns & Inouye, 1997). Urban grasslands are sensitive to disturbance, and most have been changed forever for human settlement and replaced wildlife with domestic animals (van der Walt et al., 2015). Livestock grazing and other intensive management practices can modify the plant community and alter the pollinator's density by making a difference in nesting resources and insect life-history traits in grasslands (Hanley & Goulson, 2003).

Apart from land-use changes, seasonal changes in precipitation and temperature can also alter the abundance and flowering period of plant species, influencing pollinators' activity period and shifting the range of plant and pollinator species (Osborne et al., 1999). For instance, the seasonal shift can change the phenological patterns of flowering plant species and reduce the floral resources available to pollinators, causing a decline in pollinators and plant-pollinator interactions (Memmott et al., 2007). Also, seasonal changes can affect the overwintering behaviour of insect pollinators or their pupation stage and their foraging season by reducing the early or late season forage for establishing colonies (e.g., in bees, the survival of queens and whole colony) (Memmott et al., 2007).

In Norway, the northern ecosystem has a short seasonal activity for both flowering plant species and foraging pollinators (Willmer, 2011). Besides, semi-natural habitats like hay-making land and grazing land have declined dramatically during the past hundred years (Norderhaug & Johansen, 2011), which may have reduced the resources for plant and pollinator community by increasing fragmentation. Such semi-natural habitat types with high species richness and abundance are in decline today. This decline in biodiversity related to pollination service and based on information about Norwegian pollinating fauna and flora reported by Totland et al. (2013) concluded that more studies of pollination service in Norway are needed to improve knowledge in this field. Therefore, this study will try to find more information on pollination services concerning the Norwegian ecosystem. Many relevant studies have studied pollination systems through the plant-pollinator interaction network approach (e.g., (Bendel et al., 2019; Fründ et al., 2010)), so similarly, it will be the primary approach of this study.

## **1.2 Plant-pollinator interaction**

Plant-pollinator mutualistic interaction involves exchanging goods or services between the species that have been crucial in the generations of Earth's biodiversity (Bascompte & Jordano, 2007). Flowers must rely on pollination agents, and many pollinators get their nourishment from the plants (Potts et al., 2010). Although some species depend upon abiotic vectors for pollen transfer, more than 90% of the planet's angiosperms depend on pollinators to complete their reproductive stage (Kearns et al., 1998). Many individual plant species can self-pollinate without the help of animals. However, long-term self-pollination by all individuals would end inter-breeding among individuals of the same species or are genetically self-incompatible (Ollerton et al., 2011). The pollinators maintain the structure and functions of a wide range of natural communities and enhance the aesthetic, recreational, and cultural aspects of human activity.

Worldwide, around 300,000 species are estimated to be the flower-visitors of which bee species contribute for 25,000-30,000 alone and other pollinators like butterflies, flies, moths, wasp, beetles, birds, and mammals (Kearns & Inouye, 1997; Nabhan & Buchmann, 1997). Around 352,000 species of angiosperms exist globally, of which 90% species are found to be biotically pollinated in the biodiversity, and 60 to 80 % of wild floral species need animal pollinators for their existence in nature, while only 35 % of the world's crop production benefits from animal pollinators (Kearns et al., 1998; Potts, Imperatriz Fonseca, et al., 2016). Among the pollinators, insects are the most common pollinators. Insect pollinators are crucial for the maintenance of biodiversity and global food security. Around 75% of crop species and up to 88% of flowering plant species rely on insect pollinators; among them, wild insect pollinators contribute substantially to the productivity of many crops and seed setting of wildflowers (Powney et al., 2019). That is why a plant-pollinator relationship is a key interaction with implications for human livelihoods and wild ecosystems.

## **1.3 Plant-pollinator network**

Plant-pollinator networks include species involved in pollination service and represent all interactions between co-existing plants and their flower visitors within a researcher-defined site. The plant-pollinator network is structured and determined by various factors like the co-occurrence of species in space and time and morphological and physiological traits of interacting species (Bartomeus et al., 2016). Recent studies on pollination systems have greatly

advantaged the plant-pollinator interactions through examining the pollination network (Bascompte & Jordano, 2007; Vázquez et al., 2009). These studies delineated community functioning and allowed inferences to be determined about community structure and resilience, like identifying the aspects of networks that are vulnerable to disturbance and how they can be conserved (Tylianakis et al., 2010). A pollination network is a bipartite mutualistic network with two levels, where plant species and pollinators act as the nodes and the interactions between them as the links (Fonkalsrud, 2014). Pollination network diagrams illustrate the degree or number of species interacting with each other and the interaction strength between the two levels and see their responses independently to the disturbances (Elle et al., 2012). Several descriptive metrics like species richness, abundance, linkage density, links per species, interaction diversity, network specialization ( $H_2'$ ), and so on can be calculated from the pollination network (Chacoff et al., 2018; Dormann et al., 2009). Such indices of pollination networks can be essential to study and better understanding the relationships existing in interacting plant-pollinator communities and compared with relevant communities through which biodiversity management decisions can be made.

#### **1.4 Main pollinators**

Within the insect pollinators, bees are the most dominant and frequent visitors to flowering species (Neff & Simpson, 1993; Winfree et al., 2011). Bees are obligate florivores throughout their different life stages and use pollen and nectar as their foods, so they are special floral visitors. Bee species have various morphological adaptations like a different length of tongues, cubacula, or scopa, which helps to exploit many several floral designs and transfer pollen more efficiently, resulting in more interactions with flowers than other pollinators (Danforth et al., 2006). Honeybees are the most valuable pollinators economically as they pollinate crop monocultures globally and act as the alternatives for wild bees to ensure pollination in agriculture fields (Klein et al., 2007). Non-*Apis* species (wild bees) are significant for wild plant pollination and are also equally effective or better than honeybees for some crops (Winfree, 2010). Bumblebees (*Bombus spp.*) are wild bee species common in temperate and colder habitats and primarily distributed throughout the northern hemisphere (Abrol, 2011). Bumblebee species can carry and transfer more pollen from anther to stigma than other insects (including *Apis mellifera*) and forage floral resources for more extended periods of the day, even in poor weather conditions, so they are more effective and active pollinators among the bee pollinators (Abrol, 2011).

After the bees, flies are second in their importance as floral visitors, and despite their poor pollen carrying capacity, their sheer abundance makes a considerable impact on pollination service. Hoverflies (flower flies) are well known as the best flower foraging flies, which feed on both nectar and pollen. They are even compared with bees in importance as pollinators in some tropical and semi-arid zones and where bees are uncommon, like in cold and high-altitude habitats (Willmer, 2011). Other insect pollinators like butterflies, moths, beetle, thrips, and wasps usually encounter many flower species that support pollination mechanisms.

### **1.5 Pollinator decline**

The pollinator populations are shifting, and a global decline has been noticed in different parts of the world (Kearns et al., 1998; Potts et al., 2010). The pollinator richness has diminished in the last 50 years, undergoing a significant decline in some species while some have become extinct (Goulson et al., 2015). Despite the worldwide increase of managed honey bee colonies, both wild and managed bees have undergone marked declines in Europe and North America over several decades (vanEngelsdorp et al., 2011). Evidence is in the form of case studies reported by the researchers. Assessment of long-term data from Britain (Scotland, England, and Wales) between 1980 to 2013 suggests a broad difference in the trends and reductions in richness and abundance of managed and wild pollinators. Within this period, 33% of wild pollinator species have decreased, while about 10 % increased in number, including bees pollinating crops (Powney et al., 2019). Although the common species are increasing, rarer species are decreasing, so overall biodiversity is being lost. The loss of this service will also reduce the pollination activities, further hindering the ecological balance of biodiversity. A pollinator decline limits pollen carry and deposition, resulting in reduced plant reproductive success, which deteriorated plant-pollinator interaction and threatened natural populations' extinction (Biesmeijer et al., 2006). This loss of ecosystem functions could create problems in the future, including growing food crops and risk long-term food security.

Plant and pollinator biodiversity is threatened by a combination of many land-use changing drivers, including land clearing and conversion to agriculture or pasture land, extensive grazing, monocultures, pesticide, and herbicide use, and introduction of commercial bees (Bradshaw et al., 2009; Potts, Ngo, et al., 2016). This declining plant and pollinator population trend accentuates the need to understand better pollination services and plant-pollinator interactions (Elle et al., 2012).



## 1.6 Status of pollination in Norway

Norway has relatively few activities and studies in pollination ecology compared to other Scandinavian countries. Totland et al. (2013) have reported about the status and characteristics of pollination service in Norway. Insects are the only pollinating fauna in Norway. The number of pollinator species is lower in Norway compared to other northern countries. Species richness and abundance of solitary bees are comparatively low in contrast to southern Europe. Despite that, bumblebee species richness is higher compared to other European countries. Bumblebee species and various flies have dominated the Norwegian pollinator fauna (Totland et al., 2013). The geographical conditions and topography of Norway contrast with the rest of Europe, so the distribution and population of pollinators seem different and limited in survival and dispersal in Norway.

According to Totland et al. (2013), most Norwegian floral species show a generalization pattern of interaction, despite some species showing specialization, which often has zygomorphic (bisymmetric) long corolla and are pollinated by long-tongued bumblebees like *Bombus hortorum* and *Bombus consobrinus*. Norway has a relatively low number of pollinators, and due to the short season, flowering must be achieved in this short period which causes both inter and intra-specific competition for any available pollinators (Willmer, 2011). Similarly, bee and fly species must forage in the short flowering period from the limited flora available, and due to low pollinator richness, it leads to more generalization interacting patterns for their survival and existence.

## 1.7 Objectives

The main objective of this study is to see how land-use changes and seasonal changes affect flowering plant communities and plant-pollinator networks in urban grasslands in Trondheim. With the main objective, there are three sub-objectives of this study: (a) to quantify the abundance and diversity of flowering plant species and pollinators in successional and semi-natural grasslands, b) to describe plant-pollinator interactions in grassland, and c) to observe plant-pollinator networks in the working grasslands along with seasonal shift. For each sub-objective, we have the following respective hypotheses:

- a. **Change in land use will change the abundance and richness of the flowering plant species existing in that environment:** Species have their specific habitat requirements and are sensible to land-use change. This study will examine the effect of land-use changes in the abundance and richness of flowering plants in different habitat types. Heggøy (2021) examined the change in pollinator communities in the same habitats with the same data sources as in this study.
- b. **Increase in the availability of flowering plants and resources will positively influence the plant-pollinator networks:** More pollination services are expected when there are high or increased species richness and abundance of flowering plants and resources. The abundance and diversity of pollinators have been positively correlated with pollination services. With more pollination services through increased availability of floral resources, positive influence in the plant-pollinator networks is also expected. This study will also examine the patterns of pollination interaction network with change in plant and pollinator composition by observing network indices like links per species, Shannon diversity, and Specialization Index (H2').
- c. **Plant-pollinator networks will change throughout the growing season due to resource availability in working grassland types:** Availability of flowering plants and resources for pollination services also depend upon the period of flowering. The life cycle of plants goes through a different season, which affects the availability of resources to the pollinators and interaction patterns in the existing grasslands. This thesis will also study the change in plant-pollinator networks throughout the growing season in the given land-use types.

