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# The influence of nesting resources on bee-flower interactions, revealed through functional traits, network structure and geology

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# Preface

This thesis was written as the final work of my master's degree in Natural Resource Management at the Norwegian University of Life Sciences (NMBU). The Directorate of Public Roads supported the project financially.

I would like to thank my supervisors Marit H. Lie and Markus K. A. Sydenham at NMBU, without whose brilliant guidance, this thesis would have been a much more challenging, and less inspiring task. I would also like to thank Astrid Brekke Skrindo at the Directory of Public Roads for superb support throughout the whole project. The collaboration with Kaj-Andreas Hanevik, during field and laboratory work, has been invaluable, and for this I want to thank him specially.

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# Abstract

Bees are the major pollinators in most parts of the world, but their diversity have declined as a consequence of environmental changes, during the last century. To counteract this decline, an understanding of the bees and their ecology is essential. Bees are closely connected to the flowers they interact with, and the strength and distribution of these interactions, are to a large extent decided by the functional traits of the interacting species. Bees are also dependent on nesting resources, and this may be a more important driver of bee community assembly, than previously thought. In this study, I assessed the influence of nesting resources, and trait-based ecological filtering on bee-flower interactions, using sandy sediments as a proxy for nest site availability for ground nesting bees.

I sampled bees in roadsides on glaciofluvial (n=8) and marine sediments (n=8), i.e. sandy versus non-sandy sediments. I tested how the probability of floral visitation and number of floral visits, was related to bee and floral functional traits, like sociality, nesting behaviour, tongue-length and flower morphology, as well as to sediment type. I analysed network structure by comparing nestedness and speciality, between sediment types and against null-models.

I found that the probability of floral visitation to actinomorphic flowers, and by short tongued bees was higher on glaciofluvial, than on marine sediments, and that short-tongued bees preferred actinomorphic flowers, while long-tongued preferred zygomorphic flowers. Furthermore, I found the network on glaciofluvial sediments to be less nested and more specialized than the network on marine sediments, and both networks to be less nested and more specialised than what could be expected by chance.

My findings show that bee-flower interactions are filtered on different scales. On a larger spatial scale, by environmental factors connected to nest site availability, and on a smaller scale, within habitats, by trait-matching of tongue length and flower morphology. The patterns of floral visitation, and variation in network structure can be explained by a greater occurrence of specialist interactions of mining bees on glaciofluvial sediment. Mining bees are dependent on sandy soils for excavating their nests, thus revealing the role of geological processes in shaping bee-flower interactions through the allocation of nesting resources.

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# Introduction

Land-use changes and other environmental changes has caused a decline in pollinator diversity in most of the world (Burkle et al., 2013; FAO, 2008; Kearns et al., 1998; Potts et al., 2010). An estimated 87.5 % of all angiosperms are pollinated by animals, and typically by insects (Ollerton et al., 2011). These plants and their pollinators constitutes one of the world's most important interaction networks and contribute greatly to both global biodiversity and ecosystem function (Burkle & Alarcón, 2011). Bees are generally considered the most specialised pollinators (Buchmann & Ascher, 2005) and are also the major pollinators in most geographic regions (Michener, 2007; Ollerton, 2017).

In Europe, 9 % of the assessed bee species are threatened as a consequence of agricultural intensification, climate change and urban development, during the last century (Nieto et al., 2014; Ollerton et al., 2014). In Norway, this number is over 30 % (Ødegaard, 2018). Habitat loss and disturbance has been suggested as the strongest drivers of the decline, especially in areas with extensive human land-use (Winfree et al., 2007; Winfree et al., 2009). This is in accordance with the reported declines of bees and bee pollinated plants in heavily populated parts of western Europe (Biesmeijer et al., 2006). As human land-use is predicted to increase, the prospects for bees are nor very good (Winfree et al., 2009). This has raised concern, and initiatives aiming for protection has come from all over Europe, as well as the European Union (IBPES, 2016). However, the development of effective management practises, rely on an understanding of the bees and their ecology (Murray et al., 2012; Potts et al., 2003).  Currently, we know too little about more than half of the bees in Europe to accurately assess their status, revealing an urgent need for more research on bee ecology (Nieto et al., 2014).

Studies on bee diversity typically focus on the richness and abundance of species, even though the interactions between species also are an important part of biodiversity (Bastolla et al., 2009; Olesen et al., 2007; Ollerton, 2017; Trøjelsgaard & Olesen, 2016). Bees are closely connected to the flowers they interact with, and knowledge about these interactions, are important to understand the species distribution and responses to environmental changes (Carman & Jenkins, 2016; Ollerton, 2017; Pellissier et al., 2017). Bee-flower interaction networks are, like other plant-pollinator networks, mutualistic bipartite networks that consist of two interacting groups of species, plants and pollinators, that both benefit from the interaction (Trøjelsgaard & Olesen, 2016), and were only interactions between the two levels are considered. A flower visitor is not necessarily a pollinator, since only visitation to a flower is observed. However, Ballantyne et al. (2015) found, by comparing pollination efficiency networks with flower-visitation networks, that even if the level of specialization often is underestimated in visitation networks, all flower visitors could be considered potential pollinators.

The stability and coexistence in a network are, to a great extent, decided by the structure of the network (Bastolla et al., 2009). Understanding of network structure, and how it is affected by disturbances, is therefore essential to address the loss of biodiversity (Butchart et al., 2010; Elle et al., 2012; Olesen et al., 2007; Pellissier et al., 2017). Plant-pollinator networks have a few typical characteristics (Elle et al., 2012). They are often highly nested (Bascompte et al., 2003), which means that specialists only interact with generalists while generalists interact with both specialists and generalists (James et al., 2012) or in other words, the specialists only interact with a small selection of the species that the generalists interact with (Bascompte et al., 2003). The nestedness adds to network stability (Bascompte & Jordano, 2007; Thebault & Fontaine, 2010) and can increase the number of interacting species (Bastolla et al., 2009), while the possibility for extinction cascades decreases as the most specialized species interact with the most generalised (Nielsen & Totland, 2014), but see James et al. (2012), which states that the only real predictor of stability is the number of links within networks.

As most mutualistic networks are highly nested (Bascompte et al., 2003), a majority of interactions are asymmetric, which means that one of the interacting partners is more specialized than the other (Bascompte & Jordano, 2007). Asymmetric specialisation is common in plant-pollinator networks (Vázquez & Aizen, 2004), and is believed to increase stability, by preserving coexistence and biodiversity (Bascompte et al., 2006). The level of specialisation for the entire network can be measured by a weighted mean of the specialisation of each species within the network (Blüthgen et al., 2007). A high level of specialisation, can possibly, reduce network stability (Elle et al., 2012), but the overall stability is often more influenced by the presence of one or a few important species (Ives & Carpenter, 2007). Most species have few interactions, and only a few have more interactions than what could be expected by chance (Nielsen & Totland, 2014). Most interactions are also quite generalised and totally obligate interactions are rare (Kearns et al., 1998). Specialization can also be linked to abundance, meaning that in networks were species are not equally abundant, parts of the specialization can be explained by species various abundances (Dormann et al., 2017).

Recently, it’s been emphasized that studies of networks also should include information about functional traits (Tylianakis & Morris, 2017), as they can influence network structure by selecting for some interactions before others (Hagen et al., 2012; Maglianesi et al., 2014;

Pellissier et al., 2017). A species functional trait is a well-defined, comparable, property that has a strong impact on the fitness of individuals and explains differences in the average performance of species (McGill et al., 2006). Functional traits are therefore also related to ecosystem functioning (Cadotte et al., 2011).

The responses of species to environmental disturbance are not random, but are to a large extent, decided by their traits (Aguirre-Gutiérrez et al., 2016), and both abiotic and biotic factors can function as a trait-based ecological filter, excluding species with unfavourable traits (Houseman & Gross, 2006). Solitary bees are often more negatively affected by disturbance, than social bees, at least in northern Europe, where bumble bees are the only wild, obligate, social species (Murray et al., 2012; Steffan-Dewenter et al., 2002; Winfree et al., 2009). Specialist species may also be more negatively affected by disturbance than generalist species (Biesmeijer et al., 2006), which can be connected to sociality as solitary species are typically more specialized than social species (Michener, 2007). There are also indications that disturbance can be positive for ground nesting bees, as this increase the availability of bare soil, but negative for aerial nesting bees, since land use often leads to destruction of nest sites above ground (Williams et al., 2010). A functional traits approach can focus on many species at a time, and is therefore well suited to address climate and land-use changes (McGill et al., 2006). However, it is not fully understood how the species response to long-term changes, is influenced by their functional traits (Aguirre-Gutiérrez et al., 2016).

Agricultural areas have been shown to be important for bees (Winfree et al., 2007). These areas might also provide good opportunities for effective conservation efforts (Carman & Jenkins, 2016), especially since moderate levels of human land-use can be combined with management practises (Winfree et al., 2007). During the last Century a lot of semi natural grassland have been converted to other land use types, reducing the amount of suitable habitat for bees in anthropogenic landscapes (Murray et al., 2012; Steffan-Dewenter et al., 2002; Stoate et al., 2009; Tilman et al., 1994), and as little as 1 % of the hay meadows that once occurred in Europe, still remains (Norderhaug & Svalheim, 2009). Agricultural intensification also results in the disappearance of field edges, as documented in both England and Norway (Fry et al., 1998; Goulson, 2003). There are indications that there is a positive correlation between the amount of semi-natural patches in the local area and the diversity of solitary bees (Steffan-Dewenter et al., 2002). Artificially disturbed areas, like roadsides, can therefore be important to conserve wild bees (Cousins, 2006; Holzschuh et al., 2007), and roadsides are considered substitute habitat for many species dependent on open-semi natural grasslands (Hopwood, 2008; Saarinen et al., 2005). However, some aspects of roadsides may not be positive. The road may act as barrier for many insects (Bhattacharya et al., 2003; Muñoz et al., 2015), and for bees and wasp, this effect, are often stronger on small species with inferior dispersal abilities (Andersson et al., 2017). Roads can also cause high mortality rates of insects trying to cross (Baxter-Gilbert et al., 2015; Muñoz et al., 2015). Nevertheless, roadside management, which means repeated disturbances through cutting of the vegetation, give roads the same ecological characteristics as traditionally mowed biotopes (Tikka et al., 2001), and there are indications that roadsides can function as dispersal corridors in strongly fragmented landscapes (Hopwood, 2008). The loss of  flowers is one of the reasons for bee declines in agricultural areas (Gathmann et al., 1994; Ollerton et al., 2014), and in areas where flowers are scarce, roadsides can be turned into good foraging habitats, by sowing preferred foraging plants (Pywell et al., 2005). In North America, Hopwood (2008) found that restored roadsides, planted with native plants, contained more bees than unrestored.

