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Effects of land-use on bumblebees and other pollinators in urban grasslands

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Abstract

Semi-natural grasslands are one of the most important habitats for bumblebees and other pollinator taxa, but changes in land use threaten this habitat type. Abandonment and subsequent encroachment of bushes and trees is considered one of the most important threats today. Additionally, urbanization has led to an increased pressure, fragmentation, and isolation of habitat patches, and urban green-space areas are managed intensively. These land-use changes are causing declining numbers and diversity of pollinators and important floral resources. In this study we examined: (1) effects of land use on bumblebees and other pollinator taxa in urban grasslands by comparing semi-natural and successional grasslands within the urban and suburban parts of Trondheim. (2) effects of various factors including season, land-use in the surrounding landscape, and flower species richness and abundance on species richness and abundance of bumblebees and other pollinator taxa. Generalized linear mixed models were used to assess the relationship between pollinators and land-use, seasons, flowers, surrounding landscape and weather conditions including temperature and cloud cover. A NMDS ordination analysis was used to assess the relationship between composition of observed pollinators, grasslands, and their land-use.

We found a significant difference in pollinator richness and abundance in semi-natural and successional grasslands. Similarly, there was a significant difference in variation of bumblebee abundance and species richness between semi-natural and successional grasslands, with a higher variation among the semi-natural grasslands. Total abundance of pollinators did not differ significantly between land-use types, neither did the variation. Number of pollinators increased during the summer, and numbers in May and June differed significantly from July and August. Bumblebees and other pollinators were positively affected by species richness and abundance of flowering plants, increasing proportion of non-habitat, and temperature. The ordination analysis showed no significant difference in species composition between land-use types, but revealed some pattern related to the different pollinators' preferences for specific habitats. Results of this study indicate that Trondheim present a variety of characteristics among semi-natural grasslands and suggest that maintenance of the semi-natural grasslands' characteristics is of importance for the conservation of urban pollinator- and plant communities. Additionally, management strategies promoting heterogeneity and connectivity at the landscape level can be important for the conservation of pollinators and plants in urban areas.

Samandrag

Semi-naturlege grasmarker er eit av dei viktigaste habitata for humler og andre pollinatorar, men endringar i arealbruk truer denne habitattypen. Opphøyr av skjøtsel, med påfølgande gjengroing er truleg ein av dei viktigaste truslane mot semi-naturlege grasmarker i dag. I tillegg har urbanisering ført til auka press, fragmentering og isolering av habitatflekkar, og urbane grønt-områder er sterkt modifisert. Slike arealbruksendringar fører til nedgang i diversiteten av pollinerande insekt og viktige blomsterressursar. I denne studien undersøkte me: (1) effektar av arealbruk på humler og andre pollinatorar i urbane grasmarker ved å samanlikne semi-naturlege grasmarker og suksessive grasmarker. (2) effekten av ulike faktorar, inkludert sesong, blomsterressursar og arealbruk i omkringliggande landskap, på antall av humler og andre pollinatorar. Generaliserte lineære blanda modeller vart brukt til å vurdere forholdet mellom pollinatorar og arealbruk, sesong, antall blomar, omkringliggande landskap, temperatur og skydekke. Ein NMDS-ordinasjonsanalyse vart brukt til å vurdere forholdet mellom samansetning av observerte pollinatorar, grasmarker og arealbruk.

Me fann at artsrikdom og antall av humler var signifikant forskjellig i semi-naturlege og suksessive grasmarker. Det var også ein signifikant forskjell i variasjonen av artar og antall av humler i dei to typane grasmarker, med høgast variasjon i semi-naturlege grasmarker. Totalt antall av pollinatorar var ikkje signifikant forskjellig i dei to typane grasmarker, heller ikkje variasjonen. Artsrikdom og antall av humler og andre pollinatorar auka gjennom sommaren, og mai og juni var signifikant forskjellig frå juli og august. Humler og andre pollinatorar var positivt påverka av auka antall blomar, større andel ikkje-habitat, og høgare temperatur. Ordinasjons-analysen viste ingen signifikant forskjell i arts samansetnad i semi-naturlege og suksessive grasmarker, men analysen viste samanhengar relatert til pollinatorars preferansar for habitat. Resultata i denne studien viser ein stor variasjon innanfor semi-naturlege grasmarker i Trondheim, med eit mangfald av vedlikehald og karaktertrekk. Riktig bevaringsarbeid av grasmarker og urbane grønt-areal kan bidra til auka diversitet av pollinatorar og plantar i framtida. I tillegg kan forvaltningstiltak som fremmer heterogenitet og konnektivitet på landskapsnivå vere viktig for å bevare biodiversitet av pollinatorar og plantar i urbane områder.

Preface

This project was performed in collaboration with another master student, Ajay Dhukuchhu. His thesis focuses on the effect of land-use on plants and plant-pollinator networks in the same grasslands based on the same data set. Thus, all plant results are referred to as Dhukuchhu 2021.

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I would like to thank my supervisors Frode Ødegaard and Gunnar Austrheim for their help, support, and guidance through field work and the writing of this thesis. I would also like to thank Sandra Åström for the help with the field methods, and Sondre Dahle for the demonstration of methods in the field. Onwards I would like to thank Ajay Dhukuchhu for the cooperation and company through the work on this project. Thanks to friends and family for continued encouragement and support. Lastly, my fellow master students deserve a special thanks, for their understanding, company, long coffee breaks, and nice conversations through the work of this thesis.

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1 Introduction

Pollinators play an essential role as one of nature's benefits to people through the production of food and the reproduction of many wild plants (Potts et al., 2016, Norwegian Ministries, 2018). However, an increasing number of studies report declining numbers of pollinators in several parts of the world, stressing the urgent need to include pollinators in future conservation efforts (Williams and Osborne, 2009, Cardinale et al., 2012, Potts et al., 2016, Bendel et al., 2019). The Assessment Report on Pollinators, Pollination and Food Production published by IPBES in 2016 highlights habitat destruction, fragmentation and degradation, along with conventional intensive land management practices as important causes for the reduction or alteration of the pollinators' food and nesting resources, causing declining densities and diversity of the pollinating insects (Potts et al., 2016, Díaz et al., 2019). Urbanization, in addition to agricultural expansion and intensification, is considered one of the most important causes to land-use change, leading to loss of resources and habitats for pollinating insects (Potts et al., 2016). Semi-natural grasslands are recognized as one of the most important habitats for pollinators (Totland, 2013, Ødegaard et al., 2015b), but experience a decline due to the cessation of traditional agriculture and subsequent abandonment or intensified management (Öckinger and Smith, 2007, Hovstad et al., 2018, Squires et al., 2018, Jakobsson and Pedersen, 2020). In urban and suburban areas, semi-natural grasslands and other green space areas may play an essential role as habitats for both plants and pollinators, but correct management is needed to maintain their semi-natural characteristics (Moog et al., 2002, Öckinger et al., 2009, Noordijk et al., 2009, Klaus, 2013, Aguilera et al., 2019). Knowledge about how pollinators are affected by urbanization and how habitats and resources should be managed in the best possible way will become increasingly important in the future, as the urban land cover is expected to expand (Winfree et al., 2011, Gunnarsson and Federsel, 2014, Potts et al., 2016, Díaz et al., 2019).

1.1 Pollinators and their interaction with plants

Pollinators and plants form the mutualistic process of pollination, where plants get their reproductive gametes spread by insects, and insects receive energy and protein in the form of nectar and pollen from the plants in return (Willmer, 2011, Totland, 2013). The strong correlation between pollinator and plant diversity in a community is supported by several previous studies (Fontaine et al., 2005, Ebeling et al., 2008, Theodorou et al., 2020), and they

point out that a high diversity of pollinators and plants is crucial for the sustainability of ecosystems. A higher richness of functional insect groups is expected to promote a high diversity of plants, as various groups of insects have plant-species specific preferences (Fontaine et al., 2005, Willmer, 2011). This will benefit insects in a longer perspective, since successful pollination enhances the future availability and diversity of food, thus contributing to the temporal stability and maintenance of pollinator communities (Ebeling et al., 2008). Enhanced diversity of pollinators may also increase the likelihood that some species will have the ability to adapt to changing environments. Moreover, increased functional redundancy increase the probability that surviving species can compensate for potentially extinct species (Zamora, 2000, Potts et al., 2016). Greater floral abundance is also beneficial as this contribute to a higher resource availability for pollinators (Potts et al., 2006). Worldwide, it is estimated that almost 90% of flowering plants are fully or partly dependent on animal pollination (Potts et al., 2016). In Norway, the seed production of probably nearly 80% of wild plant species depends upon insect pollination (Totland, 2013).

Pollination plays a vital role as one of nature's benefits to humans (Potts et al., 2016, Norwegian Ministries, 2018). It is a regulating service contributing to the gene flow and maintenance of biodiversity in wild plant communities (Vanbergen and Initiative, 2013). Moreover, pollinators are essential in the production of food worldwide, including agricultural crops such as fruits, vegetables, oils, seeds and nuts (Vanbergen and Initiative, 2013). Beyond food provisioning, pollinators contribute directly to medicines, biofuels, fibres, construction materials, recreational activities and as sources for inspiration in for instance religion, education, and art (Potts et al., 2016). In Norway, there is no prepared estimates of the economic significance of pollination, but pollinators play an important role in the production of both oil crops, legumes, fruits, and wild berries (Totland, 2013).

1.1.1 Bees and bumblebees

Bees (Apiformes) and bumblebees *(*Bombus*)* are considered the most important groups of pollinators in the northern hemisphere (Totland, 2013). In Norway, there is a high diversity of bees, with a total of 208 species observed, including one species of honeybee, 35 species of bumblebees, and 172 species belonging to different groups of wild bees (Artsdatabanken, 2014). Today, about one third of the bees found in Norwegian ecosystems are listed on the Norwegian red list over threatened species (Ødegaard, 2014, Ødegaard and Lønnve, 2015). This include 5 species of bumblebees, where 3 of these are classified as threatened (Ødegaard et al., 2015a).

Bees and bumblebees are dependent on nectar- and pollen producing plants as a source of energy and protein for both adult and larval nutrition (Willmer, 2011). The bees and bumblebees represent different levels of sociality (Artsdatabanken, 2014, Ødegaard et al., 2015b, Miljødirektoratet, 2019), where solitary bees are the most common (Willmer, 2011). Solitary bees do not form communities, but live as separate, independent individuals where each female is making and stocking her own nest (Willmer, 2011, Totland, 2013). Social (eusocial) bees live in colonies and behave in a way that best benefit the whole community (Totland, 2013). Among the 35 bumblebee species found in Norway, 28 species are social and the remaining 7 are social parasites, infiltrating the nests of their host (Totland, 2013, Ødegaard et al., 2015b). The bumblebee queen is the only fertile individual, producing workers (infertile females), males, and new queens throughout the summer. In northern ecosystems, bumblebees have an annual life cycle starting in the spring when the queen wakes up from hibernation. The queens are mainly active outside the nest in the spring, collecting resources for producing their first brood of workers inside the nest. As the summer passes on, workers do tasks inside and outside the nest, including foraging for nectar and pollen. Males and new queens are produced in late summer and leave the nest almost immediately after maturation (Goulson, 2003, Willmer, 2011, Totland, 2013, Ødegaard et al., 2015b). Bees and bumblebees nest either above or in the ground, often in old burrows of small rodents or in layers of mosses or grass (Ødegaard et al., 2015b). The social bees are dependent on a constant availability of flowering plant species from early spring to late summer for the colony to survive (Goulson et al., 2010, Totland, 2013). Solitary bees have a shorter lifespan, and are thus more dependent on availability of specific resources at the time they are active (Totland, 2013).

1.1.2 Butterflies and moths

Butterflies and moths (Lepidoptera) are regarded as poorer pollinators than bees as they are less directly linked to the plants; they have their primary source of protein in the vegetative parts of the plants, and they do not collect pollen (Willmer, 2011, Totland, 2013). Butterflies and moths are representing a relatively large order; there are around 175 000 species worldwide, represented by approximately 2200 species in Norway (Aarvik and Elven, 2014). Among butterflies and moths, 459 species are red listed on the Norwegian red list over threatened species. Among these, 319 are classified as threatened (Aarvik, 2015).

Butterflies (Papilionoidea) are diurnal and associated with warm and relatively still summer weather (Willmer, 2011). By contrast, the vast majority of moths are active at night-time (Willmer, 2011). The butterflies form their own superfamily, consisting of 5 families and

approximately 100 species in Norway. These butterflies are larger than the moths, and often have conspicuous paintings on their wings (Aarvik and Elven, 2014). Butterflies have a life cycle where they undergo metamorphosis though four stages: egg, caterpillar, pupa, and imago. Females usually oviposit on the leaves of a hostplant, in which the larvae (caterpillar) feed on after hatching. As soon as the larvae has reached full length and weight, it reaches the pupa stage. The larvae are dependent on adequate warm temperatures to be able to reach full size in time. Thus, in years with cold and rainy summers there might be lower numbers of butterflies. After becoming an adult, butterflies spend most of their time looking for a mate and hopefully producing another batch of fertilized eggs. (Aarvik et al., 2009)

1.1.3 Other pollinators

Among other insect taxa, both flies, beetles, and wasps occasionally visit flowers (Willmer, 2011). Many groups of true flies (Diptera) feed on nectar or pollen from flowers, but are regarded as rather inefficient pollinators due to a non-hairy body surface. (Willmer, 2011, Totland, 2013) An exception is the hoverflies which are exceedingly hairy (Totland, 2013). Among the beetles, most species visiting flowers in our ecosystems are probably quite inefficient pollinators (Totland, 2013). Some subgroups of Hymenoptera, including different groups of wasps, occur in flowers and may in this regard act as pollinators (Totland, 2013).

1.2 Semi-natural grasslands and successional changes

For pollinators to thrive in a given habitat, characteristics including a high diversity of plants, availability of nest-building materials and suitable nesting sites are essential (Ødegaard et al., 2015b). Semi-natural grasslands meet most of these needs and have been recognized as an especially important habitat for pollinating insects and plants globally (Öckinger and Smith, 2007, Totland, 2013, Ødegaard et al., 2015b, Squires et al., 2018). These grasslands have been formed through low-intensive human activity, such as forest clearing and subsequent grazing or traditional agriculture over a long period of time (Totland, 2013, Artsdatabanken, 2016, Jakobsson and Pedersen, 2020). The natural succession into forest has been prevented by grazing, haymaking, or mowing, and this process has created a unique, open habitat containing a high-density, species rich flora and fauna (Totland, 2013). However, the cessation of traditional agricultural practices has led to abandonment or intensification of many of these grasslands (Hovstad et al., 2018, Jakobsson and Pedersen, 2020). The usage of fertilizers, ploughing, and cultivation have led to great changes in the species composition and soil characteristics (Hovstad et al., 2018). Additionally, encroachment of woody plants in abandoned grasslands has led to a declining biodiversity. Consequently, semi-natural

grasslands have experienced a considerable decline during the last 50-60 years (Hovstad et al., 2018). The 2018 red list for nature types listed Semi-natural meadow as vulnerable. Additionally, hay meadows were listed as critically endangered (Hovstad et al., 2018). Moreover, these grasslands are the main habitat for several of the red listed species of plants and insects (Henriksen and Hilmo, 2015).

Semi-natural grasslands are typically dominated by grasses and herb species (Aalberg Haugen et al., 2019), often characterized as small, uncompetitive, stress tolerant, and light demanding. The species composition of plants within the grasslands is highly determined by the local environmental conditions including light availability, soil moisture and nutrients, as well as the regional species pool (Kull and Zobel, 1991, Moen et al., 1993). Management regimes such as grazing or mowing can be favourable to maintain the characteristics of these grasslands (Moog et al., 2002, Carvell, 2002). Grazed grasslands often display a relatively heterogenous species composition, normally dominated by herbs. Grazing includes removal of plant material and livestock trampling, which create gaps, thus less competitive species has the possibility to coexist with more competitive species (Kalamees and Zobel, 2002). Similarly, mowing or cutting of grass once or twice during the summer prevent overgrowth, and may at the same time make the conditions suitable for the plants growing there (Moog et al., 2002, Noordijk et al., 2009, Aagaard et al., 2018).

The lack of management leads to successional changes and encroachment of trees and shrubs, resulting in a low light availability and altered soil-nutrient content (Hovstad et al., 2018). Thus, species thriving in semi-natural habitats will be outcompeted by less light-dependent and more competitive plant species, resulting in a reduction of the total species richness (Niedrist et al., 2009, Bohner et al., 2020). Additionally, successional changes will increase the total above ground biomass and an accumulation of litter, which hamper seed germination and the establishment of seedlings (Foster and Gross, 1997). Accumulation of litter will contribute to an increase in the soil nutrient content, promoting fast-growing plants thriving in nutrient rich conditions such as tall herbs and grasses (Prévosto et al., 2011, Hovstad et al., 2018). These changes within the plant community may have knock-on negative effects on pollinators, as important food resources will be lost (Walcher et al., 2017).

