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# How Introducing Flower Meadows in Cities Affect the Diversity of Plant-Bee Interactions

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# Abstract

Urbanization poses a significant threat to wild bee populations and the pollination services they provide, primarily due to habitat loss and fragmentation. To mitigate these challenges, initiatives such as establishing flower meadows in cities have gained prominence. One such initiative was the newly established Mother Meadow in Oslo city center. This study investigated the diversity and abundance of wild bees and their interactions with plants within the Mother Meadow, comparing the findings to data collected from pollinator-friendly habitats in the surrounding urban landscape. Despite the Mother Meadow exhibiting a lower diversity of wild bee species and unique plant-bee interactions compared to the surrounding landscape, it attracted a higher abundance of wild bees than the pollinator-friendly habitats in the surrounding areas. The spatially isolated Mother Meadow was predominantly visited by wild bee species with larger foraging ranges, such as bumblebees. This isolation can be a limiting factor for wild bee species richness, as species with smaller foraging ranges are less likely to reach the meadow. Despite its isolation the Mother Meadow may function as a steppingstone for wild bees from habitats on different sides of the inner Oslo fjord due to a general resource limitation of flowering plants in the city center. The Mother Meadow provided floral abundance for wild bees in the resource-limited environment and offered nutritional diversity by introducing plants occurring at lower frequencies in the surrounding landscape. An analysis of wild bees in the Oslo Meta Network showed that most of the observed species were common generalist species often observed in urban settings. Additionally, I found that wild bee communities and their interactions with plants were highly localized, indicating limited species movement between habitat fragments. The observed wild bees particularly favored blue-violet flowers with bilateral symmetry, late phenology, and high abundance, which has important implications for wild bee conservation in urban environments. My study provides a foundation for improving the establishment of future flower meadows to enhance wild bee diversity in urban and fragmented landscapes. It emphasizes the importance of implementing biodiverse and florally abundant meadows adjacent to other green areas to facilitate wild bee movement.

# Sammendrag

Urbanisering utgjør en betydelig trussel mot populasjoner av ville bier og pollineringstjenestene de tilbyr, hovedsakelig på grunn av tap av viktige habitater og fragmentering. For å avbøte disse negative effektene av urbanisering har initiativer som etablering av blomsterenger i byer fått økende oppmerksomhet. Et slikt tiltak var opprettelsen av 'The Mother Meadow' i Oslo sentrum. Denne studien undersøkte artsmangfold og forekomst av ville bier samt deres interaksjoner med planter i 'The Mother Meadow', og sammenlignet funnene med observasjoner fra pollinatorvennlige habitater i det omkringliggende urbane landskapet. Til tross for at The Mother Meadow hadde lavere artsmangfold av ville bier og færre unike interaksjoner mellom planter og bier sammenlignet med habitater i det omkringliggende landskapet, ble The Mother Meadow besøkt av flere ville bier enn de pollinatorvennlige habitatene i nærområdet. Den isolerte The Mother Meadow ble hovedsakelig besøkt av større biearter som kan fly lengre avstander, slik som humler. Denne isolasjonen kan være en begrensende faktor for artsmangfold av ville bier, da arter med kortere flygeevne er mindre sannsynlig å nå engen. Til tross for sin isolasjon kan The Mother Meadow fungere som et mellomlandingspunkt for ville bier fra habitater på forskjellige sider av indre Oslofjord på grunn av en generell ressursbegrensning av blomster i sentrum. Samlet sett tilbød The Mother Meadow et rikt blomsterutvalgt for ville bier i det ressursbegrensete miljøet og bidro med næringsmessig mangfold ved å tilføre planter som forekommer sjeldnere i det omkringliggende landskapet. Videre viste en analyse av ville bier i Oslo meta-nettverket at de fleste observerte artene var generalister som ofte observeres i urbane omgivelser. I tillegg fant jeg at populasjonene av ville bier og deres interaksjoner med planter var sterkt stedbundne, noe som indikerer begrenset forflytning av arter mellom fragmenterte habitater. De observerte ville biene foretrakk særlig blåfiolette blomster med bilateral symmetri, sen fenologi og høy abundans, noe som har betydelige implikasjoner for bevaring av ville bier i urbane miljøer. Min studie legger et godt grunnlag for å forbedre etableringen av fremtidige blomsterenger for å øke mangfoldet av ville bier i urbane og fragmenterte landskap. Funnene mine understreker viktigheten av å etablere artsrike og blomsterrike enger med tilgrensende grøntområder for å fremme forflytning av ville bier mellom habitatfragmenter.

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# 1.0 Introduction

Biodiversity hotspots are not only attractive to wildlife but also appealing for human settlement due to easy access to natural resources and suitability for agriculture (Cincotta et al., 2000; Luck, 2007). Human population densities are considerably higher in these hotspots compared to the global average leading to increased urbanization (Cincotta et al., 2000; Williams, 2013). While some cities can support diverse wildlife, urbanization is usually destructive and results in extensive losses of native species, habitat fragmentation, environmental degradation, and high rates of species extinctions associated with large-scale landscape transformations (Hansen et al., 2005; McKinney, 2008). Today, more than half of the world's human population lives in cities, a number which is expected to increase to almost 70% by 2050 (United Nations, 2019). As population densities rise, the wildlife in the remaining green patches (i.e., parks, gardens, cemeteries, flower meadows) are increasingly threatened (McKinney, 2008), including insect pollinators and their interactions with flowering plants (Wenzel et al., 2020).

There is a consensus that a large proportion of insect populations worldwide are in decline (Hallmann et al., 2017; Lister & Garcia, 2018; Sánchez-Bayo & Wyckhuys, 2019), with similar trends documented in pollinating insect populations (Potts et al., 2010). For instance, drastic declines have been shown in bumblebees (*Bombus*) and solitary bees in Western Europe, primarily due to changes in their environment (Biesmeijer et al., 2006; Goulson et al., 2008; Potts et al., 2010). Evidence points to habitat loss and fragmentation as main drivers of the decline (Potts et al., 2010), which are further exacerbated in urban landscapes (McKinney, 2008). This has profound implications for the ability of cities to function as reservoirs for wild bees and thereby support ecosystem services in and around urban areas (Hall et al., 2017; Wenzel et al., 2020).

The majority of flowering plants (>80%) depend on animal-mediated pollination for sexual reproduction with bees being considered the most dominant pollinating taxon (Ollerton et al., 2011; Willmer et al., 2017). Urban development threatens the diversity of plant-bee interactions through the replacement of pollinator habitats by impervious surfaces (i.e., buildings, roads, and pavements) (Harrison & Winfree, 2015). Bee species abundance and richness are negatively correlated with the proportion of impervious surfaces, with higher degrees of urbanization often leading to declines in wild bees and their pollination services surfaces (Banaszak-Cibicka & Żmihorski, 2012; Geslin et al., 2013; Wenzel et al., 2020).

In line with the optimal foraging theory, some studies have documented altered flower visitation behavior in urban bees (Andrieu et al., 2009; Pyke, 1980). Bees avoid smaller, isolated flower patches for the benefit of larger patches to maximize their net energy intake (Andrieu et al., 2009). Plants in these smaller patches receive fewer visitors, limiting pollination success and reducing gene flow (Kwak et al., 1998). The foraging range of bees is typically within a 200-300m radius of the nesting site (Gathmann & Tscharntke, 2002; Wolf & Moritz, 2008; Wright et al., 2015), although some bees can travel more than 1000m from their nests (Osborne et al., 2008). Variations in bee foraging behavior are observed along the urbanization gradient based on the availability of nesting areas and the quality, access, and distance between floral resources (Dupont et al., 2024; Gathmann & Tscharntke, 2002). Understanding urban bee foraging behavior is crucial for strategic urban green space planning to incorporate effective habitat conservation and promote connectivity between these habitats.

Urbanization is likely to affect bee diversity through species-specific habitat requirements and tolerances to habitat isolation. Greenleaf et al. (2007) demonstrated a positive association between body size and foraging ranges, indicating that larger bees typically cover greater distances than smaller bees while foraging. As the proportion of impervious surfaces increases, bare ground decreases and distances between green patches increases (Banaszak-Cibicka & Żmihorski, 2012). As a result, highly urbanized areas tend to promote large-bodied bees that nest above ground in cavities while discriminating against smaller ground-nesting bees (Banaszak-Cibicka & Żmihorski, 2012; Geslin et al., 2013). Generalist species with a broad dietary range are also found to benefit more in urban landscapes than specialist species with narrow diets (Biesmeijer et al., 2006).

Despite a global decline in bee species, recent urban pollinator studies reveal that cities focusing on the conservation and protection of various interconnected green infrastructures, such as gardens, cemeteries, flower meadows, river embankments, and parks, often have diverse populations of thriving wild bees (Hall et al., 2017; Wenzel et al., 2020). In some instances the diversity of bees in and around cities has been reported to be higher than in nearby rural areas (Hall et al., 2017). These green areas are vital for pollinators and have profound implications for wild bee conservation (Ministry of Agriculture and Food & Ministry of Climate and Environment, 2018), highlighting the importance of enhancing the value of these areas for pollinators in urban settings.

Norway has implemented a 'National Pollinator Strategy' (2018) through an 'Action Plan for Wild Pollinating Insects, 2021-2028' (2021) to mitigate and reverse the national and global

pollinator decline. The Norwegian National Pollinator Strategy aims to ensure viable populations of wild bees, including other pollinating insects, through increasing scientific knowledge, preserving habitats, preventing habitat loss and communicating information about pollinators to the public (Ministry of Agriculture and Food & Ministry of Climate and Environment, 2018). The Action Plan for Wild Pollinating Insects presents specific measures to address habitat loss and degradation, while also strengthening considerations for wild pollinators in municipal management (Klima- og miljødepartementet et al., 2021). Central to the strategy and action plan is improving our knowledge of the effectiveness of different wild bee conservation actions.

Following these Norwegian pollinator initiatives, restoring pollinator habitats in urban areas through the establishment of flower meadows has gained prominence as a tool for mitigating the negative effects of urbanization and providing nutritional diversity to wild bees (Aamlid & Svalheim, 2020). These flower meadows often comprise a mix of locally sourced native flowering plants, sharing many of the same plant species with semi-natural meadows (Aamlid & Svalheim, 2020). To improve conditions for pollinating insects, Oslo municipality established a flower meadow in the highly urbanized city center in 2020. The introduced meadow, hereafter referred to as the Mother Meadow, is located on a newly created pier and is surrounded by the inner Oslo fjord and tall concrete buildings. The closest larger pollinator-friendly habitats are more than 300m away, which is further than the typical foraging range of many bees and potentially limits the effectiveness of the Mother Meadow in supporting the local wild bee populations. Through the 'HiMotherBee' project researchers from the Norwegian Institute of Nature Research (NINA) and the Norwegian University of Life Sciences (NMBU) were tasked with investigating the impacts of the Mother Meadow on plant-bee interactions throughout the wider cityscape.