Unlike their wasp ancestors, bees are dependent on floral resources both in the juvenile and adult stages (Michener, 2007) and are, typically well equipped, with feathery hairs and pollen baskets (scopa), to collect it (Schoonhoven et al., 2005). Bees also have a specialised tongue to gather nectar, and the length of it, decides to a large extent their flower preferences and forage efficiency (Michener, 2007; Schoonhoven et al., 2005), and can together with other traits such as body size and flower morphology be determinants of possible interactions (Dormann et al., 2017). Some bees, especially bumblebees, can also bite trough the side of the flowers and extracting nectar without going near the anthers, thereby depriving the plant of pollination (Michener, 2007).

Bees exhibits various levels of dietary specialisation. Many of the solitary bees are very specialized and utilises only a flower species within a single genus (so-called oligolectic). However, the majority of species, are more generalised (so-called polylectic), and visits many different flower species, even if they often show a preference for a few specific families (Michener, 2007). The period of flight activity for solitary bees can sometimes be as short as a couple of weeks, and therefore it is possible for them to specialise in flowers with short blooming seasons. Social bees on the other hand, are often active for longer periods than most flower species bloom, and must therefore utilize many different flower species to sustain them throughout the season (Hagen et al., 2012; Michener, 2007). Because of their dependence on floral resources the species composition within bee communities is closely related to the species composition within plant communities (Potts et al., 2005) and floral diversity and abundance have been shown to play an important role in structuring bee communities (Potts et al., 2003).

In addition to flower resources bees also need a place to rear their young (Michener, 2007), so the quality of their habitat is dependent on both forage and nesting resources (Potts et al., 2005). Bees are central place foragers, as the female forage from the nest, and the floral resources available are determined by the location of the nest and the flight distance of each species. (Murray et al., 2009; W. Schoener, 1979; Westrich, 1996).

Bees have a diverse set of nesting strategies. They can be miners that excavate their own nests in the ground, masons that use pre-existing cavities, and carpenters that excavate their own nests in woody material, while social species use different type of nests, both below and above ground (O' Toole & Raw, 1991). Social species form colonies, with an egg-laying queen, and workers that do the foraging and take care of the broods. The solitary species, rely on the female to unaided construct the nest and provide food for the young (Michener, 2007). In addition to social and solitary species, there are cleptoparasitic species, which lay their eggs in other bees nests, and the larvae feeds on food provided by the host (Potts et al., 2005). Sociality can have a large influence on network structure, because of the great difference in abundance of individuals between solitary and social species, which ranges from a few to several thousand individuals in each nest (Hagen et al., 2012).

The majority of bees are miners and excavate tunnels in the ground (Michener, 2007), but there are also ground nesting species, typically bumble bees, that use pre-existing cavities (Goulson, 2003). Both the amount of bare ground and the quality of the soil are proposed as, important factors for ground nesting bees (Potts et al., 2005). Also other environmental characteristics like, litter cover (Grundel et al., 2010), slope of the ground (Burkle & Alarcón, 2011), soil compaction (Wuellner, 1999) and the amount of cracks or holes in the ground (Potts et al., 2005), have been suggested as factors influencing nest site availability.

Many ground-nesting bees are dependent on sandy soils (Cane, 1991; Potts & Willmer, 1997), and the amount of sand in the soil varies between different types of sediment. In Norway, and in other mountainous areas at high latitudes, the distribution of sediments is to a large extent, decided by events during the last ice-age (Fossen, 2008; Olsen et al., 2013). Large areas contain exposed bedrock, or bedrock with a thin layer of sediment (Andersen, 2000; Olsen et al., 2013). In areas with a thicker sediment cover, this consists largely of till, but also of marine and glaciofluvial sediments (Olsen et al., 2013). Marine sediment consists of silt and clay, deposited at the bottom of the sea, and consequently these areas are situated below the postglacial marine limit (c.200 m a.s.l.) (Fossen, 2008; Olsen et al., 2013). Sand can occur in small patches, both natural and artificial, but the majority of the area is dominated by finer material. Glaciofluvial sediments, on the other hand, consist almost exclusively of sand and gravel, deposited by rivers of glacial meltwater. The material was deposited when these rivers reached the edge of the ice-cap, and in places where the retraction of this edge stopped for long periods of time, large glaciofluval deltas where created (Olsen et al., 2013). As these geological processes have distributed certain resources throughout the landscape, they may also have influenced the distribution of organisms dependent on these resources. The availability of nest sites for many bee species may coincide with the presence of sandy soils, and can therefore be explained by these processes. In this study, I assessed the influence of nesting resources and trait-based ecological filtering on bee-flower interactions, using sandy sediments as a proxy for nest site availability for ground nesting bees. Specifically, I hypothesized that:

1. Sediment type functions as an environmental filter by selecting for bees according to their functional traits. Ground nesters should prefer sandy sediments, due to a better nest site availability, while aerial nesters, which are dependent on nesting resources, not necessarily coherent with sediment type, should be unaffected.
2. Within habitats, species functional traits will influence bee-flower interactions, particularly through the trait-matching of tongue-length and flower morphology.
3. Network structure will be affected by sediment type, and because of higher nest site limitation on the marine sediments, this network should be less nested and less specialized, than the network on glaciofluvial sandy sediments. Based on the typical characteristics of other mutualistic networks (Bascompte et al., 2003; Blüthgen et al., 2007), both networks should be more nested and more specialized than what could be expected by chance.

# Method

## Study area

I established study sites within 16 stretches of roadside, along county roads in south-eastern Norway, (between latitudes 60,09- 60,32 N and longitudes 11,19- 10,99 E). The study area was chosen because it contained areas dominated by sediment with sandy soils (glaciofluvial), or by sediment without sandy soils (marine) (Fig. 1), and was therefore well suited to examine the influence of sand on the bee community. Roadsides are also relatively similar across environmental gradients, and are well suited to be compared across these gradients. The area is 27 by 7 km, located in the southern boreal vegetation zone, slightly oceanic vegetation section (Moen et al., 1998), and heavily affected by human-land use. Parts of the area constitutes Norway´s largest glaciofluvial delta (Olsen et al., 2013) and consists of large deposits of sand and gravel from the last ice-age. The landscape in the area on glaciofluvial sediments is dominated by boreal forests and semi-natural open areas, and the main land use are forestry, building ground and extraction of sand and gravel. Several areas are protected due to their special geology, limnology and flora. Marine sediment consists mostly of silt and clay and the main land-use is agriculture, but the landscape is crossed by rivers and ravines, with both coniferous and deciduous forests. Some of the ravine-landscapes, and some of the larger connected agriculture areas, are protected, as they are relatively rare and constitute valuable habitat for both fauna and flora (Wold et al., 2012).

## Study design

My study sites where established in places where they were not completely surrounded by forest, and where the Directorate of Public Roads, considered it safe to work, i.e. where we were easily detected by traffic. All sites where 50 m long, between 3 and 6 m wide, and contained at least three different angiosperm families when inspected in June. Minimum distance between sites was 1000 m, which is farther than most solitary bees fly to forage (Gathmann & Tscharntke, 2002), but within flight distance of most bumblebees (*Bombus sp.*) (Walther-Hellwig & Frankl, 2000). The abundance of bee nests can be difficult to quantify, so proxies for potential nest site availability are often used (Sardiñas & Kremen, 2014). I made the assumption that the availability of nesting sites for ground nesting bees is dependent on access to sandy soils, and eight of the sites (s1 to s8), where located on glaciofluvial sediment, and eight (m1 to m8), on marine sediment (fig 1). Numbers ‘1’- ‘8’ reflect a south to north gradient where ‘1’ is the southernmost and 8 the northernmost. I used quaternary geological maps (NGU, 2017), to identify areas with different sediments.

In Norway, where this study was conducted, roadsides are managed for traffic safety, which often comprises cutting once or twice a year (Vegdirektoratet, 2014). My study sites where marked with posts in the beginning of June, and the vegetation was left uncut until the samplings where finished in August. The roadsides outside my sites, where cut at least once during the summer. Honeybees (*Apis mellifera*) were not the focus of this study, and were excluded from the analyses. 163 Honeybees were sampled in sites s1-s8, and 44 in sites m1-m8. Their nesting availability are decided by humans and not environmental factors, and the higher abundance on s1-s8, probably reflects the beekeepers want to have the honeybee hives in areas with heather, i.e. sandy areas.

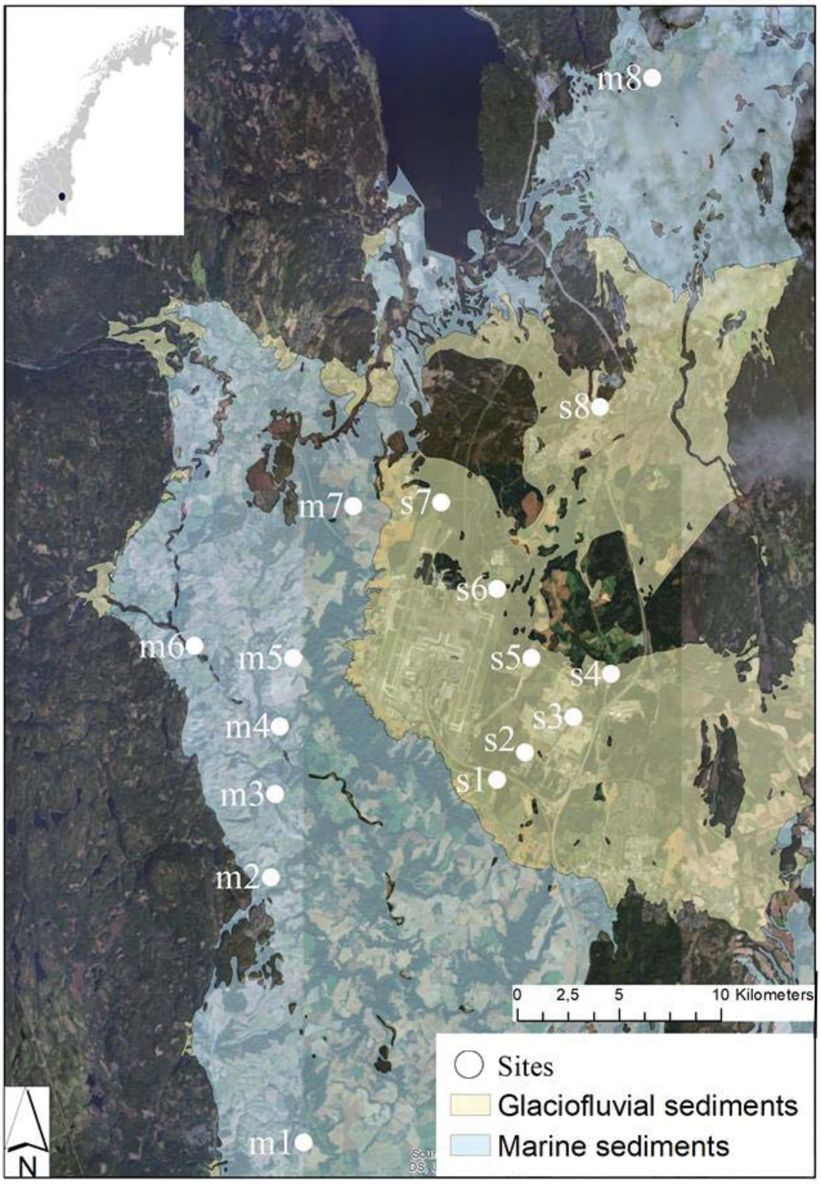


**Figure 1.** Maps of the study sites with sediment types within the study area (NGU, 2017).

Study area selection, site selection, field work and laboratory work were conducted in collaboration with a fellow student, Kaj-Andreas Hanevik. The data set used in this study was also used in a master’s thesis on bee species richness and abundance (see Hanevik, 2018).

