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The influence of nest-site limitation on the species richness and abundance of bees: Linking biodiversity and geology

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Management of Natural Recourses

Preface

This thesis concludes my master's degree in Natural Recourse Management at the University of Life Sciences, Ås. In particular, it was my interest in biodiversity which inspired me to do this thesis, and being allowed to work with both bees and plants has been truly fascinating.

I want to express my sincere gratitude to my supervisors, Astrid Skrindo, Kari Klanderud, Markus Sydenham and Marit Helene Lie, whom have all helped me greatly throughout the process of completing this thesis. I want to thank my father, Arne Hanevik, for linguistic consultations during the process of writing. I also want to thank geologist Mona Henriksen for taking her time to discuss the geological basis for this study. Lastly, I am grateful for having had such a great working partner in Daniel Skoog; field work and laboratory work would not have been the same alone. The overall idea for the study was proposed by Markus Sydenham, and the Directorate of Public Roads supported the project financially.

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Abstract

There is mounting evidence of declines in global biodiversity. Declining wild bee populations are subject to concern because bees are considered the most important pollinators worldwide, contributing to the production of agricultural crops and reproduction of wild plants. A suitable habitat for bees must include both foraging recourses and nesting recourses. While the link between flowers and bees has been shown innumerable times, the importance of nesting recourses is poorly documented. A large portion of the Norwegian bee fauna are solitary mining bees, because of their habits of not nesting on colonies *and* excavating subterranean nests in, most often, sandy soils. Due to enhanced nesting recourses for such mining bees, I hypothesised that sediment type would influence on the species richness and abundance of bees. To test this, I sampled bees in road verges on sediments with differing textures, comparing the bee fauna on glaciofluvial (sandy) versus marine (clayey/silty) sediments. The influence of sediment type was larger for the solitary compared to the social bees, and both the species richness of bees, as well as the species richness and abundance of solitary bees were higher on glaciofluvial compared to marine sediments. These results indicate *nest site limitation* as an important ecological factor influencing bee communities, implying that geological processes control the distribution of nesting recourses for mining bees in areas affected by glaciation processes.

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1 Introduction

There is mounting evidence of declines in global biodiversity (Butchart et al., 2010; IPBES, 2018), and there are clear indications of declines in bee populations specifically (Ana Nieto et al., 2014; Biesmeijer et al., 2006; Goulson et al., 2008; Ollerton et al., 2014; Potts et al., 2010a; Rasmont et al., 2005). Although collapsing honey bee-colonies are a well-known phenomenon (Potts et al., 2010b) coined "Colony collapse disorder", wild bee populations are also evidently regressing (Potts et al., 2010a). Drivers for declines in wild bee populations highlighted by Potts et al. (2010a) are land-use change including loss and fragmentation of habitats (Goulson et al., 2005; Goulson et al., 2008; Müller et al., 2006; Steffan-Dewenter et al., 2002); pesticides (Kevan et al., 1998; Rortais et al., 2005); decreased recourse diversity (Müller et al., 2006); alien species (Thomson, 2006); spread of pathogens (Furst et al., 2014); and climate change (Rasmont et al., 2015; Williams et al., 2007). Although there are no documented declines in wild bee populations, loss of suitable habitat and an increased fragmentation of populations have resulted in 30% of the Norwegian species to be red listed (considered at risk of going nationally extinct) (Henriksen & Hilmo, 2015), where 12 species are already considered nationally extinct (Ødegaard et al., 2015a).

An estimated 87.5 % of all flowering plant species are pollinated by animals (Ollerton et al., 2011). As an ecosystem service, pollination contributes significantly to agricultural food production (IPBES, 2018; Kleijn et al., 2015). Pollination has been shown to positively influence the production of 70% of our agricultural crop-species (Klein et al., 2007), with an estimated value of 153 billion euro worldwide (Gallai et al., 2009). However, crop pollination ecosystem service arguments alone are not sufficient managing threatened bees (Kleijn et al., 2015). Furthermore, the bees as a group constitute an ecologically important taxon due to their role as the most important pollinator of wild plants (Michener, 2007). Understanding what drives the distribution of bees is thus important in order to conserve and manage this ecologically and economically important, as well as biologically interesting taxon.

Bees are central place foragers (Orians & Pearson, 1979) and suitable habitats must therefore include foraging recourses within the flight distance of the female's nest (Westrich, 1996). Foraging recourses are generally viewed as the main factor driving bee communities (Potts et al., 2003; Roulston & Goodell, 2011), and bee diversity and abundance increases with that of flowering plants (Ebeling et al., 2008; Fründ et al., 2010; Grundel et al., 2010; Holzschuh et al., 2006; Roberts et al., 2017; Steffan-Dewenter & Tscharntke, 2001). This link seems to be

caused by the nectar (Potts et al., 2003) or pollen (Müller et al., 2006) resources produced by the plants, or likely a combination of both.

Besides food in the form of nectar and pollen, bees also require nesting recourses; which means both the substrate they nest within as well as the materials used for nest construction (Murray et al., 2009). Bees exhibit a wide array of nesting strategies, which can be divided into three guilds based on their nesting habits (O' Toole & Raw, 2004): Ground or above-ground nesting, and cleptoparasites. These three nesting guilds may again be divided based on how the nests are created (O' Toole & Raw, 2004). *Miners* excavate subterranean tunnels. *Carpenters* also excavate nests, but in woody material, most often dead wood. The *masons* make use of pre-existing cavities for their nests, such as hollow plant stems, cavities in rock or wood, or even snail shells. *Social nesters* also build their nests in pre-existing cavities but utilize larger cavities like abandoned mice nests or hollow tree stems that may support large social colonies. *Cleptoparasites* lay their eggs in other species' nests, and let their young be provisioned for by the host. There is reason to suspect nesting recourses to be a potential limiting factor for bees, but a meta-study on the factors affecting bees concludes there is little actual evidence supporting this (Roulston & Goodell, 2011). On the other hand, nesting recourses have been shown to be a factor influencing bee communities (Grundel et al., 2010; Murray et al., 2012; Potts & Willmer, 1997; Potts et al., 2005; Sardiñas & Kremen, 2014; Steffan-Dewenter & Schiele, 2008), and Cane (1991) suggested that the distribution of some species of bees may be limited by the availability of suitable nesting substrates. As nesting recourses is one of two basal spatial habitat requirements for bees (the other being foraging recourses), grasping its impact may greatly improve our understanding of the ecology of bees.

Landscape factors are also known to potentially influence bee communities, and various studies points to the positive relationship between landscape heterogeneity and bees (e.g. Boscolo et al., 2017). Assumably, this may be due to more heterogenous landscapes offering a greater variety of recourses for bees, potentially making a wider array of niches available. Furthermore, a reduction in landscape heterogeneity has been shown to potentially cause species loss (Moreira et al., 2015), and bee communities in areas with little remaining natural vegetation can possibly be upheld by high environmental heterogeneity (Kennedy et al., 2013). Not all bees react the same way to landscape factors (Steffan-Dewenter et al., 2002), and non-bombus taxa may be more sensitive to landscape-scale differences in adjacent habitats (Murray et al., 2012).

Because bees typically depend on early successional habitats, some anthropogenic landscape elements offer high-quality habitats for bees, such as open semi-natural calcareous grasslands (Murray et al., 2012). Agricultural field edges (Sydenham et al., 2014), power line clearings (Russell et al., 2005; Sydenham et al., 2016) and forest clearings due to silviculture (Roberts et al., 2017) has also been shown as potentially suitable habitats for bees. Road verges constitute another type of anthropogenically affected landscape element which in many ways is managed as a semi-natural grassland, first and foremost by regular cutting of the vegetation, stopping the invasion of later succession-species and reforestation. Roadside management may greatly impact the bees in road verges (Noordijk et al., 2009), and road verge restoration from weedy to flower-rich plant communities can have a profound positive effect on bee communities (Hopwood, 2008). Additionally, road verges can be viewed as one of few potentially bee-friendly landscape elements that is steadily increasing its extent today. Alas, roads as landscape elements are known to be not solely positive for bees (Tamayo et al., 2014) as they may impose barrier effects (Andersson et al., 2017; Bhattacharya et al., 2003) as well as bee mortality due to collisions with cars (Baxter-Gilbert et al., 2015; Keilsohn et al., 2018). As roads amount to the largest part of Norway's developed area (Statistisk sentralbyrå, 2016), road verges subsequently cover huge areas, one estimate being 1131 km^2 (Auestad et al., 2000). The geographical extent of this potentially bee-friendly habitat makes road verges an interesting habitat in the study of bees.

