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When do ungulates override the climate? Defining the interplay of two key drivers of northern vegetation dynamics

Thesis for the degree of Philosophiae Doctor

Trondheim, April 2021

Norwegian University of Science and Technology
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To Phony pilgrim,
Island wind,
Frigate bird,
Smiley hunter,
Fly fisher,
Poker player,
and Spider man.

Contents

Acknowledgements

If the individual I was four years ago would meet the individual I am now, she would not recognize me. After embarking on the quest of PhD, I have grown not just as a researcher but also as a person. While I myself was changing, I had privilege to study the fascinating changes in ecosystems: changes in plants, changes in climate, changes in herbivore populations. It has been a joy to learn to understand better both myself and the biosphere around me, and for this opportunity, I'm forever grateful.

None of the research presented in this thesis would have been possible without my supervisors. James D. M. Speed was always there with original project plans, advanced analysis ideas, and educated enthusiasm, yet also ready to answer elementary questions about R-coding. Gunnar Austrheim eagerly shared his knowledge on ungulates, especially with regards to sheep and moose in Norway. Jean-Pierre Tremblay helped me to organize my research stay in Canada and introduced me to the exclosure experiments in Gaspésie. Alison Hester showed me the Scottish Highlands and kept me on the right path whenever my deer interaction scribblings started to wander to the misty moors of ambiguity. The core funding for the project was provided by the Research Council of Norway (project 262064).

I'm also obliged to a myriad of people who brought me over obstacles that I could not have overcome by myself. Particularly, I would like to thank Anders L. Kolstad for introducing the path analysis approach, Shaila J. Rao for guiding me to access Cairngorms National Park, and Marc Daverdin for helping to retrieve climate and spatial data whenever online interphases provided too mazy for me. I'm also thankful for Isla Myers-Smith, Brage B. Hansen, Mathilde Le Moullec and Lauri Oksanen who were not afraid to give sharp criticism when it was urgently needed.

Most of the data used in this thesis is not collected by myself, but results from a vast collaboration network spanning across space and time. Some of the experimental designs were initiated when I was still a seedling of a biologist, unaware of the ungulate fences and vegetation plots that were popping up here and there around the tundra and boreal forest biomes. Over the years, myriad people have contributed to data collection at these sites, enabling the large-scale analyses presented here. Yet, I have had a privilege to bring in my own part for the data collection and conduct enjoyable fieldwork for all the appended papers.

A special thanks belongs to the trees and shrubs used to construct growth chronologies, allowing me to reach even further back in time. The oldest individual of this thesis started to grow under the cold skies of Greenland before even my grandparents were born.

Working on my PhD took me into distant places my climate conscience would never have allowed me to fly to for personal reasons. I found myself rock climbing in Nunavik, hiking in Swiss Alps, peeking into the depths of Loch Ness, feasting lobster on the coast of French Canada, skiing past the volcanic pools of Iceland, and tenting amid the golden colours of the Ural mountains. Naturally, not all the travels were without challenges. I managed to walk off some toenails while looking for tree samples in Scotland, and almost got stuck in Reykjavík when the COVID-19 pandemic started shaking the world. Perhaps one of the most memorable moments occurred after a shrub sampling trip when the motor of our overloaded boat died in the creeping darkness of Siberia. Yet, none of the challenges were too formidable to be overcome with help from my friends and colleagues.

Back home in Trondheim I was always welcomed by our lovely museum community. Other PhD students provided wonderful peer support, and especially Tanja Petersen never failed to make me laugh with good – and bad – humour. I would also like to thank the department and my supervisors for all the flexibility I got with regards to practicalities of my PhD. This enabled me to guide a BBC documentary group, work on several articles outside my PhD, and to follow my passion in science popularizing while writing the thesis.

Over the years, my dad and my siblings helped me to keep things in the right perspective by asking, from time to time: “What was is again that you were studying?” I also have extraordinary luck to have a mom who I could talk about p-values, and be understood.

Finally, I’m indebted to my *kjæreste* for carrying me through the final year of my PhD with love, passion and witty discussions both on and beyond my PhD. No one can conference like the Woodbuck and the Unicorn.

Katariina E. M. Vuorinen

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List of papers

I. Vuorinen K. E. M., Rao S. J., Hester A. J. & Speed J. D. M. (2020) Herbivory and climate as drivers of woody plant growth: Do deer decrease the impacts of warming? Ecological Applications 30(6): e02119. 10.1002/eap.2119.

II. Vuorinen K. E. M., Kolstad A. L., De Vriendt L., Austrheim G., Tremblay J.-P., Solberg E. J. & Speed J. D. M. (2020) Cool as a moose: How can browsing counteract climate warming effects across boreal forest ecosystems? Ecology 101(11): e03159. 10.1002/ecy.3159

III. Vuorinen K. E. M., Austrheim G., Tremblay J.-P., Myers-Smith I., Hortman H. I., Frank P., Barrio I. C., Dalerum F., Björkman M. P., Björk R. G., Ehrich D., Sokolov A., Sokolova N., Ropars P., Boudreau S., Normand S., Prendin A. L., Schmidt N. M., Pacheco A., Post E., John C., Kerby J., Sullivan P. F., Sandal L., Le Moullec M., Hansen B. B., Pedersen Å. Ø., van der Wal R., Gough L., Young A., Li B., Magnússon R. Í., Sass-Klaassen U., Buchwal A., Welker J., Grogan P., Andruko R., Morrissette-Boileau C., Volkovitskiy A., Terekhina A. & Speed J. D. M. Herbivores counteract the effects of warming on Arctic shrub growth at intermediate temperatures. (*unsubmitted manuscript*)

IV. Vuorinen K. E. M., Austrheim G., Mysterud A., Gya R., Vandvik V., Grytnes J.-A. & Speed J. D. M. Alpine plant community traits show long-term resistance to changing sheep densities across elevational gradients. (*unsubmitted manuscript*)

Author contributions

Paper I: K. E. M. Vuorinen and J. D. M. Speed designed the dendroecological part of the study, and K. E. M. Vuorinen and A. J. Hester conducted the related fieldwork. S. J. Rao designed the tree monitoring part and conducted related fieldwork. K. E. M. Vuorinen conducted the analyses with help from J. D. M. Speed. K. E. M. Vuorinen wrote the manuscript with comment contributions from all co-authors; **Paper II**: Field experiments were designed and managed by E. Solberg, G. Austrheim, J. D. M. Speed, and J.-P. Tremblay. K. E. M. Vuorinen, A. Kolstad, L. De Vriendt, E. Solberg, G. Austrheim, J. D. M. Speed, and J.-P. Tremblay contributed to field work. K. E. M. Vuorinen planned and conducted the analyses with help from J. D. M. Speed, J.-P. Tremblay, G. Austrheim, A. Kolstad, and L. De Vriendt. K. E. M. Vuorinen wrote the manuscript with comment contributions from all co-authors; **Paper III**: K. E. M. Vuorinen planned and conducted the analyses with help from J. D. M. Speed and I.-M. Smith. All co-authors provided data and contributed comments at the writing phase; **Paper IV**: Field experiments were designed and managed by A. Mysterud, J. D. M. Speed and G. Austrheim. K. E. M. Vuorinen J. D. M. Speed, G. Austrheim, and J.-A. Grytnes contributed to field work. K. E. M. Vuorinen planned and conducted the analyses with help from J. D. M. Speed, G. Austrheim, and J.-A. Grytnes. R. Gya and V. Vandvik contributed trait data. K. E. M. Vuorinen wrote the manuscript with comment contributions from all co-authors.

Introduction

During the past decades, the discussion on the future of the biosphere has often been dominated by aspects related to global warming. Increasing mean temperatures are expected to have profound effects on the vegetation systems of the Earth, and cascade through ecosystems from bottom-up (Björkman et al., 2018; Myers-Smith et al., 2015a; Peñuelas and Filella, 2009; Pugnaire et al., 2019). With changing climate, plant growth rates (Brecka et al., 2018; Myers-Smith et al., 2015a), functional traits (Björkman et al., 2018; Ma et al., 2017), species distributions (Lenoir et al., 2008; Pauli et al., 2012; Steinbauer et al., 2018; Stewart et al., 2018; van Vuuren et al., 2006), and community assemblages (Gallagher et al., 2019; Rumpf et al., 2018; Stewart et al., 2018; Vuorinen et al., 2017) are changing, transforming ecosystems all over the world. Northern biomes are expected to be particularly strongly affected, as they are experiencing the most drastic climatic shifts (Pachauri et al., 2014).

However, ecological processes rarely work like a one-way street. Top-down effects of herbivores have potential to change climate-driven baseline vegetation, and thus plant patterns do not necessarily follow climatic patterns directly, neither in time nor space. For example, insect outbreaks can have high impacts on boreal forests and northern treeline ecotones (Babst et al., 2010; Ivantsova et al., 2019), and effects of rodent peaks on vegetation can even be seen from space (Olofsson et al., 2012). Many northern ecosystems, despite warming, have not been going through expected vegetation changes (Berner et al., 2020; Björkman et al., 2020; Myers-Smith et al., 2020), perhaps due to various biotic modifiers of climatic effects. Many of these top-down factors affecting northern vegetation are outside of human control. Yet, there is one biotic ecosystem element that is profoundly affected – and often intentionally managed – by human across the tundra and boreal forests, namely ungulate herbivores, such as deer, moose, reindeer/caribou, muskox, and sheep.

In boreal forests, deer and moose are managed to balance between hunting interests, traffic safety, and forests damage prevention (Beguin et al., 2016; Boertje et al., 2010; Lavsund et al., 2003). Reindeer/caribou are hunted and herded in semi-domesticated populations around the Arctic, and they have high importance for several indigenous cultures (Vors and Boyce, 2009). Muskox populations, both endemic and introduced, are similarly controlled under different policy regimes (Cuyler et al., 2020). Also domesticated sheep have been an important part of the livelihoods of diverse northern societies since time immemorial, and in many regions, continue to be a central management interest for meat and wool production (Ross et al., 2016). While human might have drastic impacts on northern vegetation *via* climatic changes, we also shape it indirectly by affecting ungulates that change plant communities by browsing, grazing, and trampling (Fig. 1).

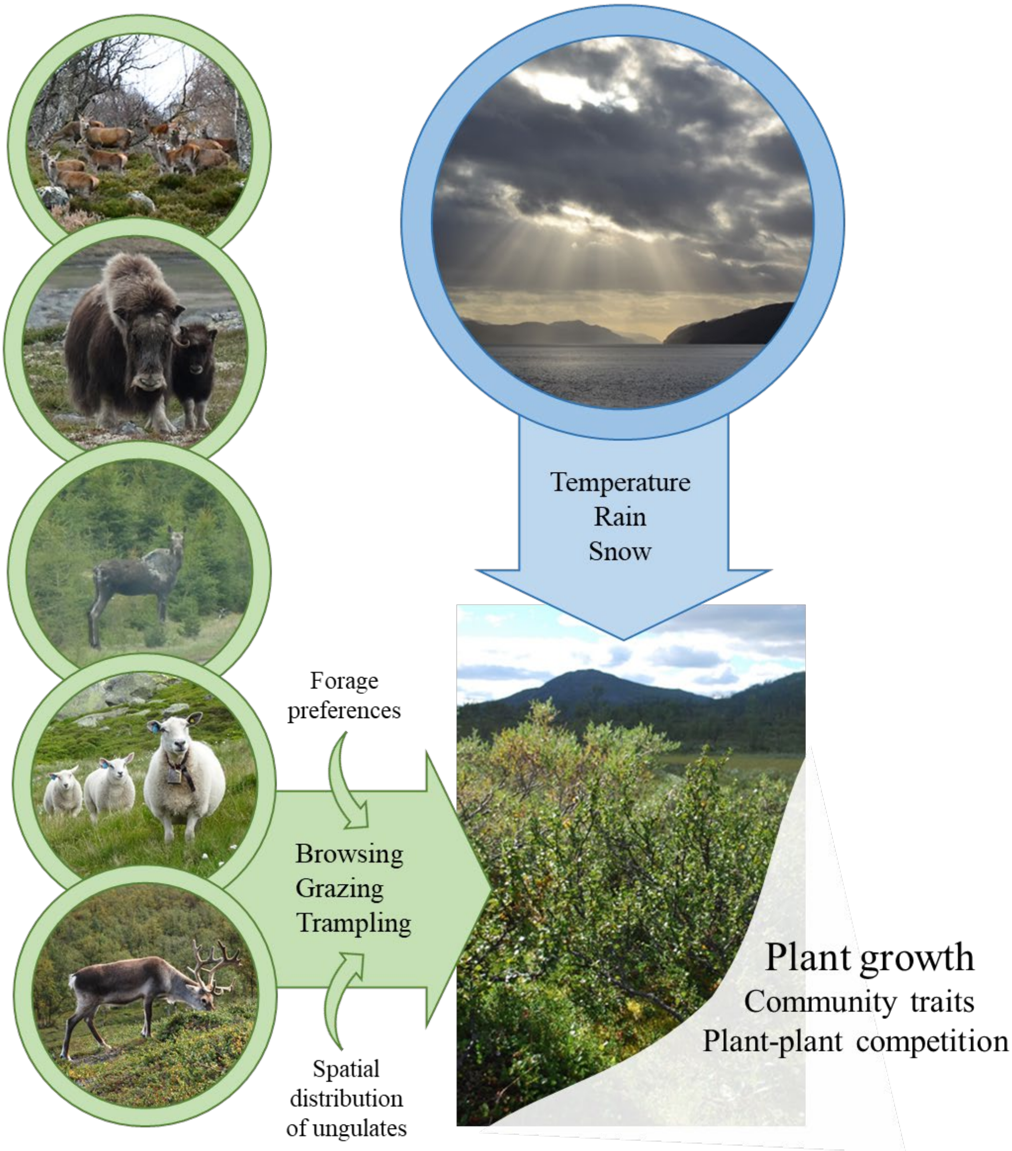

Figure 1. A schematic illustration of the studied effects. Different ungulate herbivore species affect plants by browsing, grazing and trampling, depending on their forage preferences and distribution in space. Temperature, rain and snow effects may be additive or interactive to herbivore effects. Ungulates and climate affect the growth of individual plants, which reflects to community level traits and plant-plant competition.