In Norway, there is a variation of characteristics of semi-natural grasslands today, caused by a differences in environmental factors, land-use history, fertilizer application, and management regimes (Hovstad et al., 2018, Jakobsson and Pedersen, 2020). In abandoned semi-natural grasslands, successional changes starts immediately, and the successional pathways may show

large variations (Prévosto et al., 2011). Similarly, fertilization of grasslands may cause regional differences in characteristics and growing conditions (Totland, 2013, Jakobsson and Pedersen, 2020). Detailed knowledge about semi-natural grasslands and their direction of changes, including successional changes or degree of fertilization, is scarce in Norway today (Jakobsson and Pedersen, 2020). Recognizing important indicators representing the various states of semi-natural grasslands can be an important aid in monitoring programs for the semi-natural nature types, and can give valuable information for future management planning (Jakobsson and Pedersen, 2020).

1.3 Grasslands as habitats in the urban landscape

The rapid growth of urban areas has led to an increased pressure and destruction of natural and semi-natural habitats (Potts et al., 2016, Díaz et al., 2019). As a result, habitats have been altered into small, fragmented and isolated patches (Geslin et al., 2013, Potts et al., 2016). Depending on the extent of changes in land-use, urbanization has shown varied effects (negative, neutral, or positive) on the pollinator- and plant community structure. The most negative responses are found where land-use changes have been most extreme, whilst moderately changed systems reveal more varied responses within the pollinator community (Koh and Sodhi, 2004, Öckinger and Smith, 2006, Bergman et al., 2008, Winfree et al., 2011, Theodorou et al., 2020). Even though urbanisation is recognized as a significant factor in both current and predicted species extinction (McDonald et al., 2008), researchers emphasize that correct management of urban green areas can potentially promote biodiversity and viable populations of pollinators and plants (Blair and Launer, 1997, Öckinger et al., 2009, Gunnarsson and Federsel, 2014, Potts et al., 2016), and there is an increasing awareness of their inclusion in urban planning and global biodiversity conservation actions (Elmqvist et al., 2013).

Urban grasslands comprise a broad diversity of green spaces, including parks and playgrounds, road verges, meadows in residential areas, old wastelands and other habitat types located in densely populated areas (Klaus, 2013). Among the variety of green spaces there is a diversity of management regimes, ranging from heavily managed traditional public parks to irregularly managed semi-natural grasslands and ruderal patches (Blair and Launer, 1997). The management regimes of grasslands can be an important factor determining the specific traits and composition of the local plant- and pollinator community (Carvell, 2002, Bertoncini et al., 2012). Additionally, characteristics such as habitat connectivity and heterogeneity in surrounding landscapes becomes increasingly important along the urban gradient and can be a contributing factor in the dynamics of urban plant populations (Tommasi et al., 2004, Öckinger

and Smith, 2006, Potts et al., 2016, Aguilera et al., 2019). The island biogeography theory has been used as a conceptual framework to explain the regional processes that promote urban biodiversity (Fattorini et al., 2018). This theory explains species richness on islands as a dynamic equilibrium between immigration and extinction rates, where size of the island and distance to the source of colonization are important determinants (MacArthur and Wilson, 2016). Comparable to the habitat islands described in the theory of island biogeography, urban green spaces vary in size, have different degrees of isolation and fragmentation, and are separated by an environment that is more or less inhospitable (MacArthur and Wilson, 2016, Fattorini et al., 2018). The species-area relationship predicts that larger habitats increase habitat diversity and can support larger populations. Furthermore, the metapopulation theory predicts that the risk of species extinction can be reduced by proximity between natural fragments, thus increasing the chances of sustaining a meta-population (Jones and Leather, 2013, Fattorini, 2016). In urban landscapes, lawns, road verges, railway banks, and flower beds, often abundant in city-near areas, contributes to an increased landscape connectivity and proximity between habitat patches, thus may play an essential role for the maintenance of urban pollinator- and plant communities (Westrich, 1996, Dearborn and Kark, 2010, Potts et al., 2016, Phillips et al., 2020).

1.4 Norway and Trondheim

Detailed knowledge about the actual plant-pollinator interactions is crucial to be able to understand the importance of pollinators, their role in the ecosystem (Carman and Jenkins, 2016), and to make efficient management plans (Totland, 2013). In Norway, there is still limited knowledge about pollination as an ecosystem process (Totland, 2013). The national pollinator strategy, established in 2018, highlights three focus areas to achieve the goal of viable populations of pollinators: increasing scientific knowledge, providing good habitats, and improving communication on the subject (Norwegian Ministries, 2018). The strategy emphasizes the need of more knowledge about how areas important for pollinators should be managed, and that these management strategies should be set into play to ensure pollinators a continuous availability of floral resources.

In Trondheim, there is an ongoing systematic work to maintain cultural land and improve conditions for pollinators, with implementation of a plan for the use and management of valuable cultural landscapes in the municipality, including several sites in Bymarka and one site at Lade, Grønlia (Øien 2010, Øien 2018). This work can give us valuable knowledge about

efficient management practices and can be an important step into future management planning promoting pollinators in urban areas.

1.5   Aims and hypotheses

In this study, we aim to investigate the effects of land-use change on bumblebees and other pollinator taxa within urban grasslands. This will be done by comparing two different grassland types; semi-natural grasslands and successional grasslands (1); investigate how species richness and abundance of pollinators changes between seasons (2) assess the importance of plant species richness and abundance within semi-natural and successional grasslands (3); and examine how the surrounding landscape affect pollinators within grasslands (4).

We hypothesize that the species richness and abundance of pollinators will be higher in semi-natural grasslands compared to successional grasslands (1); that species richness and abundance of pollinators will differ between seasons (2); that species richness and abundance of pollinators will increase with increasing species richness and abundance of flowering plants (3); that high proportion of non-habitat such as roads and built-up areas in the surrounding landscape will affect species richness and abundance of pollinators within grasslands negatively (4).

2 Methods

2.1 Study location

The study was conducted in Trondheim municipality in Trøndelag county (63°26′24″N 10°24′0″E). Trondheim lies in central Norway, located relatively close to the Norwegian Sea. This gives Trondheim a slightly oceanic climate, typically cool and humid (Moen et al., 1993). Most of the area lies within the southern boreal zone, but the upper parts of Bymarka reaches the middle boreal zone (Lyngstad et al., 2002). The Area resource Map (AR5) and categorizations made by Kleppe (2019) was used as a basis for selection of field sites. In her study, grasslands were categorized into different land-use categories based on current land-use, the degree of succession, and state of area (Kleppe, 2019). The AR5 map is a national standard map provided by Trondheim municipality, which is designed for use at a scale of 1:5 000 and describes the land-use, forest quality and basic conditions (NIBIO, 2021). We selected 12 sites situated within the urban and suburban parts of Trondheim by a stratified random sampling method (figure 1). 6 sites were categorized as semi-natural and another 6 as successional (figure 1, table 1). See appendix B for picture of the sites.
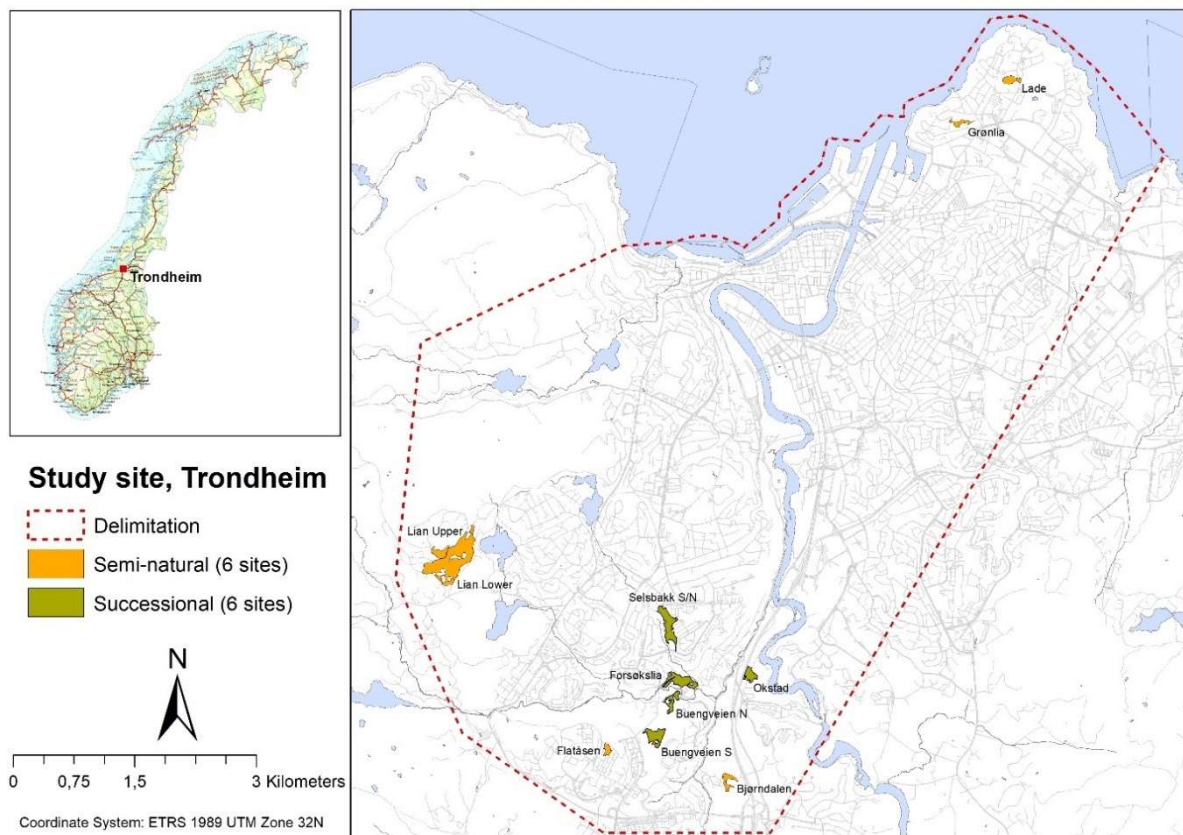
Figure 1. Map of the selected study sites (six semi-natural and six successional) in Trondheim municipality. The delimitation marks the border for the selected urban area in Kleppe (2019).

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The semi-natural sites are characterized by a high diversity of plants and insects (figure 2), dominated by grass and herb species (Artsdatabanken, 2016). Semi-natural grasslands are relatively nutrient poor, and typical plant species include harebell (*Campanula rotundifolia*) and common bent (*Agrostis capillaris*) (Moen et al., 1993). Successional sites are habitats that has undergone successional changes towards scrub and woodland, dominated by tall grasses, weeds and wooden plants (figure 3) (Artsdatabanken, 2016, Bohner et al., 2020). Species typically found in grasslands in a successional state includes fireweed (*Epilobium angustifolium*), European raspberry (*Rubus idaeus*) and meadowsweet (*Filipendula ulmaria*) (Moen et al., 1993). The area of semi-natural sites varied between 9 155-167 791 m^2 and the area of successional sites varied between 18 218-47 494 m^2 (table 1). Landscapes surrounding the sites were dominated by a mixture of forest, built-up areas, building estates, roads, grasslands and some agricultural areas (Figure 1, table 1). Some criteria were set for the sites, including that they should be large enough for containing 5 transects on a size of 50x5 meters. The minimum distance between transects were 5 meters and the minimum distance from the transects to the edge of the site were 10 meters. Additionally, the sites should be distributed at different elevation (table 1), with at least one site of each land-use type represented at the different elevations if possible.
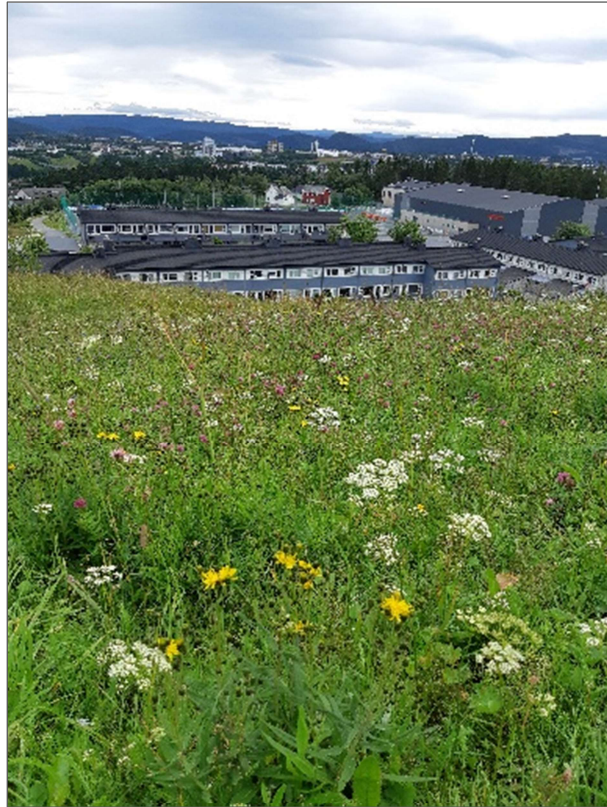
Figure 2 Flatåsen, one of the semi-natural grasslands included in the study. (Photo: H. Heggøy)

Figure 3. Okstad, one of the successional grasslands included in the study. (Photo: Ajay Dhukuchhu)

Table 1. An overview over the selected study sites, their land-use category, size, characteristics of the surrounding landscape (values between 0 and 1 representing proportion. 0 = 0% cover of the specific land-use type, whilst 1 = 100% cover in the surrounding landscape), and meters above sea level (Kartverket, 2021).

Site	Size (m²)	Land-use	Proportion of non-habitat	Proportion of forest	Proportion of grassland	Meters above sea level
Flatåsen	9 155	Semi-natural	0.22	0.27	0.10	182
Grønlia	10 918	Semi-natural	0.29	0.09	0.14	43
Lade	15 590	Semi-natural	0.20	0.14	0.21	57
Bjørndalen	15 653	Semi-natural	0.14	0.36	0.09	110
Lian Upper	18 279	Semi-natural	0.06	0.54	0.19	305
Lian Lower	167 791	Semi-natural	0.05	0.64	0.05	265
Okstad	18 218	Successional	0.19	0.40	0.05	45
Buengveien N	18 401	Successional	0.14	0.27	0.25	85
Buengveien S	32 460	Successional	0.14	0.28	0.21	105
Forsøkslia	42 657	Successional	0.19	0.29	0.16	70
Selsbakk N/S	47 495	Successional	0.27	0.14	0.10	120

2.2   Field work

The sampling was performed on four occasions during the 2020 field season: late May, late June, late July, and early August. Sampling took place on sunny or partly sunny days with a minimum temperature of 10 degrees in May and a minimum of 15 degrees in June, July, and August. The sampling was performed between 10:00 in the morning and 17:00 in the afternoon. At each site, 5 fixed transects were established in a parallel manner (Figure 4). At each sampling day, there were done registrations on temperature and cloud cover at starting time for each transect. Plant- and pollinator registrations were completed by the same two observers throughout the field season. A standardized form was used to register pollinators and plants in the field (see appendix C).

Figure 4. Transects were measured up before the field season. (Photo: H. Heggøy)

2.2.1 Pollinator data

Bumblebees, butterflies, and other pollinators were counted while walking slowly along the mid-line of the transects, observing the area of 2.5 meters on each side of the mid-line. Bumblebees and butterflies were identified at species level. In cases of uncertainty, individuals were captured with a sweep net for photographing or put in a transparent glass vial for easier identification (Figure 5). Difficult individuals of bumblebees were euthanized by freezing and brought to the lab for identification. Only workers and males of bumblebees were brought to the lab, thus no bumblebee-queens were killed in the study. All butterflies caught by sweep net were released in the field.

Figure 5. Difficult individuals were captured in a glass vial for easier identfication. (Photo: H. Heggøy)

In the case of the common *Bombus lucorum*, there are two less common "sibling species", *B. cryptarum* and *B. magnus*, which are hard to distinguish in field (Ødegaard et al., 2015b). In this study, these individuals were counted as the common species *B. lucorum* (*B. lucroum group*). In total, 108 (15%) individuals of bumblebees were not identified to species. These bumblebees were included in the analyses of the number of individuals but not of species richness.

Other taxa of pollinators, including wild bees, hoverflies, honeybees, and wasps were registered and counted if they were observed within the transect, similarly to bumblebees and butterflies.

Flies and beetles were registered only if they were observed sitting on a flowering herb, since these taxa are regarded as more occasional pollinators (Willmer, 2011, Totland, 2013). If a pollinator were observed sitting on a flower, the species of the flowering herb was registered along with the pollinator.