Nesting recourses for ground-nesting bees may be particularly scarce in mountainous regions such as Norway, with vast areas with little to no soil-depth (European Commission, 2005). The distribution of sediments in Norway are primarily controlled by quaternary-geological processes (Jørgensen et al., 2013), and geological processes may therefore shape the distribution of nesting recourses for ground nesting bees. Sediments in Norway vary more over short distances compared to the more southernly parts of Europe that have not been icebound to the same extent (European Commission, 2005). This makes Norway a suitable model-area to study how sediment type influence the bee-fauna, because the short distances between different sediments eliminate the effects of climatic variation. Glaciofluvial sediments consist of particles that glacial rivers have transported and deposited under, along and in front of glaciers (Jørgensen et al., 1997). In contrast, marine sediments consist of particles accumulated on the seafloor, that have been elevated above sea level due to isostatic uplift (Jørgensen et al., 1997). Glaciofluvial sediments mainly consist of sand and gravel while the lighter particles have been washed away, whereas marine sediments consist of silt

and clay. Because of the wide array of bees in the Norwegian fauna being *miners* with nest sites linked to sandy soils (Cane, 1991; Ødegaard, 2018a), the road verges on sandy sediments are, compared to the silty/clayey sediments, likely to harbour a greater variety and number of bees. This depends on whether the availability of nest-sites is limiting the species richness and abundance of bees. If so, the bee communities should differ between sediment-types. I used road verges as a model system to test if sediment type influences the species richness and abundance of bees.

I hypothesised that:

(1) The influence of sediment type on bee abundance differ between solitary and social bees, because of the large proportion of miners among the solitary bees.
(2) The species richness and abundance of bees, and especially the solitary bees, are higher in road verges located on glaciofluvial compared to marine sediments, due to enhanced nesting recourses on glaciofluvial sediments.
(3) Floral foraging resources and landscape diversity influence the species richness and abundance of bees, and this influence is related to sediment type.

2 Methods

2.1 Study area

The study was conducted along road verges in Ullensaker, Nannestad and Eidsvoll municipalities in Akershus county, of south-eastern Norway. The study area is situated in the southern boreal vegetation zone, slightly oceanic vegetation section (Moen et al., 1998). This area has nationally renowned quaternary geological assets, with Norway's largest glaciofluvial delta consisting of sand and gravel, and large areas with marine sediments consisting of silt and clay (fig. 1) (Jørgensen et al., 1997). The rich geological history causes the landscape to vary largely between ravine landscape and dry pine forests, kettle holes, overgrown aeolian sand dunes and intensively farmed agricultural land to mention some. From a Norwegian perspective, this area is known to harbour a diverse and rare entomological community (Artskart.artsdatabanken.no, 2018; Ødegaard et al., 2015a).

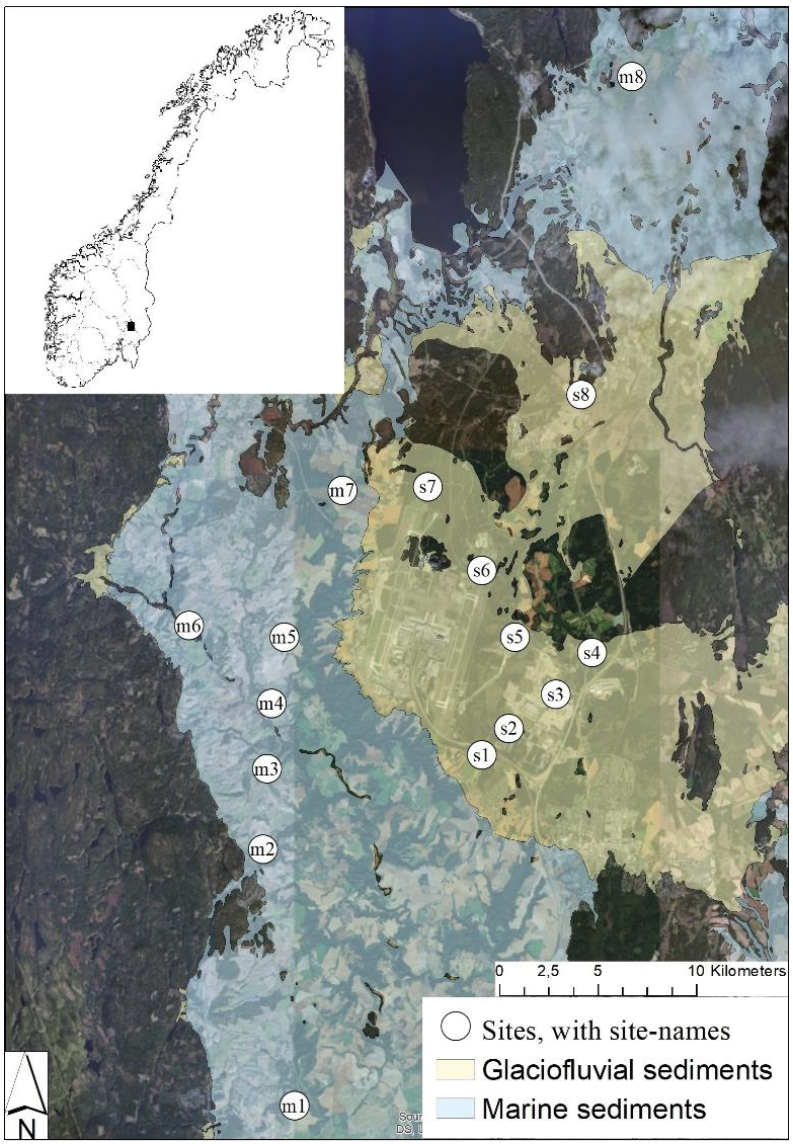


Figure 1: Map showing study area, sites (white dots) with site-names, and the prevalence of glaciofluvial- and marine sediments in the area. Top left corner: Geographical placement of the study area in Norway. See appendix 4 for coordinates.

The choice of study area was made because of the large coherent area with glaciofluvial sediments and the coherent area with marine sediments partially encircling the glaciofluvial sediments (fig. 1).

2.2 Site selection

I will define a *road verge* as a narrow strip of ground next to a road, usually covered with vegetation that is being regularly cut for safety reasons. A total of

16 road verges were selected, eight on glaciofluvial sediments and eight on marine sediments, using sediment maps from Geological Survey of Norway (NGU, 2017). All sites were separated by at least 1000 m in order to achieve independency between sites. Even though 1000 m technically is within the foraging distance of some large social bees (Greenleaf et al., 2007; Zurbuchen et al., 2010), significant autocorrelation in bee species composition has been shown to occur mostly at distances < 950 m (Torné-Noguera et al., 2014).

To ensure similarity and comparability between sites, all road verges had a width of at least 3 m, were at least 50m long, and contained at least three different plant families which provide floral foraging recourses for bees. The sites were inspected in the field in April 2017. All sites had high levels of sun-exposure and were not located within forests.

In the site selection, no emphasis was laid on the road verge to be an ideal biotope for bees, but merely offering a certain minimum of foraging possibilities. To ensure that the vegetation in our road verges wasn't being cut before the bee sampling was completed, an agreement was made with the local entrepreneur responsible for the road-side cutting in the area.

2.3 Vegetation survey

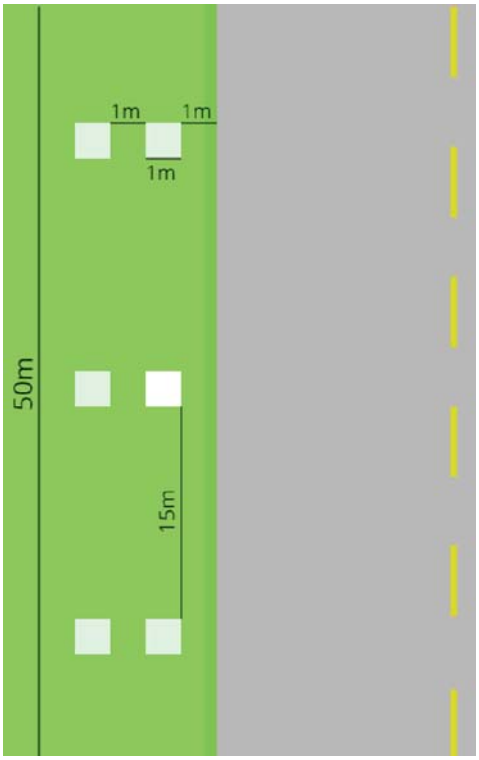


Figure 2: Graphical display of the vegetation survey's study design.

To be able to account for, and to quantify the floral resources along the road verges, the vegetation covering six 1 m^2 quadrats were carefully examined at each site. To strive for a representative image of the vegetation in the whole 50 m road verge segment, the quadrats were arranged in a pairwise manner. The first pair was placed in the middle of the 50 m segment, and the two other pairs were placed 15 m to each side of the middle pair (fig. 2). The paired quadrats were arranged so that the quadrat closest to the road was put either at the end of the roadcut, or one meter from the road if the roadcut was shorter than one meter. The second quadrat was placed one meter from the end of the first quadrat, perpendicularly to the road. If the road

verge was too narrow for this arrangement, the distance between the quadrats was shortened accordingly.

