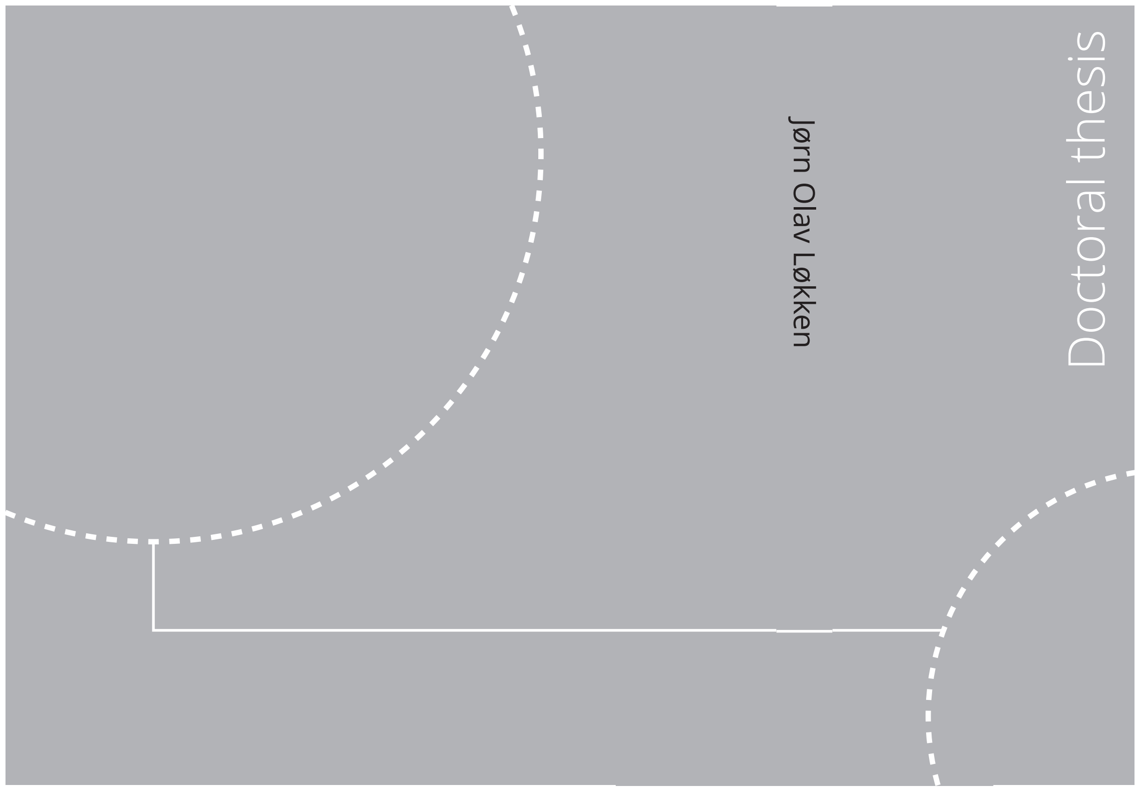
ISBN 978-82-326-4990-7 (printed ver.)
ISBN 978-82-326-4991-4 (electronic ver.)
ISSN 1503-8181



Doctoral thesis

Jørn Olav Løkken

Doctoral theses at NTNU, 2020:321

NTNU
Norwegian University of
Science and Technology
Thesis for the degree of
Philosophiae Doctor
Faculty of Natural Sciences
Department of Biology

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effects of climate warming and herbivory

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PRINTED IN
NORWAY
NO - 1598

NORDIC SWAN ECOLABEL
Printed matter
2041 0731

Printed by Skipnes Kommunikasjon AS

Preface

What a long, strange trip it's been, and a lot of people have crossed my path through this seemingly never-ending story. But now's the time that we've at the end of the line. It's time for the thanks:

First of all, I want to thank my supervisors: Annika Hofgaard, Marianne Evju, Lars Söderström and Richard Strimbeck. In particular Annika, for teaching me the scientific crafts, your impressive ecological knowledge and ability to read nature like an open book, and your attention to details: "It's a sophism that in ecology simple answers can be given to seemingly simple questions". Marianne for teaching me the value of doing it badly and worry later, and for guiding me through data analysis without losing track of what's important: "Do not get the proverbial statistical chart in front of your ecological horse". I would also like to thank Håkan Hytteborn and Linda Dalen for their contribution to the Kongsvoll-paper, and particularly to Håkan for getting me started in the treeline business all those years ago!

I would thank the ECOFUNC team; In particular my fellow PhD-student Lars Rød-Eriksen for always being on the other side of that tiny desk wall and battling through the ups and downs of PhD-life alongside me, and for valuable inputs on life, ecology and R-scripts (not necessarily in that order..). Finishing up this from my home office just isn't the same when I can't whisper "Lars! Lars! Lars!" over that tiny wall in times of need. Nina Eide, for holding the project together and for your support through the ups and downs, Stefan Blumentrath for providing GIS data, and all the rest of you for support and for insight into the ecology of arctic and not so arctic foxes.

I would also like to thank everyone who contributed to the field work: Anaïs for keeping up with me as only company for the majority of a summer. The field team in Grødalen: Anna, Lasse and Isabel for your dedication, hard work and good humour even when it snows in August, and to my uncle Per for helping me out with the last stretch. The accommodation and employees at Gjøra camping for shelter and support. The Dahlbergs for housing us during the stay in Bjerka, and for feeding us waffles and wiener pecans when we needed it the most. Länsstyrelsen Västerbotten and in particular Tomas Staafjord for the exceptionally fast application processing, giving us the permission to conduct our study in Vindelfjällen nature reserve on a days' notice. Also, thanks to Barbro Dahlberg, who counted a majority of the tree rings.

Colleagues at NINA, Signe CD, your view from ahead of the curve have always been a great support (I still regret losing that manuscript submission contest though…). Anne and Lasse, it was a pleasure to see the PhD-legacy of NINA continued, and in particular with such fine specimens as you. Heidi for teaching me the ropes of NiN nature mapping which I swore to never do again… Signe N, Inga and Jørgen for being there when I needed you. Thank you to all the other at NINA I have interacted with through the years (in particular those interested in botany and Pokémon's) for the work hours in field and office, lunches, Friday cakes and other scientific and social gatherings, discussing weird species (ants!), biology and the mysteries of life.

My new colleagues at NaturRestaurering AS for trusting me, even though I hadn't finished what I've started, and for giving me the time to finish what I started, for teaching me how to bash out text at highspeed and being the best colleagues I could ask for!

All the people who made the life part of the work-life balance enjoyable and full of shenanigans: the climbers, the capoeiristas, the quizzer, the bacalao aficionados, the MUDers, the punks, the geeks, the freaks, and all the others. Childhood friends, old friends, new friends and not so new friends, I would name you all, but I don't know where to start or where to end…

My family for your ever-present, never-ending well of support: mamma, pappa and syster!

Linnea for keeping me company in my home office during the last stretch.

Siri, you are the most important of all. Your love is my rock in the weary land, my shelter from the storm.

Styggen på ryggen: Du kan ta deg en bolle.

Jørn Olav Løkken,
Ås, April 2020

Abstract

The transition between closed forest and alpine areas, the forest-tundra ecotone (FTE), is on the global scale expected to be coarsely regulated by temperature. Thus, due to predictions for climate warming the ecotone is anticipated to change, with upward altitudinal shifts and reorganizing of mountain vegetation. However, at local scales, responses often deviate from the global trend due to counteracting abiotic and biotic factors.

The aim of this thesis is to investigate some of the factors affecting mountain birch FTE dynamics at a local scale, with a focus on climate warming and land-use, and the interaction between them. The research questions were addressed by an experimental study comparing effects of sheep grazing and climate warming on sapling growth and ground-layer composition, a resurvey of vegetation composition and forest structure in permanent plots along altitudinal transects covering a time-period of 22 years, and a dendroecological study of age structure and physiognomics of treeline trees and saplings along coast-inland and altitudinal gradients.

The experiment revealed sheep grazing to be a strong factor counteracting warming effects on sapling growth. Ground-layer composition responded stronger to warming than the sapling layer, but with timing differences, illustrating the importance of long-term experiments. The resurvey revealed a consistent upward shift of field-layer vegetation, but responses were highly species dependent. However, there was no upward shift of neither the tree layer nor the sapling layer. The tree layer showed no overall changes in physiognomics (height, number of trees), although there was a turnover of trees in the 22-year period. The dendroecological study showed that a difference along the coast-inland gradient with higher treeline altitude and growth rate, and larger trees in the inland site compared to the coastal site. Both the resurvey and the dendroecological study showed saplings to be present hundreds of altitudinal meters beyond the tree-/forest line.

Jointly considering the results of these studies, grazing by domestic sheep is found to be a factor strongly counteracting effects of climate warming on the FTE, in particularly restricting growth of saplings into tree size. Vegetation in the field-layer did, however, respond more to the warming than the sapling- and tree-layer. This layer discrepancy stands in contrast to the common assumption that an upward shift of saplings and trees will precede upward movements of the field-layer. This thesis shows how different methods are complementary in gaining deeper insight into FTE dynamics. In light of climate warming and land-use change in detailed site studies provide valuable local scale data for upscaling and calibration of models projecting future scenarios.

Sammendrag

Overgangen mellom tett skog og fjellområder, skog-tundra-økotonen, er globalt i stor grad regulert av temperatur. Økt temperatur som følge av klimaendringer forventes å påvirke økotonen, med høydeforflytning av vegetasjon oppover i landskapet og endret artssammensetning. På lokal skala avviker responsene i økotonen ofte fra den globale trenden på grunn av motvirkende abiotiske og biotiske faktorer.

Målet med denne avhandlingen er å undersøke noen av faktorene som påvirker lokal dynamikk i fjellbjørkdominerte skog-tundra-økotoner, med fokus på temperaturøkning og arealbruk og samspillet mellom disse faktorene. Forskningsspørsmålene ble undersøkt ved hjelp av et eksperimentelt studium som sammenlikner effekter av sauebeite og økt temperatur på småbjørk og vegetasjonssammensetningen i feltsjiktet, en re-kartlegging (etter 22 år) av vegetasjonssammensetning og skogstruktur i permanente ruter langs høydetransekter, og et dendroøkologisk studium av aldersstruktur og fysiognomi hos tregrensetrær og småbjørk langs kyst-innlandsgradienter og høydegradienter.

Eksperimentet viste at sauebeite motvirker effekten av oppvarming på veksten av småbjørk. Vegetasjonen i feltsjiktet responderte sterkere på oppvarming enn busksjiktet, men med klare tidsforskjeller mellom artsgrupper, noe som illustrerer viktigheten av eksperimenter som går over lengre tidsperioder. Re-kartleggingen viste en jevn høydeforflytting av vegetasjonen i feltsjiktet oppover i landskapet, men at responsene varierte fra art til art. Verken tresjiktet eller busksjiktet forflyttet seg oppover i samme periode. Tresjiktet viste heller ingen generelle endringer i fysiognomikk (høyde, antall trær), selv om det foregikk en utskiftning av trær i 22-årsperioden. Den dendroøkologiske studien viste en forskjell mellom kyst og innland der tregrensen, vekstraten og trehøyden var høyere i innlandet sammenlignet med ved kysten. Både gjentaksstudiet og den dendroøkologiske studien viste at småbjørk var til stede hundrevis av høydemeter over tregrensen.

Resultatene fra disse studiene viser at sau på utmarksbeite er en faktor som sterkt motvirker effekten av temperaturøkning på skog-tundra-økotonen, særlig ved å begrense veksten hos mindre bjørkeindivider til trestørrelse. Vegetasjonen i feltsjiktet reagerte derimot mer på oppvarmingen enn småtrærne og tresjiktet. Denne forskjellen i respons mellom de ulike sjiktene står i kontrast til den generelle antakelsen om at busk- og tresjiktet vil respondere før feltsjiktet. Denne avhandlingen viser hvordan ulike metoder kompletterer hverandre og kan gi dypere forståelse for dynamikken i skog-tundra-økotonen. Sett i lys av klimaendringer og endringer i arealbruk kan detaljerte feltstudier gi verdifulle data for oppskalering og kalibrering av modeller for fremtidige scenarier.

List of papers

I. Løkken, J. O., Hofgaard, A., Dalen, L., Hytteborn, H. 2019. Grazing and warming effects on shrub growth and plant species composition in subalpine dry tundra: An experimental approach. *Journal of Vegetation Science* 30(4): 698-708

II. Løkken, J. O., Evju, M., Söderström, L., Hofgaard, A. Vegetation response to climate warming across the forest-tundra ecotone: species-dependent upward movement. *Re-submitted to Journal of Vegetation Science 19.03.2020*

III. Løkken, J. O., Evju, M., Söderström, L., Hofgaard, A. Tree and sapling turnover but no advance of the forest-tundra ecotone over a 22-year warming period in Central Norway. *Manuscript*

Author contributions

Paper I:
HH & AH initiated and designed the study. LD lead the field sampling and provided the data from 1999-2002. AH, HH & JO provided the data 2005-2017. JOL performed the analysis with input from AH and HH. JOL drafted the paper in collaboration with all co-authors (AH, HH, LD). Final version of the manuscript read and approved by all co-authors.

Paper II & III:
AH initiated and designed the study and provided the 1994 data. JOL lead the field sampling in 2016. JOL performed the analysis with input from ME and AH. JOL drafted the papers in collaboration with all co-authors (AH, ME, LS). Final version of the manuscript read and approved by all co-authors.

General introduction:
JOL lead the field sampling and provided the age data. Initial drafts of the manuscripts read and commented upon by AH and ME.

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General introduction

Introduction

The ecotone between the dense forest and the treeless alpine areas, the forest-tundra ecotone (FTE; i.e. including forest line, treeline and species line) is a visually striking boundary between ecosystems that have intrigued ecologists for centuries (cf. Holtmeier, 2009 and refences therein). Early in the 20th century, the mechanisms behind the position of the FTE started to be investigated. Temperature was among the first factors regarded as a regulator of tree growth and development, and in particular the 10°C isocline of the warmest month was linked to the upper position of trees (Andersson, 1902; Daubenmire, 1954; Grace, 1989; Wardle, 1971). More recent research into temperature limitation of the FTE has narrowed the global range to a mean root zone temperature of 6.7 °C ±0.8 during the growth season (Körner & Paulsen, 2004). This is linked to a lower temperature threshold for growth and tissue formation (Hoch & Körner, 2009; Körner et al., 2016), and more specifically, freeze tolerance of tissue in spring and length of the photoperiod for maturation of tissue (Körner et al., 2016).

During the last decades, high-latitude and high-altitude areas have experienced increasingly warmer temperatures, and the increase is predicted to continue in the current century (IPCC, 2014). This warming has sparked a renewed interest in FTE dynamics, as the ecotone is assumed to advance with increasing temperatures (ACIA, 2005; Grace, Berninger, & Nagy, 2002). An advance of the boreal forest into alpine ecosystems would lead to fragmentation and loss of alpine areas (ACIA, 2005; Chapin, Shaver, Giblin, Nadelhoffer, & Laundre, 1995), as well as a reduction of albedo and a possible decrease of total ecosystem carbon pools (de Wit et al., 2014; Sørensen et al., 2017). Climate warming is expected to cause alterations in ecological systems, including changes in plant species distribution, composition and growth (Bjorkman et al., 2018; Elmendorf et al., 2012; Steinbauer et al., 2018). The presence of a tree-layer is important for the composition of vegetation in the field-layer (Hofgaard & Wilmann, 2002; Sundqvist, Björk, & Molau, 2008). However, vegetation in the field-layer has been found to be less sensitive to air temperature than the tree-layer (Lenoir et al., 2013; Scherrer & Körner, 2010). The field-layer vegetation might therefore respond independently from the tree-layer to a warming climate (Batllori, Blanco-Moreno, Ninot, Gutiérrez, & Carrillo, 2009; Camarero, Gutierrez, & Fortin, 2006).

Studies of forest encroachment rate, and consequences to biodiversity and ecosystem interactions, require detailed data from natural environmental gradients in combination with long-term monitoring and experimental data. A range of methods exist to assess and predict ongoing and future changes of plant communities as well as FTE dynamics (Danby, 2011; Elmendorf et al., 2015). Methods include resurveys of field plots and transects, repeat photography, dendrochronology, use of historical records, remote sensing, monitoring and experiments (Danby, 2011; Elmendorf et al., 2015). The temporal and spatial scale of these methods vary, as do the limitation and benefits of each method (Danby, 2011). To untangle the variation in FTE responses to climate warming and assess and calibrate future models of change all these methods must be used in interaction at both global and local scales (Bryn & Potthoff, 2018; Danby, 2011).

A global meta-study of altitudinal FTE advance over the last century found that only ca. half (52%) of the included FTE sites showed an upward movement, a small fraction (2%) downward, while remaining sites (46%) were stationary (Harsch, Hulme, McGlone, & Duncan, 2009). This heterogeneity in responses, including lack of advancing behaviour for ca. half of the sites, calls for consideration of the importance of a diversity of abiotic and biotic drivers and their interactions when addressing the topic of FTE advance (Hofgaard, Harper, & Golubeva, 2012; Holtmeier & Broll, 2005).

At the local landscape scale, a broad range of regulating factors come into play, leading to a larger variation and complexity in the position of and responses to temperature change of the FTE (Holtmeier & Broll, 2005). In a review of FTE changes in Norway, Bryn and Potthoff (2018) acknowledge that there is large inter-site variation and need for a better understanding of "the role of proximate and ultimate drivers, and especially interactions and feedbacks among them". Land-use in the form of livestock grazing and summer farms is a central factor in Norwegian mountains (Olsson, Austrheim, & Grenne, 2000), often hampering growth of tree species, and restricting upwards advancement due to warming (Aune, Hofgaard, & Söderström, 2011; Hofgaard, Løkken, Dalen, & Hytteborn, 2010; Speed, Austrheim, Hester, & Mysterud, 2010). However, it is often difficult to disentangle the effect of climate warming from the effect of changed land-use practices on the FTE (Bryn, 2008; Gehrig-Fasel, Guisan, & Zimmermann, 2007).

Mountain birch (*Betula pubescens* spp. *tortuosa* (Ledeb.) Nyman) is a low stature tree species typically making up the FTE in Scandinavia. The species can grow in a variety of forms; from shrubby multi-stemmed individuals to tall single-stemmed individuals (Wielgolaski, 2005). Mountain birch is an important food source for a range of wild, semi-domestic and domestic herbivores (including foliovorous insect herbivores such as the autumnal moth (*Epirrita autumnata* (Borkhausen)) and winter moth (*Operophtera brumata*

(L)) (Moen, Cairns, & Lafon, 2008; Tenow, 1996; Van Bogaert, Jonasson, De Dapper, & Callaghan, 2009). Studies of FTEs in Norway is challenging and interesting since it is largely dominated by a deciduous species (mountain birch), maintains long legacies of land-use, and encompasses large topographic variation (Bryn & Potthoff, 2018; Olsson et al., 2000).

Questions

In this thesis I investigate some of the factors affecting mountain birch FTE dynamics at a local scale, with a focus on climate warming and land-use, and the interaction between them. The main study sites were located in central Norway (Fig. 1). Additional data collected on age structure and physiognomics of birch trees and saplings along two altitudinal gradients in the central Scandes mountain are presented in this general introduction (hereafter referred to as "**age data**"). This is used to highlight conclusions drawn from the main studies. This data area geographically complement available age structure data from similar studies done along coastal – inland gradients (Albertsen, 2012; Aune et al., 2011; Kermagoret, 2015) and a latitudinal gradient (Dalen & Hofgaard, 2005; Hofgaard, Dalen, & Hytteborn, 2009). Specifically, I ask:

1) How has the FTE changed over the last decades, a time period characterized by climate warming (**II**, **III**, **age data**)

2) Does change in plant biodiversity in the field-layer track the rate of change of the tree layer (**I**, **II**, **III**)

3) How does land-use affect FTE dynamics, and how do these effects interact with climate warming (**I**, **II**, **III**, **age data**)

4) How can different methods (experiment, resurvey and dendroecology) work together to gain better insight into FTE dynamics (**I**, **II**, **III**, **age data**)

These questions were addressed by:

a) An experimental study comparing the effects of domestic sheep grazing and climate warming on sapling growth and field-layer vegetation (**paper I**).
b) A resurvey of plant biodiversity and forest structure along altitudinal transects (**paper II & III**).
c) Age and physiognomic data of treeline trees and saplings collected along altitudinal transects (**age data**)

Methods

Study areas

Field work for this thesis was carried out at four different study sites (Fig. 1). The study in **paper I** was conducted at Kongsvoll, Dovre Mountains, Central Norway (62°18′ N, 9°37′ E), at 1090 m a.s.l. in the ecotone between the closed mountain birch forest at lower altitudes and the treeless region at higher altitudes. The studies in **paper II** & **III** were conducted along the transition from the boreal forest to the open alpine tundra in Grødalen, Central Norway (Lat. 62°30’N-62°36’N, Long. 8°50’E-9°13’E). The study site at Kongsvoll have a slightly continental climate characterized by low annual precipitation, cold winters and relatively warm summers, while Grødalen is slightly oceanic characterized by high precipitation and relatively warm winters and cool summers (Moen, 1999). The temperature at both study sites increased significantly during the study periods. The mean annual temperature increased by 1.1°C over the 18-year study period at Kongsvoll, and 1.2°C over the 22-year study period in Grødalen (Norwegian Meteorological Institute, 2019). For further details on climate, see the respective papers.

The **age data** were collected in two areas in the central Scandes mountains: Bjerka, Norway (Lat. 66°17’N, Long. 13°9’E) and Hemavan, Sweden 65°51' N E14° 54'E). Bjerka has a slightly oceanic climate (Moen, 1999), while Hemavan is more continental. Mean annual temperature at Hemavan (1960-2014) was –0.3°C, and 0.9°C at Bjerka. At both sites temperature increased substantially over the period. Total annual precipitation at Hemavan was 810 mm while at Bjerka it was 1458 mm. Precipitation did not change substantially during this period in any of the sites. (Norwegian Meteorological Institute, 2020; Swedish Meteorological and Hydrological Institute, 2020) (See appendix 1 for temperature trends). Both study areas are located in the transition between the boreal forest and the alpine zone. According to statistics on domestic grazing (available 1992-present) the study site at Bjerka has not been used for domestic grazing in the period with available data (NIBIO, 2020). The site at Hemavan is grazed by semi-domestic reindeer, belonging to Ubmeje “sameby”. Although our site is managed within a year-round grazing area, the study site is mainly used (spring, summer, autumn) with peak in late summer (The Sami Parliament, 2020).

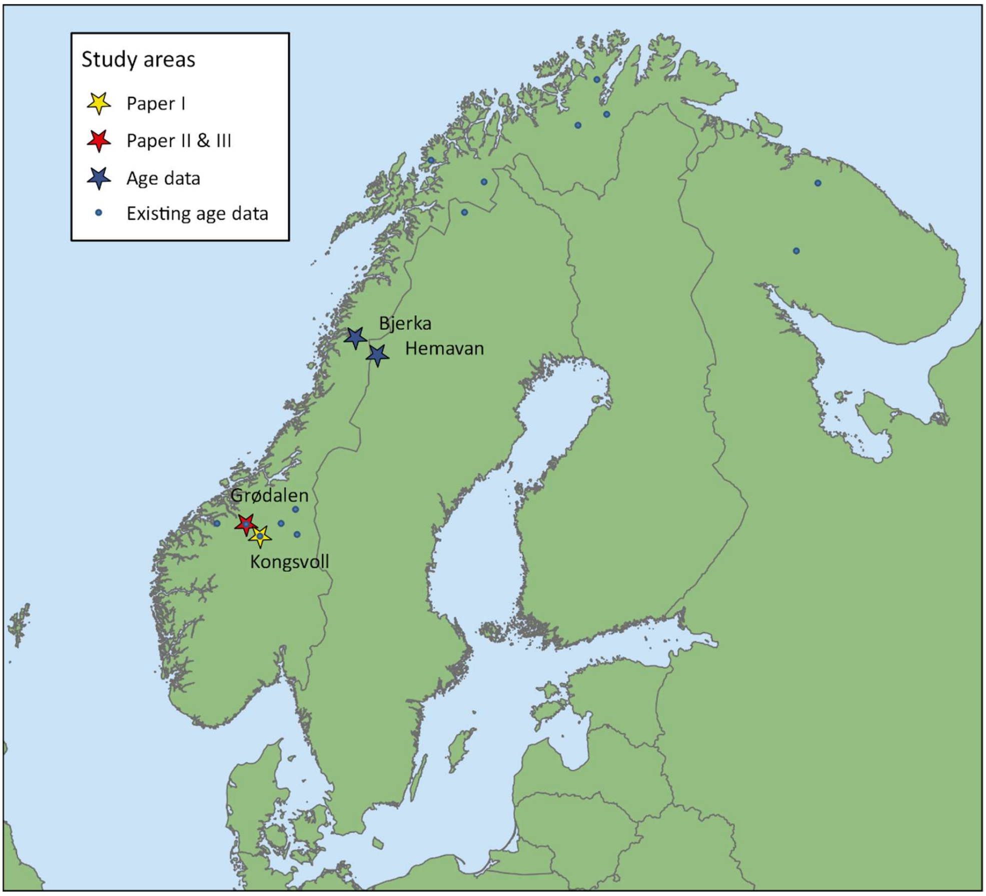


Fig. 1. Map of the study areas and their associated papers. Blue dots show study sites for previously collected age data.

Study design

Paper I used a nested, three-factorial experiment with plots distributed among three treatments: ambient grazing and ambient temperature, no grazing and ambient temperature using exclosures, and no grazing combined with experimental increased temperature using exclosures and open-top chambers (Fig. 2. See paper I or Molau and Mølgaard (1996) for a description of the open-top chambers). In each plot changes in shrub height, shrub cover and ground-layer composition (joint bottom- and field-layer) were measured every third year over a 18-year period from 1999 to 2017.

Fig 2. The experimental site at Kongsvoll.

Paper II & **III** used data from permanent 10 × 10m plots along altitudinal transects from forest to high alpine areas (Fig 3). The initial analysis was conducted in 1994 and the plots were resurveyed in 2016, thus covering a 22-year period. Along the transects data on identity, distribution and abundance of vascular plant species were recorded in 1 × 1m quadrats within the plots (**paper II)**. Data on tree distribution, stand structure and recruitment were collected at the plot level (**paper III**). Environmental factors related to local topography and bedrock were also recorded (**paper II** & **III**).

Fig. 3. Work in one of the plots in the study for paper II & III in Grødalen.

