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# Diversity of wild bees in semi-natural grasslands in southeast Norway is related to temperature and amount of edge habitat in the surrounding landscape

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Master of Science in Ecology

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# *Abstract*

The declines in diversity and abundance of wild bees are mainly attributed to the intensification of agricultural practices and the resulting loss of semi-natural grassland habitats. Furthermore, the effect of climate change (i.e., rising temperatures) pose an additional concern for wild bees (and other insect pollinators). However, the potential interactive effects of rising temperatures and habitat characteristics are poorly understood.

The aim of this study was to explore the interactive effects of temperature and different landscape attributes (amount of edge habitat, amount of semi-natural grasslands, distance to coastline, landscape diversity). I sampled wild bees from 20 semi-natural grasslands in southeast Norway to supplement an existing dataset containing data from 32 such grasslands. Using data from all 52 sites, I analysed how bee species richness, total abundance and Shannon diversity varied across the sites, in relation to temperature, distance to the coastline, and area-dependent landscape attributes quantified within radii of 250, 450 and 650 m around each site.

My results indicate that rising temperatures and habitat area (amount of edge habitat) have a positive effect on wild bee diversity. However, the positive effect of edge habitat was modified by temperature, and the importance of edge habitat decreased with increasing temperature. Consequently, the amount of habitat area (edge) was only important for wild bee diversity at lower temperatures.

My findings suggest that within southeastern Norway, climatic factors were more important for wild bee diversity than availability of suitable habitat. However, wild bees undergoing thermal stress from colder temperatures showed increased dependancy on habitat amount (edges). With the impending implications of climate change, a better understanding of the interactive effects of climatic conditions and the surrounding landscape context could help ensure the viability of wild bee communities in the future.

## *Table of contents*

# *1. Introduction*

Wild bees provide important pollination services, and contribute to agricultural productivity and diversity of natural ecosystems (Öckinger and Smith, 2006; Potts et al. 2010; Ødegaard et al. 2013; Reilly et al., 2020). However, the global decline of wild bees and other insect pollinators are raising concerns for future pollination efficiency, and the implications on ecosystems (Williams et al 1991; FAO 2008; Potts et al. 2010). While there are several factors contributing to the (current, past, and potentially future) decline of wild bees, such as invasive species (Stout et al. 2009; Rasmussen et al. 2021; Renner et al. 2021), pesticides (Van Der Valk et al. 2012; Park et al. 2013) and diseases (Abrol 2012), land-use change is attributed as the main driver (Biesmeijer et al. 2006; Ollerton et al. 2014; Papanikolaou et al. 2017; Jeroen et al. 2018). Anthropogenic land-use change have caused habitat loss and fragmentation of suitable habitats for wild bees (Öckinger & Smith 2006; Ødegaard et al. 2013; Carrié et al. 2017). Specifically, the intensification of agriculture and abandonment of traditional practices have resulted in loss of semi-natural grasslands, such as pastures and flower meadows (Potts et al. 2010; Ødegaard et al. 2013). Semi-natural grasslands are considered important habitat for wild bees by providing nesting sites and high density of diverse floral resources (Ødegaard et al. 2013; National Pollinator Strategy 2018), as the management of these areas (i.e. grazing animals, cutting or mowing) allows for more diverse plant assemblages by benefiting slow growing and specialist plants (Öckinger & Smith 2006). Thus, to prevent further loss of semi-natural grasslands and their associated biodiversity, Norway implemented a national action plan in 2009, and declared flower meadows a threatened (CR) nature type in 2011 (Miljødirektoratet, 2021).

Other studies have found that the surrounding landscape composition is important for wild bee diversity (Steckel et al. 2014; De Palma et al. 2015; Mallinger et al. 2016; Papanikolaou et al. 2017). More specifically, high amounts of semi-natural grassland habitat (Papanikolaou et al. 2017), landscape heterogeneity (Mallinger et al. 2016), and availability of floral resources (Kratschmer et al. 2019) in the surrounding landscape context have a positive effect on wild bee diversity. However, as remnants of semi-natural grasslands are scattered throughout the modern cultural landscape (National Pollinator Strategy 2018), wild bees are found to forage in alternative habitats, like in edge habitats (i.e. the transitional areas between different habitat types) (Sydenham et al. 2016; Kallioniemi et al. 2017). These different edge habitats, like forest edges and road verges, typically hold early succession vegetation, resembling that of semi-natural grasslands, and can have similar plant species assemblages with high floral density (Kallioniemi et al. 2017; Phillips et al. 2019). Thus, wild bees can find valuable habitat for nesting and foraging alongside agricultural fields (Sydenham et al. 2012; Kallioniemi et al. 2017), alongside roads (Phillips et al. 2019), and in forest edges and clearings (Eldegard et al. 2017; Sydenham et al. 2016; Jeroen et al. 2018). Furthermore, wild bees are dependent on relatively close proximity to different suitable habitats for floral resources, as smaller solitary bees only tend to forage a few hundred meters from the nest (Gathmann & Tscharntke 2002; Zurbuchen et al. 2010). Hence, wild bee diversity is especially sensitive to landscape composition at the local-scale (Murray et al. 2012).

Wild bee diversity is also influenced by climatic conditions (Clarke & Gaston 2006; Sunday et al. 2014; Corbet et al. 2016; Phillips et al. 2018). Hence, climate change pose an additional threat to wild bees, and is expected to influence bee communities in multiple ways (Oliver et al. 2014; Papanikolaou et al. 2017; Kammerer et al. 2021). One of the major aspects of climate change is the predicted rise in temperature, and the impact is predicted to vary geographically (IPCC 2018). Furthermore, ecosystems in different regions of the world are expected to have varying responses to warming, as the species in these ecosystems would have different thermal tolerances (Sunday et al. 2014). Hence, rising temperatures are expected to increase bee diversity in boreal areas (Hoiss et al. 2012), while several studies predict decreased bee diversity in temperate ecosystems (Papanikolaou et al. 2017; Kammerer et al. 2021). This is because temperature tend to be a limiting factor for biodiversity in boreal regions, as a result of seasonal variation, thus warmer temperatures would generally increase biodiversity (Klanderud et al. 2003; Grabherr et al. 2010; Vanneste et al. 2017). An additional aspect of climate change is the changes in seasonal weather patterns and frequency of extreme weather events (IPCC 2018). This is expected to be challenging for pollinators, both directly by imposing abiotic stresses and indirectly by altering plant-pollinator interactions (Polce et al. 2014; IPCC 2018). Hence, the initial positive effect of warming temperatures expected in boreal ecosystems, could be abated by the implications of abnormal weather patterns and more extreme events (like drought). Consequently, increased frequency and intensity of drought is expected to negatively affect pollination (Oliver et al. 2014; Thomson 2016; Phillips et al. 2018; Rankin et al. 2020; Hung et al. 2021). Direct consequences of drought can cause bees to overheat when foraging and thirst, because suitable water sources (i.e. shallow puddles) tend to dry up quickly in the sun (Rankin et al. 2020). While indirect consequences of drought conditions can affect the availability of floral resources (e.g. reduction in flower size, number of flowers per plant) (Oliver et al. 2018), floral nutritional quality for pollinators (less pollen and nectar) (Gallagher et al. 2017; Rankin et al. 2020) and cause mismatch between plant-pollinator relationships (Phillips et al. 2018). Thus, rising temperatures, especially combined with increased occurrence of drought conditions, have the potential to affect wild bee communities in a number of ways.

While the implications of climate change is expected to vary in different regions of the world, it is also predicted to vary within the same region(s) (IPCC 2018). Hence, different ecosystems within southeast Norway could then experience climate change effects differently; like wild bee communities residing in coastline ecosystems compared to inland habitats. Following this, coastline ecosystems are found to have less annual temperature variance than further inland (Sutton et al. 2007). This is because the oceans heat capacity is much greater than that of land, and as a result it take longer to heat up or cool down; i.e. the ocean slowly warms in the summer, keeping air cool, and it slowly cools in winter, keeping the air warm. Thus, the further distance from the ocean the more extreme the climate is likely to be (Sutton et al. 2007).

However, the threats to the diversity of wild bee communities are not isolated, but act in concert. Oliver et al. (2014), among others, have pointed out the importance of studying the interactive effect of threats on biodiversity (i.e. interactive effect of landscape context *and* climate factors), with the premise of them having antagonistic or synergic implications. A study by Papanikolaou *et al.* (2017) explored the potential of semi-natural grasslands mitigating the detrimental effect of warmer temperatures on wild bee communities in Germany. Furthermore, Hung et al. (2021) investigated whether habitat fragmentation worsened the effect of drought on wild bees. In similar fashion, drought-sensitive butterflies were found to be more resilient (in population recovery) in less fragmented landscapes in Great Britain after extended drought conditions (Oliver et al. 2015). In this context, wild bee communities are likely to respond differently to climate change (i.e. rising temperature) in different landscape contexts. Therefore, identifying which attributes within a landscape that can dampen or amplify wild bees interactions with climate change, can be valuable when implementing management strategies to these landscapes. Thus, the aim of this study was to investigate the interactive effects of rising temperatures and different landscape attributes on wild bee diversity in southeast Norway. I made the following predictions:

*i)* Rising temperatures will have a negative effect on wild bee communities. More specifically, the implications of prolonged high temperatures in synergy with little precipitation, resulting drought conditions.

*ii)* Increased amounts of semi-natural grassland habitat will have a positive effect on local wild bee communities (i.e. species richness, abundance and diversity).

*iii)* Increased diversity (heterogeneity) in the surrounding landscape will have a positive effect on local wild bee communities.

*iv)* Increased amounts of edge habitat will have a positive effect on wild bee communities.

*v)* Closer proximity to coastline will have a positive effect on wild bee communities, compared to bee communities further away from the coast (inland).

# *2. Methods*

## *2.1 Study area and site selection*

The study was conducted in semi-natural grasslands in southeast Norway, in the three counties of Viken, Oslo and Innlandet (between latitudes 58.99-60.49 N, and longitudes 10.08-12.00 E). The study area stretches from the island landscapes of Hvaler (59°04'19.5"N, 10°54'59.7"E) in the south, to forested inland habitats close to Hamar (60°29'28.1"N, 11°06'36.0"E) in the north. The distribution of the dominant land-use and habitat types according to AR5 maps were: forest (65%), freshwater bodies (8.4%), infrastructure (7.9%), cultivated soil (tilled) (5.4%), open land (4.9%), roadwork/ transport (1.7%), ocean (1.6%), pasture (infield) (1.2%) and non-tilled cultivated areas (0.1%) (within 650m radii). This distribution of landscape context was the average within 650 meter radii of the study sites, and would be representative of the agricultural land-use in a wider region. Elevation ranges from 2.7- 537 m.a.s.l., and the mean temperature during the flowering season (April-August) was 12.4˚C. Field work was conducted in the summers (April-August) of 2019 and 2020.

Study sites were selected along a gradient of landscape context, and vary in management regime, conservational value (national and regional levels of importance in line with DN 2009, *Ministry of the Environment*), elevation and distance to sandy areas. The selected sites were at least 1000 meters apart to prevent re-sampling of the same local wild bee communities, as foraging distances for most wild bees are typically shorter than 1000 meters (Gathmann & Tscharntke, 2002). A total of 52 study sites were selected (32 sites in 2019, and 20 sites in 2020) (Figure 1). All sites (except one in 2020) reside within registered semi-natural grasslands; albeit in different forms: forest clearings, flower meadows, scrap lands/wastelands (*skrotemark*) and grazed pastures (actively and periodically at the time of field work/data collection).