The vegetation survey was carried out between 9/6-2017 and 23/6-2017. Each 1 m^2 quadrat was divided into 16 equally large sub-quadrats, and the vegetation was registered by examining each of the 1/16 sub-quadrats for every plant providing floral recourses for bees, thus excluding grasses and other wind-pollinated species. Each plant, when possible, was identified to the species level. Every species' abundance was also estimated as a total coverage percentage for the whole 1 m^2. Overlapping vegetation was taken into account, meaning that a total cover over 100% was possible within quadrats.

The quadrats in the vegetation survey were also used to measure potentially relevant environmental conditions for the bees, including coverage of grasses, ligneous plants, and percentage coverage of bare soil.

Additionally, a second method of quantifying the floral foraging resources for the bees was conducted at the end of each bee-sampling. This was more superficial than the vegetation survey, but gave temporal insight on how much food was available in the road verge at the time. Specifically, this was done by registering which species were blooming, and the abundance of each species in bloom. A score from 1 to 3 was given, combining the amount of each registered species *in addition* to blooming. 1 meaning between 1 and 10%, 2 meaning between 10 and 50%, and 3 meaning between 50 and 100% coverage of the road verge bees were sampled from.

2.4 Bee sampling

Bees were sampled twice at each site. Sampling round number one was in July between 4/5-2017 and 13/7-2017, and number two was in August between 4/8-2017 and 17/8-2017. The sampling rounds were temporally separated to cover more of the phenological variation of both plants and bees. To minimize potential weather-effects on the bee sampling, four prerequisites were established: All sampling was to be performed between 11 o'clock in the morning and six o'clock in the evening, a minimum of 15 degrees Celsius at the start of the sampling, no more than 5 m/s wind-velocity, and no precipitation 30 mins prior to and during the sampling. Additionally, the sites from the two sediment types were paired in a south-north manner, making the southernmost site on glaciofluvial and marine sediments pair 1 and so forth (fig. 1, where site S1 and M1 = pair 1 etc.). In order to minimise the variation in weather conditions between the sediment types, the sites were visited in this pairwise manner, each

sampling round starting at the southernmost site-pair moving north. Weather-information was gathered from YR.no (Meterologisk institutt, 2017).

To minimize the effects of seasonality, each sampling round was carried out over a short period as possible. All sampling was conducted by the same two collectors, each of us starting at each end of the 50 m road verge transect. The sampling was conducted by calmly walking back and forth the transect, catching flower-visiting bees using sweep nets. The plant species on which the bee was visiting was identified to the species level, noted, and then the bee was put into a plastic container along with a note carrying information on the location, sampling round, collector, and plant species on which bee was caught foraging. The sampling effort put into each site was even.

2.5 Laboratory work

All the bees were brought to the entomology-lab at the Norwegian University of Life Sciences, dried and put on a pin. Except for the subgenus *Bombus sensu stricto* (*B. lucorum, B. cryptarum and B. magnus*), every individual was identified to the species level by Daniel Skoog and me. Identification-keys and literature used were Falk (2016), Ødegaard et al. (2015b), and Løken (1985). In addition, the species identification as to the solitary bees was controlled by Markus Sydenham.

Study area selection, site selection, field work and laboratory work were conducted in collaboration with Daniel Skoog. The dataset is also used in a master's thesis on bee-flower interactions (see Skoog, 2018).

2.6 Landscape analysis

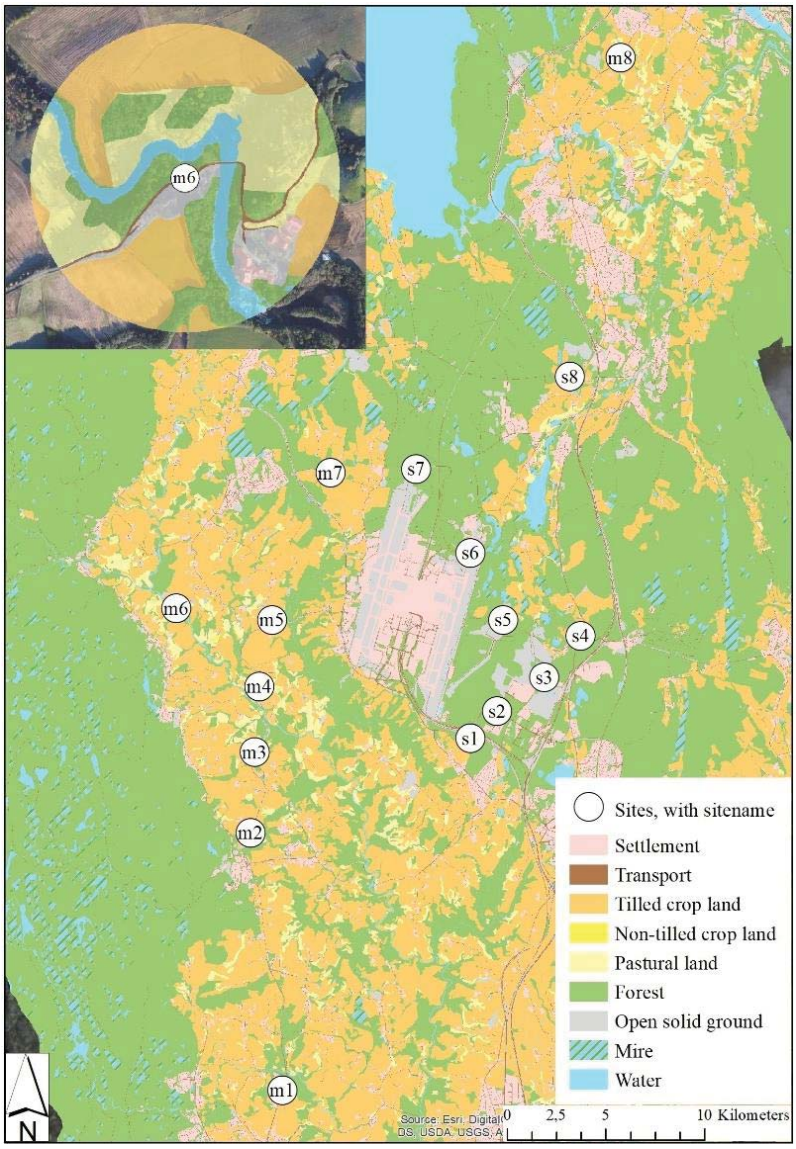


Figure 3: Map showing study area, sites and coverage of surface types (Ahlstrøm et al., 2014) used in the landscape analysis. Top left corner: Example of a 300 m buffer zone with surface types, from site m6.

Landscape analysis was performed using the GIS-software ArcMap 10.5 (ESRI, 2016). Landscape features were extracted from the digital map Ar5 (Ahlstrøm et al., 2014), specifically utilizing the information about surface types. The surface types are divided into eleven categories, nine of which are present in my study area: *Tilled crop land, non-tilled crop land, pastural land, forest, open solid ground, mire, water, transport,* and *settlement*. The data on surface types were extracted from 300 m buffer zones around the centroid of each road verge (fig. 3). A distance of 300 m was preferred as approximately this distance has been shown to be correlated to the species richness of wild bees (Steffan-Dewenter et al., 2002). Landscape diversity was calculated on the basis of the data on surface types within the buffer zones, applying the Shannon diversity index (Shannon & Weaver, 1949). These indices were calculated from the total coverage of the surface types present in each buffer zone. Sites scoring a high Shannon diversity index has therefore a high richness of surface types, and the total coverage among these has a high evenness.

2.7 Statistical analysis

In order to quantify the floral resources at each site, and to find the best floral-explanatory variable for the bee response variables, several calculations were made: (i) Floral abundance was calculated from the total coverage of every registered species in the vegetation survey, all six quadrats added up. (ii) Another calculation of floral abundance was made based on the plant-registration conducted after the bee-sampling, with both collection rounds added up. Every registered species was here given a percentage cover that represent the average of that species' coverage-interval (1=5%, 2= 35%, 3=75%). (iii) Plant genus richness from the vegetation analysis, with all six quadrats added up. Genus richness was preferred over species richness because even highly specialized bees are generally not constrained to visit one plant species (Michener, 2007). Plant genus richness also had a higher correlation coefficient to all response variables compared to plant species richness. (iiii) Floral diversity, calculated applying the Shannon diversity index following *Equation* 1, based on the genera's percentage cover from the vegetation survey, with all six quadrats added up.

$$H' = -\sum_{i=1}^{R} p_i \ln p_i$$

Equation 1, where p is the proportion of individuals belonging to the ith species in the dataset (Shannon & Weaver, 1949).

The plant percentage cover data from the vegetation survey were also used to perform *non-metric multidimensional scaling* (NMDS). Specifically, the ordination was executed using the metaMDS-function in the vegan-package (J. Oksanen et al., 2017) in R. This function combines the recommendations for ecological ordination, as proposed by Minchin (1987), into one command. The NMDS was performed in order to distil the vast amounts of information obtained from the vegetation survey. Specifically, the NMDS-analysis collapses the information about the different sites, and from the two groups of sites (sediment types), into two dimensions to enable visualisation and analysis of the data. To test if the relative differences in plant species composition influence the bees, the individual axis 1- and 2-scores of each site were included in the statistical analysis.

