

Tuija Maliniemi

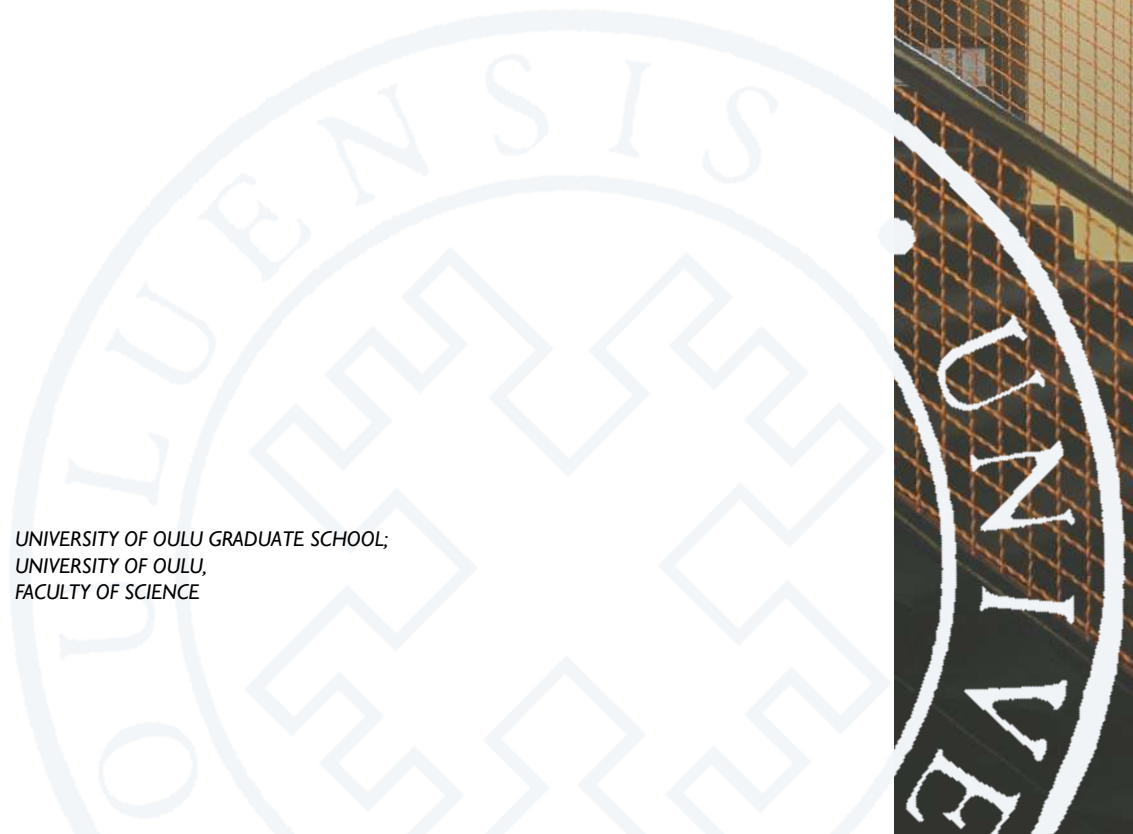
DECADAL TIME-SCALE VEGETATION CHANGES AT HIGH LATITUDES

*RESPONSES TO CLIMATIC AND NON-CLIMATIC
DRIVERS*

UNIVERSITY OF OULU GRADUATE SCHOOL;
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TUIJA MALINIEMI

**DECADAL TIME-SCALE
VEGETATION CHANGES AT HIGH
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Responses to climatic and non-climatic drivers

Academic dissertation to be presented with the assent of the Doctoral Training Committee of Technology and Natural Sciences of the University of Oulu for public defence in Keckmaninsali (HUI06), Linnanmaa, on 28 September 2018, at 12 noon

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Abstract

Boreal and arctic plant communities are responding to anthropogenic climate change that has been exceptionally rapid during the recent decades. General responses include increased productivity, range expansions and biodiversity changes, all of which affect ecosystem functions. Vegetation dynamics are however controlled by multiple drivers, and the outcomes under the changing climate are not yet fully clear. As high latitude areas often lack long-term monitoring of vegetation, alternative methods are required to observe and understand vegetation changes and dynamics. Recently, resurveying historical vegetation data has become a valuable method of studying vegetation changes over the past few decades. In this thesis, I studied multidecadal (23–60 years) vegetation changes in forest and treeless heath and tundra plant communities along a latitudinal gradient in northern Fennoscandia using both vegetation resurveys and long-term experimental data. In addition to examining climate-driven vegetation changes, I related changes in plant communities to key local drivers of each context including mesotopography, grazing, soil moisture and soil fertility.

General trends among the resurveyed treeless heath sites were the pronounced increase of the dwarf shrub *Empetrum nigrum* ssp. *hermaphroditum* in snow-protected habitats and the decrease of lichens throughout. Southernmost heath communities showed strong responses to multidriver effects and had shifted towards new community states. The long-term experiment in the tundra confirmed that depending on driver combinations, tundra communities evolve towards divergent alternative states, highlighting the importance of local drivers in modifying tundra vegetation over time. Communities in fertile forest sites experienced greater temporal turnover compared to infertile forest sites, suggesting that the soil fertility level is a key predictor of vegetation changes under climate change. This particularly important finding previously relied mainly on experimental evidence. Despite these generalities, changes in diversity, plant groups and species varied under a rather uniform climatic warming trend and were often habitat- or region-specific. Thus, the results of my thesis highly motivate continued monitoring and resurveying of vegetation under rapid environmental change and also form baseline time-series data for future studies.

Keywords: boreal forests, bryophytes, climate change, community ecology, lichens, long-term studies, plant communities, plant diversity, reindeer grazing, treeless heaths, tundra, vascular plants, vegetation dynamics, vegetation resurvey

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Tiivistelmä

Poikkeuksellisen nopea ilmastonmuutos on johtanut viime vuosikymmenten aikana muutoksiin boreaalisisissa ja arktisissa kasviyhteisöissä. Muutoksiin lukeutuvat tuottavuuden lisääntyminen, levinneisyysrajojen siirtyminen sekä muutokset biodiversiteetissä, mitkä kaikki muuttavat ekosysteemien toimintaa. Kasvillisuuden dynamiikkaa säätelevät kuitenkin useat paikallistason tekijät, minkä seurauksena ei ole täysin selvää, miten kasvillisuus on eri alueilla ja habitaateissa muuttunut. Koska kasvillisuuden jatkuva monitorointi on harvinaista pohjoisilla alueilla, vanhojen kasvillisuusaineistojen uudelleenkartoituksista on tullut tärkeä menetelmä muutosten havaitsemiseksi. Tutkin väitöskirjassani vuosikymmenten kuluessa tapahtuneita (23–60 vuotta) kasvillisuusmuutoksia Pohjois-Fennoskandian metsissä, puuttomilla kankailla ja tundralla uudelleenkartoitusten ja kokeellisen tutkimuksen avulla, ja kytkin ne ilmastonmuutokseen sekä tärkeimpiin paikallisiin tekijöihin.

Yleisiä trendejä uudelleenkartoitetuilla puuttomilla kankailla olivat variksenmarjan (*Empetrum nigrum* ssp. *hermaphroditum*) voimakas lisääntyminen lumensuojaisissa habitaateissa sekä jäkäläien väheneminen kaikkialla. Yhteisöjen kokonaisuutos oli voimakkainta eteläisillä puuttomilla kankailla, jossa se korreloi yhtä aikaa lisääntyneiden lämpötilojen ja laidunpaineen kanssa. Kokeellinen tutkimus tundralla osoitti, että kasviyhteisöt kehittyvät hyvin erilaisiksi paikallisten tekijöiden voimakkuussuhteista riippuen, jotka voivat joko hidastaa tai nopeuttaa ympäristömuutoksista johtuvia kasvillisuusmuutoksia. Metsien uudelleenkartointi osoitti yhteisöjen kokonaisuutoksen olevan pitkällä aikavälillä suurempaa tuottavilla maaperillä lehtometsissä verrattuna karumpiin kangasmetsiin. Tutkimuksen mukaan maaperän tuottavuus on avaintekijä, joka ennustaa kasvillisuusmuutosten voimakkuutta ilmastonmuutoksen aikana. Tästä tärkeästä löydöstä oli aiemmin pääasiassa vain kokeellista tutkimustietoa. Yleisistä trendeistä huolimatta, muutokset diversiteetissä, kasviryhmissä ja yksittäisissä lajeissa olivat kuitenkin vaihtelevia ja usein habitaatti- tai aluesidonnaisia. Väitöskirjani tulokset, jotka muodostavat myös aikasarjan tuleville tutkimuksille, osoittavat kasvillisuuden monitoroinnin ja uudelleenkartoitusten olevan ensisijaisen tärkeitä, jotta kasvillisuuden dynamiikkaa voidaan ymmärtää paremmin nopeasti muuttuvissa olosuhteissa.

