



**INSTITUTIONEN FÖR BIOLOGI OCH  
MILJÖVETENSKAP**

# **MOUNTAIN ROADS AND THE HOMOGENIZATION OF PLANTS**

A study on plant communities and their traits along  
the elevational gradient



**Violetta Chernoray**

---

Degree project for Bachelor of Science with a major in Biology.

BIO603 Biology: Degree project 30 hp

First cycle

Semester/year: Spring/Autumn 2022

Supervisor: Anne Bjorkman, Department of Biological and Environmental Sciences

Examiner: Åslög Dahl, Department of Biological and Environmental Sciences

*Front page image by Violetta Chernoray.*

# Table of contents

Abstract.....	1
Sammanfattning .....	1
1 Introduction .....	2
1.1 Roads and the spread of non-native species .....	2
1.2 The importance of plant traits .....	3
1.3 Homogenization by roads .....	3
1.4 Project aim .....	4
1.4.1 Hypotheses.....	5
2 Methods.....	5
2.1 Datasets .....	5
2.2 Analyses .....	6
2.2.1 Data preparation.....	6
2.2.2 Plotting non-native species and their traits .....	7
2.2.3 Calculating dissimilarity estimates .....	7
2.2.4 NMDS analysis .....	8
2.2.5 ANOSIM and testing for significance .....	8
3 Results .....	9
4 Discussion.....	11
4.1 Effect of road proximity .....	11
4.2 Effect of elevation.....	12
4.3 Limitations and future work.....	13
5 Conclusion.....	14
6 Acknowledgments.....	14
7 References .....	14
8 Attachments.....	17

## Abstract

Overexploitation, land use, and other anthropogenic disturbances have increased in recent years, and are expected to increase even further. A very common anthropogenic disturbance, that can be seen even as far as in mountain regions, is roads. Roads are known to fragment landscapes, modify environmental conditions, and help distribute plants (including non-native). Furthermore, they have been seen to have a homogenizing effect on plant species communities, making them more similar to each other. However, although there have been studies on how roads and elevational gradients in the mountains affect species composition, little is known about their effect on plant trait assemblage and functional diversity. Do roads and elevation homogenize the functional diversity of plant communities? By using plant trait data for three different traits, and abundance data covering different road proximities and elevations, this project aimed to answer this question. Analyses were done in R (v. 4.2.0) with the help of the *vegan* package, which made it possible to make dissimilarity plots, NMDS ordinations, and an ANOSIM analysis of the data. The results showed that the plant communities closest to the road were different from the communities in the natural vegetation, both in species and trait assembly, and that they had the least variation in trait and species composition. Moreover, the trait assemblage along the elevational gradient was not that different in the three road proximities, indicating little abiotic filtering of traits due to elevation. In conclusion, roads did have a homogenizing effect on both plant and trait communities, and this difference could be because of disturbances and different abiotic conditions. It would be a good idea to explore this relationship further, but at a more local level to include more abiotic factors than just the elevation, and by looking more into depth at the traits of non-native species.

*Key-words: anthropogenic disturbance; spatial ecology; Northern Scandes; functional traits; roadsides; beta-diversity.*

## Sammanfattning

De senaste åren har människans markanvändning och överexploatering av naturen ökat; och på grund av den stigande mänskliga populationen väntas ingen minskning. En mycket vanlig typ av markanvändning som sker även högt uppe i bergen, är bygget och underhållet av vägar. Detta är den vanligaste antropogena störningen i alpina miljöer som påverkar den omgivande naturen. Vägar fragmenterar landskapet, förändrar abiotiska faktorer, och bidrar till spridningen av växter och deras frön – inklusive av främmande arter. Utöver det, har vägar också noterats ha en homogeniserande effekt på plant-biotan, vilket innebär en förändring i artmångfalden. Dessvärre, har det inte skett mycket forskning om huruvida samma effekt kan observeras i sammansättningen av växters funktionella egenskaper. Har vägar en homogeniserande effekt även där? Med hjälp av data som berör växters egenskaper, samt deras förekomst längst med vägar och på olika höjder över havet, så var arbetets syfte att besvara denna fråga. Detta gjordes i R (v. 4.2.0) med hjälp av paketet *vegan*, som gjorde det möjligt att grafiskt visa skillnaden mellan olika replikat, samt utföra analyserna "NMDS" och "ANOSIM". Resultaten tydde på att växtsamhällena närmast vägkanten skilde sig från de stickprov som var längre bort från vägen, både vad gäller arter och deras egenskaper. Områdena närmast vägen hade minst variation i dessa sammansättningar. Dessutom visade det sig att sammansättningen av växtegenskaper inte skiljde sig så mycket oavsett avstånd till vägen och höjd över havet, vilket tyder på att höjden över havet inte verkar förändra de abiotiska faktorerna tillräckligt för att påverka egenskaperna hos växterna. Sammanfattningsvis, visade vägar minska diversiteten av arter och deras egenskaper. Detta hade varit intressant att utforska vidare, fast på en mer lokal nivå, för att inkludera effekterna av småskaliga abiotiska faktorer, samt undersöka om egenskaperna skiljer sig hos de främmande arterna jämfört med de lokala arterna.

*Nyckelord: markanvändning; Skanderna; funktionell ekologi; vägkanter; beta-diversitet.*

# 1 Introduction

Habitat conversion and anthropogenic disturbances greatly affect biodiversity and species distributions. Changing conditions for plants are normal, but human activity, such as land use, has increased the speed by which these changes occur (Körner, 1999). Overexploitation, tourism, and demands for cultivated land have increased in recent years and pose a danger to the natural vegetation. This is especially true in mountain regions, which historically have remained relatively pristine due to their inaccessibility and extreme temperatures. Nevertheless, in recent years, there has been an increase in human activity in those areas, and said human activity is expected to increase even further (Körner, 1999; Haider & Lembrechts *et al.*, 2022). Mountain regions are very characteristic in their climate and landscape, and it is not unusual for them to have special cultural heritage and unique species –which is why preserving them through sustainable management is so vital (Körner, 1999). One example of a common anthropogenic disturbance that often gets overlooked is roads – which have made many previously remote alpine regions more accessible (Haider & Lembrechts *et al.*, 2022). Roads are one of the most common anthropogenic land-use disturbances in remote areas, and their density is expected to increase in the future (Lembrechts *et al.*, 2014; Haider & Lembrechts *et al.*, 2022). Roads fragment landscapes, modify environmental conditions (by changing the microclimate, soil pH, compaction, and nutrient status), and act as vectors for the dispersal of plants by vehicles, footwear, clothing, and other equipment (Lembrechts *et al.*, 2014; Lembrechts *et al.*, 2016; Pollnac *et al.*, 2012; Taylor *et al.*, 2012).

## 1.1 Roads and the spread of non-native species

Roads create corridors for plants to move and colonize new areas. This can be beneficial for some species, and species richness is often greater closer to roadsides (Lembrechts *et al.*, 2014). For instance, seeds can adhere to cars and be transported hundreds of kilometers under dry conditions, helping them disperse to areas they wouldn't be able to reach otherwise (Taylor *et al.*, 2012). However, this can also apply to alien and invasive plants, which in a similar fashion can spread to adjacent native vegetation. Therefore, although mountains are known to be relatively free of non-native species, anthropogenic disturbances like roads are increasingly funneling them to higher elevations (Lembrechts *et al.*, 2016).

Native plant abundance has been noted to be lower closer to roadsides, while the opposite is true for non-native plants (Pollnac *et al.*, 2012; Jauni *et al.*, 2015; Gelbard & Belnap, 2003). This could be because of the disturbance intensity, as it is greater closer to traffic and can change the local habitat (Lembrechts *et al.*, 2014). The abiotic conditions at these sites often benefit alien species the most, favoring their establishment in these sites. The reason behind this is that non-native plant species often are better adapted the disturbances, alien substrates, and the microclimate along roads (Lembrechts *et al.*, 2014; Lembrechts *et al.*, 2016; Pollnac *et al.*, 2012; Jauni *et al.*, 2015).