T-tests were performed to examine whether the floral recourses and landscape diversity differ significantly between sediment types. Shapiro-tests were used to examine whether data was normally distributed or not.

To find the best fitted floral explanatory variable for each model, the floral measurement with its highest Spearman rank correlations to the response variable was selected for each model. Spearman rank correlations (rho) between explanatory variables were checked, and in the

event of correlation > 0,5 only one of the variables were included in the models. NMDS axis-2 scores as explanatory variable was correlated with plant genus richness (0.65). Because plant genus richness is a more intuitive explanatory variable, NMDS axis-2 score was excluded from all models. *Bare soil* was omitted as explanatory variable because five out of the sixteen sites, all on marine sediments, had estimates of zero. *Grass coverage* was also omitted as explanatory variable due to its high correlation coefficients with plant genus richness (-0.70). *Coverage of ligneous plants* was omitted as explanatory variable as nine sites had estimates of zero.

2.8 Model selection

All analyses were conducted by applying the data from the two sampling rounds added up, since no temporal variation was of interest. The honeybee (*Apis mellifera)* was omitted from every analysis because they are managed animals and therefore not affected by the same factors as wild bees, hence not of interest in this study. Out of Norway's 208 known bee species, apart from the 35 bumblebees (*Bombus)* and the honeybee, the rest are so called solitary bees (Michener, 2007). To test hypothesis (1), that sediment-type influences the abundance of solitary bees differently than the social bees, a generalized linear mixed-effects model assuming a poisson distribution was performed. The bee abundance was split between solitary- and bumblebee-abundance, and a model was fitted with abundance as response variable, an interaction-term between sediment-type and sociality (solitary or social) as explanatory variable, and site as random variable. In addition to the honeybees, all cleptoparasites (n=63) were excluded from the GLMM on abundance of solitary- and social bees.

To test hypothesis (2) (higher species richness and abundance of bees in road verges on glaciofluvial compared to marine sediments), and (3) (foraging recourses and landscape diversity influences the species richness and abundance of bees) generalized linear models (GLMs) were fitted with a log-link, assuming a poisson distribution. Response variables were species richness of bees, species richness of solitary bees, and abundance of solitary bees. GLM on the total abundance of bees was discarded due to the large number of individuals (84 %) being bumblebees, thus not suitable to test my hypothesis of higher abundance of bees on glaciofluvial sediments because of enhanced nesting recourses for mining bees.

Explanatory variables included in the GLMs were (i) the floral measurement with the highest correlation coefficient to the response variable, (ii) sediment type, (iii) NMDS axis-1 score,

(iiii) landscape diversity as a Shannon-index, (iiiii) the interaction term between *sediment type* and *the floral measurement with the highest correlation coefficient to the response variable*, and (iiiiii) the interaction term between *sediment type* and *landscape diversity*. The interaction terms were included in the model selection because the influence of these specific explanatory variables may differ between the sediment types. The constituent terms of the interactions were also included in the models, as argued by Brambor et al. (2005).

A pre-selection for each explanatory variable was performed by fitting individual models, omitting variables with $p > 0,05$ from the full models.

Stepwise backward elimination was used to exclude explanatory variables from the full models if their influence on the response variable was not statistically significant ($p > 0.05$). To check for the poisson-distribution's prerequisite of *equidispersion*, dispersion-tests (Cameron & Trivedi, 1990) were performed for every step of the backwards elimination. The dispersion-tests showed that the model for *species richness of bees* was under-dispersed, while the models for *abundance of solitary bees* and the GLMM testing the abundance of bees and the interaction term sediment type*sociality were over-dispersed. These models were therefore re-fitted assuming a negative binomial distribution using the R-package "MASS" (Venables & Ripley, 2002). Despite quasipoisson-distributions being preferred in the event of under-dispersion, all models were refitted assuming a negative binomial distribution as it made no difference in the statistical outputs. Lastly, the models were validated through graphical validation.

Data management was carried out using Excel and R (R Development Core Team, 2018).

3 Results

In sum, 1117 bees were collected, including 766 bombus, 207 Apis melifera and 144 solitary bees. A total of 45 species were identified, counting the taxa *Bombus sensu stricto* as one species (see appendix 1 for species inventory list).

3.1 The abundance of bees, sociality and sediment type

The significant interaction term between sediment type and sociality shows that the influence of sediment type differs between solitary and social bees (table 1). Also, solitary bees are more positively influenced by the presence of glaciofluvial sediments compared to the social bees (fig. 4).

Table 1: Results from GLMM on bee abundance divided between sociality (solitary and social), both sampling rounds added up, with interaction-term between explanatory variables sociality and sediment type, using site as a random variable.

	estimate	std. error	z-value	p-value
Intercept	3.5303	0.1432	24.645	< 2e-16
Sediment type	0.3497	0.1992	1.756	0.0791
Socialitysolitary	-2.3722	0.1991	-11.916	< 2e-16
Sediment type:sociality	1.1066	0.2267	4.881	1.05e-06

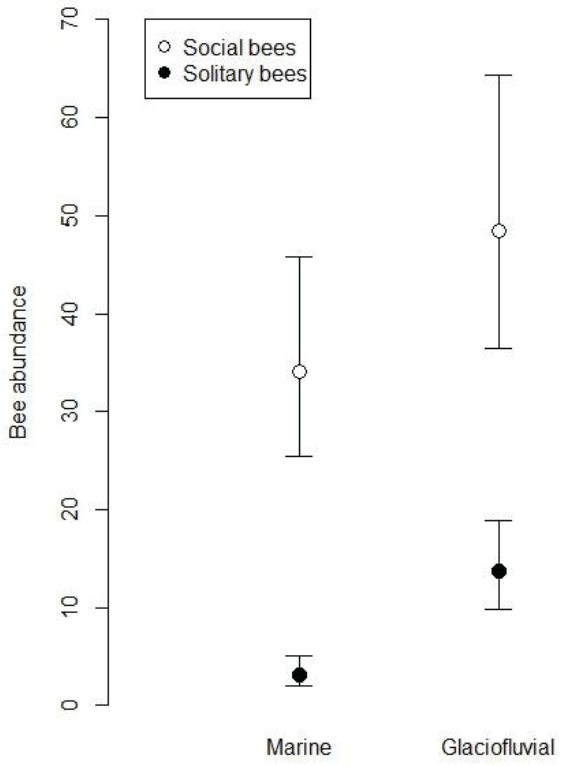


Figure 4: Plot graphically displaying the influence of sediment type on the abundance of social- and solitary bees specifically, including intervals for standard deviation. For details on the statistical analysis, see table 1.

3.2 Total species richness

The species richness of bees was highest in road verges on glaciofluvial sediments (fig. 5). In sum, 42 species were identified from the sites on glaciofluvial sediments, compared to only 23 from the sites on marine sediments. Interestingly, the glaciofluvial sites harbour 22 unique (only found on one sediment type) species compared to only three on marine sediments. The significant interaction-term between sediment type and landscape diversity shows that the influence of landscape diversity on the species richness of bees differ significantly between sediment types (table 2).

Table 2: Results from GLM on bee species richness (both sampling rounds added up). Explanatory variables kept through model selection, assuming a negative binomial distribution, are sediment type, landscape diversity and the interaction between landscape diversity and sediment type.

	estimate	std.error	z-value	p-value
Intercept	1.154	0.583	1.979	0.048
Sediment type	2.249	0.689	3.260	0.001
Landscape-diversity	0.882	0.465	1.896	0.058
Sediment type:Landscape-diversity	-1.499	0.597	-2.508	0.012

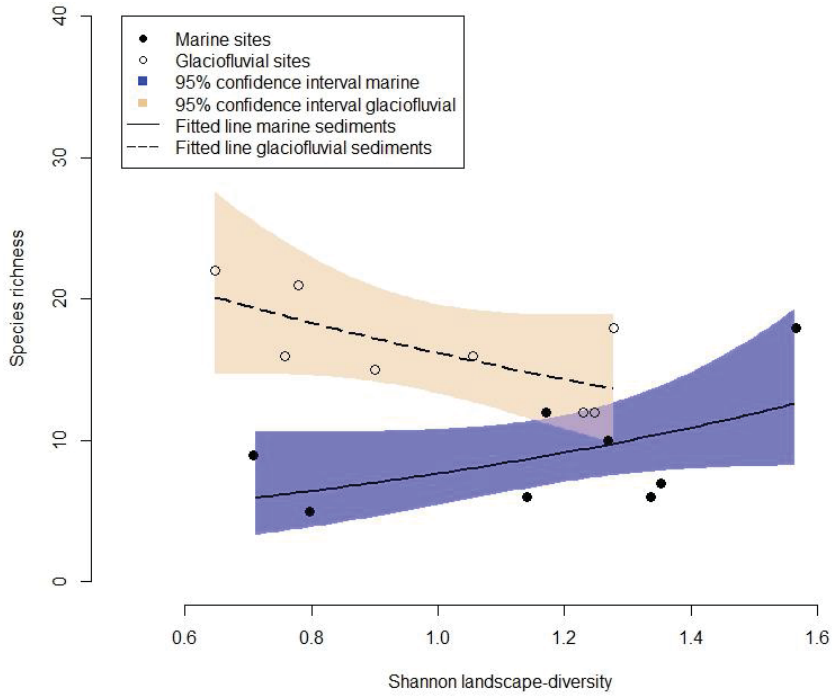


Figure 5: Plot graphically displaying the influence of Shannon landscape-diversity and sediment type the species richness of bees. Specifically showing fitted lines and 95% confidence intervals from the GLM on bee species richness. Fitted lines and confidence intervals only displayed for the intervals of the explanatory variable there is actual data for. For details on the statistical analysis, see Table 2.