## Data sampling

I sampled bees twice at each site together with K. A. Hanevik. The first sampling was conducted between the fourth and thirteenth of July and the second between the fourth and seventeenth of August. Species with flight times outside of these periods could not be sampled. However, the periods are within the time of peak activity for the majority of bee species in Norway, so our samplings should have the potential to cover a large proportion of species. Of the 117 different bee species that have been observed foraging in Norway, between 2008 and 2017, 68 species or 58 % have been observed during July or August (table 1).

To minimize variation in weather conditions between the samplings on different sediment types, one site from each sediment type, were always sampled on the same day and these pairs where sampled from South to North. This means, that on the first day of each sampling round, we sampled the southernmost site on marine sediment, m1, and the southernmost site on glaciofluvial sediment, s1, and on the last day we sampled the two northernmost sites on each sediment type, m8 and s8. We sampled for one hour, between 11 am and 6 pm, on days with little or no clouds with temperatures above 15 C, and wind speeds below 5 m/s. There was no precipitation, 30 min prior to, and during the samplings. Sampling was conducted by Kaj-Andreas Hanevik and myself, walking back and forth, along a fixed transect (50m) running parallel to the road, catching flower-visiting bees with sweep nets. For each sampled specimen, the visited flower species was registered, as well as the identity of the collector. The bees were collected in plastic containers, containing 96 % ethanol, and brought back to the entomology laboratory at NMBU for identification.

**Table 1.** Number of bee species observed foraging per month in Norway 2008-2017, in total, 117 species have been registered during this time (Artsdatabanken, 2018).

| Month | Number of species |
|---|---|
| January | 0 |
| February | 0 |
| March | 10 |
| April | 24 |
| May | 52 |
| June | 73 |
| July | 77 |
| August | 60 |
| September | 28 |
| October | 6 |
| November | 1 |
| December | 0 |

Weather conditions such as, temperature, wind speed, and time of day, was registered for each sampling, as this could, potentially have an effect on the result (Appendix 1). However, the pairwise sampling scheme, and the limits for temperature and wind speed, restricts possible variation between these measures for each sampling, and it is unlikely that weather had a considerable impact on the results.

The floral resources were quantified by estimating the coverage of angiosperms in bloom immediately after each collection-round. Only plant species with one or more recorded bee-visits, were included. Three levels where used for flower abundance, and each species was categorized as, more than 50 %, between 10 and 50 % or less than 10 %, in each plot. When merging these two estimates, all values over 50%, where set to 75, all values between 10% and 50%, where set to 30, and all values less than 10%, where set to 5. So, for example, a plant with and estimated coverage of over 50 % at both samplings at a site, ended up with a total coverage of 150 for that site. Subsequently this value no longer reflects the percentage coverage, but is a relative value, only useful to compare sites in this study. Shannon diversity and species richness was calculated from the abundance measures after the two indexes for each site was merged. Shannon diversity was calculated with function "diversity", in Vegan package (Oksanen et al., 2017) in R. I used t-tests in R to test if the vegetation differed between sediment types. Shannon diversity, species richness and flower abundance of zygomorphic and actinomorphic flowers at each site were tested separately for differences between sediment types.

## Laboratory work

All collected bees were pinned, labelled and identified to species in the entomology laboratory at NMBU, by Kaj-Andreas Hanevik and myself. A reliable separation of *Bombus lucorum, B. terrestris, B. cryptarum* and *B. magnus*, is not possible to do without the use of DNA (Falk & Lewington, 2015), and since we had no possibility for DNA analysis, these species were all labelled *Bombus sensus strictu*. Species identifications were verified by Markus A.K. Sydenham (NMBU). Keys used for the identifications, was (Falk & Lewington, 2015; Løken, 1985; Ødegaard et al., 2015). A leg from each of the solitary bees was pulled of, labelled and put on ethanol, to enable future molecular identification.

## Statistical analyses

### Functional traits

The functional traits analyses were done to quantify the effect of species traits and environmental conditions on the occurrence and abundance of species. Clepto-parasitic bees, 63 individuals, of 6 different species were excluded, since their occurrence in an area, to a large extent, is decided by their hosts. The structuring of the data was done by the method explained by Jamil et al. (2013), and comprises the creation of three data tables: a bee species by traits table; a site by environment table; and a bee species abundance per site table. In the bee species by traits data table (Appendix 3), all bees where assigned as solitary or social, ground or aerial nesting and short- or long-tongued. Information on traits where obtained from the literature (Falk & Lewington, 2015; Ødegaard et al., 2015; Ødegaard, 2018). Taxonomically all bumblebees belong to the long-tongued bees, so the tongue length of the bumblebees refers to the length of their tongue relative to other bumblebees. In the site by environment table (Appendix 4), the flowering plants in each site, were divided according to flowersmorphology, into zygomorphic or actinomorphic, for which Shannon diversity, species richness and abundance was calculated separately. Information about flower morphology where obtained from the literature (Lid et al., 2005). All traits were selected on the basis of their relevance to this study, but also because of their widespread use in studies of bees, in general. The site by environment table also contained information about substrate type. Information on substrate where obtained from a sediment database (NGU, 2017). The site by bee species abundance table, is a quantitative interaction matrix with bee species in rows and flowering plants in columns (information available in fig. 2 & 3).

These three data tables where then merged into one data table, with all possible species-by-site combinations. The flowering plants at each site was divided according to flower morphology, so each site was treated as two sites, one with actinomorphic and one with zygomorphic flowers. This means a total of 32 sites. Two columns were added, one where all species where registered as present or absent (1/0), and one were abundance of each species was registered. I tested for non-independence among the quantitative variables. Species richness of flowering plants was excluded due to a strong correlation with Shannon diversity of flowering plants (cor. = 0.729), while *Shannon diversity* and *flowerabundance* was assessed as independent (cor.=0.096).

I tested if the probability of floral visitation was related to trait-environment interactions. I used a binomial generalized mixed effects model (GLMM) in R library lme4 (Bates et al., 2015) to modell the presence or absence of bees on zygomorphic or actinomorphic plants within sites. To account for the variation in occurrences between sites and species, and to address possible pseudo replication, species and site identity, were included as random effects. The variable flower abundance variable was log-transformed (ln (x+1)) because I expected species occurrences and abundances to show non-linear increases with resource availability. Effect of collector, was tested by setting collector as a single explanatory variable and performing a likelihood ratio test (LRT). Collector was not significant for *probability of floral visitation* (LRT= 0.214, P= 0.644) and was not included in the analysis.

I tested if the abundance of floral visits made by bees were related to trait-environment interactions. Before the analysis of number of floral visits, all rows with abundance 0, were removed from the data set. Abundance in this analysis, therefore refers to abundance after presence has been established (Boulangeat et al., 2012). The effects were analysed by fitting a generalized mixed effects model (GLMM) in R library lme4 (Bates et al., 2015), with *number of floral visits* as response. Species and site identity, were included as random effects. I assumed that flower abundance had an effect on the abundance of bees (Potts et al., 2003), and to neutralize the variation in flower abundance between sites, *flowerabundance*, was set as an offset variable. Effect of collector, was tested by setting collector as a single explanatory variable. A likelihood ratio test (LRT) was performed. Collector was not significant for *number of floral visits* (LRT= 0.018, P=0.893), and was not included in the analysis. I first fitted a Poisson GLMM but because of dispersion issues the model was refitted using a negative binomial mixed effect model.

For both models, I conducted a pre-selection of variables, where all interaction-terms, where tested separately (Chi-square test, $p < 0,05$). Then a sequential backwards elimination of non-significant terms ($p>0.05$), using likelihood ratio tests (LTRs), were performed with function “drop1”. None of the final models reached convergence so I used an optimization procedure to address this issue, function “glmercontroll”, method=bobyqa, package optimx in R. Model validation was done graphically with QQ-plots.

### Network structure

I created two bee-flower visitation networks by pooling the 16 samplings on plots S1 to S8, to one network, called S-web and the 16 samplings on plots M1 to M8, to a second network, called M-web. Bees were in rows and plants in columns and the interactions were quantified by the number of interactions between species. The networks were analysed as bipartite networks, using the *bipartite* package and *vegan* package, in R (Dormann et al., 2008; Oksanen et al., 2017). As proposed by Elle et al (Elle et al., 2012) I analysed networks for nestedness, specialisation and specialization asymmetry. (Dormann et al., 2017). Connectance and modularity are other often used measures of network structure (Elle et al., 2012), but since they may be strongly affected by network size (Blüthgen et al., 2006; Olesen & Jordano, 2002; Olesen et al., 2007; Winemiller, 1989) they are not used in this study. In the analysis of network structure, cleptoparasites were included.

