

The effects of geodiversity on temporal shifts in alpine plant communities.

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“If I have seen further, it is by standing on the shoulders of Giants”

Isaac Newton, 1675

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Abstract

Climate warming is inducing compositional shifts in alpine species communities across Europe. However, there are variations in the magnitude and direction of these shifts related to variations in the abiotic environment. Increased number of micro-climates in a habitat, where species can “escape” the changes in the general environmental, is theorized to increase the temporal stability of species compositions. To study such relationships between the abiotic and biotic environment, researchers has collected different aspects of the abiotic environment under the term geodiversity. Novel techniques for quantifying geodiversity are being presented and include aspects such as geology, geomorphology, hydrology, and topographical heterogeneity. All these have been found to influence species composition, and geomorphology has been related with temporal stability in species communities. It is expected that the number of geodiversity features in a habitat lowers the magnitude of compositional shifts and increases biodiversity. In this thesis I study the temporal shifts in vascular plant species compositions of in the alpine research area of Hirkjølen, Norway. I use Pythagorean distance to measure the size of compositional shifts from 1932 to 2020 in 40 permanent plots in a Non-metric Multidimensional Scaling ordination. I found that georichness, especially geomorphology, lowers the magnitude of compositional shifts. Also, plots at higher elevations experience smaller shifts than those at lower elevation. This could be due to increased anthropogenic disturbance, such as grazing or cabin construction, at lower elevations. There was also a difference in direction of shifts along the elevational gradient. At lower elevations species communities are becoming more similar to low-georichness habitats with higher presence of *Picea abies* and berry heather forest-species. At higher elevations there were shifts toward both alpine and lowland species compositions. This was likely due to relaxed temperature constraints and competition release from climate warming, but also grazing is likely to have induced these shifts. It will be of interest if future studies look at how georichness influence changes in species compositions caused by such anthropogenic influence. There is also a need to look into on how individual geodiversity components influence temporal development as I found them to have varying degree of influence. This has been the first study to look at plot-scale geodiversity and relate it to temporal development of species communities. Currently, there is a great need to study the relationship between geodiversity and biodiversity, especially in the face of climate warming, and a lack of studies on geodiversity.

The effects of geodiversity on temporal shifts in alpine plant communities.

Tags: Geodiversity, Climate-change, Alpine, Sub-alpine, Abundance, Ordination, Permanent plots, Vegetation resurvey.

Introduction

Climate warming have been linked to shifts in plant community composition across Europe (Harrison, 2020; Kapfer & Grytnes, 2017; Pauli et al., 2012). Especially in alpine regions, species communities have been found to shift towards both warmer and colder species habitats. The direction and velocity of shifts has been found to vary depending on both elevation (Loarie et al., 2009; Roth et al., 2014) and the local environment (Hjort et al., 2012; Lenoir et al., 2013; Potter et al., 2013; Roth et al., 2014; Serrano et al., 2007). From this, it can be theorized that change in species composition is better predicted by variations in the habitat than variations at landscape level. For instance, vascular plants experience different temperatures than the general ambient temperatures due to variations in surface topography (Scherrer & Körner, 2011). Up to now, however, the relationship between the abiotic environment and development of species composition has mainly been studied using individual or a few abiotic variables at a time. There is also a general lack of studies on how the overall abiotic environment play into temporal development of species community composition. To remedy these aspects, multiple components of the abiotic environment, i.e. geology, geomorphology, hydrology and topographical heterogeneity have been collected under the novel term of geodiversity (Alahuhta et al., 2020).

Geodiversity aims to describe and quantify variations in the abiotic environment (Brilha et al., 2018), and can give insight into both species distribution and composition (Bailey et al., 2018; Hjort et al., 2012). For instance, habitats with a wide range of geodiversity components are expected to house increased biodiversity through the presence of varied microhabitats (Brilha et al., 2018; Hutchinson, 1992; Knudson et al., 2018). These microhabitats cover an extent of niches which dictate which species can thrive in the area. Examples of this are soil nutrients, temperature variation, and water availability (Brilha et al., 2018; Kerr & Packer, 1997; Richerson & Lum, 1980). Habitats that contain a wide range of geodiversity features are defined as having high georichness. This can be quantified as the number of geodiversity features in an area, and it is expected to affect the temporal development of habitat biodiversity (Alahuhta et al., 2020).

High georichness can be expected to support and maintain higher biodiversity and more stable community compositions over time compared to sites with lower georichness (Alahuhta et al., 2020; Knudson et al., 2018; Virtanen et al., 2010). As habitats consist of a mosaic of microhabitats with varying environments (Hjort et al., 2015; Scherrer & Körner, 2011), species can escape to more suited microhabitats when the general environment becomes unfavourable (Bertrand et al., 2011; Knudson et al., 2018). Although much of the environmental variation comes from varied topography and differences in vegetation cover (Loarie et al., 2009; Potter et al., 2013; Roth et al., 2014), the remaining geodiversity features are expected to greatly add to it (Serrano et al., 2007). In general, variations in surface

structure have been found to slow down and change the direction of compositional change of species in habitats to an extent of being completely decoupled from the general climate (Lenoir et al., 2013; Roth et al., 2014; Scherrer & Körner, 2011). Therefore, the inclusion of geodiversity in ecological studies is of great interest as species communities shift in the face of climate change (Alahuhta et al., 2020).

Unfortunately, the current knowledge on the relationship between geodiversity and species composition stem from biodiversity based approaches, such as richness counts (Bailey et al., 2017; Benito et al., 2020; Hjort et al., 2012; Jačková & Romportl, 2012; Räsänen et al., 2016; Tukiainen et al., 2017), and rely mainly on data on landscape scale (Knudson et al., 2018) which is not optimal for finer-scale studies (Bailey et al., 2017). Furthermore there is a lack of research on how fine-scale geodiversity affect species composition in general (Benito et al., 2020), and no studies on its effect on changes in species compositions over time.

In this thesis I study the relationship between geodiversity and the temporal development of species compositions. To do this, I use a novel technique for quantifying geodiversity at plot-scale together with temporal data on vascular plant communities from the alpine region of Hirkjølen, Norway. The data represent a unique opportunity for analysis as it spans almost 90 years between the original survey (1932) and re-sampling (2020) of permanent plots.

By looking at environmental factors such as elevation, plot location relative to the treeline, geodiversity, and its separate components (hydrology, geology, geomorphology), and topographical heterogeneity I ask if geodiversity is related to temporal stability in vascular plant species compositions in alpine communities.

Geodiversity

Since geodiversity play such a central role in this thesis I will in the following provide some information on the history of the concept of geodiversity. I will also provide short descriptions of the geodiversity features I use in my analyses, and their relationships with the local biotic environment.

History

Beier et. al (2015) present an overview of the history of geodiversity as a movement from wanting to protect areas of geophysical interest, to an acknowledgement of it forming a basis of biodiversity, and finally to being a surrogate measure of biodiversity in conservation planning. It was first introduced as a strategy for selecting the extent of the first national park in 1972, Yellowstone National Park. Later in 1988, it was attributed the reason behind the palaeoecological findings of 8000 years old shifts in plant communities, and suggested as a probable, but coarse, way to locate areas which maintained high biodiversity over time. This was also the beginning of the idea of Conserving Natures Stage (CNS). Through the following years additional ideas and theories were added to the CNS. The use of physical features to find geophysical diverse areas, such as elevation gradients, soil type, and flood areas. In 2010 CNS was proposed as a way to identify areas with high climate resilience. This is where the idea of geodiversity as a coarse filter for habitats with high resilience and biodiversity have further developed from. Many different quantitative and qualitative approaches have been used to test the relationship environment and the species communities, but scientists have up to now not been able to agree on one single method of assessing geodiversity. Fortunately, there are research teams which design and present novel methods which might help standardize the methods used for geodiversity assessment. One of which is used in this thesis.

Individual geodiversity features:

The approach to assessing environment heterogeneity by looking at geodiversity aims to be modular by including four different aspects of the habitat abiotic composition (Knudson et al., 2018). These are aspects of geology, geomorphology, hydrology and topography (Hjort et al., 2012). It is possible to add other aspects to this list, such as soil sample analysis and bedrock assessment, since the features are mainly treated separate. This modular approach allows the geodiversity assessment to be fitted to the data which is available or which would be suitable to collect in field work.

Geodiversity has earlier been included in temporal studies through the study of how slow-changing variables affect fast-changing variables in a habitat. One example of this is a study into restoration of irrigated fishponds. Here, the presence of native plants was found to be higher in areas with sedimented nutrient-rich soil after disturbance events (Knudson et al., 2018). The nutrient content in the soil was in this study considered slow-changing, while the presence of plants was considered a fast-changing variable. Which rate of change that is found depends of course on the type of variables which are studied. The bedrock type in an area, for instance, is unlikely to change faster than the presence of ponds or the vegetation cover. Geodiversity has from the CNS approach been studied as slow changing variables (Beier et al., 2015), which allows for treating them as fixed variables in analyses of biodiversity (Alahuhta et al., 2020).

The method I use in this thesis include aspects of the abiotic environment which are all linked to habitat biodiversity and species composition stability. A full list of geodiversity features used in the field work can be found in Appendix I. Here follows short descriptions of the features and how they affect their local environment:

Geology

The aspect of geology in geodiversity give insight into soil structure. Examples of geology feature are exposed bedrock, coarseness of the soil like gravel or till, and presence of peat in the habitat. It has been found to be a good predictor of species compositions and species richness in geodiversity assessments (Lobo et al., 2001). Especially when considering dominant vegetation types, geology is considered a good predictor (Anderson et al., 2015) as it includes information on the availability of important substrates and to an extent water and nutrients for plant species (Anderson et al., 2015; Hjort et al., 2012).

Geomorphology

Geomorphology includes a wide variety of environmental erosional and depositional processes. These processes are for instance deposition of rocks and soil from glaciers, streams and landslides, or erosion from acidic rain, wave action or glacial melt water streams. Peat deposits and hummocks are also included into this category. Features which would be categorized as geomorphological have been found to promote temporal stability and increased biodiversity under climate warming (Hjort et al., 2012; Virtanen et al., 2010). This is due to the large influence it has on habitat variability through inclusion of features of different sizes. This size range contribute to the number of microclimates and their ecological characteristics (Hjort et al., 2012).

Hydrology

Water is an integral part of geodiversity (Brilha et al., 2018) and it is regarded as one of the most important resource limitations in plant ecology (Hawkins et al., 2003). In geodiversity it is assessed through features such as the presence of running water, dry channels, and ponds. In biodiversity studies, water has been found to dictate both species composition (Yu & Ehrenfeld, 2010) and habitat response to climate warming (Harrison, 2020; Virtanen et al.,

2010). This comes from the well-known fact that plant species have different water requirements depending on their adaptations. And thus, we find different species compositions based on how much water is present in a habitat (Harrison, 2020).

Topographical heterogeneity

Topography is maybe the most studied aspect of geodiversity (Hjort et al., 2012; Tukiainen et al., 2017). It is regarded as strong predictor of habitat diversity (Anderson et al., 2015; Falk et al., 2006; Räsänen et al., 2016) as it creates environmental variability on both landscape and microclimatic scale (Roth et al., 2014). Large scale features such as elevation, slopes, and cliffs create variations in snow cover, lapse rate, radiation exposure, and precipitation rates (Loarie et al., 2009). Meanwhile, smaller topographical features such as snow beds, ridges, boulders, escarpments, and screes create local variations in temperature (Loarie et al., 2009; Potter et al., 2013; Roth et al., 2014) as well as shade coverage and soil moisture (Falk et al., 2006; Potter et al., 2013; Tukiainen et al., 2017). As such, topography affects habitat composition on multiple scales. The novelty of topography in geodiversity studies is the estimation of plot scale surface roughness, also known as topographical heterogeneity. This gives a closer reflection of the local environment than analyses which utilize for instance slope heterogeneity or just elevation.

Methods:

Study area

The demonstration area of Hirkjølen was established in 1932 by Professor Elias Mork and is located in the eastern part of Ringebu county, Norway (61° 40' N, 10° 30' E). It spans from 779 to 1089 m.a.s.l from the sub-alpine mountain plateau, past the treeline at approx. 1000 m.a.s.l. and into to the alpine peak of Skjerdingfjellet (Figure 1). It is situated in the northern boreal zone and is regarded as having warm summers and cold winters, although the mean annual temperatures have increased in recent years (Figure 2) (Karger et al., 2017). The annual precipitation rates of the area lay around 730 mm, measured from 2007-2020 at the weather station of Venabu (Norwegian Meteorological Institute and the Norwegian Broadcasting Corporation, 2021).

It is considered to be an area which is rich and diverse in species due to variations in habitat environment, water availability, and bedrock and soil types. Most of the research area is dominated by berry heather and old spruce (*Picea abies*) forests. But there are also habitats with tall herbs, younger birch (*Betula pubescens*) forests, moraine ridges, and open alpine heather fields (figure 3).