Asiasanat: boreaaliset metsät, diversiteetti, ilmastonmuutos, jäkälät, kasvillisuuden dynamiikka, kasviyhteisöt, laidunnus, pitkäaikaistutkimukset, putkilokasvit, puuttomat kankaat, sammalet, tundra, uudelleenkartointi, uudelleenotanta, yhteisöekologia

To my family

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Oulu, July 2018

Tuija Maliniemi

Original publications

This thesis is based on the following publications, which are referred throughout the text by their Roman numerals:

- I Maliniemi, T., Kapfer, J., Saccone, P., Skog, A. & Virtanen, R. (2018). Long-term vegetation changes of treeless heath communities in northern Fennoscandia: links to climate change trends and reindeer grazing. *Journal of Vegetation Science*, 29(3), 469–479. doi:10.1111/jvs.12630
- II Maliniemi, T., Happonen, K. & Virtanen, R. (2018). Soil fertility level influences temporal turnover of high latitude vegetation under changing climate. *Manuscript*.
- III Saccone, P., Pyykkönen, T.*, Eskelinen, A. & Virtanen, R. (2014). Environmental perturbation, grazing pressure and soil wetness jointly drive mountain tundra toward divergent alternative states. *Journal of Ecology*, 102(6), 1661–1672. doi:10.1111/1365-2745.12316

* Maliniemi *nee* Pyykkönen

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1 Introduction

Terrestrial vegetation, which is the basis for ecosystem functioning and human wellbeing, is reacting to changing conditions in climate and land use in ecosystems across the globe. The impacts of anthropogenically driven climate change are regarded as a particularly serious threat to northern ecosystems (Seddon, Macias-Fauria, Long, Benz, & Willis, 2016), which are expected to face most pronounced warming in the future (IPCC, 2014). During the recent decades, boreal and arctic ecosystems have experienced substantial alterations (Myers-Smith et al., 2011; Post et al., 2009; Sundberg, 2014), as climate has already shifted towards warmer and milder regimes. Increased atmospheric CO₂ concentrations, rising temperatures and changes in precipitation have widely been recognized to cause considerable changes in species distributions, species interactions, phenology, productivity and multiple ecosystem processes (Parmesan & Yohe, 2003). The responses of high latitude vegetation to a changing climate are anticipated to grow even stronger in the future, which could prominently alter ecosystem functions and amplify positive climate warming feedbacks (Chapin et al., 2005; Kaplan et al., 2003; Pearson et al., 2013). Global change effects on species, communities and ecosystems are thus among the current research priorities in ecology (Sutherland et al., 2013).

Northern plant communities live in stressed environments, where growth conditions are characterized by low temperatures, short growing seasons and low nutrient availability (Chapin, Jefferies, Reynolds, Shaver, & Svoboda, 1992), which are regarded as the main determinants of the composition of northern plant communities (Körner, 2003). As a result, communities are considered less dynamic, as both the succession and ecological responses are slow (Grime, 2001). Long life spans, clonal reproduction, low intensity of flowering and changing seed production explain the slow reaction to changes (Jonasson, Callaghan, Shaver, & Nielsen, 2000). As pronounced changes in climate regimes are taking place, it is crucial to understand if high latitude systems are more prone to changes in climate, or if they are after all more stable due to their characteristics, and if there is variation among communities and habitats. Moreover, increasing number of results deviate from general climate-related trends, which highlights the importance of non-climatic drivers as modifiers of community compositions (Vanneste et al., 2017). Considering the large-scale outcomes that follow high latitude vegetation responses to climate change, there is an urgent need to understand the influence of several drivers on vegetation dynamics and study local and regional changes that have occurred over time.

In order to understand the temporal dynamics of vegetation and the processes behind them, long-term observations are inherently fundamental. Long-term continuous monitoring of vegetation spanning decades is however rare, even at a global scale, yet some long-term experimental monitoring programmes studying plant community responses to changing conditions have been running for decades (see e.g. Henry & Molau, 1997; Silvertown et al., 2006) and many have been found just recently. The uniqueness of long-term monitoring mainly results from the lack of resources, the long duration of projects and the commitment of people as monitoring ecological responses ideally continues for generations. Thus, shorter-term studies are clearly more common. Even though short-term studies provide important information on immediate changes and responses of plant communities to changing conditions, they rarely succeed in predicting long-term dynamics and outcomes of plant community responses to changes (Kapfer, Virtanen, & Grytnes, 2012) or in capturing the overall influence of environmental drivers, many of which operate over long time-spans. This is especially of importance in high latitude ecosystems, where communities dominated by long-living and slow-growing species respond rather slowly to changing conditions. Indeed, there might be a delay in the compositional changes of slow-growing high latitude species in relation to changes in climate (Alexander et al., 2018).

Resurveying historical vegetation data has recently been recognized as a highly valuable tool for observing long-term vegetation changes and compensating for scarce monitoring (Hédli, Bernhardt-Römermann, Grytnes, Jurasinski, & Ewald, 2017). Observational resurveys also support experimental studies, as it is acknowledged that experiments conducted in controlled environments cannot directly be expected to correspond and do not always correspond to observed responses of plant communities in natural environments (Parmesan & Hanley, 2015). Plant community responses are more complex in natural environments, and when they deviate from experiments, it is important to study what is behind the observed responses. However, both approaches are fundamental, as experimental studies can reveal driver-specific and multi-driver causations that are generally difficult to distinguish from observational studies. Resurveys along with long-term monitoring data can contribute to current research priorities and answer fundamental ecological questions that are still unclear (Sutherland et al., 2013; Verheyen et al., 2017). In northern systems, these include the rate of which different habitats react and if plant communities show notable responses to global changes (sensitivity), are able to recover from disturbances (resilience) or show temporal stability by remaining virtually unchanged over time (resistance).

1.1 Expected and observed climate driven vegetation changes at high latitudes

Competition is acknowledged as a key element behind central ecological theories that explain species dominance and diversity in plant communities. The direct and indirect responses of plant communities to changing key resources, such as rising temperatures, depend largely on how communities are structured. If plant species are presumed to possess equal competitive abilities along productivity gradients, changes in vegetation can be expected to be strongest in areas that experience the largest change in key resources (Tilman, 1982, 1988). A warmer climate would thus mean substantial changes for vegetation in high latitude areas that are predicted to warm fast. As warming potentially induces accelerated mineralization of soils in nutrient-poor systems (Chapin, Shaver, Giblin, Nadelhoffer, & Laundre, 1995), competition for minerals would shift towards competition for light, as nutrient restriction becomes relaxed. Such a process likely favours tall-growing plants over low-growing plants and thus predicts pronounced changes for habitats that are composed mainly of low-growing species.

However, plants within a community or a habitat are rarely equal in competitive abilities and this applies especially to high latitude systems where the ability to persist under harsh conditions is generally more important for survival. According to plant strategy theory (Grime, 1974, 2001), different life history strategies of plants along the productivity gradient determine community responses to environmental changes. Plants are categorized into one of three groups, representing competitors that can take the maximum advantage of resources in productive habitats, stress-tolerators that survive in nutrient-poor habitats and ruderals that thrive in disturbed habitats under low stress. This theory predicts that communities on fertile soils, usually consisting of competitors or ruderals, are able to respond quickly to changing resource levels, such as rising temperatures, whereas communities inhabiting infertile soils, consisting mainly of stress-tolerators, could better resist environmental changes. Moreover, species with competitive abilities can shift their range or increase their abundance when resources increase.

The theories above are not mutually exclusive and predicted responses have been observed throughout high latitudes. The widely reported increase of shrub abundance in the tundra is one of the most distinct consequences of climate warming impacts on productivity throughout the circumpolar Arctic (Elmendorf et al., 2012; Hudson & Henry, 2009), yet the sensitivity of shrub growth to warming

is heterogeneous and depend on local conditions (Myers-Smith et al., 2015). The expansion of shrubs can alter nutrient cycling and plant phenology or even stabilize the composition of plant communities. For example, in a study by Daniëls, de Molenaar, Chytrý, and Tichý (2011), vegetation types dominated by single species and comparative dense canopies remained unchanged for decades. Another distinct phenomenon is the northward and upward range shift of species (Lenoir, Gegout, Marquet, de Ruffray, & Brisse, 2008) and treelines (Kullman, 2002; Rundqvist et al., 2011), as growth conditions have become more favourable for southern and low elevational species to establish. This poses a considerable threat for many high latitude and altitude species and communities, whose habitats are contracting at the expense of species expanding their range. However, boreal species have better opportunities for range expansions, while arctic and alpine species can do this only if there is enough space to migrate upward or northward or if microclimatically suitable niches are found (Grabherr, Gottfried, & Pauli, 1994; Wilson & Nilsson, 2009). Advancing treelines and the shrubification of the tundra have the potential to further work as a feedback mechanism, since taller vegetation may not be completely covered by the snow and thus can reduce the albedo.

The changing climate inevitably affects snow cover, which is one of the key elements affecting plant community composition in northern environments. Further on, mesotopography determines snow accumulation across a landscape, influencing habitat types and related plant communities. Species and communities that depend on snow are regarded as highly sensitive to climate change. Of the tundra habitats, snowbed plant communities are considered particularly vulnerable to changes in climate (Björk & Molau, 2007; Kapfer et al., 2012), as the species inhabiting these sites become restricted by a growing season length, soil moisture and availability of phosphorus.