I calculated the nestedness of each network using the index, $\text{NODF}_{\text{weighted}}$, in function “networklevel”. $\text{NODF}_{\text{weighted}}$, is based on NODF (Almeida-Neto et al., 2008), which is an nestedness estimator for presence/absence data, but in accordance with the estimator WNODF (Almeida-Neto & Ulrich, 2011), it estimates nestedness using quantitative data. Both NODF and WNODF have shown greater consistency and accuracy than other measures of nestedness (Almeida-Neto et al., 2008; 2011). High values indicate high levels of nestedness. Nestedness may increase with network size (Bascompte et al., 2003), but is quite robust against sampling effort (Nielsen & Bascompte, 2007). To test if the observed $\text{NODF}_{\text{weighted}}$ was statistically significant, I used null-models with 1000 permutations and fixed row and column marginal sums, in function “null-model”. Gotelli (2000) showed, that the use of fixed row and column marginal totals in null models, do not prevent the detection of patterns. Standardized values were calculated with equation 1.

$$z - score = \frac{(observed - mean, null)}{se, null}$$

**Equation 1**: z-score is the standardised value, observed, is the observed value, mean, null is the mean value from the null-models, and se, null is the standard error from the null-models. Z-score <-2 or >2 means the difference between observed and null model values are significant.

Specialization was calculated, using index H2, which is a measure of the overall level of selectiveness or specialization in bipartite networks, and is comparable between networks as it is rather unaffected by network size and asymmetry (Blüthgen et al., 2006; Fründ et al., 2016). H2 describes to which extent an observed network differs from a network with random interactions, and is derived from the weighted sum of the specialization (d’) of the species in the network. H2 ranges from 0 to 1, where 0 means no specialization, and 1 means complete specialization. For the entire networks, H2 was calculated using function “networklevel”. Also for specialization, null-models, with 1000 permutations and fixed row and column marginal sums, function “null-model”, was used to determine the difference in specialization of observed networks with networks of random interactions. Standardized values where derived with equation 1.

Specialization asymmetry was calculated by calculating specialization (H2) for plants and bees separately, according to (Blüthgen et al., 2007). d’ was derived from function “dfun”, and H2 was calculated with equation 2.

$$\frac{H2 = \sum_{i=1}^{n} d'_i * n_i}{n}$$

**Equation 2**: H2 is derived from d’ for each species weighted by its number of individuals. For plants, individuals mean visits.

Distinction from random networks for the separate levels was derived from null-models, with 999 permutations and fixed row and column marginal sums, in function “permatfull”. Standardized values where derived with equation 1.

# Results

A total of 910 individuals of 45 species of wild bees visiting 41 different species of flowering plants were sampled (Appendix 2). On marine sediment (Fig. 2), 336 individuals of 23 species of bees were sampled on 23 species of flowering plants (Appendix 2). On glaciogluvial sediment (Fig. 3), 574 individuals of 42 species of bees were sampled on 31 species of flowering plants (Appendix 2).

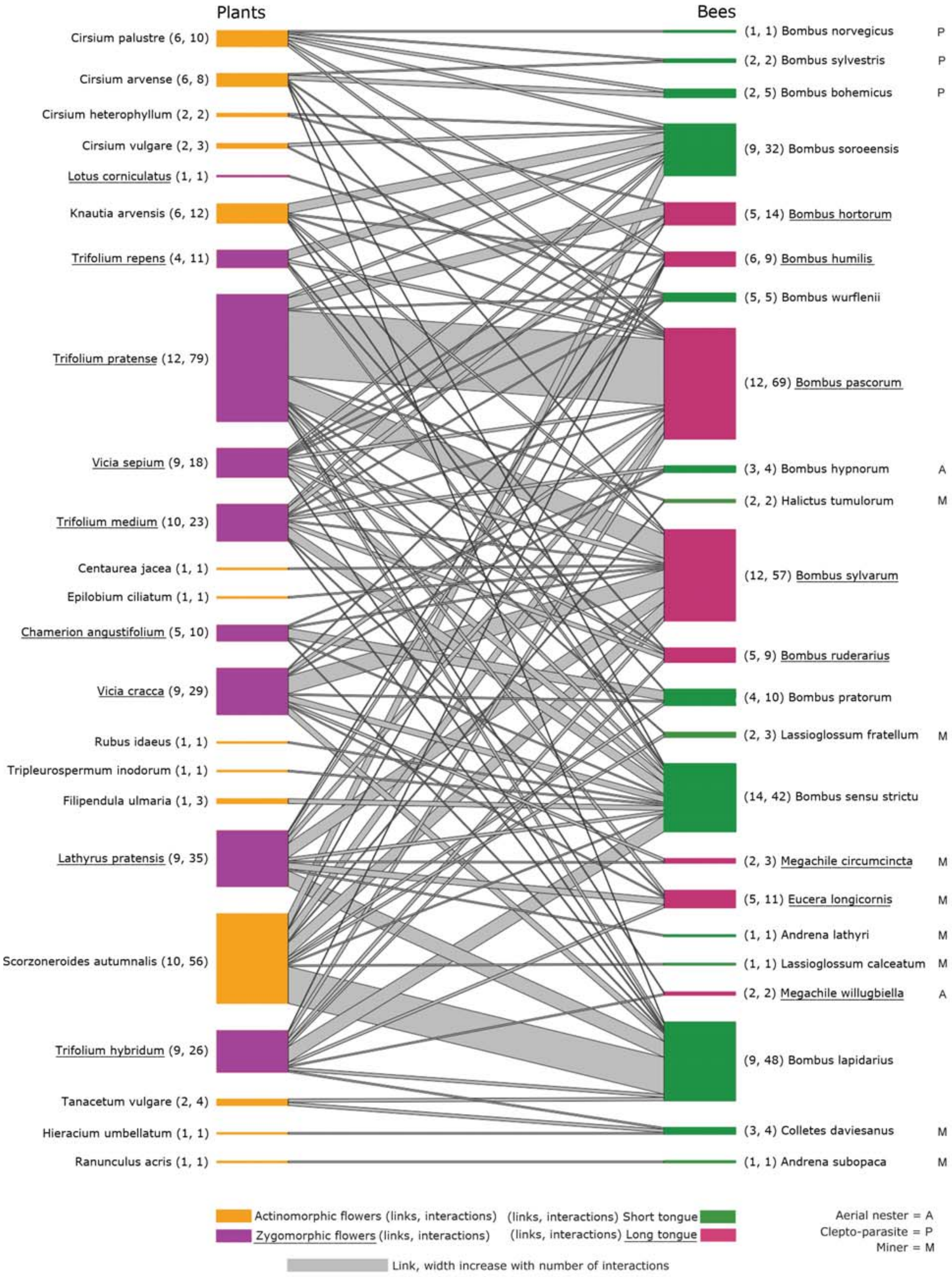


**Figure 2.** The network sampled in roadsides on marine sediments, sites m1-m8. A link is the presence of one or more interactions between a pair of species, while an interaction is between two individuals. The same pair of species can only have one link, but several interactions. All non-Bombus are solitary, while all Bombus, except the clepto-parasites, are social. All non-miners and non-aerial nesting species, are ground nesters that use pre-existing cavities. The figure is made with function "plotweb in package bipartite (Dormann et al., 2008) in R.

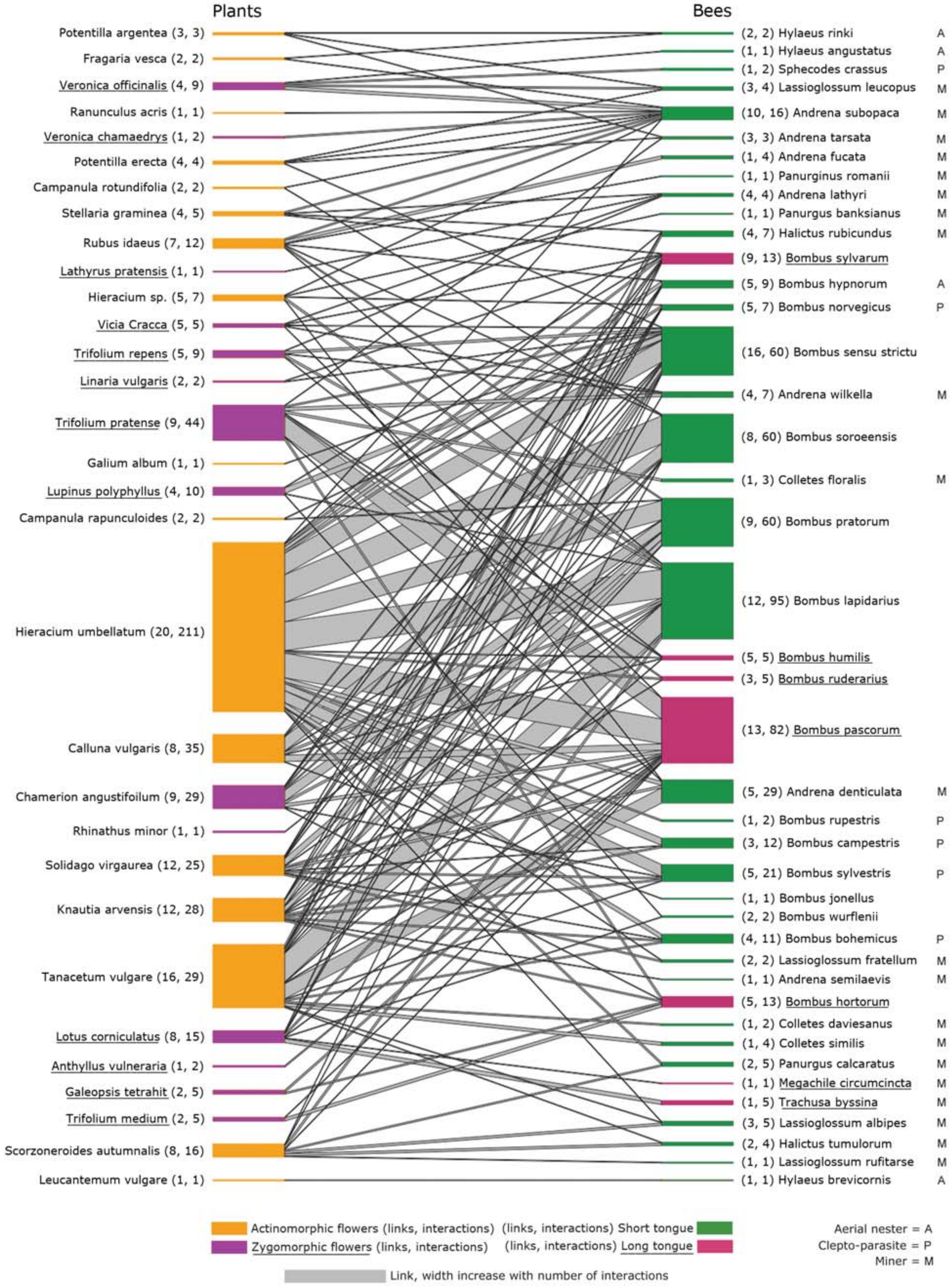


**Figure 3**. The network sampled in roadsides on glaciofluvial sediments, sites s1-s8. A link is the presence of one or more interactions between two species, while an interaction is between two individuals. The same pair of species can only have one link, but several interactions. All non-Bombus, except the clepto-parasite S. crassus, are solitary, while all Bombus, except the clepto-parasites, are social. All non-miners and non-aerial nesting species, are ground nesters that use pre-existing cavities. The figure is made with function “plotweb”, package bipartite (Dormann et al., 2008) in R.