The field work to collect **age data** was carried out in august 2015. The study was established at gentle, south-facing slopes at each study site. The altitude and location of the ten uppermost tree individuals taller than 2 m height (i.e. treeline markers), and at least 50 m horizontal distance to the next individual tree or small group of trees were identified. These trees are hereafter referred to as “treeline trees”. To determine the age at establishment, all treeline trees were cored using an increment borer at the base of the stem. The treeline trees were also cored at 2 m height to determine the time spent to reach tree size. Cores were mounted on wooden supports, dried and transported to the lab for age determination. In addition, the height, basal diameter, crown diameter (length and width), and stem diameter at breast height (DBH) of each treeline tree were recorded. The treeline altitude was calculated as the mean altitude of treeline tree positions. Number of saplings / ha was calculated for each individual plot. Growth rate was calculated as height/age. Crown size was calculated by using this formula:

$$\text{crown size} = \pi((\text{width}+\text{length})/4)^\wedge 2)$$

To assess age structure and physiognomics of the sapling pool above the treeline, we established 50 × 20 m plots from the treeline to the summit. Plots were placed with an altitudinal distance of 50 meters from (and including) the treeline altitude (i.e.: TL, 50, 100, 150, 200, 250). The highest plot was located at 200 and 250 meter above the treeline at Hemvan and Bjerka, respectively. At each altitude level, plots were established until a minimum number of 100 saplings, or a maximum of 8 plots had been analyzed.

Within each plot, all birch saplings were identified, and the following physiognomic variables were recorded: height (cm), crown diameter, basal diameter, GPS location and surrounding vegetation. Finally, all saplings were cut at the base and a basal disc collected for age determination. Growth rate and crown size of saplings were calculated in the same way as for the treeline trees.

Age was determined in the lab using cores from the treeline trees and basal discs from the saplings. Cores and discs were smoothed with a scalpel and smeared with zinc ointment to improve ring visibility (Fig. 4). Age was determined by counting the tree rings using a stereomicroscope (6-40×).

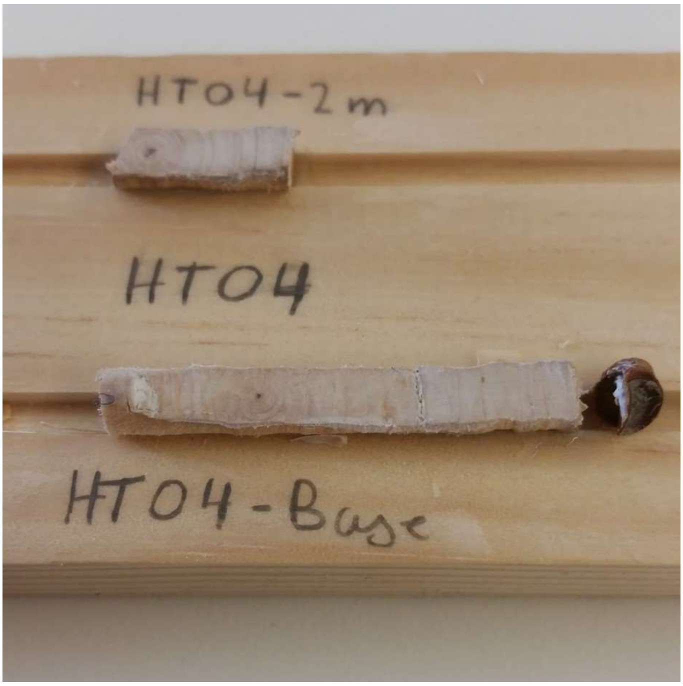


Fig. 4. Mounted and smoothed cores from treeline trees.

Results

Experimentally testing the effects of sheep grazing and warming on sapling growth and field-layer composition in **paper I** revealed sheep grazing to be a strong factor counteracting warming effects on sapling growth. The study also revealed stronger effects of warming on the composition in the ground-layer, but with timing differences between responses, most notably an initial rapid decline of lichens and an accumulation of litter over time. **Paper II** and **III** highlight the layer-specific responses found in **paper I**: We found no altitudinal advance of the FTE or significant increase in number of trees or saplings in **Paper III**. The study of field-layer changes in **paper II** did, however, reveal a change in vegetation composition with an estimated upward shift rate of 0.5±0.1 m yr^{-1}, with a homogenization of vegetation across the ecotone. Further, the study showed a general increase in species diversity, with the strongest increase in the lower end of the transects. Change in species abundance varied between species, and species responses varied within the respective functional groups. In **paper III** we found a turnover of both saplings and trees in the ecotone, but no altitudinal advance of either. Further, we did not find significant change in tree layer physiognomics (height and number of trees). Despite no significant overall change in the number of saplings, there was a significant interaction with altitude. This interaction revealed a decline in the number of saplings in the forested part accompanied by an increase above the forest line. Both the sapling layer and the tree layer physiognomics was to some extent regulated by local topography and bedrock.

The **age data** show that at Hemavan the mean treeline was located at 791 m a.s.l., 171 m higher than at Bjerka where it was located at 620 m a.s.l. (Table 1). The trees at the treeline were established in the mid 1960s at both sites (1966 and 1962, respectively). The treeline trees at Hemavan spent on average 21 ±10.2 years growing into tree size (2 m), while at Bjerka it took 39 ±16.0 years. The average year for growing into tree size was 1987 for Hemavan , and 2001 for Bjerka (Table 1, Fig. 5). There was a difference in height of the treeline trees at the two sites, where the mean height was 409 cm at Hemavan, and 268 at Bjerka.

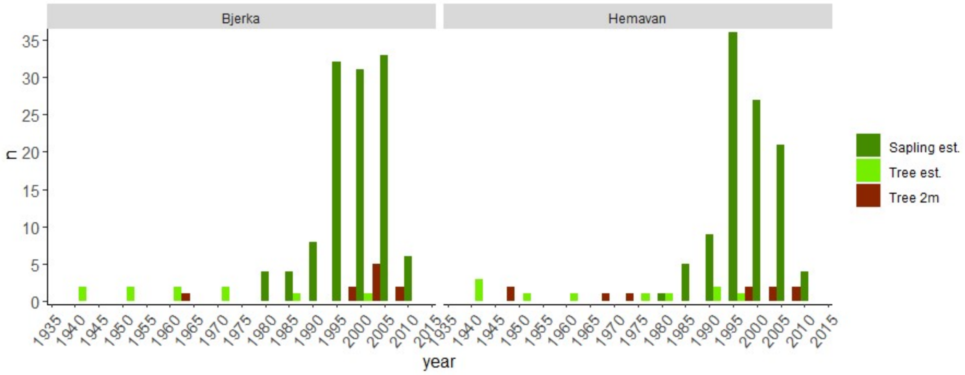


Fig. 5. Time of establishment of trees and saplings, and growth into treeline tree (2 m tall), at treeline altitude for the two sites (data is aggregated at 5-year spans).

Table 1. Main properties of treeline trees.

Site	**treeline (altitude)**	**SD**	**established (year)**	**SD**	**2 m level (year)**	**SD**	**time to tree (years)**	**SD**	**height (cm)**	**SD**
Hemavan	791	9.3	1966	23.4	1987	24.4	21	10.2	409	132
Bjerka	620	8.2	1962	18.9	2001	13.1	39	16.0	268	61

The majority of saplings at Hemavan established 1998 ± 7 years, and at Bjerka 1999 ± 7 years. At both sites there were saplings up to 200 altitudinal meters above the treeline (Fig. 6, appendix 2). This was the highest plots at Bjerka, and no saplings were found beyond this. At Hemavan no saplings were found in the plots at 250 m above the treeline. All tested variables characterizing sapling age, no/ha, and physiognomy significantly correlated with distance to the treeline, but with large differences in correlation factor (Kendall's non-parametric correlation coefficient tau; τ): Number of saplings per ha correlated best (–0.34, Table 2), while age had a low correlation factor. The correlation between altitude and physiognomics was weaker at Bjerka than at Hemavan, and the correlation between altitude and age was not significant at Bjerka (p=0.831, Table 2). Age was significantly correlated with all physiognomic variables, but correlated strongest with stem diameter (0.45, Table 2).

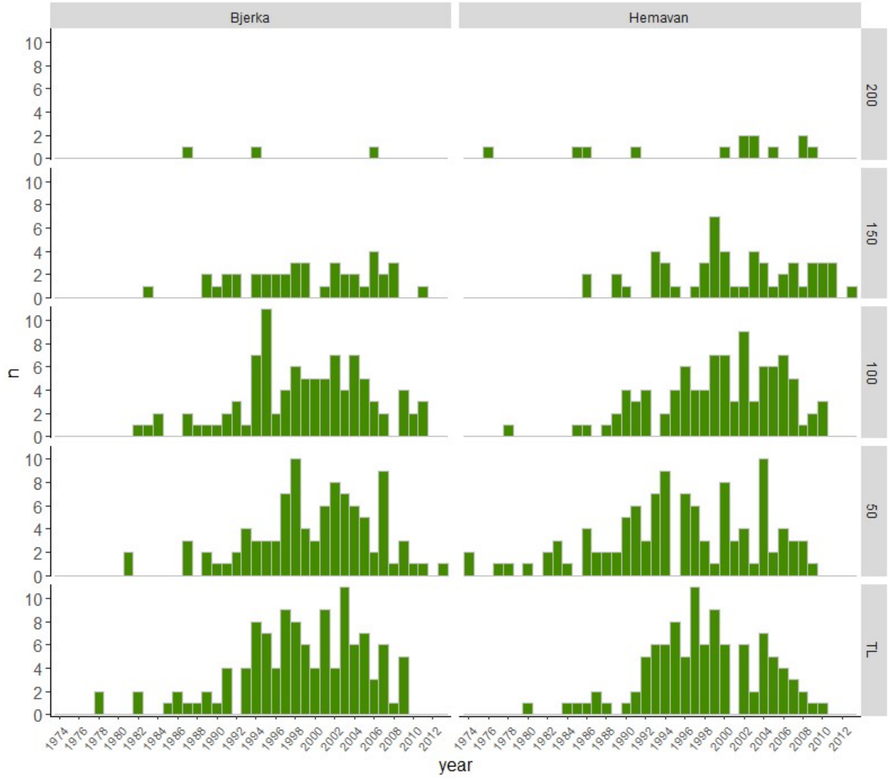


Fig. 6. Time of establishment of saplings, split in area and distance to treeline.

Table 2. Kendall's non-parametric correlation coefficient (τ) and associated p-value between a) altitude and sapling age, saplings per ha and physiognomic measures (stem diameter, crown size and height), and growth rate, and b) between sapling age and the physiognomic measures.

		overall		**Hemavan**		**Bjerka**	
	variable	**τ**	**p**	**τ**	**p**	**τ**	**p**
altitude	age	−0.06	0.023	−0.12	0.002	−0.01	0.831
	no/ha	−0.43	<0.001	−0.41	<0.001	−0.37	<0.001
	stem diameter	−0.27	<0.001	−0.40	<0.001	−0.14	0.001
	crown size	−0.31	<0.001	−0.41	<0.001	−0.19	<0.001
	height	−0.34	<0.001	−0.48	<0.001	−0.22	<0.001
	growth rate	−0.29	<0.001	−0.34	<0.001	−0.24	<0.001
age	stem diameter	0.45	<0.001	0.44	<0.001	0.46	<0.001
	crown size	0.33	<0.001	0.27	<0.001	0.40	<0.001
	height	0.24	<0.001	0.17	<0.001	0.32	<0.001
	growth rate	−0.19	<0.001	−0.32	<0.001	−0.07	0.066

Discussion

Most predictions expect increased growth of woody species and elevational advance of the forest-tundra ecotone due to climate warming (ACIA, 2005; Grace et al., 2002; IPCC, 2014). However, the experimental study in **paper I** identified sheep grazing as a strong counteracting regulator of birch sapling growth. Growth restriction of saplings caused by sheep grazing is most likely partly responsible for the lack of FTE advancement observed in **paper III**, since there is no lack of sapling recruitment in the areas above the forest line. The role of herbivory in restricting the growth of saplings and thus advancement of the FTE is known from other studies in Scandinavia (Olofsson et al., 2009; Speed et al., 2010). Thus, we hypothesise that grazing is at least partly responsible for the lack of recruitment from the sapling layer to the tree layer and lack of altitudinal advance of the FTE over the 22-year timespan in **paper III**.

The **age data** reveal local variation in treeline position, tree growth and tree physiognomy. Age distributions at the 2 m level of the treeline trees suggest that both of our study sites have stable to slightly advancing treelines (Dalen & Hofgaard, 2005), but with some variation: At Bjerka, trees were small and had reached tree size recently, while at Hemavan, the trees were taller and the age distribution at the 2 m level slightly more even, suggesting this site to be more stable than the coastal site (Aune et al., 2011; Dalen & Hofgaard, 2005). The slower growth rate and lower height of the treeline trees at Bjerka is in line with those examined along a latitudinal gradient (ranging central to northern Norway) in Dalen and Hofgaard (2005). The treeline trees in Hemavan were both taller and had faster growth rates compared to those recorded along the latitudinal gradient (Dalen & Hofgaard, 2005), but reflects the coast-inland trends of a gradient north of the **age data** sites (Aune et al., 2011).

Both **paper III** & **age data** found saplings far beyond the treeline, and in both studies the number and height of saplings declined with increasing altitude, as would be expected if growth and survival is climate dependent. There was, however, low correlation between the age and increasing altitude in the **age data**, which is found in other studies of birch establishment as well (Aune et al., 2011; Kermagoret, 2015). As mountain birch is not seed limited, and seeds can travel by wind far into the alpine zone (Molau & Larsson, 2000), it is hypothesis that climatic favourable years are likely to have stimulated birch seedling establishment (Kullman, 2002). Some have linked higher seedling establishment to warmer than average summers (Kullman, 2002), while other have found effect of higher precipitation in the non-growing season (Aune et al., 2011). As precipitation in the non-growing season mainly comes as snow, this is causally linked to the presence of a protecting snow cover during winter (Aune et al., 2011; Sturm et al., 2001). Thus, as there is substantially more precipitation at the coastal **age data** site, the difference in correlation between the sites might be partly linked to snow cover. Further, the presence of individuals of all age classes at all altitudes show how once established, saplings can survive for a long time in favourable sites far above the treeline. The effect of solar radiation and local topography on the distribution of saplings in **paper III**, underlines that depressions and other forms of shelter, such as boulders and shrubs are important for sapling recruitment and survival (Albertsen, 2012; Dalen & Hofgaard, 2005; Kermagoret, 2015).

Compared to the sapling cohorts in Aune et al. (2011) and Hofgaard et al. (2009), the **age data** cohorts are skewed towards the younger ages (mean age was around 16 years, with the oldest saplings being around 40 year old), and small (mean height 30-40 cm, and only a few reaching past 1 m). At both **age data** sites, the age distribution of treeline trees and saplings is overlapping indicating a climate-related stationary situation (Aune et al., 2011). Assuming the observed growth rate is stable it would take approximately 60 years before the mean population height at treeline altitude reached tree size in Hemavan, and close to 90 years at Bjerka. Jointly considering the growth rate of treeline trees in the **age data** and the small changes of the FTE found in **paper II** & **III** underlines the need to carefully consider time span of studies as the actual climatic response can be hard to separate from what should be considered normal population dynamics (Bryn & Potthoff, 2018; Körner, 2007).

The 22-year study in **paper III** showed no overall changes of the physiognomics of the tree layer, although there was a turnover of trees during the time period. The stable FTE in this study thus falls in line with the 46% of FTE studies with no response to increased temperatures (Harsch et al., 2009). Further, **paper III** reveals, a regulating effect on height and distribution of trees from environmental factors that vary at small spatial scales, as local topography, bedrock and solar radiation. Thus, underlining how the timing and dynamics of change at local scale is contingent on regional-scale factors (Dalen & Hofgaard, 2005; Danby & Hik, 2007; Resler, 2006). Tree mortality varied within the study area, being particularly high in one of the transects (**paper III**). The high mortality is likely causally linked to outbreaks of defoliating insects. As such outbreaks are predicted to increase in both magnitude and frequency in the future because of climate change, they will most likely also play a larger role in regulating FTE dynamics in the future (Seidl et al., 2017; Wielgolaski, Hofgaard, & Holtmeier, 2017).

In contrast to the stability of the sapling-/tree-layer found in **paper III**, the field layer vegetation in **paper II** shifted upwards at a rate of 0.5±0.1 m yr^{-1}. This shift is moderate compared to the increase in temperature over the same period: Assuming a lapse rate of 0.6°C per 100 m of altitude the temperature increase of 1.4°C in the 22-year period represents an upward temperature shift of more than 200 altitudinal meters. Compared to field studies of vegetation change, however, the recorded shift is at a similar order of magnitude as most calculated rates of shifts in species' optimums (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; le Roux & McGeoch, 2008; Lenoir, Gegout, Marquet, de Ruffray, & Brisse, 2008), but in contrast to other studies reporting minor or no signs of upward shifts (Virtanen et al., 2010; Vittoz, Randin, Dutoit, Bonnet, & Hegg, 2009; Wilson & Nilsson, 2009).

The discrepancies in climate responses between the field-layer and the sapling-/tree-layer in the resurvey (**paper II** and **III**) was also found in the experimental study (**paper I**). Both studies found a stronger response to warming in the field-layer compared sapling-/tree-layer. This is somehow surprising given that the field-layer is more decoupled from the climate than the tree-layer, and thus the tree-layer is expected to respond more to climate warming (Lenoir et al., 2013; Scherrer & Körner, 2010). Similar discrepancies are however observed in a FTE study in Finland, where they found changes in the field- and bottom-layer, but no treeline advancement (Vuorinen et al., 2017). Taken together with the findings in **paper II** of species-specific responses, the result might indicate a transition towards novel combinations of tundra and boreal species, or possibly the degeneration of tundra ecosystems (Post et al., 2009; Vuorinen et al., 2017).

Future considerations

This thesis explored some of the local variation in mountain birch FTE dynamics by using a range of methodological approaches. The results from my studies suggest that FTE responses to climate warming will be both layer- and species specific (**paper I**, **II** and **III**), and that interactions with local environmental factors and on-going and changing land-use practices affect these responses. Herbivory will, in particular, cause a restriction on height growth of birch saplings into tree size. This reflects the call for studies of other life stages than trees, such as seeds, seedlings and saplings to fully understand FTE dynamics in a changing climate (Hofgaard, Harper, & Golubeva, 2012; Smith, Germino, Johnson, & Reinhardt, 2009; Sveinbjörnsson, Hofgaard, & Lloyd, 2002). As a decline in the use of remote areas for grazing is commonly seen in Norway and elsewhere in Europe (Austrheim, Solberg, & Mysterud, 2011; Wielgolaski et al., 2017) and saplings are frequently present in the forest–

tundra ecotone and adjacent tundra in the Scandinavian mountains (Aune et al., 2011; Hofgaard et al., 2009; **paper III**; **age data**), a likely future scenario would be increased growth of saplings and subsequent encroachment of the previously treeless tundra areas (Cairns, Lafon, Moen, & Young, 2007; Speed et al., 2010; **paper I**).

This thesis shows how different methods are complementary in gaining deeper insight into FTE dynamics. In light of climate and anthropogenic changes, long-term monitoring and resurveys, in particular of permanent plots will become an invaluable tool to understand FTE responses (Bakker, Olff, Willems, & Zobel, 1996; Bryn & Potthoff, 2018; Kapfer et al., 2016). In the words of Kullman (2010): “An unbiased projection of the art and amplitude of biotic consequences of altered climatic conditions can only be accomplished by long-term in situ monitoring”. The studies conducted in this thesis display some of the strengths and weaknesses of monitoring and experiments. Even though the resurvey study covered 22 years, we detected only minor differences. This underlines the long timespans needed, at least at some sites such as mine, to see statistically strong patterns. Thus, when monitoring studies do not cover long enough timespans, or the driving factors behind the observed changes isn’t clear, other approaches such as dendroecology and experiments can be used to gain more insight. Dendroecology provides data with high temporal resolution, and can provide insight into the dynamics in the time gaps between resurveys, where field recordings, as in **paper III**, can be decades apart (Danby, 2011). Experiments, such as open-top chambers altering temperature, can help untangle the relative importance of factors driving observed changes, yet have shortcomings, such as the risk of experimental artefacts (De Boeck et al., 2015; **paper I**). Detailed site studies form valuable insights at local scales, and can in combination with methods used at larger spatial and temporal scales provide valuable data and insight for upscaling and calibrating of models projecting future scenarios (Bryn & Potthoff, 2018; Danby, 2011; Sveinbjörnsson et al., 2002).

References

ACIA. (2005). *Arctic Climate Impact Assessment*. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

Albertsen, E. (2012). *Tree recruitment in the forest-tundra ecotone. Limitation and facilitation processes in contrasting climatic regions.* (MSc). NTNU, Norway.

Andersson, G. (1902). Zur Pflanzengeographie der Arktis. *Geographische Zeitschrift, 8*(1), 1-23. Retrieved from www.jstor.org/stable/27804181

Aune, S., Hofgaard, A., & Söderström, L. (2011). Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula. *Canadian Journal of Forest Research, 41*(3), 437-449. doi:10.1139/x10-086

Austrheim, G., Solberg, E. J., & Mysterud, A. (2011). Spatio-temporal variation in large herbivore pressure in Norway during 1949-1999: has decreased grazing by livestock been countered by increased browsing by cervids? *Wildlife Biology, 17*(3), 286-298. doi:10.2981/10-038

Bakker, J. P., Olff, H., Willems, J. H., & Zobel, M. (1996). Why do we need permanent plots in the study of long-term vegetation dynamics? *Journal of Vegetation Science, 7*(2), 147-156. doi:10.2307/3236314

Batllori, E., Blanco-Moreno, J. M., Ninot, J. M., Gutiérrez, E., & Carrillo, E. (2009). Vegetation patterns at the alpine treeline ecotone: the influence of tree cover on abrupt change in species composition of alpine communities. *Journal of Vegetation Science, 20*(5), 814-825. doi:10.1111/j.1654-1103.2009.01085.x

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Ruger, N., Beck, P. S. A., . . . Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature, 562*(7725), 57-62. doi:10.1038/s41586-018-0563-7

Bryn, A. (2008). Recent forest limit changes in south-east Norway: Effects of climate change or regrowth after abandoned utilisation? *Norsk Geografisk Tidsskrift - Norwegian Journal of Geography, 62*(4), 251-270. doi:10.1080/00291950802517551

Bryn, A., & Potthoff, K. (2018). Elevational treeline and forest line dynamics in Norwegian mountain areas – a review. *Landscape Ecology, 33*(8), 1225-1245. doi:10.1007/s10980-018-0670-8

Cairns, D. M., Lafon, C., Moen, J., & Young, A. (2007). Influences of animal activity on treeline position and pattern: implications for treeline responses to climate change. *Physical Geography, 28*(5), 419-433. doi:10.2747/0272-3646.28.5.419

Camarero, J. J., Gutierrez, E., & Fortin, M.-J. (2006). Spatial patterns of plant richness across treeline ecotones in the Pyrenees reveal different locations for richness and tree cover boundaries. *Global Ecology and Biogeography, 15*(2), 182-191. doi:10.1111/j.1466-822X.2006.00211.x

Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., & Laundre, J. A. (1995). Responses of Arctic Tundra to Experimental and Observed Changes in Climate. *Ecology, 76*(3), 694-711. doi:10.2307/1939337

Chen, I. C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science, 333*(6045), 1024-1026. doi:10.1126/science.1206432

Dalen, L., & Hofgaard, A. (2005). Differential Regional Treeline Dynamics in the Scandes Mountains. *Arctic, Antarctic, and Alpine Research, 37*(3), 284-296. doi:10.1657/1523-0430(2005)037[0284:Drtdit]2.0.Co;2

Danby, R. K. (2011). Monitoring forest–tundra ecotones at multiple scales. *Geography Compass, 5*(9), 623-640. doi:0.1111/j.1749-8198.2011.00447.x

Danby, R. K., & Hik, D. S. (2007). Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology, 95*(2), 352-363. doi:10.1111/j.1365-2745.2006.01200.x

Daubenmire, R. (1954). Alpine timberlines in the Americas and their interpretation. *Butler University Botanical Studies, 11*(8/17), 119-136. Retrieved from www.jstor.org/stable/41822517

De Boeck, H. J., Vicca, S., Roy, J., Nijs, I., Milcu, A., Kreyling, J., . . . Beier, C. (2015). Global Change Experiments: Challenges and Opportunities. *BioScience, 65*(9), 922-931. doi:10.1093/biosci/biv099

de Wit, H. A., Bryn, A., Hofgaard, A., Karstensen, J., Kvalevag, M. M., & Peters, G. P. (2014). Climate warming feedback from mountain birch forest expansion: reduced albedo dominates carbon uptake. *Global Change Biology, 20*(7), 2344-2355. doi:10.1111/gcb.12483

Elmendorf, S. C., Henry, G. H., Hollister, R. D., Bjork, R. G., Bjorkman, A. D., Callaghan, T. V., . . . Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters, 15*(2), 164-175. doi:10.1111/j.1461-0248.2011.01716.x

Elmendorf, S. C., Henry, G. H., Hollister, R. D., Fosaa, A. M., Gould, W. A., Hermanutz, L., . . . Walker, M. D. (2015). Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. *Proceedings of the National Academy of Sciences, 112*(2), 448-452. doi:10.1073/pnas.1410088112

Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. E. (2007). Tree line shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science, 18*(4), 571-582. doi:10.1111/j.1654-1103.2007.tb02571.x

Grace, J. (1989). Tree lines. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 324*(1223), 233-245. doi:10.1098/rstb.1989.0046

Grace, J., Berninger, F., & Nagy, L. (2002). Impacts of climate change on the tree line. *Annals of Botany, 90*(4), 537-544. doi:10.1093/aob/mcf222

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters, 12*(10), 1040-1049. doi:10.1111/j.1461-0248.2009.01355.x

Hoch, G., & Körner, C. (2009). Growth and carbon relations of tree line forming conifers at constant vs. variable low temperatures. *Journal of Ecology, 97*(1), 57-66. doi:10.1111/j.1365-2745.2008.01447.x

Hofgaard, A., Dalen, L., & Hytteborn, H. (2009). Tree recruitment above the treeline and potential for climate-driven treeline change. *Journal of Vegetation Science, 20*(6), 1133-1144. doi:10.1111/j.1654-1103.2009.01114.x

Hofgaard, A., Harper, K. A., & Golubeva, E. (2012). The role of the circumarctic forest–tundra ecotone for Arctic biodiversity. *Biodiversity, 13*(3-4), 174-181. doi:10.1080/14888386.2012.700560

Hofgaard, A., Løkken, J. O., Dalen, L., & Hytteborn, H. (2010). Comparing warming and grazing effects on birch growth in an alpine environment – a 10-year experiment. *Plant Ecology & Diversity, 3*(1), 19-27. doi:10.1080/17550871003717016

Hofgaard, A., & Wilmann, B. (2002). Plant distribution pattern across the forest-tundra ecotone: The importance of treeline position. *Ecoscience, 9*(3), 375-385. doi:10.1080/11956860.2002.11682725

Holtmeier, F.-K. (2009). *Mountain timberlines: ecology, patchiness, and dynamics* (Vol. 36): Springer Science & Business Media.

Holtmeier, F.-K., & Broll, G. (2005). Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography, 14*(5), 395-410. doi:10.1111/j.1466-822X.2005.00168.x

IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]*. Retrieved from Geneva, Switzerland:

Kapfer, J., Hedl, R., Jurasinski, G., Kopecky, M., Schei, F. H., & Grytnes, J. A. (2016). Resurveying historical vegetation data - opportunities and challenges. *Applied Vegetation Science, 20*(2), 164-171. doi:10.1111/avsc.12269

Kermagoret, A. (2015). *Understanding the characteristics of forest encroachment into tundra ecosystems along environmental gradients in central Norway.* (MSc). Sorbonne Université, France.

