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Flower Power: Which plant species attract which wild bee species? And do plant–bee species interactions depend on bee traits?

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Abstract

Insects constitute the world's most diverse class of animals and are vital for ecosystem function, services, and human welfare. Bees are considered some of the world's most important pollinators, and declining bee richness and abundance could have devastating effects on agricultural productivity and ecosystem stability. Habitat destruction has led to declines in food resources for bees in agricultural areas, entailing serious negative impacts on pollinator communities. To help mitigate this loss, increasing flower resource availability is essential, for example by sowing flower strips. The establishment of flower strips is an environmental scheme used throughout Europe, to increase the food resources available for pollinating insects in agricultural areas and prevent the decline in richness and abundance of pollinators. Nevertheless, the knowledge of how plant species composition affects bee diversity is limited.

This thesis aims to assess how different plant species contribute to wild bee richness and to bee diversity within distinct trait groups i.e., sociality: social vs solitary, diet preference: specialist vs generalist, or taxonomic family. Thirty-two locations in Southeast Norway were sampled. Resource-seeking bees within the transects were collected using netting. In one-half of the locations, bees were sampled along transects with a sown flower strip on one side and roadside vegetation on the other. In the second half of the locations, bees were sampled along transects with a grain field on one side and roadside vegetation on the other. To assess plant species composition and abundance at different sites, vegetation squares were used to conduct a vegetation analysis.

This study found that there was a great variance in which plant species bees were attracted to. Several key plant species stood out as popular plant species, contributing to both bee abundance and diversity. Additionally, bee traits, i.e., sociality, diet niche and taxonomic family, influenced the plant–bee interactions (attraction). Moreover, flower strips differed from the roadside in both abundance and species composition.

This study provides insight into the network of interactions between wild bee species and plant species, and the plant preferences of bees based on some traits. This knowledge could improve the effect of flower strips as an environmental scheme, potentially improving the quality of flower strips to support a larger variety of bee species.

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Introduction

In the last decade, there have been alarming reports of global insect decline (Hallmann et al., 2017; Wagner et al., 2021). Insects make up almost 40% of all known species, making them the world's most diverse taxonomic class (Bar-On et al., 2018). Several known drivers of insect decline include agricultural intensification, land-use change, and climate change, but the relationship among them is often complex (Cardoso et al., 2020; Didham et al., 2020). The decline of insects could have devastating impacts on ecosystem function, services, and human welfare (Wagner et al., 2021). One of the ecosystem services provided primarily by insects is pollination (Vanbergen & Initiative, 2013) Over 70% of our crop depends on or benefits from insect pollination, and the annual estimated value of pollination by insects in the US alone is over 3 billion US dollars (Losey & Vaughan, 2006). According to Potts et al. (2016), the most important pollinators are bees, which can pollinate over 90% of global pollinator-dependent crops.

Wild bees are an important group of pollinators, vital for pollinating most of our crops and wild plants (Kuppler et al., 2023; Potts et al., 2010) but bee populations are under pressure from habitat loss, degradation and fragmentation (Cardoso et al., 2020; Wagner et al., 2021). Indeed, in the last centuries, anthropogenic changes in agricultural practices have led to a decline in bee biodiversity and abundance due to fewer flower resources (Potts et al., 2010). The decline of bees could have large consequences for agricultural success and wild plant reproduction (Biesmeijer et al., 2006). Bees depend on flower resources and undisturbed nesting areas throughout their lives (Goulson et al., 2015). For a single offspring to reach adulthood, large amounts of pollen are needed. For example, one single individual of *Anthidium punctatum* requires pollen from more than two hundred flower heads (Kuppler et al., 2023; Müller et al., 2006). Therefore, flower resources are often a limiting factor for the abundance of bees due to their dependency on pollen, especially in highly intensified agricultural landscapes (Bretagnolle & Gaba, 2015).

To prevent the loss of flower resources in agricultural areas, environmental compensation, and agricultural schemes such as Agri-Environmental Schemes (AES) have been implemented in several European countries (Albrecht et al., 2020; Hellwig et al., 2022). AES has financially motivated farmers to sow flower strips since 2001 (Haaland et al., 2011). Different EU countries vary in their flower strip design, width, management, and species composition following current regulations (Haaland et al., 2011). Flower strip mixes range from annual flower seed mixes containing easily accessible seeds from species such as *Phacelia tanacetifolia* and *Trifolium* spp., to perennial mixes containing native flora (Hadrava et al., 2022). In Norway, a state-funded project was launched in 2019 aimed to increase food recourses for pollinators by giving funding to farmers to sow flower strips in field edges (Statsforvalteren, 2020a). These flower strips should be 2 meters wide, and not fertilised or sprayed with pesticides. In 2020, the number of applications for flower strip funding increased by almost 100, from 55 the previous year to 145. This shows the increasing interest and demand for agricultural schemes that promote insect pollination (Statsforvalteren, 2020c). Several studies have shown that AES such as flower strips have positively impacted wild bee population richness and abundance, but the relationship between flower strips and their impact is complex and largely still unknown (Albrecht et al., 2020; Buhk et al., 2018; Wood et al., 2015b). Several important factors impact this relationship, for instance, species composition, the surrounding area, or the age of the flower strip. Studies have shown that flower strips older than 3 years increase in efficiency (Albrecht et al., 2020).

Different species of bees have evolved different 'traits: a functional trait (here forward referred to as trait) is generally described as an individual physical, morphological or phenological measurable attribution such as home range size, body mass, habitat preference, diet preference, etc. (Birks, 2020; Galán-Acedo et al., 2019). The use of traits can contribute to understanding interactions in ecosystems, specifically through the use of interaction networks. These networks can help identify the roles and relationships between different species and how they contribute to ecosystem functioning (Dawson et al., 2021). Because bee species differ in their behaviour and ecology, their response to the same disturbance may be different, which is vital knowledge in conservation (Danforth et al., 2019). Hence, studying certain traits can provide a deeper understanding of interaction networks and contribute to conservation actions (Moretti et al., 2016). Among the traits that can impact bees' attraction to plant species is their dietary niche. Bee species differ in their dietary niches and the widths of their niches (Bommarco et al., 2010; Ritchie et al., 2016). Bee species that prefer a large variety of pollen from several different plant species and families are categorised as polylactic (resource generalist). Bees with a restricted preference for pollen ranging from only one species to a genus of plants are categorised as oligolectic (resource specialists) (Ritchie et al., 2016). Around two-thirds of European bee species that collect pollen are estimated to be polylectic in studies done by Zurbuchen and Müller (2012), and Bogusch et al. (2020). Studies have shown that species with more specialization have a stronger risk of extinction and make up a larger part of red-listed bee species than generalists (Bogusch et al., 2020; Winfree et al., 2007). A study conducted by Biesmeijer et al. (2006) showed a shift in pollinator assembly in Britain and the Netherlands because of changes in land-use practices, leading to habitat degradation. The study concluded that the decline of specialist bees was linked to a change in plant community composition. This knowledge is vital to the conservation of specialised bees to preserve and promote habitats with suitable flower resources.

Another trait that can impact a bee species' preference is their sociality. Bees are one of the few insects that have evolved different types of social structures, from solitary bees that make individual nests to social bees that live in colonies, such as bumblebees (Peters et al., 2017). More than 75% of all species are solitary bees, whereas less than 10% are social, and the remainder are parasites (Danforth et al., 2019). Solitary and social bees have different life spans: solitary bees are usually adults for only a few weeks, while social bees are active over a longer period (several months) with several overlapping generations(Biesmeijer et al., 2006). Many solitary bees are philopatric, meaning they prefer to stay at the site from which they emerged, in some cases reusing the nest they emerged from. Due to their small foraging ranges (often 400 meters or less) and the fact that their females are philopatric, solitary bees have less dispersal than social bees (Danforth et al., 2019).

The spatial distribution of flower resources and the distance between suitable nesting areas in agricultural landscapes can limit bee dispersal (Gathmann & Tscharntke, 2002). In a study by Williams and Kremen (2007), flower resources distributed throughout the landscape and solitary bee reproductive success were linked. The authors urged that increased landscape diversity and connectivity could benefit solitary bee populations. Because solitary bees have limited dispersal, connectivity in the landscape is vital to conserve their populations (Danforth et al., 2019). This was further supported by Sutter et al. (2017), highlighting the importance of plant species diversity in agricultural landscapes. The authors found that when plant diversity increases, key floral resources increase, supporting a greater diversity and abundance of bees. Hence, increasing plant diversity in combination with connectivity in agricultural landscapes may be an effective strategy for bee conservation.

Yet, to my knowledge, very few studies have examined the effects of mitigating efforts in agricultural areas (flower strips) on wild bee functional trait diversity. To address this knowledge gap, I use our current knowledge of bee traits and bees sampled, to investigate whether plant composition is essential for explaining the presence of different functional trait groups of bees.