The time used on each transect is assumed to be the same when the time used on handling insects and taking notes is subtracted from the total time used from start to end.

2.2.2 Plant data

Registrations of plants were performed at five subplots on a size of 1x1 meter within each transect. Only flowering herbs were registered. A quadrat (1x1 meter) containing 16 sub-quadrats was used as a tool for the plant registrations (Figure 6). The species of the flowering plants observed within the quadrat were registered, and number of sub-quadrats where a species was present represented abundance of the species within the quadrat. For the abundance of flowering plants at the transect-level, the abundance of the five subplots were summarized together. Additionally, the height of the vegetation at each subplot was measured.

Figure 6. Plant quadrat used for registrations of flowering plants. (Photo: Gunnar Austrheim)

2.3   Statistical analyses

Data preparation and statistical analyses were performed in R, version 4.0.2. (R Core Team, 2020). The data on bumblebee species richness, bumblebee abundance and pollinator abundance represented counts and were non-normally distributed, thus only non-parametric statistical tests were applied (Hollander, 1973) (see appendix D). All figures were made by using the package "ggplot2" (Wickham et al., 2016)

A Wilcoxon rank sum test was carried out to compare the distribution of abundance and species richness of bumblebees and abundance of pollinators in semi-natural and successional grasslands (Hollander, 1973). A Fligner-Killeen test was carried out to test homogeneity of variances within land-use types (Conover et al., 1981). Furthermore, differences in abundance and species richness of bumblebees and abundance of pollinators between seasons were investigated with a Kruskal-Wallis test (Hollander, 1973). A pairwise Wilcoxon rank sum test with corrections for multiple testing was used to calculate pairwise comparisons between the seasons. The functions *wilcox.test(), fligner.test(), kruskal.test(),* and *pairwise.wilcox.test(),* from the package "stats" were used for Wilcoxon rank sum test, Fligner-Killeen test, Kruskal-Wallis test and pairwise Wilcoxon rank sum test, respectively (R Core Team, 2020).

A non-metric multidimensional scaling (NMDS) was performed to investigate differences in species composition of bumblebees and pollinator groups among sites and land use types. Ordination analyses were performed using the function *metaMDS* from the package "vegan" (Oksanen et al., 2016). The number of reduced dimensions were three, and the dissimilarity distance matrix were calculated by using the Bray-Curtis dissimilarity. The function *anosim()* in the package "vegan" were used to test if there was a significant difference in species composition between semi-natural grasslands and successional grasslands (Oksanen et al., 2016).

Generalized linear mixed models with Poisson or negative binomial error distribution and a logarithmic link function were used to analyse the effect of land use, flowering plants, and landscape parameters on the species richness and abundance of pollinators (Bolker et al., 2009). Either species richness (per transect) of bumblebees, abundance (the sum of surveyed individuals within transects) of bumblebees, or abundance of pollinators (the sum of surveyed individuals within transects) were used as response variable (Table 2). Proportion of forest, grasslands and non-habitat, flower species richness and abundance, land use, season, temperature, cloud cover and size of site were the a priori explanatory variables (Table 2).

Transects nested within sites were included as random factors (Table 2). Flowering plant abundance, temperature, cloud cover and size of site were scaled to overcome convergence problems (*(predictor-mean)/standard deviation*).

The proportion of forest cover, buildings, roads, and grasslands characterized as *Home field grazing (HFG)* and *Open firm ground (OFG)* (Kleppe, 2019, NIBIO, 2021) within a radius of 500 meter from the edge of each study site was determined by using ArcMap 10.8 (table 1) (ESRI, 2019) and national standard AR5-resource map provided by Trondheim municipality (NIBIO, 2021). A radius of 500 meters were chosen based on assumed foraging distances from the nest site (Goulson et al., 2010, Ødegaard et al., 2013). "Analysis tools" and the *proximity*-function *buffer* was used to create buffer zones surrounding the study sites. The *overlay*-function *intersect* was used to determine proportion of the three categories within each buffer-zone. Buildings and roads were summarized to represent proportion of non-habitat.

A Spearman's rank correlation test was performed to evaluate the strength of association between explanatory variables and the direction of the relationship (Crawley, 2012). A value of $r = \pm 1$ indicates a perfect association between two variables, while $r = 0$ reflects the absence of a relation between the two variables. The correlation test were carried out using the function *rcorr()* in the "Hmisc" package (Harrell Jr and Harrell Jr, 2019). To measure relationships between categorical and continuous variables, Kruskal-Wallis eta-squared were calculated by using the function *kruskal_effsize()* from the "Rstatix"- package (Kassambara, 2020). Values $\geq$ 0.26 were determined as strong relationships (Bakeman, 2005). Highly correlated variables ($r \geq 0.5$, $\eta^2 \geq 0.26$) were removed from the model (Rumsey, 2016). Flowering plant species richness was highly correlated with several variables, including abundance of flowering plants (Spearman's rank correlation; $r = 0.88$, $p < 0.01$), season ($\eta^2 > 0.26$), and size of site (Spearman's rank correlation; $r = -0.62$, $p < 0.13$). Since flowering plant abundance is expected to have much of the same effect as flowering plant species richness, only plant abundance was included in further model selection. Proportion of forest and proportion of non-habitat were also highly correlated (Spearman's rank correlation; $r = -0.99$, $p < 0.001$), but proportion of non-habitat was a central factor of this study, thus the latter were excluded from further analyses. There was also a high correlation between temperature and cloud cover, and temperature was chosen for further analyses since this was expected to be more informative. Final explanatory variables were land-use, season, flowering plant abundance, proportion of non-habitat, proportion of grassland, size of site, and temperature. Model selection was performed by excluding non-significant variables from analysis one by one. The best model were selected by ranking a priori

defined models according to Akaike Information Criterion (Burnham and Anderson, 2002). Generalized linear mixed models were analysed using the function *glmer()* in the package "lme4" in R (Bates et al., 2012). The "Dharma" package was used to validate models by plotting the residuals and test for overdispersion, homoscedasticity and zero-inflation (Hartig, 2016). Overdispersion was detected in the model including pollinator abundance as response variable, thus this model was fitted with a negative-binomial distribution. A simple regression analysis was performed with flowering plant species richness as the only explanatory variable to investigate the direction of the relationship between flowering plant species richness and the three response variables. Further details on correlations and model selection are presented in appendix H.

Table 2. Detailed description of the response variables, a priori predictor variables and random factors.

Variables	Type of variable	Description
Bumblebee species richness	Continuous, response	Number of species observed within a transect
Bumblebee abundance	Continuous, response	Number of individuals observed within a transect
Pollinator abundance	Continuous, response	Number of individuals observed within a transect
Land use	Categorical, predictor	Two categories; semi-natural and successional grassland
Season	Categorical, predictor	Four seasons; early May, late June, late July, early August
Flowering plant abundance	Continuous, predictor	Number of sub-quadrats with one or more flowering plants present. All sub-quadrats within the transect were summarized together to represent abundance.
Flowering plant species richness	Continuous, predictor	Number of flowering plant species present within the 5 plant quadrats in the transect.
Proportion of non-habitat	Continuous, predictor	Percentage of total area of 500-meter buffer zone surrounding the sites
Proportion of forest		
Proportion of grassland		
Area	Continuous, predictor	Size of site, measured in m^2
Temperature	Continuous, predictor	Air temperature, measured in degrees Celsius (°C)
Cloud cover	Continuous, predictor	Percentage (%) of cloud cover
Site	Categorical, random factor	12 sites
Transect	Categorical, random factor	5 transect nested within site

3 Results

3.1   Pollinator diversity and abundance

A total of 1527 individuals of pollinators were registered. Among these, there were in total observed 706 individuals of 12 species of bumblebees, and 44 individuals of 8 species of butterflies (Table 3). Additionally, there were found 504 individuals of honeybees and 273 individuals belonging to other insect taxa, including flies, beetles, wasps (Vespidae and Symphyta), and wild bees (Table 3). Among all sites, *B. lucorum gr.* was the predominating species of bumblebees (191 ind.), and *Pieris napi* was the predominating species of butterflies (9 ind.) See appendix A and D for detailed number on pollinators at the different sites.

Table 3. Total number and percentage of different pollinator taxa observed in semi-natural (SN) and successional (SS) grasslands. Percentages are given as percentage of total number of pollinators within each land-use type. Wasps represent individuals belonging to the family Vespidae and the suborder Symphyta.

Pollinator taxa	SN (abundance) *(species richness)*	SN (%)	SS (abundance) *(species richness)*	SS (%)	Total number
Bumblebees	447 (*12*)	60.2	259 (*7*)	34.12	706 *(12)*
Butterflies	27 (*8*)	3.63	17 (*1*)	2.24	44 *(8)*
Honeybees	164	22.07	340	44.80	504
Flies	51	6.86	77	10.14	128
Wasps	20	2.69	33	4.35	53
Hoverflies	20	2.69	22	2.90	42
Wild bees	14	1.88	11	1.45	25
Beetles	13	1.75	12	1.58	25
Total	743	100	759	100	1527

3.1.1 Semi-natural sites

In semi-natural sites*,* a total of 447 individuals of bumblebees were observed*,* and 12 species were represented (Table 3). The most frequently observed bumblebee species was *B. lucorum gr.* (121 ind.), *B. pascuorum* (104 ind.) and *B. lapidarius* (52 ind.) (Table 4). Total number of individuals per site observed during a visit ranged from 0 individuals to 95 individuals.

A total number of 27 individuals of butterflies were observed during the sampling period, represented by 8 species (Table 3). The most frequently observed species was *Erebia ligea* (5 ind.). Numbers of individuals found per site per visit ranged from 0 individuals to 6 individuals.

There were registered 164 individuals of honeybees (Table 3). Total number of honeybees observed per site ranged from no individuals to 42 individuals. Other pollinators were represented by 118 individuals (Table 2).

All seasons summarized; the total number of pollinators found at a site ranged from 32 individuals to 239 individuals, total number of bumblebees ranged from 18 to 192 individuals, and species richness of bumblebees ranged from 3 to 11 species. "Grønlia" was the most numerous site both in abundance of pollinators and in abundance of bumblebees (239 ind. and 192 ind., respectively. Additionally, "Grønlia" had the highest species richness of bumblebees, with a total of 11 species observed. "Flatåsen" was the second most abundant site, both in total number of pollinators and total number of bumblebees (table 5). Similarly, it was the second most species rich site for bumblebees (table 5).

3.1.2 Successional sites

In successional sites, a total of 259 individuals of bumblebees were observed, and seven species were represented (Table 3). The most frequently observed species was *B. lucorum gr.* (70 ind.), *B. pascuorum* (60 ind.) and *B. soroeensis* (34 ind.) (Table 4). The total number of individuals observed per site during a visit ranged from no individuals to 55 individuals.

A total number of 17 individuals of butterflies were observed, represented by one identified species (9 individuals were not taken to species) (Table 3). The most frequently observed species was *Pieris napi* (8 ind.). Number of individuals observed per site during a visit ranged from no individuals to four individuals. There were in total registered 340 individuals of honeybees. Total number of honeybees observed per site during a visit ranged from no individuals to 122 individuals. Other pollinators were represented by 155 individuals (Table 3).

All seasons summarized, total number of pollinators found at a site ranged from 45 to 230 individuals, total number of bumblebees ranged from 14 to 78 individuals, and total number of species of bumblebees observed ranged from two to six individuals. Among successional sites, "Forsøkslia" was most numerous in pollinators, with a total of 230 individuals observed, where 28 individuals were bumblebees (table 5). Second most numerous was "Selsbakk N", with a total of 220 individuals observed, including 54 individuals of bumblebees (table 5). The most abundant site in bumblebees was "Selsbakk S", with a total of 78 individuals of bumblebees observed during the summer, represented by four species (table 5) In total, there were observed 128 pollinating insects at "Selsbakk S". The most species rich site and second most abundant in terms of bumblebees was "Buengveien N", with a total of six species and a total number of

60 individuals of bumblebees (table 5). Total number of pollinators at "Buengveien N" was 95 (table 5).

Table 4. Abundance and percentage of the different species of bumblebees in semi-natural (SN) and successional (SS) grasslands. Percentages are given as percentage of total number of bumblebees identified to species within each land-use type. Tongue length is given in mm. For social bumblebees, tongue lengths are taken from Ødegaard et al. (2013). Cuckoo bumblebees are assumed to have a small tongue on a length of 8-11 mm (Willmer, 2011).

Species	SN (abundance)	SN (%)	SS (abundance)	SS (%)	Tongue length
B. lucorum gr.	121	29,7	70	36,7	8.5
B. pascuorum	104	25,60	60	31,4	10.6
B. lapidarius	52	12,70	0	0	10.9
B. soroeensis	46	11,30	34	17,8	8.8
B. terrestris	41	10,10	1	0,5	10.1
B. pratorum	12	3,00	0	0	9.3
B. hypnorum	8	2,00	21	11	9.2
B. jonellus	6	1,50	0	0	8.1
B. campestris	6	1,50	0	0	8-11
B. hortorum	5	1,20	2	1,1	14.4
B. norvegicus	3	0,70	0	0	8-11
B. bohemicus	3	0,70	3	1,6	8-11

Table 5. Total number of pollinators, bumblebees and species of bumblebees observed at each site. Land-use is given as semi-natural (SN) grasslands and successional (SS) grasslands.

Site	Land-use	All pollinators (abundance)	Bumblebees (abundance)	Bumblebees (species richness)
Grønlia	SN	239	192	11
Flatåsen	SN	165	135	9
Lade	SN	143	18	6
Lian Upper	SN	115	62	6
Bjørndalen	SN	62	18	3
Lian Lower	SN	32	22	5
Forsøkslia	SS	230	28	4
Selsbakk N	SS	220	54	5
Selsbakk S	SS	128	78	4
Buengveien N	SS	95	60	6
Okstad	SS	53	25	5
Buengveien S	SS	45	14	2

3.1.3 Variation between and within land-use types

Species richness and abundance of bumblebees differed significantly between semi-natural habitats and successional habitats (Species richness; $w = 8518.5$, $p = 0.007$ abundance; $w = 8263.5$, $p = 0.038$, Wilcoxon rank sum test, Figure 7a, 7b). There were on average observed 3.08 ± 0.65 species of bumblebees in semi-natural sites, compared to 1.46 ± 0.27 species in successional sites. The mean abundance of bumblebees in semi-natural and successional sites were 18.63 ± 5.81 individuals and 10.79 ± 2.86 individuals, respectively. Total number of pollinators did not differ significantly between semi-natural and successional sites ($w = 7857.5$, $p = 0.218$, Wilcoxon rank sum test, Figure 7c). On average per site, there was found 30.96 ± 6.69 individuals in semi-natural habitats and 31.63 ± 8.11 individuals in successional habitats. Comparing the different pollinator taxa, bumblebees was the most frequently observed pollinator in the semi-natural sites, whilst honeybees was the most frequently observed taxa in successional sites (Table 3).