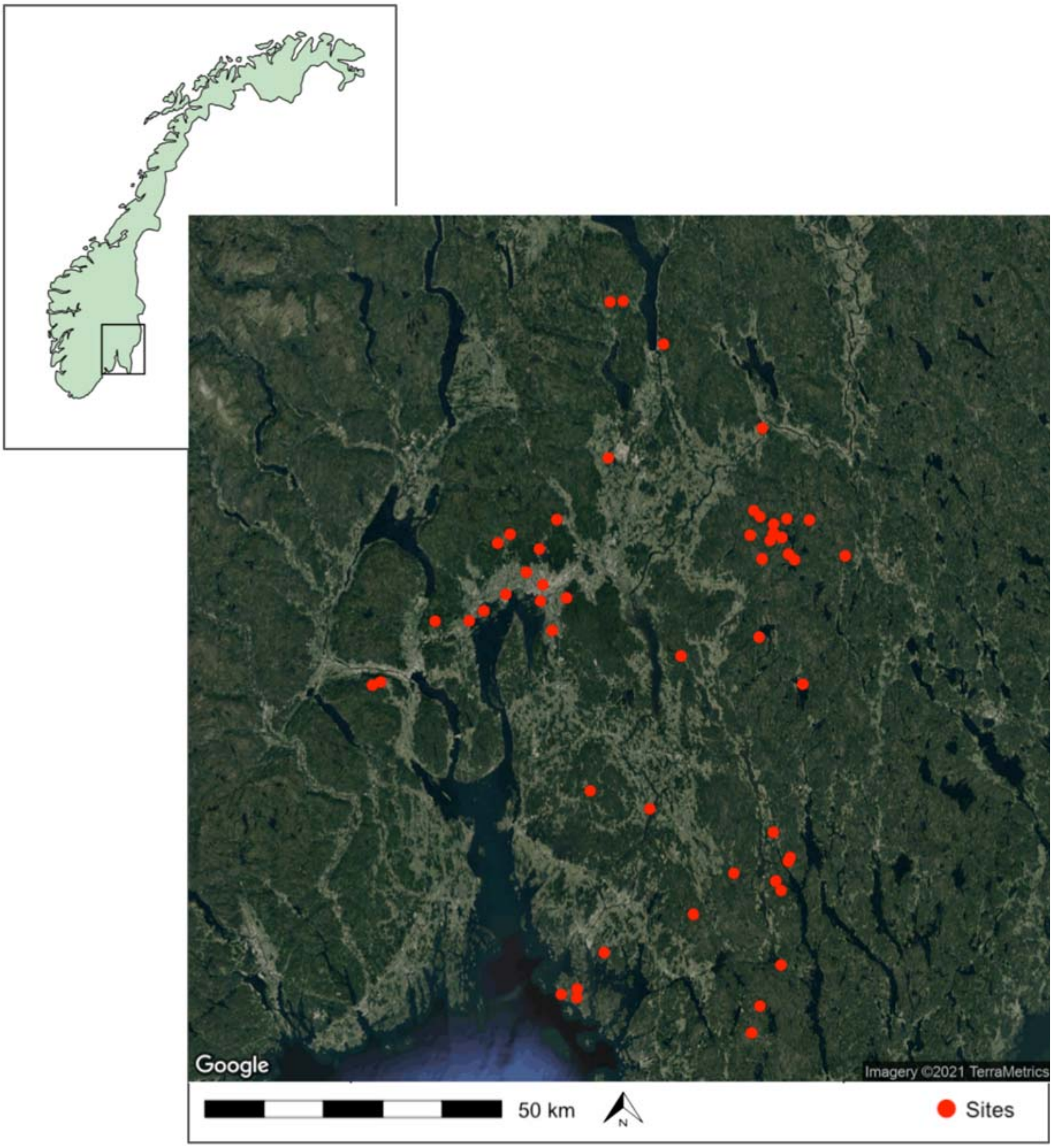


**Figure 1:** Map of study area in southeast Norway, and the 52 study sites. Map made in Rstudio Version 1.4.1103 (2020), using packages *ggmap* (Kahle & Wickham 2020), *ggplot2* (Wickham 2016), and satellite map by Google Maps (2021).

## *2.2. Data collection*

### *2.2 Bee sampling*

I followed the field protocol for bee sampling from 2019, and extended the study by 20 additional sites in 2020. However, this time with two pan traps per site, instead of three. I sampled bees with pan traps, which is a standardised method for registering wild bees, and efficient when sampling multiple sites during the same time period (Gezon et al. 2015; O'Connor et al., 2019). The pan trap consists of three plastic bowls (Ø = 30cm), one painted fluorescent blue (Sparvar 3107 blue Fluorescent), one fluorescent yellow (RAL 1026 Fluorescent yellow), and one left unpainted (white). The bees are attracted to the colours, reminiscent of flowers, and drown in the water. Pan traps were installed at least 20 meters apart, to avoid "trap-competition", in vegetated areas with sun exposure (Figure 2b-c). Repeated bee sampling by pan traps throughout the flowering season do not inherently affect the composition of the local bee communities (Gezon et al. 2015). I sampled bees four times during the 2020 flowering season: 1) 13.-16. May, 2) 25.-28. May, 3) 14.-17. June, 4) 14.-19. July.  Pan traps were deployed when there were four consecutive days with sun, with little wind (<5m/s) and temperatures above 15°C during the day. Albeit, the risk of some variation in weather conditions throughout the region over the course of the sampling period (4 days).

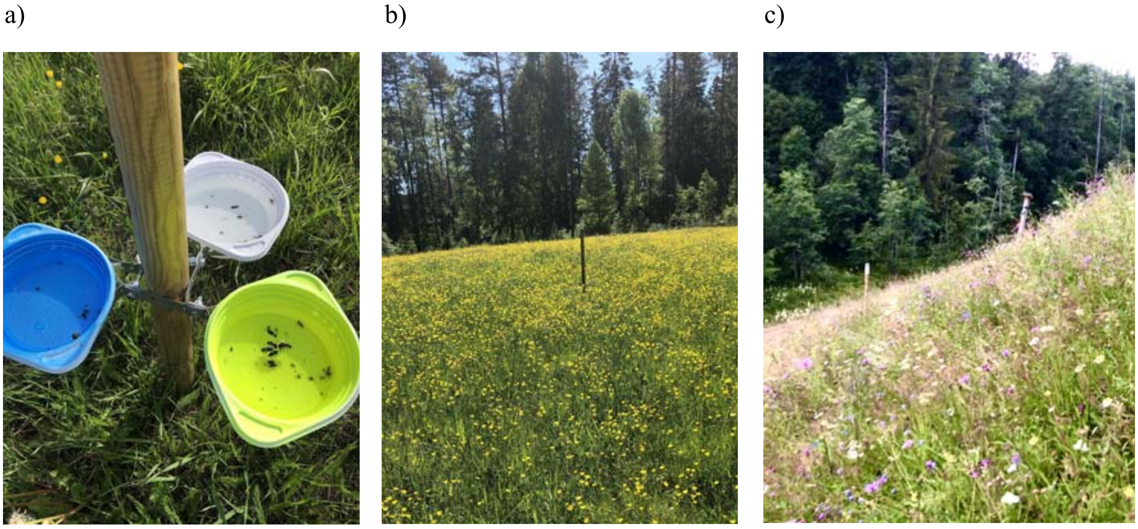


**Figure 2:** Pan traps after 48 hours (a). Pan traps were installed in sun exposed areas, with pans deployed levelled with the surrounding vegetation (b, c).

On sampling days, pan traps were filled with water (2 cm from the top) and a small amount of dish soap (Zalo) to break the surface tension. After 48 hours the traps were emptied by sifting the contents through a a sieve and coffee filters, and the insect material was transferred to jars filled with 99% Ethanol until further processing. The jars were marked on site. The collected bees were dried, pinned, and identified to species level by myself and Mikaela E.G.P. Olsen. Species identification was then verified by Markus A.K. Sydenham (Norwegian Institute for Nature Research).

## *2.3. Data pre-processing*

### *2.3.1 Bee data*

The focus of this study was solitary bees, and bumblebees (sp. *Bombus)* and the domesticated honeybee (*Apis mellifera)* were not included in the analyses. To prepare the raw data (bee registration) for analysis, I calculated species richness, total bee abundance and Shannon diversity for each sample unit (trap within site within year). I used the R software (version 3.6.2) and the *Vegan* package (Oksanen et al. 2020) to calculate richness and Shannon diversity.

### *2.3.2 Landscape data*

The landscape context data were based on digital AR5-maps (NIBIO), using the R software version 3.6.2. I created buffers around each study site with radii of 250, 450 and 650 meters, and used these when quantifying the landscape variables below. These radii were selected because the distance is within the foraging range for most wild bees (also smaller solitary species), thus it gives a good indication of the habitat conditions experienced by local bee communities (Steffan-Dewenter et al. 2002). Secondly, to avoid the buffers extending into Sweden I chose 650 m radii as maximum radius (the country border is ca 700m away from a few of the sites). Four main landscape variables were extracted: elevation, the amount of valuable habitat nearby, landscape diversity, and distance to coastline:

1) *Elevation*:

Site elevation for each sample unit (Site_Trap_Year) was obtained from Norgeskart.no (Kartverket).

2) *Amount of valuable habitat nearby:*
   a) *Amount of registered semi-natural grasslands*

   I opted to quantify the amount of *registered* meadows, because it gives an indication of a stable habitat/resource in a temporal perspective. I calculated the amount of registered meadows for each site within the buffers (250m, 450m, 650m). I downloaded nature-type maps (DN-13 registered) from Naturbase (*Ministry of the Environment*), and aggregated by nature-type to establish all areas with meadows. I then intersected this with my trap locations, to get the total area of meadows (m2) within each buffer radii. In contrast to the rest of the sites, one study site in 2020 (POLLI_22_2020) was not installed within a registered meadow, and has therefore no meadow amount. I used the packages *geosphere* (Hijmans 2019), *sp* (Bivand et al. 2013), *raster* (Hijmans 2020), *maptools* (Bivand & Lewin-Koh 2020), *ggmap* (Kahle & Wickham 2020), *rgeos* (Bivand & Rundel 2020) and *rgdal* (Bivand et al. 2020) in R, to calculate the amount of registered meadow around my sites.

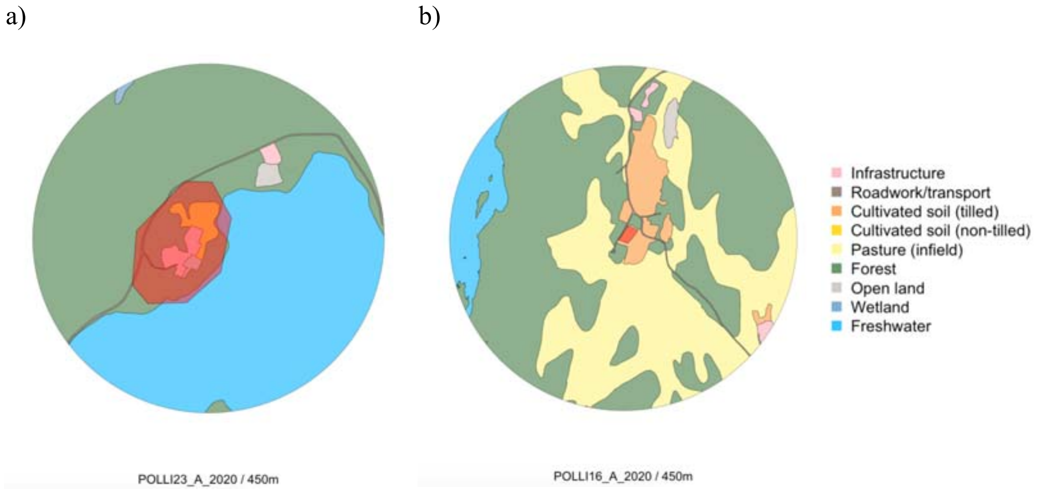


**Figure 3:** Visualisation of the sites with highest (a) and lowest (b) amount of registered meadows within 450m buffers. The site with zero meadow amount is not pictured. Meadows are shown as red polygons in the maps. Digital maps (AR5) worked in RStudio.

*b) Quantification of edge habitat*

I chose to define *edge habitat* as the transitional area between different habitats types. Therefore, I had to combine all smaller neighbouring polygons with the same habitat type in my AR5-maps, into one big polygon instead (i.e. two neighbouring forest polygons had to be combined into one big forest polygon). This however, caused me to potentially lose some edge habitat, like from corridors alongside neighbouring fields as an example. Still, I chose to rather underestimate the true amount of edge habitat, and simply calculate the edges between different the habitat types. Thus, I split and aggregated my AR5-maps by habitat type. By aggregating I was able to combine all the neighbouring polygons with the same habitat type, and then quantify the amount of edges (m). I used the packages *geosphere* (Hijmans 2019), *sp* (Bivand et al. 2013, *raster* ((Hijmans 2020), *maptools* (Bivand & Lewin-Koh 2020), *ggmap* (Kahle & Wickham 2020), *rgeos* (Bivand & Rundel 2020) and *rgdal* (Bivand et al. 2020) in R.

