



Plant community responses to 15 years of nitrogen and phosphorus fertilization along an elevational gradient in the subarctic tundra

Gaya Marike ten Kate

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Swedish University of Agricultural Sciences, SLU

Faculty of Forest Sciences, department of Forest Ecology and Management

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Gaya Marike ten Kate

Supervisor: Maja Sundqvist, Swedish University of Agricultural Sciences, Department of Forest Ecology and Management
Assistant supervisor: Zsófia Réka Stangl, Swedish University of Agricultural Sciences, Department of Forest Ecology and Management
Examiner: Lenka Kuglerová, Swedish University of Agricultural Sciences, Department of Forest Ecology and Management

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Swedish University of Agricultural Sciences
Faculty of Forestry
Department of Forest Ecology and Management

Abstract

Climate change in the Arctic has profound effects on tundra vegetation, directly through increasing temperatures and indirectly through changes in plant community composition and nutrient cycling. Fertilization experiments are widely used to study the effects of increased nutrient availability on arctic tundra vegetation. This study investigated the effects of 15 years of nitrogen (N) and phosphorus (P) addition along an elevational gradient in subarctic heath and meadow vegetation in northern Sweden. It shows that vegetation type strongly interacted with elevation, time, N and P addition to influence plant communities and hence that different vegetation types can have highly different responses to increased nutrient availability over time. In both vegetation types, N was the main limiting nutrient, but combined fertilization with N and P generated the greatest change in plant community composition, whereby slow-growing species were replaced by one or two dominant graminoids, which was associated with a decrease in species richness, Simpson's diversity and Shannon diversity. The effect of N addition on plant community composition was stronger in the nutrient-poor heath, whereas species richness declined more in the nutrient-rich meadow. During 15 years of nutrient addition, the fastest and greatest change in plant community composition, species richness and diversity occurred at the warmer sites in the heath and the colder sites in the meadow, but after ten years of fertilization, the colder sites in the heath also responded to increased nutrient availability, implying that temperature mediates the effect of fertilization on heath vegetation. The results of this study highlight the complex responses of different vegetation types in the tundra to increased nutrient availability over time and show that short-term responses to fertilization may persist on the long-term, but additional changes may occur after more than ten years of nutrient addition in more temperature and nutrient limited plant communities.

Keywords: arctic tundra, climate change, fertilization, nitrogen, phosphorus, plant community composition, species richness, Simpson's diversity, Shannon-Wiener diversity, elevational gradient

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Abbreviations

ANOVA	Analysis of variance
LMM	Linear mixed model
N	Nitrogen
NMDS	Non-metric multidimensional scaling
P	Phosphorus
PERMANOVA	Permutational analysis of variance
SMHI	Swedish Meteorological and Hydrological Institute

1. Introduction

Climate change is occurring at more than double the rate in the Arctic compared to the rest of the world (Francis et al., 2017). Positive feedbacks amplify warming in the Arctic, because reduced snow and ice cover resulting from atmospheric warming causes shifts in albedo, cloud cover and ocean streams, which further increase atmospheric temperatures (Walsh, 2014). Between 1966 and 2003 surface air temperatures in the Arctic increased with an average of 0.4°C per decade (ACIA, 2005). Several environmental changes have been observed in the arctic tundra in response to elevated temperatures, such as a longer growing season (Niittynen et al., 2020), earlier snowmelt (Stone et al., 2002), and increased precipitation (Box et al., 2019), all of which influence plant growth. As a result, climate change has shown profound effects on arctic tundra vegetation, directly by enhancing plant growth (Elmendorf et al., 2012a), and indirectly through increasing microbial activity and decomposition of organic matter (Chapin et al., 1995). For example, research has reported a greening of the Arctic (Walker et al., 2012; Berner et al., 2020), an expansion of shrubs (Tape et al., 2006; Mekonnen et al., 2018), and a northward movement of the tree line (Danby & Hik, 2007; Bjorkman et al., 2018). Moreover, several studies have shown an increase in nutrient turnover in tundra soils at increased temperatures (Chapin et al., 1995; Rinnan et al., 2008), likely due to changes in soil temperature and soil moisture, rendering an increase in nutrients available to plants. This is likely to relieve parts of the nutrient limitation currently imposed on plant growth in the arctic tundra, where nitrogen (N) and phosphorus (P) are major limiting nutrients (Shaver & Chapin, 1980; Shaver et al., 1986; Jonasson, 1992; Chapin et al., 1995). An important reason for the low N and P availability in tundra soils is that a substantial proportion of the nutrients is locked up in organic material with a long turnover time, or is immobilized by microbes, leaving most of these nutrients unavailable to plant roots (Jonasson & Michelsen, 1996).

Global warming, resulting from climate change, could induce a shift in plant community composition in the arctic tundra from nutrient-conservative species to species that require higher amounts of nutrients (Miller, 1982; Mekonnen et al., 2018). However, regional differences have been observed in response to warming (Elmendorf et al., 2012b). For example, in a synthesis of 61 warming experiments

in the Arctic, the proportion of shrubs was found to increase with warming in sites with a relatively high ambient summer temperature (Elmendorf et al., 2012b). By contrast, graminoids increased in proportion mainly at colder sites, and vascular plant diversity (Simpson's diversity index; Peet, 1974) declined only in sites with high soil moisture (Elmendorf et al., 2012b). Hence, long-term variation in the regional climate across arctic sites can be a strong mediator of plant community responses to rising temperatures.

Landscape heterogeneity plays an important role in the differential responses of tundra vegetation to climate change. The arctic tundra is characterized by a mosaic landscape where different vegetation types, associated with different dominant plant functional groups, are found in close proximity to each other (Björk et al., 2007). This patchiness in the landscape results largely from small-scale topographic differences which affect water and nutrient availability, because water and nutrients move downwards on hillslopes and accumulate in topographic depressions (Peterson & Billings, 1980; Young et al., 1997). For example, in the Fennoscandian tundra two vegetation types, heath and meadow, are commonly found within short distances from each other. Heath vegetation occurs in nutrient-poor patches and is mainly dominated by evergreen and deciduous shrubs, whereas meadow vegetation occurs in more fertile patches and is dominated by forbs and graminoids (Molau & Alatalo, 1998). Nitrogen availability in the soil has been found to be more than three times higher in meadow versus heath vegetation (Björk et al., 2007), which has been suggested to relate to stronger N limitation of plant growth in the heath (Chu et al., 2011). Further, the plant N:P ratio is higher in the meadow, which has been suggested to impose a larger P limitation on meadow vegetation, although the differences between vegetation types are small (Giesler et al., 2012). Since heath and meadow are inherently different in terms of nutrient dynamics and plant functional groups, these vegetation types can respond very differently to changes in temperature and increased nutrient availability (Sundqvist et al., 2014a).

Fertilization experiments are widely used to study the effect of increased nutrient availability on plant communities in the tundra. A common finding in these studies is a shift in dominant functional groups towards an increase in fast-growing deciduous species and graminoids at the cost of slow-growing evergreen species (Chapin et al., 1995; Press et al., 1998; Bret-Harte et al., 2008; Veen et al., 2015). Multiple fertilization studies have also reported an increase in the biomass of deciduous shrubs (Chapin et al., 1995; Jonasson et al., 1999; DeMarco et al., 2014) and graminoids (Bret-Harte et al., 2008; Liu et al., 2020) with nutrient addition. Another study in alpine tundra in Colorado, USA, found that plant diversity (Shannon-Wiener index; Peet, 1974) increased with N+P fertilization in dry meadow, but diversity decreased with the same treatment in wet meadow

(Theodose & Bowman, 1997), which highlights the fundamental differences between the responses of different vegetation types to nutrient addition.

Nitrogen is often believed to be the main limiting nutrient in the arctic tundra (Aerts & Chapin, 1999), but the role of P in driving patterns of biodiversity in the tundra is less well understood (McLaren & Buckeridge, 2019). Full-factorial fertilization experiments which explored the separate and interactive effects of N versus P addition on vegetation found the largest response to treatment in the combination of N and P fertilization (Shaver & Chapin, 1980; Jonasson et al., 1999), indicating that N and P have a co-limiting effect on tundra ecosystems (Giesler et al., 2012). Similarly, Zamin et al. (2014) found an interactive effect between N and P addition, where combined fertilization with N and P showed a lower inorganic N availability in the soil than when the same amount of N was added without P. Furthermore, an experiment of N and P addition in the alpine tundra in Colorado, USA, found that N addition significantly reduced species richness, whereas P addition alone did not affect species richness (Seastedt & Vaccaro, 2001). Nevertheless, McLaren and Buckeridge (2019) suggest that, besides a universal N-limitation, there is a more complex P-limitation in the tundra, which is generally less well studied and understood.

Most fertilization experiments report short-term (< 10 years) responses to nutrient addition, and long-term studies are few. However, short-term responses to nutrient addition do not necessarily match long-term results (McLaren & Buckeridge, 2019). For example, McLaren & Buckeridge (2019) found that the relative proportion of plant functional groups in moist acidic tundra continued to change after 26 years of fertilization, where short-term results predicted the direction, but not the magnitude of long-term change. In several cases, decoupled effects of above- and belowground responses to fertilization have been reported (Wardle et al., 2013; McLaren & Buckeridge, 2019). In one experiment the microbial community needed more than 10 years to respond to fertilization (Rinnan et al., 2007), which in turn influences the vegetation. As a result, short-term fertilization experiments may not mirror the longer term responses of plant communities to nutrient addition (Farrer et al., 2015), and very little is known about how long-term fertilization interacts with long-term changes in temperature to affect tundra plant communities. Elevational gradients serve as powerful tools to study long-term temperature effects on vegetation, as long as other abiotic variables remain relatively constant, due to the natural decrease in temperature that is associated with increasing elevation (Körner, 2007; Sundqvist et al., 2013; Müller et al., 2017). This allows for the opportunity to study long-term natural temperature effects on an ecosystem. Nevertheless, few studies have combined fertilization experiments with elevational gradients.

In order to better understand how nutrient supply and temperature interact to influence plant community composition and diversity in the subarctic tundra, I studied how heath and meadow vegetation respond to long-term nutrient addition along an elevational gradient. This was tested in a full-factorial study of N and P fertilization between 2008 and 2022 in Abisko, northern Sweden (Sundqvist et al., 2011, 2014a). An observational study on this elevational gradient found that N concentrations, species richness and Simpson's diversity were higher in meadow than in heath (Sundqvist et al., 2011). Further, soil P availability has been found to decrease consistently with elevation in both vegetation types (Vincent et al., 2014), whereas patterns of soil mineral N concentrations across elevations in this study system were less clear and decreased with elevation in the heath, but were highly variable along the elevational gradient in the meadow (Sundqvist et al., 2011, 2014b). After two years of fertilization it was concluded that N was the main limiting nutrient in both heath and meadow, but in both vegetation types the largest response to fertilization was observed when N and P were added together (Sundqvist et al., 2014a). Vegetation density significantly increased with N+P addition in both vegetation types, and this effect was strongest at the low elevation for the heath and at the high elevations for the meadow (Sundqvist et al., 2014a). This suggests that the cold temperatures at high elevations are likely more limiting than nutrients for heath vegetation, while nutrients are more limiting at high elevations for the meadow vegetation (Sundqvist et al., 2014a). Since long-term responses often differ from short-term responses to fertilization, the current study follows up on Sundqvist et al. (2014a) with the aim to analyze long-term (15 years) responses of subarctic heath and meadow vegetation to N and P addition along an elevational gradient. I test the hypotheses that:

1. After 15 years of fertilization, N addition will continue to have a greater effect on heath and meadow vegetation than P addition (Aerts & Chapin, 1999; Sundqvist et al., 2014a), but combined fertilization with N+P will generate the greatest change in plant community composition and diversity for both vegetation types (Shaver & Chapin, 1980; Jonasson et al., 1999; Sundqvist et al., 2014a).

2. There will be a shift in plant community composition in N and N+P fertilized plots from conservative and slow growing species towards faster growing plants (Chapin et al., 1995; Press et al., 1998; Bret-Harte et al., 2008; Veen et al., 2015), which over time will decrease diversity (Chapin et al., 1995; Press et al., 1998). This effect will be greater in the nutrient-poor heath vegetation than in the more nutrient-rich meadow vegetation (Molau & Alatalo, 1998).

3. After 15 years of fertilization, plant communities in N and N+P fertilized plots at the low elevation in the heath and the high elevations in the meadow will be almost entirely dominated by graminoids (Sundqvist et al., 2014a), which is associated with a decrease in species richness and diversity. At the high elevations in the heath and the low elevations in the meadow there will be little to no effect of fertilization.

2. Methods

2.1 Study site

This experiment was conducted on Mt. Suorooaivi (1193m), located 20 km south-east of Abisko, Sweden (68°21'N, 18°49'E). This elevational gradient faces north-east and ranges between 450 to 1000 meters in elevation, as is previously described by Sundqvist et al. (2011, 2014a). The climate is characterised as subarctic, with long, cold winters and short summers. The average growing season is approximately three months between June and September and the average temperature in Abisko during the growing season is 10.3 ± 2.8 °C, based on measurements between 2000 and 2020 acquired from the Swedish Meteorological and Hydrological Institute (SMHI) (SMHI, 2023). Previous air temperature measurements across this study system showed a decline in temperature of approximately 2-3 °C between 400 and 1000 meters elevation (Sundqvist et al., 2011, 2020; Blume-Werry et al., 2018). The mean precipitation in Abisko during the growing season is 226 mm, with July being the wettest month (73.3 mm) and June being the driest month (46.6 mm) (SMHI, 2023). Summer precipitation previously measured in proximity of the study area ranged between 230 and 290 mm and showed little variation across elevations (Karlsson et al., 2005; Sundqvist et al., 2011).

At the study site, heath and meadow vegetation grow in patches in a mosaic pattern (Figure 1). Mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest grows at the base of the mountain until the treeline, with the forest line located between 500 and 650 meters elevation. The heath vegetation consists mainly of evergreen and deciduous dwarf shrubs and is dominated by *Betula nana*, *Empetrum nigrum*, *Vaccinium vitis-idaea*, and *Vaccinium uliginosum*. The meadow vegetation is characterized by forbs and graminoids, with common forb species including *Bistorta vivipara*, *Ranunculus nivalis*, *Solidago virgaurea* and *Viola biflora*, and common graminoids including *Carex bigelowii* and *Deschampsia flexuosa*. Pteridophytes are found in the forest in both vegetation types, but are rare above the treeline.