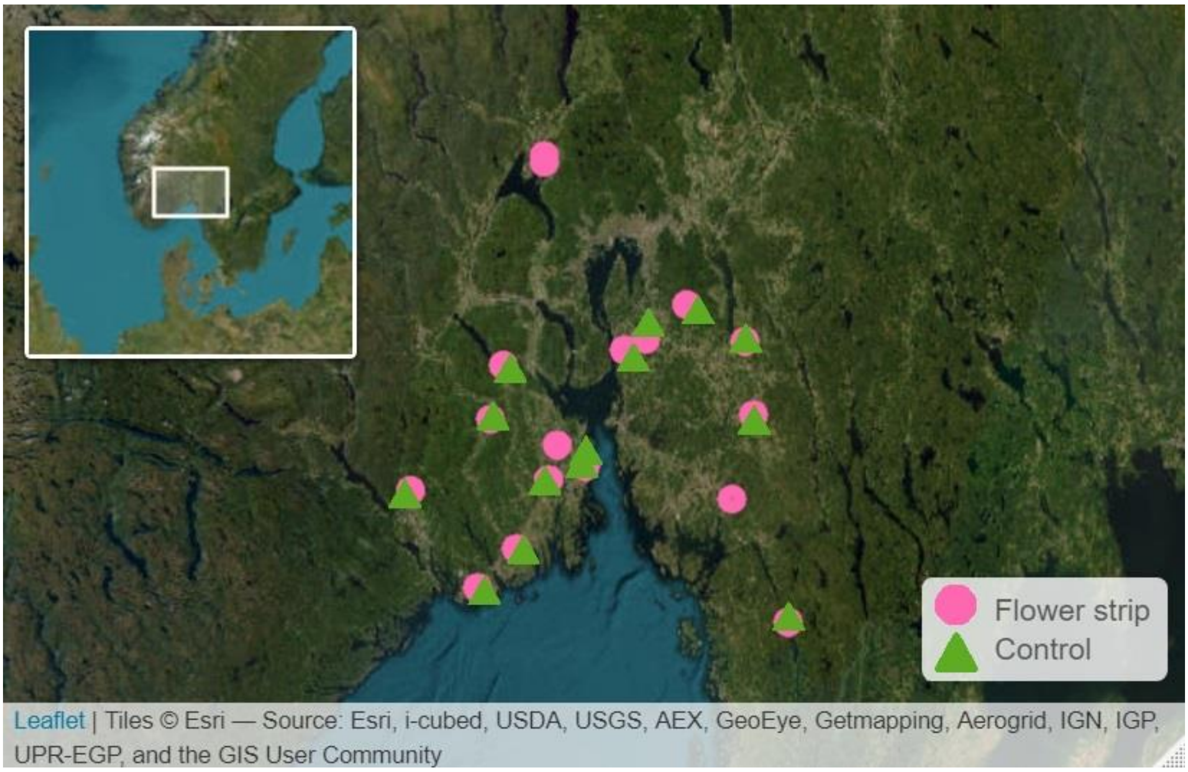
The overall aim of my thesis is to (1) describe plant-bee interactions i.e., which plant species attract which bee species, (2) investigate if plant-bee interactions can be explained by bee traits i.e., sociality: social vs solitary: diet niche: specialist vs generalist, or taxonomic family, and (3) investigate whether the flower strips contribute with unique plant species (flowers) that are not found in the roadside habitat.

Methods

2.1 Study area and site selection

The study was carried out in the southeast of Norway at 32 locations in Vestfold og Telemark, and Viken counties (Figure.1). The study locations were organised in pairs containing one flower strip site (FLWRSTR) and one control site (CONTROL) per location (Figure 1 and 2). However, the focus of this study was to investigate plant-bee interactions regardless of treatment; data from the two treatments were pooled in this thesis.

The selection criteria for the study sites were set and selected by the POLLIEFFECT project. The sites were chosen based on prediction values for species richness (from Sydenham et al. (2022)) flower strip, and road width. The selected flower strips should preferably be older than 2 years old. This proved challenging, therefore, flower strips < 2 years old were also included if there were no better alternatives. The control site was 1-5km from the flower strip and had the same prediction value. The width of the road next to the site was important because the width of the road was correlated with the width of the road ditch size and the speed limit. Therefore, the sites were located next to a road with a speed limit between <60km/h - >90km/h.



Leaflet | Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community

Figure 1 Map of the study area with sites. Created in R studio using the package leaflet (Agafonkin 2010-2023).

2.3 Site design

Each site was separated into two sub-habitats: field edge (with or without flower strip) and road ditch (Figure 2). This was done to counteract any bias towards flower strips or road ditches. A 50-meter transect was used to collect the bees in the two sub-habitats. Resource-searching bees were collected for 20 minutes in each sub-habitat per location using netting; using a butterfly net and Falcon tubes with 96% ethanol. A coin was flipped to determine which sub-habitat was to be collected first. After 20 minutes, the other sub-habitat was collected. For each collected specimen, 30 seconds were added to the collection time after the initial collection time was up. This was done to account for the handling time of the bees. The collected bees from the different sub-habitats were kept in separate labelled sampling glasses.

During the collection period, there were times when sites were without flowers due to roadside mowing or growth. In these cases, the site was not sampled due to the absence of flowers.

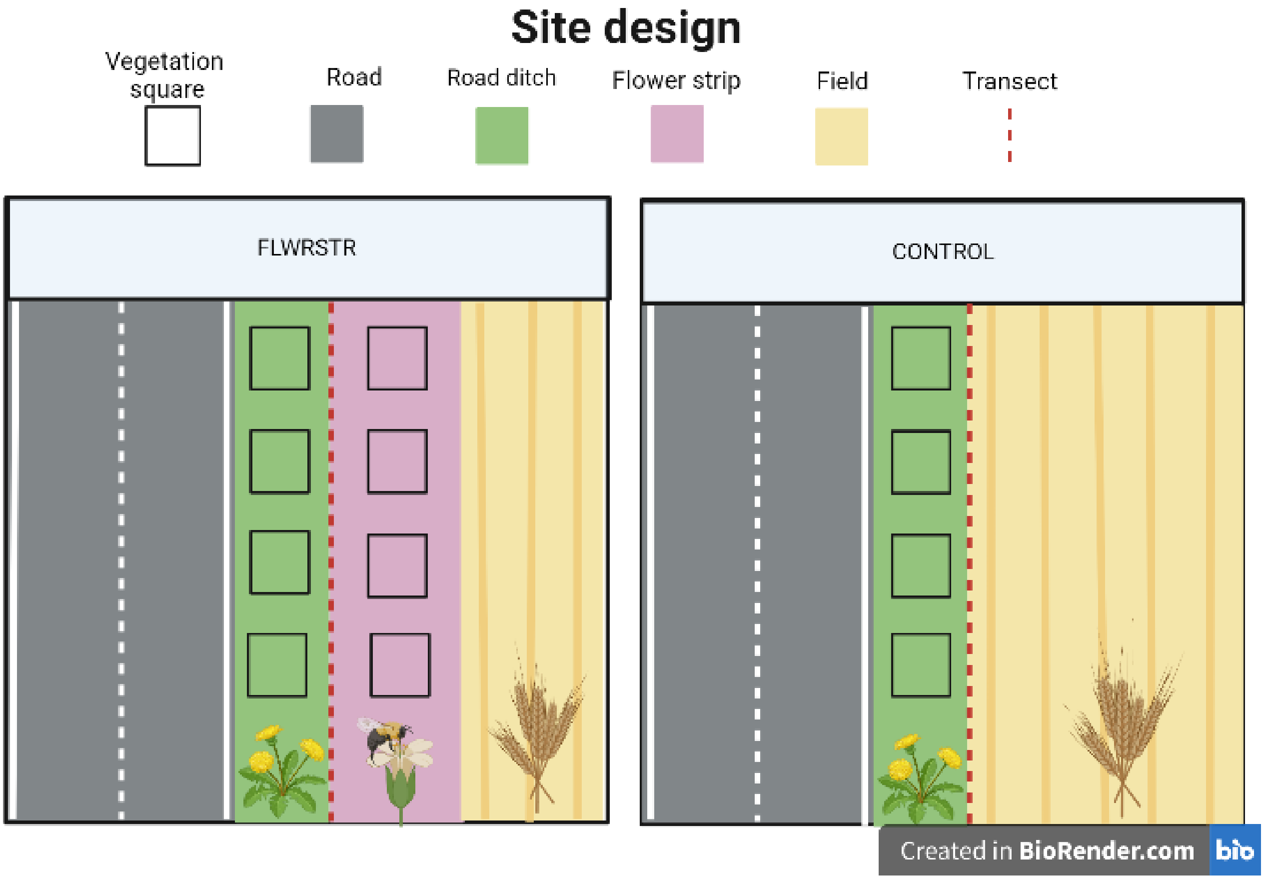


Figure 2 The two site treatments: flower strip (FLWRSTR) and control. Each location was made up of two sub-habitats: roadside and field-edge. Flowerstrip locations had a flower strip in the field-edge sub-habitats, and the control location only has a field edge. A 50-meter transect separated the roadside and field edge/flower strip. Data from the two treatments were pooled in this thesis. Five vegetation squares were placed along the transect for two sub-habitats during the vegetation analysis. Created with BioRender.com

2.4 Bee sampling

Field sampling was carried out from May 2022 to the end of July 2022 using netting (Figure. 3b). Netted bees were put in sampling tubes with labels that contained information about the collection site, collection period (date), sub-habitat and the plant species the bee was caught. There were three collection periods: the first in May, the second in early July, and the last collection in late July.

Weather conditions impact pollinator flight and forage activity (Karbassioon et al., 2023; Wratt, 1968). Therefore, sampling was only conducted on days with temperatures above 15 degrees, low wind conditions (<5ms/s), and low cloud cover (Figure 3a). Similar criteria are used for sampling butterflies in the protocol by Butterfly Conservation Europe (Swaay et al., 2012). To cover more sites in a short amount of time, the fieldwork was conducted by three field workers (Kaj Andreas Hanevik (COWI), Marianne Strand Torvanger (UiO) and myself). To standardize the protocol, all field technicians had an in-person revision of the data collection to reduce human errors and biases. The collection in any one sampling period should preferably not extend more than 10 days from the first collection. Because of this, some sites were not sampled in the first collection period due to undesirable weather conditions and too great a time interval between the samplings in the collection period.