Kullman, L. (2002). Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology, 90*(1), 68-77. doi:10.1046/j.0022-0477.2001.00630.x

Kullman, L. (2010). Alpine flora dynamics - a critical review of responses to climate change in the Swedish Scandes since the early 1950s. *Nordic Journal of Botany, 28*(4), 398-408. doi:10.1111/j.1756-1051.2010.00812.x

Körner, C. (2007). Climatic Treelines: Conventions, Global Patterns, Causes (Klimatische Baumgrenzen: Konventionen, globale Muster, Ursachen). *Erdkunde, 61*(4), 316-324. Retrieved from www.jstor.org/stable/25648043

Körner, C., Basler, D., Hoch, G., Kollas, C., Lenz, A., Randin, C. F., . . . Turnbull, M. (2016). Where, why and how? Explaining the low-temperature range limits of temperate tree species. *Journal of Ecology, 104*(4), 1076-1088. doi:10.1111/1365-2745.12574

Körner, C., & Paulsen, J. (2004). A world-wide study of high altitude treeline temperatures. *Journal of Biogeography, 31*(5), 713-732. doi:10.1111/j.1365-2699.2003.01043.x

le Roux, P. C., & McGeoch, M. A. (2008). Rapid range expansion and community reorganization in response to warming. *Global Change Biology, 14*(12), 2950-2962. doi:10.1111/j.1365-2486.2008.01687.x

Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science, 320*(5884), 1768-1771. doi:10.1126/science.1156831

Lenoir, J., Graae, B. J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G., . . . Svenning, J. C. (2013). Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology, 19*(5), 1470-1481. doi:10.1111/gcb.12129

Moen, A. (1999). *National Atlas of Norway: Vegetation*. Hønefoss: Statens Kartverk.

Moen, J., Cairns, D. M., & Lafon, C. W. (2008). Factors structuring the treeline ecotone in Fennoscandia. *Plant Ecology & Diversity, 1*(1), 77-87. doi:10.1080/17550870802246664

Molau, U., & Larsson, E.-L. (2000). Seed rain and seed bank along an alpine altitudinal gradient in Swedish Lapland. *Canadian Journal of Botany, 78*(6), 728-747. doi:10.1139/b00-049

Molau, U., & Mølgaard, P. (1996). *ITEX manual*. Retrieved from Copenhagen: https://www.gvsu.edu/itex/library-8.htm

NIBIO. (2020). NIBIO. Retrieved from https://nibio.no/tema/landskap/kart-over-beitebruk-og-seterdrift/beitestatistikk

Norwegian Meteorological Institute. (2020). eKlima. *eKlima.* Retrieved from http://sharki.oslo.dnmi.no/

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology, 15*(11), 2681-2693. doi:10.1111/j.1365-2486.2009.01935.x

Olsson, E. G. A., Austrheim, G., & Grenne, S. N. (2000). Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960–1993. *Landscape Ecology, 15*(2), 155-170. doi:10.1023/a:1008173628016

Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., . . . Aastrup, P. (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science, 325*(5946), 1355-1358. doi:10.1126/science.1173113

Resler, L. M. (2006). Geomorphic Controls of Spatial Pattern and Process at Alpine Treeline. *The Professional Geographer, 58*(2), 124-138. doi:10.1111/j.1467-9272.2006.00520.x

Scherrer, D., & Körner, C. (2010). Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology, 16*(9), no-no. doi:10.1111/j.1365-2486.2009.02122.x

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., . . . Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change, 7*(6), 395-402. doi:10.1038/nclimate3303

Smith, W. K., Germino, M. J., Johnson, D. M., & Reinhardt, K. (2009). The Altitude of Alpine Treeline: A Bellwether of Climate Change Effects. *The Botanical Review, 75*(2), 163-190. doi:10.1007/s12229-009-9030-3

Speed, J. D. M., Austrheim, G., Hester, A. J., & Mysterud, A. (2010). Experimental evidence for herbivore limitation of the treeline. *Ecology, 91*(11), 3414-3420. doi:10.1890/09-2300.1

Steinbauer, M. J., Grytnes, J. A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., . . . Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature, 556*(7700), 231-234. doi:10.1038/s41586-018-0005-6

Sturm, M., Holmgren, J., McFadden, J. P., Liston, G. E., Chapin, F. S., & Racine, C. H. (2001). Snow–Shrub Interactions in Arctic Tundra: A Hypothesis with Climatic Implications. *Journal of Climate, 14*(3), 336-344. doi:10.1175/1520-0442(2001)014<0336:Ssiiat>2.0.Co;2

Sundqvist, M. K., Björk, R. G., & Molau, U. (2008). Establishment of boreal forest species in alpine dwarf-shrub heath in subarctic Sweden. *Plant Ecology & Diversity, 1*(1), 67-75. doi:10.1080/17550870802273395

Sveinbjörnsson, B., Hofgaard, A., & Lloyd, A. (2002). Natural causes of the tundra-taiga boundary. *Ambio, Spec No 12*, 23-29. doi:10.2307/25094572

Swedish Meteorological and Hydrological Institute. (2020). SHMI weather data. Retrieved from https://www.smhi.se/data

Sørensen, M. V., Strimbeck, R., Nystuen, K. O., Kapas, R. E., Enquist, B. J., & Graae, B. J. (2017). Draining the Pool? Carbon Storage and Fluxes in Three Alpine Plant Communities. *Ecosystems, 21*(2), 316-330. doi:10.1007/s10021-017-0158-4

Tenow, O. (1996). Hazards to a Mountain Birch Forest: Abisko in Perspective. *Ecological Bulletins*(45), 104-114. doi:http://www.jstor.org/stable/20113188

The Sami Parliament. (2020). Karta över årstidsland. Retrieved from ftp://ftp.sametinget.se/webb/sameby/ars/142_ubmeje_arstid.pdf

Van Bogaert, R., Jonasson, C., De Dapper, M., & Callaghan, T. V. (2009). Competitive interaction between aspen and birch moderated by invertebrate and vertebrate herbivores and climate warming. *Plant Ecology & Diversity, 2*(3), 221-232. doi:10.1080/17550870903487456

Virtanen, R., Luoto, M., Rämä, T., Mikkola, K., Hjort, J., Grytnes, J.-A., & Birks, H. J. B. (2010). Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. *Global Ecology and Biogeography, 19*(6), 810-821. doi:10.1111/j.1466-8238.2010.00570.x

Vittoz, P., Randin, C., Dutoit, A., Bonnet, F., & Hegg, O. (2009). Low impact of climate change on subalpine grasslands in the Swiss Northern Alps. *Global Change Biology, 15*(1), 209-220. doi:10.1111/j.1365-2486.2008.01707.x

Vuorinen, K. E. M., Oksanen, L., Oksanen, T., Pyykonen, A., Olofsson, J., & Virtanen, R. (2017). Open tundra persist, but arctic features decline-Vegetation changes in the warming Fennoscandian tundra. *Global Change Biology, 23*(9), 3794-3807. doi:10.1111/gcb.13710

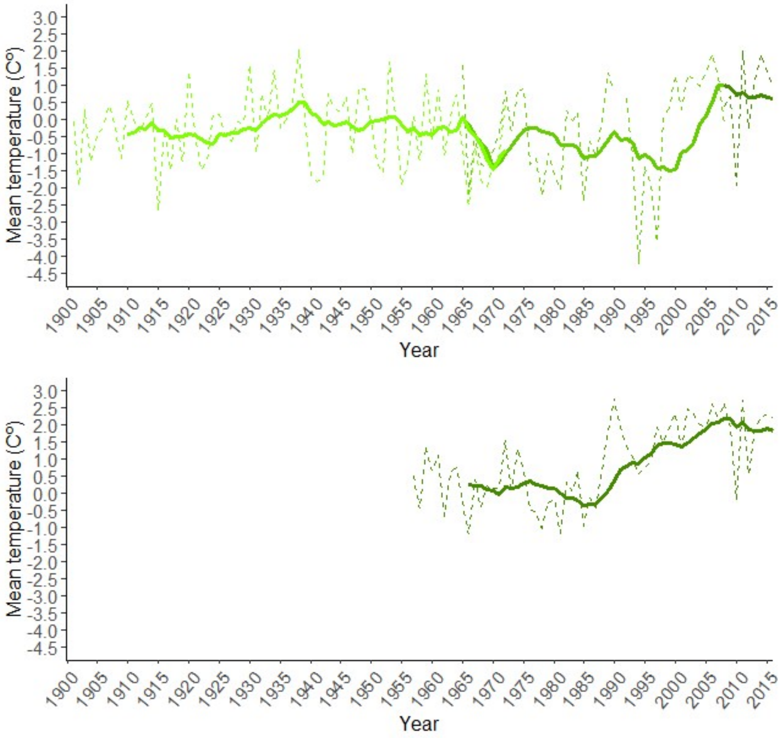
Wardle, P. (1971). An explanation for alpine timberline. *New Zealand Journal of Botany, 9*(3), 371-402. doi:10.1080/0028825X.1971.10430192

Wielgolaski, F. E. (2005). *Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests* (M. M. Caldwell, G. Heldmaier, R. B. Jackson, O. L. Lange, H. A. Mooney, E.-D. Schulze, U. Sommer, F. E. Wielgolaski, P. S. Karlsson, S. Neuvonen, & D. Thannheiser Eds. Vol. 180). Berlin/Heidelberg: Springer-Verlag.

Wielgolaski, F. E., Hofgaard, A., & Holtmeier, F. K. (2017). Sensitivity to environmental change of the treeline ecotone and its associated biodiversity in European mountains. *Climate Research, 73*(1-2), 151-166. doi:10.3354/cr01474

Wilson, S. D., & Nilsson, C. (2009). Arctic alpine vegetation change over 20 years. *Global Change Biology, 15*(7), 1676-1684. doi:10.1111/j.1365-2486.2009.01896.x

Appendix



Appendix 1: Annual mean temperature (dashed line) and ten-year running means (solid line) for annual temperature at Hemavan (upper panel) and Bjerka (lower panel). Data for Hemavan is from three different weather stations: 1900-1972 Tärnaby, 1965-2008 Hemavan, 2008-2015 Hemavan Flygplats. Data for Bjerka is interpolated data for the treeline altitude (1957-2015). Note that the meterological stations at Hemavan is located at 450-482 m a.s.l., while the data for Bjerka is interpolated for 620 m a.s.l. Data source: the Swedish Meteorological and Hydrological Institute (smhi.se) and Norwegian meteorological institute (met.no).

Appendix 2: Properties of the sapling pools at the different altitudes. Plots with * marks altitude levels where less than maximum number of plots were laid out, due to difficult and/or not suitable terrain.

site	**altitude**	**established (year)**	**SD**	**stem diameter (cm)**	**SD**	**crown size (cm²)**	**SD**	**height (cm)**	**SD**	**growth rate (cm/year)**	**SD**	**no / ha**	**SD**	**saplings**	**plots**
Hemavan	TL	1998	5.9	1.1	0.6	776.0	1138.8	44.4	39.8	2.6	1.6	599	466	103	3.25
	50	1995	8.0	0.9	0.8	199.3	365.2	22.9	10.1	1.4	0.8	728	108	107	1.5
	100	1999	6.3	0.6	0.2	56.1	99.4	17.5	7.4	1.3	0.9	307	95	96	3.5
	150	2001	6.9	0.5	0.2	20.2	35.1	12.5	5.6	1.1	0.7	279	50	54	2.0 *
	200	1998	10.4	0.5	0.3	34.0	72.9	12.1	3.9	0.9	0.4	36	12	13	4.0 *
	250	-	-	-	-	-	-	-	-	-	-	-	-	0	2.0
Bjerka	TL	1999	6.6	0.9	0.5	455.1	940.4	31.0	22.1	1.9	1.3	733	254	118	2.0
	50	2000	6.3	0.8	0.4	193.9	447.1	26.1	16.0	1.8	1.2	747	297	98	1.75
	100	1999	6.6	0.7	0.4	235.8	749.6	22.1	15.1	1.4	1.0	260	62	97	4.0
	150	1999	6.6	0.6	0.4	76.1	153.4	13.7	9.5	0.9	0.6	234	138	41	2.6 *
	200	1996	9.6	0.8	0.3	85.7	105.5	15.4	5.3	0.9	0.2	30	1	3	1.0 *

Paper I

Received: 24 March 2018 | Revised: 25 February 2019 | Accepted: 12 March 2019

DOI: 10.1111/jvs12752

RESEARCH ARTICLE

Journal of Vegetation Science

IAVS

Grazing and warming effects on shrub growth and plant species composition in subalpine dry tundra: An experimental approach

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Funding information
The European Commission (ENV4-CT97-0586); NTNU; NINA; The Research Council of Norway (176065/S30, 172529/S30 and 244557/E50).

Co-ordinating Editor: Ingolf Kühn

Abstract

Questions: Vegetation in the forest–tundra ecotone faces changes in both climate and land-use. While climate warming is an important driver of vegetation growth and composition, herbivory may have opposing effects. In the present study, we experimentally test how removal of sheep herbivory affects the vegetation in an alpine forest–tundra ecotone, and how responses are manifested at higher temperatures.

Location: Dovre Mountains, Central Norway.

Methods: Shrub growth (height and cover) and ground layer composition were analysed each third year over an 18-year period in a nested, three-factorial experiment (ambient temperature and herbivory; ambient temperature and no herbivory; increased temperature and no herbivory). Fencing and open-top-chambers were used as expedients. Treatment effects and interactions over time were analysed using linear mixed effects models and ordination.

Results: Shrub height and cover increased over time due to reduced herbivory, but without additional warming effect. Lichen cover declined in all treatments over time, but more rapidly and earlier under warming treatment (significant after three years). Contrary to expectations, there was no statistically significant increase in woody species due to warming, although evergreen woody species displayed a trend shift after six years, comprising a sharp decline towards year twelve. Litter accumulated in all treatments, but at higher rates under warming (significant after nine years).

Conclusions: Our results disclose removal of sheep herbivory as a prominent driver of shrub growth, with warming as a subordinate driver in the studied alpine vegetation. The warming-driven increased litter abundance may, however, be caused by the decrease of wind inside chambers and the subsequent absence of wind-driven removal of litter. This chamber effect and the displayed timing differences in vegetation responses call for the critical use of short-term experimental data in predictions of long-term consequences of environmental change.

KEYWORDS
alpine vegetation, climate warming, exclosure, experimental warming, forest–tundra ecotone, herbivory, long-term experiment, OTC, plant community, shrub growth

1 | INTRODUCTION

During the last decades, high-latitude and high-altitude areas have experienced increasingly warmer temperatures, and the increase is predicted to continue in the current century (IPCC 2013). This warming is expected to cause alterations in ecological systems, including changes in plant species distribution, composition and growth (Bjorkman et al., 2018; Callaghan et al., 2004; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; IPCC, 2013).

In northern European alpine areas, land-use in the form of sheep herbivory is an important driver interacting with the warming (Ross et al., 2016). While climate warming affects vegetation change in terms of increased growth and as driver of community changes, herbivory may have a dampening or opposing effect (Hofgaard, 1997; Kaarlejärvi, Eskelinen, & Olofsson, 2013; Olofsson et al., 2009; Post & Pedersen, 2008). Herbivory affects plant species and communities through biomass removal, and by hampering growth, reproduction, and recruitment (Augustine & McNaughton, 1998; Mulder, 1999). Further, selective foraging and changes in nutrient cycling may favour certain species over others (Augustine & McNaughton, 1998; Mobæk, Mysterud, Loe, Holand, & Austrheim, 2009).

In the forest–tundra ecotone, the open tundra meets the boreal forest, and with rising temperatures, boreal forest is expected to advance into the tundra (Chapin et al., 2005; Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; Tape, Sturm, & Racine, 2006). However, as shown over recent years there is a considerable inertia in this response, causing a mismatch between predictions and observed changes (Harsch, Hulme, McGlone, & Duncan, 2009; Hofgaard, Tømmervik, Rees, & Hanssen, 2013; Van Bogaert et al., 2011; Vittoz, Randin, Dutoit, Bonnet, & Hegg, 2009). The growth and abundance of woody erect species such as trees and shrubs, are detrimental to both the prevalence and structure of tundra ecosystems in a changing climate (Callaghan et al., 2002; Hofgaard, 1997; Hofgaard, Dalen, & Hytteborn, 2009; Holtmeier & Broll, 2005; Myers-Smith et al., 2011; Tape et al., 2006) and several studies have shown that the presence of large herbivores can affect both the structure and location of the forest–tundra ecotone, as well as mitigate the effects of climate warming (Hofgaard, Løkken, Dalen, & Hytteborn, 2010; Speed, Austrheim, Hester, & Mysterud, 2010; Vowles et al., 2017; Wielgolaski, Hofgaard, & Holtmeier, 2017).

The impact of herbivores is spatiotemporally variable, as their habitat and forage selection vary throughout the growing season (Mobæk et al., 2009). Although this spatiotemporally variable grazing impact may be central for the resilience of tundra ecosystems under the threat of climate change-driven shrub encroachment (Hoset et al., 2017), it is often difficult to disentangle the impact of herbivory on vegetation from the effects of increased temperature (Hofgaard et al., 2010; Speed, Austrheim, Hester, & Mysterud, 2011; Speed, Austrheim, & Mysterud, 2013).

Tundra ecosystems are assumed to be particularly vulnerable to climate warming (Callaghan et al., 2011; Post et al., 2009) and indeed temperature-driven changes in both composition and diversity of tundra vegetation have been shown (Arft et al., 1999; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Walker et al., 2006). Tundra vegetation responses to increased temperature show large spatial variation, where for example dry tundra generally is more resistant towards vegetation changes in response to increased temperature compared to mesic tundra (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012). Although there are few general patterns, a common trend is an increase in shrubs (especially deciduous, low and tall shrubs) and dead plant material, at the expense of lichens and mosses (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012).

Increased growth and abundance of shrubs might have multiple influences on the ecosystem and the ground layer vegetation (Myers-Smith et al., 2011). The increase in canopy cover and height, as well as enhanced litter production, will lead to a shading of the ground layer (Blok et al., 2010), as well as reduced albedo and alternation of the carbon cycle (de Wit et al., 2014; Sturm, Douglas, Racine, & Liston, 2005; Väisänen et al., 2014). Further, erect woody species act as traps for wind-redistributed snow, resulting in changes in snow accumulation patterns (depth and amount). This may affect shrub size growth and vegetation composition, through increased winter soil temperature, protection from damage caused by wind abrasion and browsing or grazing, change in growing season length, and change in soil moisture (Dalen & Hofgaard, 2005; Holtmeier & Broll, 2005; Sturm et al., 2001).

The spatio-temporal nature of herbivory, the heterogeneity of tundra ecosystems, and the observed differences between short-term and long-term vegetation responses to climate change (Alatalo, Jägerbrand, & Molau, 2015; Arft et al., 1999; Chapin, Shaver, Giblin, Nadelhoffer, & Laundre, 1995; Hollister, Webber, & Tweedie, 2005) call for more long-term, local-scale data (Barrett, Hollister, Oberbauer, & Tweedie, 2015; Hollister et al., 2015) to disentangle the relative importance of different drivers. Particularly needed are data where climate regulation is tested in combination with other regulating factors such as herbivory (Cairns, Lafon, Moen, & Young, 2007; Hofgaard, Harper, & Golubeva, 2012; Sveinbjörnsson, Hofgaard, & Lloyd, 2002). This is important especially in dry tundra sites, where responses are slower (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012) and the effects of changes in drivers might not be observable during short study periods.

In the present study, we experimentally test how the removal of sheep herbivory affects the vegetation in an alpine forest–tundra ecotone, and how the responses are manifested in warmer temperatures. Further, we address the importance of the length of experimental periods in unravelling timing differences in vegetation responses, and in scenarios for tundra vegetation change. The experiment consists of three nested treatments: grazing exclosures to regulate herbivory, open-top chambers (OTCs) to increase temperature and controls with ambient grazing and temperature.

2 | METHODS

2.1 | Study area

The study was conducted in the Dovre mountain area in central Norway (62°18′ N, 9°37′ E), at 1,090 m a.s.l., in the ecotone between the closed Mountain birch (*Betula pubescens* subsp. *tortuosa* (Ledeb.) Nyman) forest at lower altitudes and the treeless alpine region at higher altitudes. The climate is slightly continental (Moen, 1999) characterised by low annual precipitation, cold winters, and relatively warm summers. Climate data from Fokstua Meteorological Station 27 km south of the study area (973 m a.s.l) for the 30-year period prior to the experiment (1971–2000) showed a mean annual temperature of −0.2°C, the warmest month being July and the coldest January, with a mean temperature of 10.3°C and −7.6°C, respectively. Mean annual precipitation for the 30-year period was 454 mm, and the snow cover generally lasted from October to late May. Mean annual temperature in the study period was 1.1°C higher (i.e. 0.9°C; $p < 0.001$) than for the prior 30-year mean, while mean annual precipitation was not significantly different (456 mm) (for monthly variation in the two periods see Appendix S1; Norwegian Meteorological Institute, 2017). The two-year overlap between the 30-year period and the study period has no impact on presented mean values.

The study area is located on a dry, west-facing alpine tundra slope characterised by a sparse layer of shrub-sized mountain birch (i.e. <2 m tall), dwarf shrubs and some herbs in the field layer, and lichens in the bottom layer. Mountain birch is a low-stature tree species common to the forest–tundra ecotone in Scandinavia and is a preferred forage to a range of herbivores, including semi-domestic and domestic browsers/grazers and folivorous insect herbivores such as the autumnal moth (*Epirrita autumnata* (Borkhausen, 1794)) (Moen, Cairns, & Lafon, 2008; Van Bogaert, Jonasson, De Dapper, & Callaghan, 2009). Although *Epirrita* outbreaks are common in mountain birch forests (Tenow, 1996), only one outbreak period (2015–2017) was recorded in the study area during the experiment (A. Hofgaard unpubl.) but without affecting the experimental area. Mountain birch grows in various forms, from upright single or multi-stemmed small trees, to shrubby krummholz or shrubs. The shrub-form of mountain birch constitutes, together with dwarf birch (*B. nana* L.), the dominating shrub layer species in dry and mesic areas of the Scandinavian forest–tundra ecotone.

Main dwarf shrubs are *Empetrum nigrum* L., *Vaccinium uliginosum* L., *Vaccinium vitis-idaea* L., *Arctostaphylos uva-ursi* (L.) Spreng. and *Betula nana*. The most common lichen species is *Alectoria ochroleuca* (Hoffm.) Massal. In addition to lichens, the bottom layer consists of small patches of moss, litter, and mineral soil including stones. The soil in the area is mainly podzolic, but with some azonal soils characteristic for the altitudinal alpine podzolization boundary (Låg, Juve, & Gust, 1983), derived from an underlying schist bedrock (Norwegian Geological Survey, 2018), and typically covered by an organic layer of ~3 cm thickness (range at the study area 0–6 cm). The area is used by a number of herbivores with domestic sheep (*Ovis aries* Linnaeus) being the most common, which use it as grazing ground during the growing season (June–September). Others, but less frequent, are mountain hare (*Lepus timidus* Linnaeus), grouse (*Lagopus* spp. Linnaeus), microtine rodents, insects such as autumnal moth, and occasionally moose (*Alces alces* Linnaeus) and reindeer (*Rangifer tarandus* Linnaeus). The mountain areas of Norway have been used as summer grazing grounds for domestic stocks for centuries, and this form of land use has been central in shaping the mountain vegetation's composition and stature (Olsson, Austrheim, & Grenne, 2000).

2.2 | Study design and experimental set-up

The 18-year experiment was established in 1999 and visited at least twice annually for maintenance. The experimental area spanned ca. 200 m × 40 m and included three exclosure areas, of ~20 m × 15 m each, in the non-fenced surrounding. The experiment consisted of three nested treatments: ambient grazing and ambient temperature regimes (AGA), no grazing and ambient temperature using exclosures (NGA), and no grazing combined with experimentally increased temperature using exclosures and OTCs (NGW). The treatment combining warming and ambient grazing was not included in the study design. Fifty birch saplings with surrounding vegetation (henceforward named plots) within the enclosed areas were randomly appointed to the NGA and the NGW treatment (25 plots for each), and 25 plots were randomly appointed to the AGA treatment in the subalpine heath surrounding the exclosures. The mean height of selected saplings was 9.6 cm at the start of the experiment. Corner positions of the plots were permanently marked, to ensure exact placement during reanalysis.

The exclosures, including both NGA and NGW plots, eliminated sheep herbivory, but smaller herbivores (invertebrates, hares, birds and rodents) had free access. We used standard sheep fencing (90 cm tall with a 15 cm × 20 cm mesh size) used by farmers of the region to construct the exclosures. The OTCs used for warming were hexagonal, 32 cm high and with a top diameter of 52 cm, and a bottom diameter of 85 cm (Molau & Mølgaard, 1996). OTCs do not exclude small mammals such as lemmings and voles (see e.g. Kaarlejärvi et al., 2013), and the NGA and NGW treatments are thus similar in their exclusion of herbivores. Ground surface air temperature and soil temperature (at 5 cm depth) during the snow-free season were recorded hourly in two OTCs and two ambient temperature plots during the early part of the study (1999–2002 for air temperature, and 1999–2001 for soil temperature). Recorded OTC temperatures were 1.6°C higher at the ground surface and 1.1°C higher in the soil, compared to the ambient temperature plots (Dalen, 2004). This temperature enhancement is within the lower range of recent model scenarios of future climate in the region (ACIA, 2005; IPCC, 2013), but was at the mean range when the experiment started (IPCC, 2001).

2.3 | Data collection

In the present study, we randomly selected ten out of the 25 plots per treatment to analyse shrub height, shrub cover and ground layer changes over time. The plots were 50 cm × 50 cm, divided into nine sub-plots (16.7 cm × 16.7 cm), with the focal birch sapling located in the centre of the central sub-plot. Ground layer was used as joint naming for the field- and bottom layers. All recordings were performed at peak growing season (late July or early August), every third year from 1999 to 2017 (i.e., 1999, 2002, 2005, 2008, 2011, 2014 and 2017). These years are henceforward named year 0, year 3 etc. with last year being year 18. There were no height recordings in years 9 and 12. Due to trampling activity by grazing animals, and animals removing marking sticks, some of the plots in the AGA treatment were lost during the study period. Consequently, in year 6 nine of the initial ten AGA plots could be resampled, in years 9 and 12 seven plots, while in years 15 and 18 only five and four plots, respectively, were included in the reanalyses. This loss of experimental units might have caused a conservative estimate of grazing effect in the last two years of the experiment.

Recording of the shrub layer and ground layer cover was done at the sub-plot level as visually estimated percentages of each species/component (see Appendix S2 for a list of all components). The height of the shrub layer was measured at the plot level as the distance from the ground to the highest (living) part of the sapling. All data for vascular plants and lichens were recorded at the species level, whereas for mosses we recorded the total cover. In addition, we recorded the cover of bare soil (mineral soil and stone), and litter. The total estimated percentage per sub-plot of the ground layer had to sum up to 100%. The shrub layer cover was recorded separately and could vary between 0% and 100%.