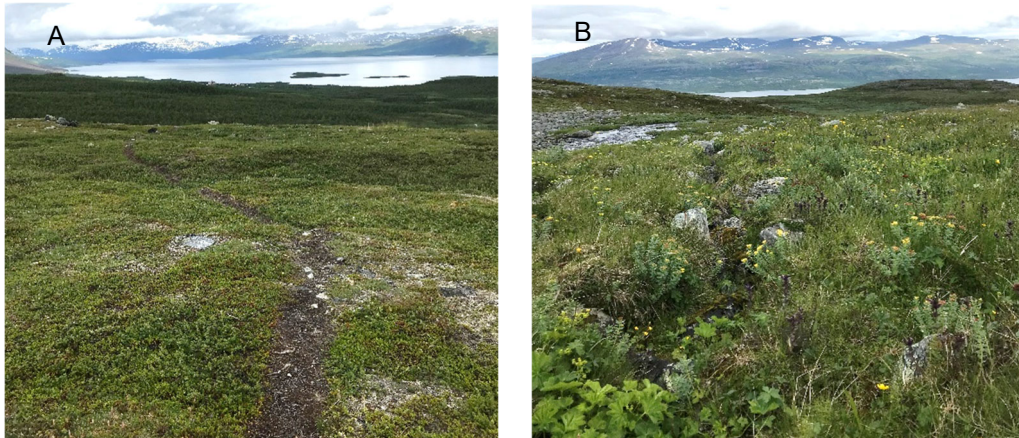


Figure 1: Heath vegetation (A) and meadow vegetation (B) at the study site.

The subarctic is sensitive to cyclical outbreaks of autumnal moths (*Epirrita autumnata*) in birch forests (Parker et al., 2017) and lemmings in the tundra (Oksanen & Oksanen, 1992). In 2012-2013 and 2022 the sites located at 500 meters in the mountain birch forest were subject to an outbreak of *Epirrita autumnata*, which killed a large proportion of the forest. Moreover, in 2015 there was an outbreak of lemmings, which led to a strong reduction of vegetation cover in several plots in this study system at 800 and 1000 meters.

2.2 Study design

A full-factorial experiment of N and P fertilization was set up at 500, 800 and 1000 meters elevation in the summer of 2008. Sixteen replicate plots of 1x1 m were installed at each elevation in heath and meadow vegetation, resulting in a total of 96 plots. These 16 plots were divided into four independent blocks, within which each plot was randomly assigned one of the following treatments: control, N fertilization, P fertilization, or N + P fertilization (Figure 2). The mean distance between the two nearest plots with the same treatment was ~10 m (Sundqvist et al., 2014a), which is assumed to be enough to ensure independence between plots (Sundqvist et al., 2011), because of the high degree of heterogeneity in the landscape due to variations in soil fertility depending on small-scale topographical differences (Björk et al., 2007).

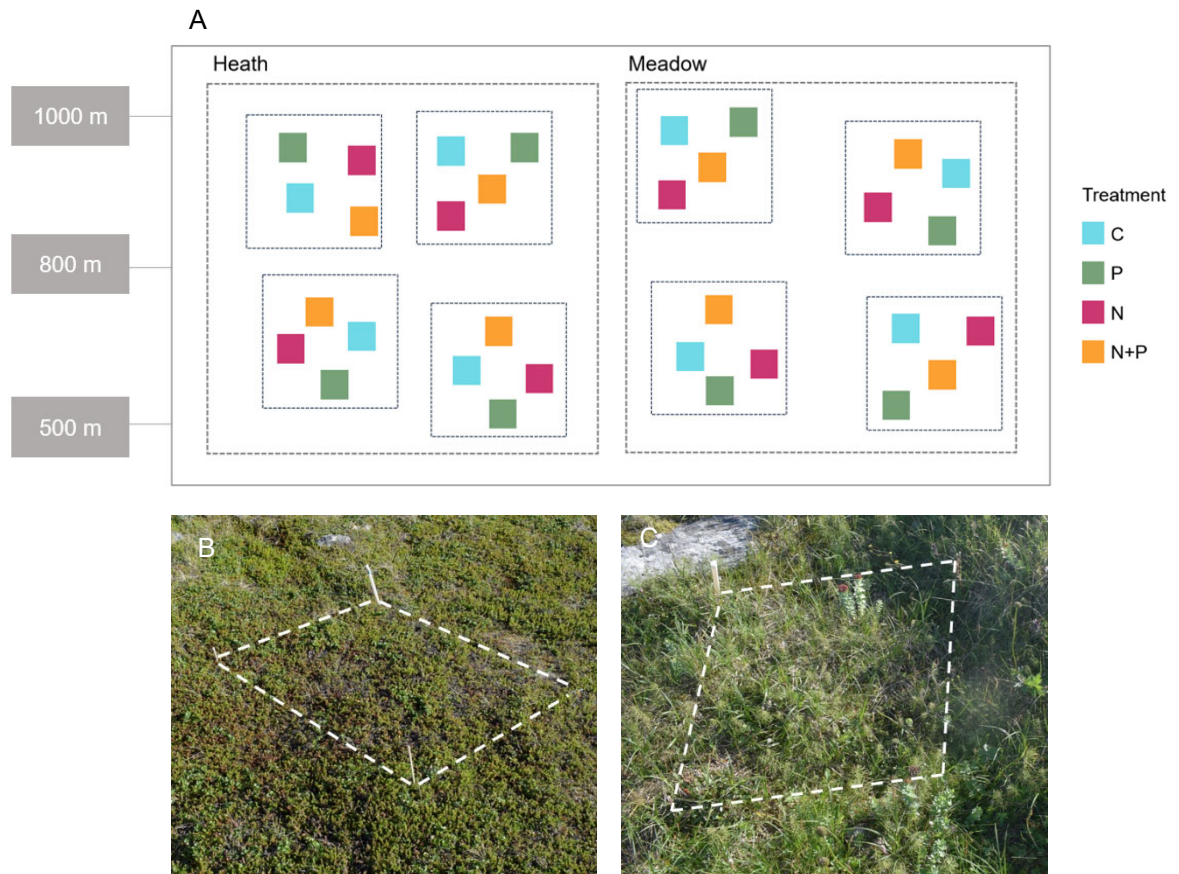


Figure 2: A schematic overview of the experimental design of this study (panel A). At all elevations (500, 800 and 1000 meters) and in both vegetation types (heath and meadow) there were sixteen plots, which received one of the four treatments: control (C), phosphorus fertilization (P), nitrogen fertilization (N) or combined fertilization with nitrogen and phosphorus (N+P). Plots that received the same treatment in each vegetation type were divided over four randomly positioned blocks. Example plots located in heath (panel B) and meadow (panel C) vegetation are shown. Photo credit: Eliška Kutakova.

Plots assigned to fertilization have been fertilized annually since 26 July 2008. During the summers of 2009 and 2010, half of the annual amount of fertilizer was added when the plots were snow free and the other half was added three weeks later (Sundqvist et al., 2014a). Since 2011, all plots were fertilized with the full amount of fertilizer at once in the last week of June or early July each year. Fertilized plots received $10 \text{ g N m}^{-2} \text{ yr}^{-1}$ in the form of NH_4NO_3 and/or $5 \text{ g P m}^{-2} \text{ yr}^{-1}$ in the form of $\text{Ca}(\text{H}_2\text{PO}_4)_2 \cdot \text{H}_2\text{O}$. These amounts were chosen to alleviate any N and P limitation imposed on this ecosystem and are based on previous amounts of fertilizers used in nutrient limitation studies with this same purpose in the Arctic (Jonasson, 1992; Chapin et al., 1995).

2.3 Vegetation measurements

The vegetation in each plot was measured in July 2008 (prior to the first fertilization), 2010, 2012, 2015, 2018 and 2022 by means of point intercept analysis, a method described by Goodall (1952). A straight line of ten downward-facing pins was placed at the edge of each plot and moved ten times within the plot, resulting in a grid with a total of 100 points where measurements of species presence was recorded. Each time a vascular plant touched a pin the species was noted, including when the same individual plant touched the pins multiple times. Further, the bottom hit of each pin (e.g. moss, lichen, litter, rock, bare soil, etc.) was recorded. The presence of any additional vascular plant species that occurred in a plot that was not recorded by the point intercept method was also registered to be able to calculate the species richness in each plot. Plants that could not be identified to species were identified to genus level. Likewise, any genus that could not be identified was classified at a plant functional group level. Finally, each species was assigned one of five functional groups based on Shaver & Chapin (1991) and Sundqvist et al. (2014a): deciduous shrubs, evergreen shrubs, forbs, graminoids and pteridophytes.

To correct for occasional deviations from the 100 pins due to errors made in the field, the number of total vascular plant hits per species was divided by the total number of bottom hits and multiplied by 100, assuming that the relative occurrence of each species was similar across the entire plot. Additional species in each plot were included in the data as one divided by the total number of corrected vascular plant hits to give each additional species the same relative occurrence per plot per year.

2.4 Data analysis

All analyses were performed in R version 4.2.1 (R Core Team, 2022). For all statistical tests, $\alpha < 0.05$ was used as a threshold level for significance. All graphs were created with the “ggplot2” package in R (Wickham, 2016).

2.4.1 Plant community composition

To investigate the effects of fertilization treatment on the proportion of different plant functional groups, I created stacked bar plots showing the relative abundance of each functional group for each year per vegetation type, elevation and treatment. To further study the effects of fertilization treatment on an individual species level, I used non-metric multidimensional scaling (NMDS), an ordination method that arranges original data points in a multidimensional space as accurately as possible

based on pair-wise distances between data points (Kruskal, 1964). I performed the NMDS with a Bray-Curtis dissimilarity matrix on the pinpoint data (excluding additional species) for all years and both vegetation types. I used the *metaMDS* function in the “vegan” package in R (Oksanen et al., 2022) to perform the NMDS analysis and I used a Shepard diagram and goodness of fit test to assess how well data points in a two-dimensional space represented the original data. Since I found a clear separation between the community compositions at each vegetation type and elevation, I subsequently performed separate NMDS analyses for each vegetation type and elevation to further investigate the effects of fertilization treatment on community composition. I then performed a PERMANOVA analysis with the *adonis2* function in the “vegan” package in R (Oksanen et al., 2022) to test for differences between the species composition of plots that received a different treatment at each vegetation type and elevation in 2008 and 2022. The PERMANOVA was based on a Bray-Curtis distance and used to test if the centroids of each treatment at a given vegetation type, elevation and year differ significantly from each other. Additionally, I used a PERMANOVA to further investigate if the species composition of plots within a given treatment, vegetation type, and elevation significantly changed over time.

2.4.2 Diversity indices

To explore how plant species richness and diversity were affected by fertilization, I analyzed the effects of fertilizer treatment, vegetation type, elevation and time on species richness, Simpson’s diversity index (D) and the Shannon-Wiener diversity index (H'). Species richness was counted as the total number of species present per plot. Simpson’s diversity index and the Shannon-Wiener diversity index were calculated with the “vegan” package in R (Oksanen et al., 2022). Simpson’s D measures the probability that two randomly chosen individuals from one sample belong to the same species (Peet, 1974), with values ranging between 0 and 1, where a lower value indicates a larger diversity. The Simpson’s diversity index is calculated as follows (Oksanen et al., 2022):

$$D = \sum_{i=1}^n p_i^2 \quad [1]$$

Where n is the total number of species and p_i is the proportional abundance of species i .

On the other hand, the Shannon-Wiener index measures the uncertainty about the species identity of an individual within a sample, which depends on species evenness and sample size (i.e. uncertainty increases with evenness and sample size) (Peet, 1974). Values of the Shannon-Wiener index generally range between 1.5 and

3.5, where lower values indicate a higher diversity. The Shannon diversity index is calculated as follows (Oksanen et al., 2022):

$$H' = - \sum_{i=1}^n p_i \ln p_i \quad [2]$$

Where n is the total number of species and p_i is the proportional abundance of species i .

The data was tested for the assumptions of normality and heterogeneity by means of the combination of a histogram and Shapiro-Wilk test. Since there was a clear variation in species composition among plots and blocks at the start of the experiment, I decided to normalize the data for species richness, Simpson's diversity and Shannon diversity on a plot level to the 2008 value. I did this by subtracting the 2008 value for species richness and both diversity indices per plot from all following years in the same plot. This allowed me to compare differences in the direction of change over time between different treatments.

I used linear mixed models (LMMs) with the normalized data to assess the effects of vegetation type, elevation, time, N and P fertilization and their interactions on species richness, Simpson's diversity index and the Shannon-Wiener diversity index. Plot nested in block was included as a random factor in the model to account for natural variation between plots over time. I used the *lmer* function within the "lme4" package in R to create the LMMs (Bates et al., 2014). Since vegetation type strongly interacted with elevation, time, N and P, I also ran the models separately for heath and meadow. The LMMs were followed by a type III ANOVA with Kenward-Roger's approximation for degrees of freedom. The ANOVA results were used to evaluate the amount of variance in species richness, Simpson's diversity and Shannon diversity that was explained by each fixed factor and the interactions between these factors.

3. Results

3.1 Community composition

3.1.1 Functional group level

Changes occurred in the relative abundance of plant functional groups in both heath and meadow along the elevational gradient (500, 800, 1000 meters) after fertilization with N and P (Figure 3). In the heath vegetation, a large shift in plant community composition was found in N and N+P fertilized plots at all elevations, but the strongest and fastest shift occurred at 500 meters and in the N+P treatment. Over time, at all elevations in the heath the relative abundance of graminoids increased with N and N+P fertilization, whereas the relative abundance of shrubs decreased, but the magnitude of this shift in functional groups was strongest at 500 meters elevation. At 500 meters, the proportion of graminoids in N and N+P fertilized plots increased rapidly in the first eight years of fertilization, whereas at 800 and 1000 meters, graminoids in N and N+P fertilized plots clearly started to increase after 11 and 15 years of fertilization, respectively. In addition, at 800 and 1000 meters, there was an increase in forbs in the N+P treatment after 15 years of fertilization. In the first years after the start of the experiment in 2008, the relative abundance of pteridophytes in the heath increased slightly in the control, P and N treatments at 500 meters, but they remained nearly absent in the N+P treatment.

