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Climate Change and Alpine Vegetation Shifts on Mountaintop Summits in Norway

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Preface

The field work and data collection for this thesis was carried out within the framework of the third vegetation sampling campaign of the Global Observation Research Initiative in Alpine Environments (GLORIA). In 2015, the field work was financed by the Norwegian Environment Agency (*Miljødirektoratet*), whereas the field work in 2001 and 2008 was financed by the GLORIA-Europe project within the 5th RTD - Framework Program of the European Union and the Norwegian Directorate for Nature Management, respectively. Moreover, with the help of their technician, Manfred Bardy-Durchhalter, I was able to access the complete temperature and vegetation dataset from 2001 and 2008.

I would like to thank my supervisors Pieter De Frenne and Kris Verheyen for their excellent guidance and support during the writing process of this thesis. Not only did they provide me with some relevant comments and corrections, but they also assisted with the statistical analysis.

In addition, I would like to express my gratitude to the people who assisted me during the field work, in particular Magni Olsen Kyrkjeeide, Rozália Kapás, Sigrid Lindmo and Ottar Michelsen. With their help, I acquired some valuable local plant knowledge and was able to schedule and carry out the field work within the provided time period. Furthermore, I acknowledge Ottar Michelsen for helping me to read out the temperature loggers and providing me with additional data for the malfunctioning loggers. I also thank Håkon Holien and Kristian Hassel for determining the altitudinal ranks of the lichens and bryophytes.

Finally, I would also like to thank Bente Jessen Graae for arranging the accommodation and Mia Vedel and her team for keeping me alive and, above all, well-fed with the delicious vegetarian cooking during my four-week stay at the *Villreinsenter* in Hjerkinn, Norway.

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List of abbreviations

a.s.l.	above sea level
ACIA	Arctic Climate Impact Assessment
ANOVA	Analysis of Variance
E	East
ENSO	El Niño - Southern Oscillation
GCM	General Circulation Model
GLORIA	Global Observation Research Initiative in Alpine Environments
Gt	Gigatons
HSP	Highest Summit Point
IPCC	Intergovernmental Panel on Climate Change
KOL	Kolla (one of the mountains under study)
LAI	Leaf Area Index
MATA	Mean Annual Temperature Anomaly
N	North
NAO	North Atlantic Oscillation
NINA	Norwegian Institute for Nature Research
NMDS	Non-metric Multidimensional Scaling
PERMANOVA	Permutational Multivariate Analysis of Variance
ppb	parts per billion
ppm	parts per million
RPC	Representative Concentration Pathway
S	South
S.D.	Standard Deviation
S.E.	Standard Error of the Mean
SAS	Summit Area Sections
SKI	Storkinn (one of the mountains under study)
SST	Sea Surface Temperature
VAR	Vesle Armodshøkollen (one of the mountains under study)
VKO	Veslekolla (one of the mountains under study)
W	West

Abstract

Global temperatures have risen with c.a. 0.85 °C during the past century and are predicted to increase even further at an accelerated rate in the coming decades. These changes in the climate system are having a profound impact on the distribution and composition of plant communities. Mountain ecosystems are considered to be extremely sensitive since their vegetation is generally constraint by low temperatures. Within the framework of the international observation network *Global Observation Research Initiative in Alpine Environments* (GLORIA), medium-term changes in species diversity and composition of vascular plants, lichens and bryophytes were investigated on four study summits in the National Park of Dovrefjell, Norway. These four summits were situated along an elevational gradient from the low alpine (1161 m a.s.l.) to the high alpine vegetation zone (1845 m a.s.l.). In 2015, vegetation data indicated that the species richness of vascular plants decreased significantly with increasing elevation. In addition, compared to the previous surveys in 2001 and 2008, no significant change in vascular plant species richness was found, whereas a significant decrease in lichen species richness (with an average loss of two species over a period of 15 years) was observed. Changes in species composition of vascular plants were strong, however, and could be attributed to a significant increase in cover of shrubs, dwarf shrubs and graminoids. Moreover, thermophilization of vascular plants (i.e. the increasing abundance of warm-adapted species and/or decreasing abundance of cold-adapted species) was more pronounced on the two lowest summits and on the north-facing slopes. Also, this process primarily occurred during the period 2001-2008. Lichens generally showed less thermophilization than vascular plants and the process mainly took place on the two highest summits between 2008 and 2015. For the bryophytes, thermophilization was only noticed on two summits during the period 2001-2015. To conclude, climate change can be considered as the prominent driver for the observed changes in vegetation. However, since this is only a medium-term observational study, other factors, such as plant-herbivore interactions, should also be taken into account and could be assessed with further experimental research.

Samenvatting

De globale temperatuur steeg met circa 0.85 °C gedurende de voorbije eeuw. Bovendien wordt voorspeld dat deze opwaartse trend zich in de komende decennia versneld zal doorzetten. Verscheidene studies toonden reeds aan dat deze klimaatverandering een doorgedreven impact heeft op de ruimtelijke verdeling en samenstelling van plantengemeenschappen, voornamelijk in bergecosystemen die gelimiteerd worden door lage temperaturen. In het kader van het internationaal lange-termijn observatienetwerk *Global Observation Research Initiative in Alpine Environments* (GLORIA) werden veranderingen in de soortenrijkdom en -samenstelling van hogere planten, korstmossen en mossen onderzocht op vier bergen in het massief van Dovrefjell, Noorwegen. Deze bergen werden geselecteerd langsheen een hoogtegradiënt die strekt van de lage alpine (1161 m boven zeeniveau) tot de hoge alpine zone (1845 m boven zeeniveau). Enerzijds bleek uit de verzamelde data van 2015 dat de soortenrijkdom van hogere planten sterk daalde met toenemende hoogte. Anderzijds werd geen significante verandering in de soortenrijkdom van hogere planten vastgesteld, vergeleken met de vorige vegetatieanalyses in 2001 en 2008. De soortenrijkdom van de korstmossen daalde echter wel significant (met een gemiddelde van twee soorten) gedurende de periode 2001-2015. Deze verandering in de soortensamenstelling van hogere planten kon voornamelijk worden toegeschreven aan een toename in de bedekking van struiken, dwergstruiken en grasachtigen zoals grassen, zegges en russen. Ten slotte bleek uit de vegetatiedata dat thermofilisatie van hogere planten (d.w.z. de verhoogde abundantie van warmteminnende soorten en/of de verlaagde abundantie van koudeminnende soorten) voornamelijk voorkwam op de twee laagste bergen en op de noordflanken. Bovendien bleek dat het proces zich grotendeels voordeed in de periode 2001-2008. Voor de korstmossen werd over het algemeen minder thermofilisatie waargenomen en het effect was voornamelijk merkbaar op de twee hoogste bergen gedurende de periode 2008-2015. Thermofilisatie van de mossen werd echter slechts op twee bergen waargenomen tijdens de periode 2001-2015. Deze vaststellingen komen sterk overeen met voorgaande klimaatimpactstudies in vergelijkbare omstandigheden. Bijgevolg kan de klimaatverandering beschouwd worden als de meest aannemelijke drijvende kracht achter de vastgestelde veranderingen in vegetatie. Echter, het effect van andere factoren, zoals plant-herbivoor interacties, kan niet verwaarloosd worden en vormt het onderwerp van verder onderzoek.

Introduction

As a result of the contemporary enhanced concentrations of greenhouse gasses in the atmosphere, the global climate is changing. Temperatures have been rising significantly by approximately 0.85 °C all across the world (IPCC, 2013). Europe has warmed more than the global average, with an annual average surface temperature increase of about 1.3 °C between 1850 and 2009 (European Environmental Agency, 2010). Moreover, precipitation has increased on mid-latitude land areas of the Northern Hemisphere since 1901. For other latitudes, long-term positive and negative trends in precipitation were observed, but with a much lower confidence (IPCC, 2013). The average duration of the growing season has increased with 10.8 days since the beginning of the 1960s (Menzel & Fabian, 1999). In Arctic regions, however, the effect of climate warming seems to be even more severe and studies indicate a warming rate of almost twice the global average. Norway has experienced an increase in the mean annual temperature of about 0.9 °C during the period 1900-2008 (Ministry of the Environment of Norway, 2009). However, the mean annual temperature increase varies strongly depending on the geographical region and ranges between 0.5 and 1.5 °C for the period 1874-2004 (Hansen-Bauer, 2005).

Recent climate impact studies assessed the effects of climate warming on a wide range of habitats around the world (Walther et al., 2002; Root et al., 2003; Parmesan, 2006; Gottfried et al., 2012). A large variety of changes in the distribution of plant and animal species and the composition of communities has already been observed (Parmesan et al., 1999; Thomas et al., 2001; Pounds et al., 2006; Berg et al., 2010; Urban, 2015). Mountain ecosystems are generally limited by low temperatures and are therefore considered to be highly sensitive to climate warming (Chapin & Körner, 1994; Aerts et al., 2006). As a result, these ecosystems are often used as indicators for the impacts of climate-induced warming (Price & Barry, 1997). Prolonged temperature increases gradually remove local environmental boundaries, allowing a warming-induced range shift of alpine plant species towards higher altitudes. Hence, species richness is expected to increase in the high alpine and nival belt. However, in the low alpine belt, species diversity might decrease due to the stronger competition of highly productive thermophilic species with the potential to overgrow local alpine plants (Callaway et al., 2002; Pauli et al., 2003; Wipf et al., 2006; Wipf & Rixen, 2010). This increasing dominance of warmth-loving (low-altitude) species and the subsequent decline of cold-adapted (high-altitude) species was termed *thermophilization* (Gottfried et al., 2012). Previous studies also indicated a climate-induced change in species composition with an increasing dominance of dwarf shrubs, such as *Betula nana* and *Vaccinium vitis-idea*, and a growing abundance of graminoids[1], viviparous[2] and hemiparasitic[3] species (Bahn & Körner, 2003; Virtanen et al., 2003). Furthermore, in situ experimental warming studies report that the abundance of deciduous shrubs and graminoids increased significantly in tundra environments with a 1 – 3 °C warming, whereas the cover of cryptogams (lichens and bryophytes) significantly declined (Walker et al., 2006; Elmendorf et al., 2012).

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[1] From ecological point of view, graminoids are defined as herbaceous plants with a grass-like morphology. Common plant families included in this group are among others: *Poaceae*, *Cyperaceae* (sedges) and *Juncaceae* (rushes). These species often dominate in open habitats, e.g. grasslands and marshes (Schulze et al., 2005).
[2] Viviparous plants generally produce seeds or embryos that start to develop prior to the detatchment of the parent plant (Schulze et al., 2005).
[3] Hemiparasitic plants are naturally parasitic (i.e. obtain nourishment from their host), however they photosynthesize as well. A popular example is mistletoe (*Viscum album*) (Zuber, 2004).

In order to investigate the impacts of climate change on mountain ecosystems, an international long-term observation network was established, named GLORIA (*Global Observation Research Initiative in Alpine Environments*). In 2001 and 2008, GLORIA's researchers already performed field work and vegetation analysis on mountains in 18 target regions scattered across the European continent. During the summer of 2015, a third sampling campaign was carried out in order to detect possible changes in in vegetation composition and abundance in the different mountain plots (Grabherr et al., 2000; Pauli et al., 2005; Grabherr et al., 2010; Michelsen et al, 2011). One of these target regions is located at Dovrefjell, an extensive national park on the Norwegian mainland (Michelsen et al., 2009; Michelsen et al., 2011). The set-up comprises four mountaintop summits which are carefully selected using the instructions summarized in the GLORIA manual (Pauli et al., 2015), namely Vesle Armodshøkollen, Veslekolla, Kolla and Storkinn. The main purpose of this study is to examine whether the species diversity, evenness and composition of vascular plants, lichens and bryophytes changed significantly on the GLORIA summits at Dovrefjell compared to the previous field surveys in 2001 and 2008. Moreover, it will be investigated whether climate change and the subsequent temperature increase can be addressed as the main driver for potential changes in vegetation. The influence of other factors, such as grazing, trampling, eutrophication, invasive species, etc., will be considered as well.

Literature review

Tundra ecosystems

The name 'tundra' is closely related to the Lappish word *tundar* which was formally used to indicate the treeless northern regions in Finland. The word literally means 'marshy plains'. However, the name 'tundra' as such was introduced by the Russians in 1841 in order to describe a distinctive ecological realm which is characterized by levelled or undulating treeless plains and primarily occurs in the northern Arctic regions (Online Etymology Dictionary, 2015; Webster, 2015). The tundra biome can be subdivided into two major zones, namely the Arctic tundra and the Alpine tundra (**figure 1**). The Arctic tundra envelopes a vast area of marshy, moss-covered plains north of the Arctic circle whereas the Alpine tundra is generally found above the treeline on higher mountain peaks (Moore, 2006; Encyclopedia Britannica, 2015).

The global extent of all major tundra ecosystems accounts for approximately 10 % of the entire Earth's land surface area. The Arctic tundra stretches up to the northern edge of the coniferous forest belt which is situated at 60° N in North America and Eurasia. About 80 % of the Arctic tundra is situated less then 100 km off the coast, making it predominantly a maritime biome (Walker et al., 2005; Bhatt et al., 2010). The Alpine tundra, on the other hand, is mainly restricted to the Northern Hemisphere and covers about 3 % of the Earth's surface. These tundra ecosystems generally occur at higher elevations, typically in mountain ranges (e.g. the Alps or the Pyrenees), where the low temperatures and high wind velocities prohibit tree growth (Moore, 2006). According to Körner and Paulsen (2004), the position of the alpine treeline is determined by the location of the 10 °C isotherm of the warmest month of the year.
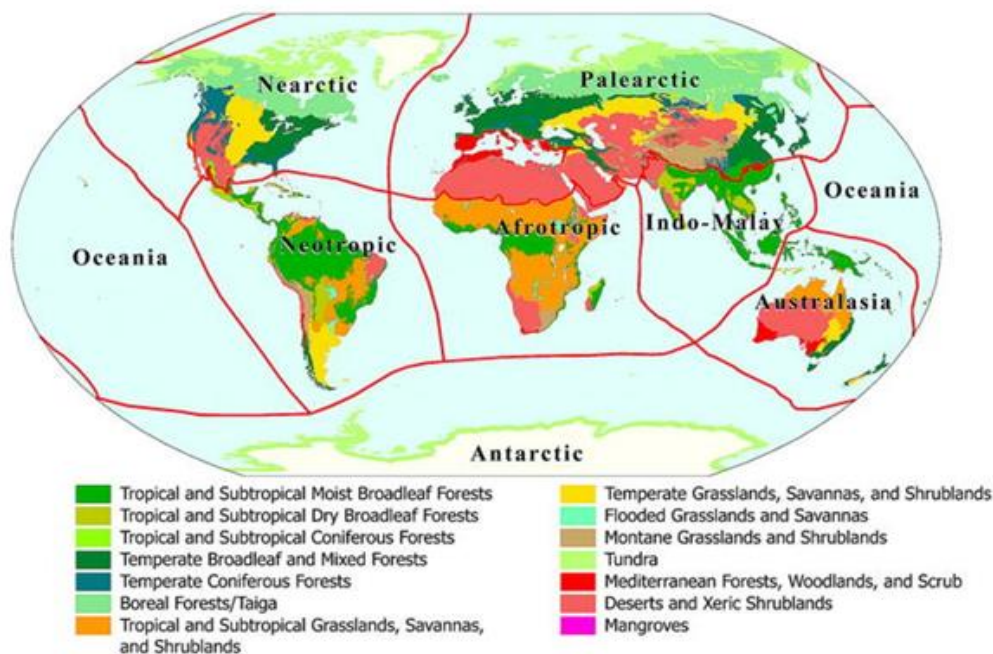
Figure 1: Map of the terrestrial ecoregions of the World. In order to facilitate representation, the ecoregions are categorized within 14 different biomes and eight biogeographic realms (Olsen et al., 2001).

Tundra ecosystems are characterized by a large variety of (extreme) climatic conditions. In fact, the tundra biome comprises a gradient of approximately 10 °C in average summer temperature and spans over a moisture gradient from polar deserts to wetlands (Epstein et al., 2004; Elmendorf et al., 2012). The most extreme conditions can be found in the Arctic regions, whereas the Alpine tundra is defined by a more moderate climate with cool summers (3 – 12 °C) and temperate winters. Moreover, the annual precipitation in the Arctic regions is, on average, higher than in the Alpine tundra, nonetheless it only reaches up to 380 mm. Approximately, two-thirds of this amount can be attributed to summer rains, while the remaining part falls as snow. Snowstorms, in combination with the characteristic strong winds, cause distinctive snow-drift patterns which constantly scape the landscape during the winter months. Furthermore, heavy precipitation events during the summer influence the landscape through erosion (ACIA, 2001; Körner, 2003). The growing season is usually short, e.g. the average length of the growing period ranges between 50 – 60 days in Arctic areas and corresponds to approximately 180 days in Alpine tundra regions (University of California: Museum of Paleontology, 2015).

Soils in the Arctic tundra can be described by the presence of a permafrost layer (Muller, 2008) which generally obstructs the downward movement of percolating precipitation or melt water (Moore, 2006). As a result, the Arctic lowlands can easily become saturated and waterlogged during the summer thaw. In addition, this phenomenon leads to *solifluction* or downward creep of the overlying active layer (Kerfoot, 1972). Alpine tundra ecosystems, however, generally lack a continuous permafrost layer. In combination with the inclination of alpine slopes, this contributes to a better drainage of melt water. Subsequently, soils in alpine regions contain lower amounts of water despite the higher annual amounts of snowfall (Moore, 2006). Depending on the classification system, most soils in the tundra biome can be classified as Gelisols or Cryosols (Soil Survey Staff, 1999; FAO, 2014; Kimble, 2013). These soil types are highly erodible and defined by the presence of an active surface layer which is continuously shaped by freeze-thaw cycles (Kimble, 2013). These alternating periods of freezing and thawing are caused by the seasonal variations in temperature and have a major influence on the landscape of tundra ecosystems. Furthermore, soil pH, soil organic matter content and nutrient availability varies significantly among tundra soils (Epstein et al., 2004; Elmendorf et al., 2012). For example, pH values in a tundra environment range between 3 – 4 for moist acidic soils and between 6 – 7 for moist non-acidic soils (Hobbie et al., 2004). In addition, organic carbon contents in tundra region range between 3.9 – 5.4 kg m^{-3} and 27.2 – 72.6 kg m^{-3} for turbic[4] and non-cryoturbated Cryosols respectively (Kimble et al., 2000; Tarnocai, 2005; Weintraub & Schimel, 2005; Beermann et al., 2014).

The Arctic tundra biome is generally marked by a low plant and animal species diversity and shows a decreasing vegetation productivity and complexity with increasing latitude. However, patterns of species richness vary and local high diversity can be found in various old, topographically and geologically complex regions. Arctic regions support a large variety of rare or endemic plant and animal species which have adapted to the local, often extreme, climatic conditions (Arctic Biodiversity Assessment, 2013; Munson & Sher, 2015). Therefore, mountain ranges can often be described as true *hotspots* of diversity. This can be largely attributed to high rates of species turnover across substantial

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[4] Turbic Cryosols are mineral soils with permafrost within 2 m of the soil surface and with distinctive evidence of cryoturbation (i.e. mixing of soil material from different horizons upon an alternating freeze-thaw cycle). Due to the instability of active turbic sites and the exposure of parent material at the soil surface, vegetation is scarce or even completely absent on this type of soils. The other great groups of the Cryosolic order are Organic and Static Cryosols, which respectively consist of organic and mineral parent material and have a permafrost layer within 1 m depth from the soil surface (Kimble et al., 2000).

climatic and edaphic[5] gradients (Munson & Sher, 2015). Hence, the tundra biome can be considered as an important contributor to global biodiversity (ACIA, 2001; Arctic Biodiversity Assessment, 2013).

Predator-prey and food-feeder relationships are seemingly simple in the tundra, making the ecosystem's stability susceptible to the extinction of critical species (Winner, 2003). With respect to the vegetation, the spatial distribution of plant communities is controlled by local abiotic conditions such as soil drainage, snow cover, time of melt and microclimates (Billings, 1973; Billings & Mooney, 1968). For example, coastal tundra plains are mainly dominated by cotton grass (*Eriophorum sp.*), sedges (*Carex sp.*) and mosses (*Bryophyta*) while more elevated areas above wet, peaty soils contain more willows (*Salix sp.*), grasses (*Poaceae*) and rush species (*Juncus sp.*). Gentle slopes with sufficient soil development are covered with vast meadows and cushion plants occur predominantly on ridges which are continuously exposed to desiccating winds. At higher elevations and on exposed rocky slopes, vascular plants only occur in scattered patches. Finally, on top of high mountain peaks, lichens and bryophytes generally grow on rocks and the vascular plant limit is situated close to the line of permanent snow cover (Zwinger & Willard, 1996). A lot of plant species in tundra ecosystems have adapted to the local climate (Bliss, 1962; Billings & Mooney, 1968). On the one hand, prolonged periods of temperatures below freezing point have led to the evolutionary advantage of a rapid life cycle completion. On the other hand, a lot of tundra plant species are perennial as a response to the short growing season. Most plant species are short and group together in order to resist freezing temperatures and protect against snow during winter months. Some species also photosynthesize at lower temperatures and lower light intensities, e.g. some tundra grasses photosynthesize sugars at temperatures below freezing point (-4 °C) due to the production of antifreeze keeping the cell liquid sufficiently fluid (Griffith et al., 2005). Some plant species still continue to develop after being exposed to freezing temperatures and even produce seeds upon thawing. Other plants largely depend on budding and underground shoots or runners for reproduction, e.g. some members of the heath family (*Ericaceae*). Furthermore, species like cotton grass (*Eriophorum sp.*), lousewort (*Pedicularis sp.*) and some willows (*Salix sp.*) have hairy flower stalks with the capacity to retain warm air (Bliss, 1962; Billings & Mooney, 1968). Other species have the ability to raise their temperature by generating heat in the mitochondria of their cells, e.g. *thermogenic* plants (Meeuse, 1966; Meeuse, 1975).

The extensive treeless plains of the tundra provide a living environment for some extraordinary birds and mammals. Local fauna includes predators like the polar bear (*Ursus maritimus*), the Arctic fox (*Alopex lagopus*), the Arctic wolf (*Canis lupus*) and snow owl (*Nyctea scandiaca*), but include some characteristic large herbivores as well, e.g. the wild reindeer (*Rangifer tarandus tarandus*) and the musk ox (*Ovibus moschatus*) (Winner, 2003; Dublin et al., 2001). Most of these animals have adapted to the local environment and climatic conditions. For example, large mammals such as the musk ox thrive in areas above the timberline during the growing season and descend to graze in the lowlands during the colder winter months. Other animals, e.g. the Arctic ground squirrel (*Spermophilus parryii*), hibernate during the cold winter period when a major food source is absent (Winner, 2003). Next to fauna and flora, bacteria and fungi have a key role in the ecosystem functioning of the tundra biome as well. Microbial communities contribute to a series of biochemical processes in the soil, e.g. nutrient cycling and their composition largely depends on the local soil temperature, soil moisture availability and carbon content of the soil (Wallenstein et al., 2007). However, almost all biological life in tundra

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[5] Edaphic factors are related to or caused by particular soil conditions, e.g. texture, drainage properties, chemical characteristics, etc. Edaphology is, next to pedology, one of the main divisions of soil science and describes the influence of soil characteristics on living organisms, especially plant indiviuduals and communities (Buckman & Brady, 1960).

soils is restricted to the active surface layer which varies in thichness between 10 cm and a few meters, depending on the maximum summer temperature (Margesin, 2008).

In conclusion, the species composition and distribution in tundra ecosystems is mainly controlled by temperature (Klanderud & Birks, 2003; Pauli et al., 2004; Walker et al., 2005; Elmendorf et al., 2012). However, other abiotic, biotic and anthropogenic factors such as precipitation and soil moisture, the presence of predators or an essential food source, invasive species, grazing, trampling, land-use changes, urbanization and industrialization, tourism, resource extractions, pollution, etc. play a significant role too. Climate impact studies indicate that an increasing temperature, as a result of the ongoing global climate change, can trigger a wide range of ecological and even evolutionary responses among plant and animal species (Parmesan et al., 1999; Thomas et al, 2001; Whalter et al., 2002; Parmesan & Yohe, 2003; Parmesan, 2006; Pounds et al., 2006). Consequently, local and regional species compositions and distributions are expected to change through various processes such as migration or adaptation (Parmesan, 2006; Berg et al., 2010). Generally, species tend to shift their distributions towards higher latitudes in flat regions and higher altitudes in mountainous areas (Klanderud & Birks, 2003; Parmesan & Yohe, 2003; Parmesan, 2006). In tundra regions, however, some species already occur at the limits of their physiological capacities with relatively narrow environmental tolerances. In addition, most high-latitude or high-altitude species are characterized by their limited geographical ranges (Pauli et al., 1996; Thuiller et al., 2005; Munson & Sher, 2015). Therefore, some of these species are unlikely to migrate and change biome, despite the fact that polar as well as alpine ecosystems will contract as a result of global warming (Cox & Moore, 2010). Hence, they are highly threatened with extinction (Parmesan, 2006). This global extinction risk is not only predicted to increase, but will probably also accelerate as global temperatures rise in the coming decades (Uban, 2015). Finally, climate-induced changes in tundra vegetation could have a wide range of consequences in the future. For instance, plant composition highly influences other processes, like nutrient cycling, productivity and decomposition, active layer depth above permafrost, forage quantity and quality, snow distribution and land surface albedo (Chapin et al., 1996; Sturm et al., 2005; Cornelissen et al. 2007; Blok et al., 2010). In addition, the net effect of climate warming on the extensive carbon stocks contained in tundra soils highly depends on whether the warming-induced increase in primary productivity counterbalances the increase in heterotrophic soil respiration and methanogenesis and the subsequent carbon dioxide (CO_2) and methane (CH_4) release in thawing permafrost soils (Euskirchen et al., 2009; McGuire et al, 2009; Tarnocai et al., 2009). These unique ecosystem services provided by the tundra biome, in combination with the future climate predictions and the subsequent ecological responses, increase the incentive of performing climate-warming studies in tundra environments (Elmendorf et al., 2012).

Climate change: history, processes, causes and effects and future projections

Long-term observations of weather station, buoy, ship and satellite data indicate that global temperatures are rising significantly. This significant warming trend is now visible in all archives of datasets and using all statistical methods. The Fifth Assessment Report of the IPCC (Intergovernmental Panel on Climate Change from the United Nations) reported that the globally averaged combined land and ocean surface temperature increased with approximately 0.85 ± 0.2 °C between 1880 and 2012 (IPCC, 2013) (**figure 2**).
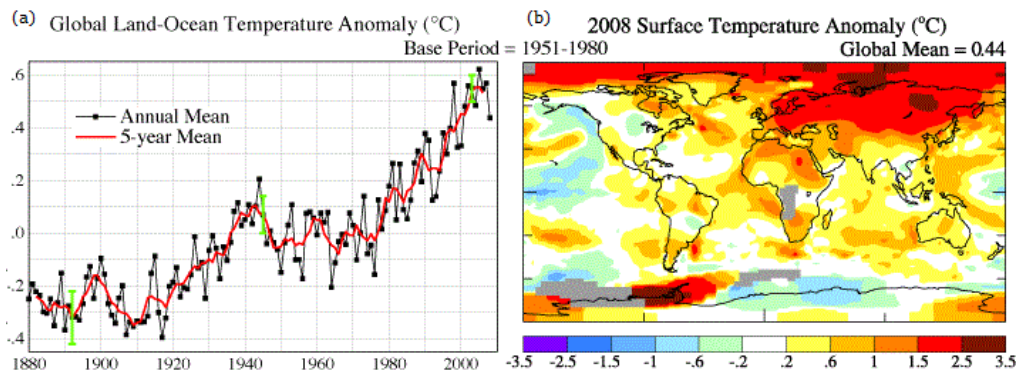
Figure 2: (a) Annual mean global land-ocean temperature anomaly relative to the base period of 1951-1980 together with a 5-year moving average trendline. (b) Map of the global annual mean surface temperature difference between the base period of 1951-1980 and 2008 (NASA, 2008).

Despite the overall upward trend, global mean surface temperature measurements generally show a high degree of decadal and inter-annual variability on a short time scale. These fluctuations can be largely attributed to natural causes, e.g. variations in solar irradiance or the intensity of an El Niño[6] event. Hence, observed trends which are based on short-term records tend to be highly susceptible to the selection of beginning and end dates. A popular example that is related to the misinterpretation of short-term trends is the myth of 'Global Cooling'. This trend indicates a stalling of ongoing temperature rise, but is only temporary on a long time scale. Possible causes for this transient levelling are a weak solar maximum and a strong El Niño (Peterson et al., 2008). Moreover, the IPCC predicts a further increase of overall surface temperatures in the course of the 21st century based on a wide range of model projections using four different greenhouse gas concentration trajectories or Representative Concentration Pathways (RCPs). These hypothetical trajectories range between serious emission reductions (RCP 2.6) and a business-as-usual scenario (RCP 8.5) (IPCC, 2013) (**figure 3**).
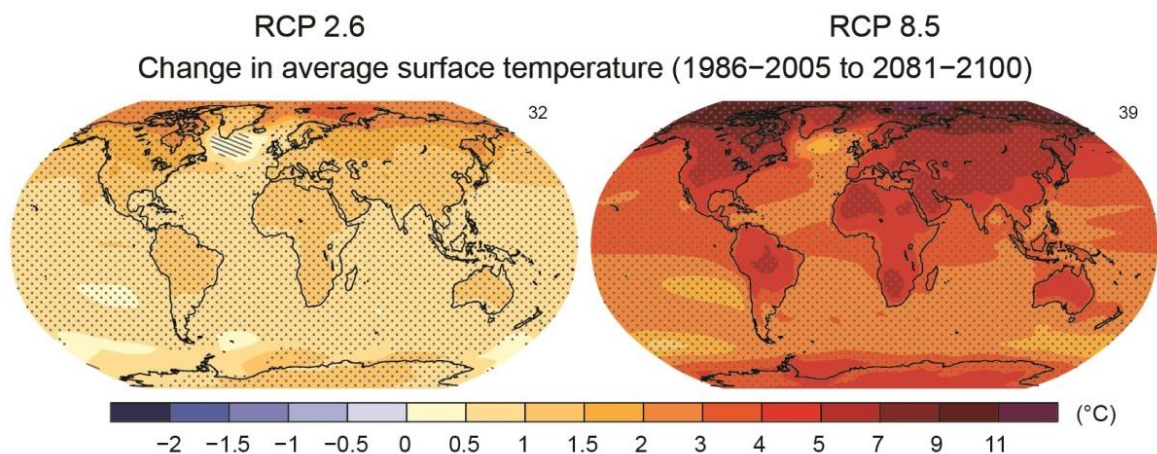
Figure 3 Map of the projected global annual mean surface temperature change for the late 21st century based on two scenarios (a best-case scenario, RCP 2.6 and a worst-case scenario, RCP 8.5) (IPCC, 2013).

Anthropogenic activities, notably fossil fuel burning and land-use changes, play a key role in these recent changes (IPCC, 1995). One of the most decisive motivations for this human influence on the

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[6] El Niño is a naturally occurring phenomenon which is responsible for a periodical warming along the equator and the eastern Pacific Ocean. El Niño typically lasts for a period of six months and the sea surface temperature around the equator can rise with about 3 °C above the normal temperature for that time of the year (KNMI, 2015).

global climate is that climate models simply fail to predict the recent elevations in the global surface temperature without the inclusion of anthropogenic forcings (see **figure 4**).
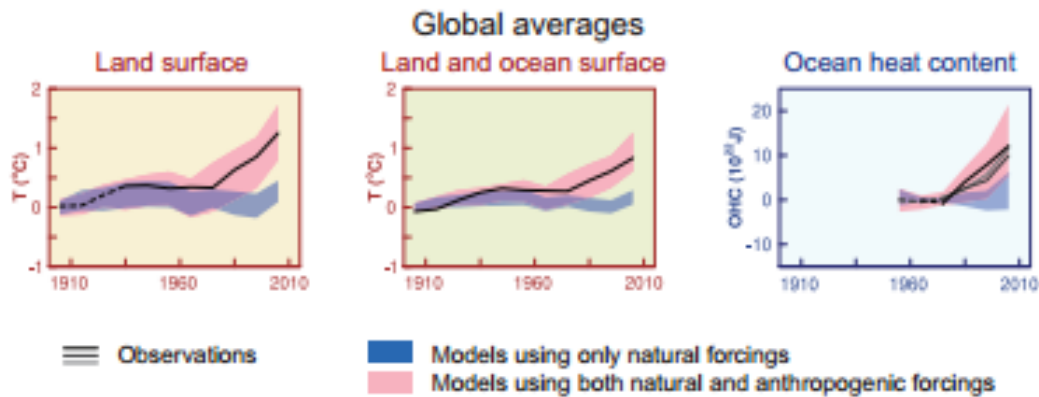
Figure 4: Comparison of the observed and simulated climate change between 1880 and 2012. The blue model predictions only include natural forcings while the red model predictions take into account anthropogenic forcings as well. Anomalies are calculated relative to 1880-1919 for surface temperatures and relative to 1960-1980 for ocean heat content. Observations are illustrated using a solid line when data coverage is good and high in quality. However, in case of insufficient data coverage and thus larger uncertainties, observations are indicated with a dashed line. Finally, all time series represent decadal averages (IPCC, 2013).

Greenhouse gasses have been continuously emitted into the atmosphere as a result of human activities, e.g. fossil fuel use, land-use change and agriculture. Hence, the atmospheric concentrations of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) increased significantly since pre-industrial times (conventionally since 1750) (IPCC, 2013). In 2011, concentrations for these three main well-mixed greenhouse gasses reached a level of respectively 391 ppm, 1803 ppb and 324 ppb. This corresponds with an increase of about 40 %, 150 % and 20 % compared to the pre-industrial levels of 1750. Greenhouse gasses are characterized by a certain radiative forcing, i.e. the amount of energy (W/m^2) that is absorbed in the atmosphere due to the presence of these gasses and would otherwise be lost to space. In total, the overall anthropogenic radiative forcing equals a positive value of 2.29 W m^{-2} relative to 1750 (IPCC, 2013) which in turn leads to the observed surface warming.

About 50 % of the anthropogenic CO_2 emissions is directly absorbed by the terrestrial biosphere (25 %) and by the ocean through *oceanic downwelling* (25 %). The higher partial pressure of CO_2 in the atmosphere stimulates plant productivity, but only in temperature limited regions, like tundra ecosystems or boreal forests, and in the wet tropics. As a result, higher amounts of CO_2 are taken up by the biosphere each year, however this process is marked by a high inter-annual variability and partly counteracted by the increased temperature sensitivity of heterotrophic soil respiration[7] and subsequent oxidation of organic matter by microorganisms in boreal and Arctic wetlands. **Figure 5** represents the seasonal variations in the atmospheric CO_2 concentration due to the uptake and release of the terrestrial biosphere. The Northern (red) and the Southern (black) Hemisphere show an anti-phased curve. However, the characteristic saw-tooth pattern is much less pronounced in the Southern Hemisphere due to the fact that this part of the Earth's surface is predominantly covered by oceans. On a long time scale, both Hemispheres show an exponential upward trend.

The combustion of fossil fuels and the burning of biomass also goes hand in hand with the emissions of short-lived tropospheric aerosols. These dust particles reflect the incoming solar radiation and

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[7] Heterotrophic soil respiration refers to the release of carbon dioxide upon the decomposition of organic materials (e.g. plant structural elements) in the soil by heterotrophic organisms (i.e. organisms that cannot fix carbon and rely on an organic source of carbon for growth) (Schulze et al., 2005).

therefore generate a cooling effect. In addition, aerosols serve as cloud condensation nuclei and subsequently contribute to the formation of clouds. Moreover, the same amount of water vapor is distributed over a larger amount of droplets. As a result, the droplets will be significantly smaller, which in turn gives rise to brighter clouds with a higher albedo. Consequently, more incoming solar radiation is reflected back to space. This explains the aerosols' overall negative radiative forcing of approximately -0.9 $\pm$ 1.0 W/m^2 (IPCC, 2013). The cooling effect of air pollutants is commonly referred to as 'Global Dimming' (Wild, 2012).
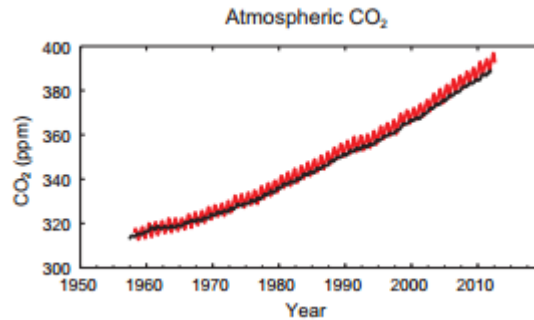
Figure 5: Seasonal variations in the atmospheric CO$_2$ concentration since 1958, with the Northern (Mauna Loa-red) and the Southern (South Pole-black) Hemisphere anti-phased. The long-term trend is exponential and the seasonal amplitude increases as the elevated partial pressures of CO$_2$ contribute to a fertilization effect (IPCC, 2013).

In addition, climate change significantly intensifies the hydrological cycle. On average, the total amount of annual precipitation is predicted to increase as a result of the higher water content of the atmosphere (cfr. law of Clausius-Clapeyron: warm air can hold more water). However, some regional differences can be observed with an increase of precipitation at high latitudes, in the tropics and in Eastern Asia and a decrease in the subtropics, notably in the Mediterranean and the Caribbean (see **figure 6**). Moreover, the seasonality in the annual precipitation is predicted to increase as well. In general, wet regimes will likely get wetter while dry regimes are predicted to get drier. Also, extreme rainfall events will presumably occur more frequently, with longer dry periods in between (Trenberth, 1999; Ramanathan et al., 2001; Miralles et al.; 2014; IPCC, 2013).
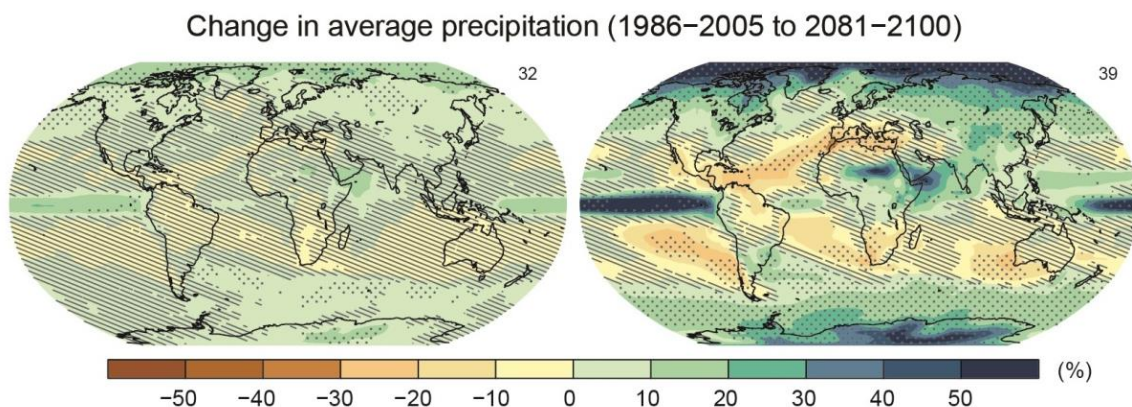
Figure 6: Map of the projected global annual mean precipitation change for the late 21st century based on two scenarios (RCP 2.5 and RCP 8.5) (IPCC, 2013).

With respect to the cryosphere, the average rate of ice loss has increased substantially around the globe. In addition, the Greenland and Antarctic ice sheets have been losing considerable amounts of ice mass. The average rate of ice loss from the Greenland ice sheet has increased from 34 $\pm$ 40 Gt per year over the period 1992-2001 to about 215 $\pm$ 61 Gt per year over the period 2002-2011. For Antarctica, a similar increase of approximately 30 $\pm$ 67 Gt per year over the period 1992-2001 to about

147 ± 75 Gt per year over the period 2002-2011 was recorded (Gregory, 2004; Maslanik et al., 2007; IPCC, 2013). In addition, observations also show a rapid decline in the Arctic sea-ice extent and the Northern Hemisphere spring snow cover. However, the rate of this process shows a high spatial variability with substantial regional differences (IPCC, 2013). Furthermore, a considerable reduction in the thickness and areal extent of the permafrost layer was observed in Arctic regions, boosting the local soil microbial activity. As a result, enormous carbon stocks could eventually be released into the atmosphere as CO_2 due to microbial respiration which in turn initiates a substantial climatic feedback reaction. Apart from the cryosphere, the hydrosphere and the hydrological cycle are affected by global warming as well. The global sea level has risen approximately 30 cm since pre-industrial times, partly as a result of natural warming in the aftermath of the Little Ice Age[8], and about 18 cm since 1900. The annual rate of this sea level rise approximates a value of 1.8 mm per year since 1961 and 3.1 mm per year since 1993. So far, this rise can mainly be attributed to thermal expansion of the ocean's surface (45 %) and melting of alpine glaciers (25 %) (Church & White, 2006; IPCC, 2013).

Tundra environments have been subjected to increasing temperatures as well. Most Arctic regions have experienced warmer temperatures since the mid-1800s (Overpeck et al., 1997; Walker et al., 2006). However, this warming has been accelerating substantially during the last decades (Overpeck et al., 1997; Serreze et al., 2000; ACIA, 2004; Walker et al., 2006). In the past 40 years, surface air temperatures in Arctic regions have increased at an average rate of about 0.4 °C per decade. In other words, polar latitudes warm almost twice as fast compared to lower latitudes (Kattsov et al., 2005; McBean et al., 2005; Walker et al., 2006; Anisimov et al., 2007). In addition, most General Circulation Models (GCMs) predict that air temperatures will continue to rise most rapidly at higher latitudes (IPCC, 2007). For example, an early climate sensitivity analyses indicated that a doubling of the global CO_2 concentrations would cause a temperature increase of about 12 K in the northern regions (Manabe & Wetherald, 1975; Bigelow et al., 2003). As a result, almost 40 % of the present tundra surface area could eventually be replaced by boreal forests by the year of 2100 (ACIA, 2004; Walker et al., 2006). High-latitude climates are presumably more susceptible to climate warming due to two distinctive positive feedback mechanisms (Bigelow et al., 2003). On the one hand, climate warming contributes to changes in the extent and duration of sea-ice cover in the Arctic Ocean (Ganopolski et al., 1998a; Braconnot et al., 1999; Vavrus, 1999; Bigelow et al., 2003). Bhatt et al. (2010) showed that there is a significant correlation between the decline in sea-ice and the additional increase in land surface temperatures in tundra environments. Secondly, changes in the land surface albedo as a consequence of the ongoing disappearance of snow cover, induces a supplementary warming effect as well (Bonan et al., 1992; Foley et al., 1994; Bigelow et al., 2003). As the areal extent of snow cover diminishes at higher latitudes, the albedo of the land surface lowers. Subsequently a significantly higher amount of the incoming solar radiation is absorbed, which in turn gives rise to an additional surface warming. This process is also referred to as the 'Albedo Feedback' (Winton, 2006).