3.3 Species richness of solitary bees

The species richness of solitary bees was highest in road verges on glaciofluvial compared to marine sediments, but the magnitude of this difference depends on the plant genus richness (fig. 6 and table 3). Additionally, the average solitary bee species per site was only 1.8 on marine compared to 6.9 on glaciofluvial sediments. An increase in floral foraging recourses seem to have a positive influence on the solitary bee species richness on marine sediments while showing no trend on glaciofluvial sediments.

Table 3: Results from GLM of solitary bee species richness (both sampling rounds added up), containing the explanatory variables selected through model selection, assuming a poisson distribution. Explanatory variables kept are sediment type, plant genus richness, and the interaction between the two.

	estimate	std. error	z-value	p-value
Intercept	-1.924	1.135	-1.695	0.090
Sediment type	3.451	1.274	2.708	0.007
Plant genus richness	0.165	0.067	2.445	0.014
Sediment type:Plant genus richness	-0.145	0.073	-1.988	0.047

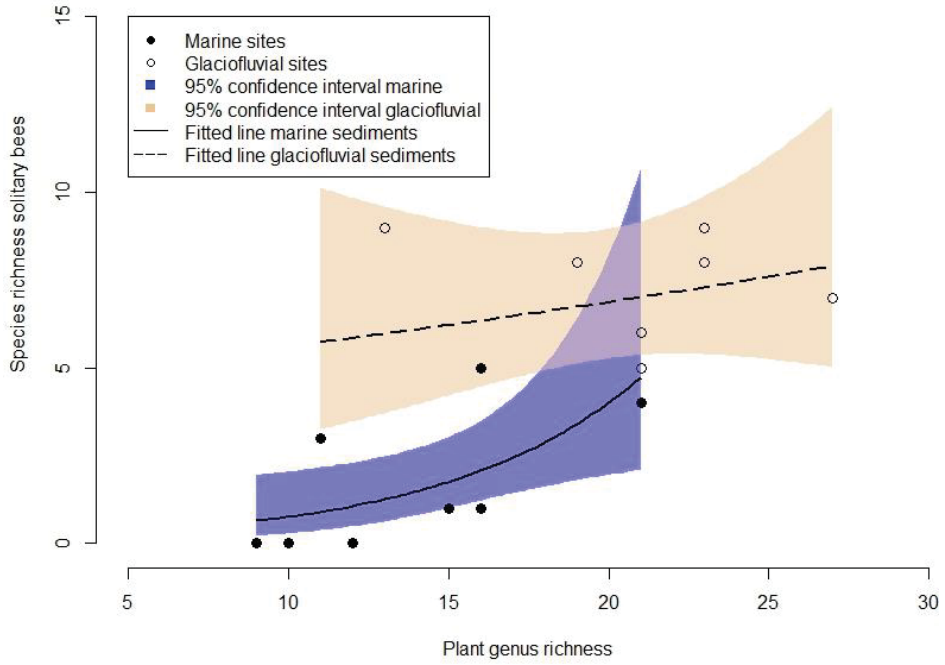


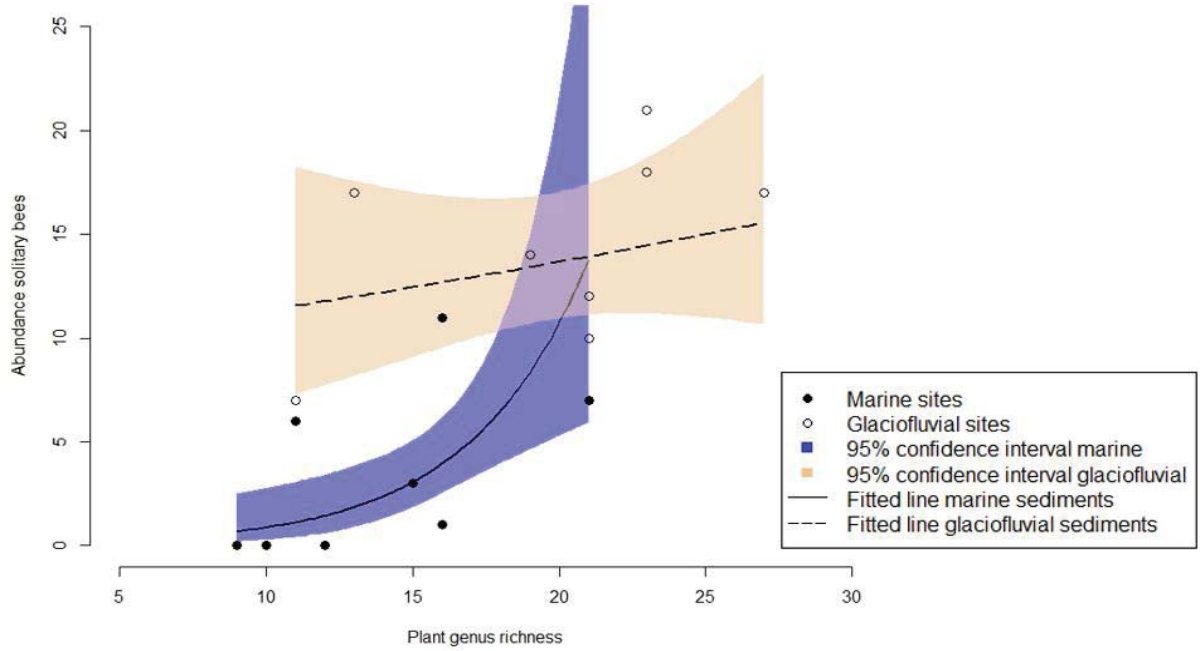
Figure 6: Plot graphically displaying the effects of plant genus richness and sediment type on solitary bee species richness. Specifically, it shows fitted lines and 95% confidence intervals for GLM on the interaction term between sediment type and plant genus richness. Beige confidence interval=glaciofluvial sediments, blue confidence interval=marine sediments. Points represent the different sites; black points for sites on marine sediments and red points for the glaciofluvial sites. Fitted lines and confidence intervals only displayed for the intervals of the explanatory variable there is actual data for. For details on the statistical analysis, see Table 3.

3.4 Abundance of solitary bees

In total, 28 individuals of solitary bees were sampled from the road verges on marine sediments, compared to 117 on glaciofluvial sediments (Appendix 1), and the abundance of solitary bees was clearly highest on glaciofluvial sediments (fig. 7). The significant interaction terms between sediment type and plant genus richness, and sediment type and landscape diversity, shows that the magnitude of this difference between sediment types depends on both the plant genus richness and landscape diversity. Additionally, an increase in floral foraging recourses seem to have a positive influence on the species richness of solitary bees on marine sediments while showing no particular trend on glaciofluvial sediments (fig. 7, table 4).

Table 4: Results from GLM of solitary bee abundance, containing the explanatory variables selected through model selection, assuming a negative binomial distribution. Explanatory variables kept in the model for abundance amongst the solitary bees are sediment type, genus richness from the vegetation analysis, landscape diversity, the interaction between sediment type and genus richness vegetation analysis, and the interaction between sediment type and Shannon landscape-diversity.

	estimate	std. error	z-value	p-value
Intercept	-3.578	1.475	-2.425	0.015
Sediment type	6.202	1.547	4.008	6.12e-05
Plant genus richness	0.250	0.073	3.442	0.001
Landscape diversity	2.125	0.829	2.564	0.01
Sediment type:Plant genus richness	-0.231	0.075	-3.072	0.002
Sediment type:Landscape diversity	-2.984	0.902	-3.307	0.001