For the meadow vegetation, over time the greatest shift in plant functional group composition was found in the N and N+P fertilized plots, but this response was weaker in the meadow than in the heath vegetation. The strongest shift in plant functional group composition in the meadow occurred in the N and N+P fertilized plots at 800 and 1000 meters, compared to little response to any fertilization treatment at 500 meters. At 800 and 1000 meters, the relative abundance of graminoids increased in the first five years and after 11 years of N and N+P addition, whereas at 500 meters, the relative proportion of plant functional groups did not change over time. Unlike the heath, the shift in plant functional group composition in the meadow showed little difference between the N and N+P treatments. In both N and N+P fertilized plots at 800 and 1000 meters there was an increase in graminoids, together with a decrease in shrubs, although the proportion of shrubs in the meadow was low from the start of the experiment. At 800 and 1000 meters in the N+P treatment there was a clear reduction in graminoids in 2015 compared to previous years.



Figure 3: The relative proportion of plant functional groups in heath (A) and meadow (B) between 2008-2022 at 500m, 800m and 1000m elevation in control plots (C), phosphorus fertilized plots (P), nitrogen fertilized plots (N) and nitrogen and phosphorus fertilized plots (N+P).

3.1.2 Species level

Distinct differences were found between the species composition of plots in heath and meadow and between 500, 800 and 1000 meters elevation, which clearly represents the elevational gradient in this study (Figure 4). The species composition in plots in heath and meadow vegetation were significantly different from each other (PERMANOVA: $F_{1,54} = 203.01$, $p < 0.001$). In both vegetation types the species composition at 500 meters differed significantly from the vegetation at 800 and 1000 meters (PERMANOVA: $F_{1,34} = 108.86$, $p < 0.001$), but there was an overlap between plots at 800 and 1000 meters. Over time, the species composition between heath and meadow did not become more or less similar to each other.

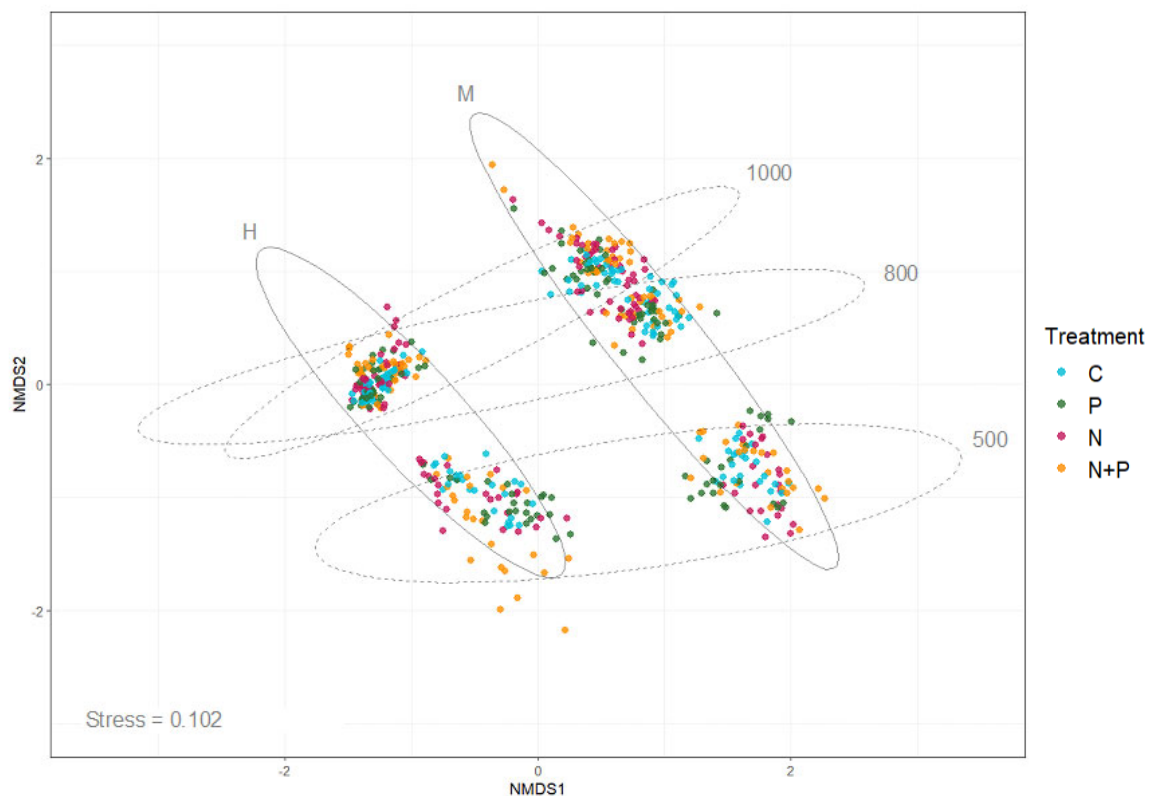


Figure 4: NMDS ordination with Bray-Curtis distance for pinpoint data for all years. Points display plots, where a smaller distance between points indicates a closer similarity in species composition. Ellipses display 95% confidence range per elevation (500, 800, 1000 meters) and vegetation type (heath and meadow). The stress value represents how well the plotted dissimilarity between plots corresponds with the original dissimilarity. A stress value around 0.1 is considered a fair fit.

Although there were initial differences between the species compositions of plots at a given elevation and vegetation type, there were no significant differences in 2008 between plots that received different nutrient addition treatments (Appendix

B). The PERMANOVA showed that over time, significant changes occurred in the species composition of plots within each fertilization treatment per vegetation type and elevation. Between 2008 and 2022, the species composition in control plots changed significantly at all elevations in the meadow and at 500 meters in the heath (Table 1). In P fertilized plots, there were significant changes in the species composition of plots in the meadow at 800 and 1000 meters and in the heath at 800 meters (Table 1). In N fertilized plots, there was a significant change in the species composition of plots in the meadow at 800 and 1000 meters and in the heath at 500 and 800 meters (Table 1). The species composition in N+P fertilized plots changed significantly at all elevations in both heath and meadow (Table 1).

*Table 1: PERMANOVA testing differences in the species composition over time (2008, 2010, 2012, 2015, 2018, 2022) for each treatment, vegetation type and elevation. Only significant results are displayed. Stars indicate the significance level: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.*

Treatment	Vegetation type	Elevation	PERMANOVA	
			F	p
C	Heath	500	2.14	0.012*
	Meadow	1000	2.01	0.008**
		800	1.40	0.048*
		500	1.86	0.019*
P	Heath	800	2.33	0.005**
	Meadow	1000	1.71	0.015*
		800	2.49	<0.001***
N	Heath	800	2.50	0.018*
		500	9.87	<0.001***
	Meadow	1000	2.75	<0.001***
		800	2.80	<0.001***
N+P	Heath	1000	3.18	<0.001***
		800	3.70	<0.001***
		500	20.00	<0.001***
	Meadow	1000	4.72	<0.001***
		800	2.59	<0.001***
		500	2.43	<0.001***

In 2022, there were large differences in species composition between plots that received different nutrient addition treatments at all elevations and vegetation types, except for the plots at 500 meters in the meadow (Figure 5).

In the heath at 1000 meters, the shrubs *Cassiope tetragona*, *Empetrum nigrum* and *Vaccinium vitis-idaea* were present in all control and fertilization treatments, but were more common in control and P fertilized plots than N and N+P fertilized plots (Figure 5A). The shrub *Betula nana* appeared in all plots, but was slightly more abundant in N and N+P fertilized plots than in control and P fertilized plots. Further, *Calamagrostis lapponica* was frequently registered in N and N+P fertilized plots, but less abundant in control and P fertilized plots. In addition, *Rubus chamaemorus* was abundant in one N+P fertilized plot, but absent in all other plots.

In the meadow at 1000 meters, all plots were associated with the presence of the graminoids *Carex bigelowii* and *Calamagrostis lapponica*, but these were much more abundant in N and N+P fertilized plots than in control and P fertilized plots (Figure 5B). Moreover, in N+P fertilized plots the graminoid *Calamagrostis lapponica* was dominant, whereas in N fertilized plots *Calamagrostis lapponica* and *Carex bigelowii* were equally abundant. The graminoid *Festuca vivipara* was only present in control and P fertilized plots, with the exception of one N fertilized plot. In addition, the forbs *Bistorta vivipara*, *Saussurea alpina* and *Viola biflora* were present in all treatments, but had a relatively low cover in all plots.

In the heath at 800 meters, the shrubs *Empetrum nigrum* and *Vaccinium vitis-idaea* were present in all plots, but were more common in control and P fertilized plots than in N and N+P fertilized plots (Figure 5C). *Betula nana* appeared in all plots, but was slightly more common in N and N+P fertilized plots than in control and P fertilized plots. Furthermore, the graminoid *Calamagrostis lapponica* was registered in all plots, but had a high abundance in N+P fertilized plots, compared to a low abundance in control, P and N fertilized plots.

In the meadow at 800 meters, all treatments were associated with a similar absolute abundance of the forbs *Bistorta vivipara* and *Viola biflora*, but these were relatively more abundant in control and P fertilized plots (Figure 5D). In N and N+P fertilized plots there was a high abundance of the graminoids *Calamagrostis lapponica* and *Carex bigelowii*, which had a similar abundance in N+P fertilized plots, but *Carex bigelowii* dominated in N fertilized plots. Furthermore, the graminoid *Anthoxanthum alpinum* was more abundant in N and N+P fertilized plots than in control and P fertilized plots, but less abundant than *Calamagrostis lapponica* and *Carex bigelowii*.

In the heath at 500 meters, the graminoid *Deschampsia flexuosa* was present in all plots, but dominated in N and, to an even greater extent, in N+P fertilized plots. The shrub *Empetrum nigrum* was present in all control plots and two P fertilized plots, but absent in N and N+P fertilized plots. The shrub *Vaccinium myrtillus* was

present in all plots, but was more common in control, P and N fertilized plots than in N+P fertilized plots (Figure 5E).

In the meadow at 500 meters, the forbs *Cicerbita alpina*, *Geranium sylvaticum* and *Rumex acetosa* were present in all treatments, as well as the graminoid *Milium effusum* and the pteridophytes *Equisetum* sp. and *Gymnocarpium dryopteris* (Figure 5F).

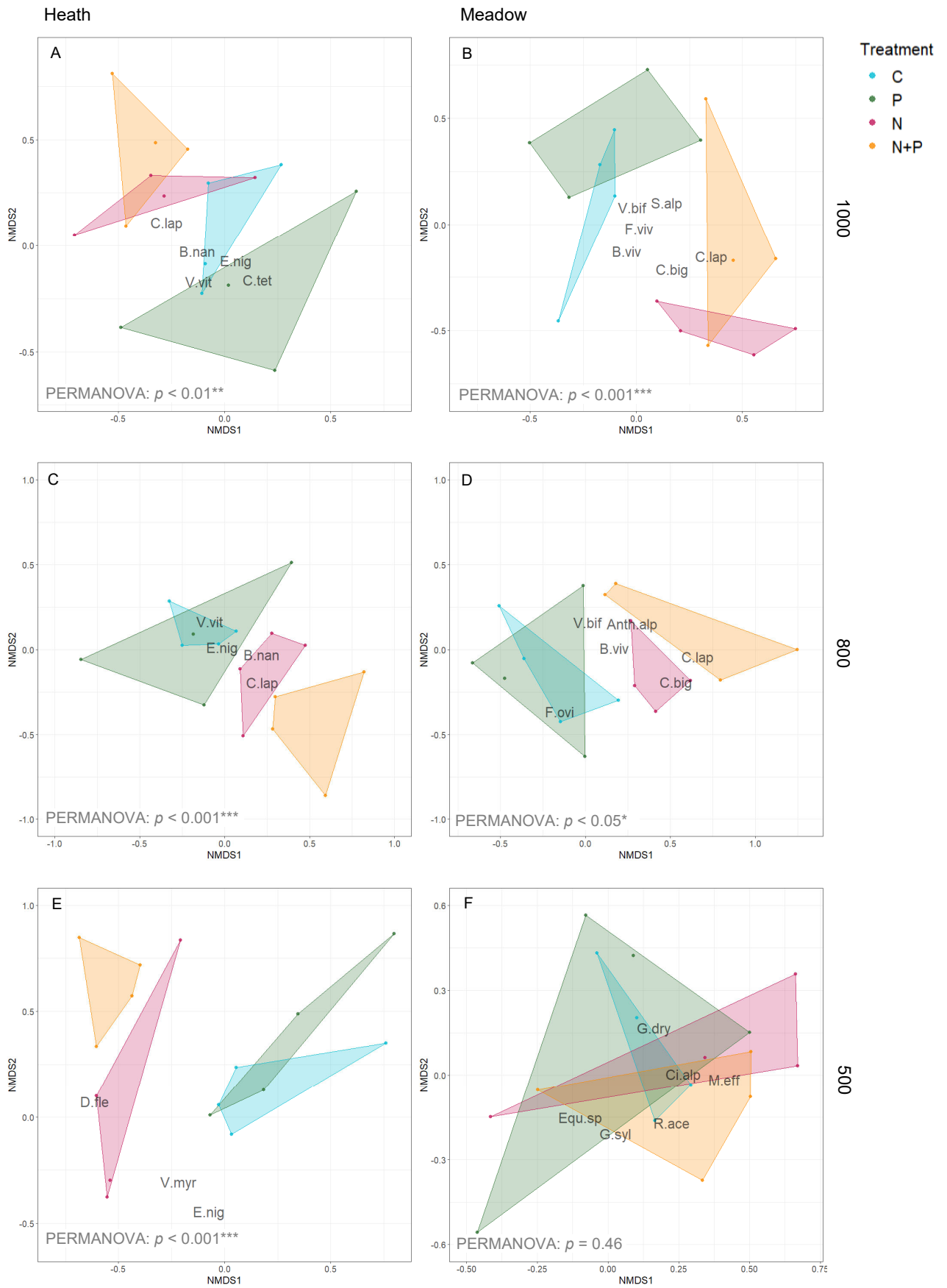


Figure 5: NMDS ordination with Bray-Curtis distance for pinpoint data from all years, but where the image is only displaying plant community data for 2022. Points display plots, where a smaller distance between points indicates a closer similarity in species composition. Species scores are the weighted average plot scores with weights based on the abundance of species per plot. In each panel (A-F), species are shown which had a cover > 5% in that vegetation type and elevation: *Anth.alp* = *Anthoxanthum alpinum*, *B.nan* = *Betula nana*, *B.viv* = *Bistorta vivipara*, *C.big* = *Carex bigelowii*, *C.lap* = *Calamagrostis lapponica*, *C.tet* = *Cassiope tetragona*, *Ci.alp* = *Cicerbita alpina*, *D.fle* = *Deschampsia flexuosa*, *E.nig* = *Empetrum nigrum*, *Equ.sp* = *Equisetum sp.*, *F.ovi* = *Festuca ovina*, *F.viv* = *Festuca vivipara*, *G.dry* = *Gymnocarpium dryopteris*, *G.syl* = *Germanium sylvaticum*, *M.eff* = *Milium effusum*, *R.ace* = *Rumex acetosa ssp. lapponica*, *S.alp* = *Saussurea alpina*, *V.bif* = *Viola biflora*, *V.myr* = *Vaccinium myrtillus*, *V.vit* = *Vaccinium vitis-idaea*

Note: axes cannot be compared between panels (A-F), because each panel displays a separate NMDS analysis.