Variation within land-use types in species richness and abundance of bumblebees differed significantly between semi-natural and successional grasslands, with a higher variation within the semi-natural sites (Species richness; $F = 26.96$, $df = 1$, $p < 0.001$, abundance; $F = 5.62$, $df = 1$, $p = 0.018$, Fligner-Killeen test, Figure 7a, 7b). The variation in pollinator abundance within land-use types did not differ significantly between semi-natural sites and successional sites ($F = 3.09$, $df = 1$, $p = 0.079$, Fligner-Killeen test, Figure 7c).
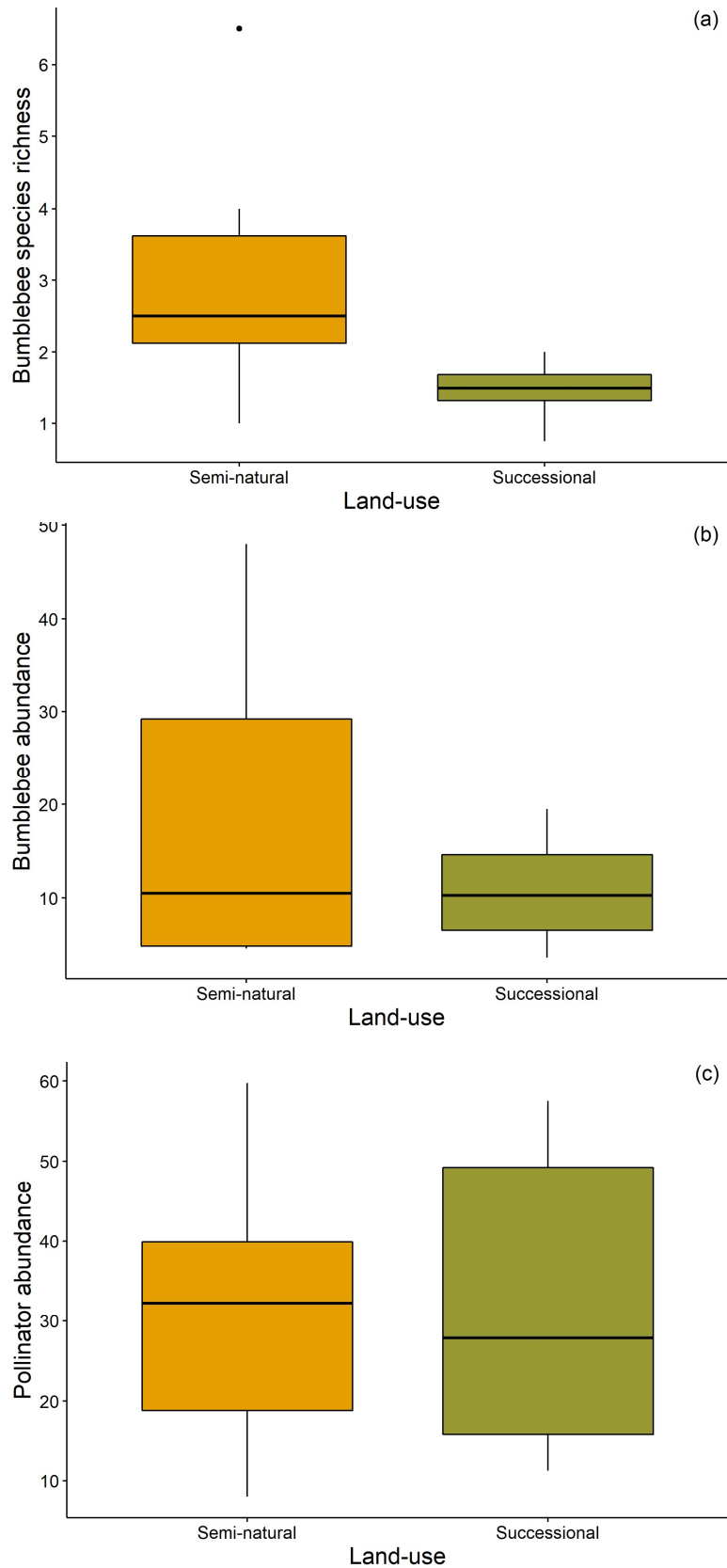
Figure 7. Differences between and within semi-natural and successional grasslands for species richness of bumblebees (a), abundance of bumblebees (b) and abundance of pollinators (c).

3.1.4 Variation between seasons

Number of pollinators observed differed between seasons, and increased during the summer, with 60 individuals observed in May, 192 individuals observed in June, 597 individuals observed in July and 678 individuals observed in August (Figure 8). Number of bumblebees observed increased during the summer, and both species richness and abundance of bumblebees were highest in July (Figure 8a, Figure 8b), which differed compared to the total number of pollinators which had the highest observed number of individuals in August (Figure 8c). Bumblebees were the most abundant taxa in all months except from June, where honeybees represented the highest number. The abundance of honeybees was also high in July and August, with a total of 154 and 285 individuals, respectively. Flies represented a reasonably abundant group both in June, July, and August, but numbers of flies were relatively low in comparison with honeybees and bumblebees. Numbers of butterflies observed were relatively low throughout the summer, with the highest number observed in June. For detailed numbers of the various pollinator taxa in the different seasons, see appendix E.
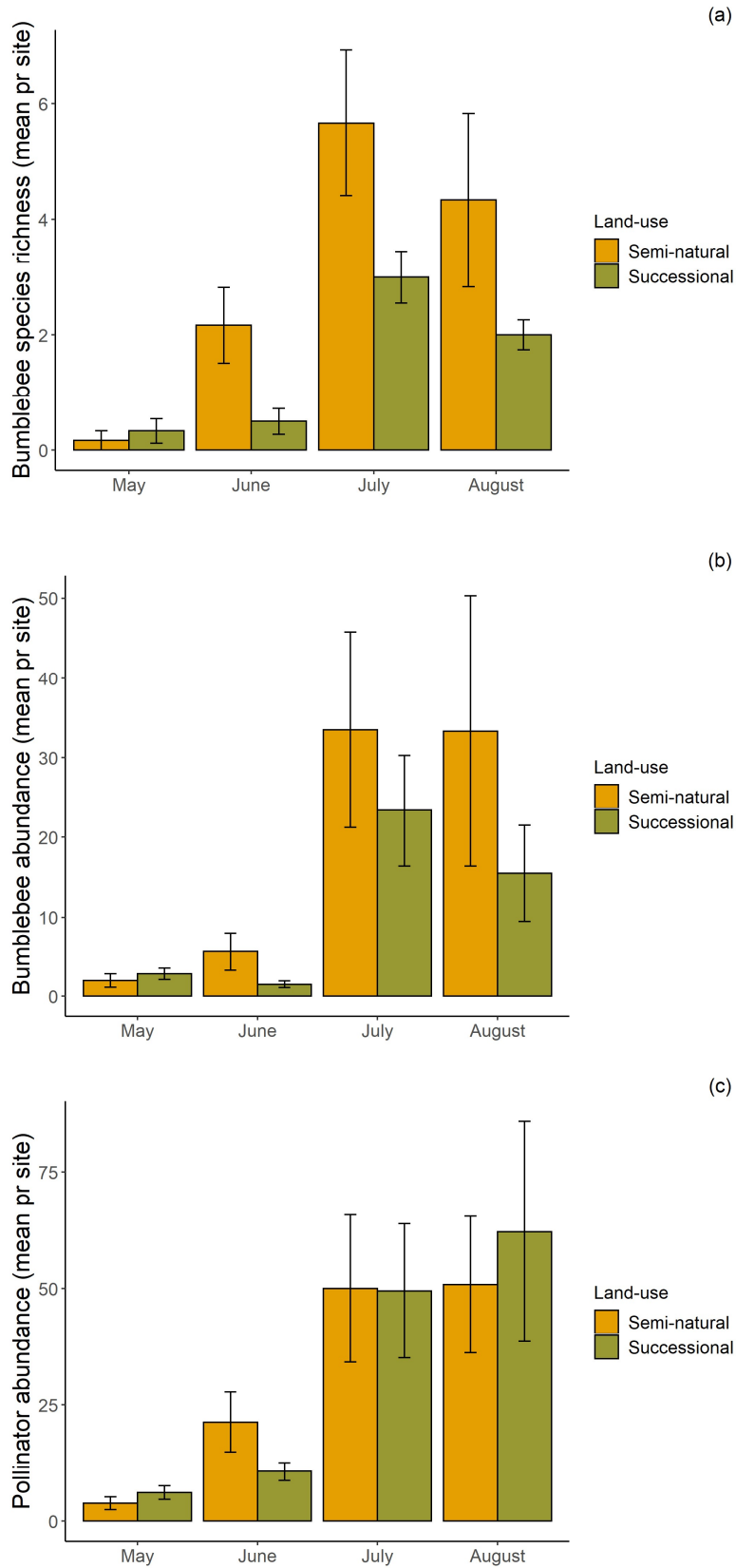
Figure 8. Species richness of bumblebees (a), abundance of bumblebees (b) and abundance of pollinators (c) in semi-natural grasslands in May, June, July, and August. Error bars represent standard error (SE).

3.2   Species composition

3.2.1   Bumblebees

A NMDS of bumblebee species (n = 12) and sites resulted in a 3-axis optimal solution, with final stress 0.047 (Figure 9, see appendix G for stress plot). An ANOSIM test showed no significant difference between species composition in semi-natural grasslands and successional grasslands (r = 0.1222, p = 0.156). Among successional sites, the ordination plot reveals some clustering along the NMDS1 axis, and a more distributed pattern along the NMDS2 axis. The different species of bumblebees are distributed relatively even among the successional sites, but three species (*B. hortorum, B. soroeensis, B. pratorum*) show some clustering around "Selsbakk N". Among the semi-natural sites, some clustered pattern can be seen along the NMDS1 axis, where "Lian U", "Grønlia" and "Forsøkslia" form one group close to the origin, and "Lian L", "Bjørndalen" and "Lade" form another group in the left part of the plot. Four species of bumblebees (*B. norvegicus, B.terrestris, B.campestris, B. jonellus*) stand out from the remaining species with a location in the right part of the plot, closest to the two semi-natural sites "Flatåsen" and "Grønlia".
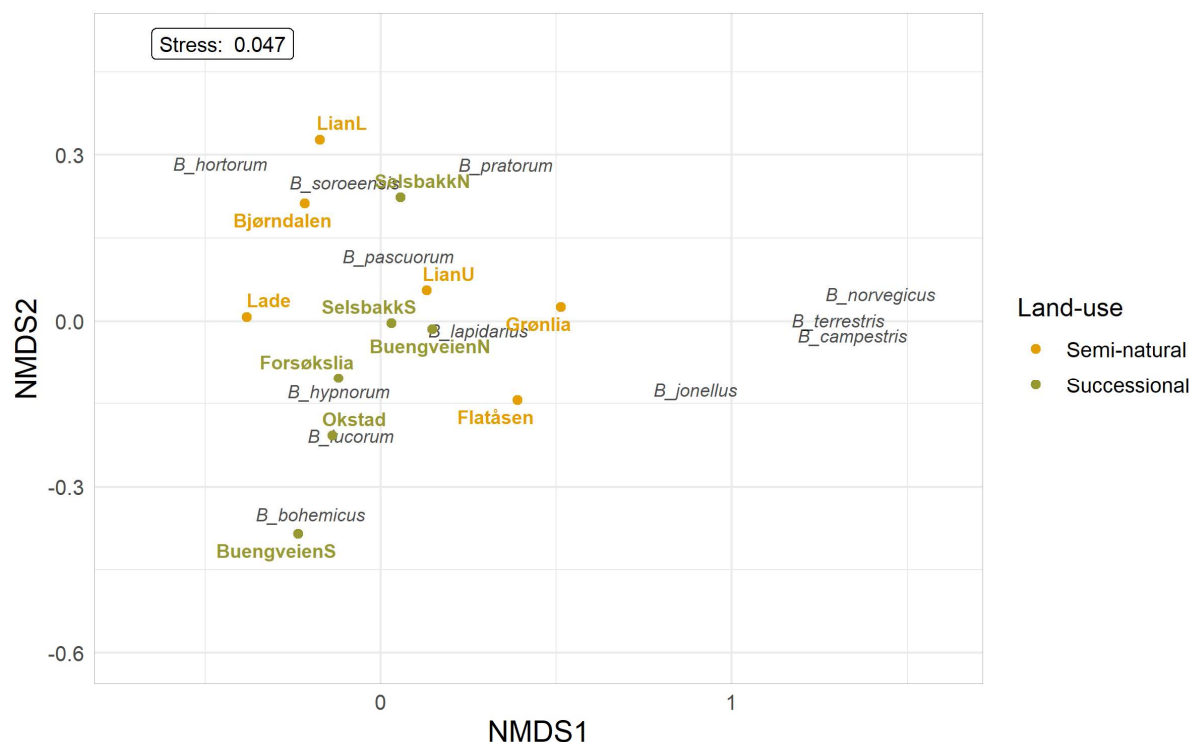
Figure 9. Ordination plot of sites (semi-natural sites = yellow, successional sites = green) and bumblebee species (italic) along a non-metric multidimensional scaling (NMDS) axis 1 (MDS1) and 2(MDS2).

3.2.2 Pollinator taxa

A NMDS of the different pollinator taxa resulted in a 3-axis optimal solution, with final stress 0.027 (Figure 10, see appendix G for stressplot). An ANOSIM test showed no significant difference between pollinator composition in semi-natural grasslands and successional grasslands ($r = -0.1204$, $p = 0.837$). The ordination plot reveals no clear clustering according to the land-use types, but some clear groupings among sites and pollinator taxa can be seen. In the lower right corner of the plot, honeybees, social wasps (Vespidae) and sawflies (Symphyta) are located nearby the successional site "Forsøkslia" and the semi-natural site "Lade". Additionally, the location of "Selsbakk N" indicate some association with honeybees. The semi-natural sites "Flatåsen" and "Grønlia", placed in the upper right part of the plot, suggest association with bumblebees (Bombus). Among the other sites, "Okstad", "Buengveien S", and Bjørndalen are clustered together and are located close to flies and hoverflies. "Buengveien N", "Lian U", and "Selsbakk S", located close to the origin, suggest association with wild bees, butterflies (Papilionoidea) and bumblebees.
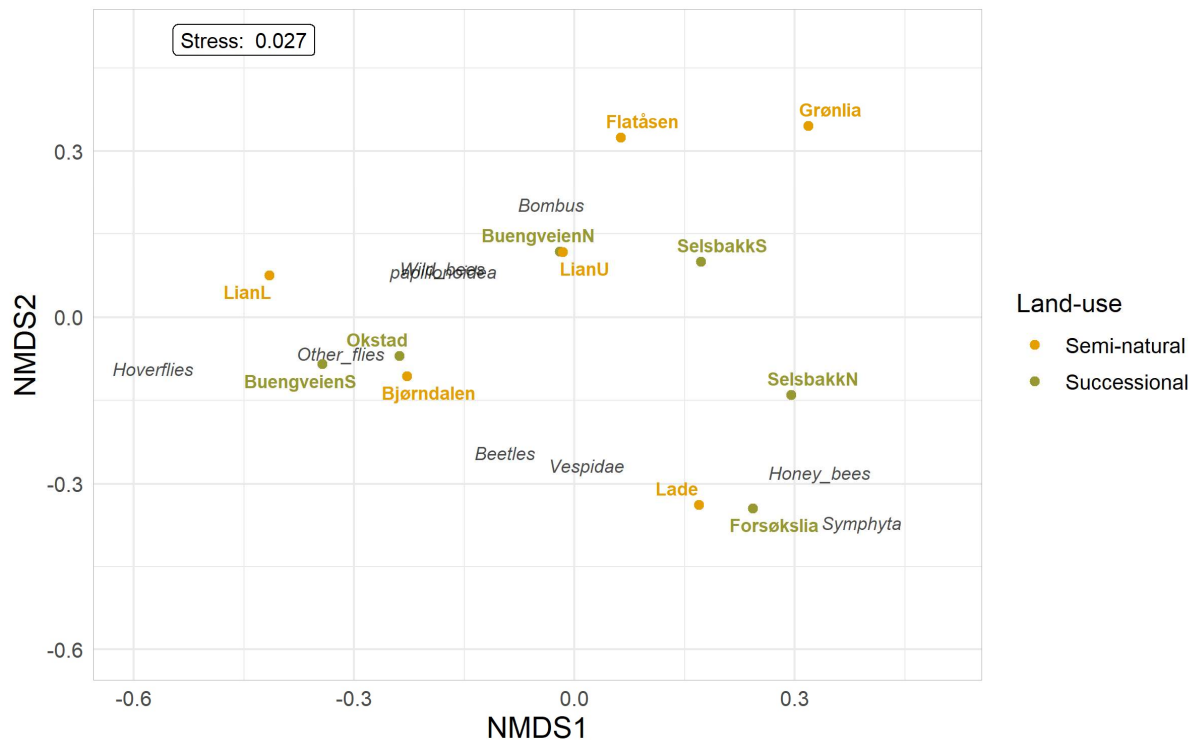
Figure 10. Ordination plot of sites (semi-natural sites = yellow, successional sites = green) and pollinator taxa (italic) along a non-metric multidimensional scaling (NMDS) axis 1(MDS1) and 2 (MDS2).

3.3 Factors affecting bumblebees and other polliantors within grasslands

To investigate which factors that affect the abundance of bumblebees, species richness of bumblebees, and abundance of pollinators, similar model selections were performed on the three different response variables (see appendix H, model selection). Model selection included seven variables: land-use, season, flowering plant abundance, proportion of non-habitat, proportion of grasslands, size of site and temperature. The simple regression analysis performed to investigate the effect of flowering plant species richness revealed that plant richness has a strong positive effect on species richness and abundance of bumblebees, and total abundance of pollinators when no other variables are included in the model (see appendix H).