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[8] The Little Ice Age (1300-1850) was a period of temporary cooling after the Medieval Climate Optimum (900-1300). During this large-scale event, glaciers expanded their range in several mountain areas, e.g. the European Alps, New Zealand, Alaska and the southern Andes. However, a considerable difference in the timing of these glacial advances was observed, suggesting the occurrence of largely independent climate changes, rather than a globally-synchronous glacial event. Various causes have already been proposed, among others cyclical lows in solar radiation, changes in the ocean circulation, natural variability in volcanic activity, etc. (Matthews, 1977; Mann, 2002)

Ecological and evolutionary responses of tundra ecosystems to climate change

General consensus

Recent climate impact studies quantified the overall effects of the ongoing climate change on a wide range of habitats around the world (Walther et al., 2002; Root et al., 2003; Parmesan, 2006; Gottfried et al., 2012). A large variety of changes in the distribution of species and the composition of communities has already been observed (Parmesan et al., 1999; Thomas et al., 2001; Pounds et al., 2006; Berg et al., 2010). Tundra ecosystems tend to be extremely susceptible to global warming as they are largely controlled by climatic constraints (Klanderud & Birks, 2003; Walker et al., 2006; Elmendorf et al., 2012). Most tundra plant species already occur close to their climatic limits of survival and within a restricted geographical range (e.g. at high latitudes or altitudes) making them more prone to eventual extinction (Parmesan, 2006; Crisp et al., 2009; Cox & Moore, 2010). However, many recent climate-change experiments have indicated species-specific responses in plant growth and reproduction (Chapin & Shaver, 1985; Arft et al., 1999; Walker, 2006; Elmendorf, 2011). In addition, a wide range of predictive models forecast distinctive changes in species distribution as a response to rising temperatures (Gottfried et al., 1999; Klanderud & Birks, 2003). During the last few decades, substantial shifts in the distribution, composition, total biomass, diversity and homogenity of Arctic and alpine plant communities have been observed (Grabherr et al., 1994; van Wijk et al., 2004; Tape et al., 2006; Hudson & Henry, 2009; Post et al., 2009; Callaghan et al., 2011; Hill & Henry et al., 2011). Many of these environmental change studies only focus on the response of single species and do not take into account fundamental biotic interactions, such as competition, predation and facilitation[9] (Berg et al., 2010). Moreover, climate-induced changes in species distribution and composition affect the entire structure and functioning of tundra ecosystems (Berg et al., 2010; Elmendorf et al., 2012; Bellard et al., 2013). As a result, a more holistic approach is required in order to study the ecological footprint of global warming. These ecological responses have to be investigated at the level of plant communities, taking multispecies interactions on a long time scale into consideration (Parmesan & Yohe, 2003; Berg et al., 2010).

Phenology changes

Rapidly increasing temperatures can induce phenology changes of Arctic and alpine vegetation (Walker et al., 1995; Oberbauer et al., 2015; Munson & Sher, 2015). In this case, species try to cope with the changing climatic conditions by adjusting their life cycle, instead of tracking the shifting isotherms as with distribution shifts. This thermal response is particularly important for rare and endemic[10] species, which can be abundantly found in mountain ecosystems and are marked by their limited abundances, restricted spatial distributions and low capacity for long-distance dispersal (Munson & Sher, 2015). In addition, the rate of phenology changes is expected to be significantly higher in mountain ecosystems due to the fact that these regions are already characterized by extreme environmental conditions, stronger temperature increases and the distinctive sensitivity of plant growth initiation to cold temperatures and snowpack formation (Inouye, 2008). For example, alpine

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[9] Facilitation is defined as the interaction between species in which both participants benefit (*mutualism*) or in which one species benefits and the other remains unaffected (*commensalism*) (Stachowicz, 2001).

[10] Endemic species are unique to a distinctive geographical location and are not found outside that region (Schulze et al., 2005)

shrub- and grassland ecosystems are constraint by the local extreme environmental conditions, e.g. short growing period for vegetation and long-lasting snow cover, and are therefore expected to be highly susceptible to climate change. Hence, the predicted future temperature increases, altered precipitation regimes and prolonged growing seasons are likely to induce local changes in plant phenology and growth. These climate-induced changes in the growth and development of plant species also have the potential to alter species competition, productivity and consequently affect consumers of plant resources, such as humans and herbivores (Munson & Sher, 2015). Moreover, phenological responses to climate change strongly vary among species (Parmesan, 2006; Berg et al., 2009; Walther, 2010) and depend to a large extent on the habitat type (Munson & Sher, 2015). Some species show a higher sensitivity to changing environmental conditions and respond faster, whereas other species display only a minor response. Interactions between species with a different sensitivity might result in a potential mismatch of temporal associations and subsequently affect their fitness. In some cases, this disruption of biotic interactions might cascade down the food chain and influence the entire ecosystem functioning (Berg et al., 2009).

Phenological changes in high-latitude and mountainous environments involve, for example, an earlier onset of growth due to shorter winter periods (Keller et al., 2000) or a substantial response of flowering phenology to earlier snowmelt in subalpine and alpine ecosystems (Dunne et al., 2003; Wipf, 2006; Rixen et al., 2008; Wipf & Rixen, 2010). This results in an enhanced green-up, which has already been observed in Arctic regions using remote sensing techniques and long-term satellite leaf area index (LAI) records (Myneni et al., 1997; Zhu et al., 2016). Several studies have been performed to investigate phenological responses of plant species in alpine ecosystems. For example, according to Rammig et al. (2010), a significantly earlier melt out of the snow cover and start of the vegetation period was observed on summits in the Swiss Alps. As a result, the onset of plant growth occurred earlier in the year, giving rise to a longer growing season, considerably taller plant individuals (+77 %) and a larger accumulation of aboveground biomass (+45 %). Munson and Sher (2015) demonstrated a significant acceleration of the flowering date of several rare plant species in the Rocky Mountains by approximately 42 days over the last 137 years, which corresponds with an average rate of change of 3.1 days per decade. In addition, they found that the growing season of all investigated plant species at the highest elevations was restricted by the extreme environmental conditions, while less restrictive climates at lower altitudes gave rise to more individualistic phenological responses. Species in lower elevation habitats accelerated their flowering date as a response to increasing temperatures much earlier in the year than at higher elevations. However, despite the fact that multiple studies have already reported substantial phenological shifts of alpine plant species (CaraDonna et al., 2014), further increases in temperatures and continued alterations of precipitation regimes might eventually lead to a strong population decline of already vulnerable endemic species with severe ecological and evolutionary constraints (Munson & Sher, 2015; Urban, 2015).

Distribution shifts

Species are expected to shift their distribution towards higher latitudes in flat regions and towards higher altitudes in mountainous areas in order to keep up with the shifting isotherms (Walther et al., 2002; Parmesan & Yohe, 2003; Neilson et al., 2005). On average, species shift their ranges 6.1 ± 2.4 km per decade more towards the poles (or meters per decade upward in mountainous areas) (Parmesan & Yohe, 2003). These directional range shifts can be largely attributed to the influence of changing climatic regimes on species-specific physiological thresholds of temperature and precipitation tolerance (Woodward & Williams, 1987; Hoffman & Parsons, 1997). Driven by warming temperatures, these distinctive *climatic envelopes* are predicted to shift in a poleward or upward direction, depending on local topographic characteristic of the landscape (Walther et al., 2002).

However, for some species (e.g. reef-building corals) the latitudinal distribution is predominantly constraint by other climatic factors, such as light. As a result, a shift in distribution is unlikely to occur despite the local temperature changes (Hoegh-Guldberg, 1999).

Climate-induced distribution shifts along latitudinal and altitudinal gradients have already occurred during the 20th century across a wide range of taxonomic groups and geographical regions (Hughes, 2000; Easterling et al., 2000; McCarty, 2001; Walther et al., 2001; Walther, 2003). However, ambiguous correlations with temperature changes were often not observed (Walther et al., 2002). Most distribution shifts tend to be episodic rather than gradual or monotonic and are frequently affected by the occurrence of local climate extremes (Easterling et al., 2000). In addition, rates of distribution shifts can vary substantially among and within species depending on individual dispersal abilities and local landscape conditions (Walther et al., 2002). For example, Lenoir et al. (2008) observed significantly larger shifts in optimum elevation for mountainous species compared to ubiquitous[11] species in French temperate and Mediterranean mountain forest ecosystems. On the other hand, Le Roux and McGeoch (2008) reported a much faster response and upslope migration of habitat generalists compared to habitat specialists on the sub-Antarctic Marion Island. Also, the magnitude of the upslope distribution shifts of alpine vegetation generally lags behind the isothermal shift of about 8 – 10 m per decade (Grabherr et al., 1994), whereas most butterfly species tend to keep up with the shifting isotherms (Karl et al., 1996).
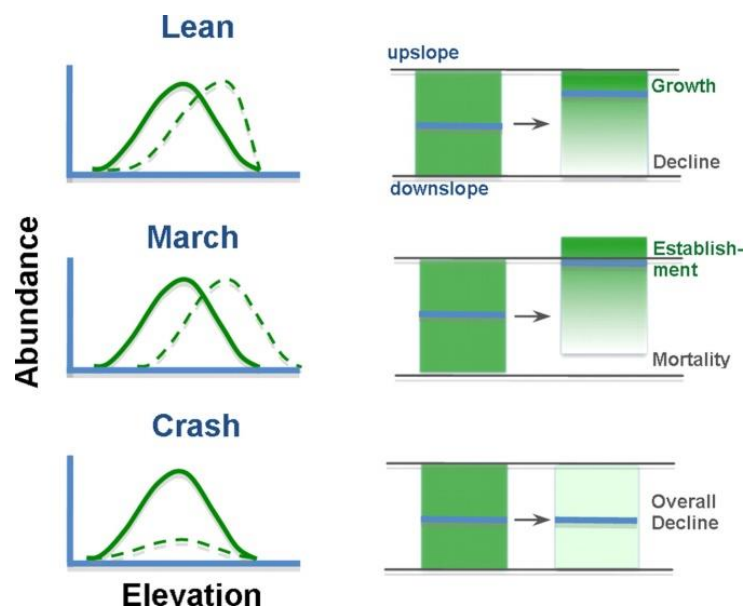
Figure 7: Types of species distribution shifts along an elevational gradient, resulting from changes in growth, establishment, decline and mortality of plants (Breshaers et al., 2008).

Altitudinal, as well as latitudinal, range shifts can be subdivided into three main categories (**figure 7**). (Breshaers et al., 2008). At first, *lean* range shifts can be described as a change in species distribution where the outer edges remain constant, but the central tendency shifts significantly. Secondly, the process of *march* can be distinguished, where the upper and lower boundary of species ranges experiences a parallel shift and the species distribution as a whole moves in an upward (or poleward) direction. Finally, if mortality appears to be widespread throughout the current species range, the distribution change is referred to as a *crash*. On the one hand, species migration can occur as a rather slow local process whereby a species shifts its distribution as a front in short steps. On the other hand, range shifts can also take place as a rapid movement or jump which is mediated by long-distance

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[11] Ubiquitous species are species that typically thrive in a wide range of environments (Schulze et al., 2005).

dispersal events (Neilson et al., 2005). In addition, a sustained long-distance migration generally consists of two distinctive processes: a long-distance jump which is immediately followed by the establishment and sufficient local spread of local populations in order to provide a large seed source and subsequently increase the odds of a later long-distance jump (Clark et al., 2001). A successful local spread depends on four main components, namely the reproductive output or *fecundity*, the *dispersal ability*, germination and seedling survival or *establishment* and *growth* to reproductive maturity. Furthermore, a successful long-distance migration and local spread may take years or even decades, depending on the species' generation time. Another important regulating factor is the mode of long-distance dispersion. Most terrestrial plant species generally migrate through wind dispersal (*anemochory*) or dispersal by animals (*zoochory*) (Neilson et al., 2005).

Human activities affect plant migration patterns as well, mainly through the accidental or deliberate introduction of exotic species and the alteration and fragmentation of the natural landscape and land use. These influences dominate in densely populated areas and can be largely attributed to agricultural and forestry activities (Hodkinson & Thompson, 1997). Recent anthropogenic activities have shaped the landscape as well, giving rise to a highly fragmented environment with a large amount of isolated forest patches. In turn, local plant population sizes, seed production and the amount of suitable habitats might diminish substantially. Habitat fragmentation presents a severe limit for species dispersal and highly increases the risk of local extinction (Walther et al., 2002; Fahrig, 2003 Hof et al., 2011). Many regions that might become climatically suitable with future warming are often located beyond the dispersal capacity of several plant and animal species. Hence, species with a lower dispersal capacity might become caught by the dilemma of a warming-induced range shift and the low likelihood to find a new suitable habitat with sufficient nutritional and reproductive resources. Finally, human activities such as resource exploitation and the mismanagement of vast natural lands highly increase the pressure on the local ecosystem, eventually pushing it beyond the tolerances of its limits (Walther et al., 2010). **Figure 8** illustrates the potential changes in species ranges as a result of climate change and the aggravating effect of human-induced habitat fragmentation.
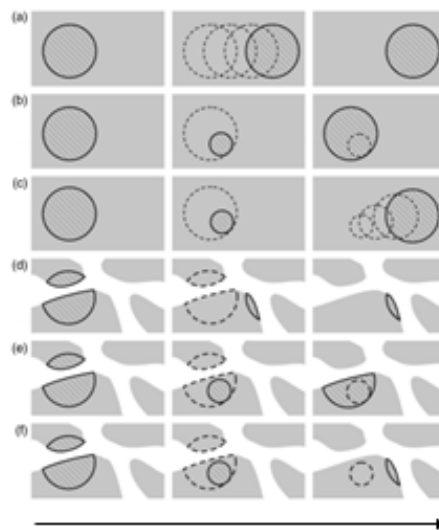
Figure 8: Six scenarios of range shifts of species over time as a result of climate change and the interaction with habitat fragmentation (time proceeds from left to right) (a) Gradual climate change without fragmentation: species track shifting isotherms. (b) Rapid climate change: species survive by residing in small local areas with a suitable microclimate or *refugia* and expand again when favorable climatic conditions return. (c) Species also endure in local *refugia*, but subsequently track suitable climatic conditions. (d)-(f) Similar processes as in (a)-(c), but with habitat destruction and fragmentation. This results in even smaller areas with a suitable microclimate and hence a reduced probability of survival or successful range shifts (Hof et al., 2011).

In situ experimental warming studies indicated that the abundance of deciduous shrubs and graminoids increased significantly in tundra environments as a result of a 1 – 3 °C warming, whereas the population of cryptogams (lichens and bryophytes) significantly diminished (Walker et al., 2006; Elmendorf et al., 2012). Considerable spatial and temporal differences were observed as well. (**figure 9**) (Elmendorf et al., 2012). In areas that were already relatively warm, the total shrub abundances showed the largest long-term positive effect on experimental warming, whereas in colder regions the initial positive response of shrubs could not be sustained. Consequently, Elmendorf et al. (2012) reports that in the next few decades cold tundra regions continue to show resistance against shrub encroachment. In addition, the restricted amount of bioavailable nitrogen and slow species turnover largely constrain shrub expansion in High Arctic regions (Epstein et al., 2000). Nonetheless, long-distance migration and gene-flow could eventually overcome these genetic constraints, thereby increasing shrub abundance in these colder environments in a long run (Alsos et al., 2007; Aitken et al., 2008). Most initial positive responses of shrubs could be attributed to low-growing and deciduous shrubs. Evergreen shrubs, on the other hand, showed no significant response to changing summer temperatures, but were highly affected by local moisture conditions. Furthermore, tall shrubs considerably increased their cover in a tundra environment after at least 10 years of additional warming, while the abundance of dwarf shrubs substantially decreased. These differences can be largely attributed to an increase in light competition with warming as the canopy of taller shrubs gradually closes. According to the same study, forbs and total graminoids showed no consistent temporal trend after being subjected to a 10 year period of experimental warming. However, graminoid abundance increased most at colder sites, while neutral to negative responses were observed at warmer sites. Among graminoids, grass, rush and sedge species, variable responses along a distinctive moisture gradient were found. However, some changes in abundance also resulted from opposing species responses, whereby the gains of one group of species counterbalance the losses of another group. Grasses increased their abundance most in dry sites, whereas sedges showed the greatest positive long-term response in wetter regions. Rush abundance showed no consistent response to experimental warming, although a slight tendency for negative responses was observed in dry sites.
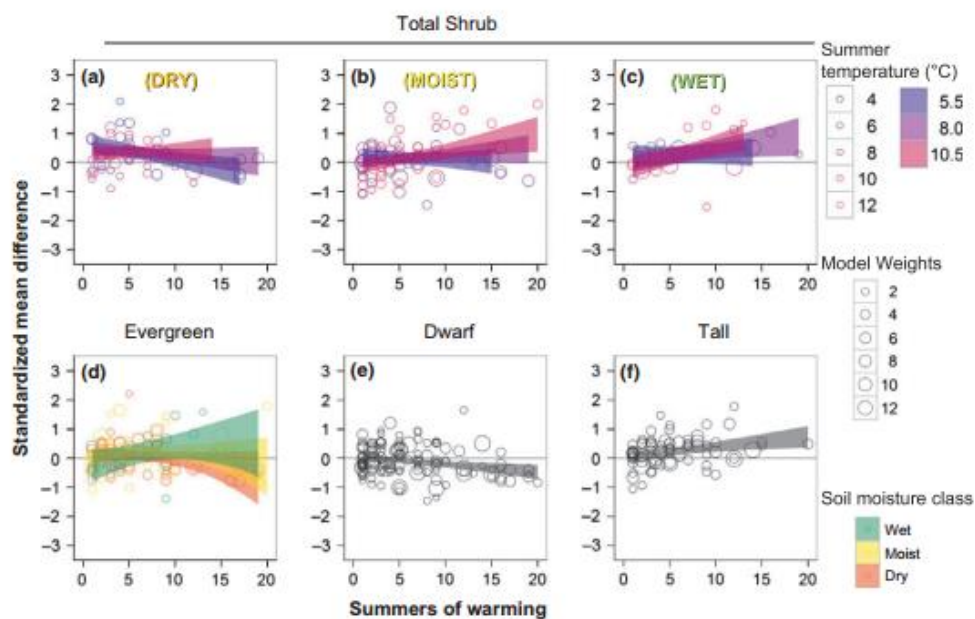
Figure 9: Total shrub response in dry (a), moist (b) and wet (c) conditions to experimental warming as well as the warming-induced changes in evergreen (d), dwarf (e) and tall shrubs (Elmendorf et al., 2012).

Non-vascular cryptogams such as lichens (especially foliose[12] and fruticose[13] lichens) considerably declined in abundance irrespective of local moisture and temperature conditions. Moss abundance, however, primarily decreased in moist areas. Recent studies indicated that not the ambient summer temperature, but moisture availability explains the climate-induced changes in the abundance of bryophytes (Lang et al., 2009). Bryophyte species are characterized by the absence of true roots, which in turn makes them more vulnerable to water deficiency in warmer, drier environment (Potter et al., 1995). Lang et al. (2012) performed a study on the responses of Arctic bryophyte diversity and abundance to an increasing temperature, confirming the previous statement. Most bryophyte species, except for *Sphagnum* and some pleurocarpous mosses[14], showed a significant decrease in abundance upon warming in three separate environmental warming experiments and along a natural temperature gradient. The susceptibility of lichen species to climate warming can be attributed to the increased shade due to a higher biomass production of vascular plants in tundra ecosystems. Especially in lower Arctic tundra and low-altitude environments, where shrub encroachment appears to be most significant, severe reductions in lichen abundance could be observed after 10 years of warming (Cornelissen et al. 2001; Elmendorf et al., 2012). However, on a shorter time scale lichens show a larger degree of resistance against warming in the high Arctic regions (Walker et al., 2006). Other components of the ecosystem are affected by a decline in lichen abundance as well due to the fact that they serve as an important source of animal forage and nitrogen inputs (Elmendorf et al., 2012) (**figure 10**).
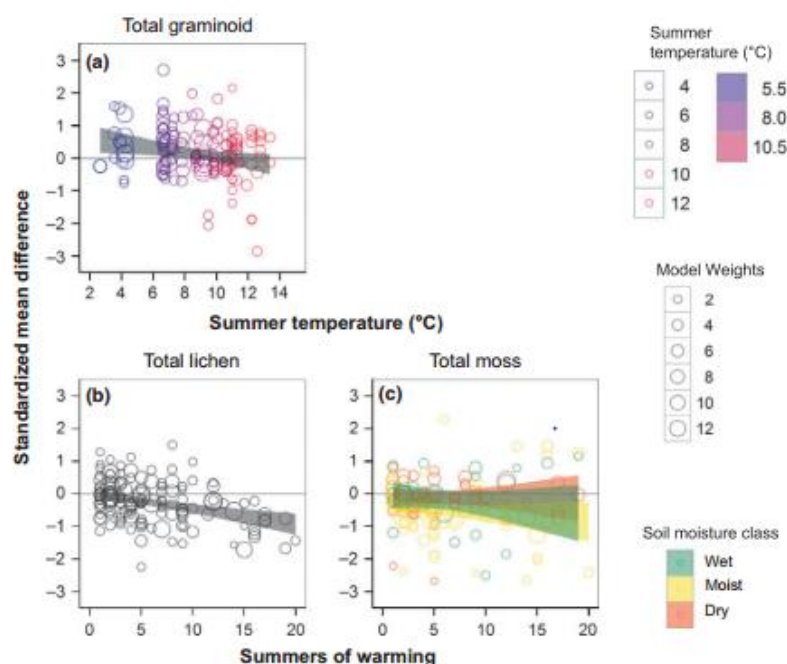
Figure 10: Total graminoid (a), lichen (b) and moss (c) response to experimental warming, including variations with summer temperature, soil moisture and time (Elmendorf et al., 2012).

In addition to moisture conditions, also altitude, migration corridors (e.g. roads) and the presence of a favorable rooting substrate play a key role in the ability of plant species to expand their ranges and colonize new ecosystems within Arctic and alpine regions (Klanderud & Birks, 2003; Lembrechts et

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[12] Foliose lichens are characterized by their flattened leafy thalli and upper and lower cortex with hyphae. These hyphae are used to attach on various substrates (Nash, 2012).

[13] Fruticose lichens have a shrubby or bushy growth structure and are marked by their relatively slow growth. This type of lichens commonly occurs in extreme habitats, such as tundra ecosystems (Nash, 2012).

[14] Pleurocarpous mosses are moss types in which the archegonia (i.e. sex organs) and capsules (i.e. spore-bearing structures) are borne on short, lateral branches rather than at the tips of the stems or branches (Allaby, 1998).

al., 2016). Klanderud and Birks (2003) observed the distribution and frequency changes of vascular plant species at several summits in Jotunheimen, central Norway. The aim of this long-term research was to examine possible shifts in species distribution and changes in species richness along an altitudinal gradient at a multi-decadal time scale. With respect to changes in species distribution, this study concluded that snow-bed species and a collection of locally rare alpine species of open habitats proved to be most vulnerable (Sætersdal & Birks, 1997; Holten, 1998). In addition, some regional alpine taxa and vegetation types are severely threatened with extinction (Holten, 1990; Grahberr et al., 1995) in absence of local *refugial habitats* (Gottfried et al., 1999). Moreover, Klanderud and Birks (2003) reported that summits with a corresponding topography, geomorphology and geographic situation are marked by similar patterns of change in vegetation distribution and species richness. Also, species with comparable environmental demands appeared to respond similarly to climate-induced changes. On average, an annual elevational advance of approximately 1.2 m was observed. Furthermore, oligotrophic plant species, which generally thrive in a wide range of ecological conditions and altitudes, showed the largest positive response. Local lee-slope species (e.g. *Avenella flexuosa*, *Vaccinium myrtillus*, *Vaccinium uliginosum*, *Phyllodoce caerulea* and some *Salix* species) enlarged their present range, not only at elevations where they already occurred, but also towards higher elevations. Species that commonly thrive on more exposed ridges (e.g. *Juncus trifidus*, *Luzula spicata*, *Festuca vivipara* and some *Carex* species) expanded their range as well during the 68-year long sampling period. However, the dwarf shrub *Empetrum nigrum* showed the most significant positive response with an upward movement of about 200 m. The increased abundance of dwarf shrubs, such as *Vaccinium myrtillus*, *Vaccinium uliginusum* and *Empetrum nigrum* can be related to an increase in both the length of the snow-free period and the length of the growing period. These species mainly belong to mesophilous heaths[15] and are expected to invade snow beds together with other lee-slope species as the duration of snow cover gradually decreases. Species of less extreme snow-beds (e.g. *Omalotheca supina*, *Veronica alpina*, *Sibbalidia procumbens* and *Casiope hypnoides*) have increased their frequency as well, which could also be attributed to a longer growing season. On the other hand, species that are characteristic for extreme late-melting snow beds (e.g. *Oxyria digyna*, *Cerastium cerastoides*, *Ranunculus pygmaeus* and several *Saxifraga* species) showed a declining frequency in most occupying sites due to the fact that an earlier snow melt contributed to a significant decrease in soil moisture and nutrient availability during the summer months. Finally, high altitude species (e.g. *Ranunculus glacialis, Poa flexuosa* and *Trisetum spicatum*) largely vanished from their low altitude habitats, but substantially increased their abundance at the highest sites of the Jotunheimen mountain range.

Virtanen et al. (2003) observed some similar changes in two alpine environments in Finland and Norway between 1920 and 1999 and reported them quantitatively. With respect to the heath vegetation, *Empetrum nigrum* (+8.1 %) and *Salix herbacea* (+1.7 %.) significantly increased their cover, whereas other vascular plant species, such as *Arctous alpinus* (-7.4 %) and *Loiseleuria procumbens* (-37.1 %) showed a diminishing cover percentage. *Euphrasia frigida* completely disappeared during the sampling period. Also, some common lichen species considerably declined or even vanished from the monitoring site: *Cladonia sp.* (-2.1 %), *Flavocetraria nivalis* (-12.8 %) and *Solorina crocea* (-2.6 %). On the other hand, bryophyte species, such as *Gymnomitrion sp.* (+9.5 %) and *Racomitrium lanuginosum* (+13 %) substantially increased their cover in the heath areas. In snow-bed areas, vascular plant species, such as *Carex bigelowii* (-13.6 %), *Carex vaginata* (-2.2 %) and *Salix herbacea* (-13.5 %), and lichen species, such as *Cetraria islandica* (-3.6 %) and *Cladonia gracilis* (-9.7 %), significantly declined. Less extreme snowbed species, *Bistorta vivipara* (+3 %) and

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[15] Mesophilious species are organisms that grow best at moderate temperatures (Schulze, 2005).

Solidago virgaurea (+2.1 %), locally increased their cover. Other species, which were normally absent in these snow-bed areas, like *Geranium sylvaticum* (+1.7 %), *Luzula multiflora* (+1.8 %) and *Ranunculus acris* (+2.6 %), recently established. Finally, in the alpine mires a decline in vascular plants species was observed, especially for high altitude species like *Carex bigelowii* (-5.4 %) and *Carex rupestris* (-6.3 %), grasses like *Festuca vivpara* (-4.6 %) and other perennial herbs like *Pedicularis oederi* (-4 %) and *Pinguicula vulgaris* (-2 %).

Another important change that is observed in Arctic and alpine ecosystems, is a shift in the position of the treeline (Mindas et al., 2000; Kullman, 2002; Penuelas & Boada, 2003; Sanz-Elorza et al., 2003; Camarero & Gutiérrez, 2004; Parmesan, 2006; Gehrig-Fasel et al., 2007; Shiyatov et al., 2007). In the last few decades, treelines have moved in a poleward direction in Sweden (Kullman, 2001; Moen et al., 2004) and in an eastern direction in Canada (Lescop-Sinclair & Payette, 1995). Also, in Russia (Meshinev et al., 2000) and in New Zealand (Wardle & Coleman, 1992) the treeline has significantly shifted upward. The position of the treeline is determined by a wide range of complex interactions between past and present climatic conditions and disturbances (Oksanen et al., 1995; Hofgaard, 1997a; Hofgaard, 1997b; Körner, 1999). In addition, several studies have already been performed, correlating climatic indices (e.g. summer mean temperature and temperature sums) to the location of the treeline (Körner, 1999; Grace et al., 2002). Moreover, Kullman (1998) and Holten and Carey (1992) indicated that the treeline position is a sensitive indicator of climate change. The ecotone between forest and treeless alpine heaths can be considered as an important feature of mountain ecosystems. However, ecologically valuable alpine heaths are severely fragmented by an advance in the treeline position. Especially in the future, lower lying treeless valleys would gradually become covered by forest, breaking up the landscape into a patchwork of smaller areas (Moen, et al., 2004). Fragmentation in turn decreases species population's abundance and significantly enlarges dispersal distances, eventually contributing to an increased susceptibility to local extinctions. Furthermore, together with climate warming, gradual afforestation in alpine ecosystems stimulates the upward movement of alpine plant species (Moen et al., 2004). **Figure 11** illustrates the upward advance of the treeline position with approximately 125m on Mt. Mettjeburretjakke, Sweden between 1915 and 2007.
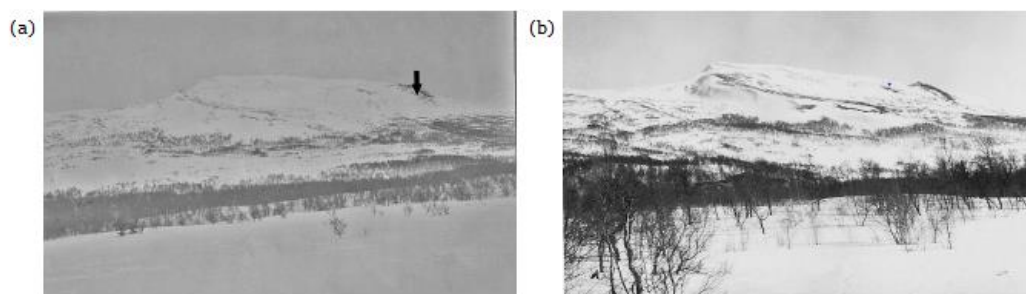
Figure 11: Change in the position of the treeline on Mt. Mettjeburretjakke (855 m a.s.l.) in mid-central Sweden between 1915 (a) and 2007 (b) (Kullman, 2010).

Community reorganization and ecosystem responses

Climate-induced spatial and temporal changes in the distribution and behavior of individual species probably also disrupt interactions with other species at the same or adjacent trophic levels. Hence, species that are closely interacting or competing might respond differently or show a divergent susceptibility to the ongoing climate change, giving rise to a considerable alteration of their interactions at a multispecies level and as a result limiting range expansions of single species (Walther et al., 2002; Berg et al., 2009; Walther, 2010). These interactions include among others mutualism, facilitation, competition and predation. Furthermore, distribution shifts at a lower trophic level might set in motion a series of distinctive bottom-up effects through ecological networks and eventually

induce possible feedback processes (Walther, 2010). The variability in the dispersal rate of interacting species might disrupt spatial associations (Callaway et al., 2004) in a way that migrating species become temporarily released from certain soil pathogens (van Grunsven et al., 2007). Subsequently, this spatial mismatch gives rise to a less negative plant-soil feedback for migrants compared to native species in the new locality (Berg et al., 2009). In addition, a lot of species with a specialist lifestyle prove to be indirectly constraint by the distribution of prey or host plants (Kinlan & Gaines, 2003; MacLachlan et al., 2005). For example, specialist herbivores (e.g. insects) generally show a larger dispersal capacity and have the ability to keep up with the shifting isotherms. However, this expansion will be largely constraint due to the fact that their plant resource moves at a slower rate and commonly lags behind (Kinlan & Gaines, 2003; Berg et al., 2009).

Top-down effect in plant and animal communities have also been observed. Those effects proved to have a considerable influence and the community responses as well (Walther, 2010). For example, the susceptibility to climate warming seems to increase significantly along trophic levels with a considerably larger thermal response of top trophic level organisms. As temperatures increase, this asymmetry might eventually lead to a community destabilization with cascading effects down the food web (Voigt et al., 2003). Post and Pedersen (2008) performed a warming experiment, indicating that the response of plant communities was strongly depending on the presence or absence of herbivores. The study showed that in absence of herbivores, the plant community changed from graminoid-dominated to dwarf-birch dominated after being subjected to increased temperatures for a certain amount of time. In this case, the primary productivity and plant community composition was predominantly regulated by the changing climatic conditions. Nonetheless, if musk oxen and caribou grazed on the experimentally warmed plots, no consistent alteration in the plant community composition was observed.

Arctic plant communities show a climate-induced alteration in species composition with a significantly diminishing macrolichen abundance and an increasing abundance of vascular plants (Harte & Shaw, 1995; Cornelissen et al., 2001; Walther, 2003). Likewise, substantial population increases of the two native vascular plant species (*Colobanthus quitensis* and *Deschampsia antarctica*) have been observed on the Antarctic Peninsula (Fowbert & Smith, 1994). On the one hand, native tundra species increase their abundance and distribution by claiming areas which have recently been exposed by the retreat of ice, but on the other hand a large variety of vascular plant and bryophyte species invade from lower latitudes and successfully establish a viable population in the warming tundra biome and locally increasing species richness (Kennedy, 1995; Convey, 2001; Walther, 2003). However, short-term warming experiments (e.g. Walker et al., 2006) in a wide variety of tundra ecosystems report the opposite effect, with a strong local decline in biodiversity. These observations are inconsistent with the broad patterns of increasing biodiversity along natural gradients of increasing temperatures in response to climate change (Walker, 1995) and can be largely explained by differences in short-term and long-term warming effects. On a short time scale, local extinctions and changes in the dominance of certain species presumably occur before the introduction of new migrants (Sala et al., 2000; Walker et al., 2006). Consequently, according to Walker et al. (2006) tundra ecosystems will initially show a decline in biodiversity due to a distinctive species loss and shift of the vegetation towards an increased shrub dominance.

In alpine ecosystems, a warming-induced range shift of species towards higher altitudes is observed (Gottfried et al., 1999; Engler et al., 2011), gradually transforming mountain plant communities (Gottfried et al., 2012). In general, cold-adapted species, with an optimal performance at lower temperatures, show a decreasing trend, whereas warm-adapted species tend to flourish in response to the warming climate. Gottfried et al. (2012) referred to this process as *thermophilization*. Observations

of these trends have been recorded during the last decade, with a significant increase of thermophilic species between 2001 and 2008 on several mountain summits all across Europe. Thermophilization of mountain plant communities proved to be more pronounced with an increasing degree of climate warming. As a result, prolonged temperature increases might cause stronger competition in the lower alpine belt by highly productive species, which accumulate a lot of biomass in a short period of time and potentially overgrow other species (Callaway et al., 2002; Wipf et al., 2006; Wipf & Rixen, 2010). However, in the high alpine belt and the nival belt, species richness is expected to increase as a consequence of thermophilization (Walther et al., 2005; Gottfried et al., 2012). The concept of thermophilization was only recently introduced and has been applied for vascular plants (e.g. Gottfried et al., 2012; De Frenne et al., 2013) and butterfly, fish and bird species (e.g. Devictor et al., 2012). For cryptogams such as lichens and bryophytes, however, this concept has not yet been studied.

Next to species richness, species evenness is also affected by climate warming (Walker et al., 2006) with some important consequences for the ecosystem as well (Chapin et al., 2000). Walker et al. (2006) reported a decrease in evenness for tundra ecosystems after a certain period of experimental warming. In other words, the dominance structure of tundra plant communities is predicted to change significantly with a shift towards fewer species producing a greater fraction of the cover. Climate-induced changes in the interactions between species at a plant community level can also show more complex patterns, for example along an altitudinal gradient (Callaway et al., 2002). Callaway et al. (2002) focused on positive interactions (i.e. facilitation) between plant species and their importance relative to competition. Such positive effects include among others the accumulation of nutrients, the protection against grazing and tramping by herbivores, the provision of shade, etc., each enhancing the performance of neighboring species. The report published two main conclusions. Firstly, they found that biomass, growth and reproduction of alpine plants significantly increased when other plants were growing in the direct vicinity. Secondly, negative species interactions (such as competition) primarily occurred at lower elevations where abiotic conditions proved to be physically less stressful. At these lower elevations, an invasion of competitively stronger species could lead to a diminished abbundance of less competitive snow-bed species and high-altitude species growing at their lower-elevation limits (Klanderud & Birks, 2003). However, at higher altitudes, where abiotic stress prevails, mostly positive effects (such as facilitation) were observed. Likewise, positive species interactions dominated at sites with a lower temperature, whereas competition prevailed in warmer areas. In conclusion, general interactions will shift along an altitudinal gradient from competition to facilitation with an increasing degree of abiotic stress. This shift can be mainly attributed to fundamental physiological limitations: at lower elevations resource availability limits growth and reproduction of plants, while at higher elevations non-resource factors such as temperature, wind scouring and soil instability appear to be the greatest constraints. In this case, neighboring species contribute to an enhancement of abiotic stresses, thereby favoring plant growth to a larger extent than the competition with the neighboring plants (Grime, 1979).

Climate change not only influences the community structure and ecosystem process through an increase in temperature alone (Dukes & Mooney, 1999; Travis, 2003; Walther et al., 2009; Walther, 2010). For example, Bhatt et al. (2010) observed that vegetation shifts in the Arctic tundra were significantly correlated with the recent decline of near-coastal sea-ice. Summer sea-ice considerably declined in cover (Stroeve et al., 2007) and thickness (Rothrock et al., 2008; Kwok & Rothrock, 2009) during the last few decades. As a result, the land surface temperatures increased even more, leading to an increase in tundra productivity (Bhatt et al., 2010). Other important determinants of the community composition are soil moisture and nutrient availability (Walker et al., 2006). In general, areas with a

mesic regime[16] are characterized by the most significant response to climate warming and in turn the largest impact on species biodiversity (Grime, 2001). Walker et al. (2006) indicated that Low Arctic mesic sites showed the largest increase in canopy height after experimental warming. However, also the cover density of tundra plant communities plays a substantial role. Higher canopy densities limit lateral expansion and therefore stimulate growth in a vertical direction. High Arctic ecosystems showed little response to climate warming, which can most likely be attributed to the fact that these regions are characterized by a low nutrient availability (Robinson et al., 1995).

In conclusion, warming-induced community reorganization not only gives rise to a reshuffling of the existing species, but also leads to the introduction of new species. Those species tend to mix with the present communities and eventually compose new assemblages (Walther et al., 2004; Williams & Jackson, 2007; Hobbs et al., 2009). As a result, the entire ecological network and ecosystem functioning might be modified on a long time scale (Dukes & Mooney, 2004). Furthermore, species dynamics at range boundaries are more prone to climate-induced changes compared to the dynamics within the interior of a species range (Parmesan & Yohe, 2003). Finally, the effect of global warming on plant communities can be both direct, as a result of higher temperatures or a decrease in water availability (Van Mantgem & Schwilk, 2009), or indirect, for example through an insect outbreak and subsequent tree mortality (Kurz et al., 2008).

Feedbacks of biodiversity changes on ecosystem processes

Shifts in the local composition and frequency of plant species affect ecosystem processes as well, triggering a wide range of feedbacks (Walker et al., 2006; Walther, 2010; Elmendorf et al., 2012). For example, the gradual transition of a herb-dominated to a woody tundra will lead to a significant alteration of the ecosystem functioning (e.g. shrub invasion in water-limited ecosystems disturbs the ecosystem water balance with potential implications for the area's hydrological cycle) and causes a positive climate feedback (Caldeira et al., 2015). As shrub height and cover increases in tundra regions, the surface albedo and roughness changes as well, which in turn alters the entire surface energy budget (Chapin et al., 2000; Sturm et al., 2001). Generally, shrub-dominated canopy covers tend to go hand in hand with a greater leaf density and a lower surface albedo. As a result, more incoming solar radiation will be absorbed by the land surface, amplifying local atmospheric warming (Foley et al., 1994; Sturm et al., 2001). Likewise, Thomson et al. (2004) proved that shrub expansions in tundra environments contribute to an increase of the summer sensible heat flux and a decrease in the winter surface albedo. In addition, due to the modification of surface energy fluxes, shrub establishment gives rise to the creation of microclimatic conditions with a significant increase in nighttime air temperature, especially during the winter months. These microclimatic conditions effectively reduce the exposure of other plant species to minimum air temperatures and subsequently affect the community composition through facilitation (D'Odorico et al., 2010; Myers-Smith et al., 2011). Finally, shrub encroachment and the shift towards a woody tundra affect the ecosystem carbon balance (e.g. by increasing the plant and soil carbon stocks and decreasing the atmospheric CO_2 levels) and nutrient dynamics (e.g. through a change in the amount of litter that is added to tundra soils) (King & Neilson, 1992; Smith & Shugard, 1993; Sturm et al., 2001; Jackson et al., 2002; Walker et al., 2004; Neilson et al., 2005). Elmendorf et al. (2012) also recently reported that the amount of dead plant material significantly increased in plots which were subjected to experimental warming. Along with an increased shading effect, the additional production of recalcitrant leaf litter with a slow turnover may

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[16] A mesic soil moisture regime is characterized by a mean annual soil temperature ranging between 8 – 15 °C and a difference between the mean summer and winter temperature larger than 5 °C at 50 cm below the soil surface (USDA, 1999).

have a buffering effect on climate warming due to the reduced soil heterotrophic respiration (Cornelissen et al., 2007; Blok et al., 2010). In addition, water supply and quality seemed to be affected by terrestrial vegetation shifts (Gitay et al., 2001; Neilson et al., 2005). Finally, indirect climate feedbacks have also been observed. For example, warmer temperatures can stimulate insect outbreaks and in turn cause a widespread tree mortality. Consequently, ecosystem functioning of entire forests was altered, converting this carbon sink into a massive net carbon source (Kurz et al., 2008).