3.2 Diversity indices

The LMMs revealed different responses of species richness, Simpson's diversity and Shannon diversity to N and P addition in heath and meadow vegetation across the elevational gradient over the duration of the study period (2008-2022; Figure 6-8, Table C.1-3).

3.2.1 Species richness

In total 106 species were recorded in the study system, of which 46 species occurred in the heath and 100 species occurred in the meadow (Appendix A). On average, there were 8.84 species per plot in the heath and 18.87 species per plot in the meadow. In the heath, the average number of species per plot was 10.38 at 500 meters, 6.96 at 800 meters and 9.20 at 1000 meters. In the meadow, the average number of species per plot was 15.83 at 500 meters, 22.55 at 800 meters, and 18.23 at 1000 meters. In both vegetation types and at all elevations, the species richness was lower in N and N+P fertilized plots than in control and P fertilized plots, with the exception of the heath at 1000 meters (Table 2).

Table 2: The mean species richness per vegetation type, elevation and treatment over the duration of the study period (2008-2022).

Vegetation type	Elevation	Treatment	Species richness	
			Mean	SD
Heath	1000	C	9.67	2.94
		P	9.00	1.98
		N	8.82	1.19
		N+P	9.67	1.58
	800	C	7.29	0.95
		P	7.25	1.03
		N	6.67	1.24
		N+P	6.63	0.77
	500	C	11.04	2.61
		P	12.13	2.56
		N	9.50	3.12
		N+P	8.80	2.14
Meadow	1000	C	18.58	2.64
		P	19.25	4.02
		N	17.67	3.77
		N+P	17.42	4.29
	800	C	23.96	3.93
		P	24.58	4.69
		N	21.46	4.35
		N+P	20.21	4.93
	500	C	16.83	3.69
		P	16.71	2.42
		N	15.26	2.26
		N+P	15.17	3.56

Overall, the species richness was significantly influenced by the interaction between vegetation type, elevation, time and N fertilization, whereby heath and meadow showed different temporal responses at different elevations to N addition. Further, vegetation type also significantly interacted with time, N and P fertilization (Table C.1; Figure 6).

Specifically for the heath, there was a significant interaction between N addition, elevation and time, whereby N addition had a negative effect on species richness

only at the low elevation over the study period (Figure 6A). Further, although the response to P addition varied among plots, species richness declined slightly in most P fertilized plots in the heath (Figure 6A-C).

In the meadow, N and P fertilization interacted significantly with time, with generally larger negative effects of N addition on species richness when N was added together with P. At all elevations, the largest decline in species richness with N and N+P addition occurred in the first eight years of fertilization (Figure 6D-F). Further, the effect of N addition in the meadow interacted significantly with elevation and time, whereby over the duration of the study period N addition had a negative effect on species richness at all elevations (Figure 6D-F), but this effect was larger and occurred faster at 800 and 1000 meters than at 500 meters. Moreover, during the study period changes in species richness showed different patterns at different elevations. At 500 meters, the control and N+P fertilized plots showed a decrease in species richness between 2012 and 2015, whereas the species richness in the P and N treatments changed little over time (Figure 6D). At 800 meters there was a clear decrease in species richness in all plots between 2012 and 2015, whereafter species richness increased in all treatments. Further, in 2022 the P treatment showed a larger species richness than the control, N and N+P fertilized plots at 800 m (Figure 6E). At 1000 meters, there was a reduction in species richness in N and N+P fertilized plots until 2015, after which richness did not change much (Figure 6F). At all elevations, the species richness changed much more over time in the meadow than in the heath.

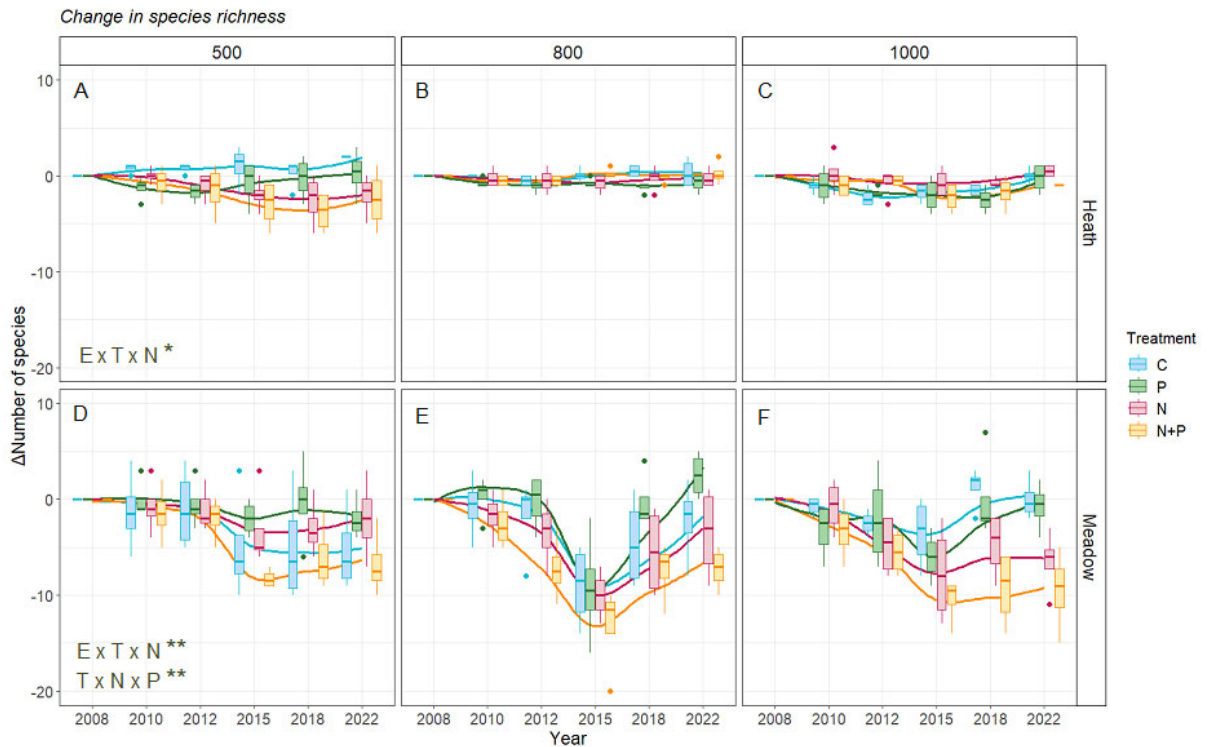


Figure 6: The change in species richness over time per treatment, elevation and vegetation type. Values for each year are compared on a plot level to the 2008 value. Boxes represent the range between the 1st and 3rd quantile and whiskers show the upper and lower quantiles. Outliers are displayed as dots. Significant interaction effects found in the LMMs with elevation (E), time (T), nitrogen fertilization (N) and phosphorus fertilization (P) as fixed factors, and plot nested in block as a random factor, are displayed separately for heath and meadow. Stars indicate the significance level of an interaction effect: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

3.2.2 Simpson's diversity index

Simpson's diversity index was significantly influenced by the interaction between vegetation type, elevation, time, N and P fertilization (Table C.1), whereby heath and meadow showed different responses to nutrient addition along the elevational gradient over the study period (Figure 7).

In the heath, the effect of N addition on Simpson's diversity interacted significantly with elevation and time, whereby N addition had a negative effect on Simpson's diversity over the study period only at the low elevation (500m). Further, the effect of N and P addition interacted significantly with elevation, where N addition at 500 meters elevation had the strongest negative effect when N was added together with P (Figure 7A). Moreover, the effect of P addition interacted significantly with time, whereby Simpson's diversity declined over time in most P fertilized plots, although

there was high variation among plots. Specifically at 800 meters, the P addition treatment had a negative effect on Simpson's diversity from 2018 onwards (Figure 7B), while the other treatments showed little effect on diversity.

In the meadow, the effect of N and P fertilization on Simpson's diversity interacted significantly with elevation and time, whereby N addition had a negative effect on Simpson's diversity at 800 and 1000 meters elevation only, especially when N was added in combination with P. At 800 meters, the fastest decline in diversity occurred in N+P fertilized plots during the first four years of fertilization, after which diversity increased slightly. In comparison, in N fertilized plots diversity continuously declined from the fourth year of fertilization onwards, resulting in the lowest Simpson's diversity at 800 meters in N fertilized plots at the end of the study period (Figure 7E). At 1000 meters, Simpson's diversity declined only after seven years of N and N+P fertilization (Figure 7F).



Figure 7: The change in Simpson's diversity index (D) over time per treatment, elevation and vegetation type. Values for each year are compared on a plot level to the 2008 value. Boxes represent the range between the 1st and 3rd quantile and whiskers show the upper and lower quantiles. Outliers are displayed as dots. Significant interaction effects found in the LMMs with elevation (E), time (T), nitrogen fertilization (N) and phosphorus fertilization (P) as fixed factors, and plot nested in block as a random factor, are displayed separately for heath and meadow. Stars indicate the significance level of an interaction effect: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

3.2.3 Shannon-Wiener diversity index

The Shannon-Wiener diversity index was significantly influenced by the interaction between vegetation type, elevation, N and P fertilization (Table C.1), whereby heath and meadow showed different responses to nutrient addition along the elevational gradient (Figure 8). Furthermore, the effect of N and P addition on Shannon diversity in both vegetation types interacted significantly with elevation and time, where different responses to nutrient addition were found along the elevational gradient over time.

Specifically for the heath, the response of Shannon diversity to N and P addition interacted significantly with elevation, whereby N addition declined Shannon diversity only at the low elevation, especially in combination with P. At 500 meters, diversity declined rapidly in N and N+P fertilized plots in the first seven years of fertilization, after which diversity did not change much (Figure 8A). Nitrogen addition also interacted significantly with elevation and time, where over time the negative effect of N addition on Shannon diversity was only visible at 500 meters. Further, P addition interacted significantly with time, where P addition slightly decreased Shannon diversity over the study period.

In the meadow, N and P addition interacted significantly with elevation and time, whereby N addition had a negative effect on Shannon diversity at all elevations over the study period, especially in combination with P, but this effect was strongest at the high elevations. At 500 meters, diversity declined in the control and all fertilization treatments, revealing little difference between fertilization treatments (Figure 8D). At 800 meters in N+P fertilized plots there was a strong decline in Shannon diversity directly after the start of the experiment, whereas in N fertilized plots diversity started to decline only after four years of fertilization (Figure 8E). At 1000 meters, Shannon diversity declined in N and N+P fertilized plots only after four years of fertilization, but the strongest decline occurred in N+P fertilized plots (Figure 8F).



Figure 8: The change in Shannon-Wiener diversity index (H') over time per treatment, elevation and vegetation type. Values for each year are compared on a plot level to the 2008 value. Boxes represent the range between the 1st and 3rd quantile and whiskers show the upper and lower quantiles. Outliers are displayed as dots. Significant interaction effects found in the LMMs with elevation (E), time (T), nitrogen fertilization (N) and phosphorus fertilization (P) as fixed factors, and plot nested in block as a random factor, are displayed separately for heath and meadow. Stars indicate the significance level of an interaction effect: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

4. Discussion

In this study, I investigated how heath and meadow vegetation in the subarctic tundra have responded to 15 years of N and P addition along an elevational gradient. The combination of a long-term fertilization experiment with an elevational gradient enabled me to explore how nutrient limitation interacts with climate to affect plant community dynamics. Therefore, this study gives a unique insight into the possible effects of climate change on subarctic tundra vegetation.

4.1 Nitrogen and phosphorus dynamics

Based on early results from this study system (Sundqvist et al., 2014a) and other fertilization experiments in the subarctic tundra (Shaver & Chapin, 1980; Aerts & Chapin, 1999; Jonasson et al., 1999), it was expected to over time find the greatest response to fertilization in plots that were fertilized with N, especially in combination with P. Overall, I found large shifts in plant community composition and diversity in N and N+P fertilized plots in both vegetation types, compared to a small effect of P addition, which supports this first hypothesis. However, although N addition drove changes in community composition and diversity in both vegetation types, P addition appears to have a more complex effect on the subarctic tundra (McLaren & Buckeridge, 2019). This is reflected by a reduction in diversity (Simpson's and Shannon diversity) with the addition of P (without N addition) over time in the heath, but an increase in species richness and Shannon diversity in the meadow, at 800 meters. A possible explanation for the differential responses of heath and meadow to P addition is the higher fungal to bacterial ratio in soils in the heath than in the meadow (Sundqvist et al., 2011). Neurauter et al. (2023) found that bacteria in tundra soils are limited by carbon, N and P, whereas fungi are limited only by carbon and N, which implies that meadow vegetation is stronger P limited than heath vegetation. This is in line with findings by Giesler et al. (2012), who found that N:P ratios in plant tissue of the same species was lower in the heath than in the meadow, suggesting that P-uptake relative to N is higher in the heath. Thus, alleviation of P limitation in the meadow could favor P-rich species. To illustrate, I found that P fertilization in the meadow generated an increase in forbs *Cerastium alpinum* and *Ranunculus nivalis*, compared to no effect of P addition on graminoids, thereby increasing species richness and diversity. On the other hand,

the decrease in species diversity in the heath with P addition probably occurred because of a decrease in the deciduous shrub *Betula nana* compared to control plots, whereas evergreen shrubs appear to be unaffected by P addition. Since N:P ratios in plant tissue vary less than soil N:P ratios (Bowman, 1994), it is possible that P addition without N leads to an imbalance in N:P ratio in species that have a high demand for N, thereby increasing N-limitation. Possibly, the high nutrient demand and rate of nutrient uptake in deciduous shrubs relative to evergreen shrubs induces an N-limitation on *Betula nana*, when P is added without N.