This study aimed to determine the importance of the recently established Mother Meadow for the general diversity and abundance of wild bees and their interactions and to compare findings from the Mother Meadow with pollinator-friendly meadows in the surrounding landscape. I explored the following research questions:

(1) Do wild bees utilize the Mother Meadow, and if so, which species are observed in the meadow?

Despite the isolation of the Mother Meadow, I expected to record wild bee activity in the meadow based on evidence that some bee species can fly these distances (Gathmann &

Tscharntke, 2002; Goulson, 2003; Wolf & Moritz, 2008). I also expect to find common, pollen generalist wild bee species, as these are more likely to profit in urban areas compared to specialists (Biesmeijer et al., 2006).

(2) How do plant-bee interaction abundance, richness and diversity compare between the Mother Meadow and the meadows in the nearby surrounding landscape?

Green corridors in fragmented urban landscapes, such as parks, roadside vegetation, and flower strips, facilitate increased pollinator movement (Van Rossum & Triest, 2012). I anticipated observing more varied and diverse interactions in the surrounding landscape than in the Mother Meadow as these areas have higher green patch connectivity.

(3) Which plant-bee interactions are collectively observed in the Mother Meadow and the surrounding landscape? Which specific plant traits (i.e., phenology, petal color, symmetry, and nectar production) enhance a plant's attractiveness to a wider range of wild bee species?

Given that wild bees have diverse dietary preferences and foraging ranges depending on sociality and body size (Greenleaf et al., 2007; Grüter & Hayes, 2022), I expected bumblebees and solitary bees to visit different plant species. Based on which plants wild bees prefer, it is possible to identify beneficial plant species for wild bees, increasing knowledge of urban plantbee interactions in Oslo and providing recommendations for plant species composition when establishing flower meadows specifically targeting wild bees in the future.

# 2.0 Methods

# 2.1 Study design

## 2.1.1 Study Area

Fieldwork was conducted in Oslo, Norway, from the beginning of June to the end of July 2023 as part of the 'HiMotherBee' project. The study area was in Oslo city center encompassing a circular area within a radius of 900 meters centered around the focal meadow (see section 2.1.2 Study Transects). The 900-meter radius was selected based on evidence that some bee species can fly these distances (Gathmann & Tscharntke, 2002; Goulson, 2003; Wolf & Moritz, 2008). Oslo City center is a highly urbanized and densely populated area, dominated by roads, buildings, and other impervious surfaces (Figure 1). Green spaces are fragmented, appearing as small, spread-out patches. Given the city center's coastal location, approximately half of the study area is in the inner Oslo fjord comprised of open ocean water surfaces.

Oslo municipality falls within the boreal-nemoral vegetation zone characterized by a transition between coniferous forest and deciduous forests, with a temperate climate (Moen, 1998). The annual mean temperature in Oslo in 2023 was 8.0°C (The Norwegian Meteorological Institute, n.d.). During the months of fieldwork, June and July, monthly average temperatures ranged from 17.4 to 20.0°C with a recorded minimum of 7.5°C and a maximum of 31.6°C (The Norwegian Meteorological Institute, n.d.). The monthly mean precipitation in Oslo in 2023 was 71.9mm, averaging 33.3mm in June and 119.0mm in July (The Norwegian Meteorological Institute, n.d.).



**Figure 1.** Aerial photo of study area showing the location of the 8 transects divided into three main transect groups. Transects were established within a 900m radius (green circle) of the focal meadow, the Mother Meadow consisting of two transects (red dots). In the surrounding landscape, one transect was established in Sara's Meadow (blue dot), and five shorter transects, collectively called the Minor Meadows (yellow dots), were established. The satellite image was sourced from Esri World Imagery and the small map in the top left corner was sourced from CartoDB Positron.

## 2.1.2 Study Transects

A total of 11 irregular transects were established within the study area. The transects were deliberately placed in relatively undisturbed patches and meadows with high floral abundance and plant diversity, ensuring their potential to attract wild bees. Three of the transects were consistently mowed during the sampling period resulting in flowerless conditions, which ultimately led to their exclusion from the study. The focus was therefore narrowed down to the remaining eight transects (Table 1). These transects showed minimal variation in elevation above sea level, typically 1-10m above sea level, but one transect, placed in Ekebergskråningen, had an elevation of 60m (Statens kartverk, n.d.). Transect lengths varied between 15 and 96m and were generally proportional to the size of pollinator-friendly patches and meadows. Each transect was set to a width of 1m to facilitate efficient bee capture using an entomological butterfly net. See Appendix A (Table A1) for coordinates indicating the starting and ending points of each transect.

The eight transects that were retained through the study were categorized into three groups: the Mother Meadow, Sara's Meadow and Minor Meadows (Figure 1, Table 1). The Mother Meadow (established in 2020), served as the focal meadow and included two transects. One transect was placed in Sara's Meadow (established in 2018), a relatively newly established meadow located in the surrounding landscape with a similar plant community to the Mother Meadow. Unlike the Mother Meadow, Sara's Meadow was close to other habitats suitable for pollinators. In contrast to the newly established meadows, the Minor Meadows consisted of six transects situated in various urban green spaces such as roadside flower strips, hiking areas and unmown sections of parks and gardens.

**Table 1.** Overview of all transects in their respective transect group, including transect length and approximate distance from the Mother Meadow. Distance is calculated using the start coordinates for each transect compared to the start coordinates for HMB\_01 (latitude: 59.90499, longitude: 10.75417). "HMB" is an abbreviation of HiMotherBee. See Appendix A (Table A1) for transect metadata including coordinates for transect start and end.

Transect Group	Transect ID	Transect Length (m)	Dist. from Mother Meadow (m)
Mother Meadow	HMB_01	96	-
	HMB_02	15	-
Sara's Meadow	HMB_08	63	867
Minor Meadows	HMB_03	36	495
	HMB_04	36	513
	HMB_05	18	367
	HMB_06	19	381
	HMB_07	95	883

## The Mother Meadow

To help mitigate the negative effect of urbanization on the diversity of pollinators and their interactions with plants, Oslo municipality's Agency for Cultural Affairs (Kulturetaten) established the flower meadow in the city center in 2020. Situated on Inger Munch's pier, a scenic park that juts out into the fjord south of the Munch Museum, the flower meadow features the notable sculpture "The Mother" by Tracey Emin. To follow up on the impacts of the meadow, the Agency for Cultural Affairs commissioned NINA to plant-bee interactions in the wider cityscape (project "HiMotherBee). My study is primarily focused on the Mother Meadow, with the other transects for comparison. Of the eight transects used in this study, two transects (HMB\_01 and HMB\_02) were established in the Mother Meadow.

J & L Gibbons Landscape Architects (with Holo & Holo as the Norwegian subcontractor) established the Mother Meadow in spring 2020, incorporating over 50 wildflowers and plants native to Oslo's costal climate (Oslo kommune, n.d.). Both seeds and plug plants were locally

sourced. NIBIO Landvik, a Norwegian competence center for flower meadows and natural seeds, delivered seeds from a seed mix for dry meadows in south-eastern Norway. The seed mix consisted of 25 different species (NIBIO, n.d.). The Ljono Stauder company (n.d.), specializing in perennial plants, provided ca. 5.000 plug plants. A comprehensive list of plant species is included in Appendix B (Table A3). In addition, sandy soil pockets were strategically introduced to enhance nesting habitats for wild bees and promote increased pollination (Oslo kommune, n.d.).

#### Sara's Meadow

Sara's Meadow is located just under 900 meters from the Mother Meadow. The meadow neighbors the Armed Forces Museum, which in turn connects to several larger park areas clearly visible on the aerial photo of the study area (Figure 1). Sara's Meadow was established in June 2018 as a part of "Budding Oslo" (Spirende Oslo), the municipality's investment program in urban agriculture run by the Agency for Urban Environment (Bymiljøetaten). One of the eight transects used in the study (HMB\_08) was established in Sara's Meadow.

The primary focus of establishing Sara's Meadow was to plant species native to Oslo and Eastern Norway (G. H. Jacobsen, advisor at the Agency for Urban Environment and project leader during the establishment of Sara's Meadow, personal communication, March 7, 2024). Approximately 6000 seeds from at least 20 different species were propagated in botanical gardens, and later re-planted into Sara's Meadow in June of 2018. Seeds from *Leucanthemum vulgare* and *Campanula rotundifolia* were purchased from NIBIO. The remaining seeds were personally collected by G. H. Jacobsen. A representative plant species list, including the most common species, is included in Appendix B (Table A4).

#### **Minor Meadows**

The Minor Meadows transect group represents the flowering green spaces in the urban landscape that are not newly established meadows, such as roadside flower strips, hiking areas and areas that are difficult to mow. The plant communities along these transects vary greatly from each other and those found in the Mother Meadow and Sara's Meadow, providing nutritional diversity to pollinators.

Two transects were situated in a recreational park east of the Mother Meadow, with one transect spanning a sandy meadow (HMB\_03) and the other following along the ruins of an old stone wall foundation (HMB\_04). Two other transects (HMB\_05 and HMB\_06) were established in

the outskirts of Losæter, a small urban agricultural garden run by the Agency for Urban Environment, featuring a combination of roadside vegetation and garden vegetation. The last transect (HMB\_07) was situated in the nature reserve 'Ekebergskråningen', a hiking and recreational area. Permission to sample and map wild bees in the nature reserve was granted by The County Governor of Oslo and Viken (Statsforvalteren i Oslo og Viken, reference number 2023/19407).

#### 2.2 Data Collection

## 2.2.1 Plant-Bee Interaction Data Collection

Over three rounds in 2023 – beginning of June, end of June, and July –flower-visiting bees were collected by both Markus A. K. Sydenham (researcher at NINA and bee specialist) and I using standardized transect walks. Such walks, conducted with a butterfly net, are recognized for their efficiency in collecting bees and serve as a good indicator of species richness (Popic et al., 2013; Westphal et al., 2008). All study transects were sampled between 10:30 and 18:00 in a randomized sequence.

Sampling periods were flexible to accommodate variation in weather conditions, as this is highly important to capture a broader diversity of bees. Pollinator activity increases with favorable conditions, such as a minimum temperature of 15°C, low wind, dry vegetation, no rain, and little to no cloud cover (Westphal et al., 2008). The first two sampling rounds were done under optimal weather conditions. July 2023 experienced a 25% increase in precipitation compared to average precipitation records characterized predominately by cloudy and rainy weather (Gangstø et al., 2023). Consequently, the final sampling round in late July occurred under sub-optimal weather conditions with slight cloud coverage and wind above 5 m/s.

We focused exclusively on collecting bees actively foraging to assess the diversity of plant-bee interactions. The collected bees were put in falcon tubes (plastic containers) filled with 96% ethanol until pinned for identification. Each tube was labeled with site ID, date, and time of sampling, along with the name of the visited plant species. Additional details regarding the identification of the visited plants are provided in section 2.2.2.

To account for varying transect lengths, we standardized the sampling time by dividing transect length by three, representing an average sampling time of 20 seconds per meter. This duration was chosen to allow ample time to sample interactions along each transect and effectively cover all transects within 2-3 days. Sampling time varies between pollinator studies utilizing the same transect walk method but typically ranges from 10 to 50 seconds per meter (Sydenham et al.,

2024; Westphal et al., 2008). See Appendix A (Table A1) for the specific sampling time for each transect. After the specified sampling time at each transect, we tallied the number of bees collected and added an additional 30 seconds per bee to account for handling time.