In recent decades, a massive decline in overall global biodiversity due to global changes has been reported (Butchart et al., 2010). Scenarios suggest that among various global change actors, climate change effects will have the strongest impact on boreal and arctic biodiversity (Sala et al., 2000). However, local patterns of biodiversity changes highly vary. In the absence of major land use effects, the local plant diversity has shown increases, decreases or no changes, which can ultimately result in overall distribution of temporal trends showing minor or no changes (Vellend et al., 2013). Currently, it is difficult to predict habitat- or ecosystem-specific trends in climate-related diversity changes without observations, which makes it highly important to study temporal changes in local species richness that

however still involves substantial uncertainty due to a lack of data of long time spans (Vellend et al., 2017).

Species' gains and losses can either increase or decrease the compositional similarity of communities over time (Baeten et al., 2014). The decline of compositional dissimilarity, i.e. biotic homogenization, is regarded as a serious threat in current biodiversity decline (McKinney & Lockwood, 1999). In this process, communities become more similar regarding taxonomy, functional roles or genetic variation (Olden & Rooney, 2009), and such trends are not much investigated in northern ecosystems.

1.2 The influence of herbivory on northern vegetation

Even though the climate is an important large-scale driver of plant community composition and dynamics, the composition of plant communities is nevertheless a result of complex interactions of multiple and often dynamic local-scale drivers. The findings on local complexity of vegetation changes under the same climate regime (e.g. Van Bogaert et al., 2011) support the idea that multiple environmental factors are behind the changes observed in high latitude plant communities, and that several interactions are yet to be revealed. Thus, the effects of the changing climate on vegetation can be expected to differ among sites, even within a spatially limited area.

One of the most essential local-scale drivers in northern systems is reindeer (*Rangifer tarandus* L.), which has highly adapted to high latitude nutrient-limited environments and can forage a variety of ground vegetation. Lichens form the main diet in the winter time, whereas graminoids, forbs and leaves of shrubs and deciduous trees are feed in the summer. The most distinct response of vegetation to intense grazing is indeed the decline of lichen-dominated vegetation types (Tømmervik et al., 2004). In worst cases, damagingly eaten systems may never recover. Decreasing lichen biomass deteriorates the nutrition of reindeer, which the decrease of nutritionally rich plants of snowbed habitats can worsen.

In high latitude ecosystems, plant-herbivore interactions are very important processes that modify vegetation (Olofsson, Hulme, Suominen, & Oksanen, 2004). In low-productive tundra communities, the impact of herbivores on vegetation through food web dynamics together with strong top-down control are suggested to favour species that resist or tolerate grazing (Oksanen & Oksanen, 2000). Thus, the redistribution of competitive species as a result of a relaxation of resources could be prevented by herbivores. The retarding effect of grazing pressure on

climate-driven vegetation changes has been increasingly reported (Olofsson et al., 2009; Post & Pedersen, 2008; Ravolainen, Bråthen, Yoccoz, Nguyen, & Ims, 2013). These studies show that grazing may prohibit tree saplings and shrub species from spreading in the tundra despite beneficial climatic conditions. Indeed, grazers can have a profound effect on the composition of species compared to grazer-free areas where vegetation have been reported to be temporally more stable (Daniëls et al., 2011; Kapfer et al., 2012). However, the effects of reindeer grazing on vegetation have often resulted in divergent results and conclusions, and thus, the impact of reindeer grazing on vegetation is not completely clear and seems highly dependent on local biotic and abiotic conditions, different management systems and grazing history (Bernes, Bråthen, Forbes, Speed, & Moen, 2015).

Outbreaks of autumnal moths (*Epirrita autumnata*) can have a crucial impact on vegetation in the forest-tundra ecotone. The effect of these climate-driven species invasions on northern vegetation can be abrupt and profound and are considered a driver that can quickly change the vegetation state of dominant oligotrophic mountain birch forests in particular (Karlsen, Jepsen, Odland, Ims, & Elvebakk, 2013).

1.3 Long-term state shifts in plant communities

Ecosystems and communities exist in one of the possible alternative stable states after persisting as such for a relatively long time-span. Changes in ecological conditions can cause an ecosystem or a community to become more unstable or to shift into a transitional state (Fukami & Nakajima, 2011). Intense grazing is such a driver in northern systems that can cause transitional changes in vegetation. Van der Wal (2006) proposed alternative states of boreal and tundra vegetation along increasing grazing pressure. Initially, a shift could be seen from lichen- to bryophyte-dominated vegetation as a consequence of heavy trampling and selective feeding. A shift to graminoid-dominated state would further follow under continued heavy grazing. Graminoids have a better tolerance for grazing in general but they also benefit from reduced soil moisture, increased soil temperatures and consequent increase in nutrient cycling rates (Olofsson, Stark, & Oksanen, 2004), all of which are typical conditions for graminoid-dominated state.

In theory, anthropogenically driven global changes are regarded as forces with high potential to move the composition of current ecosystems and communities into novel species compositions and relative abundances that have not previously occurred in a given community or system (Hobbs et al., 2006). Such novelty can

emerge in a process where natural systems shift outside of their historical range of variability (Landres, Morgan, & Swanson, 1999). In this process (Fig. 1), initial communities are pushed outside their historical range of environmental conditions, or they change through species' gains or losses. Once a community composition shifts as a result of abiotic or biotic forcing, yet still resembles more initial composition than novel, interactions under new conditions further modify species abundances which can ultimately result in novel community composition. Even though shifts in community compositions are plausible to occur in northern communities, formation of completely novel communities remain more theoretical option, regarding rather slow responses of northern vegetation.

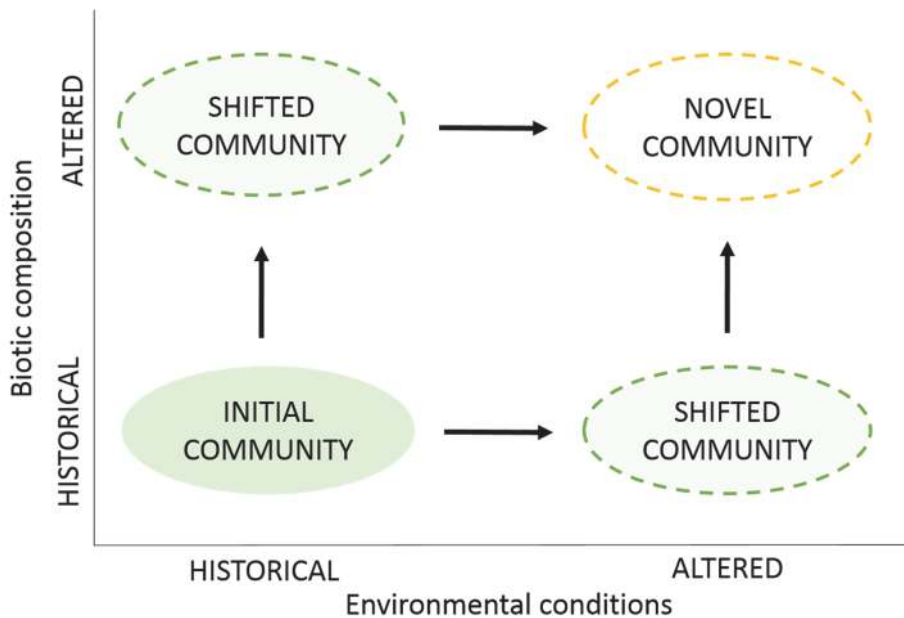


Fig. 1. Development of community shifts and novel communities via changing environmental and biotic conditions (modified from Suding, Gross, & Houseman, 2004 and Seastedt, Hobbs, & Suding, 2008). The initial community, having a range of historical abiotic and biotic characteristics, shifts into a new state as a result of direct environmental forcing (e.g. climate change) that pushes the community outside of its historical range of environmental conditions. The gains and losses of important species have a similar ability to shift the community into a new state. Restructuring of the shifted community due to new abiotic or biotic interactions further modifies the species

composition as species abundances or biogeochemical processes change leading to novel community composition.

1.4 Aims of this thesis

In this thesis, I studied decadal time-scale vegetation dynamics in forest and treeless heath and tundra habitats along a bioclimatic gradient in northern Fennoscandia by resurveying historical vegetation sample plots and using long-term experimental data. The main focus was to reveal long-term plant community changes that had taken place under recent rapid climatic warming by offering detailed evidence on changes in individual species, different plant functional and strategy groups, diversity and community state shifts, all of which are not sufficiently known in the study area. By relating and testing the effects of potential underlying drivers to observed vegetation changes, the purpose of this thesis is to help understand long-term community dynamics and the importance of key drivers whose impacts on vegetation dynamics are not yet fully understood in the field of ecology. Studied vegetation sites were not impacted by direct or major human disturbances (i.e. they represent rather late successional stages), which made it easier to distinguish possible climate but also other local driver effects on vegetation.

I investigated long-term vegetation changes and their potential drivers in three separate studies addressing the following research questions:

1. How have treeless heath plant communities changed over time, and do changes show links with regional climate trends and reindeer grazing?
2. Is the soil fertility level a general ecosystem property influencing the magnitude of forest vegetation changes under the changing climate?
3. Do environmental perturbation and varying local conditions lead to divergent plant community trajectories in mountain tundra over time?

More precisely, study I explored vegetation changes (46–50 years) in treeless heath and tundra sites that were differentiated by region and mesotopography (wind-exposed and snow-protected sites), and observed changes were linked to regional climate and grazing pressure trends. My expectations were to observe climate-driven vegetation changes, but with regional variation due to grazing pressure and mesotopography.