The strength of ungulate effects on vegetation can be comparable to strength of climatic effects. For example, the borders of tundra and savannah biomes are shaped not only by temperature and precipitation, but also by browsing and grazing (Bråthen et al., 2017; Staver et al., 2009; Van Langevelde et al., 2003). Interestingly, the effects of ungulates on tundra and boreal forest vegetation are typically counteracting that of temperature – higher temperatures lead to increased biomass production, whereas ungulates remove biomass. This is why ungulates have been proposed to function as a buffer against warming: higher mean temperatures may increase the tree production in boreal forests, but deer can bring tree growth down (Fisichelli et al., 2012b); treelines may be advancing towards the north and higher elevations, but sheep can decrease them (Speed et al., 2010); shrubs may be spreading to open tundra, but their encroachment can be slowed down by reindeer (Christie et al., 2015; Olofsson et al., 2009; Verma et al., 2020; Vowles et al., 2017); temperatures may alter alpine plant species communities, but sheep can reverse these trends (Speed et al., 2012).

The interplay of climate and ungulates in shaping the vegetation of tundra and boreal forests has multitudinous tangible consequences for how we may want to manage ungulate populations. Moose and deer may reduce forestry production and slow down reforestation programmes (Kolstad et al., 2018; Rao, 2017), whereas warming may result in desired increased tree growth rates (Boisvenue and Running, 2006). On tundra, in contrast, increasing biomass production leads into undesired closing-up of the vegetation, loss of arctic species, and even feedback loops further warming the climate (Myers-Smith et al., 2011), and there, the buffer effects of reindeer/caribou, muskox and sheep, counteracting warming effects, can be seen as positive. Recently, there has been a lot of discussion on how to rewild ecosystems by herbivore management to preserve and bring back threatened ecosystem dynamics (Cromsigt et al., 2018; Macias-Fauria et al., 2020; Olofsson and Post, 2018). However, to adapt ungulate management to the prevailing and future climatic conditions for preserving and achieving desired vegetation states, knowledge on the combined effects of climate and ungulates is urgently needed.

Yet, there is only limited information on how climate and herbivores together affect vegetation. As climatic effects and herbivore effects are rarely quantified simultaneously, we do not know what levels of ungulate pressures are needed to counteract certain degrees of climatic change. Thus, defining the relative effect sizes of climatic factors and ungulates is of vital importance. Furthermore, it is possible that ungulate and climate effects are not simply additive but interactive, changing each other's effects. For example, ungulate effects on a plant species may decrease with increasing temperature, if temperature decreases the palatability of this plant species, or increase if the high temperatures expose browsed plants to detrimental water loss. For quantifying climate and ungulate effects under different climatic conditions and ungulate pressures, it is crucial to take the potential interactions into account instead of simply assuming additive relationships.

Various biotic and abiotic factors further complicate the interplay of climate and ungulates in northern ecosystems. Ungulate effects on plants need not be solely negative, but positive effects may occur for example *via* effects on nutrient cycling (Cherif and Loreau, 2013). While plant species preferred by ungulates experience direct negative browsing and grazing effects, less preferred plant species may experience indirect positive effects when ungulates lower the prevalence of competing plants (Pastor and Naiman, 1992). Plant herbivore resistance and tolerance also affect which parts of the vegetation are most vulnerable to ungulates. This implies that plant community-level effects of ungulates are likely differ considerably from species-specific effects. By favouring plants with certain traits over others, ungulates may change plant community traits, driving plant resource economics and vegetation structure. Furthermore, ungulates may have differing effects on different plant characteristics, such as height growth, radial growth and establishment of new plant individuals.

Also effects of climatic factors may vary depending on ecological context. Temperature may have not just positive, but also negative consequences for plants if warming is too extreme or connected to detrimental abiotic conditions, such as drought (Buchwal et al., 2020) or icing events (Le Moullec et al., 2020). In boreal forests, growth conditions may become suboptimal for certain tree species, and there is a possibility for increased wind and fire damage risk (Venäläinen et al., 2020). Increased tree mortality may even outpace increased growth rates (Brecka et al., 2018). Both temperature and ungulate effects can be expected to depend on moisture conditions, as water availability changes plants' compensatory growth potential and response to warming (Myers-Smith et al., 2015a). Snow cover may have similar modifying effects, for example by shortening the growth period and protecting plants from herbivory (Ossi et al., 2015b; Ueda et al., 2002).

In principle, ungulates may be able to counteract any increase in plant growth driven by climate – providing that the ungulate pressure is high enough. Yet, we do not know how high are the required ungulate pressures, and under which conditions are ungulate buffers more likely to work. Only by taking into account the prevailing abiotic and biotic conditions, and interactions of ungulates and climate, can we answer the question: When do ungulates override the climate?

Objectives

The primary objective of this thesis is to define the interplay of climate and ungulates in affecting the vegetation of tundra and boreal forests within multiple different ecological contexts. With this approach, I aimed at identifying conditions under which ungulates are likely to counteract climatic effects, including: a) detecting interactive effects of temperature and herbivores, b) defining crucial temperature and herbivores thresholds, and c) quantifying the relative strengths of temperature and herbivores. To achieve this, I asked four specific study questions:

- Are the effects of red deer (*Cervus elaphus*) and temperature on woody plant growth additive or interactive, and how high deer densities and browsing intensities are needed to counteract a certain degree of warming? (Paper **I**)
- Under which abiotic and biotic conditions are moose (*Alces alces*, *A. americanus*) more likely to counteract the warming effects on boreal tree growth at early successional stages? (Paper **II**)
- Does the growth response of tundra shrubs to reindeer/caribou (*Rangifer tarandus*), muskox (*Ovibos moschatus*) and sheep (*Ovis aries*) depend on temperature? (Paper **III**)
- Does the response of alpine tundra vegetation trait composition to sheep depend on elevation? (Paper **IV**)

I wanted to answer these questions in ways that would not just be ecologically relevant, but that would also provide knowledge useful for ungulate management. The study of Paper **I** aimed at producing information of tree and shrub growth rates for reforestation and deer management purposes of a national park in Scottish Highlands. The study of Paper **II** was designed to assess how managed moose affect the growth of economically important tree species in forestry clear-cuts under different climatic conditions. The study of Paper **III** aimed at assessing whether the potential of tundra ungulates to buffer warming effects on tundra shrubs can be expected to work all across the Arctic. And finally, the study of Paper **IV** assessed whether sheep management might be used to prevent warming-induced changes in alpine plant community traits in heavily grazed southern Norwegian mountains.

Methods

To tackle the broad questions of the dynamics of vegetation, ungulates and climate, I applied a multi-site, multi-species approach looking into woody plant growth and plant community traits as a response to ungulate pressure and climatic factors.

Each paper had different spatial scope to address the specific study question related to different ungulate species. The study of Paper **I** looked into deer effects and was conducted in a Scottish national park. The study of Paper **II** looked into moose effects and was conducted at multiple boreal sites in Norway and Canada. The study of Paper **III** looked into reindeer/caribou, muskox and sheep effects and spanned across the Arctic biome. The study of Paper **IV** looked into sheep effects and was conducted at two alpine sites in southern Norway. (Fig. 2)

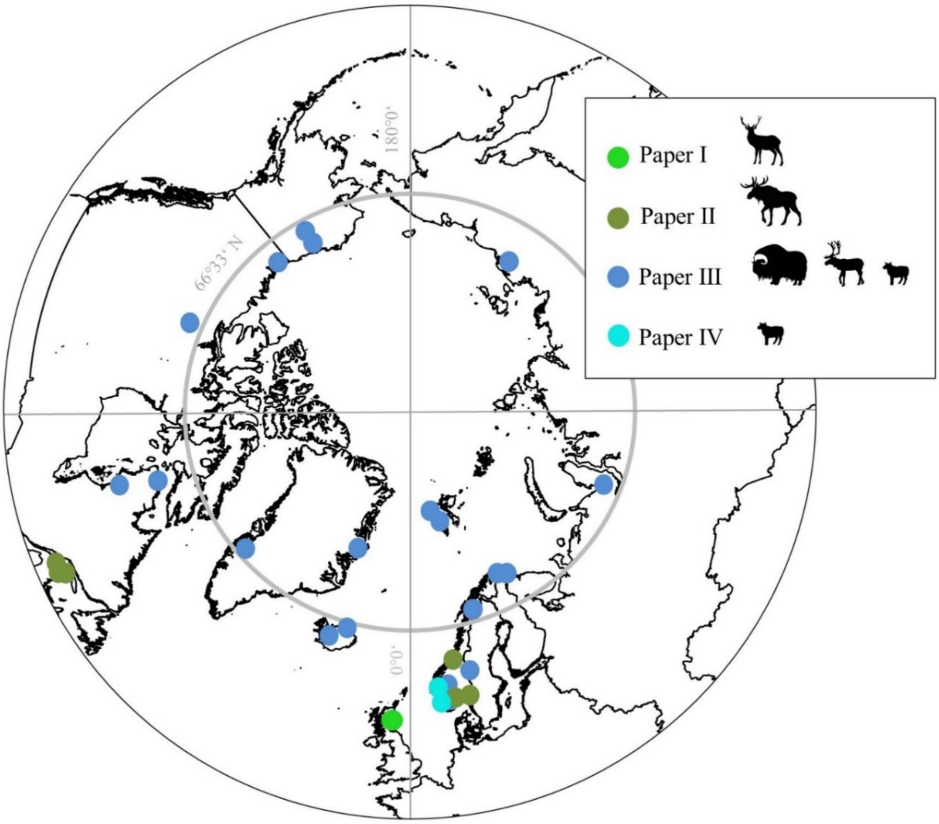

Figure 2. Study locations of each paper, with indication of the studied ungulate. Paper **I** looked into the effects of deer, Paper **II** into the effects of moose, Paper **III** into the effects of reindeer/caribou, muskox, and sheep, and Paper **IV** into the effects of sheep.

Three approaches were used to quantify responses of plants: height growth measurements (Papers **I** and **II**), growth ring measurements (Papers **I** and **III**; Myers-Smith et al., 2015b), and plant species surveys (Paper **IV**; Fig. 3). The two first methods targeted annual height and radial growth of woody plants that play key roles in the study ecosystems, namely trees (Paper **I** and **II**) and shrubs (Papers **I** and **III**). The third method targeted a wider set of vegetation community properties including plant size, reproduction, and resource economics (Paper **IV**).

Two main approaches were used to quantify the ungulate pressure in all papers: ungulate presence-absence, based on experimental ungulate exclusion fences, and observational ungulate density varying in time and/or space, based on various direct and indirect ungulate density estimation methods. In addition, Papers **I** and **II** included field measurements on ungulate faeces and browsing pressure. Climatic data was acquired from local meteorological stations (Paper **I**) and from national and global climate models (Papers **II**-**IV**). We only looked into the effects of observed climatic variation, i.e. climatic factors were not manipulated.

All papers took advantage of long-term plant, ungulate and climate records, necessary to disentangle the ungulate and climatic effects. The study periods spanned over up to 25, 11, 45, and 19 years, for Papers **I**-**IV**, respectively.

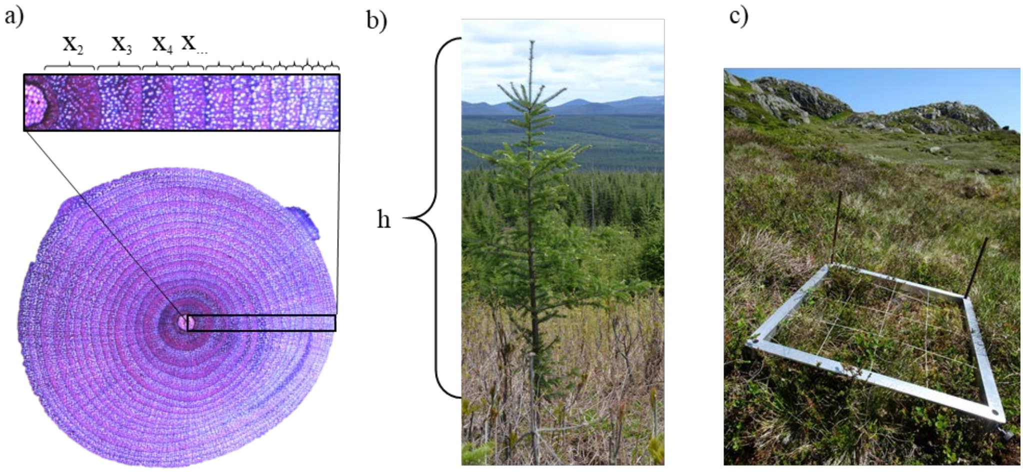

Figure 3. Illustration of the three methods used for quantifying vegetation response: growth ring measurements (a), height growth measurements (b), and plot-based plant community composition surveys (c).

Results

High ungulate densities may hamper the growth of trees at early successional stages of boreal forests (Kolstad et al., 2018; Rao, 2017). In contrast, higher temperatures may benefit tree growth (Boisvenue and Running, 2006). These dynamics have a pronounced management relevance in areas such as the Scottish Highlands where reforestation is often negligible due to high numbers of deer (Rao, 2017). In Paper **I**, we conducted a study in the Cairngorms National Park and showed that the effects of temperature and deer density on the radial and height growth of Scots pine were additive: the growth increase caused by expected warming of 2–3.5°C was predicted to be nullified by an increase of 6–11 and 2–4 deer km^{-2} (for radial and height growth, respectively). Models using deer faeces counts instead of deer density yielded similar results. However, we also found an interactive effect of browsing intensity and temperature: pine height growth decreased under warming when more than 60% of shoots were browsed, suggesting that high browsing intensities may be efficient in reversing temperature trends. Furthermore, deer presence resulted in pines responding more strongly to temperature, possibly because deer reduced the growth constraints caused by plant-plant competition and exposed pines to bigger temperature variations (Karlsson, 2000; Oerlander and Karlsson, 2000). Taken together, the results of Paper **I** showed that deer have high potential to both counteract and modify temperature responses of pines in the national park.

Paper **I** also yielded some evidence for deer density and temperature interacting in affecting the radial growth of heather in the field layer. Growth decreased with increasing deer density when temperatures were above 6°C, but increased with increases in deer densities below 6°C. This might reflect indirect effects of high snow cover, related to low temperatures: when snow reduced access to shrubs (Ossi et al., 2015b; Ueda et al., 2002), deer might have browsed trees more frequently, and thus potentially reduced tree shading, benefitting heather.