Other possible drivers of ecological responses in tundra ecosystems

Next to climate warming, other factors might be responsible for vegetation distribution shifts and biodiversity changes in the tundra biome, e.g. atmospheric nitrogen (N) deposition, grazing, land-use changes, invasive species and natural succession (Klanderud & Birks, 2003; Parmesan & Yohe, 2003). At first, Klanderud and Birks (2003) considered the effect of N deposition on local species diversity. N deposition through precipitation significantly increased to about 2000 mg m^{-2} year^{-1} (or 20 kg ha^{-1} year^{-1}) in the Jotunheimen mountain range during the last century (Tørseth & Semb, 1997). These depositions are expected to fertilize alpine heath ecosystems, largely influencing regional plant communities (Chapin & Shaver, 1985) and stimulating species diversity in otherwise low productive areas (Teodose & Bowman, 1997). However, N deposition reaches significantly higher values at low elevation areas, close to industrial and agricultural activities, and are therefore often considered as a lowland problem. Nonetheless, mountain vegetation shows a much larger response due to its selection for survival in a nutrient poor environment (Körner, 2013). This was also observed by Hiltbrunner et al. (2005) in the Central Swiss Alps, where alpine plants already responded sensitively to an annual N deposition rate of 5 – 10 kg per hectare.

Secondly, the effect of grazing on plant communities and their responses to climate change has been widely demonstrated. Austrheim and Eriksson (2001) concluded that the ongoing grazing activities on low-productive snow-beds and alpine heath ecosystems within the Scandinavian mountains substantially decreased local species richness. On more productive lands, however, moderate grazing showed the opposite effect with an increase in species diversity (Chapin & Körner, 1995; Körner, 1999; Austrheim & Eriksson, 2001). Extreme snow-bed plant species are highly susceptible to an increase in grazing as well, since they are extremely attractive to reindeer at higher altitudes (Gaare & Skogland, 1970). Moreover, according to Gaare and Skogland (1970), alpine grazers such as reindeer and sheep are rather selective and generally prefer grasses to shrubs. Hence, moderate grazing might contribute to shrub encroachment and the consequent transition of grassland to shrub-dominated vegetation (Jefferies & Bryant, 1995). Subsequently, keeping the effect of herbivores into account, Klanderud and Birks (2006) concluded that the increased abundance of dwarf shrubs at lower elevations in the Jotunheimen mountain range resulted either from grazing activities or a synergy between grazing and climate change. Herbivores also have the ability to modify and slow down (or even halt) the upward movement of the treeline (Moen et al., 2004). Climate-driven treelines show a gradual transition with progressively smaller tree individuals as the climatic conditions become less and less favorable, whereas treelines in grazed areas appear to be more abrupt (Ellenberg, 1988). The browsing activity of herbivores leads to a depletion of resources from individuals, that are already occurring at the limits of their survival, and increases mortality near the border of the treeline. In addition, browsing is expected to prevent regeneration, which in turn reduces the amount of saplings and young trees. Hence, the upward movement of the treeline might be stalled, or even completely stopped, due to the fact that herbivores feed on seedlings that are already severely weakened by

unfavorable climatic conditions and increased competition from field layer plant species (Moen et al., 2004).

The herd density also plays a key role in the alteration of vegetation composition and ecosystem productivity (McNaughton et al., 1989; Bråthen et al., 2007). Studies indicate that the aboveground primary productivity can be both positively or negatively affected by an increase in herbivore stock density, depending on how the species composition shifts under the present grazing regime (McNaughton et al., 1989; Hobbs, 1996; Augustine & McNaughton, 1998). In some cases, the composition of plant communities showed clear resistance against changes in the grazing regime, whereas in other cases plant communities shifted towards an increased dominance of persistent growth forms with a substantially lower productivity (Bestelmeyer et al., 2004). Bråthen et al. (2007) demonstrated that high-density reindeer herds have the ability to homogenize the biomass and abundance of palatable plants across environmental productivity gradients. They observed that a persistent high reindeer grazing pressure eventually led to a reduction of plants with facilitating or neutral effect on ecosystem productivity. For example, in high-density districts the abundance of palatable plants (e.g. grasses, tall dicotyledons and N-facilitators) on resource-rich sites decreased to that of less fertile areas. Along with grazing, tourism contributes to the creation of microsites where the germination and survival of seedlings is highly promoted (Eriksson & Ehrlen, 1992). For example, near hiking trails in mountain areas species richness might increase due to increased shelter possibilities and the presence of a suitable rooting substrate. On the other hand, hiking activity tends to go hand in hand with extensive trampling, increasing the probability of a local drop in species richness along the trails.

Another possible driver of plant community shifts in tundra ecosystems is the effect of natural succession. This process seems to be delayed in most extreme environments, such as Arctic and alpine regions, but can be substantially accelerated as a response to climate warming, increased N deposition and higher grazing- or tourism-related pressures (Klanderud & Birks, 2003). Presently, vegetation in tundra ecosystems is still recovering from the Little Ice Age. Hence, many tundra plant species have not reached a distribution that corresponds with the current climate forcings. For instance, in Jotunheimen, most of the species that showed a decreasing abundance in the last few decades (e.g. *Oxyria digyna*, *Trisetum spicatum* and some *Cerastium* and *Saxifraga* species) can be categorized as pioneers and are characteristic for early successional stages. As succession gradually proceeds towards a more mature plant community, these species will be easily substituted by species that are more characteristic for a later successional stage (e.g. *Avenella flexuosa*, *Empetrum nigrum* and some *Vaccinium* and *Salix* species) (Matthews & Whittaker, 1987; Matthews, 1992). However, at higher altitudes (above 1500 m) an invasion of lowland shrubs as a result of natural succession is prevented by the shorter growing season (Matthews, 1992).

Finally, a wide range of human activities constantly modifies the structure of plant communities and therefore considerably influences biodiversity and the entire ecosystem functioning. Thuiller (2007) concluded that vast land-use changes and climate warming have presumably been the most important drivers of 20th century ecological responses of plants and animals. In addition, habitat fragmentation as a result of extensive resource extractions, agricultural activities and urbanization significantly altered plant and animal communities as well, sometimes even up to the point of local species extinctions (Walther et al., 2002). Moreover, the introduction of non-native, exotic species in a new area and the subsequent spread is often mediated by human activities. After crossing the geographical boundaries of a new habitat, these exotic species have to overcome local abiotic and biotic restrictions in order to grow and reproduce. Subsequently, they will gradually expand their distribution and become *invasive*. Exotic species generally lack a certain enemy and outcompete native species within the new locality,

thereby reducing species richness (Walther et al., 2002). Common examples of alien species in tundra ecosystems are among others Himalayan balsam (*Impatiens glandulifera*) and the garden lupine (*Lupinus polyphyllus*) (Norwegian Biodiversity Information Centre, 2012; Global Invasive Species Database, 2015).

Aims

In the light of these climate-induced vegetation responses, several monitoring initiatives and networks were established all across the globe. Among others, the *Global Observation Research Initiative in Alpine Environments* (GLORIA) was founded in order to assess long-term climate change impacts on plant communities in high-mountain ecosystems (Pauli et al., 2015). Within the scope of this international research initiative, comparable data are collected in different mountain areas around the world. One of these target regions is situated in the Dovrefjell National Park, Norway, and the set-up consists of four summits representing an elevational gradient. These summits were previously monitored in 2001 and 2008 and some substantial spatial and temporal changes in vegetation were observed (Michelsen et al., 2011). This study reported a significant increase in species richness and a considerable change in cover and abundance of certain vascular plant species, especially an increase of woody plants and graminoids. In 2015, local plant species were re-inventoried in order to determine whether these trends continued throughout the years and whether these changes in vegetation can be attributed to the ongoing changes in climate conditions during the same period. The practical part of this master thesis summarizes the results of the most recent monitoring campaign at Dovrefjell and assesses the impact of climate change, as well as the influence of other possible drivers. In particular, the following research questions will be addressed:

[1] Is there a significant positive change in soil temperature between 2001 and 2015?

[2] Is there a significant effect of the summit characteristics (altitude and/or aspect) on the change in soil temperature?

[3] Did a significant change in plant, lichen and bryophyte species richness and community composition occur between 2001 and 2015? Which species have disappeared and which species are new? Can we related species' functional traits to their change in frequency over time?

[4] Is it possible to relate the observed changes in local vegetation patterns to the observed changes in temperature? Which other drivers might have an influence?

Materials and methods

Study area

The study area is located in the Dovrefjell-Sunndalsfjella National Park (Norwegian: *Dovrefjell-Sunndalsfjella nasjonalpark*), one of the largest continuously protected nature reserves on the Norwegian mainland. Together with the surrounding protected areas, the National Park covers about 4367 km^2, including a large part of the Dovrefjell mountain range (Nasjonalparkene, 2015). In this region, four mountain summits were selected in order to study possible vegetation shifts as a result of climate change along an elevational gradient: Vesle Armodshøkollen (62°15'40.5'' N, 9°39'55.4'' E, 1161 m a.s.l.), Veslekolla (62°18'23.6'' N, 9°27'25.2'' E, 1418 m a.s.l.), Kolla (62°17'30.5'' N, 9°29'12.7'' E, 1651 m a.s.l.) and Storkinn (62°20'48.2'' N, 9°26'27.1'' E, 1845 m a.s.l.). The summits are situated in two Norwegian municipalities, namely the Oppdal (Sør-Trødelag county) and Dovre municipality (Oppdal county), and are chosen to represent an altitudinal gradient from the low alpine zone up to the high alpine zone in the Dovrefjell mountain region. **Figure 12** shows a map of the study area, together with the exact location of the four selected summits.
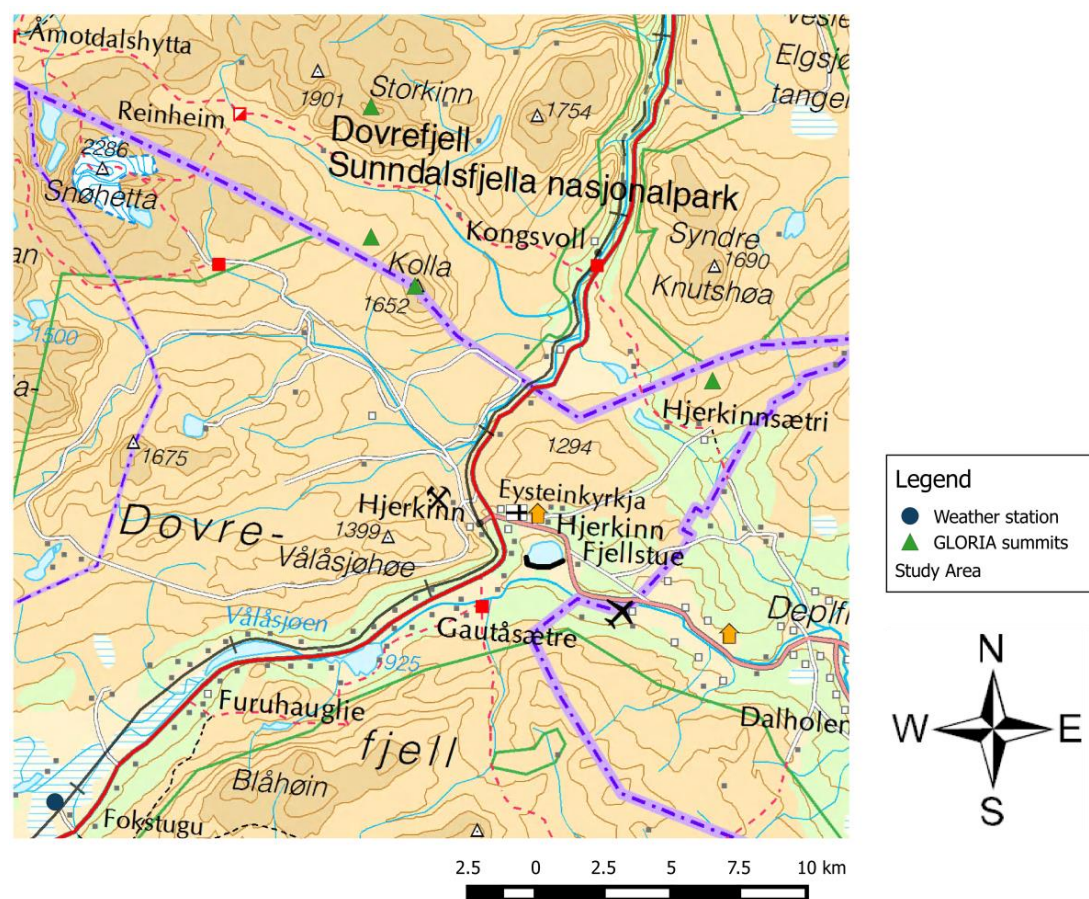
Figure 12: Topographic map of Dovrefjell with the location of the four selected GLORIA summits and the nearby weather station of Gammel-Fokstugu; basemap: N500 Raster, UTM 33, Norway-country, MrSID; coordinate system: WGS 84 / UTM zone 33N (Kartverket, 2015) (Edited in QGIS 2.6.0-Brighton).

Geography

The Dovrefjell-Sunndalsfjella National Park is located on the mainland of Norway, about 370 km north of Oslo and 200 km south of Trondheim. The nature reserve stretches over areas that belong to three different Norwegian counties, namely Oppdal, Sør-Trødelag and Møre og Romsdal. Together with the Dovre National Park, it includes the famous Dovrefjell mountain range, a natural habitat for a large range of rare plant and animal species. The highest summit in this mountain region is Snøhetta (2256 m a.s.l.) which has become a popular tourist attraction during the last decades. In addition, the river Driva takes its rise in the Dovrefjell mountain range, after which it runs north through the Oppdal county. The national park can be reached via the main south-north highway (E6) or the celebrated railway *Dovrebanen* which runs through the Dovrefjell mountain region (Nasjonalparkene, 2015).

Geology

Approximately 400 million years ago, the Caledonian mountain range was thrust up, giving birth to a large part of the Scandinavian Mountains. As a result of this intensive mountain chain folding, enormous mountain peaks were created, some of them reaching even higher than the summits in the Himalaya today. However, during a period of about 100 million years of erosion, those peaks were eventually levelled off, leaving only the roots of the original mountain chain. This flat plateau remained present in the Norwegian landscape for another few 100 million years. During the Tertiary period (70 – 2.5 million years ago), the western part of the Scandinavian plate was lifted up just off the coast of Norway. The eastern part of Sweden remained lower, causing the entire plate to angle. As a result, all rivers giving rise in the Scandinavian mountains flow in an eastern direction. The higher west side, which was formed during this period of uplifting, stretches over the entire length of Scandinavia and also includes the Dovrefjell mountain range (Nasjonalparkene, 2015; The Geological Survey of Norway, 2015).

Two types of parent material can be found at Dovrefjell. In the west, the mountains are mainly dominated by ancient Precambrian bedrock. This 1000 million year old bedrock is predominantly composed of less weatherable and heavily metamorphosed rocks such as gneiss. Other areas in this region consist mainly of mineral-rich sandstone, such as feldspar which dates back to approximately 600 – 700 million years ago. The summits in the neighborhood of Snøhetta are composed of those mineral-rich rock species and are therefore characterized by a large variety of interesting minerals. Moreover, younger rock produces a considerable amount of nutrients upon weathering. These nutrient-rich soils provide the excellent environment for the establishment of a species-rich alpine vegetation. The eastern part of the Dovrefjell mountain range on the other hand, is dominated by the Cladonian mountain chain which mainly consists of strongly folded rock. Phyllite, mica schist and greenstone are the predominant rock types typically found in this region, which is often indicated as the 'Trondheim field' (Nasjonalparkene, 2015).

Three of the selected summits (Veslekolla, Kolla and Storkinn) are situated west of the Drivdalen valley, which is formed by the river Driva and runs north through the Oppdal municipality in the Sør-Trødelag county. Veslekolla and Storkinn are characterized by bedrock that is mainly composed of strongly metamorphosed sandstone. On the other hand, the summit Kolla predominantly consist of gneiss, granite and anorthosite. Finally, the lowest summit, namely Vesle Armodshøkollen, is located east of the Drivdalen valley and the bedrock is composed of greenstone and amphibolite (Bretten et al., 1994; Syverhuset, 2009; The Geological Survey of Norway, 2015).

Finally, with respect to soils, Dovrefjell is mainly dominated by Podsols (Soil Map of Norway, 1983) (**figure 13**). This is a typical soil type for coniferous or boreal forests and is predominantly derived from quartz-rich sand material, sandstones or sedimentary debris of magmatic rocks. In areas with a

sufficient amount of precipitation, Podsols generally form from any type of parent material. This coarse-textured soil type is mostly not suitable for agricultural purposes, given the fact that the high sand fraction barely contributes to the retention of plant-essential nutrients. Moreover, sandy soils are also characterized by a low water holding capacity. Therefore, the recommended agricultural practice for *podsols* is grazing (Spaargaren, 2008). The World Reference Base (WRB) for Soil Classification by the FAO describes Podsols as soils with either a hardened *petroplinthic* horizon starting within 50 cm from the soil surface, a *plinthic* horizon starting within 50 cm from the soil surface or a *plinthic* horizon starting within 100 cm from the soil surface in combination with either an underlying *albic* horizon or a horizon with recognizable *stagnic*[17] properties.

Legend:
- ▲ Study summits
- ■ Podsols with a thick to medium bleached layer, partly with a hardpan and accompanied by swamp soils and brown earths
- ■ Podsols with a medium bleached layer with swamp soils, Lithosols and brown earths
- ■ Azonal soils which were formed above the podsolization boundary (Crudaplsols), Lithosols and Podsols
- ■ Podsols with a medium bleached layer, Lithosols, bown earths, swamp soils, rankerlike soils and Redzinas
- ■ Podsols with a humus or ferric humus layer

Figure 13: Soil map of Dovrefjell. This map belongs to the much larger Soil Map of Norway (Jorbunnskart) which was published by J. Lag and the Norges Landbrukshogskole in 1983 and is characterized by a scale of 1:2000000 (European Soil Portal, 2015; Soil Map of Norway, 1983).

Macroclimate

The eastern part of the Dovrefjell-Sunndalsfjella National Park is characterized by a highly fluctuating annual precipitation rate (approximately 400-500 mm on average). In the western part of the national park, significantly higher values for the annual precipitation rate are registered. The regions east of the Snøhetta mountain range are influenced by a typical continental climate with relatively warm summers and cold winters (Nasjonalparkene, 2015).

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[17] Stagnic properties develop upon (temporary) saturation of the soil with surface water for a period long enough to allow reducing conditions to occur (WRB, 2014).

Weather stations in Dovrefjell are located at Snøheim (1505 m a.s.l.), Kongsvoll (930 m a.s.l.) and Gammel-Fokstugu (972 m a.s.l.). Data gathered at the weather station of Gammel-Fokstugu, approximately 25 km from the study area, indicated a long-term mean annual temperature of approximately -0.1 °C between the period of 1961-1990. Generally, the highest temperatures were measured in the month of July with a mean monthly temperature of 9.8 °C, while the coldest temperatures were registered in January with a mean monthly temperature of -8.8 °C. In addition, the average annual precipitation at the weather station of Gammel-Fokstugu approached a value of about 435 mm (Syverhuset, 2009; Norwegian Meteorological Institute, 2015). **Figure 14** shows the mean annual temperature anomaly relative to the normal period of 1961-1990 for this weather station. On an annual basis, the long-term average temperature between 1961-1990 approximated a value of 0.8 °C.
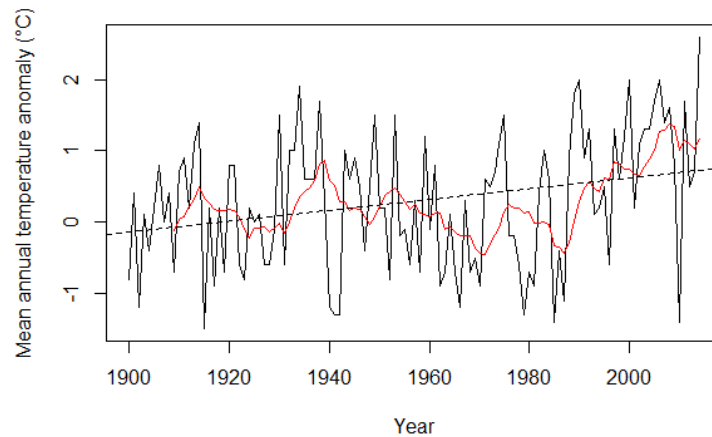
Figure 14: Anomaly of the mean annual temperature relative to the baseline period of 1961-1990 at the weather station of Gammel-Fokstugu. The dashed line shows the long-term linear trend, whereas the red line represents a 10-year running average.

The mean annual temperature measurements at Gammel-Fokstugu showed a visible upward trend throughout the period of 1900-2014. A statistical analysis (ANOVA) confirmed the fitted linear trendline to be significantly increasing over time (F = 8.96, n = 114, P = 0.00338) (**table 1**).

Table 1: ANOVA results for fitting a linear trendline to the mean annual temperature anomaly (MATA) measurements. The code (**) corresponds with a significance level of 0.01 or 1 %.

Effect	Df	SSR	MSR	F-value	p-value
MATA	1	9315	9315.2	8.96	0.00338 **
Residuals	113	117415	1039.1		

Figure 15 represents the change of the mean seasonal temperature anomaly relative to the normal period of 1961-1990 at Gammel-Fokstugu. The long-term average seasonal temperatures for the spring, summer, autumn and winter were respectively -0.1 °C, 10.2 °C, 1.6 °C and -8.4 °C.

Based on these seasonal temperature graphs, it could be concluded that winter temperatures clearly showed the largest inter-annual variability in the study area. These results are consistent with the assessment report of the European Environmental Agency (2013) which also observed a significantly higher inter-annual temperature variability in Europe during the winter months. According to Hurrell (1995), this phenomenon is mainly caused by the inter-annual variability in the atmospheric

circulation, associated with the North Atlantic Oscillation[18] (NAO) and the subsequent fluctuations in the surface westerlies across the North Atlantic Ocean onto the European continent.
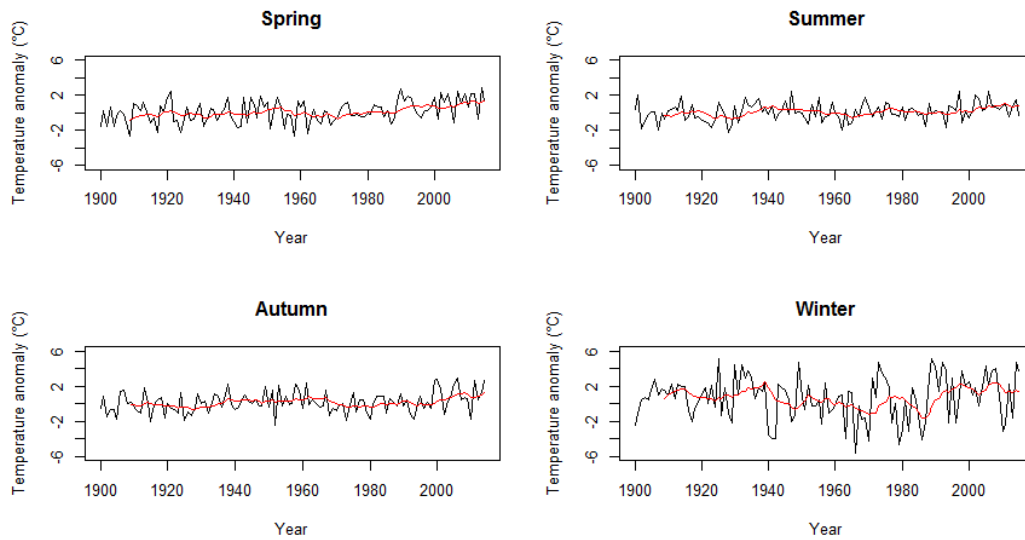
Figure 15: Mean seasonal temperature anomaly at Gammel-Fokstugu weather station relative to the baseline period of 1961-1990. For each season, the red line represents a 10-year running average.

The annual amount of precipitation at the weather station of Gammel-Fokstugu showed a large variation throughout the measuring period. Some years proved to be rather wet, whereas other years were marked by a particularly lower amount of rainfall. Nonetheless, Dovrefjell is considered as one of the drier regions on the Norwegian mainland (Norwegian Meteorological Institute, 2015). **Figure 16** illustrates the percentage anomaly of the mean annual precipitation. The blue bars indicate the relative deviation of the annual amount a precipitation in comparison to the long-term average annual precipitation for the normal period of 1961-1990.
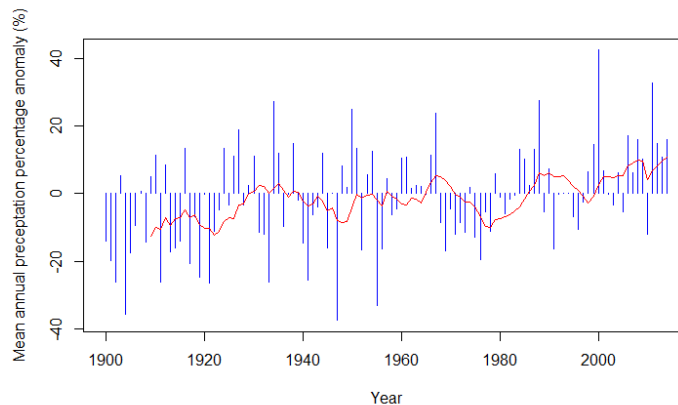
Figure 16: Percentage anomaly of the mean annual precipitation relative to the normal period of 1961-1990 at the weather station of Gammel-Fokstugu. The red line represents a 10-year running average.

The explicit inter-annual variability in the amount of precipitation was also represented in the four seasonal graphs. However, no clear long-term trend could be distinguished during the measuring

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[18] The North Atlantic Oscillation is one of the most prominent teleconnection patterns in the Northern Hemisphere and is driven by changes in the atmospheric sea level pressure between the Artic and the subtropical Atlantic. Climate anomalies associated with this event are largest during boreal winter months (Hurrel, 1995).

period. This is illustrated by **figure 17** showing the percentage anomaly for the mean seasonal precipitation with respect to the normal period of 1961-1990 at Gammel-Fokstugu.
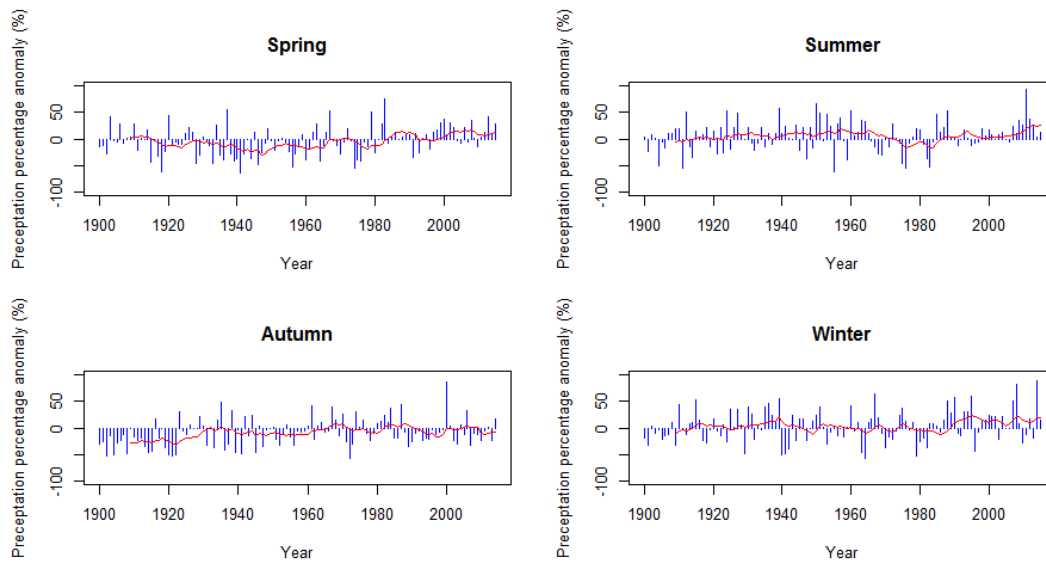
Figure 17: Percentage anomaly of the mean seasonal amount of precipitation relative to the normal period of 1961-1990. The red line indicates a 10-year running average for each season.

Ecology

Flora

The Dovrefjell area is characterized by a large variety of climatic conditions and geological features which provides a wide range of abiotic conditions and possible habitats. As a result, the area is covered with a highly species-rich alpine vegetation. The vegetation zones range from the northern boreal zone to the high alpine zone within the study area (Moen et al., 1999; Syverhuset, 2009). The four GLORIA summits are selected in a way that each mountain is located within a different vegetation zone: Vesle Armodshøkollen is situated in the low alpine zone, while the summit of Veslekolla can be found in the transition between the low and middle alpine zone. The two highest summits, Kolla and Storkinn, are respectively located in the transition between the low and the high alpine zone and the high alpine zone (Syverhuset, 2009). Moreover, many different vegetation alliances or characteristic plant communities are found within the study area. The exposed ridges with only small amounts of snow cover are predominantly covered with plant communities belonging to the *Loiseleurio-Arctostaphylio* alliance. In addition, the vegetation cover on the lee sides of the summits mainly consists of *Phyllodoco-Vaccinion* and *Nardo-Carcion bigelowii* alliances. The late-melting snow beds are generally covered with plants from the *Cassiopo-Salicion herbaceae* alliance (Syverhuset, 2009; Elven et al., 1996). Finally, it should be noted that Vesle Armodshøkollen is characterized by a rather species-rich alpine flora, while the GLORIA summits located to the west of the Drivdalen valley have a remarkably lower species richness (Michelsen et al., 2011; Syverhuset, 2009).

Fauna

The areas around the mountain range of Dovrefjell are characterized by a varying vegetation cover and therefore provide an excellent habitat for numerous bird species, e.g. the golden eagle (*Aquila chrysaetos*), the gyrfalcon (*Falco rusticolus*) and the rough-legged buzzard (*Buteo lagopus*). In addition, some larger mammals thrive within the borders of the national park. Wolverines (*Gulo gulo*),

for example, were able to establish a viable population, but they are rarely seen by humans in the wild (Norway's National Parks, 2015). The Arctic fox (*Vulpes lagopus*) is also native to the Dovrefjell area, however its population has been declining dramatically during the last decades.

Another unique mammal housing in the Dovrefjell area, is the musk ox (Ovibos moschatus). In 1931, it was reintroduced to the region from Greenland and according to most recent survey it has increased its population up to approximately 300 animals (Bretten, 1990; Syerhuset, 2009). Most of these musk oxen stay to the west of the Drivdalen valley (Syverhuset, 2009; Michelsen et al., 2011). The wild reindeer (*Rangifer tarandus tarandus*), commonly known as the Snøhetta reindeer, occur both to the west (Snøhetta area) and to the east (Knutshø area) of the Drivdalen valley (Syverhuset, 2009). Finally, also sheep are typically herded in the Dovrefjell area. Multiple farmers in the municipality of Oppdal let their sheep graze to the east of the Driva river, mainly in the Knutshø area. In total, over 6000 animals presently occur in this region. Sheep herds from the Folldal municipality are grazing in the area around the summit Vesle Armodshøkollen. These herds generally move in the direction of Kongsvoll at the end of the summer (Syverhuset, 2009; Michelsen et al., 2011). More information on fauna in the Dovrefjell National Park can be found in **Appendix A**.

In conclusion, a wide variety of animals presently occur within the study area, each with different food preferences. As a result, every one of these animals has a particular influence on the occurrence and distribution of the vegetation. Also trampling of grazers has a distinctive impact on the soil and vegetation (e.g. resulting in soil compaction). Wild reindeer, for example, generally feed on lichen-covered ridges which are commonly found at Vesle Armodshøkollen. Sheep on the other hand prefer grasses such as the Wavy hair-grass (*Avenella flexuosa*) and do not graze on these lichen patches. Nonetheless, sheep herds use those lichen-covered areas as a resting place, thereby influencing the present vegetation due to trampling activity (Syverhuset, 2009; Michelsen et al., 2011).

Management

Dovrefjell was the first region on the Norwegian mainland to receive the status of a 'Charter Park', meaning that it currently has an internationally recognized plan for a sustainable tourism development. Europe counts about 45 different charter parks, which are all bound to a general certification of national parks and protected areas. The certification criteria are set out by an overarching federation called EUROPARC (Midnorsknatur, 2015; Den Norske Turistforening, 2015; EUROPARC Conference, 2015). The current management objective for the Dovrefjell National Park is to preserve an extensive, continuous and predominantly untouched mountain area together with its cultural heritage. In addition, the preservation of the local alpine ecosystem along with its natural diversity, landscape morphology and remarkable geological deposits forms a main concern for regional policy makers. This challenge includes among others a large-scale cleaning of the former local military domain. Finally, with respect to fauna and flora, local authorities attempt to safeguard the regional variation in habitats and ensure the long-term preservation of wild reindeer stocks on the west (Snøhetta area) and the east side (Knutshø area) of the Drivdalen valley (Midnorsknatur, 2015).

The GLORIA project

The *Global Observation Research Initiative in Alpine Environments*, otherwise known as the GLORIA project, was first presented to an international auditorium in September 2000 during the First International Conference on Mountain Biodiversity in Rigi/Kaltbad, Switserland (Grahberr et al., 2000a; GLORIA, 2015). The global monitoring program was founded in order to establish an

international research network with the objective to assess the impact of the ongoing climate change on mountain ecosystems.

Apart from some old records on the dynamics of mountain flora in the European Alps (1835-1953), long-term and large-scale observations of the impacts of rising temperatures on high-mountain ecosystems lacked for most of the past century (Grabherr et al., 2000a). As a result, the GLORIA research initiative was created in order to provide a long-term observation network for a comparative study of climate change impacts on mountain biodiversity and gather large-scale data on the composition and distribution of vegetation patterns in alpine ecosystems (Pauli et al., 2003; Pauli et al. 2004). Furthermore, all major mountain ranges are monitored according to a standardized field protocol, the 'Multi-Summit Approach', which is described in the GLORIA Field Manual (Pauli et al., 2004) and summarized in the following section. Today, 42 GLORIA monitoring sites or 'target regions' have been established all over the world (GLORIA, 2015) (**figure 18**).
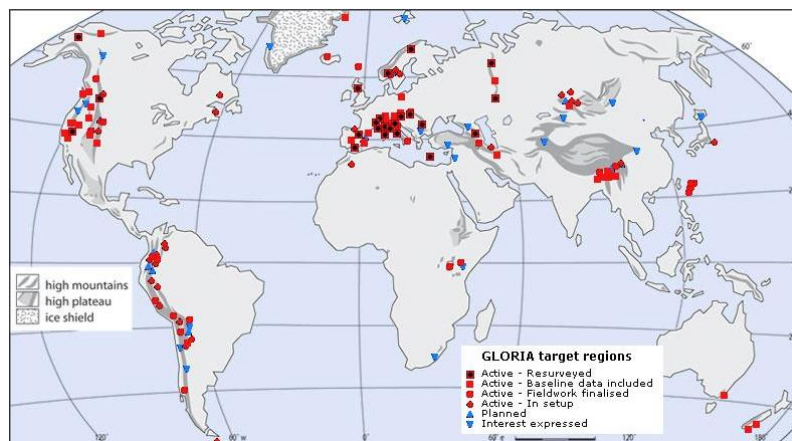
Figure 18: Map of the GLORIA target regions. The different symbols make a distinction between the active and planned monitoring sites (GLORIA, 2015).

The GLORIA project focusses on the alpine life zone or high-mountain biome, which is described as all areas above the natural high-elevation and low-temperature determined treeline and encompasses three different vegetation zones, namely the treeline ecotone, the alpine elevation zone and the nival elevation zone (Pauli et al., 2004). High-mountain environments are generally shaped by the enormous force of moving glaciers and pedogenesis as physical soil structure is continuously influenced by freeze and thaw cycles, resulting from seasonal variations in temperature (Gutiérrez, 2005). Direct anthropogenic influences remain largely absent in these high-mountain habitats, compared to the lower elevations. Consequently, the alpine life zone can be considered as an ideal region for comparative studies of climate change impacts on local biodiversity (Pauli et al., 2004).

However, there exist other reasons for focusing on these environments as well. For example, the alpine life zone comprises areas at all latitudes and in all *zonobiomes*. As a result, the high-mountain regions provide the only terrestrial biome where all climate change impacts on biological processes can be compared along all fundamental climatic gradients, i.e. altitudinal, latitudinal and longitudinal. Secondly, high-mountain ecosystems are mainly controlled by abiotic ecological factors that are often related to changes in climatic conditions, making them more easily comparable. This can be attributed to the fact that the effect of biotic interactions (e.g. competition) decreases with altitude. Some studies even indicate that positive species interactions (e.g. facilitation), dominate at sites with low temperatures, while competition prevails in warmer areas at lower elevations (Callaway et al., 2002). Mountain ecosystems are also characterized by steep ecological gradients due to the compression of thermal life zones. As a result, alpine environments provide a habitat for a wide range of endemic species (Quézel, 1953; Hedberg, 1969; Pawlowski, 1970; Grabherr et al., 2000b) and are known for

their high degree of organismic diversity (Barthlott et al., 1996). Hence, these areas prove to be much more prone to potential losses as a result of climate changes. Finally, vegetation boundary shifts in mountain areas can be easily recognized due to the presence of narrow ecotones. Most alpine vegetation generally consists of long-lived perennial plant species. Subsequently, most species will be visible within the same growing season, making multiple monitoring events within one season unnecessary. Long-lived species also tend to be more suitable for monitoring the impacts of climate change as they are generally less susceptible to short-term climate fluctuations. Prolonged changes in climatic conditions, however, trigger plant distribution shifts and in the long run threaten certain species with extinction (Pauli et al., 2004).

In order to study the effect of climate change on this alpine life zone and assess the risk of local biodiversity losses, in situ observations at a species level are required. This is due to the fact that single species do not respond separately to a changing environment, but the entire structure and functioning of the ecosystem is affected (Ammann, 1995; Grahberr et al., 1995; Gottfried et al., 1998; Berg et al., 2009). A lot of the previous studies regarding environmental changes only focused on the response of individual species and therefore neglected the fundamental biotic interactions at a species level such as predation and competition, but also positive species interaction such as mutalism. Individual species can have a contrasting sensitivity to increasing temperatures causing an entire disruption of community interactions and ecosystem functioning. Possible examples are mismatches in phenology or dispersal patterns and the disruption of predator-prey and flower-pollinator interactions (Whalter et al., 2002; Berg et al., 2009). Within the context of previous conclusions, the GLORIA project aims to (Pauli et al., 2004):

- Provide a standardized data set on the altitudinal differences in species richness and composition, vegetation cover, soil temperature and length of the snow-cover period in mountain ranges all over the world;
- Quantify temporal changes in alpine biodiversity and ongoing shifts in vegetation patterns;
- Contribute to a baseline for the long-term observation of plant communities in order to reveal climate-induced changes in vegetation cover, species composition and distribution, migration patterns, etc. (observation intervals range between 5 to 10 years);
- Provide a detailed risk assessment for biodiversity losses as a result of global warming by comparing the present-day distribution patterns of alpine plant species along latitudinal and altitudinal gradients.

Study design

During the fieldwork at Dovrefjell, a standardized method and study design was applied which is referred to as the 'Multi-Summit Approach' and published in the GLORIA Field Manual of 2004 (Pauli et al., 2004) and the revised version of 2015 (Pauli et al., 2015). This combination of guidelines for a standardized field application forms the basis of the GLORIA monitoring network and was designed to be universally applicable in numerous alpine ecosystems all over the world, ranging from polar to tropical latitudes. Presently, already 18 different mountain areas have been selected as 'Multi-Summit Sites' on the European mainland. In order to qualify for a target region, the mountain area has to contain at least four different summits, representing an altitudinal gradient of vegetation patterns from the natural treeline ecotone up to the vascular plant limit or, when this limit is not reached, up to the uppermost vegetation zone (**figure 19**). Ideally, the arrangement of summits is selected in the following way:

- Summit 1: treeline ecotone

- Summit 2: transition between the lower and the upper alpine zone
- Summit 3: transition between the upper alpine zone and nival zone
- Summit 4: close to the limits of vascular plant life

In the target region of Dovrefjell, this corresponds with the following arrangement of summits. The lowest summit, Vesle Armodshøkollen (1161 m a.s.l.), is located above the treeline in the low alpine zone. The second highest summit, Veslekolla (1418 m a.s.l.), is situated in the transition zone between the low and the middle alpine vegetation belt. The second highest summit, Kolla (1651 m a.s.l.), is located in the transition zone between the middle and the high alpine vegetation belt. Finally, the highest summit, Storkinn (1845 m a.s.l.), is located in the high alpine zone. Moreover, the configuration represents a perfect elevation gradient and is preferred because climate-induced changes often occur first in transition zones of vegetation (Yu et al., 2008).
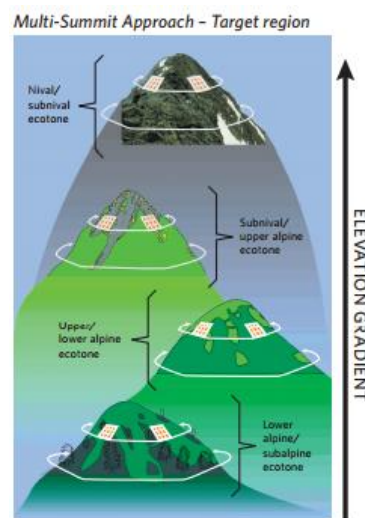
Figure 19: Visual interpretation of an elevation gradient of vegetation zones which consists of four summits in a target region. The white lines represent the lower boundaries of the 5-m and 10-m summit areas (Pauli et al., 2015).

All summits in a target region were selected in the direct vicinity of each other and possible climatic variations could only be attributed to a difference in altitude. Furthermore, the manual suggests to select two or more target regions in more extensive mountain systems in order to avert a distribution of summits across a major climatic shed. For example, it should be avoided at all time that summits which are situated on the prominent windward side of a mountain chain, are located in the same target region as summits which are situated at the leeward side. Also, summits which can be found in the humid outer part of a mountain system cannot belong to the same target region as summits which are located in the drier inner part. The individual GLORIA summits within a distinctive target region have to fulfill a broad range of geological, geomorphological and land-use requirements as well. All those criteria are listed in the GLORIA manual and include for example that the summits should not be affected by anthropogenic or agricultural land-use practices such as trampling, grazing and fertilizing. Finally, a 'moderate' geomorphological shape of the summit is also required (Pauli et al., 2004).