Changes in boreal and mountain birch forest communities (33–57 years) were investigated in study II. The main target was to test whether soil fertility level is a general modulator of the magnitude of long-term vegetation changes and whether

this applies along a bioclimatic latitudinal gradient. Here, I hypothesized that communities on fertile soils have experienced greater changes over time based on earlier experimental evidence (Grime et al., 2000, 2008).

Study III was an experimental study of local driver impacts on long-term changes (23 years) in mountain tundra vegetation. Here, the effects of environmental perturbation, grazing pressure and soil wetness on plant community trajectories were studied on a tundra snowbed site. This experimental study complements the observational study I by offering information on the effects of multiple local drivers on plant community changes in mountain heath habitats. For this study, it was hypothesized that following environmental perturbation, the joint effects of grazing pressure and soil moisture conditions determine the long-term trajectories of heath communities.

2 Materials and methods

This thesis is based on vegetation resurveys that were conducted using both historical observations (I and II) and long-term experimental data (III).

2.1 Vegetation resurveys

Resurveying historical vegetation datasets has become an increasingly adopted method for studying vegetation changes in different habitats over the past few decades (Daniëls et al., 2011; Grabherr et al., 1994; Kapfer et al., 2012; Lenoir et al., 2008; Steinbauer et al., 2018), the period of the most pronounced anthropogenic climate change. High latitude environments are mostly remote and hard to access, which are the main reasons for the lack of permanent plots and continuous environmental monitoring. Thus, resurveying historical vegetation data is the primary method for observing long-term vegetation changes in these areas. Despite increasing use of the method, the number of resurveys from high latitude areas is still limited. One of the underlying reasons is that the historical vegetation plots generally lack coordinates and are thus non-permanent, i.e. with information for approximate relocation (semi-permanent plots) or completely lacking information on plot location (non-traceable plots). This becomes a confronting problem, as the method is based on comparing the same vegetation plots sampled at different periods. Successful relocation of old vegetation plots depends on the accuracy of plot-specific information (e.g. topographical variables, description) in the historical data. A study from Kopecký and Macek (2015) shows that the data resurveyed from approximately relocated plots do not considerably vary from the same plot relocated precisely. Thus, a resurvey of semi-permanent vegetation data is relatively robust to uncertainties in the precision of location, yet depend on the quality of old data and local spatial heterogeneity (Ross, Woodin, Hester, Thompson, & Birks, 2010). Along with the use of semi-permanent plots and considering all the location information available for successful relocation, Kapfer et al. (2017) suggest other important criteria to minimize the inevitable relocation error. These include the control for seasonal variability in vegetation by conducting a resurvey at the same time of the year as the original sampling was carried out, the use of experienced observers for low observer bias and the standardization of datasets for comparability.

2.2 Study area and resurveys of old vegetation datasets

Studies I and II are based on resurveying old high-quality vegetation data from forest and treeless heath habitats in northern Fennoscandia, which were originally sampled in 1957–1981 (Table 1). Together, these data sets cover a latitudinal gradient from central Finland to northern Norway, encompassing middle boreal, northern boreal and oroarctic bioclimatic zones (Fig. 2). All the old vegetation data include diverse and detailed information on sample plot locations, which are in most cases a specific area, an elevation, a slope, an aspect, a description of the surroundings and a plot location on a paper map. Thus, all the old vegetation data are regarded as ‘semi-permanent’ (*sensu* Kapfer et al., 2017).

Abundance estimates for complete species composition (vascular plants, bryophytes and lichens) were recorded in the original sampling for each data set, along with various data-specific variables, all of which were digitized in the beginning of this project. *Post hoc* georeferencing of old vegetation plots was conducted using ArcMap software (v. 10.2), and relocation accuracy was further improved on site using data-specific information on plot location. Vegetation resurveys were carried out in 2013–14, bearing the original sampling seasons in mind as much as possible. The percentage cover of all species was estimated using the same scale that was used in each of the original sampling, and most of the associated data-specific variables were measured again. Additionally, soil samples were taken from each plot for pH measurement that was conducted in a laboratory. Human impact was estimated visually for each plot *in situ* at plot-scale, and using land cover data in ArcMap for the surroundings (details in Walz & Stein, 2014). After resurveys, species identities for many bryophytes and lichens were confirmed using a microscope. Eventually, conducted resurveys met all the criteria suggested for minimizing the inherent error in resurveyed data (Kapfer et al., 2017).

Before analyses, old and new species data were harmonized for taxonomy and some taxa, especially small cryptogamic species substantially similar to each other, were treated collectively or at a generic level. For each study, species data was pooled into generally used morphological plant groups of boreal and arctic vegetation. For study II, species data was also categorized into plant strategy theory classes (Grime, 1974, 2001) after Heikkinen and Kalliola (1990), Grime, Hodgson and Hunt (2007) and Pierce, Brusa, Vagge and Cerabolini (2013). The nomenclature of vascular flora, bryophytes and lichens in each study (I–III) follows Hämet-Ahti, Suominen, Ulvinen and Uotila (1998), Ulvinen, Syrjänen and Anttila (2002) and Vitikainen, Ahti, Kuusinen, Lommi and Ulvinen (1997), respectively.

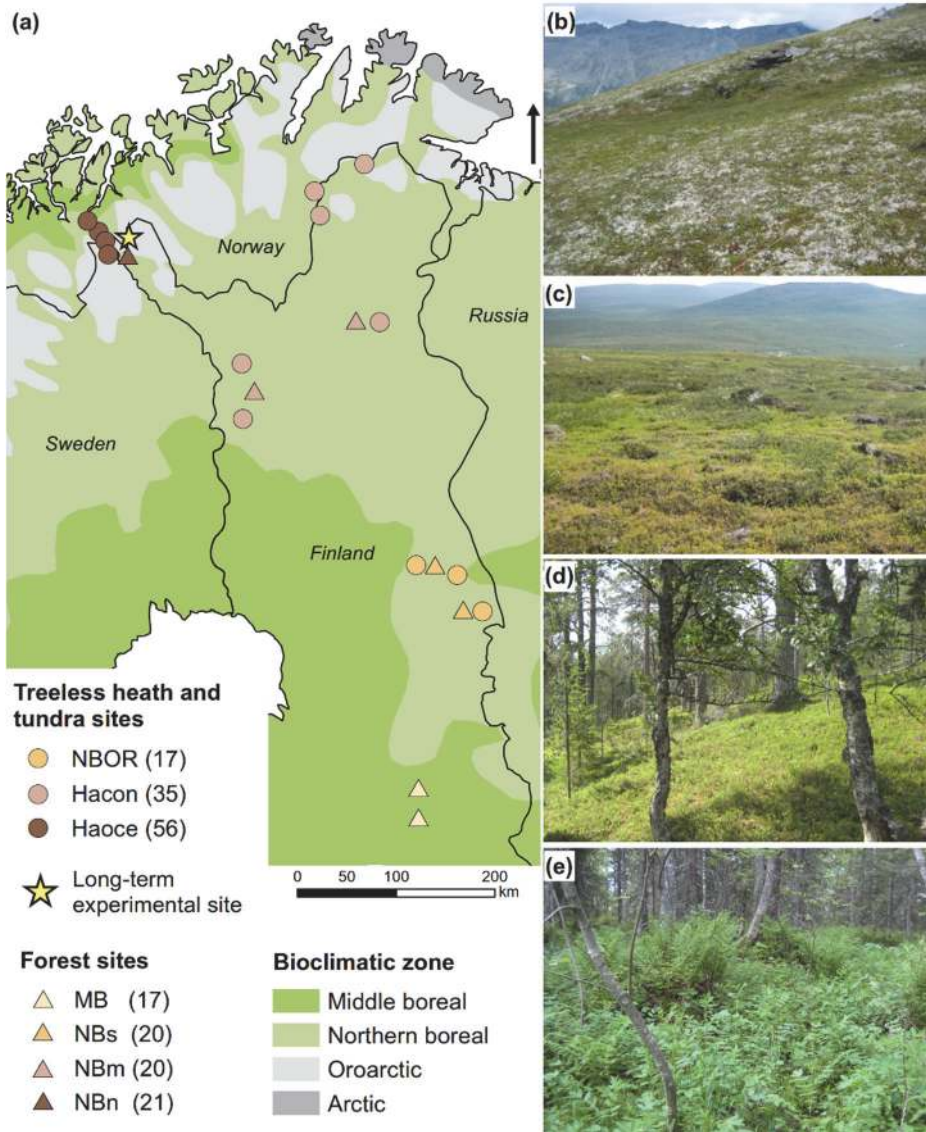


Fig. 2. a) Study area and studied vegetation types with the number of plots for resurveyed sites (site names correspond to names used in original publications) that included: b) treeless wind-exposed *Empetrum hermaphroditum* heaths, c) treeless snow-protected *Calluna vulgaris*, *Vaccinium myrtillus* and *Betula nana* heaths, d) infertile forests and e) fertile herb-rich forests. The bioclimatic zonation is after Moen (1999) and Virtanen et al. (2016). Photos: Tuija Maliniemi.

Table 1. The resurveyed old vegetation datasets used in studies I and II with original sampling years, vegetation type of each data, plot sizes used for coverage estimations of field and shrub layer species, number of resurveyed plots and information on which paper data is used.