## Functional traits

The functional traits analyses, consisted of 847 individuals of 39 species of bees (cleptoparasites excluded). Of them 705 individuals (83 %) were bumblebees (Bombus spp.), and 142 individuals (17 %) solitary bees. In total, 298 bees were long-tongued and 549 were short-tongued. The vast majority of the bees, 828 (97,8 %), were ground nesters and only 19 individuals of five different species were aerial nesters. A total of 41 species of plants where visited, 16 of them had zygomorphic flowers, and 25 had actinomorphic flowers.

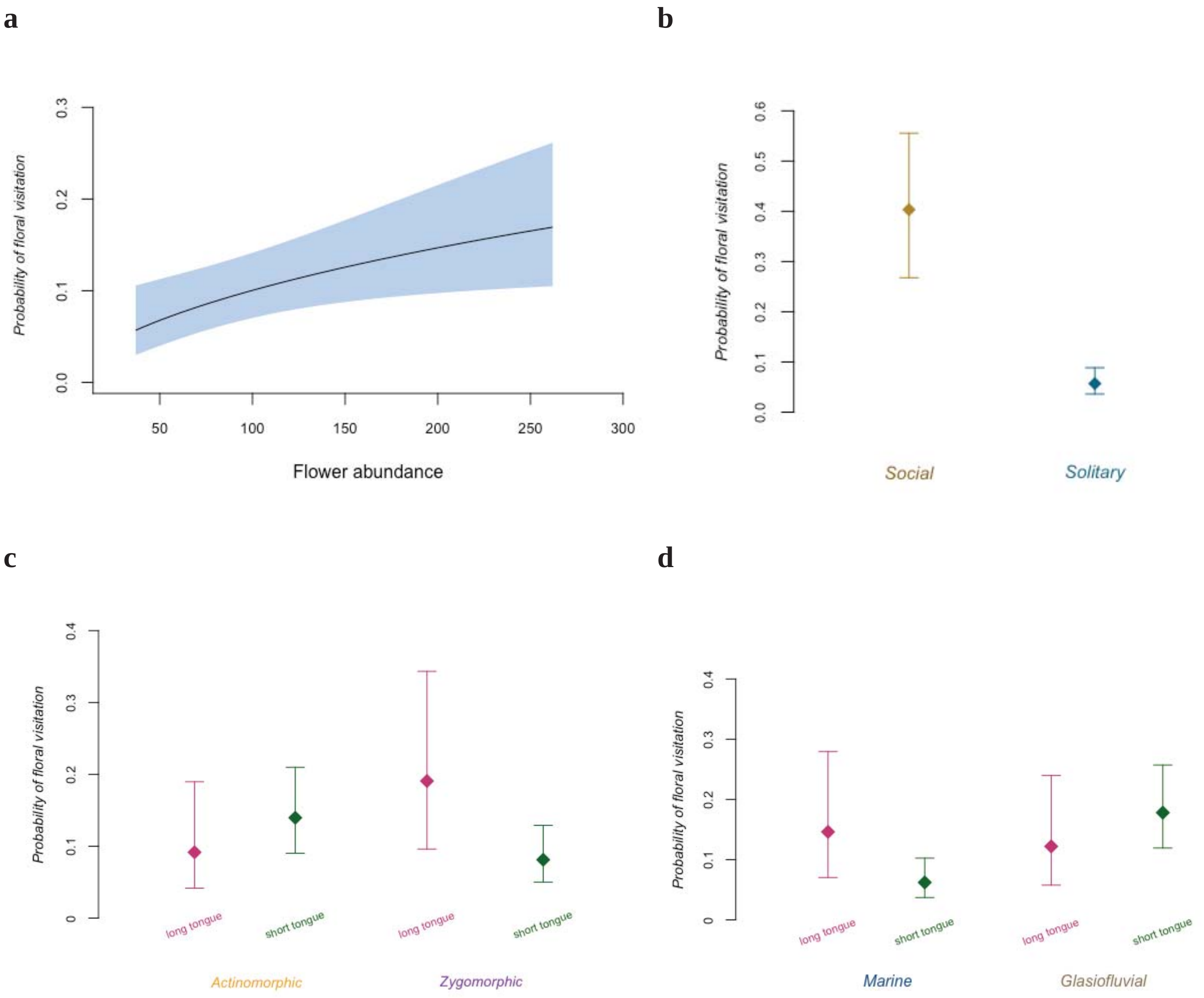
### Probability of floral visitation

The final model included the main effect term *log(flowerabundance+1* (LRT=6.21, P<0.05), showing that the probability of floral visitation of an average bee increased with increasing abundance of flowers (Table 2, Fig. 4). The other main effect term included in the model was *Sociality* (LRT=26.34, P<0.001), showing that the probability of floral visitation was higher for social than solitary bees (Table 2, Fig 4).

The interaction term *Flowermorphology* × *tongue* (LRT=13.79, P<0.001), showed that the probability of floral visitation of long tongued bees was higher on zygomorphic than on actinomorphic flowers, while the probability of floral visitation of short-tongued bees was higher on actinomorphic flowers (Table 2, Fig. 4).

The interaction term *Sediment* × *tongue* (LRT=12.38, P<0.001), showed that short-tongued bees was affected by sediment type. The probability of visitation for short-tongued bees was higher on glaciofluvial, than on marine sediments, while the long-tongued bees, were seemingly unaffected by sediment type (Table 2, Fig. 4).

The interaction term *Flowermorphology* × *sediment* (LRT=5.08, P<0.05), showed that sediment had an effect on the probability of floral visitation on actinomorphic flowers, but not on zygomorphic flowers. The probability of visitation, on actinomorphic flowers, was higher on glaciofluvial sediments, than on marine sediments (Table 2, Fig. 4).



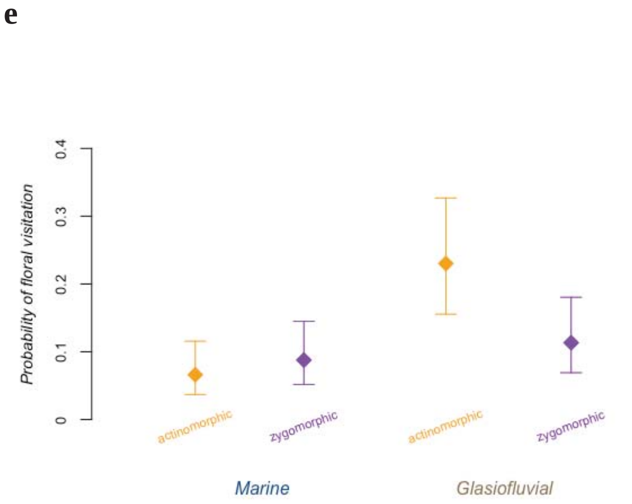


**Figure 4.** Probability of floral visitation at different flower abundances (a), and for social and solitary bees (b). Blue shaded region shows 95% confidence interval. Probability of floral visitation, by long and short-tongued bees, on actinomorphic and zygomorphic flowers (c), by long and short-tongued bees on marine and glaciofluvial sediments (d), and on actinomorphic and zygomorphic flowers on marine and glaciofluvial sediments (d).

**Table 2.** Analysis of probability of floral visitation. Results from binomial GLMM.

| **Fixed effects** | B | SE | Z | P |
|---|---|---|---|---|
| *Intercept* | -*3.85* | *1.22* | *3.16* | *< 0.01* |
| *Sociality (solitary)* | -*2.42* | *0.39* | -*6.18* | *< 0.001* |
| *log(flowerabundance+1)* | *0.63* | *0.25* | *2.51* | *< 0.05* |
| *Flowermorphology × sediment* | -*1.16* | *0.49* | -*2.38* | *< 0.05* |
| *Sediment × tongue* | *1.39* | *0.39* | *3.53* | *< 0.001* |
| *Flowermorphology × tongue* | -*1.46* | *0.39* | -*3.72* | *< 0.001* |
| **Random effects** | variance | SD | Obs. | groups |
| *Species identity (intercept)* | *0.85* | *0.92* | *1248* | *39* |
| *Site identity (intercept)* | *0.13* | *0.36* | *1248* | *32* |

### Number of floral visits

*Sociality* was included as a main effect also in this model (LRT=16.96, P < 0.001), and the number of floral visits was higher for social than for solitary bees (Fig. 6a, table 5).

The number of floral visits was affected by tongue-length and flower morphology, and as in the analysis of probability of floral visitation, the interaction term *Flowermorphology x tongue* was included in the final model (LRT=13.34, P < 0.001). On sites with registered visits, the number of visits of long tongued bees was higher on zygomorphic, than on actinomorphic flowers, while the number of visits of short-tongued bees was higher on actinomorphic than on zygomorphic flowers. (Table 3, Fig.5).

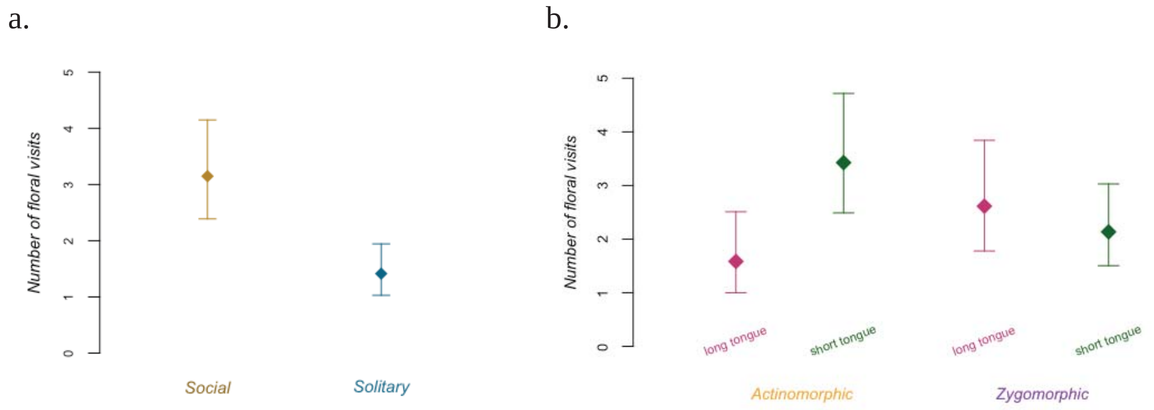


**Figure 5.** Number of floral visits by (A) social and solitary bees, and (B) long and short-tongued bees on actinomorphic and zygomorphic flowers.