The geology of Hirkjølen is dominated by glacial processes (Høitomt et al., 2017; Mork & Heiberg, 1937). At higher elevations, nutrient poor slates of sparagmite cover layers of limestone and other calcareous rocks. There are, however, patches of nutrient rich soil where glacial processes have broken up the sparagmite slates. Such rich soil becomes more common down the hillside, especially along the western side, and below the scree- and moraine ridges of the south-east side. Nutrient rich brown soil can be found in large areas along the north-western side due to run-off water carrying and eroding nutrients from calcareous rocks. These streams and seepages also create areas of varying wetness, and especially at lower elevation there are both dry and wet habitat types.

There are some areas of Hirkjølen research area which have been transformed by humans. Especially at lower elevations near the hotel of Skjerdingen (Figure 1), cabin and road construction, animal husbandry and a ski lift were found to influence the landscape. Furthermore, along the hillsides one can find patches where experiments into forest rejuvenation through planting and forestry have been conducted (Mork & Heiberg,

1937). These factors are likely to have influenced species composition in close proximity and should be taken into consideration when assessing the species composition in the area.

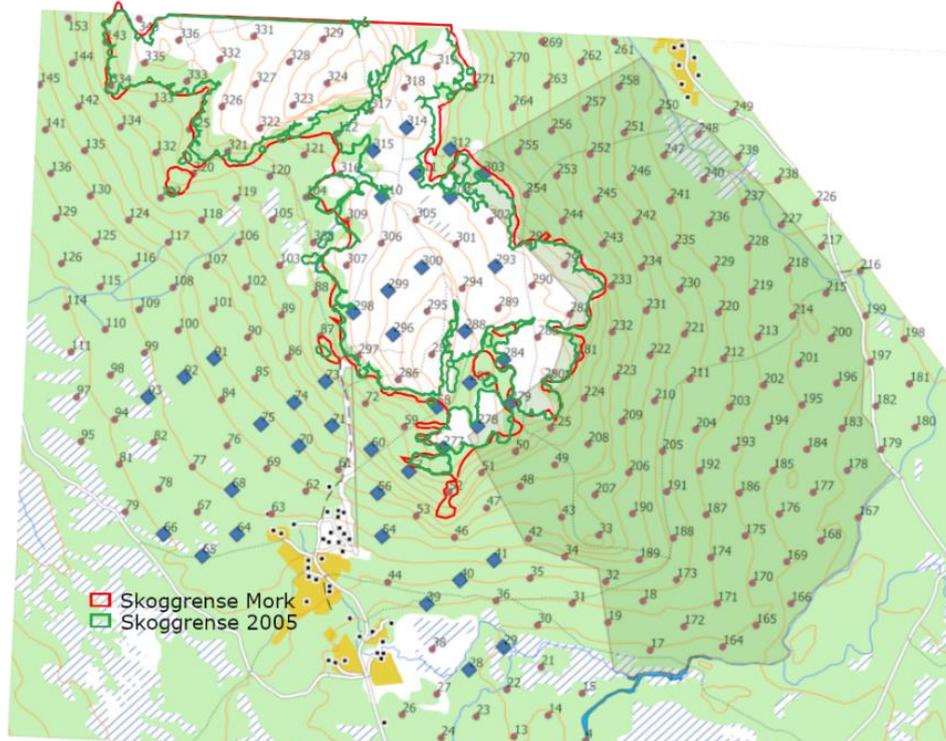


Figure 1: Map over research area Hirkjølen with plot number and geographical data. Blue squares were resampled in 2020, red dots were not resampled in 2020, green line marks the treeline in 2005, and red line mark treeline found by professor Mork.

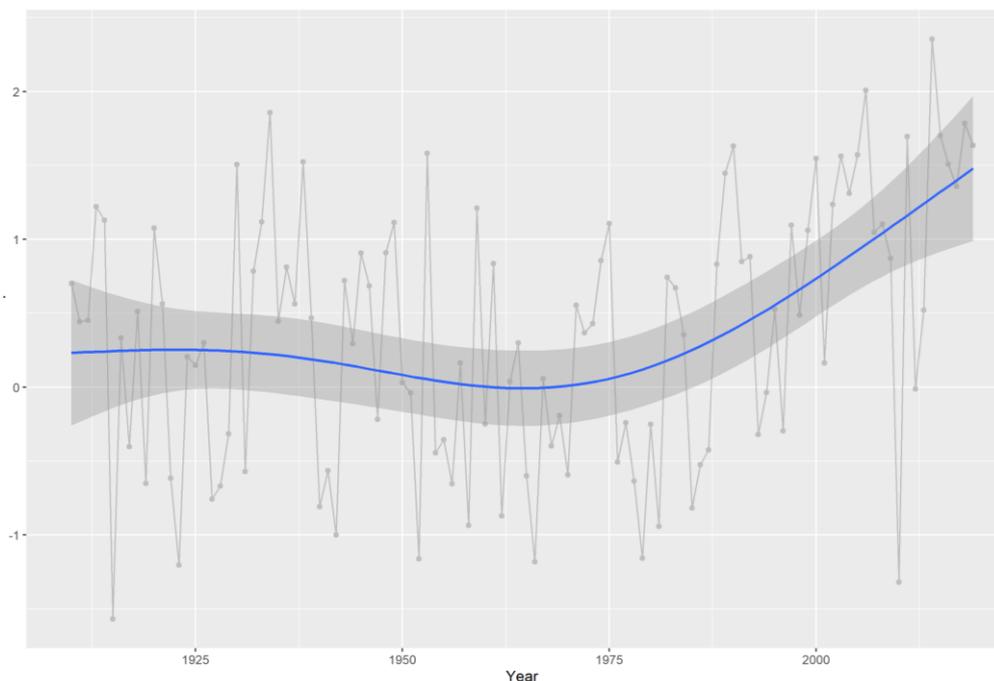


Figure 2: General additive model showing change in annual mean temperature from 1910 to 2019. Data is retrieved from CHELSA database and Norwegian weather stations.



Figure 3: Examples of 6 different habitat types found in Hirkjølen. Upper right: Top of moraine ridge south east of the peak of Skjerdingen, Upper middle: Plot with old dense vegetation south of the peak, Upper left: Open grazed birch forest at the lowest elevation, Lower right: Closed wet forest at lower elevation, Lower middle: Open heather field on the mountain plateau north of the peak of Skjerdingen, Lower right: Moraine hillside where birch (*Betula pubescens*) forest meets spruce (*Picea abies*) forest.

Vegetation resurvey

In my analyses I used composition and abundance data on the Hult-Sernander scale (Appendix II) to assess the development from 1932 to 2020. We included data from 40 the original 347 permanent plots which were established by prof. Mork in 1932 (Mork & Heiberg, 1937; Nygaard & Ødegaard, 1999). The same 40 plots were resampled using the same scale during field work in the summer of 2020. The plots were chosen on the basis of having high biodiversity, covering the elevational gradient, having proper markings (Figure 4), and having a history of low human interference. The latter was done by selecting the plots from a list of 150 plots which have to a low degree been influenced by forest rejuvenation experiments and cabin construction. Each plot was located using GPS UTM-32 coordinates in combination with map and compass. During the field work we combined the maps and GPS-coordinates into an updated higher resolution map which allowed for easier navigation (Figure 1). Comparison with map of human interacted plots also became easier.

Each plot was originally marked with 4 red corner markers and one large white pole (Figure 4) which made them easy to locate. Some plots had some missing or moved corner sticks due to melt water, snow movement streams or animals. In these cases we used the remaining corners to estimate plot area and temporarily marked it with white ropes. If the corner markers were found they were returned to their approximate corner location. In some plots one or two of the corner sticks were replaced by erected stones or cairns but these were easy to identify.

Each plot was documented with five pictures. One picture from each corner of the plot using a wide lens and pointing inwards toward the centre. And one 360 degrees panorama picture, standing in the centre of the plot pointing outwards. This summed up to a total of 200 pictures which were used for reference of geodiversity after field work.

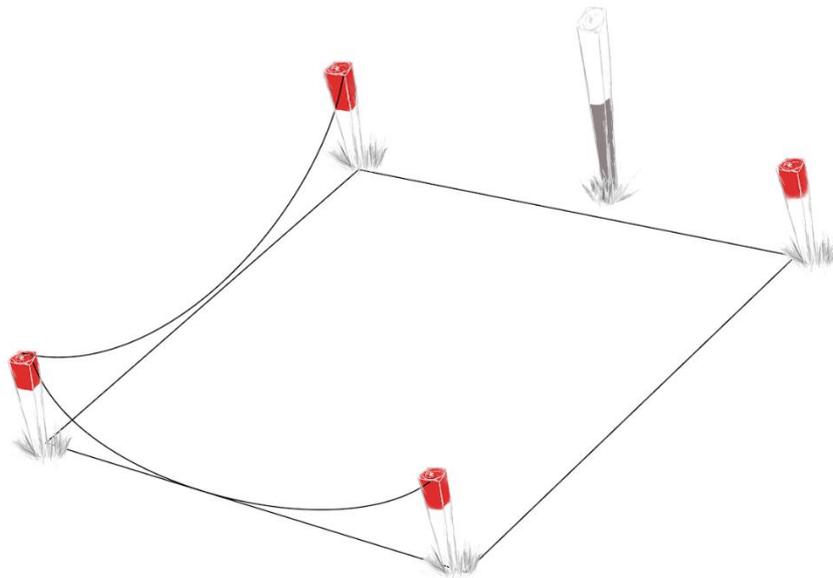


Figure 4: Illustration of permanent plot markings. Red markers at each corner of a 10x10 meter square, and a white pole on one side. White pole had metal plaque with plot number. Illustration also includes example placement of 10 meter white ropes for easier distinction of plot area in field. Illustration: Halvor Dahl Reisæter-Thu

Mapping of plot-scale geodiversity

The geodiversity assessment was performed using the field form designed by Hjort et al. (2021, see Appendix I for a simplified version). The method relied on visual identification of landform and surface features and processes in a 10-meter radius circle from the vegetation plot centre. This extended beyond the 10x10 meter plot in order to cover as many of the geodiversity features which could influence plot species composition. The topographical heterogeneity was scored from 1 (completely flat surface) to 5 (very rough surface), disregarding any general slope in the plot.

Here follows a short description of the normal routine of a plot assessment before a more in-depth look at the individual geodiversity features:

Performing the abundance assessment of vascular plant species took on average between 40 – 90 minutes. This time was also partly spent looking for geodiversity features which were noted down upon observation. These were mostly the easier observable features such as running water, presence of peat or escarpments. After plant species assessment was complete, 10-15 minutes was spent trailing the 10-meter radius boundary from the plot centre

before crossing the plot in straight lines to cover the entire area. Care was taken to not trample the plots severely. Smaller geodiversity features such as deposits and erosion from water, soil structure and weathering of rocks were typically identified during this. Lastly, the topographical heterogeneity of the plot was assessed when we had got a good feel of the plot. After the field work, the georichness was estimated as the sum of geology, geomorphology and hydrology features which were found in the plot. All plots were also re-assessed with the pictures taken to verify the geodiversity which was observed.

Data cleaning

Cleaning of the species and geodiversity data, and statistical analyses were done using R v1.3.959 (R Core Team, 2020). Elevation for each plot was estimated using a 10-meter resolution digital elevation model (DEM) from GEONORGE v Sprint 10.1. The DEM was analysed in the geographic information system QGIS v3.14.15-Pi. Lastly, we looked at plot location in relation to the treeline in 1930 and 2005, by assessment of treeline maps supplied by NIBIO. Each plot was categorized as either above or below for each year.

We homogenized the species composition data we collected in 2020 with that prof. Mork collected in 1932 (Aksnes, 2021). During this process, some species had to be merged due to observer error from similarities in field and possible misidentification.

Post analysis, all cleaned geodiversity and species composition data was made available at the ECKO data consortium (Appendix IV).

Temperature data

The mean annual temperature for each plot from 1910-2019 was estimated with data from the CHELSA database V1.0, for the years 1910-2016, (Karger et al., 2017; Karger & Zimmermann, 2018) and Norwegian weather stations, for the years 2017-2019. This was done by calculating the mean temperature between all plots from a 1-km resolution raster which was interpolated from these data.

Analysis of compositional shifts

Vegetation data on the Hult-Sernander scale was recorded as discrete values on a logarithmic scale. Because of this the data did not fulfil the assumption of linearity without a linear transformation. This is sometimes overlooked in statistical analysis and cause faulty results (Oksanen et al., 2019). I therefore utilized analyses which used rank-order transformations to force the data onto a linear relative scale. The advantages of this will be discussed in the following.

Testing for differences in species composition

The effects of the environmental and temporal variables on species composition were explored through an Analysis of Similarities (ANOSIM). This method was chosen since it:

- Uses rank-transformations on the data to become non-metric
- Allows for inclusion of dissimilarity matrices
- Analyses the data iteratively
- Tests the data against an appropriate H_0
- Has many similarities with the ordination techniques used for analysis into temporal shifts

(Anderson & Walsh, 2013; Clarke, 1993; Oksanen et al., 2019).