The invasion of non-native plants can be problematic, because some of these species have been seen to negatively impact plant communities, resulting in a biodiversity loss and shift in ecosystems. This is because, when a species reaches a sufficiently high abundance, it will influence the species in its environment, not only by competing with them for resources but also by altering the microhabitat (Vilà *et al.*, 2011). Consequently, alien plant species can, for instance, inhibit the spread and growth of endemic plants, alter ecosystem processes and change the vegetation structure (Curtis, 2005; Jauni *et al.*, 2015). One example is the dwarf bamboo *Sasa kurilensis* in Japan, which has spread upwards to snow-meadows in alpine areas and decreased species richness there (Kudo *et al.*, 2011). However, the effect an alien species might have on a community isn't necessarily always negative. A meta-analysis by Vilà *et al.* (2011) concluded that although the invasion of alien species decreased the abundance and diversity of local plants, it increased the total production (measured in biomass and Net Primary Production) by an average of 58% after the invasion. The way an alien species can do this is for example by changing the microbial activity, pH, salinity, or

nutrient content in the soil, or by affecting the litter decomposition rate in the ecosystem (Vilà *et al.*, 2011).

Furthermore, the non-native plant species that manage to spread to higher elevations, tend to have traits that promote adaptability and tolerance to different temperatures and habitats (Alexander *et al.*, 2010). They often share traits that promote fast growth, efficient dispersal, and high fitness, making them good roadside colonizers (Jauni *et al.*, 2015). Consequently, specialized local species with narrow climatic ranges, that can't adapt to human-altered environments, can be outcompeted and replaced by these non-native species if they have more suitable traits (McKinney *et al.*, 1999; Alexander *et al.*, 2010).

## 1.2 The importance of plant traits

As previously mentioned, traits serve an important role in how species adapt to environmental conditions. The traits of a plant species or individual are also to some extent what determine the ecosystem processes and functions in a community (Bruelheide *et al.*, 2018). Indirectly, the trait composition is affected by factors in the environment, such as elevation, since they influence species richness, function and distribution (Severin *et al.*, 2015; Andersen *et al.*, 2015). When it comes to elevation, there is often a decline in non-native species richness as elevation increases (Alexander *et al.*, 2010; Andersen *et al.*, 2015). Most likely, this decline is the result of extreme environmental conditions (Alexander *et al.*, 2010). Since not all species that are found in mountain regions can survive the conditions at high elevations, those habitats are often called “limiting”. This means that in order to grow and survive there, and not have its tissues freeze if it gets too cold and dry, a plant needs to have physiological traits suitable for that environment (Körner, 1999). For example, plants in the alpine region are often characterized by a compact cushion form with small leaves and a short height. This growth form is efficient for trapping heat and litter to survive cold, windy regions with nutrient-poor soil (Körner, 1999). Moreover, environmental and biotic filtering can also include factors such as land use – which may shape species distributions and cause variations in the physiology of plants (Bruelheide *et al.*, 2018).

Many traits are thought to have functional roles specifically tied to important plant strategies, which can vary depending on environmental conditions such as light availability and soil nutrient content (Dwyer *et al.*, 2014). Three fundamental factors that most often are measured in plants are establishment, survival, and dispersal (Díaz *et al.*, 2016; Weiher *et al.*, 1999). These factors can be measured by looking at different traits. For example, a tall plant height can make a plant grow above short plants and capture more light; giving good fecundity and competitive ability if that trait is suitable for the conditions that the plant grows in (Díaz *et al.*, 2016). Notably, a lot of traits correlate with each other, which makes it possible to predict a community's response to changes in the environment – even by measuring just a few traits (Thomas *et al.*, 2020; Dwyer *et al.*, 2014; Weiher *et al.*, 1999). A simple model that supposedly captures all of these three factors is Westoby's leaf-height-seed model (Weiher *et al.*, 1999). In this model “leaf” indicates specific leaf area (SLA, light capturing leaf area per unit dry leaf mass), “height” is the canopy height of an adult plant, and “seed” indicates seed mass (Westoby, 1998; Dwyer *et al.*, 2014). SLA and plant height can both be used to predict plant establishment and persistence, while seed mass can be used as a proxy for dispersal and establishment success. As a result, by measuring these traits, it is possible to look at the most vital factors in the life cycle of a plant, and make predictions about the effect different gradients or disturbances can have on the floral composition and ecosystem function (Dwyer *et al.*, 2014).

## 1.3 Homogenization by roads

There have been records of roads having a homogenizing effect on plant communities, meaning that they become more similar to each other through time (Alexander *et al.*, 2016; Dunnett *et al.*, 1998; Haider *et al.*, 2018; McKinney & Lockwood, 1999). Such an effect can be measured by

looking at the community dissimilarity of the plant biota, also known as *beta diversity* (Haider *et al.*, 2018). Beta diversity looks at the difference in species composition or turnover between different regional assemblages, and can be used to study how they change along different gradients. A high beta diversity indicates that the compared samples or environments differ markedly from each other (Koleff *et al.*, 2003).

Homogenization of plant communities can occur if unique indigenous species, that are sensitive to land use and/or environmental change, get replaced by non-native or already widespread species that have a broader environmental tolerance (McKinney & Lockwood, 1999). In other words, species that can establish in new, disturbed areas, and spread with the help of roads, have a good chance of out-competing some less common local plant species. This effect can further be amplified if different roads are constructed and managed in similar ways, since that will give rise to homogenous abiotic conditions and similar disturbances between areas (Haider *et al.*, 2018).

Additionally, the filtering of species due to human land use, such as the construction and usage of roads, can lead to a convergence in plant traits. Plants at high elevations tend to be specialized and have narrow climatic ranges (Alexander *et al.*, 2010; Körner, 1999), but the species found along roadsides are mostly disturbance-tolerant, generalist plants that thrive in disturbed landscapes (Alexander *et al.*, 2010; Lembrechts *et al.*, 2014). Consequently, although their abundance normally decreases with elevation, if such species get introduced to higher elevations – for instance with the help of humans – then it becomes possible for them to spread upwards towards higher elevations (Alexander *et al.*, 2010; Andersen *et al.*, 2015; Lembrechts *et al.*, 2014), leading to a convergence of traits in the plant community (Dwyer *et al.*, 2014; McKinney & Lockwood, 1999).

With this in mind, because each species has a set of functional traits, a decrease in species richness can also lead to a decrease in functional diversity, which is the variation of functional traits in a community. Low functional diversity could lead to reduced ecosystem functioning, since species richness generally correlates with primary productivity and community stability (Begon & Townsend, 2021). Most commonly, this positive relationship is explained by two hypotheses: the complementarity hypothesis, which states that species use resources in complementary ways due to niche differentiation, and the selection hypothesis, which proposes that a community is by chance more likely to have highly productive species if there are more species in total. Correspondingly, diverse communities will often have higher production and functional richness compared to communities that have a lower species richness, thanks to their underlying traits (Begon & Townsend, 2021; Cardinale *et al.*, 2011). Since the environment can affect what species grow where, a change in the environment – such as a disturbance, or the effect of high elevation as a stressor – can also affect functional diversity and ecosystem functioning (Cardinale *et al.*, 2011). As a result, homogenization can lead to simpler and less unique ecosystems (McKinney & Lockwood, 1999; Wolf *et al.*, 2021).

#### **1.4 Project aim**

Previous studies have noted homogenization of plant species along roadsides, as well as the importance of roads as dispersal vectors for both native and non-native plant species (Dunnett *et al.*, 1998; Pollnac *et al.*, 2012; Taylor *et al.*, 2012; Haider *et al.*, 2018). A study by Lembrechts *et al.* (2014) covered the same location as mentioned in this paper, with data collected in 2012. Lembrechts *et al.* (2014) came to the conclusion that roadside plots have higher richness and abundance of non-native plants than in the adjacent vegetation. They also suggested there is an interaction between road proximity and elevation; that it affected richness of non-native plant species, and that plots at the highest elevations were the most variable in terms of species composition (Lembrechts *et al.*, 2014). For this reason, this paper also briefly looks at elevation as a factor of homogenization.