The collected bees were stored in pure ethanol until they could be pinned and prepared for determination. The sampled bees were brought to the lab at NMBU where the majority were labelled and pinned (Figure. 3c); the rest were pinned up at the NINA office in Oslo. The pinned bees were species identified by Markus Sydenham (researcher, NINA) and were deposited at the Norwegian Institute for Nature Research (NINA). Species of bumblebees belonging to the sub-genus 'sensu stricto' (*Bombus cryptarum, B. lucorum, B. terrestris, B. magnus)* are cryptic; therefore, all collected bumblebees belonging to this subgenus were species identified to the sub-genus and not species. (Williams et al., 2012)

Figure 3: Recollection of laboratory and fieldwork. A control location with good weather conditions (a). The process of netting bees in the field (b). Pinned up bees ready for species identification (c).

2.5 Vegetation surveys

Vegetation surveys were conducted by Kaj Andreas Hanevik (COWI) at the end of July to evaluate plant species composition and abundance. Vegetation squares (1m^2) were placed at 10-meter intervals along the transect in each of the two sub-habitats, making a total of 10 vegetation squares per site. Within each vegetation square, the number of 0.5×0.5m squares (1-4) occupied per plant species was recorded.

2.6 Bee specialization

I used Bees Wasps & Ants Recording Society (2023a) and Artsdatabanken (2023) to determine the dietary niche (Generalist/specialist), taxonomic family and sociality (Social/solitary) of each bee species. Eight species of solitary bees were classified as specialists at BWARS.com: *Andrena denticulata, Andrena lathyri, Andrena wilkella, Colletes daviensanus, Colletes similis, Dasypoda hirtipes, Macropis europaea* and *Panurgus calcaratus.*

2.7 Statistical analysis

I used R Studio (R version 4.2.2) to perform the statistical analysis (R Core Team, 2022). The study centred on wild bees, and as a result, honeybees (*Apis millifera*) were not included in the collected bees due to their classification as domestic animals as done in the studies by Ockermüller et al. (2023) and Burkle et al. (2020). Similarly, cleptoparasitic and cuckoo bumblebee bees were also excluded as they do not collect pollen and the host determines their distribution (Litman et al., 2013).

2.7.1 Preliminary analysis

Before starting statistical analyses, I followed the protocol by Zuur et al. (2010) for data exploration to investigate for outliers and as a preventative measure for statistical errors. Statistical analysis only included sites with three collection periods. As such, six sites were excluded from the analysis because they did not meet the criteria. In addition, one site turned out to be a clear-cut forest instead of a field edge, this site was also excluded. When the locations were selected, one control site turned out to be an unregistered flower strip at the time and therefore not in the Norwegian agricultural directory registry. As a result, one site pair each comprised a flower strip rather than one flower strip and one control. This site was reclassified as flower strips and kept in the analysis because there were still enough control locations to have a representative sample size.

2.7.2 Plant–bee interaction webs

To visualize which flowers attracted which bees, I used the package 'bipartiteD3' to create interaction webs between bees and flower species (Terry, 2021). The dataset was subsetted to depict the interaction between bee and plant species more clearly, and three interaction webs were made. One interaction web was made specifically for solitary bees as their preferences were easily overshadowed by those of bumblebees due to their lower abundance. Another interaction web was made for all bumblebees. Lastly, an interaction web was made of bumblebees with the exclusion of *Bombus sensu stricto.* Because *B. sensu stricto* makes up the majority of bumblebees caught (>60%), excluding them will more clearly show the differences between other bumblebee species.

2.7.3 Traits

To investigate the effect of bee traits and plant species on the abundance of bee species I conducted three Generalized linear models (GLM) using the package "stats" (R Core Team, 2022). The three GLMs were made to test how specific traits influenced the floral preferences of bees: Model 1 = sociality, model 2 = dietary niche, and Model 3 = taxonomic bee family (Table 1). To inspect the residuals and distribution of the data, diagnostic plots were made using the code *"plotResiduals"* from the package 'DHARMa' (Hartig, 2022). The 'DHARMA' diagnostic plots showed that the data was under-dispersed for all the traits models, because of this, I used GLM with family quassipoison to analyse the models.

Table 1 model overview for the traits: sociality, diet niche and taxonomic family. Plant abundance was logarithmically transformed.

Model	*Trait*	*GLM*
Model 1	Sociality	glm(BeeSpecies~traitSocial/Solitary*PlantSpecies + LPlantAbundance.001, family = quasipoisson, data = SS)
Model 2	Diet niche	glm(BeeSpecies~traitGeneralist/Specsialist*PlantSpecies + LPlantAbundance.001, family = quasipoisson, data = GS)
Model 3	Taxonomic family	glm(BeeSpecies~traitTaxonomicBeeFamily*PlantSpecies + LPlantAbundance.001, family = quasipoisson, data = Fam)

The response variable was the abundance of bee species for all three models. The explanatory variables for Model 1 were plant species and the trait: sociality(Social VS solitary). For Model 2 the explanatory variables were plant species and traits: diet niche (Generalist VS specialist). Lastly, for model 3 the explanatory variables were plant species and the trait: taxonomic bee family.

As a result of the vegetation analysis, several species of plants had an abundance of zero in some sites. To be able to logarithmically transform the variable for plant abundance, 0 was replaced by 0.001. This was done to avoid undefined values. To visualise the models, I used the package 'emmeans' (Lenth, 2023) to create figures of the three trait models. The ANOVA outputs of the models were made by using the package "car" in R studio(Fox & Weisberg, 2019).

2.7.4 Plant species composition in sub-habitats

To explore the plant species composition in the sub-habitats a bubble plot of the plant species was made. Plant species abundance was calculated using data from the vegetation survey. The data was subset and summarized into two datasets, one for each sub-habitat. The package "Dplyr"(Wickham et al., 2023) was used to make a table for each sub-habitat containing plant species visited at least once by a bee. This table was used to create the bubble plot over plant species composition in the two sub habitats by using the r package "ggplot2" (Wickham, 2016). To check for independence between sub-habitat and plant species, Fisher's test was used. Fisher's test was used instead of the chi-square because the sample size was too small, and several species had an estimated <5 frequency that would have led to the chi-square result not being reliable (Soetewey, 2020).

Results

3.1 Which plant species attract which bee species?

The most visited plant species by solitary bee individuals were *Taraxacum* spp.(28,5%), which also attracted eight different solitary bee species (Figure 4). Other popular plant species among solitary bees were *Hieracium* spp*. (10%), Galium album (6,2%), Lotus corniculatus (7,7%), Trifolium repens (6,2%),* and *Tripleurospermum inodorum (9,2%)*. Figure 4 shows that there is a great variety among which bees visit which plant species with the majority of plants visited at < 5% by bees. Some plant species attracted a larger diversity of bee species such as *Taraxacum* spp., while others such as *Solidago virgaurea* only attracted one species of solitary bee. The plant species that contributed the most to the diversity of solitary bee species were *Taraxacum* spp. (8), *Barbarea vulgaris* (5), *Hieracium* spp. (5), *T. inodorum* (5), *T. repens* (4), *Stellaria graminea* (4) and *G. album* (4).

Only 130 out of the 1194 collected bee individuals were solitary bees in this study. The most abundant solitary bee species were *Halictus tumulorum* with 28 individuals collected (21,5% of all solitary bees) and *Andrena denticulata* with 12 individuals collected (9%). All other solitary bees had a percentage lower than 6%, meaning less than eight individuals of this species were caught.

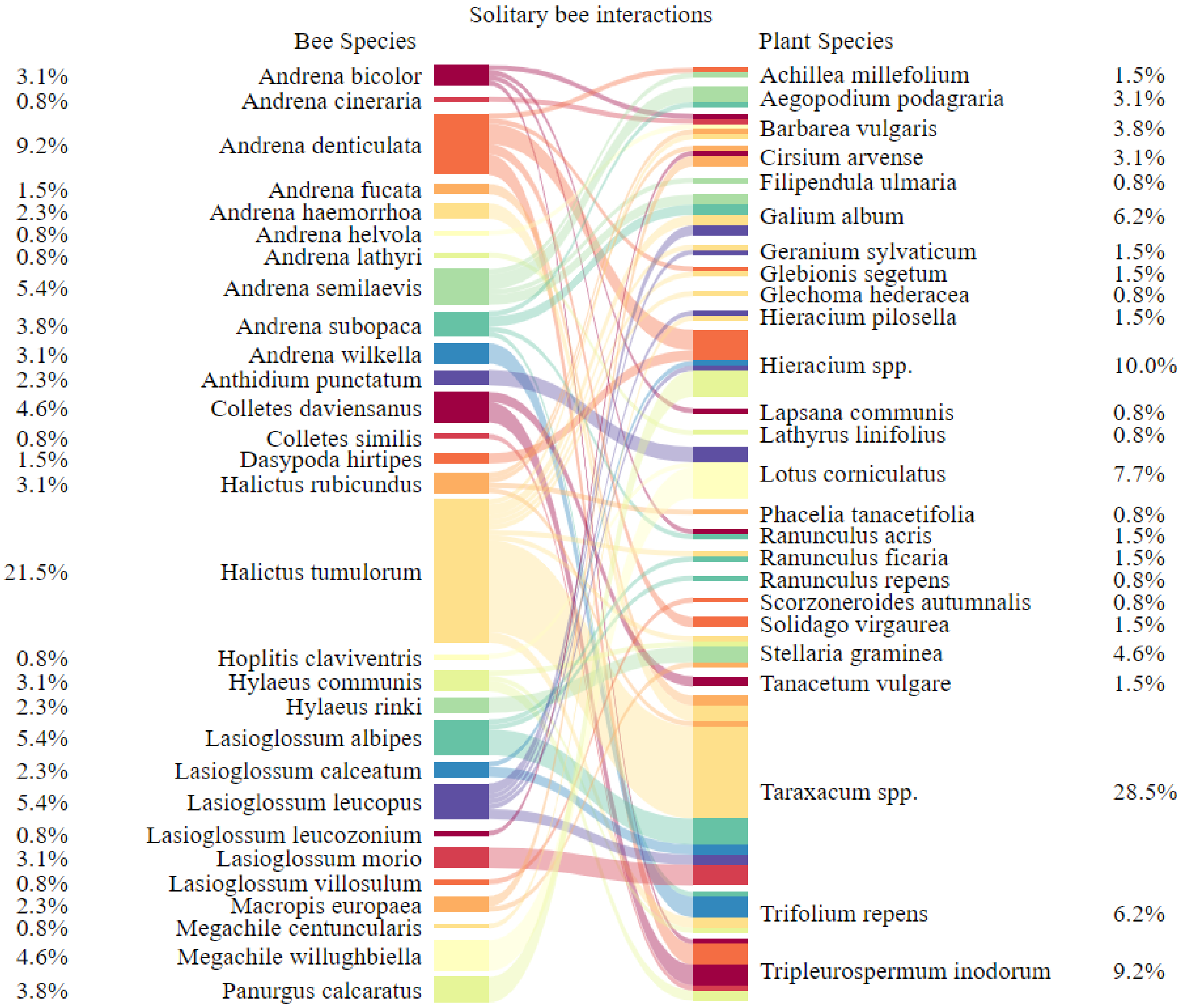


Figure 4 Interaction web of solitary bees. The percentage of solitary bee individuals is shown to the left of the bee species, while the percentage of solitary bee visitation is shown to the right of the plant species.