3.3.1 Bumblebee species richness

Two models explaining bumblebee richness were found to be within ΔAIC = 2, with a difference in AIC of 0.65 (see appendix H, model selection). Both models included land use, season, proportion of non-habitat, temperature and the interaction between season and temperature. The model with a slightly higher AIC additionally included flowering plant abundance, which had a positive, but not significant, effect (Figure 11a). The model not including plant abundance explains 64% of the variation observed. Comparing the effect of land-use types, the effect of successional sites differed significantly from semi-natural sites, with a more negative effect in sites categorized as successional grasslands (table 6). Between seasons, July and August differed significantly from May and June (Chi-square = 76.088, df = 3, p = < 0.001, Kruskal-Wallis test, appendix F). The effect of seasons became more positive throughout the summer (table 6). An increase in proportion of roads and buildings in the surrounding landscape had a significant positive effect on the species richness within sites (Figure 11b, table 6). Similarly, an increase in temperature had an overall positive and significant effect on the number of species of bumblebees, but in interaction with season, the effect differed between seasons (Figure 11c, table 6). In July and August, there was a decreasing number of species with increasing temperatures, and this differed significantly from May, where increasing temperatures had a positive effect on species richness of bumblebees.
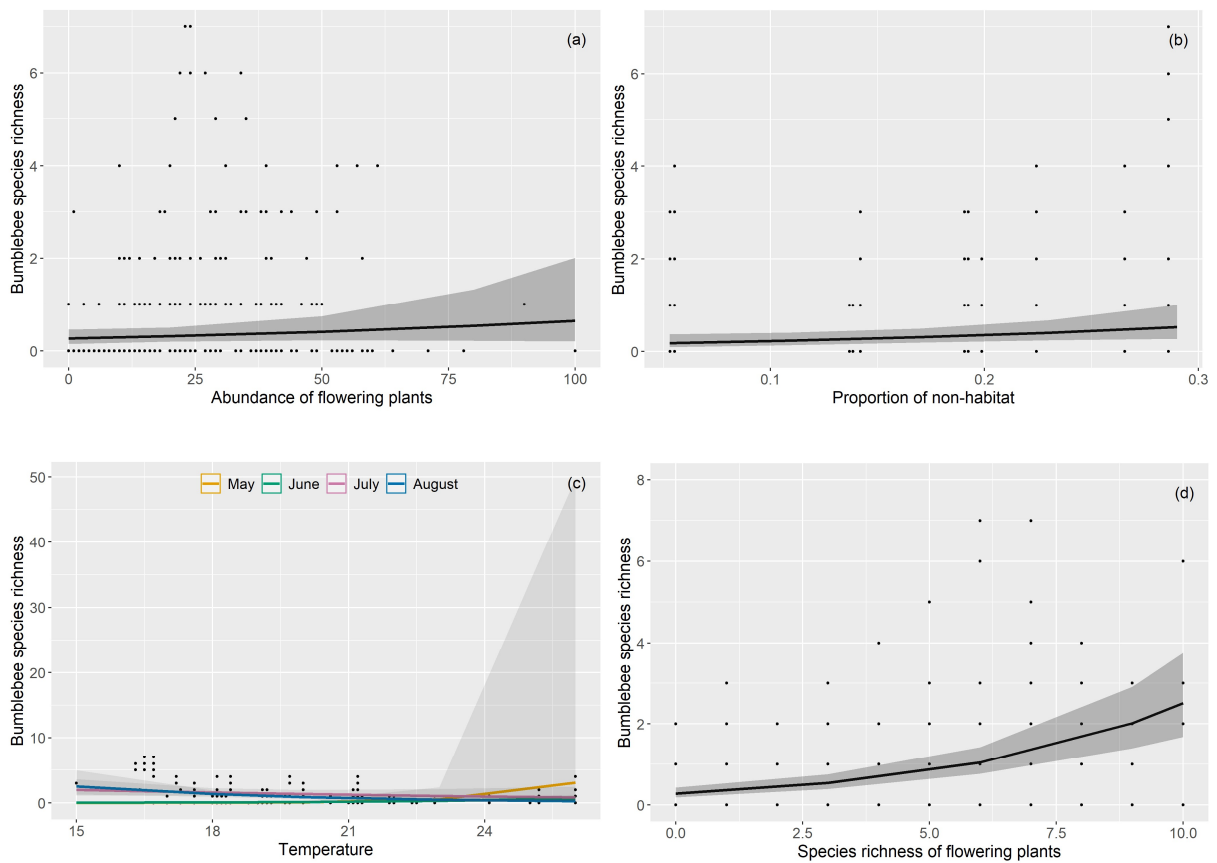
Figure 11. Relationship between bumblebee species richness and proportion of non-habitat (a), flowering plant abundance (b), temperature within seasons (c) and species richness of flowering plants (d). Figure (d) is fitted with the model including only plant species richness as a predictor. Grey area represents confidence intervals.

Table 6. Results from generalized linear mixed model (GLMM) on how species richness of bumblebees is affected by different factors. Values include estimate, standard error (SE), Z-value, confidence interval (CI) and P-value (P).

Predictors	Estimate	SE	Z-value	CI	P
(Intercept)	-3.09	0.69	-4.46	-4.45 - 1.74	< 0.001
Land-use (SS)	-0.72	0.32	-2.27	-1.35 - 0.10	< 0.05
June	0.47	0.77	0.60	-1.05 – 1.98	0.546
July	2.99	0.59	5.11	1.84 – 4.14	< 0.001
August	2.62	0.59	4.41	1.46 – 3.79	< 0.001
Non-habitat	4.45	2.10	2.13	0.35 – 8.56	< 0.05
Temperature	1.51	0.64	2.38	0.27 – 2.76	< 0.05
June:temperature	-0.79	0.70	-1.14	-2.16 – 0.57	0.254
July:temperature	-1.71	0.65	-2.63	-2.98 - 0.43	< 0.01
August:temperature	-2.05	0.67	-3.06	-3.36 - 0.74	< 0.01

3.3.2 Bumblebee abundance

Bumblebee abundance was effectively described by the model including land-use, season, proportion of non-habitat, flowering plant abundance, temperature and the interaction between temperature and season (Table 7, appendix H, model selection). This model explains 87% of the variation observed. The effect of semi-natural and successional sites had no significant difference, but the estimates suggest a more negative effect in successional sites (Table 7). There was a significant difference between the two first summer months and the two last summer months, with and increasing trend during the summer, and the most positive effect found in July (chi-square = 63.001, df = 3, p = < 0.001, Kruskal-Wallis test, appendix F). Increasing abundance of flowers within sites had a significant positive effect on the number of bumblebees (Figure 12a, Table 7). Additionally, an increasing proportion of non-habitat in the surrounding landscape had a positive effect on the number of bumblebees within the sites (Figure 12b, Table 7). Temperature had an overall positive effect on the abundance of bumblebees, but the effect varied within the seasons, with a decreasing trend in abundance of bumblebees in higher temperatures in both July and August (Figure 12c, Table 7). The interaction effect in July and August differed significantly from the effect in May, which had a positive effect on abundance of bumblebees with increasing temperatures.
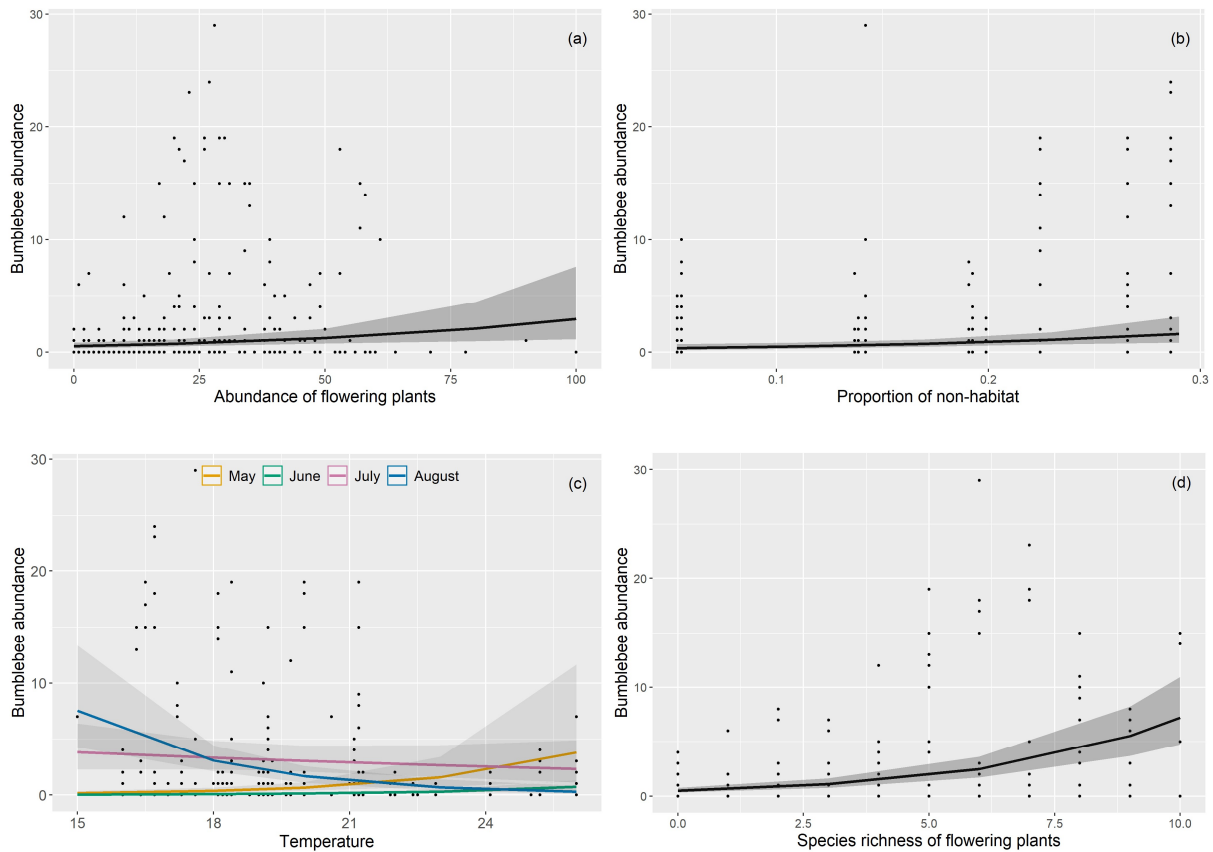
Figure 12. Relationship between bumblebee abundance and abundance of flowering plants (a), proportion of non-habitat (b), seasonal temperature (c) and species richness of flowering plants (d). Figure (d) is fitted with the model including only plant species richness as a predictor. Grey area represents confidence intervals.

Table 7. Results from generalized linear mixed model (GLMM) on how bumblebee abundance is affected by different factors. Values represent estimates, standard error (SE), Z-value, confidence interval (CI) and P-value (P).

Predictors	Estimate	SE	Z-value	CI	P
(Intercept)	-1.43	0.50	-2.85	-2.42 - 0.45	< 0.01
Land-use (SS)	-0.57	0.37	-1.54	-1.31 - 0.16	0.124
June	-1.67	0.45	-3.69	-2.56 – 0.78	< 0.001
July	1.67	0.22	7.54	1.24 – 2.11	< 0.001
August	1.18	0.23	5.16	0.73 – 1.63	< 0.001
Non-habitat	6.54	2.47	2.65	1.70 – 11.37	< 0.01
Plant abundance	0.31	0.10	3.04	0.11 – 0.52	< 0.01
Temperature	0.74	0.19	3.86	0.37 – 1.12	< 0.001
June:temperature	0.01	0.28	0.03	-0.54 – 0.56	0.975
July:temperature	-0.86	0.22	-3.86	-1.29 – 0.42	< 0.001
August:temperature	-1.51	0.26	-5.87	-2.02 – 1.01	< 0.001

3.3.3 Pollinator abundance

The simplest model that best explains the total abundance of all pollinators observed included the same variables as for bumblebee abundance; land-use, season, proportion of non-habitat, flowering plant abundance, temperature and the interaction between temperature and season (table 8, appendix H, model selection). This model was the least complex model within ΔAIC = 2 and explains 49% of the variation observed. Three other models had an AIC within ΔAIC = 2, and additionally included grassland and size of site as a predictor (appendix H, model selection). Both proportion of grassland and size of site had had a positive, but not significant effect on the abundance of pollinators. The abundance of pollinators in July and August were significantly different from the abundance in May and June, with August having the most positive effect (table 8, Chi-square = 128.6, df = 3, p = < 0.001, Kruskal-Wallis test, appendix F). Increasing floral abundance within the sites (Figure 13a), increasing proportion of non-habitat in the surrounding landscape (Figure 13b), and increasing temperatures had an overall significant positive effect on the number of pollinators within the grasslands (table 8). The interaction between season and temperature reveals that higher temperature became less important for the pollinators in July and August, and the effect was significantly different between May and July and between May and August (Figure 13c, table 8).
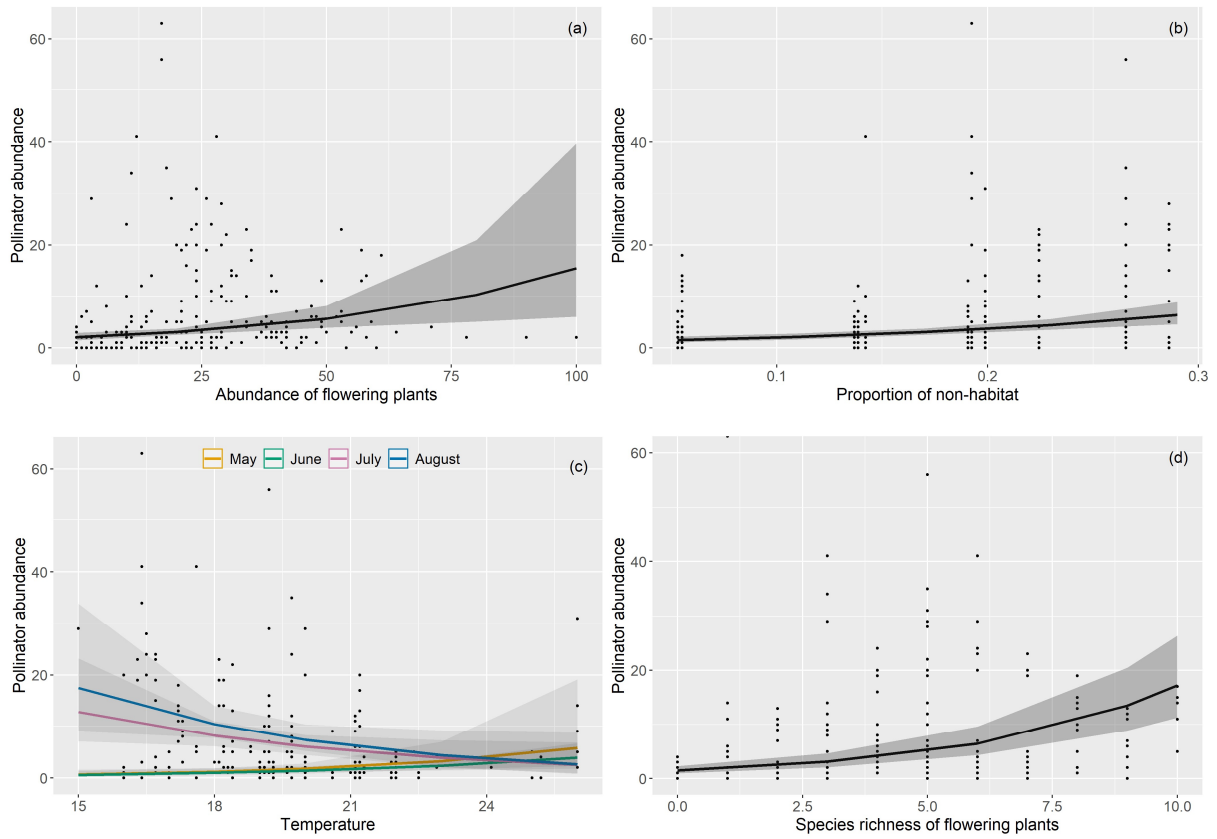
Figure 13. Relationship between pollinator abundance and flowering plant abundance (a), proportion of non-habitat (b), seasonal temperature (c), and species richness of flowering plants (d). Figure (d) is fitted with the model including only plant species richness as a predictor. Grey area represents confidence intervals.

Table 8. Results from generalized linear mixed model (GLMM) with negative binomial distribution on how pollinator abundance is affected by different factors. Values include estimate, standard error (SE), Z-value, confidence interval (CI) and P-value (P).

Predictors	Estimate	SE	Z-value	CI	p
(Intercept)	-0.61	0.29	-2.15	-1.17 – 0.05	< 0.05
Land-use (SS)	-0.07	0.20	0.35	-0.32 – 0.47	0.726
June	-0.24	0.37	-0.64	-0.97 – 0.49	0.523
July	1.37	0.27	5.09	0.84 – 1.90	< 0.001
August	1.57	0.25	6.18	1.07 – 2.07	< 0.001
Non-habitat	6.00	1.27	4.74	3.52 – 8.48	< 0.001
Plant abundance	0.38	0.12	3.24	0.15 – 0.61	< 0.01
Temperature	0.50	0.20	2.51	0.11 – 0.89	< 0.05
June:temperature	-0.06	0.26	-0.22	-0.58 – 0.46	0.826
July:temperature	-0.88	0.25	-3.47	-1.38 – 0.38	< 0.001
August:temperature	-0.95	0.29	-3.31	-1.50 – 0.39	< 0.001

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4 Discussion

Today, land-use change is considered one of the most important factors threatening the abundance, diversity and health of pollinators and the provisioning of pollination (Potts et al., 2016). The aim of the present study was to examine how pollinators and especially bumblebees are affected by land-use in urban grasslands by comparing semi-natural and successional grasslands within a delimited area of Trondheim municipality. In addition, abundance and species richness of flowering herbs, surrounding landscape and time of season were investigated as potential important factors determining the abundance and species richness of pollinators within grasslands.