## 2. MATERIALS AND METHODS

### 2.1 Site description

The study was conducted in 2020 (May-August) at nearby grasslands in Trondheim municipality, Trøndelag, Norway (63°26'24"N 10°24'0"E). Trondheim is located at 18 m above sea level on the south shore of Trondheim Fjord at the Nidelva river's mouth. The climate type is cool and humid; winters are long and cold with short days and relatively low precipitation, mainly snowfall, while summers are short and mild with long days and moderate rainfall (Merkel, 2020). The annual mean temperature of Trondheim is 7.1 °C, and the average rainfall of 875.3 mm annually (Klimaservicesenter, 2020)

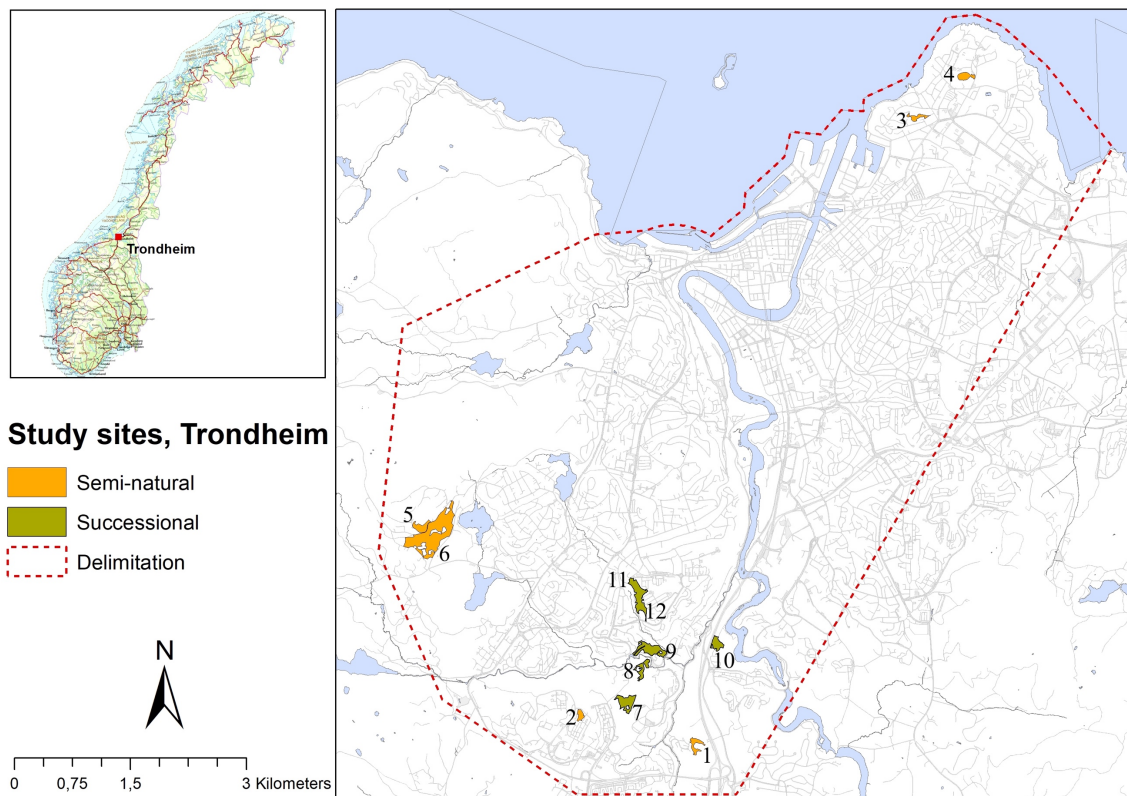


Figure 1. Map of the study sites with the delimitation showing the border for selected urban areas in Trondheim municipality

Based on the Area Resource Map (AR5) of Trondheim municipality and the delimitation map modified from Kleppe (2019), two land-use categories, successional and semi-natural grasslands, were identified within the municipality. The AR5 is a standard national map that classifies the area based on land use and primary environmental conditions (NIBIO, 2020). Twelve sites were selected with a stratified design within the Trondheim city, six sites of each land-use type.

Table 1. Sites selected for land-use types with their locality ID and area (m<sup>2</sup>) according to AR5 map.

Land-use type	S.No.	Sites	ID	Area (in m <sup>2</sup> )
Semi-natural	1.	Bjørndalen	7002	15653.293
	2.	Flatåsen	13534	9154.775
	3.	Grønlia	23748	10917.576
	4.	Lade	16320	15589.905
	5.	Lian Upper	23948	18278.888
	6.	Lian Lower	27627	167791.195
Successional	7.	Buengveien N	28321	18400.627
	8.	Buengveien S	27629	32460.200
	9.	Forsøkslia	2964	42657.035
	10.	Okstad	3761	18218.487
	11/12.	Selsbakk N/S*	6732	47494.892

\*Two sites from the Selsbakk area were selected and named as Selsbakk N (6732a) and Selsbakk S (6732b) for this study.



Figure 2. Successional (a. *Forsøkslia*) and semi-natural (b. *Flatåsen*) grassland in Trondheim. (Photo: Dhukuchhu A.)

Semi-natural grasslands were near to the human settlement, agricultural land, and with low-intensity management practices like grazing in some sites. Those grasslands were dominated by small grass and herb species with some trees and shrubs. On the other side, successional grasslands were near to forest or riverside that were left undisturbed now or previous management has been stopped and were bushy with tall weeds and invaded by shrubs and trees which are in a successional state now (Kleppe, 2019).

## 2.2 Data Collection

Four surveys were done from late spring (May) 2020 to late summer (August) 2020 to sample the plant-pollinator community composition. After site selection, a standardized transect sampling method, as reviewed by Gibson et al. (2011), was used. Five transects, each about 50 metres long per site, were fixed according to Öberg (2010), and a 5 metre distance was maintained between the two transects using a measuring tape and at least 10 m inside the site's edges (Figure 3). Coordinates of both starting and ending points were recorded with the help of a GIS (Geographic Information System) device and marked with a peg to have a reference for the next sampling period.

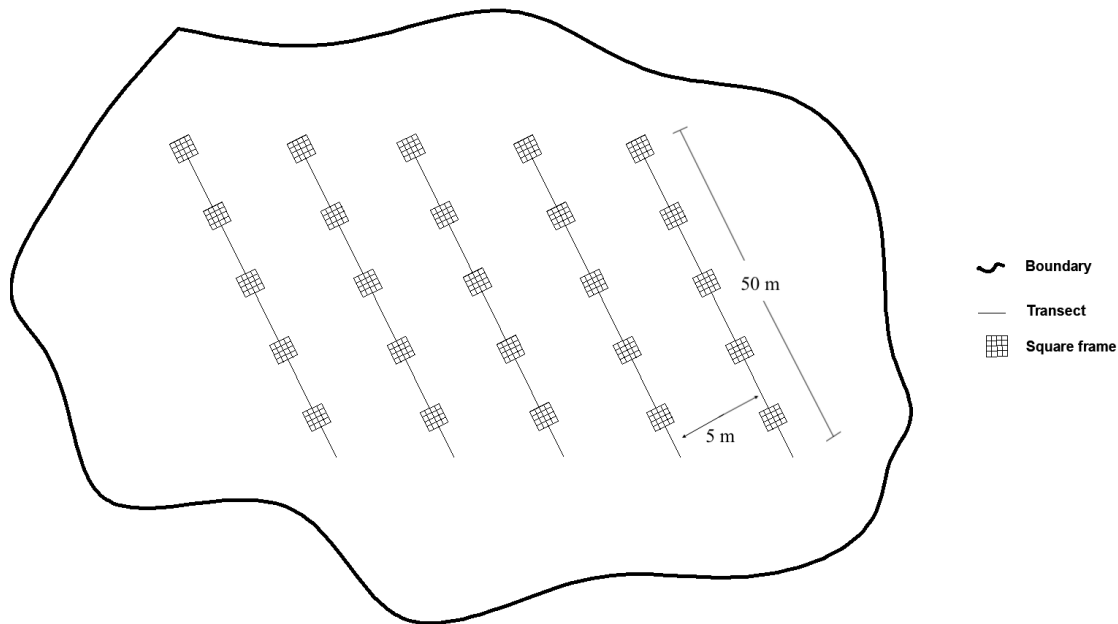


Figure 3. Fixed transects within the site and square frames in each transect.

After fixing the transects, sampling was done on sunny days between 10:00 to 17:00 hours, with a temperature of more than 15°C and sustained winds <15 km/h (Moranz et al., 2012; Popic et al., 2013). During site selection in early May, the temperature was lower than 15°C, so as the temperature increased in late May, sampling was started. With a thermometer, the ambient air temperature was measured at every starting point of each transect, and cloud cover as a percent of the sky covered by cloud at the sampling time. Pollinator species were identified by walking along the transect at a slow pace within approximately 2.5 m distance from the transect and recorded in the standard survey form (Appendix C). An aerial insect net was used to collect floral visitors.

### 2.3 Pollinator identification

All pollinators observed in the field were identified systematically. The unknown visitors were collected in small glass vials to identify them correctly. Simultaneously, some were stunned with carbon dioxide for a short period to identify them in the lab by assigning them a unique identification code related to the habitat type and date they were collected. Precautions were taken while observing to avoid killing queens; only males and workers were collected in a vial. Pollinators like a bumblebee, honey bee, butterfly, hoverfly, wasp, wild bee, beetle, and other insect pollinators were observed. All bumblebee species were identified to species level using the book "Humler I Norge" (Ødegaard et al., 2015). As most of the bumblebee species were identified at species levels, three unidentified species were named as sp1, sp2, and sp3. Some

butterfly species were also identified at the species level, whereas other pollinating insects were identified at the genus or family level.

## **2.4 Floral sampling and taxonomic identification**

Information about the abundance and species richness of flowering herb plants is needed to know the plant community composition in those grasslands. Data concerning flowering plant species were collected while conducting a transect walk. After the pollinator individuals were netted on a flower, the associated floral species where the pollinator was foraging were determined. In contrast, for floral abundance, a separate plant sampling was done using a standardized square frame. The frame was placed systematically along the transect at five different points with a 10m distance apart (Figure 3). The frame had 16 minor square subplots, and the number of subplots where a floral species occurred was counted for an abundance of each species. The same species found in the same subplot were counted as one even though there is more than one individual. All floral species were identified at the species level. In addition, the plant height of dominated species at each point where the frame was placed is measured by measuring scale (Figure 4f).



Figure 4. Data sampling and identification: (a) Transect walk and sampling pollinators, (b) Observing pollinator, (c) Identifying bumblebee species: *Bombus pascuorum*, (d) Sampling flowering plants (e) Floral species: *Leucanthemum vulgare*, and (f) Identifying and quantifying floral species and filed layer height within a square frame. (Photo Credit: Heggøy H., Austrheim G.)



## 2.5 Statistical analysis

All statistical analyses were done with R version 4.0.4 (R Core Team, 2021). The floral and pollinator communities' primary metrics, including their mean richness, and mean abundance from transect level data, were calculated to see the pattern of floral and pollinator species in different seasons. Mean plant height was also calculated to observe the productivity of each grassland type. The generalized linear mixed-effects models were fitted in R, using *lme4* packages to test land-use change and seasonal effect on the floral abundance and floral richness. Land-use type and season (month of the survey) were explanatory variables, temperature and cloud cover (%) were other predictor variables, whereas sites and transects nested in sites were random variables. According to Batushansky et al. (2016), the threshold of  $r \geq |\pm 0.5|$  was set up, and a correlation matrix was constructed to remove highly correlated variables (Appendix D). Floral richness was highly correlated with floral abundance ( $r = 0.62$ ) so, these variables were selected as a response variable separately in two different tests.

Firstly, to see the effect of land-use and seasonal change on floral abundance, the models were fitted. The temperature and cloud cover data were standardized to obtain a relatively well-fitted model for the data. The dispersion test was performed to check the overdispersion, and data were overdispersed. That is why models were again fitted with negative binomial distribution for generalized linear mixed effect modelling. The Second-order Akaike Information Criterion (AICc) model selection, using the *AICmodavg* package in R, was conducted to find the best model. The model explaining the change in floral abundance by the explanatory variables land-use type, change in season (i.e., month) and their interaction, and the additional effect of temperature variable gave the best-fitted model (Appendix E). Secondly, to see the effect of land-use change on a floral richness, the models were fitted. There was no overdispersion, so the models were fitted using Poisson distribution for generalized linear mixed effect models. Model explaining the interaction effect of land-use type and change in the season gave the best model to see the effect on floral richness. Parameter estimates were obtained from the best-fitted models with maximum likelihood (Laplace Approximation). The underlying model assumptions were verified and met by graphing the data and checking the random effects' linearity, homoscedasticity, and normality (Appendix F).