The Interplay of ungulates and climate has pronounced effects for boreal forests also in a wider forest management context. Commercial tree production may shape boreal landscapes stronger than climate or ungulate effects, but within the framework set by forestry, browsing and temperature can have pronounced effect on tree growth. After clear-cutting, trees are vulnerable to ungulates until they escape browser reach (Kolstad et al., 2018), yet their growth is also affected by plant-plant competition, temperature, snow and rain. In Paper **II**, we illustrated the relative effects of moose on height growth of different tree species in relation to other biotic and climatic factors in Norway and Canada. High temperatures increased the growth of many deciduous trees, but not that much for coniferous trees, suggesting imbalanced benefits of warming for different species. However, also the negative effects of moose presence were most pronounced for the deciduous species, implying that moose may even out the imbalanced benefits of warming. We also found that moose presence strengthened the temperature response of balsam fir in Canada, in a same way as deer presence strengthened the temperature response of Scots pine in Paper **I**. Winter precipitation decreased browsing intensity, and it seems likely that snow may play a crucial role in modifying the effects of moose on tree growth. In contrast, moose density and local forage availability increased browsing pressure. We found weak evidence that moose affected some species positively by reducing plant-plant competition. In sum, the results of Paper **II** showed that moose presence may override the temperature effects especially for preferred forage species, but that this counteracting effect may be modified by snow, moose density, and local forage availability.

In Papers **III** and **IV**, we changed the focus from boreal forests to alpine and arctic tundra. The model of Paper **III** predicted that reindeer/caribou, muskox and sheep were most efficient at counteracting temperature effects on shrub radial growth at summer temperatures of around 7.5°C across the Arctic, while their effects decreased as conditions became either colder or warmer. It is possible that we were unable to detect ungulate effects in the warmer parts of the Arctic because there, high ungulate densities were associated with high summer and winter precipitation that may counteract ungulate effects: summer rain and a longer snowy period may increase shrubs' potential for compensatory growth and decrease herbivore exposure (Jespersen et al., 2018; Ossi et al., 2015a; Ueda et al., 2002; White et al., 2009). The lack of observed ungulate response in the colder parts of the Arctic, in contrast, may be due to the fact that the shrub species in this area were small, prostrate species that may take less ungulate damage in comparison to erect shrub species (Vowles and Björk, 2019). However, it is also possible that we failed to observe ungulate effects at cold temperatures because our data captured relatively low variation in ungulate densities. Several other biotic factors, such as shrub palatability, ungulate species, and ungulate landscape use may also contribute to the results. Overall, it was hard to pinpoint the exact mechanisms behind the observed shrub growth patterns, but our results suggest that ungulate temperature buffer potential may vary between climatically different parts of the Arctic.

In Paper **IV**, we took spatially more focused, local scope, but scaled up to the community level by looking into multiple traits of multiple plant species. This allowed us to take a wider ecological perspective and model not just changes in plant height, but also in other size traits, resource dynamics, and reproduction. Our analyses showed that Southern-Norwegian alpine plant communities with long grazing history (Daugstad et al., 2014; Hayward, 1948) were highly resistant to changes in sheep densities, regardless of elevation. Yet, elevation had some moderate effects for community trait composition, high vegetative height, specific leaf area, leaf area, and leaf fresh mass being associated to lower elevations, and leaf dry matter content and woodiness to middle and high elevations at one of the two study sites. Furthermore, we also observed small increases in traits related to size and growth potential, happening simultaneously with increased temperature and precipitation. These results suggest that sheep may not be efficient in overriding climate effects on alpine plant communities within time periods <20 years. This may be because these communities have been developing resistance to ungulates over centuries. Likely resistance mechanisms include high compensatory growth potential, slow species turnover, and intense plant-plant competition in the field and ground layer (Cingolani et al., 2005; Lemaire, 2001; Milchunas et al., 1988).

Discussion

Climate and herbivores shape northern plants together (Bryant et al., 2014; Christie et al., 2015; Fisichelli et al., 2012a; Niemelä et al., 2001; Olofsson et al., 2009). Thus, considering their effects in isolation may give misleading impression of the dynamics of tundra and boreal forests. In this thesis, I have shown that climate and ungulate effects on plants may depend on each other, and that their effects vary between different ecological contexts across northern biomes. These interactions and context dependencies need to be acknowledged if we are to use rewilding and ungulate management (Cromsigt et al., 2018; Macias-Fauria et al., 2020; Olofsson and Post, 2018) to preserve and restore desired vegetation characteristics in a warming climate (Mbow et al., 2017; Pachauri et al., 2014).

I identified multiple cases where ungulate and temperature responses were interactive, suggesting complex vegetation dynamics. This applied to the pine and heather responses to temperature, deer presence and browsing intensity in Scottish Highlands (Paper **I**), responses of a fir and a rowan species to temperature and moose presence in boreal forests (Paper **II**), and the growth of shrubs across the Arctic (Paper **III**). In certain other cases, temperature and herbivore effects were additive, suggesting that herbivore presence and/or sufficient herbivore density may counteract a certain degree of warming linearly. This applied to the pine response to temperature and deer density in Scottish Highlands (Paper **I**), and several preferred forage tree species in boreal forest (Paper **II**). However, even if herbivores played many crucial roles in changing vegetation dynamics, I also found that in some cases climate-centric view of vegetation dynamics may be justified, as plants responded to temperature but not to ungulates. This suggests that ungulates might not always have buffering power against warming. This applied to the least preferred forage tree species in boreal forests (Paper **II**), and alpine plant community traits with long grazing history (Paper **IV**). (Fig. 4)

Multiple abiotic factors may explain why plant responses to ungulates and climatic variables differed in such profound ways both on local scale and across tundra and boreal forests. Firstly, nutrient availability is a key driver of plant productivity, likely affecting plant growth responses to both climatic factors and ungulates. Secondly, tundra and boreal forest ecosystems are seasonal, meaning that snow cover modifies plant exposure to ungulates (Oksanen et al., 2020). In Papers **I-III**, I showed direct and indirect evidence that snow may protect heather and boreal trees from deer and moose browsing, and tundra shrubs from arctic ungulates. Thirdly, high local water availability may increase plants' potential to compensate biomass loss caused by herbivory, and to respond positively to warming (Björkman et al., 2018). This might explain why tundra shrub growth did not respond negatively to ungulates under high temperatures and precipitation values (Paper **III**). On the other hand, herbivory may expose plants to water loss. This might be why we observed a negative temperature response for the highly browsed pines in the Scottish Highlands (Paper **I**). Increased precipitation may also have contributed to the minor plant size trait

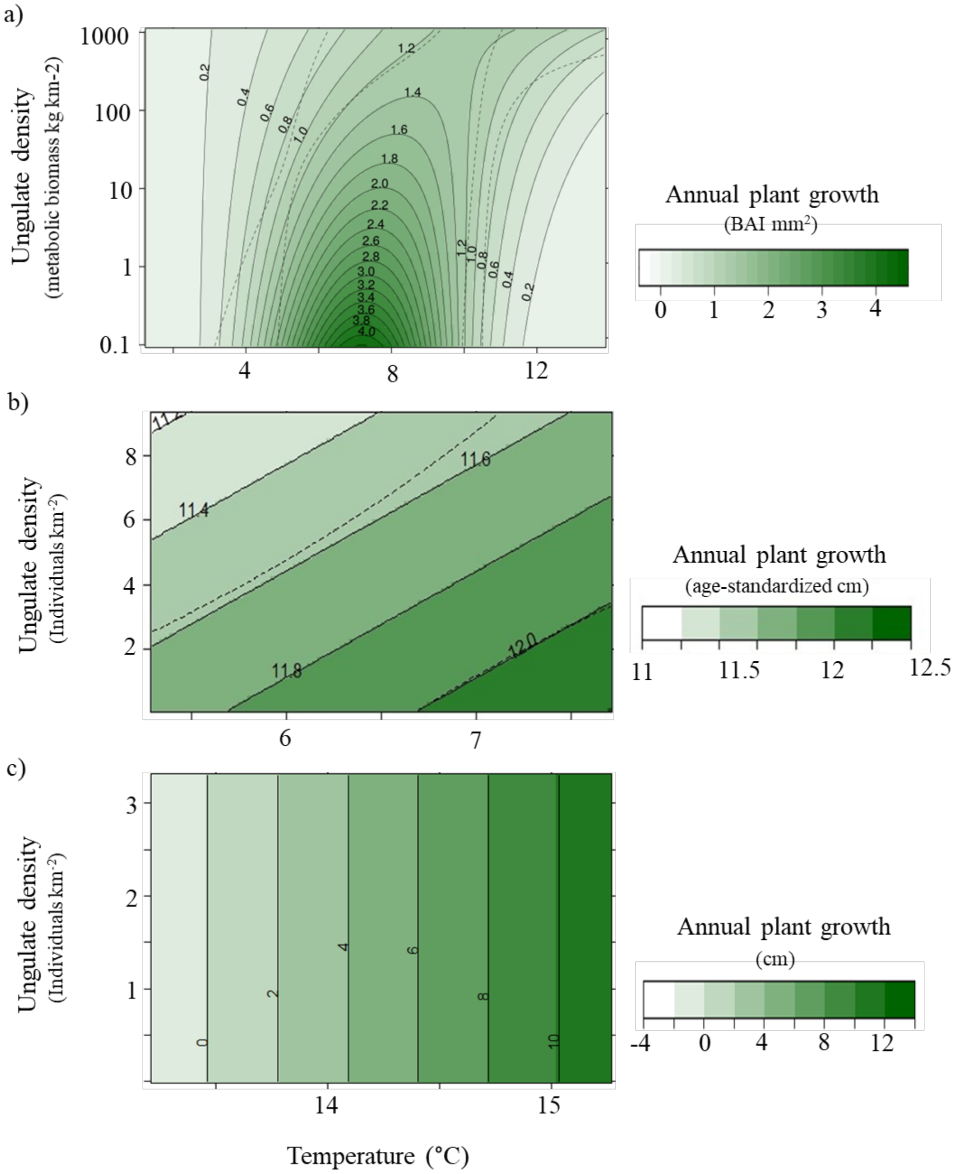

Figure 4. Three examples of different detected ungulate effect types: interactive ungulate-temperature effect (a), additive ungulate-temperature effect (b), and no ungulate effect (c). Annual plant growth prediction is presented as green colour on the plane of ungulate density and temperature: the darker the green, the higher the growth. The more vertical the growth isoclines are, the stronger the temperature effect; the more horizontal they are, the stronger the ungulate effect. Panel a is based on data from Paper **III**, where basal area increment (BAI) of tundra shrubs responded to interactive effects of ungulate density and temperature; panel b is based on data from Paper **I**, where height growth of a pine species responded positively to temperature and negatively to ungulate density; panel c is based on data from Paper **II**, where height growth of a spruce species responded positively to temperature but there was no response to moose density. In panels a and c, temperature is growth period average, whereas in panel b, temperature is annual average. Note also different units of the ungulate density and plant growth axes between the panels.

increases we observed in alpine Norwegian plant communities (Paper **IV**). All these abiotic factors and their relative role in shaping vegetation dynamics vary between and within the studied ecosystems, potentially shaping the observed interplay of climatic factors and ungulates.

Biotic factors are another explanation for why observed plant responses to ungulates and climate were so variable. Ungulate forage preferences and plant palatability (Bryant et al., 2014; Pastor and Naiman, 1992) change the potential of ungulates to override climatic effects, and thus we expect to find differing effects depending on plant and ungulate species. As we showed, moose did not have strong effects on the growth of less preferred forage tree species, whereas more preferred species were highly affected by it (Paper **II**). The lack of observed ungulate response in the coldest parts of the Arctic may also reflect the fact that low-stature shrubs of these areas are not necessarily heavily damaged by ungulates, in comparison more sensitive, erect shrubs (Paper **III**). Furthermore, the way ungulates are using the landscape (Schmidt et al., 2016; Skarin et al., 2020) may have consequences for the local ungulate effects. For example, Paper **II** showed that moose browsing intensity increased with local forage availability, suggesting that browsing may be concentrated on areas with highest forage value. Herbivory and trampling pressure may vary spatially also due to other factors, such as predation risk (Ripple and Beschta, 2003), which may make ungulate effects on plants uneven across the landscape. The lack of ungulate responses at the coldest and warmest areas in Paper **III** may also be explained by low local ungulate pressure besides high landscape-level ungulate densities. In sum, vegetation responses to ungulates and climate are dependent on the behavioural and physiological characteristics of the ungulate and plant species in question.

Plant-plant interactions can also change the way ungulates and temperature affect vegetation (Bråthen and Lortie, 2016; Pastor and Naiman, 1992; Speed et al., 2013). Paper **II** showed some evidence for moose having minor indirect positive effects on the growth of certain species *via* reducing the amount of competing species. Also in Paper **I**, we suggested that positive response of heather to deer at low temperatures might have been due to reduced competition pressure from browsed trees. Paper **III** showed some evidence for a moderate positive ungulate effect on shrub growth under conditions typical for sheep-dominated sites, which we suggest might be because sheep may have been targeting competing plant species rather than shrubs. Plant-plant interactions may also have played a role for the stability observed in Paper **IV**: long grazing history might have led to alpine plant communities with high plant-plant competition close to the ground level (Cingolani et al., 2005; Lemaire, 2001; Milchunas et al., 1988), and thus to slow species turnover. Plant competition conditions varied between and within studied ecosystems, and thus they may have had a substantial role in shaping the observed climate and ungulate effects.

As the variable results showed, the answer to the question of when ungulates override the climate depends on the biotic and abiotic conditions of the system in question. In this thesis, I have studied ungulate and climate effects at both local scale (Papers **I** and **IV**) and closer to biome level (Papers **II** and **III**), but also in the papers with the wide scope, the explanations of observed patterns tend to came down to local factors such as plant-plant competition, different plant and ungulate species, and how ungulates behave in landscape. This conclusion has clear implications for management, calling for case-specific evaluations of ungulate and climate effects, including their potential interactions, to decide for appropriate management actions.

The results imply that in the case of boreal reforestation, deer densities need to be kept low if the expected increase in mean temperatures is desired to translate into increased pine growth (Paper **I**). Same applies to moose densities in commercially managed boreal forests with regards to deciduous species (Paper **II**). However, certain coniferous may not respond to or be targeted by moose browsing, especially in presence of more preferred forage species, and thus moose management may not be that crucial for their growth. Coniferous may have weaker positive responses to warming in comparison to deciduous species, or they may even respond to it negatively (Way and Oren, 2010; Paper **II**), meaning that moose presence may help us to sustain the current tree species composition in boreal forests by supressing growth of deciduous trees. The optimal ungulate densities depend on what tree species are desired, and how fast they are wished to grow. However, managers also need to consider that browsing effects are likely to be uneven in landscape e.g. due to foraging optimizing behaviour of ungulates (Milligan and Koricheva, 2013; Paper **II**). Furthermore, if climatic change results into higher winter precipitation, the browsing pressure on trees may decrease considerably, whereas lower winter precipitation and/or shorter snowy period (Soja et al., 2007) may increase it (Paper **II**).