4.1 Variations within and between semi-natural and successional grasslands

4.1.1 Pollinators and plants

Abandonment is considered one of the greatest threats towards semi-natural grasslands today (Potts et al., 2016, Hovstad et al., 2018, Jakobsson and Pedersen, 2020). The cessation of management practices including grazing, mowing or traditional agriculture leads to encroachment of bushes and trees in many grasslands (Morris, 2000, Potts et al., 2016, Hovstad et al., 2018). Consequently, these grasslands experience a change in plant species composition, and an overall decline in number and species of plants (Bohner et al., 2020). Additionally, an increase in management intensity of grasslands, especially in urban areas has led to a decrease in biodiversity (Potts et al., 2016). These factors are expected to have a knock-on negative effect on pollinators (Potts et al., 2016, Walcher et al., 2017). Supporting our hypothesis, results on bumblebees revealed a significantly higher number of individuals and species in semi-natural sites compared to successional sites. Similarly, butterflies, wild bees and beetles were slightly more abundant in semi-natural grasslands compared to successional grasslands, even though less distinct than bumblebees. Similar results were found in the study by Walcher et al. (2017) in the Austrian and Swiss Alps, with a higher bumblebee abundance and species richness in extensively managed meadows compared to abandoned meadows. A higher plant species richness and flower cover within grasslands is proven to benefit bumblebee richness (Ebeling et al., 2008), and successional changes threaten the high diversity of important floral resources. Social bumblebees living in colonies are dependent on a constant food supply throughout the colony's life span, and a diverse plant community can provide this. Furthermore, a species rich meadow would have the potential to provide flowers with both shorter and longer corollas, thus

also benefiting bumblebees with a variation of tongue lengths (Willmer, 2011). The significant difference in bumblebee abundance and species richness in the two grassland types in our study indicate that the semi-natural grasslands are important habitats providing a high abundance of resources preferred by bumblebees.

Contradictory to what we expected, total number of pollinators observed were slightly higher in successional grasslands compared to semi-natural grasslands. Other pollinator taxa are not as dependent on floral resources as the bees (Willmer, 2011), and this could partly explain the different results when all pollinator taxa observed are included. An exception is the butterflies, which is dependent on host plants for egg laying. Studies investigating effects of land-use on butterflies has found negative effects of abandonment (Öckinger et al., 2006b) but late successional stages is assumed to have the most clear negative effects (Öckinger et al., 2006a). In line with these studies, we found a higher number of butterflies in semi-natural grasslands compared to successional grasslands, indicating that semi-natural grasslands are more preferred habitats. However, it is important to point out that numbers of butterflies were very low in our study and may not be representative for the real population. Numbers of honeybees were substantially higher in successional grasslands compared to semi-natural grasslands. A factor potentially explaining the marked difference is the existence of beehives in the neighbouring landscape of some of the successional sites ("Forsøkslia" and "Selsbakk N") (Mattilsynet, 2021), leading to "hotspots" of honeybees in grasslands located in the beehives' proximity. Moreover, honeybees are considered as "supergeneralists", going to almost any flowers in most of the habitats where they occur (Willmer, 2011), indicating that they may be satisfied with the less diverse floral composition provided by the successional grasslands in their proximity.

Flowers recorded in this study displayed a similar trend as the bumblebees, with a higher abundance and species richness in semi-natural grasslands, but also great variation within land-use types (Dhukuchhu, 2021). This is in accordance with the results of the study conducted by Kleppe (2019) two years earlier in the same grasslands. She found a high variation in plant species richness among low-intensively managed grasslands, but no significant difference between land-use categories. The review by Winfree et al. (2011) assessed the impacts of human-induced land-use change, and one of their concluding remarks suggest that "*pollinators respond more consistently to the directionality of change in floral resources with land-use change than they do to land-use change itself*". Thus, how floral resources respond to land-use change may explain some of the diversity of responses among pollinators. Pollinators rely on flowers as a food resource, and the importance of floral resources is strongly supported in

literature (Fontaine et al., 2005, Roulston and Goodell, 2011, Winfree et al., 2011). In line with our hypothesis, there was a significant positive relationship between floral abundance and pollinators within the grasslands. The exception was bumblebee species richness, which was positively but not significantly affected by flowering plant abundance. Plant species richness was not included in our analyses due to the high correlations with several of the explanatory variables, but it is expected that this is an important factor promoting species richness of bumblebees (Ebeling et al., 2008, Roulston and Goodell, 2011). The simple regression exploring the relationship between bumblebee species richness and plant species richness suggest a positive relationship, but the strength of this relationship when accounting for other factors is unknown.

4.1.2 Effects of management

Semi-natural grasslands represent a relatively broad category, and in urban ecosystems these grasslands can be exposed to a variation of management intensity, ranging from an intensive mowing regime to no management at all (Klaus, 2013). Additionally, there is a variation in the application of fertilizers or manure from grazers, leading to variations in soil nutrient content (Willmer, 2011, Hudewenz et al., 2012). In this study, the management intensity of the sites was not included as a factor in the analyses but could be an explanation for some of the variation within the semi-natural category. Among the semi-natural study sites there was indeed a variety in management. "Lian Lower" was the only site used for grazing during the sampling period. "Lian Upper" is usually used for grazing but was not grazed during the sampling period. Depending on the intensity, grazed grasslands have the potential to be highly suitable pollinator habitats indirectly by a high diversity of pollinator-friendly plants (Lazaro et al., 2016). Studies investigating effects of grazing suggest that moderately grazed grasslands will promote the highest biodiversity (Lazaro et al., 2016). If the grazing pressure is too high, plants are more prone to damage on parts of or the whole flower, making them less attractive for pollinators (Willmer, 2011). Also, the soil characteristics may change due to high-intensity trampling, potentially making the soil less suitable for ground-nesting insects (Sjödin, 2007, Sjödin et al., 2008). Moreover, the pollinators' responses may differ between the pollinator taxa, for instance due to differences in life-history traits and nesting requirements. Additionally, the flower resources utilized by various groups of pollinator taxa may be differently affected by grazing (Goulson, 2003). Finally, the type of livestock grazing at a given site might be a significant factor determining the direction of the pollinators' responses (Willmer, 2011). Comparison of numbers of pollinators at Lian Lower and Lian Upper reveals substantially lower numbers in

the grazed site, suggesting the ongoing grazing to be a factor affecting pollinators negatively, but that grazing can make suitable growing conditions for a diversity of plants, supported by a high diversity of plants at both Lian Lower and Upper.

At "Grønlia", there is an ongoing management regime including cutting of grass and removal of trees and bushes once a year (Aagaard et al., 2018, Øien, 2018). This regime is suggested to promote a high diversity of plants and pollinators (Johansen et al., 2019, Wehn et al., 2020), which is supported in the results of this study by the high abundance and species richness of both pollinators and plants (Dhukuchhu, 2021). Another site with a high abundance and species richness of bumblebees and overall high numbers of pollinators is "Flatåsen". To our knowledge, there is no ongoing management at this site, but our results indicate that earlier management regimes have made this grassland particularly suitable for a high diversity of pollinators and plants (Dhukuchhu, 2021). Differently, in the semi-natural site "Lade", located nearby "Grønlia", numbers of pollinators observed were comparable with several of the successional sites. This site is not managed in any way, but still is classified as a semi-natural grassland. However, relatively high grasses and emergence of raspberry (*Rubus idaeus*) suggest it to be in a transition phase towards a later successional state (Dhukuchhu, 2021). It is important to point out that the high diversity at "Grønlia" and "Flatåsen" may have had a potentially strong effect on the results as outliers among the semi-natural sites.

A potentially important mechanistic factor underlying pollinator responses to land-use change is the availability of nest or oviposition sites. Above ground nesters typically build their nest in dead wood, in forb or shrub stems, or in perennial grass, all substrates that is likely to be removed if habitats are converted (Williams et al., 2010). Below ground nesters can be exposed if the change in land-use leads to changes in ground, for instance by compacting the soil (Williams et al., 2010). The meta study by Williams et al. (2010) found that location of bee-nests significantly affected response to habitat loss, where species nesting above ground were on average more negatively affected by intensive land-use than below ground nesters. Below-ground nesters like bumblebees often nest in cavities or abandoned nests of small mammals or rodents (Ødegaard et al., 2015b). Management such as high-intensity grazing correspond to high-intensity trampling, which may affect these pollinators directly by compacting the soil and filling or destroying their nests, potentially leading to direct mortality (Sjödin, 2007, Kimoto et al., 2012). However, less intensive grazing might facilitate nesting resources by creating areas of bare soil, desired by ground-dwelling pollinators (Kimoto et al., 2012, Murray et al., 2012). Other management regimes such as mowing may be more beneficial for ground-nesting bees

compared to above-ground nesting bees. Intensive mowing is non-selective and cuts the vegetation to a uniform height, thus topographical features and potential above-ground nesting sites such as grass tussocks may be destroyed (Morris, 2000, Potts et al., 2016). Moreover, mowing may lead to direct mortality of eggs and larvae and a sudden removal of almost all floral resources which serve as host-plants for butterflies and food for bumblebees (Johst et al., 2006). Non-managed meadows that are in an early stage of becoming overgrown due to a lack of management, but still are relatively open, have also been shown to be suitable nesting sites for bumblebees (Svensson et al., 2000), suggesting that some of the successional grasslands may still be important despite the lower floral diversity. In this study, characteristics and structures within the grasslands or in the surrounding landscape that could serve as potential nesting sites where not surveyed, but this could give valuable information and knowledge about the quality of the sites.

4.2   Land-use in the surrounding landscapes

Maintenance of connectivity and heterogeneity in landscapes surrounding urban grasslands has been highlighted by researchers as potential important measures to maintain biodiversity in cities (Öckinger et al., 2009, Potts et al., 2016). Green spaces within the urban matrix can serve as both habitats, foraging patches, and corridors for dispersal, promoting diversity of both pollinators and plants. In contrast to our hypothesis, a higher proportion of non-habitat in the surrounding landscape had a strong positive effect on the abundance and species richness of pollinators within the grasslands. The highest proportions of non-habitat within the buffer zones were found at "Grønlia" and "Flatåsen", with a percentage of 29% and 22%, respectively. These sites were also the most numerous in pollinators. Compared to other studies, this percentage can be considered low-to-medium high, and the "anthropogenic disturbance" only moderate (Winfree et al., 2009). The study by Winfree et al. (2007) found similar effects of intermediate disturbance on bees, and they argued that disturbed landscapes provide a variety of successional stages, thus promoting a higher diversity due to different preferences for habitats among bees. However, more extreme changes has been found to affect pollinators negatively (Winfree et al., 2009), suggesting that negative effects might occur when natural and semi-natural landcover falls below some threshold.

According to the metapopulation theory, proximity between natural fragments increases species richness (Fattorini et al., 2018). In this study, the proportions of grasslands in the surrounding landscape were relatively low or equal to the proportion of forest and non-habitat, and had no significant effect on pollinators observed, suggesting that other attributes of the landscape had

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a higher impact. The proportion of forest was not included in our analyses due to a high correlation with proportion of non-habitat, but previous studies have found varied effects of a high proportion of forest cover and it is suggested that forests and forest-edges can potentially provide overwintering sites and nesting places for insects (Winfree et al., 2007, Diaz-Forero et al., 2011).

Characteristics such as proportion of lawns, road verges and other potential sources for food and nesting sites were not measured, but this could be factors contributing to the positive trends observed in our study. An increasing proportion of buildings and roads in the proximity may correspond with an increasing proportion of private gardens and road verges. Road verges has been emphasized by studies as important early or mid-successional habitats providing a rich diversity of floral resources and opportunities for reproduction in larval hostplants (Gardiner et al., 2018, Jakobsson et al., 2018, Phillips et al., 2020). Additionally, they could serve as corridors for movement and dispersal to other nearby populations and habitats. The management of edges along roads commonly include cutting of vegetation and grass to improve the sight for vehicles, often limited to a few times throughout the summer season (Jakobsson et al., 2018). This management regime is recognized as beneficial for promoting a high diversity of floral resources (Noordijk et al., 2009). Similarly, lawns have the potential to provide both food and nesting places for pollinators, and are often abundant in cities (Bertoncini et al., 2012), thus contributing to increased heterogeneity and connectivity within the urban landscape.

Our analyses were based on large-scale maps and in that sense not a relevant scale for pollinators. Compared to a homogenous landscape dominated by grasslands, an urban, fragmented landscape including built-up areas and roads may provide a higher diversity of land-use and habitat types, possibly including both suitable nesting sites and floral resources. Among solitary bees, the majority are ground-nesters and typically nest in dry and sandy or rocky patches of bare soil and in sun-faced, warm slopes with little vegetation, for example in road verges (Willmer, 2011), all characteristics that can be related to urban landscapes. Those nesting in substrates above ground often find suitable nesting sites in dead, sun-faced branches with old insect exits, beneath stones and in old plant stalks, but may also exploit constructions built by people, including roofs, crevices and holes in walls, or timber walls (Totland, 2013). This indicate that human-disturbed landscapes in many contexts may be as suitable habitats as less disturbed natural grasslands in terms of nesting sites.

4.3　Temporal variation

Consistent with our hypothesis, there was a clear variation between seasons, with the highest number of pollinators observed towards the end of the summer. Considering the life cycle of the social bees, a higher number of individuals in late summer is expected, as more workers, and eventually also males and queens, are produced (Willmer, 2011). In early spring, the bee communities mainly consist of queens, and the production of workers has yet not started. Thus, one could expect fewer active individuals and consequently a lower sample size of bees compared to later in the summer. The number of individuals observed increased considerable from May to June, indicating that colonies were established, and workers had started the emergence from the nest. Registrations on whether a bumblebee was a queen, worker or male was not implemented, but this could give valuable information about the stage of the colonies' lifecycle. There was an increase in both abundance and species richness of plants from May to June, which fits well with the increase in number of pollinators (Dhukuchhu, 2021). Species richness of plants continued increasing throughout the summer, supporting the increase in bumblebee species throughout the summer (see appendix E). By contrast, abundance of plants decreased after June. However, this is not reflected in the numbers of pollinators, suggesting that even though floral resources were less abundant, they found sufficient food resources either within or in neighbouring grasslands. In addition to phenological aspects, climate and weather conditions can be important determinants for the activity among pollinators, both indirectly through the floral resources available, but also directly through their preferences for warm and dry climatic conditions (Totland, 2013). This may affect pollinators and can be an explanation for the low numbers of pollinators observed in May and June.

In line with our results, an overall higher activity at higher temperatures throughout the summer is expected as most taxa of pollinators thrive in warm, sunny and still summer weather (Willmer, 2011). Investigating the effect of temperature within seasons revealed a varied pattern, with a positive relationship between pollinators and increasing temperatures in May and June, followed by a negative relationship in July and August. Unnormal high or low temperatures at the days field work was carried out might have caused a bias of pollinators at high or low temperatures.

4.4　Species composition

4.4.1　Bumblebees
The NMDS showed no significant difference between the semi-natural and successional sites in species composition of bumblebees, but some patterns among the species' location and

characteristics of the sites could be seen. *B. terrestris* is a species that thrive in cultural and city-near landscapes (Ødegaard et al., 2015b), and its location close to "Flatåsen" and "Grønlia" fits well with the characteristics of their surrounding landscape with a high percentage of non-habitat. The sites' central location within the plot also reflects their high species richness. Moreover, the location of *B. soroeensis* close to Lian, fits well with its preferences for landscapes with a combination of cultural landscapes and forests, and a high abundance of harebell (*Campanula rotundifolia*) (Ødegaard et al., 2015b, Dhukuchhu, 2021). Among the cuckoo bumblebees, only *B. bomhemicus* had a close location to its host, *B. lucorum.* However, total number of cuckoo bumblebees were relatively low, and their distribution shown in the ordination plot might not reflect their real distribution. A variation of management regimes and successional stages both within and in the surroundings of grasslands have in previous studies shown to cause differences in species composition of plants (Bertoncini et al., 2012, Bohner et al., 2020), thus potentially affecting the species composition of bumblebees. In this study, most species observed were generalists, and all except from two were short-tongued, thus their flower preferences are expected to be more generalized than specialized (Ødegaard et al., 2015b). Still, the variation of habitat types within the urban matrix can potentially support a high diversity of bumblebees, including species with specific preferences such as *B. terrestris* and *B. soroeensis*, stressing the importance of maintaining semi-natural grasslands both in urban and suburban parts.