Both pollinators and interacting plant species datasets were used to explore the patterns of plant-pollinator relationship with seasonal shift. There were insufficient interaction data in the first

survey (May), so the change in plant-pollinator interaction network properties was observed only for the last three survey data. The *bipartite* package (Dormann, 2020) in R was used to get the interaction network and properties. Data were pooled at land-use type level for each observation period with the output of three plant-pollinator interactions for each land-use type. In this thesis, we focused on bumblebee species. It is the primary pollinator of a northern ecosystem, so the pollination network was analysed at the species level for both floral and bumblebee species. On the other hand, to observe the overall performance of other insect pollinator groups in interactions, the second version of interaction networks was analysed on plant family and pollinator groups' taxonomic levels. Each connecting line between the bumblebee species and flowering plant species or between the pollinator groups and plant family show which species from one trophic level made interactions with another trophic level in each land-use type. The same pollinator species may interact with different plant species in other habitats due to the availability of plant resources. Following network parameters for all pollination networks describing their properties were calculated:

1. **Links per species:** The mean number of species from the other level with which each plant or pollinator species interacts in the network.
2. **H2':** The specialization index developed by Blüthgen et al. (2006) derived from Shannon entropy, which helps to compare different interactions network and analyse variations between them. The H2' ranges from 0 representing most generalized or a perfectly nested network to 1 are showing most specialized network (Blüthgen et al., 2006).
3. **Shannon diversity:** It shows the diversity of the network entries.

H2' score was used to evaluate the specialization and generalization in networks throughout the growing season in both successional and semi-natural grasslands. Null models were generated to examine the differences between the observed network and a random network structure. Here, 1000 null models were created according to the "r2dtable" method (Patefield, 1981) for the observed networks. Random networks were generated in this method by keeping row and column sums constant. The statistical significance of observed interaction networks with the respective null models were tested by using the z-score and a two-sided p-value. Then, the differences between the two observed networks were tested through null-model entire analysis approach (Dormann, 2020) in which intended analysis on observed network index (H2' for this study) was carried out by repeating it 1000 times with null models of each network.

### 3. RESULTS

#### 3.1 Plant composition

Throughout the survey, 50 flowering plant species from different plant families were recorded. Species list and their abundance are provided in appendix A. Out of 50 plant species, 49 plant species were observed in semi-natural and 27 in successional grasslands. Twenty-six flowering plant species were observed in both land-use types, whereas 21 different species were recorded only in semi-natural and 3 in successional grasslands.

In the first survey in May 2020, fewer floral species and even no floral species were observed in some sites. However, in the following three surveys; June, July, and August, more floral species were observed (Figure 5A). From the transect level data, the overall mean and standard error of floral richness was  $5.34(\pm 0.29)$  in semi-natural and  $2.67(\pm 0.17)$  in successional land-use type. The highest richness was observed in August for semi-natural  $6.87(\pm 0.51)$ , but for successional, it was in June  $3.78(\pm 0.19)$  and lowest for both land-use types in May (Figure 5A). Floral species were increasing from May to August in semi-natural grasslands, whereas it increased from May and reached a maximum in June and decreased later in July and August in successional grasslands. However, there was no similar pattern of changing floral abundance like floral richness. Floral abundance increased rapidly from May (lowest abundance) to June (highest abundance) but decreased in both land-use types (figure 5B) later in July and August. In June, the mean floral abundance was  $44.5(\pm 3.5)$  in semi-natural and  $35.5(\pm 2.67)$  in successional grasslands (Figure 5B). While between the two land-use types, the mean floral abundance was  $28.01(\pm 1.78)$  in semi-natural, whereas  $17.78 (\pm 1.42)$  in successional grasslands overall.

In May, plant species from Ranunculaceae (e.g., *Anemone nemorosa*) dominated both grasslands and Rosaceae species; *Alchemilla vulgaris*, was highly abundant in semi-natural grasslands only. In June, *Anthriscus sylvestris*, *Lathyrus pratensis*, and *Vicia species* dominated both grasslands. *Alchemilla vulgaris* and *Stellaria graminea* were observed more in semi-natural than in successional grasslands. It seems that flowering species from Asteraceae and Fabaceae were in an increasing pattern. More species from those two families were observed with more distribution in semi-natural grasslands in July and August. A new species, *Epilobium angustifolium* from Onagraceae, was emerging in successional grasslands, and later in August,

more number was observed. One flowering species, *Stellaria graminea*, was observed throughout the sampling period in high numbers in all sampling rounds in both land-use types. Many species were observed and different species dominated at each period. In response to plant height, generally the average height of plant species was higher in successional compared to semi-natural grasslands. The average height was maximum in June for both successional (119.18 cm) and semi-natural (50.5 cm) grasslands (Appendix G).

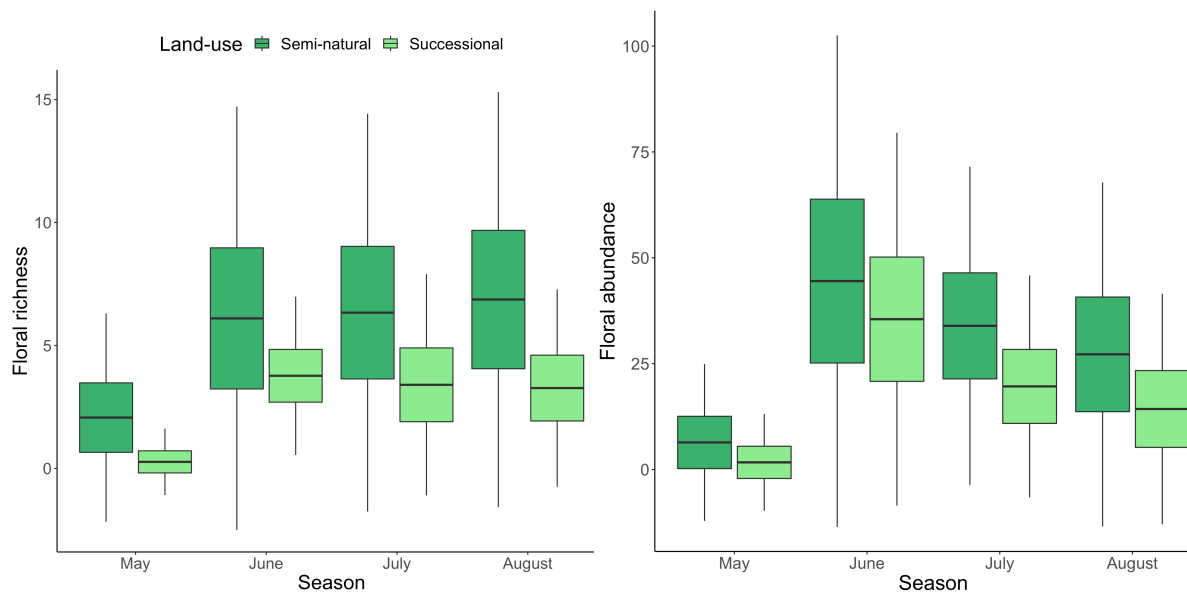


Figure 5. Mean floral species richness (A) and mean floral abundance (B) across semi-natural and successional land-use types in different seasons.

### 3.1.1 Change in plant community composition

There was great variation observed in floral richness and abundance between two land-use types within a different period. Based on AICc model selection, the model with the interacting effect of land use and season (month of the survey) and effect of temperature was best fitted to see the change in floral abundance. The floral abundance of semi-natural grasslands was significantly different from successional grasslands ( $z$ -value= -5.225,  $p < 0.001$ , table 1). The plot shows that floral abundance was higher in June than in May and gradually decreased in July and August (Figure 5B). This trend follows in both land-use types, and while comparing land-use types, there was always higher floral abundance in semi-natural grasslands compare to successional grasslands (Figure 5B). The interaction effect of land use and the season and the additive effect of temperature had also significantly affected the abundance of floral species (Table 2).

Similarly, the model fitted with the interacting effect of land use and season was best fitted to see the change in floral richness. Flowering plant species richness of successional grasslands was also significantly different (z-value= -5.113,  $p < 0.001$ , table 1) from semi-natural grasslands. Semi-natural grasslands have more floral richness than successional grasslands. The interacting effect of land-use change and the season in floral richness was significant in June, July, and August compared to May (Table 2).

Table 2. Results from generalized linear mixed effect model on how land use, season, and temperature affect the floral abundance and floral richness. (Number of observations= 240, Sites= 12, Transect: Sites= 60)

<b>Floral abundance</b>				
<b>Predictors</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>z-value</b>	<b>Pr(&gt; z )</b>
(Intercept)	3.530	0.515	6.859	<0.001
Land use (Successional)	-1.278	0.245	-5.225	<0.001
Season(June)	2.575	0.241	10.682	<0.001
Season(July)	1.719	0.151	11.358	<0.001
Season(August)	1.596	0.158	10.095	<0.001
Temperature	-0.096	0.028	-3.402	0.001
Land use(Successional): Season(June)	0.667	0.287	2.320	0.02
Land use(Successional): Season(July)	0.857	0.247	3.466	0.001
Land use(Successional): Season(August)	0.519	0.255	2.037	0.042
<b>Floral richness</b>				
<b>Predictors</b>	<b>Estimate</b>	<b>Std. Error</b>	<b>z-value</b>	<b>Pr(&gt; z )</b>
(Intercept)	0.692	0.157	4.400	<0.001
Land use(Successional)	-2.030	0.397	-5.113	<0.001
Season(June)	1.082	0.147	7.378	<0.001
Season(July)	1.120	0.146	7.670	<0.001
Season(August)	1.201	0.145	8.303	<0.001
Land use(Successional): Season(June)	1.566	0.393	3.980	<0.001
Land use(Successional): Season(July)	1.426	0.394	3.615	<0.001
Land use(Successional): Season(August)	1.305	0.394	3.309	0.001

### 3.2 Pollinator composition

Different pollinator species were observed during the field survey. Among the observed pollinators, twelve bumblebee species and nine butterfly species were recorded at the species level, while honey bee, wasp, hoverfly, wild bee, and beetle at the genus level.

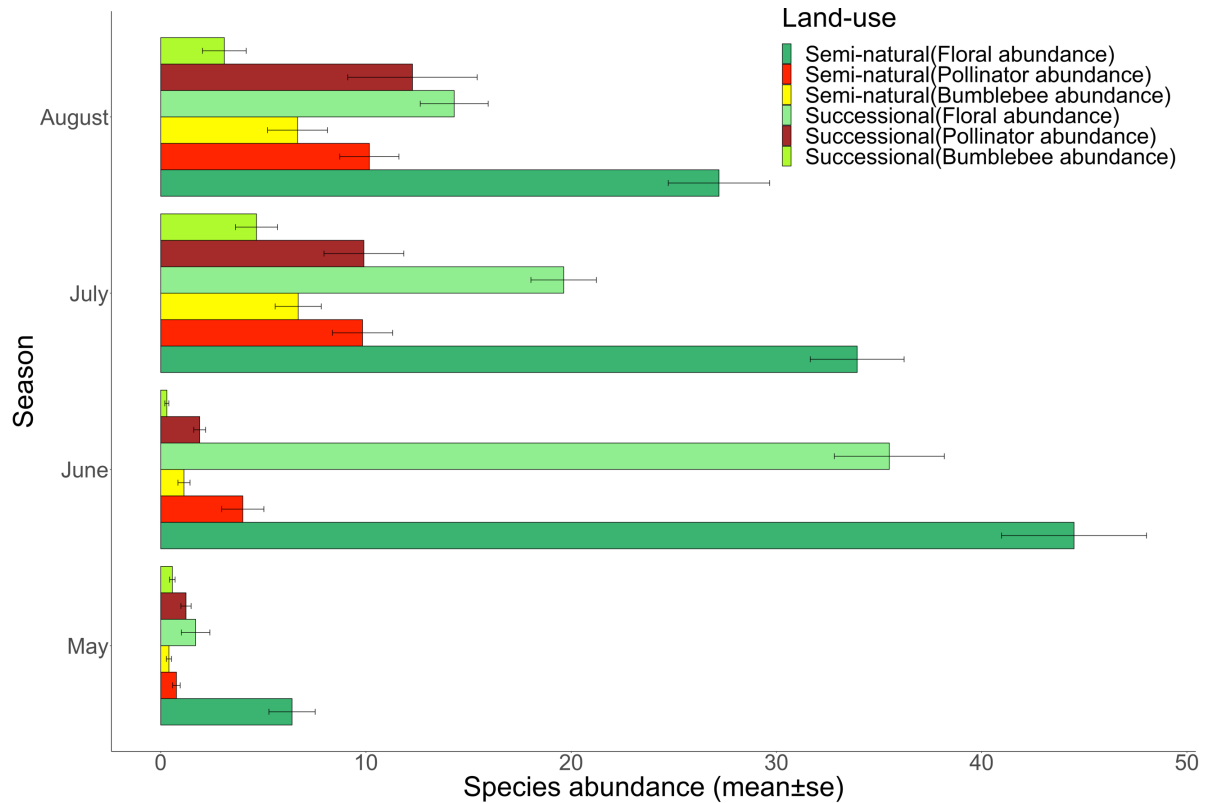


Figure 6. Mean floral, total pollinator, and bumblebee abundance across semi-natural and successional grasslands at different seasons.