**Table 3.** Analysis of the number of floral visits of bees. Results from negative binomial GLMM. The response, shall be understood as the number of floral visits after presence has been established, since all sites with an abundance of 0, was removed from the data set before the analysis was done.

| **Fixed effects** | B | SE | Z | P |
|---|---|---|---|---|
| *Intercept* | *-4.12* | *0.23* | *-17.67* | *< 0.001* |
| *Sociality (solitary)* | *-0.80* | *0.19* | *-4.12* | *<0.001* |
| *Flowermorphology x tongue* | *-0.97* | *0.24* | *-4.01* | *< 0.001* |
| **Random effects** | variance | SD | Obs. | groups |
| *Species identity (intercept)* | *0.12* | *0.33* | *239* | *39* |
| *Site identity (intercept* | *0.13* | *0,37* | *293* | *32* |

## Network structure

In contrast to my hypothesis the network on marine sediments (M-web) was more nested than the network on glaciofluvial sediments (S-web), and both networks were significantly less nested then what could be expected by chance (Table 4).

In line with my hypothesis the level of specialisation was highest for the S-web, and significantly higher than expected by chance for both networks. The two levels, separately was also more specialized than what could be expected by chance. Bees and plants, separately, where also more specialised in the S-web than the M-web. This also means that the plants were more specialised than bees in both networks. Even if the z-scores were higher for plants than bees, in the S-web.

In the S-web 58 % of the species were bees, and 42 % plants, which yields a web asymmetry of 0.15. In the M-web there were as many bees as plants, and subsequently the web asymmetry was 0. As clepto-parasitic species were included, all bees represented in figure 2 and 3, were included in the network structure analysis.

**Table 4.** Observed values for M-web and S-web, mean values (mean) and standard error (se) for null models, and z-score (equation 1). Z-score <-2 or >2 means that the difference between observed and null model values are significant. Calculations were done using *bipartite package (Dormann et al., 2008) in R. NODF*$_{weighted}$ *is the index for nestedness, and H2 is the index for specialisation.*

| | observed | mean null | se null | z-score |
|---|---|---|---|---|
| **NODF** $_{\mathbf{weighted}}$ | | | | |
| M-web | 25.57 | 39.90 | 3.28 | -4.37 |
| S-web | 13.23 | 33.60 | 2.67 | -7.63 |
| **H2 total** | | | | |
| M-web | 0.29 | 0.11 | 0.01 | 15.79 |
| S-web | 0.36 | 0.11 | 0.01 | 25.06 |
| **H2 Plants** | | | | |
| M-web | 0.26 | 0.09 | 0.01 | 17.74 |
| S-web | 0.31 | 0.10 | 0.01 | 25.43 |
| **H2 bees** | | | | |
| M-web | 025 | 0.10 | 0.01 | 16.40 |
| S-web | 0.27 | 0.09 | 0.01 | 28.29 |

## Vegetation

The vegetation did not show any significant differences ($P<0.05$) between the two different sediment types, even though the difference in flower abundance of actinomorphic flowers, was nearly significant with a t-test p-value of 0.066 (Table 5, for data on each site see Appendix 4). Plants were separated by flower morphology, because many bees prefer flower of one morphology, and are more or less, unaffected by the distribution of plants with the other type of flower morphology. This might also have yielded a different result than if all plants were quantified together.

**Table 5.** Mean values of Shannon diversity, species richness and flower abundance, for actinomorphic and zygomorphic flowers separately on marine and glaciofluvial sediments. Derived from Appendix 4.

| Substrate | Flower morphology | Shannon diversity | Species richness | Flower abundance |
|---|---|---|---|---|
| *marine* | *zygomorphic* | 1.3 | 6.2 | 146.1 |
| *marine* | *actinomorphic* | 1.4 | 6.5 | 93.8 |
| *glaciofluvial* | *zygomorphic* | 1.5 | 6.6 | 106.6 |
| *glaciofluvial* | *actinomorphic* | 1.5 | 7.2 | 145.4 |

# Discussion

As I hypothesized, sediment type acted as an ecological filter selecting for bees according to their functional traits, which was shown by the higher probability of floral visitation on actinomorphic flowers, and by short-tongued species, on glaciofluvial sediment (Fig. 4). Nest site availability can explain the higher visitation rates of short tongued bees on glaciofluvial sediment, as miners which constituted a majority (67%) of the short-tongued species, are dependent on sandy soils to excavate their nests (Cane, 1991; Potts & Willmer, 1997). The higher probability of visitation to actinomorphic flowers on glaciofluvial sediments (Fig. 4), can also be explained by visitation of short-tongued bees, as both flower visitation of long-tongued species and bee-visits to zygomorphic flowers, were unaffected by sediment type (Fig. 4). I did not find any effect of sediment type on the number of floral visits, which means that when presence was established, abundance was unaffected by sediment type (Fig. 5).

Other studies have found that the environment's filtering of functional traits can explain species distribution (Aguirre-Gutiérrez et al., 2016; Steffan-Dewenter & Westphal, 2008; Sydenham et al., 2014; Tylianakis & Morris, 2017), with nesting behaviour suggested as one of the most influential traits (Williams et al., 2010). Furthermore, nesting resources have been found to be an important factor for ground nesting bees (Sardiñas & Kremen, 2014), and, most likely, a limiting factor for some bee species (Cane, 1991; Wuellner, 1999). Potts et al. (2003; 2005), found that between 5 and 10 % of bee community structure may be determined by nesting resources, and as much as 40 % of the variation in species abundances can be explained by availability of nest sites.

Roulston and Goodell (2011) and Torné-Noguera et al. (2014), did not find any influence of nesting resources on the bee community. However, Roulston and Godell (2011) did state, that some sort of influence of nesting resources is plausible, while Torné-Noguera quantified nesting resources for ground nesting bees by the amount of bare soil in the bee-sampling transects. This approach may be inadequate, since most bees can have their nests, in a radius of several hundred meters from where they are caught (Gathmann & Tscharntke, 2002). The quality of the soil was neither taken into account, making it uncertain if bare ground implies nest site availability (Potts et al., 2005). Other properties that could enhance nest site availability for ground nesting bees, are suitable slopes, pre-existing burrows (Potts et al., 2005), litter cover (Grundel et al., 2010), and soil compaction (Wuellner, 1999), but these are necessary to quantify over large areas, and therefore also resource demanding. The method used in this study can, on the other hand, be used to identify potential nest site availability for all areas were quaternary maps are available. This is a resource efficient approach, and if satisfactory, it will enable a wider use of sediment-based quantification of nest site availability in the future.

My prediction that ground nesters should prefer sandy sediments was not supported. A potential explanation for this may be that the trait, ground vs. aerial nester, is unsuited to assess this effect. Bumblebees (*Bombus spp*.) are assigned ground nesters, but use pre-existing cavities (renters), or dense herbage on the surface (Michener, 2007), and are therefore not as dependent on sandy soils, as species that excavate their nests themselves (miners). This makes the assumption that ground nesters, as a whole, are dependent on sandy soils imprecise. Furthermore, there were only 19 aerial nesting individuals (2.2%) in the study, making the distribution of nesting traits extremely skewed. This can to some extent be explained by the sampling periods, which excluded bees with flight times in spring or early summer, and/or a scarcity of aerial nest sites in the vicinity of our sampling sites. Nevertheless, I do believe my samples give a representative picture of the bee community in the study area, as I did sample during the period of peak activity for bees in this area (Table 1), and sampled a large proportion of the bee species one could expect to find during this period (Table 1).

In line with my hypothesis, I found that bee-flower interactions were influenced by the trait-matching of tongue length and flower morphology. The probability of floral visitation from long tongued bees was higher on zygomorphic than on actinomorphic flowers, while this pattern was the opposite for short tongued bees (Fig. 4). As shown in other studies, trait-matching like this can determine the strength of interactions (Maglianesi et al., 2014), and in some cases which interactions that are possible (Dormann et al., 2017; Olesen et al., 2011; Poisot et al., 2015). Many short tongued bees are not able to reach the nectar in zygomorphic flowers with deep corollas and subsequently prefer actinomorphic flowers, with short corollas, like Apiacea (Michener, 2007). Long tongued bees are able to reach the nectar of both type of flowers, but can be less efficient on some flower types (Michener, 2007), even if they have been shown to forage without preferences (Pacheco Filho et al., 2015). The number of floral visits showed the same pattern as probability of floral visitation (Fig. 5), which indicates that these preferences were also significant within the bumblebees (*Bombus spp.),* as they are a majority of individuals (84%), but a minority of species (31%). This is supported by Carvell (2002) who found that short tongued bumblebees preferred flowers with short corollas and long-tongued bumblebees preferred flowers with long corollas. It have also been found that long-tongued bumblebees are more sensitive to disturbance and fragmentation, than short tongued (Bommarco et al., 2012), which can imply differences in flower preferences.

Contrary to my hypothesis the network on glaciofluvial sediment (S-web) was less nested, than the network on marine sediment (M-web), but was, in line with my hypothesis, more specialized (Table 4). The same pattern was shown by the z-scores, but it is uncertain if the comparison of networks, using z-scores are reliable (Pellissier et al., 2017; Song et al., 2017), so in this case, z-scores are only used to compare networks against null-models. Species functional traits can influence network structure by selecting for some interactions over others (Hagen et al., 2012; Maglianesi et al., 2014; Pellissier et al., 2017), and low nestedness can be caused by a high evolutionary specialization and more specialist interactions (Hagen et al., 2012; Traveset et al., 2016). Species, with favourable traits may also account for a larger proportion of the links within the network under suitable environmental conditions (Tylianakis & Morris, 2017), like the miners, and their interactions, that are favoured in areas where they have access to sandy soils. As all miners in my study were solitary, and solitary species typically are more specialised (Michener, 2007), sediment can explain the less nested and more specialized structure of flower visitations in the S-web, with the presence of specialist interactions of solitary mining bees. These are interactions that were absent from the M-web, tentatively due to nest site limitation, as marine sediments contain very little accessible sand. Competition can also explain a less nested structure as dominant species may force other species away from some flowers (Dormann et al., 2017). In habitats without nest site limitation, competition for flower resources may be harder, which can explain the less nested structure of the S-web, and is also consistent with the higher abundance of bees in this network.