Data, published	Original sampling year	Vegetation type	Plot size (m) (field / shrub layer)	No. of resurveyed plots	Data in paper
Haapasaari, 1988	1964–86	Treeless heaths / tundra	2x2 / 2x2	108	I
Hämet-Ahti, 1963	1957–60	Mountain birch forests	10x10 / 10x10	21	II
Lyytikäinen, 1983	1980	Heath forests	1x1 ¹ / 25x25	10	II
Mikkonen-Keränen, 1982	1980–81	Heath forests	1x1 ² / 30x30	10	II
Leinonen, 1984	1980–81	Heath and herb-rich forests	1x1 ³ / 10x10	9	II
Kaakinen, 1971	1968–70	Herb-rich forests	5x5 / 5x5	8	II
Kaakinen, 1974	1971–72	Herb-rich forests	5x5 / 5x5	10	II
Kaakinen, unpublished	1974–76	Herb-rich forests	5x5 / 5x5	10	II

Plot data averaged from ¹ four 1 x 1 m ² two to four 1 x 1 m ³ five 1 x 1 m vegetation grids

Only sites that were estimated to stay outside direct human disturbance over time were selected for studies I and II, and thus, studied plots represent relatively natural states of vegetation. In study I, treeless heaths (altogether 108 plots) represent the northern boreal and hemiarctic mountain heath and tundra sites that are predominant above the treeline. Studied plots were divided into three subregions (NBOR, HAcon, HAOce; Fig. 2a) based on geographic location, differences in climate regimes and original community composition. To account for habitat-specific changes, heaths were further divided according to mesotopographical position and consequent snow accumulation affecting species composition. Wind-exposed sites with relatively thin snow cover in subregions HAcon and HAOce were dominated by *Empetrum nigrum ssp. hermaphroditum* (Fig. 2b) and snow-protected sites with mostly intermediate to thick snow cover in places were dominated by *Calluna vulgaris* in subregion NBOR and *Vaccinium myrtillus* and *Betula nana* (Fig. 2c) in subregions HAcon and HAOce. Forest sites (altogether 78 plots) in study II were selected so that equal number of sites represented both infertile and fertile site types (Fig. 2d, e) in four subregions along the latitudinal gradient (MB, NBs, NBm and NBn). Fertile forest types represent herb-rich forest vegetation that is scattered among the dominant infertile coniferous heath forest types. In subregion NBn, both site types represent mountain birch forests.

The reindeer is the main large herbivore in the study area and their numbers have been high since the late 1800's (Bernes et al., 2015). Defoliation of mountain

birch and some ground layer shrubs by autumnal moths were reported from 2004–06 (Kopisto, Virtanen, Pekkanen, Mikkola, & Kauhanen, 2008) and also observed during the resurvey in Kilpisjärvi area (HAoce, I; NBn, II).

2.3 Environmental variables

Daily surface temperature and precipitation data for the study period were derived from E-OBS raster (25 x 25 km) dataset (Haylock et al., 2008). Data on annual reindeer numbers within reindeer herding districts was received from the Natural Resources Institute Finland (former Finnish Game and Fishery Research Institute), and municipal-level information was used for plots in located in Norway (Tømmervik & Riseth, 2011). First, long-term subregion-specific trends for thermal sums (I, II), growing season and annual precipitation (I, II, respectively), winter temperatures (I) and grazing pressure (I, II) were constructed. For calculating thermal sums, the length of growing seasons was first determined to start and to end from the day following at least ten subsequent days with a daily average temperature $\geq +5$ °C to mark the start and $< +5$ °C to mark the end. Daily temperatures exceeding the +5°C threshold during the growing season were then summed to gain thermal sums. Precipitation values were gotten by adding daily data, and winter temperatures were averaged from daily values in January and February. Grazing pressure was calculated by dividing the number of reindeer by the area of the reindeer herding district.

Changes in climate and grazing variables over each relevant study period were quantified for each plot. In study I, ten-year averages of climate variables and five-year averages of grazing pressure before each sampling were used to calculate the difference between samplings. In study II, linear regressions for each dataset were first formed using the original sampling year as a starting point and the resurvey year as an ending point. The slope of linear regression was then multiplied by the number of years between the original survey and the resurvey to achieve comparability between datasets that vary in time spans.

2.4 Experimental design and long-term experimental data

The long-term experiment for study III is located in the low-productive mountain tundra of Mt. Jehkats in the Kilpisjärvi area (Fig. 2, 3a). The experiment, established in 1989, includes altogether 30 blocks (40 x 50 cm) of *Vaccinium myrtillus* heath vegetation, which were first dug out. Ten blocks were then

transplanted within the original heath site for control plots to account for the transplantation effect. The remaining 20 blocks were transplanted into a snowbed site 150 m higher in elevation, near the limit of altitudinal distribution of *V. myrtillus*, to test the effect of environmental perturbation. To test the effects of grazing and soil moisture on community composition, half of these blocks were protected from mammalian herbivores using metal mesh fences (Fig. 3), and half were left grazed. Moreover, as soil wetness varied within the snowbed site, blocks were divided belonging to either dry or wet conditions determined based on gravimetric soil moisture measurements. As a result, the experiment contained five treatments: control plots, grazed plots and exclosures on dry snowbed, and grazed plots and exclosures on wet snowbed. The vegetation was sampled from the central part of each block (12.5×12.5 cm) in 2012.



Fig. 3. Long-term experimental site in Mt. Jehkats in Kilpisjärvi. Blocks of *Vaccinium myrtillus* dominated heath vegetation, typical for the sloping sites with intermediate snow cover in the study area, were transplanted into a snowbed site representing sedge-grass meadows that varied in soil moisture conditions. Half of the blocks were fenced for testing the effect of reindeer grazing to temporal changes in plant community composition. Photo: Risto Virtanen.

2.5 Statistical analyses

Species-specific changes (I, II) and changes in plant morphological (I, II) and plant strategy groups (II) were tested using t-test for independent samples. Changes in species frequencies (I, II) were tested using χ^2 -tests. Compositional changes in

studied plant communities (I, II, III) over time were illustrated with non-metric multidimensional scaling (NMDS) ordinations using the vegan package (Oksanen et al., 2012, 2018) in R software (R Development Core Team, 2013) using Bray-Curtis distances and species abundance data. Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001) from vegan was used to test the effects of time, habitat and subregion (I) and experimental treatments (III) to compositional dissimilarities visualized in NMDS ordinations. In study I, correlation vectors of climate and grazing variables were fitted onto the subregion-specific ordinations to estimate their contribution to community changes. Moreover, Spearman's correlations were calculated between observed vegetation changes and changes in climate and grazing pressure across the whole study area.

Species richness or α -diversity were calculated at plot-level (I, II) and treatment-level (III). Plot-level changes were tested using t-tests for independent samples, and the difference among treatments was tested using one-way generalized linear models (GLM). The magnitude and/or the direction of community dissimilarities, i.e. community turnover or changes in β -diversity over time, were tested in each study. For testing the magnitude of temporal dissimilarities at the plot-level (I, II) and site-level (I), abundance-based Bray-Curtis dissimilarities were calculated between old and new community data using simba (I, Jurasinski & Retzer, 2015) and betapart (II, Baselga, Orme, & Villeger, 2013) packages. In addition, for study II, abundance-based Bray-Curtis dissimilarities were partitioned into balanced variation in abundance and abundance gradients to account for varying patterns in species abundance changes (Baselga, 2013). Site-level β -diversity in study II was based on the effective numbers of distinct communities (Jost, 2007). For testing the direction of community turnover, i.e. if community compositions show rising similarity or dissimilarity over time, community turnover rates were calculated for each site using the vegetarian package (Charney & Record, 2015). In study III, β -diversity was calculated at the treatment-level using the Sørensen index of dissimilarity (Sørensen, 1948), and differences among treatments were tested using Permutational Multivariate Dispersion Analyses (PERMDISP; Anderson, Ellingsen & McArdle, 2006) using the vegan package.

Linear models were fitted to test the responses of compositional changes (Bray-Curtis dissimilarity and its partitioned components) to soil fertility and location (II). Spatial autocorrelation of model residuals were tested based on Moran's I values using the spdep package (Bivand et al., 2017). To test the effect of soil fertility and location on turnover rate changes ($n=8$), permutation tests for linear models were

applied from the `lmPerm` package (Wheeler & Torchiano, 2016). Two-way Generalized Linear Models (GLM) were used to test the effects of environmental perturbation, grazing pressure, soil wetness and grazing pressure x soil wetness interaction on plant groups, diversity indices and dominant shrubs. One-way GLMs were used to test the difference among treatments for plant groups and diversity indices followed by *post-hoc* tests for testing pairwise differences among treatments.

3 Results and discussion

During the study period, increased warming and precipitation were recorded throughout the study area as also reported for northern Fennoscandia by Kivinen, Rasmus, Jylhä and Laapas (2017). A clear shift in thermal sums occurred in the latter half of 1990s, and thus, regardless of varying duration of studied datasets, the resurvey time since the temperature-related changes is equal in time spans. Despite the general trends observed, the magnitude of climatic changes showed some regional variability. In general, climate records showed that long-term increases in thermal sums were stronger in the southern and middle parts of the study area compared to the northwest (Kilpisjärvi) area (HAoce, I; NBn, II; III), where initially lower temperatures and shorter growing seasons were recorded. Grazing pressure also showed an increasing trend over the study period throughout the study area (excluding subregion MB in study II that is located outside the reindeer herding district), with region-specific fluctuations.