Less number of pollinators were observed in May and June than the July and August (Figure 6). There was a gradual decrease in floral abundance for both land-use types after reaching maximum in June whereas. However, the variation in pollinator abundance was not like changing floral abundance (Figure 6). The highest pollinator abundance was recorded in August for both semi-natural ( $10.17 \pm 1.44$ ) and successional ( $12.27 \pm 3.15$ ) land-use types. There was no much difference in pollinator abundance between the land-use types. The average pollinator abundance throughout the sampling periods was ( $6.33 \pm 1.02$ ) in successional grasslands and ( $6.19 \pm 0.68$ ) in semi-natural grasslands. Among the total pollinator abundance, a significant portion of abundance was occupied by bumblebees (Figure 6).

Similarly, there was also no much difference in bumblebee abundance in May and June between the two land-use types compared to July and August. The highest bumblebee abundance was

recorded in July for both land-use types ( $6.67 \pm 1.12$  for semi-natural and  $4.67 \pm 1.02$  for successional). Semi-natural land-use types have almost similar abundance in July and August.

### 3.2.1 Change in bumblebee community composition

There was little difference between the two land use categories for bumblebee richness. Variations within the bumblebee species were observed during the sampling periods. A different pattern was found between floral richness and bumblebee richness. Though the floral richness was highest in August for semi-natural and in June for successional land-use types, the bumblebee richness peaked in July for both land-use types and decreased in August (Figure 7). The average bumblebee richness was  $2.46 (\pm 0.37)$  in semi-natural and  $1.23 (\pm 1.02)$  for successional land-use types in July.

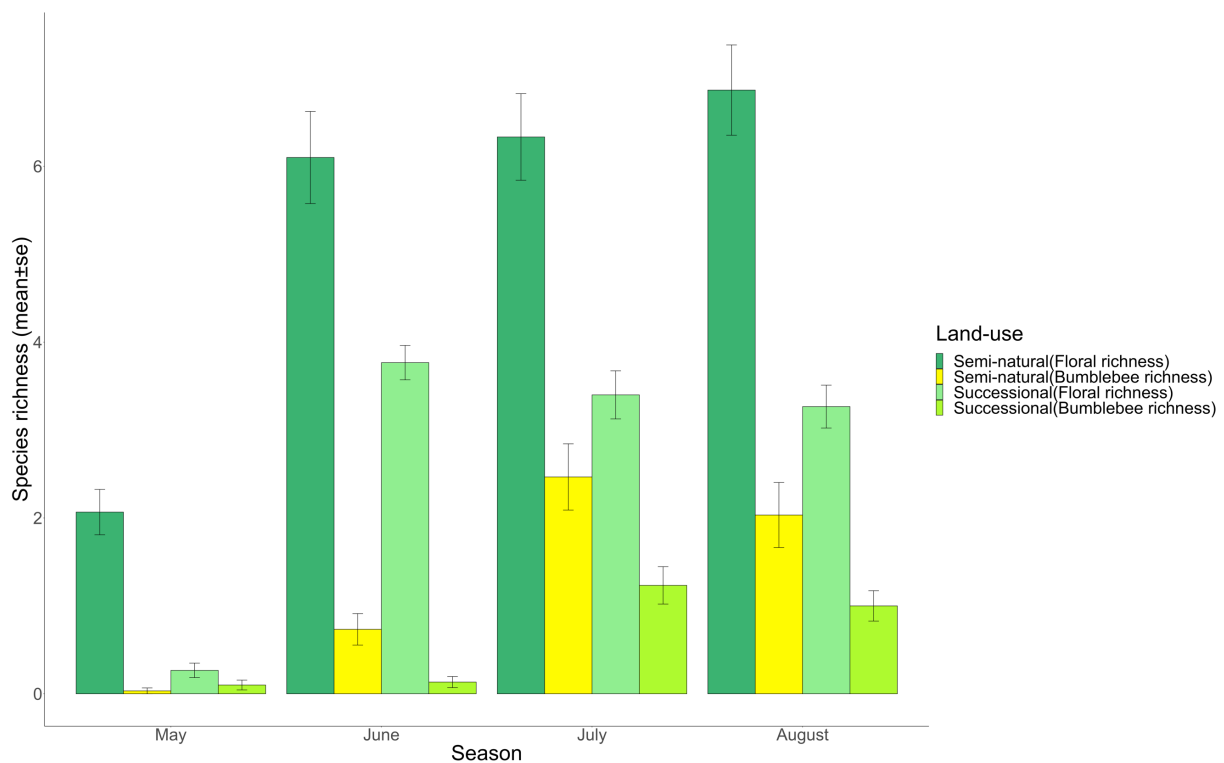


Figure 7. Mean floral richness and bumblebee richness across semi-natural and successional grasslands at different seasons.

Among the twelve different bumblebee species observed in the survey, three species (*Bombus terrestris*, *Bombus norvegicus*, and *Bombus campestris*) were recorded only in the semi-natural grasslands, whereas other nine species were recorded in both land-use types (Appendix B). *Bombus lucorum* and *Bombus pascuorum* were found most in both land-use types and similarly distributed around the sites of each habitat type. *Bombus lapidarius* species was also observed more in semi-natural, though few were observed in successional grasslands. One of the semi-



natural grassland sites, Grønliå, was found with more bumblebee species than other semi-natural sites.

### 3.3 Plant-pollinator interaction network

Interaction networks also changed with a change in season in both land-use types. Twelve bumblebee species with three other unidentified species interacted with 26 different flowering plant species. Among the pollinator groups, nine pollinator groups had interacted with 17 different plant families. There was variation within the same species when it interacted with different plant species at different times.

#### 3.3.1 Bumblebee species level interaction network

Fewer interactions between bumblebee and plant species were observed in June than for other periods. The most common interactions in the network were for *Bombus soroeensis* and *Campanula rotundifolia* in semi-natural grasslands. However, the highest observation of interactions was for *Bombus hypnorum* and two floral species in successional (Figure 8a). Specialization Index ( $H_2'$ ) was less in successional grasslands (0) than in semi-natural grasslands (0.75), and the difference was highly significant ( $p < 0.001$ ) with the land-use type (Appendix I). Interaction network was almost generalized in successional and more specialized in semi-natural (Figure 8a). The average links per species in successional was 0.63 and 0.86 in semi-natural (Table 3).

The number of floral species and bumblebee species increased in July, so more interactions were observed in both land-use types than in June (Figure 8b). In the July network, the most common interactions were for *Bombus soroeensis* and *Campanula rotundifolia* in semi-natural, and *Bombus hypnorum* with *Epilobium angustifolium* in successional grasslands. However, *Bombus lucorum* was the most commonly observed bumblebee species in both land-use types (Figure 8b). Many of the interactions were observed in fewer numbers, seen as narrow interaction lines (Figure 8b). The average number of links per species was 1.07 in successional and 1.58 in semi-natural (Table 3). The specialization index ( $H_2'$ ) was 0.34 and 0.46 in successional and semi-natural, respectively (Figure 8b) and significantly different ( $p = 0.034$ , Appendix I).

There was not a significant difference ( $p=1.392$ ) in the specialization index (H2') between successional (0.32) and semi-natural (0.33) in August. However, there were fewer interactions in successional than in semi-natural grasslands. The most common interactions were between *Bombus lucorum* and *Hieracium spp.* in successional and the same bumblebee species, *B. lucorum*, and *Epilobium angustifolium*, in semi-natural (Figure 8c). In terms of links per species, it was 0.94 and 1.68 in successional and semi-natural, respectively (Table 3).

Differences were observed between the bumblebee species and floral species from the plant-pollinator interaction networks. Networks from June in semi-natural and July in successional had more bumblebee species. In contrast, more floral species were recorded in August at successional and in July and August at semi-natural grasslands. On the other hand, there was less but an equal number of both floral and bumblebee species in June at successional (Figure 8). A higher interaction diversity (Shannon diversity) was observed in July for both land-use types than other sampling rounds (Table 3). With the calculation of z-score and p-value, all observed networks were significantly different ( $p<0,001$ ) from respective null models except for successional land-use type in June ( $p=0.734$ ; Appendix H). Overall the semi-natural grasslands were more specialized than successional grasslands for the bumblebee interaction networks and significantly different from each other (Table 3; Appendix I). Variations found in the network indices for two land-use types at different seasons suggest that seasonal change can shift the network structures and affect their properties.

Table 3. Network indices from the bumblebee interaction network for both land-use types in June, July and August.

Network indices	Successional grassland			Semi-natural grassland		
	June	July	August	June	July	August
Links per species	0.625	1.067	0.938	0.875	1.576	1.68
Shannon diversity	1.609	2.37	2.069	2.313	3.434	3.057
H2'	0	0.343	0.323	0.753	0.456	0.325

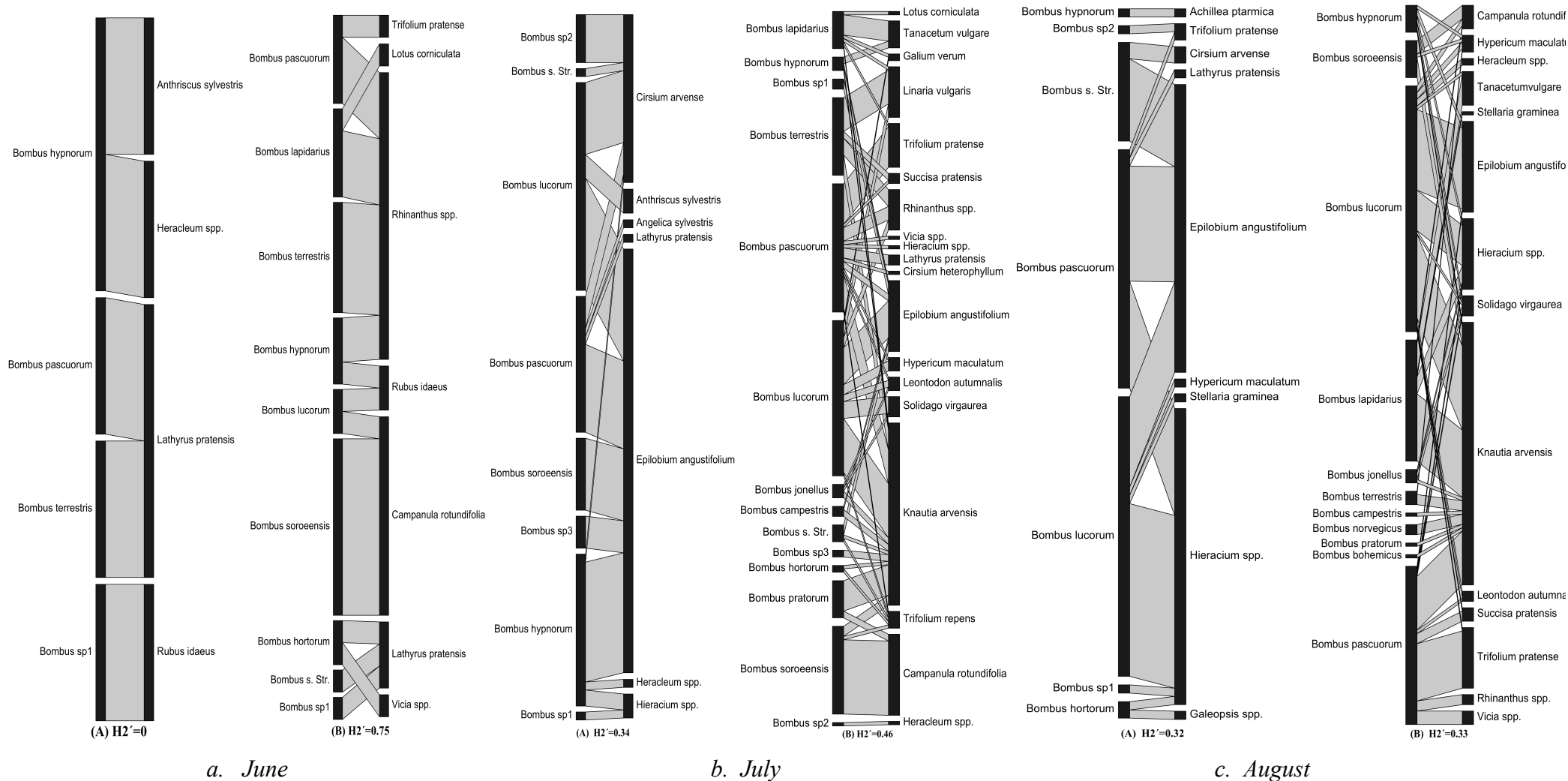


Figure 8. Interaction networks for bumblebee species and flowering plant species in June, July and August at successional (A) and semi-natural grasslands (B). Specialization Index ( $H2'$ ) for each observed network was included to indicate the level of network interaction.