However, although there has been research on how elevation and roads in mountain regions influence species richness and composition, little is known about their effect on functional diversity

(Haider *et al.*, 2018; Lembrechts *et al.*, 2014; Lembrechts *et al.*, 2016). Since the assemblage of traits is important at both an individual and at a community level, understanding the effect roads and elevation have on functional traits is crucial. By looking at how these factors affect the diversity of plant traits, better predictions can be made about how progressing anthropogenic disturbances such as roads can affect plant ecosystems and their processes. Such understanding can help decide on how changing, and sensitive, areas such as the mountain regions can be managed sustainably, as well as help prevent any unwanted impacts that might arise due to increased infrastructure and touristic pressure (Körner, 1999; Haider & Lembrechts *et al.*, 2022).

#### 1.4.1 Hypotheses

Due to roads functioning as dispersal corridors, and the elevation having a filtering effect on the vegetation, it is expected that both of these factors will have a homogenizing effect on the plant biota and their traits. The study, therefore, aims to test two hypotheses:

- 1) The plots closest to the road will be compositionally and functionally different from the plots further away from the road. The reason behind this is that the disturbance will give rise to an environment that not all species can tolerate, but that is instead better suited for generalists and disturbance tolerant species, including non-natives.
- 2) The plots at the highest elevation will be compositionally and functionally more similar to each other, compared to the plots at the lower elevations. This would be thanks to environmental filtering (colder temperatures etc.) which will hinder non-native species, and species that are not adapted to those environments from spreading upwards.

## 2 Methods

### 2.1 Datasets

The main dataset in this study was acquired from the Mountain Invasion Network (MIREN, [www.mountaininvasions.org](http://www.mountaininvasions.org)). The MIREN data was collected according to a published protocol and included a total of 5072 observations (Haider & Lembrechts *et al.*, 2022). The data that was investigated in this project was collected in 2017, along three roads in the Northern Scandes close to Narvik, Norway (Fig. 1). The roads were constructed approximately forty years ago, and still hold regular traffic by both tourists, locals, and industrial traffic (Lembrechts *et al.*, 2014).

Selected roads covered elevation gradients from 13.2 m to 703.3 m, from 18.3 m to 610.4 m, and from 15 m to 634.3 m (Haider & Lembrechts *et al.*, 2022). Each road was divided into 19 equally wide elevation bands, giving 20 sample sites which were located at the splits between the bands (Haider & Lembrechts *et al.*, 2022). Each sample site consisted of three plots, where species abundance was collected. The abundance was measured by three value classes ranging from 1-3; where 1 = 1-10 individuals, 2 = 11-100 individuals and 3 = > 100 individuals of a species (Haider & Lembrechts *et al.*, 2022). The data also included the status of each species (native/alien). The criteria for an alien species were that it was introduced to northern Norway from another region. However, none of the species were yet classified as invasive (Lembrechts *et al.*, 2014). The purpose of dividing the sample sites into three plots was to cover different road proximities, where the first plot was a roadside plot that was parallel to the road, and the other two go from its middle and into the adjacent natural vegetation (Haider & Lembrechts *et al.*, 2022).

The plant trait data for the chosen traits specific leaf area ( $\text{mm}^2/\text{mg}$ ), vegetative plant height (m), and seed mass (mg) mostly came from the public Tundra Trait Team (TTT) database. This dataset contains field collected data of a total of 18 traits and 978 vascular plant species growing in tundra habitats. It includes 91 970 measurements collected in places such as Alaska, Greenland, Siberia, and the Australian and European Alps, during the time period 1964-2018 (Bjorkman *et al.*, 2018). Additionally, when trait measurements for a particular species were not available from the TTT database, gap-filled trait data was acquired from the TRY trait database. This was done for approximately 16% of the trait values, mostly for the trait “seed mass” (Kattge *et al.*, 2020).



**Figure 1: Location of MIREN survey sites in northern Norway.** (a) Position of the whole sample area ( $68^{\circ}26'18''$  N,  $17^{\circ}25'40''$  E) near Narvik, Norway. (b) Close up of the position of the three sampled roads and their overlap: RO in green, SO in blue, NO in orange, and NO + SO in violet. The NO and SO roads share the same road at their base. (c) Representation of a site (T-transect) and how it is divided into three plots. Each plot is 50 m long and 2 m wide. Plot 1 is laid out along the roadside at the location of the first plant, and goes 2 m into the vegetation. Note that sites in panels (b) and (c) are not to scale. Maps were created with QGIS 3.26.0 using the Bing base map.

## 2.2 Analyses

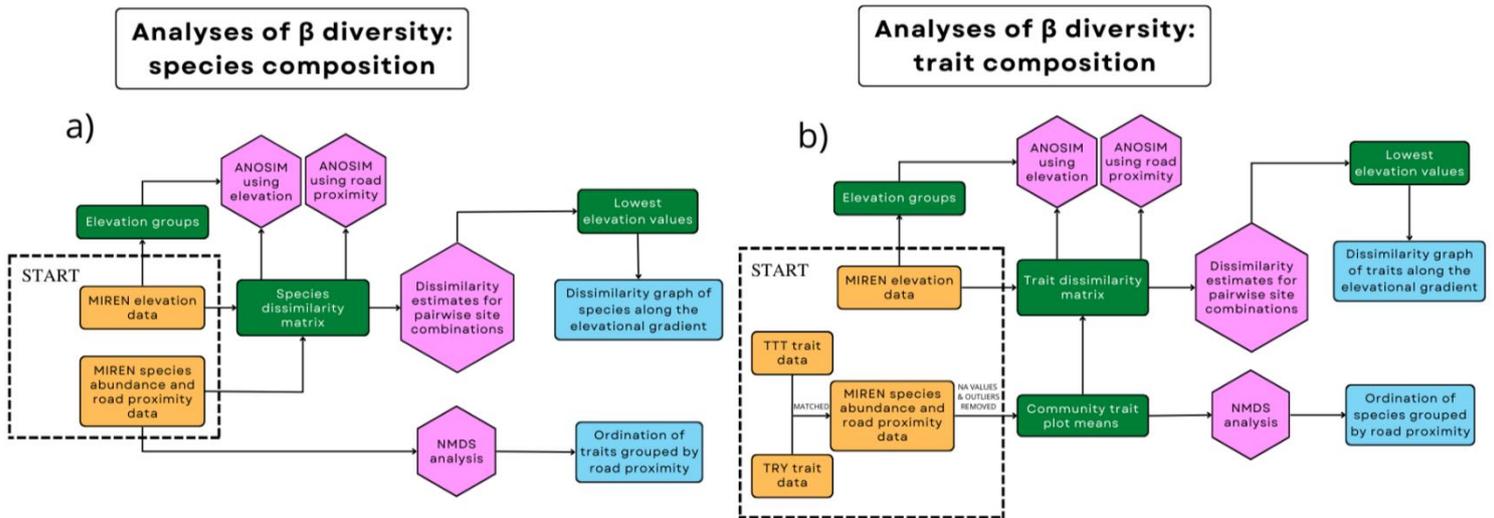
### 2.2.1 Data preparation

All statistical analyses were generated in R v. 4.2.0 (R Core Team, 2020) with the help of the packages *vegan* and *dplyr*, and plotted with *ggplot2*. A summary of the process is shown in Fig. 2.

All the species abundance and road proximity data were used when doing the analyses which compared the three road proximities. From the TTT database, only the measurements that were made on individuals or that show mean values such as the plot mean, were used. Minimum and maximum values (e.g., maximum height in a plot) were removed. Using these, together with the trait data from TRY, median trait values were calculated for each trait across all species. The reason

the median was used was that it is less affected by extreme outliers, and because histograms for the three traits showed that the values for each trait were not normally distributed.

The median trait values per species were then merged with the MIREN dataset, and any missing trait values were filled in using the data from TRY. In the end, 6% of the entries were removed because they lacked trait data. Most of these were entries that were not identified to species level, such as unknown *Taraxacum* and *Salix* species. Furthermore, the seed mass for *Corylus avellana* (593.374 mg) was removed as it was too much of an outlier compared to the other seed masses. In the end, the community weighted mean trait values were calculated for each trait and each plot using the *weighted.mean* function (from the *dplyr* package), which were then used in the analyses.