A rank-order transformation replaces the species abundance values with ranks ordered on a monotone scale from the most- to the least common species. If two or more species share abundance values, they also share rank order. The result is a linear dataset without any assumptions of linear relationships in the real-world data. It actually removes any unit of

measurement from the data, it becomes non-metric, which decreases the chance for unaccounted effects on the analysis, like the arch-effect in Principal Component Analysis (PCA). It should also be noted that this removes any direct measurement of magnitude of difference in the real-world data, and instead produce relative measurements between plots.

The inclusion of dissimilarity/distance matrices allows for choosing the different aspects of the data which is of interest. Examples of these are Bray-Curtis dissimilarity and Jaccard similarity which focuses on changes in species composition, Euclidean distance which focus on changes in total and individual species abundance, and chi-squared which look at weighted relative changes in species abundance (Anderson & Walsh, 2013). I choose Bray-Curtis dissimilarity matrix for the exploratory analysis of my species abundance data. This is due to the consequences of using Bray-Curtis on ranked data and relative counts. When Bray-Curtis is applied onto ranked data, only the shape of the species counts is analysed. The shape is which species has high and which species has low values. The size of each species count is removed and only information on changes in the rank-order is provided (Greenacre & Primicerio, 2013). In this way one avoids a result which includes an unknown amount of information on shape and size, and instead is provided a result which includes only shape.

Some statistical analyses suffer from susceptibility to providing results based on local optima in the data. Especially algorithms which chooses a starting point and then analyses the rest of the data from there runs the danger of finding a result which is only the best when seen from that specific starting point. Performing multiple iterations, with multiple starting points, and comparing the results from each one remedies this by choosing many starting points and then finding the best result from all iterations. In these analyses, for instance, 9999 iterations were used for all permutational tests.

A part of data analysis in ecology which is often overlooked is finding the test with the appropriate H_0 -testing criteria (Clarke, 1993). Since I am testing variation between plots with different environments, I find the ANOSIM- H_0 a good fit: *The within group distances are greater or equal to the between group distances*. In my case this translates to analysing whether it is better to group species communities which have similar or different environments together, or not. In comparison there is the Permutational Analysis of Variance (PERMANOVA) which uses a H_0 that is: *There is no difference in centre location between of any of the groups*. This is not as clear as the H_0 for the ANOSIM.

As ANOSIM is somewhat less known than PERMANOVA there are two things which should be noted. Firstly, ANOSIM is more prone to estimating liberal P-values when analysing heterogeneous data compared to more popular tests like the PERMANOVA (Anderson & Walsh, 2013; Oksanen et al., 2019). Care with interpreting the results is therefore a must. And secondly, ANOSIM does not report the commonly used R^2 -statistics or similar explained variance measurements. It instead reports the R-statistics which provides insight on degree of similarity between groups. It ranges from -1 to 1 where a value close to 1.0 reflects high similarity within groups and high dissimilarity between groups. A value close to -1 reflects the opposite. If the ANOSIM provides a value close to 0 it means that the data has an even distribution of species ranks between and within groups.

The variables I included in these analyses were elevation, georichness, topographical heterogeneity and richness of geology, geomorphology, and hydrology. I also tested for difference in geodiversity composition along the elevational gradient and above/below the 2005 and 1930 treeline.

Visualizing differences in species composition

To visualize, and later analyse, the changes in plant community composition I performed a Non-metric Multidimensional Scaling ordination (NMDS) with a Bray-Curtis dissimilarity matrix, using 'metaMDS()' function in the *Vegan*-library (Oksanen et al., 2019). Such ordinations map multivariate data onto simplified ordination spaces with decreased number of dimensions. This allows for easier interpretation of complex data through one-, two- or three-dimensional plots. An NMDS ordination is regarded as the most robust method for unconstrained ordination in community ecology (Minchin, 1987). It uses a rank-order transformation on the data and analyses it through multiple permutations. The advantages of this are discussed earlier under the heading *Testing for differences in species composition*. Another advantage of the NMDS is the ability to map environmental trend lines onto the ordination plot for easier interpretation by use of the function 'envfit()' (Oksanen et al., 2019). The function uses the ordination scores and finds the direction of most change for each environmental variable in ordination space. This maximises the correlation between the environmental variables and the species composition in ordination space. The trend lines from this are also scaled according to their associated R^2 value which means that the length of the arrow reflects their correlation with species composition. The result is a plot which give insight into non-metric variations in species compositions, and how the environment relates to it. Although without direct information on absolute differences. I can, however, still interpret the magnitude of differences in species community composition shape due to using ranked data with Bray-Curtis dissimilarity, and since the function 'metaMDS()' performs a PCA on the results before plotting it. This maximises the explained variance of data shape, by the ordination axes. Lastly, one can easily account for pseudo-replication in resampled data in the NMDS by preventing permuted analyses within paired plots. This is done by including the 'strata' term in the NMDS.

To study the differences in species composition caused by temporal shifts and environmental variables I mapped the topographical heterogeneity, year of sampling, elevation, whether the plot was above or below the treeline, and georichness to the ordination.

Measuring differences in species composition over time

I then measured the magnitude of compositional change in each plot from 1932 to 2020 as the Pythagorean distance, $\Delta NMDS$, in the ordination using the following formula:

$$\sqrt{\Delta NMDS1^2 + \Delta NMDS2^2} = \sqrt{(NMDS1_{2020} - NMDS1_{1932})^2 + (NMDS2_{2020} - NMDS2_{1932})^2} = \Delta NMDS$$

Here the Pythagorean distance ($\Delta NMDS$) was measured as the root of the sum of the squared values for the degrees of change along the two first ordination axis ($NMDS1_{2020} - NMDS1_{1932} = \Delta NMDS1$ and $NMDS2_{2020} - NMDS2_{1932} = \Delta NMDS2$). By this definition I got a measure of the relative degree of change in species composition which encompassed the highest degree of explained change in the ordination. I could still apply Pythagorean, distances which is a Euclidean distance, despite using the non-Euclidean dissimilarity measurement of Bray-Curtis. This is due to my method treating the data as relative counts through rank-transformation. This makes the Bray-Curtis distance similar to the Manhattan distance which is a Euclidean-distance measurement. Furthermore, the maximised explained variance from the PCA in the 'metaMDS()' code carries into the $\Delta NMDS$ estimate.

General Additive Models

The $\Delta NMDS$, magnitude of compositional change in species, were then applied in a set of General Additive Models (GAMs) to study their relationships to environmental variables. GAMs serve as a middle ground between simple models (i.e., linear regression) and complex models (i.e., machine learning). They allow for fitting non-parametric smoothers, as well as

linear relationships, without deciding on a mathematical formula beforehand, whilst remaining interpretable through plotting. These were fit using the *mgcv*-library in R (Wood, 2011). I used a Gaussian-distribution with Restricted Maximum Likelihood for the models. It is regarded as the most effective method to avoid overfitting the model by penalizing increased “*wiggleness*” in the model. The number of knots, *k*, was adjusted based on GAM diagnostics from `'gam.check()'` (Wood, 2011).

Univariate GAMs were used to determine response of Δ NMDS to variations in the environmental variables plot elevation (*k* = 4), georichness (*k* = 10), and counts of geomorphology (*k* = 6), hydrology (*k* = 3), and topographical heterogeneity (*k* = 4) were fitted as smoothed predictors of the Δ NMDS. Geology was fitted as a linear response due to low number of covariate combinations. Test for multivariate interaction responses were fitted with georichness and elevation, as well as georichness and treeline as predictor variables for degree of composition change.

And lastly, GAMs for change in georichness with elevation, and difference in georichness from below to above the treeline, was fitted to study the between-variable relationships. I also checked correlations between variables with the *corrplot*-library (Wei & Simko, 2017). This was to uncover possible strong correlations between variables and to avoid testing with non-independent predictors.

Results:

Data summary

A total of 182 species were identified in the 40 plots used in the analysis. In the 1932 data the total number of species recorded was 168, ranging from seven to 66 species per plot, and with a mean of 33 species in each plot. During the resampling of 2020, fewer species were found as the total ended up at 137 species. The mean and maximum per plot were lower, at 27 and 57 species in a plot, but the minimum remained the same at seven species

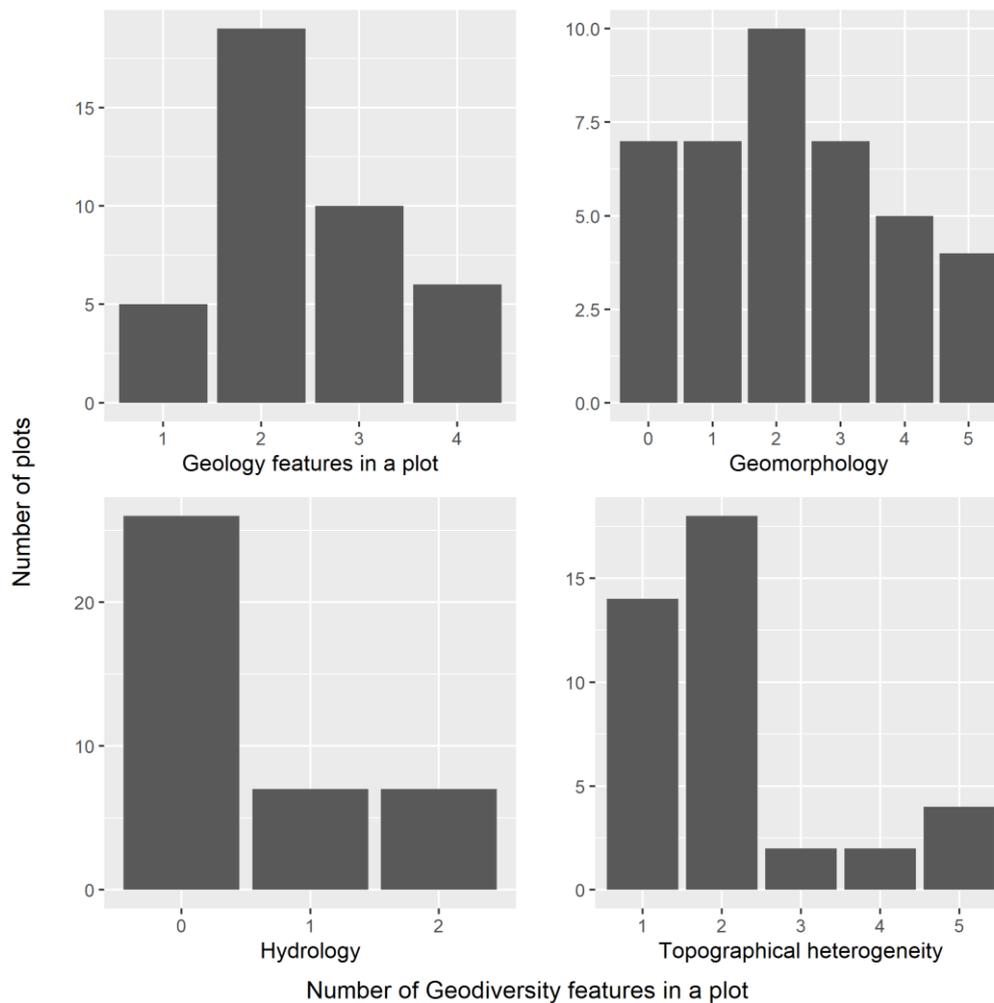


Figure 5: Barplot summarizing the number of plots with different counts of geodiversity features.

Looking at georichness I found an average of five features in each plot, with a maximum of 11 and a minimum of one. Of the different categories, geology proved to be the most common with an average of 2.4 features, just above geomorphology which ended up at 2.2 features per plot. Hydrology was the least common geodiversity feature and was found on average once every other plot, 0.5. The surface roughness was on average scored to be 2.1 on the topographical heterogeneity scale (Figure 5).

Distribution of species

The exploratory analyses performed with the ANOSIM showed a significant change in species composition over time (R -value = 0.23, $P < 0.01$), which was also found in the NMDS (Figure 6). The species compositions were also found to differ along the elevational gradient (R -value = 0.57, $P < 0.01$) and when separating between plots above and below the treeline. Comparing the elevation variable with the two treeline bipartitions showed a surprisingly low correlation between them (Figure 7). It was therefore interesting to see if the variables uncovered different patterns in species composition. When looking at the treeline analyses, the 2005-treeline provided a greater distinction between communities above and below the treeline (R -value = 0.57, $P < 0.01$) than the 1930-treeline (R -value = 0.54, $P < 0.01$). I therefore choose to use the 2005-treeline in all further analyses when the treeline was of interest.