### 3.3.2 Pollinator groups level interaction network

As mentioned in many studies, bees and flies are the primary pollinators in the northern region. In this study also, these groups dominated the interaction patterns in both landscapes. In June, flies had the most common interactions with Apiaceae in successional, whereas honey bees with Rosaceae in semi-natural grasslands (Figure 9a). Between two grasslands networks, the specialization index ( $H2'$ ) was more specialized in semi-natural (0.58) than in successional (0.40) and significantly different ( $p < 0.001$ ) from each land-use type (Appendix I).

In July, the mean number of links per species was similar in both landscapes. However, the interaction diversity was higher in semi-natural (2.59) compared to successional (1.91) (Table 4). The semi-natural network was more specialized ( $H2' = 0.43$ ) than successional ( $H2' = 0.33$ ), and the difference was significant ( $p = 0.012$ ). The bumblebees had dominated the networks in both land-use types. Floral species from Asteraceae and Onagraceae families had more interactions with pollinators in successional and Caprifoliaceae in a semi-natural habitat (Figure 9b).

Similar trends were observed in August between the two land-use types as in July. Semi-natural had a more specialized network, mean links per species, and interaction diversity than in successional grasslands (Figure 9c, Table 4). There was a significant difference ( $p < 0.001$ ) between the two land-use types in the specialization index (Appendix I). Bumblebees and honey bees had the most common interactions with Onagraceae and Asteraceae in successional, whereas bumblebees dominated interactions with Caprifoliaceae and Asteraceae (Figure 9c).

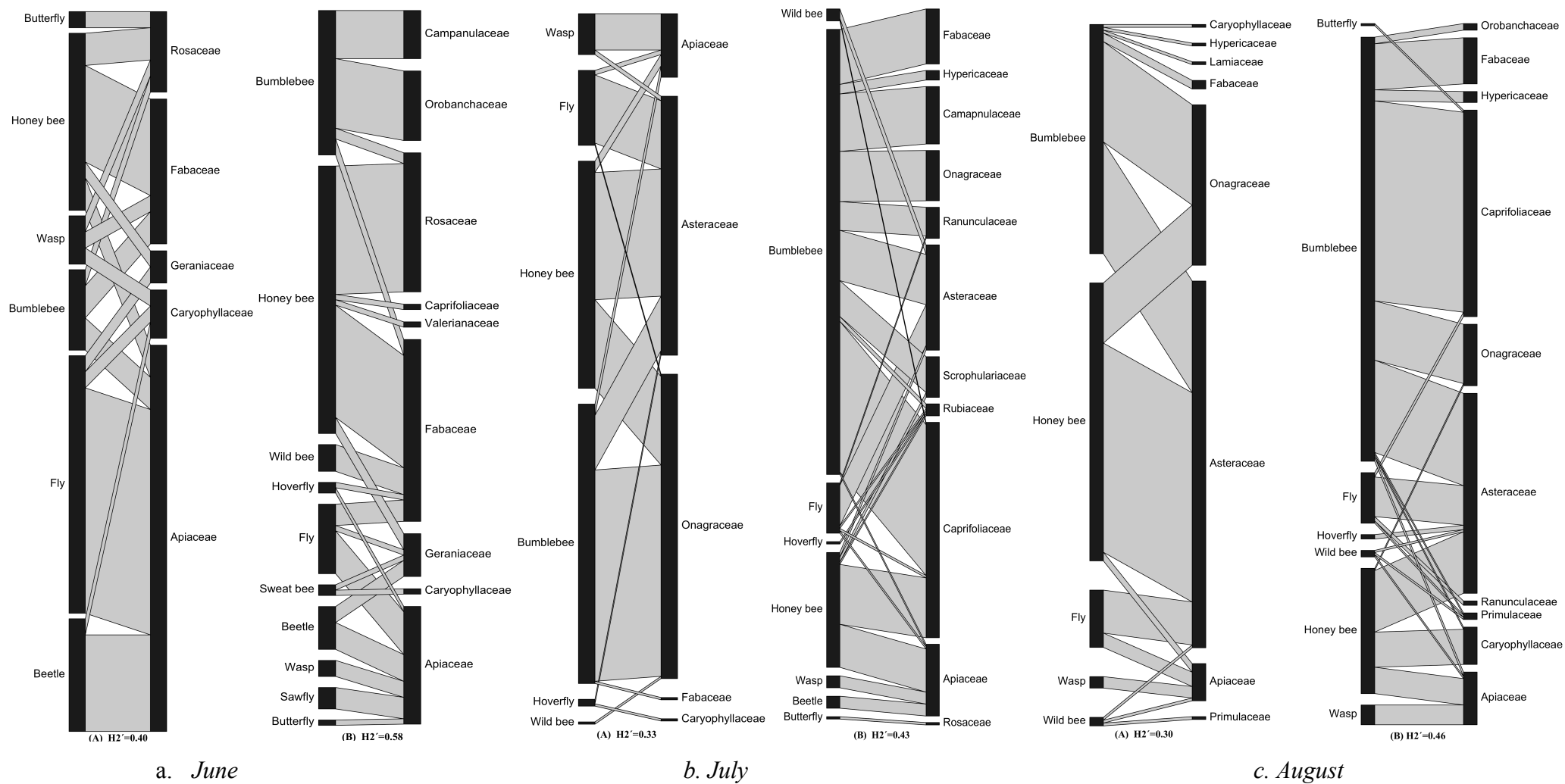


Figure 9. Interaction networks for pollinator groups and plant families in June, July, and August at successional (A) and semi-natural grasslands (B). Specialization Index ( $H_2'$ ) for each observed network was included to indicate the level of network interactions.

Changes in network indices were observed between the landscape types and the same grasslands in different sampling rounds (Table 4). Networks were comparatively specialized in June for both land-use types than in July and August. With the change in time or season, network properties also get influenced as the abundance of both floral and pollinator groups was affected by time and environment variables. Overall in the pollinator group also, the specialization index was higher in semi-natural grasslands than in successional grasslands. The interaction networks obtained from pollinator groups and floral families were not randomly allocated and significantly different from respective null model networks (Appendix H). The specialization index values were also different in group-level networks and significant ( $p < 0.001$ ) between successional and semi-natural grasslands (Appendix I).

*Table 4. Network indices from the pollinator group level interaction network for both land-use types in June, July and August.*

	Successional grassland			Semi-natural grassland		
Network indices	June	July	August	June	July	August
Links per species	1.455	1.364	1.154	1.158	1.368	1.353
Shannon diversity	2.273	1.913	1.861	2.556	2.592	2.272
H2'	0.399	0.331	0.303	0.577	0.425	0.458

## **4. DISCUSSION**

This study examined the effect of land-use changes and seasonal changes on the pollinated floral community. Then a change in the pattern of pollinator communities, and floral communities and plant-pollinator interactions were observed. The results showed that changes in land-use types or properties of a landscape and seasonal changes determine the floral communities. Concerning that, Heggøy (2021), used the same data source; land-use change and seasonal changes also significantly affected pollinator composition. Floral communities in working grasslands had also affected the composition of pollinator communities. Such change in floral communities and then in pollinator communities can directly affect the interaction network, which was observed between the successional and semi-natural grasslands in the observed sites along with the seasonal shift.

### **4.1 Plant resources**

Urban grasslands are closely related to human habitation. The structural properties of soil and plant resources available there are remarkably altered by human settlement activities and production processes. Urban habitats may be deficient in soil nutrients than natural habitats due to the deposition of toxic substances or substrates from the pollution occurring in the city areas. Such changes can affect the plant resources existing in those habitats as soil resources are essential for their existence. Along with soil resources, the light resource is also vital for the plant's survival. Abiotic soil properties like soil surface temperature, soil nutrient, and moisture availability can mediate the flowering phenology and affect the changing floral diversity in the respective landscapes (Wolf et al., 2017).

In this study, two land-use types, semi-natural and successional habitats in the urban grasslands, were studied. Based on the observed characteristics, semi-natural grasslands were quite open and near to the settlement area. Despite being near to the human habitat, those habitats were in a natural state. Due to the original condition and openness, it might support many floral species. Also, some sites had managed grazing practices that helped increase the openness of the land and enriched the soil with organic manure. As mentioned earlier, the relationship between soil resources and light resources determines the existence of plant resources. When the habitat is open, light can reach soil surface level, and emerging plant communities do not need to compete for light to grow. Small floral species also get equal opportunity to grow and flowers up to full bloom stage. With these advantages, many floral species were observed in semi-natural sites.

Most species related to plant family like Rosaceae (e.g., *Alchemilla ptarmica*), Rubiaceae (e.g., *Galium verum*), Caryophyllaceae (e.g., *Stellaria graminea*), and Fabaceae (e.g., *Trifolium pratense*) dominated the semi-natural grasslands. Besides, flowers were observed in mass blooming patterns. In contrast, successional sites were closed to forest areas and in a successional state as left undisturbed where management practices were stopped. As successional sites were entirely covered with tall grassy weeds and bushes, small floral species had to compete with those species to get enough light and soil nutrients for survival and proper flowering. Average plant height was higher in successional than in semi-natural, which was evident in this study as tall grass, herbs, and non-flowering species were observed in successional grassland compared to small and many flowering plant species in semi-natural grasslands. So, higher vegetative growth was observed rather than reproductive growth in successional than in semi-natural grasslands as they had to compete for the nutrient available there. Some sites were isolated too, which may hinder the dispersal of seeds from abiotic factors. So, such remains of old management practices, isolation, and deposition of foreign materials might cause those sites to have fewer floral communities. Even though fewer floral resources were found, flowers were observed in patches. Floral species from plant family Onagraceae (e.g., *Epilobium angustifolium*), Fabaceae (e.g., *Lathyrus pratensis*, *Vicia spp.*), Asteraceae (e.g., *Cirsium arvense*), and Caryophyllaceae (e.g., *Stellaria graminea*) dominated those successional sites. Variations in floral abundance throughout the survey were found and statistically also significantly different among the land-use type, which delineates that land-use change determines resource availability and thus the diversity of flowering plant species and their abundance.

#### **4.2 Pollinator community**

Many studies suggested that increasing urbanization and human settlement areas impacted land-use change and negatively affecting the pollinators (Williams et al., 2010; Winfree et al., 2009; Winfree et al., 2011). Pollinators' response to land-use change might be determined by the type and level of anthropogenic activities in those landscapes (Hogsden & Hutchinson, 2004; Kremen et al., 2002; Öckinger & Smith, 2006; Tews et al., 2004; Winfree et al., 2009; Winfree et al., 2011). The responses also depend upon the study methods, being mostly negative when compared between the landscapes along the gradients and mostly positive when compared at local land-use types level (Winfree et al., 2011)



According to our hypothesis, we expected land-use change to affect the abundance and diversity of flowering plants and subsequently pollinators. Change in plant community composition along the different land-use types has affected the pollinator richness (bumblebee richness), and their response was significantly different between the floral richness of the two land-use types (Heggøy, 2021). Pollinators share flowers as their food resources; that is why floral resources can limit the abundance and richness of pollinators (Öckinger & Smith, 2006; Roulston & Goodell, 2011; Summerville & Crist, 2001). Floral resources respond to land-use change, and with change in floral resources, pollinators respond correspondingly, like when floral resources increase, pollinators also increase and vice versa (Winfree et al., 2011). Nevertheless, the results showed that floral abundance was maximum in June and decreased gradually in July and August, whereas pollinators' abundance increased gradually from May to August. That means not only increment in floral availability will increase pollinator diversity, but also other variables can influence the pollinators, such as growing season, their foraging behaviour, nesting resources, and environment variables like temperature, which determine the growth and activity of pollinators. As a result, season and temperature also significantly affected the bumblebee richness (Heggøy, 2021). In May, during the site selection, the weather was cool, windy, and humid, and in late May, fewer pollinators were recorded. As the season changed in June, July, and August, temperature also increased, and a moderate increase in temperature favoured the pollinators and increased their activity. However, on a hot day or when a high temperature was recorded during July and August, fewer pollinator species were observed, explaining the fluctuating pollinator response with changes in temperature and season.