2.4 | Data treatment and statistical analyses

During the course of the experiment, the summed percentage recorded for some ground layer sub-plots deviated from the required 100% total value due to summing mistakes during field work. Therefore, an acceptance range of 95%–105% was established. Sub-plot recordings with a total value outside this range for a particular year were excluded from the analysis (*n* = 107). The cover of the component bare soil showed some apparent pre-treatment-related differences, with a larger mean value in the AGA treatment (33.2% vs 12.5% in NGA and 14.9% in NGW, respectively) at the start of the experiment. This difference was not statistically significant, however (AGA vs NGA; $p = 0.260$, AGA vs NGW; $p = 0.446$; linear mixed effects model).

The cover data for individual ground layer components were merged into the following component groups: deciduous woody species, evergreen woody species, herbs, graminoids, lichens, mosses, litter and bare soil (see Appendix S2 for details).

To investigate the consistency effect of warming and herbivory on shrub cover and height, and ground layer composition over time, we used separate linear mixed effect models with shrub height, and shrub layer and component groups cover as response variables, respectively. The response variables were square-root transformed to attain normality and equal variances. Treatment (AGA, NGA and NGW), year (0–18, categorical variable) and the interaction between treatment and year were used as fixed factors. As sub-plots were nested in plots (spatial autocorrelation) and were repeatedly analysed (temporal autocorrelation) we used plot as a random factor and an autocorrelation factor of 1 (corAR1()) to account for this (cf. Crawley, 2008). In models where a significant interaction between treatment and time was found, we used a Tukey HSD test to investigate the contrast between year 0 and the subsequent years to identify when the responses turned significant, and to identify pairwise differences between treatments in each of the years.

To investigate compositional changes of the ground layer in response to grazing exclusion and warming a two-dimensional global nonmetric multidimensional scaling (GNMDS), with Bray–Curtis dissimilarity measure (sensu Davey, Heegaard, Halvorsen, Kauserud, & Ohlson, 2013) was used. In addition, a canonical correspondence analysis (CCA; Lepš & Šmilauer, 2003) was used to test for an interaction effect between treatment and time.

All statistical analyses were performed in the R statistical environment (Version 3.3.2., R Core Team, Vienna, Austria), using the following packages: 'nlme' and 'multcomp' for the linear mixed effects models, and 'vegan' and 'MASS' for the multivariate analyses.

3 | RESULTS

3.1 | Shrub layer

Over the course of the experiment, shrub height decreased from 11.1 to 10.1 cm in the AGA treatment, but increased from 10.5 to 52 cm in the NGA treatment, and from 11.7 to 76.3 cm in the NGW treatment (Figure 1a), with no main effect of treatment ($p = 0.438$), but a significant treatment × year effect ($p < 0.001$). In both NGW and NGA, the height increase was significant over time. The increase turned significant in year 3 ($p < 0.001$) for the NGW and in year 6 for NGA ($p = 0.013$). NGW was significantly taller than AGA from year 6 onward ($p < 0.01$), and NGA became significantly taller than AGA in year 18 ($p < 0.01$). There was no significant difference between NGW and NGA (See Appendix S3 for details on main effects in the linear mixed effects model, and Appendix S4 for details on the Tukey HSD post-hoc test).

Shrub cover decreased from 3.8% to 2.2% in the AGA treatment, but increased from 3.6% to 16.4% in the NGA treatment and from 2.7% to 26.3% in the NGW treatment during the 18-year experiment, with a significant main effect of treatment ($p = 0.028$) and a significant treatment × year effect ($p < 0.001$). The shrub cover showed negligible changes in all three treatments in the first six years, but a strong significant increase was seen after this initial period in both the NGA and the NGW treatments (Figure 1b). For the NGW treatment, the increase in cover turned significant in year 9 ($p < 0.01$) and for the NGA treatment in year 12 ($p < 0.001$). There were no significant changes in the AGA over time. NGW became significantly larger than AGA in year 18 ($p < 0.01$). There was no significant difference between any of the other treatments.

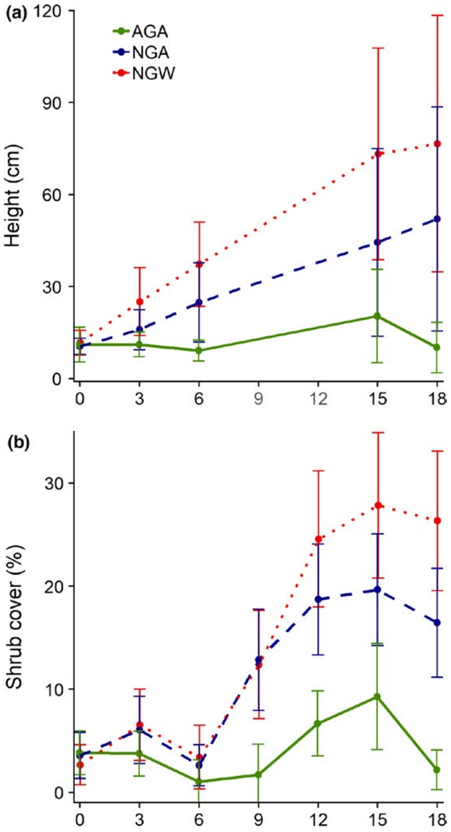

FIGURE 1 Change in shrub layer height (a), and shrub layer cover (b) for the three treatments over the 18-year experimental period. Treatment abbreviations: AGA, ambient grazing and ambient temperature; NGA, no grazing and ambient temperature; and NGW, no grazing and experimentally increased temperature. Points show the mean measured values and error bars the 95% confidence interval. Grey font for *x*-axis values in panel (a) marks years where height recordings are lacking

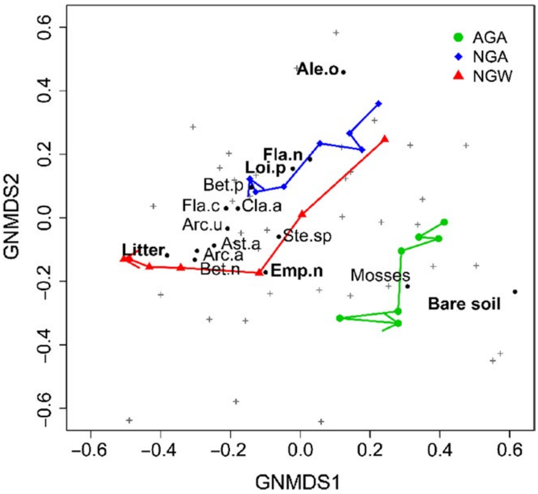

FIGURE 2 Change in ground layer composition over the 18-year experimental period shown by trajectories of mean plot values in a global nonmetric multidimensional scaling (GNMDS) ordination in the treatments AGA, NGA and NGW (see Figure 1 for an explanation of the acronyms). Crosses represent ground layer components with <1% cover. Dots with attached text represent more than 1% cover, and bold font is used for components with over 5% cover. Positions of text labels were adjusted to increase readability. For full component list, see Appendix S2

3.2 | Ground layer

The GNMDS revealed a time-related change in ground layer composition in all treatments (Figure 2), which was confirmed by the CCA ($p = 0.001$; Appendix S5). The main pattern was a change towards higher cover of litter (mainly shrub leaves) (axis 1) and lower cover of the lichen *Alectoria ochroleuca* (axis 2), with a significant difference between treatments ($p = 0.001$, Figure 2; Appendix S3). The strongest response along both axes was shown by the trajectory of the NGW treatment (Figure 2).

The change in ground layer composition varied largely between treatments and component groups (Figure 3). The linear mixed effects models showed significant treatment × year interactions for the cover of evergreen woody species, lichens and litter ($p < 0.001$, $p = 0.021$ and $p < 0.001$, respectively). For evergreen woody species, the cover increased in both the AGA and the NGA treatment, and the change turned significant in year 12 for both; ($p = 0.015$ and $p = 0.031$, respectively; Figure 3a). These significances were, however, not sustained in years 15 and 18. The NGW treatment showed no significant change from year 0, but a visual inspection of the trend line revealed a sharp decline in evergreen woody species cover between years 6 and 12 (from 41.9% to 25.9%; $p < 0.001$).

Lichens were the dominating ground layer component group in all treatments in year 0 and declined significantly over the study period for all treatments (Figure 3e). The decline was faster and stronger in the NGW treatment, where the decrease turned significant already in year 3 ($p < 0.001$). In the AGA and the NGA treatments, the decline turned significant in year 12 ($p < 0.01$). This decline in lichen cover led to loss of its dominance in the NGW treatment in year 3 (27.5%), and in year 9 in the AGA treatment (23.8%), but the initial dominance prevailed in the NGA treatment throughout the experiment (39.8% in year 18).

Litter cover increased in all treatments, but with apparent differences between treatments ($p < 0.001$). The largest increase over time was seen in the NGW treatment (Figure 3g), with a significant increase after three years ($p = 0.028$), and with a cover peak in year 12 after a strong increase in year 9 ($p < 0.001$). The cover of litter was consistently higher in NGW than in the other treatments from year

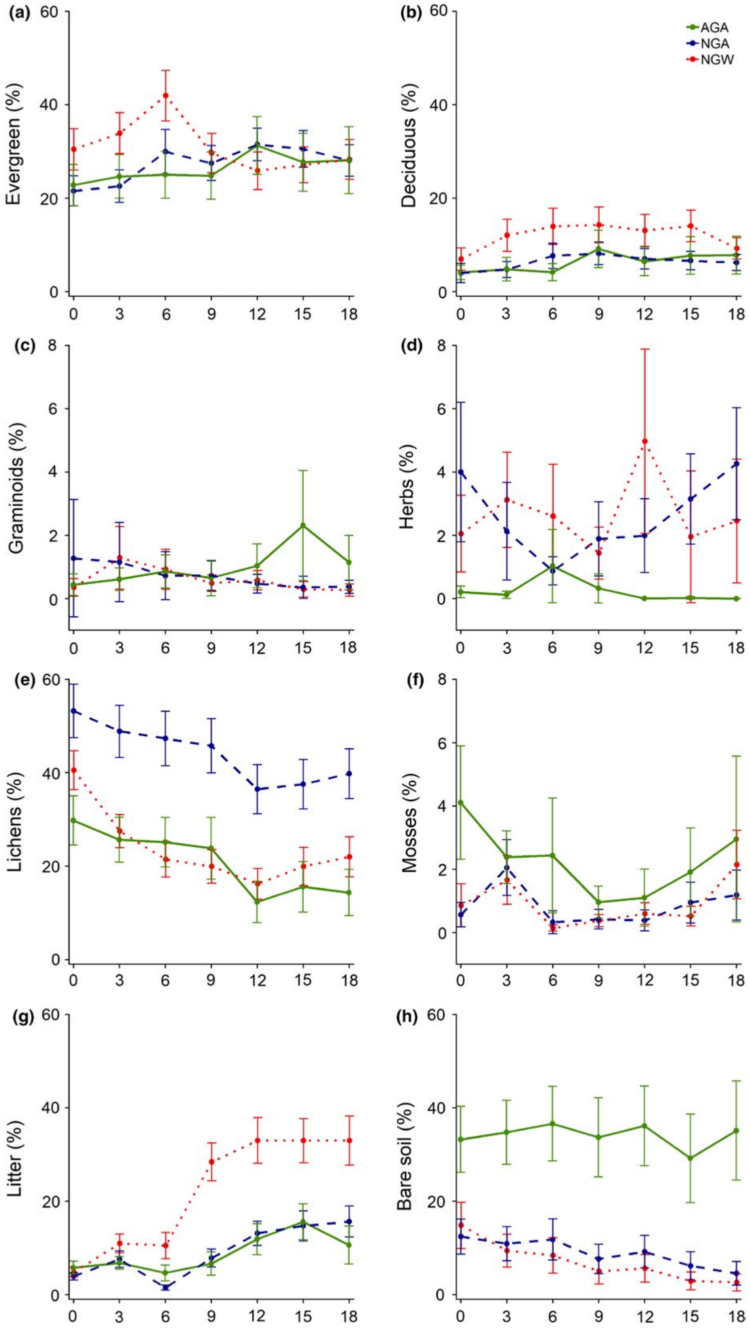

FIGURE 3 Change in mean cover (%) of ground layer component groups over the 18-year experimental period, for the treatments AGA, NGA and NGW (see Figure 1 for an explanation of the acronyms). (a) Evergreen woody species, (b) deciduous woody species, (c) graminoids, (d) herbs, (e) lichens, (f) mosses, (g) litter, and (h) bare soil. Points show the mean measured values and error bars the 95% confidence interval. Note different *y*-axis scales

9 onwards ($p < 0.001$). In the NGA treatment litter cover was significantly lower in year 6 than at the start of the experiment ($p < 0.001$), before it increased toward the end of the experiment. The increase turned significant in year 12 ($p < 0.001$). In the AGA treatment there were negligible changes in litter cover the first nine years, but a small significant ($p < 0.01$) increase was seen in year 15.

The cover of ground layer deciduous woody species varied through time ($p < 0.001$, Figure 3a), but the change was not different between treatments ($p = 0.562$). For herbs, on the other hand, there were significant cover differences between treatments ($p < 0.001$), but no significant variation over time ($p = 0.606$, Figure 3d). Mosses varied in cover over time with a close to significant difference between treatments ($p = 0.080$), but with no treatment × year interaction ($p = 0.140$, Figure 3f). Finally, the cover of bare soil was generally higher in the AGA treatment than in the two other treatments and varied over time ($p < 0.001$), but with no treatment × year interaction ($p = 0.249$, Figure 3h).

4 | DISCUSSION

The lack of shrub growth responses to warming stands in contrast to expectations of increased shrub growth in the forest–tundra ecotone in response to climate warming (ACIA, 2005; IPCC, 2013). Instead, the results highlight the importance of herbivory, with its strong controlling effect on shrub layer growth, but with only a weak effect on ground layer composition through time. However, combined warming and herbivore exclusion caused an initial rapid decline of lichen cover. This, further and importantly, shows that short-term vegetation responses may differ from long-term responses, thus highlighting the importance of experimental period. This understanding is particularly important regarding tundra communities that are in general slow to respond (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012).

4.1 | Effects of herbivore removal

The observed control of shrub layer growth by herbivores is in line with previous studies showing herbivory as a more important factor than temperature in regulating growth of shrub-sized birch in the forest–tundra ecotone (Hofgaard et al., 2010; Olofsson et al., 2009; Speed et al., 2010). Accordingly, any change to the grazing pressure would have an apparent impact on shrub growth and subsequently on the structure of the shrub layer and the ecotone, similar to the effects of climate change on the structure and location of the forest–tundra ecotone (Batllori & Gutierrez, 2008; Vitali, Urbinati, Weisberg, Urza & Garbarino, 2018; Wielgolaski et al., 2017). As a decline in the use of remote areas for domestic livestock grazing is commonly seen in Norway and elsewhere in Europe (Austrheim, Solberg, & Mysterud, 2011; Wielgolaski et al., 2017), and saplings are frequently present in the forest–tundra ecotone and adjacent tundra in the Scandinavian mountains (Aune, Hofgaard, & Söderström, 2011; Hofgaard et al., 2009; Kullman, 2002), a likely future scenario would be increased growth of shrubs and their subsequent encroachment of the previously shrubless tundra areas (Cairns et al., 2007; Hofgaard et al., 2010; Olofsson et al., 2009; Speed et al., 2011). However, caution is needed when assessing how experimentally defined effects scale up to the ecosystem level (Post & Pedersen, 2008). This is further complicated by the spatiotemporal nature of herbivory (Mobæk et al., 2009; Post & Pedersen, 2008).

4.2 | Effects of warming combined with herbivore removal

The reduction in the cover of lichens with added warming in our experiment is in line with results from other warming experiments (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Lang et al., 2012; Wahren, Walker, & Bret-Harte, 2005; Walker et al., 2006), and is commonly attributed to an increased cover of vascular plants, and a subsequent increase in shade and litter (Alatalo, Jägerbrand, Chen, & Molau, 2017; Cornelissen et al., 2001). While there was some increase in woody species in the warming treatment, the increase in litter and shading shrub cover in the first six years of the experiment, when the major lichen decline took place, was minor. As there was no similar response in the ungrazed ambient treatment, our results thus suggest a response to increased temperature as such, or to other side effects of the OTC treatment. The decline in lichens was mainly attributed to one single species: *Alectoria ochroleuca*, whereas other lichen species showed a more stable cover. A strong decline of *Alectoria* species has been observed in another long-term experiment using OTCs in a dry tundra site (Hollister et al., 2005). Changes in lichen cover are not assumed to be closely linked to changes in temperature (Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012). However, a recorded species-specific response, and sensitivity of one species in particular, calls for attention beyond functional group-level (St. Martin & Mallik, 2017).

Although non-significant, warming added to shrub layer growth differences between the non-grazed treatments. Increases in both air and soil temperatures are reported to promote the growth of mountain birch (Weih & Karlsson, 2001). Thus, the observed effect of warming, even after the saplings overtopped the chambers, might be a result of growth-promoting increases in soil temperature and warmer air temperature conditions in the surroundings of the lower parts of the sapling. Furthermore, the OTC wind-sheltering effect and contribution to the build-up of an insulating snow cover by hindering snow redistribution during the winter might add to the increased growth (cf. Bokhorst et al., 2013, 2011).

Contrary to reports of an increase in woody species abundance with increased temperature in tundra ecosystems (Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012), we saw no such (significant) positive effect for warming on the cover of deciduous or evergreen woody species in the ground layer. In contrast, we observed a rapid decline in the cover of the evergreen woody species after six years of warming. This decline could be due to winter warming events or a reduction in snow cover (Bokhorst, Bjerke, Tømmervik, Callaghan, & Phoenix, 2009). However, as this response in evergreen woody species is seen in the warming treatment only, and OTCs generally reduce the rate of freeze–thaw events and also increase snow accumulation in and around the chambers (Bokhorst et al., 2011), this is not a very likely scenario. Also, there are no meteorological data indicating any extraordinary weather events in this time period (Norwegian Meteorological Institute, 2017). As the decrease in evergreen woody species coincides with the period of the largest litter accumulation, it is instead likely that these responses are linked. The increased amount of litter in the ground layer might suppress the growth of evergreen woody species through shading and the accumulation per se.

The increased litter accumulation in warmed plots, mainly consisting of shrub leaves, corresponds to findings in similar experiments (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Jónsdóttir, Magnusson, Gudmundsson, Elmarsdottir, & Hjartarson, 2005; Wahren et al., 2005). It is suggested that litter accumulates because increased evapotranspiration due to increased temperature lowers the litter moisture to the point where fungal decomposition activities become inhibited (Christiansen et al., 2017). This is in line with an earlier study that proposed that moisture plays a more important role than temperature in litter decomposition (Sjögersten & Wookey, 2004). Further, climate warming is assumed to lead to an increase in species with more recalcitrant litter, such as shrubs and woody vegetation, with subsequent ecosystem-level consequences (Cornelissen et al., 2007). However, studies of the microclimatic impacts of OTCs have shown that in addition to representing an "average" future climatic scenario OTCs also have unwanted side effects, including temperature extremes, higher evaporation, lower soil moisture and changed wind pattern (Bokhorst et al., 2013, 2011; Dalen, 2004). Consequently, the observed litter accumulation inside the chambers is likely to a large degree a chamber effect, where litter is trapped inside the chambers, fragmentation due to wind tumbling is reduced to a minimum, and where limited redistribution of litter can occur due to inhibited ambient wind. Accordingly, the ceased litter accumulation in warmed plots in the last year of the experiment likely relates to the increased height of the saplings and that they are overtopping the chambers. With a mean height three times the chamber height most leaves are exposed to ambient wind dispersing them away from the OTC opening.

4.3 | Short- and long-term effects

Most experimental studies of climate warming in the tundra usually last for a short time (but see e.g. Alatalo et al., 2017; Barrett & Hollister, 2016; Hudson & Henry, 2010), and as a result, knowledge regarding long-term plant community responses will largely rely on model projections of short-term data (Barrett & Hollister, 2016; De Boeck et al., 2015). Long-term studies are particularly important in dry tundra sites, where community responses are commonly slow (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012), and for sites where different vegetation layers or species can be assumed to show deviating response patterns to environmental change (Vuorinen et al., 2017). A slow or delayed response can lead to underestimation of responses, while transient initial responses followed by a stabilization can lead to overestimation (De Boeck et al., 2015). Our experiment with its 18-year time span, enables some unravelling of the timing differences between responses in different vegetation layers and components, and their implications regarding predictions of long-term consequences. Extrapolation from short-term study data could be misleading as long-term responses might differ from the short-term responses (Alatalo et al., 2015; Hollister et al., 2005). As an example, extrapolation of the responses from years 0 to 6 would lead to an overestimation of the warming effect for the evergreen woody species increase and an underestimation for shrub growth. Further, the shown slow decline in lichens and the increase in evergreen woody species in the ambient temperature treatments (significant in year 12) could not have been foreseen based on short-term data.

5 | CONCLUDING REMARKS

The shown discrepancy between the fast response of some ground layer components to warming and the lack of effects of warming on the shrub layer emphasise the species-specific and layer-specific character of climate- and herbivory-driven vegetation change in the forest–tundra ecotone, including the advance of boreal species into the tundra (Vuorinen et al., 2017). Taken together, the result might indicate a transition towards novel combinations of tundra and boreal species, or possibly the degeneration of tundra ecosystems (Post et al., 2009; Vuorinen et al., 2017). Although our study shows only minor changes for most vegetation components due to warming, even in the long term, the rapid and strong reduction effect on *Alectoria ochroleuca* calls for attention regarding the responses of the lichen community. Further, the accumulation of litter within OTCs has to be seen from the point of view of a chamber effect, and not as a result of warming alone. This chamber effect calls for caution when using experimental data in predictive models of climate change effects on vegetation and ecosystem structure and functioning. It also points to the need for combining experimental data with observational ambient condition data (De Boeck et al., 2015). Our results also underpin the importance of considering multiple drivers, as the use of combined abiotic (temperature) and biotic (herbivory) drivers in our study approach gives a deviating picture of how the system may change over time (Post & Pedersen, 2008).

ACKNOWLEDGEMENTS

We would like to thank Tord Bretten and Frode Thorsteinsen for their help with establishing the field site; Brita Hytteborn, Sølvi Wehn, and Andreas Forberg for field assistance; Siri Lie Olsen for statistical help, and we are grateful for the logistic support from Kongsvold Biological Station.

DATA ACCESSIBILITY

The data is available at Open Science Framework (https://doi.org/10.17605/OSF.IO/XKAVJ).

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REFERENCES

ACIA (2005). *Arctic Climate Impact Assessment*. Cambridge, UK: Cambridge University Press.

Alatalo, J. M., Jägerbrand, A. K., Chen, S., & Molau, U. (2017). Responses of lichen communities to 18 years of natural and experimental warming. *Annals of Botany*, *120*(1), 159–170. https://doi.org/10.1093/aob/mcx053

Alatalo, J. M., Jägerbrand, A. K., & Molau, U. (2015). Testing reliability of short-term responses to predict longer-term responses of bryophytes and lichens to environmental change. *Ecological Indicators*, *58*, 77–85. https://doi.org/10.1016/j.ecolind.2015.05.050

Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., … Wookey, P. A. (1999). Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, *69*, 491–511. https://doi.org/10.1890/0012-9615(1999) 069[0491:Rotpte]2.0.Co;2

Augustine, D. J. & McNaughton, S. J. (1998). Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management*, *62*, 1165–1183. https://doi.org/10.2307/3801981

Aune, S., Hofgaard, A., & Söderström, L. (2011). Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula. *Canadian Journal of Forest Research*, *41*, 437–449. https://doi.org/10.1139/x10-086

Austrheim, G., Solberg, E. J., & Mysterud, A. (2011). Spatio-temporal variation in large herbivore pressure in Norway during 1949–1999 has decreased grazing by livestock been countered by increased browsing by cervids? *Wildlife Biology*, *17*, 286–298. https://doi.org/10.2981/10-038

Barrett, R. T. & Hollister, R. D. (2016). Arctic plants are capable of sustained responses to long-term warming. *Polar Research*, *35*(1), 25405. https://doi.org/10.3402/polar.v35.25405

Barrett, R. T. S., Hollister, R. D., Oberbauer, S. F., & Tweedie, C. E. (2015). Arctic plant responses to changing abiotic factors in northern Alaska. *American Journal of Botany*, *102*, 2020–2031. https://doi.org/10.3732/ajb.1400535

Batllori, E. & Gutierrez, E. (2008). Regional tree line dynamics in response to global change in the Pyrenees. *Journal of Ecology*, *96*, 1275–1288. https://doi.org/10.1111/j.1365-2745.2008.01429.x

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., … Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, *562*, 57–62. https://doi.org/10.1038/s41586-018-0563-7

Blok, D., Heijmans, M. M. P. D., Schaepman-Strub, G., Kononov, A. V., Maximov, T. C., & Berendse, F. (2010). Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Global Change Biology*, *16*, 1296–1305. https://doi.org/10.1111/j.1365-2486.2009.02110.x

Bokhorst, S. F., Bjerke, J. W., Tømmervik, H., Callaghan, T. V., & Phoenix, G. K. (2009). Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. *Journal of Ecology*, *97*, 1408–1415. https://doi.org/10.1111/j.1365-2745.2009.01554.x

Bokhorst, S., Huiskes, A., Aerts, R., Convey, P., Cooper, E. J., Dalen, L., … Dorrepaal, E. (2013). Variable temperature effects of Open Top Chambers at polar and alpine sites explained by irradiance and snow depth. *Global Change Biology*, *19*, 64–74. https://doi.org/10.1111/gcb.12028

Bokhorst, S., Huiskes, A., Convey, P., Sinclair, B. J., Lebouvier, M., Van de Vijver, B., & Wall, D. H. (2011). Microclimate impacts of passive warming methods in Antarctica: Implications for climate change studies. *Polar Biology*, *34*, 1421–1435. https://doi.org/10.1007/s00300-011-0997-y

Cairns, D. M., Lafon, C., Moen, J., & Young, A. (2007). Influences of animal activity on treeline position and pattern: Implications for treeline responses to climate change. *Physical Geography*, *28*, 419–433. https://doi.org/10.2747/0272-3646.28.5.419

Callaghan, T. V., Björn, L. O., Chernov, Y., Chapin, T., Christensen, T. R., Huntley, B., & Ims, R. A. (2004). Biodiversity, distributions and adaptations of Arctic species in the context of environmental change. *Ambio*, *33*, 404–417. https://doi.org/10.1579/0044-7447-33.7.404

Callaghan, T. V., Crawford, R. M., Eronen, M., Hofgaard, A., Payette, S., Rees, W. G., … Werkman, B. R. (2002). The dynamics of the tundra-taiga boundary: an overview and suggested coordinated and integrated approach to research. *Ambio*, Spec No *12*, 3–5. https://doi.org/10.2307/25094569

Callaghan, T. V., Tweedie, C. E., Åkerman, J., Andrews, C., Bergstedt, J., Butler, M. G., … Zemtsov, V. A. (2011). Multi-decadal changes in tundra environments and ecosystems: synthesis of the International Polar Year-Back to the Future project (IPY-BTF). *Ambio*, *40*, 705–716. https://doi.org/10.1007/s13280-011-0179-8

Chapin III, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., & Laundre, J. A. (1995). Responses of Arctic tundra to experimental and observed changes in climate. *Ecology*, *76*, 694–711. https://doi.org/10.2307/1939337

Chapin, F. S., Sturm, M., Serreze, M. C., McFadden, J. P., Key, J. R., Lloyd, A. H., … Welker, J. M. (2005). Role of land-surface changes in arctic summer warming. *Science*, *310*, 657–660. https://doi.org/10.1126/science.1117368

Chen, I-C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*, 1024–1026. https://doi.org/10.1126/science.1206432

Christiansen, C. T., Haugwitz, M. S., Priemé, A., Nielsen, C. S., Elberling, B., Michelsen, A., … Blok, D. (2017). Enhanced summer warming reduces fungal decomposer diversity and litter mass loss more strongly in dry than in wet tundra. *Global Change Biology*, *23*, 406–420. https://doi.org/10.1111/gcb.13362

Cornelissen, J. H. C., Callaghan, T. V., Alatalo, J. M., Michelsen, A., Graglia, E., Hartley, A. E., … Aerts, R. (2001). Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, *89*, 984–994. https://doi.org/10.1111/j.1365-2745.2001.00625.x

Cornelissen, J. H. C., Van Bodegom, P. M., Aerts, R., Callaghan, T. V., Van Logtestijn, R. S. P., Alatalo, J., … M. O. L. Team (2007). Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters*, *10*, 619–627. https://doi.org/10.1111/j.1461-0248.2007.01051.x

Crawley, M. J. (2008). *The R book*. Chichester, UK: John Wiley & Sons.