**Figure 2: Summary of the work process for the data analyses.** Close-ups can be found under “Attachments”. The original datasets are illustrated in orange, the analyses in violet, and the final output in blue. The green boxes illustrate what was calculated from the datasets to fit each respective analysis. (a) Workflow of the analyses done to look at beta diversity for species composition. The original datasets that were used were MIREN elevation data, species abundance, and road proximity. (b) Workflow of the analyses done to look at beta diversity for the trait composition. Here, additional trait data was matched to the species abundance and road proximity data.

### 2.2.2 Plotting non-native species and their traits

To get a visualization of how the abundance of non-native plant species varies with road proximity, their occurrence was plotted in a boxplot. The percentage of non-native species was calculated for each plot at each site ( $n = 60$ ) and grouped by the three road proximities.

Furthermore, a boxplot was made to investigate how the trait values varied for native species relative to the trait values of the non-natives. The boxplot was made using log-transformed median trait values for each trait across all species excluding *Corylus avellana*.

### 2.2.3 Calculating dissimilarity estimates

Dissimilarity estimates were calculated for pairwise site combinations using the Bray Curtis dissimilarity index. The Bray Curtis dissimilarity index is a proportional index that ranges from 0 (plots are identical in their composition) to 1 (plots are as different as they could be), which is often used to compare how sites differ (Bobbitt, 2021). Here, the plots at the first site at the lowest elevation ( $< 15$  m) were compared to all other sites along the elevational gradient. This was done to see how similar the sites are when taking into account the elevation gradient and the road proximity groups (roadside, intermediate, interior). Two dissimilarity matrices were made using the *vegdist* function, one using species abundance data and the second one using the weighted mean

trait data. The result was graphed using the “lm” method and  $y \sim x$  formula in *geom\_smooth* that is part of *ggplot*.

#### 2.2.4 NMDS analysis

A Non-Metric Multidimensional Scaling (NMDS) analysis was made to look for patterns in the data; particularly whether roads had a significant effect on species beta diversity and trait beta diversity. NMDS is an ordination-based analysis that is used to portray a distance or dissimilarity matrix in a multidimensional space, using a reduced number of dimensions (often two or three) (Zuur *et al.* 2007). The analysis itself is non-parametric, meaning that it is based on ranks and ignores actual values. It uses numerical optimization methods (“trial and error”) to visualize what plots or families are similar to each other, meaning that points close to each other in the ordination are the most similar (Zuur *et al.* 2007). The goodness of fit for the points is measured with a value called *stress*, which is the pairwise distances between the observed and fitted dissimilarities (Zuur *et al.* 2007). The stress value ranges from between 0 and 1 and needs to be as low as possible while still retaining few dimensions – as anything above three dimensions makes presentation and interpretation too difficult (Zuur *et al.* 2007, Legendre & Legendre 1998). The general idea is that a stress value below 0.05 is considered perfect, anything between 0.05-0.1 is likely reliable, values above 0.1 should be interpreted with caution, and anything above 0.2 is considered to be poor and most often unusable (Zuur *et al.* 2007).

The ordination was made in order to plot the different sites along the three road transects and to give a visualization of how they might differ. In this scenario, pairwise dissimilarities were calculated using the three road proximity groups with the *metaMDS* function, running twenty tries at two dimensions ( $k=2$ ). The results were graphed using *ggplot* giving two ordinations, where one represented the weighted average of species in the plots based on just species abundance, and the second one represented the weighted trait composition (calculated using the species abundance and their median trait values) for the same plots.

#### 2.2.5 ANOSIM and testing for significance

Finally, an ANOSIM (Analysis of Similarities) was made to calculate the p-statistic and R-values for the communities to see whether they were functionally and compositionally different from each other. ANOSIM is a non-parametric statistical test that looks at how similar groups of samples are using a dissimilarity matrix. It uses the statistic *R*, which is based on the difference in average ranks between groups ( $r_B$ ) and within groups ( $r_W$ ) of samples:

$$R = (r_B - r_W) / (N(N - 1) / 4)$$

Where *N* is the total number of samples.

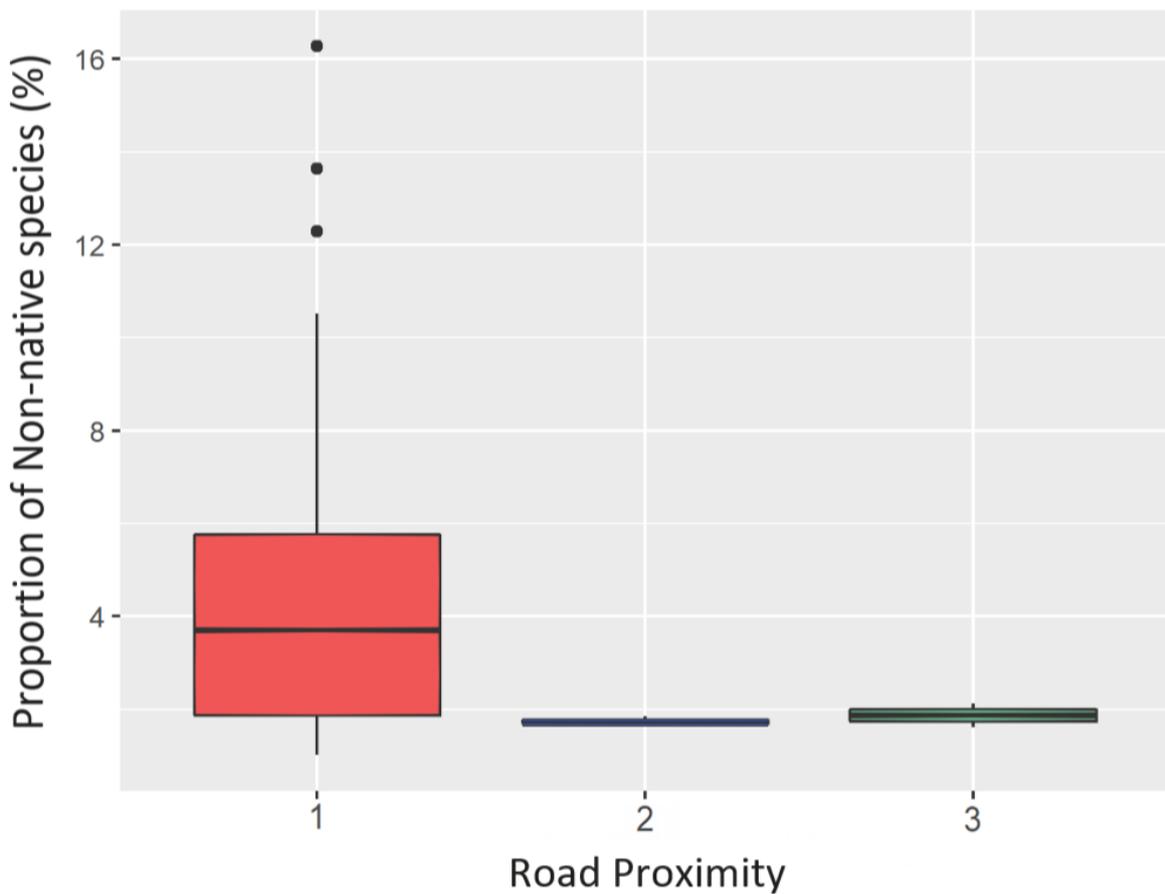
The ANOSIM *R* statistic ranges from +1 to -1, where the null hypothesis is represented by an *R*-value of 0. The null hypothesis that is tested in an ANOSIM is that there is no difference between the means of ranked dissimilarities among the groups of samples, where  $R=0$  indicates that samples are not very different from each other (Sommerfield *et al.*, 2021; Chapman & Underwood, 1999). A value of  $R = 1$  means that the groups are as dissimilar as they can be, meanwhile a value less than 0 suggests that samples within groups are less similar than samples between groups. A value substantially less than 0 should normally not occur, and can be a sign of a faulty design (Sommerfield *et al.*, 2021; Chapman & Underwood, 1999). The goal behind this analysis was to statistically test whether the road proximity or the elevation had a homogenizing effect on the plant compositions.