### **4.3 Interactions network**

One objective of this study was to map the plant-pollinator interactions in two land-use types in different seasons and observe the change in network interactions and their properties. This study also showed various interaction networks with varying properties in each sampling round as many studies had found variation in species composition and pollination network in different periods (Alarcón et al., 2008; Dupont et al., 2009).

Pollinator species have different preferences to interact with other species and respond according to plant communities' composition. Pollinator species interacting with specific flowering plants might change their interaction if other plant species dominated that area. They also depend upon the rewards provided by the new plant species or the nature of the pollinator,

which might be specialists or generalists. For instance, in this study, *Bombus soereensis* has most common interactions with *Campanula rotundifolia* in semi-natural grasslands and foraged in same species till the abundance of that plant species was high. As abundance decreased, bumblebee species interacting with other flowering plant species were observed, but still, interactions with *Campanula rotundifolia* were more than with other species. Nevertheless, in successional grasslands, *Campanula rotundifolia* was not observed so *Bombus soereensis* interacting with another species *Epilobium angustifolium* was found. This determines that *Bombus soereensis* shows constancy and might prefer *Campanula rotundifolia* over other species and reason behind it might be due to the rewards it provides or the attractiveness of flower (Ødegaard, 2015). Bumblebees can show good level of flower constancy and can be good generalists by foraging a lot of flowering plant species to get rewards or rather can act as specialists by foraging mainly on a single flower if it gives much reward at less expense of energy and sometimes they go checking out some other species (Willmer, 2011). This shows the generalization and specialization level of a same species at different period and depends upon the availability of floral resources. The observed networks in this study also resulted more specialization when more flowering plants were observed and more generalization when the diversity and abundance was low which was indicated by specialization index (H2') for both land-use types.

One of the main findings of this study was that *Bombus pascuorum* and *Bombus lucorum* were recorded as the most commonly observed bumblebee species during the survey, which was also supported by the status of bumblebees in Norway (Åström et al., 2018). Both species had more interactions with different flowering species. Long-tongued species like *B. pascuorum* can take out all nectar from all flowering species where other species cannot and can interact with many species, whereas short-tongued species like *B. lucorum* can forage various bowl-shaped flowers and short tubular corollas as well as can theft nectar from the longer tube by making holes at the base with their strong mandibles (Willmer, 2011). That is why tongue length, the size, and strength of bumblebee are also critical for them and helps to determine which species they can or prefer to forage.

On the other trophic level side, flowering plant species like *Lathyrus pratensis*, *Rhinanthus species*, *Epilobium angustifolium*, *Knautia arvensis*, and many others had more interactions with different bumblebee species. This study already showed that bumblebee richness is influenced by floral richness, many floral species existing in semi-natural grasslands interacted

with many bumblebee species compared to successional grasslands. This was expected from one of our hypotheses, stating that change in land-use and plant community composition will influence the pollinator richness and the interacting patterns. In contrast, floral abundance might not support more interactions always. For instance, *Stellaria graminea*, an herbaceous perennial species with short slender stems with small white flowers, was observed abundantly in all sampling seasons. However, some interactions with bumblebee were rarely observed. The reasons behind it might be the rewards it provides may not be sufficient, or a small flower size with a slender stem may not provide a landing stage for bumblebee. That is why the interacting process also depends upon the flower morphology and rewards it offers to the pollinator.

In a group-level interaction network, most of the interactions were observed for bee and fly groups. Bumblebees, honey bees, and flies have more interactions with various plant families than other groups like butterflies, beetle, and wasps. Bees can adapt to a wide range of flowers as they can be more generalist with more floral species, whereas a fly group is a diverse group of insects, so various flies have various ways of foraging more flowers (Willmer, 2011). Within the bee group, bumblebee mostly prefers floral species from Fabaceae, Lamiaceae, and Scrophulariaceae. Fabaceae is a major pollen source for bumblebees (Goulson et al., 2008). The data of flowering plant species in this study also shows that Fabaceae species were observed more in semi-natural than in successional grasslands. Bumblebees' interactions with Fabaceae species like *Lathyrus pratensis*, *Trifolium pratense*, *Trifolium repens*, and *Vicia species* were also found more in semi-natural grasslands. However, the observed networks showed fewer interactions of bumblebees with Fabaceae and more with other families in later sampling rounds, showing the variation in networks in different seasons. This shift of bumblebees to other families might be due to the reduction of Fabaceae plants and interaction with other species (Goulson et al., 2005). More interactions for each pollinator group were observed in semi-natural than in successional as more plant families were recorded in semi-natural.

Loss of habitat or intensive management practices destroys the nesting sites and food sources of pollinators (Williams, 1982). Along with that, it affects the foraging behaviour of pollinators. For instance, bees make their foraging routes and pathways during the flight and can remember them for a long time. Habitat fragmentation can spoil their routes and their preferred species, making them vulnerable to decline in that habitat (Knight et al., 2005). This suggests that change in land use impacts the pollination network by changing the foraging behaviour of the pollinators and their preference over the flowers.

Besides, throughout the growing season, environmental variables also changed, impacting the growth stage of both plants and pollinators. Ecological change is most seen in urban areas where anthropogenic activities emit greenhouse gases and cause environmental change (GRIMMOND, 2007). Plant-pollinator interaction could be vulnerable to change in environment variables when interactions depend upon them. For instance, bees are active on sunny days with warm temperatures and forage the flowers. Environmental variation can impact the flowering period causing a mismatch and disrupt the interactions between bees and flowering plant species (Goulson et al., 2015). Such changing environmental conditions could shift flower phenology, and pollinators may not show such shifts concerning flowering plants, affecting their interacting patterns.

#### **4.4 Limitations of the study**

Field sampling was performed in 2020, from late spring (May) to late summer (August). In May 2020, there was a fluctuation in the weather. The weather was cold and the temperature below 15°C in earlier May (Klimaservicesenter, 2020), so sampling started in late May. The earlier climatic conditions might have affected the growth and development of flowering plant species and might delay the rise of pollinator species. During the sampling period, rainy and windy days were avoided, which might have affected the abundance of pollinators. Grazing practices have been found in some semi-natural sites, which might have affected species diversity. In future studies, such practices could be an essential factor to see the effect of land use on species richness. Except for bumblebee and butterfly, other pollinators were identified at genus level only, so it has been less effective in predicting the total pollinator richness in those landscapes. Identification of every pollinator at the species level in future studies could be better for observing the effect of land use on pollinator richness.

#### **4.5 Management Implications**

The dataset from this study can be integrated into meta-analysis and used in future studies for comparing plant species composition and pollinator communities across the grasslands in Trondheim. Trondheim grasslands are providing a substantial ecological niche to many pollinators group, especially bumblebee species. That is why policies and strategies for maintaining biodiversity and urban planning should be promoted to support habitat establishment and enhancement for pollinators and floral diversity in urban landscapes through

proper research and study. The conservation practices like low intensive management of grasslands, creation of green parks and recreational space, roadside hedgerows, home gardens, green roofs, and walls can be managed to support floral species and potential pollinators. Modern practices like "bee hotels" (MacIvor & Packer, 2015) and bumblebee nest boxes (Gaston et al., 2005) can be promoted to provide nesting sites for nesting bees or bumblebees. Restoration techniques like promotion of existing local species, leaving the edges of agricultural fields naturally for the local plant species, establishing natural corridors for the isolated grasslands, and so on should be promoted and adapted to alleviate challenges for plant-pollinator conservation.

## 5. CONCLUSION

The main aim of this study was to see the effects of land-use changes and seasonal changes in flowering plant communities and plant-pollinator networks in urban grasslands, which provide essential ecosystem services by functioning and balancing the existing biodiversity. This study showed an effect of land-use changes and seasonal shift on flowering plant species and causing the subsequent decline in the food resources, which has affected the pollinator composition. Plant-pollinator networks investigated in grassland working landscapes found that floral resources availability influenced interaction network and pollinator abundance throughout the sampling period. In general, links per species and diversity of species increased, and networks were more specialized in semi-natural grasslands than in successional grasslands for both species level and group level interaction network where pollinator species became more generalists to get rewards from limited resource availability. This study has also shown a realistic outlook of pollinator communities' interactions with the floral resources and contributed to understanding the plant-pollinator networks in grassland working landscapes. Results and supportive findings suggest that plant-pollinator networks will change throughout the growing season due to seasonal shifts and resource availability in existing landscape types. Nevertheless, more knowledge and understanding about the impacts of land-use change in plant-pollinator interaction is needed. Overviewing the change of landscapes and their impact on plant-pollinator compositions and interactions, biodiversity of urban grasslands can be understood up to some extent indicating conservation is vital to support these ecosystem services.

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## 7. APPENDICES

### Appendix A. Flowering plant species observed in semi-natural and successional grasslands across Trondheim in May, June, July and August.

Plant family	Flowering plant species	Semi-natural grasslands				Successional grasslands			
		May	June	July	August	May	June	July	August
<b>Apiaceae</b>	<i>Aegopodium podagraria</i>	0	0	0	21	0	6	24	10
	<i>Angelica sylvestris</i>	0	0	0	0	0	0	4	4
	<i>Anthriscus sylvestris</i>	0	61	41	57	0	441	25	0
	<i>Heracleum sp.</i>	0	0	0	3	0	14	9	2
<b>Asteraceae</b>	<i>Achillea millefolium</i>	0	14	40	19	0	3	22	23
	<i>Achillea ptarmica</i>	0	0	27	53	0	0	48	60
	<i>Cirsium arvense</i>	0	1	5	3	0	0	73	59
	<i>Cirsium heterophyllum</i>	0	7	0	0	0	0	9	13
	<i>Hieracium umbellatum</i>	0	4	11	0	0	0	0	0
	<i>Hieracium sp.</i>	0	24	0	36	0	0	0	20
	<i>Leontodon autumnalis</i>	0	0	15	12	0	0	0	0
	<i>Leucanthemum vulgare</i>	0	38	20	8	0	3	0	0
	<i>Solidago virguarea</i>	0	0	4	15	0	0	0	0
	<i>Tanacetum vulgare</i>	0	0	10	28	0	0	18	8
	<i>Taraxacum officinale</i>	19	0	0	0	0	0	0	0
<b>Brassicaceae</b>	<i>Arabidopsis thaliana</i>	4	0	0	0	0	0	0	0

Plant family	Flowering plant species	Semi-natural grasslands				Successional grasslands			
		May	June	July	August	May	June	July	August
<b>Campanulaceae</b>	<i>Campanula rotundifolia</i>	0	34	90	37	0	0	0	0
<b>Caprifoliaceae</b>	<i>Knautia arvensis</i>	0	0	32	35	0	0	1	0
	<i>Succissa arvensis</i>	0	0	9	2	0	0	0	0
	<i>Valeriana sambucifolia</i>	0	5	0	0	0	0	13	2
<b>Caryophyllaceae</b>	<i>Cerastium fontanum</i>	2	0	0	0	0	0	0	0
	<i>Stellaria graminea</i>	0	157	236	217	0	24	88	110
<b>Fabaceae</b>	<i>Lathyrus pratense</i>	0	98	10	16	0	357	66	17
	<i>Lotus corniculata</i>	0	12	11	0	0	4	0	1
	<i>Trifolium pratense</i>	0	87	55	32	0	0	10	1
	<i>Trifolium repens</i>	0	9	58	7	0	0	4	0
	<i>Vicia sp.</i>	6	62	4	5	0	131	3	11
<b>Geraniaceae</b>	<i>Geranium sylvaticum</i>	0	27	0	0	0	46	7	1
<b>Hypericaceae</b>	<i>Hypericum maculatum</i>	0	0	50	38	0	0	0	2
<b>Lamiaceae</b>	<i>Galeopsis tetrahit</i>	0	0	0	0	0	0	12	6
	<i>Prunella vulgaris</i>	0	0	4	1	0	0	0	0
<b>Onagraceae</b>	<i>Epilobium angustifolium</i>	0	0	12	22	0	25	148	78
<b>Orchidaceae</b>	<i>Orchis sp.</i>	0	3	0	0	0	0	0	0
<b>Orchidaceae</b>	<i>Platanthera chlorantha</i>	0	19	0	0	0	0	0	0
<b>Orobanchaceae</b>	<i>Euphrasia officinalis</i>	0	0	1	2	0	0	0	0