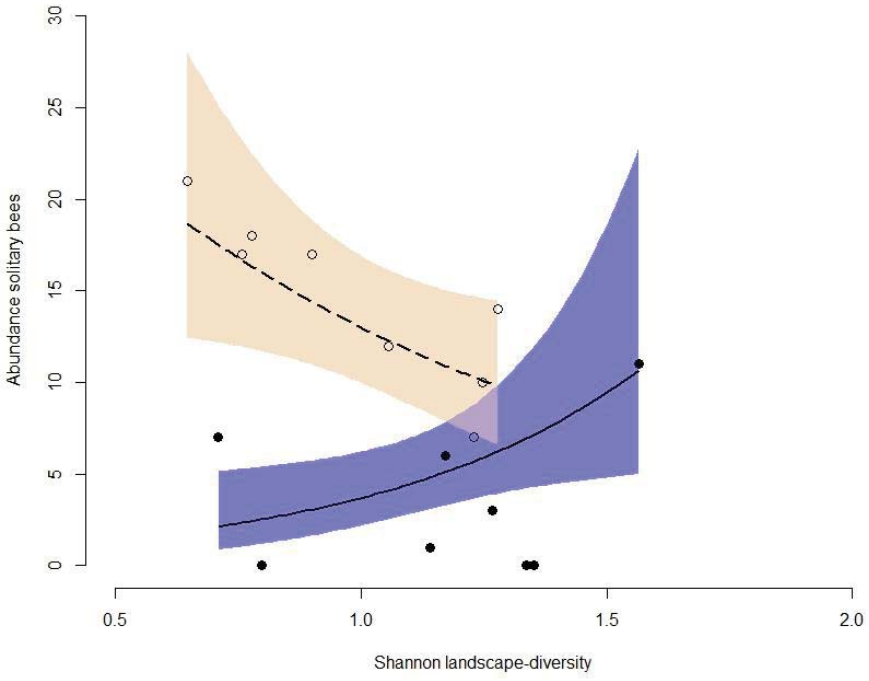
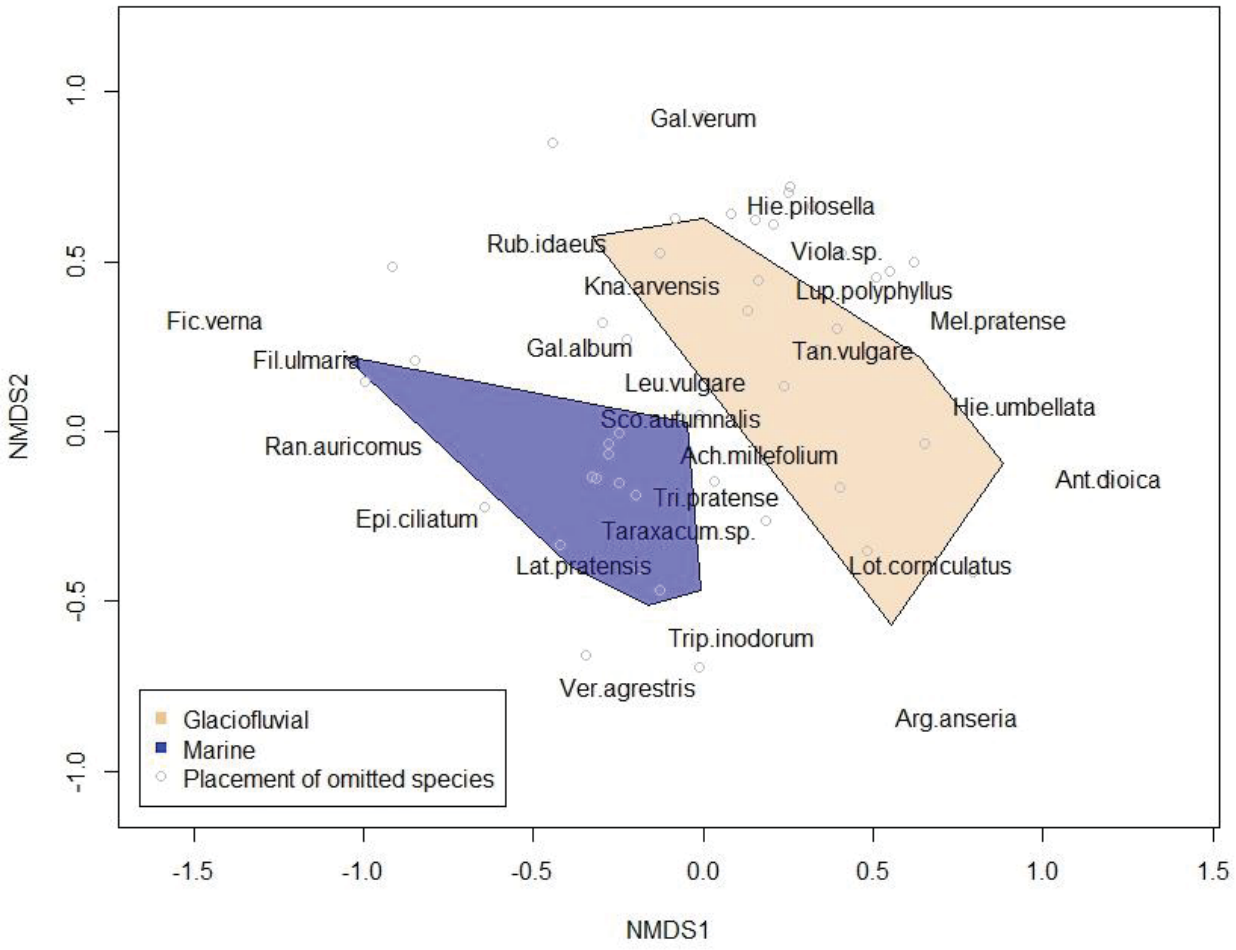


Figure 7: Plots graphically displaying the influence of plant genus richness and sediment type, as well as landscape-diversity and sediment type on the abundance of solitary bees. Specifically, it shows fitted lines and 95% confidence intervals for the interaction terms sediment type*plant genus richness, and sediment type*landscape diversity, respectively. Fitted lines and confidence intervals only displayed for the intervals of the explanatory variables there is actual data for. For details on the statistical analysis, see Table 4.

3.5 Vegetation analysis

A total of 82 taxa were recorded in the vegetation survey. 52 taxa were identified in the road verges on marine sediments, compared to 70 on the glaciofluvial sediments. The NMDS-ordination shows that there are clear differences in plant species composition between the road verges the two sediment types (2 dimensions, stresslevel = 0.15) (fig. 8).



Genus name abbreviations: Ach=Achillea, Ant=Antennaria, Arg=Argentina, Epi=Epilobium, Fic=Ficaria, Fil=Filipendula, Gal=Galium, Hie=Hieracium, Kna=Knautia, Lot=Lotus, Lat=Lathyrus, Leu=Leucanthemum, Lup=Lupinus, Mel=Melampyrum, Ran=Ranunculus, Rub=Rubus, Sco=Scorzoneroides, Tan=Tanacetum, Tri=Trifolium, Trip=Tripleurospermum.

Figure 8: NMDS-plot visualizing the differences in plant species composition between the road verges on the two sediment types (2 dimensions, stresslevel = 0.15). Some species are omitted from the graphical display to make visualisation more straightforwardly. Omission of overlapping species names in the ordination-plot is done by prioritising the more abundant species.

Due to correlation > 0.5 with the floral recource-measurements and NMDS axis-2 score, only the sites' NMDS axis-1 scores were included in the model selection, but proved to be insignificant for either model.

T-tests showed that there is a significant difference in plant genus richness and NMDS axis-1 scores between the two sediment types. This do not apply for Shannon plant-diversity, neither floral abundance-measurements, nor the Shannon landscape-diversity (95 % confidence intervals) (table 5).

Table 5: Statistical output from t-tests performed on the explanatory variables between the two sediment types.

	t	df	mean glaciofluvial	mean marine	p-value
Plant genus richness	-2.546	12.962	19.75	13.75	0.04
Floral abundance (vegetation analysis)	0.45	8.721	361.75	389.5	0.664
Shannon plant-diversity	-1.624	13.978	1.943	2.267	0.127
Floral abundance (at bee-sampling)	-0.014	13.157	263.125	263.75	0.989
Shannon landscape-diversity	1.420	13.677	0.415	0.473	0.681
NMDS axis-1	-3.588	13.936	-0.33	0.33	0.003