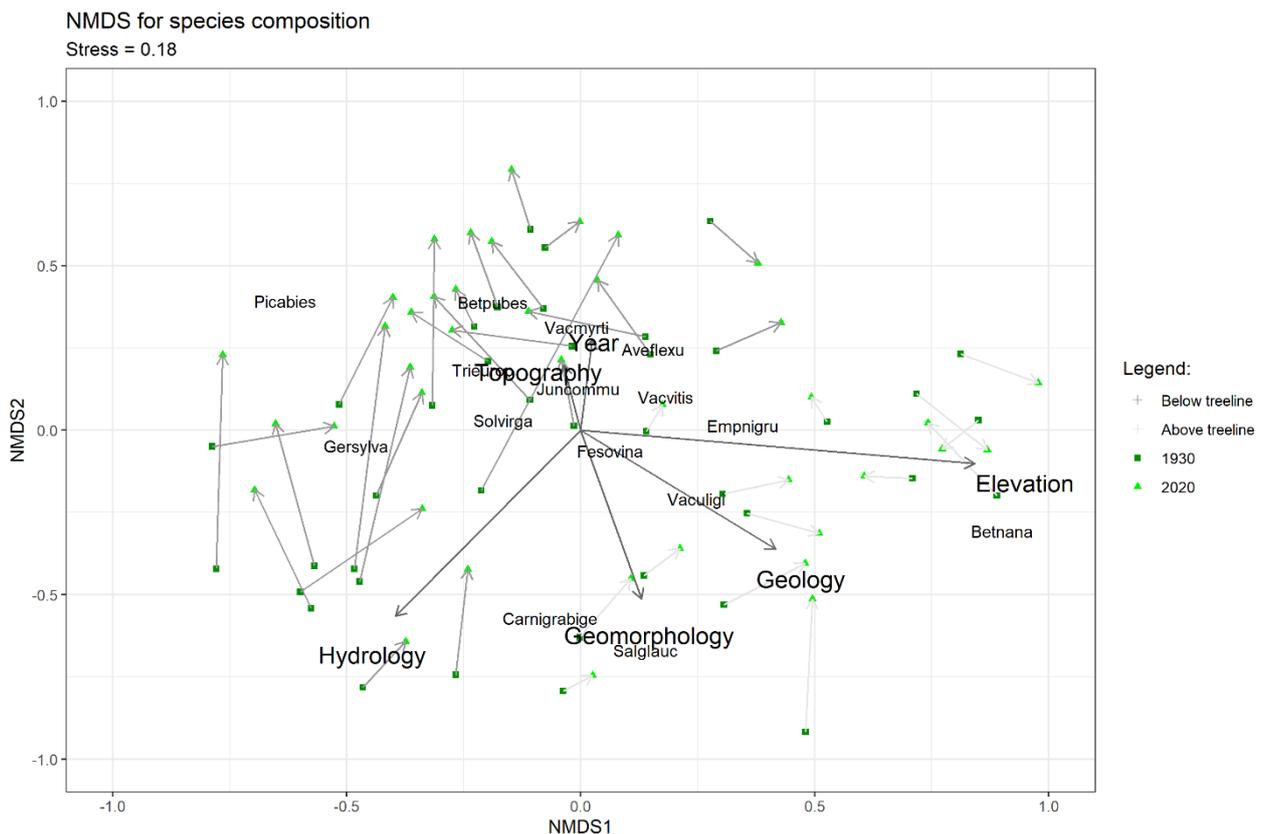


Figure 6: Result from Non-metric Multi-dimensional Scaling species composition in each plot. Environmental variables year of sampling, elevation, topographical heterogeneity (Topography), geology, geomorphology and hydrology are mapped onto the ordination. Colour and shape of points represent year of sampling and are connected by arrows which show direction of temporal shift in species composition. Arrows are colored by whether the plot was located above or below the 2005-treeline. The centroid of the 20 most abundant species are added as abbreviations. Their location represent their optima in abundance for all plots. These are: *Avenella flexuosa*, *Betula nana*, *Betula pubescens*, *Bistorta vivipara*, *Carex nigra bigelow*, *Empetrum nigrum*, *Festuca ovina*, *Geranium sylvaticum*, *Gymnocarpium dryopteris*, *Hieracium sp.*, *Juniperus communis*, *Luzula pilosa*, *Melampyrum sylvaticum*, *Picea abies*, *Salix glauca*, *Solidago virgaurea*, *Trientalis europaea*, *Vaccinium myrtillus*, *Vaccinium uliginosum* and *Vaccinium vitis-idaea*.

Moving from the temporal and spatial analyses of species composition to the analyses with geodiversity, I found the total geodiversity to significantly affect species composition (R-value = 0.21, $P < 0.01$). Of the features which sum up to the total geodiversity, hydrology (R-value = 0.23, $P < 0.01$) and geomorphology (R-value = 0.09, $P < 0.01$) proved significant, while geology did not (R-value = 0.01, $P = 0.33$). Topography, which was the last aspect of geodiversity to be assessed also did not prove to be a significant predictor of species composition (R-value = -0.06, $P = 0.98$).

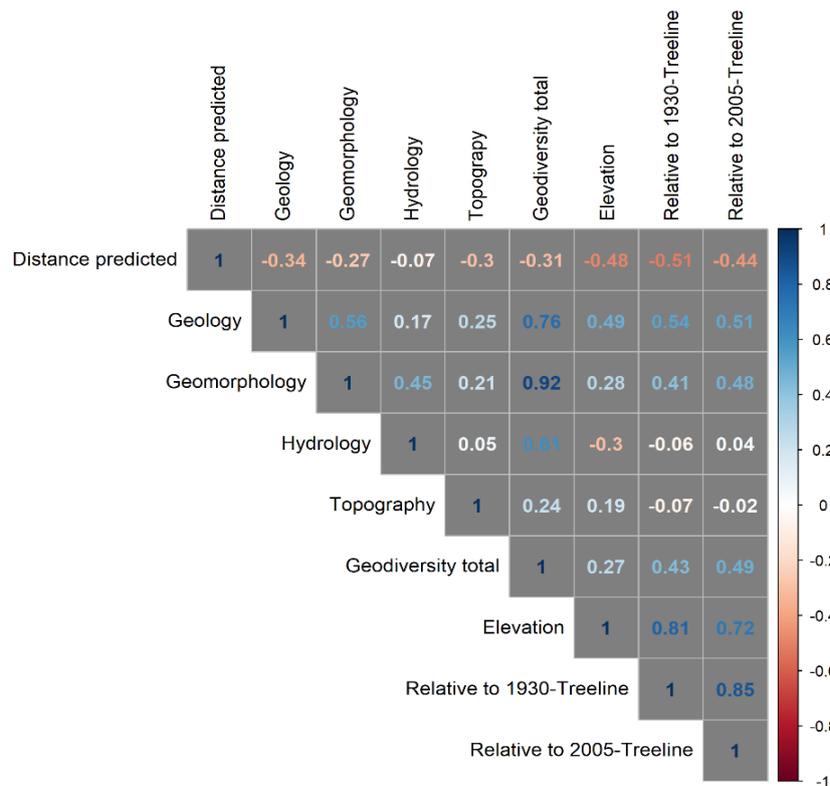


Figure 7: Correlation matrix which show correlation between all variables used in the analysis. Distance predicted is the Pythagorean distance between the 1932- and 2020-location of a plot in the ordination analysis

After testing univariate ANOSIMs I looked at interaction between variables and their effects on species composition. Along the elevational gradient the response of species composition was found to be similar between 1932 and 2020 (the interaction between elevation and time: R-value = -0.12, P= 0.34). Comparing species compositions for 1930 and 2020 and their associated georichness in contrast showed something different. My analyses showed species compositions with similar georichness to develop differently over time (the interaction between georichness and time: R-value 0.24, P< 0.01). Species communities varying responses to georichness was found to be significantly different at both elevations (the interaction between georichness and elevation R-value = 0.80, P< 0.01) and in the treeline bipartition (the interaction between georichness and 2005-treeline: R-value = 0.16, P = 0.02). To see if these findings were due to the georichness alone, or if the composition of geodiversity variables played into the results, I performed a set of ANOSIMs with geodiversity composition as the response variable. What I found was there being no significant difference in geodiversity composition along the continuous elevational gradient (R-value = -0.04, P = 0.54). However, separating the plots into above or below the treeline showed a significant difference in geodiversity composition (R-value = 0.14, P = 0.01).

Temporal development of species composition

In the general additive models I found the number of geodiversity features to influence the magnitude of shifts in species composition (Figure 8 and Table 1). Of the individual geodiversity features, diversity in geomorphology provided the highest explanatory power for magnitude of change in species composition, followed by diversity in geology. Topographical heterogeneity and hydrology were not found to have an effect on the degree of compositional change.

The GAMs for elevation showed a difference in degree of change in species composition along the elevational gradient (Table 1). To see if this was in some way related to georichness I ran a GAM for georichness with elevation (Figure 9 and Table 1). I did not find any evidence of this. However, I did find a difference in plot georichness between the plots above and those below the treeline. Using bivariate analysis to test for interaction between georichness and elevation, and georichness and plot location relative to the treeline, we found georichness to have lower explanatory power than the elevation and treeline variables (Table 2). Unfortunately, due to low number of plots in the data I considered the loss of statistical power to be too great for separate analyses of plots above, and below, the treeline

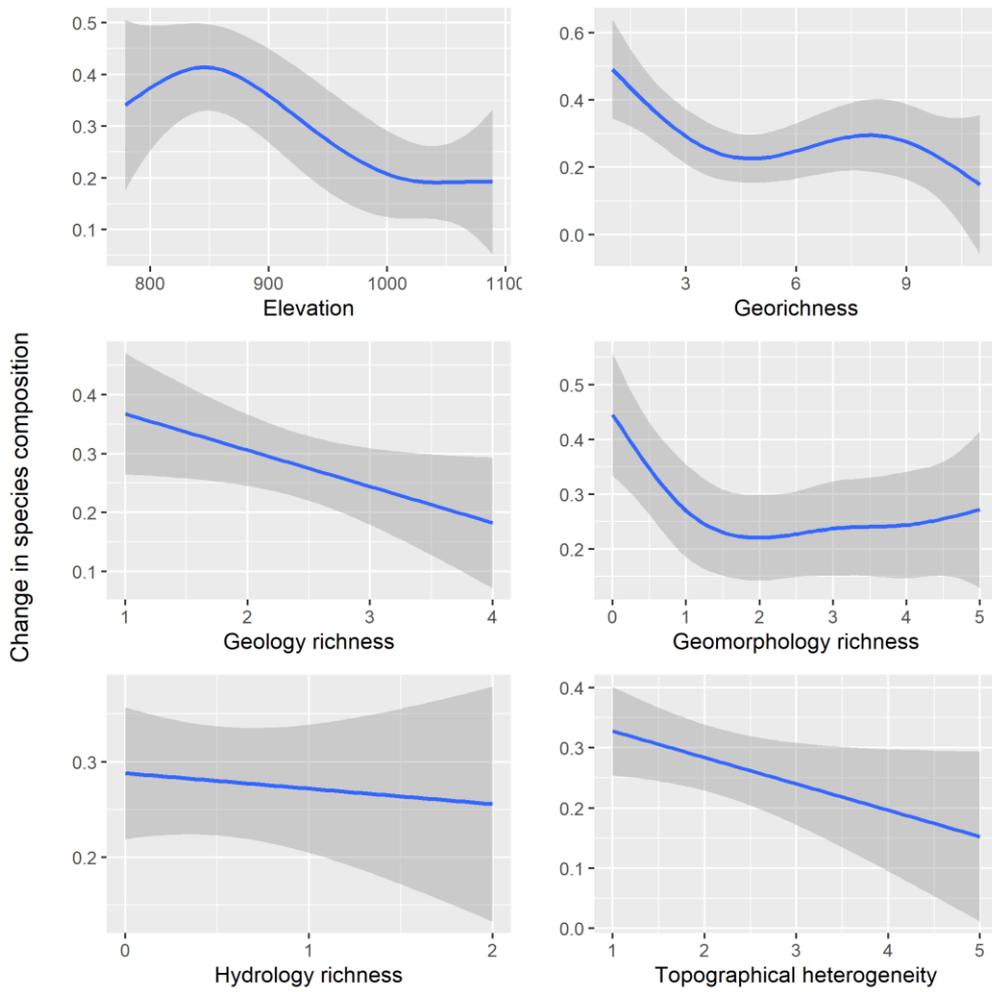


Figure 8: Results from General Additive Models with change in species composition as estimated by ordination with elevation, richness for both combined and separate geodiversity variables, and topographical heterogeneity.

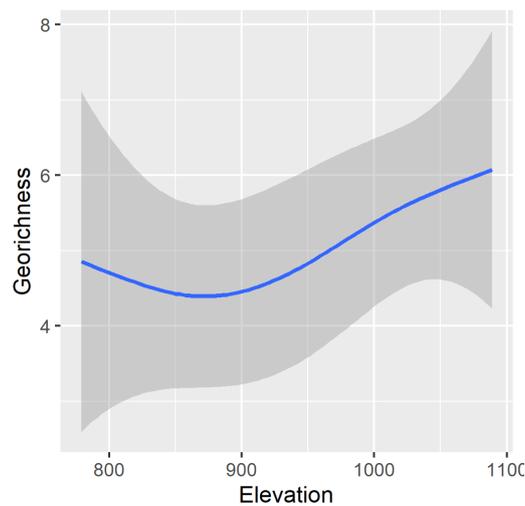


Figure 9: Results from General Additive Models which predict number of geodiversity features with elevation.