Several changes were observed in the composition of resurveyed plant communities that varied between regions and habitats. Among the general trends were the pronounced changes of snow-protected habitats among studied heath sites and generally stronger changes of fertile forests sites. However, one of the main findings was that despite rather uniform climate trends across subregions, relatively inconsistent vegetation changes have taken place. This was also demonstrated in the experimental study, that showed prominent variation among the studied communities. Changes among regions were profound especially in the southern part of the northern boreal zone (subregion NBOR, I; NBs, II), where changes in climate were also relatively large.

3.1 Observed vegetation changes in plant communities over time

3.1.1 Changes in species and plant groups

In treeless heath communities (I), the most distinct change in the abundance of an individual species was the increase of the evergreen dwarf shrub *Empetrum nigrum* spp. *hermaphroditum*. This change had taken place specifically on snow-protected habitats where it was reflected in the increased coverage of evergreen shrubs as a whole. The increase of *Empetrum* is in line with other studies from several tundra areas in Fennoscandia (Virtanen et al., 2010; Vowles et al., 2017; Vuorinen et al.,

2017). There are both empirical (Felde, Kapfer, & Grytnes, 2012; Wilson & Nilsson, 2009) and experimental evidence (Kaarlejärvi et al., 2012), indicating that the expansion is promoted by climate warming, yet when tested across the whole study area, no significant correlation between warming and increased *Empetrum* cover was found. Nevertheless, the increasing *Empetrum* abundance has various effects on tundra systems, as it produces recalcitrant litter, has allelopathic effects on vegetation and immobilizes soil nutrients (Nilsson, 1994).

In contrast with the increasing cover of *Empetrum*, the cover of the deciduous dwarf shrub *Vaccinium myrtillus*, formerly the most dominant species in snow-protected habitats, had decreased. The cover of deciduous shrubs did not increase anywhere, and only few shrub species had increased in subarea HAOce. Despite the potential for resident trees and shrubs (e.g. *Betula nana*, *Salix* spp., *Juniperus communis*) to expand their abundance over decades, such a development was not detected. It is noteworthy, that the deciduous dwarf shrub *Arctostaphylos alpinus* had increased in frequency through the subregion HAOce, yet more clearly in wind-exposed sites, where it has been inherently more abundant. This may be a locally important process, as shady prostrate growth form and relatively big litter formation, also applicable to *Empetrum*, could suppress smaller and ground layer species (Cornelissen et al., 2001).

Lichens had significantly decreased throughout the study area over decades. Considering that lichen cover had already been under intensive consumption and trampling by reindeer during the original sampling (Haapasaari, 1988), the further decrease is alarming. However, it was not the common fruticose reindeer lichens that had notably decreased, as their cover was rather low to begin with, and some species experienced even local increases. The decreased species were mainly cup- and horn-form *Cladonia* species and formerly relatively abundant N-fixing species (*Stereocaulon* spp., *Nephroma* spp. and *Peltigera* spp.).

Along with major changes described above, treeless heaths of subregion NBOR also experienced other prominent species-specific changes. These included the complete absence of formerly recorded low-stature species *Diphasiastrum alpinum*, *Lycopodium clavatum* (club mosses), *Festuca ovina* (a graminoid) and *Trientalis europaea* (a forb). *Sphagnum* spp. (peat mosses) were recorded as immigrant species along with a distinct increase of several boreal forest mosses.

The responses of plots transplanted into snowbed site (III) differed in many ways from observed changes in snow-protected and wind-exposed sites (I). *V. myrtillus* generally persisted in control and transplanted plots in study III, and no sign of increasing *Empetrum* cover was seen. Along with treatment-specific

responses of shrubs and bryophytes and the decline of lichens throughout the snowbed site (III), among the general trends were the strong contribution of graminoids and forbs that established relatively equally in transplanted plots as a result of an immigration from the local species pool.

In forest communities (II), species- and plant group-specific changes highly varied among study sites, and no general trends along fertility or latitudinal gradient were found. However, pronounced changes in fertile sites were observed among bryophytes and certain graminoid species, yet with varying species identities or signs of change. Contrary to expectations of climate-driven responses, no general increase of tall shrubs (excluding subregion MB), forbs or pure competitor species (*sensu* Grime, 2001) was observed neither in fertile or infertile sites but rather a decrease.

It has been suggested that analyses of plant community changes in relation to global changes benefit from a generalized plant strategy or trait-based approaches (Parmesan & Hanley 2015). Establishing possible links between plant functional traits and their long-term dynamics for these high-latitude systems is well on its way (The Tundra Trait Team, 2018), yet the trait data on cryptogamic ground layer plants that often cover 50% or even more is still limited (Martin & Mallik, 2017). Species assignments into the Grime's CSR system (II) likely contain much of the trait variation and can inform about underlying processes (competitive pressure and disturbance). On the other hand, most recent analyses favour examining one or a few traits, thereby attempting to infer links between functional changes and changes in possible drivers (Harrison, Damschen, Fernandez-Going, Eskelinen, & Copeland, 2014). Yet, there is no firm knowledge of how different traits react to different environmental or biotic drivers. Here, a combination of analyses on species abundances, community composition, generalized plant morphology and strategy groups could probably provide the most transparent picture of the functional changes in communities. As forest communities on fertile and infertile soils strongly differ in their composition and responses, stratified analyses along soil fertility gradients are clearly necessary.

3.1.2 Changes in species richness and community turnover

Plot-scale vascular plant species richness remained stable in treeless heaths (I) over time, which has been a general trend in multiple tundra sites during the recent decades (Elmendorf et al., 2012). It has been shown that increased *Empetrum* coverage negatively affects vascular plant species richness (Bråthen & Ravolainen,

2015), and that the impact is even stronger under abiotically milder conditions (Mod, Heikkinen, le Roux, Wisz, & Luoto, 2016). Thus, it may have a more pronounced impact on vascular plant species richness in subregion NBOR in the future. Even though plot-scale decreases of vascular plant richness was not observed in subregion NBOR, site-level losses of vascular plants and a substantial decrease in the total number of species was recorded. Also, in forest communities (II), vascular plant richness remained unchanged, excluding fertile sites in the northernmost subregion NBn where a major increase was observed in a plot-scale (11 species on average, $p < 0.001$).

In treeless heath sites (I), plot-scale lichen richness decreased locally in subregion NBOR and in wind-exposed sites of subregion HAcon. Notable increases in bryophyte richness were in turn recorded in forest communities throughout subregions NBs and NBn (II). Changes in a single plant group (vascular plants, bryophytes or lichens) richness were mostly reflected in the changes of total species richness, which can be thus tracked down to the change in a certain plant group richness. This is highly important if only total species richness is studied, as changes in plant group diversities may help to understand the varying patterns in temporal biodiversity trends that have shown tremendous variability in general and high context-dependency at a local scale during the recent decades (Vellend et al., 2017). High local variability and context-dependency in species richness was also recorded in study III.

Among the resurveyed communities (I, II), the magnitude of compositional turnover over time was most pronounced in snow-protected heath sites (I) and in fertile forest sites (II) throughout subregions (Fig. 4). Even though turnover was stronger in these sites, it was still relatively high in infertile forest and wind-exposed heath sites; thus, the results do not necessarily suggest that these sites have remained unchanged but showed more resistance over time. Interestingly, the direction of compositional turnover in forest sites (II) showed subregion-specific signs in changes, so that communities in both fertile and infertile sites showed signs of heterogenization in subregions MB and NBn and homogenization in NBs and NBm.

The results from study II and III revealed that changes in species richness are not necessarily directly comparable with changes in beta-diversity, i.e. community turnover. In fertile forest communities, for example, the increase in local richness was associated with increased turnover in subregion NBn while it was associated with decreased turnover in subregion NBs. The conflicting trends between local richness and compositional turnover support the need for an analytic exploration of

multiple biodiversity facets: focus on only one may not inform anything about other important biodiversity changes.

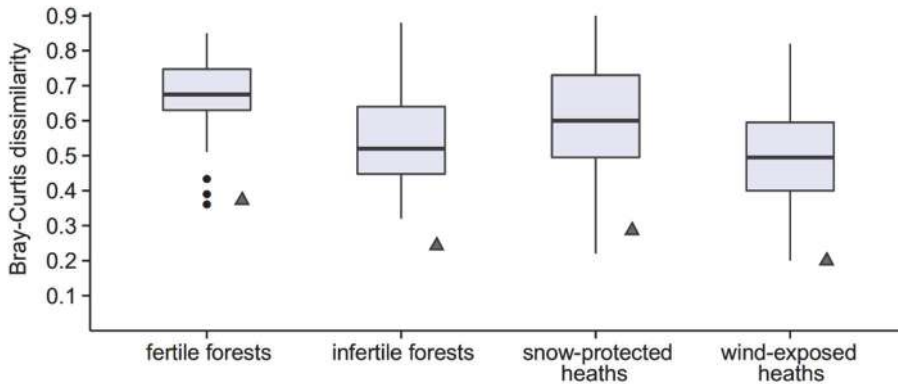


Fig. 4. The magnitude of compositional change, i.e. community turnover at plot-level measured as abundance-based Bray-Curtis dissimilarities between original and resurveyed sites in snow-protected ($n = 68$) and wind-exposed ($n = 40$) treeless heaths in study I and fertile ($n = 38$) and infertile ($n = 40$) forests in study II. Triangles indicate site-level turnover between samplings, averaged from plot-level species abundances.