For each summit in the target region of Dovrefjell, a standard procedure was followed in order to set up the equipment and establish the monitoring site. The different steps of this procedure are summarized in **Appendix B** and **C**. After putting the equipment into place, a fine-scaled vegetation analysis was performed within each of the four 3 x 3 m² quadrat clusters. Each of those grids consists of nine different 1 m² quadrats which are indicated with a unique code (**figure 20**). However, only within the four corner quadrats (code: 11, 31, 13 and 33) a detailed vegetation analysis is performed due to the fact that the other squares might be damaged by trampling during the recording procedure.

The top cover[19] of all surface types (e.g. vascular plants, lichens, bryophytes, solid rock, scree, litter and bare ground) and the species cover[20] of all vegetation types (e.g. vascular plants, lichens and bryophytes) was recorded in a standard way within the sixteen 1 m² quadrats. This recording procedure consisted of the following steps. First, possible disturbances by grazing mammals were documented. This included for example grazing-related features such as feces, browsing damage and trampling indications. Subsequently, the top cover percentage of all surface types was determined. This survey included vascular plants, lichens and bryophytes that were growing on soil and were not covered vascular plants, solid rocks[21] and scree[22]. Finally, the top cover of bare ground and litter material was included as well. Secondly, the top cover of some subtypes was estimated. These subtypes represent a fraction of the present vascular plants, solid rock or scree and were therefore estimated as a percentage of the surface types cover. The following subtypes were included in the quadrat's survey: lichens and bryophytes growing below a layer of vascular plants, *epilithic* lichens and bryophytes growing on solid rock units and *epilithic* lichens and bryophytes growing on scree or mobile debris material. Bryophytes that were growing in micro-fissures where the soil is no longer visible were included in this percentage cover.
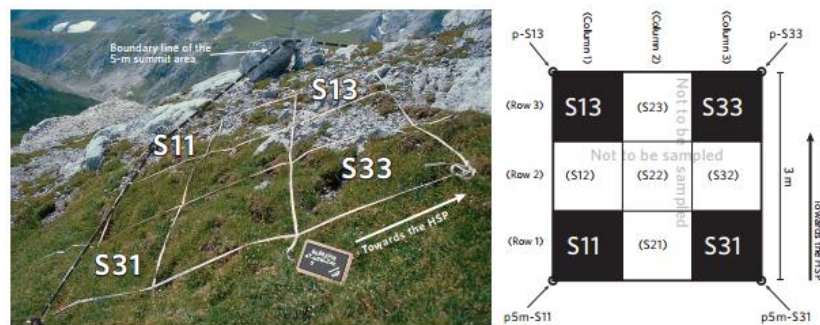
Figure 20: Schematic representation of a 3 x 3 m² grid (here in the southern section). The corner quadrats (S11, S31, S13 and S33) are used for a detailed vegetation analysis while the other squares are ignored during the recording procedure due to the fact that they are constantly damaged by trampling of the investigators (Pauli et al., 2015).

In a next step, all vascular plant, lichen and bryophyte species, occurring within the observed 1 m² quadrat, were inventoried and a visual estimation of their species cover was made. For practical monitoring purposes, these cover values were estimated as precisely as possible, particularly for species with a low abundance within the quadrat. Nonetheless, this procedure will always include a certain degree of inaccuracy. In most cases, the species cover percentage was based on the percentage scale relative to the total surface area of the quadrat (1 m^2), however a template indicating the area of 1 %, 0.5 %, 0.1 %, 0.05 % and 0.01 % could be adopted to facilitate the visual estimation procedure. In addition, a second plant cover estimation procedure was performed according to the point intercept method (Pauli et al., 2015). This method involved recording surface types (such as lichens, bryophytes, solid rock, scree, litter and bare soil) or vascular plant species that intercepted with the vertical projection of a predetermined series of points (Floyd & Anderson, 1987). The theoretical basis for this approach is elementary: the number of points intercepted or 'hits' of a particular entity should

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[19] The top cover corresponds with the vertical projection of a surface type and the total sum adds up to 100 % (Greig-Smith, 1983; Pauli et al., 2015).

[20] The species cover also takes into account the overlap between different vegetation parts and the total sum generally exceeds 100 % (Greig-Smith, 1983; Pauli et al., 2015).

[21] Solid rocks are described as fixed large and immobile boulders (Pauli et al., 2015).

[22] Scree can be described as debris material with a grain size that is larger than the sand fraction and single mobile rock fragments (Pauli et al., 2015).

correspond to its cover, within a certain degree of accuracy (Goodall, 1952; Greig-Smith, 1983; Pauli et al., 2015). In practice, the series of points was arranged according to a 10 x 10 grid which was created by an aluminium frame (**figure 21**). This frame consisted of 100 cells of 0.1 m x 0.1 m, delimited by a network of strings.
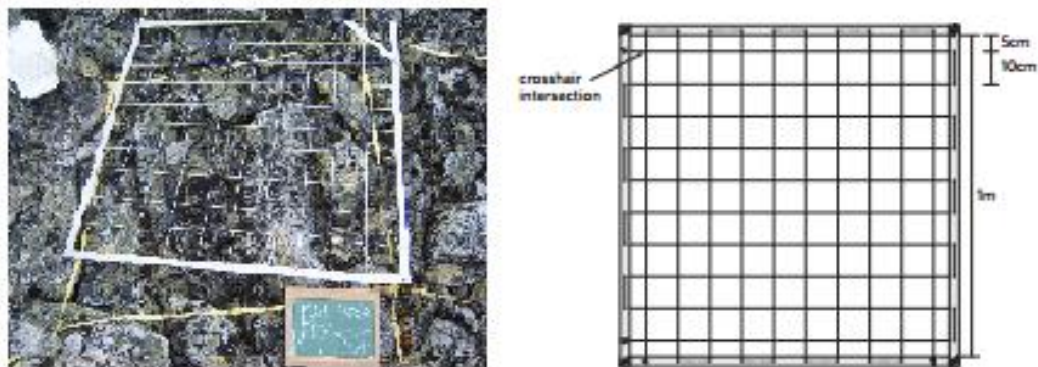
Figure 21: Schematic representation of the aluminium frame which is used for the point intercept method. The grid consists of 100 cells of 0.1 m x 0.1 m that are delimited by a network of white strings. The orientation of the frame is indicated on the figure as well (Pauli et al., 2015).

The frame was fitted on top of the observed quadrats, using photographic documentation from the previous survey in 2008. Subsequently, a wooden pin was placed vertically in the lower right corner of each grid cell and the intercepted surface types or plant species was recorded. When more than one vascular plant species was in contact with the wooden pin, all touching individuals were recorded and therefore received an additional hit. Moreover, if the wooden pin was hitting bare ground, but also solid rock, scree or litter, the latter was documented. Lastly, lichens on solid rock or scree were not taken into account during the point intercept method.

Table 2: Description of the five abundance classes or categories, used to visually estimate the species cover percentage within a summit area section (Pauli et al., 2015).

Abundance class	Symbol	Quantitative value (%)	Description
Abundant	a	50	Very abundant, making up most of the present phytomass; more or less patchy or dense vegetation layers; species covers more than 50 % of the summit area section
Common	c	10	Frequent and widespread occurrence within the section; presence is obvious at the first glance, but it covers less than 50 % of the summit area section
Scattered	s	0.5	Widespread within the section, species can hardly be overlooked, but the presence is not obvious at the first glance; individuals are not necessarily evenly dispersed over the entire summit area section
Rare	r	0.05	Some individuals at several locations that can hardly be overlooked in a careful observation
Very rare	r!	0.005	One or a few small individuals

Next to the detailed vegetation analysis in the 1 m² quadrats, the eight different summit area sections were analyzed as well. These sections were installed in the four cardinal directions between the HSP and 5 height meters below the HSP and between 5 and 10 height meters below the HSP (cfr. **Appendix C**). In each section, the percentage top cover of all surface types (vascular plants, solid rock, scree, lichens, bryophytes, bare ground and litter) was estimated visually. In addition, all present vascular plant species within a certain section were carefully inventoried in order to make a complete species list. Meanwhile, the species percentage cover was estimated as well using five distinctive *abundance classes* or *categories*. These categories were later replaced by a quantitative value

(**table 2**). The main purpose of this survey was to detect potential changes in species richness and species migrations on the investigated mountain top (Pauli et al., 2004).

Climatic data

In addition to the vegetation sampling, soil temperature was continuously recorded on the study summits using a miniature data logger. These measurement devices were buried in the substrate at a depth of approximately 10 cm below the soil surface. The mountaintop summits at Dovrefjell were equipped with the *GEO-Precision M-Log5W logger*. Each summit contained four of these temperature loggers, one in every 3 x 3 m² quadrat cluster of each cardinal direction (N, E, S and W). Normally, the loggers were buried in the middle quadrat, specified with the code 22 (see **figure 20**). However, when the substrate in the middle quadrat was unsuitable (e.g. due to the presence of massive solid rock fragments), the temperature logger was installed in a neighboring square. The temperature data could be easily read out on a laptop after installing the proper software (*GP5W-Shell*) and plugging in a wireless USB dongle with build-in antenna. Using this antenna, a certain nearby logger could be traced and subsequently identified by the software. After a correct identification, some dynamic logger parameters, such as the 'deviation to PC's clock', were displayed. If the time deviation of the selected logger were too large (i.e. within the range of a few minutes), the time settings were corrected using the 'Synchronize Clock'-button which was available on the software interface.

Statistical analyses

All statistical analyses were performed in R version 3.2.2 (R Core Team, 2015). For the temperature data from the loggers in each of the quadrat clusters, annual and seasonal (summer vs. winter) average values were calculated. In this case, the summer months corresponded with June, July and August, whereas the winter months corresponded with the December, January and February. In addition, a locally-weighed polynomial regression (*lowess*) was determined, representing a long-term trend. Furthermore, a linear mixed effect model was fit to the temperature data, specifying the summit or aspect (nested within summit) as a fixed effect and the temperature logger's code as a random effect to account for the hierarchical nature of the data and repeated measurements. Secondly, the factor year was added to this model and a χ^2-test was performed to check whether the temperature change was significant over time. In order to detect any significant differences, the change of the soil temperature throughout the period 2001-2015 (for every summit and for each aspect) was compared in a paired-wise way using a Tukey Multiple Comparison test. This procedure was repeated for the annual mean summer and winter temperatures.

The second part of the statistical analysis focussed on the vegetation data of 2015. Based on the cover data of vascular plants, lichens and bryophytes, the corresponding species richness (S), Shannon diversity index (H) and species evenness (J) were calculated and the effect of altitude and aspect on these three parameters was examined using an ANOVA test. Therefore, both variables, summit and aspect (nested within the variable summit), were included in the linear model. Main effect were tested using a significance level of 5 %, while for interaction effects a significance level of 1 % was used. The Shannon index was calculated using **equation 1**:

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

Where p_i is the proportion (n/N) of all individuals (n) of a particular species i divided by the total number of indivuals (N) and S is the total number of species. The species evenness was determined using **equation 2**:

$$J = \frac{H}{\ln S} \qquad (2)$$

Where H corresponds with the Shannon diversity index and S with total number of species in the community.

To test how the vegetation changed over time between 2001 and 2015, an ANOVA test was performed with summit, aspect (nested within summit), year and their interaction as fixed effects and the number of species, Shannon diversity index and species evenness for vascular plants, lichens and bryophytes as response variables. Next, dissimilarity indices were calculated for vascular plants, lichens and bryophytes and evaluated for the periods 2001-2008, 2008-2015 and 2001-2015 in order to quantify the corresponding β diversity. Whittaker (1960) defined β diversity as the variation of species between different sites along a spatial or temporal gradient. Moreover, this parameter is directly linked to the biodiversity at a local scale (α diversity) as well as at a wider regional scale (γ diversity). Vellend (2001) distinguished two main types of β diversity, namely *turnover* and *variation* (**figure 22**). First, *turnover* provides a measure of the change in community structure (i.e. identity, relative abundance, biomass and/or cover) between two sampling units along a distinctive spatial, temporal or environmental gradient. This measure gives an idea of the number of new species that are encountered along a previously defined gradient, the number of initial species that were lost and the proportion of unshared species when moving from one sampling unit to another along that gradient. Secondly, *variation* refers to the variation of species identity among sampling units within a certain spatial or temporal extent and provides an answer to questions as: "By how much does the total number of species in a geographical region exceed the average number of species in the sampling units?" and "Do we repeatedly encounter the same species in different sampling units?" (Anderson et al., 2006).
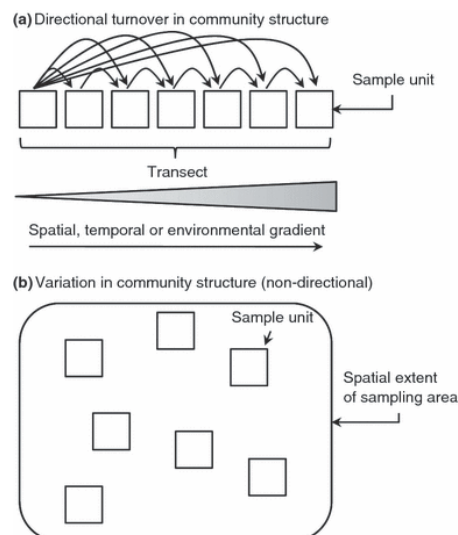
Figure 22: Schematic representation of the two main types of β diversity, namely the turnover in community structure along a previously defined gradient (a) and the variation in community structure between different sampling units (b) (Anderson et al., 2010).

A wide range of indices for β diversity have been proposed for ecological analysis (e.g. Vellend, 2001; Koleff et al., 2003; Jost, 2007). The Euclidean distance function depends to a large extent on the abundance of species in two sites and not just the species that are shared. However, in this case, more emphasis needed to be given to the extent to which certain species are shared and the alterations in

species composition or *turnover* (De Frenne et al., 2015). Hence, ecological distances were calculated using the modified Gower dissimilarity index (Gower, 1971; Gower, 1987). This index can be described as a pairwise dissimilarity measure which is based on relative abundance data, but does not include joint absences. The exclusion of joint absences indicates that two sites will not be considered as more similar when they both lack specific species (Anderson et al., 2011). The main advantage of this modified dissimilarity measure is that it explicitly weights an order-of-magnitude change in abundance the same as a change in species composition (from 0 to 1). This is achieved by specifying a log base which can be altered in order to change the emphasis placed on the compositional change vs. the change in abundance. For instance, when using a log base of 2, a doubling in abundance will correspond with a change in species composition. As a result, this dissimilarity index can be interpreted as the average change in orders of magnitude per species between two sampled plots (Anderson et al., 2006). The modified Gower dissimilarity index was calculated using **equation 3**:

$$d_{MG} = \frac{\sum_{k=1}^{\gamma} \omega_k |x'_{1k} - x'_{2k}|}{\sum_{k=1}^{\gamma} \omega_k} \tag{3}$$

Where x_{1k} provides a measure for the abundance of a species k in the first sampling unit and x_{2k} for the abundance of that same species k in the second sampling unit. However, in this formula, x_{1k} and x_{2k} are log-transformed which is indicated by the apostrophe. In addition, the weights ω_k are used in order to exclude the joint absences by specifying $\omega_k = 0$ in the case $x_{1k} = x_{2k} = 0$ and $\omega_k = 1$ elsewhere (Anderson et al., 2006). This dissimilarity index is also not limited by an upper bound. Clarke and Warwick (2001) previously stated that an ecological dissimilarity between two sites should reach a maximum value if there are no species in common at all. Nevertheless, the index might become more susceptible to erratic behavior for sparse data, a problem which is not encountered with the modified Gower dissimilarity index (Clarke et al., 2006).
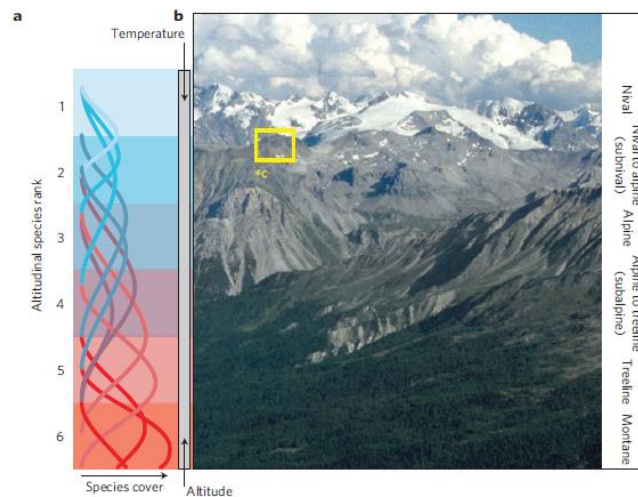
Figure 23: (a) Distribution of alpine plant species along an elevational gradient. An altitudinal indicator value is assigned to different alpine plants using six ranks ranging from 1 (blue) to 6 (red). The amplitude of the curves gives an indication of the varying species abundances. (b) Arrangement of the different bioclimatic belts along the elevational gradient (Gottfried et al., 2012).

Furthermore, in order to demonstrate the effect of climate warming on the composition of alpine plant communities at Dovrefjell, the ecological indicator concept was applied. This procedure takes into account the realized position of a plant species along an environmental gradient and quantifies thus the increasing dominance of warmth-loving (low-altitude) species (i.e. thermophilization). In this case, a difference in elevation was considered to consistently represent a thermal gradient. According to the

central European concept of vegetation belts, mountain species are distributed between different ecotones (colline, montane, subalpine or treeline, alpine and nival) depending on the ranges of their performance (**figure 23**).

All recorded plant species in the quadrats of the GLORIA summits received an altitudinal rank (**table 3**) which was originally based on the species' lower and upper margin as well as its distribution centre. For vascular plants, these ranks were derived from Gottfried et al. (2012), whereas for lichens and bryophytes the altitudinal ranks were determined in a similar manner by experts from the NTNU (Håkon Holien and Kristian Hassel). All ranks are mentioned per species in **Appendix H**.

Table 3: Description of the different altitudinal ranks for the vascular plants.

Rank	Description
1	Species with a nival distribution centre
2	Alpine to nival species, not descending to treeline
3	Alpine centered species, not descending to montane belt
4	Alpine centered species, descending to montane belt or indifferently distributed from the alpine belt to the treeline
5	Species centered in the treeline ecotone or indifferently distributed from montane to alpine belt
6	Species with a montane distribution centre or indifferently distributed from the montane belt to the treeline

Subsequently, the thermic vegetation indicator *S* was calculated for each quadrat using the **equation 4**:

$$S = \frac{\sum_i (rank(species_i) \times cover(species_i))}{\sum_i cover(species_i)} \tag{4}$$

The difference in the thermic vegetation indicator for each quadrat between 2001, 2008 and 2015 was determined. These differences are referred to as the thermophilization indicator *D* and were evaluated for the periods 2001-2008, 2008-2015 and 2001-2015 respectively. Based on an ANOVA test, the effect of summit and aspect (nested within the variable summit) on these parameters was tested. Due to uncertain identification of the bryophyte species in 2008 (as, for instance, indicated by the total γ-diversity numbers), it was decided not to include the thermophilization indicators for the periods involving the year 2008, i.e. 2001-2008 and 2008-2015.

Potential changes in the species composition of vascular plants, lichens and bryophytes on the GLORIA summits at Dovrefjell during the period 2001-2015 were determined using a Permutational Multivariate Analysis of Variance (PERMANOVA) based on distance matrices. These matrices were calculated using the modified Gower (*altGower*) dissimilarity index. The variables summit, aspect (nested within the variable summit), year and the corresponding interaction effects were included in the linear model in order to investigate their effect on the species composition. The change in species composition of vascular plants throughout the sampling period of 2001-2015 was also investigated using an NMDS (Non-Metric Multidimensional Scaling) plot. The main purpose of NMDS is to reproduce the original position of a community in a multidimensional environment using a minimal number of (principal) dimensions. However, NMDS uses the rank order of species in a community instead of the absolute abundance, making the technique much more flexible with respect to the input data type. In this case, a distance matrix based on the modified Gower dissimilarity index was calculated and used as an input for the NMDS procedure. The final NMDS plot showed the different plots (or quadrats) on the GLORIA summits for both sampling campaigns (2001 and 2015), together with the vascular plant species, plotted along the two selected principal axis.

Finally, a linear mixed effect model was used to investigate whether the cover percentage of the individual species on the GLORIA summits changed significantly between 2001 and 2015. In this model, the variable year was specified as a fixed effect, whereas the variable summit was defined as a random effect.

Results

Microclimate

The change of the mean annual soil temperature in the quadrat clusters of the GLORIA summits at Dovrefjell during the period 2001-2015 is represented by **figure 24** (Vesle Armodshøkollen), **25** (Veslekolla), **26** (Kolla) and **27** (Storkinn).
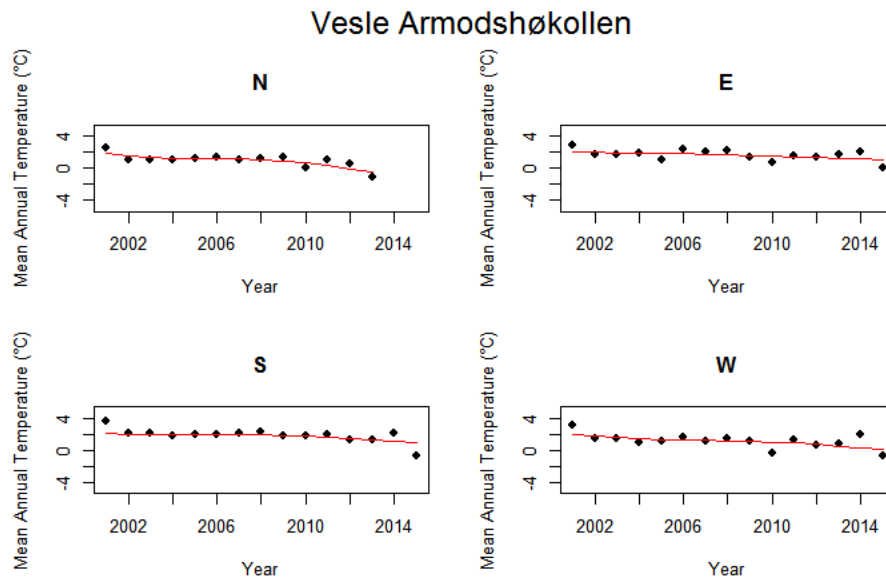
Figure 24: Mean annual soil temperature in the quadrats at Vesle Armodshøkollen (1161 m a.s.l.), located in the four cardinal directions (N, E, S and W). The red line represents a locally-weighed polynomial regression.
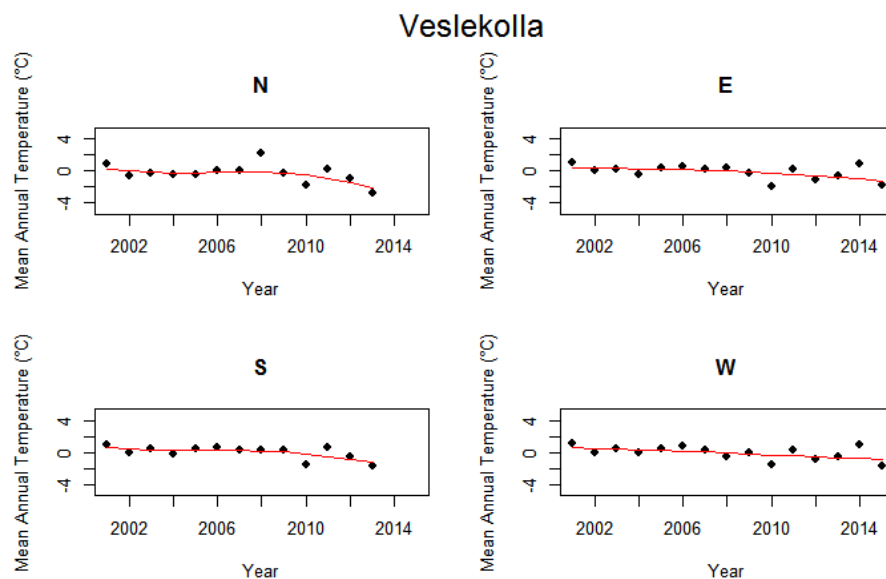
Figure 25: Mean annual soil temperature in the quadrats at Veslekolla (1418 m a.s.l.), located in the four cardinal directions (N, E, S and W). The red line represents a locally-weighed polynomial regression.
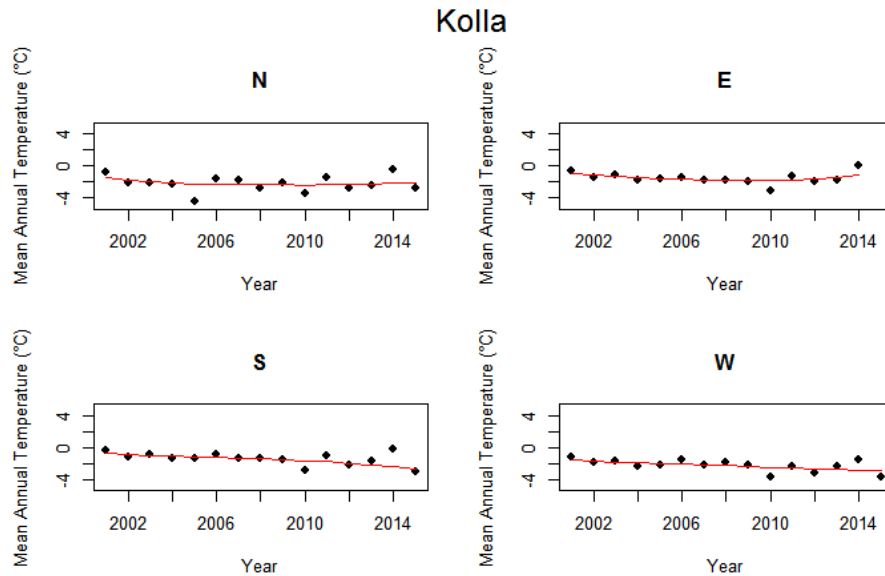
Figure 26: Mean annual soil temperature in the quadrats at Kolla (1651 m a.s.l.), located in the four cardinal directions (N, E, S and W). The red line represents a locally-weighed polynomial regression.
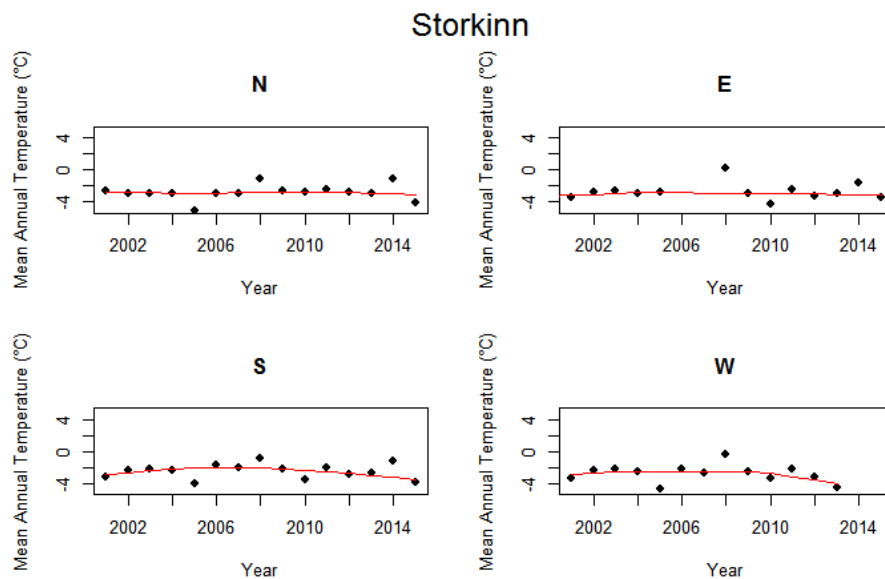
Figure 27: Mean annual soil temperature in the quadrats at Strokinn (1845 m a.s.l.), located in the four cardinal directions (N, E, S and W). The red line represents a locally-weighed polynomial regression.

Across the four summits, a significant decrease in the annual mean soil temperature was found during the period 2001-2015 (χ^2-test, P < 0.0001). Moreover, significant differences in the mean soil temperature were noticeable between Vesle Armodshøkollen, Veslekollla and Kolla (Multiple comparison test, P < 0.001) and between Kolla and Storkinn (Multiple comparison test, P = 0.00822). However, no significant temperature differences were detected depending on the aspect. For the annual mean summer temperature, a significant negative trend was observed (χ^2-test, P < 0.0001), whereas for the annual mean winter temperature a positive trend was found (χ^2-test, P = 0.00103). Figure 28 shows the overall mean annual temperature throughout the measuring period of 2001-2015 for all temperature loggers combined. The mean annual summer and winter temperatures for all temperature loggers are indicated as well.
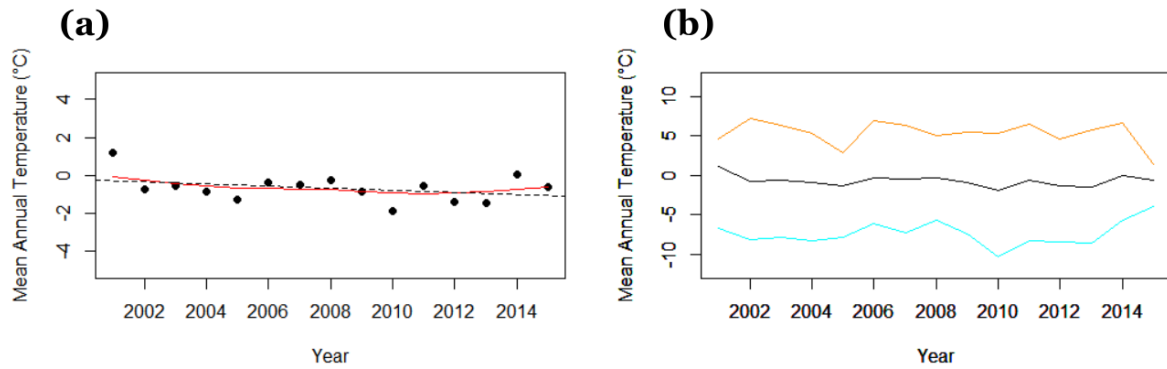
Figure 28: (a) Mean annual soil temperature averaged for all temperature loggers in the target region of Dovrefjell throughout the period 2001-2015. The dashed line indicates a long-term linear trend, whereas the red line represents a locally-weighed polynomial regression. **(b)** Mean annual soil temperature (black) and Mean annual summer (orange) and winter temperature (blue) averaged for all temperature loggers in the target region of Dovrefjell throughout the period 2001-2015.

Vegetation

Vegetation status in 2015

Vascular plants in the quadrats and summit area sections

The species richness, Shannon diversity index and species evenness of vascular plants in the quadrats and the summit area sections differed significantly between the four summits. This indicates the highly significant effect of altitude on vascular plant species richness, diversity and evenness in the study area. For the vascular plants in the quadrats, these three parameters showed a significant difference depending on the aspect of mountain tops as well. For instance, **figure 29** illustrates a decline in species richness with increasing altitude. Furthermore, he species richness was significantly lower for the northern aspect of the lowest summit. An important remark is that the quadrats of the northern aspect of Storkinn were covered with snow and therefore not sampled. With respect to the summit area sections, no significant effect of aspect on the number vascular plant species and the Shannon diversity index was found. The effect of aspect on the species evenness of vascular plants in the summit area sections was only marginally significant (**table 4**).

Lichens and bryophytes

A significant difference in lichen species richness, Shannon diversity index and evenness was found between the four summits in the study area as well. In addition, these parameters showed significant differences depending on the aspects of each summit. For example, **figure 30** shows a higher Shannon diversity index and species evenness for lichens on the two highest summits. Similar results were found for the bryophyte species. Nonetheless, the number of bryophyte species showed only a marginally significant difference between the four summits (**table 4**).

Vascular plants in quadrats

Vascular plants in SAS

Figure 29: Mean species richness (a, d), Shannon diversity index (b, e) and species evenness (c, f) of vascular plants in the quadrats (left) and summit area section (SAS) (right) for each aspect on the GLORIA summits at Dovrefjell. The error bars give an indication of the corresponding standard errors.
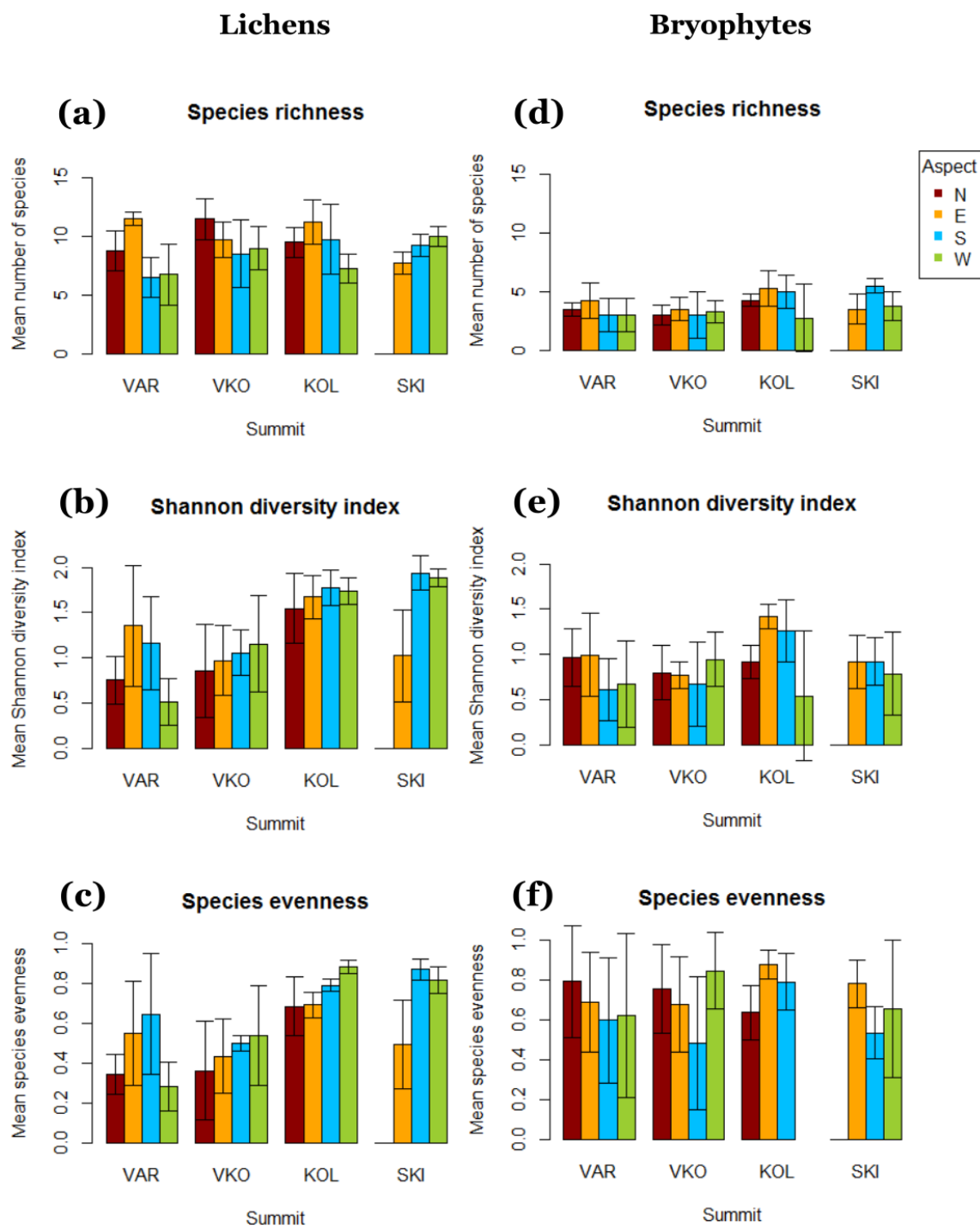
Figure 30: Mean species richness (a, d), Shannon diversity index (b, e) and species evenness (c, f) lichens (left) and bryophytes (right) for each aspect on the GLORIA summits at Dovrefjell. The error bars give an indication of the corresponding standard errors.

Table 4: ANOVA results for the effect of the variables summit and aspect (nested within summit) on the species richness, Shannon diversity index and species evenness of vascular plants, lichens and bryophytes on the GLORIA summits at Dovrefjell. . With respect to the significance codes, the following symbols were used: (***) for P < 0.001, (**) for P < 0.01, (*) for P < 0.05 and (.) for P < 0.1.

Effect	Df	SSR	MSR	F-value	P-value
Vascular plant species in the quadrats					
Species richness					
Effect of summit	3	518	173	147	< 2e-16 ***
Effect of aspect, nested within summit	12	52	4.33	3.68	<0.001 ***
Residuals	48	56.5	1.18		
Shannon diversity index					
Effect of summit	3	10.3	3.43	36.7	1.8e-12 ***
Effect of aspect, nested within summit	12	2.69	0.222	2.38	0.017 *
Residuals	48	4.49	0.094		
Species evenness					
Effect of summit	3	3	1	35.7	1.24e-11 ***
Effect of aspect, nested within summit	12	1.41	0.117	4.19	< 0.001 ***
Residuals	42	1.18	0.028		
Vascular plant species in the summit area sections					
Species richness					
Effect of summit	3	3965	13212	132.2	1.68e-11 ***
Effect of aspect, nested within summit	12	127	10.6	1.06	0.447
Residuals	16	160	10		
Shannon diversity index					
Effect of summit	3	8.51	2.84	28.8	1.1e-06 ***
Effect of aspect, nested within summit	12	1.92	0.16	1.63	0.180
Residuals	16	1.58	0.099		
Species evenness					
Effect of summit	3	0.336	0.112	6.38	0.005 **
Effect of aspect, nested within summit	12	0.426	0.036	2.027	0.099 .
Residuals	15	0.263	0.018		
Lichen species					
Species richness					
Effect of summit	3	85.6	28.5	9.45	5.14e-05 ***
Effect of aspect, nested within summit	12	371.1	30.9	10.2	1.44e-09 ***
Residuals	48	145	3.021		
Shannon diversity index					
Effect of summit	3	5.36	1.786	13.1	2.17e-06 ***
Effect of aspect, nested within summit	12	11.9	0.996	7.33	2.12e-07 ***
Residuals	48	6.5	0.136		
Species evenness					
Effect of summit	3	1	0.334	12.4	3.97e-06 ***
Effect of aspect, nested within summit	12	2.45	0.204	7.60	1.29e-07 ***
Residuals	48	1.29	0.027		
Bryophyte species					
Species richness					
Effect of summit	3	13.7	4.56	2.48	0.073 .
Effect of aspect, nested within summit	12	83.8	6.98	3.79	< 0.001 ***
Residuals	48	88.5	1.84		
Shannon diversity index					
Effect of summit	3	1.17	0.391	2.95	0.042 *
Effect of aspect, nested within summit	12	4.79	0.399	3	0.003 **
Residuals	48	6.37	0.133		
Species evenness					
Effect of summit	3	0.667	0.222	3.96	0.014 *
Effect of aspect, nested within summit	12	1.93	0.161	2.87	0.005 **
Residuals	46	2.58	0.056		

Changes over time

γ-diversity

The total number of vascular plant species in the study area (γ-diversity) increased during the period 2001-2015. For the lichens, a decrease in the total number of species was found, whereas for the bryophytes, a steady-state situation was observed between 2001 and 2015. However, a significantly lower total amount of bryophyte species was noticed for 2008 (**table 5**).

Table 5: Total number of vascular plant species for each of the GLORIA summits at Dovrefjell. The last column shows the total number of species in the entire study area for each year. In addition, the last row for each taxonomic group indicates the total number of unique species for each summit that were recorded during the period 2001-2015.

	VAR	VKO	KOL	SKI	Total (γ)
Vascular plants					
2001	56	14	21	6	67
2008	58	18	22	6	68
2015	61	16	20	8	73
Total species	75	20	26	8	85
Lichens					
2001	20	22	28	15	39
2008	18	19	19	16	28
2015	20	22	20	15	33
Total species	24	27	36	24	49
Bryophytes					
2001	13	9	9	9	20
2008	6	6	8	8	**13**
2015	13	8	13	10	21
Total species	19	12	17	16	28

α-diversity: vascular plants in quadrats and the summit area sections

For the vascular plants in the quadrats, no interaction effect between summit and year on the number of species was found. This indicates that there was no significant change in species richness on the summits separately throughout the sampling period. Furthermore, no significant change over time in the number of species was found. However, considering the entire data set, the species richness of vascular plants differed significantly between the summits and the aspects of each summit. In other words, altitude as well as aspect have a significant effect on the species richness. For instance, **figure 31** shows that the mean number of species decreased with altitude, ranging from about 7.86 ± 2.24 (S.E.) species per 1 m² quadrat on the lowest summit to only 1.11 ± 0.19 species per 1 m² quadrat on the highest summit.