Dalen, L. (2004). *Dynamics of mountain birch treelines in the Scandes mountain chain, and effects of climate warming*. (Doctoral thesis), Trondheim, Norway: NTNU.

Dalen, L. & Hofgaard, A. (2005). Differential regional treeline dynamics in the Scandes Mountains. *Arctic Antarctic and Alpine Research*, *37*, 284–296. https://doi.org/10.1657/1523-0430(2005)037[0284:Drtdit]2.0.Co;2

Davey, M. L., Heegaard, E., Halvorsen, R., Kauserud, H., & Ohlson, M. (2013). Amplicon-pyrosequencing-based detection of compositional shifts in bryophyte-associated fungal communities along an elevation gradient. *Molecular Ecology*, *22*, 368–383. https://doi.org/10.1111/mec.12122

De Boeck, H. J., Vicca, S., Roy, J., Nijs, I., Milcu, A., Kreyling, J., … Beier, C. (2015). Global change experiments: challenges and opportunities. *BioScience*, *65*, 922–931. https://doi.org/10.1093/biosci/biv099

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., … Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, *15*, 164–175. https://doi.org/10.1111/j.1461-0248.2011.01716.x

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., … Wipf, S. (2012). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, *2*, 453–457. https://doi.org/10.1038/nclimate1465

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, *12*, 1040–1049. https://doi.org/10.1111/j.1461-0248.2009.01355.x

Hofgaard, A. (1997). Inter-relationships between treeline position, species diversity, land use and climate change in the central Scandes Mountains of Norway. *Global Ecology and Biogeography*, *6*, 419–429. https://doi.org/10.2307/2997351

Hofgaard, A., Dalen, L., & Hytteborn, H. (2009). Tree recruitment above the treeline and potential for climate-driven treeline change. *Journal of Vegetation Science*, *20*, 1133–1144. https://doi.org/10.1111/j.1654-1103.2009.01114.x

Hofgaard, A., Harper, K. A., & Golubeva, E. (2012). The role of the circumarctic forest–tundra ecotone for Arctic biodiversity. *Biodiversity*, *13*, 174–181. https://doi.org/10.1080/14888386.2012.700560

Hofgaard, A., Løkken, J. O., Dalen, L., & Hytteborn, H. (2010). Comparing warming and grazing effects on birch growth in an alpine environment — a 10-year experiment. *Plant Ecology & Diversity*, *3*, 19–27. https://doi.org/10.1080/17550871003717016

Hofgaard, A., Tømmervik, H., Rees, G., & Hanssen, F. (2013). Latitudinal forest advance in northernmost Norway since the early 20th century. *Journal of Biogeography*, *40*, 938–949. https://doi.org/10.1111/jbi.12053

Hollister, R. D., May, J. L., Kremers, K. S., Tweedie, C. E., Oberbauer, S. F., Liebig, J. A., … Gregory, J. L. (2015). Warming experiments elucidate the drivers of observed directional changes in tundra vegetation. *Ecology and Evolution*, *5*, 1881–1895. https://doi.org/10.1002/ece3.1499

Hollister, R. D., Webber, P. J., & Tweedie, C. E. (2005). The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Global Change Biology*, *11*, 525–536. https://doi.org/10.1111/j.1365-2486.2005.00926.x

Holtmeier, F.-K. & Broll, G. (2005). Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, *14*, 395–410. https://doi.org/10.1111/j.1466-822x.2005.00168.x

Hoset, K. S., Ruffino, L., Tuomi, M., Oksanen, T., Oksanen, L., Mäkynen, A., … Moe, T. (2017). Changes in the spatial configuration and strength of trophic control across a productivity gradient during a massive rodent outbreak. *Ecosystems*, *20*, 1421–1435. https://doi.org/10.1007/s10021-017-0124-1

Hudson, J. M. G. & Henry, G. H. R. (2010). High Arctic plant community resists 15 years of experimental warming. *Journal of Ecology*, *98*, 1035–1041. https://doi.org/10.1111/j.1365-2745.2010.01690.x

IPCC (2001). *Climate change 2001: The scientific basis*. Cambridge, UK: Cambridge University Press.

IPCC (2013). *Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

Jónsdóttir, I. S., Magnússon, B., Gudmundsson, J., Elmarsdóttir, A., & Hjartarson, H. (2005). Variable sensitivity of plant communities in Iceland to experimental warming. *Global Change Biology*, *11*, 553–563. https://doi.org/10.1111/j.1365-2486.2005.00928.x

Kaarlejärvi, E., Eskelinen, A., & Olofsson, J. (2013). Herbivory prevents positive responses of lowland plants to warmer and more fertile conditions at high altitudes. *Functional Ecology*, *27*, 1244–1253. https://doi.org/10.1111/1365-2435.12113

Kullman, L. (2002). Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, *90*, 68–77. https://doi.org/10.1046/j.0022-0477.2001.00630.x

Låg, J., Juve, G., & Gust, J. (1983). *Nasjonalatlas for Norge*. Hønefoss, Norway: Norges Geografiske Oppmåling.

Lang, S. I., Cornelissen, J. H. C., Shaver, G. R., Ahrens, M., Callaghan, T. V., Molau, U., … Aerts, R. (2012). Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. *Global Change Biology*, *18*, 1096–1107. https://doi.org/10.1111/j.1365-2486.2011.02570.x

Lepš, J. & Šmilauer, P. (2003). *Multivariate analysis of ecological data using CANOCO*. Cambridge, UK: Cambridge University Press.

Mobæk, R., Mysterud, A., Loe, L. E., Holand, Ø., & Austrheim, G. (2009). Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. *Oikos*, *118*, 209–218. https://doi.org/10.1111/j.1600-0706.2008.16935.x

Moen, A. (1999). *National Atlas of Norway: Vegetation*. Hønefoss, Norway: Statens Kartverk.

Moen, J., Cairns, D. M., & Lafon, C. W. (2008). Factors structuring the treeline ecotone in Fennoscandia. *Plant Ecology & Diversity*, *1*, 77–87. https://doi.org/10.1080/17550870802246664

Molau, U. & Mølgaard, P. (1996). *ITEX manual*. Copenhagen, Denmark: Danish Polar Center.

Mulder, C. P. H. (1999). Vertebrate herbivores and plants in the Arctic and subarctic: effects on individuals, populations, communities and ecosystems. *Perspectives in Plant Ecology, Evolution and Systematics*, *2*(1), 29–55. https://doi.org/10.1078/1433-8319-00064

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, *6*, 045509. https://doi.org/10.1088/1748-9326/6/4/045509

Norwegian Geological Survey (2018). Norwegian Geological Survey. Retrieved from http://geo.ngu.no/kart/berggrunn_mobil/

Norwegian Meteorological Institute (2017). eKlima. Retrieved from http://sharki.oslo.dnmi.no/

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, *15*, 2681–2693. https://doi.org/10.1111/j.1365-2486.2009.01935.x

Olsson, E. G. A., Austrheim, G., & Grenne, S. N. (2000). Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960–1993. *Landscape Ecology*, *15*, 155–170. https://doi.org/10.1023/a:1008173628016

Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., … Aastrup, P. (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science*, *325*, 1355–1358. https://doi.org/10.1126/science.1173113

Post, E. & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 12353–12358. https://doi.org/10.1073/pnas.0802421105

Ross, L. C., Austrheim, G., Asheim, L.-J., Bjarnason, G., Feilberg, J., Fosaa, A. M., … Thórhallsdóttir, A. G. (2016). Sheep grazing in the North Atlantic region: A long-term perspective on environmental sustainability. *Ambio*, 45, 551–566. https://doi.org/10.1007/s13280-016-0771-z

Sjögersten, S. & Wookey, P. A. (2004). Decomposition of mountain birch leaf litter at the forest-tundra ecotone in the Fennoscandian mountains in relation to climate and soil conditions. *Plant and Soil*, *262*, 215–227. https://doi.org/10.1023/b:plso.0000037044.63113.fe

Speed, J. D., Austrheim, G., Hester, A. J., & Mysterud, A. (2010). Experimental evidence for herbivore limitation of the treeline. *Ecology*, *91*, 3414–3420. https://doi.org/10.1890/09-2300.1

Speed, J. D. M., Austrheim, G., Hester, A. J., & Mysterud, A. (2011). Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. *Forest Ecology and Management*, *261*, 1344–1352. https://doi.org/10.1016/j.foreco.2011.01.017

Speed, J. D. M., Austrheim, G., & Mysterud, A. (2013). The response of plant diversity to grazing varies along an elevational gradient. *Journal of Ecology*, *101*, 1225–1236. https://doi.org/10.1111/1365-2745.12133

St. Martin, P., & Mallik, A. U. (2017). The status of non-vascular plants in trait-based ecosystem function studies. *Perspectives in Plant Ecology, Evolution and Systematics*, *27*, 1–8. https://doi.org/10.1016/j.ppees.2017.04.002

Sturm, M., Douglas, T., Racine, C., & Liston, G. E.(2005). Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research: Biogeosciences*, *110*(G1), G01004. https://doi.org/10.1029/2005JG000013

Sturm, M., McFadden, J. P., Liston, G. E., Chapin III, F. S., Racine, C. H. & Holmgren, J., (2001). Snow–shrub interactions in Arctic tundra: a hypothesis with climatic implications. *Journal of Climate*, *14*, 336–344. https://doi.org/10.1175/1520-0442(2001)014<0336:ssiiat>2.0.co;2

Sveinbjörnsson, B., Hofgaard, A., & Lloyd, A. (2002). Natural causes of the tundra-taiga boundary. *Ambio*, Spec No *12*, 23–29. https://doi.org/10.2307/25094572

Tape, K., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, *12*, 686–702. https://doi.org/10.1111/j.1365

Tenow, O. (1996). Hazards to a Mountain birch forest — Abisko in perspective. *Ecological Bulletins*, *45*, 104–114.

Väisänen, M., Ylänne, H., Kaarlejärvi, E., Sjögersten, S., Olofsson, J., Crout, N., & Stark, S. (2014). Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nature Climate Change*, *4*, 384–388. https://doi.org/10.1038/nclimate2147

Van Bogaert, R., Haneca, K., Hoogesteger, J., Jonasson, C., De Dapper, M., & Callaghan, T. V. (2011). A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *Journal of Biogeography*, *38*, 907–921. https://doi.org/10.1111/j.1365-2699.2010.02453.x

Van Bogaert, R., Jonasson, C., De Dapper, M., & Callaghan, T. V. (2009). Competitive interaction between aspen and birch moderated by invertebrate and vertebrate herbivores and climate warming. *Plant Ecology & Diversity*, *2*, 221–232. https://doi.org/10.1080/17550870903487456

Vitali, A., Urbinati, C., Weisberg, P. J., Urza, A. K., & Garbarino, M. (2018). Effects of natural and anthropogenic drivers on land-cover change and treeline dynamics in the Apennines (Italy). *Journal of Vegetation Science*, *22*, 189–199. https://doi.org/10.1111/jvs.12598

Vittoz, P., Randin, C., Dutoit, A., Bonnet, F., & Hegg, O. (2009). Low impact of climate change on subalpine grasslands in the Swiss Northern Alps. *Global Change Biology*, *15*(1), 209–220. https://doi.org/10.1111/j.1365-2486.2008.01707.x

Vowles, T., Gunnarsson, B., Molau, U., Hickler, T., Klemedtsson, L., & Björk, R. G. (2017). Expansion of deciduous tall shrubs but not evergreen dwarf shrubs inhibited by reindeer in Scandes mountain range. *Journal of Ecology*, *105*, 1547–1561. https://doi.org/10.1111/1365-2745.12753

Vuorinen, K. E. M., Oksanen, L., Oksanen, T., Pyykönen, A., Olofsson, J., & Virtanen, R. (2017). Open tundra persist, but arctic features decline — Vegetation changes in the warming Fennoscandian tundra. *Global Change Biology*, *23*, 3794–3807. https://doi.org/10.1111/gcb.13710

Wahren, C.-H. A., Walker, M. D., & Bret-Harte, M. S. (2005). Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, *11*, 537–552. https://doi.org/10.1111/j.1365-2486.2005.00927.x

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., … Wookey, P. A. (2006). Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 1342–1346. https://doi.org/10.1073/pnas.0503198103

Weih, M. & Karlsson, P. S. (2001). Growth response of Mountain birch to air and soil temperature: is increasing leaf-nitrogen content an acclimation to lower air temperature? *New Phytologist*, *150*, 147–155. https://doi.org/10.1046/j.1469-8137.2001.00078.x

Wielgolaski, F. E., Hofgaard, A., & Holtmeier, F. K. (2017). Sensitivity to environmental change of the treeline ecotone and its associated biodiversity in European mountains. *Climate Research*, *73*, 151–166. https://doi.org/10.3354/cr01474

de Wit, H. A., Bryn, A., Hofgaard, A., Karstensen, J., Kvalevåg, M. M., & Peters, G. P. (2014). Climate warming feedback from mountain birch forest expansion: reduced albedo dominates carbon uptake. *Global Change Biology*, 20, 2344–2355. https://doi.org/10.1111/gcb.12483

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Mean monthly temperature and precipitation representing the study area.
Appendix S2 List of components.
Appendix S3 Linear mixed effects model statistics.
Appendix S4 Tukey HSD post-hoc test statistics.
Appendix S5 CCA test statistics.

How to cite this article: Løkken JO, Hofgaard A, Dalen L, Hytteborn H. Grazing and warming effects on shrub growth and plant species composition in subalpine dry tundra: An experimental approach. *J Veg Sci*. 2019;00:1–11. https://doi.org/10.1111/jvs12752

Supporting information to the paper

Grazing and warming effects on shrub growth and plant species composition in subalpine dry tundra – an experimental approach

Løkken, J.O. et al.
Journal of Vegetation Science.

Appendix S1 Mean monthly temperature and precipitation representing the study area.
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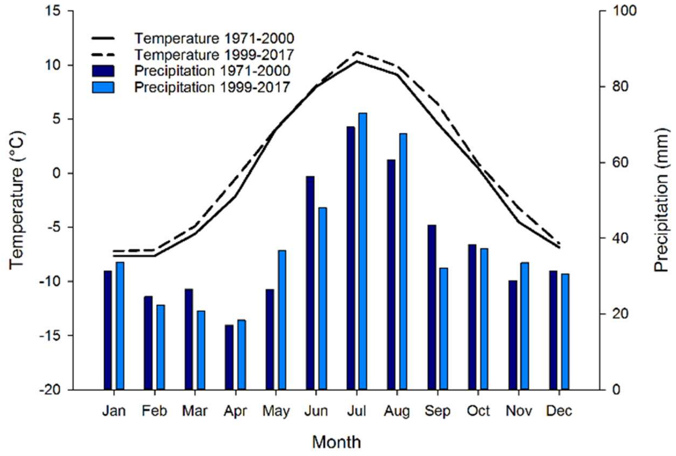

Appendix S1. Mean monthly temperature and precipitation representing the study area, here presented for the 30-year period leading up to the experiment (1971-2000) and for the study period (1999-2017) at Fokstugu meteorological station 973 m a.s.l. and 27 km south of the study area. (Source: Norwegian Meteorological Institute; www.met.no).

Appendix S2. List of components, group merging, and component abbreviations displayed in the ordination plot (Fig. 3). Nomenclature follows the Norwegian Species Nomenclature Database (Norwegian Biodiversity Information Centre 2018).

Component group	Component	Abbrevation
Deciduous woody species	*Arctostaphylos alpinus*	*Arc.a*
	Betula nana	*Bet.n*
	Betula pubescens spp. tortuosa	*Bet.p*
	Salix hastata	
	Salix phylicifolia	
	Vaccinium uliginosum	
Evergreen woody species	*Arctostaphylos uva-ursi*	*Arc.u*
	Diapensia lapponica	
	Empetrum nigrum	*Emp.n*
	Juniperus communis	
	Loiseleuria procumbens	*Loi.p*
	Vaccinium vitis-idaea	
Graminoids	*Avenella flexuosa*	
	Carex bigelowii	
	Festuca ovina	
	Juncus trifidus	
	Luzula confusa	
	Luzula multiflora	
Herbs	*Antennaria alpina*	
	Antennaria dioica	
	Astragalus alpinus	*Ast.a*
	Erigeron sp.	
	Euphrasia sp.	
	Pinguicula vulgaris	
	Primula scandinavica	
Lichens	*Alectoria nigricans*	
	Alectoria ochroleuca	*Ale.o*
	Bryocaulon divergens	
	Cetraria islandica	
	Cladonia arbuscula	*Cla.a*
	Cladonia rangiferina	
	Cladonia sp.	
	Cladonia stellaris	
	Cetraria aculeata	
	Flavocetraria cucullata	*Fla.c*
	Flavocetraria nivalis	*Fla.n*
	Peltigera aphthosa	
	Peltigera canina	
	Solorina crocea	
	Sphaerophorus globosus	
	Stereocaulon sp.	*Ste.sp*
	Thamnolia vermicularis	
Mosses	Mosses	Mosses
Litter	Litter	Litter
Bare soil	Bare soil	Bare soil

References

Norwegian Biodiversity Information Center (2018, March 18). Norwegian Species Nomenclature Database. Retrieved from http://www2.artsdatabanken.no/artsnavn/Contentpages/Hjem.aspx

Appendix S3. Linear mixed effects model statistics. Effects of treatment and year and the interaction effect between treatment and year on shrub height, shrub cover and cover of ground layer components given by the linear mixed effects model.

Response variable	Factor	numDF	denDF	F-value	P-value
Shrub height	treatment	2	27	0.85	0.438
	Year	4	90	14.92	<0.001
	treatment:year	8	90	4.83	<0.001
Shrub cover	treatment	2	29	4.07	0.028
	Year	6	1572	39.91	<0.001
	treatment:year	12	1572	3.22	<0.001
Evergreen woody species	treatment	2	28	0.68	0.514
	Year	6	1571	3.66	0.001
	treatment:year	12	1571	3.73	<0.001
Deciduous woody species	treatment	2	28	1.72	0.197
	Year	6	1571	5.37	<0.001
	treatment:year	12	1571	0.88	0.562
Herbs	treatment	2	28	47.78	<0.001
	Year	6	1571	0.75	0.606
	treatment:year	12	1571	1.04	0.407
Lichens	treatment	2	28	6.56	0.005
	Year	6	1571	28.97	<0.001
	treatment:year	12	1571	2.00	0.021
Mosses	treatment	2	28	2.29	0.080
	Year	6	1571	9.90	<0.001
	treatment:year	12	1571	1.44	0.140
Bare soil	treatment	2	28	12.52	<0.001
	year	6	1571	9.62	<0.001
	treatment:year	12	1571	1.24	0.249
Litter	treatment	2	28	14.04	<0.001
	Year	6	1571	77.83	<0.001
	treatment:year	12	1571	8.37	<0.001

Appendix S4 a) Tukey HSD-post hoc test statistics. Estimates and P-values for variables with significant year:treatment interaction. Pairwise comparison with year 0 and each sub-sequent year for the three treatments respectively. Significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	Estimates					
Response variable	**AGA**		**NGA**		**NGW**	
Shrub height						
Year 3	0.10		0.63		1.46	***
Year 6	-0.27		1.47	*	2.58	***
Year 9	N/A		N/A		N/A	
Year 12	N/A		N/A		N/A	
Year 15	0.70		2.78	***	4.59	***
Year 18	-0.09		3.26	***	4.74	***
Shrub cover						
Year 3	0.03		0.60		0.85	
Year 6	-0.67		-0.24		0.15	
Year 9	-0.50		1.24		1.63	**
Year 12	0.76		2.24	***	3.24	***
Year 15	0.84		2.38	***	3.37	***
Year 18	-0.01		1.92	***	3.31	***
Evergreen woody						
Year 3	0.46		0.15		0.33	
Year 6	0.67		0.74		0.93	
Year 9	0.76		0.72		-0.06	
Year 12	1.37	*	1.07	*	-0.51	
Year 15	1.01		0.88		-0.33	
Year 18	0.85		0.69		-0.24	
Lichens						
Year 3	-0.50		-0.38		-1.13	**
Year 6	-0.65		-0.43		-1.83	***
Year 9	-0.81		-0.60		-2.06	***
Year 12	-2.14	***	-1.37	***	-2.52	***
Year 15	-1.83	***	-1.30	***	-2.24	***
Year 18	-2.07	***	-1.09	*	-2.13	***
Litter						
Year 3	0.36		0.62		0.94	*
Year 6	-0.52		-1.02	***	0.44	
Year 9	-0.11		0.48		2.93	***
Year 12	0.93		1.11		3.25	***
Year 15	1.51	**	1.46	***	3.20	***
Year 18	0.59		1.41	***	3.09	***

Appendix S4 b) Tukey HSD-post hoc test statistics. Estimates and P-values for variables with significant year:treatment interaction. Pairwise comparison of treatments for each year. Significance levels: ° = $P < 0.1$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

		Estimates				
Response variable		**Shrub height**	**Shrub cover**	**Evergreen**	**Lichens**	**Litter**
Year 0						
	NGA vs. AGA	-0.01	-0.01	0.37	2.02	-0.18
	NGW vs. AGA	0.13	-0.36	1.21	1.20	0.04
	NGW vs. NGA	0.13	-0.35	0.83	-0.82	0.22
Year 3						
	NGA vs. AGA	0.53	0.57	0.06	2.14	0.08
	NGW vs. AGA	1.49	0.47	1.07	0.57	0.62
	NGW vs. NGA	0.96	-0.11	1.01	-1.57	0.55
Year 6						
	NGA vs. AGA	1.73	0.43	0.44	2.23 °	-0.68
	NGW vs. AGA	2.98 **	0.46	1.46	0.03	1.01
	NGW vs. NGA	1.25	0.03	1.02	-2.21 °	1.68 **
Year 9						
	NGA vs. AGA	N/A	1.74	0.34	2.22	0.41
	NGW vs. AGA	N/A	1.77	0.38	-0.05	3.08 ***
	NGW vs. NGA	N/A	0.03	0.05	-2.27 °	2.68 ***
Year 12						
	NGA vs. AGA	N/A	1.48	0.07	2.78 **	0.28
	NGW vs. AGA	N/A	2.13	-0.67	0.82	2.36 ***
	NGW vs. NGA	N/A	0.65	-0.74	-1.96	2.08 ***
Year 15						
	NGA vs. AGA	2.07	1.53	0.24	2.55 *	-0.23
	NGW vs. AGA	4.01 **	2.17	-0.13	0.79	1.74 *
	NGW vs. NGA	1.94	0.63	-0.37	-1.76	1.96 **
Year 18						
	NGA vs. AGA	3.34 **	1.93	0.22	2.99 **	0.64
	NGW vs. AGA	4.95 ***	2.96 **	0.13	1.14	2.54 ***
	NGW vs. NGA	1.61	1.03	-0.09	-1.85	1.90 **

Appendix S5. CCA test statistics. Effects of treatment, year and the interaction between treatment and year on the ground layer composition in the CCA analysis.

Analysis	Factor	Df	ChiSquare (CCA)	F	Pr(>F)
CCA	Treatment	2	0.239	38.42	0.001
	Year	1	0.088	28.28	0.001
	treatment:year	2	0.030	4.89	0.001

Paper II

Vegetation response to climate warming across the forest-tundra ecotone: species-dependent upward movement

Running head: Vegetation response in the forest-tundra ecotone

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Funding information
The Research Council of Norway (244557/E50).

Keywords
alpine vegetation, altitudinal gradients, climate warming, forest-tundra ecotone, forest vegetation, resurvey, species composition, species diversity, species-specific responses

Abstract

Questions: Rising temperatures are predicted to cause upward shifts and reorganisation of mountain vegetation. This study analyses how field-layer vegetation across the forest-tundra ecotone has responded over a 22-year period. Main questions are (i) have vegetation composition, richness and diversity changed? (ii) have abundance of functional plant groups and individual species changed? (iii) which environmental factors regulate vegetation distribution and composition?

Location: Central Norway.

Methods: The study uses vascular plant species recordings and environmental data from permanent 1x1m quadrats (n=266), established in 1994 and revisited in 2016, along transects from forest to high alpine areas (750-1500 m a.s.l.). Changes in vegetation composition (species- and functional group-level) and influence of environmental factors are analysed using ordination and mixed-effect models.

Results: Ordination shows an overall upward vegetation movement corresponding to 0.5±0.1 m yr^{-1}, and compositional homogenisation across the ecotone over time. Changes at species- and functional group-levels vary across the ecotone. Species richness and diversity increase over time due mainly to an increase of herbs and graminoids in the forested part of the ecotone. Evergreen woody species increase in abundance across the entire ecotone and most strongly above the forest. Deciduous woody species abundance is stable at group-level but shows large variation at species-level. Species-level responses deviate from group-level responses in all functional groups. Vegetation distribution and composition are environmentally explained by altitudinal distance to the treeline and microtopography.

Conclusions: Our results show how increased temperature impacts vegetation movements and reorganisation through mainly species-specific responses with low within functional group coherency. The apparent upward shift is moderate compared to the increase in temperature over the study period, but larger than in similar studies, although grazing pressure might co-control change rate. Species-specific responses and response rates highlight the need for detailed empirical data to predict and understand vegetation responses in a warming climate.

Introduction

During the last decades, global temperature has been rising, and is predicted to continue to increase (IPCC, 2014). The temperature increase has been more pronounced at high latitudes and altitudes (ACIA, 2005; IPCC, 2014; Pepin et al., 2015). With higher temperatures, a northward and upward shift of vegetation is commonly predicted, as well as loss of species and a change in dominance between species (Bjorkman et al., 2018; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Steinbauer et al., 2018).

The vegetation transition between boreal forest and the treeless tundra, the forest-tundra ecotone, is predicted to be sensitively responding to climate change with an upward shift in its location (ACIA, 2005; IPCC, 2014). Observed shifts are, however, spatiotemporally variable (Harsch, Hulme, McGlone, & Duncan, 2009), due to deviating main drivers of the ecotone (Hofgaard, Harper, & Golubeva, 2012; Holtmeier & Broll, 2005).