Table 1: Results from univariate General Additive Models: “Response” ~ “predictor variable”. Δ NMDS is the Pythagorean distance from 1932- to 2020 plot location in the ordination analysis. It indicates degree of compositional change in the species communities. * marks significant results using 0.05 significance level. Geology uses T-statistic based GAM due to having too few unique covariate combinations.

| Test | adj. R ² | Test-statistic | P-value |
|---|---------------------|----------------|---------|
| Δ NMDS ~ Georichness | 0.19 | F-value: 2.83 | 0.04* |
| Δ NMDS ~ Geomorphology | 0.21 | F-value: 2.97 | 0.03* |
| Δ NMDS ~ Geology | 0.07 | T-value: -1.97 | 0.06 |
| Δ NMDS ~ Hydrology | -0.02 | F-value: 0.32 | 0.79 |
| Δ NMDS ~ Topographical heterogeneity | 0.06 | F-value: 3.48 | 0.07 |
| Δ NMDS ~ Elevation | 0.27 | F-value: 5.07 | 0.01* |
| Georichness ~ Elevation | 0.05 | F-value: 0.99 | 0.34 |
| Georichness ~ Above/Below Treeline | 0.17 | T-value: 2.96 | 0.01* |

Table 2: Results from bivariate General Additive Models using interaction between variables: “Response” ~ “predictor variable 1” and “predictor variable 2”. Δ NMDS is the Pythagorean distance from 1932- to 2020 plot location in the ordination analysis which indicate degree of compositional change in the species communities. * marks significant results using 0.05 significance level.

| Test | adj. R ² | Variables | Test-statistic | P-value |
|--|---------------------|----------------------|----------------|---------|
| Δ NMDS ~ Georichness and Elevation | 0.24 | Georichness | F-value: 1.49 | 0.249 |
| | | Elevation | F-value: 7.26 | 0.01* |
| Δ NMDS ~ Georichness and Above/below treeline | 0.25 | Georichness | F-value: 1.55 | 0.46 |
| | | Above/below treeline | T-value: -2.31 | 0.01* |

Discussion:

The comparison of species communities in the NMDS show a shift in species composition from 1932 to 2020. This shift seems vary in both magnitude (Figure 8) and direction (Figure 6) depending on the habitat georichness and elevation. Generally, the magnitude of compositional shifts seemed to decrease with increasing georichness and altitude. These novel findings were in accordance with the theory of habitat heterogeneity supporting higher compositional stability in plant species communities over time.

The influence of geodiversity on magnitude of shifts in species composition

Higher georichness seemed to lower the magnitude of compositional shifts in an almost stepwise pattern, from low to medium, and from medium to high values. It is possible that the maximum decrease in compositional change from georichness is reached if only a few geodiversity features is present. This seem, however, unlikely as more geodiversity features are expected to increase habitat variability. It is therefore of interest to assess the different categories of geodiversity, which all showed some form of negative relationship with compositional change. Hydrology did not significantly affect the shifts in species composition (Figure 5), which was somewhat expected due to Hirkjølen being a dry area (Figure 5). The major shifts were therefore most likely not related with the presence of water-related features and processes. Also geology did not prove significant. Although, the statistics show evidence of a possible pattern which would have been uncovered with greater statistical power. Geomorphology on the other hand induced smaller compositional shifts in species composition if one or more such features were present. A reasoning for geomorphology being the only significant influence on magnitude of shifts could be due to how it is defined.

Firstly, geomorphology features are related to other aspects and processes in the environment which might be more related to temporal development than hydrology and geology. While the two latter look mostly at presence of certain features and resources, geomorphology include information on processes of erosion and deposition. These processes reflect the movement and availability of resources, e.g. erosion of minerals into the soil. A wide variety of geomorphology features in a plot would therefore reflect an environment with a possibly wide array of niches. Species would therefore be able to “escape” to different parts of the habitat with sufficient nutrients. I can however only speculate on this as an analysis of soil samples would be required to fully explain soil related processes.

Secondly, geomorphology contains more features different sizes compared to hydrology and geology. It also contains more features than the other two in total. This would make it capture a wider part of the surface heterogeneity and create greater distinction between areas with high and low georichness. The features themselves also greatly contribute to habitat variability and environment of micro-habitats, e.g. through variations in surface temperatures through surface roughness. This is however somewhat contested by topographical heterogeneity not being significant. If the variation in surface structure in geomorphology greatly influenced the shifts in species, then it would likely also be reflected in the topographical heterogeneity as a significant result. For instance, the presence of turned soil from earth slides, peat hummocks or physical weathering of rocks would all increase the topographical heterogeneity. It is therefore likely that the other aspects of geomorphology, which I have discussed, are stronger drivers for compositional stability in Hirkjølen. This could for instance be feature which are more related with erosion and deposition of nutrients than those related to topography. Geomorphology is the only geodiversity aspect which has been found to directly contribute to stability in plant composition before (Virtanen et al., 2010). Geology and hydrology lack this evidence to be fully defined as well defined stability inducing abiotic features in the environment.

In comparison to the findings of a similar geodiversity assessment from a comparable study sites in the Finnish tundra (unpublished), performed by group of local researchers, all the categories of geodiversity I assessed had lower occurrences, which might have influenced the analyses. Geomorphology for instance had 1.5 fewer occurrences per plot on average. There were also some problems regarding skewed data collection of geodiversity features (Figure 5) although the plots were relatively homogeneous in geodiversity composition. The homogeneity in the geodiversity composition can also be seen in the geodiversity composition NMDS in Appendix I.

What topographical heterogeneity does not include in terms of topographical variation, that has been found to influence compositional stability (Graae et al., 2018), is the slope of the habitat (Loarie et al., 2009). Even smaller slopes and changes in elevation produce variations in temperature and can give insight in which microclimates are present in a habitat.

The influence of elevation on magnitude of shifts

The magnitude of compositional shifts was different along the elevational gradient, i.e. below and above the treeline. At lower elevations, the magnitude of shifts followed a curve similar to a second-degree polynomial with increasing elevation. After it peaked around 850 m.a.s.l. it decreased steadily until it reached the treeline. Here it evened out at a very low degree of compositional change. This was unexpected as alpine habitats are regarded as vulnerable to climate change and are expected to change greatly with increasing environmental temperatures. I therefore expected an increase in compositional change especially around the treeline area as species are found to be moving upward. One possible explanation to this is the fact that the magnitude of shifts follows an inverse of georichness with elevation. This would likely point to the difference in magnitude being as much caused by differences in

georichness as elevation. But georichness did not prove significantly different along the continuous elevational gradient. Only by separating the plots into above or below the 2005 treeline was there a significant increase in georichness and geodiversity composition, as would be expected from smaller soil depth and less vegetation cover in the alpine (Roth et al., 2014; Scherrer & Körner, 2011). Unfortunately, it was not possible to perform statistical analyses on the separate groups due to low plot count. The loss of statistical power from separating the plots would be too great to properly assess the trends below and above the treeline.

From all of this it becomes likely that both the georichness and the types of geodiversity features in a habitat affect the magnitude of compositional shifts. There does however remain some questions regarding the how these variations in geodiversity play out at different elevations and vegetation densities. Research which includes a greater data collection and longer gradients would possibly allow for further investigation into these trends. There remains also the question of how geodiversity relates to species compositions of forest and alpine communities.

Direction of change

From the NMDS one can see a sudden change in the direction of compositional shifts from low to high elevation. At lower elevation species communities mostly shift toward species compositions associated with lower georichness. It is possible that this is due to geodiversity being harder to identify at lower elevations due to denser vegetation cover. It could also be evidence of species communities becoming more similar to low elevation plots. These plots have often a more homogeneous surface structure due denser vegetation cover than alpine habitats (Roth et al., 2014).

Looking at the associated species compositions, the temporal development seems to move toward higher presence of species such as *Vaccinium myrtillus*, *Avenella flexuosa*, *Betula pubescence*, *Vaccinium vitis-idaea* and *Trientalis*. There were also many plots which moved toward the centroid for *Picea abies*, especially at the lowest elevations. All of these species are typical forest species. In the opposite direction lay species such as *Carex nigra bigelowii* and *Salix glauca* which are often found in the alpine, as well as *Vaccinium uliginosum*. These shifts can be interpreted as an increase in spruce forests and berry heather forests, and a decrease in grey leaf willow fields. As spruce and berry heather forests can sometimes be dominated by only a few species these shifts could mean that species compositions become more similar and perhaps less resilient over time. Especially if the forests and forest floor vegetation grow denser, they may cover certain geodiversity features, making them less influential but also harder to identify.

Elevational shifts of species composition are often a reflection of change in the associated thermal conditions for the species composition. This can happen if lowland species move upward as a result of relaxation of temperature restraints, as seen as thermophilization across Europe (Erschbamer et al., 2011; Grytnes et al., 2014; Steinbauer et al., 2018; Harrison, 2020). Here the degree of change is expected to be higher in the plots the species move into, but this is not necessarily what one sees from the analyses. In the GAMs and NMDS the greatest shifts happen around 850 m.a.s.l. and these shifts were not exclusively along the elevational, temperature, gradient. Another possibility of species shifts is a downward movement from competition release at lower elevation (Lenoir et al., 2010; Roth et al., 2014). In this case, the competition release is induced by a niche suddenly becoming available for competition limited species. This can happen as a result of disturbance events such as grazing and predation, or altered interspecies-interaction from climate warming (Lenoir et al., 2010). There is also the possibility of a mixed response (Roth et al., 2014) which is what the NMDS shows. It also shows an increase in the presence of *Avenella flexuosa* which could be an indicator of such grazing induced patterns (Austrheim et al., 2008)

Exactly how geodiversity affects the direction of these specific types of shifts is uncertain. There are however some patterns on how geodiversity relates to different species compositions, on which the shifts may happen. From the ANOSIMS I found hydrology and geomorphology counts, as well as the total georichness, to provide some explanatory power to the composition of the species communities. Meanwhile, geology and topographical heterogeneity was not related with specific species communities. This raises the question if geodiversity counts are the appropriate tool for predicting specific species compositions, and to this extent their development. The study of quantifying geodiversity is still at an early stage. And so far, geodiversity counts have been proven a viable predictor of richness in some species. But since it only includes information on the number of different niches available and not the type of niche, nor the abundance of it, caution should be taken when attributing it predictive power of species compositions. For now, it seems that some geodiversity features explain more of the local variations in species compositions than others. It will be of great interest if future research looks further into how and to what degree the individual geodiversity categories can predict the type and development of individual species compositions.

Other sources of influence

It is also possible that these shifts have been facilitated by change in land-use and habitat transformation. Anthropogenic factors such as herbivory and cabin construction are well known to cause changes in community composition (Virtanen et al., 2010). A high number of free roaming cows and sheep were observed at lower elevation, especially around the hotel of Skjerdingen at 840 m.a.s.l., and along the ski resort (Figure 1). This is the same elevation we observed the highest degree of compositional change (Figure 8). Further away from the cabin and hotel area, we found evidence of grazing from moose, and reindeer at higher elevations. Since the observations of anthropogenic influence partly overlap with elevation, and I do not have explicit data on its severity, I can unfortunately neither verify nor disprove its influence. It is therefore of great interest if future research investigates how geodiversity affect resilience against grazing and other forms of anthropogenic pressure.

The next step

In the absence of empirically tested theories on how geodiversity affects temporal development of biodiversity, I hope that the findings in this thesis will promote more attention to be brought to the topic. As I see it, the next steps in the study of geodiversity would be assessing how this method perform across different arctic-alpine environments or how other methods that quantify geodiversity performs in different ecosystems. Studying the method in a variety of ecosystems would provide valuable information on not only the robustness of the method itself. It would also give insight into how the different abiotic environments, and in turn different geodiversity compositions, affect the species compositions and their development. Perhaps geodiversity features will be found to affect species compositions differently, which then allow for weighted approaches to relate geodiversity to the structure and development of species communities.

It will be of importance to gather enough data, which sufficiently covers the gradients of both geodiversity and other environmental factors. Compensating for skewed data, which often occur in environmental data, will also be important to avoid the uncertainties which my analyses suffer from. This can for instance be done through modelling techniques. Possible false negatives or inconclusive movement of species are examples of problems which might arise if data is collected without taking such measures into account. I suggest prioritizing longer elevational gradients, selecting plots with even distribution of variables, and possibly including other environmental variables, e.g. soil sample analysis. By expanding the research scope in this way, more of the environment is accounted for and one might get a clearer picture of what developmental patterns are actually in play.

Assessment of biodiversity and geodiversity is an important study, and it becomes ever more important to find good methods for studying temporal development, and its influencers. Especially in the face of climate warming and anthropogenic influence it is promising that novel methods are emerging and being tested. However, there still remain much to be uncovered and studied about the relationship between geodiversity and biodiversity.