Besides individual species responses to P addition, I found significant interactive effects between N and P addition, in combination with vegetation type, elevation and time, indicating that the effects of N versus P addition are mediated by the other nutrient. While several studies suggest that there is an independent co-limitation of N and P in the subarctic tundra (Bowman, 1994; Shaver & Chapin, 1995; Giesler et al., 2012), there might also be an interaction between N and P availability (Vitousek et al., 2010). In a factorial fertilization study in the subarctic tundra, Zamin et al. (2014) found an interaction between N and P, whereby P addition increased soil available N, possibly due to increased rates of N fixation (e.g. Eisele et al., 1989). On the other hand, in two meta-analyses it was found that N addition did not enhance P limitation in the tundra (Li et al., 2016; Deng et al., 2017). This implies that P addition has the potential to stimulate N fixation, although this might only apply under conditions of sufficient soil moisture (Zielke et al., 2005) and the presence of N-fixing organisms (Diáková et al., 2016).

4.2 Changes in community composition

Second, I expected to find a shift in plant community composition in N and N+P fertilized plots from slow growing species towards faster growing plants, and that this shift would be greater in the heath than in the meadow. In line with this hypothesis, I found that in both vegetation types, the shift in plant community composition that occurred in N and N+P fertilized plots was characterized by a loss of slow-growing species and an increase of graminoids, but the shift in plant functional groups was stronger in the heath than in the meadow. Further, changes in species composition in both vegetation types were strongly mediated by a few individual species. After 15 years of nutrient addition, one or two graminoid species dominated in almost all N and N+P fertilized plots. A similar pattern was found by Press et al. (1998) in a fertilization experiment in subarctic heath, where the abundance of the graminoid *Calamagrostis lapponica* increased with a factor 18 in plots that were fertilized with NPK, but other graminoid species did not show a clear response to nutrient addition. Moreover, I found that different species dominated in heath versus meadow and at low versus high elevations. For example,

at the low elevation in the heath, N and N+P fertilized plots were almost entirely dominated by *Deschampsia flexuosa*, which was also found by Nilsson et al. (2002) after eight years of N addition in dwarf shrub dominated alpine tundra. At the high elevations in the heath, N and N+P fertilized plots were dominated by *Calamagrostis lapponica*, which is in line with several other fertilization experiments in subarctic heath (Press et al., 1998; Little et al., 2015). In the meadow, N addition at the high elevations led to a large increase in *Calamagrostis lapponica* together with *Carex bigelowii*, but the associated shift in plant community composition was not as large as in the heath, which is in agreement with Little et al. (2015). These results highlight the differential responses of species and vegetation types to nutrient addition at different elevations. They imply that under different conditions of temperature (i.e. temperature is higher at lower elevations) and soil moisture (i.e. moisture is higher in meadow than heath), different species respond to enhanced nutrient availability, but that the general responses among plant functional groups are more consistent among vegetation types and elevations.

The extent to which species composition changes with nutrient addition is strongly influenced by the initial community composition in each plot (Gasarch & Seastedt, 2015), as well as the dominant mechanisms for seed dispersal and germination potential of different species (Müller et al. 2011). For example, *Deschampsia flexuosa* is a common graminoid at the low elevation in the heath, but this species is highly competitive only at high nutrient concentrations (Aerts & Chapin, 1999). Furthermore, the seeds of *Deschampsia flexuosa* are mainly dispersed with the wind (Scurfield, 1954), which is an effective way to quickly spread throughout an area. Thus, although *Deschampsia flexuosa* was present in all plots at the low elevation in the heath at the start of the experiment, this graminoid could only dominate when nutrients were added to the system. Additionally, the importance of initial community composition is also reflected in the responses of less common species to nutrient addition. For example, during 15 years of N+P addition in the heath at 1000 meters, the abundance of *Rubus chamaemorus* increased from 0.7 to 39% cover, but this happened only in the plot where this species was present from the start of the experiment. In contrast to *Deschampsia flexuosa*, the seed dispersal of *Rubus chamaemorus* is generally low, because this depends on the presence of different animals, which eat the plant's berries and spread its seeds in their droppings (Campbell et al., 2003). However, whether or not *Rubus chamaemorus* produces berries is dependent on pollination by insects (Brown & McNeil, 2009). Therefore, the spread of *Rubus chamaemorus* depends on both animals and pollinating insects, which probably hinders the establishment of *Rubus chamaemorus* in new areas. Thus, seed dispersal is a strong driver of plant community composition (Lenoir et al., 2012), but dominant mechanisms for

dispersal differ among species, which favours the establishment of some species over others.

4.3 Long-term effects of nutrient addition

Third, in the most responsive communities (i.e. low elevation in the heath and high elevations in the meadow; Sundqvist et al., 2014a) I expected to find a shift in community composition after 15 years of nutrient addition towards vegetation almost completely dominated by graminoids, compared to little effect in the least responsive communities. I found strong interaction effects between vegetation type, elevation, time and N addition on species richness, Simpson's diversity and Shannon diversity, which indicates that the effect of N addition over time differs per elevation and vegetation type. In the heath, the plots at the low elevations that were fertilized with N or N+P were almost entirely dominated by the graminoid *Deschampsia flexuosa*, and in the meadow N and N+P fertilized plots were dominated by graminoids *Calamagrostis lapponica* and *Carex bigelowii*, although the relative cover of graminoids was lower in the meadow than the heath. Thus, I found strong support for this third hypothesis. Moreover, after ten years of nutrient addition, similar changes occurred in the species composition and diversity in the less responsive communities in the heath, but not in the meadow. Probably, this difference between vegetation types occurred because plots at the low elevation in the meadow were already rich in nutrients at the start of the experiment, whereas the heath at high elevations is strongly nutrient and temperature limited (Sundqvist et al., 2014a), which likely delayed the vegetation response to nutrients.

Few studies have explored the long-term effects of nutrient addition on the tundra (Wardle et al., 2013; DeMarco et al., 2014; McLaren & Buckeridge, 2019), and even less studies present vegetation measurements at multiple moments in time (Wardle et al., 2013). Although it has been suggested that short-term result predict the direction of long-term change that occurs with nutrient addition (McLaren & Buckeridge, 2019), I found that different species responded to increased nutrient availabilities at different moments in time. For example, the abundance of *Anthoxanthum alpinum* in the meadow at 800 meters increased strongly in the first five years of combined fertilization with N+P, but in the following years declined in abundance, while *Calamagrostis lapponica* and *Carex bigelowii* became much more abundant in later years. Within plant functional groups, individual species differ in terms of growth strategies (Wright et al., 2004; Freschet et al., 2010), with faster growing species in the subarctic tundra generally being associated with higher soil N concentrations (Freschet et al., 2010). Probably, species with more acquisitive growth strategies therefore have the capacity to respond quicker to nutrient addition than species with more conservative growth strategies. Moreover,

these results highlight that, although short-term results indicated the shift in plant functional groups that occurred on the long-term, the short-term responses of individual species to nutrient addition did not mirror long-term responses. Therefore, more studies should investigate the responses of individual species to nutrient addition over time.

Additionally, knowledge on long-term temporal patterns is important to better understand how fertilization experiments relate to natural ecosystem dynamics, through a reflection of natural disturbances that occur within an ecosystem. For example, in 2015 the vegetation at 800 meters in the meadow was highly affected by a lemming peak, leading to a lower species richness and diversity compared to other years. Lemming peaks are a natural cyclical occurrence in the arctic tundra (Oksanen & Oksanen, 1992), and have been found to promote vegetation diversity (Kaarlejärvi et al., 2017). However, meadow vegetation appeared to be more affected by the lemming peak than heath vegetation. Thus, future studies could consider studying the possible interactive effects between vegetation type, fertilization treatment and lemming abundance on tundra plant communities.

4.4 Natural nutrient dynamics

Natural increases in nutrient availability resulting from climate change may differ from fertilization with high doses of nutrients, such as this present study, with the aim to fully alleviate N- and P-limitation (Prager et al., 2017). Low amounts of fertilizer can already generate substantial decreases in plant diversity (Prager et al., 2017) and increases in biomass (Zamin et al., 2014), although it is unclear how different plant functional groups and individual species respond to low versus high doses of fertilizer. Furthermore, in an observational study, Spasojevic et al. (2013) found that alpine tundra vegetation showed non-directional changes during a time period of 21 years. This highlights the complexity of ecological research and implies that the vegetation in field experiments is constantly changing, even without field manipulations. Thus, to be able to derive implications from fertilization studies, it is important to understand how fertilization relates to natural nutrient dynamics in tundra ecosystems.

Atmospheric N deposition is generally an important source of N in ecosystems around the world, and although atmospheric N deposition is relatively small at high latitudes (Jonasson & Michelsen, 1996), this source of N is found to increase in the Arctic along with increases in greenhouse gas emissions (Laj et al., 1992). Additional important nutrient sources are urine and feces from animals (Barthelemy et al., 2015, 2018). Furthermore, animal and insect outbreaks can lead to a dieback of plant biomass, which when decomposed creates an influx of nutrients into the

system (Oksanen & Oksanen, 1992; Parker et al., 2017). For example, in this study, the plots located in the birch forest (500m) were subject to an outbreak of *Epirrita autumnata* in 2012 and 2022, which led to a high tree mortality. Following the outbreak in 2012, Parker et al. (2017) found an increase in soil inorganic N. In response to the increased nutrient availability, I found that the species composition and species richness in control plots in the heath showed a pattern similar to N and N+P fertilized plots. Thus, natural nutrient dynamics clearly influence plant community dynamics and thereby their responses to fertilization. Therefore, long-term fertilization studies, which explore the effects of nutrient addition across different environmental conditions, give a more complete understanding of different factors that influence long-term plant community responses to increased nutrient availability.

5. Conclusion

The results from this study show the high complexity of subarctic tundra ecosystems, where small-scale differences in vegetation type have a large impact on the overall responses of tundra vegetation to nutrient addition and elevation-associated temperature over time. In both heath and meadow vegetation, N was the main limiting nutrient, but combined fertilization with N and P generated the greatest change in plant community composition, whereby shrubs were replaced by one or two dominant graminoids, which was associated with a decline in species richness and diversity. Over time, I found larger shifts in plant community composition in the nutrient-poor heath, but stronger declines in species richness in the nutrient-rich meadow. Furthermore, temperature showed to be a limiting factor for plant growth in the heath, whereby low temperatures associated with high elevations coincided with delayed responses to increased nutrient availability. Based on the results of this study, it can be expected that enhanced N availability in nutrient-poor heath will generate a shift from evergreen and deciduous shrubs towards graminoids, and this shift will be greater and occur faster under higher temperatures. In comparison, nutrient-rich meadow vegetation is expected to shift from a diverse plant community to a community dominated by a few individual graminoids. Lastly, additional long-term fertilization studies and fertilization studies based on different doses of nutrient addition are necessary to better understand the responses of tundra vegetation, especially on a species level, to increased nutrient availability over time.

References

- ACIA (2005). Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.
- Aerts, R. & Chapin, F.S. (1999). The Mineral Nutrition of Wild Plants Revisited: A Re-evaluation of Processes and Patterns. In: Fitter, A.H. & Raffaelli, D.G. (eds) *Advances in Ecological Research*. Academic Press. 1–67. [https://doi.org/10.1016/S0065-2504\(08\)60016-1](https://doi.org/10.1016/S0065-2504(08)60016-1)
- Barthelemy, H., Stark, S., Michelsen, A. & Olofsson, J. (2018). Urine is an important nitrogen source for plants irrespective of vegetation composition in an Arctic tundra: Insights from a ¹⁵N-enriched urea tracer experiment. *Journal of Ecology*, 106(1), 367–378. <https://doi.org/10.1111/1365-2745.12820>
- Barthelemy, H., Stark, S. & Olofsson, J. (2015). Strong Responses of Subarctic Plant Communities to Long-Term Reindeer Feces Manipulation. *Ecosystems*, 18(5), 740–751. <https://doi.org/10.1007/s10021-015-9856-y>
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. arXiv. <http://arxiv.org/abs/1406.5823> [2023-04-11]
- Berner, L.T., Massey, R., Jantz, P., Forbes, B.C., Macias-Fauria, M., Myers-Smith, I., Kumpula, T., Gauthier, G., Andreu-Hayles, L., Gaglioti, B.V., Burns, P., Zetterberg, P., D'Arrigo, R. & Goetz, S.J. (2020). Summer warming explains widespread but not uniform greening in the Arctic tundra biome. *Nature Communications*, 11(1), 4621. <https://doi.org/10.1038/s41467-020-18479-5>
- Björk, R.G., Klemetsson, L., Molau, U., Harndorf, J., Ödman, A. & Giesler, R. (2007). Linkages between N turnover and plant community structure in a tundra landscape. *Plant and Soil*, 294(1), 247–261. <https://doi.org/10.1007/s11104-007-9250-4>
- Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Normand, S., Rüger, N., Beck, P.S.A., Blach-Overgaard, A., Blok, D., Cornelissen, J.H.C., Forbes, B.C., Georges, D., Goetz, S.J., Guay, K.C., Henry, G.H.R., HilleRisLambers, J., Hollister, R.D., Karger, D.N., Kattge, J., Manning, P., Prevéy, J.S., Rixen, C., Schaepman-Strub, G., Thomas, H.J.D., Vellend, M., Wilmking, M., Wipf, S., Carbognani, M., Hermanutz, L., Lévesque, E., Molau, U., Petraglia, A., Soudzilovskaia, N.A., Spasojevic, M.J., Tomaselli, M., Vowles, T., Alatalo, J.M., Alexander, H.D., Anadon-Rosell, A., Angers-Blondin, S., Beest, M. te, Berner, L., Björk, R.G., Buchwal, A., Buras, A., Christie, K., Cooper, E.J., Dullinger, S., Elberling, B., Eskelinen, A., Frei, E.R., Grau, O., Grogan, P., Hallinger, M., Harper, K.A., Heijmans, M.M.P.D., Hudson, J., Hülber, K., Iturrate-Garcia, M., Iversen, C.M., Jaroszynska, F., Johnstone, J.F., Jørgensen, R.H., Kaarlejärvi, E., Klady, R., Kuleza, S., Kulonen, A., Lamarque, L.J., Lantz, T., Little, C.J., Speed, J.D.M., Michelsen, A., Milbau, A., Nabe-Nielsen, J., Nielsen, S.S., Ninot, J.M., Oberbauer, S.F., Olofsson, J., Onipchenko, V.G., Rumpf, S.B., Semenchuk, P., Shetti, R., Collier, L.S., Street, L.E., Suding, K.N., Tape, K.D., Trant, A., Treier, U.A., Tremblay, J.-P.,