The change in Shannon diversity index over time was only marginally significant. However, the effect of altitude and aspect on this parameter appeared to be highly significant. In this case, the Shannon diversity index decreased with altitude and ranged between approximately 0.85 ± 0.43 per 1 m² quadrat on the lowest summit and 0.07 ± 0.01 per 1 m² quadrat on the highest summit. Finally, the species evenness of vascular plants showed a significant increase in the quadrats during the period 2001-2015. Also, a significant effect of altitude and aspect on the species evenness was found (**table 6**).
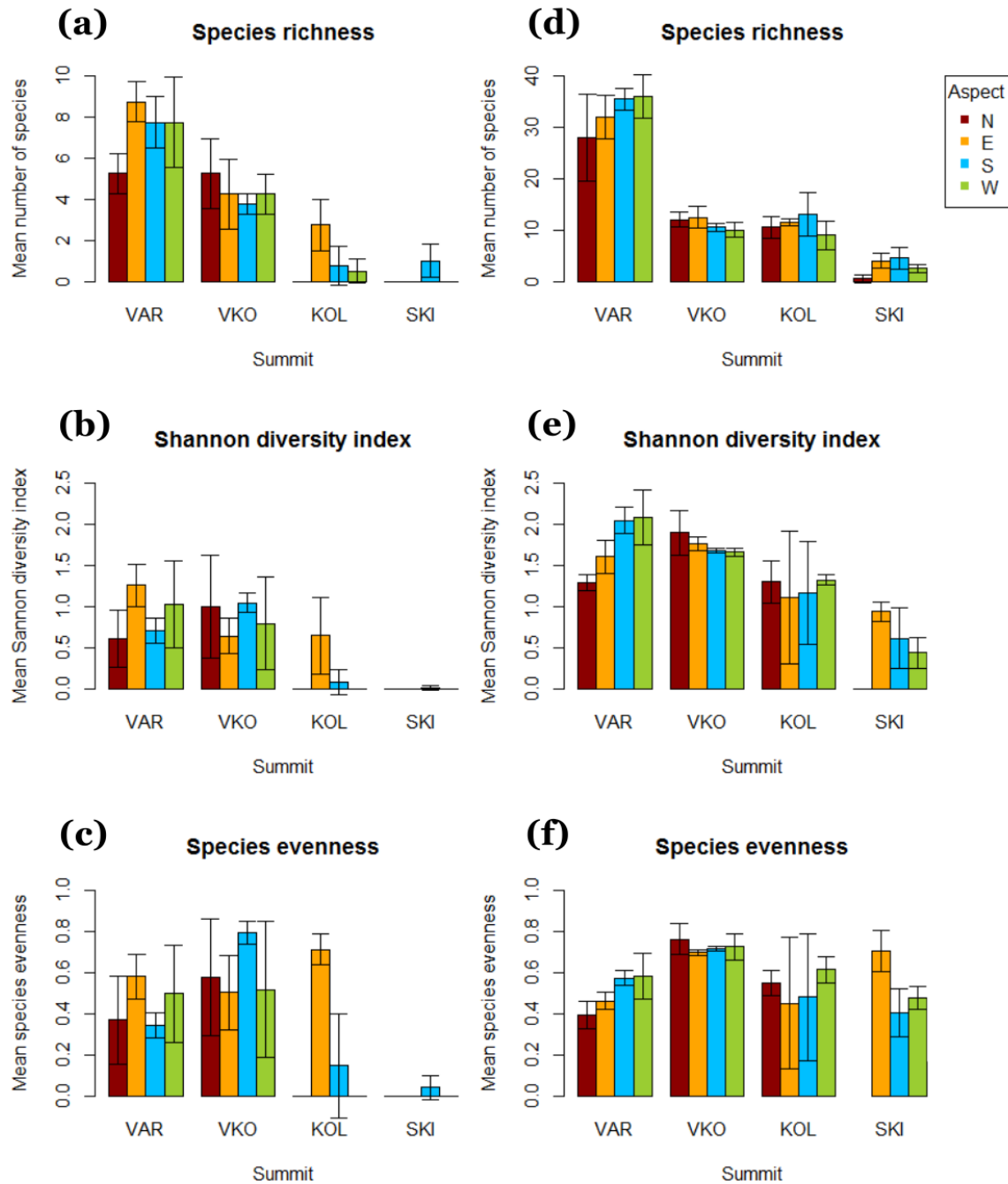
Effect of summit

Effect of aspect
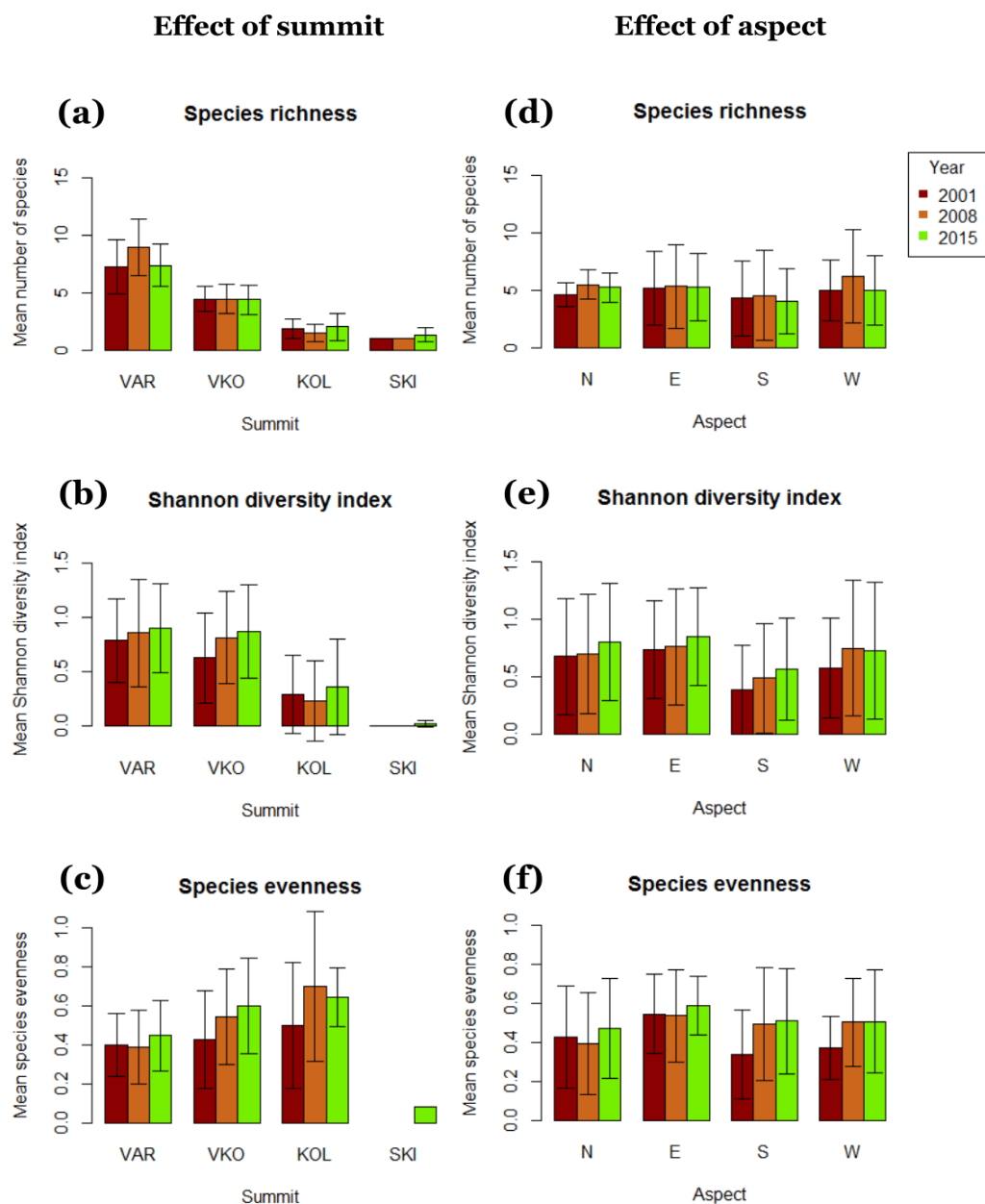
Figure 31: Mean species richness (a, d), Shannon diversity index (b, e) and species evenness (c, f) of vascular plants in the quadrats of the GLORIA summits (left) and the aspects of each summit (right) at Dovrefjell in 2001, 2008 and 2015. The error bars give an indication of the corresponding standard error.

With respect to the vascular plants in the summit area sections, a marginally significant interaction effect between summit and year on the number of species was found. Furthermore, vascular plant species richness in the sections showed a marginally significant increase over time. However, it could be concluded that the number of vascular plant species in these sections differed significantly between the four summits, again indicating a significant effect of altitude on species richness. **Figure 32** shows that the mean number of species ranged between 28.38 ± 7.95 species per section in 2001 and 32.88 ± 5.28 species per section in 2015 on the lowest summit and was therefore much higher compared to the other three summits. For instance, on the highest summit, the number of vascular plant species only ranged between 3.66 ± 1.21 species per section in 2001 and 3.28 ± 1.70 species per section in 2015. In addition, species richness differed between the aspects of the summits as well, with a somewhat higher average amount of species on southern side (about 15.92 ± 12.64 species per section) compared northern side (about 14.63 ± 8.94 species per section) of each mountain.

Similar results were found for the Shannon diversity of the vascular plants in the summit area sections. However, no significant change over time was observed. Furthermore, this diversity index decreased significantly with elevation, ranging from about 1.88 ± 0.30 per section on the lowest summit and 0.60 ± 0.32 per section on the highest summit. Also, the diversity of vascular plants appeared to be higher on the southern aspect compared to the northern aspect of each summit. Finally, for the species evenness of vascular plants in the summit area sections, significant differences were only found between the four summits and the aspects of each summit (**table 6**).

Figure 32: Mean species richness (a, d), Shannon diversity index (b, e) and species evenness (c, f) of vascular plants in the summit area sections of the GLORIA summits (left) and the aspects of each summit (right) at Dovrefjell in 2001, 2008 and 2015. The error bars give an indication of the corresponding standard error.

Table 6: ANOVA results for the effect of the variables summit, aspect (nested within summit), year and the interaction effect between summit and year on the species richness, Shannon diversity index and species evenness of vascular plants in the quadrats and the summit area sections on the GLORIA summits at Dovrefjell. With respect to the significance codes, the following symbols were used: (***) for P < 0.001, (**) for P < 0.01, (*) for P < 0.05 and (.) for P < 0.1.

Effect	Df	SSR	MSR	F-value	P-value
Vascular plant species in the quadrats					
Species richness					
Effect of summit	3	790	263	147	< 2e-16 ***
Effect of Year	1	0.1	0.1	0.058	0.810
Effect of aspect, nested within summit	8	153	19.1	10.6	7.47e-11 ***
Interaction effect between summit and year	3	0.3	0.09	0.052	0.984
Interaction effect between summit, aspect and year	8	5.2	0.64	0.359	0.939
Residuals	105	188	1.79		
Shannon diversity index					
Effect of summit	3	9.36	3.12	24.1	5.81e-12 ***
Effect of Year	1	0.455	0.455	3.52	0.063 .
Effect of aspect, nested within summit	8	6.135	0.767	5.94	2.87e-06 ***
Interaction effect between summit and year	3	0.133	0.044	0.344	0.794
Interaction effect between summit, aspect and year	8	0.176	0.022	0.171	0.994
Residuals	105	13.6	0.129		
Species evenness					
Effect of summit	3	0.643	0.214	5.20	0.002 **
Effect of Year	1	0.234	0.234	5.69	0.019 *
Effect of aspect, nested within summit	8	1.28	0.160	3.90	< 0.001 ***
Interaction effect between summit and year	2	0.062	0.031	0.758	0.472
Interaction effect between summit, aspect and year	7	0.151	0.022	0.525	0.813
Residuals	87	3.58	0.041		
Vascular plant species in the summit area sections					
Species richness					
Effect of summit	3	9801	3267	380	< 2e-16 ***
Effect of Year	1	21	21	2.43	0.124
Effect of aspect, nested within summit	12	499	42	4.84	1.7e-05 ***
Interaction effect between summit and year	3	59	20	2.30	0.088 .
Interaction effect between summit, aspect and year	12	45	4	0.435	0.943
Residuals	60	516	9		
Shannon diversity index					
Effect of summit	3	21	7.01	67.7	<2e-16 ***
Effect of Year	1	0.269	0.269	2.60	0.112
Effect of aspect, nested within summit	12	3.07	0.256	2.47	0.011 *
Interaction effect between summit and year	3	0.204	0.068	0.657	0.582
Interaction effect between summit, aspect and year	12	0.379	0.032	0.305	0.986
Residuals	60	6.22	0.104		
Species evenness					
Effect of summit	3	0.485	0.162	8.89	5.79e-05 ***
Effect of Year	1	0.059	0.059	3.22	0.078 .
Effect of aspect, nested within summit	11	0.321	0.029	1.60	0.121
Interaction effect between summit and year	3	0.040	0.013	0.73	0.540
Interaction effect between summit, aspect and year	11	0.094	0.009	0.47	0.916
Residuals	60	1.091	0.019		

α-diversity: lichens and bryophytes

No significant interaction effect between summit and year on the number of lichen species was found. When looking at the main effects, a significant decrease over time in lichen species richness was observed. In addition, the species richness showed significant differences depending on the altitude and the aspect of the study summits (**table 7**). For instance, a higher number of lichen species was found on Veslekolla and Kolla (**figure 33**).

However, for the Shannon diversity index and species evenness of lichens, a significant interaction effect between summit and year was observed (**table 7**). This indicates that these parameters changed significantly on each of the four summits separately. Lichen species diversity did not change

significantly on Vesle Armodshøkollen and the change in lichen species evenness was only marginally significant. On Kolla, however, a significant increase in lichen species diversity (P < 0.0001) and evenness (P < 0.0001) was found, whereas on Veslekolla and Storkinn no significant change over time in these parameters was noticed. Finally, lichen diversity and species evenness also showed significant differences depending on the aspects of each summit (**table 7**).

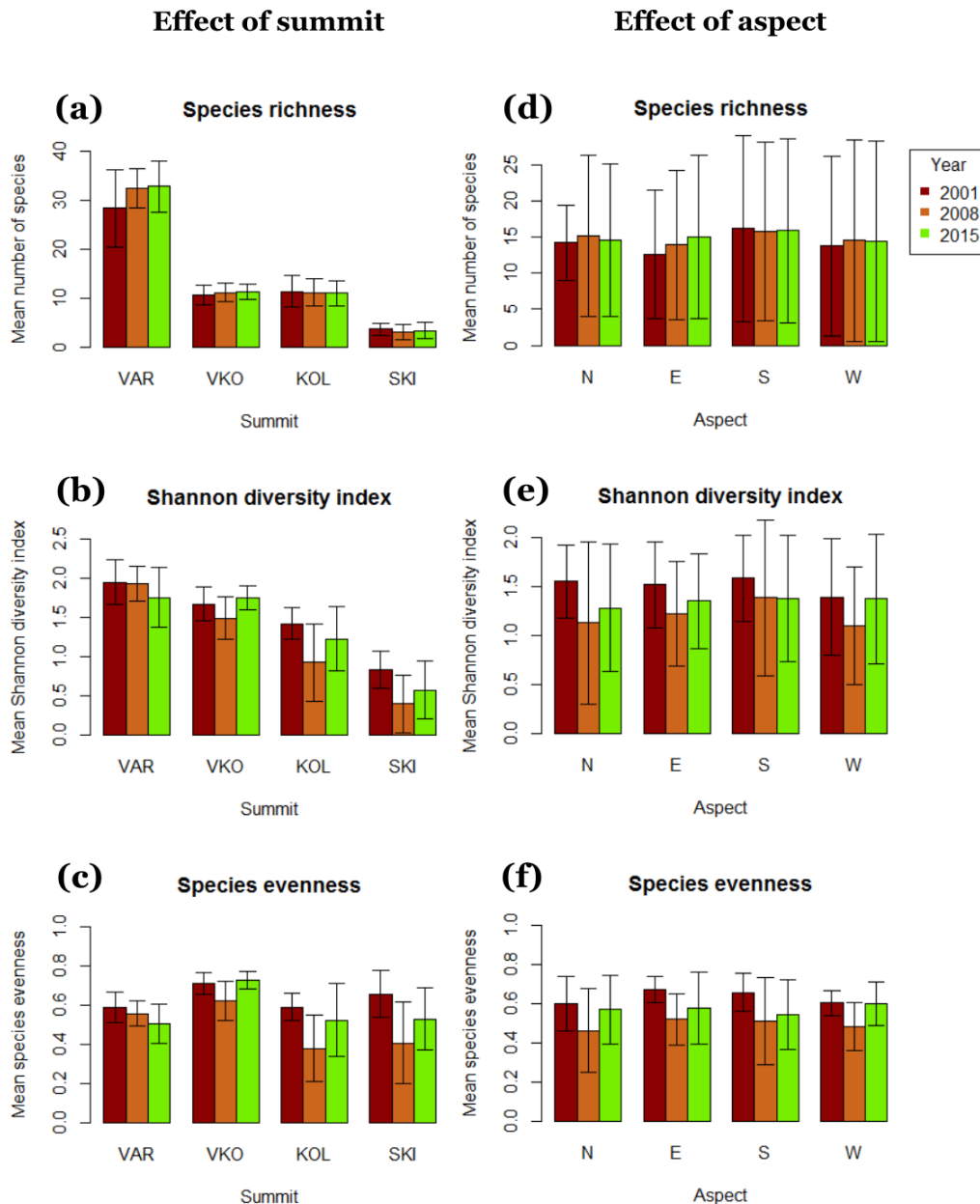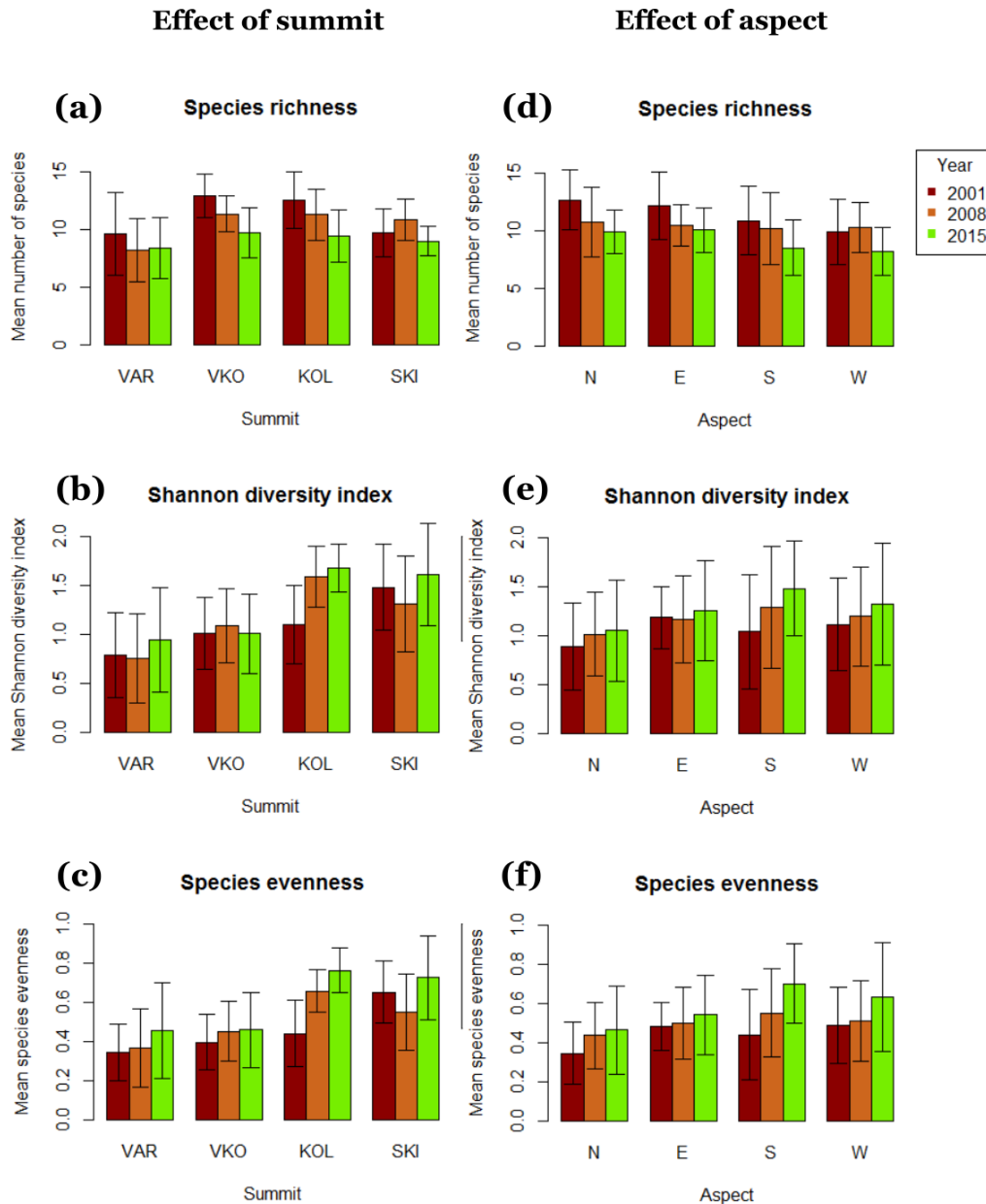**Figure 33: Mean species richness (a, d), Shannon diversity index (b, e) and species evenness (c, f) of lichens in the summit area sections of the GLORIA summits (left) and the aspects of each summit (right) at Dovrefjell in 2001, 2008 and 2015. The error bars give an indication of the corresponding standard error.**

With respect to the bryophytes, no significant interaction effect between summit and year on the species richness was found. However, a significant increase in the number of bryophytes was observed between 2001 and 2015 on the four summits combined. Furthermore, there was a significant difference in the number of bryophyte species between the summits and between the aspects of these

summits. **Figure 34** shows that the mean number of bryophyte species increased with altitude. Moreover, the species richness proved to be slightly higher on the eastern and southern aspects of the study summits. The Shannon diversity index for bryophytes increased significantly over time as well, whereas for the species evenness only a marginally significant change was found (**table 7**).
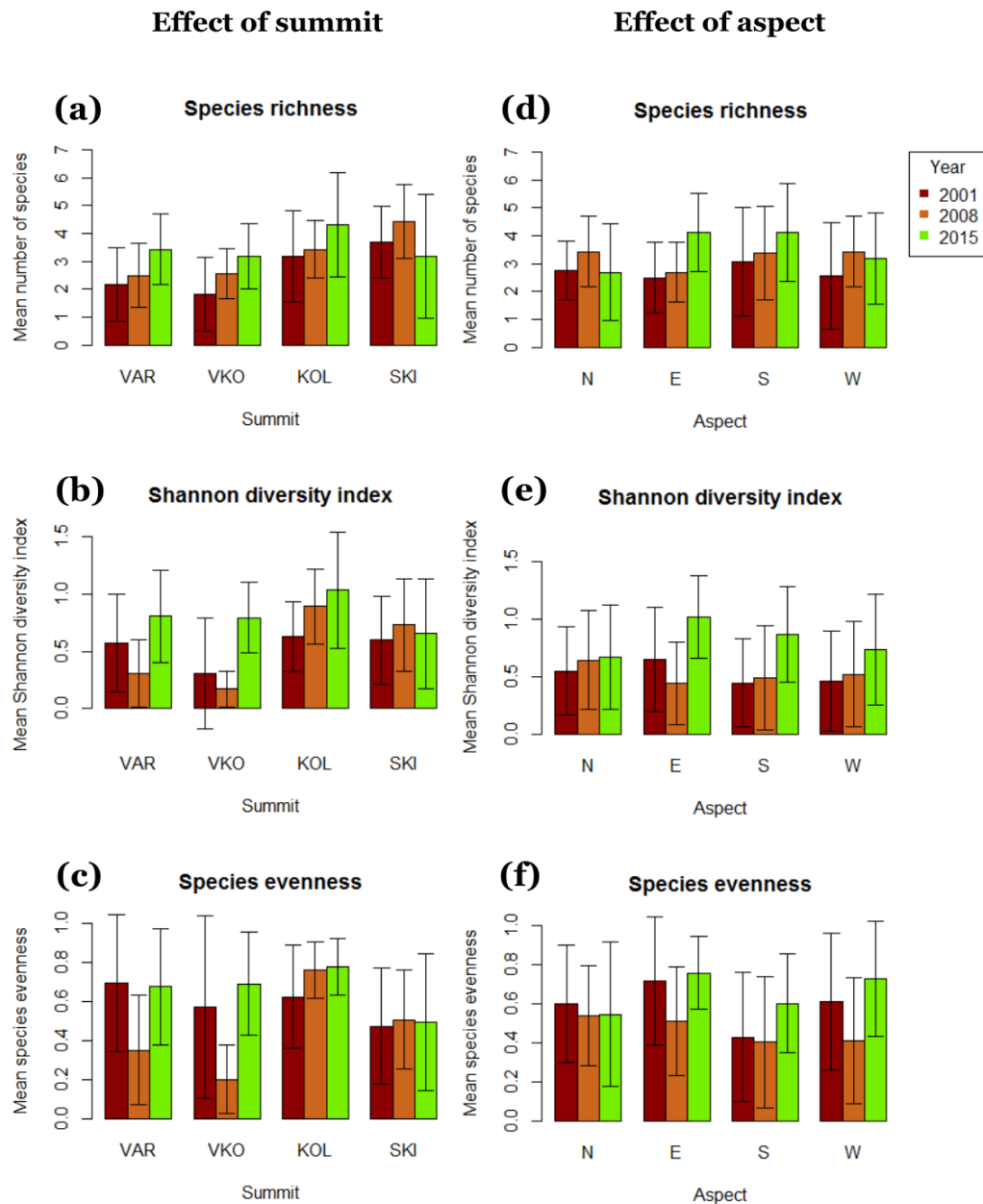
Figure 34: Mean species richness (a, d), Shannon diversity index (b, e) and species evenness (c, f) of bryophytes in the summit area sections of the GLORIA summits (left) and the aspects of each summit (right) at Dovrefjell in 2001, 2008 and 2015. The error bars give an indication of the corresponding standard error.

Table 7: ANOVA results for the effect of the variables summit, aspect (nested within summit), year and the interaction effect between summit and year on the species richness, Shannon diversity index and species evenness of lichens and bryophytes on the GLORIA summits at Dovrefjell. With respect to the significance codes, the following symbols were used: (***) for P < 0.001, (**) for P < 0.01, (*) for P < 0.05 and (.) for P < 0.1.

Effect	Df	SSR	MSR	F-value	P-value
Lichen species					
Species richness					
Effect of summit	3	208	69.2	19.4	1.12e-10 ***
Effect of Year	1	143	143	40.1	2.70e-09 ***
Effect of aspect, nested within summit	11	392	35.7	9.99	1.72e-13 ***
Interaction effect between summit and year	3	35.5	11.8	3.31	0.022 *
Interaction effect between summit, aspect and year	11	22.4	2.03	0.57	0.851
Residuals	150	536	3.57		
Shannon diversity index					
Effect of summit	3	13.6	4.53	36.4	< 2e-16 ***
Effect of Year	1	1.51	1.51	12.1	< 0.001 ***
Effect of aspect, nested within summit	11	10.8	0.98	7.91	9.49e-11 ***
Interaction effect between summit and year	3	1.54	0.51	4.13	0.008 **
Interaction effect between summit, aspect and year	11	1.17	0.11	0.87	0.585
Residuals	150	18.6	0.12		
Species evenness					
Effect of summit	3	2.20	0.733	32.5	3.12e-16 ***
Effect of Year	1	0.656	0.656	29.1	2.66e-07 ***
Effect of aspect, nested within summit	11	1.59	0.145	6.42	1.14e-08 ***
Interaction effect between summit and year	3	0.345	0.115	5.10	0.002 **
Interaction effect between summit, aspect and year	11	0.270	0.025	1.09	0.374
Residuals	150	3.39	0.023		
Bryophyte species					
Species richness					
Effect of summit	3	58.6	19.5	11.3	8.88e-07 ***
Effect of Year	1	21.1	21.1	12.2	< 0.001 ***
Effect of aspect, nested within summit	12	63.3	5.27	3.06	< 0.001 ***
Interaction effect between summit and year	3	18.6	6.21	3.60	0.015 *
Interaction effect between summit, aspect and year	12	38.3	3.19	1.85	0.045 *
Residuals	160	276	1.73		
Shannon diversity index					
Effect of summit	3	4.63	1.54	9.93	4.84e-06 ***
Effect of Year	1	2.82	2.82	18.1	3.50e-05 ***
Effect of aspect, nested within summit	12	2.51	0.209	1.35	0.197
Interaction effect between summit and year	3	0.877	0.292	1.88	0.135
Interaction effect between summit, aspect and year	12	2.55	0.213	1.37	0.186
Residuals	160	24.9	0.156		
Species evenness					
Effect of summit	3	1.58	0.526	6.16	< 0.001 ***
Effect of Year	1	0.233	0.233	2.73	0.101
Effect of aspect, nested within summit	12	2.37	0.197	2.31	0.010 *
Interaction effect between summit and year	3	0.265	0.088	1.034	0.380
Interaction effect between summit, aspect and year	12	0.839	0.070	0.819	0.631
Residuals	142	12.1	0.085		

β-diversity: modified Gower dissimilarity indices for the quadrats

With respect to vascular plants, the highest values for the modified Gower dissimilarity index were noticed for the period 2001-2015. In addition, a significant difference in the modified Gower dissimilarity index was found between the four summits for each period. **Figure 35** illustrates that the dissimilarity index for vascular plant species increased with decreasing altitude. However, only for the period 2008-2015, a significant effect of aspect was observed. Regarding the lichen species, a significant effect of altitude on the dissimilarity index was found as well. Likewise, **figure 35** shows an increase in the dissimilarity index for lichen species as the elevation decreased. In this case, the effect of aspect was only significant for the period 2001-2008. Considering the bryophytes, a

significant difference in the modified Gower dissimilarity index between the summits was observed for the periods 2001-2008 and 2008-2015. The effect of aspect was only significant for the period 2001-2008 and marginally significant for the period 2001-2015. Finally, it could also be concluded that the values for modified Gower dissimilarity index were somewhat higher for vascular plants compared to lichens and bryophytes (**table 8**).
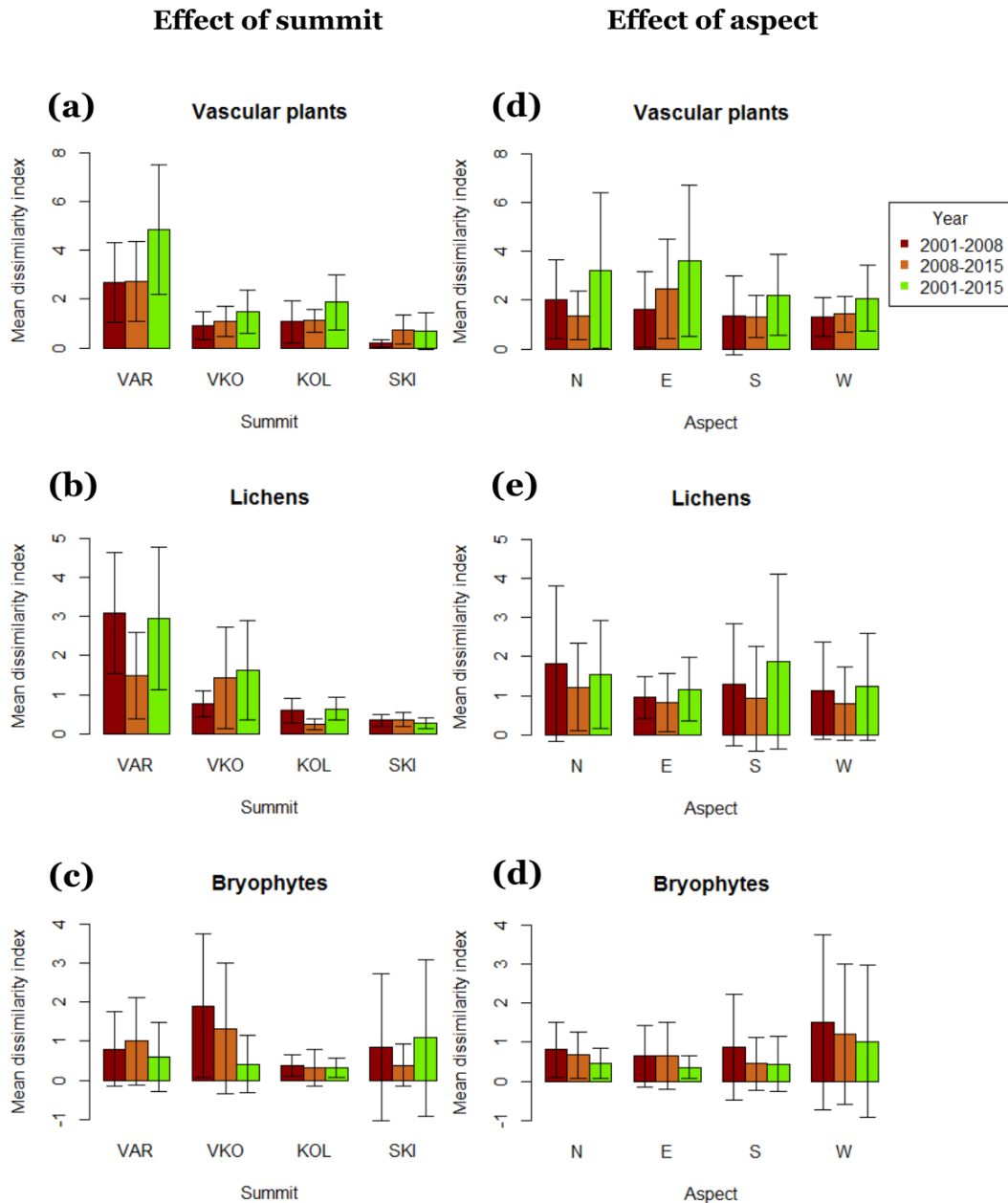

Figure 35: Mean modified Gower dissimilarity index for vascular plants (a, d), lichens (b, e) and bryophytes (c, f) in the quadrats of the GLORIA summits (left) and the aspects of each summit (right) between 2001-2008, 2008-2015 and 2001-2015. The error bars give an indication of the corresponding standard error.

Table 8: ANOVA results for the effect of the variables summit and aspect (nested within summit) on the modified Gower dissimilarity index for the vascular plants, lichens and bryophytes in the quadrats of the GLORIA summits at Dovrefjell. With respect to the significance codes, the following symbols were used: (***) for P < 0.001, (**) for P < 0.01, (*) for P < 0.05 and (.) for P < 0.1.

Effect	Df	SSR	MSR	F-value	P-value
Vascular plant species in quadrats					
Modified Gower dissimilarity index for 2001-2008					
Effect of summit	3	35	11.7	7.84	< 0.001 ***
Effect of aspect, nested within summit	8	4.41	0.55	0.370	0.928
Residuals	31	46.2	1.49		
Modified Gower dissimilarity index for 2008-2015					
Effect of summit	3	28.4	9.46	17	1.04e-06 ***
Effect of aspect, nested within summit	8	31.5	3.94	7.08	2.69e-05 ***
Residuals	31	17.3	0.557		
Modified Gower dissimilarity index for 2001-2015					
Effect of summit	3	116	38.7	13.7	7.16e-06 ***
Effect of aspect, nested within summit	8	40.4	5.05	1.79	0.117
Residuals	31	87.4	2.82		
Lichen species in quadrats					
Modified Gower dissimilarity index for 2001-2008					
Effect of summit	3	74.6	24.9	49.7	2.46e-14 ***
Effect of aspect, nested within summit	11	16.9	1.54	3.07	0.004 **
Residuals	45	22.5	0.500		
Modified Gower dissimilarity index for 2008-2015					
Effect of summit	3	20.3	6.78	8.99	8.9e-05 ***
Effect of aspect, nested within summit	11	10.4	0.95	1.26	0.279
Residuals	45	33.9	0.75		
Modified Gower dissimilarity index for 2001-2015					
Effect of summit	3	64.3	21.4	17.3	1.3e-07 ***
Effect of aspect, nested within summit	11	20.8	1.89	1.52	0.157
Residuals	45	55.8	1.24		
Bryophyte species in quadrats					
Modified Gower dissimilarity index for 2001-2008					
Effect of summit	3	18.7	6.23	4.15	0.012 *
Effect of aspect, nested within summit	11	34.2	3.11	2.07	0.046 *
Residuals	41	61.6	1.50		
Modified Gower dissimilarity index for 2008-2015					
Effect of summit	3	10.1	3.35	3.25	0.032 *
Effect of aspect, nested within summit	11	17.4	1.58	1.53	0.156
Residuals	41	42.3	1.03		
Modified Gower dissimilarity index for 2001-2015					
Effect of summit	3	4.59	1.53	1.48	0.234
Effect of aspect, nested within summit	11	20.2	1.84	1.78	0.089 .
Residuals	41	42.3	1.03		

β-diversity: Species composition

No significant interaction effect between summit and year and between summit, aspect and year on the species composition of vascular plants in the quadrats and the summit area sections was observed. In addition, no significant change over time in species composition of the vascular plants in the quadrats was found. Nonetheless, the species composition proved to be significantly different between the summits and aspects of each summit. Based on the data for the vascular plants in the summit area sections, however, species composition showed a significant temporal change during the period 2001-2015. Also, significant differences in species composition between the summits and the aspects of each summit were observed (**table 9**).

For lichens and bryophytes, a significant interaction effect between summit and year on the species composition was noticed (**table 9**). On Vesle Armodshøkollen, a marginally significant change in the lichen species composition was observed, whereas for the bryophytes a highly significant change over time ($P = 0.001$) was found. On Veslekolla, Kolla and Storkinn, both lichen ($P = 0.001$) and bryophyte

(P= 0.001) species composition changed significantly over time. Finally, species composition of lichens and bryophytes showed significant differences depending on the aspects of the study summits as well (**table 9**).

Table 9: Result from the PERMANOVA analysis with the individual effects of summit, aspect, year and interactions on the species composition of vascular plants, lichens and bryophytes on the GLORIA summits at Dovrefjell during the period 2001-2015. With respect to the significance codes, the following symbols were used: (***) for P < 0.001, (**) for P < 0.01, (*) for P < 0.05 and (.) for P < 0.1.

Effect	Df	SSR	MSR	F-value	R2-value	P-value
Vascular plant species in quadrats						
Species composition						
Effect of summit	3	21	6.99	64.5	0.481	0.001 ***
Effect of Year	1	0.058	0.058	0.531	0.001	0.825
Effect of aspect, nested within summit	8	10.8	1.350	12.5	0.248	0.001 ***
Interaction effect between summit and year	3	0.115	0.038	0.354	0.003	1.000
Interaction effect between summit, aspect and year	8	0.242	0.030	0.280	0.006	1.000
Residuals	105	11.4	0.108		0.261	
Total	128	43.6			1	
Vascular plant species in summit area sections						
Species composition						
Effect of summit	3	18.4	6.13	92.1	0.697	0.001 ***
Effect of Year	1	0.189	0.189	2.83	0.007	0.022 *
Effect of aspect, nested within summit	12	3.09	0.257	3.86	0.117	0.001 ***
Interaction effect between summit and year	3	0.398	0.133	1.99	0.015	0.019 *
Interaction effect between summit, aspect and year	12	0.322	0.027	0.402	0.012	1.000
Residuals	60	4	0.067		0.151	
Total	91	26.4			1	
Lichen species						
Species composition						
Effect of summit	3	9.48	3.16	42	0.304	0.001 ***
Effect of Year	1	2.03	2.04	27.1	0.065	0.001 ***
Effect of aspect, nested within summit	11	6.33	0.575	7.64	0.203	0.001 ***
Interaction effect between summit and year	3	1.26	0.420	5.58	0.040	0.001 ***
Interaction effect between summit, aspect and year	11	0.819	0.074	0.99	0.026	0.517
Residuals	150	11.3	0.075		0.362	
Total	179	31.2			1	
Bryophyte species						
Species composition						
Effect of summit	3	18.9	6.30	29.5	0.29297	0.001 ***
Effect of Year	1	3.38	3.38	15.8	0.05238	0.001 ***
Effect of aspect, nested within summit	11	6.32	0.57	2.69	0.09807	0.001 ***
Interaction effect between summit and year	3	3.07	1.02	4.79	0.0476	0.001 ***
Interaction effect between summit, aspect and year	11	2.92	0.266	1.24	0.04534	0.052 .
Residuals	140	29.9	0.214		0.46363	
Total	169	64.5			1	

Secondly, the change in species composition of vascular plants throughout the sampling period of 2001-2015 could also be investigated using an NMDS plot (**figure 36**). For lichens and bryophytes, the corresponding NMDS plots can be found in **Appendix D**.

Figure 36: NMDS plot for the vascular plant species on the GLORIA summits at Dovrefjell for 2001 (crosses) and 2015 (full circles). The following color code was used to indicate the different study summits: olive green = Vesle Armodshøkollen light brown = Veslekolla, grey = Kolla and black = Storkinn. The grey surface represent a convex hull and encloses the plots or quadrats for each of the GLORIA summits within the study area. The full species names and the corresponding work codes can be found in Appendix F. This figure shows the different plots on the GLORIA summits for both sampling campaigns (2001 and 2015), together with the vascular plant species, plotted along the two principal axis. Plots close to each other are more likely to have a similar species composition than plots further away from each other. In addition, species in the direct vicinity of a plot are more likely to occur within that plot than species further away from it. In addition, the grey surface represent a convex hull and encloses the plots or quadrats for each of the GLORIA summits within the study area.

Thermophilization

A significant difference in the thermic vegetation indicator (*S*) was observed between the four summits and the different aspects of each summit. On the other hand, no significant change in the thermic vegetation indicator between the three different years was found. **Figure 37** illustrates that the highest values for this parameter were calculated for the two lowest summits, whereas Kolla showed significantly lower values. However, judging from **figure 37**, the difference in the thermic vegetation indicator between the different aspects is much less obvious.