Plant family	Flowering plant species	Semi-natural grasslands				Successional grasslands			
		May	June	July	August	May	June	July	August
<b>Orobanchaceae</b>	<i>Rhinanthus angustifolius</i>	0	35	20	7	0	0	0	0
	<i>Rhinanthus minor</i>	0	11	7	3	0	0	0	0
<b>Polygonaceae</b>	<i>Bistorta vivipora</i>	0	0	8	7	0	0	0	0
<b>Ranunculaceae</b>	<i>Anemone nemorosa</i>	40	0	0	0	47	0	0	0
	<i>Ranunculus acris</i>	19	103	12	7	3	5	0	0
<b>Rosaceae</b>	<i>Alchemilla vulgaris</i>	97	387	94	22	1	0	0	0
	<i>Filipendula ulmaria</i>	0	0	0	0	0	0	5	4
	<i>Potentilla erecta</i>	0	97	13	10	0	0	0	0
	<i>Rubus sp.</i>	0	0	3	0	0	0	0	0
	<i>Rosa sp.</i>	0	2	0	0	0	4	0	0
<b>Rubiaceae</b>	<i>Galium rivale</i>	0	23	4	14	0	0	0	0
	<i>Galium uliginosum</i>	0	0	0	2	0	2	0	0
	<i>Galium verum</i>	0	15	108	75	0	0	0	0
<b>Scrophulariaceae</b>	<i>Verboscum nigrum</i>	0	0	4	0	0	0	0	0
<b>Violaceae</b>	<i>Viola sp.</i>	5	0	0	0	0	0	0	0
<b>Total richness</b>		<b>8</b>	<b>26</b>	<b>32</b>	<b>32</b>	<b>3</b>	<b>14</b>	<b>20</b>	<b>20</b>
<b>Total abundance</b>		<b>192</b>	<b>1335</b>	<b>1018</b>	<b>816</b>	<b>51</b>	<b>1065</b>	<b>589</b>	<b>432</b>

**Appendix B. Pollinators observed in semi-natural and successional grasslands across Trondheim in May, June, July and August.**

Pollinators	Semi-natural grasslands				Successional grasslands			
	May	June	July	August	May	June	July	August
<i>Bombus hortorum</i>	0	2	3	0	0	0	0	2
<i>Bombus terrestris</i>	0	6	31	4	0	0	0	0
<i>Bombus lucorum</i>	0	3	44	74	0	0	29	41
<i>Bombus soroeensis</i>	0	10	27	9	0	0	34	0
<i>Bombus lapidarius</i>	1	5	11	35	0	1	0	0
<i>Bombus jonellus</i>	0	0	2	4	0	0	0	0
<i>Bombus hypnorum</i>	0	3	2	3	0	0	18	1
<i>Bombus pratorum</i>	0	0	11	1	0	0	0	0
<i>Bombus pascuorum</i>	0	3	41	60	1	0	24	34
<i>Bombus campestris</i>	0	0	3	3	0	0	0	0
<i>Bombus bohemicus</i>	0	0	2	1	3	0	0	0
<i>Bombus norvegicus</i>	0	0	0	3	0	0	0	0
<i>B. s. str.</i>	0	0	6	0	0	0	1	12
<i>Pieris napi</i>	0	0	1	0	2	0	1	5

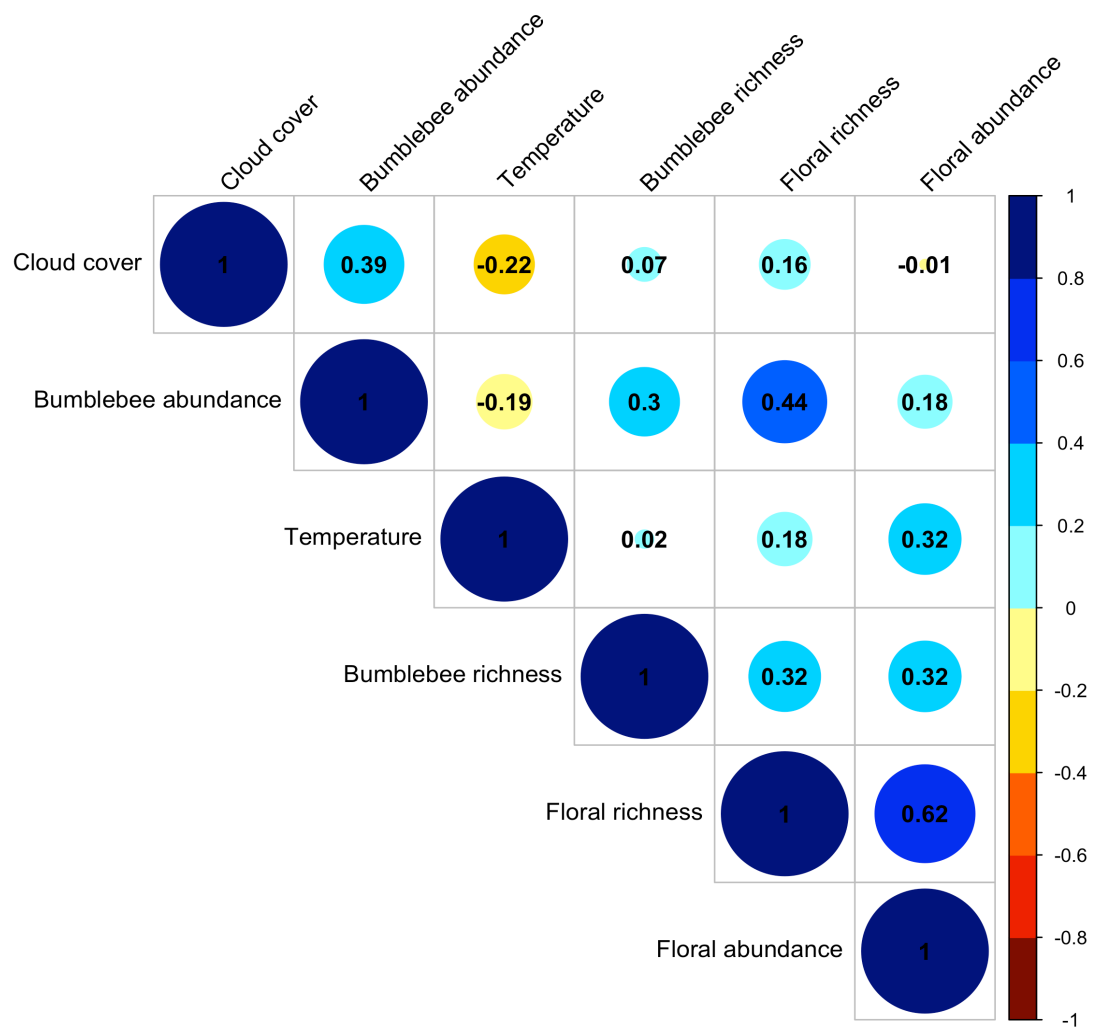
Pollinators	Semi-natural grasslands				Successional grasslands			
	May	June	July	August	May	June	July	August
<i>Pieris brassicae</i>	0	1	0	0	0	0	0	0
<i>Anthocharis cardamines</i>	0	1	0	4	1	0	0	1
<i>Polyommatus icarus</i>	0	1	1	0	0	0	0	0
<i>Callophrys rubi</i>	0	1	0	0	0	0	0	0
<i>Cupido minimus</i>	0	1	0	0	0	0	0	0
<i>Boloria selene</i>	0	4	0	0	0	0	0	0
<i>Erebia ligea</i>	0	0	3	2	0	0	0	0
<i>Lycaena hippothoe</i>	0	0	1	0	0	0	0	0
<b>Psithyrus</b>	<b>0</b>	<b>0</b>	<b>7</b>	<b>2</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
Honey bees	2	51	54	57	0	2	100	228
Wild bees	1	5	5	3	0	1	1	8
Hoverflies	1	12	4	3	9	1	2	3
Other flies	0	6	20	25	1	0	33	25
Wasp	8	3	3	0	6	1	21	13
Beetles	0	12	0	0	5	33	5	0
<b>Total abundance</b>	<b>13</b>	<b>130</b>	<b>282</b>	<b>293</b>	<b>28</b>	<b>39</b>	<b>269</b>	<b>373</b>







**Appendix D. Correlation matrix to remove highly correlated variables.**



## Appendix E. Model selection

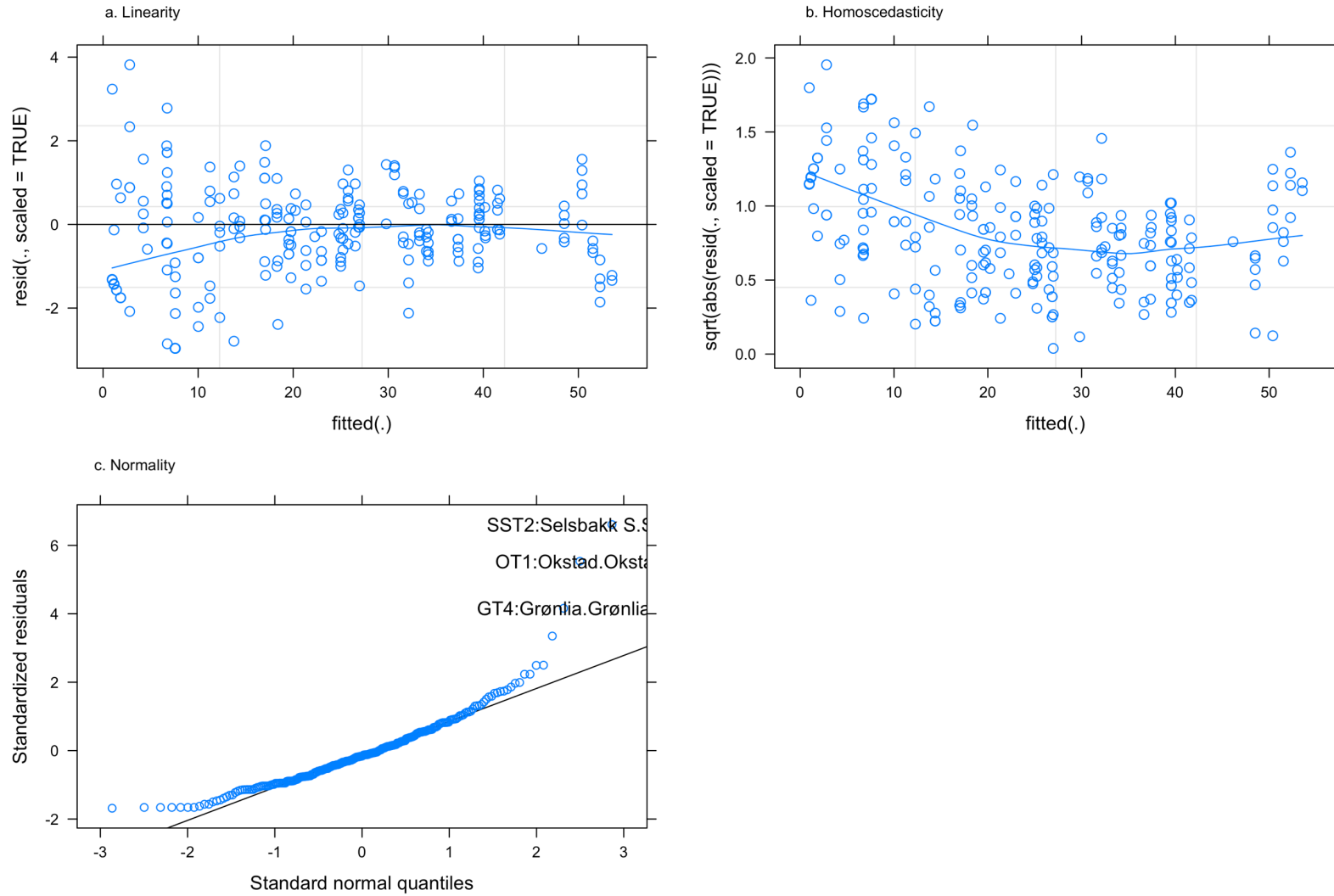
Model selection for generalized linear mixed-effects models testing the effect of land use, season, temperature and their interaction on floral abundance (A) and floral richness (B). The models are ranked by decreasing  $\Delta\text{AICc}$  value. K = number of estimated parameters for each model,  $\text{AICc}$  = Akaike information criteria,  $\Delta\text{AICc}$  = difference in  $\text{AICc}$  from the best fitted model, and  $\text{AICcWt}$  = Akaike weight.