In the case of alpine and arctic tundra, the results support the studies showing that ungulates may be used to counteract plant growth increases driven by warming (Cahoon et al., 2012; Christie et al., 2015; Olofsson et al., 2009; Plante et al., 2014; Speed et al., 2013; Vowles et al., 2017). However, Papers **III** and **IV** also make clear that increasing ungulate densities may not always be as efficient vegetation change mitigation action as some studies suggest. Tundra shrubs may tolerate ungulates if they have low stature, if they are protected by snow, and if their growth is supported by high water availability, which might mean that herbivore buffers are weaker in some parts of the Arctic (Paper **III**). It also appears that under long-term grazing pressure, whole alpine plant communities may enter into a state that is highly resistant to sheep (Cingolani et al., 2005; Lemaire, 2001; Milchunas et al., 1988). Yet, these communities may nevertheless respond to new climatic conditions. This implies that sheep are less likely to function as a countermeasure for climate-driven plant species and community trait changes in the areas where it has already historically transformed the vegetation. These constrains should be kept in mind when considering ungulate management as a means to modify climate effects on tundra.

Yet, even the areas, communities and species less sensitive to herbivores may respond to them when faced with sufficiently high browsing, grazing or trampling pressure. Thus, the most crucial aspect of the question of whether ungulates override the climate is the magnitude of the climatic response to be overcome, and whether it is realistic to aim at the ungulate pressure of corresponding magnitude. In the appended papers, I have defined certain herbivore pressure sizes needed to counteract certain degree of warming. However, these numbers are only directly applicable for specific contexts of each paper, and due to the importance of local biotic and abiotic factors described above, high caution should be paid if generalising the results to other systems and areas. I encourage for more studies looking into climate and ungulate effects in specific ecological contexts to produce realistic estimations of counteractive potential of ungulates for management purposes. Naturally, it is also essential to relate the effect sizes of ungulates to other potential drivers of vegetation dynamics, such as rodents, insect outbreaks and forestry practices, as their effect may highly exceed that of ungulate herbivores (Post and Pedersen, 2008; Prendin et al., 2020). I also emphasize the importance of research on likely modifiers of the interactions of ungulates and temperature, considering three-way interactions between ungulates, temperature and nutrient availability, and between ungulates, temperature and precipitation. Other apparent knowledge gaps include the combined effects of changing climate and changing ungulate community compositions (Speed et al., 2019), and the combined effects of changing climate and spatially uneven herbivore pressures (Schmidt et al., 2016; Skarin et al., 2020).

For successful ungulate-based vegetation management, it is crucial to notice that we affect vegetation also by changing ungulate populations in multiple inadvertent ways. Reindeer/caribou are affected by direct human disturbance and intensifying use of tundra land (Wolfe et al., 2000), and climatic changes are contributing to the decline of their numbers (Vors and Boyce, 2009). Also some muskox populations may be vulnerable to future warming (Cuyler et al., 2020). In contrast, many boreal forest deer and moose populations have been going though increases after extirpation of their natural predators and increases in forage availability driven by changes in forestry (Lavsund et al., 2003; Ripple and Beschta, 2012). If ungulate populations are to be used for modifying vegetation dynamics, it is essential that needed ungulate densities are sustained besides these unintended, indirect effects.

Even if we had full control on ungulate population densities, ungulate-based vegetation management faces crucial ecological and societal challenges, as both vegetation and ungulates play multiple biological and cultural roles. For example, sustaining high densities of moose and deer for hunting purposes can be desirable from management perspective (Scottish Natural Heritage, 2016; Storaas et al., 2001), even if it has adverse effects on tree growth. Recently introduced muskox populations (Cuyler et al., 2020) may help to preserve open tundra in warming climate, but indigenous peoples may react to locally new species suspiciously. High reindeer densities are perhaps useful for meat production and prevention of shrub advancement (Kolari et al., 2019; Verma et al., 2020), but they also suppress grazing-sensitive plant species. These type of trade-offs mean that ungulate management needs to balance between different goals related to vegetation state, cultural values, climate change mitigation, economic gains and losses, biodiversity, and ecosystem services (Fischer et al., 2018; Mbow et al., 2017).

It is also justified to ask how meaningful it is to consider temperature and herbivore as counteracting forces. Reforestation advances slow in many areas besides higher temperatures, and thus warming in unlikely to remove the need for management actions enhancing tree growth. Also, ungulate management certainly cannot replace climate change mitigation measures as a way to retain and restore ecosystem dynamics, even if it could be used locally to prevent warming effects on vegetation. We may be able to disentangle the effects of ungulates and climate on vegetation in scientific terms, but to decide how these two forces are let to shape the future of the biosphere, is another tangled bank, waiting to be unraveled.

References

Babst, F., Esper, J., Parlow, E., 2010. Landsat TM/ETM+ and tree-ring based assessment of spatiotemporal patterns of the autumnal moth (Epirrita autumnata) in northernmost Fennoscandia. Remote Sensing of Environment 114, 637-646.

Beguin, J., Tremblay, J. P., Thiffault, N., Pothier, D., Côté, S. D., 2016. Management of forest regeneration in boreal and temperate deer–forest systems: challenges, guidelines, and research gaps. Ecosphere 7, e01488.

Berner, L. T., Massey, R., Jantz, P., Forbes, B. C., Macias-Fauria, M., Myers-Smith, I., Kumpula, T., Gauthier, G., Andreu-Hayles, L., Gaglioti, B. V., 2020. Summer warming explains widespread but not uniform greening in the Arctic tundra biome. Nature communications 11, 1-12.

Björkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., 2018. Plant functional trait change across a warming tundra biome. Nature 562, 57-62.

Björkman, A. D., Criado, M. G., Myers-Smith, I. H., Ravolainen, V., Jónsdóttir, I. S., Westergaard, K. B., Lawler, J. P., Aronsson, M., Bennett, B., Gardfjell, H., 2020. Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring. Ambio 49, 678-692.

Boertje, R. D., Keech, M. A., Paragi, T. F., 2010. Science and values influencing predator control for Alaska moose management. The Journal of Wildlife Management 74, 917-928.

Boisvenue, C., Running, S. W., 2006. Impacts of climate change on natural forest productivity–evidence since the middle of the 20th century. Global Change Biology 12, 862-882.

Bråthen, K. A., Lortie, C., 2016. A portfolio effect of shrub canopy height on species richness in both stressful and competitive environments. Functional ecology 30, 60-69.

Bråthen, K. A., Ravolainen, V. T., Stien, A., Tveraa, T., Ims, R. A., 2017. Rangifer management controls a climate-sensitive tundra state transition. Ecological Applications 27, 2416-2427.

Brecka, A. F., Shahi, C., Chen, H. Y., 2018. Climate change impacts on boreal forest timber supply. Forest Policy and Economics 92, 11-21.

Bryant, J. P., Joly, K., Chapin III, F. S., DeAngelis, D. L., Kielland, K., 2014. Can antibrowsing defense regulate the spread of woody vegetation in arctic tundra? Ecography 37, 204-211.

Buchwal, A., Sullivan, P. F., Macias-Fauria, M., Post, E., Myers-Smith, I. H., Stroeve, J. C., Blok, D., Tape, K. D., Forbes, B. C., Ropars, P., 2020. Divergence of Arctic shrub growth associated with sea ice decline. Proceedings of the National Academy of Sciences.

Cahoon, S. M., Sullivan, P. F., Post, E., Welker, J. M., 2012. Large herbivores limit CO 2 uptake and suppress carbon cycle responses to warming in W est G reenland. Global Change Biology 18, 469-479.

Cherif, M., Loreau, M., 2013. Plant–herbivore–decomposer stoichiometric mismatches and nutrient cycling in ecosystems. Proceedings of the Royal Society B: Biological Sciences 280, 20122453.

Christie, K. S., Bryant, J. P., Gough, L., Ravolainen, V. T., Ruess, R. W., Tape, K. D., 2015. The role of vertebrate herbivores in regulating shrub expansion in the Arctic: a synthesis. BioScience 65, 1123-1133.

Cingolani, A. M., Noy-Meir, I., Díaz, S., 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. Ecological applications 15, 757-773.

Cromsigt, J. P., te Beest, M., Kerley, G. I., Landman, M., le Roux, E., Smith, F. A., 2018. Trophic rewilding as a climate change mitigation strategy? Philosophical Transactions of the Royal Society B 373, 20170440.

Cuyler, C., Rowell, J., Adamczewski, J., Anderson, M., Blake, J., Bretten, T., Brodeur, V., Campbell, M., Checkley, S. L., Cluff, H. D., 2020. Muskox status, recent variation, and uncertain future. Ambio 49, 805-819.

Daugstad, K., Mier, M. F., Peña-Chocarro, L., 2014. Landscapes of transhumance in Norway and Spain: Farmers' practices, perceptions, and value orientations. Norsk Geografisk Tidsskrift-Norwegian Journal of Geography 68, 248-258.

Fischer, M., Rounsevell, M., Rando, A. T.-M., Mader, A., Church, A., Elbakidze, M., Elias, V., Hahn, T., Harrison, P. A., Hauck, J., 2018. Summary for policymakers of the regional assessment report on biodiversity and ecosystem services for Europe and Central Asia of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Fisichelli, N., Frelich, L. E., Reich, P. B. J. G. C. B., 2012a. Sapling growth responses to warmer temperatures ‘cooled’ by browse pressure 18, 3455-3463.

Fisichelli, N., Frelich, L. E., Reich, P. B., 2012b. Sapling growth responses to warmer temperatures ‘cooled’ by browse pressure. Global Change Biology 18, 3455-3463.

Gallagher, R. V., Allen, S., Wright, I. J., 2019. Safety margins and adaptive capacity of vegetation to climate change. Scientific reports 9, 1-11.

Hayward, D., 1948. Transhumance in southern Norway. Scottish Geographical Magazine 64, 71-80.

Ivantsova, E. D., Pyzhev, A. I., Zander, E. V., 2019. Economic consequences of insect pests outbreaks in boreal forests: A literature review. Журнал Сибирского федерального университета. Гуманитарные науки 12.

Jespersen, R. G., Leffler, A. J., Oberbauer, S. F., Welker, J. M., 2018. Arctic plant ecophysiology and water source utilization in response to altered snow: isotopic (δ 18 O and δ 2 H) evidence for meltwater subsidies to deciduous shrubs. Oecologia 187, 1009-1023.

Karlsson, I. M., 2000. Nocturnal air temperature variations between forest and open areas. Journal of applied meteorology 39, 851-862.

Kolari, T. H., Kumpula, T., Verdonen, M., Forbes, B. C., Tahvanainen, T., 2019. Reindeer grazing controls willows but has only minor effects on plant communities in Fennoscandian oroarctic mires. Arctic, Antarctic, and Alpine Research 51, 506-520.

Kolstad, A. L., Austrheim, G., Solberg, E. J., Venete, A. M., Woodin, S. J., Speed, J. D., 2018. Cervid exclusion alters boreal forest properties with little cascading impacts on soils. Ecosystems 21, 1027-1041.

Lavsund, S., Nygrén, T., Solberg, E. J., 2003. Status of moose populations and challenges to moose management in Fennoscandia. Alces 39.

Le Moullec, M., Sandal, L., Grøtan, V., Buchwal, A., Hansen, B. B., 2020. Climate synchronises shrub growth across a high-arctic archipelago: contrasting implications of summer and winter warming. Oikos.

Lemaire, G., 2001. Ecophysiology of grasslands: dynamic aspects of forage plant populations in grazed swards. International Grassland Congress, Vol. 19, pp. 29-37.

Lenoir, J., Gégout, J.-C., Marquet, P., De Ruffray, P., Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. science 320, 1768-1771.

Ma, Z., Liu, H., Mi, Z., Zhang, Z., Wang, Y., Xu, W., Jiang, L., He, J.-S., 2017. Climate warming reduces the temporal stability of plant community biomass production. Nature Communications 8, 1-7.

Macias-Fauria, M., Jepson, P., Zimov, N., Malhi, Y., 2020. Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? Philosophical Transactions of the Royal Society B 375, 20190122.

Mbow, H.-O. P., Reisinger, A., Canadell, J., O’Brien, P., 2017. Special Report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems (SR2). Ginevra, IPCC.

Milchunas, D., Sala, O., Lauenroth, W. K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist 132, 87-106.

Milligan, H. T., Koricheva, J., 2013. Effects of tree species richness and composition on moose winter browsing damage and foraging selectivity: an experimental study. Journal of Animal Ecology 82, 739-748.

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6, 045509.

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S., Wilmking, M., Hallinger, M., Blok, D., Tape, K. D., Rayback, S. A., Macias-Fauria, M., Forbes, B. C., 2015a. Climate sensitivity of shrub growth across the tundra biome. Nature Climate Change 5, 887-891.

Myers-Smith, I. H., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S. A., Weijers, S., Trant, A. J., Tape, K. D., Naito, A. T., Wipf, S., 2015b. Methods for measuring arctic and alpine shrub growth: a review. Earth-Science Reviews 140, 1-13.

Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P. S., 2020. Complexity revealed in the greening of the Arctic. Nature Climate Change 10, 106-117.

Niemelä, P., Chapin, F. S., Danell, K., Bryant, J. P., 2001. Herbivory-mediated responses of selected boreal forests to climatic change. Climatic Change 48, 427-440.

Oerlander, G., Karlsson, C., 2000. Influence of shelterwood density on survival and height increment of Picea abies advance growth. Scandinavian journal of forest research 15, 20-29.

Oksanen, T., Oksanen, L., Vuorinen, K. E., Wolf, C., Mäkynen, A., Olofsson, J., Ripple, W. J., Virtanen, R., Utsi, T. A., 2020. The impact of thermal seasonality on terrestrial endotherm food web dynamics: a revision of the Exploitation Ecosystem Hypothesis. Ecography.

Olofsson, J., Post, E., 2018. Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. Philosophical Transactions of the Royal Society B: Biological Sciences 373, 20170437.

Olofsson, J., Tømmervik, H., Callaghan, T. V., 2012. Vole and lemming activity observed from space. Nature Climate Change 2, 880-883.

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.

Ossi, F., Gaillard, J.-M., Hebblewhite, M., Cagnacci, F. J. E. j. o. w. r., 2015a. Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer 61, 111-124.

Ossi, F., Gaillard, J.-M., Hebblewhite, M., Cagnacci, F., 2015b. Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer. European journal of wildlife research 61, 111-124.