Conclusion

In this study I have looked how geodiversity, as a measurement for abiotic variability in a habitat, relates to changes in species composition over time. This is the first study to use geodiversity in temporal assessments of species composition, and one of the first to utilize quantitative methods in the field to measure fine-scale geodiversity. By comparing composition and abundance data of vascular plant communities from 1932 and 2020 I have assessed the variations in temporal shifts in the alpine species communities in Hirkjølen, Norway. The analyses show evidence of species communities shifting with different magnitude and in different directions depending on variations in the abiotic environment and elevation. The magnitude of shifts seemed to decrease with increasing georichness, that is the total count of different geodiversity features. This was as expected. Habitat heterogeneity have been theorized to increase the variety and number of micro-climates where species can “escape” when the general environment becomes unfavourable. Especially geomorphology seemed to relate to this trend, while hydrology, geology and topographical heterogeneity seemed less important. It is therefore possible that compositional stability is most strongly related to the erosion- and deposition-processes of nutrients in Hirkjølen. And not the variations in temperature from surface roughness. Looking at broader patterns, I found a drop in magnitude, and a change in the directions, of shifts along the elevational gradient. The largest shifts happened at lower elevations. Here the shifts moved toward the species composition becoming similar to low-georichness plots with increased presence of berry heather forests and *Picea abies*-dominated species compositions. This could be worrying as homogeneous compositions, which can exist in these forest types, are expected to be more susceptible to change than heterogeneous compositions. At higher elevations, the magnitude of shift decreased steadily before evening out above the treeline. Here the shifts had mixed directions. Where the species composition became warmer and more similar to low-elevation plots species have likely moved upward as a result of relaxation of temperature restraints. In the plots where species compositions became more similar to high elevation plots, plants have most likely moved downward as a result of competition release from anthropogenic or climate disturbances. The difference in shifts between high and low elevation plot could come from anthropogenic pressure being higher at lower elevations. During the field work, free roaming cows and sheep, cabin construction and a ski-lift were among the possible influences we found. These were all centred around the 850 m.a.s.l. which had the highest magnitude of compositional shifts. How geodiversity relates to shifts in species composition from land-use change is not known, and it would be of great interest if future research would look into this. I hope that my findings of georichness lowering temporal shifts in species composition will promote more research to be done on the relationship between geodiversity and biodiversity. There is a great need of knowledge on this topic, especially in the face of climate warming, changing species compositions and a current lack of studies on geodiversity.

References:

- Aksnes, F. (2021). *Can functional traits contribute to explain elevational range shifts of vascular plant species?* University of Bergen.
- Alahuhta, J., Toivanen, M., & Hjort, J. (2020). Geodiversity–biodiversity relationship needs more empirical evidence. *Nature Ecology and Evolution*, 4(1), 2–3. <https://doi.org/10.1038/s41559-019-1051-7>
- Anderson, M. G., Comer, P. J., Beier, P., Lawler, J. J., Schloss, C. A., Buttrick, S., Albano, C. M., & Faith, D. P. (2015). Case studies of conservation plans that incorporate geodiversity. *Conservation Biology*, 29(3), 680–691. <https://doi.org/10.1111/cobi.12503>
- Anderson, & Walsh. (2013). PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs*, 83(4), 557–574. <https://doi.org/10.1890/12-2010.1>
- Austrheim, G., Myrnes, A., Pedersen, B., Halvorsen, R., Hassel, K., & Evju, M. (2008). Large scale experimental effects of three levels of sheep densities on an alpine ecosystem. *Oikos*, 117(6), 837–846. <https://doi.org/10.1111/j.0030-1299.2008.16543.x>
- Bailey, J. J., Boyd, D. S., & Field, R. (2018). Models of upland species' distributions are improved by accounting for geodiversity. *Landscape Ecology*, 33(12), 2071–2087. <https://doi.org/10.1007/s10980-018-0723-z>
- Bailey, J. J., Boyd, D. S., Hjort, J., Lavers, C. P., & Field, R. (2017). Modelling native and alien vascular plant species richness: At which scales is geodiversity most relevant? *Global Ecology and Biogeography*, 26(7), 763–776. <https://doi.org/10.1111/geb.12574>
- Beier, P., Hunter, M. L., & Anderson, M. (2015). Introduction. *Conservation Biology*, 29(3), 613–617. <https://doi.org/10.1111/cobi.12511>
- Benito, X., Vilmi, A., Luethje, M., Carrevedo, M. L., Lindholm, M., & Fritz, S. C. (2020). Spatial and Temporal Ecological Uniqueness of Andean Diatom Communities Are Correlated With Climate, Geodiversity and Long-Term Limnological Change. *Frontiers in Ecology and Evolution*, 8. <https://doi.org/10.3389/fevo.2020.00260>
- Bertrand, R., Lenoir, J., Piedallu, C., Dillon, G. R., De Ruffray, P., Vidal, C., Pierrat, J. C., & Gégout, J. C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, 479(7374), 517–520. <https://doi.org/10.1038/nature10548>
- Brilha, J., Gray, M., Pereira, D. I., & Pereira, P. (2018). Geodiversity: An integrative review as a contribution to the sustainable management of the whole of nature. In *Environmental Science and Policy* (Vol. 86, pp. 19–28). Elsevier Ltd. <https://doi.org/10.1016/j.envsci.2018.05.001>
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18(1), 117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Falk, D. A., Palmer, M. A., & Zedler, J. B. (2006). *Foundations of restoration Ecology* (1st ed.). Island Press.
- Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J. C., Hylander, K., Ehrlén, J., Speed, J. D. M., Klanderud, K., Bråthen, K. A., Milbau, A., Opedal, Ø. H., Alsos, I. G., Ejrnæs, R., Bruun, H. H., Birks, H. J. B., Westergaard, K. B., Birks, H. H., & Lenoir, J. (2018). Stay or go – how topographic complexity influences alpine plant population and community responses to climate change. In *Perspectives in Plant Ecology, Evolution and Systematics* (Vol. 30, pp. 41–50).

Elsevier GmbH. <https://doi.org/10.1016/j.ppees.2017.09.008>

- Greenacre, M., & Primicerio, R. (2013). Chapter 5 Measures of distance between samples : non-Euclidean. In *Multivariate Analysis of Ecological Data* (pp. 1–10).
- Harrison, S. (2020). Plant community diversity will decline more than increase under climatic warming. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1794). <https://doi.org/10.1098/rstb.2019.0106>
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J. F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E., & Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. In *Ecology* (Vol. 84, Issue 12, pp. 3105–3117). Ecological Society of America. <https://doi.org/10.1890/03-8006>
- Hjort, J., Gordon, J. E., Gray, M., & Hunter, M. L. (2015). Why geodiversity matters in valuing nature's stage. *Conservation Biology*, 29(3), 630–639. <https://doi.org/10.1111/cobi.12510>
- Hjort, J., Heikkinen, R. K., & Luoto, M. (2012). Inclusion of explicit measures of geodiversity improve biodiversity models in a boreal landscape. *Biodiversity and Conservation*, 21(13), 3487–3506. <https://doi.org/10.1007/s10531-012-0376-1>
- Hjort, J., Tukiainen, H., Salminen, H., Kemppinen, J., Kiilunen, P., Snåre, H., Alahuhta, J., & Maliniemi, T. (2021). *Local-scale mapping of geodiversity for plant ecology and biodiversity studies in Arctic-alpine environments (unpublished)*.
- Høitomt, G., Kistefos Skogtjenester AS, & Nygaard, P. H. (2017). *Forvaltningsplan for Skardseterlia naturreservat*.
- Hutchinson, G. E. (1992). Population studies: animal ecology and demography. In *Bulletin of Mathematical Biology* (Vol. 54, Issue 4, p. 695). Kluwer Academic Publishers. <https://doi.org/10.1007/BF02459641>
- Jačková, K., & Romportl, D. (2012). The Relationship Between Geodiversity and Habitat Richness in Šumava National Park and Křivoklátsko PLA (Czech Republic): A Quantitative Analysis Approach. *Journal of Landscape Ecology*, 1(1), 23–38. <https://doi.org/10.2478/v10285-012-0003-6>
- Kapfer, J., & Grytnes, J.-A. (2017). Large climate change, large effect? Vegetation changes over the past century in the European High Arctic. *Applied Vegetation Science*, 20(2), 204–214. <https://doi.org/10.1111/avsc.12280>
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4(1), 1–20. <https://doi.org/10.1038/sdata.2017.122>
- Karger, D. N., & Zimmermann, N. E. (2018). *CHELSAcruts - High resolution temperature and precipitation timeseries for the 20th century and beyond*. EnviDat. <https://doi.org/http://dx.doi.org/10.16904/envodat.159>
- Kerr, J. T., & Packer, L. (1997). Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, 385(6613), 252–254. <https://doi.org/10.1038/385252a0>
- Knudson, C., Kay, K., & Fisher, S. (2018). Appraising geodiversity and cultural diversity approaches to building resilience through conservation. *Nature Climate Change*, 8(8), 678–685. <https://doi.org/10.1038/s41558-018-0188-8>
- Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W., & Svenning, J.-C. (2010). Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, 33(2), 295–303.

<https://doi.org/10.1111/j.1600-0587.2010.06279.x>

- Lenoir, J., Graae, B. J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G., Bergendorff, C., Birks, H. J. B., Bråthen, K. A., Brunet, J., Bruun, H. H., Dahlberg, C. J., Decocq, G., Diekmann, M., Dynesius, M., Ejrnæs, R., Grytnes, J. A., Hylander, K., Klanderud, K., ... Svenning, J. C. (2013). Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology*, *19*(5), 1470–1481. <https://doi.org/10.1111/gcb.12129>
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*(7276), 1052–1055. <https://doi.org/10.1038/nature08649>
- Lobo, J. M., Castro, I., & Moreno, J. C. (2001). Spatial and environmental determinants of vascular plant species richness distribution in the Iberian Peninsula and Balearic Islands. *Biological Journal of the Linnean Society*, *73*(2), 233–253. <https://doi.org/10.1111/j.1095-8312.2001.tb01360.x>
- Minchin, P. R. (1987). An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio*, *69*(1–3), 89–107. <https://doi.org/10.1007/BF00038690>
- Mork, E., & Heiberg, H. H. H. (1937). Om vegetasjonen i Hirkjølen forsøksområde. *Meddelelser Fra Det Norske Skogforsøksvesen*, *5*(19), 617–684.
- Norwegian Meteorological Institute and the Norwegian Broadcasting Corporation. (2021). *Precipitation Venabu station last 13 months 2007-2021*. <https://www.yr.no/nb/historikk/graf/5-13420/Norge/Innlandet/Ringebu/Venabu>
- Nygaard, P. H., & Ødegaard, T. (1999). Sixty years of vegetation dynamics in a south boreal coniferous forest in southern Norway. *Journal of Vegetation Science*, *10*(1), 5–16. <https://doi.org/10.2307/3237155>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O’Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *vegan: Community Ecology Package*. <https://cran.r-project.org/package=vegan>
- Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J. L. B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R. F., Ghosn, D., Holten, J. I., Kanka, R., Kazakis, G., Kollár, J., Larsson, P., Moiseev, P., Moiseev, D., Molau, U., ... Grabherr, G. (2012). Recent plant diversity changes on Europe’s mountain summits. *Science*, *336*(6079), 353–355. <https://doi.org/10.1126/science.1219033>
- Potter, K. A., Arthur Woods, H., & Pincebourde, S. (2013). Microclimatic challenges in global change biology. *Global Change Biology*, *19*(10), 2932–2939. <https://doi.org/10.1111/gcb.12257>
- R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. <https://www.r-project.org/>
- Räsänen, A., Kuitunen, M., Hjort, J., Vaso, A., Kuitunen, T., & Lensu, A. (2016). The role of landscape, topography, and geodiversity in explaining vascular plant species richness in a fragmented landscape. *Boreal Environment Research*, *21*(1–2), 53–70.
- Richerson, P. J., & Lum, K. (1980). Patterns of Plant Species Diversity in California: Relation to Weather and Topography. *The American Naturalist*, *116*(4), 504–536. <https://doi.org/10.1086/283645>
- Roth, T., Plattner, M., & Amrhein, V. (2014). Plants, Birds and Butterflies: Short-Term Responses of Species Communities to Climate Warming Vary by Taxon and with Altitude. *PLoS ONE*, *9*(1),

e82490. <https://doi.org/10.1371/journal.pone.0082490>

- Scherrer, D., & Körner, C. (2011). Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, *38*(2), 406–416. <https://doi.org/10.1111/j.1365-2699.2010.02407.x>
- Serrano, E., Flano, P. R., & Valladolid. (2007). Geodiversity. A theoretical and applied concept. *Geographica Helvetica*, *62*(3), 140–147. <https://doi.org/10.5194/gh-62-140-2007>
- Tukiainen, H., Bailey, J. J., Field, R., Kangas, K., & Hjort, J. (2017). Combining geodiversity with climate and topography to account for threatened species richness. *Conservation Biology*, *31*(2), 364–375. <https://doi.org/10.1111/cobi.12799>
- Virtanen, R., Luoto, M., Rämä, T., Mikkola, K., Hjort, J., Grytnes, J. A., & Birks, H. J. B. (2010). Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. *Global Ecology and Biogeography*, *19*(6), 810–821. <https://doi.org/10.1111/j.1466-8238.2010.00570.x>
- Wei, T., & Simko, V. (2017). *R package “corrplot”: Visualization of a Correlation Matrix*. <https://github.com/taiyun/corrplot>
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society*, *73*(1), 3–36.
- Yu, S., & Ehrenfeld, J. G. (2010). Relationships among plants, soils and microbial communities along a hydrological gradient in the New Jersey Pinelands, USA. *Annals of Botany*, *105*(1), 185–196. <https://doi.org/10.1093/aob/mcp183>