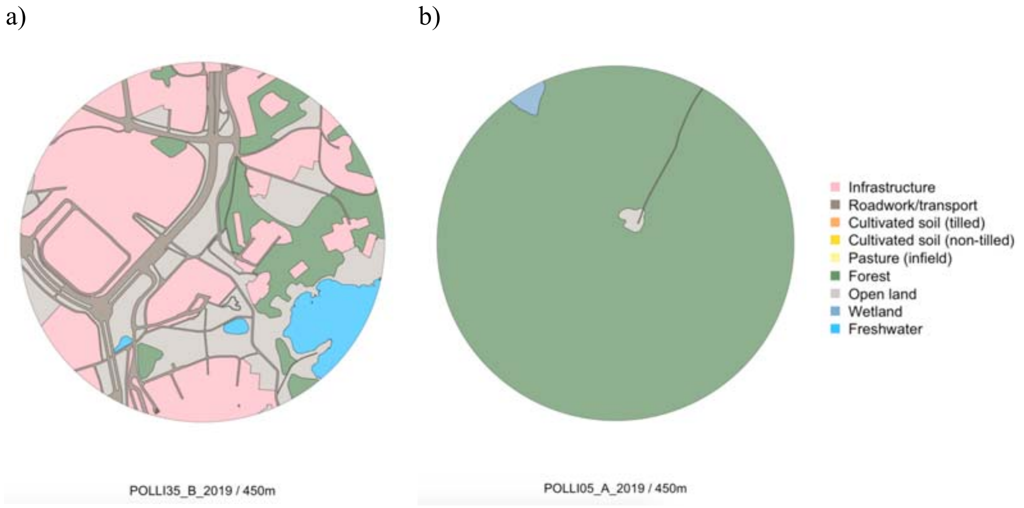


**Figure 4:** Visualisation of the sites with highest (a) and lowest (b) amount of edges within 450m buffers. Digital maps (AR5) worked in RStudio.

### 3) *Diversity (heterogeneity):*

I used the Shannon diversity index when calculating the landscape diversity (heterogeneity). First, I aggregated AR5-maps by habitat type, and calculated the area (m2) of each habitat type within the different buffer radii. Then I calculated landscape diversity by using the *geosphere* (Hijmans 2019) and *vegan* package (Oksanen et al. 2020) in R. The equation used for the Shannon diversity index was:

$$(H) = - \sum_{i=1}^{s} p_i \ln p_i$$

where p = proportion (n/N) of area of one particular habitat type (n) divided by the total amount of area (N), ln = the natural log, Σ = the sum of the calculations, and s = the number of habitat types present within the buffers.

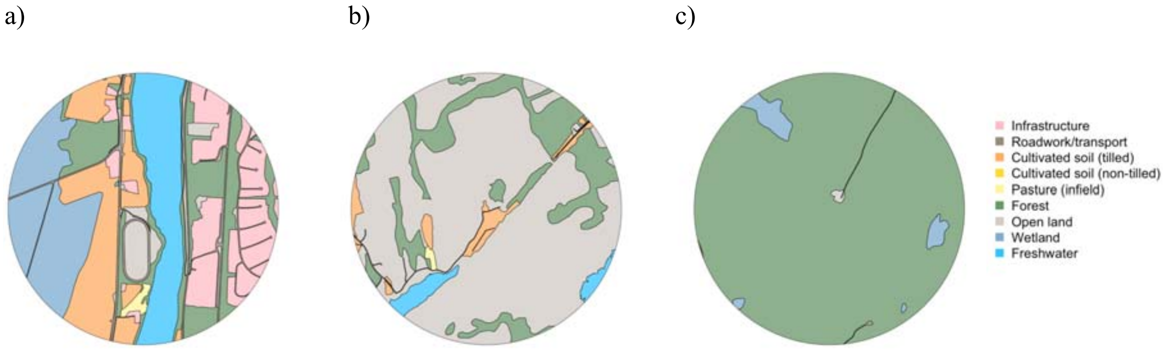


**Figure 5:** Visualisation of sites with high (a), moderate (b) and low (c) landscape diversity (within 450m buffer). Digital maps (AR5) worked in RStudio.

### 4) *Distance to coastline*

I sorted AR5-maps by habitat type and aggregated by ocean polygons. I then calculated the distance from each trap location (in m) to the nearest ocean polygon (i.e. the coastline). I used the *rgeos* package (Bivand & Rundel 2020) in R.

## *2.3.3 Climate data:*

Raster maps with mean monthly temperatures were dowloaded from seNorge.no. I extracted the temperatures (monthly mean) for each trap location (total of 136 locations over the two years), for the whole flowering season (April-August). I later used the aggregate function to calculate mean temperature for each site, as well as annual mean temperatures. I used the packages *rgdal* (Bivand et al 2020), *raster* (Hijmans 2020) and *sp* (Bivand et al 2013) in RStudio (Version 1.4.1103).

## *2.4. Statistical analysis*

Prior to statistical analyses, I explored my data to avoid common statistical problems; I carried out graphical inspection of the data to check for outliers, frequency distributions and correlation among predictor variables (Zuur et al. 2010). For statistical analyses of relationships between bee response variables (richness, abundance, Shannon diversity) and explanatory variables, I fitted generalised linear mixed-effects regression models (GLMMs), as I had dependent data (study sites were sampled with two/three traps, multiple times during the flowering season(s)), and the GLMM allowed me to include Site ID as a random effect term. Before fitting the GLMMs, I carried out a pre-selection of predictor variables, where I checked each possible pairwise combination between predictor variables and response variables by a Spearman correlation test. Only predictor variables that showed a moderate to strong signal (r >0.5) on the response were included as predictors in the GLMMs. I used the backward selection method suggested by Zuur et. al. (2010) when building my models, and the drop1 function (for Chi-square) to check for significant relationships (*stats* function). Model assumptions were tested and verified by running a DHARMa residual diagnostics, where predicted vs. observed values were plotted to estimate the models fit for the data (*DHARMa* package (Hartig 2020)). To fit my models I used the *lme4* (Bates et al. 2014), *MuMIn* (Bartoń 2020), *effects* (Fox 2003) and *DHARMa* (Hartig 2020) packages in RStudio (Version 1.4.1103).

Concerning the predictor variable *Temperature*, I chose to include both April and July temperatures, as these months had the strongest (and similar) allover correlation with the response variables. Consequently, this also allowed me to look at the temporal aspect of temperature effects over the course of the flowering season; early (April) and mid-late (July). Therefore, I fitted three main models (three response variables: species richness, abundance and Shannon diversity), each with two different temperature predictor variables, which resulted in six models total (Table 2-3). Additionally, because some landscape attributes were quantified within three different buffer radii (250m, 450m, 650m); (i.e. a*mount of edges, landscape diversity* and *amount of registered meadows,* I tested and found that the 250m buffer radius gave the strongest allover signal for all the models. Thus, I used predictor variables from the 250m buffer as predictors in the final GLMMs.

### *Species richness*

To model the relationship between number of bee species (richness) and predictor variables, I fitted a generalised mixed model (GLMM), assuming a Poisson distribution of errors. As fixed effects in the full model, I included *mean monthly temperature for April/July*, *amount of edges* and *year,* and the interaction term *amount of edges* × *mean monthly temperature for April/July.* Random effects were *Site+Year* for Model 1, and *Site+Year* and *Year* for Model 4 (see rationale in *Annual Variance* below), where the *Year* variable was a two level categorical factor. The predictor variable *amount of edges* was log-transformed to improve residual distributions.

### *Total abundance*

To model the relationship between number of bees (abundance) and predictor variables, I fitted a negative binomial generalised mixed-effects model (NBGLMM), assuming both under- and over-dispersion of the count data. As fixed effects in the full model, I included *mean monthly temperature for April/July* (continuous), *amount of edges* (continuous), *year* (categorical with two levels), and the interaction term *amount of edges×mean monthly temperature for April/July.* Random effects were *Site+Year* (categorical) and *Year* (categorical with two levels) for Model 2, and *Site+Year* for Model 5 (see reasoning in *Annual Variance* below). The predictor variable *amount of edges* was long transformed to improve residual distributions.

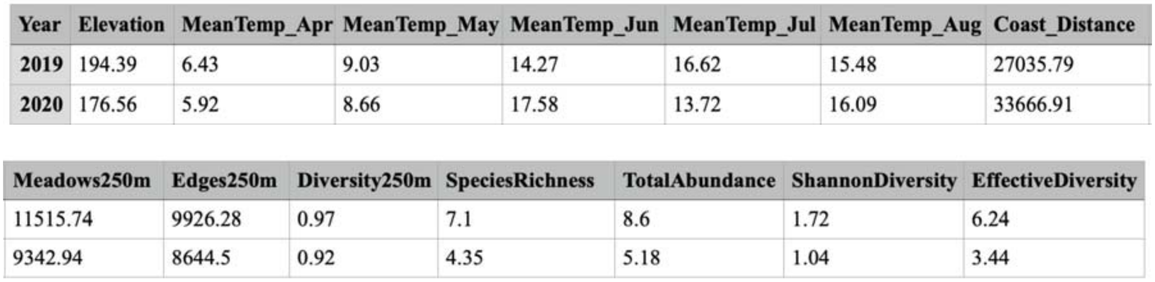
### *Shannon diversity*

To model the relationship between the proportion of species abundance (Shannon diversity) and predictor variables, I fitted a regular linear mixed-effects regression (LMM), assuming Gaussian distributed continuous data. As fixed effects, I included *mean monthly temperature for April/July* (continuous), *amount of edges* (continuous), *year* (categorical with two levels). The interaction term is *amount of edges×mean monthly temperature for April/July.* Random effects were *Site+Year* (categorical) and *Year* (categorical with two levels) for Model 3 and Model 6 (see reasoning in *Annual Variance* below). The predictor variable *amount of edges* was log-transformed to improve residual distributions.

### *Annual variance*

There was considerable annual variation in the wild bees response variables; specifically, species richness, total abundance and Shannon diversity (Table 1).

**Table 1:** Annual variance of the different variables. (See also the temperature variation between the years for June and July).



| Year | Elevation | MeanTemp_Apr | MeanTemp_May | MeanTemp_Jun | MeanTemp_Jul | MeanTemp_Aug | Coast_Distance |
|---|---|---|---|---|---|---|---|
| **2019** | 194.39 | 6.43 | 9.03 | 14.27 | 16.62 | 15.48 | 27035.79 |
| **2020** | 176.56 | 5.92 | 8.66 | 17.58 | 13.72 | 16.09 | 33666.91 |

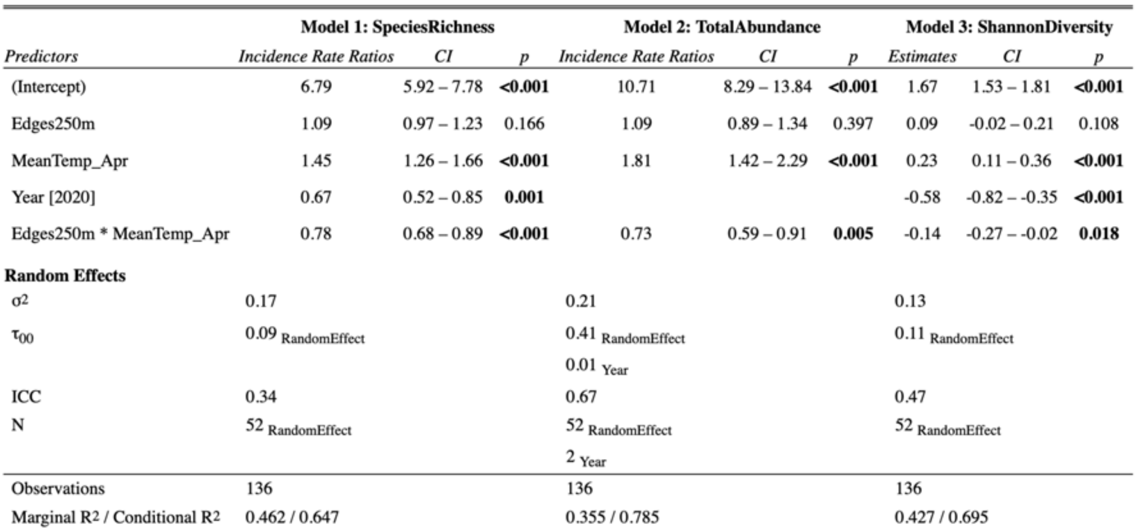
| Meadows250m | Edges250m | Diversity250m | SpeciesRichness | TotalAbundance | ShannonDiversity | EffectiveDiversity |
|---|---|---|---|---|---|---|
| 11515.74 | 9926.28 | 0.97 | 7.1 | 8.6 | 1.72 | 6.24 |
| 9342.94 | 8644.5 | 0.92 | 4.35 | 5.18 | 1.04 | 3.44 |

I did not intend to investigate the annual variance of wild bees, but rather all the wild bees gathered collectively for the two years. For this reason, *Year* should have ideally been included as a random effect for all models. However, because there was considerable annual variance, the residual distributions from some models did not conform to the distributions expected from the assumed error distributions. *Year* was therefore modelled as a fixed effect for some models, and random effect for others (Table 2-3). This was simply to get the cleanest looking models (i.e., best fit to the data), without major quantile deviation of the residuals. I do acknowledge that there was annual variance, but because sites were non-randomly distributed across environmental conditions across years, and monthly sampling intensity varied between 2019 and 2020, I could not analyse this further. Site nested in year was included as a random effects in the models, to account for the uneven amount of pan-traps between the two years and repeated sampling (dependent data) (Table 2-3).