- Tremblay, M., Venn, S., Weijers, S., Zamin, T., Boulanger-Lapointe, N., Gould, W.A., Hik, D.S., Hofgaard, A., Jónsdóttir, I.S., Jorgenson, J., Klein, J., Magnusson, B., Tweedie, C., Wookey, P.A., Bahn, M., Blonder, B., van Bodegom, P.M., Bond-Lamberty, B., Campetella, G., Cerabolini, B.E.L., Chapin, F.S., Cornwell, W.K., Craine, J., Dainese, M., de Vries, F.T., Díaz, S., Enquist, B.J., Green, W., Milla, R., Niinemets, Ü., Onoda, Y., Ordoñez, J.C., Ozinga, W.A., Penuelas, J., Poorter, H., Poschlod, P., Reich, P.B., Sandel, B., Schamp, B., Sheremetev, S. & Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, 562(7725), 57–62. <https://doi.org/10.1038/s41586-018-0563-7>
- Blume-Werry, G., Lindén, E., Andresen, L., Classen, A.T., Sanders, N.J., von Oppen, J. & Sundqvist, M.K. (2018). Proportion of fine roots, but not plant biomass allocation below ground, increases with elevation in arctic tundra. *Journal of Vegetation Science*, 29(2), 226–235. <https://doi.org/10.1111/jvs.12605>
- Bowman, W.D. (1994). Accumulation and Use of Nitrogen and Phosphorus Following Fertilization in Two Alpine Tundra Communities. *Oikos*, 70(2), 261–270. <https://doi.org/10.2307/3545637>
- Box, J.E., Colgan, W.T., Christensen, T.R., Schmidt, N.M., Lund, M., Parmentier, F.-J.W., Brown, R., Bhatt, U.S., Euskirchen, E.S., Romanovsky, V.E., Walsh, J.E., Overland, J.E., Wang, M., Corell, R.W., Meier, W.N., Wouters, B., Mernild, S., Mård, J., Pawlak, J. & Olsen, M.S. (2019). Key indicators of Arctic climate change: 1971–2017. *Environmental Research Letters*, 14(4), 045010. <https://doi.org/10.1088/1748-9326/aafc1b>
- Bret-Harte, M.S., Mack, M.C., Goldsmith, G.R., Sloan, D.B., DeMarco, J., Shaver, G.R., Ray, P.M., Biesinger, Z. & Chapin III, F.S. (2008). Plant functional types do not predict biomass responses to removal and fertilization in Alaskan tussock tundra. *Journal of Ecology*, 96(4), 713–726. <https://doi.org/10.1111/j.1365-2745.2008.01378.x>
- Brown, A.O. & McNeil, J.N. (2009). Pollination Ecology of the High Latitude, Dioecious Cloudberry (*Rubus chamaemorus*; Rosaceae). *American Journal of Botany*, 96(6), 1096–1107
- Campbell, D.R., Rochefort, L. & Lavoie, C. (2003). Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands in Quebec. *Journal of Applied Ecology*, 40(1), 78–91. <https://doi.org/10.1046/j.1365-2664.2003.00782.x>
- Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995). Responses of Arctic Tundra to Experimental and Observed Changes in Climate. *Ecology*, 76(3), 694–711. <https://doi.org/10.2307/1939337>
- Chu, H., Neufeld, J.D., Walker, V.K. & Grogan, P. (2011). The Influence of Vegetation Type on the Dominant Soil Bacteria, Archaea, and Fungi in a Low Arctic Tundra Landscape. *Soil Science Society of America Journal*, 75(5), 1756–1765. <https://doi.org/10.2136/sssaj2011.0057>
- Danby, R.K. & Hik, D.S. (2007). Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology*, 95(2), 352–363. <https://doi.org/10.1111/j.1365-2745.2006.01200.x>
- DeMarco, J., Mack, M.C., Bret-Harte, M.S., Burton, M. & Shaver, G.R. (2014). Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra. *Ecosphere*, 5(6), art72. <https://doi.org/10.1890/ES13-00281.1>
- Deng, Q., Hui, D., Dennis, S. & Reddy, K.C. (2017). Responses of terrestrial ecosystem phosphorus cycling to nitrogen addition: A meta-analysis. *Global Ecology and Biogeography*, 26(6), 713–728. <https://doi.org/10.1111/geb.12576>

- Diáková, K., Biasi, C., Čapek, P., Martikainen, P.J., Marushchak, M.E., Patova, E.N. & Šantrůčková, H. (2016). Variation in N₂ Fixation in Subarctic Tundra in Relation to Landscape Position and Nitrogen Pools and Fluxes. *Arctic, Antarctic, and Alpine Research*, 48(1), 111–125. <https://doi.org/10.1657/AAAR0014-064>
- Eisele, K.A., Schimel, D.S., Kapustka, L.A. & Parton, W.J. (1989). Effects of available P and N:P ratios on non-symbiotic dinitrogen fixation in tallgrass prairie soils. *Oecologia*, 79(4), 471–474. <https://doi.org/10.1007/BF00378663>
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Boulanger-Lapointe, N., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Dorrepaal, E., Elumeeva, T.G., Gill, M., Gould, W.A., Harte, J., Hik, D.S., Hofgaard, A., Johnson, D.R., Johnstone, J.F., Jónsdóttir, I.S., Jorgenson, J.C., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lara, M., Lévesque, E., Magnússon, B., May, J.L., Mercado-Díaz, J.A., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Onipchenko, V.G., Rixen, C., Martin Schmidt, N., Shaver, G.R., Spasojevic, M.J., Þórhallsdóttir, Þ.E., Tolvanen, A., Troxler, T., Tweedie, C.E., Villareal, S., Wahren, C.-H., Walker, X., Webber, P.J., Welker, J.M. & Wipf, S. (2012a). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, 2(6), 453–457. <https://doi.org/10.1038/nclimate1465>
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Bjorkman, A.D., Callaghan, T.V., Collier, L.S., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Fosaa, A.M., Gould, W.A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D.S., Hofgaard, A., Jarrad, F., Jónsdóttir, I.S., Keuper, F., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lang, S.I., Loewen, V., May, J.L., Mercado, J., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Pieper, S., Post, E., Rixen, C., Robinson, C.H., Schmidt, N.M., Shaver, G.R., Stenström, A., Tolvanen, A., Totland, Ø., Troxler, T., Wahren, C.-H., Webber, P.J., Welker, J.M. & Wookey, P.A. (2012b). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, 15(2), 164–175. <https://doi.org/10.1111/j.1461-0248.2011.01716.x>
- Farrer, E.C., Ashton, I.W., Spasojevic, M.J., Fu, S., Gonzalez, D.J.X. & Suding, K.N. (2015). Indirect effects of global change accumulate to alter plant diversity but not ecosystem function in alpine tundra. *Journal of Ecology*, 103(2), 351–360. <https://doi.org/10.1111/1365-2745.12363>
- Francis, J.A., Vavrus, S.J. & Cohen, J. (2017). Amplified Arctic warming and mid-latitude weather: new perspectives on emerging connections. *WIREs Climate Change*, 8(5), e474. <https://doi.org/10.1002/wcc.474>
- Freschet, G.T., Cornelissen, J.H.C., Van Logtestijn, R.S.P. & Aerts, R. (2010). Evidence of the ‘plant economics spectrum’ in a subarctic flora. *Journal of Ecology*, 98(2), 362–373. <https://doi.org/10.1111/j.1365-2745.2009.01615.x>
- Gasarch, E.I. & Seastedt, T.R. (2015). Plant community response to nitrogen and phosphorus enrichment varies across an alpine tundra moisture gradient. *Plant Ecology & Diversity*, 8(5–6), 739–749. <https://doi.org/10.1080/17550874.2015.1123317>
- Giesler, R., Esberg, C., Lagerström, A. & Graae, B.J. (2012). Phosphorus availability and microbial respiration across different tundra vegetation types. *Biogeochemistry*, 108(1), 429–445. <https://doi.org/10.1007/s10533-011-9609-8>
- Goodall, D. (1952). Some Considerations in the Use of Point Quadrats for the Analysis of Vegetation. *Australian Journal of Biological Sciences*, 5(1), 1. <https://doi.org/10.1071/BI9520001>

- Jonasson, S. (1992). Plant Responses to Fertilization and Species Removal in Tundra Related to Community Structure and Clonality. *Oikos*, 63(3), 420–429. <https://doi.org/10.2307/3544968>
- Jonasson, S. & Michelsen, A. (1996). Nutrient Cycling in Subarctic and Arctic Ecosystems, with Special Reference to the Abisko and Torneträsk Region. *Ecological Bulletins*, (45), 45–52
- Jonasson, S., Michelsen, A. & Schmidt, I.K. (1999). Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. *Applied Soil Ecology*, 11(2), 135–146. [https://doi.org/10.1016/S0929-1393\(98\)00145-0](https://doi.org/10.1016/S0929-1393(98)00145-0)
- Kaarlejärvi, E., Eskelinen, A. & Olofsson, J. (2017). Herbivores rescue diversity in warming tundra by modulating trait-dependent species losses and gains. *Nature Communications*, 8(1), 419. <https://doi.org/10.1038/s41467-017-00554-z>
- Karlsson, J., Jonsson, A. & Jansson, M. (2005). Productivity of high-latitude lakes: climate effect inferred from altitude gradient. *Global Change Biology*, 11(5), 710–715. <https://doi.org/10.1111/j.1365-2486.2005.00945.x>
- Körner, C. (2007). The use of ‘altitude’ in ecological research. *Trends in Ecology & Evolution*, 22(11), 569–574. <https://doi.org/10.1016/j.tree.2007.09.006>
- Kruskal, J.B. (1964). Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika*, 29(1), 1–27. <https://doi.org/10.1007/BF02289565>
- Laj, P., Palais, J.M. & Sigurdsson, H. (1992). Changing sources of impurities to the Greenland ice sheet over the last 250 years. *Atmospheric Environment. Part A. General Topics*, 26(14), 2627–2640. [https://doi.org/10.1016/0960-1686\(92\)90114-Z](https://doi.org/10.1016/0960-1686(92)90114-Z)
- Lenoir, J., Virtanen, R., Oksanen, J., Oksanen, L., Luoto, M., Grytnes, J.-A. & Svenning, J.-C. (2012). Dispersal ability links to cross-scale species diversity patterns across the Eurasian Arctic tundra. *Global Ecology and Biogeography*, 21(8), 851–860. <https://doi.org/10.1111/j.1466-8238.2011.00733.x>
- Li, Y., Niu, S. & Yu, G. (2016). Aggravated phosphorus limitation on biomass production under increasing nitrogen loading: a meta-analysis. *Global Change Biology*, 22(2), 934–943. <https://doi.org/10.1111/gcb.13125>
- Little, C.J., Jägerbrand, A.K., Molau, U. & Alatalo, J.M. (2015). Community and species-specific responses to simulated global change in two subarctic-alpine plant communities. *Ecosphere*, 6(11), art227. <https://doi.org/10.1890/ES14-00427.1>
- Liu, N., Michelsen, A. & Rinnan, R. (2020). Vegetation and soil responses to added carbon and nutrients remain six years after discontinuation of long-term treatments. *Science of The Total Environment*, 722, 137885. <https://doi.org/10.1016/j.scitotenv.2020.137885>
- McLaren, J.R. & Buckeridge, K.M. (2019). Decoupled above- and belowground responses to multi-decadal nitrogen and phosphorus amendments in two tundra ecosystems. *Ecosphere*, 10(7), e02735. <https://doi.org/10.1002/ecs2.2735>
- Mekonnen, Z.A., Riley, W.J. & Grant, R.F. (2018). Accelerated Nutrient Cycling and Increased Light Competition Will Lead to 21st Century Shrub Expansion in North American Arctic Tundra. *Journal of Geophysical Research: Biogeosciences*, 123(5), 1683–1701. <https://doi.org/10.1029/2017JG004319>
- Miller, P.C. (1982). Environmental and Vegetational Variation across a Snow Accumulation Area in Montane Tundra in Central Alaska. *Holarctic Ecology*, 5(2), 85–98

- Molau, U. & Alatalo, J.M. (1998). Responses of Subarctic-Alpine Plant Communities to Simulated Environmental Change: Biodiversity of Bryophytes, Lichens, and Vascular Plants. *Ambio*, 27(4), 322–329
- Müller, E., Cooper, E.J. & Alsos, I.G. (2011). Germinability of arctic plants is high in perceived optimal conditions but low in the field. *Botany*, 89(5), 337–348. <https://doi.org/10.1139/b11-022>
- Müller, M., Oelmann, Y., Schickhoff, U., Böhner, J. & Scholten, T. (2017). Himalayan treeline soil and foliar C:N:P stoichiometry indicate nutrient shortage with elevation. *Geoderma*, 291, 21–32. <https://doi.org/10.1016/j.geoderma.2016.12.015>
- Neurauter, M., Yuan, M., Hicks, L.C. & Rousk, J. (2023). Soil microbial resource limitation along a subarctic ecotone from birch forest to tundra heath. *Soil Biology and Biochemistry*, 177, 108919. <https://doi.org/10.1016/j.soilbio.2022.108919>
- Niittynen, P., Heikkinen, R.K., Aalto, J., Guisan, A., Kemppinen, J. & Luoto, M. (2020). Fine-scale tundra vegetation patterns are strongly related to winter thermal conditions. *Nature Climate Change*, 10(12), 1143–1148. <https://doi.org/10.1038/s41558-020-00916-4>
- Nilsson, M.-C., Wardle, D.A., Zackrisson, O. & Jäderlund, A. (2002). Effects of alleviation of ecological stresses on an alpine tundra community over an eight-year period. *Oikos*, 97(1), 3–17. <https://doi.org/10.1034/j.1600-0706.2002.970101.x>
- Oksanen, L. & Oksanen, T. (1992). Long-Term Microtine Dynamics in North Fennoscandian Tundra: The Vole Cycle and the Lemming Chaos. *Ecography*, 15(2), 226–236
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlenn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J. (2022). `vegan: Community Ecology Package`. R package version 2.6-2, <<https://CRAN.R-project.org/package=vegan>>.
- Parker, T.C., Sadowsky, J., Dunleavy, H., Subke, J.-A., Frey, S.D. & Wookey, P.A. (2017). Slowed Biogeochemical Cycling in Sub-arctic Birch Forest Linked to Reduced Mycorrhizal Growth and Community Change after a Defoliation Event. *Ecosystems*, 20(2), 316–330. <https://doi.org/10.1007/s10021-016-0026-7>
- Peet, R.K. (1974). The Measurement of Species Diversity. *Annual Review of Ecology and Systematics*, 5(1), 285–307. <https://doi.org/10.1146/annurev.es.05.110174.001441>
- Peterson, K.M. & Billings, W.D. (1980). Tundra Vegetational Patterns and Succession in Relation to Microtopography near Atkasook, Alaska. *Arctic and Alpine Research*, 12(4), 473–482. <https://doi.org/10.1080/00040851.1980.12004207>
- Prager, C.M., Naeem, S., Boelman, N.T., Eitel, J.U.H., Greaves, H.E., Heskell, M.A., Magney, T.S., Menge, D.N.L., Vierling, L.A. & Griffin, K.L. (2017). A gradient of nutrient enrichment reveals nonlinear impacts of fertilization on Arctic plant diversity and ecosystem function. *Ecology and Evolution*, 7(7), 2449–2460. <https://doi.org/10.1002/ece3.2863>
- Press, M.C., Potter, J.A., Burke, M.J.W., Callaghan, T.V. & Lee, J.A. (1998). Responses of a subarctic dwarf shrub heath community to simulated environmental change. *Journal of Ecology*, 86(2), 315–327. <https://doi.org/10.1046/j.1365-2745.1998.00261.x>