The most visited plant species among the bumblebee individuals were *P. tanacetifolia* (40,3%), *Trifolium pratense* (19,9%) and *Vicia cracca* (9,8%) (Figure 5). As *B.sensu stricto* makes up the majority of all collected bumblebees(>60%), it creates a bias towards this species' preference. With the removal of *B. sensu stricto,* the preference of the other bumblebee species is clearer (Figure 6). In Figure 5, *P. tanacetifolia* was the most visited plant species (40,3%), but Figure 6 shows that *P. tanacetifolia* was visited only 8,8% when *B. sensu stricto* was excluded. Among bumblebees other than *B. sensu stricto*, the most visited flowers were *T. pratense (37,5%)*, *T. repens (10%) V. cracca (9,3%)* and *P. tanacetifolia (8,8%)* while other plant species were visited <5% (Figure 6). Overall*,* bumblebees visit a variety of different plant species, but several plant species were visited by <1% of bumblebee individuals (Figures 5 & 6). Bumblebee species diversity is largely attributed to the plant species *T. pratense* (8), *T. repens* (8), *V. cracca* (7), *P. tanacetifolia* (7), *Taraxacum* spp. (6), and *Circium arvense* (6). When excluding *B. sensu stricto* the most abundant bumblebee species were *Bombus sylvarum* (28,5%), *Bombus lapidarius* (19%) and *Bombus humilis* (16,5%) (Figure 6).

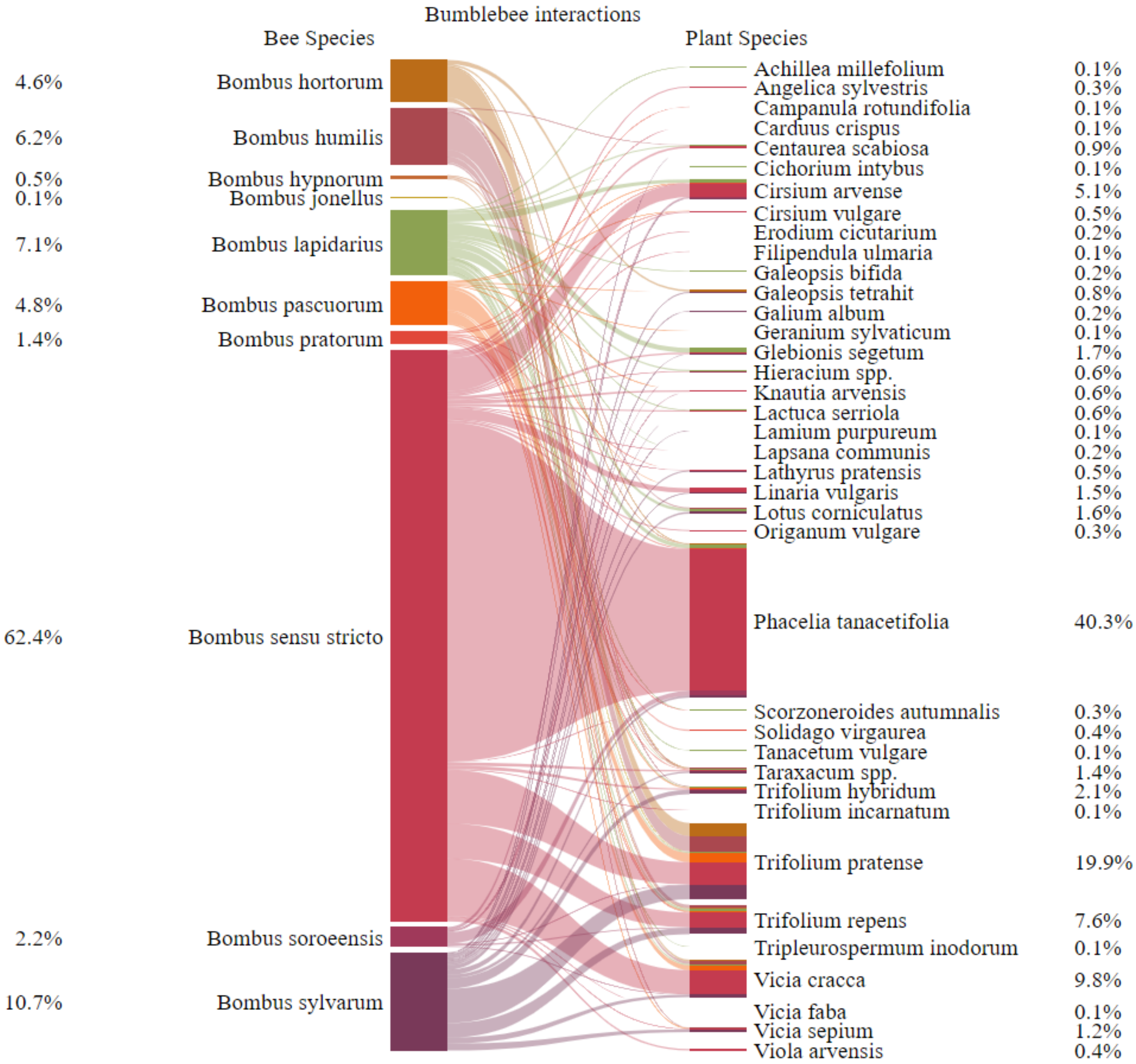


Figure 5 Interaction web of all species of Bumblebees. To the right of each plant species is the percentage of bumblebee visitation. The percentage of bee individuals is shown to the left of the bumblebee species. Each bumblebee species is represented by a unique colour.

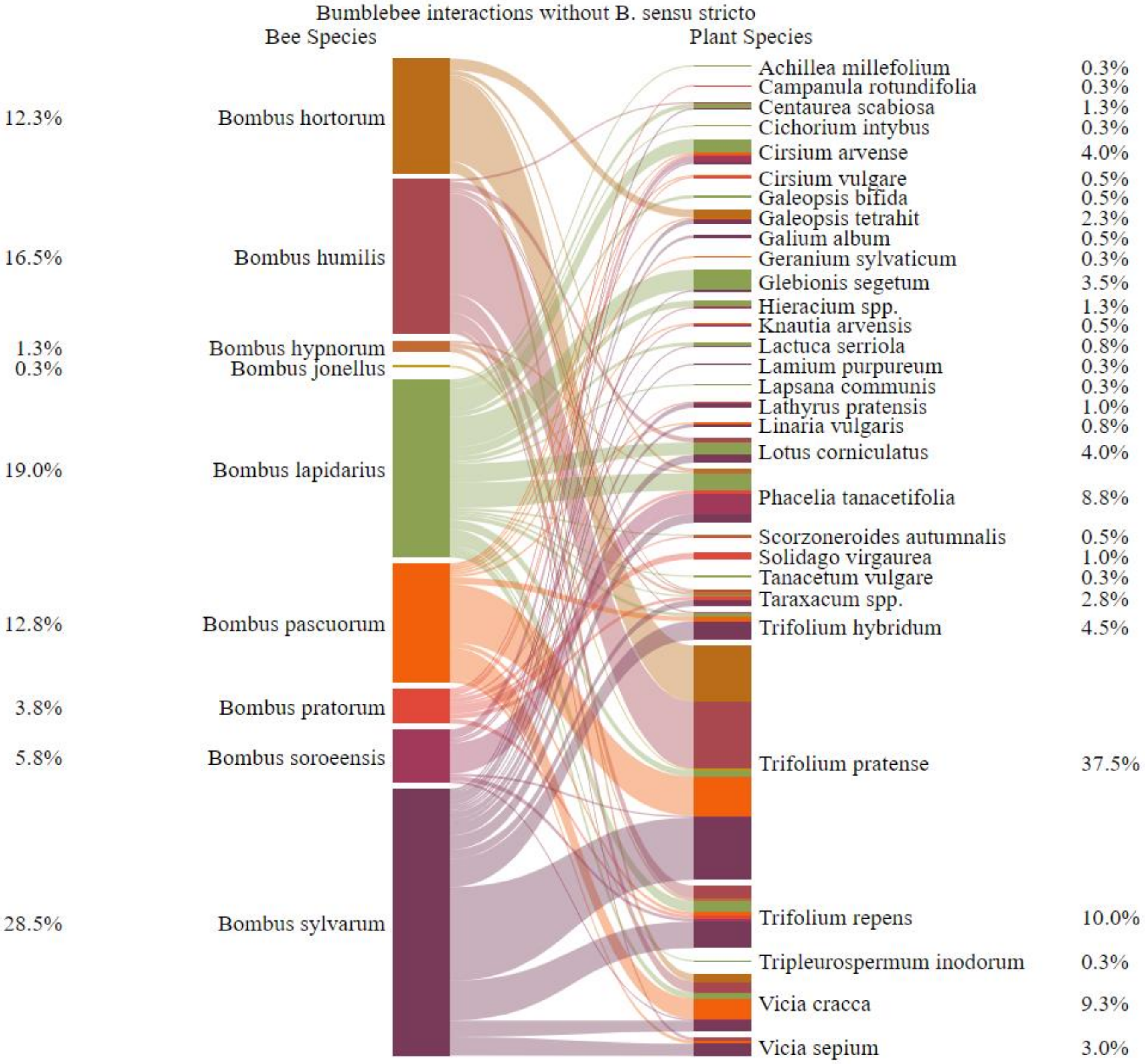


Figure 6 Interaction web of Bumblebees excluding B.sensu stricto. To the right of each plant species is the percentage of bumblebee visitation. The percentage of bee individuals is shown to the left of the bumblebee species. Each bumblebee species is represented by a unique colour.