Pachauri, R. K., Allen, M. R., Barros, V. R., Broome, J., Cramer, W., Christ, R., Church, J. A., Clarke, L., Dahe, Q., Dasgupta, P., 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. Ipcc.

Pastor, J., Naiman, R. J., 1992. Selective foraging and ecosystem processes in boreal forests. The American Naturalist 139, 690-705.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J. L. B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R. F., 2012. Recent plant diversity changes on Europe's mountain summits. Science 336, 353-355.

Peñuelas, J., Filella, I., 2009. Phenology feedbacks on climate change. Science 324, 887-888.

Plante, S., Champagne, E., Ropars, P., Boudreau, S., Lévesque, E., Tremblay, B., Tremblay, J.-P., 2014. Shrub cover in northern Nunavik: can herbivores limit shrub expansion? Polar biology 37, 611-619.

Post, E., Pedersen, C., 2008. Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences 105, 12353-12358.

Prendin, A. L., Carrer, M., Karami, M., Hollesen, J., Bjerregaard Pedersen, N., Pividori, M., Treier, U. A., Westergaard-Nielsen, A., Elberling, B., Normand, S., 2020. Immediate and carry-over effects of insect outbreaks on vegetation growth in West Greenland assessed from cells to satellite. Journal of Biogeography 47, 87-100.

Pugnaire, F. I., Morillo, J. A., Peñuelas, J., Reich, P. B., Bardgett, R. D., Gaxiola, A., Wardle, D. A., Van Der Putten, W. H., 2019. Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. Science advances 5, eaaz1834.

Rao, S. J., 2017. Effect of reducing red deer Cervus elaphus density on browsing impact and growth of Scots pine Pinus sylvestris seedlings in semi-natural woodland in the Cairngorms, UK. Conservation Evidence 14, 22-26.

Ripple, W. J., Beschta, R. L., 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184, 299-313.

Ripple, W. J., Beschta, R. L., 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biological Conservation 145, 205-213.

Ross, L. C., Austrheim, G., Asheim, L.-J., Bjarnason, G., Feilberg, J., Fosaa, A. M., Hester, A. J., Holand, Ø., Jónsdóttir, I. S., Mortensen, L. E., 2016. Sheep grazing in the North Atlantic region: A long-term perspective on environmental sustainability. Ambio 45, 551-566.

Rumpf, S. B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J., Willner, W., Zimmermann, N. E., Dullinger, S., 2018. Range dynamics of mountain plants decrease with elevation. Proceedings of the National Academy of Sciences 115, 1848-1853.

Schmidt, N. M., van Beest, F. M., Mosbacher, J. B., Stelvig, M., Hansen, L. H., Nabe-Nielsen, J., Grøndahl, C., 2016. Ungulate movement in an extreme seasonal environment: year-round movement patterns of high-arctic muskoxen. Wildlife Biology 22, 253-267.

Scottish Natural Heritage, 2016. Deer management in Scotland: report to the Scottish Government from Scottish Natural Heritage. SNH, Battleby.

Skarin, A., Verdonen, M., Kumpula, T., Macias-Fauria, M., Alam, M., Kerby, J. T., Forbes, B. C., 2020. Reindeer use of low Arctic tundra correlates with landscape structure. Environmental Research Letters.

Soja, A. J., Tchebakova, N. M., French, N. H., Flannigan, M. D., Shugart, H. H., Stocks, B. J., Sukhinin, A. I., Parfenova, E., Chapin III, F. S., Stackhouse Jr, P. W., 2007. Climate-induced boreal forest change: predictions versus current observations. Global and Planetary Change 56, 274-296.

Speed, J. D., Austrheim, G., Hester, A. J., Mysterud, A., 2010. Experimental evidence for herbivore limitation of the treeline. Ecology 91, 3414-3420.

Speed, J. D., Austrheim, G., Hester, A. J., Mysterud, A., 2012. Elevational advance of alpine plant communities is buffered by herbivory. Journal of Vegetation Science 23, 617-625.

Speed, J. D., Austrheim, G., Hester, A. J., Mysterud, A., 2013. The response of alpine Salix shrubs to long-term browsing varies with elevation and herbivore density. Arctic, Antarctic, and Alpine Research 45, 584-593.

Speed, J. D., Austrheim, G., Kolstad, A. L., Solberg, E. J., 2019. Long-term changes in northern large-herbivore communities reveal differential rewilding rates in space and time. PloS one 14, e0217166.

Staver, A. C., Bond, W. J., Stock, W. D., Van Rensburg, S. J., Waldram, M. S., 2009. Browsing and fire interact to suppress tree density in an African savanna. Ecological applications 19, 1909-1919.

Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. Nature 556, 231-234.

Stewart, L., Simonsen, C. E., Svenning, J. C., Schmidt, N. M., Pellissier, L., 2018. Forecasted homogenization of high Arctic vegetation communities under climate change. Journal of Biogeography 45, 2576-2587.

Storaas, T., Gundersen, H., Henriksen, H., Andreassen, H. P., 2001. The economic value of moose in Norway-a review. Alces 37, 97-107.

Ueda, H., Takatsuki, S., Takahashi, Y., 2002. Bark stripping of hinoki cypress by sika deer in relation to snow cover and food availability on Mt Takahara, central Japan. Ecological Research 17, 545-551.

Van Langevelde, F., Van De Vijver, C. A., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L., Bond, W. J., 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84, 337-350.

van Vuuren, D. P., Sala, O. E., Pereira, H. M., 2006. The future of vascular plant diversity under four global scenarios. Ecology and Society 11.

Venäläinen, A., Lehtonen, I., Laapas, M., Ruosteenoja, K., Tikkanen, O. P., Viiri, H., Ikonen, V. P., Peltola, H., 2020. Climate change induces multiple risks to boreal forests and forestry in Finland: A literature review. Global change biology 26, 4178-4196.

Verma, M., to Bühne, H. S., Lopes, M., Ehrich, D., Sokovnina, S., Hofhuis, S. P., Pettorelli, N., 2020. Can reindeer husbandry management slow down the shrubification of the Arctic? Journal of Environmental Management 267, 110636.

Vors, L. S., Boyce, M. S., 2009. Global declines of caribou and reindeer. Global change biology 15, 2626-2633.

Vowles, T., Björk, R. G., 2019. Implications of evergreen shrub expansion in the Arctic. Journal of Ecology 107, 650-655.

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.

Vuorinen, K. E., 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.

Way, D. A., Oren, R., 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree physiology 30, 669-688.

White, K. S., Pendleton, G. W., Hood, E., 2009. Effects of snow on Sitka black-tailed deer browse availability and nutritional carrying capacity in southeastern Alaska. The Journal of Wildlife Management 73, 481-487.

Wolfe, S. A., Griffith, B., Wolfe, C. A. G., 2000. Response of reindeer and caribou to human activities. Polar research 19, 63-73.

Paper I

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Herbivory and climate as drivers of woody plant growth: Do deer decrease the impacts of warming?

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Abstract. Vegetation at ecotone transitions between open and forested areas is often heavily affected by two key processes: climate change and management of large herbivore densities. These both drive woody plant state shifts, determining the location and the nature of the limit between open and tree or shrub-dominated landscapes. In order to adapt management to prevailing and future climate, we need to understand how browsing and climatic factors together affect the growth of plants at biome borders. To disentangle herbivory and climate effects, we combined long-term tree growth monitoring and dendroecology to investigate woody plant growth under different temperatures and red deer (*Cervus elaphus*) herbivory pressures at forest–moorland ecotones in the Scottish highlands. Reforestation and deer densities are core and conflicting management concerns in the area, and there is an urgent need for additional knowledge. We found that deer herbivory and climate had significant and interactive effects on tree growth: in the presence of red deer, pine (*Pinus sylvestris*) growth responded more strongly to annual temperature than in the absence of deer, possibly reflecting differing plant–plant competition and facilitation conditions. As expected, pine growth was negatively related to deer density and positively to temperature. However, at the tree population level, warming decreased growth when more than 60% of shoots were browsed. Heather (*Calluna vulgaris*) growth was negatively related to temperature and the direction of the response to deer switched from negative to positive when mean annual temperatures fell below 6.0°C. In addition, our models allow estimates to be made of how woody plant growth responds under specific combinations of temperature and herbivory, and show how deer management can be adapted to predicted climatic changes in order to more effectively achieve reforestation goals. Our results support the hypothesis that temperature and herbivory have interactive effects on woody plant growth, and thus accounting for just one of these two factors is insufficient for understanding plant growth mechanics at biome transitions. Furthermore, we show that climate-driven woody plant growth increases can be negated by herbivory.

Key words: adaptive management; browsing; climate change; deer; ecotone; heather; herbivory; pine; reforestation; Scotland; shrubs.

INTRODUCTION

Climate is known to determine the fundamental distribution of biomes, and we have already started to witness ecotone shifts with global warming (Sturm et al. 2001, Harsch et al. 2009, Evans and Brown 2017, Myers-Smith and Hik 2018). However, herbivory has the potential to dramatically change the realized distribution of biomes, and top-down trophic pathways have been shown to affect, for example, the distribution of open tundra ecosystems (Christie et al. 2015, Bråthen et al. 2017) and savanna (Van Langevelde et al. 2003, Staver et al. 2009, Staver and Bond 2014, Oliveras and Malhi 2016). Large herbivores are important drivers of vegetation state shifts, particularly at tree lines and other areas involving transitions between woody plant dominated states and states with low woody plant cover (Speed et al. 2011, Ripple et al. 2015, Treml et al. 2016, Cromsigt et al. 2018, Olofsson and Post 2018).

By affecting both climate and herbivore populations, human activity has created circumstances where the causes of ecotone changes are hard to disentangle (Oliveras and Malhi 2016, Stevens et al. 2016, Treml et al. 2016, Vuorinen et al. 2017). A growing body of evidence shows the importance of both climatic and top-down trophic factors in driving biome changes, but potential interactive effects between these are still poorly

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understood (see, however, Speed et al. 2011, Tremblay and Boudreau 2011, Bråthen et al. 2017, Løkken et al. 2019). In order to adapt herbivory management to prevailing and future climatic conditions, understanding potential interactions between climate and herbivory is crucial.

An example of an ecosystem state shift driven by the combination of climate and herbivores can be found in the Scottish Highlands, UK, where humans have caused one of the most dramatic biome shifts by changing many previously naturally forested areas to open moorlands by felling, fire, and grazing since the Neolithic period (Mather 2004). Concurrent climatic changes toward cooler and wetter conditions around 4000 BP also acted to reduce suitability for some tree species. Even though a reforestation trend has been apparent since the beginning of the 20th century (Mather 2004), strong increases in deer numbers since the 1960s are hampering the return of trees (Scottish Natural Heritage 2016, Rao 2017). To assist reforestation, managers in different parts of the UK have reduced deer densities (Gong et al. 1991, Scott et al. 2000, Rao 2017). Exclusion of deer is a commonly used method, but as fences can have negative effects on the landscape and other species (e.g., grouse), deer culling is also applied. Both of these strategies have resulted in successful forest regeneration (Putman 2003, Rao 2017), but it is unknown whether a warming climate has also contributed to observed tree growth changes (0.4–0.8°C increase 1901–2012; Hartmann et al. 2013) or how it will affect tree growth in the future if mean temperatures keep rising as expected (2.0–3.5°C by the 2080s across UK; Hulme 2002). Earlier studies have estimated that for successful tree regeneration, deer densities need to be at or below 3–5 red deer/km^2 (Rao 2017), but these estimates do not account for variations or change in climate.

In many ecotone areas, herbivory may act as a buffer against climate change by preventing woody plant growth increase (Speed et al. 2012, Christie et al. 2015, Bråthen et al. 2017, Vuorinen et al. 2017, Cromsigt et al. 2018). However, in the management perspective of the Scottish Highlands, this is considered as a negative effect as high deer densities make much more difficult the achievement of the target annual woodland expansion from the Climate Change Scotland Act 2009 (Cairngorms National Park Authority 2016). High deer densities also contribute to maintaining the current, heavily human-altered state of existing native woodlands (Patterson et al. 2014). Nevertheless, from a management perspective, deer are also an important game species and a natural part of highland ecosystems. Wild deer provide a source of local meat and support rural tourism and local economy through recreational visits, sport hunting, and sales of venison (Scottish Natural Heritage 2016). It has been estimated that the annual monetary benefit to the private and public sectors associated with deer is £17.6 million (Scottish Natural Heritage 2016). Thus, balancing between different management targets in a warming climate is crucial.

By assessing radial growth and height growth of key woody species under different temperatures and deer pressures, we addressed the following question: Are tree and shrub radial and height growth driven by (1) herbivore presence, density, and browsing pressure; (2) temperature; or (3) additive or interactive effects of herbivores and temperature? In addition, to inform management of deer and reforestation under future climate change and conservation requirements, we aim to estimate the increases in deer density and browsing pressure that would prevent the predicted tree growth increases under climatic warming.

Methods

Study area

The study area, located in the Mar Lodge Estate, Cairngorms National Park, Scotland, UK (57°00′ N 3°32′ W, 300–520 m above sea level), is dominated by remnant Caledonian pine forest and open moorlands. The main browser is the red deer *Cervus elaphus*, with low number of roe deer *Capreolus capreolus* and mountain hare *Lepus timidus* also occurring in the region (Rao 2017). There are no sheep or other ungulate herbivores in the study area. The study area contained 15 deer exclosures, ranging in size between 0.016 and 480 ha, with fences that were erected at different times between 1959–1999 and taken down 2012–2013 (with some exceptions, see Appendix S1: Fig. S1, Table S1). After 1995, the land owner, the National Trust for Scotland, embarked on larger-scale restoration of pine forests through reduction in numbers of deer in the whole study area of 12,487 ha through culling. This has resulted in a reduction of deer densities from approximately 15 deer/km^2 to near zero in 15 yr (Fig. 1a; for more information on deer count methods see Rao [2017]). Both red and roe deer were managed under the deer reduction program, but only red deer numbers were monitored. In addition to yearly counts of individuals, deer have been monitored by counting red deer and roe deer pellets (not separated by species) in 17 10×10 m quadrats since 2002 (Appendix S1: Fig. S1; for methods, see Rao [2017]).

The nearest weather station, located approximately 6 km east from the study area (Braemar, 57°01′ N 03°40′ W, 327 m above sea level), gave a source of daily temperature data covering the whole deer monitoring period (information provided by the National Meteorological Library and Archive—Met Office, UK; © Crown Copyright 2017). The data shows variation between 5.3°C and 7.7°C in yearly mean temperatures, with an annual average of 7.0°C, but no consistent warming trend across the study period (Fig. 1a).