The first round of sampling was conducted by Sydenham. For the second and third rounds of sampling, both Sydenham and I conducted sampling (see exceptions in Appendix A, Table A2). Transects sampled by both collectors were sampled within a week of each other (per round). In July this was not possible due to challenging weather conditions. Sydenham completed sampling in early July, while I sampled interactions in the latter half of the month.

#### 2.2.2 Vegetation Surveys

To gauge the richness of blooming plants along all transects, I conducted three standardized vegetation surveys between June 7<sup>th</sup> and July 29<sup>th</sup>, 2023. The first two surveys coincided with the first two rounds of plant-bee interaction sampling, ensuring alignment within a  $\pm$  sevenday window for each transect. This approach, comprised of sampling rounds and corresponding vegetation surveys, aimed to determine in-bloom plant availability and evaluate floral richness per transect for each round of plant-bee interaction sampling. The final plant survey was not possible to align with the interaction sampling due to weather conditions.

Using a subplot frequency analysis method (SF),  $1 \times 1m$  plots were positioned at 5-meter intervals along each transect (Figure 2). These plots were further subdivided into four 50×50cm sub-plots. The number of survey plots per transect varied with transect length with a 5-meter transect hosting one plot, a 10-meter transect accommodating two plots, and so forth. The SF methods was used in this study to register each in-bloom plant species within a plot. To quantify the abundance of in-bloom plant species, a scoring system ranging from 1 to 4 was applied to each species per plot based on its presence across subplots.

The plants were identified to species level utilizing field books (Feilberg, 2018), the Artsorakel mobile app (Artsdatabanken, 2020) for species identification though images, and the expertise of Siri Lie Olsen, plant ecologist. Plants belonging to the genera *Hieracium*, *Rumex*, *Rosa*, and *Taraxacum* were only identified to genus level due to difficulty in distinguishing them at species level. Similarly, plants within *Convolvulaceae* were only determined to family level.

Plant species cover (%) was calculated using the abundance estimates from the plant surveys conducted. The number of sub-plots in which a species was present was divided by the total number of sub-plots, then multiplied by 100. Overall, plant cover refers to the proportion of subplots a given plant was present in. Plant species that were only recorded during interaction

sampling and not abundant enough to be recorded during the plant surveys were given the lowest subplot frequency (= 1). This was done to reflect the plants' overall low abundance but also to ensure their inclusion in the plant cover (%) calculations despite a minimal contribution.



**Figure 2.** A) Schematic overview of how vegetation surveys were conducted. Yellow squares represent  $1 \times 1$ -meter plots, each comprising of four subplots for recording in-bloom plant occurrences. These plots were systematically positioned, maintaining a consistent 5-meter separation between each plot, regardless of transect length. B) Transect setup at the Mother Meadow: A 30-meter-long measuring tape was used to mark the transect line, facilitating the efficient placement and spacing of the  $1 \times 1$ -meter plots. Photograph: Bischof, A.

# 2.2.3 Bee Identification and Species Information

In total there are 210 recorded species of wild bees in Norway (Artsdatabanken, 2021; Ødegaard, 2014). Among these, there are 175 solitary bee species from six different families and 35 species of bumblebees (Artsdatabanken, 2021; Ødegaard, 2014). Approximately one-third of Norway's bees are currently on the Norwegian Red list for Species primarily due to habitat impacts (Artsdatabanken, 2021).

I pinned and prepared the wild bees sampled during fieldwork at the entomology lab of the Norwegian University of Life Sciences (NMBU). Identification of honeybees (*Apis mellifera*) was conducted by me, whereas the remaining wild bee species were identified by Sydenham using relevant sources (Amiet et al., 1999; Amiet et al., 2001; Amiet et al., 2002; Amiet et al., 2007; Amiet et al., 2010; Amiet et al., 2018). Despite collecting *A. mellifera*, I excluded the domesticated honeybee from this study to focus exclusively on wild bees and their interactions with plants. All wild bee species were determined to species level with the exception of the subgenus *Bombus sensu stricto*, a group of cryptic bumblebee species known for their difficulty in distinguishing between them (Carolan et al., 2012; Williams et al., 2012).

See Appendix C (Table A5) for details on species information of the observed wild bees in the Meta Network, including number of observations, sociality, status in the Norwegian Red List for Species, nesting preferences, dietary preferences, and urban presence.



**Figure 3. Left:** Collected wild bee specimens were pinned, labeled (locality, date, collector, bee species, and visited plant), and stored in sealed entomological display cases. **Top right:** Solitary bee *Megachile willughbiella*. **Bottom right:** Solitary bee *Anthidium manicatum*. Photos: Bischof, A.

#### 2.2.4 Plant Species Traits Information

To promote pollinator diversity, it is important to understand which plant characteristics or traits are most attractive to wild bees. Therefore, I have focused on a selection of specific plant species traits that are known to influence pollinator preference. These traits include flower symmetry (Yoder et al., 2020), flower petal color (Pichler et al., 2020), phenology (Pichler et al., 2020) and nectar production (Baude et al., 2016). Plant phenology and nectar production values were sourced from Tyler et al. (2021), a dataset with ecological indicators and trait values of Swedish vascular plants, many of which are commonly found in Norway. For taxa not identified to species level (see section 2.2.2), the average trait value of the all the plants within the taxa was calculated using the Tyler et al. (2021) dataset. The genus *Taraxacum* was not included in the Tyler et al. (2021) dataset and was consequently excluded from traits-analysis (see section 2.3.1). I also excluded the genus *Convolvulaceae* from the model due to lack of species level identification.

Nectar production was categorized using the seven-degree logarithmic scale from Tyler et al. (2021) based on data from a publication on nectar assessment in Great Britain (Baude et al.,

2016). At the lower end of the scale, plants are characterized by no nectar production (=1, 0 g), whereas on the upper end of the scale are those exhibiting high nectar production (=7, >200 g) based on expected yearly yield of grams sugar per square meter.

Plant phenology, or onset of flowering, was categorized using the continuous 15-degree scale suggested by Tyler et al. (2021). The scale is based on the climatic conditions in central Scania county in Sweden (latitude: 55.990300, longitude: 13.595800) and divides the growing season from late February (=1) to late September (=15) into 1/2-month increments. The onset of flowering in Oslo is only slightly delayed compared to central Scania as it lies somewhat further north, and the dataset is therefore applicable to the phenology in the inner Oslo fjord. This scale presents the onset of flowering and does not indicate length of flowering period, main growth period or intraspecific variation.

I divided flower petal color into four different categories: blue-violet, pink-red, yellow, and white (Figure 4) using Feilberg's (2018) field flora of wild flowers in Norway as a guide. Final decisions were based on overall personal observations of the local flora from fieldwork. It is important to note that bees have the ability to detect ultraviolet light (UV) (Kühn, 1927), which may affect the attractiveness of flowers to bees (Chittka & Raine, 2006). However, to maintain comparability with Feilberg's flora (2018), and thereby colors visible to humans, this study adhered to the light spectrum visible to humans.

Flower symmetry was categorized into two main groups: radial symmetry and bilateral symmetry (Figure 4). The identified plants were grouped using descriptions and illustrations from Feilberg's (2018) field flora and Lid's Norwegian flora (Lid & Lid, 2005) as a guide. Bilateral flowers have one plane of symmetry while radial flowers have multiple. Many plants in the aster family (Asteraceae) exhibit both radial and bilateral symmetry depending on whether single flowers or flowerheads are considered (Chapman et al., 2012). In this study, I categorized asters as having radial symmetry, as this characterizes the flower head as a whole and represents the first impression bees receive when approaching these flowers.

A more detailed description of the plant traits is included in Appendix D (Table A6), including explanations of the adaptations made.



**Figure 4.** Images of flowering plants to vizualize the flower petal color and symmetry categories. **White:** *Leucanthemum vulgare* (A). **Blue-Violet:** *Campanula rotundifolia* (B). **Yellow**: *Lotus corniculatus* (C). **Pink-Red**: *Lathyrus sylvestris* (D). A and B are examples of flowers with radial symmetry, while C and D are examples of flowers with bilateral symmetry. Photos: Bischof, A.

# 2.3 Statistical Analyses

All statistics were performed with R version 4.3.1 (R Core Team, 2023) using RStudio (Posit Team, 2023). I used the "ggplot2" package (Wickham, 2016) to plot functions in the base R package for producing figures and graphs.

## 2.3.1 Comparative Analyses

To compare the interaction abundance, richness and diversity between the Mother Meadow and the two transect groups in the surrounding landscape (Sara's Meadow and Minor Meadows), I utilized three different comparative methods: (1) rarefaction analyses, (2) linear regression models and (3) Venn diagrams. All the comparative analyses are based solely on the plant-bee interaction sampling data. It is important to note that each transect group consists of a different number of transects, and each transect varies in length. Transect length differences were addressed in the linear regression models by using the number of interactions per transect length (m), thereby ensuring comparability across transects of varying length. Rarefaction and Venn diagram analyses were based on data collected within the respective transect groups, irrespective of transect length, sampling round, or collector.

To assess the diversity of wild bees and their interactions with plants across the three transect groups, I used a sample-size-based rarefaction-extrapolation (R/E) analysis method. I used the 'iNEXT' function from the "iNEXT"-package to estimate richness (Hill number = 0) and sample coverage (sufficiency of sampling effort), based on the rarefaction and extrapolation (prediction) of Hill numbers (Chao et al., 2014; Hsieh et al., 2024). This method standardizes sampling efforts and facilitates comparisons even when dealing with groups of different sample sizes and transect lengths (Chao et al., 2014). The R/E curves were plotted with the 'ggiNEXT' function (Hsieh et al., 2024; Wickham, 2016).

To compare plant-bee interaction richness and abundance across the three transect groups, I fitted two linear regression models using the 'lm' function with transect group as the categorical predictor variable. The response variable 'interaction richness per meter' (Model 1) was calculated by dividing the total number of unique interactions observed by the transect length (m) for every combination of transect, collector and sampling round. Similarly, response variable 'interaction abundance per meter' (Model 2) was calculated by dividing the total number of observed interactions by the transect length (m) for every combination of transect, collector and sampling round. Similarly, response variable 'interaction abundance per meter' (Model 2) was calculated by dividing the total number of observed interactions by the transect length (m) for every combination of transect, collector and sampling round. I used "DHARMa" diagnostic plots of the simulated residuals (Hartig, 2022) for assessing residual distributions. Due to the left skewedness in the data, the response variables, plant-bee interaction richness per meter and plant-bee interaction abundance per meter, were log-transformed. After the transformations, assumptions of normality and homogeneity were met. If significant differences between transect groups were found, I conducted a Tukey's Honest Significant Difference (HSD) post-hoc test to further analyze pairwise differences between the transect groups.