Separate tests were done using the species-based dissimilarity matrix and the weighted mean trait-based dissimilarity matrix, testing both road proximity and the elevation groups as different factors. Since the elevation was a continuous variable, it was first divided into three groups (0-250 m, 250-500 m, 500+ m) in order to fit the analysis. This was done using the *cut* function. The testing itself was done using the *anosim* function, running at 9999 free permutations and counting  $p \leq 0,05$  as the significance threshold.

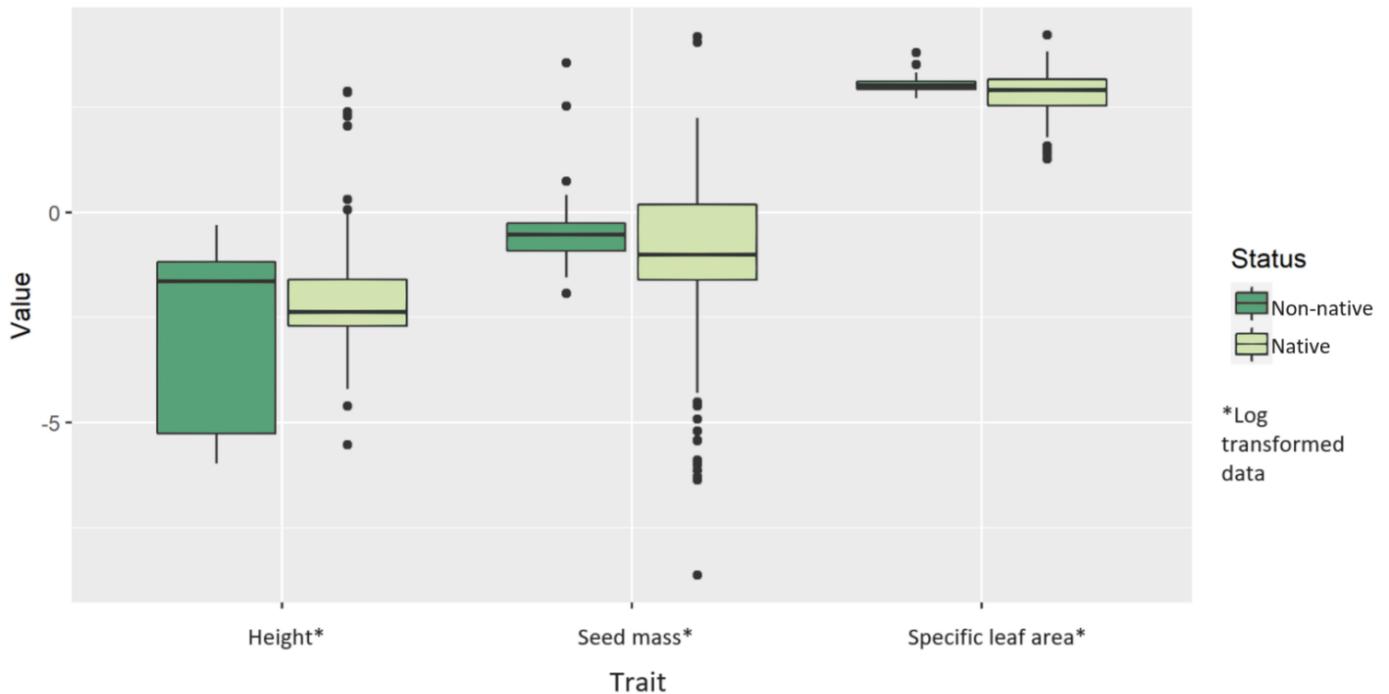
### 3 Results

A total of 208 species were used in the species community analyses, and a total of 199 species were used in the trait community analyses. Moreover, the vegetative plant height median values ranged from 0.0025 m to 17.69 m, seed mass median values ranged from 0.00018 mg to 65.17 mg, and the specific leaf area median values ranged from 3.54 mm<sup>2</sup>/mg to 68.02 mm<sup>2</sup>/mg.

The proportion of non-native plant species was greatest closest to the roads, with a median percentage of approximately 4% non-native plant species per site (Fig. 3). Both native and non-native plants seemed to cover a similar range of values when it comes to their traits (Fig. 4). The specific leaf area appeared to be about the same for both groups, but non-native plants displayed to be slightly taller on average and with slightly heavier seed mass.

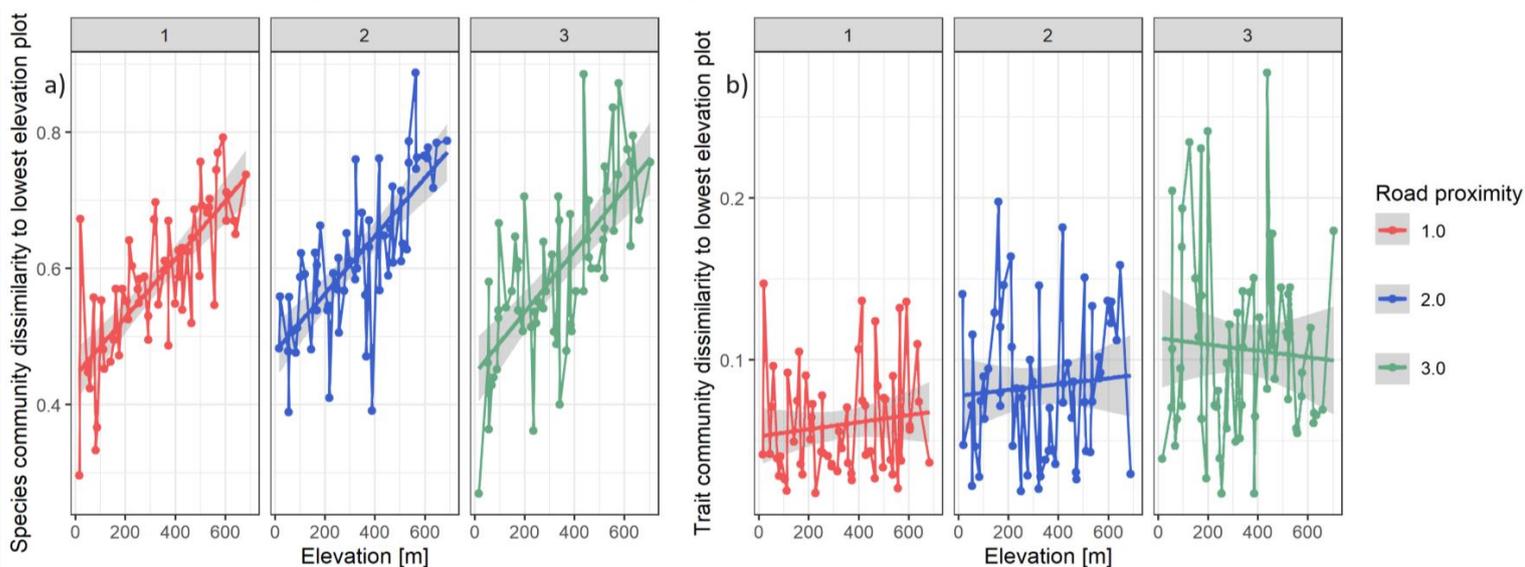


**Figure 3: Boxplot of proportion of non-native plants per site, grouped by road proximity.** Here, road proximity 1 was closest to the road ( $n_1 = 38$ ), road proximity 2 was further away ( $n_2 = 3$ ) and road proximity 3 was completely in the natural vegetation ( $n_3 = 2$ ). The median percentage of non-native plant species found closest to the road was approximately 4%, which was the largest median percentage among the three road proximities.



**Figure 4: Trait boxplot of native and non-native plants.** Shows the height, seed mass, and specific leaf area for non-native and native plant species based on log-transformed median trait values. The non-native plants ( $n_{\text{Non-native}} = 13$ ) seemed to have a slightly taller height and bigger seed mass on average compared to native plants ( $n_{\text{Native}} = 185$ ), while average specific leaf area was about the same for both.