## *3. Results*

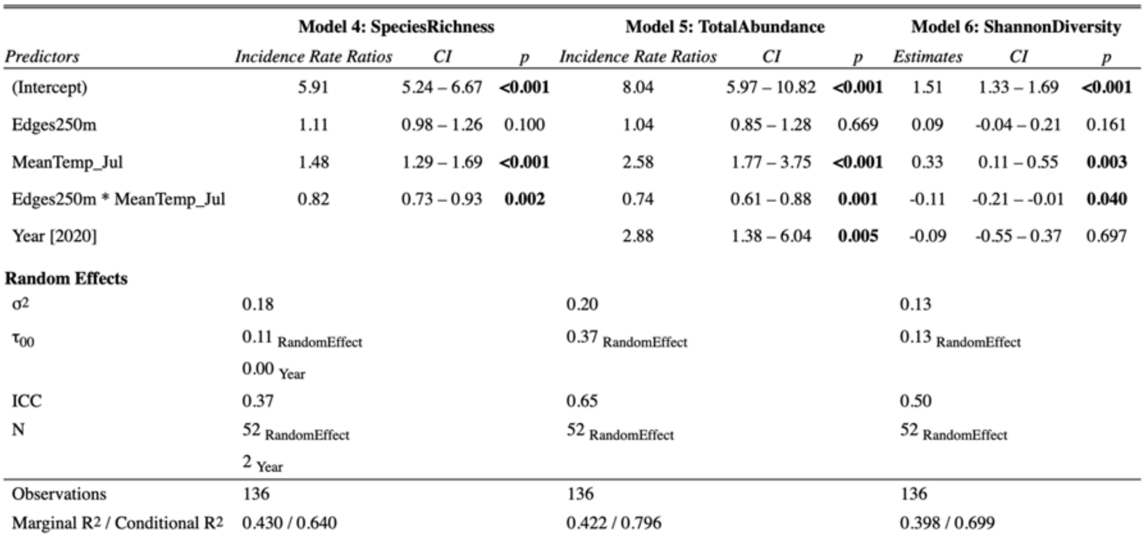
A total of 2835 bees were collected during the summers of 2019 and 2020. I excluded 72 honey bees (*Apis mellifera*) and 881 bumblebees from all analysis. The remaining 1882 individuals belonged to 87 different species of solitary bees. The most abundant solitary bee species was *Lasioglossum morio* with 267 individuals.

**Table 2:** Models and model statistics for modelling species richness, total abundance and Shannon diversity as a function of average monthly April temperature, amount of edge (m) within 250m a buffer and year (2019 [reference level] and 2020). I used a Poisson generalised linear mixed-effects model (GLMM) to model species richness, a negative binomial GLMM to model abundance and a linear mixed-effects regression (LMM) to model Shannon diversity. The amount of edges *(Edges250m)* was long transformed, to alleviate and scale (standardise) the error distribution. Site and year were included as a random effects, to account for repeated sampling throughout the flowering season. *Year* was included as a fixed effect in model 1 and 3, to account for significant annual variance, and as a random effect in model 2. Marginal R-squared is explained by fixed effects, while conditional R-squared is explained by fixed effects *and* random effects. This means that *Year* is included in conditional R-squared as a fixed effect for certain models, hence this value is likely an overestimation.



| | **Model 1: SpeciesRichness** | | | **Model 2: TotalAbundance** | | | **Model 3: ShannonDiversity** | | |
|---|---|---|---|---|---|---|---|---|---|
| *Predictors* | *Incidence Rate Ratios* | *CI* | *p* | *Incidence Rate Ratios* | *CI* | *p* | *Estimates* | *CI* | *p* |
| (Intercept) | 6.79 | 5.92 – 7.78 | **<0.001** | 10.71 | 8.29 – 13.84 | **<0.001** | 1.67 | 1.53 – 1.81 | **<0.001** |
| Edges250m | 1.09 | 0.97 – 1.23 | 0.166 | 1.09 | 0.89 – 1.34 | 0.397 | 0.09 | -0.02 – 0.21 | 0.108 |
| MeanTemp_Apr | 1.45 | 1.26 – 1.66 | **<0.001** | 1.81 | 1.42 – 2.29 | **<0.001** | 0.23 | 0.11 – 0.36 | **<0.001** |
| Year [2020] | 0.67 | 0.52 – 0.85 | **0.001** | | | | -0.58 | -0.82 – -0.35 | **<0.001** |
| Edges250m * MeanTemp_Apr | 0.78 | 0.68 – 0.89 | **<0.001** | 0.73 | 0.59 – 0.91 | **0.005** | -0.14 | -0.27 – -0.02 | **0.018** |
| **Random Effects** | | | | | | | | | |
| $\sigma^2$ | 0.17 | | | 0.21 | | | 0.13 | | |
| $\tau_{00}$ | $0.09_{\text{RandomEffect}}$ | | | $0.41_{\text{RandomEffect}}$<br>$0.01_{\text{Year}}$ | | | $0.11_{\text{RandomEffect}}$ | | |
| ICC | 0.34 | | | 0.67 | | | 0.47 | | |
| N | $52_{\text{RandomEffect}}$ | | | $52_{\text{RandomEffect}}$<br>$2_{\text{Year}}$ | | | $52_{\text{RandomEffect}}$ | | |
| Observations | 136 | | | 136 | | | 136 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.462 / 0.647 | | | 0.355 / 0.785 | | | 0.427 / 0.695 | | |

**Table 3:** Models and model statistics for modelling species richness, total abundance and Shannon diversity as a function of average monthly July temperature, amount of edge (m) within 250m a buffer and year (2019 [reference level] and 2020). I used Poisson generalised linear mixed-effects model (GLMM) to model species richness, a negative binomial GLMM to model abundance and a linear mixed-effects regression (LMM) to model Shannon diversity. The amount of edges *(Edges250m)* was log transformed, to alleviate and scale (standardise) the error distribution. Site and year was included as a random effect, to account for repeated sampling throughout the flowering season. *Year* was included as a fixed effect for model 5 and 6, only to account for significant annual variance, and as a random effect for model 4. Marginal R-squared is variation explained by fixed effects, while conditional R-squared is explained by fixed effects *and* random effects. This means that *Year* is included in conditional R-squared as a fixed effect for certain models, hence this value is likely an overestimation.



| | **Model 4: SpeciesRichness** | | | **Model 5: TotalAbundance** | | | **Model 6: ShannonDiversity** | | |
|---|---|---|---|---|---|---|---|---|---|
| *Predictors* | *Incidence Rate Ratios* | *CI* | *p* | *Incidence Rate Ratios* | *CI* | *p* | *Estimates* | *CI* | *p* |
| (Intercept) | 5.91 | 5.24 – 6.67 | **<0.001** | 8.04 | 5.97 – 10.82 | **<0.001** | 1.51 | 1.33 – 1.69 | **<0.001** |
| Edges250m | 1.11 | 0.98 – 1.26 | 0.100 | 1.04 | 0.85 – 1.28 | 0.669 | 0.09 | -0.04 – 0.21 | 0.161 |
| MeanTemp_Jul | 1.48 | 1.29 – 1.69 | **<0.001** | 2.58 | 1.77 – 3.75 | **<0.001** | 0.33 | 0.11 – 0.55 | **0.003** |
| Edges250m * MeanTemp_Jul | 0.82 | 0.73 – 0.93 | **0.002** | 0.74 | 0.61 – 0.88 | **0.001** | -0.11 | -0.21 – -0.01 | **0.040** |
| Year [2020] | | | | 2.88 | 1.38 – 6.04 | **0.005** | -0.09 | -0.55 – 0.37 | 0.697 |
| **Random Effects** | | | | | | | | | |
| $\sigma^2$ | 0.18 | | | 0.20 | | | 0.13 | | |
| $\tau_{00}$ | $0.11_{\text{RandomEffect}}$<br>$0.00_{\text{Year}}$ | | | $0.37_{\text{RandomEffect}}$ | | | $0.13_{\text{RandomEffect}}$ | | |
| ICC | 0.37 | | | 0.65 | | | 0.50 | | |
| N | $52_{\text{RandomEffect}}$<br>$2_{\text{Year}}$ | | | $52_{\text{RandomEffect}}$ | | | $52_{\text{RandomEffect}}$ | | |
| Observations | 136 | | | 136 | | | 136 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.430 / 0.640 | | | 0.422 / 0.796 | | | 0.398 / 0.699 | | |

### *3.1. Species richness*

I found a significant relationship between species richness and the interaction between temperature and amount of edge habitat within 250m buffers ($p_{April}<0.001$ and $p_{July}=0.002$, R-squared$_{April}=0.462$ and R-squared$_{July}=0.43$) (Table 2-3). The April model estimated the Incident Rate Ratio (IRR) for species richness to 6.79 (intercept), and increasing temperature increased bee species richness (IRR=1.45, p<0.001). The interactive effect of temperature and edge habitat had a positive effect on species richness (IRR=0.83, p<0.001), however the importance of edge habitat was modified by temperature. More specifically, the importance of edge habitat decreased with increased temperature. Similarly, the July model estimated the IRR for species richness to 5.91 (intercept), and increased temperature gave increased richness (IRR=1.48, p<0.001). The interactive effect of temperature and edge habitat was estimated to an IRR of 0.82 (p=0.002), where the importance of edge habitat for species richness decreased with increased temperature. The species richness models showed that increased habitat amount had a neutral effect on richness under high temperatures (75% quantile) for both April and July (Figure 6a-7a). Although, the wide confidence intervals posed some uncertainty at high temperatures (75% quantile); 25% of sites in April and 15% in July measured high temperatures, while 19% of sites had edge amount over 15000m. There was a positive slope for low temperatures (<50% quantile), where species richness increased parallel to increased habitat amount (Figure 6a-7a).

This trend was apparent for both April and July models. There was an even spread of the residual response for species richness for both April and July based models (Figure 6b-7b).

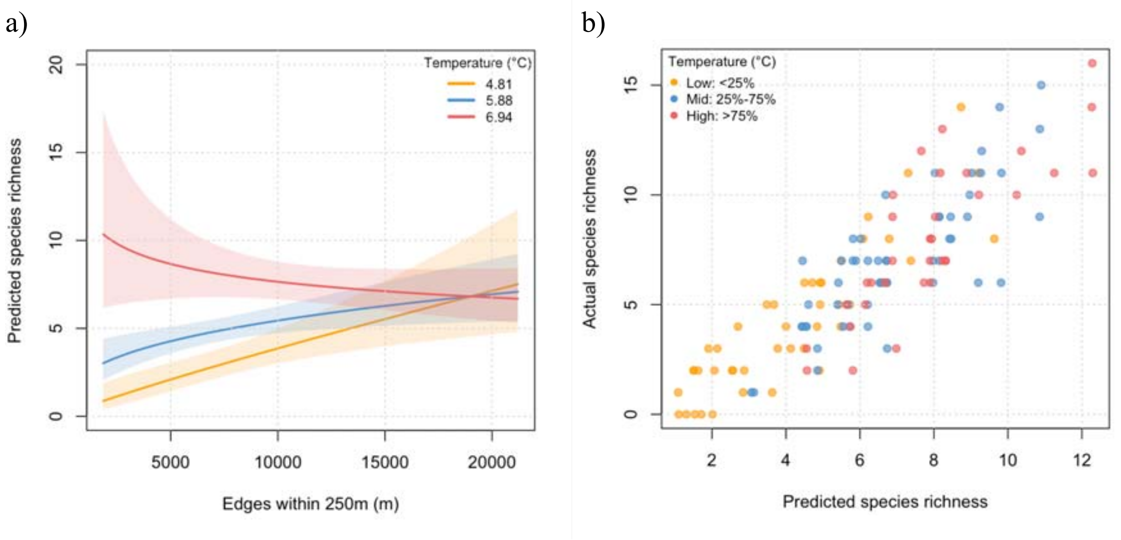

a) b)

**Figure 6:** Estimated species richness of wild bees in semi-natural grasslands as a function of the amount of edges within 250 m buffers around each site at different levels of average monthly April temperature. The influence of temperature is shown for the 25%, 50% and 75% quantiles. Shaded polygons show the 95% confidence intervals. The mean amount of edges was 9550m. The residual response plot shows the correlation between the actual and predicted species richness (b). The sites are divided into three levels of temperature: low (<25%), mid (between 25%-75%) and high (>75%). The percentage (%) refers to the quantiles (a).