The presence of a tree-layer is important for the composition of the field-layer (Hofgaard & Wilmann, 2002; Sundqvist, Björk, & Molau, 2008). However, the field-layer vegetation has been found to be less sensitive to air temperature than the tree-layer (Lenoir et al., 2013; Scherrer & Körner, 2010). The field-layer vegetation might therefore respond independently to a warming climate (Batllori, Blanco-Moreno, Ninot, Gutierrez, & Carrillo, 2009; Camarero, Gutierrez, & Fortin, 2006). Further, alpine vegetation is considered especially vulnerable in a warming climate, as alpine plant species are assumed to be weak in competition with potentially invading lower-altitude species (Körner, 2003).

Reported responses of field-layer vegetation to warming in alpine areas include increase in abundance of woody species and increased vegetation height (Bjorkman et al., 2018; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Myers-Smith et al., 2011). However, many experimental and observational studies have reported modest vegetation responses to increased temperatures in arctic and alpine ecosystems in comparison to scenarios based on correlations with changes in biotic and abiotic factors alone (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Virtanen et al., 2010; Vittoz, Randin, Dutoit, Bonnet, & Hegg, 2009; Wilson & Nilsson, 2009).

Further, studies show a large heterogeneity in observed vegetation responses to climate warming (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012), suggesting that other factors inhibit or override the effects of increased temperatures, including both biotic factors such as herbivory (Hofgaard, 1997; Post & Pedersen, 2008; Speed, Austrheim, & Mysterud, 2013), and abiotic factors such as topograhpy, snow cover and soil conditions (Eskelinen, Kaarlejarvi, & Olofsson, 2017; Graae et al., 2017; Wipf & Rixen, 2010).

A common approach to analysing complex vegetation responses is to categorise species into functional groups based on e.g. growth form or morphological characters. This approach is frequently used in studies of changes in alpine vegetation (cf. Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Wilson & Nilsson, 2009), often based on the functional groups defined in Chapin, BretHarte, Hobbie, & Zhong (1996). However, several studies have found a lack of consistent species responses within functional groups (Little, Jägerbrand, Molau, & Alatalo, 2015; Saccone, Hoikka, and Virtanen, 2017). Studies comparing the two approaches point to functional groups concealing species-specific responses, but also that species-level investigations can produce better understanding of the determinants for the functional groups (Little et al., 2015; Saccone, Hoikka, and Virtanen, 2017).

Common methods to study climate effects on vegetation are gradient studies (space-for-time), experiments, and monitoring (Elmendorf et al., 2015). While gradient studies reflect the present environment, they tend to overestimate effects of climate change as a gradient reflects the average environment over a larger timespan and thus is an expression of site history rather than present climate (Elmendorf et al., 2015). Experiments, on the other hand, yield detailed control over some selected environmental factors, but are prone to artefacts especially when used over longer timespans (De Boeck et al., 2015; Ettinger et al., 2019; Løkken, Hofgaard, Dalen, & Hytteborn, 2019).

Monitoring, or resurveying of historic vegetation plots, has received renewed interest as a means to better understand vegetation changes over time (Kapfer et al., 2016), and avoids some of the disadvantages of space-for-time studies and experiments, particularly when plots are permanently marked (Verheyen et al., 2018). Resurvey of permanent plots located along altitudinal gradients can give particularly good insights as there is potential to detect shifts and altered dynamics in different vegetation zones (Gazol, Moiseev, & Camarero, 2017; Spasojevic & Suding, 2012; Virtanen et al., 2010; Wilson & Nilsson, 2009)

The present study analyses changes in field-layer vegetation over a 22-year period by using recordings from permanent plots located along altitudinal gradients across the forest-tundra ecotone and adjacent sub-alpine forest and alpine tundra, in Central Norway. The baseline data was recorded in 1994 (Hofgaard, 1997; Hofgaard & Wilmann, 2002) and the resurvey data in 2016. During this period, the study area experienced a 1.2°C increase in mean annual temperature. Three main questions are asked: (i) How has vegetation composition, richness and diversity changed in the 22-year period, and was the rate and direction of change sustained across the forest-tundra ecotone? (ii) How has abundance of functional plant groups and individual plant species changed in the 22-year period, and how did these changes influence overall composition and diversity change? (iii) Which environmental factors regulate vegetation distribution and composition across the forest-tundra ecotone overall, and has the importance of environmental factors changed in the 22-year period?

Methods

Study area

The study area is located in Central Norway (Lat. 62°30'N-62°36'N, Long. 8°50'E-9°13'E), and is characterised by a rough topography with large altitudinal differences within short distances. Most surrounding mountain peaks reach altitudes between 1400 and 1600 m a.s.l. The area is located in the transition between the northern boreal and the alpine vegetation zone and the climate is slightly oceanic (Moen, 1999). Due to lack of nearby meteorological stations recording temperature, we used interpolated temperature data, with a spatial resolution of 1 km^2, to investigate temperature trends over the study period (Norwegian Meteorological Institute, 2019). Mean annual and summer (June-August) temperature increased with 1.2°C and 1.4°C respectively (from -0.6°C to + 0.6°C and from 7.6°C to 9.0°C, respectively; Figure 1) when comparing the 15-year period predating the 1994 measurements (1979-1993) with the 15-year period predating the 2016 measurements (2001-2015). Precipitation data are available from the Hafsås meteorological station within the study area (operational 1978-present, 698 m a.s.l.). Mean annual precipitation did not change substantially over the study period (697 mm and 678 mm in the 15-year periods 1979-1993 and 2001-2015, respectively, see Appendix S1 for details).

The study area is used as grazing ground for domestic sheep during the summer season (June-September). There are no detailed annual records on the number of sheep using the study area, however, estimates based on numbers reported by the local association of sheep farmers (Sunndalen beitelag, see Appendix S2), indicate that the number of released sheep has declined from 16.3 sheep/km^2 to 11.3 sheep/km^2 between 1994 and 2016.

The typical bedrock in the area consists of gneiss, but a band of amphibolite schist runs southwest/northwest through parts of the area (Norwegian Geological Survey, 2019) and gives rise to richer soils locally (Table 1).

The forest in the study area is dominated by mountain birch (*Betula pubescens* spp. *tortuosa* (Ledeb.) Nyman), with few scattered individuals of *Pinus sylvestris* L., *Alnus incana*

L., *Populus tremula* L. and *Sorbus aucuparia* L. The forest line, defined as the uppermost position of closed stands of birch trees at least 2 meters in height, ranged 940-1120 m a.s.l. in 1994, using an altimeter (Table 1). The treeline, i.e. the uppermost position of individual trees of at least 2 meters in height, ranged 980-1170 m a.s.l. There was no detectable altitudinal shift of neither the forest line nor the treeline between 1994 and 2016 (i.e. GPS recordings in 2016 were within the uncertainty estimates of the 1994 altimeter recordings) (Løkken et al. unpubl). The field-layer vegetation in the forest is dominated by herbs and graminoides such as *Trientalis europeae* L. and *Avenella flexuosa* (L.) Drejer, respectively, and scattered dwarf shrubs such as *Vaccinium myrtillus* L. and *Empetrum nigrum* L. Between the forest line and the treeline the abundance of herbs and graminoids declines and the vegetation becomes dominated by alpine heath communities where dwarf shrubs such as *E. nigrum*, *V. myrtillus* and *Vaccinium uliginosum* L. are the most common. Above the treeline and towards the mountain summits the vegetation becomes successively sparser with a higher dominance of low statured alpine species such as *Salix herbacea* L. and *Carex bigelowii* Torr. ex Schwein. Further details on geographical location, geology, climate and vegetation are found in Hofgaard (1997) and Hofgaard & Wilmann (2002). Nomenclature follows the Norwegian Species Nomenclature Database (Norwegian Biodiversity Information Centre, 2019).

Study design

The study consists of six transects including a total of 67 plots (10 m x 10 m, see Table 1 for transect details). The transects run from the closed forest to mountain summits and thus encompass the entire forest-tundra ecotone, including the forest, the forest line, treeline and tree species line (i.e. most advanced location of tree species specimens irrespectively of size), and adjacent alpine areas. The lower end of the transects was determined by the valley bottom or by areas with intense human land use. The plots were placed along the transects at every 50 m a.s.l. interval (e.g. 750, 800, 850 and so forth), mapped and permanently marked with plastic sticks and aluminium pipes. In the plots, the number of trees (≥2 m), stand density, height of trees, and number of saplings (<2 m) were recorded and mapped at a 5 m x 5 m sub-plot level. For recording of field-layer species four quadrats (1 m x 1 m) were located within each plot (one per sub-plot) according to a restricted random procedure (see Hofgaard (1997) for details). The quadrats were divided into 16 squares (0.25 m x 0.25 m) and presence/absence of all field-layer species was recorded in each square, giving an abundance of each species per quadrat as the frequency of occurrence in squares. In 1994 a total of 74 plots and 295 quadrats were analysed. The transects were revisited in 2015, and 69 of the original 74 plots were located and registered by GPS. Two of the plots were rejected due to signs of intensified human land use. Thus, in 2016, 67 plots and 266 quadrats were reanalysed (See Table 1 for distribution between transects).

Slope and aspect were recorded in 1994 for each quadrat. To avoid the problem with circularity of the aspect data (large values being very close to small values, i.e. 0° and 360° both represent north) we calculated the deviation in degrees from the optimal angle of aspect (205°) for solar radiation (Dargie, 1984), ranging from 0° to 180° (henceforward denoted devOpt). All plots were categorised according to bedrock type ("poorer"; plots on poor bedrock or "richer"; plots on intermediately rich bedrock) determined by comparing the GPS position of each plot to a digital bedrock map available from NGU (Norwegian Geological Survey, 2019). Distance to the forest line and treeline was defined for each plot, based on the altitudinal distance between the plot and the respective line for each transect. Topographic Position Index (TPI) (Weiss, 2001) was assessed for each quadrat, with a surrounding of a continuous circle of 250 m^2. TPI is a measure of the difference in elevation of the central point from the average surrounding elevation, relative to the slope. Positive values indicate that the centre is higher than the surrounding (convex terrain), while negative values indicate a lower central altitude than the surrounding (concave). Further, we used the height of the trees and saplings to calculate the tree-layer height in each sub-plot, as the mean height of the 5 tallest trees and/or saplings in each sub-plot.

Data treatment and statistical analyses

To identify changes in field-layer vegetation along the forest-tundra ecotone, we defined four transect sections along the ecotone, based on the grouping in Hofgaard & Wilmann (2002): Forest (>100 m below treeline), TL-100 (plots from treeline to 100 altitudinal meter below), TL+100 (treeline to 100 m above), alpine (>100 m above treeline).

Vegetation change was analysed both at species-level and functional group-level. Four functional groups were used: evergreen woody species, deciduous woody species, herbs, and graminoids. To examine changes at the species-level we selected the three most frequent species from each of the four functional groups (frequency recorded as the number of quadrats with species occurrence; see Appendix S3).

Due to a strong collinearity between environmental factors, especially those related to altitude, such as distance to treeline, and features of the tree-layer, a combination of constrained ordination (CCA) and variance inflation factor (VIF) was used to determine the relative importance of the environmental variables as well as their collinearity, and subsequently to choose a statistical and ecological useful set of environmental variables. The CCA analysis was used to determine which of the environmental variables had the strongest explanatory power on field-layer composition. Correlation between variables (Appendix S4), their explanatory power (Appendix S5) and the VIF of each variable (Appendix S5) were used to guide variable removal. With the goal that no variable in the final set of environmental variables should have a higher VIF than 5 (cf. Zuur, Ieno, & Smith, 2007), the following set of environmental variables was included in further analyses: Distance to treeline (treeline), height of tree-layer (height), aspect (devOpt), bedrock, TPI, slope, number of saplings (saplings) and year (See Appendix S6 for how these variables varied with transect section).

To investigate patterns in field-layer vegetation composition, the field-layer data, combined over years, were subjected to a global two-dimensional non-metric multidimensional scaling (GNMDS). The GNMDS was run with Bray-Curtis dissimilarity measure, 100 initial configurations, maximum 200 iterations and stress tolerance 10^{-7} (Davey, Heegaard, Halvorsen, Kauserud, & Ohlson, 2013). Unreliable Bray-Curtis distances (>0.8) were replaced by geodesic distances, using the “step-across” method (Williamson, 1978).

To assess the importance of the environmental variables on the species composition we used linear mixed-effect models with quadrat axis score as response variable and environmental variables as predictors, using quadrat nested within plot nested within transect as random factor. This method accounts for the spatial and temporal autocorrelation structure of the data. To investigate the vegetation distribution and composition across the forest-tundra ecotone and how this changed over the studied 22-year period, we constructed linear mixed-effects models including all environmental variables, transect section, year, and the two-way interaction between transect section and year. Quadrat nested within plot nested within transect was used as random factor. A backward-selection procedure was used to simplify the models (cut-off: p=0.05), and only the most parsimonious models are presented.

We constructed separate mixed-effect models for the following response variables: 1) displacement of quadrat axis scores along each of the two axes in the GNMDS analysis, 2) species richness (number of species in each quadrat), 3) Shannon’s diversity index, 4) the abundance of all four functional groups and 5) the most frequently occurring species. As the quadrat displacement along the ordination axes was calculated as the difference in axis scores between years, this model did not include year and the interaction between year and transect section. Displacement of quadrat axis scores, richness, Shannon’s diversity index and evergreen woody species were analysed with linear mixed-effects models. Abundance of the functional groups deciduous woody species, herbs and graminoids were run with generalised linear mixed-effects models, using a quasi-poisson distribution with a log link. For the individual species abundance models, we used a binominal distribution with log link.

All statistical analyses were performed using the packages 'lme4' (Bates, Maechler, Bolker, & Walker, 2015), 'lmerTest' (Kuznetsova, Brockhoff, & Christensen, 2017), 'MASS' (Venables & Ripley, 2002) and 'vegan' (Oksanen et al., 2019) in the R statistical environment (R Core Team, 2019).

Results

Species turnover and composition

The total number of species recorded was 151 in 1994 and 150 in 2016, with a mean of 15.2 ± 6.4 SD species per quadrat in 1994, and 16.0 ± 7.4 SD species per quadrat in 2016. The number of species per quadrat (species richness) was highest in the forest section and declined with altitude (Appendix S7). In total ten species were lost between 1994 and 2016 (6.6%), and nine new species (6.0% of all species) were recorded in 2016 (Appendix S8). Lost species had low occurrence (present in 1-2 quadrats in 1994) and included six herbs and four graminoids. The new species in 2016 were found in 1-3 quadrats and included six herbs, two graminoids and one deciduous dwarf shrub.

The species composition GNMDS revealed variation in both the first (range –1.56 to 1.39 half change units) and second ordination axis (range –1.65 to 0.92 half change units). The variation along the first axis was significantly explained by distance to the treeline ($p<0.001$, Table 2, Figure 2) with quadrats located in the alpine section on the negative end of the axis and forest quadrats towards the positive end. In addition, there was significant variation between years along the first axis ($p<0.001$, Table 2). Variation along the second axis was best explained by TPI ($p=0.039$, Table 2, Figure 2), and there were significant differences between years along this axis ($p<0.001$, Table 2).

The change in species composition along the first axis (displacement of axis score) was significant ($p<0.001$, Figure 2, Appendix S9), but was not explained by any of the environmental variables, i.e. the displacement was equal among quadrats. Species composition along the second axis changed significantly, and there was an effect of the height of the tree-layer, where quadrats with low tree height had higher axis displacement ($p<0.001$, Figure 2, Table 3a, Appendix S9). Thus, displacement along the second axis varied with quadrat location across the forest-tundra ecotone; quadrats below the treeline moved in a negative direction, while quadrats above the treeline moved in a positive direction (Figure 2), i.e. indicating a homogenisation of the species composition across the transect sections.

The overall change in species composition between 1994 and 2016, calculated as the average displacement of axis score per quadrat, was on average 0.04 ± 0.01 SE and 0.03 ± 0.01 SE along the first and second axes, respectively. As the total length of the first axis (which mainly correlated with altitude) was 2.95 and the altitudinal span of the altitudinal gradient was 750 m, the displacement along the first axis indicated approximately a 10.5 ± 1.7 SE m upward shift of vegetation (750*(0.04/2.95)).

Species richness & diversity

There was a general increase in both species richness and Shannon's diversity index from 1994 to 2016 (Table 3b, Appendix S9), with a stronger increase in quadrats located in the forest and TL-100 compared with TL+100 and alpine sections (significant year × section interaction; Table 3b, Appendix S9). Quadrats located in the alpine section only showed change in diversity (Table 3b, Figure 3). A general effect of bedrock was found, with highest species richness on richer bedrock.

Functional group and species-specific responses

The distribution across the ecotone and the abundance changes from 1994 to 2016 of the three most frequent species in each functional group showed a variety of coinciding and contradictory trends compared to the main trend of their respective functional group (Figure 4, Table 4).

Evergreen woody species

The mean abundance of the functional group evergreen woody species was negatively related to the height of the tree layer and distance to the treeline, and was positively related to the number of saplings (Figure 4, Table 3c, Appendix S9). The abundance of evergreen woody species increased overall from 1994 to 2016, but a significant year × transect section interaction reveal a stronger response in the alpine section (Figure 4, Table 3c, Appendix S9). *Empetrum nigrum* was the dominant species in all transect sections above the forest with highest abundance in the sections around the treeline (Figure 4, Table 4, Appendix S9). The species showed a general abundance increase, and with strongest response in the alpine section (significant year × transect section interaction). *Phyllodoce caerula* had significantly lower abundance in the forest than the other transect sections and increased in overall abundance over time (Fig. 4, Table 4, Appendix S9). *Vaccinium vitis-idaea* had its lowest abundance in TL+100 and no variation in abundance among other transect sections. There was no overall abundance change, but a significant year × transect section interaction revealed that the abundance increased slightly in the alpine section and decreased in the three other transect sections (Figure 4, Table 4, Appendix S9).

Deciduous woody species

The abundance of the functional group deciduous woody species was positively related to the number of saplings, and negatively related to TPI, distance to the treeline and tree-layer height, and consequently the abundance was lower in forest and alpine quadrats compared to TL-100 and TL+100 (Figure 4, Table 3d, Appendix S8). There was no significant change in the abundance of deciduous woody species from 1994 to 2016 (Figure 4). Of the three most frequent deciduous woody species, *Vaccinium myrtillus* was dominant at all transect sections below the alpine section. There was a significant overall abundance increase of the species, and with strongest responses in sections above the forest (Figure 4, Table 4, Appendix S9). The abundance of *Salix herbacea* was highest in the TL+100 and alpine transect sections. The species had an overall abundance decrease over time, with the strongest decrease in the TL+100 and alpine sections (Figure 4, Table 4, Appendix S9). *Vaccinium uliginosum* had its highest abundance in the TL-100 transect section and showed an overall increase from 1994 to 2016. This increase was shown in all transect sections except the section with highest abundance (TL-100) where there instead was a slight decrease (Figure 4, Table 4, Appendix S9).

Herbs

Overall the herb abundance was positively related to TPI and tree height (Figure 4, Table 3d, Appendix S8). From 1994 to 2016 herb abundance increased in the forest section but not at higher altitudes (Figure 4, Table 3d, Appendix S8). The three most abundant herb species showed somewhat deviating distribution patterns across the forest-tundra ecotone. While *Bistorta vivipara* was more abundant in the alpine transect section, *Solidago virgaurea* and *Trientalis europaea* were most abundant in the forest (Figure 4, Table 4, Appendix S9). There was no general change in abundance of *B. vivipara* between 1994 and 2016, but a significant year × transect section interaction revealed a small abundance increase in the forest (Table 4, Appendix S9). In contrast both *S. virgaurea* and *T. europaea* increased in abundance between 1994 and 2016, *S. virgaurea* mainly in the forest, but *T. europaea* along the entire gradient with emphasis on TL-100 and TL+100 (Figure 4, Table 4, Appendix S9).

Graminoids

The overall abundance of graminoids was positively related to bedrock richness and TPI (Figure 4, Table 3d, Appendix S8). Overall graminoid abundance did not change between 1994 and 2016, but a significant year × transect section interactions showed a slight increase in graminoid abundance over time in all sections except in TL+100, in which a slight decrease occurred (Figure 4, Table 3d, Appendix S8). The three most abundant graminoids showed deviating distribution patterns across the ecotone (Figure 4, Table 4, Appendix S9). The abundance of *Avenella flexuosa* was highest in the forest and decreased with increasing altitude whereas *Carex bigelowii* had highest abundance in the alpine section and a decrease towards the forest. *Anthoxanthum odoratum* was distributed evenly across the ecotone (Figure 4, Table 4, Appendix S9). Regarding change in abundance from 1994 to 2016, *A. odoratum* showed an overall decrease, *C. bigelowii* no overall change but a small increase in the forest section, and *A. flexuosa* showed no change (Figure 4, Table 4, Appendix S9).

Discussion

Changes in species composition

The estimated upward shift of 10.5 m of field-layer vegetation between 1994 and 2016, based on quadrat displacement along the first ordination axis, represents an overall vegetation movement of approximately 0.5 m yr^{-1}. Even though 22 years is a relatively short time period to detect compositional vegetation changes, the experienced increase of 1.4°C in mean summer temperature represents an upward temperature shift of more than 200 altitudinal meter (assuming a lapse rate of 0.6°C per 100 m of altitude; Wieser & Tausz, 2007). Accordingly, to keep track with the experienced warming an upward vegetation movement of approximately 10 m yr^{-1} would have been needed. In light of this the recorded upward shift of vegetation composition over the time period is moderate, but still at a similar order of magnitude as most calculated rates of shift in species optimums, with ranges from an average of ca. 1.1 m yr^{-1} to 3 m yr^{-1} (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; le Roux & McGeoch, 2008; Lenoir, Gegout, Marquet, de Ruffray, & Brisse, 2008), but in contrast to other studies reporting minor or no signs of upward shifts (Virtanen et al., 2010; Vittoz et al., 2009; Wilson & Nilsson, 2009). Even though the estimated upward movement is statistically consistent, there is large variation among plots, and thus the rate of the upwards movement must be handled with care.

Our results of species composition above and below the treeline becoming more similar during the 22-year study period, is indicative of homogenisation of the vegetation. This is also reported for a variety of other alpine plant communities as a response to climate warming (Matteodo, Ammann, Verrecchia, & Vittoz, 2016; Odland, Høitomt, & Olsen, 2010; Ross, Woodin, Hester, Thompson, & Birks, 2012), and has been causally linked to invasion of widespread and generalist species and decline of rare or specialised species (Matteodo et al., 2016). Accordingly, the individual species analysis show distribution expansion and abundance increase of species with generally high presence throughout the ecotone, particularly in the area of the the forest line and the treeline (e.g. *Empetrum nigrum*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea*) and a parallel decline in specialist species like the alpine *Salix herbacea*.

Species richness and diversity

The observed overall increase in species richness is composed of increase in the lower-elevation quadrats (where diversity was alreay high) and little to no increase in upper parts. This is in line with results from the southern Scandes Mountains (Klanderud and Birks, 2003), but in contrast to results from the norther Scandes (Wilson and Nilsson, 2009) where a general decline in species richness was found over a similar time span (20 years). However, the area of the northern study (Wilson and Nilsson, 2009), although located at comparable altitudinal range as our study, is characterised by moister climate conditions and without sheep grazing impact. These differences might thus explain the deviating results.

Further, our findings of negligible increase in species richness in the alpine section stand in contrast to reports of rapid increase in species richness at alpine summits due to climate warming (Pauli et al., 2012; Steinbauer et al., 2018). However, these studies are based upon large plots or entire summits, increasing the probability of recording rare species. Thus, the contrasting results may be due to study design (Kullman, 2010; Wilson & Nilsson, 2009).

The stronger increase in diversity in the parts of the ecotone with the initial highest diversity is contrasting the classic diversity-invasibility hypothesis (Elton, 1958), that predicts species rich communities to be more resistant to immigration by new species. However, contrasting results are reported, often referred to as the invasion paradox (cf. Fridley et al., 2007). This theory, however, places limited emphasis on abiotic constrains, and in alpine systems abiotic factors such as wind and cold exposure are found to be able to dominate over competetive interactions (Gazol et al., 2017; Spasojevic & Suding, 2012). It has also been argued that invasiveness depends on the productivity of the area, and that low productive areas experience less invasions (Davies, Harrison, Safford, &Viers, 2007), which agrees with our results and the results of Wilson and Nilsson (2009) who found stronger changes in the most productive, lower parts of the ecotone.

Individual species vs. functional groups

The results of analyses of individual species in our study underline the importance of a species approach, in addition to or instead of a functional group approach, when investigating vegetation dynamics. These mixed responses, with stronger species-specific responses, especially within the deciduous woody species group, underline how grouping species into traditional functional groups can be inadequat and even misleading to explain vegetation responses to environmental change (Klanderud, 2008; Little et al., 2015; Saccone, Hoikka, & Virtanen, 2017).

Our results suggest that the decrease in sheep abundance in the study area from 1994 to 2016 might have given foraging prone species improved resprouting and disperse conditions. For example, the increase in *Solidago virgaurea* over time, a species which has been shown to respond postively to cessasion of grazing (Evju, Austrheim, Halvorsen, & Mysterud, 2009), combined with the increase in *Vaccinium myrtillus* and a general decline in *Anthoxanthum odoratum*, indicate vegetation changes associated with a decreased grazing pressure over time (Pakeman, Fielding, Everts, & Littlewood, 2019).

Evergreen species, in particular *Empetrum nigrum,* have been found to increase in abundance in response to warming (Klanderud & Birks, 2003; Vuorinen et al., 2017; Wilson & Nilsson, 2009), suggesting that warming is a main driver of the observed increase also in our study area. Changes in tundra vegetation in response to climate warming are however, regionally variable, in particular the response of deciduous woody species (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012).

Environmental factors and drivers of change

Our analysis reveals distance to treeline as the strongest determinant of field-layer vegetation composition. Although treeline and tree height are highly correlated with altitude, the results support that precence of a tree-layer exerts controll over field-layer vegetation (Hofgaard & Wilmann, 2002). Further, the results suggest that vegetation changes above the treeline involve interactions with other drivers such as topography and substrate richness (i.e. displacement along the second ordination axis), which is in line with previously published findings (Batllori et al., 2009; Hofgaard & Wilmann, 2002; Lenoir et al., 2013; Scherrer & Körner, 2010). Even though the presence of a historic tree-layer has lingering importance for current field-layer vegetation composition (Hofgaard & Wilmann, 2002), the lack of treeline movement in the study area (Løkken et al. unpubl.) combined with an upward shift of field-layer vegetation suggest that the link with tree-layer might become weaker in a warming climate (Batllori et al., 2009; Camarero et al., 2006). These contrasting results suggest that vegetation in the forest-tundra ecotone responds in layer-specific manners to climate warming, possibly moderated by the presence of herbivores (Løkken et al., 2019; Vuorinen et al., 2017). In alpine and arctic tundra ecosystems, herbivory is a well known driver counteracting effects of climate warming on vegetation (Eskelinen et al., 2017; Olofsson et al., 2009; Speed, Austrheim, Hester, & Mysterud, 2012), that might inhibit the expansion of deciduous woody species, but with low effect on evergreen woody species (Vowles et al., 2017; Ylänne, Stark, & Tolvanen, 2015).