All the species-based dissimilarity graphs (Fig. 5, panel a) showed a positive trend in community dissimilarity, meaning that the species community composition changed along the elevational gradient. However, the trend was not as strong when looking at the traits (Fig. 5, panel b), where the dissimilarity was much lower (<0.3 compared to <0.9 for species dissimilarity) and remained more constant. Here, the sites closest to the road were the least different from each other in terms of trait composition. This suggested that in terms of trait composition, the plant communities were relatively homogenous along the elevational gradient.

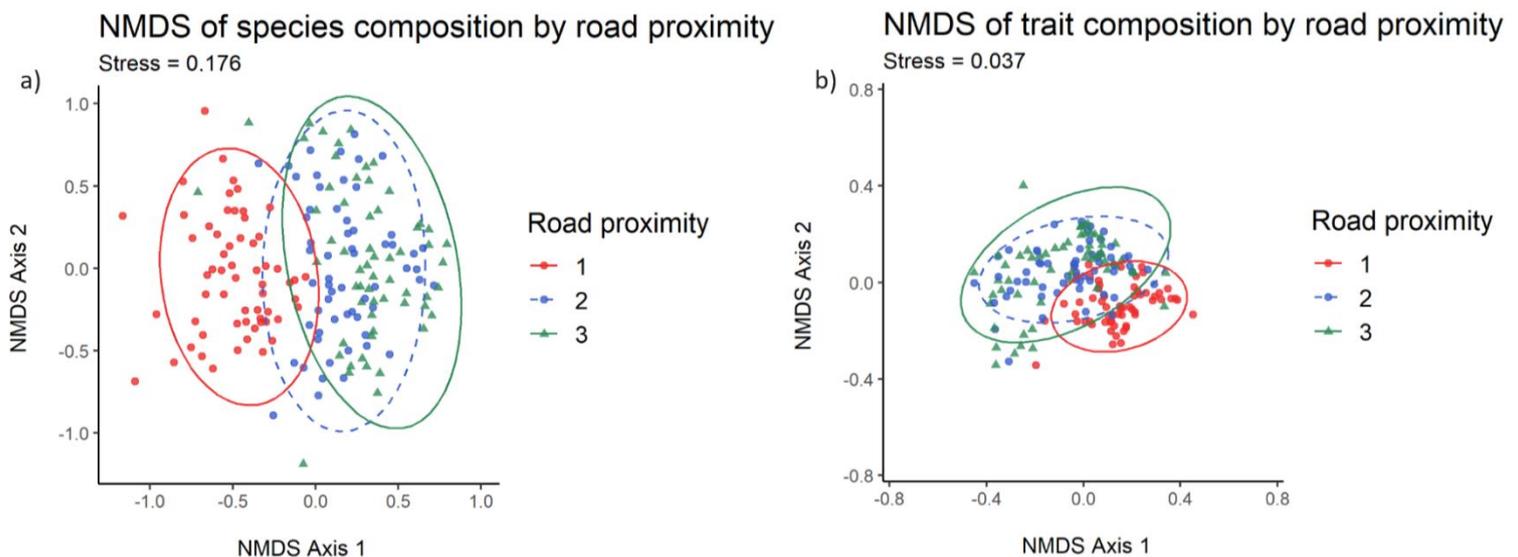


**Figure 5: Dissimilarity to lowest elevation point.** The linear graphs illustrate the pairwise dissimilarity (y-axis) between the plots at the first site (< 15 m) and the sites at higher elevations (x-axis). The calculations were done using the Bray Curtis dissimilarity index. (a) Dissimilarity between species composition, using species abundance data ( $n = 177$ ). Shows a positive trend between community dissimilarity and elevation

but no homogenization based on road proximity. (b) Dissimilarity between trait composition, using weighted mean trait data ( $n = 177$ ). Shows a positive trend for road proximity 1 and 2 but not road proximity 3. The dissimilarity for the sites was much more constant, implying homogenization.

Both species and trait composition were substantially different closest to the road (Fig. 6). These sites were the most different among the three road proximities, as they shared less overlap with the natural plots in the two-dimensional ordination. The sites closest to the road also showed the most clustering and the least variation in both their species and trait composition (Fig. 6), compared to the plots further away from the road. The stress value for the species ordination (Fig. 6a, stress = 0.176) was high and falls into the category of ordination that should be interpreted with caution, as it indicates a high pairwise distance between the observed and the fitted dissimilarities. The stress value for the trait-based ordination (Fig. 6b, stress = 0.037) was lower than 0.05 which is a fair stress value, implying a good fit between the observed and fitted dissimilarities.

The ordinations were further explored by an ANOSIM analysis, made with 9999 free permutations. The ANOSIM of the three road proximities showed a significant difference between the roadside and natural communities for both the species community composition ( $R = 0.3655$ ,  $p < 0.001$ ) and the trait community composition ( $R = 0.112$ ,  $p < 0.001$ ). The  $R$  values indicate that the communities were somewhat different when looking at species composition, but less so when looking at trait composition where the  $R$ -value was closer to 0. The ANOSIM which compared the three elevational groups (not shown in figure) were not significant ( $p > 0.05$ ), but gave low  $R$  values for both the species composition ( $R = 0.009$ ,  $p = 0.210 > 0.05$ ) and the functional trait composition ( $R = -0.006$ ,  $p = 0.666 > 0.05$ ) which means there was less difference among the samples in terms of the plant trait assemblage.



**Figure 6: NMDS ordination of plots.** a) Ordination based on species abundance data, grouped by road proximity ( $n = 180$ , stress = 0.176). Shows that road prox. 1 had a different species composition compared to road prox. 2 and 3. b) Ordination-based trait composition calculated with weighted means, grouped by road proximity ( $n = 180$ , stress = 0.037). Shows that road prox. 2 and 3 were less dissimilar to each other compared to road prox. 1 which had more of a different trait composition.

## 4 Discussion

### 4.1 Effect of road proximity

The results did indeed indicate that the plots closest to the road were compositionally and functionally different from the plots in the natural vegetation. Being that the variation in the species

and trait composition appears to be less near the road, there is strong support that the road is having a homogenizing effect on both the trait composition and species composition.

Notably, the sites closest to the road being different from the natural sites, supports the results of Lembrechts *et al.* (2014) who used abundance data from 2012 in the same location. Similarly, to what was illustrated here, Lembrechts *et al.* (2014) concluded that roadside plots had a higher species richness and abundance of non-native plants compared to the natural plots, making the roadside plots different from the ones covering the natural vegetation (road proximity 2 and 3). This is likely because of different conditions along roadsides, since traffic and biochemical effects of roads can affect microclimate and abiotic factors. They can, for instance, have better light availability and higher temperatures, which benefits some species so that they thrive along roadsides (Lembrechts *et al.*, 2014; Gelbard & Belnap, 2003). Consequently, the vegetation closest to the road can become compositionally different from the one further away from the road (Lembrechts *et al.*, 2014; Gelbard & Belnap, 2003).

In the same fashion, the difference in disturbance and abiotic conditions would also influence the functional composition in a roadside plant community (Bruelheide *et al.*, 2018). The results show that the variation in the trait assembly is much lower compared to what it is when looking at the species compositions, and there seems to be a lot of clustering and overlap between the trait assemblages. The roadside plots also displayed a higher percentage of non-native species, and when looking at how the trait composition varied for native and non-native plants, the non-native plant species appeared to have a pattern of having a slightly taller average height and bigger seed mass.

If non-native plant species are most abundant closest to the road, and these traits indeed vary between non-native and native species, then that can affect the total trait assembly. Generally speaking, a tall plant height shows good fecundity and competitive ability, as taller individuals can grow over short plants and capture more light (Díaz *et al.*, 2016). Likewise, a bigger seed mass tends to increase a plant's establishment success and is beneficial for the survival of the seedling (Díaz *et al.*, 2016). If these traits are what differentiates the native plants from the non-native ones, then that could indicate that if non-native plants are able to spread along roads, then they will have good chances of establishing in the adjacent vegetation and competing with the native species. This would especially be true if they are very tolerant of the disturbances along roads. As mentioned before, the most common type of plants found along roads are disturbance-tolerant generalists (Alexander *et al.*, 2010; Lembrechts *et al.*, 2014), and if such species are present while unique species are not very abundant, then the trait assembly can become more homogenous (McKinney & Lockwood, 1999).