To illustrate the overlap of the number of unique wild bee species, plants visited by wild bees and plant-bee interactions among the three transect groups, I used area-proportional Euler diagrams fit with ellipses from the "eulerr"-package (Larsson, 2024) to plot the figures.

#### 2.3.2 Meta Network Analyses

The second part of the statistical analyses aimed to collectively examine the data from all the eight transects in the study area, hereafter referred to as the Meta Network. The Meta Network analyses provide insight into overall (4) plant-bee interactions and (5) plant characteristics that affect visiting bee species richness.

The aim of the plant-bee interaction analysis was to gain perspective of species-specific flower preferences for wild bees in the Meta Network. To visualize the interaction network for the entire Meta Network I used the "bipartiteD3" package (Terry, 2021). The bipartite graphs were based on the interaction sampling data. Given that wild bees differ in their dietary niches and foraging ranges depending on sociality and body size (Greenleaf et al., 2007; Grüter & Hayes, 2022), I split the data into two main groups: bumblebees and solitary bees. Two bipartite figures were made based on this rough distinction in size and sociality providing insights into different dietary preferences among bumblebees and solitary bees.

The aim of the Model 3 analysis was to determine which plant traits seem to attract more species of wild bees, but also to investigate whether other factors influence bee species richness. The

response variable in the model was the total number of bee species (i.e., bee species richness) observed on a particular plant species within a transect on separate sampling rounds. To analyze the relationship between various predictor variables and the total number of bee species across all transects, I fit a Poisson generalized linear mixed-effects model (GLMM) using the 'glmmTMB' function from the "glmmTMB" package to account for zero inflation (Brooks et al., 2017). The Model 3 dataset was comprised of data collected during interaction sampling and vegetations surveys, as well as the plant trait information. The full model included four categorical fixed effects: flower symmetry, collector, sampling round, and petal color, and three continuous fixed effects: phenology, nectar production and plant cover. To account for random variations across different transects and plant families, these variables were included as crossed random effects.

I used residual diagnostic plots made using the function 'simulateResiduals' from the "DHARMa" package (Hartig, 2022) to assess if residual distribution met model assumptions. All the continuous predictor variables were standardized using the 'scale' function. Additionally, plant cover was transformed using the 'log1p' function (i.e., log(1+x)) to accurately handle values close to zero and skewedness. Model assumptions were met after standardization and transformation of the continuous predictors. Marginal  $R^2$  and conditional  $R^2$  were calculated using the 'r.squaredGLMM' function from the "MuMIn" package (Barton, 2023), and they were used to interpret the variation explained by the fixed effects and the entire model, respectively. To improve model interpretability, I reduced the full model using likelihood ratio tests (LRT) to stepwise eliminate all non-significant predictors. The LRT tests were performed using the 'drop1' function with Chi square tests allowing for identification of the least significant predictors (predictors with the highest p-value). The three fixed effects: collector, sampling round and nectar production were removed in the stated order, yielding a reduced final model with the remaining four fixed effects: flower symmetry, petal color, phenology and plant cover.

# 3.0 Results

## 3.1 Wild Bees of the Meta Network

All 27 observed wild bee taxa in the Meta Network are common species often encountered in urban landscapes (Appendix C, Table A5). Most of these species are polylectic, meaning they visit many unrelated host plants for pollen (Cane & Sipes, 2006). Three wild bee species are oligolectic and only visit taxonomically related plants. These include *Colletes daviesanus*, which mainly visits plants within the aster family (*Asteraceae*), and *Dufourea dentiventris* and *Melitta haemorrhoidalis*, which prefer plants in the *Campanula* genus and are tightly attached to *C. rotundifolia*. Nesting preferences varied among the observed species (Appendix C, Table A5) with most preferring various types of below-ground nesting. Most of the observed wild bee species are listed as 'Least Concern' (LC) in the Norwegian Red list for Species (2021). However, two solitary species (*Andrena nigriceps* and *D. dentiventris*) and one bumblebee species (*Bombus subterraneus*) are listed as 'Near Threatened' (NT).

# 3.2 Transect Group Comparison: Wild Bee and Interaction Richness

Wild bee sample coverage within transect groups was high, indicating high sufficiency in sampling effort. Sample cover was highest in the Mother Meadow (98%, n=177), followed by Sara's Meadow (95%, n=85) and the Minor Meadows (92%, n=95). An assessment of the rarefaction-extrapolation curves revealed that the Mother Meadow had the lowest expected bee species richness within the Meta Network (Figure 5), especially when compared to the Minor Meadow R/E curve. The Mother Meadow R/E curve asymptotes below those of Sara's Meadow and the Minor Meadows, indicating that even with increased sampling effort, the Mother Meadow hosted fewer species than the transects in the surrounding landscape. Of the two transects in the surrounding landscape, the Minor Meadows showed the highest expected bee species richness. Based on the R/E analysis among 100 randomly sampling individuals, one may expect 20 wild bee species in the Minor Meadows and 13 in Sara's Meadow, but only 7 in the Mother Meadow.



**Figure 5.** Sample-size-based R/E curves for expected wild bee richness (Hill number = 0: species richness) within the three transect groups as a function of sampling effort. The solid lines represent rarefaction, the dashed lines represent extrapolation and the solid symbols indicate the maximum number of observed individual bees for each of the transect groups. The transparent shading represents 95% confidence intervals from 1000 bootstrap replications.

Plant-bee interaction sample cover within the three transect groups varied from medium to high, indicating a somewhat insufficient sampling effort. Estimated sample cover was lowest in the Minor Meadows (70%), and more adequate in the Mother Meadow (94%) and Sara's Meadow (80%). The interaction rarefaction-extrapolation curves reveal the same trend as the wild bee R/E analysis with the two transects in the surrounding landscape exhibiting higher interaction richness than the Mother Meadow (Figure 6). Among 100 randomly sampled interactions one may expect to record approximately 25, 35, and 49 unique plant-bee interactions in the Mother Meadow, Sara's Meadow and Minor Meadows, respectively.



**Figure 6.** Sample-size-based R/E curves for expected plant-bee interaction richness (Hill number = 0: interaction richness) within the three transect groups as a function of sampling effort. The solid lines represent rarefaction, the dashed lines represent extrapolation and the solid symbols indicate the maximum number of observed interactions within each of the transect groups. The transparent shading represents 95% confidence intervals from 1000 bootstrap replications.

#### 3.3 Transect Group Comparison: Interaction Richness and Abundance

Despite the Mother Meadow having a lower expected wild bee (Figure 5A) and interaction richness (Figure 5B) compared to Sara's Meadow and the combination of all the Minor Meadows, the Mother Meadow attracted a significantly higher abundance of wild bees than the Minor Meadows (Figure 7B). The linear regression models revealed that there was no statistically significant difference in mean interaction richness per meter among the transect groups (Model 1, Table 2, F = 2.35, p = 0.114). There was a statistically significant difference in mean interaction abundance per meter across the transect groups (Model 2, Table 2, F = 4.40, p = 0.022). The following Tukey's HSD test revealed that the mean value of interaction abundance was significantly higher in the Mother Meadow than in the Minor Meadows. No other pairwise significant differences in mean interaction abundance values were found.



**Figure 7.** Link richness (A) and interaction abundance (B) per meter, across the three transect groups: Mother Meadow, Sara's Meadow, Minor Meadows. The green dashed line represents the mean link richness of the Meta Network (combined mean of all three transect groups). Pairwise significant differences in means (p = <0.05) are indicated with distinct lower-case letters.

**Table 2.** Summary statistics from both linear regression models with transect group as the predictor variable. The table shows variance (F statistic) and Degrees of Freedom (DF) with associated p-value. Additionally, summary statistics from post hoc test (Tukey's HSD test) for Model 2 reveal significant differences between transect groups. The number of total interaction samplings per transect differed between the groups: Mother Meadow (n=8), Sara's meadow (n=5), Minor Meadows (n=18). Bold p-values are significant and <0.05.

Model 1: Interaction Ric	chness / Meter			
Predictor		DF	F	р
Transect group		2	2.35	0.114
Model 2: Interaction Ab	undance / Meter			
Predictor		DF	$\boldsymbol{F}$	р
Transect group		2	4.40	0.022
Post Hoc Test				
(I) Transect group	(J) Transect group	Mean differen	nce (I-J)	р
Sara's Meadow	Mother Meadow		-0.19	0.937
Minor Meadows	Mother Meadow		-0.09	0.030
Minor Meadows	Sara's Meadow		-0.90	0.163

# 3.4 Transect Group Comparisons: Overlap of Unique Species and Interactions

Of the 27 bee species, 18 were observed in only one transect group (Minor Meadows = 12, Sara's Meadow = 4, Mother Meadow = 2, Figure 8A). Only three bee species occurred in at least two of the transect groups, while six wild bee species were observed in all three transect groups, including three bumblebee taxa: *Bombus hypnorum, Bombus lapidarius* and *B. sensu* 

*stricto*, and three solitary bee species: *C. daviesanus, Lasioglossum morio* and *M. haemorrhoidalis*. These six shared bees represented 86.6% of the total wild bee abundance in the dataset, implying that the remaining 21 bee species were observed considerably fewer times and in more localized parts of the landscape. Refer to Appendix E (Table A7) for full list of wild bee taxa in the Meta Network, detailing their observation frequency within each transect group.

Three plants with recorded bee visitors occurred in all the transect groups: *Achillea millefolium*, *Lotus corniculatus* and *Tanacetum vulgare*. Collectively, they accounted for a visitation frequency of 17.4% and were visited by both bumblebees and solitary bees. The Mother Meadow and Sara's Meadow shared many of the same visited plant species (n = 5), while hosting 4 and 6 unique visited plant species, respectively. In comparison, the Minor Meadows supported 17 unique plants that were visited by wild bees. A full list of plant species visited by wild bees in the Meta Network can be found in Appendix E (Table A8), including wild bee visitation frequency per transect group.

Notably, the majority of unique plant-bee interactions were observed in one single transect (82 of 96), but these made up 53.2% of the total amount of observed interactions. This means that the 14 unique plant-bee interactions occurring in at least two transect groups made up 46.7% of the observed interaction events. Two plant-bee interactions were observed across all the transect groups: *B. lapidarius* visiting *L. corniculatus* (n = 8) and *C. daviesanus* visiting *A. millefolium* (n = 28) accounting for 10.0% of the total interaction abundance.

Despite only recording two wild bee species (*Colletes floralis* and *Megachile willughbiella*) and four flowering plant species (*C. rotundifolia, Echium vulgare, Hylotelephium maximum* and *Plantago lanceolata*) unique to the Mother Meadow, the meadow notably contributed with 21 unique plant-bee interactions to the overall Meta Network (Figure 8C). This finding is noteworthy, given the number of shared plants between the Mother Meadow and Sara's Meadow (Figure 8B). The Minor Meadows had the most observed unique plant-bee interactions compared to the newly established meadows.



# OMinor Meadows OMother Meadow OSara's Meadow

**Figure 8:** Three-way Venn diagrams showing the number of shared and unique wild bee species (A), visited plant species (B) and plant-bee interactions (C) at the 3 transect groups. Interaction abundance: Mother Meadow (n = 177), Sara's Meadow (n = 85), Minor Meadows (n = 95). Refer to Appendix E for full list of wild bee taxa (Table A7) and visited plant taxa (Table A8), including transect-group specific information.