4 Discussion

4.1 Nest-site limitation

As hypothesised, I here show that sediment type is more important for the solitary compared to the social bees. Expanding on this, both the species richness of bees, as well as the species richness and abundance of solitary bees are higher in road verges located on glaciofluvial compared to marine sediments. To my knowledge, there are no previous studies systematically linking geological processes and bee diversity. My results indicate nesting recourses as a limiting factor structuring bee communities and imply that geological processes control the distribution of nesting recourses for mining bees. The notion that nesting recourses are of importance to bees has previously been shown (Murray et al., 2012; Potts et al., 2005) but the factors controlling the spatial distribution of nesting recourses are poorly studied (although fire has been argued as a factor affecting nesting recourse availability (Potts et al., 2003)). There are multiple studies that suggest nesting recourses as a partial factor structuring bee communities, but its level of impact vary in the literature. Nesting recourse diversity has been shown to only be of importance to the most abundant species, explaining 10% of the bee community structure (Potts et al., 2003). The species richness and abundance of bees have also been shown not to be related to nesting substrate availability (Torné-Noguera et al., 2014). There are probably several reasons as to why my results partially contrast these studies. One is the utilization of different nesting recourse-proxies, and another is that the actual limiting effect of nesting recourses may vary spatially. Torné-Noguera (2014) measured nesting recourses for ground nesting bees as a percentage cover of bare soil, and concluded that the geographical variation in bee communities were mainly determined by floral recourses rather than nesting recourses. Using *bare soil* as proxy for nesting recourses for mining bees does not take soil texture into account (the relative amount of sand, silt and clay), which has been shown to be of great importance to the nesting habits of ground nesting solitary bees (Cane, 1991). This methodology contrasts mine, because I specifically chose sites based on their sediments' texture. Even though Torné-Noguerra et al. (2014) utilises the same nesting recourse-proxy as other studies which finds nesting recourses to be of importance (e.g. Potts et al., 2005), it can be argued that the value of bare soil *in itself* as potential nesting recourse for mining bees could vary greatly between different geographical areas due to varying soil texture. Additionally, the method of measuring the percentage of bare soil as a proxy for nesting recourses does not consider that there may be suitable nest-sites in close proximity to the transect where bare soil is measured. This opposed to my

method which allows for a great level of certainty in knowing how the nesting recourse-proxy is spatially distributed near the sampling site. Expanding on this, Spain (Torné-Noguera et al., 2014) and Israel (Potts et al., 2003) have not been affected by glaciation-processes during the Pleistocene, in contrast to Norway (European Commission, 2005). Considering my results, which imply that the geological history influences the diversity of bee communities, the actual limiting effect of nesting recourses may vary between areas with different geological histories. Studies performed in different parts of the world thus allows for the possibility that the limiting effect of nesting recourses factually varies between areas. This naturally allows for varying results regarding nesting recourses' limiting effect for bees in different parts of the world.

Table 6: Unique solitary bee species (only found on one sediment type) for the sites on glaciofluvial sediments, including the bees' nesting strategies. Nesting strategies obtained from Ødegaard (2018a) and Cederberg (2015).

Species	Nesting strategy
Andrena denticulata	Miner
Andrena fucata	Miner
Andrena semilaevis	Miner
Andrena tarsata	Miner
Andrena wilkella	Miner
Colletes similis	Miner
Colletes floralis	Miner
Halictus rubicundus	Miner
Hylaeus angustatus	Pre-existing cavities
Hylaeus brevicornis	Pre-existing cavities
Hylaeus rinki	Pre-existing cavities
Lasioglossum albipes	Miner
Lasioglossum leucopus	Miner
Lasioglossum rufitarse	Miner
Panurginus romanii	Miner
Panurgus banksianus	Miner
Panurgus calcatus	Miner
Sphecodes crassus	Cleptoarasite
Trachusa byssina	Miner

Strengthening the argument of enhanced nesting recourses for mining bees on sandy sediments, it should be pointed out that 15 of the 19 unique (78 %) (i.e. only found on one sediment type) solitary bee species on glaciofluvial sediments are miners (table 6). The functional nesting strategies of these species gives a clear indication that the difference in species richness between sediment types is to likely be attributable to enhanced nesting resources for mining bees.

4.2 The influence of foraging recourses and landscape diversity

As hypothesised, both foraging recourses and landscape diversity influence the species richness and abundance of bees. The species richness and abundance of solitary bees show the same trends regarding the influence of foraging recourses: An increase in floral foraging

recourses seems to positively influence the bees in road verges on marine sediments while showing no trend on glaciofluvial sediments (fig. 6 and 7). This means that the difference in species richness and abundance of solitary bees between sediment types is modified by the foraging recourses available, which also has been shown for the effect of different management-schemes in Norwegian power line clearings (Sydenham et al., 2016). The difference as to how foraging recourses influences the species richness and abundance of between sediment types is likely due to the landscape-differences between the sediment types. The landscape on marine sediments is dominated by agricultural land, while on glaciofluvial sediments forest is the dominating landscape-type (See fig. 3). Moreover, in the 300 m buffer zones at each site, tilled crop land averages 57 % on marine sediments compared to 14 % on glaciofluvial sediments. In contrast, forest covers 17 % on marine compared to 53% on glaciofluvial sediments. Hence, a low landscape diversity index on glaciofluvial sediments equals a heavily forested landscape while a low landscape diversity index on marine sediments equals an extensively farmed landscape. Foraging recourses for bees in the agriculturally dominated landscape on marine sediments are likely to be patchier distributed than on glaciofluvial sediments dominated by forests, as grain-cultivation is the dominating crop (personal observation), which offer no foraging possibilities at all for bees. This may partly explain the contrasting influence of foraging recourses for the species richness and abundance of solitary bees, as flowers in road verges on marine sediments may to a greater extent act as bee-magnets in a fragmented landscape. Furthermore, the quality of the surrounding habitats become more important in landscapes with large agricultural monocultures (Kennedy et al., 2013). In effect, the landscape surrounding the road verges on marine sediments is arguably less suitable for bees than the surrounding landscape on glaciofluvial sediments, making the recourses available in road verges on marine sediments more important from a landscape-ecological point of view. There is an unquestionable relationship between floral foraging recourses and bees (Potts et al., 2003; Roulston & Goodell, 2011); the observed differences in the species richness of bees, and the species richness and abundance of solitary bees in this study could thus be proposed a result of differences in floral foraging recourses between sediment types. Such differences might be both in recourse-amount as well as systematic differences in floral community due to differing soil types and the effect of soil on the plant communities. While there is a significant difference in plant genus richness between sediment types, the other floral measurements show no differences (Table 6.). There are however clear differences in plant species composition between sediment types (fig. 8, table 6). Interestingly though, foraging recourses

proved insignificant to explain the variation in total species richness, while the results on both the species richness *and* abundance of solitary bees show that the impact of floral recourses in this study is arguably less than that of sediment type. Additionally, the relative differences in plant species composition (NMDS axis-1 scores) for the bees proved insignificant in my study. The low influence of foraging recourses might be explained by that the variation in foraging recourses and plant species composition is not large enough to unveil the real impact of foraging recourses on the bee communities. Nonetheless, the observed influence of foraging recourses does not take away from the clear influence of sediment type on the species richness and abundance of bees.

The results shown for both the species richness and abundance of solitary bees indicate no clear trends on either sediment type regarding the influence of landscape diversity (fig. 5 and 7). Landscape heterogeneity at the broad level may dilute the number of flower visitors, minimizing the landscape effect at the local level (Tscharntke et al., 2012), possibly explaining this. However, there are relative differences when comparing the influence of landscape diversity between sediment types (table 2 and 4). When compared, landscape diversity tends to have a negative effect on the bees on glaciofluvial sediments, while positive on marine sediments. There is reason to believe that this too could be related to the above-mentioned differences in landscape composition between sediment types. The intensively farmed land with extensive monocultures of agricultural crops on marine sediments are unlikely suitable habitats for bees (Holzschuh et al., 2010), especially not for ground nesting bees due to tillage and thus destruction of their nests (Ullmann et al., 2014). This may, especially at low levels, explain the differing influence of landscape diversity between sediment types.

4.3 Discussion of methods

45 bee species were identified in this study, making up almost a quarter of the extant Norwegian species. Although this is quite a high number of species for such a spatially limited area in Norway, there are several species already identified in close proximity to our road verges that were not sampled (Artskart.artsdatabanken.no, 2018). Bees were only sampled in July and August, and sampling during a more extended period of the season would probably have led to a higher species number of especially solitary bees. This is due to the fact that the solitary bees are active during shorter timespans and therefore easier to miss with only two sampling rounds, compared to bumblebees which are active throughout the season (Ødegaard et al., 2015b; Ødegaard, 2018a) and thus easier to sample despite few sampling

rounds. Because of the many solitary bees known to be linked to nest sites in sandy soils (Ødegaard, 2018a), sampling more of the season would *probably* only enhance the already observed differences between sediment types.

The bee sampling was performed by net collecting at flowers, a method chosen because we wanted data on which species of flowers the bees were foraging, even though these data are not used in my thesis (but see Skoog, 2018). Net sampling inherently carries the possibility of a certain collector bias (Westphal et al., 2008), but it is, along with observational studies, the only sampling method that allows for direct data on flower visits. Pan traps has bees argued to be the most efficient bee sampling method (Westphal et al., 2008), although there are examples of net collection outperforming pan traps (Popic et al., 2013). A combination of the two methods has been suggested assessing bee communities (Nielsen et al., 2011). Even though net sampling brings along the possibility of a collector bias, this would affect the sampling on the two sediment types in equal ways. It should also be mentioned that the sampling effort per transect meter (1 hour 50 m transect walk*2 persons*2 sampling rounds) is higher than the sampling effort made when sampling by net collection in Nielsen et al. (2011) and Westphal et al. (2008). Interestingly, the two collectors in my dataset had very similar experiences of collecting bees prior to the bee sampling, and there seems to be no collector bias in my data (see appendix 3).