Appendix I

Table 3: Table of Geodiversity components and their associated features. Based on the field form for the geodiversity assessment (Hjort et al., 2021)

| Geodiversity component | Geodiversity Process | |
|-----------------------------|---|------------------------------------|
| GEOLOGY | Exposed bedrock | |
| | Till (glaciogenic material) | |
| | Stones/blocks (continuous field) | |
| | Sand/gravel (> 5 cm thick layer) | |
| | Silt/fine sediment (> 5 cm thick layer) | |
| | Peat (> 5 cm thick layer) | |
| | Escarpment (> 45 degrees) | |
| Geomorphology | Nivation | |
| | Glaciogenic | Erosion |
| | | Deposition |
| | Glaciofluvial | Erosion |
| | | Deposition |
| | Aeolian | Erosion |
| | | Deposition |
| | Fluvial | Erosion |
| | | Deposition |
| | Littoral | Erosion |
| | | Deposition |
| | Biogenic | Peat deposits |
| | | Peat hummocks |
| | Rapid mass movements | Landslide scars |
| | | Sediment deposits |
| | Cryogenic | Cryoturbation (signs or landforms) |
| | | Solifluction (signs or landforms) |
| Weathering | Physical | |
| | Chemical | |
| HYDROLOGY | Spring (pond, pool, seepages) | |
| | Running water (river, stream, rivulet) | |
| | Dry channel / ephemeral stream | |
| | Standing water | |
| | Dry pond/pool | |
| | Wetland | |
| TOPOGRAPHICAL HETEROGENEITY | | |

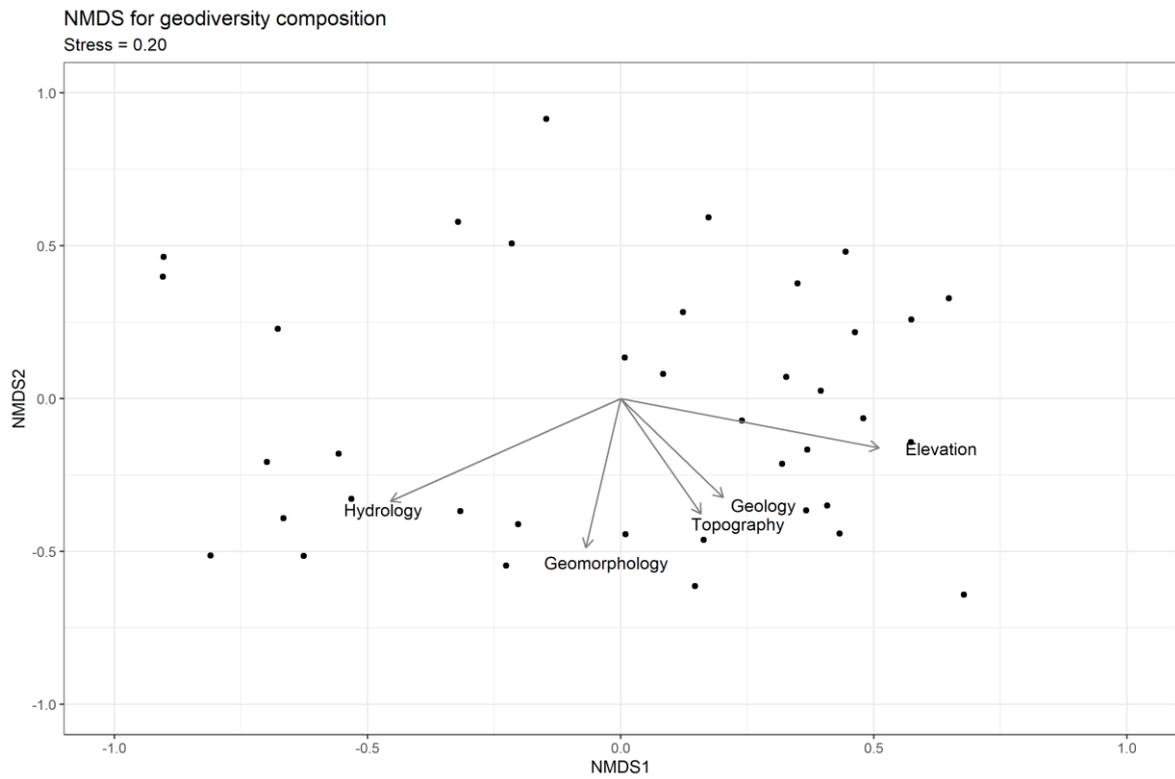


Figure 10: NMDS for geodiversity composition: Dots are plot location. Gradient of each geodiversity component are mapped onto the ordination to clarify which variables are found together.

Appendix II

Description of the Hult-Sernander scale

The cover estimates for each species in each plot were done by visual assessment. We applied the Hult-Sernander scale to score the extent of each species cover. In this we included all layers of the plot from herb- to tree-layer. The Hult-Sernander scale scores species on a scale from 1-5. A score of 1 equals a cover of less than $1/16^{\text{th}}$ or $< 8\%$ of the plot. An estimate of 2 equals a cover between $1/16^{\text{th}}$ and $1/8^{\text{th}}$ (from 8 to 12.5%). An estimate of 3 equals a cover between $1/8^{\text{th}}$ to $1/4^{\text{th}}$ (from 12.5 to 25%). An estimate of 4 equals a cover between $1/4^{\text{th}}$ and $1/2$ (from 25 to 50%). Finally, a score of 5 equals a cover of more than half of the plot.

Appendix III

Challenges with species composition data

It should be noted that this study suffers from some limitations and biases in regard to data collection and analysis. During the field work a mean of five fewer species per plot were found by the master students in comparison to the findings of prof. Mork. This decrease in species can have influenced to compositional analyses. It is possible that some plots were more dissimilar than others in terms of having rare species which were not identified during the resampling. It is also possible that some plots were more similar by having species which were similar but were classified differently. This was hopefully remedied by having prof. Grytnes at Institute for Biological Science accompanying the master students in the field and giving instructions the first few days.

Another note on the use of geodiversity in compositional analyses is that prediction of species composition with the use of geodiversity often perform better on common species compared to rarer species (Anderson et al., 2015). This would possibly increase the error from misidentified or overlooked rare species.

Improper analyses

Some analyses provided negative R-values. This means that species compositions were more similar between plots of different environments than between plots of similar environments. This is often associated with faulty assigning of categories or improper study design. In the case of topographical heterogeneity this could mean that plots were assigned the wrong topographical heterogeneity-score, but it could also just mean that it has little to no influence on species composition. It should however be taken into consideration when looking into the results.

Human influence on plots

Certain plots in Hirkjølen proved to have higher degree of human influence than other. Plots 65 and 315 were examples of this where hiking and tractor trails go directly through the plots.

Improper geodiversity assessment

Geodiversity features can sometimes be difficult to identify. In the first dataset of geodiversity composition in Hirkjølen, before re-assessing through the pictures taken, multiple plots were recorded as having zero geology related features. This is not physically possible due to how the geodiversity features are defined. The pictures were therefore used for re-assessment, to assign at least one geodiversity feature to all plots. This post-field work assignment of geodiversity features to plots can be a possible source of error. I suggest that the plots in Hirkjølen are resurveyed and the geodiversity composition re-counted in future analyses.

Diagnostics for analyses for species composition

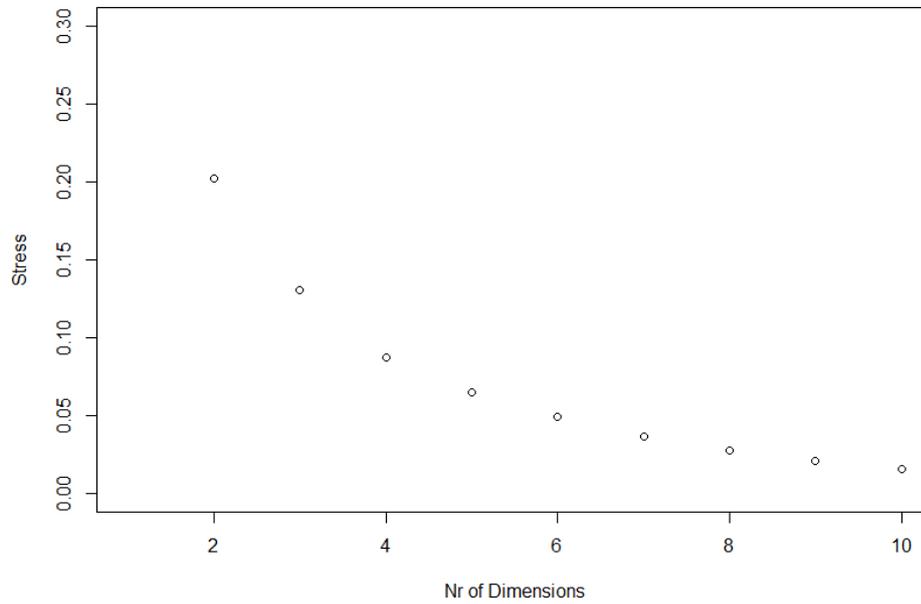


Figure 11: Scree plot for Non-metric Multidimensional Scaling of species composition. It depicts the amount of stress for different number of dimensions in the result. Stress < 0.2 is regarded a good fit.

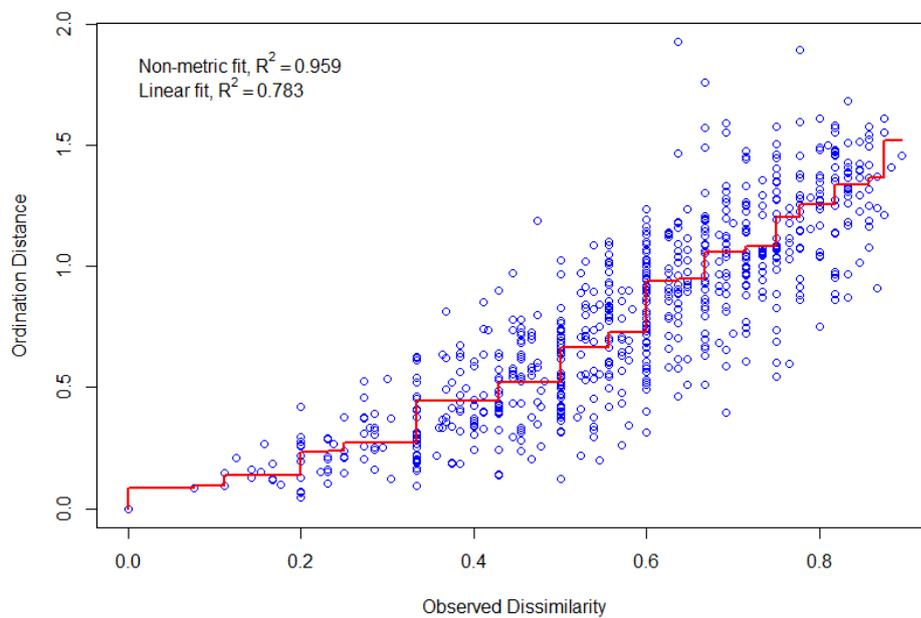


Figure 12: Shepard's diagram for Non-metric Multidimensional Scaling of species composition. Straighter red line indicates good fit.

Diagnostics for analyses of geodiversity composition

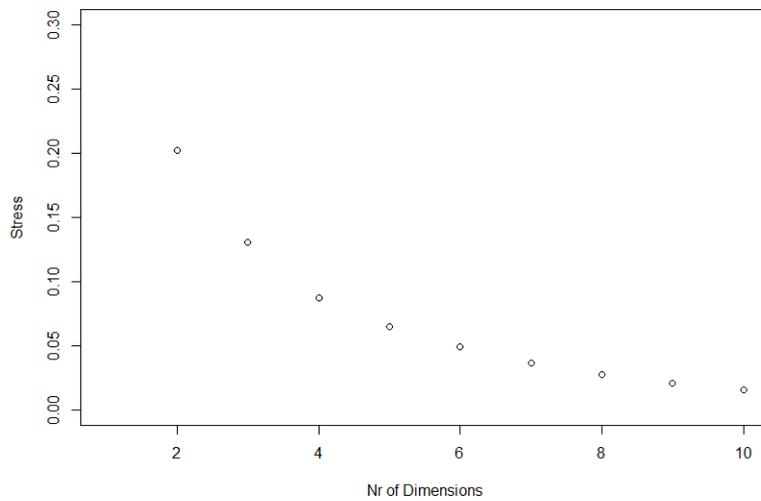


Figure 13: Scree plot for Non-metric Multidimensional Scaling of geodiversity composition. It depicts the amount of stress for different number of dimensions in the result. Stress < 0.2 is regarded a good fit.