- R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rinnan, R., Michelsen, A., Bååth, E. & Jonasson, S. (2007). Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem. *Global Change Biology*, 13(1), 28–39. <https://doi.org/10.1111/j.1365-2486.2006.01263.x>
- Rinnan, R., Michelsen, A. & Jonasson, S. (2008). Effects of litter addition and warming on soil carbon, nutrient pools and microbial communities in a subarctic heath ecosystem. *Applied Soil Ecology*, 39(3), 271–281. <https://doi.org/10.1016/j.apsoil.2007.12.014>
- Scurfield, G. (1954). *Deschampsia Flexuosa* (L.) Trin. *Journal of Ecology*, 42(1), 225–233. <https://doi.org/10.2307/2256995>
- Seastedt, T.R. & Vaccaro, L. (2001). Plant Species Richness, Productivity, and Nitrogen and Phosphorus Limitations across a Snowpack Gradient in Alpine Tundra, Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research*, 33(1), 100–106. <https://doi.org/10.1080/15230430.2001.12003410>
- Shaver, G.R., Chapin, F. & Gartner, B.L. (1986). Factors Limiting Seasonal Growth and Peak Biomass Accumulation in *Eriophorum Vaginatum* in Alaskan Tussock Tundra. *Journal of Ecology*, 74(1), 257–278. <https://doi.org/10.2307/2260362>
- Shaver, G.R. & Chapin, F.S. (1980). Response to Fertilization by Various Plant Growth Forms in an Alaskan Tundra: Nutrient Accumulation and Growth. *Ecology*, 61(3), 662–675. <https://doi.org/10.2307/1937432>
- Shaver, G.R. & Chapin, F.S. (1991). Production: Biomass Relationships and Element Cycling in Contrasting Arctic Vegetation Types. *Ecological Monographs*, 61(1), 1–31. <https://doi.org/10.2307/1942997>
- Shaver, G.R. & Chapin, F.S. (1995). Long-Term Responses to Factorial, NPK Fertilizer Treatment by Alaskan Wet and Moist Tundra Sedge Species. *Ecography*, 18(3), 259–275
- SMHI. (2023). Griddade Nederbörd- Och Temperaturdata - PTHBV. <https://www.smhi.se/data/ladda-ner-data/griddade-nederbord-och-temperaturdata-pthbv>
- Spasojevic, M.J., Bowman, W.D., Humphries, H.C., Seastedt, T.R. & Suding, K.N. (2013). Changes in alpine vegetation over 21 years: Are patterns across a heterogeneous landscape consistent with predictions? *Ecosphere*, 4(9), art117. <https://doi.org/10.1890/ES13-00133.1>
- Stone, R.S., Dutton, E.G., Harris, J.M. & Longenecker, D. (2002). Earlier spring snowmelt in northern Alaska as an indicator of climate change. *Journal of Geophysical Research: Atmospheres*, 107(D10), ACL 10. <https://doi.org/10.1029/2000JD000286>
- Sundqvist, M.K., Giesler, R., Graae, B.J., Wallander, H., Fogelberg, E. & Wardle, D.A. (2011). Interactive effects of vegetation type and elevation on aboveground and belowground properties in a subarctic tundra. *Oikos*, 120(1), 128–142. <https://doi.org/10.1111/j.1600-0706.2010.18811.x>
- Sundqvist, M.K., Liu, Z., Giesler, R. & Wardle, D.A. (2014a). Plant and microbial responses to nitrogen and phosphorus addition across an elevational gradient in subarctic tundra. *Ecology*, 95(7), 1819–1835. <https://doi.org/10.1890/13-0869.1>
- Sundqvist, M.K., Sanders, N.J., Dorrepaal, E., Lindén, E., Metcalfe, D.B., Newman, G.S., Olofsson, J., Wardle, D.A. & Classen, A.T. (2020). Responses of tundra plant community carbon flux to experimental warming, dominant species removal and elevation. *Functional Ecology*, 34(7), 1497–1506. <https://doi.org/10.1111/1365-2435.13567>

- Sundqvist, M.K., Sanders, N.J. & Wardle, D.A. (2013). Community and Ecosystem Responses to Elevational Gradients: Processes, Mechanisms, and Insights for Global Change. *Annual Review of Ecology, Evolution, and Systematics*, 44(1), 261–280. <https://doi.org/10.1146/annurev-ecolsys-110512-135750>
- Sundqvist, M.K., Wardle, D.A., Vincent, A. & Giesler, R. (2014b). Contrasting nitrogen and phosphorus dynamics across an elevational gradient for subarctic tundra heath and meadow vegetation. *Plant and Soil*, 383(1), 387–399. <https://doi.org/10.1007/s11104-014-2179-5>
- Tape, K., Sturm, M. & Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, 12(4), 686–702. <https://doi.org/10.1111/j.1365-2486.2006.01128.x>
- Theodose, T.A. & Bowman, W.D. (1997). Nutrient Availability, Plant Abundance, and Species Diversity in Two Alpine Tundra Communities. *Ecology*, 78(6), 1861–1872. [https://doi.org/10.1890/0012-9658\(1997\)078\[1861:NAPAAAS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1861:NAPAAAS]2.0.CO;2)
- Veen, G.F. (Ciska), Sundqvist, M.K., Metcalfe, D. & Wilson, S.D. (2015). Above-Ground and Below-Ground Plant Responses to Fertilization in Two Subarctic Ecosystems. *Arctic, Antarctic, and Alpine Research*, 47(4), 693–702. <https://doi.org/10.1657/AAAR0014-085>
- Vincent, A.G., Sundqvist, M.K., Wardle, D.A. & Giesler, R. (2014). Bioavailable Soil Phosphorus Decreases with Increasing Elevation in a Subarctic Tundra Landscape. *PLOS ONE*, 9(3), e92942. <https://doi.org/10.1371/journal.pone.0092942>
- Vitousek, P.M., Porder, S., Houlton, B.Z. & Chadwick, O.A. (2010). Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. *Ecological Applications*, 20(1), 5–15. <https://doi.org/10.1890/08-0127.1>
- Walsh, J.E. (2014). Intensified warming of the Arctic: Causes and impacts on middle latitudes. *Global and Planetary Change*, 117, 52–63. <https://doi.org/10.1016/j.gloplacha.2014.03.003>
- Walker, D.A., Epstein, H.E., Reynolds, M.K., Kuss, P., Kopecky, M.A., Frost, G.V., Daniëls, F.J.A., Leibman, M.O., Moskalenko, N.G., Matyshak, G.V., Khitun, O.V., Khomutov, A.V., Forbes, B.C., Bhatt, U.S., Kade, A.N., Vonlanthen, C.M. & Tichý, L. (2012). Environment, vegetation and greenness (NDVI) along the North America and Eurasia Arctic transects. *Environmental Research Letters*, 7(1), 015504. <https://doi.org/10.1088/1748-9326/7/1/015504>
- Wardle, D.A., Gundale, M.J., Jäderlund, A. & Nilsson, M.-C. (2013). Decoupled long-term effects of nutrient enrichment on aboveground and belowground properties in subalpine tundra. *Ecology*, 94(4), 904–919. <https://doi.org/10.1890/12-0948.1>
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. <https://doi.org/10.1038/nature02403>
- Young, K.L., Woo, M.-K. & Edlund, S.A. (1997). Influence of Local Topography, Soils, and Vegetation on Microclimate and Hydrology at a

- High Arctic Site, Ellesmere Island, Canada. *Arctic and Alpine Research*, 29(3), 270–284. <https://doi.org/10.1080/00040851.1997.12003245>
- Zamin, T.J., Bret-Harte, M.S. & Grogan, P. (2014). Evergreen shrubs dominate responses to experimental summer warming and fertilization in Canadian mesic low arctic tundra. *Journal of Ecology*, 102(3), 749–766. <https://doi.org/10.1111/1365-2745.12237>
- Zielke, M., Solheim, B., Spjelkavik, S. & Olsen, R.A. (2005). Nitrogen Fixation in the High Arctic: Role of Vegetation and Environmental Conditions. *Arctic, Antarctic, and Alpine Research*, 37(3), 372–378

Popular science summary

Climate change happens more than twice as fast in the Arctic than in the rest of the world. The warmer temperatures have a large effect on tundra vegetation, because it has been found that nutrients are recycled more rapidly under warmer conditions, which stimulates plant growth. Scientists use fertilization experiments to study the effects of increased nutrient availability on arctic tundra vegetation. Since nitrogen (N) and phosphorus (P) are the main limiting nutrients in the tundra, this study investigated the effects of 15 years of N and P fertilization in subarctic heath and meadow vegetation in northern Sweden. To relate this to temperature, this experiment was carried out on the slope of a mountain, whereby higher elevations correspond to lower temperatures. It was found that heath and meadow have highly different responses to increased nutrient availability over time. In both vegetation types, N was the main limiting nutrient, but combined fertilization with N and P generated the greatest change in plant community composition, whereby shrubs were replaced by one or two dominant grass species. The effect of nutrient addition was stronger in the nutrient-poor heath than in the nutrient-rich meadow vegetation. During 15 years of nutrient addition, the fastest and greatest change in plant community composition, species richness and diversity occurred at the warmer sites in the heath and the colder sites in the meadow. After ten years of fertilization, the colder sites in the heath also responded to increased nutrient availability, probably because the cold temperatures delayed the response to fertilization. The results of this study show that enhanced nutrient availability can lead to different changes in community composition, species richness and diversity among different vegetation types in the tundra.

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Appendix A

Table A: A list of species that were registered in the study system over the duration of the study period (2008-2022) in heath (H) and/or meadow (M) vegetation.

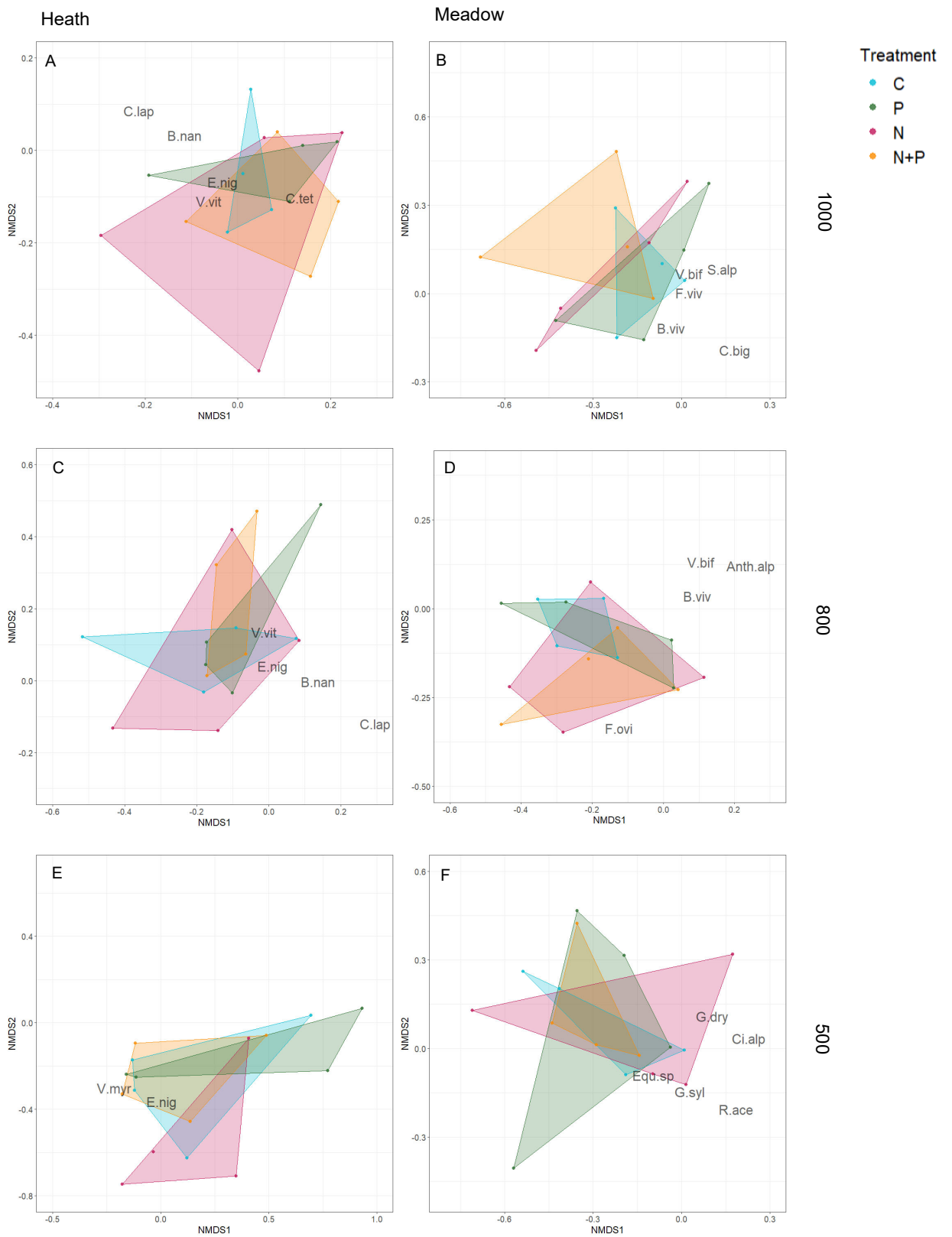
Species	Functional group	Vegetation type
<i>Agrostis</i> sp.	Graminoid	M
<i>Alchemilla</i> sp.	Forb	M
<i>Angelica archangelica</i> ssp. <i>archangelica</i>	Forb	M
<i>Antennaria alpina</i>	Forb	M
<i>Anthoxanthum alpinum</i>	Graminoid	M
<i>Anthriscus sylvestris</i>	Forb	M
<i>Arctostaphylos alpinus</i>	Deciduous shrub	H
<i>Astragalus alpinus</i>	Forb	M
<i>Bartsia alpina</i>	Forb	M
<i>Betula nana</i>	Deciduous shrub	H, M
<i>Betula pubescens</i> ssp. <i>czerepanovii</i>	Deciduous shrub	H
<i>Bistorta vivipara</i>	Forb	H, M
<i>Calamagrostis lapponica</i>	Graminoid	H, M
<i>Carex bigelowii</i>	Graminoid	H, M
<i>Carex capillaris</i>	Graminoid	M
<i>Carex dioica</i>	Graminoid	M
<i>Carex lachenalii</i>	Graminoid	M
<i>Carex vaginata</i>	Graminoid	M
<i>Carex</i> sp.	Graminoid	M
<i>Cassiope hypnoides</i>	Evergreen shrub	H, M
<i>Cassiope tetragona</i>	Evergreen shrub	H, M
<i>Cerastium alpinum</i>	Forb	M
<i>Cicerbita alpina</i>	Forb	M
<i>Cirsium helenioides</i>	Forb	M
<i>Deschampsia alpina</i>	Graminoid	M
<i>Deschampsia cespitosa</i>	Graminoid	M
<i>Deschampsia flexuosa</i>	Graminoid	H, M
<i>Diapensia lapponica</i>	Forb	H
<i>Dryas octopetala</i>	Forb	M