# 3.5 Meta Network: Plant-Bee Bipartite Networks

Overall, 357 plant-bee interactions were recorded from a pool of 96 unique pairwise plant-bee combinations among 38 plant taxa and 27 wild bee taxa across the Meta Network throughout the summer of 2023. Among these interactions, 114 occurred between 18 solitary bee species and 24 plant taxa, comprising 41 unique plant-solitary bee interactions (Figure 9). Regarding bumblebees, 9 bumblebee taxa were found interacting with 26 plants species, totaling 55 unique pairwise plant-bumblebee interactions (Figure 10).

The solitary bee bipartite analysis (Figure 9) showed that the most frequently observed species was *C. daviesanus* with 59 recordings accounting for 51,8% of all recorded solitary bees. Subsequently, 12 *M. haemorrhoidalis* (10,5%), 11 *L. morio* (9,6%) and 9 *Seladonia tumulorum* (7,9%) were observed. These four solitary bees were observed visiting five to seven different plant species. The remaining 14 solitary bees were recorded less than five times each and were only observed on one to two plants. The most visited plant species was *A. millefolium* (28,1%), attracting four different solitary bee species, while *L. vulgare* (13,2%) and *T. vulgare* (10,5%), were also highly frequented plant species.

		Interaction	
	Plants	Solitary Bees	
28.1%	Ach. millefolium	And. nigriceps And. semilaevis	1.8% 3.5%
0.9%	All. vineale*	Ant. manicatum	1.8%
3.5%	Ant. sylvestris*	Cer. cyanea	2.6%
3.5%	Cam. rapunculoides*		
3.5%	Cam. rotundifolia		
3.5%	Cir. arvense		<b>51</b> 00 /
6.1%	Convolvulaceae*	Col. daviesanus	51.8%
5.3%	Gal. album*		
0.9%	Geu. urbanum*		
1.8%	Kna. arvensis		0.0%
1.8%	Lam. album	Out dentiventris	0.9%
13.2%	Leu. vulgare*	Hop claviventris	0.9%
0.9%	Lin. vulgaris	Hyl communis	0.9%
1.8%	Lot. corniculatus	Hyl. confusus	0.9%
0.9%	Mal. moschata	Hyl hyalinatus	1.8%
1.8%	Pas. sativa		1.8%
2.6%	Pot. argentea	Las fratellum	0.9%
0.9%	Sco. autumnalis*		0.60/
2.6%	Ses. libanotis	Las. morio	9.0%
10.5%	Tan. vulgare	Meg. willughbiella	0.9%
0.9%	Taraxacum sp.*	Mel. haemorrhoidalis	10.5%
1.8%	Tor. japonica*	Osm bicolor	0.9%
2.6%	Tri. inodorum*	Sel tumulorum	7.0%
0.9%	Vic. sepium*		1.970

Interaction

**Figure 9**. Bipartite graph of the interactions between solitary bees and plant species (n = 114). On the left, a list of plant taxa visited by solitary bees is presented alphabetically, along with corresponding percentages representing frequency of visits. Plant taxa that were exclusively observed visited by solitary bees are indicated with an asterisk (\*). Plants without asterisk were visited by both solitary bees and bumblebees. On the right, the list includes all solitary bees, along with corresponding percentages representing their relative abundance. For the full Latin names of plant and wild bee taxa, refer to Appendix E (Table A7, Table A8).

Among the observed plant-bumblebee interactions (Figure 10), the most frequently observed bumblebee taxa were *B. sensu stricto* (53,5%), *B. lapidarius* (32,5%) and *B. hypnorum* (7,4%), with 130, 79 and 18 observations respectively. These three bumblebee taxa were observed interacting with 11 to 16 different plants, indicating that these species have a wider nutritional range compared to the remaining 6 bumblebee species with each interacting with only 1 to 5 different plants. The plant species most visited by bumblebees were *Hypericum perforatum* (17,7%) and *Centaurea scabiosa* (17,3%) attracting three and two bumblebee species respectively. It is important to note that the most visited plants were not necessarily the plants that attracted the highest diversity of bumblebee species. Despite having less than 5% visitation frequency, *Knautia arvensis* attracted five wild bee species and *Lamium album* attracted four. These two plants attracted the broadest diversity of bumblebee species.

		Interaction	
	Plants	Bumblebees	
2.9%	Ach. millefolium	Bom. hortorum	1.2%
0.8%	Cam. rotundifolia	Bom hypnorum	7 4%
17.3%	Cen. scabiosa*	Boin. hyphorum	7.470
0.4%	Cir. arvense		
11.1%	Ech. vulgare*		
3.3%	Hie. umbellatum*		22 504
13.6%	Hyl. maximum*	Boill. Tapidarius	52.5%
17.7%	Hyp. perforatum*		
1.2%	Hys. officinalis*		
4.9%	Kna. arvensis	Bom. pascuorum	2.9%
2.1%	Lam. album	Bom. ruderarius	0.4%
0.4%	Lat. sylvestris*		0.170
3.7%	Lin. vulgaris		
3.3%	Lot. corniculatus		
0.8%	Mal. moschata		
5.3%	Ori. vulgare*		
0.8%	Pas. sativa	Bom. sen. stricto	53.5%
0.4%	Pla. lanceolata*		
2.9%	Pot. argentea		
1.2%	Rub. idaeus*		
1.2%	Ses. libanotis		
0.4%	Sil. vulgaris*		
0.4%	Tan. vulgare	Bom. soroeensis	1.2%
1.2%	Tri. pratense*	Bom. subterraneus	0.4%
2.1%	Tri. repens*	Bom. sylvarum	0.4%
0.4%	Vis. vulgaris*		

Interaction

**Figure 10.** Bipartite graph of the interactions between bumblebees and plant species (n = 243). On the left, a list of plants species visited by bumblebees is presented alphabetically, along with corresponding percentages representing frequency of visits. Plant taxa that were exclusively observed visited by bumblebees are indicated with an asterisk (\*). Plants without asterisk were visited by both solitary bees and bumblebees. On the right, the list includes all bumblebees, along with corresponding percentages representing their relative abundance. For the full Latin names of plant and wild bee taxa, refer to Appendix E (Table A7, Table A8).

#### 3.6 Meta Network: Predictors of Plant Species' Attractiveness to Bees

A total of 72 different plant taxa were observed in the entire Meta Network. Among these, 38 taxa were visited by at least one wild bee species. Based on the vegetation surveys, the most species-rich families were *Asteraceae*, *Fabaceae*, and *Campanulaceae*, collectively accounting for approximately 46% of the total plant registrations. The most frequently recorded plant species were *H. maximum* (subplots = 154), *A. millefolium* (subplots = 112) and *Potentilla argentea* (subplots = 111).

I found that the most important drivers of plant attractiveness to bees in Oslo city center were flower petal color, flower symmetry, phenology and plant cover (Figure 11). Wild bees were favorably inclined towards blue-violet plants with bilateral symmetry, late phenology and high plant cover. The fixed effects explained 24% of the variation in bee species richness sampled on plant species, while the entire model, including both fixed and random effects explained 42% of the variation (Table 3).

Flower petal color significantly influenced the number of bee species attracted to a plant (Figure 11A, Table 3, p = 0.002). Flowers with blue-violet (i.e. *C. rotundifolia*), white (i.e. *L. vulgare*) and yellow (i.e. *L. corniculatus*) petals attracted significantly more bee species compared to pink-red flowers (i.e. *Origanum vulgare*), attracting 4.01, 3.22, 2.27 times more bee species, respectively (Appendix F, Table A9). Additionally, bee species richness was significantly related to flower symmetry (Table 3, p = 0.016) with bilaterally symmetric flowers attracting 2.56 times more bee species than flowers with radial symmetry (Appendix F, Table A9). Late blooming plants, such as *H. maximum* flowering in mid-August (phenology = 12), attracted more bee species than early blooming plants, such as *L. album* (phenology = 5), first flowering in late April. Lastly, the analysis showed that the bee species richness increased significantly with plant cover (Table 3, p = < 0.001).



**Figure 11:** Bee species richness was significantly influenced by (A) flower petal color (table 3, p = 0.002), (B) flower symmetry (Table 3, p = 0.016), (C) plant phenology (Table 3, p = <0.001) and (D) plant cover (table 3, p = <0.001). The predictors were plotted on the original scale. Bars (A, B) and colored polygons (C, D) represent the 95% confidence intervals. Plant phenology ranges from late April (= 5) to mid-August (= 12) with approximately half-month increments.

**Table 3**. Model 3: Wild bee species richness. The table shows results from the likelihood ratio tests (LRT) with corresponding p-values and Degrees of Freedom (DF) for fixed effects, including variance ( $\sigma^2$ ) and standard deviation (SD) of random effects from summary statistics. Bold p-values are significant and <0.05. Model variance is explained by marginal and conditional  $R^2$ .

p
0.002
0.016
< 0.001
< 0.001

# 4.0 Discussion

The aim of this study, located in the urbanized city center of Oslo, was to investigate the diversity and abundance of wild bees and their interactions with plants within the Mother Meadow and compare these findings with larger pollinator-friendly habitat fragments in the surrounding landscape. I found that despite the Mother Meadow exhibiting a lower diversity of wild bee species and unique plant-bee interactions compared to the surrounding landscape, it attracted a significantly higher abundance of wild bees than the Minor Meadows.

In the context of the broader Meta Network, most wild bees observed were large-bodied polylectic species that prefer to nest in below-ground cavities or sandy soil. An analysis of bee dietary preferences showed a strong inclination towards blue-violet plants with bilateral symmetry, late phenology and high plant cover. Notably, each transect group predominantly hosted unique interactions, while only a few interactions were observed across multiple transect groups. In fact, 53,2% of the total number of observed interactions in the Meta Network exclusively observed within a single transect group.

## 4.1 The Mother Meadow's Role in the Meta Network

Despite being spatially isolated, the Mother Meadow attracted a greater abundance of wild bees compared to the transects in the surrounding landscape. This is especially evident when compared to the Minor Meadows, consisting of unmanaged and sporadic flower patches in recreational areas and roadside vegetation strips with a lower floral density average. The overall presence of bees in the Mother Meadow suggests that floral resources are a limiting factor for wild bees in the surrounding urban landscape, consequently driving wild bees to extend the duration of their foraging trips to meet their energy requirements (Gathmann & Tscharntke, 2002). Furthermore, the Mother Meadow and its immediate surroundings may host several potential nesting sites facilitating easier access to the meadow. The Mother Meadow provides nutritional diversity for wild bees by introducing plants occurring at low frequencies in the surrounding landscape. This creates favorable conditions for the meadow to attract numerous wild bees and foster unique interactions not observed elsewhere. Simultaneously, the meadow may support pollination services to plants in the surrounding landscape by having a relatively high frequency of interactions that were observed elsewhere in the Meta Network but at lower rates (Crone et al., 2022; Kwak et al., 1998). This means that wild bees visiting the Mother Meadow could enhance the sexual reproduction and gene flow among plants in the Meta Network by acting as links between fragmented areas.