4.4.2 All pollinators

The NMDS including all pollinators showed no significant difference between land-use types. By contrast, sites grouped together across land-use types, indicating similarities in species composition despite the difference in successional state. For example, supporting our previous arguments, "Flatåsen" and "Grønlia" are mainly associated with bumblebees, together with one more semi-natural site ("Lian Upper") and two successional sites ("Buengveien N", "Selsbakk S"). The semi-natural site "Lade" and the successional sites "Forsøkslia" and "Selsbakk N" are located closely, and honeybees is one of the pollinator taxa especially associated with these sites. This is consistent with the outstanding high numbers of honeybees within these sites (see appendix E). A reasonable explanation for the high numbers could be the existence of beehives in the neighbouring landscape (Mattilsynet, 2021). However, several other sites with a lower number of honeybees had beehives in their vicinity (i.e. "Lian Upper" and "Lian Lower"), thus additional factors such as floral resources available within the grasslands might be a contributing factors causing the high abundance. In which degree honeybees is a significant

competitor towards bumblebees is not investigated in this study, but honeybees and wild bees are suggested to have a high overlap of food resources (Rasmussen et al., 2021), indicating that some competition might occur. This could be an important and interesting topic to examine in further studies.

4.5   Methodological considerations

Field data was recorded during the summer of 2020, which had deviations from normal climatic conditions. May was characterized by cold temperatures and high precipitation, including some days with snow (Grinde et al., 2020b). Contrastingly, June followed with high temperatures and low precipitation (Grinde et al., 2020a). These climatic conditions could have caused a delayed establishment of bee-colonies and reduced pollinator activity, and consequently a low sample size in May and June.

The AR5 map was used to investigate the landscape surrounding the grasslands. This map provides information on the broad land-use categories but features of the landscape on a more detailed scale including potential suitable nesting places, the existence of smaller floral patches or corridors, and total cover of private gardens is not investigated and could be factors giving valuable information about important characters of the urban landscape. Thus, the category "non-habitat" might mask a heterogeneity of real and important habitats on a smaller scale.

Finally, since the study employed a repeated measures design, some individuals may have been sampled repeatedly during the investigation period since flying insects move rapidly around. However, a minimum distance of 5 meters between transects was a measure to reduce resampling.

4.6   Management implications

The semi-natural grasslands in Trondheim represent a variety of characteristics and management regimes (Kleppe, 2019). Among our study sites, some grasslands maintain their semi-natural characteristics either by grazing or mowing, but some are also threatened by overgrowth of tall grasses, bushes, and trees. Even though pollinators showed varied responses among semi-natural and successional grasslands in our study, overgrowth is expected to cause declining numbers of pollinators in the future. Accordingly, management efforts should be targeted on the existing semi-natural grasslands to avoid further loss of this important habitat type. Restoration of grassland in late successional stages is also important, however restoration has been shown most beneficial in early successional states since this increases the probability that management-dependent species still are present (Öckinger et al., 2006a). Different

management types such as low intensity grazing or mowing has been shown beneficial in already managed grasslands within Trondheim municipality (Øien, 2018, Wehn et al., 2020), and several grasslands should be included in this systematic work. Wehn et al. (2020) suggest some specific measures to benefit pollinators, including that grasslands should be divided into smaller parts which are mowed at different times to ensure that pollinators have a continuous availability to floral resources. Similarly, an asynchronous management regime should be applied to neighbouring grasslands. Finally, especially important species of plants should be left out from cutting in their flowering period. Considering the timing of mowing, Johansen et al. (2019) suggest that heterogenous mowing times will be most beneficial in the perspective of pollinator conservation. Early mowed grasslands serve as the main resource of flowers in late season, whilst late mowed grasslands serve as the main pollen and nectar resource in early season, thus pollinators are ensured a constant availability to floral resources (Johansen et al., 2019). Also, removal of plant litter is of importance, as this has been shown to promote species richness and abundance of plants (Carson and Peterson, 1990). An increasing amount of plant litter left on the ground will contribute to an increased biomass and may delay or inhibit seed recruitment (Jensen and Meyer, 2001).

The role of floral resources as a necessity for pollinators should be acknowledged, and promotion of local species rather than alien species should be a part of conservation in urban green space areas and public gardens. Management efforts targeted on the total urban landscape is important to maintain dynamics and avoid complete isolation of plant- and pollinator populations within the urban matrix. This includes facilitation of suitable nesting sites for a diversity of pollinators in the proximity of grasslands, including old plant stalks, cervices and holes in walls, dead trees and branches, and south-facing sandy slopes. Information to the public about efforts that can be done on private properties such as lawns could be beneficial, as these make up a large proportion of the urban and suburban land-cover. Lastly, acknowledging small green space areas close to human infrastructure, edges between land-use types, road verges etc. as potential habitat could contribute to increased biodiversity.

5 Conclusion

The present study shows that there is a great variation in characteristics among grasslands in Trondheim, particularly among semi-natural grasslands. Both species richness and abundance of bumblebees were significantly higher in semi-natural grasslands, underpinning the importance of these grasslands as habitats for bumblebees. Other pollinators are less dependent on flower resources and may be less affected by successional changes. This is reflected in our results, with no significant difference between semi-natural and successional grasslands. However, "hot-spots" of honeybees may partly explain the high numbers of pollinators in successional grasslands. Furthermore, the land-use change itself may not be the main explanation for the pollinators' responses, but rather the change in characteristics such as floral resources available in their habitat, and small-scale features of the landscape such as suitable nesting sites, foraging patches, and dispersal corridors in the proximity of their habitat. The positive effect of an increasing proportion of non-habitat in our study indicates that moderate anthropogenic disturbances in the urban matrix may provide a heterogenic landscape with a diversity of habitats for pollinators.

Our results suggest that various land-use and management regimes both within and in the surrounding landscapes can have various effects on pollinators, and especially bumblebees may be vulnerable to changes such as abandonment of semi-natural grasslands and subsequent successional changes. Pollinator-friendly management regimes including grazing and mowing have shown a potential to promote a high diversity of pollinators and plants and should be an essential part in future urban management planning.

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Appendices

Appendix A: Bumblebees, butterflies and other pollinators observed in the 12 study sites.

Number of bumblebee species, butterfly species, and other pollinators observed in the 12 study sites in May (yellow), June (green), July (red), and August (blue).

May:

	Bjørndalen	Flatåsen	Grønlia	Lade	Lian L	Lian U	Buengv. N	Buengv. S	Forsøkslia	Okstad	Selsb. N	Selsb. S
Bumblebees												
B. hortorum												
B. terrestris												
B. lucroum												
B. soroeensis												
B. lapidarius			1									
B. jonellus												
B. hypnorum												
B. pratorum												
B. pascuorum						1						
B. campestris												
B. bohemicus										3		
B. norvegicus												
B. s.str												
Psithyrus												
Bombus	6	2	1	1	1		2	3	2	1		5

	Bjørndalen	Flatåsen	Grønlia	Lade	Lian L	Lian U	Buengv. N	Buengv. S	Forsøkslia	Okstad	Selsb. N	Selsb. S
Butterflies												
Pieris_napi								2				
Lycaena hippothoe												
Erebia ligea												
Callophrys rubi												
Pieris brassicae												
Polyommatus icarus												
Cupido minimus												
Boloria selene												
Papilionoidea	1		1									
Pieridae									1			
Satyrinae												

	Bjørndalen	Flatåsen	Grønlia	Lade	Lian L	Lian U	Buengv. N	Buengv. S	Forsøkslia	Okstad	Selsb. N	Selsb. S
Other pollinators												
Honeybees			2									
Wild bees			1									
Hoverflies	1							4			1	4
Other flies											1	
Symphyta												
Vespidae	1	2		2			1	2	2	1		1
Beetles												
Oedemeridae												
Coccinellidae												
Megachile												

June:

	Bjørndalen	Flatåsen	Grønlia	Lade	Lian L	Lian U	Buengv. N	Buengv. S	Forsøkslia	Okstad	Selsb. N	Selsb. S
Bumblebees												
B. hortorum	1			1								
B. terrestris		1	5				1					
B. lucroum			1	1	1							
B. soroeensis					8	2						
B. lapidarius			5									
B. jonellus												
B. hypnorum			2	1					2			
B. pratorum												
B. pascuorum			3								1	
B. campestris												
B. bohemicus												
B. norvegicus												
B.s.str												
Psithyrus												
Bombus	1					1		1	1	1	2	

	Bjørndalen	Flatåsen	Grønlia	Lade	Lian L	Lian U	Buengv. N	Buengv. S	Forsøkslia	Okstad	Selsb. N	Selsb. S
Butterflies												
Pieris_napi												
Lycaena hippothoe												
Erebia ligea												
Callophrys rubi				1								
Pieris brassicae			1									
Polyommatus icarus			1									
Cupido minimus			1									
Boloria selene						4						
Papilionoidea					1	1					1	2
Pieridae						1					1	1
Satyrinae												
Other pollinators												
Honeybees	4	4	1	42			2	3	1	1	2	3
Wild bees	1	1		1	2	1	1					
Hoverflies	3	2	3	2	2			4	2	1	1	
Other flies	5	1					10	3	1	4		
Symphyta		1		3								
Vespidae		1						1	1			1
Beetles							2					
Oedemeridae				3				1				
Coccinellidae	4	1						3		1		
Megachile			1									

July:

	Bjørndalen	Flatåsen	Grønlia	Lade	Lian L	Lian U	Buengv. N	Buengv. S	Forsøkslia	Okstad	Selsb. N	Selsb. S
Bumblebees												
B. hortorum		1			1	1						
B. terrestris		3	28									
B. lucroum		16	14	1	1	12		7	8	11	3	
B. soroeensis		1	7	2	4	13	4		2	1	8	19
B. lapidarius		6	4	1								
B. jonellus		1				1						
B. hypnorum		1	1				3			1	2	12
B. pratorum			7		1	3						
B. pascuorum	5	14	9	1	1	11	6		4	3	9	2
B. campestris		1	2									
B. bohemicus			2									
B. norvegicus												
B.s.str		5			1				1			
Psithyrus		2	5									
Bombus		4		4	2	1	3		1	1	7	22

	Bjørndalen	Flatåsen	Grønlia	Lade	Lian L	Lian U	Buengv. N	Buengv. S	Forsøkslia	Okstad	Selsb. N	Selsb. S
Butterflies												
Pieris_napi			1						1			
Lycaena hippothoe					1							
Erebia ligea						3						
Callophrys rubi												
Pieris brassicae												
Polyommatus icarus			1									
Cupido minimus												
Boloria selene												
Papilionoidea									1			
Pieridae												
Satyrinae												
Other pollinators												
Honeybees		3	29	19	2	1		1	48	5	18	28
Wild bees			3			2						1
Hoverflies				2	2			1				1
Other flies	1	1	1	2		15	2	1	8		22	
Symphyta												
Vespidae				5			1	1	1	1	15	
Beetles												
Oedemeridae												
Coccinellidae				5								
Megachile												

August:

	Bjørndalen	Flatåsen	Grønlia	Lade	Lian L	Lian U	Buengv. N	Buengv. S	Forsøkslia	Okstad	Selsb. N	Selsb. S
Bumblebees												
B. hortorum							1				1	
B. terrestris			4									
B. lucroum	2	36	30	2		4	22	2	4	1		12
B. soroeensis		2	4			3						
B. lapidarius		4	29	2								
B. jonellus		3	1									
B. hypnorum		2	1					1				
B. pratorum			1									
B. pascuorum	3	30	16	1	1	9	15		3		10	6
B. campestris			3									
B. bohemicus			1									
B. norvegicus			3									
B.s.str											12	
Psithyrus			2									
Bombus						1	2				1	

	Bjørndalen	Flatåsen	Grønlia	Lade	Lian L	Lian U	Buengv. N	Buengv. S	Forsøkslia	Okstad	Selsb. N	Selsb. S
Butterflies												
Pieris napi									2		3	
Lycaena hippothoe												
Erebia ligea		2										
Callophrys rubi												
Pieris brassicae												
Polyommatus icarus												
Cupido minimus												
Boloria selene												
Papilionoidea											1	
Pieridae	2					2				1		
Satyrinae						2						

Other pollinators												
Honeybees	7	7		31		12	8	1	122	2	88	7
Wild bees	1					2	5				2	1
Hoverflies	2					1	3					
Other flies	11	5	1	1	4	3		2	5	9	8	1
Symphyta												
Vespidae				9							1	3
Beetles												
Oedemeridae												
Coccinellidae									5			
Megachile												

Appendix B: Pictures of study sites

Semi-natural sites:

Figure B1. The semi-natural study sites: Bjørndalen (a), Flatåsen (b), Lade (c), Lian Lower (d), Lian Upper (e), and Grønlia (f). Photo: Frode Ødegaard, Ajay Dhukuchhu and Hildegunn Heggøy

Successional sites:

Figure B2. All the successional sites: Buengveien N (a), Buengveien S (b), Forsøkslia (c), Okstad (d), Selsbakk N (e), and Selsbakk S (f). (Photo: Ajay Dhukuchhu)

Changes in a successional grassland through seasons:

Figure B3. The successional site Okstad in four seasons, late May (a), late June (b), late July (c), and early August (d). Photo: Hildegunn Heggøy and Ajay Dhukuchhu

Appendix C: Field survey

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: ……………………….....

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

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

Appendix D: Distribution of dependent variables
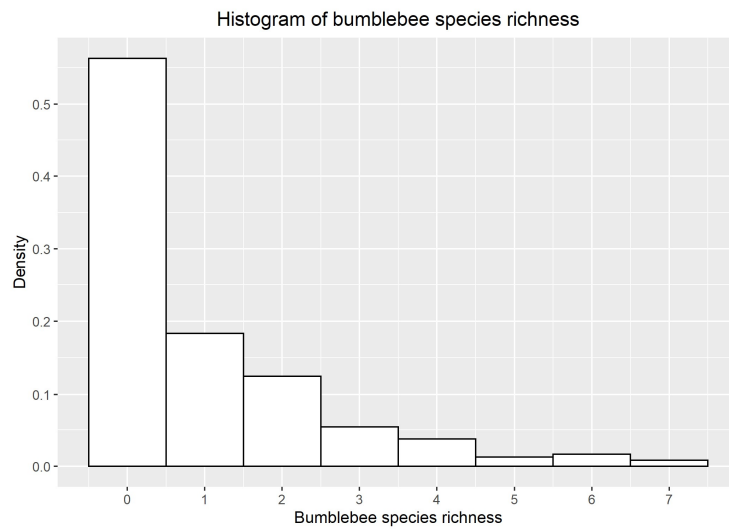
Histogram of bumblebee species richness

Figure D1. Histogram showing distribution of bumblebee species richness.
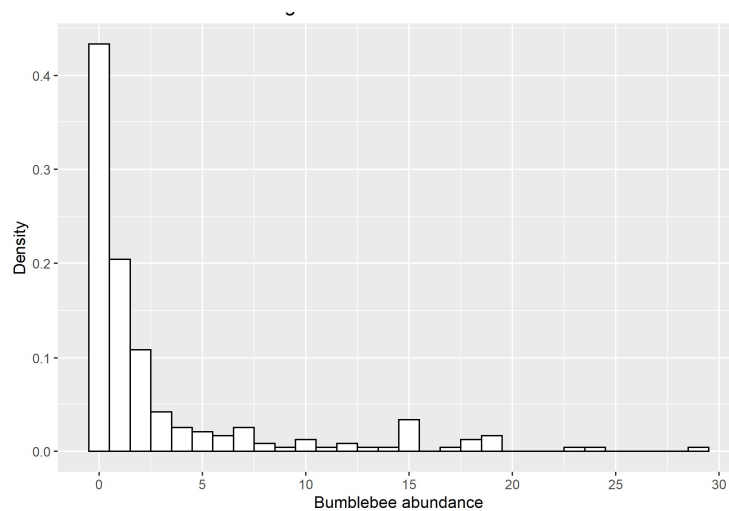
Figure D2. Histogram showing distribution of bumblebee abundance.