3.2 Trait Sociality

The sociality of the bee and plant species alone had no significant effect on the number of bee species present, but the interaction between them had a significant effect (Table 2). The interaction between sociality and plant species was a highly significant predictor of the interaction frequency between plants and bees (p-value of <0.001) indicating that solitary bees and social bees were attracted by different plant species.

*Table 2 Anova outputs for glm(BeeSpecies~traitSocial/Solitary*PlantSpecies + LPlantAbundance.001, family = quasipoisson, data = SS)*

Response: Bee species	**LR Chisq**	**Df**	**Pr(<Chisq)**
Social/Solitary	0.52	1	0.472
Plant Species	169.02	46	< 0.001
Plant Abundance	10.00	1	0.002
Trait: Plant species	316.72	46	< 0.001

Social bees were recorded on more plant species (> 30) than solitary bees (<20) (Figure 7). Across sites, after controlling for plant abundances, the most attractive plant species to social bees were: *Lactuca serriola (~4)*, *Vicia sepium* (~3.5 bee species), *T. pratense (*~3 bee species*); P. tanacetifolia; Glebonis segetum;* and *Centaurea scabiosa.* For solitary bees, the most attractive plants were *Ranuculus acris*, *Ranuculus ficaria,* and *Hieracium* spp. Social bees were recorded on 37 out of 47 plant species (78,72%) whereas solitary bees were recorded on 26 of the 47 plant species (44,68%). The large confidence intervals in Figure 7 indicate an uncertainty among several of the estimates. For instance, solitary bees respond to *Viola arvensis* at zero, but the confidence interval is large, indicating that the estimated mean is highly uncertain and the true mean for the population is somewhere in the interval. This might also be because there were no observations of bees from this trait group on those plants. i.e., their bee abundance was = 0 across all sites where they occur.

Solitary bee species responed to nine plant species that social bees had zero response to. Namely, *S. graminea, R. acris, R. ficaria, Ranuculus repens, Lathyurs linifolius, Hieracium piloselia, Glechoma haderacea, B. vulgaris* and *Aegopodium podeagraria.*

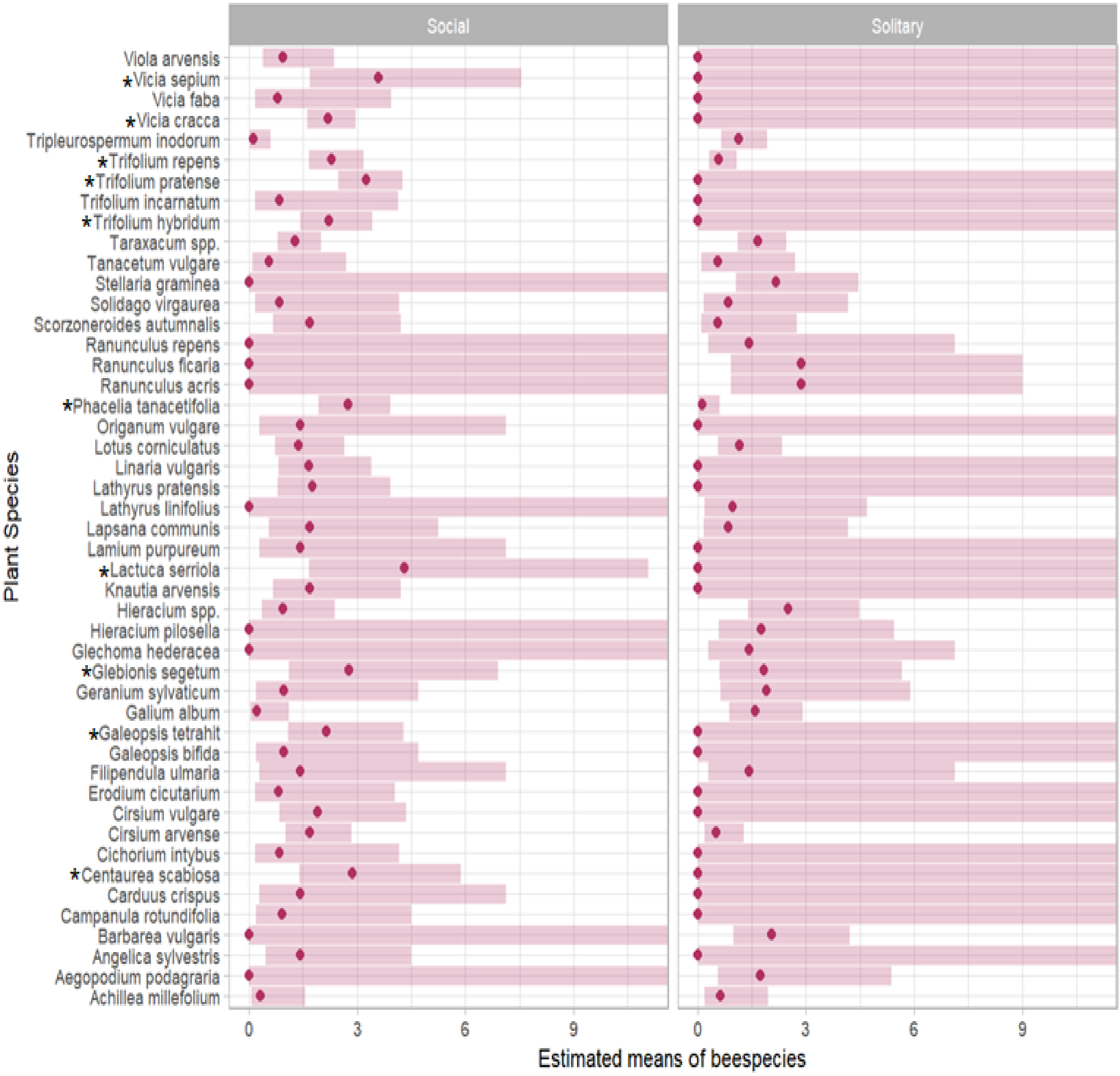


*Figure 7 shows the estimated mean number of bee species and associated 95% confidence intervals (the coloured panels) per plant species for social (left panel) and solitary (right panel) bees. Plant species with a p-value of <0.05 are marked with a * in the figure.*

3.3 Trait Diet niche

The interaction between generalists/specialists and plant species significantly affected the number of bee species present, while the other factors did not have a significant impact alone (Table 3). The interaction between the bee trait Generalist / Specialist and plant species had a high LR Chisq of 387.46 and a low p-value of <0.001 indicating a significant effect, suggesting that the attraction to specific plants differs between generalist and specialist species of bees.

*Table 3 Anova output for glm(BeeSpecies~traitGeneralist/Specsialist*PlantSpecies + LPlantAbundance.001, family = quasipoisson, data = GS)*

Response: Bee species	**LR Chisq**	**Df**	**Pr(<Chisq)**
Generalist/specialist	2.51	1	0.114
Plant Species	31.33	46	0.952
Plant Abundance	0.05	1	0.826
Trait Generalist/specialist: Plant species	387.46	46	< 0.001

Generalist bee species were recorded on all except one plant species, while specialist bee species were only recorded to visit 10 plant species (Figure 8). The only plant species that generalists were not attracted to is *L. linifolius.* Generalist bees respond to all plants with 1 bee species except *T.inodorum (~0.5), T.repens (~0.75), Tanacetum vulgare (0.5), A. millefollium (~0.5)* and *L. linifolius (0).*

Specialist bees had the largest response to *S. virgaurea* (~1), *L. linifolius (~1)* and *G. segetum (~1).* Specialist bees responded with ~0.5 to *Hieracium* spp., *T. indorum, Stellaria graminea,* and *T. vulgare,* and <0.5 to *Achillea millefolium, T. repens and C. arvense.* The confidence intervals are generally larger within specialist bee species, meaning that the estimated mean is uncertain (Figure 8). Interstingly, both *T. inodorum*, *A. millefolium* and *T. vulgare* were visited relatively much by specialist bees but less than average visitation from generalists. The same goes for *L. linifolius* which did not attract generalist bees but was one of the most visited by solitary bees. This reflects the ANOVA outputs that indicate that bees differ in visitation based on their dietary specialization.