## 4.2 Effect of elevation

The statistical analysis where elevation was a grouping factor suggested that elevation did not have a significant effect on neither species nor the trait composition in the plant communities. However, the dissimilarity graph – which used continuous values instead of grouped values for the elevation – indicated that the species compositions were more different from each other as elevation increased. This could be explained by the species richness of the different plots, which has been seen to increase with elevation (Lembrechts *et al.*, 2014).

Unexpectedly, when looking at the trends for the trait community dissimilarity, the plots closest to the road did not seem to be that different from the plots higher up along the elevational gradient. It was expected that the plants at higher elevations would be compositionally and functionally different from the plants at further down; the motivation being that the number of unique roadside species and non-native species would decrease with the elevation (Alexander *et al.*, 2016; Lembrechts *et al.*, 2014). Instead, the dissimilarity between the trait composition at the lowest elevation, compared to higher elevations, was rather constant in the three road proximities. That is surprising since high elevations have been noted to be limiting habitats, and can have extreme abiotic conditions which not all species are able to tolerate (Lembrechts *et al.*, 2014; Körner, 1999;

Alexander *et al.*, 2016). The plants at high elevations are therefore often known to be specialized in terms of their traits, for instance by being shorter and more compact (Körner, 1999), but here, the results did not show that the plants at the higher elevation had a different trait composition.

Given these points, it seems like environmental filtering might play a role in affecting the species composition, but not the trait composition. It is possible that plants, including non-native species, might be able to spread to higher elevations if they have the right traits to survive in that environment. A possible explanation for the low dissimilarity between the trait compositions in the communities, could be that generalist species are present along the elevational gradient. If generalist species are abundant even as elevation increases, then they can have a homogenizing effect on the total trait assembly along the elevational gradient (Lembrechts *et al.*, 2014).

### 4.3 Limitations and future work

There were two analyses that looked at the influence of elevation on the plant species and trait composition, but interestingly enough they showed different results. One of them indicated that the species (but not the trait) composition varied with elevation, while the second one did not give any significant results for elevation as a descriptive factor. A possible explanation could be that the ANOSIM analysis did not look at elevation as a continuous variable (but instead as three different groups), and perhaps the groups were too broad in their elevational range. Another reason for the high p-values could have been the result of too few replicates in the data, or that there was a lot of variation within the samples.

Ideally, the trait values should have been collected together with the abundance data so that the weighted mean values could have been calculated for each plot, based on individual values for that plot and the sample sites' location. The trait values in the datasets that were used for the analyses were measured in other parts of the world, and not in the Northern Scandes where the abundance data was collected. Many environmental factors can affect an individual's traits, which means that the community traits can differ between locations, even at a small scale, and it will be reflected in the trait values. At smaller levels, traits can for instance be affected by not only the elevation, but by local environmental factors such as soil nutrition and depth, topography, and biotic interactions (Bruehlheide *et al.*, 2018). Disturbance, niche partitioning, and biotic interactions all affect the trait composition in a plant community and can make it so that even plants of the same species have different traits if they grow in different environments (Bruehlheide *et al.*, 2018). With this in mind, by measuring traits at the same location as where the abundance data is collected, the local conditions influencing plant species distributions and their traits could also be considered. As a result, it would make the data more independent and representative of the sites in the Northern Scandes.

All things considered, it would be interesting to take a closer look at specifically what different species and traits can be found at each site. A useful analysis when looking at the species could perhaps be the similarity percentage analysis (SIMPER), which looks at the species distribution in different groups, and how much individual species contribute to the dissimilarity between the them (Clarke, 1993). When it comes to traits, it would be interesting to further investigate how they vary in native and non-native plant species. This was briefly done in this study but could be improved upon by collecting the traits at the actual location of the roads, and testing the difference statistically by weighting the species traits by the species abundance. In like manner, it would be of use to go into more depth on why there might be a difference between patterns in species composition and trait composition. The trait composition did not vary with increased elevation in any of the road proximities, while the species composition did, and that could have been due to other environmental factors that were not investigated here. As mentioned before, since traits are influenced by many factors, it is important to take into consideration other local environmental factors besides elevation.

## 5 Conclusion

Roads do seem to play a role in shaping plant species communities and their trait assembly, and the road proximity is homogenizing both species and trait composition. Traits heavily influence ecosystem functions and processes; therefore, it is important to pay more attention to the trait composition of different plant communities, and how they might vary with disturbances like roads, and environmental stress factors such as increased elevation. By looking at the diversity of plant traits, we can advance our understanding of the main drivers for plant trait assembly, and how the influence of different factors might be different when looking at species composition, compared to their trait composition. In other words, it will give us more knowledge of how functional diversity and ecosystem functions vary naturally and might be influenced by human-induced changes in nature. This understanding is vital for management purposes and can make it easier to prevent any unwanted ecological impacts that might arise with homogenization, and, correspondingly, help preserve healthy and productive plant ecosystems.

## 6 Acknowledgments

Several people played a decisive role in making this project possible. I want to take this opportunity to thank them for all the help and support. I could not have wished for a better supervisor than Anne Bjorkman, who helped me throughout the process, encouraged me, and gave me constructive feedback. I would also like to say a big thank you to Jonas Lembrechts from MIREN for sharing the data with me, for all the valuable comments, and for allowing me to participate in the process of collecting the 2022 MIREN data. It was a very valuable experience that taught me a lot about the subject and the data collection process, and gave me new perspectives when writing this paper. Thank you to Jan Clavel for the assistance in the field and for helping me understand the dataset better. I am also very grateful to all the kind and hardworking Master's students from Antwerp University who were part of the fieldwork, and made me feel very included in the process. Last but not least, thank you to my examiner Åslög Dahl and various students at Gothenburg University for taking interest in my work.

## 7 References

- Alexander, J.M., Kueffer C., Daehler C.C., Edwards P. J., Pauchard A., Seipel T., MIREN Consortium. (2010). Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences*, Vol. 108(2): 656-661. <https://doi.org/10.1073/pnas.10131361>
- Alexander, J.M., Lembrechts, J.J., Cavieres, L.A., Daehler, C., Haider, S., Kueffer, C., Liu, G., McDougall, K., Milbau, A., Pauchard, A., Rew, L.J., Seipel, T. (2016). Plant invasions into mountains and alpine ecosystems: current status and future challenges. *Alpine Botany*, Vol. 126: 89–103. <https://doi.org/10.1007/s00035-016-0172-8>
- Andersen, K.M., Naylor, B.J., Endress, B.A., Parks, C.G. (2015) Contrasting distribution patterns of invasive and naturalized non-native species along environmental gradients in a semi-arid montane ecosystem. *Applied Vegetation Science*, Vol. 18: 683–693. <https://doi.org/10.1111/avsc.12185>
- Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Normand, S., Thomas, H.J.D., Alatalo, J.H., Alexander, H., Anadon-Rosell, A., Angers-Blondin, S., Bai, Y., Baruah, G., te Beest, M., Berner, L., Björk, R.G., Blok, D., Bruelheide, H., Buchwal, A., Buras, A., Carbognani, M., Christie, K. ... Zamin, T. (2018). Tundra Trait Team: A database of plant traits spanning the tundra biome. *Global Ecology and Biogeography*, Vol. 27: 1402–1411. <https://doi.org/10.1111/geb.12821>
- Bobbitt, Z. (2021). Bray-Curtis Dissimilarity: Definition & Examples. *Statology Study*. <https://www.statology.org/bray-curtis-dissimilarity/>, retrieved 19-08-2022.
- Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Joménez-Alfaro, B., Hennekens, S.M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V.D., Schrodte, F., Mahecha, M.D., Peet, R.K., Sandel,