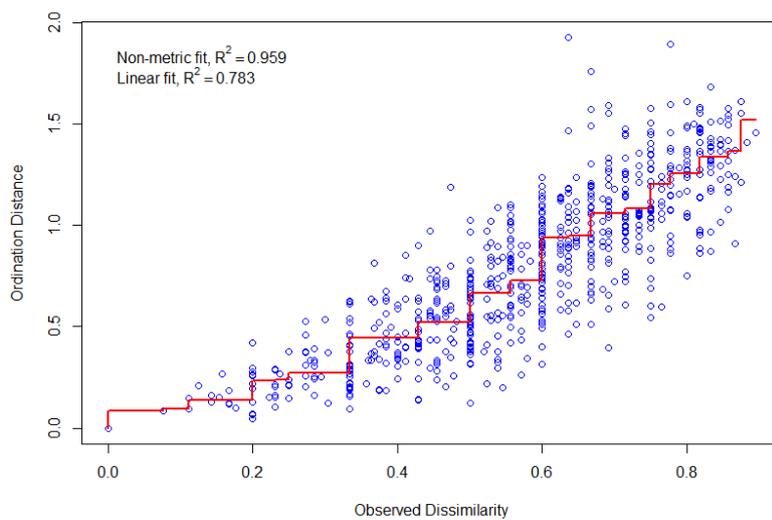


Figure 14: Shepard's diagram for Non-metric Multidimensional Scaling of geodiversity composition. Straighter red line indicates good fit.

Appendix IV

The data for this thesis can be found in the ECKO data consortium:

Geodiversity data:

Reisæter-Thu H, Aksnes F, Maliniemi T (2021), OS-2020-NO-305318, ECKO Resurvey Data Consortium, <https://ecko.uib.no/datasets/OS-2020-NO-305318>

Species composition data:

Aksnes F, Reisæter-Thu H (2021), RE-2020-NO-790115, ECKO Resurvey Data Consortium, <https://ecko.uib.no/datasets/RE-2020-NO-790115>

Appendix V

Code from all analyses

Here follows an extract from the codes used in the analyses of the data. Data cleaning and structuration of the data to fit the analyses are not included. Please contact me on hre012@uib.no if you have any questions.

Geodiversity composition

```
ANOSIM_gdc_elev <- anosim(geodiv_community, grouping =  
geodiv_community_env$elevation, distance = "jaccard", permutations = 9999)
```

```
ANOSIM_gdc_tree <- anosim(geodiv_community, grouping =  
geodiv_community_env$above_t_2020, distance = "jaccard", permutations = 9999)
```

```
## These codes perform the ANOSIM of geodiversity composition using elevation and plot  
location relative to the 2005 treeline as predictor. Jaccard-distance matrix is used due to the  
binary nature of presence/absence-data. 9999 permutations are to get a proper result
```

Species composition multivariate analyses

```
ANOSIM_GDC_year <- anosim(community_df, grouping = community_env$GDC_total *  
community_env$year, distance = "bray", permutations = 9999, strata =  
community_env$plot_nr)
```

```
ANOSIM_elev_year <- anosim(community_df, grouping = community_env$elevation *  
community_env$year, distance = "bray", strata = community_env$plot_ID, permutations =  
9999)
```

```
NOSIM_GDC_elev <- anosim(community_df, grouping = community_env$elevation *  
community_env$GDC_total, distance = "bray", strata = community_env$plot_ID,  
permutations = 9999)
```

```
## These codes perform the ANOSIM of species composition composition using  
georichness, elevation, and a combination of the two as predictors. Dissimilarity matrix Bray-  
Curtis is used. The strata term includes sampling within the same plots for both years and as  
such avoids autocorrelation. 9999 permutations are to get a proper result
```

Species composition univariate analyses

```
ANOSIM_elev <- anosim(community_df, grouping = community_env$elevation, distance =  
"bray", strata = community_env$plot_ID, permutations = 9999)
```

```
ANOSIM_gdc <- anosim(community_df, grouping = community_env$GDC_total, distance =  
"bray", strata = community_env$plot_ID, permutations = 9999)
```

```
ANOSIM_geol <-anosim(community_df, grouping = community_env$Geology_total, distance =  
"bray", strata = community_env$plot_ID, permutations = 9999)
```

```
ANOSIM_geom <-anosim(community_df, grouping = community_env$Geomorphology_total,  
distance = "bray", strata = community_env$plot_ID, permutations = 9999)
```

```
ANOSIM_h <-anosim(community_df, grouping = community_env$H_total, distance = "bray",  
strata = community_env$plot_ID, permutations = 9999)
```

```

ANOSIM_topo <-anosim(community_df, grouping =
community_env$Topographical_heterogeneity, distance = "bray", strata =
community_env$plot_ID, permutations = 9999)

ANOSIM_tree1930 <-anosim(community_df, grouping = community_env$above_t_1930,
distance = "bray", strata = community_env$plot_ID, permutations = 9999)

ANOSIM_tree2020 <-anosim(community_df, grouping = community_env$above_t_2020,
distance = "bray", strata = community_env$plot_ID, permutations = 9999)

ANOSIM_year <-anosim(community_df, grouping = community_env$year, distance = "bray",
strata = community_env$plot_ID, permutations = 9999)

```

These codes perform the ANOSIM of species composition composition using georichness, elevation, hydrology, geology, geomorphology, topographical heterogeneity, and plot location relative to the 1930- and 2005 treeline. It also includes an analysis of species composition between the two years 1930 and 2020. Dissimilarity matrix Bray-Curtis is used. The strata term includes sampling within the same plots for both years and as such avoids autocorrelation. 9999 permutations are to get a proper result

Code for Non-metric Multidimensional Scaling for species composition

```

nmds_df <- metaMDS(community_df, k = 2, trymax = 999, autotransform = F, trace =F,
distance = "bray") #Performs the NMDS ordination for species composition using Bray-
Curtis-dissimilarity

envfit_df_sep <- envfit(nmds_df, select(community_env, "elevation", "year", "Geology_total",
"Geomorphology_total", "H_total", "Topographical_heterogeneity"), permutations = 9999)
#fits separate Geodiversity and environmental vectors to the ordination

```

Code for Non-metric Multidimensional Scaling for geodiversity composition

```

nmds_geodiv <- metaMDS(geodiv_community, k=2, distance = "bray", trymax = 999,
autotransform = F, trace =F)

env_fit_geodiv <- envfit(nmds_geodiv, select(head(community_env, 40), "elevation",
"Geology_total", "Geomorphology_total", "H_total", "Topographical_heterogeneity"),
permutations = 9999) #fits separate Geodiversity and environmental vectors to the
ordination

```

Example code for measuring the Pythagorean distance

```

sqrt((NMDS1_2020 - NMDS1_1930)^2 + (NMDS2_2020 - NMDS2_1930)^2)

```

Code for univariate General Additive Models

```

gam_gdcElev <- gam(GDC_total ~ s(elevation, k=15), method = "REML", data = df_dist)
#Fits GAM of sum of GDC to elevation

par(mfrow = c(2,2)) # Allows for 4 plots at once in R. use before gam.check

gam.check(gam_gdcElev) #Print diagnostics for GAM

summary(gam_gdcElev) #Print summary statistics for GAM

```

```
pgam_gdc_elev <- plot.gam(gam_gdcElev, xlab = "Elevation", ylab = "Geodiversity", pch = 16, residuals = TRUE) #Print plot of gam
```

```
gam_gdcTree <- gam(GDC_total ~ above_t_2020, k=15, method = "REML", data = df_dist)  
#Fits GAM of sum of GDC to elevation
```

```
summary(gam_gdcTree)
```

```
gam_elev<- gam(dist_pred ~ s(elevation, k=4), method = "REML", data = df_dist)#Fits GAM  
to distance predicted by NMDS to elevation
```

```
par(mfrow = c(2,2))# Allows for 4 plots at once in R. use before gam.check
```

```
gam.check(gam_elev) #Print diagnostics for GAM
```

```
summary(gam_elev) #Print summary statistics for GAM
```

```
par(mfrow = c(1,1))
```

```
plot(gam_elev, residuals = TRUE, pch = 16, xlab = "Elevation", ylab = "Change in species  
composition") #Print plot of gam
```

```
gam_gdc <- gam(dist_pred ~ s(GDC_total, k=10), method = "REML", data = df_dist)#Fits  
GAM to distance predicted by NMDS to GDC_total
```

```
par(mfrow = c(2,2))# Allows for 4 plots at once in R. use before gam.check
```

```
gam.check(gam_gdc, pages = 1)#Print diagnostics for GAM
```

```
summary(gam_gdc) #Print summary statistics for GAM
```

```
plot(gam_gdc, residuals = TRUE, pch = 16, xlab = "Geodiversity richness", ylab = "Change  
in species composition") #Print plot of gam
```

```
gam_geology <- gam(dist_pred ~ s(Geology_total), method = "REML", data = df_dist)#Fits  
GAM to distance predicted by NMDS to geology components
```

```
par(mfrow=c(2,2))# Allows for 4 plots at once in R. use before gam.check
```

```
gam.check(gam_geology)#Print diagnostics for GAM
```

```
par(mfrow=c(1,1)) #Reset R plot to plotting one plot at a time
```

```
summary(gam_geology)#Print summary statistics for GAM
```

```
plot(gam_geology, all.terms = TRUE, residuals = TRUE, pch = 16, xlab = "Geology  
richness", ylab = "Change in species composition") #Print plot of gam
```

```
gam_geomorph <- gam(dist_pred ~ s(Geomorphology_total, k=6), method = "REML", data =  
df_dist)#Fits GAM to distance predicted by NMDS to geomorphology components
```

```

par(mfrow=c(2,2))# Allows for 4 plots at once in R. use before gam.check
gam.check(gam_geomorph)#Print diagnostics for GAM
par(mfrow=c(1,1))#Reset R plot to plotting one plot at a time
summary(gam_geomorph)#Print summary statistics for GAM
plot(gam_geomorph, all.terms = TRUE, residuals = TRUE, pch=16, xlab = "Geomorphology
richness", ylab = "Change in species composition") #Print plot of gam

```

```

gam_topography <- gam(dist_pred ~ s(Topographical_heterogeneity,k=4), method =
"REML", data = df_dist)#Fits GAM to distance predicted by NMDS to topographical
heterogeneity

```

```

par(mfrow=c(2,2))# Allows for 4 plots at once in R. use before gam.check
gam.check(gam_topography)#Print diagnostics for GAM
par(mfrow=c(1,1))#Reset R plot to plotting one plot at a time
summary(gam_topography)#Print summary statistics for GAM
plot(gam_topography, all.terms = TRUE, residuals = TRUE, pch = 16, xlab = "Topographical
heterogeneity", ylab = "Change in species composition") #Print plot of gam

```

```

gam_h <- gam(dist_pred ~ s(H_total,k=3), method = "REML", data = df_dist)#Fits GAM to
distance predicted by NMDS to nr of hydrology components

```

```

par(mfrow=c(2,2))# Allows for 4 plots at once in R. use before gam.check
gam.check(gam_h)#Print diagnostics for GAM
par(mfrow=c(1,1))#Reset R plot to plotting one plot at a time
summary(gam_h)#Print summary statistics for GAM

```

```

pgam_dist_h <- plot(gam_h, all.terms = TRUE, residuals = TRUE, pch = 16, xlab =
"Hydrology richness", ylab = "Change in species composition") #Print plot of gam

```

Code for multivariate General Additive Models

```

gam_gdc_elev_lin <- gam(dist_pred ~ s(GDC_total, k=11) + s(elevation), data=df_dist,
method = "REML") #GAM for distance predicted by NMDS by GDC and Elevation

```

```

par(mfrow=c(2,2))# Allows for 4 plots at once in R. use before gam.check
gam.check(gam_gdc_elev_lin)#Print diagnostics for GAM
plot(gam_gdc_elev_lin, pages= 1, cex= 1, pch =1)
summary(gam_gdc_elev_lin) #Print summary statistics for GAM

```

```

gam_gdc_forest2020 <- gam(dist_pred ~ s(GDC_total, k = 11) + as.factor(above_t_2020),
method = "REML", data=df_dist)

```

```

par(mfrow=c(2,2))# Allows for 4 plots at once in R. use before gam.check
gam.check(gam_gdc_forest2020)#Print diagnostics for GAM
summary(gam_gdc_forest2020)#Print summary statistics for GAM
plot(gam_gdc_forest2020, pages = 1, all.terms = TRUE, rug = TRUE, residuals = TRUE,
pch= 1, cex= 1)#Print plot of gam

```

```

gam_trees <- gam(dist_pred ~s(GDC_total, k = 11) + Betpubes_diff + Picabies_diff, method
= "REML", data = df_dist)

```

```

par(mfrow=c(2,2))# Allows for 4 plots at once in R. use before gam.check
gam.check(gam_trees)#Print diagnostics for GAM
summary(gam_trees) #Print summary statistics for GAM
plot(gam_trees, all.terms = TRUE)#Print plot of gam

```

Code for correlation plot

```

cor_dist <- df_dist %>%
  select(-c(1:5)) %>%
  select(-c("has_changed", "Picabies_diff", "Betpubes_diff")) %>%
  as.matrix() %>%
  cor() #Creates a matrix with correlation values for all variables except those related to
change in tree abundance of Picea abies and Betula pubescence.

corrplot(cor_dist, method = "number", is.corr = TRUE, type = "upper", tl.col = "black", bg =
"gray50") #Creates the correlation plot with colours and values for correlation between
values.

```