4.4 Implications for conservation and management

In general, my results indicate that sediments should be taken into account while managing natural recourses, and in particular in the management of bees. Secondly, areas with sandy sediments should generally be considered potentially rich in bees, with obvious relevance to schemes aimed towards bee-conservation. As road verges may harbour a variety of bees, enhancement of the floral foraging recourses available in the road verges could be an effective means for the responsible authorities managing road verges (see Noordijk et al., 2009), although this may prove costly. Such measures could be especially important in areas with extensive monocultures and fragmented landscapes where the road verges offer important foraging possibilities in the landscape matrix. As nesting recourses seem to be limiting the species richness and abundance of bees, measures aimed at enhancing nesting recourses specifically, should be considered.

4.5 Conclusions

My findings show that nest-site limitation is an important ecological factor influencing bee communities, and that the distribution of nesting recourses for mining bees are controlled by geological processes. Furthermore, road verges offer suitable habitats for bees, potentially hosting a variety of species (Appendix 1). However, the suitability of the road verge varies with both the sediment type, the landscape diversity and the floral foraging recourses available. Evidently, areas with sandy sediments should be considered potentially rich in bees, of significance to both management- and conservation-schemes. My findings are likely attributable to the parts of the world that has been affected by extensive glaciation processes during the Pleistocene, where marine- and glaciofluvial sediments are prevalent. More research is needed attempting to grasp the role of nesting resources for bees, and to understand the processes affecting nesting recourses' spatial distribution.

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6 Appendix

6.1 Appendix 1, species inventory list of bees

Species name	Glacio-fluvial sediments (n)	Marine sediments (n)	Red list status	Nesting strategy
Andrena denticulata	29			Miner
Andrena fucata	4			Miner
Andrena lathyri	4	1		Miner
Andrena semilaevis	1			Miner
Andrena subopaca	16	1		Miner
Andrena tarsata	3			Miner
Andrena wilkella	7			Miner
Bombus bohemicus	11	5		Cleptoparasite
Bombus campestris	12			Cleptoparasite
Bombus hortorum	13	14		Social
Bombus humilis	5	9		Social
Bombus hypnorum	9	4		Social
Bombus jonellus	1			Social
Bombus lapidaries	95	49		Social
Bombus norvegicus	7	1		Cleptoparasite
Bombus pascorum	82	69		Social
Bombus pratorum	60	10		Social
Bombus ruderarius	5	9	VU	Social
Bombus rupestris	2			Cleptoparasite
Bombus sensu stricto	60	42		Social
Bombus sorensis	60	32		Social
Bombus sylvarum	13	57		Social
Bombus sylvestris	21	2		Cleptoparasite
Bombus wurflenii	2	5		Social
Colletes daviesanus	3	4		Miner
Colletes floralis	3			Miner
Colletes similis	4			Miner
Eucera longicornis		11		Miner
Halictus rubicundus	7			Miner
Halictus tumulorum	4	2		Miner
Hylaeus angustatus	1			Pre-existing cavity
Hylaeus brevicornis	1			Pre-existing cavity
Hylaeus rinki	2			Pre-existing cavity
Lasioglossum albipes	5			Miner
Lasioglossum calceatum		1		Miner
Lasioglossum fratellum	3	3		Miner
Lasioglossum leucopus	4			Miner

Lasioglossum rufitarse	1			Miner
Megachile circumcincta	1	3		Miner
Megachile willugbiella		2		Pre-existing cavity
Panurginus romanii	1			Miner
Panurgus banksianus	1		VU	Miner
Panurgus calcaratus	2			Miner
Sphecodes crassus	2			Cleptoparasite
Trachusa byssina	5			Miner

Appendix 1: Bee species inventory list, all sites and sampling rounds pooled. Including number of individuals on each sediment type, each species' status on the Norwegian red list if not (LC) (Ødegaard et al., 2015a), and the species' nesting habits. Nesting habits taken from (Cederberg., 2015; Ødegaard et al., 2015b; Ødegaard, 2018a).

On the distribution of *Colletes floralis*

With a total of three individuals, *Colletes floralis* was identified in two road verges, both on glaciofluvial sediments (Appendix 1). *Colletes floralis* is believed to be bound to coastal environments in Norway (Ødegaard, 2018b), a distribution pattern my findings contradict. My identifications are more in line with the Swedish distribution, with many known inland locations (Artfakta.artdatabanken.se, 2018). My observations are located approximately 35 km away from the nearest previously observed individual (Artskart.artsdatabanken.no, 2014), shifting the Norwegian northern distribution-limit around 28 km north.

6.2 Appendix 2, species inventory list of plants

Species name	Total abundance	Species name	Total abundance
Achillea millefolium	599	*Lotus corniculatus*	63
Aegopodium podagraria	32	*Lupinus polyphyllus*	210
Ajuga pyramidalis	1	*Melampyrum pratense*	10
Anemone nemorosa	31	*Melampyrum sylvaticum*	6
Antennaria dioica	3	*Myosotis arvensis*	18
Anthriscus sylvestris	383	*Myosotis sp.*	4
Argentina anseria	1	*Noccaea caerulescens*	3
Barbarea vulgaris	5	*Omalotheca sylvatica*	2
Calluna vulgaris	34	*Oxalis acetosella*	3
Campanula rotundifolia	1	*Pimpinella saxifraga*	50
Carum karvi	5	*Potentilla argentea*	17
Cerastium fontanum	16	*Potentilla erecta*	21
Cerastium glomeratum	1	*Ranunculus acris*	163
Cerastium sp.	3	*Ranunculus auricomus*	9
Chamerion angustifolium	40	*Ranunculus repens*	164
Circium vulgare	7	*Ranunculus sp.*	4
Cirsium arvense	120	*Rhinanthus minor*	34
Cirsium palustre	5	*Rubus idaes*	35
Epilobium ciliatum	1	*Salix caprea*	7
Epilobium sp.	18	*Salix sp.*	25
Erysimum cheiranthoides	0	*Sambucus rasemosa*	1
Euphrasia sp.	4	*Scorzoneroides autumnalis*	30
Ficaria verna	1	*Sorbus aucuparia*	2
Filipendula ulmaria	235	*Stellaria graminea*	32
Fragaria vesca	112	*Tanacetum vulgare*	116
Galeopsis sp.	6	*Taraxacum sp.*	383
Galium album	309	*Trifolium hybridum*	61
Galium boreale	5	*Trifolium medium*	315
Galium verum	27	*Trifolium pratense*	426
Geranium sylvaticum	18	*Trifolium repens*	105
Glechoma hedaracea	7	*Trifolium sp.*	140
Hieracium pilosella	92	*Tripleurospermum inodorum*	61
Hieracium sp.	61	*Tussilago farfara*	122
Hieracium umbellata	167	*Vaccinium myrtillus*	3
Hypercium maculatum	12	*Veronica agrestris*	2
Hypercium perforatum	1	*Veronica chamaedrys*	151
Knautia arvensis	29	*Veronica officinalis*	31
Lathyrus linifolius	32	*Viccia sepium*	224
Lathyrus pratensis	235	*Vicia cracca*	50
Leucanthemum vulgare	27	*Viola sp.*	92
Linnaria vulgaris	39	*Viola tricolor*	4

Appendix 2: Plant species inventory list, with total abundance (all sites added up, using the percentage coverage estimates from the vegetation survey).

6.3 Appendix 3, collector bias

Appendix 3, table 1: The species richness and abundance of bees, divided by collector. DJS=Daniel Jeuderan Skoog, KAH=Kaj-Andreas Hanevik.

	Collector 1 (KAH)	Collector 2 (DJS)
Individuals (n)	556	561
Species (n)	41	40
Solitary bee species (n)	24	23
Bumblebee species (n)	17	17

Appendix 3, table 2: Statistical output from t-test performed on the species richness and abundance of bees sampled at each site, between collectors. DJS=Daniel Jeuderan Skoog, KAH=Kaj-Andreas Hanevik.

	t	df	Mean collector=DJS	Mean collector=KAH	p-value
Species richness	0.2	28.553	9.816	9.5	0.843
Abundance	0.14	29.673	28.813	28.063	0.89

6.4 Appendix 4, sites with coordinates

Appendix 4: The coordinates of each site (see fig. 1). Also including old site names, as these are the site-names the collected bees are labelled with.

Site	X	Y	Old site-name
m1	11,03904	60,085292	M11
m2	11,024455	60,143665	M10
m3	11,026504	60,161903	M9
m4	11,02852	60,176813	M8
m5	11,034328	60,191842	M12
m6	10,990725	60,194455	M13
m7	11,060839	60,225118	M6
m8	11,192735	60,318768	M4
s1	11,124372	60,165043	S11
s2	11,136672	60,171149	S1
s3	11,1581	60,17885	S14
s4	11,174608	60,188283	S12
s5	11,139472	60,191864	S10
s6	11,12441	60,206994	S9
s7	11,09974	60,225974	S8
s8	11,169753	60,246846	S7

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