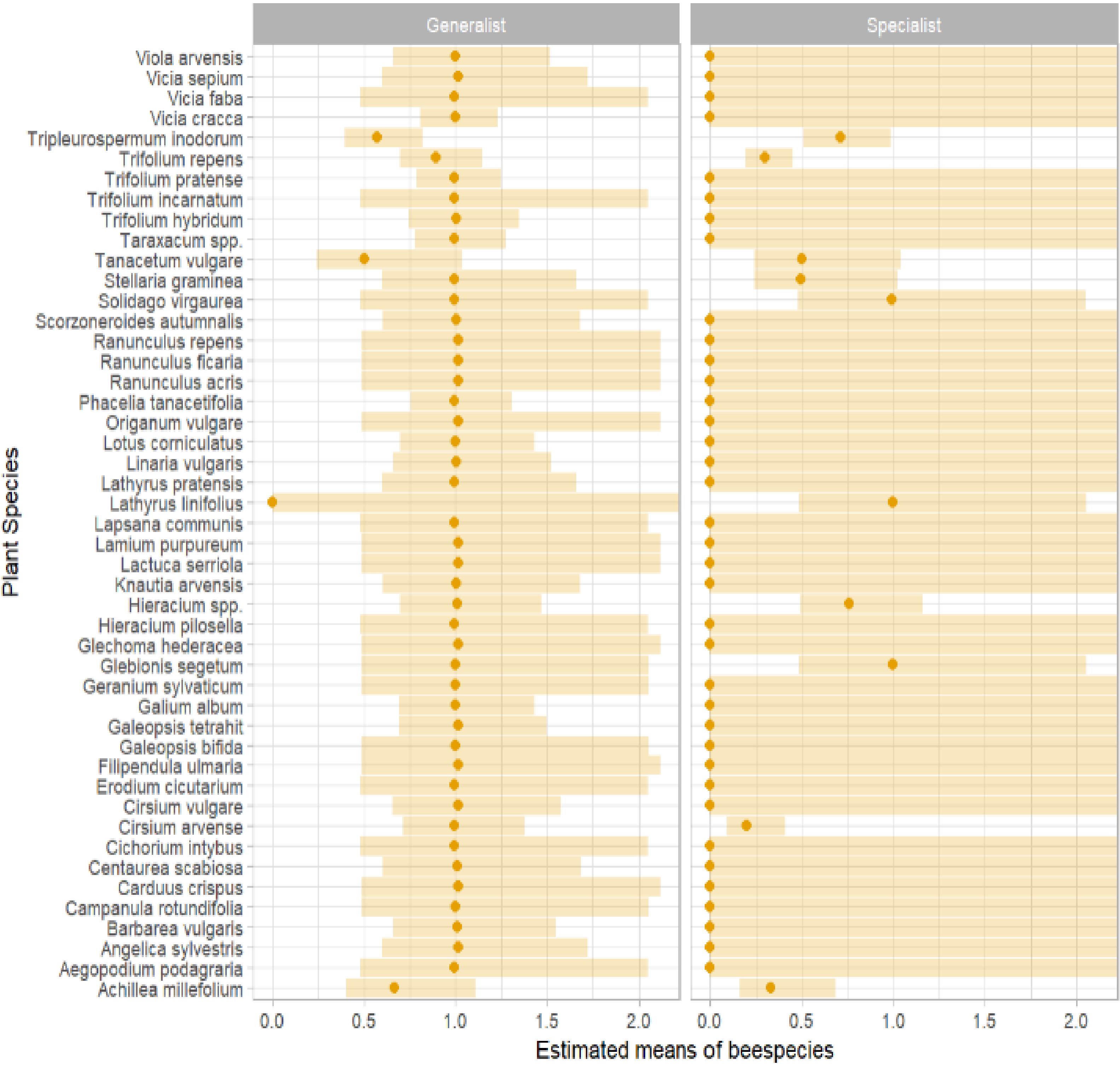


Figure 8 shows the estimated mean number of bee species and associated 95% confidence intervals per plant species for generalists (left panel) and specialist (right panel) bees. Not a single plant species had a significant effect on the GLM output. The confidence intervals are reflected in the coloured panels.

3.4 Trait Taxonomic Bee family

The trait taxonomic family had a strong effect on the response variable (LR chisq = 1249.97, p <0.001), regardless of the other variables in the model (Table 4). The interaction between the bee family and plant species had an LR Chisq of 1353.56 and a p-value of <0.001, indicating a strong association between the interaction and the response variable. This suggests that the effect of the bee family could depend on the particular species of plants. Plant species had a low LR Chisq value of 71.51 and a p-value of 0.01011 indicating that there is no significant association between plant species and response variable after taking the other factors in the model into account.

*Table 4 Anova outputs for glm(BeeSpecies~traitTaxanomicBeeFamily*PlantSpecies + LPlantAbundance.001, family = quasipoisson, data = Fam)*

Response: Bee species	**LR Chisq**	**Df**	**Pr(<Chisq)**
Taxonomic bee family	1248.97	5	< 0.001
Plant Species	71.15	46	0.011
Plant Abundance	3.50	1	0.062
TraitTaxonomic bee family: Plant species	1353.56	230	< 0.001

The different families of bees differ in their attraction to plant species (Figure 9). Although it should be noted that there is a difference in the abundance between the taxonomic families that can directly impact these results, some families of bees made up a larger part of collected bees. For instance, bumblebees (Apidea) made up almost 90% of all bee individuals caught in this study (1065 out of 1195 individuals).

Overall, Apidea has the largest response to plant species, responding to 37 of 47 plant species (78,7%) and Megachillidae responded to the least amount of plant species with 2 of 47 (4,2%). Further, Andrenidea responded to 14 out of 47(29,7%) plant species, Colletidae responded to four out of 47 (8,5%), Halictidae responded to 15 out of 47 (31.9%) and Melittidae responded to three out of 47 (6,3%). None of the bee families had a response stronger than 1,5 bee species.

The plant species that attracted the largest amount of bee species from different bee families are *T. repens (~4), and Hieracium* spp. (~4), *T.inodorum(~3), Taraxacum.*spp(~3), *S.graminea (~3), G.segetum(~3), G.album(~3), C.arvense(~3). Hieracium* spp. attracted species from all families except Colletidea and Megachillidae: Andrenidae(~1), Apidea(~0.5), Halictidae (~0.5), Melittidae(~0.25). Trifolium repens attracted bees from four families: Andrenaidae(~0.5), Apidae(~1),Colletidae(<0.25) and Halictidae (~0.25).

Regarding the family Apidae*,* 29 out of 37 plant species were found to attract around 1 species of bee*.* Despite this trend, there were some exceptions. Specifically, *T. repens, Hieracium* spp., *L. corniculatus, T. vulgare* and *Taraxacum* spp. only attracted around 0.5 species of bees. Lastly, three species of plants were found to attract ~0.25 bee species belonging to Apidae*,* namely, *A.millefolium, G.album,* and *T. inodorium.*

As for the species of bees belonging to the family Andrenidae*,* seven out of 14 plant species were found to attract approximately 1 species of bee*.* However, like the previous family, five species of plants were found to attract ~0.5 species of bees. These plant species were *T. inodorum, Hieracium* spp., *G. album, B.vulgaris* and *A. millefolium.* Additionally*,* two species of plants were found to attract ~0.25 species of bees, namely, *T. repens* and *Taraxacum* spp.

Among bee species belonging to the family Halictidae, six out of 15 plant species were found to attract around 1 species of bee. Despite this, only 0.5 species of bees are attracted to the majority of plant species, namely *G. album, C. arvense, B. vulgaris, Hieracium* spp.*, Scorzoneroides autumnalis, Taraxacum* spp.*,* and *T.repens*. Interestingly *P. tanacetifolia* were the only plant species that attracted ~0.25 species of bee.

Compared to the other bee families Megachilidae, Melittidae and Colletidae were attracted by the least amount of plant species. Specifically, Megachilidae was only attracted by *L.coniculatus (~1)* and *H. piloseila (~1).* Meanwhile, Melittidae were attracted by three plant species, including *S. graminea* (~0.5), *Hieracium* spp.(~0.5) and *C. arvense* (~0.25). Lastly, Colletidae were attracted by plant species *T. inodorum* (~0.5), *T. repens* (<0.25) *T. vulgare* (~0.5), and *S. graminea (~1).*