It has been suggested that landscape fragmentation and disturbance can lead to a decreased nestedness (Hagen et al., 2012; Vanbergen et al., 2017), with the more intensive agricultural land-use on the marine sediments implying higher levels of disturbance and fragmentation. Management practises can also contribute to a higher disturbance in roadsides on marine sediments. The frequency of the mowing is determined by the growth rate of the vegetation (Vegdirektoratet, 2014), and marine sediments are typically more productive than glaciofluvial sediments, and are, in addition, often affected by fertilizers from adjacent fields. This means that these roadsides are mowed more frequently, and therefore may be more disturbed than roadsides on glaciofluvial sediments. However, the floral diversity was comparable between sediment types and the network on marine sediments were more nested (Table 4), despite its supposedly higher levels of fragmentation and disturbance. Making it unlikely that fragmentation and disturbance were the cause of the difference in nestedness in this study. Nestedness is also believed to increase with network size (Bascompte et al., 2003;

Nielsen & Bascompte, 2007), but in this study, there was a lower nestedness of the larger sized network, and vice versa (Table 4).

The level of specialisation can also decrease with increasing disturbance and fragmentation (Ewers & Didham, 2006), and specialist species may be more negatively affected by disturbance than generalist species (Aizen et al., 2012; Biesmeijer et al., 2006; Peralta et al., 2017). More abundant species may also be less specialized, simply because their higher abundance let them interact with more species by chance (Poisot et al., 2015). The S-web is more specialized (Table 4), despite its higher abundance, and it is not unlikely that this, in part, can be explained by lower levels of fragmentation and disturbance on the glaciofluvial sediments.

In contrast to my hypothesis, both networks, were less nested than what could be expected by chance (Table 4), which is contrary to the typical plant-pollinator network (Bascompte et al., 2003; Bastolla et al., 2009). A lower nestedness than the null-models can be explained by competition, as mentioned previously (Dormann et al., 2017). In this study, it could be a consequence of the high abundance of bumblebees (Bombus spp.) in both networks. Many bumblebees are super generalists and may have excluded some solitary bees from the most generalized flower species, making their interactions more specialized, and the networks less nested. On the other hand, Dormann et al. (2009) found that the null-model Patefield, which is used in this analysis, constructs more nested networks than the observed. I believe that the difference between the null-models and the observed are attributed to the null-model properties, rather than environmental conditions.

As I hypothesized both networks were more specialized than networks of random interactions (Table 4), which could be expected for mutualistic networks (Blüthgen et al., 2007). The observed specialization was higher for plants, than for bees, in both networks, but in the S-web, the z-score was higher for the bees. The higher observed specialisation of the plants in the S-web, could be explained by the higher number of bee, than plant species in this web. This type of asymmetry can cause a higher specialization of  the less numerous level in mutualistic networks, including networks of random associations (Blüthgen et al., 2007). The higher z-score of the bees cannot, on the contrary, be explained by asymmetry. The higher number of bee than plant species in the S-web, gives the bees fewer possible links, and thereby a lower potential for their specialisation to deviate from the null-model (Carstensen et al., 2018). The higher z-score of the bees therefore emphasizes the higher specialization of the bees in this network, and is in line with my argumentation that the differences in network structure is caused by the higher occurrence of specialized interactions of mining bees in the S-web.

As the stability of networks may decrease with specialization (Elle et al., 2012) and increase with nestedness (Bascompte & Jordano, 2007; Thebault & Fontaine, 2010), both networks were less stable than what could be expected by chance. Consequently, the S-web were also less stable than the M-web, as it were less nested and more specialized (Table 4). In addition, the interactions between specialist, that were more prevalent in the S-web, are more vulnerable to disturbances than other interactions (Aizen et al., 2012), and could further decrease stability.

A difference between the functional traits, and network analyses is the presence of parasitic species. These were excluded from the functional traits analyses because their occurrences within habitats are not decided by their own traits exclusively, but largely by those of their hosts. In the network analyses, on the other hand, they were included, as they may have contributed to network structure independent of their habitat preferences, and their exclusion would give a wrong impression of the actual structure and stability of the network. Parasitic species were more abundant and had more species on glaciofluvial sediment, which could have made their influence on the two networks dissimilar. However, if glaciofluvial sediments, to a larger extent, are preferred by "popular" hosts, their parasites are a predictable consequence of this environment, and should be included. The higher abundance and species richness of parasitic species on glaciofluvial sediment can also indicate that there are more nests on this sediment type.

One obvious difficulty with the comparison of bee-flower interactions on different sediment types, is dissimilarities in other important environmental factors. In the functional traits analyses, dissimilarities of flowering plants have been taken into account, but it cannot be ruled out that some of the difference in network structure, are attributed to differences in some other aspects of the environment. However, the registration of flowering plants during the bee samplings, showed no significant difference, in neither abundance nor richness, between the two sediment types, and flower resources have been shown to be the most important factor in structuring bee communities (Potts et al., 2003; Roulston & Goodell, 2011)

Most ecological networks suffer from incomplete sampling in some way or the other. In bee-flower visitation networks, the flowers are often more completely sampled than the bees, largely because of their more continuous presence in the plots or transects (Dormann et al., 2017). Specialization may also be overestimated in networks with few observations (Fründ et al., 2016), and the fact that we did not sample throughout the season, may result in a higher specialization, as some species can have additional partners outside of our sampling periods, and therefore seem more specialized than they are (Blüthgen, 2010; Olesen et al., 2011).

However, the main objective was to compare networks on different sediment types, and as both these networks was sampled with the same intensity, sampling bias should not have a large influence on the results. In addition, quantitative metrics, as H2 and $\mathrm{NODF}_{\mathrm{weighted}}$ used in this study, are typically less sensitive to sampling bias than qualitative metrics (Blüthgen, 2010), and when non-interacting species, are excluded, as was done in this study, sampling bias can be further reduced (Nielsen & Bascompte, 2007).

## Implications for management

The roadsides in this study were widely used as forage sites, and a diverse set of bee-flower interactions was observed. My results show that bees have various preferences with regards to flower morphology. So, if the roadsides should be potential forage sites for as many bees as possible, both actinomorphic and zygomorphic flowers should be present. The network on marine sediment could have been subject to nest site limitation due to an absence of sandy soils. It could therefore be argued that improved nest site availability may be a more effective management practise, than increased flower resources, in these roadsides. If flower resources should be improved, this should be done in combination with an increase of nesting resources (Fortel et al., 2016). To improve nesting conditions for ground nesting bees, and especially miners, sand could be added to the soil. This can be done in areas outside of the roadsides, but if the bees should be able to utilize the flower resources in the roadsides it should be done within flight distance of the road. It is unclear how important the roadsides are as nesting sites, but we did not observe any nests within our study plots, during the field work for this study.

On glaciofluvial sediments where there is no apparent limitation of nest sites, an increase in floral resources may be effective. My results also show that this network may be less stable against disturbances. It could therefore be argued that conservation efforts may be more important here.

The outcome of any restoration efforts may also differ with the type of habitat and species (Henriksen & Langer, 2013; Murray et al., 2009; Sydenham et al., 2016), and these should therefore also be taken into consideration when roadsides are chosen for particular management practices. In addition, land-use changes, and the impact they might have on nesting and floral resources, should be taken into account (Murray et al., 2009; Potts et al., 2005).

It can be argued that the plants visited by most different species of bees, are the most important for the bee community as a whole. If so, the most important plant species in this study were, on marine sediments *T. pratense, S. autumnalis, L. pratensis, V. cracca and T. hybridum* (fig. 2), and on glaciofluvial sediments, *H. umbellatum, T. vulgare, S. virgaurea, K. arvensis, C. angustifolium and T. pratense* (fig. 3). The invasive plant, *Lupinus pollyphyllus,* which were present in some roadsides on glaciofluvial sediments, had just a few links, and not any that were exclusive. Its removal should therefore be unproblematic with regard to the bees, at least for bees that are active during July and August.

# Conclusion

My findings show that bee-flower interactions are filtered on different scales. On a larger spatial scale, distribution of interactions, are driven, in part, by environmental factors connected to nest site availability, and the functional responses of the bees to these factors. On a smaller scale, within habitats, realised interactions and interaction strengths are to a large extent decided by trait-matching of tongue length and flower morphology. The patterns of flora- visitation, and variation in network structure can be explained by a greater occurrence of specialist interactions of solitary mining bees on glaciofluvial sediment. This is in turn caused by the mining bee’s dependency on sandy soils for excavating their nest, thus revealing the role of geological processes in shaping bee-flower interactions through the allocation of nesting resources.

Future studies, should primarily aim at establishing the knowledge from this study on a more general basis, by doing similar studies in other areas and biotopes. If possible, bees should also be sampled throughout the entire season to enable the sampling of all species and interactions. This may generate larger networks from each site, and enable the analysis of more networks per sediment type, thereby decreasing the statistical uncertainty. In addition, the data from this and other similar studies, can be analysed in more detail with regards to single species, thus, providing a more detailed picture of the species roles in the networks. Information that may prove important in the efforts to protect the bees and the species with which they interact.

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# Appendix 1

**Appendix 1.** Information of sites, weather and timing for each sampling. Site names referred to in this study was changed according to a South-North gradient. Site names on the pinned specimens refer to old site names. There was no significant difference between neither temperature (P=0.4), or windspeed (P=0.6), between samplings on different sediment types, t-tests was done with function "t.test" in R.