Concluding remarks

Our results of vegetation change over a 22-year period with substantial warming, demonstrate how increased temperature impacts vegetation in complex species-specific manners, dependent on initial vegetation composition and local variability in biotic and abiotic factors such as the presence of a tree-layer, microtopography, soil richness and grazing pressure. The estimated upward vegetation shift of 0.5 m yr^{-1} is, even though moderate in comparison with the temperature change in the area, larger than what is found in most observational studies. In addition, the observed contrasting responses between the individual species, in particular within functional groups, underline the importance of considering the species-level when studying climate change-related vegetation changes (Klanderud, 2008; Little et al., 2015; Saccone et al., 2017). Further, insights from a range of study approaches at local scales are important to feed realistic predictions of vegetation change, both reorganisation of species and rates, under climate warming (De Boeck et al., 2015).

Acknowledgments

We would like to thank Anaïs Kermagoret, Anna Haukedal Andreassen, Lasse Topstad, Isabell Negri, Eirik Ryvoll Åsheim, Per Steinar Løkken and Siri Lie Olsen for their help with the field work, and Gjøra Camping for accomodation during the field work.

Contributions

AH initiated and designed the study, and provided the 1994 data. JOL lead the field sampling in 2016. JOL performed the analyzes with input from ME and AH. JOL drafted the paper in colaboration with all co-authors. Final version of the manuscript read and approved by all co-authors.

Data accesibility

The original data sets are stored in the NINA database, and are available upon formal request addressed to the last author.

References

ACIA. (2005). *Arctic Climate Impact Assessment*. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, 67(1)*, 1-48. doi:10.18637/jss.v067.i01

Batllori, E., Blanco-Moreno, J. M., Ninot, J. M., Gutierrez, E., & Carrillo, E. (2009). Vegetation patterns at the alpine treeline ecotone: the influence of tree cover on abrupt change in species composition of alpine communities. *Journal of Vegetation Science, 20*(5), 814-825. doi:DOI 10.1111/j.1654-1103.2009.01085.x

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Ruger, N., Beck, P. S. A., . . . Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature, 562*(7725), 57-62. doi:10.1038/s41586-018-0563-7

Camarero, J. J., Gutierrez, E., & Fortin, M. J. (2006). Spatial patterns of plant richness across treeline ecotones in the Pyrenees reveal different locations for richness and tree cover boundaries. *Global Ecology and Biogeography, 15*(2), 182-191. doi:10.1111/j.1466-822x.2006.00211.x

Chapin, F. S., BretHarte, M. S., Hobbie, S. E., & Zhong, H. L. (1996). Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, *7*(3), 347-358. doi:Doi 10.2307/3236278

Chen, I. C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science, 333*(6045), 1024-1026. doi:10.1126/science.1206432

Dargie, T. C. D. (1984). On the integrated interpretation of indirect site ordinations: a case study using semi-arid vegetation in southeastern Spain. *Vegetatio, 55*(1), 37-55. doi: 10.1007/BF00039980

Davey, M. L., Heegaard, E., Halvorsen, R., Kauserud, H., & Ohlson, M. (2013). Amplicon-pyrosequencing-based detection of compositional shifts in bryophyte-associated fungal communities along an elevation gradient. *Molecular Ecology, 22*(2), 368-383. doi:10.1111/mec.12122

Davies, K. F., Harrison, S., Safford, H. D., & Viers, J. H. (2007). Productivity Alters the Scale Dependence of the Diversity–Invasibility Relationship. *Ecology, 88*(8), 1940-1947. doi:10.1890/06-1907.1

De Boeck, H. J., Vicca, S., Roy, J., Nijs, I., Milcu, A., Kreyling, J., . . . Beier, C. (2015). Global Change Experiments: Challenges and Opportunities. *BioScience, 65*(9), 922-931. doi:10.1093/biosci/biv099

Elmendorf, S. C., Henry, G. H., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., . . . Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters, 15*(2), 164-175. doi:10.1111/j.1461-0248.2011.01716.x

Elmendorf, S. C., Henry, G. H., Hollister, R. D., Fosaa, A. M., Gould, W. A., Hermanutz, L., . . . Walker, M. D. (2015). Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. *Proceedings of the National Academy of Sciences, 112*(2), 448-452. doi:10.1073/pnas.1410088112

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., . . . Wipf, S. (2012). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change, 2*(6), 453-457. doi:10.1038/Nclimate1465

Elton, C. S. (1958). *The ecology of invasions by animals and plants*. London: Methuen and Company.

Eskelinen, A., Kaarlejarvi, E., & Olofsson, J. (2017). Herbivory and nutrient limitation protect warming tundra from lowland species' invasion and diversity loss. *Global Change Biology, 23*(1), 245-255. doi:10.1111/gcb.13397

Ettinger, A. K., Chuine, I., Cook, B. I., Dukes, J. S., Ellison, A. M., Johnston, M. R., . . . Wolkovich, E. M. (2019). How do climate change experiments alter plot-scale climate? *Ecology Letters, 22*(4), 748-763. doi:10.1111/ele.13223

Evju, M., Austrheim, G., Halvorsen, R., & Mysterud, A. (2009). Grazing responses in herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem. *Oecologia, 161*(1), 77-85. doi:10.1007/s00442-009-1358-1

Fridley, J. D., Stachowicz, J. J., Naeem, S., Sax, D. F., Seabloom, E. W., Smith, M. D., . . . Von Holle, B. (2007). The invasion paradox: reconciling pattern and process in species invasions. *Ecology*, 88(1), 3-17. doi:10.1890/0012-9658(2007)88[3:Tiprpa]2.0.Co;2

Gazol, A., Moiseev, P., & Camarero, J. J. (2017). Changes in plant taxonomic and functional diversity patterns following treeline advances in the South Urals. *Plant Ecology & Diversity, 10*(4), 283-292.

Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J.-C., Hylander, K., . . . Bråthen, K. A. (2018). Stay or go–how topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology, Evolution and Systematics*, 30, 41-50. doi: 10.1016/j.ppees.2017.09.008

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters, 12*(10), 1040-1049. doi:10.1111/j.1461-0248.2009.01355.x

Hofgaard, A. (1997). Inter-relationships between treeline position, species diversity, land use and climate change in the central Scandes Mountains of Norway. *Global Ecology and Biogeography, 6*(6), 419-429. doi:Doi 10.2307/2997351

Hofgaard, A., Harper, K., & Golubeva, E. (2012). The role of the circumarctic forest–tundra ecotone for Arctic biodiversity. *Biodiversity, 13*(3-4), 174-181. doi:10.1080/14888386.2012.700560

Hofgaard, A., & Wilmann, B. (2002). Plant distribution pattern across the forest-tundra ecotone: The importance of treeline position. *Ecoscience, 9*(3), 375-385. doi:10.1080/11956860.2002.11682725

Holtmeier, F. K., & Broll, G. (2005). Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography, 14*(5), 395-410. doi:10.1111/j.1466-822x.2005.00168.x

IPCC. (2014). *Summary for policymakers. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir,M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy,S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)].* . Cambridge, United Kingdom and New York, NY, USA, : Cambridge UniversityPress.

Kapfer, J., Hedl, R., Jurasinski, G., Kopecky, M., Schei, F. H., & Grytnes, J. A. (2016). Resurveying historical vegetation data - opportunities and challenges. *Applied Vegetation Science, 20*(2), 164-171. doi:10.1111/avsc.12269

Klanderud, K. (2008). Species-specific responses of an alpine plant community under simulated environmental change. *Journal of Vegetation Science, 19*(3), 363-U109. doi:10.3170/2008-8-18376

Klanderud, K., & Birks, H. J. B. (2003). Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene, 13*(1), 1-6. doi:10.1191/0959683603hl589ft

Kullman, L. (2010). Alpine flora dynamics - a critical review of responses to climate change in the Swedish Scandes since the early 1950s. *Nordic Journal of Botany, 28*(4), 398-408. doi:10.1111/j.1756-1051.2010.00812.x

Körner, C. (2003). *Alpine plant life: functional plant ecology of high mountain ecosystems*: Springer Science & Business Media.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software, 82(13)*, 1-26. doi:10.18637/jss.v082.i13

le Roux, P. C., & McGeoch, M. A. (2008). Rapid range expansion and community reorganization in response to warming. *Global Change Biology, 14*(12), 2950-2962. doi:10.1111/j.1365-2486.2008.01687.x

Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science, 320*(5884), 1768-1771. doi:10.1126/science.1156831

Lenoir, J., Graae, B. J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G., . . . Svenning, J. C. (2013). Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology, 19*(5), 1470-1481. doi:10.1111/gcb.12129

Little, C. J., Jägerbrand, A. K., Molau, U., & Alatalo, J. M. (2015). Community and species-specific responses to simulated global change in two subarctic-alpine plant communities. *Ecosphere*, *6*(11), art227. doi:10.1890/es14-00427.1

Løkken, J. O., Hofgaard, A., Dalen, L., & Hytteborn, H. (2019). Grazing and warming effects on shrub growth and plant species composition in subalpine dry tundra: An experimental approach. *Journal of Vegetation Science, 0*. doi:10.1111/jvs.12752

Matteodo, M., Ammann, K., Verrecchia, E. P., & Vittoz, P. (2016). Snowbeds are more affected than other subalpine-alpine plant communities by climate change in the Swiss Alps. *Ecology and Evolution, 6*(19), 6969-6982. doi:10.1002/ece3.2354

Moen, A. (1999). *National Atlas of Norway: Vegetation*. Hønefoss: Statens Kartverk.

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., . . . Hik, D. S. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters, 6*(4), 045509. doi:10.1088/1748-9326/6/4/045509

Norwegian Biodiversity Information Centre. (2019). Norwegian Species Nomenclature Database. Retrieved from http://www2.artsdatabanken.no/artsnavn/Contentpages/Hjem.aspx

Norwegian Geological Survey. (2019). Norwegian Geological Survey. Retrieved from http://www.ngu.no/

Norwegian Meteorological Institute. (2019). eKlima. *eKlima.* Retrieved from http://sharki.oslo.dnmi.no/

Odland, A., Høitomt, T., & Olsen, S. L. (2010). Increasing Vascular Plant Richness on 13 High Mountain Summits in Southern Norway since the Early 1970s. *Arctic Antarctic and Alpine Research, 42*(4), 458-470. doi:10.1657/1938-4246-42.4.458

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., . . . Wagner, H. (2019). vegan: Community Ecology Package (Version 2.5-6.) [R package]. Retrieved from https://CRAN.R-project.org/package=vegan

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology, 15*(11), 2681-2693. doi:10.1111/j.1365-2486.2009.01935.x

Pakeman, R. J., Fielding, D. A., Everts, L., & Littlewood, N. A. (2019). Long-term impacts of changed grazing regimes on the vegetation of heterogeneous upland grasslands. *Journal of Applied Ecology, 0*. doi:10.1111/1365-2664.13420

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Benito Alonso, J. L., . . . Grabherr, G. (2012). Recent plant diversity changes on Europe's mountain summits. *Science, 336*(6079), 353-355. doi:10.1126/science.1219033

Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., . . . Yang, D. Q. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change, 5*, 424. doi:10.1038/nclimate2563

Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences, 105*(34), 12353-12358. doi:10.1073/pnas.0802421105

R Core Team. (2019). R: A Language and Environment for Statistical Computing (Version 3.3.2.). Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org

Ross, L. C., Woodin, S. J., Hester, A. J., Thompson, D. B. A., & Birks, H. J. B. (2012). Biotic homogenization of upland vegetation: patterns and drivers at multiple spatial scales over five decades. *Journal of Vegetation Science, 23*(4), 755-770. doi:10.1111/j.1654-1103.2012.01390.x

Saccone, P., Hoikka, K., & Virtanen, R. (2017). What if plant functional types conceal species-specific responses to environment? Study on arctic shrub communities. *Ecology, 98*(6), 1600-1612. doi:10.1002/ecy.1817

Scherrer, D., & Körner, C. (2010). Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology, 16*(9), 2602-2613. doi:10.1111/j.1365-2486.2009.02122.x

Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology, 100*(3), 652-661.

Speed, J. D. M., Austrheim, G., Hester, A. J., & Mysterud, A. (2012). Elevational advance of alpine plant communities is buffered by herbivory. *Journal of Vegetation Science, 23*(4), 617-625. doi:10.1111/j.1654-1103.2012.01391.x

Speed, J. D. M., Austrheim, G., & Mysterud, A. (2013). The response of plant diversity to grazing varies along an elevational gradient. *Journal of Ecology, 101*(5). doi:10.1111/1365-2745.12133

Steinbauer, M. J., Grytnes, J. A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., . . . Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature, 556*(7700), 231-234. doi:10.1038/s41586-018-0005-6

Sundqvist, M. K., Björk, R. G., & Molau, U. (2008). Establishment of boreal forest species in alpine dwarf-shrub heath in subarctic Sweden. *Plant Ecology & Diversity, 1*(1), 67-75. doi:10.1080/17550870802273395

Venables, W. N., & Ripley, B. D. (2002). Modern Applied Statistics with S: Springer. Retrieved from http://www.stats.ox.ac.uk/pub/MASS4

Verheyen, K., Bazany, M., Checko, E., Chudomelova, M., Closset-Kopp, D., Czortek, P., . . . Baeten, L. (2018). Observer and relocation errors matter in resurveys of historical vegetation plots. *Journal of Vegetation Science, 29*(5), 812-823. doi:10.1111/jvs.12673

Virtanen, R., Luoto, M., Rama, T., Mikkola, K., Hjort, J., Grytnes, J. A., & Birks, H. J. B. (2010). Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. *Global Ecology and Biogeography, 19*(6), 810-821. doi:10.1111/j.1466-8238.2010.00570.x

Vittoz, P., Randin, C., Dutoit, A., Bonnet, F., & Hegg, O. (2009). Low impact of climate change on subalpine grasslands in the Swiss Northern Alps. *Global Change Biology, 15*(1), 209-220. doi:10.1111/j.1365-2486.2008.01707.x

Vowles, T., Gunnarsson, B., Molau, U., Hickler, T., Klemedtsson, L., & Björk, R. G. (2017). Expansion of deciduous tall shrubs but not evergreen dwarf shrubs inhibited by reindeer in Scandes mountain range. *Journal of Ecology, 105*(6), 1547-1561. doi:10.1111/1365-2745.12753

Vuorinen, K. E. M., Oksanen, L., Oksanen, T., Pyykonen, A., Olofsson, J., & Virtanen, R. (2017). Open tundra persist, but arctic features decline-Vegetation changes in the warming Fennoscandian tundra. *Global Change Biology, 23*(9), 3794-3807. doi:10.1111/gcb.13710

Weiss, A. (2001). *Topographic position and landforms analysis.* Paper presented at the Poster presentation, ESRI user conference, San Diego, CA.

Wieser, G., & Tausz, M. (2007). *Trees at their upper limit: treelife limitation at the alpine timberline* (Vol. 5). Dordrecht: Springer Science & Business Media.

Williamson, M. H. (1978). The ordination of incidence data. *The Journal of Ecology, 66*, 911-920.

Wilson, S. D., & Nilsson, C. (2009). Arctic alpine vegetation change over 20 years. *Global Change Biology, 15*(7), 1676-1684. doi:10.1111/j.1365-2486.2009.01896.x

Wipf, S., & Rixen, C. (2010). A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Research, 29*(1), 95-109. doi:10.1111/j.1751-8369.2010.00153.x

Ylänne, H., Stark, S., & Tolvanen, A. (2015). Vegetation shift from deciduous to evergreen dwarf shrubs in response to selective herbivory offsets carbon losses: evidence from 19 years of warming and simulated herbivory in the subarctic tundra. *Global Change Biology, 21*(10), 3696-3711. doi:10.1111/gcb.12964

Zuur, A., Ieno, E. N., & Smith, G. M. (2007). *Analyzing ecological data*: Springer Science & Business Media.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Precipitation statistics.
Appendix S2 Sheep density statistics.
Appendix S3. Individual species frequency.
Appendix S4 Correlation table for environmental variables.
Appendix S5 CCA statistics and VIF for the environmental variables.
Appendix S6. Characteristics of the environmental factors.
Appendix S7 Diversity and richness summary statistics.
Appendix S8 Species turnover.
Appendix S9 Summary tables.

Figures

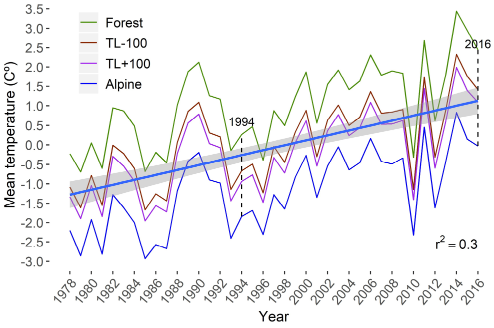


Figure 1. Mean annual temperature for the different transect sections (forest, treeline ± 100 m., alpine), and a regression line with 95% confidence interval, for the overall trend 1978 to 2016, from interpolated temperature data (Source: Norwegian Meteorological Institute; www.met.no).

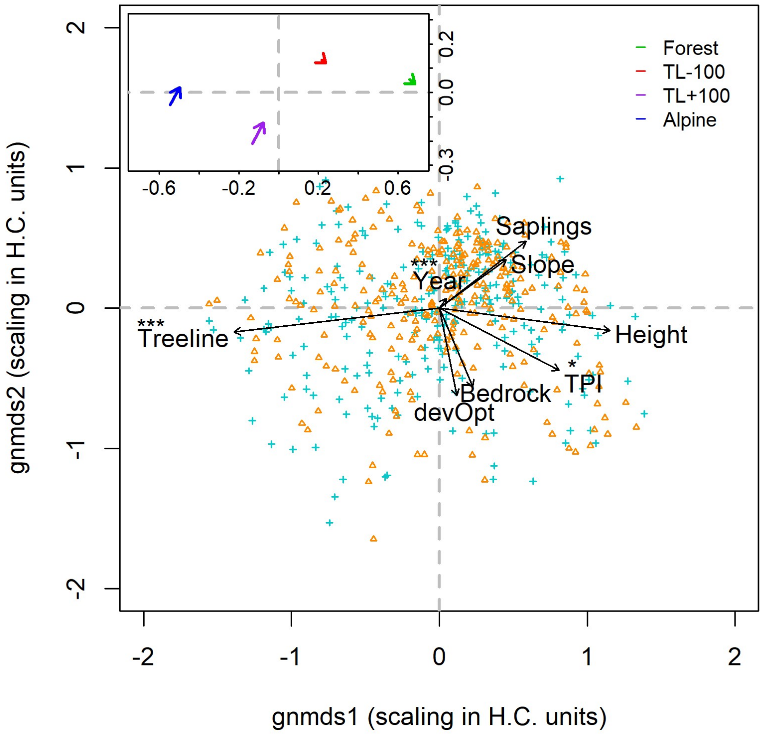


Figure 2. GNMDS biplot of the field-layer composition. Cyan crosses represent quadrats in 1994, while yellow triangles represent quadrats in 2016. Arrows in the main figure show the fitted environmental variables with stars indicating significant relationship with the ordination axes (See table 2 for p-values). Arrows in the inset display the mean displacement of quadrat scores from 1994 to 2016 in the four transect sections Forest, TL-100, TL+100 and Alpine.

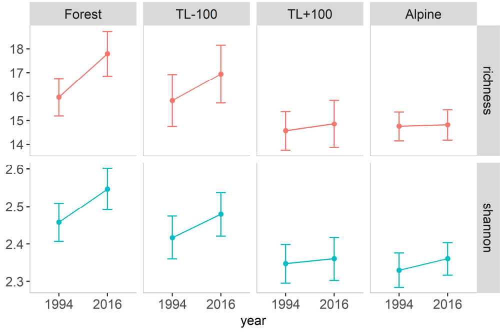


Figure 3. Mean species richness and Shannon diversity index values in 1994 and 2016 in the four transect sections. Vertical bars show the standard error.

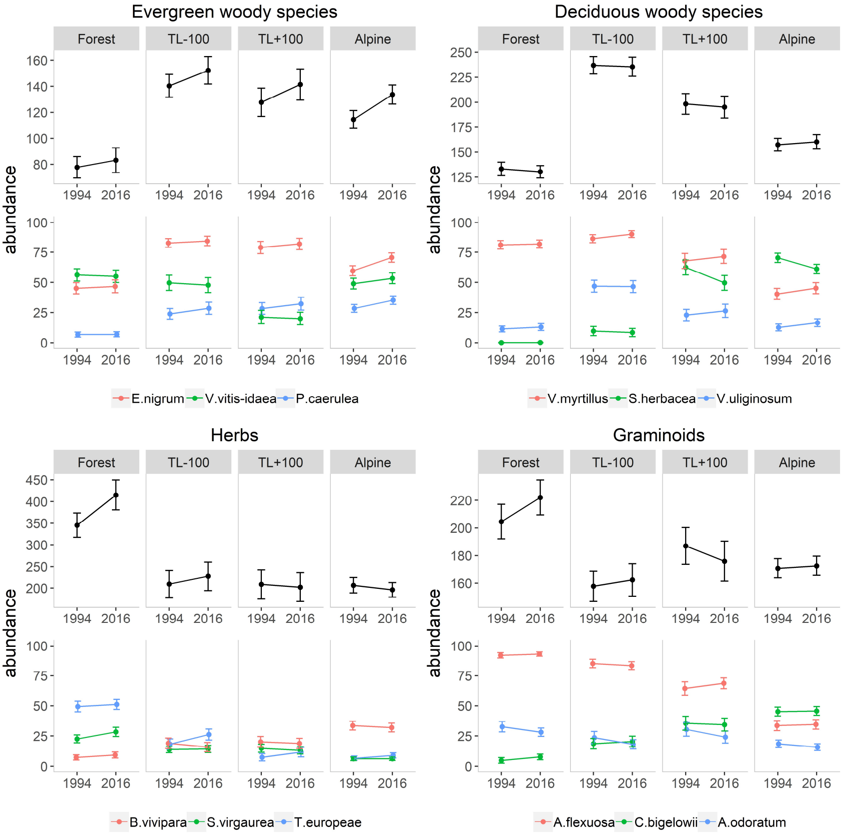


Figure 4. Mean abundance of functional groups and individual species within each functional group in 1994 to 2016. The upper panels (black lines) in each figure part show the total sum of the abundance of all species within each functional group per transect section, and lower panels (coloured lines) show the three most abundant species per group and section. Error bars represent the standard error. Note difference in y-axis score for functional groups.

Tables

Table 1. Transect characteristics and distribution of analysed plots. MGG is mylonitic gneiss, MI is mica chist, Qu is quartzites and mylonitic gneiss, occasionally amphibolite, Au is augengneiss.

transect	Aspect	Geological substrate	Altitudinal range	Forest line position 1994	Treeline position 1994	Number of plots (quadrats) in 2016	Number of species 1994	Number of species 2016
A	E-NE	MGG	750-1300	970	1000	12 (47)	63	61
B	W-SW	MGG	750-1400	940	980	13 (52)	65	68
C	NE	Mi	750-1400	960	1050	14 (56)	112	116
D	SW	Qu	850-1400	1060	1130	12 (48)	83	86
E	S	Ag	850-1150	1120	1170	5 (20)	34	38
F	SE	Mi, Qu	950-1500	970	1100	12 (48)	76	75

Table 2. Parameter estimates for all environmental factors and associated p-value from the linear mixed-effects model of axis score on GNMDS axis 1 and 2. Year = year of survey, treeline = altitudinal distance to treeline, bedrock = bedrock quality, slope = slope of the quadrat in degrees, TPI = topographic position index, devOpt = deviation from optimal aspect, height = height of the tree-layer, saplings = number of saplings.

	GNMDS1		**GNMDS2**	
Env.fact.	**Estimate**	**p-value**	**Estimate**	**p-value**
(Intercept)	0.114	0.192	0.101	0.472
Year	0.041	<0.001	0.034	<0.001
Treeline	-0.003	<0.001	-0.001	0.074
Bedrock	0.061	0.506	-0.036	0.787
Slope	-0.001	0.501	0.001	0.596
TPI	0.004	0.190	-0.008	0.039
DevOpt	0.000	0.390	-0.001	0.053
Height	0.008	0.234	-0.006	0.478
Saplings	-0.004	0.228	0.002	0.601

Table 3. Anova tables for the optimal models, found by backwards selection with an inclusion criteria of $p < 0.05$. a) Change in quadrat score along GNMDS axis 2 modelled by a linear mixed-effects model. b) Species richness and Shannon diversity index modelled by linear mixed-effects models. c) Abundance of evergreen species, modelled with linear mixed-effects model using Satterthwaite method, d) abundance of deciduous woody species, graminoids and herbs modelled with generalized mixed-effects model using the Wald chi-square method. In all models, quadrat nested in plot nested in transect are used as random variables, except a) which used plot nested in transect.

a) Response variable	**Factor**	**F-value**	**P-value**
GNMDS axis 2	Height	17.4	<0.001
b) Response variable	**Factor**	**F-value**	**P-value**
Richness	Year	18.89	<0.001
	Bedrock	16.36	0.002
	Section	1.66	0.185
	year×section	5.34	0.001
Shannon	Year	24.53	<0.001
	Bedrock	20.55	0.001
	Section	1.46	0.235
	Year×Section	2.97	0.033
c) Response variable	**Factor**	**F-value**	**P-value**
Evergreen	Year	22.96	<0.001
	Height	4.30	0.039
	Treeline	12.52	<0.001
	Saplings	7.14	0.008
	Section	6.65	<0.001
	Year×Section	4.83	<0.001
d) Response variable	**Factor**	**ChiSqr**	**P-value**
Deciduous	TPI	3.97	0.046
	Height	3.98	0.046
	Treeline	8.14	0.004
	Saplings	6.13	0.013
	Section	37.31	<0.001
Herbs	Year	9.30	0.002
	Height	4.85	0.028
	TPI	7.23	0.007
	Section	8.65	0.034
	year×Section	28.21	<0.001
Graminoids	Year	1.68	0.195
	Bedrock	10.47	0.001
	TPI	5.61	0.018
	Section	5.54	0.136
	Year×Section	8.40	0.038

Table 4. Anova table results of generalized linear mixed-effects models of abundance of individual species as a response of year, transect section and year×section, chi-square showing results of model comparison by the Wald chi-square method, and stars denoting significance level of the anova test; *** p < 0.001, ** p < 0.01, and * p < 0.05. N/A = response variables not included in the final model.

Response variable	**Year**	**Transect section**	**Year × Section**
Empetrum nigrum	67.11***	23.20***	38.65***
Vaccinium vitis-idaea	1.76	10.15*	25.15***
Phyllodoce caerulea	40.75***	18.41***	N/A
Vaccinium myrtillus	37.45***	27.70***	20.76***
Salix herbacea	128.90***	68.46***	9.14*
Vaccinium uliginosum	16.13***	24.73***	21.58***
Bistorta vivipara	2.43	18.22***	11.9**
Solidago virgaurea	4.27*	14.46**	12.92**
Trientalis europaea	34.10***	37.66***	25.69***
Avenella flexuosa	N/A	56.26***	N/A
Carex bigelowii	2.57	38.29***	13.44**
Anthoxanthum odoratum	51.60***	N/A	N/A

Supporting information to the paper

Vegetation response to climate warming across the forest-tundra ecotone: species-dependent upward movement

Løkken, J.O. et.al.