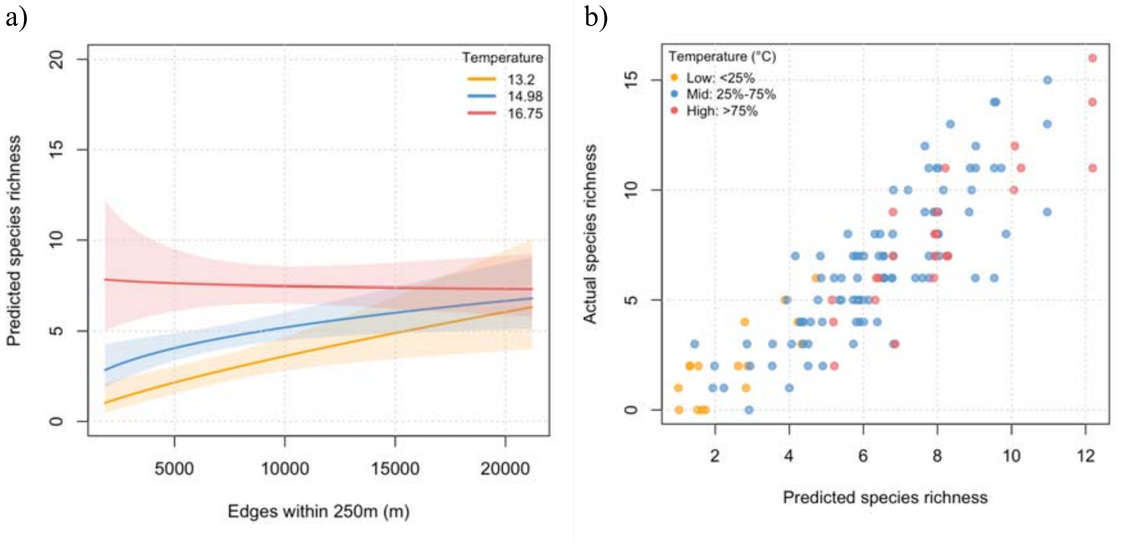

a) b)

**Figure 7:** Estimated species richness of wild bees in semi-natural grasslands as a function of the amount of edges within 250 m buffers around each site at different levels of average monthly July temperature. The influence of temperature is shown for the 25%, 50% and 75% quantiles. Shaded polygons show the 95% confidence intervals. The mean amount of edges was 9550m. The residual response plot shows the correlation between the actual and predicted species richness (b). The sites are divided into three levels of temperature: low (<25%), mid (between 25%-75%) and high (>75%). The percentage (%) refers to the quantiles (a).

I found no significant relationship between species richness and the amount of meadows, surrounding landscape diversity or distance to coastline (Table 4).

### *3.2 Total abundance*

I found that total bee abundance depended on an interaction between temperature and amount of edge habitat within 250m buffers ($p_{April}$ =0.001 and $p_{July}$ =0.005, R-squared$_{April}$ =0.355 and R-squared$_{July}$ =0.422) (Table 2-3). The April model estimated the IRR for species richness to 10.71 (intercept), and increasing temperature indicate increasing bee abundance (IRR=1.81, p<0.001). The interactive effect of temperature and edge habitat gave increased bee abundance (IRR=0.73, p<0.001), however the importance of edge habitat was modified by temperature. More specifically, the importance of edge habitat decreased with increased temperature. Similarly, the July model estimated the IRR for bee abundance to 8.04 (intercept), and increased temperature gave increased abundance (IRR=2.58 , p<0.001). The interactive effect of temperature and edge habitat was estimated to an IRR of 0.74 (p=0.001), where the importance of edge habitat decreased with increased temperature. The abundance models showed that habitat amount had a neutral effect bee abundance under high temperatures (75% quantile), which could be seen for both April and July models (Figure 8a-9a). Although, the wide confidence intervals posed some uncertainty at high temperatures (75% quantile). There was a positive slope for low temperatures (<50% quantile), where abundance increased parallel to increased habitat amount (Figure 8a-9a). This trend was apparent for both April and July models. The residual response plot indicated heteroscedasticity, because of over-dispersion of actual abundance contra predicted abundance (Figure 8b-9b). This was especially apparent for the study sites with mid and high temperatures, for both April and July.

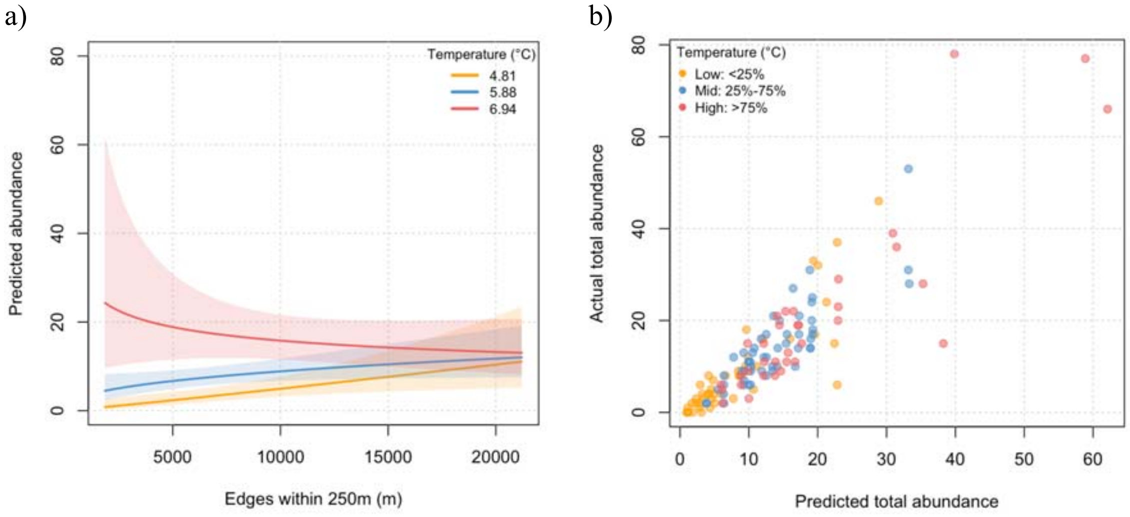


**Figure 8:** Estimated total abundance of wild bees in semi-natural grasslands as a function of the amount of edges within 250 m buffers around each site at different levels of average monthly April temperature. The influence of temperature is shown for the 25%, 50% and 75% quantiles. Shaded polygons show the 95% confidence intervals. The mean amount of edges was 9550m. The residual response plot shows the correlation between the actual and predicted species richness (b). The sites are divided into three levels of temperature: low (<25%), mid (between 25%-75%) and high (>75%). The percentage (%) refers to the quantiles (a).

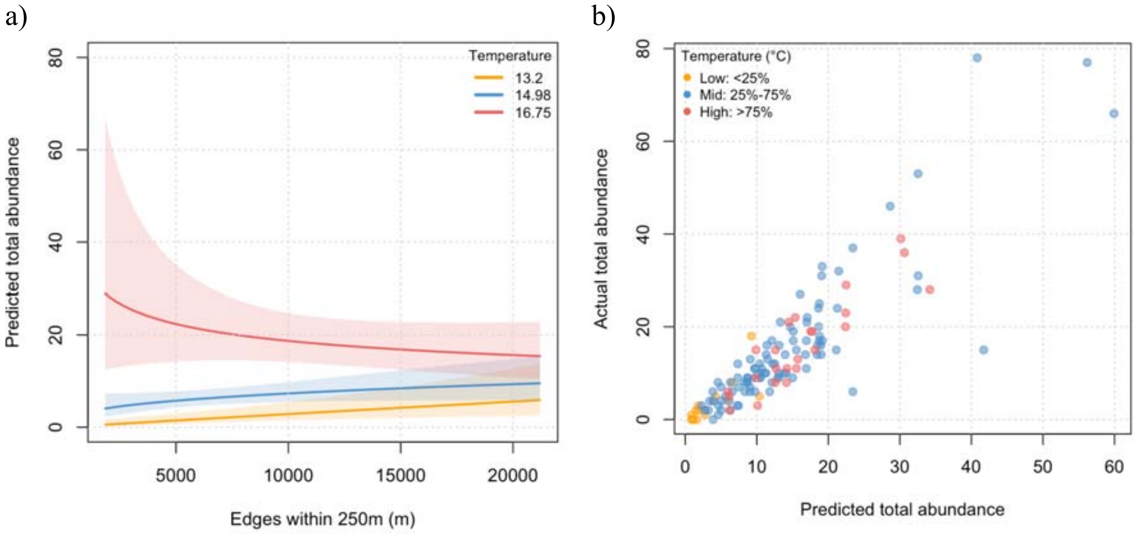


**Figure 9:** Estimated total abundance of wild bees in semi-natural grasslands as a function of the amount of edges within 250 m buffers around each site at different levels of average monthly July temperature. The influence of temperature is shown for the 25%, 50% and 75% quantiles. Shaded polygons show the 95% confidence intervals. The mean amount of edges was 9550m. The residual response plot shows the correlation between the actual and predicted species richness (b). The sites are divided into three levels of temperature: low (<25%), mid (between 25%-75%) and high (>75%). The percentage (%) refers to the quantiles (a).

I found no significant relationship between total abundance and the amount of meadows, surrounding landscape diversity or distance to coastline (Table 4).

### *3.3 Shannon diversity*

I found a significant relationship between diversity and the interaction of temperature and amount of edge habitat ($p_{April}$ =0.018 and $p_{July}$ =0.040, R-squared$_{April}$ =0.427 and R-squared$_{July}$ =0.398) (Table 2-3). The April model estimated diversity intercept to 1.67 (p<0.001), and a rise in temperature indicated an increase in diversity (0.23, p<0.001). The interactive effect of temperature and edge habitat on Shannon diversity was estimated to -0.14 (p=0.018), where the importance of edge habitat was modified by temperature. More specifically, the importance of edge habitat decreased with increased temperature. Similarly, the July model estimated the intercept for diversity to 1.51 (p<0.001), and increased temperature gave increased diversity (0.33, p=0.003). The interactive effect of temperature and edge habitat was estimated to -0.11 (p=0.040), where the importance of edge habitat decreased with increased temperature. Both Shannon diversity models showed that habitat amount had a neutral effect bee diversity under high temperatures (75% quantile) (Figure 10a-11a). Although, the wide confidence intervals pose some uncertainty at the extremes of edge amount for all temperature quantiles. There was a positive slope for low temperatures (<50% quantile), where bee diversity increased parallel to increased habitat amount (Figure 10a-11a). Although, the positive slope flattened out around mean edge amount (9550m), and increased habitat amount from this point on had a neutral effect on Shannon diversity. This signal was especially apparent for the July model. The residual response plot indicated heteroscedasticity, because of under-dispersion of actual diversity vs. predicted diversity (over-dispersion zeroes) (Figure 10b-11b). This was especially apparent for the study sites with low April temperatures and low-mid temperatures in July.