With respect to the thermophilization indices (*D*) for the periods 2001-2008 and 2001-2015, a significant effect of altitude and aspect was noticed. However, for the period 2008-2015, no significant effect of summit and only a marginally significant effect of aspect was found. On the one hand, regarding the periods of 2001-2008 and 2001-2015, positive values of the thermophilization dominated at Vesle Armodshøkollen and Veslekolla, whereas negative values were calculated for Kolla. With respect to Storkinn, which is the highest summit, the thermophilization indicator appeared to be negligibly small. Furthermore, the northern aspect obviously showed the highest positive values, followed by the eastern and western aspect. For the southern aspect, however, negative values were observed. Considerably smaller negative values of the thermophilization index of Vesle Armodshøkollen and Veslekolla were found for the period 2008-2015. Also, considering this period, the northern and eastern aspect showed a negative thermophilization index (**table 10**).
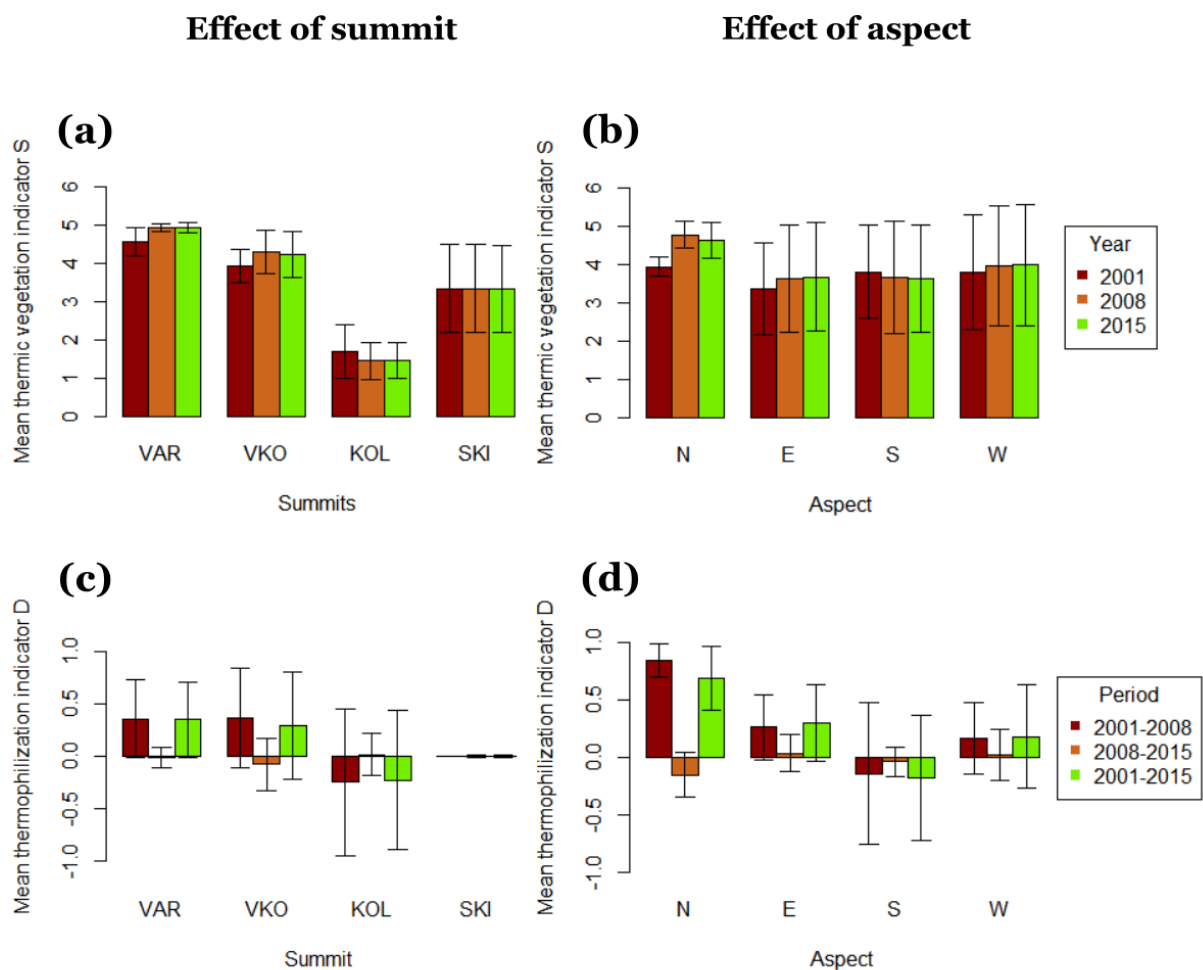

Figure 37: Mean vegetation indicator for the vascular plants in the quadrats of the different GLORIA summits (a) and the aspects of each summit (b) in 2001, 2008 and 2015. Mean thermophilization indicator for the vascular plants in the quadrats of the different GLORIA summits (c) and the aspects of each summit (d) during the period 2001-2008, 2008-2015 and 2001-2015.

Table 10: ANOVA results for the effect of the variables summit, slope, year and the interaction effects on the thermic vegetation indicator *S* and the thermophilization indices *D* for the GLORIA summits at Dovrefjell. With respect to the significance codes, the following symbols were used: (***) for P < 0.001, (**) for P < 0.01, (*) for P < 0.05 and (.) for P < 0.1.

Effect	Df	SSR	MSR	F-value	P-value
Thermic vegetation indicator					
Effect of summit	3	180	60.1	269	<2e-16 ***
Effect of Year	2	1.32	0.660	2.95	0.057 .
Effect of aspect, nested within summit	8	6.27	0.780	3.51	0.001 **
Interaction effect between summit and year	6	1.56	0.260	1.16	0.333
Interaction effect between summit, aspect and year	16	3	0.190	0.839	0.639
Residuals	93	20.8	0.220		
Thermophilization indicator for 2001-2008					
Effect of summit	3	2.55	0.850	6.09	0.002 **
Effect of aspect, nested within summit	8	4.57	0.571	4.09	0.002 **
Residuals	31	4.33	0.140		
Thermophilization indicator for 2008-2015					
Effect of summit	3	0.06	0.020	0.71	0.553
Effect of aspect, nested within summit	8	0.48	0.060	2.13	0.063 .
Residuals	31	0.88	0.028		
Thermophilization indicator for 2001-2015					
Effect of summit	3	2.07	0.690	4.22	0.013 *
Effect of aspect, nested within summit	8	3.96	0.495	3.03	0.012 *
Residuals	31	5.07	0.163		

For the lichen species, a significant difference in the thermic vegetation indicator (*S*) was noticed between the four study summits (P < 0.001) and between the different aspects (P < 0.001) of these summits. Furthermore, this indicator decreased significantly over time (P = 0.020) on the four summits combined. For the thermophilization indicator (*D*), no significant effect of altitude was found, except for the period 2008-2015, where thermophilization increased with elevation (P = 0.034). Also, no significant effect of aspect was observed for the three periods. **Figure 38** shows that, for the period 2001-2008, generally negative values for thermophilization indicator of the lichen species were found, whereas smaller positive values were observed for the period 2008-2015. This fluctuation was more pronounced on the two highest summits and on the southern and western aspects.

For the bryophytes, a significant difference in the thermic vegetation indicator (*S*) was noticed between the four study summits (P < 0.001) and between the different aspects (P < 0.001) of these summits as well. This indicator also increased significantly over time (P < 0.001) across the four summits. Furthermore, for the thermophilization indicator (*D*) of the bryophytes, no significant differences between the four study summits and between the aspects of each summit were noticed. **Figure 38** shows a positive thermophilization indicator for Veslekolla and Storkinn during the period 2001-2015. For Vesle Armodshøkollen and Kolla, however, the thermophilization indicator approached a value of zero. In addition, a positive thermophilization indicator was found for all aspects for the period 2001-2015.
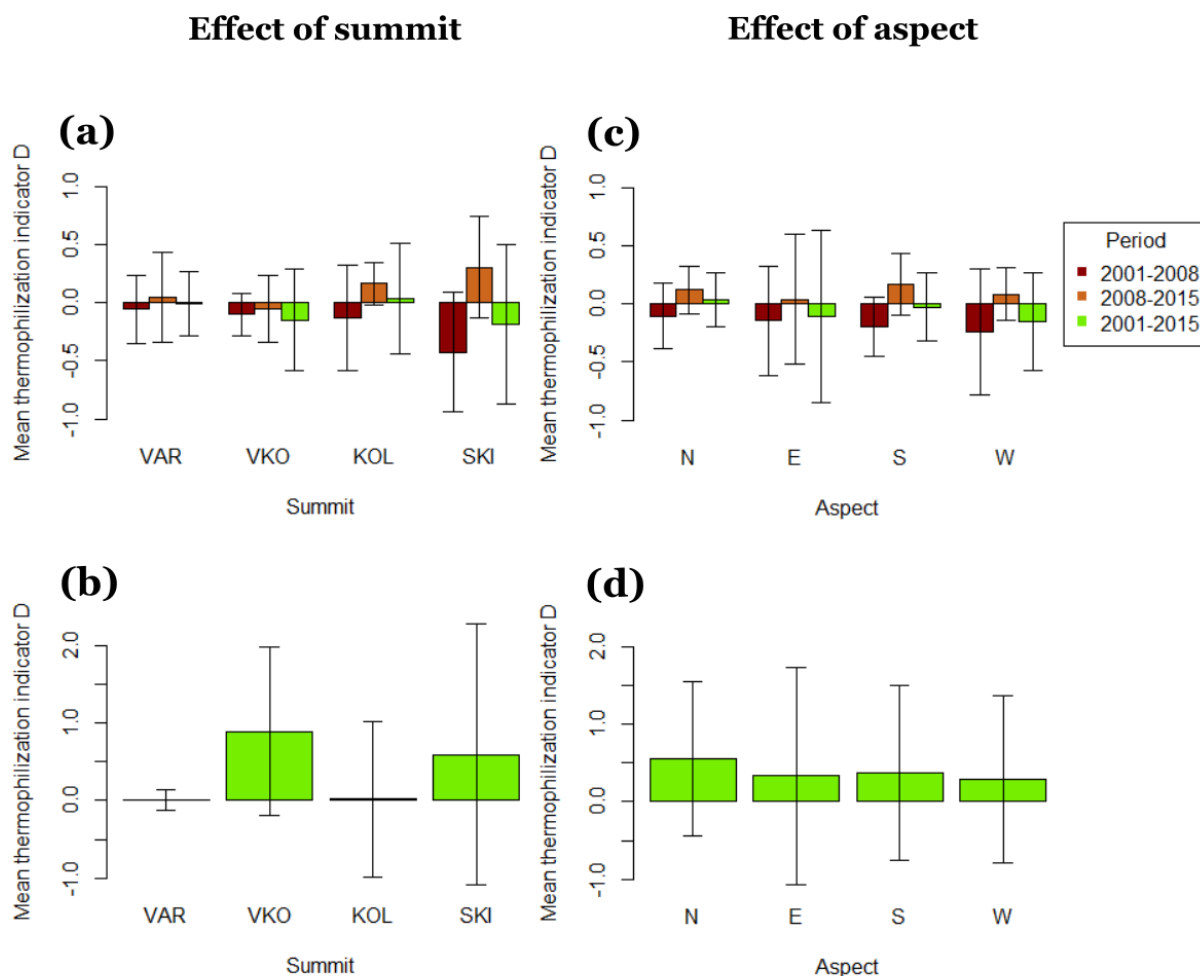
Figure 38: Mean thermophilization indicator in the quadrats of the GLORIA summits (a, b) and the aspects of each summit (c, d) for the lichens (top) and the bryophytes (bottom) during the period 2001-2008, 2008-2015, 2001-2015.

Responses of individual species

With respect to the vascular plants, three dwarf shrubs (*Betula nana*, *Vaccinium uliginosum* and *Vaccinium vitis-idea*) and two graminoids *(Festuca ovina* and *Juncus trifidus)* showed a significant increase in cover. For lichen species, a decreasing cover percentage was observed for *Cladonia arbuscular*, *Ochrolechia sp.* and *Umbilicaria sp.*, whereas an increasing cover percentage was found for *Bryocaulon divergens*, *Thamnolia vermicularis*, *Lophozia cf. ventricosa*. Finally, bryophyte species like *Polytrichum juniperinum* showed an increasing cover (**table 11**). Furthermore, two interesting vascular plant species showed a highly significant decrease in the number of hits from the point intercept method, namely *Campanula rotundifolia* (P = 0.0191) and *Salix herbacea* (P = 0.0007).

Some vascular plant species were recorded for the first time on the study summits at Dovrefjell. At Vesle Armodshøkollen, species like *Comastoma tenellum*, *Corallorhiza trifida*, *Erigeron sp.*, *Geranium sylivaticum*, *Luzula confusa*, *Silene acaulis* and even a conifer tree like *Pinus sylvestris* were added to the list. In addition, at Veslekolla, the dwarf shrub *Arctous alpinus*, the herb *Hieracium sp.* and the graminoid *Luzula confusa* appeared for the first time. At the two highest summits (Kolla and Storkinn), species like *Antennaria dioica* and *Empetrum nigrum* and *Poa sp.* respectively made their entrance.

Table 11: Vascular plant (V), lichen (L) and bryophyte (B) species with a significant change in cover percentage on the GLORIA summits at Dovrefjell between the period 2001-2015. The P-values are from linear mixed effect models.

Species	Taxonomic groups	Change in mean cover percentage (%)	P-value
Betula nana	V	+3.06	0.041
Festuca ovina	V	+0.442	< 0.001
Juncus trifidus	V	+0.184	< 0.001
Vaccinium uliginosum	V	+0.084	0.039
Vaccinium vitis-idea	V	+0.532	0.022
Bryocaulon divergens	L	+0.305	< 0.001
Cladonia arbuscula	L	-0.553	0.025
Ochrolechia sp.	L	-0.373	< 0.001
Pseudephebe sp.	L	-1.72	0.011
Thamnolia vermicularis	L	+0.063	0.002
Umbilicaria sp.	L	-1.35	<0.0001
Anthelia sp.	B	+0.118	< 0.001
Lophozia cf. ventricosa	B	+0.075	0.020
Pogonatum sp.	B	+0.116	0.009
Pohlia sp.	B	+0.078	<0.0001
Polytrichum juniperinum	B	+0.458	0.030

Finally, some of the vascular plant species at Dovrefjell were only recorded on a single study summit. As a result, these species are typical and unique for the different vegetation zones along the elevational gradient (**table 12**). For instance, some herb species like *Campanula rotundifolia* and *Geranium sylvaticum* were only found on the lowest summit (low alpine zone). Other species, like *Ranunculus glacialis*, *Festuca vivipara* and *Eriophorum scheuchzeri* were constraint to higher altitudes (middle and high alpine zone).

Table 12: Unique vascular plant species for each of the GLORIA summits at Dovrefjell in 2015.

| Summit	Unique vascular plant species
VAR	*Antennaria alpine, Anthoxantum odoratum, Arctostaphylos uva-ursi, Astragalus alpinus, Astragalus frigidus, Astragalus norvegicus, Bartsia alpine, Betula nana x pubescens, Betula pubescens, Bistorta vivipara, Campanula rotundifolia, Carex atrata, Carex rupestris, Carex vaginata, Cerastium alpinum, Comostoma tenellum, Corallorhiza trifida, Diphadiastrum alpinum, Draba glabella, Epilobium angustifolium, Erigeron sp., Euphrasia sp., Geranium sylvaticum, Juniperus communis, Kobresia mysuroides, Luzula multiflora, Melampyrum pretense, Oxytropis lapponica, Pedicularis lapponica, Pedicularis oederi, Pinguicula vulgaris, Poa pratensis, Potenilla crantzii, Primula scandinavica, Pulsatilla vernalis, Salix glauca, Salix philicifolia, Salix reticulate, Saussurea alpine, Saxifraga oppositifolia, Silene uralensis, Solidago virgaurea, Vaccinium myrtillus, Viola biflora*
VKO	*Diapensia lapponica, Hieracium sp.*
KOL	*Agrostis mertensii, Ranunculus glacialis, Cardamine bellidifolia, Festuca vivipara, Harrimanella hypnoides, Trisetum spicatum*
SKI	*Eriophorum scheuchzeri, Poa flexuosa*

Discussion

Temporal changes in climate

A significant decrease in the mean annual soil temperature was found for the temperature loggers on the summits at Dovrefjell during the period 2001-2015. This negative trend was even more obvious during the period 2008-2015. Similar results were found for the minimum and maximum soil temperature on the study summits. However, the sampling period of 15 years is still quite short and temperature measurements on a long time scale are required in order to get the broader picture. Nonetheless, this downward trend in temperature was also observed during the last ten years of the long-term temperature record (1900-2014) for the weather station of Gammel-Fokstugu. Furthermore, at a global scale, an apparent slowdown or *hiatus* in global warming has been observed since the start of the 21st century (Easterling & Wehner, 2009; Foster & Rahmstorf, 2011; Kosaka & Xie, 2013; Karl et al., 2015) (**figure 39**).
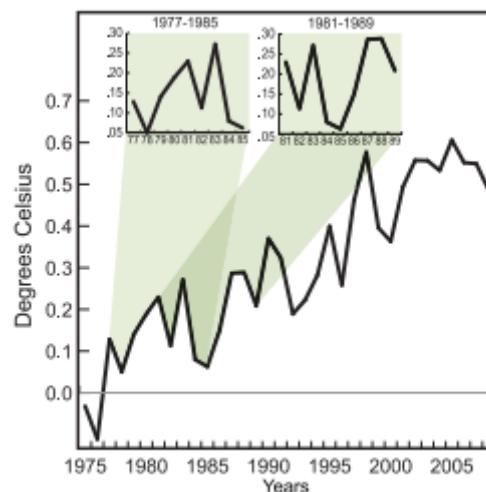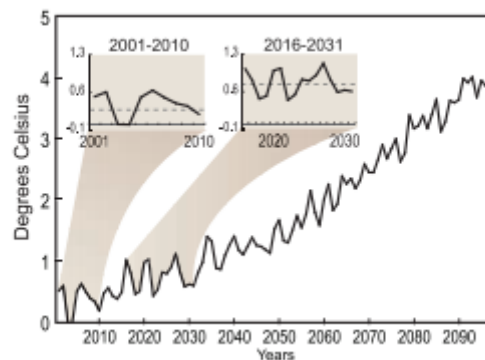

Figure 39: Globally averaged surface air temperature for land and ocean based data sets during the period 1975-2008. Note the apparent hiatus in global warming between 2000 and 2010 (Easterling & Wehner, 2009).

The global mean surface temperature experienced a significantly smaller increasing trend during the period 1998-2012 compared to the past 30 or 60 years (IPCC, 2013). A wide range of mechanisms were proposed for causing this phenomenon, but most of these theories are still being debated (Solomon et al., 2011; Kaufmann et al., 2011; Meelh et al., 2011; Kosaka & Xie, 2013). Easterling and Wehner (2009) concluded that several short periods of no warming or even cooling occurred superimposed on the long-term warming trend throughout the last century. These temperature plateaus, also referred to as *cooling spells*, are mainly caused by naturally-occurring fluctuations in the global climate and generally last for a few decades. Next to variations in the solar activity (Lean & Rind, 2009) and fluctuations in stratospheric water vapor content (Solomon et al., 2010) and tropospheric aerosols (Kaufmann et al., 2011), the El Niño - Southern Oscillation[23] (ENSO) can be addressed as one of the possible drivers for these natural fluctuations (Easterling & Wehner, 2009). In the aftermath of an El Niño event, an unusual increase in the sea surface temperature can be observed

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[23] ENSO is a naturally occurring phenomenon with a profound influence on winds and sea surface temperatures over the tropical Pacific Ocean. The warming phase (El Niño) is periodically alternated by a cooler period (La Niña). This process drives global rainfall patterns, surface air temperature, river discharge, agricultural production, ecosystems, tropical cyclones, etc. (Holbrook et al., 2012).

for the eastern tropical Pacific. This has substantial effects on the global temperatures as well. As result of an exceptional El Niño, the year 1998 was one of the warmest on record since 1850. This outlier in the overall warming trend gave the appearance of a slowdown in the warming rate during the period 1998-2008. However, after removing this outlier from the data set, Easterling and Wehner (2009) observed a significant temperature increase between 1999 and 2008. Moreover, Karl et al. (2015) performed an updated global surface temperature analysis, casting serious doubt on the existence of a slowdown in global warming. They concluded that the warming rate during the last 15 years was at least as high as the last half of the 20th century. In other words, the general scientific consensus still remains indefinite. On a longer time scale, however, the global trend in surface temperatures is still significantly positive and has even been projected to increase in the future (**figure 40**).

Figure 40: Projected globally averaged surface air temperature for the period 2000-2100 using the ECHAM5 coupled climate model with the SRESA greenhouse gas increase scenario for the 21st century (Easterling & Wehner, 2009).

With respect to the period 2001-2015, a significant negative trend was also found for the annual summer temperatures on the GLORIA summits. However, for the winter temperatures, a significant increase was observed, especially during the past five years. These observations correspond with the current consensus on climate change, predicting maximum warming trends driven by anthropogenic forcings in the higher latitudes of the Northern Hemisphere during winter (Cohen et al., 2012). Moreover, climate-change scenarios previously indicated a significantly higher warming trend during winter in Northern Europe and during summer in Southern and Central Europe (IPCC, 2007). This increase in winter temperatures exerts a major impact on natural ecosystems, especially in mountainous areas. Changes in the winter climate go hand in hand with alterations in snowfall which is considered as one of the most prevailing environmental factors in alpine ecosystems (Wipf et al., 2009). On a short time scale, changes in the timing of snowmelt and alterations in the depth and duration of snow cover influences plant growth and phenology (Walker et al., 1993). In the longer run, vegetation composition might be affected as well (Welch et al., 2005). In the scope of this hypothesis, Wipf et al. (2009) studied the species-specific effect of an earlier snowmelt and decreasing snow depth on alpine tundra plants in the Swiss Alps. As a result of an earlier snowmelt and the subsequent increasing susceptibility to frost damage (Inouye et al., 2002; Inouye, 2008), three of the four studied dwarf shrub species experienced a significant decrease in aboveground growth. However, *Loiseleuria procumbes* appeared to benefit from the advanced snowmelt and can be considered as a specialist for wind exposed growing areas with little snow cover.

A significant difference in the mean soil temperature was observed among the four summits. This can be attributed to the fact that temperatures generally decrease with increasing elevation. As a result, higher summits will be subjected to lower temperatures and a shorter snow-free period. However, no

significant temperature differences were found depending on the aspect. Nonetheless, it can be assumed that the temperatures on the northern mountainside will be somewhat lower compared to the other mountain aspects since this side receives considerably lower inputs of solar radiation on a daily basis.

Despite the apparent slowdown in the temperature increase at Dovrefjell, lag effect of past changes in climatic conditions on vegetation should be taken into account when attempting to explain the observed changes in vegetation. Various studies have already indicated a lag between the contemporary climate change and subsequent biotic responses of plants and animals (e. g. Doak & Morris, 2010; Lenoir et al., 2008). For instance, Doak and Morris (2010) found that two North American tundra species (*Silene acaulis* and *Polygonum viviparum*; both also occurring at Dovrefjell) showed compensatory changes in demographic rates (e.g. higher individual growth rates), buffering southern populations against the negative impact of climate warming and slowing their northward range shifts. Alpine and Arctic plants are mostly long-lived (de Witte & Stoecklin, 2010) and the internal processes in plant communities occur at a slow rate (Körner, 2003). Therefore, changes in the distribution of alpine plants will show a distinct trend over time rather than inter-annual variability. In addition, a wide variety of alpine plants (e.g. *Salix herbacea*, *Empetrum nigrum*, *Carex bigelowii*, etc.) are characterized by slow-responding traits such as clonal growth. Clonal reproduction enhances longevity of these plant species and thus affects community stability and vegetation responses to present and future climate warming (de Witte & Stoecklin, 2010). Therefore, possible changes in plant species richness and composition that are presently recorded in mountain areas, might be a delayed effect of climate warming during the last decades of 20th century. Long life spans and clonal reproduction strategies also enable mountain plant species to retard extinction and persist in local climate conditions that are already unsuitable for their long-term survival. Hence, a fairly modest future loss in the distribution area of alpine high-mountain flora (on average 44 to 50 % by the end of the 21st century) is predicted. These results, however, warn against drawing over-optimistic conclusions since the final impact of climate change on mountain plants is delayed by a number of decades (Dullinger et al., 2012).

Nonetheless, other studies found contrasting results. For example, Kelley and Goulden (2008) observed rapid shifts in the distribution of mountain vegetation in Southern California, USA, as a response to climate warming, at least in areas where the dispersal of species is not a major constraint. These findings are also supported by Cannone et al. (2007) for alpine and nival belts in the European Alps. Furthermore, the magnitude of the lag effects also depends on the intensity of climate warming, which differs strongly between lowland and highland areas. Bertrand et al. (2011) compared temperature trends to temperature records reconstructed from plant assemblages during a 44-year period in France. In this study, both floristically (i.e. temperature trends reconstructed from observed alterations in plant assemblages) and climatically (i.e. temperature trends reconstructed from instrumental records and climatic models) reconstructed temperatures were determined. In the period before contemporary climate warming (1965-1986), only small differences between the floristically and climatically reconstructed temperatures were observed, indicating changes in plant community composition close to the magnitude of climate change. However, larger differences were found during the current climate warming period (1987-2008), suggesting that the warming-induced reshuffling in plant communities lags behind climate change and providing evidence for a rather slow recovery of the climate-flora equilibrium. This difference was observed for both lowland and highland areas. However, in lowland forests temperature lags between climate and plant community composition were much more obvious (**figure 41**). This could be attributed to the greater velocity of climate change in lowland areas (Loarie et al., 2009), the higher proportion of species with a greater ability for local

persistence (Thuiller et al., 2005), a lower opportunity for short-distance range shifts (Jump et al., 2009) and a greater habitat fragmentation.

In order to create more certainty on the existence of lag effects in the response of vegetation to climate change at Dovrefjell, more long-term observation data are required. Moreover, other climatic parameters such as relative air humidity, the amount of snowfall and atmospheric CO_2 concentrations have a substantial effect on plant productivity and species composition as well and are believed to shape the overall response of species to changes in the mean climate. However, the effects of these parameters were not quantified for this research as local data, with the desired spatial and temporal resolution, were not available.
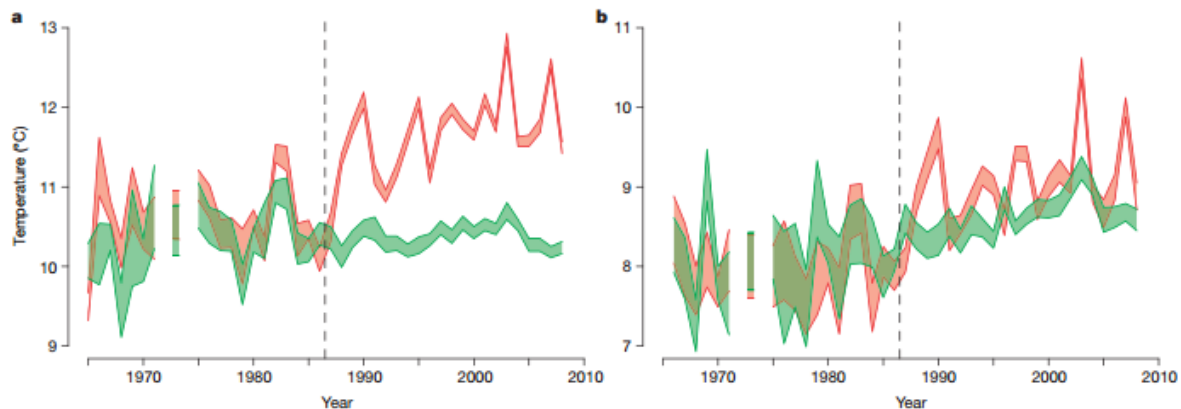

Figure 41: Comparison of the floristically (green) and climatically (red) reconstructed temperature trends during the period 1965-2008 for lowland (a) and highland (b) forest plant communities. The dashed line indicates the start of the present-day climate warming period (1987-2008) (Bertrand et al., 2011).

Vegetation analysis

Changes with elevation and aspect (2015)

Vascular plants

A significant decrease in species richness and diversity of vascular plants was observed with increasing altitude. The highest species richness was noticed on the lowest summit, located in the lower alpine belt, and declined considerably towards the middle and high alpine belt. Many theories have already been proposed in order to explain the variation in species distribution and species richness with elevation (Whittaker, 1972; Palmer, 1994; Nagy et al., 2003). Particularly gradients in biotic and abiotic conditions in mountainous areas are considered to have a substantial potential to explain species distributions and species richness patterns (McCain & Grytnes, 2010). In addition, space availability, species interactions and productivity play a significant role as well.

At a broad scale, the relationship between species richness and productivity is often monotonically positive (Mittelbach et al., 2001) (**figure 42**). In mountain ecosystems, the linear decrease in temperature with increasing elevation (approximately 0.6 °C for every 100 m) exerts a considerable influence on the pool of potential species that are able to thrive in the increasingly extreme conditions. As elevation increases, the species pool size and species richness commonly declines. Hence, local species communities at a higher elevation consist of small samples of the regional species pool (Bruun et al., 2006). This theory is known as Huston's productivity or temperature-physiography hypothesis (Huston, 1999). Microrelief is expected to play a significant role as well, as it affects habitat-type

richness (Nagy et al., 2003). Theurillat et al. (1998) stated that habitat-type richness generally decreases with increasing elevation as the potential growth area diminishes and the slope of the terrain increases. Moreover, a steeper terrain is more susceptible to erosion which in turn promotes the convergence of habitats. Winter length also increases substantially at higher elevations, leading to a reduction in fluvial and an increase in periglacial[24] phenomena. Consequently, landscape homogenization is enhanced at higher altitude and habitat-type richness is decreased.

On a local scale, both biotic factors (i.e. a declining migration of ubiquitous species with increasing elevation) and abiotic factors play a significant role in determining the patterns of species richness along the elevational gradient (Bruun et al., 2006). In particular, these patterns prove to be the result of two apparently opposing driving forces, namely a diminishing species pool and a decreasing competition intensity with elevation. Therefore, a *humped-back* relationship between species richness and productivity was found at finer scales (Mittelbach et al., 2001). In more productive lowland areas, species pools are generally larger, but species richness is restricted by competitive exclusion[25]. At an intermediate elevation, local species richness increases and reaches a maximum value as the negative impacts of a diminishing species pool size are counterbalanced by the positive impacts of a relaxed competition. At higher elevations, however, local species richness decreases again as a result of biotic depauperation (Bruun et al., 2006) (**figure 42**).
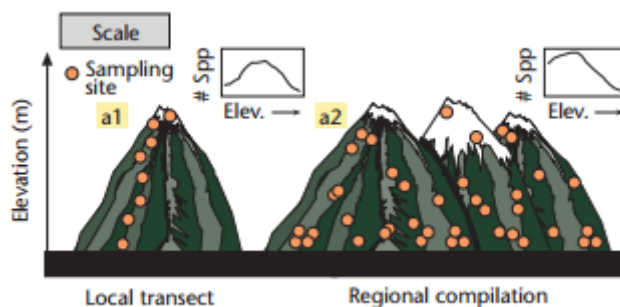
Figure 42: Patterns of plant species richness along an elevational gradient for a local transect on a single summit (a1) and a regional compilation of summits (a2) (McCain and Grytnes, 2010).

Another possible explanation for the higher species richness on the lowest summit is the difference in the composition of bedrock. Vesle Armodshøkollen mainly consists of a calcareous bedrock (Michelsen et al., 2011). This type of parent material is known to be high in nutrients which in turn could potentially support a higher productivity and vascular plant species richness (Rey Benayas & Scheiner, 2002; Virtanen et al., 2003). This hypothesis is also supported by Pausas and Carreras (1995) and by Rey Benayas and Scheiner (2002) in the eastern Pyrenees, observing the highest mean local species richness on calcareous bedrock types.

In addition, a significantly higher species richness and diversity of vascular plants was observed on the southern aspect compared to northern aspect of the summits. The higher biotic richness of south-facing aspects was more apparent with respect to the species diversity. In general, south-facing slopes receive higher daily inputs of solar radiation compared to north-facing slopes. As a result, temperature, soil moisture, nutrients and soil aggregation processes are affected. This has a substantial effect on local vegetation as well (Klemmedson & Wienhold, 1992; Sternberg & Shoshany, 2000). Northern

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[24] Periglaciation is a typical geomorphological process in tundra environments resulting from seasonal thawing of snow in areas with permafrost. As a result, the ground surface is continuously modified due to the displacement of soil material, groundwater flow, etc. (Pidwirny, 2006).

[25] Competitive exclusion means that two species competing for the same resource cannot coexist at constant population values, provided that all other ecological factors remain constant. On the longer term, one of the two competitors - with only the slightest advantage - will always dominate the other (Palmer, 1994).

aspects, on the one hand, typically provide more favorable abiotic conditions which in turn favors the dominance of certain species, especially perennials with a competitive advantage over annuals. South-facing slopes, on the other hand, are marked by more extreme conditions, in particular higher temperatures, lower soil moisture contents and more severe climate fluctuations. Consequently, small changes in the surface cover of nearby soil patches are commonly associated with considerable differences in vegetation characteristic, among others species richness and diversity (Kutiel, 1994; Nevo, 1995; Kutiel, 1999). With respect to the summit area sections, this significant effect of aspect on species richness and diversity was not found. However, this can be attributed to the fact that these sections cover a much larger area of the summit and are not exactly facing the cardinal directions at all points.

Some highly significant differences in the distribution of individual species were observed along the elevational gradient. Certain vascular plant species were only found on one of the study summits, whereas other species were recorded in the entire study area. For instance, herb species like *Bartsia alpina*, *Bistorta vivipara*, *Cerastium alpinum*, *Epilobium angustifolium*, *Geranium sylvaticum*, etc. and shrub species like (*Betula nana x pubescens* and *Juniperus communis*) were restricted to the lowest summit. These species are generally warm-adapted and have an optimal performance in the treeline ecotone or the low alpine zone. Other vascular plant species like *Diapensia lapponica*, *Ranunculus glacialis*, *Carex bigelowii*, *Cardamine bellidifolia, Huperzia selago* and *Trisetum spicatum* only occurred in the transition zone between the low and the high alpine zone. Species like *Eriophorum scheuchzeri* and *Poa flexuosa* were restricted to the highest summit and high alpine zone. These are typical high-altitude species which are adapted to the extreme environmental conditions such as low temperatures, high radiation intensities, desiccating winds and poor resource availability. In addition, most of these species are marked by a rather narrow altitudinal range and are therefore more prone to extinction as a result of changing environmental conditions. Other species, however, are characterized by a wide altitudinal range, e.g. *Salix herbacea*, occuring over a vertical range of about 1600 m (Nagy et al., 2003). At Dovrefjell, this dwarf shrub species was found an each of the four study summits, along with the shrub *Empetrum nigrum*. These species are commonly widespread or *ubiquitous*, which means they are adapted to a wide range of environmental conditions. Species like *Festuca ovina*, *Juncus trifidus*, *Phyllodoce caerulea* and *Vaccinium vitis-idea* were recorded in both the low and the middle alpine vegetation belt. These species are adapted to a broader range of environmental conditions as well, but they cannot cope with the extreme abiotic environment in the high alpine zone where freezing temperatures prevail during most parts of the year.

Lichens and bryophytes
For the lichen species richness, this significant altitudinal effect was observed as well. However, no clear linear trend along the elevational gradient could be found. On the one hand, the intensity of competition between lichen and vascular plant species decreases with increasing elevation. Hence, lichen species will be less affected by shading and more space becomes available for colonization. This hypothesis is supported by Virtanen et al. (2013), suggesting that lichens (and bryophytes) are better adapted to extreme mountain conditions and are therefore more susceptible to competition for light. On the other hand, fewer lichen species are able to cope with the extreme abiotic conditions at higher elevations. Also, the impact of herbivorous mammals (especially reindeer) on lichen communities also declines above a certain altitude (Oksanen, 1980). These factors have an opposing effect on the species richness of lichens and might explain the lack of a trend along the elevational gradient. Bruun et al. (2006) observed a peak in macrolichen species richness in northernmost Fennoscandia at about 400 m vertically above the treeline (250-1525 m a.s.l.) and a decreasing lichen

species richness at higher altitude. This peak could be attributed to small, heliophilic[26] Arctic-alpine specialists that are easily outcompeted by more competitive plants in the low alpine zone. For the lichen species evenness, a significant increase was noticed with elevation. At the lowest summit, lichen cover was dominated by species like *Cladonia stellaris* which typically forms continuous mats over relatively large areas. This could account for the lower lichen species evenness at a lower altitude.
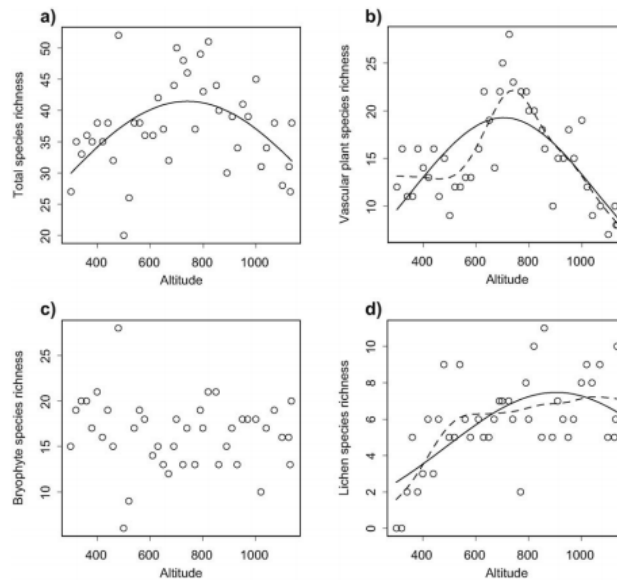
Figure 43: Scatterplots of relationship between species richness and altitude for total number of species (a), vascular plants (b), bryophytes (c) and lichens (d) in a mountain ecosystem in western Norway, approximately 300 km from our study area (Grytnes et al., 2006).

With respect to the bryophytes, a slight increase in species richness with elevation was found. This corresponds with Bruun et al. (2006), who also found an increasing trend for the richness of bryophytes and liverworts along the altitudinal gradient. In other words, the distribution patterns of bryophytes with increasing elevation clearly deviates from the temperature-physiography hypothesis. Nagy et al. (2003) concluded that the distribution of bryophytes at lower elevations depends to a large extend on the presence of special microhabitats or *refugia*, e.g. trunks, rivulets and humid or shaded rocks. Therefore, species richness of bryophytes at a lower elevation will be less affected by the temperature gradient compared to the vascular plants. At higher altitude, however, microhabitats follow the processes as described by the temperature-physiography hypothesis.

Bryophytes are also known for their ability to survive in extreme climates, such as Antarctica and the High Arctic islands (Virtanen et al., 1997), and typically benefit from a so-called pioneer strategy (Bruun et al., 2006). Hence, bryophytes respond positively to the increased amount of bare mineral soil at higher elevations. Moreover, a greater number of suitable microhabitats for epilithic and epiphytic[27] bryophyte species could be found at higher altitude. Nonetheless, another study by Grytnes et al. (2006) in western Norway reported that bryophytes mainly respond to fine-scale environmental changes and heterogenity. Fine-scale differences in moisture conditions and random variations in the type and number of local microhabitats have a much larger effect on bryophyte communities (**figure 43**). For this reason, it becomes more difficult to predict a coherent pattern in bryophyte species richness along the elevational gradient.

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[26] Heliophilic species are adapted or attracted to sunlight (Schulze, 2005).

[27] Epiphytic species grow non-parasitically on the surface of other plants (Nash, 2012).

Changes over time (2001-2015)

Vascular plants

No significant change in the species richness of vascular plants was found during the period 2001-2015. Of course, the sampling period of 15 years is still relatively short and a further increase in species richness could be expected as a consequence of future climate warming. Various studies already indicated this upward distribution shift and increased species richness of alpine vegetation in European mountain areas during the 20th century (e.g. Grabherr et al., 1994; Pauli et al., 2007; Parolo & Rossi, 2007; Holzinger et al., 2008). For instance, Holzinger et al. (2008) found an increase in vascular plant species richness of about 11 % per decade in the alpine-nival ecotone of several summits in the Alps. Moreover, this study reported an upward migration rate within the range of several meters per decade, which corresponds to those previously observed by Grabherr et al. (1994).

Lenoir et al. (2008) even found a warming-induced upward shift in the optimum elevation range of vascular plant species averaging 29 m per decade. This shift was even more significant for species with an optimal performance in mountain habitats and grass species, which are generally marked by faster population turnover. Significant changes in species richness were observed over shorter time periods as well. For example, Pauli et al. (2007) reported that the mean number of species per square meter increased by approximately 11.8 % at Mount Schrankogel, Austria, during the period 1994-2004. Moreover, Walther et al. (2002) concluded that this overall trend of upward movement is accelerating over time. A recent article by Wolf et al. (2016) in California, USA, also reported a substantial difference in the upward range shift of species with different naturalization statuses. About 12 % of the endemic taxa showed a significant upward distribution shift, whereas a much larger proportion (27 %) of the introduced taxa shifted upward during the last century. However, in this case, the upward movement of naturalized invasive species may not be attributed to climate warming, but more likely to the expansion of these non-native species in a secondary environment. Nonetheless, as these species are continuously invading their preferred climatic niches, changes in climatic conditions will potentially extend or accelerate the rate of their spread. These findings highlight the importance of taking into account the interaction factors of climate-induced changes in vegetation and the invasion of new species.

Similar results were noticed in Scandinavian mountain areas (e.g. Klanderud & Birks, 2003; Kullman, 2007). Klanderud & Birks (2003) observed an upward distribution shift and increase of species richness in the Jotunheimen mountain range, Norway, over a period of 68 years, primarily on the lower summits. These altitudinal advances were most prominent for lowland species, dwarf shrubs and species with a wide ecological range. Some studies also noticed a higher increase in species richness in the transition zone between the alpine and nival ecotone than in the adjacent vegetation belts (e.g. Grabherr et al., 1994; Walther et al., 2004; Pauli et al., 2007; Erschbamer et al., 2008). Moreover, Felde et al. (2012) found that species with a preference for lower temperatures showed a larger upward range shift compared to species preferring higher temperatures in a mountain ecosystem in Sikkilsdalen, central Norway (**figure 44**). However, these altitudinal differences in the increase of vascular plant species richness and upward range shifts over time were not found on the summits at Dovrefjell.

Lichens and bryophytes

For the lichen species, a decrease in species richness was detected over time at Dovrefjell. This trend is consistent with Elmendorf et al. (2012) and Virtanen et al. (2003) and can be attributed to the increased competition of vascular plants due to climate warming. According to this hypothesis, a

potential increase in temperature at high elevations might contribute to a higher biomass production of vascular plants, which in turn creates more shade. Particularly in low-altitude environments, where shrub encroachment appears to be most significant, severe reductions in lichen abundance were observed over time. Furthermore, only on Kolla, a significant increase in lichen diversity and species evenness was noticed. A possible explanation would be that the change in environmental conditions over time was most pronounced on Kolla compared to the other summits. In addition, compared to Kolla and Storkinn, a higher modified Gower index and, therefore, stronger turnover of lichen species was observed on the two lowest summits (**figure 35**). This could explain why the number of lichen species on the two lowest summits remained relatively constant over time. On Storkinn, however, no significant change in lichen species evenness was found, despite the lower turnover. This could be attributed to a wide range of factors, such as the more extreme environment, a reduced accessibility by herbivores and especially the cold summer of 2015. Moreover, the increased lichen diversity and species evenness at Kolla could also be related to an altered interaction with vascular plants under climate warming. However, this topic requires further investigation, as studies on a species level of non-vascular plants are often lacking and a comparison with the results of other research remains difficult. Finally, observation and determination errors during the field work cannot be ruled out, e.g. whether or not epilithic lichen species - which are predominantly occurring on Kolla - were included during monitoring.
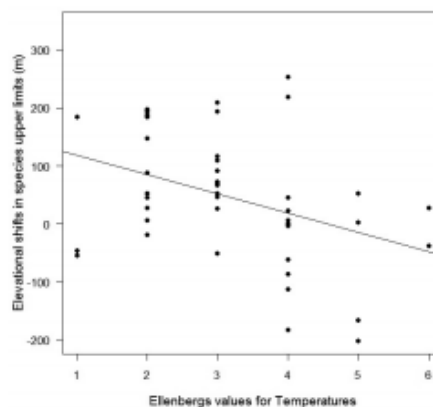
Figure 44: Changes in upper altitudinal limits of vascular plants in function of the Ellenberg values for temperature (Felde et al., 2001).