<i>Empetrum nigrum</i>	Evergreen shrub	H, M
<i>Epilobium angustifolium</i>	Forb	M
<i>Equisetum</i> sp.	Pteridophyte	H, M
<i>Erigeron</i> sp.	Forb	M
<i>Eriophorum</i> sp.	Graminoid	M
<i>Euphrasia frigida</i>	Forb	M
<i>Festuca ovina</i>	Graminoid	H, M
<i>Festuca vivipara</i>	Graminoid	H, M
<i>Geranium sylvaticum</i>	Forb	M
<i>Gnaphalium norvegicum</i>	Forb	H, M
<i>Gnaphalium supinum</i>	Forb	M
<i>Gymnocarpium dryopteris</i>	Pteridophyte	H, M
<i>Hieracium</i> sp.	Forb	H, M
<i>Huperzia selago</i>	Pteridophyte	H, M
<i>Juncus trifidus</i>	Graminoid	M
<i>Linnaea borealis</i>	Forb	H
<i>Listera cordata</i>	Forb	M
<i>Luzula arcuata</i>	Graminoid	M
<i>Luzula multiflora</i> ssp. <i>multiflora</i>	Graminoid	M
<i>Luzula multiflora</i> ssp. <i>frigida</i>	Graminoid	M
<i>Luzula multiflora</i> ssp. <i>spicata</i>	Graminoid	M
<i>Luzula pilosa</i>	Graminoid	M
<i>Luzula spicata</i>	Graminoid	M
<i>Luzula sudetica</i>	Graminoid	M
<i>Luzula wahlenbergii</i>	Graminoid	M
<i>Luzula</i> sp.	Graminoid	H, M
<i>Lycopodium annotinum</i>	Pteridophyte	H, M
<i>Melampyrum sylvaticum</i>	Forb	H, M
<i>Milium effusum</i>	Graminoid	M
<i>Molinia</i> sp.	Graminoid	M
<i>Myosotis decumbens</i>	Forb	M
<i>Orthilia secunda</i>	Forb	H, M
<i>Oxyria digyna</i>	Forb	H, M
<i>Pedicularis hirsuta</i>	Forb	H
<i>Pedicularis lapponica</i>	Forb	H
<i>Petasites frigidus</i>	Forb	M
<i>Phleum alpinum</i>	Graminoid	M
<i>Phyllodoce caerulea</i>	Evergreen shrub	H, M
<i>Poa alpina</i>	Graminoid	M
<i>Poa pratensis</i> ssp. <i>alpigena</i>	Graminoid	M
<i>Poa</i> sp.	Graminoid	M

<i>Potentilla crantzii</i>	Forb	M
<i>Pyrola</i> sp.	Forb	H, M
<i>Ranunculus nivalis</i>	Forb	H, M
<i>Rhodiola rosea</i>	Forb	M
<i>Rubus chamaemorus</i>	Forb	H, M
<i>Rubus saxatilis</i>	Deciduous shrub	H, M
<i>Rumex acetosa</i> ssp. <i>lapponicus</i>	Forb	H, M
<i>Salix glauca</i>	Deciduous shrub	H, M
<i>Salix herbacea</i>	Deciduous shrub	H, M
<i>Salix lanata</i>	Deciduous shrub	H, M
<i>Salix lapponum</i>	Deciduous shrub	M
<i>Salix polaris</i>	Deciduous shrub	H, M
<i>Salix reticulata</i>	Deciduous shrub	M
<i>Salix</i> sp.	Deciduous shrub	H, M
<i>Saussurea alpina</i>	Forb	M
<i>Saxifraga oppositifolia</i>	Forb	M
<i>Selaginella selaginoides</i>	Pteridophyte	H, M
<i>Sibbaldia procumbens</i>	Forb	M
<i>Silene acaulis</i>	Forb	H, M
<i>Silene dioica</i>	Forb	M
<i>Solidago virgaurea</i>	Forb	H, M
<i>Sorbus aucuparia</i>	Forb	H, M
<i>Stellaria</i> sp.	Forb	M
<i>Taraxacum</i> sp.	Forb	M
<i>Thalictrum alpinum</i>	Forb	M
<i>Trientalis europaea</i>	Forb	H, M
<i>Trisetum spicatum</i>	Graminoid	M
<i>Trollius europaeus</i>	Forb	M
<i>Vaccinium myrtillus</i>	Deciduous shrub	H, M
<i>Vaccinium uliginosum</i>	Deciduous shrub	H, M
<i>Vaccinium vitis-idaea</i>	Evergreen shrub	H, M
<i>Veronica</i> sp.	Forb	M
<i>Viola biflora</i>	Forb	H, M
<i>Forb1</i>	Forb	M
<i>Graminoid1</i>	Graminoid	M
<i>Pteridophyte1</i>	Pteridophyte	M

Appendix B

NMDS ordination with Bray-Curtis distance for pinpoint data including all years, where this image is only displaying plant community data for 2008. Points display plots, where a smaller distance between points indicates a closer similarity in species composition. Species scores are the weighted average plot scores with weights based on the abundance of species per plot. In each subplot (A-F), species are shown which had a cover > 5% in that vegetation type and elevation: Anth.alp = Anthoxanthum alpinum, B.nan = Betula nana, B.viv = Bistorta vivipara, C.big = Carex bigelowii, C.lap = Calamagrostis lapponica, C.tet = Cassiope tetragona, Ci.alp = Cicerbita alpina, D.fle = Deschampsia flexuosa, E.nig = Empetrum nigrum, Equ.sp = Equisetum sp., F.ovi = Festuca ovina, F.viv = Festuca vivipara, G.dry = Gymnocarpium dryopteris, G.syl = Germanium sylvaticum, M.eff = Milium effusum, R.ace = Rumex acetosa ssp. lapponica, S.alp = Saussurea alpina, V.bif = Viola biflora, V.myr = Vaccinium myrtillus, V.vit = Vaccinium vitis-idaea



Appendix C

*Table C.1: Type III Analysis of Variance Table with Kenward-Roger's method for linear mixed models with vegetation type, elevation, time, nitrogen and phosphorus as fixed factors and plot nested in block as random factors. The model is run with different dependent variables: 1) species richness, 2) Simpson's diversity index (D) and 3) Shannon-Wiener diversity index (H'). Only significant results are displayed. Stars indicate the significance level: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.*

Variable	df	Species richness		Simpson's diversity index (D)		Shannon-Wiener diversity index (H')	
		F	p	F	p	F	p
Vegetation type	18	28.11	<0.001***	1.72	0.21	16.89	<0.001***
Elevation	18	0.47	0.63	10.07	<0.01**	4.85	<0.05*
Time	286	54.99	<0.001***	45.63	<0.001***	51.52	<0.001***
Nitrogen	54	17.56	<0.001***	86.38	<0.001***	138.43	<0.001***
Phosphorus	54	3.12	0.08	24.87	<0.001***	8.50	<0.01**
Vegetation type x Elevation	18	1.09	0.36	7.34	<0.01**	1.16	0.34
Vegetation type x Time	286	39.12	<0.001***	1.98	0.10	3.86	<0.01**
Elevation x Time	286	5.70	<0.001***	7.26	<0.001***	5.10	<0.001***
Elevation x Nitrogen	54	0.03	0.97	15.58	<0.001***	2.96	0.06
Vegetation type x Nitrogen	54	10.47	<0.01**	0.26	0.61	17.83	<0.001***
Vegetation type x Phosphorus	54	0.00	0.98	16.10	<0.001***	6.95	<0.05*

Time x Nitrogen	286	10.03	<0.001***	15.86	<0.001***	13.93	<0.001***
Time x Phosphorus	286	0.92	0.45	2.46	<0.05*	0.63	0.64
Nitrogen x Phosphorus	54	4.08	<0.05*	5.81	<0.05*	7.34	<0.01**
Vegetation type x Elevation x Time	286	8.15	<0.001***	7.73	<0.001***	3.96	<0.001***
Vegetation type x Elevation x Nitrogen	54	4.23	<0.05*	51.66	<0.001***	45.43	<0.001***
Vegetation type x Time x Nitrogen	286	3.13	<0.05*	5.40	<0.001***	3.49	<0.01**
Elevation x Time x Nitrogen	286	1.97	0.05	5.54	<0.001***	2.79	<0.01**
Vegetation type x Elevation x Phosphorus	54	0.75	0.48	11.38	<0.001***	7.50	<0.01**
Vegetation type x Time x Phosphorus	286	0.97	0.42	2.56	<0.05*	1.82	0.13
Elevation x Time x Phosphorus	286	1.25	0.27	2.94	<0.01**	2.93	<0.01**
Vegetation type x Nitrogen x Phosphorus	54	6.28	<0.05*	0.45	0.50	4.35	<0.05*
Time x Nitrogen x Phosphorus	286	2.73	<0.05*	0.69	0.60	1.33	0.26
Vegetation type x Elevation x Time x Nitrogen	286	3.78	<0.001***	12.96	<0.001***	8.11	<0.001***

Vegetation type x Elevation x Time x Phosphorus	286	0.76	0.64	2.78	<0.01**	3.00	<0.01**
Vegetation type x Elevation x Nitrogen x Phosphorus	54	1.20	0.31	15.11	<0.001***	7.18	<0.01**
Vegetation type x Time x Nitrogen x Phosphorus	286	2.74	<0.05*	0.49	0.74	0.57	0.68
Elevation x Time x Nitrogen x Phosphorus	286	1.28	0.25	3.15	<0.01**	2.22	<0.05*
Vegetation type x Elevation x Time x Nitrogen x Phosphorus	286	0.74	0.65	2.48	<0.05*	1.93	0.06

Table C.2: Type III Analysis of Variance Table with Kenward-Roger's method for linear mixed models focused on heath vegetation with elevation, time, nitrogen and phosphorus as fixed factors and plot nested in block as random factors. The model is run with different dependent variables: 1) species richness, 2) Simpson's diversity index (D) and 3) Shannon-Wiener diversity index (H'). Only significant results are displayed. Stars indicate the significance level: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Variable	df	Species richness		Simpson's diversity index (D)		Shannon-Wiener diversity index (H')	
		F	p	F	p	F	p
Elevation	9	1.20	0.35	18.56	<0.001***	10.63	<0.01**
Time	143	6.24	<0.001***	27.95	<0.001***	26.24	<0.001***
Nitrogen	27	2.44	0.13	29.36	<0.001***	33.98	<0.001***
Phosphorus	27	8.09	<0.01**	30.87	<0.001***	18.45	<0.001***
Elevation x Time	143	1.76	0.09	13.00	<0.001***	8.67	<0.001***
Elevation x Nitrogen	27	9.59	<0.001***	46.98	<0.001***	42.20	<0.001***
Elevation x Phosphorus	27	1.04	0.37	3.60	<0.05*	2.03	0.15
Time x Nitrogen	143	3.94	<0.01**	16.87	<0.001***	17.33	<0.001***
Time x Phosphorus	143	0.37	0.83	5.17	<0.001***	3.86	<0.01**
Elevation x Time x Nitrogen	143	2.50	<0.05*	16.17	<0.001***	11.54	<0.001***
Elevation x Nitrogen x Phosphorus	27	1.50	0.24	11.00	<0.001***	5.15	<0.05*

Table C.3: Type III Analysis of Variance Table with Kenward-Roger's method for linear mixed models focused on meadow vegetation with elevation, time, nitrogen and phosphorus as fixed factors and plot nested in block as random factors. The model is run with three different dependent variables: 1) species richness, 2) Simpson's diversity index (D) and 3) Shannon-Wiener diversity index (H'). Only significant results are displayed. Stars indicate the significance level: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Variable	df	Species richness		Simpson's diversity index (D)		Shannon-Wiener diversity index (H')	
		F	p	F	p	F	p
Time	143	58.31	<0.001***	20.25	<0.001***	28.26	<0.001***
Nitrogen	27	15.21	<0.001***	70.06	<0.001***	109.77	<0.001***
Elevation x Time	143	8.37	<0.001***	2.81	<0.01**	2.88	<0.01**
Elevation x Nitrogen	27	1.36	0.27	8.23	<0.01**	11.28	<0.001***
Elevation x Phosphorus	27	0.58	0.57	10.03	<0.001***	5.67	<0.01**
Time x Nitrogen	143	7.34	<0.001***	5.24	<0.001***	5.24	<0.001***
Nitrogen x Phosphorus	27	5.65	<0.05*	6.89	<0.05*	9.87	<0.01**
Elevation x Time x Nitrogen	143	2.99	<0.01**	3.43	<0.01**	3.04	<0.01**
Elevation x Time x Phosphorus	143	1.07	0.39	4.00	<0.001***	3.57	<0.001***
Elevation x Nitrogen x Phosphorus	27	0.58	0.57	4.20	<0.05*	3.82	<0.05*
Time x Nitrogen x Phosphorus	143	3.46	<0.01**	0.90	0.46	1.15	0.33
Elevation x Time x Nitrogen x Phosphorus	143	1.08	0.38	3.52	<0.001***	2.60	<0.05*

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