As anticipated, the surrounding landscape exhibited more diverse wild bee communities and higher plant-bee interaction diversity than the Mother Meadow. This difference in species richness is likely attributed to the proximity of the surrounding transects to larger parks, forests and other green infrastructures, allowing greater movement and interaction opportunities for the wild bees (Librán-Embid et al., 2021; Van Rossum & Triest, 2012). Thus providing wild bees in the surrounding landscape access to a larger pool of plants species to interact with compared to those in the Mother Meadow. My findings indicate that habitat isolation can be a limiting factor for wild bee species richness in the Mother Meadow, but despite its isolation, the Mother Meadow might also function as a steppingstone for wild bees from habitats on different sides of the inner Oslo fjord due to a general resource limitation in the Meta Network.

Considering that flight capacity in bees increases with body size (Greenleaf et al., 2007), I expected to primarily observe larger bodied bees, such as bumblebees, in the Mother Meadow, which is located more than 300 meters from green areas that are larger or of similar size. My findings confirmed this expectation, as more than 85% of the wild bees observed in the Mother Meadow were bumblebees (*B. hypnorum, B. lapidarius, B. sensu stricto*, and *B. soroeensis*). Bumblebees were also found to be the most dominating taxa in the Meta Network although to a lesser extent. This is further discussed in section 4.2.

Surprisingly, five solitary bee species (*C. daviesanus, C. floralis, L. morio, M. willughbiella*, and *M. haermorrhoidalis*) were also observed in the Mother Meadow, although at a much lower frequency than the bumblebees. Smaller bees, such as solitary bees, are generally more vulnerable in highly fragmented landscapes due to lower flying capacity and stationary behavior which can further decrease foraging range (Gathmann & Tscharntke, 2002). One reason for the presence of solitary bees in the Mother Meadow may be that some of the species are among the larger solitary species observed in the Meta Network, which typically corresponds to a greater foraging range indicating that these bees are more likely to reach the meadow (Greenleaf et al., 2007). Additionally, these solitary bees may have used "micro patches", such as potted plants, flower beds, patches of roadside vegetations and rooftop gardens, between the larger green areas as resting stops to reach the meadow.

#### 4.2 The Meta Network of Oslo City Center

As predicted, most of the recorded wild bee species in the Meta Network were common pollen generalist species that are known to visit a variety of taxonomically unrelated plants to fulfill their energy requirements. Observations in other European countries such as Denmark (Dupont et al., 2024), Poland (Banaszak-Cibicka & Żmihorski, 2012), France (Geslin et al., 2013) and Germany (Librán-Embid et al., 2021) have also shown a predominance of polylectic bees in urban and fragmented environments. Collectively, these findings suggest that polylectic bees are more likely to thrive in highly fragmented landscapes. One reason for this may be that fragmented urban landscapes are often resource limited with suitable habitats being rare and widely dispersed (McKinney, 2008). Therefore, opportunistic and polylectic bees, which have little preference for habitat and a broad diet, are more likely to profit in highly urbanized settings because they can utilize most resources available (Banaszak-Cibicka & Źmihorski, 2012; Librán-Embid et al., 2021). Specialized bees, particularly oligolectic and monolectic bees, have specific habitat and dietary requirements, which limits the resources they are able to utilize, a challenge that may be further exacerbated in fragmented landscapes (Biesmeijer et al., 2006). Despite most species being common generalists, Oslo city center also functions as a habitat for red-listed species, including two solitary species (A. nigriceps and D. dentiventris) and one bumblebee species (B. subterraneus), listed as 'Near Threatened' (NT). This highlights the importance of urban environments for not only generalist species but also as a refuge for threatened species, emphasizing the critical roles cities can play in the conservation of wild bees.

In addition to dietary generalization, my findings suggest that body size can be an important factor when considering wild bee suitability in urban environments. Most bees are doorstep foragers, meaning that their foraging range is centered around their nesting site (Bell, 1990), resulting in highly localized communities of wild bees. In cities and other highly fragmented landscapes, larger bees are more likely to thrive, as their size enhances their ability to move freely between fragmented habitats (Banaszak-Cibicka & Żmihorski, 2012; Greenleaf et al., 2007; Librán-Embid et al., 2021). My findings support this, as bumblebees accounted for 68,0% of total bee abundance in the Meta Network. In addition to their larger foraging ranges, bumblebees have higher energy requirements due to body size, which may be challenging to satisfy in resource limited environments such as cites (Wenzel et al., 2020). However, in colonies of eusocial bees, such as bumblebees, size polymorphism is often observed (Cholé et al., 2019). This variation in body size provides ecological flexibility by increasing variation in foraging range and energy requirements within a colony (Cholé et al., 2019; Grüter & Hayes, 2022), further enhancing a colony's ability to efficiently forage resources in fragmented cityscapes.

Another reason for the higher sampling rates of bumblebees in my study area may be their larger size and relatively loud buzzing, which makes them easier to spot compared to solitary bees. During plant-bee interaction sampling, the collectors prioritized recording new interactions over previously recorded ones within the same transect. This method helped counteract collector bias towards more noticeable bees by ensuring that a wider range of interactions were recorded. This encouraged the collectors to actively search for new interactions, which included less prominent bees, such as solitary bees, and their plants of preference.

Only 14 of 92 unique plant-bee interactions occurred in at least two transect groups, although these made up 46,7% of the total observed interaction events. These shared interactions between the local plant-bee communities indicate connectedness within the Meta Network (Emer et al., 2018). The wild bee species observed across multiple transect groups are most likely play central roles in the Meta Network, as they act as links between the fragmented habitats, increasing gene flow between plant communities and the local pools of pollinators (Librán-Embid et al., 2021). Therefore, it is crucial to implement green corridors to function as steppingstones between the fragmented habitats for the central wild bees (Librán-Embid et al., 2021; Van Rossum & Triest, 2012).

## 4.3 Minor Meadows as Crucial Biotopes

Although the Mother Meadow attracted an abundance of bees, most unique plant-bee interactions were observed in the Minor Meadows. My findings show that the Minor Meadows, comprising of transects in various unmanaged meadows and flower strips, harbored numerous transect-group specific interactions that were not observed elsewhere in the Meta Network. This suggests high local variation in species composition with each small biotope contributing to high interaction diversity. Individually, the Minor Meadow transects are less diverse, likely due to limitations in size and flower density. Larger fragments, on the other hand, generally support more species and interactions overall due to their greater size and resources (Librán-Embid et al., 2021; Vega & Küffer, 2021). Despite the small size of the Minor Meadows, my observations indicate that smaller pollinator-friendly habitats are collectively fundamental for supporting wild bee diversity and their interactions with plants in urban landscapes (Librán-Embid et al., 2021; Van Rossum & Triest, 2012). In line with my findings, recent studies on habitat fragmentation revealed that, collectively, many smaller fragments of pollinator-friendly habitats tend to harbor more unique species and interactions than one large fragment of the same total area (Librán-Embid et al., 2021; Vega & Küffer, 2021).

Although most unique interactions were observed in the Minor Meadows (n = 44), it is important to mention that both the Mother Meadow (n = 18) and Sara's Meadow (n = 20) hosted numerous unique plant-bee interactions that were not observed in other transect groups. In fact, each transect group predominantly hosted unique interactions with 53,2% of the total number of observed interactions in the Meta Network exclusively observed within a single transect group. The highly localized and vulnerable nature of urban wild bee communities is likely a consequence of habitat fragmentation, which limits the movement of pollinators. In fragmented landscapes, small habitats can host many unique species and interactions because fragmentation prevents homogenization of species composition through limited species flow (Leibold et al., 2004; Librán-Embid et al., 2021). The loss of any one of the transect groups would lead to the further loss of local and unique interactions, and significantly impact the interaction diversity of the Meta Network, which may have unknown consequences for the pollination services and ecological functions that wild bee communities provide (Librán-Embid et al., 2021). A counteracting solution, as observed in similar studies focusing on pollinators in urban environments, is to enhance connectivity between fragments to facilitate increased pollinator movement, especially for wild bees with restricted forging ranges (Banaszak-Cibicka & Żmihorski, 2012; Van Rossum & Triest, 2012). This would make vulnerable species less susceptible if habitats were to disappear.

## 4.4 Dietary Preferences and Drivers of Plant Attractiveness to Wild Bees

From a conservation point of view, the primary objective in establishing or restoring flower meadows in cities and other severely fragmented landscapes is to provide a place of refuge for pollinators and to foster the diversification and abundance of local wild bee communities (Hall et al., 2017; M'Gonigle et al., 2015). I found that solitary bees and bumblebees clearly have different dietary preferences as only 12 of 38 visited plant taxa were shared between these two groups. Twelve plant species exclusively had solitary bee visitors, while 14 plants were exclusively visited by bumblebees. The floral preferences in bees are driven by differences in their sensory ecology (Chittka & Raine, 2006), tongue length (Goulson et al., 2008; Ranta & Lundberg, 1980), flower handling ability and foraging strategies (Greenleaf et al., 2007; Muth et al., 2015). Additionally, floral preferences of wild bees may be impacted through competition with managed honeybees (*A. mellifera*) for available floral resources (Mallinger & Gaines-Day, 2017). My findings demonstrate the importance of creating flower meadows that cater to both solitary bees and bumblebees by incorporating a diverse array of flowering plants.

The analysis of wild bee dietary preferences in the Meta Network showed a strong inclination towards blue-violet plants with bilateral symmetry, late phenology and high plant cover. These findings can be useful in the development and establishment or restoration of new flower meadows to further increase their attractiveness for wild bees. Considering the different dietary preferences observed in bumblebees and solitary bees, it is important to note that the bumblebees heavily influenced the model, as most of the observed interactions involved bumblebees. While this may not be applicable in all conservation settings, in urbanized and fragmented environments such as Oslo, the wild bees sampled during fieldwork provide a representative sample of the wild bee community. This is supported by the wild bee richness rarefaction-extrapolation analysis which indicated that sampling effort sufficiently captured a significant portion of wild bee species in the Meta Network.

I found that plant species that were more abundant along a transect were more likely to attract a broader richness of bee species, while rarer plants attracted fewer bee species. This is expected because a higher abundance of certain plants will naturally result in more interactions with wild bee species. Bees have shown a tendency towards restricting their visits to a specific plant species they have learned to recognize for more efficient flower-handling (Darwin, 1876; Waser, 1986).To minimize the time it takes to learn how to handle more flowers, it is reasonable to assume that some generalist bees learn to recognize plant species that are especially abundant within their foraging range. In relation to the establishment of flower meadows, it is well demonstrated that meadows or habitat fragments with high flower richness attract a greater diversity of wild bees (M'Gonigle et al., 2015; Theodorou et al., 2020). In addition to introducing meadows with high flowering plant richness, my findings further emphasize the importance of incorporating plant species that complement each other and do not outcompete one another, aiming to create florally abundant meadows where most flowering species are approximately equally abundant.