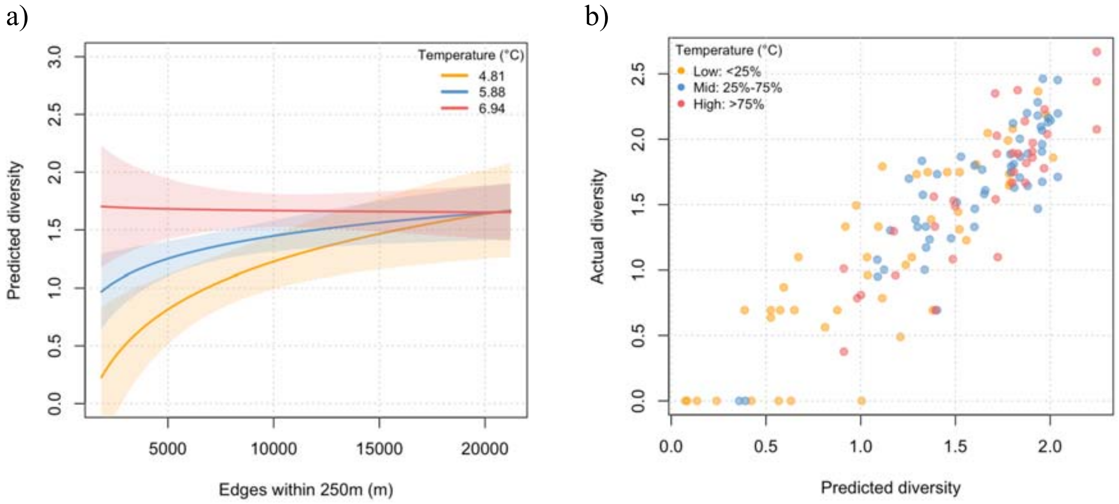


**Figure 10:** Estimated Shannon diversity of wild bees in semi-natural grasslands as a function of the amount of edges within 250 m buffers around each site at different levels of average monthly April temperature. The influence of temperature is shown for the 25%, 50% and 75% quantiles. Shaded polygons show the 95% confidence intervals. The mean amount of edges was 9550m. The residual response plot shows the correlation between the actual and predicted species richness (b). The sites are divided into three levels of temperature: low (<25% ), mid (between 25%-75%) and high (>75%). The percentage (%) refer to the quantiles (a).

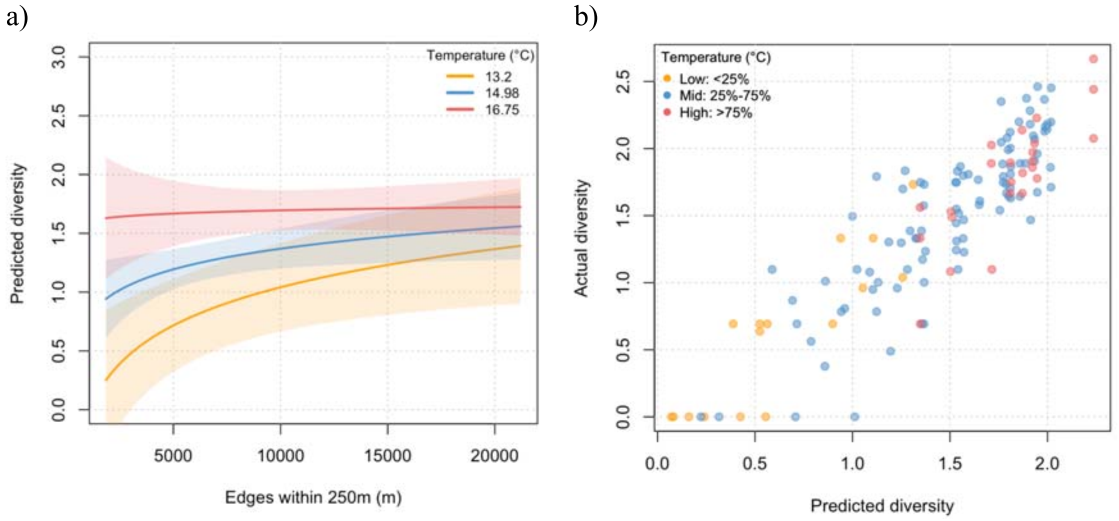


**Figure 11:** Estimated Shannon diversity of wild bees in semi-natural grasslands as a function of the amount of edges within 250 m buffers around each site at different levels of average monthly July temperature. The influence of temperature is shown for the 25%, 50% and 75% quantiles. Shaded polygons show the 95% confidence intervals. The mean amount of edges was 9550m. The residual response plot shows the correlation between the actual and predicted species richness (b). The sites are divided into three levels of temperature: low (<25% ), mid (between 25%-75%) and high (>75%). The percentage (%) refer to the quantiles (a).

I found no significant relationships between Shannon diversity and the amount of meadows or distance to coastline, but I found a significant relationship between the landscape diversity and bee diversity ($p_{April} = 0.019$, $p_{July} = 0.029$) (Table 4).

**Table 4:** Model statistics for predictor variables within 250m buffers, with parameter estimates (beta), standard error, z/t values and p value. Cells filled blue show significant relationship ($p<0.05$).

| Predictor variables | Month | Species richness | | | | Total abundance | | | | Shannon diversity | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Beta | Std. Error | z value | p | Beta | Std. Error | z value | p | Beta | Std. Error | t value | p |
| Amount of meadow | April | -0.009 | 0.067 | -0.145 | 0.88 | -0.068 | 0.105 | -0.651 | 0.51 | -0.001 | 0.063 | -0.019 | 0.98 |
| | July | -0.045 | 0.062 | -0.736 | 0.46 | -0.058 | 0.104 | -0.561 | 0.57 | -0.002 | 0.064 | -0.032 | 0.97 |
| Landscape diversity | April | 0.091 | 0.063 | 1.451 | 0.15 | 0.087 | 0.102 | 0.848 | 0.39 | 0.136 | 0.058 | 2.343 | 0.02 |
| | July | 0.089 | 0.063 | 1.405 | 0.16 | 0.066 | 0.103 | 0.641 | 0.52 | 0.131 | 0.059 | 2.180 | 0.03 |
| Distance to coastline | April | -0.031 | 0.081 | -0.381 | 0.70 | -0.002 | 0.133 | -0.012 | 0.99 | -0.013 | 0.078 | -0.169 | 0.87 |
| | July | -0.046 | 0.073 | -0.631 | 0.53 | 0.111 | 0.146 | 0.759 | 0.45 | 0.007 | 0.088 | 0.083 | 0.93 |

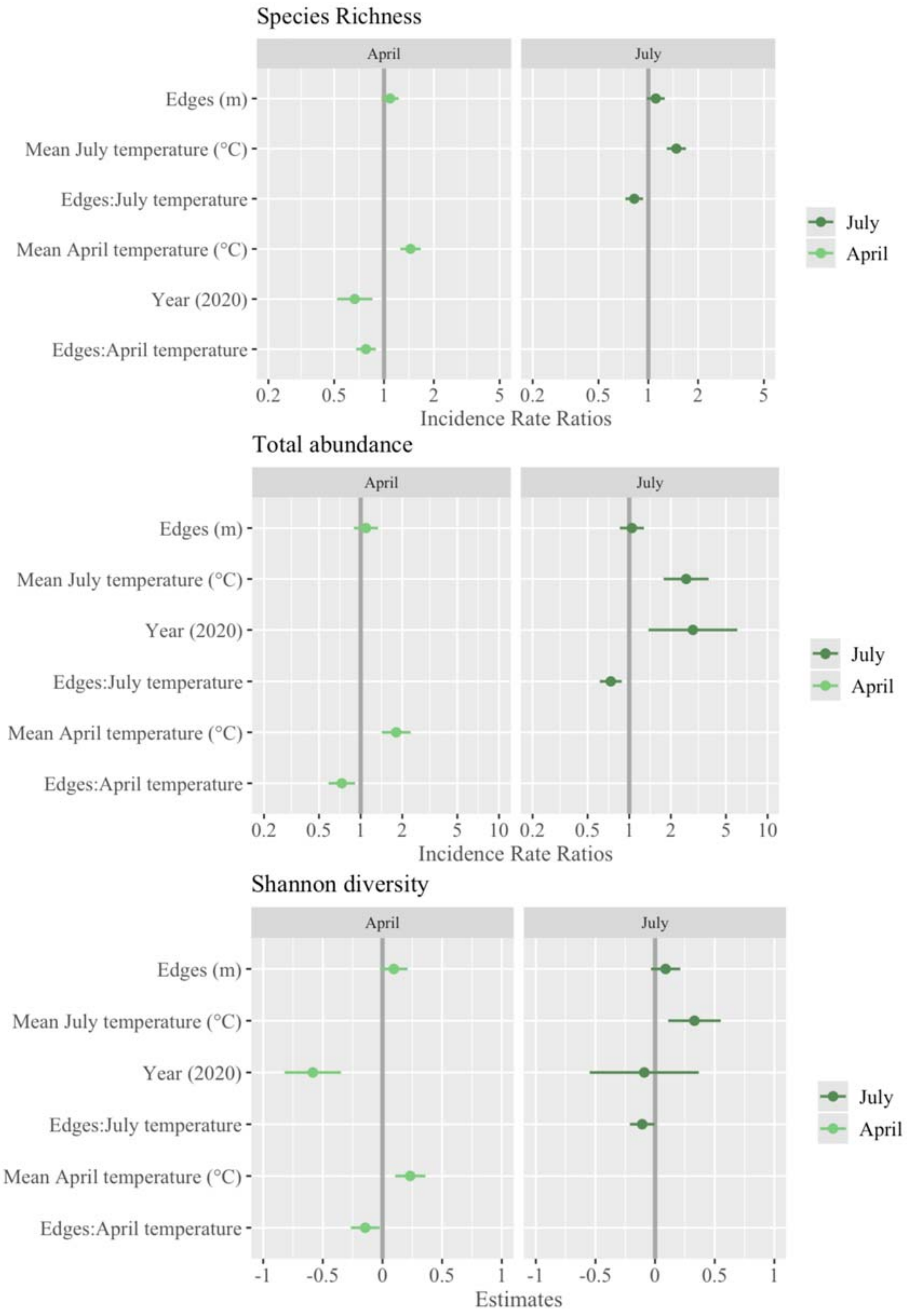


**Figure 12:** Incident Rate Ratios/Estimates and confidence intervals for the predictor variables (from Tables 2-3) influencing Species richness, abundance and Shannon diversity of wild bee communities. Estimates for models based on April temperatures are shown in light green and estimates for models based on July temperatures are shown dark green.

# *4. Discussion*

The aim of my study was to investigate the potential interactive effects of temperature and habitat availability in the wider landscape on wild bee diversity within semi-natural grasslands. More specifically, if certain landscape attributes could have mitigating or aggregating effects for wild bees when the temperature increased (in relation to climate change). I found that temperature, as simply an additive effect, had a positive effect on bee diversity (i.e., species richness, total abundance and Shannon diversity). Furthermore, I also found that wild bee diversity was affected by the interactive effect of temperature and amount of edge habitat. However, the modifying effect of amount edge habitat was only important when the temperature was low. More specifically, increased edge habitat had a positive effect for wild bees under low temperatures, but had a neutral effect under higher temperatures. Furthermore, increased temperatures gave all-over higher bee diversity along the gradient of edge amount, compared to lower temperatures. Consequently, climatic conditions were an important conditioning factor for wild bee diversity in my study region. Even though landscape composition is generally known to be an important driver for wild bee diversity, I found no significant interactions for species richness nor bee abundance with the amount of registered meadow, surrounding landscape diversity or distance to coastline (as additive or interactive effects). In contrast, there was a significant interaction between Shannon diversity and the surrounding landscape diversity, but not for the amount of registered meadow or distance to coastline.

## *4.1 Temperature*

I found that temperature was the most important driver for wild bee diversity, which coincide with previous research stating that temperature has a direct impact on the survival, dispersal range and species diversity (richness and abundance) of bees (Straka et al. 2014; Kammerer et al. 2021). Furthermore, my results indicate that increased temperatures had a positive effect on species richness, abundance and Shannon diversity. This pattern was apparent for both the April and July models, however high temperatures were especially indicative for wild bee abundance in the July model. My results, apparently contradict my prediction that high temperatures will have a negative effect on wild bees. However, it is important to clarify that the *high temperature* referred to in my interpretation of my results were above-mean monthly temperatures from this particular study (i.e., >50% of quantile temperatures in figures 7a-12a), which was >5.88 °C and >14.98 °C, for April and July respectively. My prediction was built on the assumption that high temperatures, and the *implications* that comes with, would ultimately have a negative effect on wild bee diversity. More specifically, the implications of prolonged high temperatures, in synergy with little precipitation, resulting in drought conditions (Thomson, 2016; Phillips et al 2018). Direct consequences of drought can cause bees to overheat when foraging and thirst, because suitable water sources (i.e. shallow puddles) tend to dry up quickly in the sun (Rankin et al. 2020). Hence, commercial beekeepers are encouraged to make watering stations for their honeybees, so that they can sustain the colony even in warmer weather. Wild bees, however, do not have the luxury of constant water sources, consequently leaving them more susceptible to dehydration. Following this, there were drought conditions in June 2020, followed by an uncommonly cold July with a lot of rainfall. Based on my findings of how wild bee diversity was modified by temperature, one can assume that these climatic conditions could be one explanation for why there were significantly less bees in 2020 compared to 2019. However, some of the annual variance could also be a consequence of the unequal sampling intensity for certain months (May and July) between the years. It is also possible that the measures of weather data for this study did not capture the variation of the local climatic conditions (Murray 2012); I used monthly mean temperatures, and did not include measures of precipitation. Therefore, the (potential) implications of daily and/or weekly variations in temperature for wild bee diversity were not quantified.