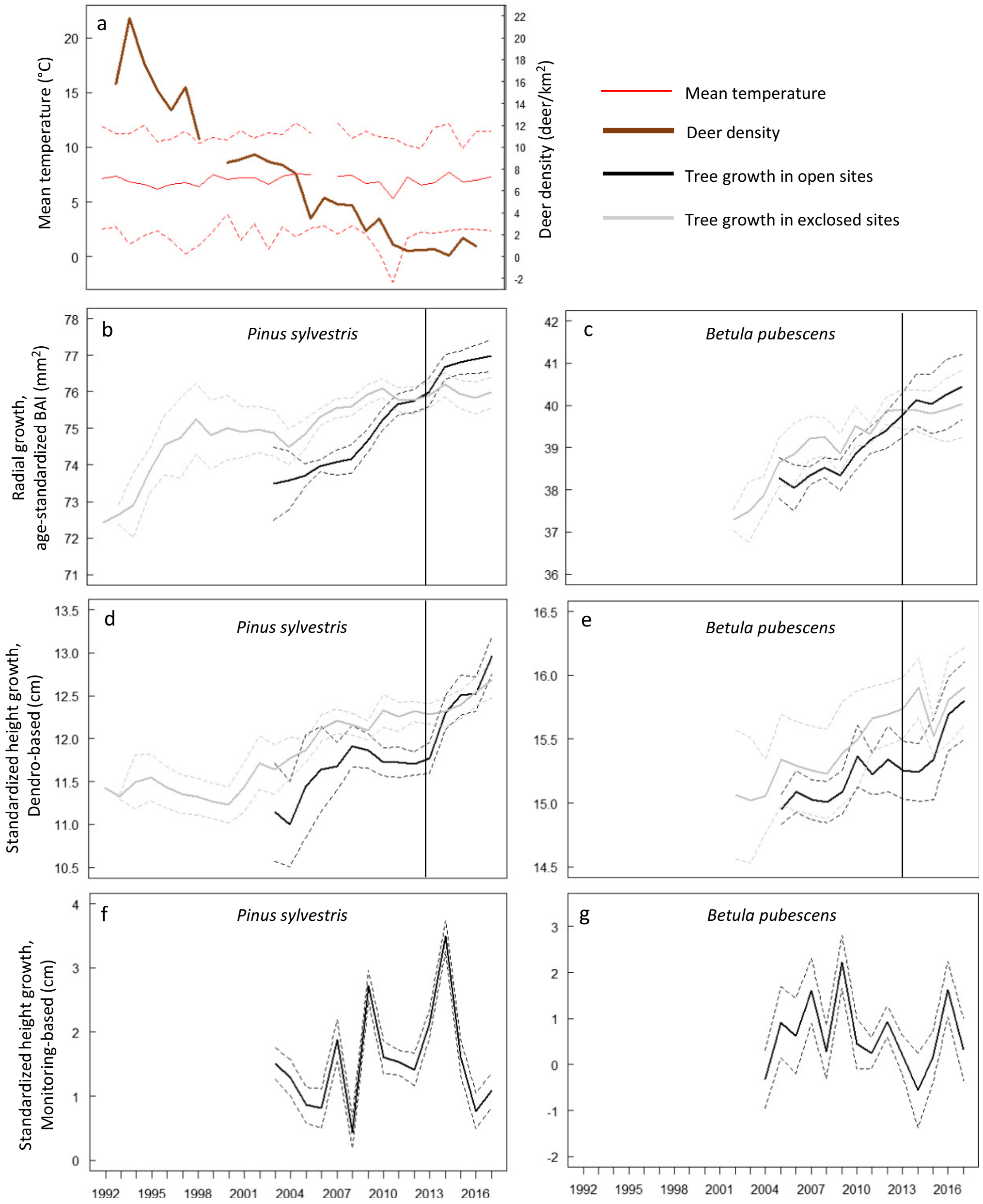

FIG. 1. Temperature, deer density, and tree growth trends 1992–2017. (a) Mean annual temperatures, summer (June–August), and winter (December–February) temperatures (upper and lower dashed red lines, respectively) recorded at Braemar weather station (Information provided by the National Meteorological Library and Archive—Met Office, UK; © Crown Copyright 2017), and red deer densities (Rao 2017). (b–e) Radial growth (BAI, basal area increment) and height growth of pine and birch, based on dendroecological measurements (mean ± SE [dashed lines]). (f, g) Height growth of pine and birch, based on monitoring measurements (mean ± SE [dashed lines]). Data points of years with less than three individuals have been excluded. Note that, even though most of the fences were taken down 2012–2014 (vertical lines), they are depicted here as exclosures. In 1997, the deer survey was not undertaken and, in 2005, temperature information lacked from some summer months, resulting in missing data from these years. The oldest individuals from open plots shown in the graph were not established before 2002, and thus there is no growth data available before that year. For an equivalent graph on heather growth, see Appendix S1: Fig. S2.

Dendroecological methods

A dendroecological approach was used to study the effects of deer presence and red deer density. We sampled paired individuals of three species playing central roles for reforestation, vegetation structure, and composition: Scots pine (*Pinus sylvestris*), downy birch (*Betula pubescens*), and heather (*Calluna vulgaris*). We sampled one individual inside of an exclosure and one outside, at each sampling spot in October–November 2017. As we were only permitted to destructively sample a small number of individuals, we standardized our sampling by first subjectively defining paired areas that matched in their growing conditions inside and outside the fence to minimize the variation caused by environmental variables not relevant for our study question. When selecting these areas, slope, aspect, field layer vegetation, moisture conditions, amount of rocks and tree shading were considered (Appendix S1: Fig. S2). However, as precisely similar sites were not always found outside and inside the exclosure, we also measured slope, aspect, and tree shading at each sampling location. Tree shading was estimated by establishing a 10 m radius circle around each individual, measuring the height and the distance to the sampled individual of all tree individuals growing inside the circle, and by summing the height : distance ratio of these tree individuals (Appendix S1: Fig. S3).

Within the paired areas, we selected a random primary starting spot and sampled the nearest individual of each target species, excluding individuals >220 cm in height and as such out of red deer browse-reach, and individuals located ≤5 or ≥25 m from the fence line, to standardize potential edge effects. Due to tree-regeneration management restrictions, we were permitted to sample only one pair of each species at each small fenced area (<10 ha) and two pairs at each large fenced area (>10 ha). Species absence in some areas constrained sampling further (Appendix S1: Table S1), resulting in a sample size of 13 pairs for pine, 6 for birch, and 18 for heather, with no significant height or diameter differences between exclosure and open plot individuals.

Sampled trees were cut at ground level. Shrubs stems were cut at 10–15 cm (length) below the base, but no root collar was reached. One disc at the base of each stem was cut and stored at room temperature in a well-ventilated space. Discs were prepared for reading of growth rings by taking thin sections of 20–30 μm with a GSL1 microtome (Fritz Hans Schweingruber, Birmensdorf, Switzerland) (Gärtner and Schweingruber 2013). Sections were stained by using a solution of aqueous Astra Blue 1 g/1,000 mL and aqueous Safranin O Dye 1 g/1,000 mL (1:1) (Gärtner and Schweingruber 2013) and a staining time of 3 minutes, which turns lignified structures pink and the cellulose of unlignified cells blue (Vazquez-Cooz and Meyer 2002). After dehydration with ethanol (Gärtner and Schweingruber 2013), sections were fixed permanently on microscope slides with Canada Balsam, applied on the sections and dried in an oven at 60°C for at least 12 h (Gärtner and Schweingruber 2013, Tardif and Conciatori 2015). Growth ring widths were measured manually with the Leica Application Suite program (LAS version 4.5.0, Core), using a Leica M165 C microscope system with MV170 HD camera (Leica Microsystems, Wetzlar, Germany). For each disc, four radii separated by 90° were measured when possible to account for irregularities in growth (Myers-Smith et al. 2015), with the exception of symmetrical large pines and birches, for which only two radii separated by 180° were measured (in these cases, a 1 cm wide piece was cut along diameter of the disc for micro-sectioning). Measurements of radii were averaged for each growth ring and converted to basal area increment (BAI; wedging rings were accounted for as zeros when absent at a certain radius), assuming that ring circumference can be approximated by a circle (Biondi and Qeadan 2008), using the dplR-package (Bunn 2008). To account for the growth increase induced by increasing age, data for each species were standardized using a linear model with log-transformation for BAI values, $\log_e(\text{BAI}) = a + b \times \text{Age}$. The back-transformed residuals from these models were then used as response variable in the analysis (Speed et al. 2011). These values allow us to model the average growth responses of the population comprising of trees with different heights.

Radial growth might not be a good indicator of height growth, as herbivores might keep shrubs and trees low in a "browsing trap" (Staver and Bond 2014, Olofsson and Post 2018), even if radial growth is not constrained. Thus, studying only ring widths may produce results not relevant for management that is concentrated on reforestation and establishing trees that grow tall enough to escape browsing. To overcome this constraint, we estimated annual height growth for sampled trees by taking four additional discs at regular intervals along the main stem (Myers-Smith et al. 2015), counting the number of rings and calculating annual height growth based on disc cut heights. When discs were too far from each other to capture annual growth, linear growth was assumed across years. Height growth values were standardized in the same way as ring growth values.

Population-level tree monitoring

As the dendroecological approach incorporates both direct (browsing) and indirect (e.g., plant–plant competition) effects of deer, we also took advantage of the long-term tree height and browsing monitoring conducted in the study area to be able to analyze direct browsing effects. This monitoring was done at the same quadrats that were used for deer pellet monitoring (Appendix S1: Fig. S1). In 2002, 17 10 × 10 m quadrats were established and 20 tree individuals marked for monitoring in each quadrat (unless the number of individuals was lower than 20, in which cases all individuals were marked). In 2007 and 2012, new tree cohorts were added, varying from 4 to 20 individuals per each quadrat. Each year 2002–2017 in July–August, the height of all marked trees was measured and the number of browsed twigs counted. This resulted in height observations of 870 pine individuals and 78 birch individuals, but due to gaps in browsing and temperature data, some of the observations were left out of the analyses. Height observations were converted to yearly height growth values and standardized as described above for trees sampled for the dendroecological analyses, but using tree height rather than age.

It is important to note that the tree monitoring approach is not directly comparable with the dendroecological approach, since the study locations differed (Appendix S1: Fig. S1). Furthermore, these two approaches differ in the part of the tree population they address, giving complementary information: the dendroecological approach only includes individuals that have survived to the sampling date, and thus addresses the growth potential of surviving trees at the individual level; the monitoring approach takes into account individuals that have shown negative growth (i.e., severe browsing of the leading shoot) or have even been killed by browsing, thus addressing the average growth at tree population level.

Statistical analyses

All analyses were carried out within the R environment (R version 3.5.1, R Core Team, R Foundation for Statistical Computing, Vienna, Austria). We modeled annual age-standardized BAI, and age- and height-standardized tree height growth as a function of mean temperature at Braemar weather station for corresponding years, different types of deer factors, their interaction, and measured environmental covariates (slope, aspect, shading caused by trees) by using the lme function of the nlme package (Bates 2007), separately for each species. See justification for using mean temperature as a climate variable in Appendix S1: Fig. S4. In the first model versions, we also included “exclusion time” (years since the fence was erected) as a covariate, but as it was never significant, we ran the final models without it.

Three versions of the above-described models were constructed to assess three types of deer effects (i.e., deer presence, red deer density, and browsing) separately. (1) To study whether deer presence (related to fencing program) alters growth response to temperature, the deer exclosure treatment (open vs. exclosed site) was used as a binary explanatory variable. (2) To study the effects of herbivore density (related to culling program), red deer density data was used as a continuous explanatory variable. As an additional analysis, we also used deer pellet counts from the nearest pellet monitoring site, as they are often used to indicate the density of herbivores but may give a different result than direct deer density measurements due to spatial heterogeneity in habitat use. If the nearest pellet monitoring site was located on the other site of the river that flows thought the study area, data from the nearest site on the same site of the river was used. For these models, only plants sampled outside the exclosures were included to make the study design more balanced (i.e., not biased toward zero deer values). (3) To study the local effects of browsing intensity, the proportion of browsed twigs was used as a continuous explanatory variable.

Random intercepts were fitted to account for the nesting of individuals within sites for each model. After this, there was no spatial autocorrelation detected in the model residuals (Appendix S1: Table S2). After applying model selection, we found that multiple models had a similar degree of support based on AIC values, and thus applied model averaging to avoid model selection uncertainty (Johnson and Omland 2004, Cade 2015, Dormann et al. 2018). For model averaging, we used the MuMIn package (Barton 2016): all possible models between null model and a full model with all explanatory variables and the interaction of climate and herbivory factors were built using the dredge function, and coefficient estimates were averaged across these models (weighted by AIC) by using the model.avg function. See goodness of fit of the models in Appendix S1: Table S3.

To provide a tool to estimate the increase in deer pressure that would counter the predicted tree growth increase through expected climatic warming, we visualized predictions from all models that included a continuous deer factor by using heat-maps of tree growth across temperature and deer factor axes. Note that full deer factor and temperature factor data ranges are used for predictions even when all deer and temperature combinations were not present in our data set. Thus, the further away a coordinate is from the observation points, the less reliable the prediction is.

Results

Trends in time

Dendroecological measurements resulted in growth series for the period 1992–2017 for pine, 2002–2017 for birch, and 1994–2017 for heather. Tree growth (both pine and birch) increased in the exclosures since the years in which the fences were erected, and increased outside the exclosures at later dates in line with the deer culling program (Fig. 1a–e). However, the tree height monitoring data did not show consistent increasing trend (Fig. 1f, g). We also found no consistent trends in heather growth over time (Appendix S1: Fig. S5).