| Site | Sediment | lat | lon | Date | Start | Stop | Temp C° | Wind m/s | Old site name |
|---|---|---|---|---|---|---|---|---|---|
| m1 | marine | 60,246846 | 11,169753 | 2017-07-04 | 15:11 | 16:11 | 18 | 5 | m11 |
| m1 | marine | 60,246846 | 11,169753 | 2017-08-07 | 11:03 | 12:03 | 18 | 4 | m11 |
| m2 | marine | 60,225974 | 11,099740 | 2017-07-05 | 11:45 | 12:45 | 17 | 3 | m10 |
| m2 | marine | 60,225974 | 11,099740 | 2017-08-08 | 12:40 | 13:40 | 18 | 4 | m10 |
| m3 | marine | 60,206994 | 11,124410 | 2017-07-05 | 16:33 | 17:33 | 20 | 5 | m9 |
| m3 | marine | 60,206994 | 11,124410 | 2017-08-08 | 14:00 | 15:00 | 19 | 4 | m9 |
| m4 | marine | 60,191864 | 11,139472 | 2017-07-06 | 12:58 | 13:58 | 21 | 5 | m8 |
| m4 | marine | 60,191864 | 11,139472 | 2017-08-10 | 11:19 | 12:19 | 19 | 3 | m8 |
| m5 | marine | 60,188283 | 11,174608 | 2017-07-06 | 14:17 | 15:17 | 22 | 5 | m12 |
| m5 | marine | 60,188283 | 11,174608 | 2017-08-10 | 16:58 | 17:58 | 21 | 3 | m12 |
| m6 | marine | 60,178850 | 11,158100 | 2017-07-07 | 11:00 | 12:00 | 16 | 1 | m13 |
| m6 | marine | 60,178850 | 11,158100 | 2017-08-07 | 12:56 | 13:56 | 17 | 3 | m13 |
| m7 | marine | 60,171149 | 11,136672 | 2017-07-07 | 16:19 | 17:19 | 21 | 3 | m6 |
| m7 | marine | 60,171149 | 11,136672 | 2017-08-16 | 11:06 | 12:06 | 18 | 2 | m6 |
| m8 | marine | 60,165043 | 11,124372 | 2017-07-13 | 15:06 | 16:06 | 18 | 3 | m4 |
| m8 | marine | 60,165043 | 11,124372 | 2017-08-17 | 11:00 | 12:00 | 17 | 3 | m4 |
| s1 | glaciofluvial | 60,318768 | 11,192735 | 2017-07-04 | 13:31 | 14:31 | 17 | 5 | s11 |
| s1 | glaciofluvial | 60,318768 | 11,192735 | 2017-08-07 | 12:40 | 13:40 | 19 | 5 | s11 |
| s2 | glaciofluvial | 60,225118 | 11,060839 | 2017-07-05 | 13:18 | 14:18 | 18 | 4 | s1 |
| s2 | glaciofluvial | 60,225118 | 11,060839 | 2017-08-08 | 11:04 | 12:04 | 15 | 3 | s1 |
| s3 | glaciofluvial | 60,194455 | 10,990725 | 2017-07-05 | 14:46 | 15:46 | 18 | 3 | s14 |
| s3 | glaciofluvial | 60,194455 | 10,990725 | 2017-08-08 | 16:00 | 17:00 | 19 | 3 | s14 |
| s4 | glaciofluvial | 60,191842 | 11,034328 | 2017-07-06 | 11:00 | 12:00 | 17 | 2 | s12 |
| s4 | glaciofluvial | 60,191842 | 11,034328 | 2017-08-10 | 13:22 | 14:22 | 20 | 3 | s12 |
| s5 | glaciofluvial | 60,176813 | 11,028520 | 2017-07-06 | 15:41 | 16:41 | 21 | 4 | s10 |
| s5 | glaciofluvial | 60,176813 | 11,028520 | 2017-08-10 | 15:00 | 16:00 | 20 | 3 | s10 |
| s6 | glaciofluvial | 60,161903 | 11,026504 | 2017-07-07 | 13:02 | 14:02 | 18 | 2 | s9 |
| s6 | glaciofluvial | 60,161903 | 11,026504 | 2017-08-14 | 11:12 | 12:12 | 15 | 2 | s9 |
| s7 | glaciofluvial | 60,143665 | 11,024455 | 2017-07-07 | 14:30 | 15:30 | 21 | 3 | s8 |
| s7 | glaciofluvial | 60,143665 | 11,024455 | 2017-08-16 | 12:40 | 13:40 | 19 | 4 | s8 |
| s8 | glaciofluvial | 60,085292 | 11,039040 | 2017-07-13 | 11:03 | 12:03 | 16 | 3 | s7 |
| s8 | glaciofluvial | 60,085292 | 11,039040 | 2017-08-17 | 12:23 | 13:23 | 18 | 4 | s7 |

# Appendix 2

**Appendix 2.** All sampled bees. KAH is Kaj-Andreas Hanevik, DJS is Daniel Skoog. Species of flowers means different species of flowering plants on which bees were caught.

| | Glaciofluvial | Marine | Total |
|---|---|---|---|
| **No. of bee species** | 42 | 23 | 45 |
| Social | 12 | 11 | 12 |
| Solitary | 24 | 9 | 27 |
| Cleptoparasites | 6 | 3 | 6 |
| **No. of bee individuals** | 574 | 336 | 910 |
| Social | 405 | 300 | 705 |
| Solitary | 114 | 28 | 142 |
| Cleptoparasites | 55 | 8 | 63 |
| Females | 416 | 272 | 688 |
| Males | 158 | 64 | 222 |
| Collected KAH | 303 | 146 | 449 |
| Collected DJS | 271 | 190 | 461 |
| **Species of flowers** | 31 | 23 | 41 |

# Appendix 3

**Appendix 3.** Bee species and their traits. Information of traits obtained from the literature (Falk & Lewington, 2015; Ødegaard et al., 2015; Ødegaard, 2018). Taxonomically all bumble bee belongs to the long-tongued bees, so the tongue length of the bumblebees refers to the length of their tongue relative to other bumblebees. Clepto-parasite are not included in this table, as they were not included in the functional traits analysis.

| Bee species | Tongue length | Nesting behaviour | Sociality |
|---|---|---|---|
| *Andrena denticulata* | short | ground | solitary |
| *Andrena fucata* | short | ground | solitary |
| *Andrena lathyri* | short | ground | solitary |
| *Andrena semilaevis* | short | ground | solitary |
| *Andrena subopaca* | short | ground | solitary |
| *Andrena tarsata* | short | ground | solitary |
| *Andrena wilkella* | short | ground | solitary |
| *Bombus hortorum* | long | ground | social |
| *Bombus humilis* | long | ground | social |
| *Bombus hypnorum* | short | aerial | social |
| *Bombus jonellus* | short | ground | social |
| *Bombus lapidarius* | short | ground | social |
| *Bombus pascorum* | long | ground | social |
| *Bombus pratorum* | short | ground | social |
| *Bombus ruderarius* | long | ground | social |
| *Bombus sensu strictu* | short | ground | social |
| *Bombus soroeensis* | short | ground | social |
| *Bombus sylvarum* | long | ground | social |
| *Bombus wurflenii* | short | ground | social |
| *Colletes daviesanus* | short | ground | solitary |
| *Colletes floralis* | short | ground | solitary |
| *Colletes similis* | short | ground | solitary |
| *Eucera longicornis* | long | ground | solitary |
| *Halictus rubicundus* | short | ground | solitary |
| *Halictus tumulorum* | short | ground | solitary |
| *Hylaeus angustatus* | short | aerial | solitary |
| *Hylaeus brevicornis* | short | aerial | solitary |
| *Hylaeus rinki* | short | aerial | solitary |
| *Lasioglossum albipes* | short | ground | solitary |
| *Lasioglossum calceatum* | short | ground | solitary |
| *Lasioglossum fratellum* | short | ground | solitary |
| *Lasioglossum leucopus* | short | ground | solitary |
| *Lasioglossum rufitarse* | short | ground | solitary |
| *Megachile circumcincta* | long | ground | solitary |
| *Megachile willugbiella* | long | aerial | solitary |
| *Panurginus romanii* | short | ground | solitary |
| *Panurgus banksianus* | short | ground | solitary |
| *Panurgus calcaratus* | short | ground | solitary |

| | | | |
|---|---|---|---|
| *Trachusa byssina* | long | ground | solitary |

# Appendix 4

**Appendix 4.** Vegetation measures from all sites divided by flower morphology. Three levels where used for flower abundance, and each species was categorized as, more than 50 %, between 10 and 50 % or less than 10 %, in each plot. When merging these two estimates, all values over 50%, where set to 75, all values between 10% and 50%, where set to 30, and all values less than 10%, where set to 5. Shannon diversity and species richness was calculated from the abundance measures after the two indexes for each site was merged. Shannon diversity was calculated with function "diversity", in Vegan package (Oksanen et al., 2017) in R.

| Site | Sediment type | Flower morphology | Shannon diversity | Species richness | Flower abundance |
|---|---|---|---|---|---|
| m1_actino | marine | Actinomorphic | 1.30 | 8 | 192 |
| m1_zygo | marine | Zygomorphic | 1.35 | 4 | 37 |
| m2_actino | marine | Actinomorphic | 1.32 | 7 | 148 |
| m2_zygo | marine | Zygomorphic | 1.59 | 7 | 98 |
| m3_actino | marine | Actinomorphic | 1.42 | 6 | 59 |
| m3_zygo | marine | Zygomorphic | 1.26 | 7 | 224 |
| m4_actino | marine | Actinomorphic | 0.93 | 6 | 110 |
| m4_zygo | marine | Zygomorphic | 1.59 | 8 | 180 |
| m5_actino | marine | Actinomorphic | 1.75 | 6 | 41 |
| m5_zygo | marine | Zygomorphic | 1.77 | 9 | 176 |
| m6_actino | marine | Actinomorphic | 1.68 | 8 | 78 |
| m6_zygo | marine | Zygomorphic | 1.53 | 7 | 262 |
| m7_actino | marine | Actinomorphic | 1.52 | 6 | 83 |
| m7_zygo | marine | Zygomorphic | 0.9 | 3 | 78 |
| m8_actino | marine | Actinomorphic | 1.56 | 5 | 39 |
| m8_zygo | marine | Zygomorphic | 0.8 | 4 | 114 |
| s1_actino | glaciofluvial | Actinomorphic | 1.42 | 6 | 65 |
| s1_zygo | glaciofluvial | Zygomorphic | 1.89 | 7 | 60 |
| s2_actino | glaciofluvial | Actinomorphic | 0.78 | 5 | 111 |
| s2_zygo | glaciofluvial | Zygomorphic | 1.83 | 8 | 101 |
| s3_actino | glaciofluvial | Actinomorphic | 1.69 | 9 | 167 |
| s3_zygo | glaciofluvial | Zygomorphic | 1.59 | 7 | 107 |
| s4_actino | glaciofluvial | Actinomorphic | 2.16 | 11 | 193 |
| s4_zygo | glaciofluvial | Zygomorphic | 0.91 | 5 | 93 |
| s5_actino | glaciofluvial | Actinomorphic | 2.01 | 10 | 194 |
| s5_zygo | glaciofluvial | Zygomorphic | 1.6 | 6 | 134 |
| s6_actino | glaciofluvial | Actinomorphic | 1.21 | 8 | 185 |
| s6_zygo | glaciofluvial | Zygomorphic | 1.42 | 8 | 165 |
| s7_actino | glaciofluvial | Actinomorphic | 1.11 | 4 | 156 |
| s7_zygo | glaciofluvial | Zygomorphic | 1.59 | 7 | 111 |
| s8_actino | glaciofluvial | Actinomorphic | 1.71 | 7 | 92 |
| s8_zygo | glaciofluvial | Zygomorphic | 1.3 | 5 | 82 |

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