I found that plant taxa with late phenology were more likely to attract numerous wild bee species. These results may have been influenced by the timing of mid-summer fieldwork making it impossible to capture interactions between wild bees and the plants with early spring phenology or late fall phenology. Banaszak-Cibicka and Żmihorski (2012) showed that bees exhibiting late phenology prefer the city center more than wild bee species that emerge earlier in the year, likely due to lack of spring blooming floral resources. In relation to my findings, this suggests that if most bee species in highly urbanized settings are more active later in the season, one would expect them to interact primarily with plant species that also exhibit later

phenology. This suggests that further studies are needed to explore the role and distribution of spring flowering shrubs and trees in Oslo city center, as these are often considered invaluable resources for wild bees with early phenology (Banaszak-Cibicka & Żmihorski, 2012).

The wild bees observed in the Oslo Meta Network showed a strong affinity for bisymmetrical flowers. This is surprising as bilateral plants generally have fewer potential visitors due to their complex and specialized structures, which is thought to result in more consistent and specialized groups of pollinators visiting these plants (Yoder et al., 2020). On the other hand, radial flowers are simpler and offer easily accessible floral nutrients to an array of pollinators (Jiang & Moubayidin, 2022). Wild bees have shown innate preferences for floral symmetry with some exhibiting a predisposed affinity for bilateral plants (Rodríguez et al., 2004), and others favoring larger and more symmetrical flowers (Møller, 1995). Some wild bees can learn how to manipulate complex flowers with bilateral symmetry, despite innate preferences, when the floral benefits are high and outweigh the initial cost of learning (Muth et al., 2015). In resource limited and fragmented landscapes, such as Oslo city center, it may therefore be cost-effective to interact with bisymmetrical flowers with high rewards.

Wild bees have innate color preferences; however, many have shown a particularly strong affinity for blue-violet flowers due to their UV blue-green photoreceptors (Chittka & Raine, 2006; Ings et al., 2009). My findings are in line with this, as most observed wild bee species were attracted to blue-violet flowers, followed by white, yellow and lastly pink-red flowers. I have highlighted the plant species in the Meta Network (Table 4) that, according to the plant-trait attractiveness model, are the most attractive to wild bees, meeting the criteria for later phenology (blooming in June or later) within the four-color categories. Bilaterally symmetric flowers are indicated in bold.

Table 4	<b>I.</b> Li	ist of	plant	species	that	are	most	attrac	tive t	to	wild	bees	in	the	Oslo	Meta	Netw	/ork	within	the	four
respecti	ve c	color	catego	ories, ad	cord	ing t	to the	trait-	attrac	ctiv	venes	s mo	del	. Th	ese j	olants	meet	the	criteria	for	late
phenolo	ogy (	bloo	ming i	n June o	or late	er). E	Bilater	ally s	ymm	etr	ric flo	wers	are	ind	icate	d in bo	old.				

Blue-Violet	Yellow	White	Pink-Red
Campanula rapunculoides	Hierarcium umbellatum	Achillea millefolium	Allium vineale
Campanula rotundifolia	Hylotelephium maximum	Galium album	Lathyrus sylvestris
Centaurea scabiosa	Hypericum perforatum	Seseli libanotis	Malva moschata
Cirsium arvense	Potentilla argentea	Silene vulgar	Origanum vulgare
Hyssopus officinalis	Scorzoneroides autumnalis Tanacetum vulgare	Torilis japonica	

Note that the plant species in Table 4 are listed without consideration for whether plant species are native or considered to be weeds or invasive species, as most urban wild bees have not been shown to discriminate between native and non-native flowers (Martins et al., 2017; Matteson & A., 2011). Despite their indifference to whether plants are native or non-native, it is crucial to use locally native species to avoid invasive alien species from displacing native species through competition and altering the structure of natural habitats (Mooney & Cleland, 2001; Roy et al., 2023).

# 5.0 Synthesis and Future Applications

My findings show that the Mother Meadow is already supporting wild bee populations and the pollination services they provide. The long-term importance of the Mother Meadow is likely to grow as it matures. Due to the Mother Meadow being relatively new, first established in 2020, its importance for wild bees and other pollinating insects in Oslo is expected to increase over time. Species richness in restored habitats has previously been found to increase over time in highly fragmented landscapes (M'Gonigle et al., 2015), as well as in small urban greening initiatives (Mata et al., 2023). This highlights the importance of long-term monitoring of the Mother Meadow to better understand the effects of establishing new flower meadows in highly urbanized areas and to accurately assess the colonization rate and persistence of pollinators (M'Gonigle et al., 2015).

In highly fragmented landscapes, such as Oslo city center, the loss of any one pollinator-friendly habitat could lead to the loss of unique interactions, and subsequently, result in unknown consequences on the ecological functions wild bees provide (Librán-Embid et al., 2021). Conversely, the establishment of new habitats, such as the Mother Meadow, can mitigate these effects. My study provides a good foundation for improving the establishment of future flowers meadows to enhance wild bee diversity in urban and fragmented landscapes. It emphasizes the importance of implementing biodiverse and florally abundant meadows of various sizes adjacent to other green areas, while also incorporating wild bees' preferences for late-blooming, blue-violet and bilaterally symmetric flowers. Future research should investigate the role of micro-habitats (i.e., potted plants, rooftop gardens, flowerbeds) within urban landscapes as steppingstones, including their configuration, size and specific species they support.

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# Appendix A – Transect Metadata

# Appendix A provides detailed metadata regarding fieldwork conducted at transects during the summer of 2023.

Table A1. Overview of transect metadata, including longitudinal (Long.) and latitudinal (Lat.) coordinates for transect start and end, transect length (m) and sampling time (min).

	Tra	nsect Start	1	Fransect end	<b>T</b> ( <b>1</b> ( )	
Transect ID –	Lat.	Long.	Lat.	Long.	Length (m)	Sampling time (min)
HMB_01	59.90499	10.75417	59.90486	10.75428	96	32
HMB_02	59.90465	10.75391	59.90474	10.75410	15	5
HMB_03	59.90513	10.76304	59.90545	10.76314	36	12
HMB_04	59.90329	10.76272	59.90322	10.76209	36	12
HMB_05	59.90246	10.75843	59.90260	10.75828	18	б
HMB_06	59.90244	10.75872	59.90254	10.75864	19	6
HMB_07	59.89721	10.75721	59.89791	10.75771	94	31
HMB_18	59.90442	10.73867	59.90494	10.73825	63	21

Sampling round 1	Collector AB	Collector MAKS
HMB_01	-	06.06.2023
HMB_02	_	06.06.2023
HMB_03	_	06.06.2023
HMB_04	_	06.06.2023
HMB_05	_	06.06.2023
HMB_06	_	06.06.2023
HMB_07	_	06.06.2023
HMB_08	_	08.06.2023
Sampling round 2	Collector AB	<b>Collector MAKS</b>
HMB_01	07.07.2023	23.06.2023
HMB_02	07.07.2023	-
HMB_03	28.06.2023	23.06.2023
HMB_04	28.06.2023	23.06.2023
HMB_05	28.06.2023	-
HMB_06	28.06.2023	-
HMB_07	28.06.2023	23.06.2023
HMB_08	07.07.2023	22.06.2023
Sampling round 3	Collector AB	<b>Collector MAKS</b>
HMB_01	29.07.2023	08.07.2023
HMB_02	29.07.2023	08.07.2023
HMB_03	27.07.2023	08.07.2023
HMB_04	27.07.2023	-
HMB_05	27.07.2023	-
HMB_06	27.07.2023	-
HMB_07	27.07.2023	-
HMB_08	29.07.2023	08.07.2023

Table A2. Overview of which transects were sampled by each collector (AB = Aurora Bischof, MAKS = Markus A. K. Sydenham), including date of interaction sampling.

# Appendix B – Supplementary Information for Introduced Meadows

Initial lists of plants sown in the two introduced meadows; Mother Meadow and Sara's Meadow. The list of plants sown in the Mother Meadow was provided by Lily Vikki (Project Manager of City of Oslo Art Collection), while Gro Hilde Jacobsen (advisor at the Agency for Urban Environment and project leader during the establishment of Sara's Meadow) provided the list of plants sown in Sara's Meadow.

Mother Meadow: Plant species						
Artemisia campestris subsp. maritima	Achillea millefolium					
Agrostis capillaris	Anthyllis vulneraria					
Avenula pratensis	Betula pendula					
Campanula persicifolia	Campanula rotundifolia					
Carum carvi	Centaurea jacea					
Centaurea scabiosa	Dianthus deltoides					
Echium vulgare	Festuca ovina					
Festuca rubra	Filipendula vulgaris					
Fragaria vesca	Fragaria viridis					
Galium verum	Geranium sanguineum					
Geum rivale	Glechoma hederacea					
Hypericum perforatum	Hypochaeris maculata					
Inula salicina	Knautia arvensis					
Leontodon autumnalis	Leucanthemum vulgare					
Lotus corniculatus	Origanum vulgare					
Plantago lanceolata	Plantago media					
Poa alpina	Primula veris					
Prunus spinosa	Sedum acre					
Sedum telephium subsp. maximum	Silene vulgaris					
Solidago virgaurea	Succisa pratensis					
Thymus pulegioides	Trifolium medium					
Viscaria vulgaris						

Table A3. List of plant species incorporated during the establishment of the Mother Meadow in 2020.

Table A4. Noncomprehensive list of plant species incorporated during the establishment of Sara's Meadow in 2018.

Sara's Meadow: Plant Species			
Campanula rotundifolia	Carum carvi		
Centaurea scabiosa	Dianthus deltoides		
Hieracium umbellatum	Hylotelephium maximum		
Hypericum perforatum	Knautia arvensis		
Leucanthemum vulgare	Linaria vulgaris		
Lotus corniculatus	Origanum vulgare		
Pimpinella saxifraga	Silene dioica		
Silene vulgaris	Solidago virgaurea		
Thymus pulegioides	Trifolium pratense		
Viscaria vulgaris			

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# Appendix C – Wild Bee Species Information

Detailed species information on the observed wild bees in the Meta Network:

- Sociality provides insight into social behavior. Two categories: eusocial and solitary.
- **n** = number of observations.
- **Conservation Status** provides information about the current status of the bee species in the Norwegian Red List for Species (2021). Red-listed and threatened species are classified as Critically Endangered (CR), Endangered (EN), Vulnerable (VU) (Artsdatabanken, 2021). Species with viable populations and little to no risk of extinction are listed as Least Concern (LC) (Artsdatabanken, 2021).
- Pollen Foraging Preferences refers to diet width. Three categories: polylectic (visits many unrelated host taxa), oligolectic (visits a select few related host taxa), monolectic (visits one host taxa) (Cane & Sipes, 2006). Species pollen foraging preferences were determined using species information sourced from the British Bees Wasps & Ants Recording Society (n.d.) and the Swedish Artfakta (SLU Artdatabanken, n.d.). Preferences in polylectic bumblebees were sources from Wood et al. (2021).
- Nesting Preferences refers to preferred choice of nesting site. Species preferences determined using species information sourced from the British Bees Wasps & Ants Recording Society (n.d.) and the Swedish Artfakta (SLU Artdatabanken, n.d.).
- Urban presence referred to whether a species, according to Swedish Artfakta (SLU Artdatabanken, n.d.), is commonly observed in urban landscapes. Simple Yes/No categories.