Effect of deer presence on temperature response

Pine growth was more sensitive to temperature changes in the presence of deer than the absence of deer, as shown by significant interaction terms (for radial growth, $z = 2.1$, $P = 0.038$; for height growth, $z = 3.4$, $P < 0.001$; for full model output, see Appendix S1: Table S4). Outside the exclosures, pine growth responded positively to increasing temperatures: with a 1°C temperature increase, radial growth increased by

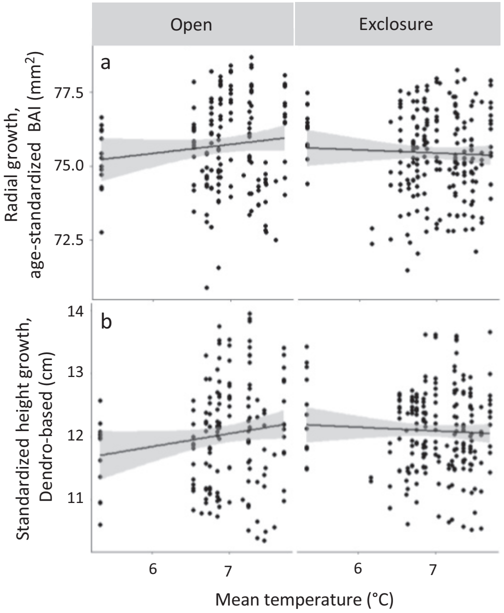

FIG. 2. Pine radial and height growth along a gradient of mean annual temperature in each deer herbivory treatment. Black points depict raw data and black lines linear growth–temperature relationship with SEs (gray), based on a model with deer as a presence-absence explanatory variable.

0.26 ± 0.16 mm^2 (mean ± SE; Fig. 2a) and height growth by 0.27 ± 0.07 cm (Fig. 2b). Inside the exclosures, there was no trend to be seen (for radial growth, slope -0.01 ± 0.05, and for height growth -0.02 ± 0.06). Differences in slopes between treatments were small, however. We observed no significant interactive effects of deer presence and temperature on birch or heather growth (Appendix S1: Table S4).

Deer density effects and temperature effects

For pine, both deer density and mean temperature affected radial and height growth, but there was no evidence of interactive effects (Table 1). Model-based predictions showed that pine growth responded positively to mean temperature, but that red deer have the potential to suppress the growth increase (Fig. 3a, b). Model predictions indicate that 1°C of warming equates to an increase of 0.4 mm^2 in annual radial growth. From our findings, this was negated by an increase of 1 deer/km^2 density (Fig. 3a). The same degree of warming was found to equate to an increase of 0.2 cm in annual height growth, which could be negated by an increase of 3 deer/km^2 density (Fig. 3b). The effects of pellet density and mean temperature on pine height growth showed the same type of patterns but, for radial growth, we found a pellet × temperature interaction where responses weakened when temperature increased and pellet number decreased (Appendix S1: Fig. S6, Table S5). For birch, no significant effects were found.

For heather, we found a significant interaction effect of deer density and temperature ($z = 1.54$, $P = 0.043$; Table 1). At low annual temperatures (<6.0°C), radial growth increased with increasing deer density and was negatively related to increasing temperature. At high temperatures (>6.0°C), growth was negatively related to both deer density and temperature (Fig. 4). The deer pellet model showed no significant effects on heather growth (Appendix S1: Table S5).

Deer browsing effects and temperature effects

We found an interactive effect of mean temperature and browsing intensity (percentage of shoots browsed) on pine height growth (Table 2). When <60% of pine shoots were browsed, height growth increased with increasing temperature and decreased with increases in deer browsing damage: 1°C warming equated to an increase of 0.3–1.5 cm annual growth, depending on browsing intensity, which could be negated by increase from 15% to 40% on the browsing intensity scale, depending on mean temperature. When >60% of shoots were browsed, height growth of pines was negatively related to increasing temperature (Fig. 3c). In general, the tree height monitoring data (which included trees that since died, as previously explained) indicated lower annual pine growth rates than the dendroecological approach (which included only trees surviving at time of sample in 2017), with a maximum of 3.6 cm/yr even at moderate browsing pressure (Fig. 3c). We found no significant effects of browsing intensity on birch growth (Table 2).

DISCUSSION

In this study, we have found evidence showing that herbivory and climate interact to determine woody plant growth at a forest–moorland ecotone. The temperature responses of pine and heather varied with herbivory pressure, and this demonstrates how herbivory might counteract or amplify the effects of temperature for these species. Temperature responses of radial and height growth of pine individuals were stronger in the presence of deer, and growth was driven by counteractive forces of temperature and herbivore density. At the tree population level, pine height growth was driven by the interactive effects of browsing and temperature, with temperature response differing below and above a threshold of 60% browsing intensity. Furthermore, we found some support for heather radial growth also being affected by interactions between temperature and herbivory, indicating different growth responses to deer density below and above a threshold of 6.0°C. Our results highlight the vital need to understand interactive and additive impacts to be able to responsively manage large herbivore dynamics in a changing climate.

TABLE 1. Coefficients for the models with the effects of deer density, mean temperature, and covariates on tree and shrub growth by analysis, conducted separately for each growth measurement type.

Parameters	Importance	Estimate	SE	*z*	*P*
Pine (n = 138)					
Radial growth					
Intercept		73.16	2.03	35.84	<0.001
Mean temperature × Deer density	0.73	−0.15	0.13	1.08	0.28
Mean temperature	0.92	0.39	0.15	2.64	**0.008**
Deer density	1	−0.39	0.05	7.37	**<0.001**
Tree shading	0.29	−0.01	0.02	0.15	0.882
Slope	0.29	−0.01	0.03	0.12	0.902
Aspect	0.74	0.01	0.01	0.65	0.517
Elevation	0.3	0	0.01	0.13	0.898
Height growth					
Intercept		10.41	1	10.34	<0.001
Mean temperature × Deer density	0.79	−0.11	0.06	1.69	0.09
Mean temperature	0.93	0.2	0.07	2.71	**0.007**
Deer density	0.81	−0.06	0.03	2.23	**0.026**
Tree shading	0.72	−0.02	0.01	0.39	0.694
Slope	0.72	−0.04	0.02	0.46	0.646
Aspect	0.72	0.01	0	0.45	0.654
Elevation	0.26	0	0	0.04	0.971
Birch (n = 74)					
Radial growth					
Intercept		42.864	5.7	7.5	<0.001
Mean temperature × Deer density	0.07	−0.098	0.08	1.2	0.24
Mean temperature	0.34	0.225	0.25	0.9	0.38
Deer density	0.44	0.042	0.32	0.1	0.9
Tree shading	0.52	0.039	0.02	0.4	0.66
Slope	0.55	−0.107	0.06	0.4	0.69
Aspect	0.56	−0.046	0.03	0.3	0.77
Elevation	0.25	−0.002	0.01	0	0.98
Height growth					
Intercept		15.543	1.43	10.8	<0.001
Mean temperature × Deer density	0.02	−0.005	0.03	0.1	0.88
Mean temperature	0.28	−0.048	0.09	0.5	0.59
Deer density	0.25	−0.003	0.06	0	0.97
Tree shading	0.25	−0.002	0.01	0.1	0.95
Slope	0.25	−0.01	0.03	0.1	0.96
Aspect	0.28	−0.007	0.01	0.1	0.9
Elevation	0.26	0.002	0	0.1	0.94
Heather (n = 148)					
Radial growth					
Intercept		3.02	1.61	1.86	0.062
Mean temperature × Deer density	0.89	−0.05	0.03	1.54	**0.043**
Mean temperature	0.56	0	0.13	0	0.5
Deer density	0.78	0.06	0.18	0.35	0.23
Tree shading	0.76	−0.03	0.01	0.5	0.615
Slope	0.27	−0.02	0.04	0.08	0.94
Aspect	0.32	0	0.01	0.13	0.897
Elevation	0.3	0	0.01	0.09	0.93

Notes: Sample numbers given for each analysis refer to the number of growth observations. The relative importance of each variable reflects the sum of the Akaike weights over all of the models in which the term appears, SEs are averaged square roots of variance estimators (based on Burnham and Anderson 2004 equations), z values are regression coefficients divided by SEs, and Pr(>|z|) values are probabilities of calculated z > tabulated z. Significant P values are shown in boldface type.

Our data demonstrate an overall positive effect of the deer reduction program on pine growth over time at the study area (see also Rao 2017), but show that temperature also plays a role in determining pine growth. We found that pine individuals growing in the presence of deer were more responsive to temperature. This might reflect reduced intraspecific plant–plant competition outside the exclosures (Appendix S1: Fig. S3; Saunders

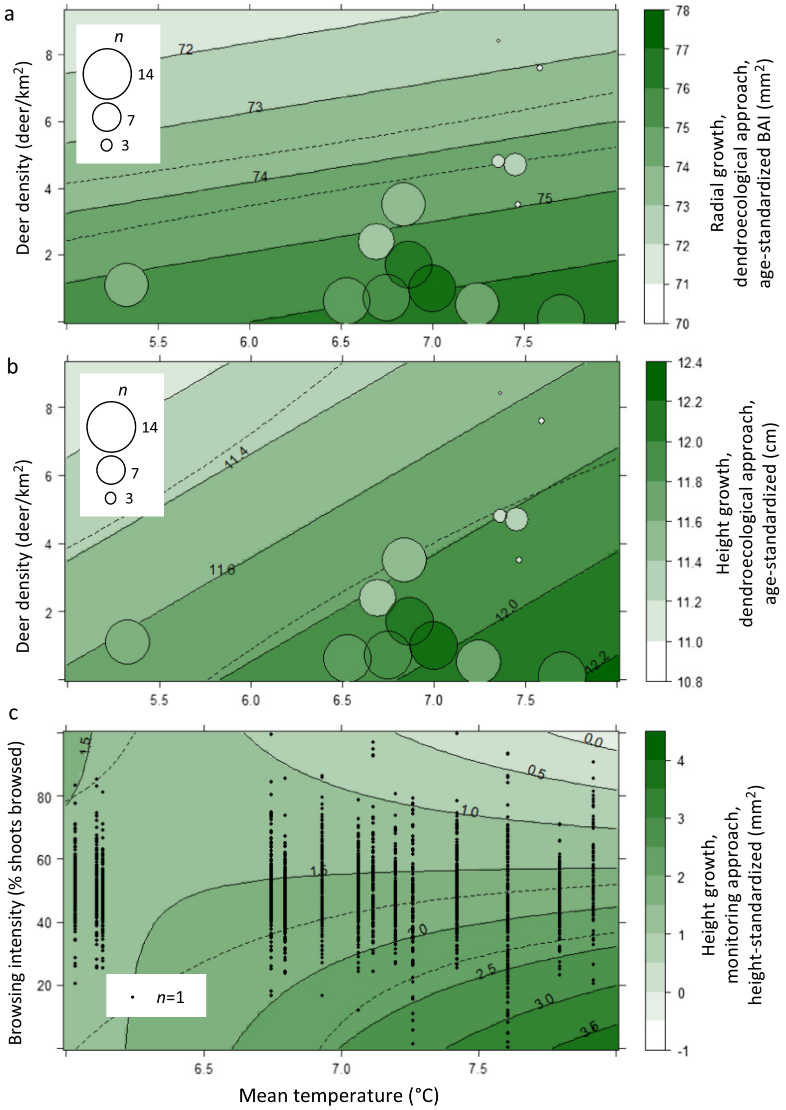

FIG. 3. Predicted pine (a) radial and (b, c) height growth along temperature, deer density (a, b), and browsing intensity (c) gradients as predicted by the respective models (Table 1): y-axis indicates deer pressure, x-axis indicates temperature, and color shows predicted growth. Standard errors are plotted for contour lines (a) 74 mm^2, (b) 11.6 cm, and (c) 2.0 cm with dashed lines. Observation points are depicted as circles with size representing sample size at each point and color the mean growth in panels a and b, and as black points in panel c. Note that model predictions get less reliable when moving further away from the data points. The difference between model prediction (color on background) and observation points (color in circles) represents the deviation between model prediction and the average observed values on each circle.

and Puettmann 1999, Nishizawa et al. 2016). In the landscape kept open by deer, solitary tree individuals might be able to take advantage of rising temperatures more effectively than individuals in dense stands where higher tree density can constrain growth. Furthermore, increased vulnerability of lone trees to cold temperatures might contribute to observed trends (Speed et al. 2011): individuals with no shelter provided by neighboring trees and with potentially browsing damage might suffer from cold periods more than unbrowsed individuals in fences where higher tree density potentially moderates temperature changes (Karlsson 2000, Oerlander and Karlsson 2000, Heithecker and Halpern 2006). Thus, herbivory presence per se does not seem to prevent potential

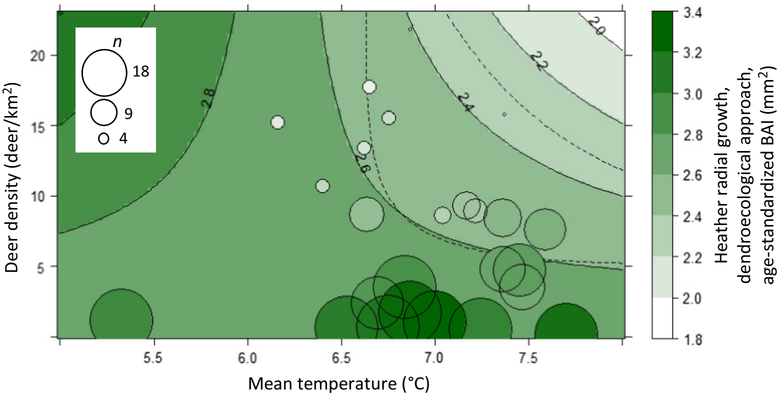

FIG. 4. Heather radial growth along temperature and deer density gradients as predicted by the model with deer density. The *y*-axis indicates deer pressure, *x*-axis indicates temperature, and color shows predicted growth. SE limits are plotted to contour line 2.4 with dashed lines. Observation points are depicted as circles with size representing sample size on each point and color the mean growth. Note that model predictions get less reliable when moving further away from the data points. The difference between model prediction (color on background) and observation points (color in circles) represents the deviation between model prediction and the average observed values on each circle.

TABLE 2. Coefficients for the models with the effects of browsing and mean temperature on tree height growth by analysis.

Parameters	Importance	Estimate	SE	*z*	*P*
Pine ($n = 2{,}784$)					
Height growth					
Intercept		−3.12	5.15	0.61	0.545
Mean temperature × Browsing intensity	0.72	−0.02	0.01	1.9	**0.047**
Mean temperature	0.85	0.95	0.69	1.37	0.17
Browsing intensity	1	0.07	0.1	0.72	0.474
Birch ($n = 412$)					
Height growth					
Intercept		−0.264	2.3	0.1	0.91
Mean temperature × Browsing intensity	0.06	0.019	0.02	0.9	0.38
Mean temperature	0.48	0.293	0.42	0.7	0.49
Browsing intensity	0.34	−0.019	0.09	0.2	0.83

Notes: Sample numbers given for each analysis refer to the number of growth observations. The relative importance of each variable reflects the sum of the Akaike weights over all of the models in which the term appears, SEs are averaged square roots of variance estimators (based on Burnham and Anderson 2004 equations), *z* values are regression coefficients divided by SEs, and $\Pr(>|z|)$ values are probabilities of calculated $z >$ tabulated z. Significant *P* values are shown in boldface type.

growth increases in response to temperature increase, but it might actually strengthen the response of individual trees through indirect effects. However, differences in temperature responses between treatments were small, suggesting a negligible management significance of the interaction. In addition, further modeling makes clear that herbivory has the potential to suppress positive temperature effects on growth when browsing pressure is high enough.