Appendix S1 Total annual precipitation.

Appendix S2 Sheep density statistics.

Appendix S3. Individual species frequency.

Appendix S4 Correlation table for environmental variables.

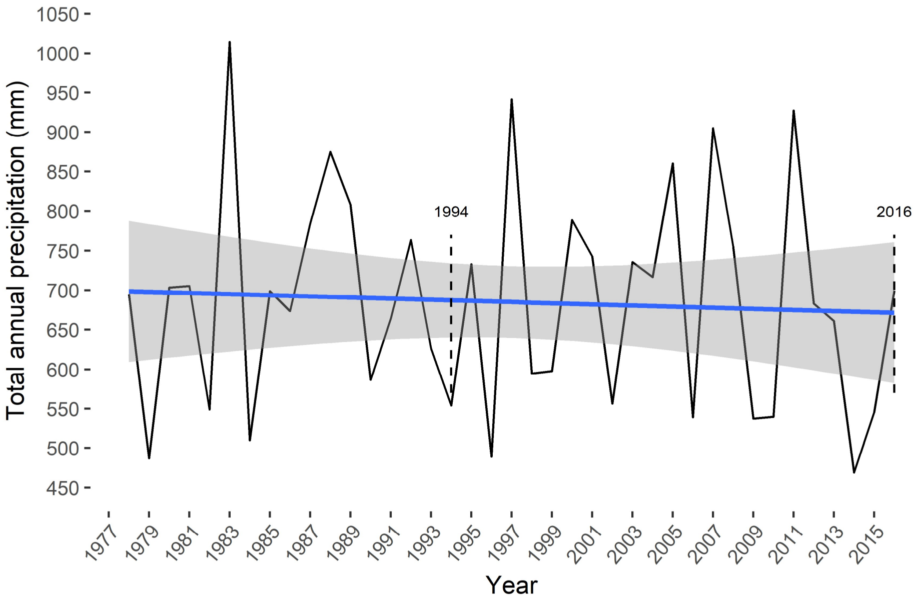
Appendix S5 CCA statistics and VIF for the environmental variables.

Appendix S6. Characteristics of the environmental factors.

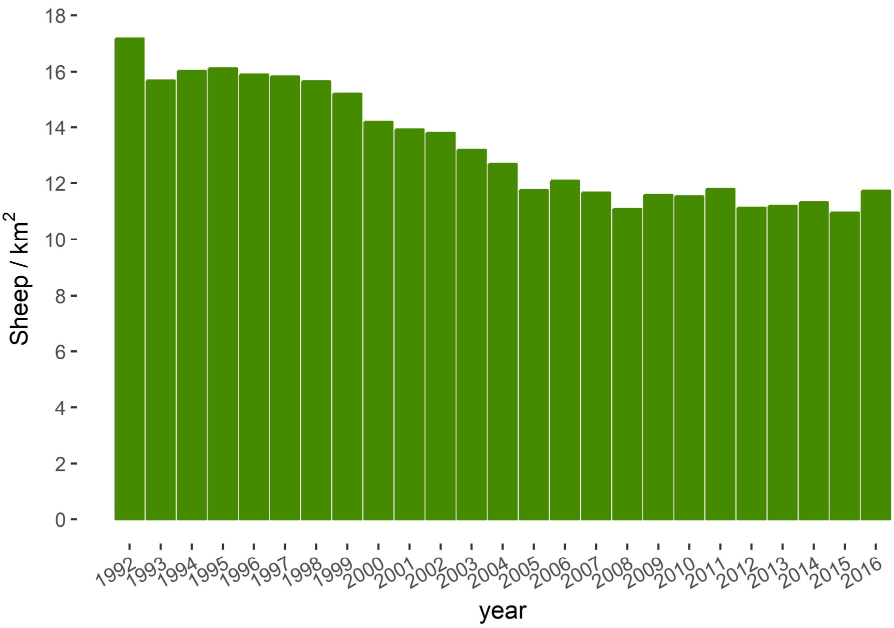
Appendix S7 Diversity and richness summary statistics.

Appendix S8 Species turnover.

Appendix S9 Summary tables.



Appendix S1 Total annual precipitation (black solid line), and the linear regression of the overall trend 1978 to 2016 (blue line, shaded area is the 95% confidence interval). Vertical dashed lines mark sampling years. The data refer to the Hafsås meteorological station, located within the study area (698 m a.s.l.). (Source: Norwegian Meteorological Institute; www.met.no).



Appendix S2 Sheep density statistics. Data on the number of domestic sheep released for summer grazing each year is available at grazing association level (NIBIO; www.nibio.no) The sheep density is thus calculated for an area including and surrounding our study area (460 km^2). Provided that the spatial distribution of sheep throughout the grazing association area is even, the sheep density was 16.3 sheep/km^2 in 1992-1994, and 11.3 sheep/km^2 in 2014-2016.

Appendix S3 Individual species frequency. Number and percentage of quadrats where the three most common species in each functional group were present in 1994 and 2016.

		1994		**2016**	
Group	**Species**	**No. of quadrats**	**%**	**No. of quadrats**	**%**
Evergreen	*Empetrum nigrum*	224	84.2	222	83.5
	Vaccinium vitis-idaea	159	59.8	155	58.3
	Phyllodoce caerulea	133	50.0	138	51.9
Deciduous	*Vaccinium myrtillus*	204	76.7	214	80.5
	Salix herbacea	131	49.2	127	47.7
	Vaccinium uliginosum	109	41.0	116	43.6
Graminoids	*Avenella flexuosa*	212	79.7	220	82.7
	Carex bigelowii	129	48.5	138	51.9
	Anthoxanthum odoratum	123	46.2	128	48.1
Herbs	*Bistorta vivipara*	120	45.1	113	42.5
	Solidago virgaurea	111	41.7	113	42.5
	Trientalis europaea	101	38.0	113	42.5

Appendix S4 Correlation table for environmental variables. Kendall's non-parametric correlation coefficient (τ) between all initial environmental variables. Bold font marks correlations larger than 0.5. Forest line = distance to forest line, treeline = distance to treeline, bedrock = bedrock quality, slope = slope of the quadrat in degrees, TPI = topographic position index, devOpt = deviation from optimal aspect, height = height of the tree-layer, density = stand density, trees = number of trees, saplings = number of saplings.

	Altitude	**Forest line**	**Treeline**	**Bedrock**	**Slope**	**TPI**	**DevOpt**	**Height**	**Density**	**Trees**	**Saplings**
Altitude	▨										
Forest line	**0.88**	▨									
Treeline	**0.84**	**0.91**	▨								
Bedrock	-0.01	-0.02	-0.14	▨							
Slope	-0.19	-0.22	-0.25	0.17	▨						
TPI	-0.37	-0.38	-0.41	0.30	0.12	▨					
DevOpt	-0.14	-0.05	-0.05	0.05	-0.04	0.05	▨				
Height	**-0.63**	**-0.66**	**-0.67**	0.06	0.20	0.36	-0.03	▨			
Density	**-0.63**	**-0.62**	**-0.64**	0.03	0.11	0.38	0.07	**0.76**	▨		
Trees	**-0.64**	**-0.64**	**-0.65**	0.00	0.13	0.37	0.03	**0.78**	**0.85**	▨	
Saplings	-0.47	-0.49	-0.48	-0.06	0.23	0.26	-0.13	**0.61**	0.44	0.48	▨

Appendix S5 CCA (Canonical Correspondence Analysis) statistics and VIF (Variance inflation factor) for the environmental variables. The CCA was run on the field-layer composition. Environmental factors are sorted by order of inclusion in the CCA (backward selection). The column Df is degrees of freedom, AIC is Akaike information criterion, F is the F-value, Pr(>F) is the P-value, VIF is the variance inflation factor with all variables included, while final VIF is after the exclusion of variables. Forest line = distance to forest line, treeline = distance to treeline, bedrock = bedrock quality, slope = slope of the quadrat in degrees, TPI = topographic position index, devOpt = deviation from optimal aspect, height = height of the tree-layer, density = stand density, trees = number of trees, saplings = number of saplings.

Env.var	**Df**	**AIC**	**F**	**Pr(>F)**	**VIF**	**Final VIF**
Treeline	1	1718.3	30.5	0.002	80.4	3.2
Height	1	1708.3	12.0	0.002	6.6	2.3
DevOpt	1	1700.0	10.3	0.002	1.8	1.1
Bedrock	1	1692.8	9.2	0.002	2.5	1.3
Forest line	1	1688.4	6.3	0.002	79.0	
Altitude	1	1685.0	5.4	0.002	24.6	
TPI	1	1681.6	5.3	0.002	1.6	1.6
Slope	1	1679.1	4.5	0.002	1.3	1.3
Density	1	1677.5	3.6	0.002	6.1	
Saplings	1	1676.2	3.2	0.002	1.5	1.4
Trees	1	1675.5	2.6	0.002	5.1	
Year				Non-sign.	1.1	1.0

Appendix S6. Mean values and standard deviation values for the (numerical) evironmental variables, averaged across quadrats in the four transect sections. Treeline = altitudinal distance to treeline, slope = slope of the quadrat in degrees, TPI = topographic position index, devOpt = deviation from optimal aspect, height = height of the tree-layer, saplings = number of saplings.

Transect section	Treeline	Slope	TPI	devOpt	Height 1994	Height 2016	Saplings 1994	Saplings 2016
Forest	-201.3 ±62.4	21.8 ±8.6	1.8 ±6.8	83.1 ±66.9	5.0 ±2.2	4.4 ±2.4	4.6 ±3.9	3.5 ±3.3
TL-100	-58.5 ±31.9	27.6 ±10.3	0.6 ±7.9	85.9 ±53.0	1.4 ±1.4	1.9 ±1.9	3.4 ±3.6	2.8 ±3.2
TL+100	59.2 ±44.9	20.6 ±10.4	-7.2 ±14.6	98.0 ±57.8	0.0 ±0.1	0.1 ±0.1	1.3 ±2.9	1.2 ±3.2
Alpine	251.1 ±82.7	15.4 ±9.0	-11.7 ±10.6	75.0 ±44.9	0.0 ±0.1	0.1 ±0.0	0.2 ±0.5	0.2 ±0.5

Appendix S7 Diversity and richness summary statistics. Mean overall Shannon diversity index in 1994 and 2016. Mean species richness in 1994 and 2016 both overall and for each of the functional groups for each transect section.

	Section	Year	Forest	TL-100	TL+100	Alpine
Shannon	Overall	1994	2.46 ±0.42	2.42 ±0.42	2.35 ±0.36	2.33 ±0.45
		2016	2.55 ±0.45	2.48 ±0.42	2.36 ±0.40	2.35 ±0.44
Richness	Overall	1994	16.0 ±6.4	15.8 ±7.9	14.6 ±5.6	14.7 ±6.0
		2016	17.8 ±7.8	16.9 ±8.7	14.9 ±6.8	14.8 ±6.3
	Evergreen	1994	1.5 ±0.9	2.1 ±0.9	2.0 ±1.1	2.3 ±1.2
		2016	1.2 ±1.0	2.3 ±1.0	2.1 ±1.1	2.4 ±1.3
	Deciduous	1994	2.5 ±1.0	3.8 ±1.2	2.7 ±1.1	2.3 ±1.1
		2016	2.6 ±1.0	4.0 ±1.2	2.8 ±1.1	2.5 ±13
	Herb	1994	7.6 ±5.0	6.1 ±5.5	6.0 ±4.6	6.0 ±4.2
		2016	9.2 ±6.3	6.5 ±5.9	6.0 ±5.7	5.7 ±4.2
	Graminoid	1994	3.4 ±1.8	3.1 ±2.0	3.5 ±1.9	3.6 ±1.4
		2016	3.9 ±2.0	3.3 ±2.5	3.6 ±2.5	3.5 ±1.5

Appendix S8 Species turnover in the full data set, with No Quad showing how many quadrats they were lost or found in, and section showing in which transect section the species was found (F = forest, TL-100 = treeline to 100 altitudinal m below, TL+100 = treeline to 100 altitudinal m above, A = alpine).

Lost species 1994-2016	**No Quad**	**section**	**New species 2016**	**No Quad**	**Section**
Ajuga pyramidalis	2	F	*Aconitum lycoctonum*	3	F
Calamagrostis phragmitoides	1	F	*Dactylorhiza maculata*	1	F
Elymus caninus	2	F	*Myosotis sylvatica*	3	F
Equisetum pratense	2	F	*Deschampsia alpina*	2	TL-100
Viola riviniana	2	F/TL-100	*Festuca rubra*	2	TL-100
Stellaria graminea	1	TL-100	*Salix hastata*	1	TL-100
Carex canescens	1	TL-100	*Comastoma tenellum*	2	TL-100/+100
Carex norvegica	1	TL+100	*Equisetum palustre*	1	TL+100
Hieracium vulgatum agg	1	TL+100	*Oxytropis lapponica*	3	A
Taraxacum croceum agg	1	A			

Appendix S9 Summary tables for the optimal mixed-effects models.

S9 a) Summary table for the optimal linear mixed-effects model on displacement of axis score in the GNMDS. Plot nested in transect is used as a random factor.

Response variable	Factor	Estimate	Std.error	DF	t-value	p-value
GNMDS1	(Intercept)	0.04	0.01	65.9	4.44	<0.001
GNMDS2	(Intercept)	0.06	0.01	67.9	5.08	<0.001
	Height	-0.02	0.00	75.3	-4.17	<0.001

S9 b) Summary table for the optimal linear mixed-effects model on richness and Shannon diversity index. In all models, quadrat nested in plot nested in transect is used as a random factor (TL = treeline).

Response variable	Factor	Estimate	Std.Error	Df	t-value	p-value
Richness	(Intercept)	12.15	1.38	13.6	8.83	<0.001
	2016	0.06	0.30	262.0	0.20	0.839
	Bedrock	6.78	1.68	12.1	4.05	0.002
	Forest	0.08	1.64	64.5	0.05	0.960
	TL-100	0.57	1.77	64.2	0.32	0.749
	TL+100	-3.01	1.86	62.6	-1.62	0.111
	2016:Forest	1.76	0.47	262.0	3.75	0.000
	2016:TL-100	1.05	0.51	262.0	2.08	0.039
	2016:TL+100	0.23	0.52	262.0	0.44	0.658
Shannon index	(Intercept)	2.16	0.08	15.4	26.89	<0.001
	2016	0.03	0.02	262.0	1.97	0.050
	Bedrock	0.44	0.10	9.6	4.53	0.001
	Forest	0.06	0.11	63.4	0.56	0.578
	TL-100	0.05	0.11	63.1	0.47	0.643
	TL+100	-0.15	0.12	61.9	-1.23	0.224
	2016:Forest	0.06	0.02	262.0	2.39	0.018
	2016:TL-100	0.03	0.03	262.0	1.22	0.225
	2016:TL+100	-0.02	0.03	262.0	-0.65	0.518

S9 c) Summary table for the optimal model on the functional groups. Evergreen is a linear mixed-effects model, while deciduous woody species, herbs and graminoids are generalized linear mixed-effects models with a quasi-poisson distribution. In all models, quadrat nested in plot nested in transect is used as a random factor.

Response variable	Factor	Estimate	Std.Error	DF	t-value	p-value
Evergreen	(Intercept)	198.86	26.40	56.7	7.53	<0.001
	2016	18.80	4.01	260.8	4.69	<0.001
	Height	-6.93	2.46	436.4	-2.82	0.005
	Saplings	3.04	0.99	461.4	3.06	0.002
	Treeline	-0.33	0.09	57.9	-3.56	<0.001
	Forest	-175.77	45.62	59.3	-3.85	<0.001
	TL-100	-79.43	33.63	57.3	-2.36	0.022
	TL+100	-50.73	25.07	57.3	-2.02	0.048
	2016:Forest	-20.36	6.54	276.6	-3.11	0.002
	2016:TL-100	-4.60	7.00	270.2	-0.66	0.511
	2016:TL+100	-5.62	7.02	260.7	-0.80	0.424
Deciduous	(Intercept)	5.31	0.14	264.0	37.19	<0.001
	Height	-0.03	0.01	264.0	-1.98	0.049
	TPI	-0.02	0.00	198.0	-1.98	0.049
	Saplings	0.01	0.01	264.0	2.46	0.015
	Treeline	0.00	0.00	57.0	-2.47	0.017
	Forest	-0.61	0.26	57.0	-2.36	0.022
	TL-100	0.08	0.19	57.0	0.44	0.660
	TL+100	-0.03	0.14	57.0	-0.18	0.857
Herb	(Intercept)	5.13	0.28	261.0	18.21	<0.001
	2016	-0.05	0.04	261.0	-1.32	0.189
	Height	0.05	0.02	261.0	2.18	0.030
	TPI	0.03	0.01	198.0	2.66	0.008
	Forest	0.06	0.31	58.0	0.21	0.836
	TL-100	-0.41	0.31	58.0	-1.30	0.200
	TL+100	-0.49	0.29	58.0	-1.68	0.099
	2016:Forest	0.27	0.05	261.0	4.90	0.000
	2016:TL-100	0.11	0.07	261.0	1.74	0.083
	2016:TL+100	0.02	0.07	261.0	0.28	0.779
Graminoids	(Intercept)	5.08	0.10	262.0	50.16	<0.001
	2016	0.01	0.03	262.0	0.36	0.718
	Bedrock	0.31	0.10	57.0	3.21	0.002
	TPI	0.01	0.00	198.0	2.35	0.020
	Forest	-0.04	0.12	57.0	-0.33	0.743
	TL-100	-0.26	0.13	57.0	-1.98	0.052
	TL+100	-0.10	0.13	57.0	-0.80	0.425
	2016:Forest	0.07	0.04	262.0	1.70	0.091
	2016:TL-100	0.02	0.05	262.0	0.37	0.714
	2016:TL+100	-0.07	0.05	262.0	-1.46	0.146

S9 d) Summary table for the optimal model on the functional groups. For Evergreen a linear mixed-effects model is used, while for deciduous woody species, herbs and graminoids generalized linear mixed-effects models with a quasi-poisson distribution are used. In all models, quadrat nested in plot nested in transect is used as a random factor (TL = treeline).

Response variable	Factor	Estimate	Std.error	z-value	p-value
Empetrum nigrum	(Intercept)	0.97	0.97	1.01	0.314
	2016	1.22	0.12	9.82	<0.001
	Forest	-1.66	1.00	-1.66	0.097
	TL-100	2.41	1.09	2.22	0.027
	TL+100	3.58	1.16	3.10	0.002
	2016:Forest	-1.07	0.18	-5.78	<0.001
	2016:TL-100	-0.97	0.23	-4.23	<0.001
	2016:TL+100	-0.66	0.26	-2.59	0.010
Phyllodoce caerulea	(Intercept)	-2.38	0.65	-3.64	<0.001
	2016	0.46	0.07	6.38	<0.001
	Forest	-3.96	0.98	-4.05	<0.001
	TL-100	-0.48	0.94	-0.51	0.608
	TL+100	-0.46	0.95	-0.48	0.630
Vaccinium vitis-idaea	(Intercept)	-1.51	1.06	-1.43	0.154
	2016	0.65	0.14	4.69	<0.001
	Forest	1.93	1.59	1.21	0.227
	TL-100	-0.49	1.79	-0.28	0.782
	TL+100	-4.87	2.06	-2.36	0.018
	2016:Forest	-0.78	0.20	-3.86	<0.001
	2016:TL-100	-0.98	0.25	-3.98	<0.001
	2016:TL+100	-0.99	0.31	-3.21	0.001
Vaccinium myrtillus	(Intercept)	-2.36	1.29	-1.83	0.067
	2016	1.09	0.18	6.12	<0.001
	Forest	6.60	1.42	4.63	<0.001
	TL-100	7.00	1.54	4.53	<0.001
	TL+100	6.03	1.63	3.70	<0.001
	2016:Forest	-1.01	0.23	-4.39	<0.001
	2016:TL-100	-0.45	0.27	-1.68	0.092
	2016:TL+100	-0.30	0.30	-1.02	0.307
Salix herbacea	(Intercept)	1.93	0.79	2.46	0.014
	2016	-1.04	0.12	-8.40	<0.001
	Forest	-13.18	2.02	-6.54	<0.001
	TL-100	-9.34	1.46	-6.39	<0.001
	TL+100	-0.57	1.39	-0.41	0.681
	2016:Forest	1.79	1.27	1.40	0.160
	2016:TL-100	0.35	0.40	0.89	0.375
	2016:TL+100	-0.53	0.23	-2.29	0.022
Vaccinium uliginosum	(Intercept)	-7.10	0.84	-8.46	<0.001
	Forest	1.62	1.14	1.42	0.155
	TL-100	6.62	1.23	5.38	<0.001
	TL+100	2.66	1.27	2.10	0.036
	2016	1.00	0.19	5.38	<0.001
	Forest:2016	-0.77	0.25	-3.11	0.002
	TL-100:2016	-1.03	0.23	-4.51	<0.001
	TL+100:2016	-0.49	0.27	-1.78	0.075

Response variable	**Factor**	**Estimate**	**Std.error**	**z-value**	**p-value**
Bistorta vivipara	(Intercept)	-2.17	0.97	-2.25	0.025
	2016	-0.16	0.11	-1.41	0.158
	Forest	-5.46	1.23	-4.45	<0.001
	TL-100	-3.19	1.35	-2.36	0.018
	TL+100	-2.46	1.29	-1.91	0.057
	2016:Forest	0.66	0.24	2.73	0.006
	2016:TL-100	-0.31	0.22	-1.39	0.164
	2016:TL+100	-0.01	0.22	-0.06	0.955
Solidago virgaurea	(Intercept)	-5.64	0.62	-9.03	<0.001
	2016	0.00	0.18	0.00	1.000
	Forest	2.78	0.87	3.20	0.001
	TL-100	2.35	0.94	2.51	0.012
	TL+100	2.44	0.96	2.54	0.011
	2016:Forest	0.52	0.22	2.36	0.018
	2016:TL-100	0.05	0.24	0.23	0.820
	2016:TL+100	-0.21	0.25	-0.84	0.400
Trientalis europaea	(Intercept)	-8.08	0.92	-8.78	<0.001
	Forest	7.68	1.24	6.21	<0.001
	TL-100	4.14	1.32	3.13	0.002
	TL+100	1.23	1.38	0.89	0.371
	2016	0.63	0.19	3.38	<0.001
	Forest:2016	-0.52	0.22	-2.39	0.017
	TL-100:2016	0.31	0.26	1.23	0.219
	TL+100:2016	0.61	0.35	1.75	0.080
Avenella flexuosa	(Intercept)	-2.60	0.92	-2.84	0.004
	Forest	7.81	1.10	7.11	<0.001
	TL-100	5.96	1.13	5.29	<0.001
	TL+100	4.22	1.12	3.77	<0.001
Carex bigelowii	(Intercept)	-0.95	0.68	-1.40	0.160
	2016	0.04	0.10	0.40	0.686
	Forest	-6.55	1.05	-6.24	<0.001
	TL-100	-3.47	1.09	-3.20	0.001
	TL+100	-0.45	1.07	-0.42	0.676
	2016:Forest	0.87	0.27	3.24	0.001
	2016:TL-100	0.22	0.21	1.05	0.296
	2016:TL+100	-0.16	0.19	-0.83	0.410
Anthoxanthum odoratum	(Intercept)	-3.43	0.80	-4.28	<0.001
	2016	-0.53	0.07	-7.18	<0.001

Paper III

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture

1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway

1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	*Acesta oophaga* and *Acesta excavata* – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania

2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, *Taeniopygia guttata*
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches

2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density

2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis):* Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (*Salmo trutta* L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment

2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholipase A2

2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: *Calanus*, little auks (*Alle alle*) and black-legged kittiwakes (*Rissa tridactyla*)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.

2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (*Lycaon pictus*) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on *Arabidopsis thaliana*
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon (*Salmo salar*)
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological contex to functional integration
2019	Mominul Islam Nahid	PhD Biology	Interaction between two Asian cuckoos and their hosts in Bangladesh

2019	Knut Jørgen Egelie	Phd Biology	Management of intellectual property in university-industry collaborations – public access to and control of knowledge
2019	Thomas Ray Haaland	Phd Biology	Adaptive responses to enviromental stochasticity on different evolutionary time-scales
2019	Kwaslema Malle Hariohay	Phd Biology	Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania
2019	Mari Engvig Løseth	Phd Biology	Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle (*Haliaeetis albicilla*) nestlings
2019	Joseph Mbyati Mukeka	Phd Biology	Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates
2019	Helene Løvstrand Svarva	Phd Biology	Dendroclimatology in southern Norway: tree rings, demography and climate
2019	Nathalie Briels	Phd Biology	Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field studies
2019	Anders L.Kolstad	Phd Biology	Moose browsing effects on boreal production forests – implications for ecosystems and human society
2019	Bart Peeters	Phd Biology	Population dynamics under climate change ad harvesting: Results from the high Arctic Svalbard reindeer
2019	Alex Kojo Datsomor	Phd Biology	The molecular basis of long chain polyunsaturated fatty acid (LC-PUFA) biosynthesis in Atlantic salmon (*Salmo salar L*): In vivo functions, functional redundancy and transcriptional regulation of LC-PUFA biosynthetic enzymes
2020	Ingun Næve	Phd Biology	Development of non-invasive methods using ultrasound technology in monitoring of Atlantic salmon (*Salmo Salar*) production and reproduction
2020	Rachael Morgan	Phd Biology	Physiological plasticity and evolution of thermal performance in zebrafish
2020	Mahsa Jalili	Phd Biology	Effects of different dietary ingredients on the immune responses and antioxidant status in Atlantic salmon (*Salmo salar L.):* possible nutriomics approaches
2020	Haiqing Wang	Phd Biology	Utilization of the polychaete Hediste diversicolor (O.F. Millier, 1776) in recycling waste nutrients from land-based fish farms for valueadding applications'
2020	Louis Hunninck	Phd Biology	Physiological and behavioral adaptations of impala to anthropogenic disturbances in the Serengeti ecosystems
2020	Kate Layton-Matthews	Phd Biology	Demographic consequences of rapid climate change and density dependence in migratory Arctic geese
2020	Amit Kumar Sharma	Phd Biology	Genome editing of marine algae: Technology development and use of the CRISPR/Cas9 system for studies of light harvesting complexes and regulation of phosphate homeostasis
2020	Lars Rød-Eriksen	Phd Biology	Drivers of change in meso-carnivore distributions in a northern ecosystem
2020	Lone Sunniva Jevne	Phd Biology	Development and dispersal of salmon lice (*Lepeophtheirus salmonis Krøyer*, 1837) in commercial salmon farming localities
2020	Sindre Håvarstein Eldøy	Phd Biology	The influence of physiology, life history and environmental conditions on the marine migration patters of sea trout

2020	Vasundra Touré	Phd Biology	Improving the FAIRness of causal interactions in systems biology: data curation and standardisation to support systems modelling applications