- B., van Bodegom, P., Altman, J., Alvarez-Dávila, E., Khan, M.A.S.A., Attorre, F. ... Jandt, U. (2018). Global trait–environment relationships of plant communities. *Nature Ecology & Evolution*, Vol. 2: 1906–1917 <https://doi-org.ezproxy.ub.gu.se/10.1038/s41559-018-0699-8>
- Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'connor, M.I., Gonzalez, A. (2011). The functional role of producer diversity in ecosystems. *American Journal of Botany*, Vol. 98 (3): 572-592. <https://www.jstor.org/stable/41149206>
- Chapman, M.G. & Underwood, A.J. (1999). Ecological patterns in multivariate assemblages: information and interpretation of negative values in ANOSIM tests. *Marine Ecology Progress Series*, Vol. 180: 257-265.
- Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, Vol. 18: 117–143.
- Curtis D.C., (2005). Upper-montane plant invasions in the Hawaiian Islands: Patterns and opportunities. *Perspectives in Plant Ecology, Evolution and Systematics*, Vol. 7(3): 203-216. <https://doi.org/10.1016/j.ppees.2005.08.002>
- Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., Garnier, E., Bönsch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.M., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Wright, S.J., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D. (2016). The global spectrum of plant form and function. *Nature*, Vol. 529: 167–171. <https://doi-org.ezproxy.ub.gu.se/10.1038/nature16489>
- Dunnett, N. P., Willis, A. J., Hunt, R., Grime, J. P. (1998). A 38-Year Study of Relations between Weather and Vegetation Dynamics in Road Verges near Bibury, Gloucestershire. *Journal of Ecology*, Vol. 86(4): 610–623. <http://www.jstor.org/stable/2648425>
- Dwyer, J. M., Hobbs, R. J., & Mayfield, M. M. (2014). Specific leaf area responses to environmental gradients through space and time. *Ecology*, Vol. 95(2): 399–410. <http://www.jstor.org/stable/43494353>
- Gelbard, J. L., Belnap, J. (2003). Roads as Conduits for Exotic Plant Invasions in a Semiarid Landscape. *Conservation Biology*, Vol. 17(2): 420–432. <http://www.jstor.org/stable/3095361>
- Haider, S., Kueffer, C., Bruelheide, H., Seipel, T., Alexander, J.M., Rew, L.J., Ramón Arévalo, J., Cavieres, L.A., McDougall, K.L., Milbau, A., Naylor, B.J., Speziale, K., Pauchard, A. (2018) Mountain roads and non-native species modify elevational patterns of plant diversity. *Global Ecology Biogeography*, Vol. 27: 667–678. <https://doi.org/10.1111/geb.12727>
- Haider, S. & Lembrechts, J.J., McDougall, K., Pauchard, A., Alexander, J.M., Barros, A., Cavieres, L.A., Rashid, I., Rew, L.J., Aleksanyan, A., Arévalo, J.R., Aschero, V., Chisholm, C., Clark, R., Clavel, J., Daehler, C., Dar, P.A., Dietz, H., Dimarco, ... Seipel, T. (2022) Think globally, measure locally: The MIREN standardized protocol for monitoring plant species distributions along elevation gradients. *Ecology and Evolution*, Vol. 12(2): e8590. <https://doi.org/10.1002/ece3.8590>
- Jauni, M., Gripenberg, S., Ramula, S. (2015). Non-native plant species benefit from disturbance: a meta-analysis. *Oikos*, Vol 124: 122–129. <https://doi.org/10.1111/oik.01416>
- Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Colin Prentice, I., Leadley, P., Tautenhahn, S., Werner, D.A.W.G., Aakala, T., Abedi, M., Acosta, A.T.R., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H., Alcántara, J.M., Alcázar, C.C., Aleixo, I., Ali, H ... Wirth, C. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, Vol. 26: 119– 188. <https://doi.org/10.1111/gcb.14904>
- Koleff, P., Gaston, K.J., Lennon, J.J. (2003) Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, Vol. 72: 367–382. <https://doi.org/10.1046/j.1365-2656.2003.00710.x>
- Kudo G., Amagai Y., Hoshino B., Kaneko M. (2011). Invasion of dwarf bamboo into alpine snow-meadows in northern Japan: pattern of expansion and impact on species diversity. *Ecology and Evolution*, Vol. 1: 85–96. <https://doi.org/10.1002/ece3.9>
- Körner C. (1999) Alpine plant life: Functional Plant Ecology of High Mountain Ecosystems. 2<sup>nd</sup> Edition. Springer: Berlin; New York.

- Legendre, P., Legendre, L. (1998). Numerical ecology. 2<sup>nd</sup> Edition. ScienceDirect (Online service): Amsterdam; New York.
- Lembrechts J.J., Milbau A., Nijs I. (2014) Alien Roadside Species More Easily Invade Alpine than Lowland Plant Communities in a Subarctic Mountain Ecosystem. *PLoS ONE*, Vol. 9(2): e89664. <https://doi.org/10.1371/journal.pone.0089664>
- Lembrechts, J.J., Alexander, J.M., Cavieres, L.A., Haider, S., Lenoir, J., Kueffer, C., Mcdougall, K., Naylor, B.J., Nuñez, M.A., Pauchard, A., Rew, L.J., Nijs, I., Milbau, A. (2016). Mountain roads shift native and non-native plant species' ranges. *Ecography*, Vol 40: 353–364. <https://doi.org/10.1111/ecog.02200>
- McKinney, M.L., Lockwood, J.L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, Vol. 14(11): 450-453. [https://doi.org/10.1016/S0169-5347\(99\)01679-1](https://doi.org/10.1016/S0169-5347(99)01679-1)
- Pollnac, F., Seipel, T., Repath, C., Rew L.J. (2012). Plant invasion at landscape and local scales along roadways in the mountainous region of the Greater Yellowstone Ecosystem. *Biol Invasions*, Vol 14: 1753–1763. <https://doi.org/10.1007/s10530-012-0188-y>
- R Core Team. (2020). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>
- Severin D. H. Irl, David E. V. Harter, Steinbauer, M.J., Puyol, G., Fernández-Palacios, J.M., Jentsch, A., Beierkuhnlein, C. (2015). Climate vs. topography – spatial patterns of plant species diversity and endemism on a high-elevation island. *Journal of Ecology*, Vol. 103 (6): 1621-1633.
- Somerfield, P. J., Clarke, K. R., Gorley, R. N. (2021). A generalised analysis of similarities (ANOSIM) statistic for designs with ordered factors. *Austral Ecology*, Vol. 46. <http://dx.doi.org/10.1111/aec.13043>
- Taylor, K., Brummer, T., Taper, M. L., Wing, A. & Rew, L. J. (2012). Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. *Diversity and Distributions*, Vol. 18: 942–951. <https://doi.org/10.1111/j.1472-4642.2012.00926.x>
- Thomas, H.J.D., Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Kattge, J., Diaz, S., Vellend, M., Blok, D., Cornelissen, J.H.C., Forbes, B.C., Henry, G.H.R., Hollister, R.D., Normand, S., Prevéy, J.S., Rixen, C., Schaepman-Strub, G., Wilmking, M., Wipf, S., Cornwell, W.K., Beck, P.S.A. ... de Vries, F.T. (2020). Global plant trait relationships extend to the climatic extremes of the tundra biome. *Nature Communications*, Vol. 11: 1351. <https://doi.org/10.1038/s41467-020-15014-4>
- Vilà, M., Espinar J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, Vol. 14: 702–708. <https://doi.org.ezproxy.ub.gu.se/10.1111/j.1461-0248.2011.01628.x>
- Weihner, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. (1999). Challenging Theophrastus: A Common Core List of Plant Traits for Functional Ecology. *Journal of Vegetation Science*, Vol. 10(5): 609–620. <https://doi.org/10.2307/3237076>
- Wolf, A.A., Funk, J.L., Selmants, P.C., Morozumi, C.N., Hernández, D.L., Pasari, J.R., Zavaleta, E.S. (2021). *PNAS*, Vol. 118 (26): e2022757118. <https://doi.org/10.1073/pnas.2022757118>
- Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, Vol. 199: 213–227.
- Zuur, A.F., Ieno, E.N., Smith, G.M. (2007). Analyzing Ecological Data. Springer: New York.

## 8 Attachments

Figure 2