3.2 Influence of local drivers on plant community changes under climate change

In treeless heath sites (I), mesotopography played a key role in the magnitude of vegetation changes over decades. In general, more pronounced compositional changes were observed in communities that are dependent on more snow cover. Without detailed information on snow cover conditions during both surveys, the results suggest the importance of altered snow cover conditions on vegetation changes or sensitivity of snow-protected communities to abiotic or biotic changes in case of unchanged snow-cover. In the latter case, species on snow-protected sites would be outcompeted by species that benefit from changed environmental conditions. Nevertheless, these results are associated with predictions and earlier evidence on sensitivity of snow cover-dependent communities to on-going climate change.

Earlier evidence has shown that reindeer grazing effectively retards the expansion of deciduous shrubs (Olofsson et al., 2009; Vowles et al., 2017), which is the most likely reason that the potential expansion was not detected here (I). Additionally, it has been reported that grazing does not prohibit the increase of

Empetrum (Bråthen, Gonzalez, & Yoccoz, 2017; Vowles et al., 2017) that thrive in the study area. Also, in the snowbed site (III), shrub growth was prohibited in grazed plots but not in enclosures, suggesting that abiotic conditions alone cannot inhibit shrub expansion. Grazing may also contribute to the homogenization of forest communities (II) (Rooney, 2009) of which there were indications in the reindeer herding district excluding subregion NBn, where the relatively high local species pool may have a buffering effect.

One likely reason for the missing link between the increasing *Empetrum* cover and a warmer climate when all sites were considered together (I) may be the habitat dependency of *Empetrum* cover changes. Indeed, our study only showed an increase in snow-protected, and not in wind-exposed habitats, which may hinder the warming link when all the habitats are considered together. As a dominant species in wind-exposed sites, *Empetrum* can hardly gain much more abundance, whereas in snow-protected sites, greater expansion is possible. In relation to many common tundra species, *Empetrum* is highly competitive, especially early in the growing season (Wipf, 2010), which has become longer in northern Fennoscandia during the past decades due to pronounced increases in temperatures during spring and autumn months (Kivinen et al., 2017). This variation in species-specific phenology and capacity to acquire resources in the early season may strongly modify species abundance relations (Brooker, 2006). Prolonged growing season and shortened snow cover duration possibly enhance *Empetrum*'s encroachment to the snow-protected sites but may also drain these sites to some degree, which is unfavourable for formerly dominant species *V. myrtillus*. Moreover, *V. myrtillus* likely becomes exposed to more frequent frost events and grazing and is thus eventually outcompeted by *Empetrum*. On the other hand, a moth outbreak during the resurvey most probably had a considerable negative impact on *V. myrtillus* cover in subregion HAoce. Nevertheless, the decline of *V. myrtillus* under grazed snowbed conditions (III) further suggested that environmental constraints, grazing and soil wetness may jointly filter shrub species from the tundra.

However, environmental perturbation or harshness seemed to prohibit *Empetrum* expansion into the snowbed site (III) where *V. myrtillus* were keeping its dominance over time. Along with the long-term persistence of typical snowbed vegetation (graminoids and forbs), this suggests that in harsh environments, such as snowbed conditions, the importance of competition is rather low compared to snow-protected sites (I), where abiotic conditions were generally milder (mean altitude of all snow-protected plots 531 a.s.l.) (Callaway et al., 2002). However, this may also be due to the shorter duration of study III compared to study I,

especially as this was also the case in the transplantation control site located within some of the studied snow-protected heath sites of the area (I).

In the snowbed site (III), increasing soil wetness tended to decrease shrub cover and increase the abundance of bryophytes as expected, which probably increased beta-diversity in wet conditions, as bryophyte mats can harbour multiple species with varying identities. Waterlogged snowbed conditions made lichens decrease in general; however, grazing ultimately determined the magnitude of these changes. Thus, site-dependent joint effects of multiple drivers eventually regulated the community composition.

Greater temporal turnover in fertile forest communities (II) throughout the study area indicate, that soil fertility may well be a general driver influencing the magnitude and rate of vegetation changes in boreal forests. Few studies have investigated the effect of soil fertility on vegetation changes in natural environments (Harrison et al., 2014; Virtanen et al., 2010), and thus, this finding is highly important, as general predictors of vegetation changes under environmental changes are not many.

The more pronounced compositional turnover of communities on fertile soils likely results from contrasted plant functional types and related soil conditions between communities of fertile and infertile soils. On fertile soils, plants representing competitive categories (*sensu* Grime, 2001) or ‘fast’ dynamics (*sensu* Reich, 2014) are relatively abundant. In contrast, on infertile soils, communities are composed of virtually entirely more stress-tolerant species (*sensu* Grime, 2001) or plants with ‘slow’ dynamics (*sensu* Reich, 2014). Even though the contrasted difference in plant functional composition accompanied with differences in soil fertility likely contributes to the observed differences in turnover, it remains less certain to what extent the higher turnover is linked to climatic warming. However, it is possible that the high turnover of communities on fertile soils can be indicative of their generally higher sensitivity to climatic changes.

Varying local drivers need further consideration in forest sites. The decline in forest overstorey cover across the subregion NBn was due to the defoliation by recent moth outbreaks. These events have shown to increase the cover of graminoid *Deschampsia flexuosa* in mountain birch forests (Karlsen et al., 2013) that was observed both on fertile and infertile sites and most likely together with warmer climate and continued intense grazing explain the strong increase of graminoids in both sites and bryophytes in fertile sites.

Finally, the effects of atmospheric deposition on vegetation changes was not assessed in these studies. The study area receives the lowest nitrogen and sulphur

depositions in Europe (Fowler et al., 2007; Harmens et al. 2011), which is why the effects of atmospheric depositions may often be neglected. However, studies from European heathlands (Britton & Fisher, 2008; Ross, Woodin, Hester, Thompson, & Birks, 2012) suggest that even correspondingly low levels of nitrogen input may enhance the capability of pre-existing species with good competitive abilities to gain even more dominance. Thus, it can be assumed that nitrogen input, even low, interplays with other drivers in the study area and its effects, especially on the naturally oligotrophic systems, may in fact be prominent in the long-term.

3.3 Evidence of long-term shifts in local and regional plant community compositions

Temporal shifts in plant community composition were observed both in treeless heath and forest habitats. The community compositions of snow-protected communities (I) in subregions HAcon and HAoce shifted towards those of wind-exposed habitats, which seems at least partly a result from distinctly changed abundance relations of dominant species. This congruence may also be interpreted as early evidence of a long-term homogenization process, yet the directional shift of snow-protected communities can also represent more transient dynamics. Moreover, there was some variation in the compositional changes of snow-protected communities between subregions, emphasizing the effects of local drivers to state changes.

The most pronounced community shifts among studied treeless heath sites (I) took place in the southernmost subregion NBOR, where heaths are located in boreal forest-tundra ecotone or its immediate vicinity compared to more northern sites that probably allowed a higher rate of immigration from the boreal forest. This was also the only subregion where increased temperatures, precipitation and grazing pressure all correlated positively with compositional shift, indicating a strong combined effect that was not seen in other subregions. One of the studied sites (Riisitunturi) in subregion NBOR is undergoing a paludification process, which was evident in the new species assemblage and likely contributes to the compositional shift. Nevertheless, these sites represent only one third of plots resampled in this subregion, and moreover, strong overall changes in vegetation were also observed in both forest sites of this subregion (NBn, II). One possible reason for the enhanced community responses is low microclimatic heterogeneity due to relatively homogenous topography, where communities do not have as good opportunities to cope with climate change compared to topographically

heterogenous areas with a high microclimatic heterogeneity (Graae et al., 2017). Considering this, results suggest that heath communities are more sensitive in topographically homogenous areas and more resistant in topographically complex areas.

To track down and understand vegetation state changes, it is necessary to include ground layer species, such as bryophytes and lichens, which have so far been relatively poorly studied over long time-scales at high latitudes (Callaghan et al., 2011). Our results from resurveyed treeless heaths (I) show evidence of moderate state shifts from lichen-rich towards more bryophyte-rich dwarf shrub tundra that can occur due to intensive grazing (van der Wal 2006). Yet, there is no evidence of the replacement of dwarf-shrub dominated heaths with grass or graminoid dominated vegetation that was observed in the experimental study (III) and in other Fennoscandian tundra sites (Olofsson, 2006). Interestingly, in a recent study by Vowles, Lovehav, Molau and Björk (2017) a shift from graminoid- to shrub-dominated (*Empetrum*) state was detected along with increasing temperatures and longer growing seasons but regardless of continued grazing pressure. This suggests that in *Empetrum* dominated heath types, as in the study area, climatic factors may have the potential to override grazing effects on state changes in the long-term.