A.	Model	K	AICc	$\Delta\text{AICc}$	AICcWt
	Landuse*Season+Temperature	12	1757.860	0	0.843
	Landuse*Season+Season*Temperature	15	1762.548	4.687	0.081
	Landuse+Season+Temperature	9	1763.889	6.029	0.041
	Landuse+Season*Temperature	12	1764.760	6.900	0.027
	Landuse*Season	11	1767.186	9.326	0.008
	Landuse+Season	8	1783.549	25.689	0
	Season	7	1794.147	36.287	0
	Landuse+Temperature	6	1983.497	225.637	0
	Temperature	5	1988.234	230.373	0
	Landuse	5	1991.694	233.834	0
	Constant	4	1998.703	240.843	0

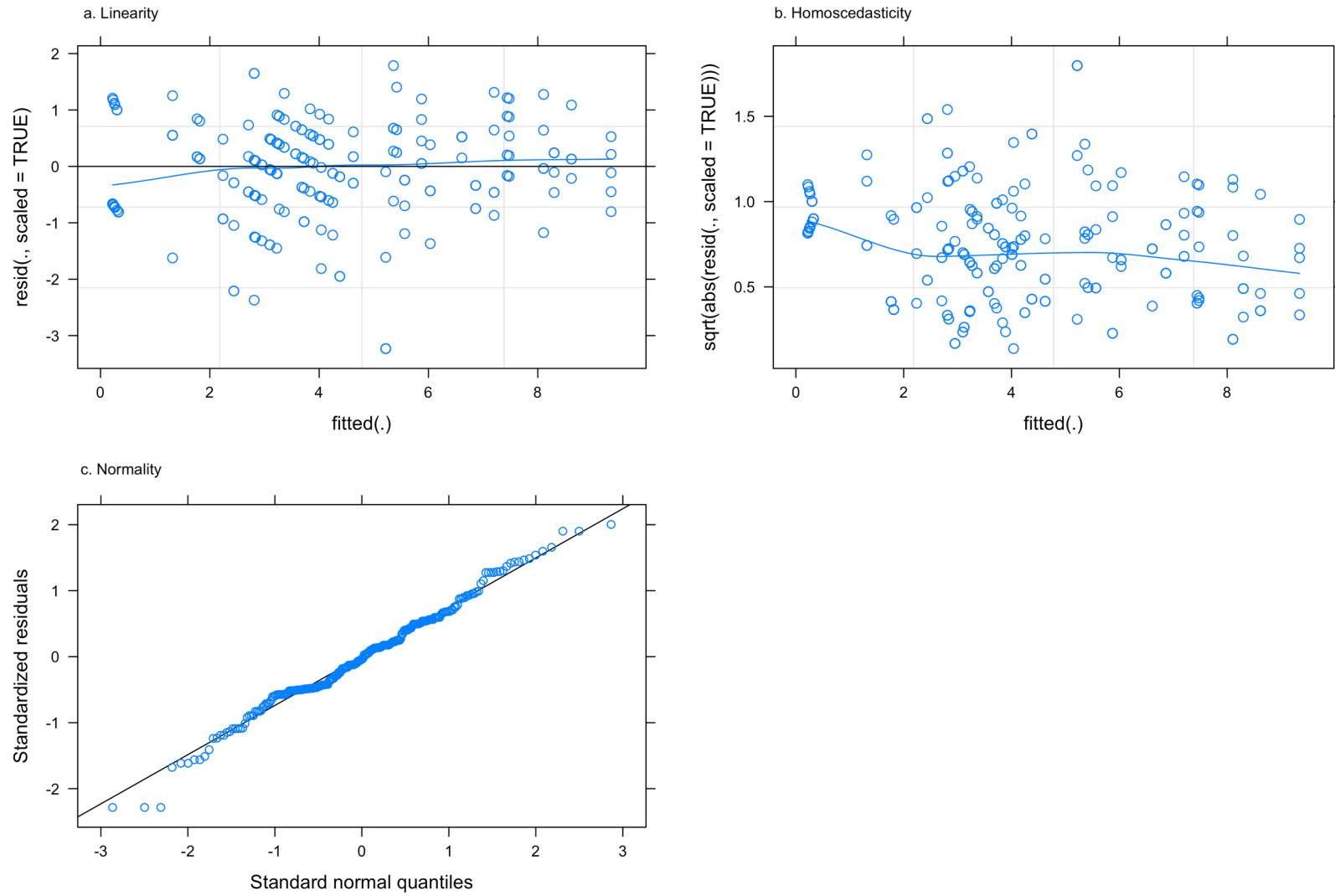
<b>B.</b>	<b>Model</b>	<b>K</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>AICcWt</b>
	Landuse*Season	10	896.88	0,00	0.718
	Landuse*Season+Temperature	11	898.93	2.05	0.258
	Landuse*Season+Season*Temperature	14	903.78	6.90	0.023
	Landuse+Season*Temperature	11	909.77	12.89	0.001
	Landuse+Season	7	912.06	15.18	0
	Landuse+Season+Temperature	8	912.45	15.57	0
	Season	6	921.99	25.11	0
	Temperature+Season	7	923.05	26.17	0
	Landuse+Temperature	5	1101.34	204.46	0
	Temperature	4	1110.14	213.26	0
	Landuse	4	1111.65	214.77	0
	Constant	3	1121.64	224.76	0

## Appendix F. Diagnosis of model assumptions

A. Verifying the model assumptions of floral abundance by checking the random effects' linearity, homoscedasticity and normality.



B. Verifying the model assumptions of floral richness by checking the random effects' linearity, homoscedasticity and normality.



**Appendix G. Mean plant height (cm) with standard error in different periods across semi-natural and successional grasslands.**

	<b>Semi-natural grasslands</b>	<b>Successional grasslands</b>
<b>May</b>	18.93±0.93	37.11±1.01
<b>June</b>	39.75±1.85	114.51±1.81
<b>July</b>	50.51±2.2	119.19±2.05
<b>August</b>	49.95±2.04	119.03±6.3

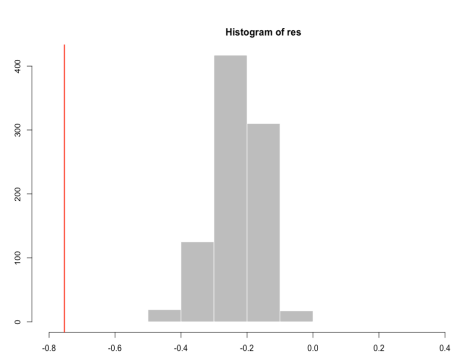
**Appendix H. H2' score, Z-score value and p-value for the bumblebee species and pollinator groups interaction networks to test significance against the respective null models.**

		<b>Bumblebee species interaction network</b>			<b>Pollinator groups level interaction network</b>		
Land-use	Time	H2'	Z-score	p-value	H2'	Z-score	p-value
<b>Successional grasslands</b>	June	0	-0.338	0.734	0.391	4.708	<0.001
	July	0.343	5.998	<0.001	0.331	34.117	<0.001
	August	0.323	6.089	<0.001	0.303	13.108	<0.001
<b>Semi-natural grasslands</b>	June	0.753	6.788	<0.001	0.577	18.719	<0.001
	July	0.456	16.278	<0.001	0.425	21.96	<0.001
	August	0.325	11.265	<0.001	0.458	28.544	<0.001

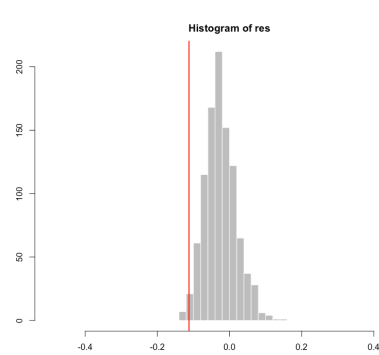


## Appendix I. Test of Specialization Index (H2') for observed networks between two land-use types.

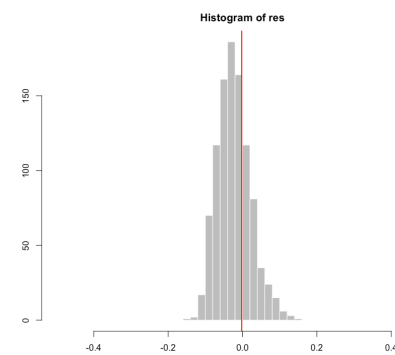
### Part 1: Bumblebee species level interaction network



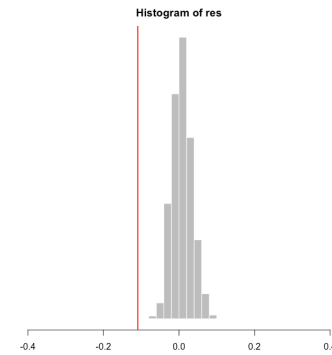
a. June ( $p < 0.001$ )



b. July ( $p = 0.034$ )

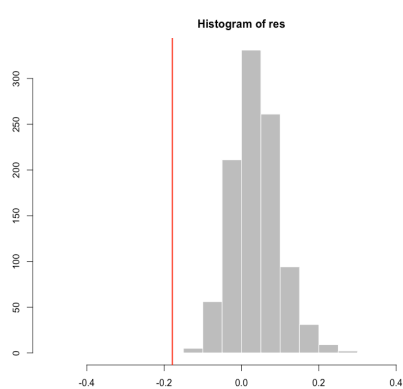


c. August ( $p = 1.392$ )

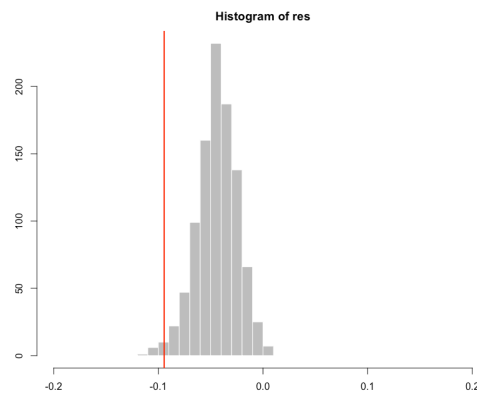


d. All seasons ( $p < 0.001$ )

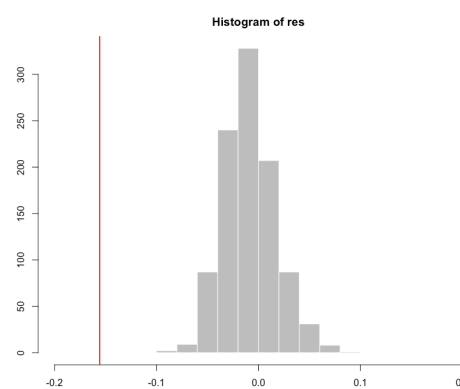
### Part 2: Pollinator groups level interaction network



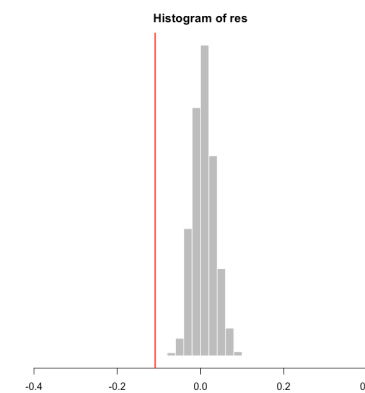
a. June ( $p < 0.001$ )



b. July ( $p = 0.012$ )



c. August ( $p < 0.001$ )



d. All seasons ( $p < 0.001$ )