My findings contradict a similar study from Germany, which found that increasing temperature led to a strong decline in bee diversity, even when correcting for phenology (i.e., functionality groups) (Papanikolaou et al. 2017). Similarly, a study of wild bees from northeast USA found that climate factors (temperature and precipitation) where more important drivers for wild bee diversity than the surrounding landscape (Kammerer et al. 2021). More specifically, the results by Kammerer et al. (2021) indicated that wild bees active in the spring were more sensitive to precipitation, while summer and fall active bees were more sensitive to temperature (although the effects varied substantially between species and functional groups). The fact that my results are not in line with studies from other climatic regions was not necessarily surprising, as the effects of rising temperature are expected to give different responses in temperate and boreal ecosystems (i.e., Germany vs. Norway) (IPCC 2018). Temperature tends to be the most prominent limiting factor for biodiversity in boreal areas (Klanderud & Birsk, 2003; Grabherr et al. 2010; Vanneste et al. 2017), and decreasing temperature generally coincide with decreasing diversity. Clarke & Gaston (2006) discuss various temperature limitation theories of how temperature affect diversity and the distribution of species. The consensus was that warmer areas are able to support more diversity, as temperature influence the rate of various processes in the link between energy supply and diversity within an ecosystem; where increased biomass/abundance of plants would in turn increase diversity for higher trophic levels. Furthermore, boreal ecosystems have rather extreme seasonal variation in temperature, which would influence the availability of nutrients and transpiration for plants (Clarke & Gaston 2006), as well the life cycle and physiology of other species living there. Thus, as a result of warming temperatures, studies have found an increase in alpine plant diversity (Klanderud & Birsk, 2003; Grabherr et al. 2010), while warmer temperatures in early spring have been correlated to earlier budding (Schwartz & Karl 1990) and increased availability of surrounding flower resources, benefitting spring active bees (Schwartz & Karl 1990; Kammerer et al. 2021). Furthermore, thermophilic insects such as alpine butterflies, and potentially also bees, respond to warming with increased flight ranges (Buckely & Kingslover 2012). Hence, my results are consistent with the assumption that increased temperature in boreal regions would likely give higher diversity of bees (Clarke & Gaston 2006; Hoiss et al. 2012; Straka et al 2015).

Furthermore, wild bees' responses to rising temperatures are likely dependent on temporal scale; *when* temperature rise occurs (i.e., the time of day, point in flowering season), and for *how long* (i.e., a few warm days/weeks vs. a whole season). Following this, results by Papanikolaou et al. (2017) indicated that increased "longer-term temperature" (i.e., annual mean over 6 years) actually had a positive effect on bee diversity, while increased "short-term temperature" (i.e., fortnightly mean temperature) had a negative effect. This suggests that the implications of the temporal scale of temperature variation can have different, and even opposing, responses within the same study. By comparison, Kammerer et al. (2021) results indicated that the mean temperature the year before sampling were most explanatory of the variance in wild bee species richness. Similarly, there are other studies indicating that temperatures one year can create ripple effects the following years; e.g. less bees after an especially warm summer the year prior (Thomson 2016; Kammerer et al. 2021), as well as the implication of warmer winters; causing overwintering adults to emerge earlier with reduced fitness (i.e., weightless and shorter life) (Bosch & Kemp, 2004; Fründ et al. 2013). Consequently, the temporal scale of temperature variation can influence wild bee diversity in different ways, and these nuances would not be reflected within the mean monthly temperature I used in this study. Hence, how temperature is measured (i.e. the temporal scale) within a study has potential to show different aspects of how changing temperatures could influence wild bee communities.

When interpreting bee community responses to changes in temperature, species-specific responses should be taken into account (Kammerer et al. 2021). This is because, while two areas can have the same exact species richness, the species composition could be different. Thus, these bee communities could respond differently to temperature change. Different wild bee species are expected to respond differently to rising temperatures, as a result of varying thermal limitations and physiological/ecological traits (Sunday et al. 2013). Consequently, species with narrow thermal niches can be more susceptible to temperature changes, than bee species with boarder thermal niches (Kühsel & Blüthgen 2015; Papanikolaou et al. 2017). Wild bees have different ways to deal with heat stress when the thermal threshold is crossed (Sunday et al. 2014; Corbet et al. 2016). Corbet et al. (2016) suggest "cooling flights" as an adaption to heat stress by smaller bees, as being suspended in air would make them cooler than residing in sunlit flowers. While insects are found less likely to rely on behavioural habitat-use to avoid exposure to high temperatures (to release thermal stress), compared to reptiles or amphibians (Sunday et al. 2014), bees have been observed to seek cover under leaves when it rains, and to avoid overheating (Corbet et al. 2016; Kammerer et al. 2021). And due to their small body size, they can seek shade in cooler micro-environments, such as under leaves or in small crevices when the temperature is high (Pincebourde & Woods 2012; Sunday et al. 2014). However, as a result of a warmer climate there is a general trend for species to shift their ranges poleward or up in elevation (Vanneste et al. 2017); where heat-tolerant species are able to move northward as the warming expands their habitable area, and heat-sensitive species move northward to avoid warming, reducing their southward expansion (Klanderud et al. 2003; Grabherr et al 2010). Although, not all species are able to make such shifts, and as a result might experience more rapid declines (Kerr et al 2015).

### *4.2 The interactive effect of temperature and edge habitat*

I found that the interactive effect of temperature and amount of edge habitat influenced wild bee species richness, total abundance and Shannon diversity. My findings suggest that the positive influence of increased amount of habitat (edge) on wild bee diversity is modified by temperature. While increased amount of habitat had a positive effect on wild bee diversity when the temperature was low, there was a neutral effect along the gradient of edge amount when the temperature was high. Additionally, increased temperature resulted in an overall higher diversity of bees along the gradient of edge, compared to lower temperatures. This pattern was consistent for species richness, total abundance and Shannon diversity for both the April and July models. Hence, climatic conditions were more important for wild bee diversity than the availability of suitable habitat in this study. Thus, my results corroborates the assumption that temperature would be an important limiting factor in this region (Klanderud et al. 2003; Grabherr et al. 2010; Sunday et al. 2014).

While my findings support my prediction that increased amount of edge habitat would have a positive effect on wild bees, I did not anticipate the importance to depend on temperature to this degree. Papanikolaou et al. (2017) also found that the interactive effect of temperature and amount of habitat influenced bee diversity. In contrast, they found that suitable habitat was the most important factor for bee diversity. However, and perhaps more interestingly, they found that increased amount of semi-natural grasslands mitigated the negative effect of rising temperature on wild bees. Their results suggest that bee communities in areas with higher coverage (range 4-17%) of semi-natural grasslands would be more resilient to the effect of rising temperatures. In comparison, assuming my edges were on average 2m wide, the average coverage of edge habitat in my study equates to 9.7%, although the amount ranges from 1.9-21.7%. This however, would be a conservative estimate of habitat amount per site, as there would likely be other habitat patches within the 250m radii (i.e., the sites were situated within a registered semi-natural grassland). Furthermore, areas of grassland, hedgerows and shrubland were included in their coverage of semi-natural grassland habitat, while I only included an estimate amount of edges. Thus, my study likely have higher coverage of suitable habitats than Papanikolaou et al. (2017), as my site with the lowest amount of edge habitat (1.9%) had additional 10% coverage of semi-natural grassland area. While my study showed a broader range in habitat amount across sites (1.9-21.7% compared to 4-17%), I still did not find the same dependancy on habitat amount under higher temperatures as Papanikolaou et al. (2017). Although, my findings could suggest that there were already sufficient amount of suitable habitat within my buffer radii, and I might have seen a different dependancy on habitat area if the amount was much smaller. However, while my findings did not show the same dependancy on habitat as Papanikolaou et al. (2017) under high temperatures, it did for colder temperatures. My findings showed that high temperatures, while increasing wild bee diversity, ultimately cancelled out the positive effect of increased habitat amount. However, in colder temperatures wild bee diversity increased with increased amount of habitat. This could suggest that habitat dependancy were more-so modified by temperature related stress, and the cause of thermal stress (either high or low temperatures) would therefore vary in different regions. Thermal stress (by high or low temperatures) would likely make it too costly for bees to forage larger distance (Straka et al. 2014; Sunday et al. 2014; Corbet et al. 2016), thus making them more dependent on the amount of habitat nearby. Hence, high temperatures caused thermal stress for wild bees in Germany, which was why increased amount of available resources alleviated some of the negative effects of heat-stress (Papanikolaou et al. 2017). While thermal stress in Norway was rather caused by colder temperatures, and bees were more dependent on habitat amount under these conditions. Consequently, my initial speculation that certain landscape attributes (like amount of habitat area) had a potential to dampen or amplify the effect of rising temperatures on wild bee diversity (as found by Papanikolaou et al. (2017)), was not corroborated by my results. However, my results rather indicated that amount of available habitat had a positive effect on wild bee diversity under low temperatures, suggesting that amount of habitat dampened the negative effects of colder weather conditions. Having said that, the potential of surrounding habitat to alleviate thermal stress for wild bees need further research.

My findings suggests that when temperatures was no longer a limiting factor, there was something other than the available amount of habitat (edge) that limited wild bee diversity. I did not find this surprising, as what limits wild bee diversity in different systems are likely a synergy of several environmental factors (biotic and biotic) (Steffan-Dewenter et al 2002; Hoiss et al 2012; Ollerton et al 2014; Gallagher et al. 2017; Jeroen et al 2018) and bees ecological traits (floral preferences, nesting preferences, flight range) (Gathmann & Tscharntke 2002; Carriè et al. 2017; Sydenham et al. 2016; Kammerer et al. 2021). In relation to my study, sites with high amount of edge habitat indicated a more fragmented landscape context (demonstrated in Figure 4). The negative effects of habitat fragmentation for wild bees have been a topic of previous studies (Steffan-Dewenter et al. 2002; Xiao et al. 2016; Jeroen et al. 2018), and especially the reduction of initial habitat area as a result. However, other studies question the importance of habitat fragmentation for pollinator diversity (Carrié et al 2017; Hung et al. 2021). Wild bees, and other pollinating species, are generally not as affected by the higher edge to core ratio typically associated with habitat fragmentation, as they tend to prefer areas with low succession plant assemblages (Carrié et al. 2017). This coincides with my findings, where wild bee diversity increased with increasing amount of edge habitat (Figure 7a-12a). A study by Hung et al. (2021) investigated the interactive effect of drought and habitat fragmentation on wild bees. Their findings indicated that the impact of drought was stronger than the impact of fragmentation on wild bee diversity. Furthermore, drought effects were consistently greater in larger habitats than in the fragments, which suggested that fragmentation had redundant effects with drought. Interestingly, Hung et al. (2021) suggested that fragmentation could have ameliorated effects of drought by enhancing bees' availability to floral resources, especially in urban environments.

The composition of the fragmented landscape could also be of importance when discussing the effects on wild bee communities, as there would be a difference for bees to navigate through big bodies of water, urbanised areas or agricultural fields (Kennedy et al 2013; Carrié et al. 2017; Kallioniemi et al. 2017). In reference to my findings, all the study sites with very high amount of edge habitat

(>15000m edge within 250m radii) were situated in highly urbanised areas (within Bærum, Asker and Oslo). Following this, Kammerer et al. (2021) found a strong pattern of exotic bees in urbanised areas, which they assumed could cause resource competition for wild species. Similarly, Fitch et al. (2019) found that urbanised areas had a positive influence on exotic bee species. Furthermore, they found a negative correlation between native and exotic bees, suggesting competition for food and resources. As discussed by Fitch et al. (2019), while competition for resources could be one aspect, the ecological filtering apparent in urban areas (i.e. lack of sandy areas, tall obstacles, etc.) could be more detriment for native species than exotic species. Thus, while urbanised areas were found to support diverse bee communities (Fitch et al. 2019), wild bee species could be more sensitive to fragmentation into this land-use. However, both Fitch et al. (2019) and Kammerer et al. (2021) showed findings from northern USA, thus the rate of urbanisation and the (potential) effect on wild bees could be different in my study region. Consequently, while the initial act of fragmentation might not negatively influence wild bee communities (Carrié et al. 2017; Jeroen et al. 2018; Hung et al. 2021), the surrounding land-use (i.e. urbanised areas) could pose challenges for wild bees (Fitch et al. 2019).