With respect to the bryophytes, an increase in species richness was observed over time, especially on the lower summits and on the eastern and southern aspects of these summits. Previous studies found mixed effects of climate change on bryophytes in mountainous ecosystems (e.g. Lang et al., 2012). These contrasting response patterns have been largely attributed to competitive interaction between cryptogams and vascular plants and their adaptation to light competition (Alatalo, 1998). For instance, bryophyte species previously showed highly different responses to shading effects (Jägerbrand & During, 2005).

According to Hassel et al. (2012), bryophyte cover and species richness will potentially decline in the future as a consequence of climate warming and the subsequent increased shading and litter deposition by vascular plants. This study predicted a considerable warming-induced effect on bryophyte communities with the highest increase in water stress or with altered snow accumulation patterns. However, an increase in the intensity and frequency of precipitation, which in turn increases local humidity, might level out this effect. On the other hand, Bergamini et al. (2009) found a significant

mean increase in altitude of cryophilous[28] bryophyte species with approximately 24 m per decade in the Swiss Alps. On a longer term, this upward distribution shift might lead to an increased species diversity at higher elevations.

Species composition

Species composition of vascular plants in the quadrats and the summit area sections also differed significantly between the four summits. This can be attributed to the fact that each summit was selected within a different vegetation zone along the elevational gradient. Each vegetation zone is marked by different environmental conditions (e.g. temperature, humidity, soil composition, solar radiation, etc.) with a distinctive effect on the pool of species with an optimal performance in that specific zone. Vascular plant communities in the treeline ecotone and low alpine belt are commonly covered by a close vegetation carpet which is dominated by alpine meadows, heaths and dwarf shrubs. At a higher elevation, vegetation becomes more subjected to frost and desiccating winds. In the alpine vegetation belt, vascular plants generally occur in patches and at locations which provide sufficient shelter from heavy winds. This zone is typically, occupied by patchy grassland, sedges and rush heats. In the nival belt and close to the limits of plant survival, snow cover occurs during a large part of the year and vegetation is strictly limited to a few rare alpine species that are adapted to the extreme environmental conditions (Nagy & Grabherr, 2009).

A significant effect of aspect on species composition of vascular plants in the quadrats and the summit area sections was noticed as well. On the one hand, south-facing slopes typically contained more light-loving species which are resistant to the lower soil moisture supply. On the other hand, northern aspects are characterized by lower inputs of solar radiation and a higher resource availability. This effect was previously demonstrated by Kutiel (1993) in Mediterranean mountain ecosystems, reporting a higher abundance of annual herbaceous plants on south-facing slopes.

In addition, species composition of vascular plants changed significantly over time in the summit area sections of all four summits. This change can be attributed to the increased cover of shrubs like *Betula nana* (3.06 %), dwarf shrubs like *Vaccinium uliginosum* (0.084 %) and *Vaccinium vitis-idea* (0.532 %) and graminoids like *Festuca ovina* (0.442 %) and *Juncus trifidus* (0.184 %), especially at lower elevations. These findings are consistent with Klanderud and Birks (2003), also indicating an increasing cover of local lee-slope species (e.g. *Avenella flexuosa*, *Vaccinium myrtillus*, *Vaccinium uliginosum*, *Phyllodoce caerulea* and some *Salix* species) in Jotunheimen, Norway, not only at elevations where they already occurred, but also towards a higher altitude. Furthermore, typical species of exposed ridges (e.g. *Juncus trifidus*, *Luzula spicata*, *Festuca vivipara* and some *Carex* species) expanded their range within the study area. Also, shrubs like *Empetrum nigrum* and dwarf shrubs like *Vaccinium uliginosum* and *Vaccinium myrtillus* showed the largest response over time. Their upward range shift could be largely attributed to an increase in both the length of the snow-free period and the length of the growing period due to the ongoing climate change. Moreover, these species mainly belong to mesophilous heaths and are expected to invade snow beds together with other lee-slope species as the duration of snow cover gradually decreases. These observation were also made by Bahn and Körner (2003), reporting that graminoids, dwarf shrubs and viviparous and hemiparasitic species showed the largest increase in cover in the Austrian Alps over a period of about 13 years. In addition, they made notice of a distinctive shrub invasion of grasslands by *Vaccinium uliginosum* in the alpine vegetation belt.

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[28] Cryophilous species generally prefer and thrive in cold envirnoments (Schulze, 2005).

At Dovrefjell, the shrub species *Betula nana* showed the most substantial change in cover percentage with an increase of about 3 % over a period of 15 years. This rate is similar to the one reported by Cannone et al. (2007), who found an average increase in the cover of shrubs and dwarf shrubs of approximately 1.9 % per decade, with the highest expansion rates in the alpine vegetation belt. According to this study, dwarf shrubs which are typical for windswept areas (e.g. *Loiseleuria procumbens, Vaccinium uliginusum* and *Vaccinium vitis-idea*) showed an increase in cover as a response to a shorter snow cover season. Alpine grassland experienced an upward migration as well, replacing the gradually disappearing snow beds (**figure 45**). However, on the study summits at Dovrefjell, this increase was only found for the two *Vaccinium* species.

Finally, lichens and bryophytes also showed a significant change in species composition over time. According to a climate-warming experiment by Elmendorf et al. (2012) and a field study in Alaska by Chapin et al. (1995), lichen species generally respond with a decrease in cover to warming temperatures. Most probably, this could be mainly attributed to the expansion and eventual overgrowth of lichen species by vascular plants, especially dwarf shrubs. However, the interaction with other abiotic and biotic factors such as reindeer grazing could not be ruled out (Cornelissen et al., 2001). This decrease in cover was also observed at Dovrefjell for *Cladonia arbusculata* and *Umbilicaria*, *Ochrolechia* and *Pseudephebe* species. Moreover, another study by Trivedi et al. (2008a) confirmed that lichens associated with montane heaths (e.g. *Cladonia arbuscula* and *Cladonia uncialis*) are expected to lose suitable bioclimatic change as a result of climate warming. For the bryophytes, Jägerbrand et al. (2012) found a negative effect of the increasing abundance of deciduous and evergreen shrubs in heath areas. Moreover, bryophyte species are characterized by the absence of true roots, which makes them more susceptible to a water deficiency in a warmer, drier environment (Potter et al., 1995). These factors might explain the change in bryophyte species composition over time.
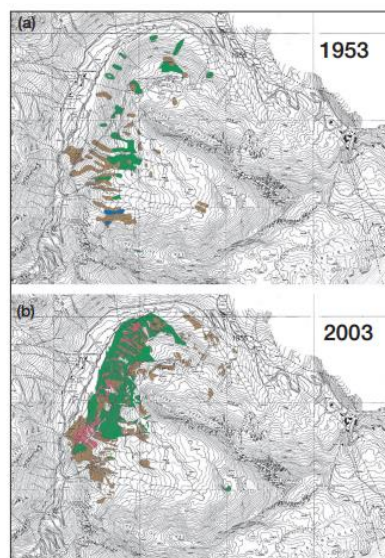
Figure 45: Shrub distribution on the Stelvio Pass, central Italian Alps in 1953 (a) and 2003 (b). Color codes: brown = dwarf shrub association (*Loiseleurietum-Cetrarietum*), green= mosaic between dwarf shrubs and alpine grassland, blue = mosaic between dwarf shrubs and snowbeds, magenta = alpine shrub association (*Rhodoreto-Vaccinietum*) (Cannone et al., 2007).

The highest values for the modified Gower dissimilarity index of vascular plants were noticed for the period 2001-2015. For the periods 2001-2008 and 2008-2015, relatively similar values for the dissimilarity index for vascular plants were found on all summits, except Storkinn. In other words, species composition of vascular plants in the quadrats experienced a much larger change over the entire sampling period of 15 years compared to the two sub-periods. This is in line with Gottfried et al.

(2012), stating that alpine plants are long-lived (de Witte & Stoecklin, 2010) and the internal processes in plant communities occur at a slow rate (Körner, 2003). Hence, species cover will show a distinct trend over time rather than inter-annual variability. This statement supports the hypothesis of a lag-effect in the response of vegetation to climate warming and might also explain why changes in species richness and distribution are still being observed at Dovrefjell despite the current absence of a clear upward trend in temperature.

In addition, the modified Gower dissimilarity index for vascular plants and lichens decreased with increasing elevation. This indicates that the species composition altered to a much larger extent at a lower elevation, namely in the treeline ecotone and low alpine zone. At higher altitude, especially near the limits of plant life, species composition largely remained unchanged over time. This could also be attributed to the prominent invasion of shrubs and dwarf shrubs at lower elevations which was previously observed in other mountain areas by Bahn and Körner (2003) in Austria and Cannone et al. (2007) in Italy. As a result of this increased cover of shrubs, lichens are gradually overgrown which in turn also explains the highest change in lichen species composition at a lower altitude. Moreover, Michelsen et al. (2011) concluded that the lowest study summit at Dovrefjell contained more potential invaders and a larger number of species with the ability to respond to environmental changes over time by expanding or diminishing their cover. This study also showed that temperature changes and the subsequent warming-induced effect on vegetation were more pronounced at the two lowest summits during the period 2001-2008.

Thermophilization

The significant effect of altitude on the thermic vegetation indicator of vascular plants can be attributed to the fact that each summit was selected in a different vegetation zone along the elevational gradient. As a result, these summits each contain typical species with an optimum performance in that specific vegetation zone. For instance, the lower summits generally contain warm-adapted species with an optimum performance in lower positions along the altitudinal gradient, especially in the treeline ecotone or alpine zone, and are marked with a higher altitudinal rank. Consequently, lower summits generally have a significantly higher thermic vegetation indicator. However, the lowest values were found for Kolla, which is only the second highest summit. In the quadrats of Kolla, generally cold-adapted species with a low altitudinal rank were found, namely *Carex bigelowii* (2), *Luzula arcuata* (2), *Ranunculus glacialis* (1), *Salix herbacea* (3) and *Saxifraga cespitiosa* (2), whereas in the quadrats of Storkinn, only two vascular plant species were recorded, including *Huperzia selago* with a high altitudinal rank (4). Furthermore, a higher amount of warm-adapted species and higher thermic vegetation indicator is expected for the southern aspect since this side of the mountain receives substantially higher inputs of solar radiation on a daily basis and has therefore a higher temperature. On the other hand, quadrats on the northern aspects are expected to contain more cold-adapted species which results in a lower higher thermic vegetation indicator. This hypothesis is only confirmed for the lowest summit.

With respect to the thermophilization indicator of the vascular plants, positive values were found for the two lowest summits during the period 2001-2008. These results indicate the occurrence of thermophilization (i.e. the decline in the abundance of cold-adapted species and the increase in the abundance of thermophilic species in mountain ecosystems) and might result from an increased cover and/or migration of species with a higher rank and a lower elevational range (thermophilic species) and/or the decline of species with a lower rank and a higher elevational range (cryophilic species). These results are in line with Gottfried et al. (2012), reporting an upward shift in the distribution of

vascular plants in European mountain ecosystems and a transformation in the magnitude of approximately 5 % of one vegetation belt after only seven years.

On the other hand, no thermophilization of vascular plants was observed for the highest summit, whereas a negative thermophilization indicator was found for Kolla. According to Gottfried et al. (2012), thermophilization of alpine plant communities mirrors the degree of warming and is therefore more distinct in locations with a higher increase in temperature. Moreover, Michelsen et al. (2011) observed a significant temperature increase at Dovrefjell in nine logger time series during the period 2001-2008, especially on the two lowest summits, which in turn explains the altitudinal differences in the thermophilization indicator. Thermophilization was also more pronounced for the northern aspect of the summits. In other words, this mountainside is marked by a stronger abundance increase of thermophilic species over time. These observation can probably also be explained by a higher warming rate compared to the other aspects. In addition, northern-facing slopes generally contain more cold-adapted species due to lower daily temperatures. Consequently, the effect of thermophilization will be more significant as these species disappear out of their current distribution range. For the period 2008-2015, generally small negative values were found for the thermophilization indicator of vascular plants, indicating the absence of thermophilization. These results can be attributed to the fact that during this period no upward temperature trends were observed and most of the logger time series even showed a significant decrease in soil temperature. Most probably, this is the reason why thermophilization temporarily slowed down at Dovrefjell after the summer of 2008.

In general, lichens showed less thermophilization than the vascular plants. Cryptogams, such as lichens and bryophytes, typically produce a large number of tiny sexual or asexual spores which can easily become airborne and disperse over larger distances. As a result, lichens and bryophytes commonly have a higher dispersal ability compared to seed plants (Lenoir et al., 2011), which in turn improves their ability to track the upwards shifting isotherms (Fuller et al., 2015). Local alpine lichen species will hence likely experience a greater upward distribution shift than vascular plants, which might enable the population to persist in a warmer environment and counteracts the increasing dominance of fast-growing, thermophilic species.

Also, thermophilization of lichens occurred primarily between 2008 and 2015. This is somewhat contrasting with the observations for the vascular plants, as indicated by the slowing down of the thermophilization during that period. Moreover, the amount of thermophilization generally mirrors the degree of warming (Gottfried et al., 2012). However, no warming (even cooling) was observed at Dovrefjell between 2008 and 2015. Hence, the increased dominance of warm-adapted lichen species during that period can probably be attributed to other factors (e.g. N deposition). In fact, lichens are considered to be highly sensitive to N deposition and typically show a declining abundance along gradients of increased N loads. In particular, epiphytic lichens experience a severe decline in diversity under high N deposition (Johansson et al., 2012). Fast-growing, warm-adapted lichen species, on the other hand, might persist under higher nutrient conditions. Nonetheless, a possible lag effect in the response of lichens to the increased temperatures from a previous period cannot be ruled out. Furthermore, thermophilization of lichen species during the period 2008-2015 was greater on the two highest summits. These summits are particularly constraint by low temperatures and small changes in the environmental conditions might induce substantial shifts in local plant communities. For this reason, thermophilization will probably be more pronounced at higher elevations, mainly due to the disappearance of light-demanding and slow-growing cold-adapted species.

Finally, for the bryophytes, no thermophilization was noticed on Vesle Armodshøkollen and Kolla between 2001 and 2015. In other words, the bryophyte community did not experience any changes over time on these summits. Most probably, this can be attributed to the low turnover of bryophyte species during the sampling period (**figure 35**). On Storkinn and Veslekolla, however, a somewhat

higher turnover of bryophytes was observed, which in turn could explain the positive thermophilization index. The thermophilization indicators for the periods 2001-2008 and 2008-2015 were not included in the analysis due to unrealistic results. Most likely, these errors can be attributed to an uncertain determination of bryophyte species during the survey of 2008.

Other possible drivers of the observed vegetation changes

Climate change is only one of the possible drivers of the observed changes in vegetation at Dovrefjell during the period 2001-2015. Other factors (e.g. grazing, trampling, N deposition and natural succession) might play a significant role as well. These factors and their predicted influence on alpine plant communities is described in the following paragraphs. However, it seems most likely that the observed changes are the result of an interaction between a wide range of factors, among others climate warming and plant-herbivore interactions.

According to Gaare (1997), extensive lichen mats, like the ones on Vesle Armodshøkollen, are commonly formed in Norwegian mountain ecosystems by a small group of perennial fruticous lichen species (e.g. *Flavocetraria nivalis*, *Cladonia stellaris* and *Stereocaulon paschale*). These lichen mats catch most water from small precipitation events, thereby causing serious water shortage problems for vascular plants. However, after decomposition, these lichen species add humus to the topsoil, hence increasing the soil water storage capacity. Grazing of herbivores creates large holes in the lichen mats, thereby increasing soil erodibility. As a result, the humus layer erodes over time, leaving only the coarse gravel particles, which severely reduces the water holding capacity of the topsoil. On the other hand, reduced grazing contributes to a gradual buildup of soil humus which in turn enhances the soil water storage capacity. Hence, vascular plants are enabled to compete with and eventually replace lichen species. In the long run, this increased competition could account for the observed invasion and expanding cover of shrubs, dwarf shrubs and graminoids in Arctic and Alpine tundra ecosystems.
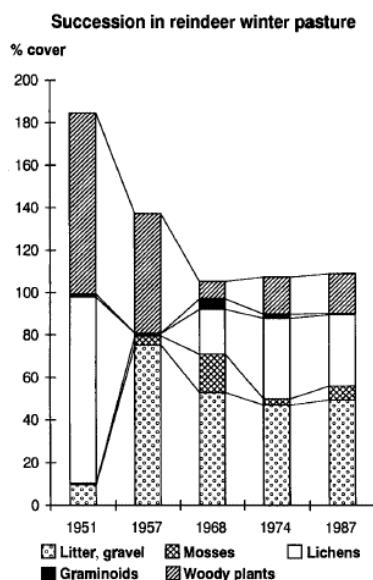
Figure 46: Recovery of winter pastures (percentage cover of litter, gravel, graminoids, mosses, wordy plants and lichens) in the Snøhetta mountain range after the population high in the 1950s (Gaare 1997).

Michelsen et al. (2011) reported that Vesle Armodshøkollen presumably experiences little or even no grazing by sheep and reindeer populations. According to Gaare (1997), reindeer grazing considerably declined in the areas around Vesle Armodshøkollen as a consequence of the railway construction in 1921. This anthropogenic barrier divided the Snøhetta range, thereby temporarily preventing the use of

the natural east-west migration route by the small reindeer population. Despite the presence of this railway and a parallel highway, former migration routes were re-established when the local reindeer population started to grow again (Skogland & Mølmen, 1980; Skogland, 1986). According to the local residents, these routes were frequently used for spring and autumn migration during the period 1957-1983. However, the use of the eastern winter ranges subsequently declined and has not been reported ever since 1985. As a result, grazing pressure from reindeer was restricted in that area before the first analysis in 2001 which could have created excellent conditions for the establishment of a soil humus layer and the predicted increase in cover of vascular plants at the expense of lichens (Michelsen et al., 2011) (**figure 46**).

Michelsen et al. (2011) also proposed that the difference in the tolerance to grazing between coexisting shrub species can be addressed as a possible indicator for the observed changes in a plant community over time. For instance, according to a study by Pajunen et al. (2008) in a forest-tundra ecotonal area in northwestern Finnish Lapland, the total cover of vegetation, along with the cover and height of shrubs, dwarf shrubs, forbs and grasses, increased significantly after an 8-year exclusion of grazing reindeer (**figure 47**). More specifically, willow shrubs that are commonly preferred by reindeer (e.g. *Salix glauca* and *Salix phylicifolia*) experienced a substantial increase in cover. This was consistent with previous studies in Arctic-alpine ecosystems (e.g. Quellet et al., 1994; Manseau et al., 2004). In addition, the cover of *Betula nana* increased in the absence of reindeer grazing, primarily in low-productive tundra heaths. In more productive habitats, the effect of exclosures on *Betula nana* seemed much less obvious and depended to a large extent on small-scale habitat heterogeneity. Furthermore, Austrheim et al. (2008) showed that *Betula nana* increases its cover under moderate grazing, whereas its cover decreases under a higher grazing pressure. The exclusion of reindeer grazing also contributed to an increase in cover of dwarf shrubs, however, opposed to willows and *Betula nana*, the effect of reduced grazing was independent of the habitat type. Dwarf shrubs like *Vaccinium vitis-idea* and *Empetrum nigrum* are commonly not preferred by reindeer as a forage plant (Warenberg et al., 1997), however, on a long time scale, reindeer grazing is expected to reduce their abundance. Moreover, *Vaccinium vitis-idea* is a slow-growing evergreen plant that cannot compensate biomass losses under a high grazing pressure and frequent trampling. Finally, Austrheim and Eriksson (2001) observed an increase in vascular plant species richness in the most productive areas and a decline in the low-productive habitats.

In addition, trampling is held responsible for the extirpation of rare species, the creation of more bare ground surfaces and a gradual speed up of local erosion processes (Zika, 1991). A trampling experiment by Cole and Monz (2002) in five high-elevation plant communities in the Wind River Mountains (Wyoming, USA) showed that low levels of trampling leaded to a strong reduction in vegetation cover and height, whereas a higher trampling intensity was associated with a much lower rate of change. Moreover, different plant communities were characterized by a varying ability to tolerate the disturbance from trampling, suggesting that the use of more tolerant plant communities could be adopted as an appropriate mitigation strategy to reduce the impacts of trampling. In particular, plant communities dominated by a woody, chamaephytic groundcover were much less resilient than plant communities dominated by turf-forming, caespitose graminoids or forbs with a matted or rosette growth form.

Grazing and trampling pressure by reindeer has not yet been quantified for this study area, leaving a considerable uncertainty about what response to expect from vegetation. Nonetheless, observations from Syverhuset (2009) indicated that the number of herbivores increased in the Dovrefjell mountain range during the last years (Syherhuset, 2009). Consequently, a potential increase of the grazing pressure might also be addressed as one of the possible drivers of the increased vascular plant species richness, especially on the lowest summit. However, this hypothesis is not supported by the observed

response of individual species in the study area. For instance, the shrub *Betula nana* showed the largest increase in cover on the two lowest summits during the period 2001-2015. In addition, willow species like *Salix glauca*, *Salix phylicifolia* and *Salix herbacea* and dwarf shrubs like *Vaccinium vitis-idea* and *Empetrum nigrum* also expanded their cover, although not always statistically significant. Keeping the observations from Pajunen et al. (2008) in mind, these changes in cover could not be the result of an increase in the grazing intensity. Vistnes and Nellemann (2008) reported that some graminoid species (e.g. *Juncus trifidus*) showed a positive response to a higher intensity of grazing by herbivores and sometimes even established at heavily grazed sites. In the scope of these findings, the increase in herbivores, especially musk oxen, might have caused the significant increase in cover of *Juncus trifidus* on Veslekolla.
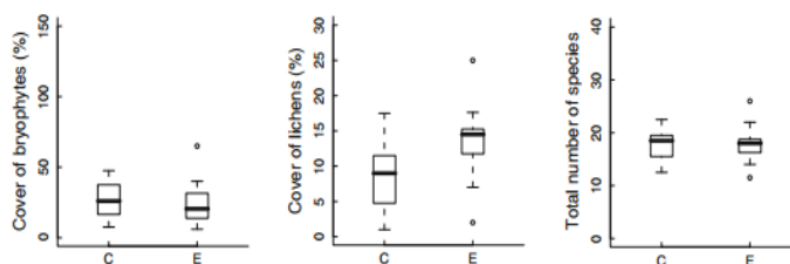

Figure 47: Cover of bryophytes, lichens and the total number of species in a tundra heath ecosystem. Control plots are indicated with the symbol (C), whereas exclosures are marked as (E) (Pajunen et al., 2008).

Pajunen et al. (2008) also concluded that lichen cover remained unaffected by the exclusion of reindeer grazing (**figure 47**), even though earlier studies previously reported that reindeer grazing and trampling severely reduced lichen abundance (Helle & Aspi, 1983). Nonetheless, this lack of response might be attributed to the slow recovery of lichens after disturbance. Therefore, grazing and trampling could also be a possible explanation for the significant decrease in the cover of lichens at Dovrefjell during the period 2001-2015. However, this is not consistent with the assumptions of Syverhuset (2009), indicating a rather low grazing pressure within the study area. Moreover, Ross et al. (2012) concluded that the ongoing homogenization of montane vegetation and the decreasing abundance of Arctic-alpine heathland lichens (e.g. *Flavocetraria nivalis*) are a consequence of climate change and the subsequent summer dryness.

The dynamics of bryophyte communities are affected by interaction with herbivores (e.g. lemmings), disturbances from geese and grazing or trampling by musk oxen as well (Hassel et al., 2012). According to Pajunen et al. (2008), reduced reindeer grazing leaded to a decline in the cover and species richness of bryophytes, especially in more productive areas where the competition with forbs increased as a response to the absence of grazing. Moreover, Oksanen and Ranta (1992) hypothesized that lemming grazing typically favors colonizing bryophyte species (e.g. *Pohlia sp.*) in mountain snowbeds. Consequently, the sharp increase in the cover of *Pohlia sp.* at Dovrefjell might also be attributed to diminished lemming grazing. Kauserud et al. (2008) observed a strong decline in lemming populations in Norway during the last decades. This was attributed to the fact that winters in southern Norway had been significantly warmer since 1994, preventing females from raising the large broods that commonly lead to lemming outbreaks (Kauserud et al., 2008). This theory is supported by Hörnfeldt (2004), indicating that winter conditions have a considerable effect on the demography of high-latitude rodents. Norway's lemmings and other Fennoscandian rodents thrive in the subnival zone where they benefit from thermal insulation, access to forage plants and the protection from predators (e.g. foxes and owls) (Stenseth, 1993). Profound changes in the condition of subnivean

habitats, such as an increased snowmelt, are likely to affect the performance of rodents through flooding, food shortage and enhanced predator access (Hörnfeldt, 2005). Virtanen (2000), however, suggested that most colonizing bryophyte species have the ability to cope with different levels of grazing. In other words, the effect remains uncertain.

Various studies also considered the effect of nitrogen (N) deposition on vegetation in Norway (e.g. Klanderud & Birks, 2003). These depositions are expected to fertilize alpine heath ecosystems, largely influencing regional plant communities (Chapin & Shaver, 1985) and stimulating species diversity in otherwise low productive areas (Teodose & Bowman, 1997). Despite the fact that N deposition is often regarded as a lowland problem, Baron (1992) stated that alpine communities tend to be extremely sensitive to changes in N deposition due to the combined effect of a short growing season, strong seasonal fluctuations in moisture availability and temperature, shallow and poorly developed soils, steep slope gradients and low primary productivity. These factors tend to limit the N uptake and retention capacity of the ecosystem. In addition, ecosystems in the low-alpine zone are potentially exposed to higher levels of N deposition compared to the surrounding lowlands since they are subjected to higher rainfall amounts (Burns, 2003) (**figure 48**).
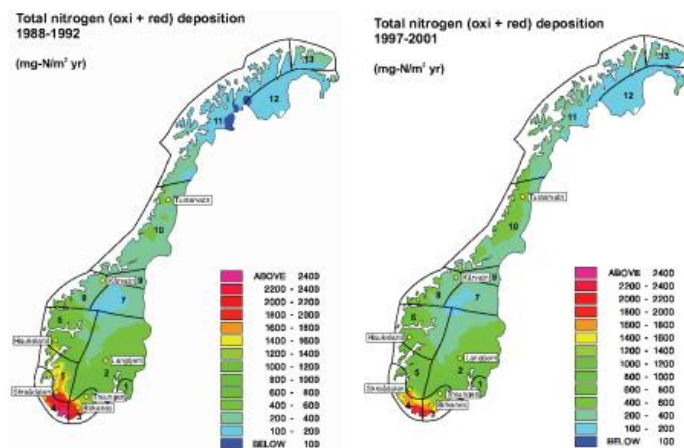
Figure 48: Total N depositions (oxidized + reduced) during the periods 1988-1992 and 1997-2001 in mg N m^{-2} year^{-1}. (Hole and Tørseth, 2002).

Mountain ecosystems are generally N-limited (Burns, 2004), but small changes in atmospheric deposition might induce saturation and a subsequent loss of N retention capacity (Baron et al., 2000). Higher N inputs contribute to an increased availability to some plant species, thereby promoting competitive exclusion of characteristic plant species by nitrophilic species (Bobbink et al., 1998). Most plant species in natural and semi-natural habitats are typically adapted to soils with a low N content (Ellenberg, 1988). Hence, N enrichment in areas with an intermediate nutrient availability will cause a serious decline in biodiversity. On nutrient-poor soils, species diversity will potentially increase as a response to increased N deposition due to the invasion of species that could not survive in the former extreme conditions (Huston, 1979). The effects on N deposition on Alpine tundra vegetation were also investigated by Jin et al. (2015) and Zong et al. (2016) in an Alpine tundra ecosystem in the Changbai Mountains, Northeast China. These studies reported a significant change in the community structure of alpine vegetation with an overall positive impact of simulated N deposition on plant growth. Moreover, Jin et al. (2015) concluded that the dwarf shrub *Vaccinium uliginosum* might become the dominant species in the future, thereby transforming the current Alpine tundra into Alpine meadow. Lichen species, on the other hand, are extremely sensitive to N deposition and experience a subsequent decline in species richness. This was also illustrated by Fremstad et al. (2005) showing a decrease in the cover of lichen species like *Alectoria ochroleuca* and *Flavocetraria nivalis* in low- and mid-alpine regions in Norway at the lowest dose of approximately 7 kg N ha^{-1} year^{-1}. N

deposition should also be taken into account when trying to explain the changes in species richness and composition at Dovrefjell. However, the annual N deposition rate at Dovrefjell is only estimated at about 2 to 4 kg N ha^{-1} year^{-1} (Paal et al., 1997). Also, total N deposition decreased in Norway from about 154856 tons per year to 140321 tons per year between 2002 and 2011 (Aas et al., 2012). Therefore, it seems less plausible that aerial fertilization was responsible for the observed changes in vegetation in the study area.

Finally, the ongoing changes in vegetation at Dovrefjell might also be considered as a long-term lag-response to postglacial warming. Svenning and Skov (2007) investigated the probability of Ice Age legacies in the geographical distribution of tree species richness on the European continent. They concluded that many tree species (e.g. *Querus robur* and *Fagus sylvatica*) have probably not reached an equilibrium with the prevailing climatic conditions in Central and Northern Europe since the Last Glacial Maximum (21.000 years ago). Hence, tree species distribution in these regions has not yet reached its potential range under the current climate and tree migration rates are therefore experiencing an impact of the previous glacial climate conditions (**figure 49**).
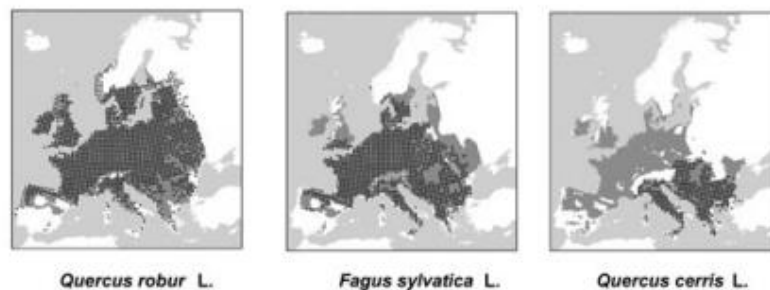
Figure 49: Current native distribution of temperate tree species (dots) and their climatic potential range (shading) estimated using a bioclimatic envelope model (Svenning & Skov, 2007).

Moreover, vegetation in tundra ecosystems is still recovering from the Little Ice Age. Many tundra plant species still have not reached a distribution that corresponds with the current climate forcings. Hence, plant community shifts in tundra ecosystems and shrub encroachment can also be considered as a delayed effect of natural succession. Klanderud and Birks (2003) reported that most of the species that showed a decreasing abundance in the last few decades at Jotunheimen (e.g. *Oxyria digyna*, *Trisetum spicatum* and some *Cerastium* and *Saxifraga* species) can be categorized as pioneers and are characteristic for early successional stages. However, as succession gradually proceeds towards a more mature plant community, these species will be easily substituted by species which are more characteristic for a later successional stage (e.g. *Avenella flexuosa*, *Empetrum nigrum* and some *Vaccinium* and *Salix* species). This is also in line with the observations at Dovrefjell where willow species as well as dwarf shrubs experienced an increase in cover and abundance throughout the last decade. Therefore, natural succession cannot be ruled out as a possible driver for the observed vegetation changes.

Conclusion

The long-term temperature record from the weather station of Gammel-Fokstugu showed a strong and significant upward trend throughout the period 1900-2014. However, during the last decade, the rate of warming air temperatures slowed down. These observations are consistent with the current hiatus in global warming. This was also reflected in the soil temperature data from the GLORIA summits from the Dovrefjell target region, indicating a significantly declining soil temperature during the measuring period 2001-2015. The cause of this phenomenon has been previously discussed in scientific literature and might be attributed to natural fluctuations in the global climate which are related to ENSO and variations in the sea surface temperature. Precipitation data from Gammel-Fokstugu showed a large inter-annual variation. However, during the last 15 years, significantly higher precipitation amounts were recorded compared to the long-term average from the period 1961-1990.

Species richness of vascular plants at Dovrefjell decreased significantly with elevation from the low alpine to the high alpine belt. Higher levels of species richness were found on south-facing slopes as compared to north-facing slopes. Over time species richness of vascular plants did not change during the period 2001-2015. On the other hand, lichen species richness experienced a significant decline over time in the study area. These observations are in line with other studies in similar conditions and might be attributed to global warming. However, for the bryophytes, an increase in species richness was observed which is somewhat contrasting to our expectations. Nonetheless, responses of bryophytes to a changing environment depend to a large extent on the available microhabitats. In addition, the species composition of vascular plants on the study summits changed significantly as well. Most likely, this change is the result of a significantly increased cover and abundance of shrubs, dwarf shrubs and graminoids, especially at higher elevations. The invasion of shrubs in Alpine tundra ecosystems has been previously reported and is often referred to as 'shrub encroachment'. Furthermore, three lichen species (*Ochrolechia sp.*, *Pseudephebe sp.* and *Umbilicaria sp.*) showed a substantial decline in cover which, according to previous studies, can be attributed to an increased competition with vascular plants. Finally, thermophilization of vascular plants (i.e. the increasing dominance of thermophilic species) was more pronounced on the two lowest summits and on the northern aspects of these summits. The migration of thermophilic vascular plant species occurred primarily during the period 2001-2008, which was marked by a higher warming rate. During the following years, thermophilization of vascular plants slowed down, most likely as a result of the observed short-term negative trend in temperature since 2008. Lichens showed less thermophilization than vascular plants, probably due to their higher dispersal ability. Also, in contrast to the vascular plants, the process mainly took place on the two highest summits between 2008 and 2015. For the bryophytes, thermophilization was only noticed on Veslekolla and Storkinn for the period 2001-2015. On Vesle Armodshøkollen and Kolla, turnover of bryophyte species was much lower during that period and the community experienced almost no changes over time.

In conclusion, most of the observed changes in vegetation at Dovrefjell are consistent with climate warming and confirm previous experimental and/or field studies. Consequently, climate warming is probably the main driver for these changes. However, this is an observational study which has only been carried out over 15 years. Other possible driving factors (e.g. grazing, trampling and eutrophication) might have a substantial influence on vegetation as well and cannot be ruled out. Most likely, the recorded changes in species richness and composition are a combined effect of climate change and plant-herbivore interactions.

Future perspectives

Since this is an observational field study, the effect of extern factors like grazing and trampling from herbivores, atmospheric N deposition, invasive species and land-use changes cannot be ruled out. This emphasizes the need for more experimental studies, enabling researchers to distinguish between the different drivers of changes in plant communities and capturing possible lag-effects in the response of vegetation.

In addition, more research is required, not only within the study area, but also in other mountain regions, in order to investigate whether changes in vegetation propagate through time and space and whether they can be related to a long-term trend in climate change. Also, comparing the observed changes of lichen and bryophyte species at Dovrefjell with the results of other studies remains difficult due to the fact that there are relatively few studies on species level of non-vascular plants. Hence, further investigation is required with respect to the interaction between different taxonomic groups (i.e. vascular plants, lichens and bryophytes) and their overall response to climate warming.

Finally, field observations at Dovrefjell could also be completed with experimental research, e.g. experiments with open-top chambers and infrared heaters, in order to study the interactive effects of elevated CO_2 levels and increased air temperature on local vegetation. Furthermore, temporaly replicated observations, such as vegetation resurveys, are indispensable for an accurate calibration and validation of environmental niche or species distribution models. In turn, these models could provide more insight into the impacts of climate warming on plant communities across space and time.

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Appendix

Appendix A: fauna in the Dovrefjell National Park

The areas around the mountain range of Dovrefjell are characterized by a varying vegetation cover and therefore provide an excellent habitat for numerous bird species. Next to some ptarmigans and small birds, also larger raptors such as the celebrated golden eagle (*Aquila chrysaetos*), the gyrfalcon (*Falco rusticolus*) and the rough-legged buzzard (*Buteo lagopus*) are commonly spotted in this region. In addition, some larger mammals thrive within the borders of the national park. Wolverines (*Gulo gulo*), for example, were able to establish a viable population, however they are rarely seen by humans in the wild (Norway's National Parks, 2015). They generally feed on small rodents, hares and grouse, however sheep commonly occur on their daily menu as well (Midnorsknatur, 2015).

Along with the wolverine, the Arctic fox (*Vulpes lagopus*) is also native to the Dovrefjell area, but its population has been declining dramatically during the last decades. Apparently, the mortality rate has been remarkably higher than the reproduction rate, notwithstanding the fact that this species has been continuously preserved since the 1950s. The reason for this rapid drop in the Arctic fox's abundance remains still a mystery, however two main probable causes have been recently suggested. On the one hand, environmental changes such as human-induced climate change, an expansion of the red fox population, the absence of large predators and variations in the dynamics of small rodents could be at the basis of the decline. On the other hand, some researchers also suggest the changes in the Arctic fox's demographics (e.g. negative effects of inbreeding) might cause this dramatic ecological response. Numerous monitoring projects have been established in order to protect the Arctic fox from being extinct in Scandinavia. The Norwegian Institute for Nature Research (NINA), for example, has recently founded a project, namely the 'Arctic Fox Conservation Ecology', which is responsible for the preservation of a viable Arctic fox population in the wild. This project not only involves monitoring and assessing the number and spatial distribution of individuals, but also sustainable management decisions have to be made (Midnorsknatur, 2015; Norwegian Institute for Nature Research, 2015; Landa et al., 2008).

Another unique mammal housing in the Dovrefjell area, is the musk ox (*Ovibos moschatus*). During the last glacial period, this animal established a natural habitat which covered the entire northern part of the Eurasian continent. Nonetheless, after the Last Glacial Maximum (11700 years ago), the musk ox completely disappeared from the Dovrefjell area (Midnorsknatur, 2015). In 1931, it was reintroduced to the region from Greenland. Yet, this limited population was extinct by 1945. Between 1947 and 1953, 21 individuals were again released in the Dovrefjell mountains. By 2006, the population had grown up to 213 individuals, but a large fraction was extirpated during the summer of that same year as a result of a *pasteurellosis* outbreak. In 2008, only 190 individuals were registered, however the most recent survey already indicates an increase up to approximately 300 animals in the area (Bretten, 1990; Syerhuset, 2009). Most of these musk oxen stay to the west of the Drivdalen valley (Syverhuset, 2009; Michelsen et al., 2011).

The wild reindeer (*Rangifer tarandus tarandus*), commonly known as the Snøhetta reindeer, occur both to the west (Snøhetta area) and to the east (Knutshø area) of the Drivdalen valley (Syverhuset, 2009). From a genetic point of view, this reindeer species is closely related to the original Scandinavian wild reindeer (Midnorsknatur, 2015; Kaltenborn et al., 2014). Therefore, its preservation is of major importance to conservation ecologists. Despite the fact that this species constantly migrates

over large distances through the landscape in search of food, the Snøhetta area forms its main natural habitat. In this area two principal wild reindeer stocks can be distinguished, which are managed in a different way. At first, the Snøhetta east population thrives in the valley of Eikesdalen to the east of Lake Aursjøen. Along with the nearby road between Jore and Eikesdalen, this lake forms a natural barrier which restricts the wild reindeer of migrating between both stocks. In order to preserve this stock, the target winter stock size is set at a population of 1800 individuals. Nonetheless, the population only contained half this number in 2003. As a result, hunting the wild reindeer was prohibited in this area in the autumn of 2003. Secondly, the smaller Snøhetta west population houses west of lake Aursjøen. For this herd, a winter stock size of approximately 500 animals is targeted (Midnorsknatur, 2015; Kaltenborn et al., 2014). In total, the Snøhetta wild reindeer herd counted around 8000-12000 animals in the 1950s. However, this number rapidly decreased to approximately 2000 as a result of frequent hunting activities in the following decades. By 2003, the lowest number of individuals, only 653, was registered which seriously stimulated some preservation measures. In 2006, the Snøhetta herd reached up to 1849 individuals, while in 2008 the population size dropped again to 1741 animals (Sørensen et al., 2009; Syverhuset, 2009). To the east of the Driva river, the Knutshø herd expanded from a population of 1164 animals in 2001 up to 1526 individuals in 2008 (Sørensen et al., 2009; Syverhuset, 2009).

Finally, also sheep are typically herded in the Dovrefjell area. For example, multiple farmers in the municipality of Oppdal let their sheep graze to the east of the Driva river, mainly in the Knutshø area. In total, over 6000 animals presently occur in this region. Furthermore, sheep herds from the Folldal municipality are grazing in the area around the summit Vesle Armodshøkollen. These herds generally move in the direction of Kongsvoll at the end of the summer (Syverhuset, 2009; Michelsen et al., 2011).