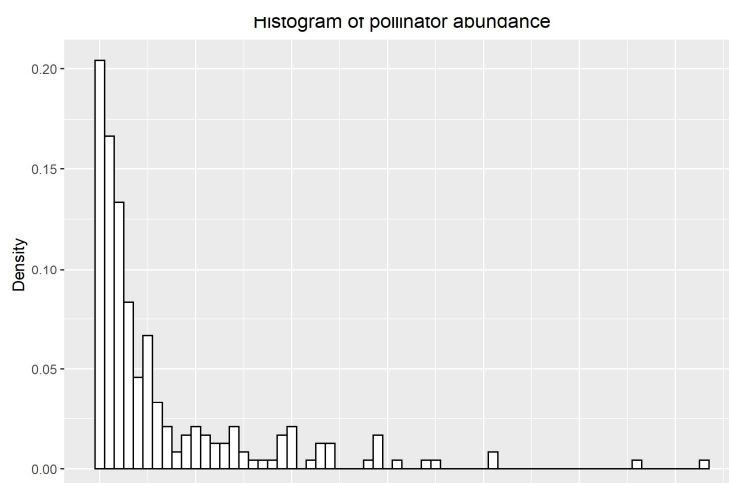Histogram of pollinator abundance

Figure D3. Histogram showing distribution of pollinator abundance.

Appendix E:

Table E1. Butterfly species (Papilionoidea) observed in semi-natural (SN) and successional (SS) grasslands.

Species	SN (abundance)	SN (%)	SS (abundance)	SS (%)
Erebia ligea	5	31,3	0	0
Boloria selene	4	25	0	0
Polyommatus icarus	2	12,5	0	0
Callophrys rubi	1	6,3	0	0
Pieris brassicae	1	6,3	0	9
Cupido minimus	1	6,3	0	0
Pieris napi	1	6,3	8	100
Pieridae	5		4	
Satyrinae	2		0	
Papilionoidea	4		5	
Total	27		17	

Table E2. Total number of individuals of various pollinator taxa observed in May, June, July, and August. Wasps are represented by Vespidae and Symphyta.

Pollinator taxa\season	May (abundance)	June (abundance)	July (abundance)	August (abundance)
Bumblebees	29	43	341	293
Butterflies	5	16	8	15
Honeybees	2	63	154	285
Flies	1	24	53	50
Wasps	12	4	24	13
Hoverflies	10	20	6	6
Wild bees	1	7	6	11
Beetles	0	15	5	5
Total number	60	192	597	678

Table E3. Total number of Honeybees observed at the sites visited.

Site	Land-use	Honeybees
Forsøkslia	SS	171
Selsbakk N	SS	108
Lade	SN	92
Selsbakk S	SS	38
Grønlia	SN	32
Flatåsen	SN	14
Lian U	SN	13
Bjørndalen	SN	11
Buengveien N	SS	10
Okstad	SS	8
Buengveien S	SS	5
Lian L	SN	2

Appendix F: Results of Pairwise Wilcoxon test

Pairwise Wilcoxon test:

P-values from pairwise Wilcoxon test investigating differences between seasons:

Table F1: Results of pairwise Wilcoxon test for bumblebee species richness.

Bumblebee species richness	May	June	July
June	<0.001	-	-
July	<0.001	<0.001	-
August	<0.001	<0.001	0.271

Table F2: Results of pairwise Wilcoxon test for bumblebee abundance.

Bumblebee abundance	May	June	July
June	0.640	-	-
July	<0.001	<0.001	-
August	<0.001	<0.001	0.11

Table F3: Results of pairwise Wilcoxon test for pollinator abundance.

Pollinator abundance	May	June	July
June	<0.001	-	-
July	<0.001	0.156	-
August	<0.001	<0.001	0.017

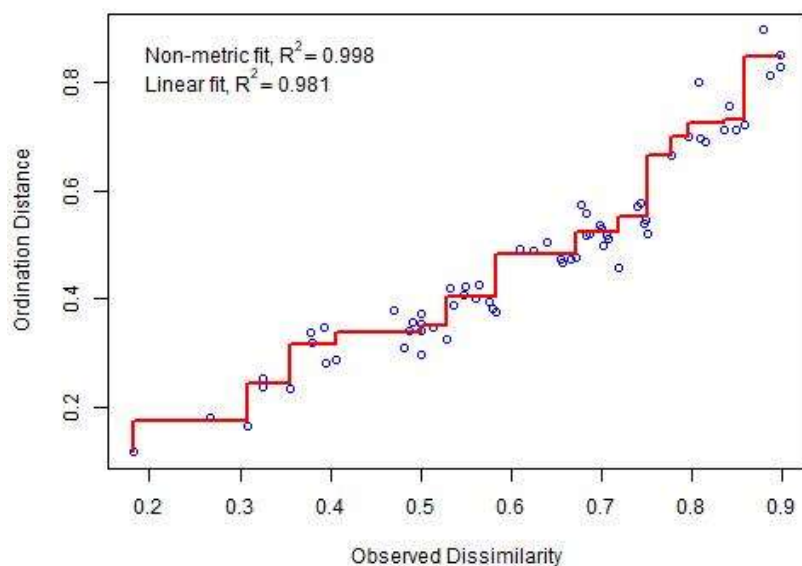**Bumblebee species richness:**

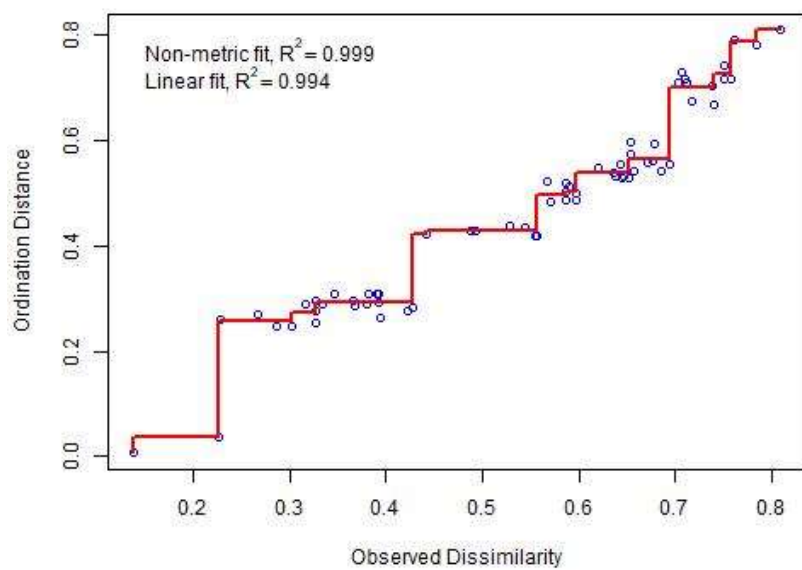*Figure G1. Stressplot of NMDS for bumblebee species.*

Pollinator taxa:

Figure G2. Stressplot of NMDS for pollinator taxa.

Appendix H: Correlation matrix and model selection

Results of correlation analyses:
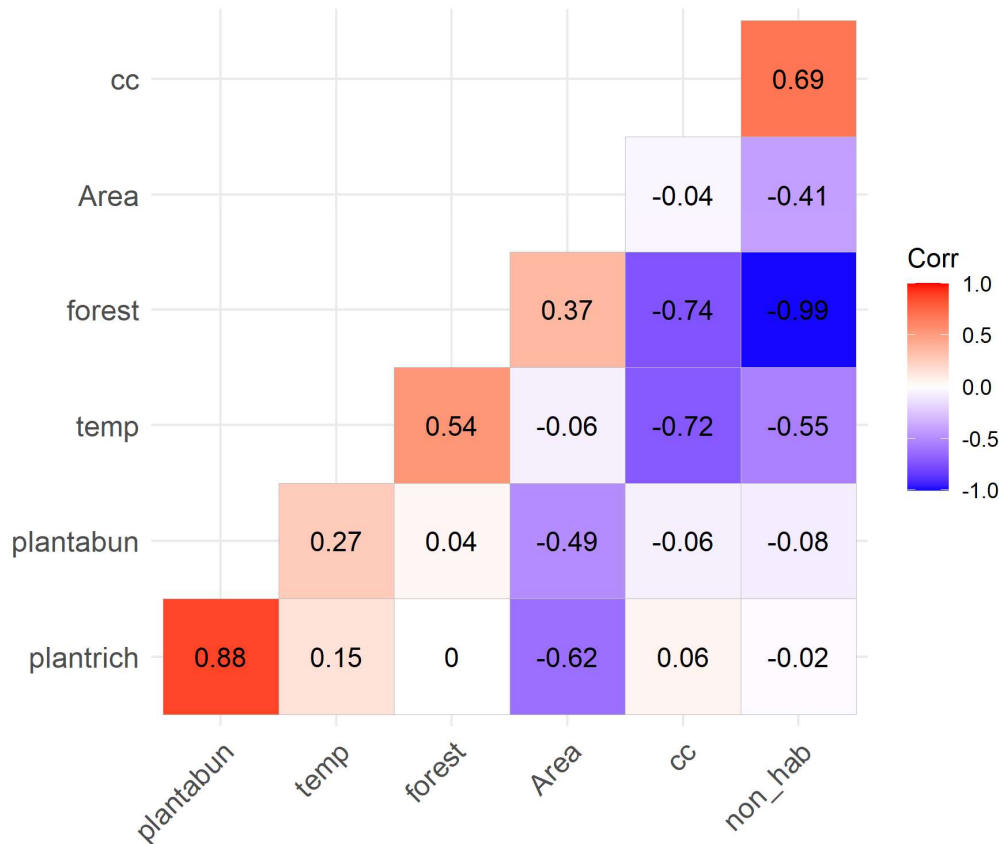
Figure H1. Correlation matrix for continuous predictor variables. "cc" = cloud cover, "area" = size of site, "forest" = proportion of forest, "temp" = temperature, "plantabun" = flowering plant abundance, "plantrich" = flowering plant species richness and "non_hab" = proportion of non-habitat.

Results from Kruskal eta-squared revealed high association between season and plant species richness. Since plant species richness was highly correlated with several variables, plant abundance was chosen as the variable representing the plant community within the grasslands in further model selection. No high correlations were found between land-use and the other predictor variables.

Model selection:

The following tables show model selection for species richness of bumblebees (Table H1), abundance of bumblebees (table H2) and abundance of pollinators (H3):

Table H1. Model selection for the model explaining species richness of bumblebees. Predictor variables include land-use (LU), season (S), proportion of non-habitat (NH), proportion of grasslands (G), size of site (A) and temperature (T). Models are fitted with a Poisson-distribution.

Model	Response	Predictor	AICc	ΔAICc	Weight
MODR1	**Bumblebee richness**	**LU + S + NH + T + S:T**	**475.7**	**0.00**	**0.557**
MODR2	**Bumblebee richness**	**LU + S + NH + PA + T + S:T**	**476.4**	**0.65**	**0.403**
MODR3	Bumblebee richness	LU + S + NH + PA + T + A + T:S	479.6	2.87	0.115
MODR4	Bumblebee richness	LU + S + NH + PA + T + A + S:T	480.8	5.08	0.043
MODR5	Bumblebee richness	LU + S + NH + PA + S:LU	486.1	10.40	0.003
MODR6	Bumblebee richness	LU + S + NH + PA	486.8	11.07	0.002
MODR7	Bumblebee richness	LU + S + NH + PA +T	487.1	11.35	0.002
MODR8	Bumblebee richness	LU + S + NH + S:LU	487.5	11.83	0.002
MODR9	Bumblebee richness	LU + S + NH	488.0	12.30	0.001
MODR10	Bumblebee richness	LU + S + NH + PA + T + S:LU	488.3	12.60	0.001
MODR11	Bumblebee richness	LU + S + NH+ G + PA + T	488.8	13.14	0.001
MODR12	Bumblebee richness	LU + S + NH + PA + T + S:PA	488.9	13.18	0.001
MODR13	Bumblebee richness	LU + S + NH + G + PA + T + A	491.1	15.35	0.000
MODR14	Bumblebee richness	LU + S + NH + G + PA + T + A + LU:S	492.6	16.91	0.000
MODR15	Bumblebee richness	LU + S + NH + G + PA + T + A + PA:S	493.0	17.29	0.000

Table H2. Model selection for the model explaining abundance of bumblebees. Predictor variables include land-use (LU), season (S), proportion of non-habitat (NH), proportion of grasslands (G), size of site (A) and temperature (T). Models are fitted with a Poisson-distribution.

Model	Response	Predictor	AICc	ΔAICc	Weight
MODA1	**Bumblebee abundance**	**LU + S + NH + PA + T + T:S**	**859.0**	**0.00**	**0.74**
MODA2	Bumblebee abundance	LU + S + NH + PA + T + G + T:S	861.1	2.10	0.26
MODA3	Bumblebee abundance	LU + S + NH + PA + T + A + T:S	863.0	4.04	0.090
MODA4	Bumblebee abundance	LU + S + NH + PA + T + PA:S	890.0	30.98	0.00
MODA5	Bumblebee abundance	LU + S + NH + PA + T + PA:S	892.0	32.96	0.00
MODA6	Bumblebee abundance	LU + S + NH + PA + T + G + PA:S	892.1	33.08	0.00
MODA7	Bumblebee abundance	LU + S + NH + PA + LU:S	893.8	34.80	0.00
MODA8	Bumblebee abundance	LU + S + NH + PA + A + S:LU	895.8	36.83	0.00
MODA9	Bumblebee abundance	LU + S + NH + PA + T + LU:S	895.9	36.95	0.00
MODA10	Bumblebee abundance	LU + S + NH + PA + T + LU:S	898.0	38.99	0.00
MODA11	Bumblebee abundance	LU + S + NH + PA + T + G + LU:S	898.2	39.17	0.00
MODA12	Bumblebee abundance	LU + S + NH + PA + T	899.4	40.36	0.00
MODA13	Bumblebee abundance	LU + S + NH + PA + T + LU:S	900.2	41.25	0.00
MODA14	Bumblebee abundance	LU + S + NH + PA + T + G + A	901.3	42.29	0.00
MODA15	Bumblebee abundance	LU + S + NH + G + PA + T	901.4	42.44	0.00

Table H3. Model selection for the model explaining pollinator abundance. Predictor variables include land-use (LU), season (S), proportion of non-habitat (NH), proportion of grasslands (G), size of site (A) and temperature (T). Models are fitted with negative binomial distribution.

	Response	Predictor	AICc	ΔAICc	Weight
MOD1	**Pollinator abundance**	**LU + S + NH + PA + T + A + S:T**	**1230.9**	**0.00**	**0.313**
MOD2	**Pollinator abundance**	**LU + S + NH + PA + T + S:T**	**1231.1**	**0.20**	**0.283**
MOD3	**Pollinator abundance**	**LU + S + NH + PA + T + G+S:T**	**1231.2**	**0.29**	**0.271**
MOD4	**Pollinator abundance**	**LU + S + NH + PA + T + G + A + S:T**	**1232.7**	**1.74**	**0.131**
MOD5	Pollinator abundance	LU + S + NH + G + PA + A + LU + S	1243.8	12.93	0.000
MOD6	Pollinator abundance	LU + S + NH + PA + T + G + LU:S	1244.0	13.10	0.001
MOD7	Pollinator abundance	LU + S + NH + G + PA + T	1245.1	14.19	0.000
MOD8	Pollinator abundance	LU + S + NH + PA + LU:S	1245.9	14.95	0.000
MOD9	Pollinator abundance	LU + S + NH + G + PA + T + A + LU:S	1246.0	15.08	0.000
MOD10	Pollinator abundance	LU +S + NH + G + PA + T + A	1247.3	16.38	0.000
MOD11	Pollinator abundance	LU + S + NH + PA + T	1248.0	17.09	0.000
MOD12	Pollinator abundance	LU + S + NH + PA + T + LU:S	1248.1	17.17	0.000
MOD13	Pollinator abundance	LU + S+ NH + PA + T + G + PA:S	1248.3	17.42	0.000
MOD14	Pollinator abundance	LU + S + NH + PA	1248.8	17.93	0.000
MOD15	Pollinator abundance	LU + S + NH + G + PA + T + A + PA:S	1250.5	19.55	0.000
MOD16	Pollinator abundance	LU + S + NH + PA + T + PA:S	1251.2	20.28	0.000

Results for generalized linear mixed models including only flowering plant species richness as a predictor:

Table H4. Results of generalized linear mixed model investigating the effect of plant species richness on bumblebee species richness.

Predictor	Estimate	SE	Z-value	P
Intercept	-1.28	0.21	-6.02	< 0.001
Plant richness	0.22	0.03	7.95	< 0.001

Table H5. Results of generalized linear mixed model investigating the effect of plant species richness on bumblebee abundance.

Predictor	Estimate	SE	Z-value	P
Intercept	-0.70	0.22	-3.24	< 0.01
Plant richness	0.27	0.02	13.38	< 0.001

Table H6. Results of generalized linear mixed model investigating the effect of plant species richness on pollinator abundance.

Predictor	Estimate	SE	Z-value	P
Intercept	0.40	0.22	1.86	0.06
Plant richness	0.24	0.01	16.46	< 0.001