### *4.3. Influence of other landscape variables*

There are numerous studies suggesting the importance of landscape composition for wild bee diversity (Steckel et al. 2014; De Palma et al. 2015; Papanikolaou et al. 2017). However, I did not find indication that wild bee species richness or abundance were influenced by my other landscape attributes: amount of meadow, surrounding landscape diversity, or closer proximity to the coastline (Table 4). Although, while wild bee Shannon diversity was influenced by the surrounding landscape diversity, I found no correlation with the amount of meadows or proximity to the coastline. However, absence of evidence is not necessarily evidence of absence, as the reality of the interactions between wild bees and their environment (biotic and abiotic factors) are both complex and dynamic.

#### *4.3.1 Amount of meadow*

Comparative to Papanikolaou et al. (2017), I did not find that increased size of meadows had a positive effect on wild bee diversity. One reason for this could be that I only included one type of semi-natural grassland, flower meadow, and wild bee diversity would not increase parallel to an increase in this habitat type alone. Secondly, all my study sites were already situated in registered meadows. This could indicate that wild bee communities with already substantial amounts of semi-natural grassland area in their immediate surroundings, would not benefit from increased amounts of grassland habitat. This would be in line with a study on habitat restoration for wild bees (Tonietto et al. 2017), indicating that increased initial habitat area was not necessarily as important as restoring suitable habitat in other fragments to make “ecological stepping stones”; proximity to different floral and nesting resources within flight range. This was also consistent with studies that have found that habitat configuration as well as composition was important for wild bee diversity (Murray et al. 2012; Steckel et al. 2014). Furthermore, it is important to note that sufficient amounts of floral density, does not necessarily mean that there are suitable nesting sites. Hence, lack of nesting sites would condition both the diversity and the amounts of wild bees (Carrié et al. 2017; Jeroen et al. 2018). Indeed, Carrié et al. (2017) found that above-ground nesters did not seem to be strongly affected by the proximity of semi-natural hay meadows in particular. Comparatively, Jeroen et al. (2018) found that the amount and proximity of semi-natural habitats had a positive effect on ground nesters, because they depend on loose sandy sediments to build nests. Thus, I might have seen a different dependancy on amount of meadows had I looked into functional groups.

### *4.3.2 Distance to coastline:*

Contrary to my expectations, I did not find indication that closer proximity to the coastline any influence on wild bee communities, nor that closeness to the coastline and temperature had any the interactive effects on wild bee diversity. I found these results surprising because of the general correlation between elevation (above sea level), temperature and distance to the coastline; where elevation tend to increase parallel to increased distance to the coastline (Young et al. 2011), and temperature decrease with increasing elevation (Hoiss et al. 2012; Sunday et al. 2014). According to Sutton et al. (2007) coastline ecosystems were found to have less annual temperature variance than further inland. Furthermore, areas close to the coast were cooler during the day compared to inland, because the ocean take longer to heat up and cool down. However, while temperature was the most important indicator of wild bee diversity in this study, I found no indication that temperature changes relating to distance to the coastline, as discussed by Sutton et al (2007), influenced bee diversity in any way. Furthermore, the importance of distance from the coast and elevation have often been linked to distribution patterns of species and ecological communities in coastal environments (Young et al. 2011). Following this, previous research has found that wild bee diversity decreases with elevation, as altitude functions as an environmental filter for wild bee functionality and diversity of (Hoiss et al. 2012). Therefore, to investigate the possible influence of proximity to the coastline on wild bees, I corrected the correlation with elevation; I extracted the residuals of coast distance from a regression of *Coast Distance×Elevation,* and tested for correlation with wild bee diversity. However, I still did not find a significant influence of distance to coastline. Young et al. (2011) argues that coastal landscapes are temporally more dynamic at the local scale, compared to more stable inland landscapes. They give the example of how the distance to the coastline changes as a response to erosion (i.e. redepositing sand) induced by increased frequency of storms. Additionally, the implications of coastal wind-flow can lead to “disturbances” for bees (i.e. salt spray and sand blowing), which only increase with closer proximity to the coastline (Young et al. 2011). Consequently, the dynamic coastline can lead to changes in environmental conditions and biotic interactions especially apparent at the local scale. Following this, Murray et al. (2012) found that bee communities were primarily sensitive to local scale factors, especially associated with nesting resources. Hence, it could be that closer proximity to the coastline would affect wild bee species differently (specific ecological traits and functional groups), which I did not look into in this study.

### *4.3.3 Surrounding landscape diversity.*

I found that landscape heterogeneity was important for wild bee Shannon diversity, but not for species richness or bee abundance. This pattern was consistent for both the April and July model. My results could suggest that rather than landscape diversity, wild bee species richness and abundance are more-so modified by what kind of floral and nesting resources are available within that landscape context (i.e. what habitat types). My findings concur with research on wild bees in vineyards across Europe, where the surrounding landscape had limited influence on species richness and abundance across functional groups (although most species were ground nesting, solitary, generalists) (Kratschmer et al. 2019). Similarly, research from apple orchards in Germany indicated that the availability of floral resources determined the positive effect of landscape heterogeneity on wild bee communities (Mallinger et al. 2016). They found that increased surrounding landscape diversity did increase wild bee diversity within orchards in bloom, because of the increased availability of different flowers. In addition, their results reflected on the importance of temporal continuity of floral resources; as flowers were most abundant in orchards during spring, and would decline over time, while flowers within grasslands (tend to) increase throughout spring and summer. Hence, continuous availability to different floral resources in the surrounding landscape context (i.e. landscape heterogeneity) would be better able to support different species requirements and higher abundance of bees (Mallinger et al. 2016).

Furthermore, I found that Shannon diversity of wild bees responded best to the surrounding landscape diversity at 250m radius, which is also the spatial scale that gave the best response for wild bee diversity and the interaction of edge habitat and temperature (Table 4). My findings support previous research indicating that solitary bees are more sensitive to their landscape context at a smaller scale (Steffan-Dewenter et al. 2002; Murray et al. 2012; Steckel et al. 2014). Steffan-Dewenter et al (2002), and later Steckel et al. (2014), found that solitary bees respond best to their local conditions at 200m radii, while bigger social bees (i.e. *Bombus* and honeybees) respond to landscape context up to 3000m. Consequently, both spatial and temporal availability to floral resources at a local scale would be more important for solitary species, because of their limited foraging range (Murray et al. 2012). Hence, landscape composition (Kennedy et al., 2013; Steckel et al. 2014), as well as the configuration (Hopfenmüller et al., 2014; Tonietto et al. 2017; Hass et al., 2018) would be important to support wild bee diversity, especially smaller solitary species.

## *5. Limitations*

Data collection in project POLLILAND, which this thesis is based on, was designed to evaluate where in the cultural landscape measures should be taken to protect insect pollinators (NINA, 2020). Thus, study sites were intentionally selected along gradients of landscape context and climatic factors over the two years, to evaluate what conditioned the diversity of wild bees (species richness and abundance) in semi-natural grasslands in southeast Norway. The fact that the study was not originally designed to answer the research questions in this thesis, can at least partly explain why I did not find that wild bee diversity was dependent on amount of semi-natural grassland nearby. My results could have been affected by the fact that all sites were already situated within registered semi-natural grasslands. My findings could therefore indicate that when initial habitat area was sufficient, a further increase of habitat area would not lead to an increase in wild bee diversity. However, I might have seen a different dependency on habitat area had my sites been distributed along a gradient of semi-natural grassland amount instead. In addition, it could be that the semi-natural grassland polygons from Naturbase were not an optimal measurement on the current conditions, as polygons may have included regrown areas, forest and agricultural land, that do not support the same function as semi-natural grassland habitats. In this case, my measurement of edge habitat might have been a better indicator of the amount of suitable habitat for wild bees within the landscape context; as edge habitats have similar plant assemblages to semi-natural grasslands, and usually support high density of flowers.

Furthermore, the study design could have influenced my results for costal distance. While I did not find that distance to the coastline had any influence on wild bees, it could be that the geographical distribution of my sites were not ideal to investigate this. Hence, I might have detected clearer spatial patterns if the sites had been distributed along a gradient of distance to coastline. However, while the dispersal abilities are quite limited for most solitary bees, the (potential) influence of the coastline might not be limited to areas with immediate proximity to the ocean. Therefore, I would suggest distributing sites within a range of 10m-50km from the coast, and perhaps try to minimise the variance in habitat quality (i.e., the proportion of habitat types) across the sites. For reference, in this study the range of costal distance was 200m-70km, and six sites were within 500m of the coastline. Furthermore, to investigate whether coastal ecosystems do experience less temperature variance than inland ecosystems, as discussed by Sutton et al. (2007), I would compare the weekly/monthly temperature variance between the sites. In addition, the possibility for other big bodies of water (i.e., freshwater lakes) to exhibit the same temperature stabilising effect should perhaps also be considered.

Lastly, as climatic factors were distributed over two years, there were among-year differences in temperature at different times in the flowering period. As an example, how did the 2°C temperature increase from June to July in 2019 (from 14°C to 16°C), compare to the 4°C decrease from June to July in 2020 (from 17.5°C to 13.7°C), in relation to affecting local bee diversity (Table 1)? In addition, there was annual variation in the monthly collection-rate of bees. In 2019 pan-traps were deployed 1x in May, 1x in June and 2x in July, while in 2020 pan-traps were deployed 2x in May, 1x in June and 1x in July. Consequently, the sites in 2020 were under-sampled in July, compared to 2019. This is important because many bee species are active in July, but not earlier in the season. Differences in the sampling intensity in July between years, therefore likely meant that bee diversity in sites sampled in 2020 would be slightly underestimated. However, while the annual variance in landscape context and climatic conditions would likely have caused some variance in the observed wild bee diversity, I accounted for between-years difference in the statistical analyses. Thus, the effects of amount of edge and landscape diversity that I *did* find should reflect the expected effects of these landscape variables in an average year. Furthermore, while I did not analyse species-specific responses to temperature change and the interactive effect of habitat, I expect the responses to vary greatly depending on their ecological traits and functionality group. Consequently, even though the study design was not optimal, my findings on how wild bee diversity was influenced by temperature (as an additive effect and as an interactive effect by modifying habitat dependency) were still relevant. My results would be reflective of the general trend of how wild bee diversity in southeastern Norway were modified by the effect of temperature change and habitat area. Furthermore, my findings suggested that habitat dependency increased when bees were subjected to thermal stress, which was caused by low temperatures in this study. These results could indicate that increased amount of suitable habitat nearby have a potential to mitigate negative effects of thermal stress conditions for wild bees, as also found by Papanikolaou et al. (2017), albeit with thermal stress in that context being high temperatures.

## *6. Conclusion*

More research is emerging looking at the interactive effects of climatic conditions and landscape context on wild bee communities in different regions; like drought conditions and habitat fragmentation in California, USA (Hung et al. 2021), and rising temperature and amount of semi-natural habitat in Germany (Papanikolaou et al. 2017). My findings showed that the interactive effect of temperature and amount of edge habitat was important for wild bee diversity. More specifically, habitat dependency was modified by temperature, indicating that temperature was the most important driver for wild bee diversity in my study. While wild bee diversity was not influenced by habitat amount under high temperatures, bee diversity increased with habitat amount under colder weather conditions. My findings suggest that wild bees undergoing thermal stress show more dependency on habitat amount in their surroundings, potentially because thermal stress makes it more costly for bees to forage for resources. This assumption is in line with research from Germany, where increased amount of habitat mitigated negative effects of rising temperatures for wild bees (Papanikolaou et al. 2017). Thus, while the cause of thermal stress would vary in different regions (i.e., high temperatures in Germany, and low temperatures in Norway), thermal stress would make wild bees more dependent on increased amount of suitable habitat nearby to compensate. This study only focused on solitary bees, which tend to be more sensitive to temperatures than social bees (like sp. *Bombus*). Hence, future studies should also investigate wild bees´ ecological traits and functional groups in relation to the interactive effect of climatic conditions and surrounding landscape. Consequently, further research is needed to investigate the implications of thermal stress for wild bees, and the potential for the surrounding landscape context to mitigate the negative effects. Improved understanding of the interactive effects of climate conditions and the surrounding landscape context can be a crucial aid in making educated management choices to conserve wild bee communities in the future.

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