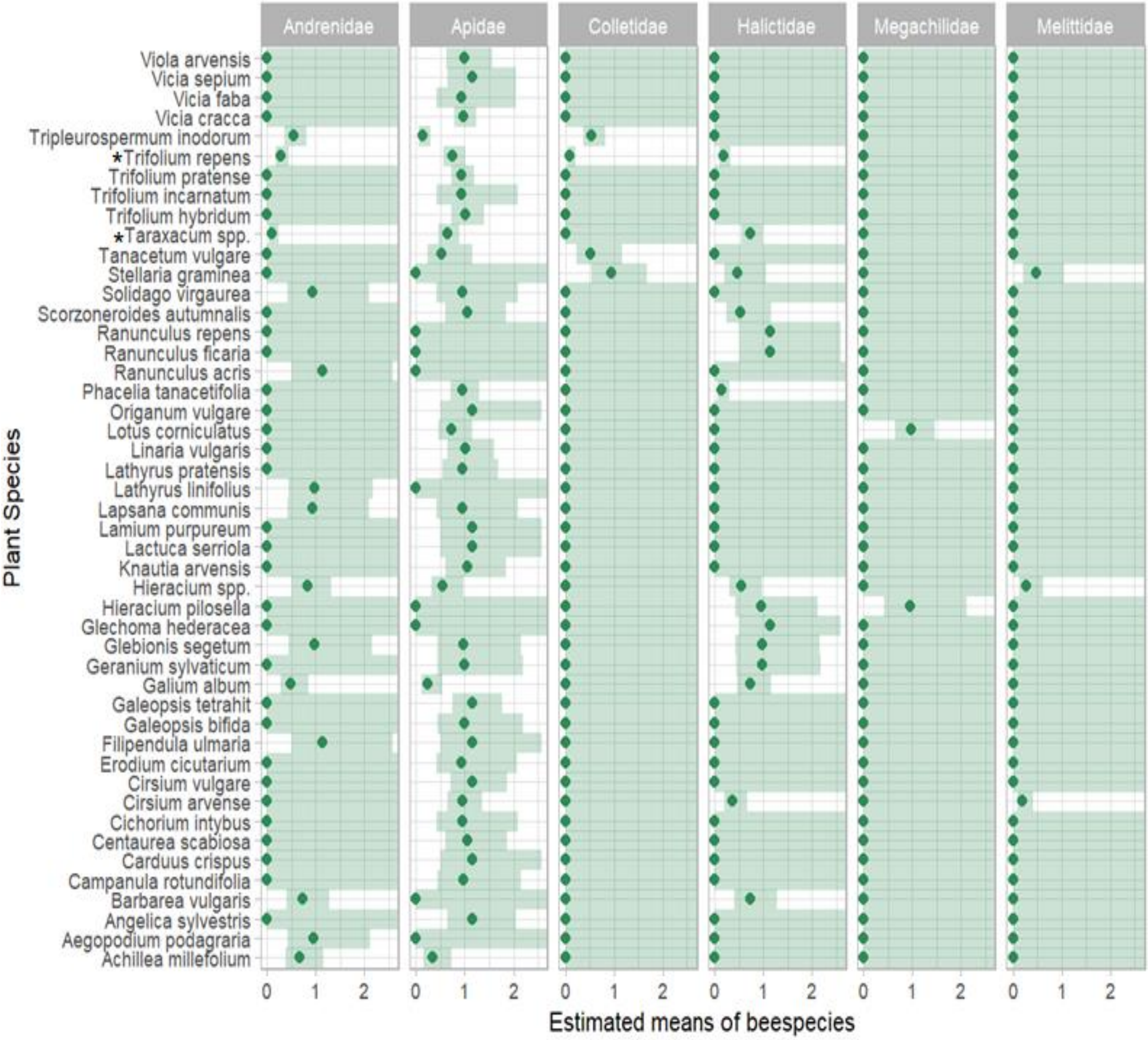


*Figure 9 shows the estimated mean number of bee species and associated 95% confidence intervals per plant species for six different families of bees. The confidence intervals are reflected in the coloured panels. Plant species with a p-value of <0.05 are marked with a * in the figure.*

3.5 Plant species composition in sub-habitats.

In total, 33 plant species were recorded in flower strips, and 39 plant species were recorded in roadsides (Figure 10). The abundance of the species found in both sub-habitats differed. For example, *A. millefolium* had a total vegetation plot frequency of 21 on flower strips and 214 on roadsides. *P. tanacetifolia* on the other hand, had a vegetation plot frequency of 104 in flower strips while the frequency at the roadside was only four. The most abundant flower species on the roadsides were *A.millefolium (214), and Taraxacum* spp. *(202)* and *T. repens (97).* The most abundant flower species in the flower strips were *T. pratense* (146), *T. repens (127),* and *P.tanacetifolia (104).* Roadside had the highest amount of unique plant species with 10 unique species, while flower strips had four unique flower species. Namely, *Vicia faba, Trifolium incarnatum, G. segetum and Chichorium intybus.* Five of the plant species registered in the vegetation survey are non-native plants Artsdatabanken (2018a) registry: *B. vulgaris, C. intybus, T. incarnatum, V. faba* and *P. tanacetifolia.*

A Fisher's Exact test indicated a significant relationship between plant species and habitat (p<0.0005; simulated p-value based on 2000 replicates). Hence, there was strong evidence of a difference between flower strips and roadside habitats concerning the abundance of the different plant species.

Figure 10: Bubble plot over species composition of the two treatments. Flower strip plant species are coloured pink and roadside plant species are coloured green.

Discussion:

The aim of my thesis was to assess if plants differ in the types of bees they attract. Such information could then guide seed mix composition for enhancing pollinator habitat enhancement schemes. The findings of this thesis revealed that the bee's sociality, diet niche, and taxonomic family trait influenced its attraction to certain plant species. It is noteworthy that the sample size for several traits was small, which leads to uncertainty in the estimates. Further, although flower strips contributed to plant species not found on roadsides, the latter had the largest number of unique species. Overall, the study sheds substantial light on the complex interactions between plants and bees and the role that bee traits play in these interactions.

4.1 Which plant species attract which bees?

The interaction webs showed a large variance among bee species, which plant species they visited and how many species were attracted by a specific plant species. Specifically, solitary bees and bumble bees were attracted by different plant species. Solitary bees and social bees have different life-history strategies which can potentially impact their attraction. According to Goulson et al. (2005), Fabaceae plant species are a major forage source for bumblebees. *T. pratense*, T. repens, and *V. cracca* all belong to the family Fabaceae and were highly visited by several bumblebee species in this study, further supporting the importance of Fabaceae plant species for bumblebee diversity.

Other studies have identified several of the same key resource plants for bees, but when comparing studies from different countries the importance of specific plant species varied (Nichols et al., 2019). Bees were significantly impacted by plants such as *O. vulgare* in a study, yet little to no visitation was observed in another (Kuppler et al., 2023; Nichols et al., 2019; Warzecha et al., 2018). This might indicate that this species has a different impact based on geographic range.

Species composition differs across geographies based on topography, climate, historic events and other environmental factors. These environmental influences shape the types of species that can survive at a given location and determine the dominant species. This, in turn, affects the overall ecosystem and the balance of the species within it. For instance, bumblebees dominate in areas with high elevations and latitudes (Orr et al., 2023). Climate change has led to a change in geographic ranges for several species, for instance, bumblebee species in Europa and North America shifted their range towards higher elevations (Kerr et al., 2015). Therefore, one cannot directly compare the species composition of two countries far from each other. Even though they may contain the same species of bees and plants, the abundance may differ between them. A species might be more dominant in certain climates or elevations but not in another. This change might also occur within the same country. Thus, AES schemes should design seed mixes based on local climatic and environmental conditions, perhaps even taking into account climate change. Furthermore, for results to be interpreted into management actions correctly, it is also essential to keep in mind the geographical differences between studies that are compared.

The spatial distribution of AES is vital to their success. If they are located too far from each other or other suitable natural habitats they might not be available for small bees with low dispersal, therefore, the placement of such schemes is just as important or even more important than the composition of the flower plantings. With increased diversity of plants and connectivity, these schemes can help support a large diversity of bees as well as other pollinators.

Flower morphology and nectar production is linked to the visitation by bees (Valadão-Mendes et al., 2022). Bumble bee species have similar morphology and behaviour, but their tongue length distinguishes species and reflects their dietary specialization. Therefore, tongue length is associated with flower preference among bumblebee species. (Goulson et al., 2005). In a study by (Sponsler et al., 2022), the flower morphology of the plant species attracted different bumblebees based on their tongue length. They found that bumblebees with a short tongue preferred flowers with head or bell morphology, while medium and long-tongued bumblebees preferred flowers that had lip, funnel or flag morphology. Interestingly, several of the most visited plant species in this study have some of the same morphological traits. Namely, *Trifolium* spp. *Taraxacum* spp., *L. corniculatus* and T. *inodorum.* The same plant species were also highlighted in other studies as key plants for bees. (Kuppler et al., 2023; Sutter et al., 2017; Warzecha et al., 2018; Wood et al., 2017). Therefore, understanding flower morphology can help explain why bees visit certain flowers.

The most visited plant species were also the plant species that contributed the most to the diversity of bees and bumblebees. For solitary bees, *Taraxacum* spp*.* were visited by the largest amount of bee species. Other plant species that contributed to the diversity of solitary bees were *Heracium* spp, *T. inodorum* and *B. vulgaris*. *Taraxacum* spp. is highlighted as a favourite plant species among all bee species in the study by Kuppler et al. (2023). *Taraxacum* spp. was highly visited but were only significant for taxonomic family. *Taraxacum* spp. blooms early in the spring and is an abundant plant species in agricultural areas. Therefore, dandelions could contribute highly sought-after pollen and nectar early in the season, but when given the option bees might choose other plant species. This might explain why it is visited by a lot of bees but is not significant for more than one trait.

4.2 Bee trait sociality, diet niche and taxonomic bee family.

In the study, I found that the bee's sociality, diet niche, and taxonomic family trait affected its preference for plant species. Bees have different life history strategies that are reflected in the trait of the bee. It is important to note that there may be an overlap between several of the traits examined in this study, which means bees can have more than one trait. For instance, solitary bees can be both specialists and generalists, while social bees tend to be generalists. In addition, different bee species within the same family may have vastly different behaviours, such as different sociality or diet niches.

All social bees in this study were bumblebees. Bumblebees are regarded as highly selective generalists due to their strong preference for certain plant species (Sponsler et al., 2022). In this study several plant species were visited by less than 1% of bumblebee individuals, this could reflect their selectiveness. It's also important to note the differences in abundance between the plant species. Such as *Trifolium* spp*.* that were highly abundant in both sub-habitats, which leads to a higher chance of visitation.

The diet niche of the bee showed a significant difference in attraction to plant species between generalists and specialists. In a study by Nichols et al. (2019), several highly attractive plant species from the Asteraceae taxa were identified. These plant species were able to attract specialised and rare bees. These plant species were *Hieracium* spp., *Taraxacum* spp., *Picris* spp., and *Centurea* spp. Several of the same plant species were highlighted in these results as significant plants for bees with different traits, further demonstrating the importance of these plants on wild bee diversity. For instance, Hieracium spp. is the most visited plant among solitary bees as well as a significant plant species in the assembly of specialist bee species. Furthermore, *Hieracium* spp. is one of several highly visited plants in the study by Kuppler et al. (2023) that also attract high visitation rates from pollen specialists, making it an essential plant species for supporting bee diversity. Moreover, the same study noted that plant species preferred by specialised bee species were generally popular among most bee species. Suggesting that catering to specialised bee species in conservation actions may benefit a large variety of bees.