Appendix B: installation of the quadrat clusters

Per mountaintop summit, the highest summit point (HSP) was located. This point serves as the principal reference point and is marked with a distinctive cross on each summit. Secondly, the location of the 3 x 3 m² grids of the quadrat clusters is determined based on the distance to the highest summit point (measured with a 50-m flexible measuring tape) and the magnetic compass direction. Subsequently, these grids are positioned at the correct location for which the corners are marked with a spike. In case of doubt, pictures from the previous survey in 2008 can be used to find the exact spot. For each summit, a single 3 x 3 m² grid is situated in the cardinal directions (N, E, S and W), which is illustrated by **figure** S**1**.
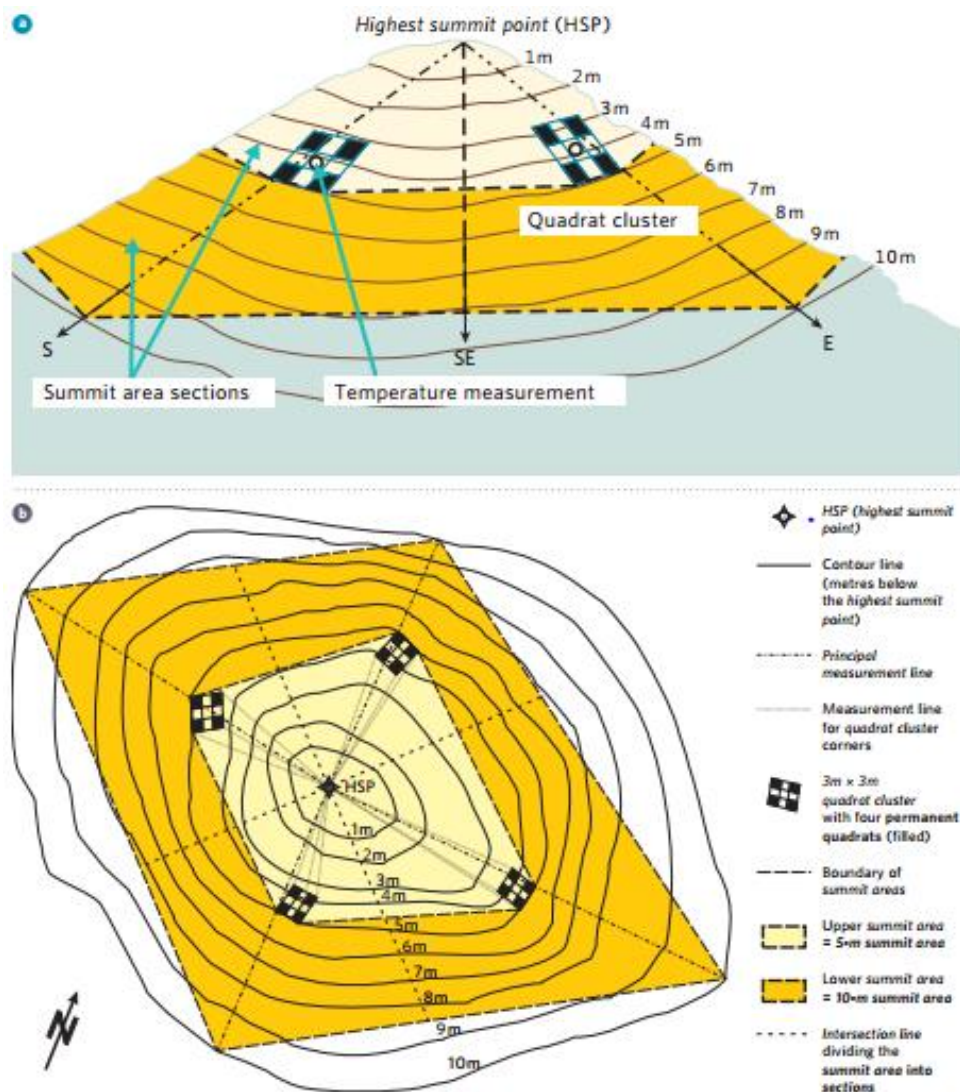
Figure S1: Schematic representation of the GLORIA Multi-Summit sampling design on a hypothetical mountain peak. a) Sideways view of the hypothetical summit with the location of the highest summit point (HSP) and contour lines at a 1 m elevation interval. b) Top view of the hypothetical summit with the location of the highest summit point (HSP) and the four 3 x 3 m² girds of quadrat clusters. The exact location of these grids depends on the nature of the sampling area and the local habitats (Pauli et al., 2015).

Appendix C: installation of the summit area sections

Next to the quadrat clusters, the boundary lines of the 5-m and 10-m summit area sections are established. These lines combine all points that are located respectively 5 m and 10 m below the highest elevation point and delimit the lower boundaries of the upper and lower summit area. The size of these summit areas is not fixed, but highly depends on the structure and steepness of the mountain slope. In practice, the (orange) ropes are fixed to a collection of corner points which are indicated by a man-made pile of rocks. On the one hand, the 5-m contour line contains eight different corner points which also represent the lower edges of the 3 m x 3 m quadrat clusters, namely p5m-N11, p5m-N31, p5m-E11, p5m-E31, p5m-S11, p5m-S31, p5m-W11 and p5m-W31. On the other hand, the 10-m contour line only counts four main corner points: p10m-N, p10m-E, p10m-S and p10m-W. The corner points are all indicated on **figure S2**. In a final step of the experimental set-up, the summit areas are divided in in four sections using another set of measuring lines, corresponding to the four major wind directions (N-5m-SA, E-5m-SA, S-5m-SA, W-5m-SA, N-10m-SA, E-10m-SA, S-10m-SA and W-10m-SA). The position of these measuring lines is marked by a number of points which are indicated on **figure S2**, but can also be determined using a compass in case of doubt.
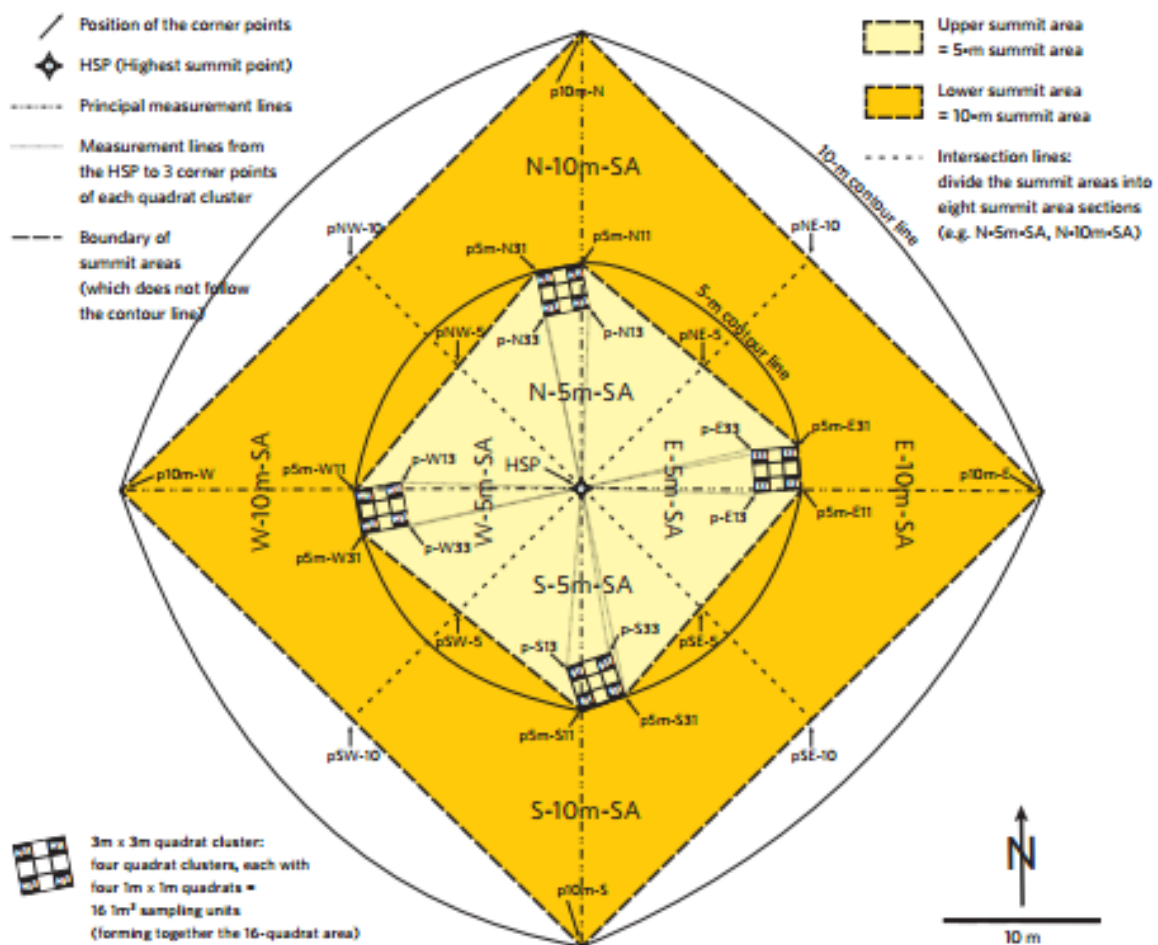
Figure S2: detailed schematic representation of the Multi-Summit sampling design with the location of the 5-m and 10-m contour lines, the different corner points and with an indication of the eight section names. (Pauli et al., 2015).

Appendix D: supplementary figures

The Euclidean and Jaccard dissimilarity indices for vascular plants, lichens and bryophytes in the quadrats of GLORIA summits at Dovrefjell were calculated and are displayed in **figure S3** and **S4**.
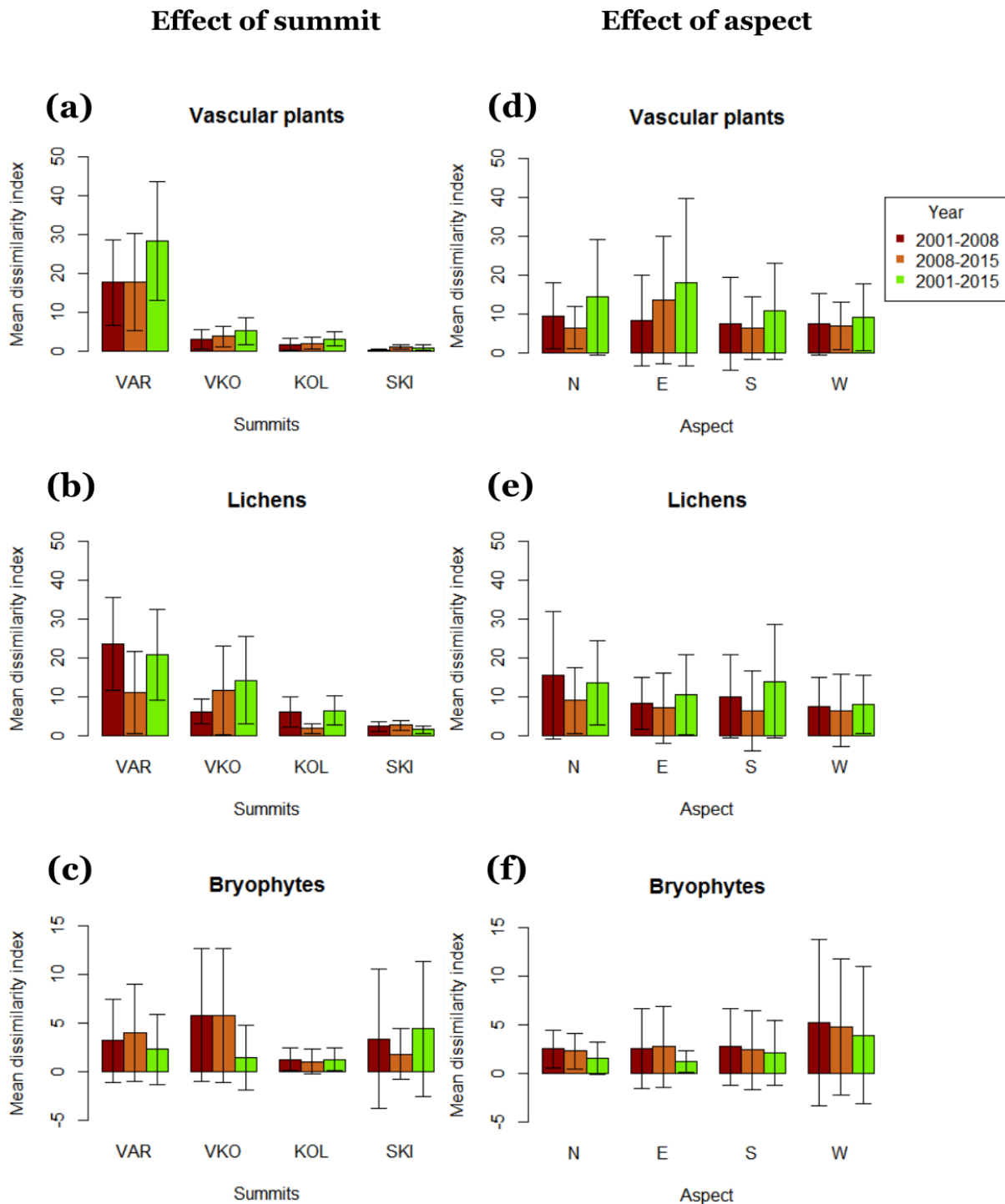
Figure S3: : Mean Euclidean dissimilarity index for vascular plants (a, d), lichens (b, e) and bryophytes (c, f) in the quadrats of the GLORIA summits (left) and the aspects of each summit (right) between 2001-2008, 2008-2015 and 2001-2015. The error bars give an indication of the corresponding standard error.

Effect of summit

Effect of aspect
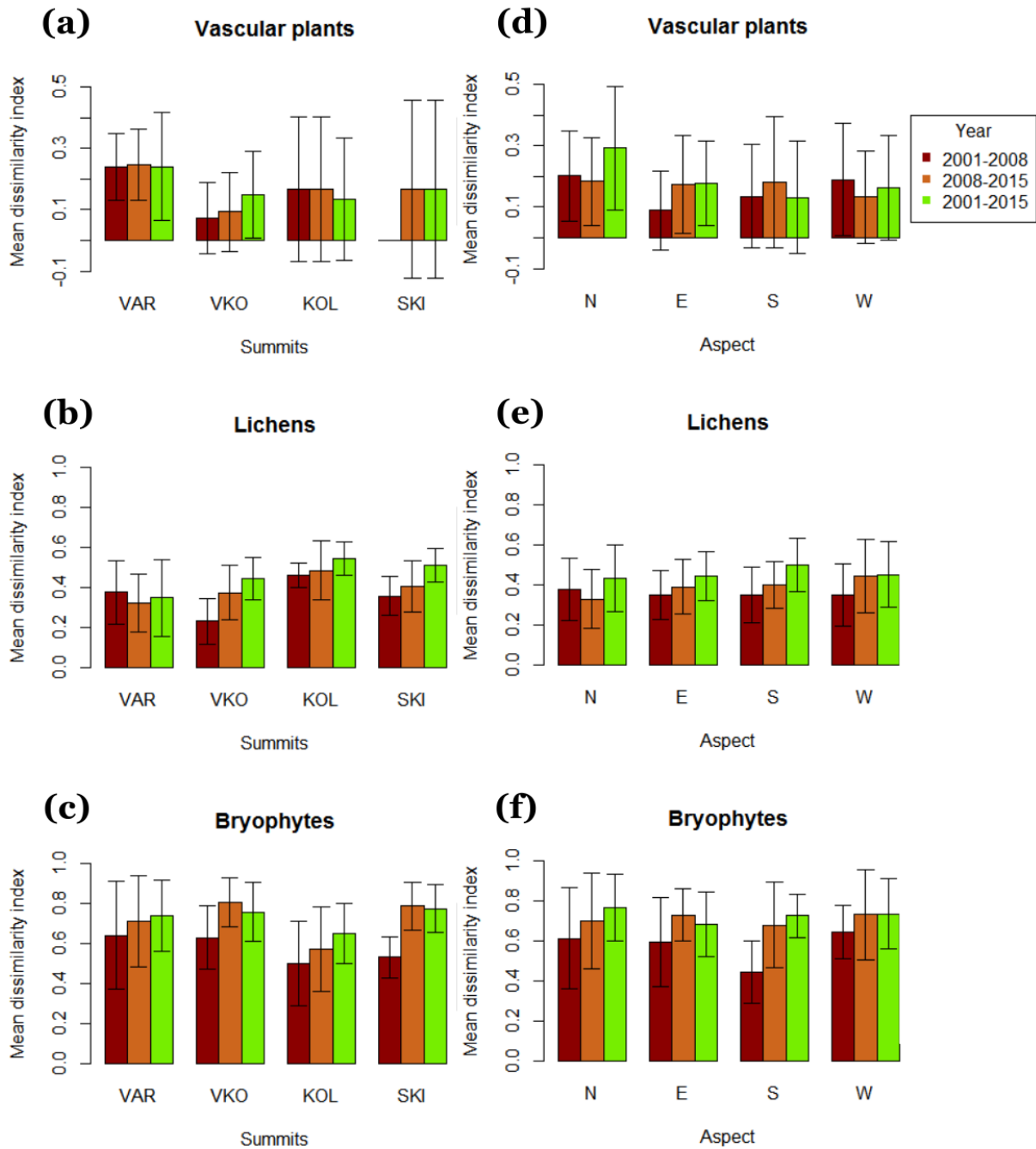
Figure S4: : Mean Jaccard dissimilarity index for vascular plants (a, d), lichens (b, e) and bryophytes (c, f) in the quadrats of the GLORIA summits (left) and the aspects of each summit (right) between 2001-2008, 2008-2015 and 2001-2015. The error bars give an indication of the corresponding standard error.

Figure **S5** and **S6** represent the NMDS plots for lichens and bryophytes in the quadrats of the GLORIA summits at Dovrefjell, respectively.

Figure S5: NMDS plot for the lichen species on the GLORIA summits at Dovrefjell for 2001 (crosses) and 2015 (full circles). The following color code was used to indicate the different study summits: olive green = Vesle Armodshøkollen light brown = Veslekolla, grey = Kolla and black = Storkinn. The grey surface represent a convex hull and encloses the plots or quadrats for each of the GLORIA summits within the study area. The full species names and the corresponding work codes can be found in Appendix F.

Figure S6: NMDS plot for the bryophyte species on the GLORIA summits at Dovrefjell for 2001 (crosses) and 2015 (full circles). The following color code was used to indicate the different study summits: olive green = Vesle Armodshøkollen light brown = Veslekolla, grey = Kolla and black = Storkinn. The grey surface represent a convex hull and encloses the plots or quadrats for each of the GLORIA summits within the study area. The full species names and the corresponding work codes can be found in Appendix F.

Appendix E: species lists

All vascular plant, lichen and bryophyte species - recorded on the GLORIA summits at Dovrefjell in 2001, 2008 and 2015 - are listed in **table S1**, **S2**, and **S3**, respectively. For every study summit, the year in which the species was found, is specified. Years between brackets indicate that only dead individuals of this specific species were recorded.

Table S1: List of vascular plant species recorded in 2001, 2008 and 2015 on the four study summits at Dovrefjell.

Species	VAK	VKO	KOL	STI
Agrostis mertensii			2001-2008	
Antennaria alpina	2001-2008-2015		2001-2008	
Antennaria dioica	2001-2008-2015		2015	
Anthoxantum odoratum	2001-2008-2015			
Arctostaphylos uva-ursi	2001-2008-2015	2008		
Arctous alpinus	2001-2008-2015	2015		
Artismesia norvegica	2001			
Astragalus alpinus	2001-2008-2015			
Astragalus frigidus	2001-2008-2015			
Astragalus norvegicus	2001-2008-2015			
Avenella flexuosa	2001-2008-2015	2001-2008-2015		
Bartsia alpina	2001-2008-2015	2008		
Beckwithia glacialis			2001-2008-2015	
Betula nana	2001-2008-2015	2001-2008-2015		
Betula nana x pubescens	2008-2015			
Betula pubescens	2001-2008-2015			
Bistorta vivpara	2001-2008-2015			
Campanula rotundifolia	2001-2008-2015			
Cardamine bellidifolia			2001-2015	
Carex atrata	2008-2015			
Carex bigelowii	2001-2008	2001-2008-2015	2001-2008-2015	2001-2008-2015
Carex rupestris	2001-2008-2015		2008	
Carex vaginata	2001-2008-2015			
Cerastium alpinum	2001-2008-2015		2001-2008	
Comastoma tenellum	2015			
Corallorhiza trifida	2015			
Diapensia lapponica	2008	2001-2008-2015		
Diphasiastrum alpinum	2001-2008-2015			
Draba fladnizensis	2001-2008		2001	
Draba glabella	2001-2008-2015			
Empetrum nigrum	2001-2008-2015	2001-2008-2015	2001-2008-2015	2015
Epilobium angustifoilium	2001-2008-2015			
Erigeron sp.	2015			
Eriophorum scheuchzeri				2001-2008-2015
Euphrasia sp.	2008-(2015)			
Festuca ovina	2001-2008-2015	2001-2008-2015	2001-2008-2015	
Festuca vivipara			2001-2008-2015	
Geranium sylvaticum	2015			
Harrimanella hypnoides			2001-2008-2015	
Hieracium alpinum	2001-2008-2015	2001-2008		
Hieracium sp.		2015		
Huperzia selago	2001		2001-2008-2015	2001-2008-2015
Juncus trifidus	2001-2008-2015	2001-2008-2015	2001-2008-2015	
Juniperus communis	2001-2008-2015			
Kobresia Mysuroides	2001-2008-2015			
Loiseleuria procumbens	2001-2008-2015	2001-2008-2015		
Luzula arcuata		2001-2008	2001-2008-2015	2001-2008-2015

	2015	2015		
Luzula confusa	2015	2015		
Luzula multiflora	2001-2008-2015			
Luzula spicata	2001-2008-2015	2008-2015	2001-2008-2015	
Melampyrum pratense	2008-2015			
Myosotis decumbens	2001			
Oxytropis lapponica	2001-2008-2015			
Pedicularis lapponica	2001-2008-2015			
Pedicularis oederi	2001-2015			
Phyllodoce caerulea	2008-2015	2001-2008-2015	2011-2008-2015	
Pinguicula vulgaris	2001-2008-2015			
Pinus sylvestris	2015			
Poa Arctica			2008	
Poa flexuosa			2001-2008	2001-2008-2015
Poa pratensis	2001-2015			
Poa sp.			2015	2015
Potentilla crantzii	2001-2008-2015		2008	
Primula scandinavica	2001-2008-2015			
Pulsatilla vernalis	2001-2008-2015			
Ranunculus sp.	2008			
Ranunculus acris	2001			
Salix glauca	2001-2008-2015			
Salix hastata	2001-2008			
Salix herbacea	2001-2008-2015	2001-2008-2015	2001-2008-2015	2001-2008-2015
Salix lapponum	2001-2008			
Salix philicifolia	2001-2008-2015			
Salix reticulata	2001-2008-2015			
Saussurea alpina	2001-2008-2015			
Saxifraga cespitosa	2001-2008-2015		2001-2008-2015	
Saxifraga oppositifolia	2001-2008-2015			
Silene acaulis	2015		2001-2008-2015	
Silene uralensis	2008-(2015)			
Solidago vigaurea	2001-2008-2015	2008		
Trisetum spicatum			2015	
Vaccinium myrtillus	2001-2008-2015			
Vaccinium uliginosum	2001-2008-2015	2001-2008-2015		
Vaccinium vitis-idea	2001-2008-2015	2001-2008-2015	2001-2008-2015	
Viola biflora	2008-2015			

Table S2: List of lichen species recorded in 2001, 2008 and 2015 on the four study summits at Dovrefjell.

Species	VAR	VKO	KOL	STI
Alectoria nigricans	2001-2008-2015	2001-2008-2015	2001-2008-2015	2001-2008-2015
Alectoria ochroleuca	2001-2008-2015	2001-2008-2015	2001-2008-2015	2001-2008-2015
Bryocaulon divergens	2001-2008-2015	2001-2008-2015	2001-2008-2015	2001-2008-2015
Bryoria sp.		2015		
Cetraria ericetorum	2001-2008-2015	2001-2008-2015	2001-2008-2015	2001-2008-2015
Cetraria islandica	2001-2008-2015	2001-2008-2015	2001	
Cladonia arbuscula	2001-2008-2015	2001-2008-2015		
Cladonia gracilis	2015	2015	2015	
Cladonia sp.	2001-2008-2015	2001-2008-2015	2001-2008-2015	2001-2008-2015
Cladonia rangiferina	2001-2008-2015	2001-2008-2015	2015	
Cladonia stellaris	2001-2008-2015	2008		
Cladonia uncialis	2001-2015	2001-2008-2015		
Flavocetraria cucullata	2001-2008-2015	2001-2008-2015	2001-2008-2015	2015
Flavocetraria nivalis	2001-2008-2015	2001-2008-2015	2001-2008-2015	2001-2008-2015
Hypogymnia physodes	2015	2015	2015	
Melanelia sp.			2015	
Ochrolechia sp.		2015		

Ochrolechia frigida		2015		
Peltigera sp.	2015			
Pseudephebe sp.		2015	2015	2015
Solorina crocea	2001-2008-2015	2001-2008-2015		
Sphaerophorus fragilis	2001-2008	2001-2008-2015	2001-2008-2015	2001-2008
Sphaerophorus globosus	2015	2015	2015	2015
Stereocaulon sp.	2001-2008-2015	2015		
Thamnolia vermicularis	2001-2008-2015	2001-2008-2015	2001-2008-2015	2001-2008-2015
Umbilicaria sp.	2015	2015	2015	2015

Table S3: List of lichen bryophyte recorded in 2001, 2008 and 2015 on the four study summits at Dovrefjell.

Species	VAR	VKO	KOL	STI
Pohlia sp.	2015	2015	2015	2015
Polytrichum juniperinum	2015	2015	2015	
Polytrichum hyperboreum	2015	2015	2015	2015
Sanionia uncinata	2015			
Dicranum sp.	2015	2015	2015	
Polytrichum piliferum	2015	2015	2015	2015
Hepatica sp.	2015			
Anthelia sp.	2015	2015		
Ceratodon purpureus	2015			
Lophozia cf. ventricosa	2015	2015		
Ptilidium ciliare	2015	2015		
Pleurozium schreberi	2015			
Barbilophozia lycopodioides	2015			
Hylocomium splendens	2015			
Andreaea rupestris			2015	2015
Tetralophozia setisformis			2015	2015
Racomitrium lanuginosum			2015	2015
Gymnomitrion concinnatum			2015	2015
Polythrichum alpinum			2015	2015
Pogonatum sp.			2015	2015
Polythrichum sp.	2015			

Appendix F: abbreviations of the names of vascular plant, lichen and bryophyte species

The abbreviations that were used to indicate the vascular plant, lichen and bryophyte species on the NMDS plots (respectively **figure 36**, **S5** and **S6**) are listed in **table S4**, **S5** and **S7**. For each species the three first letters of the genus name and the three first letters of species name were combined.

Table S4: Abbreviations of names of the vascular plant species as indicated on the NMDS plot.

Species	Abbreviation
Agrostis mertensii	Agrmer
Antennaria alpina	Antalp
Antennaria dioica	Antdio
Anthoxantum odoratum	Antodo
Arctostaphylos uva-ursi	Arcuva
Arctous alpinus	Arcalp
Artismesia norvegica	Artnor
Astragalus alpinus	Astalp
Astragalus frigidus	Astfri
Astragalus norvegicus	Astnor
Avenella flexuosa	Avefle
Bartsia alpina	Baralp
Beckwithia glacialis	Becgla
Betula nana	Betnan
Betula nana x pubescens	Betnxp
Betula pubescens	Betpub
Bistorta vivpara	Bisviv
Campanula rotundifolia	Camrot
Cardamine bellidifolia	Carbel
Carex atrata	Caratr
Carex bigelowii	Carbig
Carex rupestris	Carrup
Carex vaginata	Carvag
Cerastium alpinum	Ceralp
Comastoma tenellum	Comten
Corallorhiza trifida	Cortri
Diapensia lapponica	Dialap
Diphasiastrum alpinum	Dipalp
Draba fladnizensis	Drafla
Draba glabella	Dragla
Empetrum nigrum	Empnig
Epilobium angustifoilium	Epiang
Erigeron sp.	Eri
Eriophorum scheuchzeri	Erisch
Euphrasia sp.	Eup
Festuca ovina	Fesovi
Festuca vivipara	Fesviv
Geranium sylvaticum	Gersyl
Harrimanella hypnoides	Harhyp
Hieracium alpinum	Hiealp
Hieracium sp.	Hie
Huperzia selago	Hupsel
Juncus trifidus	Juntri
Juniperus communis	Juncom
Kobresia Mysuroides	KobMys
Loiseleuria procumbens	Loipro
Luzula arcuata	Luzarc

Luzula confusa	Luzcon
Luzula multiflora	Luzmul
Luzula spicata	Luzspi
Melampyrum pratense	Melpra
Myosotis decumbens	Myodec
Oxytropis lapponica	Oxylap
Pedicularis lapponica	Pedlap
Pedicularis oederi	Pedoed
Phyllodoce caerulea	Phycae
Pinguicula vulgaris	Pinvul
Pinus sylvestris	Pinsyl
Poa Arctica	Poaarc
Poa flexuosa	Poafle
Poa pratensis	Poapra
Poa sp.	Poa
Potentilla crantzii	Potcra
Primula scandinavica	Prisca
Pulsatilla vernalis	Pulver
Ranunculus sp.	Ran
Ranunculus acris	Ranacr
Salix glauca	Salgla
Salix hastata	Salhas
Salix herbacea	Salher
Salix lapponum	Sallap
Salix philicifolia	Salphi
Salix reticulata	Salret
Saussurea alpina	Saualp
Saxifraga cespitosa	Saxces
Saxifraga oppositifolia	Saxopp
Silene acaulis	Silaca
Silene uralensis	Silura
Solidago vigaurea	Solvig
Trisetum spicatum	Trispi
Vaccinium myrtillus	Vacmyr
Vaccinium uliginosum	Vaculi
Vaccinium vitis-idea	Vacvit
Viola biflora	Viobif

Table S5: Abbreviations of names of the lichen species as indicated on the NMDS plot.

Species	Abbreviation
Alectroria nigricans	Alenig
Alectoria ochroleuca	Aleoch
Allantoparmelia alpicola	Allapl
Brodoa sp.	Bro
Bryoria sp.	Bry
Bryocaulon divergens	Brydiv
Cetraria delisei	Cetdel
Cetraria ericetorum	Ceteri
Cetraria islandica	Cetisl
Cladonia sp.	Cla
Cladonia arbuscula	Claarb
Cladonia bellidiflora	Clabel
Cladonia cornuta	Clacor
Cladonia gracilis	Clagra
Cladonia macrophylla	Clamac
Cladonia pleurota	Clapleu
Cladonia pyxidata	Clapyx

Cladonia rangiferina	Claran
Cladonia stellaris	Clastel
Cladonia subfurcata	Clasub
Cladonia uncialis	Claunc
Coelocaulon aculetaum	Coeacu
Flavocetraria cucullata	Flacuc
Flavocetraria nivalis	Flaniv
Hypogymnia physodes	Hypphy
Hypogymnia austerodes	Hypaus
Melanelia sp.	Mel
Ochrolechia sp.	Och
Ochrolechia frigida	Ochfri
Parmelia sp.	Par
Peltigera sp.	Pel
Pertusaria sp.	Per
Pertusaria dactylina	Perdac
Pseudephebe sp.	Pse
Solorina crocea	Solcro
Sphaerophorus globosus	Sphglo
Sphaerophorus fragilis	Sphfra
Stereocaulon sp.	Ste
Thamnolia vermicularis	Thaver
Umbilicaria sp.	Umb

Table S6: Abbreviations of names of the lichen species as indicated on the NMDS plot.

Species	Abbreviation
Andreaea rupestris	Andrup
Anthelia sp.	Ant
Barbilophozia lycopodioides	Bar
Bryum sp.	Bry
Ceratadon purpureus	Cerpur
Dicranum sp.	Dic
Gymnomitrion concinnatum	Gymcon
Hepathica sp.	Hep
Hylocomium splendens	Hylsple
Kiaeria sp	Kia
Lophozia cf. ventricosa	Lop
Pleurozium schreberi	Plesch
Pogonatum sp.	Pog
Pohlia sp.	Poh
Polythrichum alpinum	Polapl
Polytrichum hyperboreum	Polhyp
Polytrichum juniperinum	Poljun
Polythrichum piliferum	Polpil
Polytrichum sexangulare	Polsex
Ptilidium ciliare	Pticil
Racomitrium lanuginosum	Raclan
Racomitrium microcarpon	Racmic
Tetraplodon mnioides	Tetmni
Tetralophozia setisformis	Tetset

Appendix G: temporal changes in percentage cover

Mean percentage cover values were calculated for all vascular plant, lichen and bryophyte species in the quadrats based on visual cover estimations in 2001 and 2015. In addition, the corresponding difference in mean percentage cover was determined between 2015 and 2001 in order to quantify the change in cover over time (**table S7**, **S8** and **S9**).

Table S7: Mean percentage cover for vascular plant species in the quadrats in 2001 and 2015 and the change in mean percentage cover over time during the period 2001-2015.

Species	Mean percentage cover 2015 (%)	Mean percentage cover 2001 (%)	Change in mean percentage cover (%)
Antennaria dioca	0.0088	0.0148	0.0061
Anthoxantum odoratum	0.0002	0.0003	0.0002
Arctous alpinus	0.0031	0.0125	0.0094
Acrtostaphylos uva-ursi	3.5000	5.0469	1.5469
Astragalus alpinus	0.0002	0.0016	0.0014
Astragalus frigidus	0.0016	0.0047	0.0031
Bartsia alpina	0.0000	0.0008	0.0008
Betula nana	2.7214	5.7781	3.0567
Bistorta vivipara	0.0008	0.0008	0.0000
Campanula rotundifolia	0.0050	0.0105	0.0055
Carex bigelowii	0.0556	0.1641	0.1084
Diapensia lapponica	0.0034	0.0125	0.0091
Empetrum nigrum	1.9864	4.7984	2.8120
Festuca ovina	0.1828	0.6250	0.4422
Hieracium alpinum	0.0017	0.0000	-0.0017
Huperzia selago	0.0055	0.0314	0.0259
Juniperus communis	0.0005	0.0000	-0.0005
Juncus trifidus	0.0359	0.2202	0.1842
Loiseleuria procumbens	1.0192	1.2922	0.2730
Luzula arcuata	0.0616	0.2578	0.1963
Luzula confusa	0.0000	0.0047	0.0047
Luzula spicata	0.0027	0.0328	0.0302
Pedicularis lapponica	0.0002	0.0016	0.0014
Phyllodoce caerulea	0.0000	0.0008	0.0008
Poa sp.	0.0000	0.0016	0.0016
Ranunculus glacialis	0.0750	0.2297	0.1547
Salix glauca	0.0000	0.0016	0.0016
Salix herbacea	0.1848	0.2048	0.0200
Salix phylicifolia	0.0313	0.1094	0.0781
Saxifraga cespitosa	0.0006	0.0016	0.0009
Solidago virgaurea	0.0000	0.0000	0.0000
Vaccinium myrtillus	0.0000	0.0031	0.0031
Vaccinium uliginosum	0.0267	0.1109	0.0842
Vaccinium vitis-idea	0.2456	0.7773	0.5317

Table S8: Mean percentage cover for lichen species in the quadrats in 2001 and 2015 and the change in mean percentage cover over time during the period 2001-2015.

Species	Mean percentage cover 2015 (%)	Mean percentage cover 2001 (%)	Change in mean percentage cover (%)
Alectroria nigricans	0.0458	0.0893	0.0435
Alectoria ochroleuca	7.1683	4.4037	-2.7647
Allantoparmelia alpicola	0.0070	0.0000	-0.0070
Brodoa sp.	0.0042	0.0000	-0.0042
Bryoria sp.	0.0000	0.5333	0.5333
Bryocaulon divergens	0.2250	0.5303	0.3053
Cetraria delisei	0.0015	0.0000	-0.0015
Cetraria ericetorum	0.1335	0.1483	0.0148
Cetraria islandica	0.0057	0.0067	0.0010
Cladonia sp.	0.0088	0.0857	0.0768
Cladonia arbuscula	0.6928	0.1395	-0.5533
Cladonia bellidiflora	0.0545	0.0000	-0.0545
Cladonia cornuta	0.0002	0.0000	-0.0002
Cladonia gracilis	0.0372	0.0753	0.0382
Cladonia macrophylla	0.0018	0.0000	-0.0018
Cladonia pleurota	0.0052	0.0000	-0.0052
Cladonia pyxidata	0.0093	0.0000	-0.0093
Cladonia rangiferina	0.2200	0.1935	-0.0265
Cladonia stellaris	3.9755	2.9675	-1.0080
Cladonia subfurcata	0.0002	0.0000	-0.0002
Cladonia uncialis	0.0002	0.0035	0.0033
Coelocaulon aculeatum	0.0598	0.0000	-0.0598
Flavocetraria cucullata	0.2557	0.2018	-0.0538
Flavocetraria nivalis	6.9323	7.1178	0.1855
Hypogymnia physodes	0.0415	0.0750	0.0335
Hypogymnia austerodes	0.0008	0.0000	-0.0008
Melanelia sp.	0.0033	0.0008	-0.0025
Ochrolechia sp.	0.4058	0.0333	-0.3725
Ochrolechia frigida	0.0133	0.0167	0.0033
Parmelia sp.	0.0367	0.0000	-0.0367
Peltigera sp.	0.0142	0.0500	0.0358
Pertusaria sp.	0.0007	0.0000	-0.0007
Pertusaria dactylina	0.0003	0.0000	-0.0003
Pseudephebe sp.	3.3335	1.6150	-1.7185
Solorina crocea	0.0217	0.0135	-0.0082
Sphaerophorus globosus	0.1512	0.0833	-0.0678
Sphaerophorus fragilis	0.0000	0.1150	0.1150
Stereocaulon sp.	0.1187	0.0302	-0.0885
Thamnolia vermicularis	0.0192	0.0817	0.0625
Umbilicaria sp.	1.5773	0.2268	-1.3505

Table S9: Mean percentage cover for bryophyte species in the quadrats in 2001 and 2015 and the change in mean percentage cover over time during the period 2001-2015.

Species	Mean percentage cover 2015 (%)	Mean percentage cover 2001 (%)	Change in mean percentage cover (%)
Andreaea rupestris	0.0336	0.0766	0.0430
Anthelia sp.	0.0000	0.1184	0.1184
Barbilophozia lycopodioides	0.0000	0.0078	0.0078
Bryum sp.	0.0069	0.0000	-0.0069
Ceratadon purpureus	0.0000	0.0109	0.0109
Dicranum sp.	0.0094	0.0358	0.0264
Gymnomitrion concinnatum	1.5552	0.3344	-1.2208
Hepathica sp.	0.0189	0.0002	-0.0188
Hylocomium splendens	0.0008	0.0625	0.0617
Kiaeria sp	0.0033	0.0000	-0.0033
Lophozia cf. ventricosa	0.0002	0.0750	0.0748
Pleurozium schreberi	0.0000	0.0078	0.0078
Pogonatum sp.	0.0000	0.1156	0.1156
Pohlia sp.	0.0003	0.0781	0.0778
Polythrichum alpinum	0.0006	0.0055	0.0048
Polytrichum hyperboreum	0.0159	0.0583	0.0423
Polytrichum juniperinum	0.0103	0.4681	0.4578
Polythrichum piliferum	0.0145	0.0234	0.0089
Polytrichum sexangulare	0.2069	0.0000	-0.2069
Ptilidium ciliare	0.0078	0.0328	0.0250
Racomitrium lanuginosum	0.1531	0.2206	0.0675
Racomitrium microcarpon	0.0428	0.0000	-0.0428
Tetraplodon mnioides	0.0013	0.0000	-0.0013
Tetralophozia setisformis	0.2281	0.1602	-0.0680

Appendix H: altitudinal ranks

The altitudinal ranks for vascular plants were derived from standard floras an calculated by Gottfried et al. (2012) (**table S10**). For the lichens and the bryophytes, the altitudinal ranks are listed in **table S11** and **S12**, respectively.

Table S10: Altitudinal ranks for the vascular plants on the GLORIA summits at Dovrefjell, derived from Gottfried et al. (2012).

Species	Altitudinal rank
Antennaria dioca	5
Anthoxantum odoratum	5
Arctous alpinus	4
Acrtostaphylos uva-ursi	5
Astragalus alpinus	4
Astragalus frigidus	5
Bartsia alpina	4
Betula nana	5
Bistorta vivipara	4
Campanula rotundifolia	6
Carex bigelowii	2
Diapensia lapponica	2
Empetrum nigrum	5
Festuca ovina	5
Huperzia selago	4
Juncus trifidus	3
Loiseleuria procumbens	4
Luzula arcuata	2
Luzula confusa	2
Luzula spicata	3
Pedicularis lapponica	4
Phyllodoce caerulea	4
Poa sp.	NA
Ranunculus glacialis	1
Salix glauca	5
Salix herbacea	3
Salix phylicifolia	5
Saxifraga cespitosa	2
Vaccinium myrtillus	6
Vaccinium uliginosum	5
Vaccinium vitis-idea	5

Table S11: Altitudinal ranks for the lichens on the GLORIA summits at Dovrefjell.

Species	Altitudinal rank
Alectroria nigricans	2
Alectoria ochroleuca	3
Allantoparmelia alpicola	2
Brodoa sp.	NA
Bryoria sp.	NA
Bryocaulon divergens	2
Cetraria delisei	3
Cetraria ericetorum	4
Cetraria islandica	5
Cladonia sp.	NA
Cladonia arbuscula	5
Cladonia bellidiflora	5
Cladonia cornuta	6

Cladonia gracilis	5
Cladonia macrophylla	4
Cladonia pleurota	6
Cladonia pyxidata	6
Cladonia rangiferina	5
Cladonia stellaris	5
Cladonia subfurcata	4
Cladonia uncialis	5
Coelocaulon aculetaum	5
Flavocetraria cucullata	2
Flavocetraria nivalis	3
Hypogymnia physodes	6
Hypogymnia austerodes	3
Melanelia sp.	NA
Ochrolechia sp.	NA
Ochrolechia frigida	4
Parmelia sp.	NA
Peltigera sp.	NA
Pertusaria sp.	NA
Pertusaria dactylina	4
Pseudephebe sp.	NA
Solorina crocea	4
Sphaerophorus globosus	5
Sphaerophorus fragilis	4
Stereocaulon sp.	NA
Thamnolia vermicularis	2
Umbilicaria sp.	NA

Table S12: Altitudinal ranks for the bryophytes on the GLORIA summits at Dovrefjell.

Species	Altitudinal rank
Andrea rupestris	6
Anthelia sp.	NA
Barbilophozia lycopodioides	6
Bryum sp.	NA
Ceratadon purpureus	6
Dicranum sp.	NA
Grimmia cf. funalis	3
Gymnomitrion concinnatum	2
Hepathica sp.	NA
Hylocomium splendens	6
Kiaeria sp	NA
Lophozia cf. ventricosa	6
Pleurozium schreberi	6
Pogonatum sp.	NA
Pohlia sp.	NA
Polythrichum alpinum	6
Polytrichum hyperboreum	4
Polytrichum juniperinum	6
Polythrichum piliferum	6
Polytrichum sexangulare	2
Ptilidium ciliare	6
Racomitrium lanuginosum	6
Racomitrium microcarpon	6
Tetraplodon mnioides	6
Tetralophozia setisformis	6