Table A5. Wild bee species information, including number of observations (n), conservation status, nesting preference, sociality, foraging preference and urban presence. For the *B. s. str.*, I used *B. lucorum* as the model species as it is the most widespread species in Norway within the subgenus.

Bee species	n	Conservation Status	Nesting Preference	Sociality	Pollen Foraging Preference	Urban Presence
Andrena nigriceps	2	NT	Bare ground	Solitary	Polylectic	Yes
Andrena semilaevis	4	LC	Bare ground	Solitary	Polylectic	Yes
Anthidium manicatum	2	LC	Cavities	Solitary	Polylectic	Yes
Bombus hortorum	3	LC	(Partially) below ground	Eusocial	Polylectic	Yes
Bombus hypnorum	18	LC	Above-ground cavities	Eusocial	Polylectic – prefer Rosaceae	Yes
Bombus lapidarius	79	LC	Below-ground cavities	Eusocial	Polylectic	Yes
Bombus pascuorum	7	LC	Above-ground	Eusocial	Polylectic	Yes
Bombus ruderarius	1	LC	(Partially) below ground	Eusocial	Polylectic – prefer Fabaceae	Yes
Bombus sensu stricto	130	LC	Below-ground cavities	Eusocial	Polylectic – prefer Apiaceae	Yes
Bombus soroeensis	3	LC	Below-ground cavities	Eusocial	Polylectic – prefer Campanulaceae	Yes
Bombus subterraneus	1	NT	Below-ground cavities	Eusocial	Polylectic	Yes
Bombus sylvarum	1	LC	(Partially) below ground	Eusocial	Polylectic	Yes
Ceratina cyanea	3	LC	Above-ground cavities	Solitary	Polylectic	Yes
Colletes daviesanus	59	LC	Cavities and sandy soil	Solitary	Oligolectic – Asteraceae	Yes
Colletes floralis	1	LC	Bare ground	Solitary	Polylectic	Yes
Dufourea dentiventris	1	NT	Bare ground	Solitary	Oligolectic – Campanula sp.	Yes
Hoplitis claviventris	1	LC	Above-ground cavities/excavator	Solitary	Polylectic - prefer Fabaceae	Yes
Hylaeus communis	1	LC	Above-ground cavities	Solitary	Polylectic	Yes
Hylaeus confusus	1	LC	Above-ground cavities	Solitary	Polylectic	Yes
Hylaeus hyalinatus	2	LC	Above-ground cavities	Solitary	Polylectic	Yes
Lasioglossum calceatum	2	LC	Bare ground	Solitary	Polylectic	Yes
Lasioglossum fratellum	1	LC	Bare ground	Solitary	Polylectic	Yes
Lasioglossum morio	11	LC	Bare ground	Solitary	Polylectic	Yes
Megachile willughbiella	1	LC	Above-ground cavities and bare ground	Solitary	Polylectic – prefer Campanula sp.	Yes
Melitta haemorrhoidalis	12	LC	Bare ground	Solitary	oligolectic - Campanula sp.	Yes
Osmia bicolor	1	LC	Cavities - empty snail shells	Solitary	Polylectic	Yes
Seladonia tumulorum	9	LC	Bare ground	Solitary	Polylectic – prefer Asteraceae	Yes

# Appendix D – Plant Trait Variables

Overview of all variables included in the analyses.

Table A6, Overview of all plant trait variables used in statistical analyses. The entire *Taraxacum* genus was omitted from Tyler et al. (2021), and therefore it was excluded from the analysis in this study. The *Convolvulaceae* genus was also omitted.

Plant trait	Definition	Units	Source
Nectar	Based on the yearly yield nectar (sugar/ $m^2$ ).	Continuous	Baude et al.
production			(2016);
	1 = no nectar production, 2 = insignificant nectar		Tyler et al.
	production (< 0.2g sugar/m <sup>2</sup> /year), $3 =$ small nectar		(2021)
	production (0.2-5g sugar/m <sup>2</sup> /year), $4 = \text{modest nectar}$		
	production (5-20g sugar/m <sup>2</sup> /year), $5$ = rather large		
	nectar production (20-30g sugar/m <sup>-</sup> /year), $0 = \text{large}$		
	hectar production (50-200g sugar/m <sup>2</sup> /year), $7 = \text{very}$		
	large neetar production (> 200g sugar/in /year).		
	Adaptations: For taxa not identified to species level,		
	the average trait value of all species present within the		
	taxa in the Tyler et al. (2021) dataset was used.		
	- <i>Hieracium</i> sp.: nectar production = 5		
	- <i>Rosaceae</i> sp.: nectar production = 3 (average		
	from genus <i>Rosa</i> )		
Dlamt	- Rumex sp.: nectar production = 1 Scale based on the elimetic conditions in Control	Continuous	Tailon et el
Plant	Scale based on the climatic conditions in Central	Continuous	(2021)
phenology	Scalla III Sweden.		(2021)
	<b>1</b> = late February, $2 = $ mid-March, $3 = $ late March, $4 =$		
	mid-April, $5 = 1$ ate April, $6 = mid-May$ , $7 = 1$ ate May,		
	8 = mid-June, $9 = $ late June, $10 = $ mid-July, $11 = $ late		
	July, $12 = \text{mid-August}$ , $13 = \text{late August}$ , $14 = \text{mid-}$		
	September, $15 = late$ September.		
	Adaptations: For taxa not identified to species level,		
	the average trait value of all species present in the		
	Tyler et al. (2021) dataset was used.		
	- <i>Hieracium</i> sp.: phenology = 7 (huge variation		
	in phenology within the different sects, but the		
	one <i>Hieracium</i> sp. recorded during fieldwork		
	was registered in early June)		
	- Rosaceae sp.: phenology = 8 (average from $R_{res}$ )		
	genus $Rosa$ ) Burner en i phonology $= 8$		
	- Rumex sp., phenology – 8 - Phacelia tanacetifolia: phenology – 8		
	(absence of phenology in Tyler et al. (2021))		
	so phenology was determined using field book		
	from Feilberg, J. $(2018) = $ June)		
Flower	Plant species were divided into four groups based on	4 categories	Feilberg
color	flower petal color: Blue-Violet, Pink-Red, Yellow	-	(2018)
	(including the plants with a greener tone), and <b>White</b> .		
Flower	I divided plant species into two groups based on	2 categories	Feilberg
symmetry	flower symmetry: radial and bilateral.		(2018); Lid

<b>Radial</b> = flowers with multiple planes of symmetry.	and Lid
<b>Bilateral</b> = flowers with one plane of symmetry	(2005)

# Appendix E – Observational Data on Wild Bee and Visited Plant Taxa

The first list (Table A7) consists of wild bee taxa observed in the Meta Network, including number of observations across the transect groups. The second list consists of plant species visited by bees, including the number of observed visits across the transect groups.

Table A7: List of wild bee species observed in the Meta Network, including observation frequency (n) within each transect group: Mother Meadow, Sara's Meadow and Minor Meadows.

Wild Bee Taxa	Mother Meadow	Sara's Meadow	<b>Minor Meadows</b>
Andrena nigriceps	0	0	2
Andrena semilaevis	0	0	4
Anthidium manicatum	0	2	0
Bombus hortorum	0	0	3
Bombus hypnorum	13	2	3
Bombus lapidarius	41	28	10
Bombus pascuorum	0	4	3
Bombus ruderarius	0	0	1
Bombus sensu stricto	98	13	19
Bombus soroeensis	1	2	0
Bombus subterraneus	0	1	0
Bombus sylvarum	0	0	1
Ceratina cyanea	0	0	3
Colletes daviesanus	17	25	17
Colletes floralis	1	0	0
Dufourea dentiventris	0	0	1
Hoplitis claviventris	0	0	1
Hylaeus communis	0	1	0
Hylaeus confusus	0	0	1
Hylaeus hyalinatus	0	0	2
Lasioglossum calceatum	0	2	0
Lasioglossum fratellum	0	0	1
Lasioglossum morio	2	1	8
Megachile willughbiella	1	0	0
Melitta haemorrhoidalis	3	3	6
Osmia bicolor	0	0	1
Seladonia tumulorum	0	1	8

Plant Taxa	Mother Meadow	Sara's Meadow	<b>Minor Meadows</b>
Achillea millefolium	14	9	16
Allium vineale	0	0	1
Anthriscus sylvestris	0	0	4
Campanula rapunculoides	0	0	4
Campanula rotundifolia	6	0	0
Centaurea scabiosa	29	13	0
Cirsium arvense	0	4	1
Convolvulaceae	0	0	7
Echium vulgare	27	0	0
Galium album	0	0	6
Geum urbanum	0	0	1
Hieracium umbellatum	0	8	0
Hylotelephium maximum	33	0	0
Hypericum perforatum	39	4	0
Hyssopus officinalis	0	0	3
Knautia arvensis	3	11	0
Lamium album	0	0	7
Lathyrus sylvestris	0	1	0
Leucanthemum vulgare	9	6	0
Linaria vulgaris	0	1	9
Lotus corniculatus	2	7	1
Malva moschata	0	0	3
Origanum vulgare	10	3	0
Pastinaca sativa	0	0	4
Plantago lanceolata	1	0	0
Potentilla argentea	0	0	10
Rubus idaeus	0	0	3
Scorzoneroides autumnalis	0	0	1
Seseli libanotis	0	6	0
Silene vulgaris	0	1	0
Tanacetum vulgare	3	9	1
Taraxacum sp.	0	1	0
Torilis japonica	0	0	2
Trifolium pratense	1	0	2
Trifolium repens	0	0	5
Tripleurospermum inodorum	0	0	3
Vicia sepium	0	0	1
Viscaria vulgaris	0	1	0

Table A8: List of plant species visited by wild bees in the Meta Network, including wild bee visitation frequency (n) within each transect group: Mother Meadow, Sara's Meadow and Minor Meadows.

# Appendix F – Supplementary Statistics

# Supplementary statistics for Model 3.

Table A9. Summary statistics of Model 3: wild bee species richness. The table shows estimated regression coefficients, standard error (SE), effect size (z), and p-value of the predictors. Bold values are significant (p < 0.05). For random effects and model variance, see Table 2. The intercept represents flowers with radial symmetry and red flower petal color.

Model 1: Wild Bee Species Richness				
Predictors	Estimate	SE	Z.	р
(Intercept)	-1.98	0.45	-4.41	< 0.001
Flower Symmetry[Bilateral]	0.94	0.41	2.27	0.023
Flower Petal Color[Blue-Violet]	1.39	0.38	3.69	< 0.001
Flower Petal Color[White]	1.17	0.42	2.83	0.005
Flower Petal Color[Yellow]	0.82	0.36	2.25	0.024
scale(Plant Phenology)	0.44	0.12	3.75	< 0.001
scale(log(Plant Cover + 1))	0.42	0.10	4.45	< 0.001

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