I found that the taxonomic bee family influenced the attraction to plant species. The number of bees caught from each family varied, indicating that the pattern of attraction for some families might not be accurate. The large confidence interval for the other families besides Apidea supports this. We cannot rule out the possibility that bees from the other families might visit other plant species than recorded because of the small sampling size. However, despite this, the figures give us an indication of what these bee families are attracted to. Further research is needed to confirm these findings, but the results do suggest a pattern of attraction to certain plant species among bee families. Understanding this pattern could be key to protecting bee populations and their habitats.

Bogusch et al. (2020) demonstrate that the specialization of bee species within taxonomic families varies greatly. The majority of bees belonging to the families Apidea, Colletidea and Halictidea were generalists, while Melittidea contained only specialists. Andrenidae and Megachilidea had equal parts generalist and specialist. In this study, the majority of specialist belongs to the family Andrenidae (4), while the rest belong to Collitidae (2) and Melittidea (2). The specialization of species within the taxonomic family might influence the overall attraction towards plant species. For instance, Megachillidea species have in a study by Marinho et al. (2018) shown a preference for Fabacaea and Asterecea plants. This can explain why in this study all species belonging to Megachillidea caught on *Lotus coniculatus* (Fabacaea*)* and *Hieracium piloseila* (Asteracea) even though they are considered generalists. In this study, the family Melittidae and Colletidae contain bee species that are specialists. For instance, the bee species *Dasypoda hirtipes* which belongs to the family Melittidae is a specialist with a strong preference for plants belonging to the family Asteraceae, such as *Hieracium* spp (Bees Wasps & Ants Recording Society, 2023b). This can help explain the low attraction to plant species for the family Collectidea, Megachilidea and Melittidae. Andrenaidea and Halictidea respond to more plant species than the three mentioned above. Andrenaidea family contains a variety of species that are both generalists and specialists, while Halicidea were all generalists in this study. Thus, the taxonomic family reflects the pattern of attraction .

Interestingly, in a study by Williams et al. (2010) bees respond to disturbances based on the trait of the bee. For instance, social bees were more sensitive towards pesticides than solitary bees. This was most likely due to the accumulation of pesticides in their nest. Consequently, management practices can be improved by taking into consideration how traits affect response to disturbances.

4.3 Plant species composition in roadsides versus flower strips

The results showed that roadsides contributed with more unique plant species than flower strips, but flower strips contained more non-native plant species than roadsides. Both flower strips and roadsides shared several plant species that were attractive to a large diversity of bees but the abundance of the plant species differed. Flower strips dominated in *Trifolium spp.* and *P.tanacetifolia* that cater to generalist and social bees such as bumblebees while roadsides were more abundant in plant species such as *Taraxacum* spp. and *A. millefolium* that were more prefered by specialists or solitary bees. The plant species *Hieracium* spp. impacted both solitary, specialised and several families of bee diversity positively. Flower strips could benefit from the add-on of these species of plants and increase the usage of native and local plant species in environmental schemes.

Considering flower strips are often sown, the seed mix used, local plant species composition and conditions can affect the species composition of the flower strip. Plant species belonging to Fabaceae are often a major component of pollinator-friendly AES because these schemes were designed to preserve rare bumblebees associated with Fabaceae. This explains their high abundance in the flower strip sub-habitat (Goulson et al., 2005; Wood et al., 2017). Seed mixes typically used in our region (Statsforvalteren (2020b)) lack species belonging to Apiaceae and Asteraceae. Both plant families have been shown in other studies to contain plant species important for red-listed and specialized bees (Kuppler et al., 2023; Wood et al., 2015a). By adding these plant species to AES schemes, one could cater to a larger diversity of bees, further emphasizing the importance of seed-mix composition in AES.

P. tanacetifolia was the most visited plant species by *B.sencu stricto,* this plant is an alien species with an unknown impact status at Artsdatabanken. Caution is advised when sowing plants non-native plants in the metanalysis by Vilà et al. (2011). Sowing species with unknown invasiveness potential such as *P. tanacetifolia* is unwise when little is known about the risk involved. The benefits and drawbacks of *P.tanacetifolia* were examined in a Mediterranean study by Petanidou (2003). The study highlighted that *P.tanacetifolia* was a beneficial nectar source for honeybees but negatively impacted the local ecosystem. Although this study was conducted in the Mediterranean, it indicates that *P.tanacetifolia* could have more negative effects than positive. In addition, if non-native plants are preferred by native bees is still largely unknown, but in a study by Seitz et al. (2020), wild bees showed no difference in forage between native and non-native plant species. According to Seitz et al. (2020), pollinators benefit from non-native plants in pollinator-enhancing flower strips because they are visited by a large number of bee species, especially in early spring and late autumn when native flowers are not as abundant. However, non-native species can be a threat to ecosystem function, composition and stability (Bartomeus et al., 2008). Considering this, the usage of non-native species with unknown risk assessment should be limited. The knowledge of how the network of non-native plants and pollinators interact is limited but it is imaginable that generalists benefit more than specialists due to their less strict preference. For instance, non-native plants can be disastrous for specialised species of bees that are ill-adapted to exploit non-native species for resources or dependent on a specific plant species that a non-native species can out-compete (Vanbergen et al., 2018). Consequently, these changes might easily be overlooked if bee abundance stays the same. Therefore, it is important to monitor bee populations closely to ensure that any changes are detected early and can be addressed. Monitoring and tracking bee populations can also provide valuable insights into the impacts of climate change and habitat loss.

Considering the already significant damage anthropogenic activity has caused ecosystems, the usage of non-native plant species as a food resource for pollinators can potentially worsen the problem. Seitz et al. (2020) recommend that non-native species, with caution, should only be contained to pollinator-friendly seed mixes in human-dominated landscapes such as gardens or parks, and only when complementing native plant species. Therefore, one should take precautionary measures by not using alien plant species due to the unknown impacts.

B. vulgaris is a non-native plant species that Artsdatabanken (2018b) has classified as a severe impact (SE) species that can devastatingly impact the ecosystem. *B. vulgaris* contributes to species richness among solitary bees, despite its relatively low abundance in the roadside sub-habitat. Plant species belonging to the Brassicaceae family provide essential flower resources for solitary bee species in spring, according to Wood et al. (2017). Therefore, it may be more attractive for bees than other plants. Furthermore, the fact that it is a highly invasive species may indicate that it spreads rapidly throughout the landscape and becomes abundant in these areas. Hence, increasing the probability of bee visitation. *B. vulgaris* visitation rates might indicate a lack of available flower recourses in early spring or with the same morphological traits that this plant offers. This should be further investigated so that this need is met, and native species identified as potential alternatives for pollinators.

4.4 Application and study limitations

Conservation of the wild bee population is vital to maintain ecosystem function, stabilisation, and services, as well as bee species' intrinsic value. This study describes the interaction network between bee species and plant species which can help bridge knowledge gaps and improve conversation actions. The knowledge of bee–plant interactions (attraction) can help increase the diversity of plant species in seed mixes used for AES schemes to support a larger diversity of bees. The diversity of plant species has been shown in multiple studies as a vital part of the conservation of wild bees((Hegland & Boeke, 2006; Ockermüller et al., 2023; Sutter et al., 2017)). As a result of large monoculture crops and mass flowering events, agricultural areas are often highly homogeneous, resulting in limited floral resources for bees (Lonsdorf et al., 2009). With increased plant diversity the area might support a larger community of bees with plant species that flower throughout the season. Therefore, AES may benefit from the knowledge of bee–plant interactions, and increased plant diversity and connectivity in their schemes. Additionally, the knowledge of how traits influence this interaction can help further fill knowledge gaps. For instance, understanding how trait patterns influence the community is key to anticipating the effects of climate change and other disturbances might have on a species with this trait. In an ever-changing world, this knowledge is vital if we are to conserve species and communities.

While this study provides valuable insights into the plant species that attract different bee species, it must be acknowledged that it has some limitations. It's imperative to consider the limitations of any study to properly interpret its findings. Since this study took place in a single year, the data collected represents a snapshot of the species composition of plants and bees at that point in time. Hence the findings might not be representative of long-term trends or for other geographic regions. Only 39 out of the 210 bee species found in Norway were recorded in this study, which gives a somewhat limited understanding of these few species (Artsdatabanken, 2021). Future studies should, therefore, seek to address these limitations and enhance our understanding of wild bee populations, their interactions with plant species and the influence of their traits. Moreover, bias might have affected the data collection in this study. For instance, larger bees are easier to spot than small bees, which might lead to an under-representation of smaller bees. Data collection may also have varied due to differences in the interpretation of the protocol among field technicians. To further validate the findings of this study, future research should focus on improving the accuracy of data collection, be long-term, and expand its geographic scope.

Conclusion

This study sheds light on bee-plant interactions (attraction) and the influence of bee trait groups. The pattern of plant species' attraction to bee species differed among bees with different traits. There is evidence both in this study and in others that several plant species belonging to Fabaceae and Asteraceae are vital for bee diversity. By including these plant species in AES schemes their effectiveness can be greatly enhanced. In particular, when catering to the needs of specialized bees which simultaneously cater to a broad diversity of bees.

Further, AES schemes such as flower strips can potentially be a crucial resource for bees in agricultural landscapes by increasing plant species diversity. Nevertheless, they also have the potential to act as a gateway for non-native plant species that threaten ecosystems. Furthermore, it is imperative to consider local conditions when creating seed mixes intended for AES schemes to ensure that conservation actions are tailored to address the specific challenges the area is facing. Moreover, due to the current climate crisis, seed mixes and other AES schemes might need to adapt to support future bee communities.

This study contributes to further understanding of the complex processes involved in bee species decline and which can enhance future conservation actions. Our conservation efforts can be made more effective and sustainable by considering the multiple factors that affect bee populations, such as trait-based interactions.

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