Results from study III showed that local drivers could have substantial effects on the trajectories of communities on the tundra snowbed, leading to alternative vegetation states over time. Environmental perturbation moved tundra communities away from their original stable state and, after decadal exposure to varying conditions on grazing and soil wetness, led to contrasting alternative states in dry conditions and more transient states in wet conditions. Even though there is not much evidence on the development of alternative states (van der Wal, 2006) on boreal forest floors (Olofsson, Moen, & Östlund, 2010), the results from study II show signs that a graminoid-dominated state may be developing locally in fertile sites of subregion NBs and both sites in subregion NBn, where grazing most likely has strong effects on vegetation.

Distinguishing climate and non-climatic driver impacts from successional changes is tedious, yet in many forest sites, canopy cover had decreased (e.g. in subregions NBs and NBn), to some degree ruling out the effects of gradual successional development of canopy cover on vegetation understory changes. Moreover, as studied communities represent rather late successional stages, relatively fast successional changes were not expected.

Even though relatively strong compositional shifts took place locally, the development of completely novel community compositions remains unlikely outcome for the studied communities given that non-native species were not observed and formation of novel compositions likely take much longer than several decades (Hobbs et al., 2006). However, structural novelty of communities is more plausible to emerge as predicted for the Eurasian tundra (Macias-Fauria, Forbes, Zetterberg, & Kumpula, 2012). The observed community shifts in the study area may well be the first signs of a process that may eventually lead to structural or functional novelty in terms of changes in current species relative abundances and thus, should not be neglected.

Taken together, the results highly suggest that the observed community shifts are not solely driven by changes in abiotic conditions nor controlled only by biotic drivers and processes but rather result from context-dependent combinations of both. Thus, despite certain generalities among community changes observed in both forest and treeless heath habitats, the direction of community shifts under the changing climate can be expected to vary across regions due to a joint effect of multiple local- and regional-scale drivers.

3.4 Remarks on the use of resurveys and long-term data

Due to the lack or scarcity of continuous vegetation monitoring, resurveys often serve as the only or among the few methods available that produce information on vegetation dynamics. This is also the case in the study area, where few long-term monitoring of vegetation are continuing to provide improved temporal sampling (Auvinen et al., 2007). Thus, these comparisons between surveys are among the few evidence on the community composition and biodiversity trends in decadal time scales in these systems. However, there are certain issues that need to be considered, of which no resurvey is free from. One obvious issue is the snapshot data and limited temporal sampling. A typical feature of observational resurveys is having data on only two time points like in studies I and II. The challenge is that the community dynamics between the studies is unknown. Even though studied plots have not been impacted by direct human disturbance, various other drivers may have affected community dynamics such as cyclic herbivory disturbances. Moreover, extreme weather conditions in either sampling points can affect species abundancies leading to over- or underestimations. Using large geographical subareas (I) and a gradient (II) to detect and interpret changes however mitigates the effects of uncontrollable local drivers. Moreover, it can be presumed that in

communities dominated by perennial slow-growing shrubs, bryophytes and lichens interannual variations in vegetation are not very sensitive to short-term variation in annual weather conditions. Even though it has been questioned whether snapshot data are sufficient for analyzing, for instance, trends in biodiversity (Cardinale, Gonzalez, Allington, & Loreau, 2018), these types of resurvey approaches can be viewed as a cost-efficient framework for providing the primary data for biodiversity and vegetation monitoring as a whole. In summary, carefully conducted resurvey produce valid data and can reveal real general trends, yet the results must be interpret with certain caution due to the limited temporal sampling. The more minor the changes the more cautiously they must be considered.

The composition of plant communities in different treatments (III) analysed after seven years (Virtanen, 1998) showed distinctly different responses compared to long-term responses of over 23 years. Short-term results suggested resistance of tundra communities to different treatments, as observed changes were mostly minor, and emphasized the importance of abiotic conditions as a predominant driver as the initially dominant dwarf shrub *V. myrtillus* declined throughout under the snowbed conditions. Comparing short-term results to long-term trajectories of plant communities in different treatments highlights the matter that long-term outcomes can be highly unpredictable from short-term responses (see also Saccone & Virtanen, 2016).

The lack of detailed information inevitably limits the use of old vegetation data but also makes plots that can be relocated particularly valuable. Despite inherent uncertainties related to the resurvey method, the results of this thesis strengthen the grounds for the semi-permanent plot resurvey approach as an invaluable tool for providing insights of climate and grazing effects on changes in plant community composition and biodiversity. Further on, they contribute to the growing number of vegetation resurvey studies that together, if not alone, can better reveal the probable drivers behind plant community changes (Verheyen et al., 2017).

4 Key findings and conclusions

Plant communities in northern Fennoscandia have undergone various changes in composition and diversity during the past few decades, which represent the period of most pronounced anthropogenic climate change. Conspicuous changes include the alteration of snow-protected treeless heath communities that have lost some of their typical characteristics while the abundance of common dwarf shrub *Empetrum nigrum* ssp. *hermaphroditum* increased on these sites. The increasing *Empetrum* cover and similarity between snow-protected and wind-exposed community compositions can be expected to negatively affect diversity by homogenizing already relatively species-poor tundra communities. The long-term ecological consequence of this could be an overall decline in community and ecosystem functioning and reduced resistance and resilience to environmental changes (Olden, Poff, Douglas, Douglas, & Fausch, 2004). Even though increasing shrub abundance contributes to positive climate warming feedback, slow decomposition rates of *Empetrum* litter can partly offset the positive feedbacks by potentially slowing down soil processes (Cornelissen et al., 2007). Increasing *Empetrum* biomass in response to warming (Bråthen et al., 2017) is a further potential threat to lichens (Cornelissen et al., 2001) that had deteriorated throughout the treeless heath communities in the study period. Such an altered vegetation structure poses growing challenges to reindeer populations and reindeer herding practices in boreal and arctic ecosystems.

The main findings from forest communities suggest generally stronger responses of communities on fertile soils under changing climatic conditions compared to communities on infertile soils. This is a particularly important finding as such generalities upon climate change impact on plant communities are not many. Even though forest communities on infertile soils may have better resistance to climatic changes, they might still turn out to be fragile, reflecting the possibility that communities with slow-growing plants might have low resilience to climatic shifts and abrupt state shifts, and if not readily evident may have relatively strong impacts in the longer-term. Despite increased species richness in many fertile forest sites, communities on fertile soils are still susceptible to biodiversity losses (demise of specialized plants and homogenization) due to their fragmented habitats and small population sizes in the study area.

Certain expected climate-driven vegetation responses, e.g. the general increase of competitive tall species, did not occur over time. Indeed, one of the key findings was that despite a rather uniform warming trend across the study area, relatively

inconsistent vegetation changes have taken place between subregions and habitats. All these suggest that non-climatic drivers play a key role in the long-term plant community dynamics, at least given the current rate of climate change. This was also clearly demonstrated in the long-term experiment on the mountain tundra snowbed that showed multi-driver effects on the development of contrasting vegetation states. Results also suggest that shrub encroachment on tundra snowbed sites will highly depend on the level of grazing pressure and soil wetness conditions. Thus, the ultimate outcome of climate change effects on plant communities throughout the study area substantially depend on many local scale factors that buffer or contribute to climatic changes and can ultimately determine plant community responses to global changes. All these aspects call for improved and continuous monitoring and resurveying of vegetation, which is clearly necessary due to distinct responses of plant communities between subregions and habitat types.

The results show that throughout the study area, the response of ground layer species, consisting of cryptogamic bryophytes and lichens, was notably strong over time. This issue is of importance, as long-term responses of ground layer species are still understudied. Observing and addressing changes in the ground layer as well will greatly improve the understanding of high latitude community dynamics.

In general, changes in resurveyed treeless heath vegetation were most pronounced in the southern parts of the study area, where overall changes in forest vegetation also tended to be greater. Among the studied regions, the southern parts were warmer to begin with. Elmendorf et al. (2012) found similarly, that warming had a positive effect on total shrub abundance in initially warmer tundra locations, and Hedwall and Brunet (2016) reported temperature-related changes in the temperate forest zone but absence in the boreal zone. This pattern suggests that vegetation changes may be lagging in the northern parts of the study area, and thus, more pronounced changes can also be expected in the north as climate change proceeds. However, the southern study area in particular can at the moment be regarded as highly indicative of relatively rapid community responses to multi-driver effects.

Several contrasted and notably varying responses of species and plant groups in different subregions and habitat types highlight the challenges in the description and prediction of vegetation trends under various climatic and non-climatic drivers. However, the results of this thesis show that long-term resurvey studies in multiple sites have an invaluable role in the investigation of the links between long-term dynamics of plant communities and often subtle and gradual global environmental

changes. Observed vegetation changes most likely have further impacts on plant communities along with expected changes in climate, and thus, future alterations in studied plant communities can be expected.

To get a better picture on long-term vegetation changes, it would be advantageous to combine existing resurveys, including the results of this thesis, to conduct meta-analyses and cross-system comparisons. Moreover, this would provide a better idea on general community responses and key drivers of each context and help detect possible lags in high latitude plant community responses.

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- I Maliniemi, T., Kapfer, J., Saccone, P., Skog, A. & Virtanen, R. (2018). Long-term vegetation changes of treeless heath communities in northern Fennoscandia: links to climate change trends and reindeer grazing. *Journal of Vegetation Science*, 29(3), 469–479. doi:10.1111/jvs.12630
- II Maliniemi, T., Happonen, K. & Virtanen, R. (2018). Soil fertility level influences temporal turnover of high latitude vegetation under changing climate. *Manuscript*.
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