Tree height monitoring showed that at the population level, average pine height growth in the area was at maximum 3.6 cm/yr, and approached zero when browsing has intensified (Fig. 3c). However, from our findings, a 2.0–3.5°C warming as predicted by the 2080s (Hulme 2002) could result in a mean increase of 2.5–4.4 cm/yr in annual pine growth, an effect size that would, over decades, have power in assisting forest regeneration, but this relationship was found to apply only if the percentage of shoots browsed remained under 60%. Above this threshold, the temperature–growth response was negative. Thus, we have shown that at a tree population level, pine height growth is driven by interactive effects of browsing intensity and temperature. We propose that this may be because heavy browsing exposes trees to stress related to higher temperatures, for example, to plant–plant competition or water stress (Bansal et al. 2013).

For the pine individuals that survived the earliest successional phase (i.e., those sampled for our dendroecological analyses), estimations of growth were higher, varying between 11.2 and 12.2 cm/yr for height growth, and 72 and 76 mm^2/yr for radial growth. However, they were less affected by temperature. If the climate warms by 2.0–3.5°C as expected by the 2080s, our results suggest that height growth could increase by 0.4–0.7 cm/yr and radial growth by 0.8–1.4 mm^2/yr (although temperatures above 7.7°C would be an extrapolation of our findings). Thus, a warmer climate might have ecologically less significant effect on growth of established tree individuals than on the average growth at tree population level, which also includes tree deaths (see also, e.g., Lutz et al. 2013, Hedwall et al. 2015). Our findings indicate that individual pine radial and height growth are driven by temperature and herbivore density, and that an increase of 6.0–10.5 and 2.0–3.5 red deer/km^2, respectively, could negate the expected increases in height and radial growth of pine along a warming climate gradient.

Combined effects of multiple factors, such as the climate × herbivory interactions revealed here, pose challenges for ecotone management. By using the model predictions illustrated in Fig. 3a, b, it is possible to define plant growth goals and determine the herbivory density that is most likely to allow such a growth rate under specific climatic conditions. For instance, if we assume a warming of 0.5°C (with expected mean annual temperature being 7.5°C), and select an example management aim of achieving mean radial growth of pine of 75–76 mm^2/yr, then deer density could be allowed to vary between 1.3 and 3.2 deer/km^2. However, there are multiple uncertainties associated with these predictions. Extrapolating outside observation points might result in erroneous predictions. Low explanatory power of the browsing intensity analyses and modest effect sizes of deer density analysis suggest that environmental variables not measured in this study, such as potential water and nutrient availability, may operate as barriers to growth increase and be as relevant for management as deer and temperature. Furthermore, as different climate variables measured at the study area were found to be collinear (Appendix S1: Fig. S4), it is also possible that instead of mean temperature, observed effects might be driven by other climatic dimensions, for example the number of frost days or minimum temperatures during growth period, and thus mean temperatures as such might not be reliable for making predictions (see also Franke et al. 2017). Furthermore, we do not know how increased CO_2 levels have contributed to observed patterns along temperature changes, or how they might affect future growth (Kurepin et al. 2018). If increasing temperatures affect plant palatability and thus change browsing pressure (see, e.g., Moreira et al. 2014, Stark et al. 2015, Kivimäenpää et al. 2017), growth predictions become even more challenging.

The management objective of the study area and of many other parts of the Scottish highlands (The National Trust for Scotland 2012, Cairngorms National Park Authority 2016, Scottish Natural Heritage 2016, Cairngorms National Park Authority 2017) is to expand native pine forest, and thus to prioritize tree growth over deer populations until forests have established. Our findings indicate that success could be achieved at different deer densities depending on prevailing temperatures. However, even though areas with trees that have already survived the first phase of forest succession might be able to tolerate browsing better in a warmer climate, even small increases in deer numbers might endanger forest regeneration in a warmer climate if browsing passes the 60% threshold that we detected here. This highlights the importance of low deer numbers for successful population-level growth even under a warmer climate. In the longer term, once woodland has been restored, regeneration should be able to proceed in the presence of a limited deer population (The National Trust for Scotland 2012, Cairngorms National Park Authority 2017).

Adapting deer management solely based on pine growth aims might have impacts on other aspects of the vegetation. We did not find an effect of browsing or temperature on the growth of birch, but our sample size of birch was limited due to its rarity at the sites, and previous studies have shown strong deer browsing effects on birch (compare, e.g., to Tanentzap et al. 2013). Furthermore, management might result in undesired changes to other species groups such as dwarf shrubs. One out of three of our heather growth models identified interactive effects of deer density and temperature, where the direction and magnitude of the deer density effect changed at a specific temperature threshold. Heather growth responded negatively to increasing temperature, which might be caused by negative collinearity of mean temperature and snow cover that protects shrubs from wind, drought stress and herbivory during winter (Ueda et al. 2002, White et al. 2009, Ossi et al. 2015, Gilbert et al. 2017). The reduction in heather growth with increasing deer density when temperatures were above 6.0°C, compared with the increase with deer densities below 6.0°C, might reflect indirect effects of snow cover: when snow reduces access to shrubs, deer more frequently browse trees (Ueda et al. 2002), and thus can reduce tree shading of heather in subsequent growing seasons. Temperature may also change the relative palatability or compensatory growth tendency of heather (Hawkes and Sullivan 2001) in relation to other forage species. Our results imply that in a warmer climate, heather growth may decrease in our study area, and that any increased browsing of heather could amplify this negative warming effect by further reducing its growth.

The Scottish highlands are an example of an environment where human intervention has extirpated large carnivores and supported increases in herbivore densities with a net result of changing the ecosystem from plant–herbivory–predation dynamics to be dominated by plant–herbivory interactions (Estes et al. 2011, Ripple et al. 2014, Svenning et al. 2016). Increases in wild ungulate numbers have occurred across many northern latitude areas, resulting in major vegetation changes (Côté et al. 2004), and in many environments domestic herbivores are primary drivers of plant system structure (Ross et al. 2016, Speed et al. 2019). In tropical regions, a prime example is African savannas where humans have decimated populations of large natural herbivores in many regions, and replaced them with livestock (Ripple et al. 2015, Hempson et al. 2017). Some ecosystems, such as arctic tundra, may naturally be two trophic-level systems, (vegetation and herbivores), as the low primary productivity precludes the third, predator trophic level (Aunapuu et al. 2007). When plant-herbivory interactions dominate, as they do in the above-mentioned ecosystems, herbivory effectively suppresses plant growth, potentially creating landscapes devoid of trees and tall shrubs. However, global warming changes this balance by increasing primary productivity. This increase in productivity can be manifested in changed vegetation structure (i.e., tree or shrub advance), or it can cascade to the herbivore trophic level, where increased herbivory may negate the warming-induced growth increases and vegetation shifts. In the Scottish Highlands, deer management has a key role in determining which one of these directions might be taken in future. To manage vegetation toward desired directions, the interactive roles of herbivory and climate, as elucidated here, need to be accounted for across the globe.

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LITERATURE CITED

Aunapuu, M., J. Dahlgren, T. Oksanen, D. Grellmann, L. Oksanen, J. Olofsson, Ü. Rammul, M. Schneider, B. Johansen, and H. O. Hygen. 2007. Spatial patterns and dynamic responses of arctic food webs corroborate the exploitation ecosystems hypothesis (EEH). American Naturalist 171:249–262.

Bansal, S., G. Hallsby, M. O. Löfvenius, and M.-C. Nilsson. 2013. Synergistic, additive and antagonistic impacts of drought and herbivory on *Pinus sylvestris*: leaf, tissue and whole-plant responses and recovery. Tree Physiology 33:451–463.

Barton, K. 2016. Multi-model inference. R package version 1.15.6. https://cran.r-project.org/web/packages/MuMIn/index.html

Bates, D. 2007. nlme: linear and nonlinear mixed effects models. R package version, 31–128. https://cran.r-project.org/web/packages/nlme/nlme.pdf

Biondi, F., and F. Qeadan. 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. Tree-Ring Research 64:81–96.

Bråthen, K. A., V. T. Ravolainen, A. Stien, T. Tveraa, and R. A. Ims. 2017. Rangifer management controls a climate-sensitive tundra state transition. Ecological Applications 27:2416–2427.

Bunn, A. G. 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26:115–124.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection, Sociological methods research. 33:261–304.

Cade, B. S. 2015. Model averaging and muddled multimodel inferences. Ecology 96:2370–2382.

Cairngorms National Park Authority. 2016. Cairngorms National Park partnership plan 2017–2022. Issues report, Priority 2: Deer management. Cairngorms National Park Authority, Grantown on Spey, Scotland.

Cairngorms National Park Authority. 2017. Cairngorms National Park partnership plan 2017–2022. Management Plans. Cairngorms National Park Authority, Grantown on Spey, Scotland.

Christie, K. S., J. P. Bryant, L. Gough, V. T. Ravolainen, R. W. Ruess, and K. D. Tape. 2015. The role of vertebrate herbivores in regulating shrub expansion in the Arctic: a synthesis. BioScience 65:1123–1133.

Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology Evolution and Systematics 35:113–147.

Cromsigt, J. P., M. te Beest, G. I. Kerley, M. Landman, E. le Roux, and F. A. Smith. 2018. Trophic rewilding as a climate change mitigation strategy? Philosophical Transactions of the Royal Society B 373:20170440.

Dormann, C. F., J. M. Calabrese, G. Guillera-Arroita, E. Matechou, V. Bahn, K. Bartoń, C. M. Beale, S. Ciuti, J. Elith, and K. Gerstner. 2018. Model averaging in ecology: a review of Bayesian, information-theoretic, and tactical approaches for predictive inference. Ecological Monographs 88:485–504.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, and J. B. Jackson. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Evans, P., and C. D. Brown. 2017. The boreal–temperate forest ecotone response to climate change. Environmental Reviews 25:423–431.

Franke, A., A. Bräuning, M. Timonen, and P. Rautio. 2017. Growth response of Scots pines in polar-alpine tree-line to a warming climate. Forest Ecology and Management 399:94–107.

Gärtner, H., and F. H. Schweingruber 2013. Microscopic preparation techniques for plant stem analysis. Verlag Dr. Kessel, Remagen, Germany.

Gilbert, S. L., K. J. Hundertmark, D. K. Person, M. S. Lindberg, and M. S. Boyce. 2017. Behavioral plasticity in a variable environment: snow depth and habitat interactions drive deer movement in winter. Journal of Mammalogy 98:246–259.

Gong, Y., M. Swaine, and H. Miller. 1991. Effects of fencing and ground preparation on natural regeneration of native pinewood over 12 years in Glen Tanar, Aberdeenshire. Forestry: An International Journal of Forest Research 64:157–168.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.

Hartmann, D. L., A. M. K. Tank, M. Rusticucci, L. V. Alexander, S. Brönnimann, Y. A. R. Charabi, F. J. Dentener, E. J. Dlugokencky, D. R. Easterling, and A. Kaplan. 2013.

Observations: atmosphere and surface. Pages 159–254 *In* T. F. Stocker, Q. Dahe, P. Gian-Kasper, T. Melinda, K. A. Simon, B. Judith, A. Nauels, X. Yu, V. Bex, and P. M. Midgley, editors. Climate Change 2013 the Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Hawkes, C. V., and J. J. Sullivan. 2001. The impact of herbivory on plants in different resource conditions: a meta-analysis. Ecology 82:2045–2058.

Hedwall, P. O., J. Skoglund, and S. Linder. 2015. Interactions with successional stage and nutrient status determines the life-form-specific effects of increased soil temperature on boreal forest floor vegetation. Journal of Ecology and Evolution 5:948–960.

Heithecker, T. D., and C. B. Halpern. 2006. Variation in microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. Forest Ecology and Management 226:60–71.

Hempson, G. P., S. Archibald, and W. J. Bond. 2017. The consequences of replacing wildlife with livestock in Africa. Scientific Reports 7:17196.

Hulme, M. 2002. Climate change scenarios for the United Kingdom: the UKCIP02 scientific report. University of East Anglia, Norwich, UK.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology & Evolution 19:101–108.

Karlsson, I. M. 2000. Nocturnal air temperature variations between forest and open areas. Journal of Applied Meteorology 39:851–862.

Kivimäenpää, M., S. Sutinen, H. Valolahti, E. Häikiö, J. Riikonen, A. Kasurinen, R. P. Ghimire, J. K. Holopainen, and T. Holopainen. 2017. Warming and elevated ozone differently modify needle anatomy of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Canadian Journal of Forest Research 47:488–499.

Kurepin, L. V., Z. R. Stangl, A. G. Ivanov, V. Bui, M. Mema, N. P. Hüner, G. Öquist, D. Way, and V. Hurry. 2018. Contrasting acclimation abilities of two dominant boreal conifers to elevated CO_2 and temperature. Plant, Cell & Environment 41:1331–1345.

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

Lutz, D. A., H. H. Shugart, D. V. Ershov, J. K. Shuman, and A. S. Isaev. 2013. Boreal forest sensitivity to increased temperatures at multiple successional stages. Annals of Forest Science 70:299–308.

Mather, A. S. 2004. Forest transition theory and the reforesting of Scotland. Scottish Geographical Journal 120:83–98.

Moreira, X., K. A. Mooney, S. Rasmann, W. K. Petry, A. Carrillo-Gavilán, R. Zas, and L. Sampedro. 2014. Trade-offs between constitutive and induced defences drive geographical and climatic clines in pine chemical defences. Ecology Letters 17:537–546.

Myers-Smith, I. H., M. Hallinger, D. Blok, U. Sass-Klaassen, S. A. Rayback, S. Weijers, A. J. Trant, K. D. Tape, A. T. Naito, and S. Wipf. 2015. Methods for measuring arctic and alpine shrub growth: a review. Earth-Science Reviews 140:1–13.

Myers-Smith, I. H., and D. S. Hik. 2018. Climate warming as a driver of tundra shrubline advance. Journal of Ecology 106:547–560.

Nishizawa, K., S. Tatsumi, R. Kitagawa, and A. S. Mori. 2016. Deer herbivory affects the functional diversity of forest floor plants via changes in competition-mediated assembly rules. Ecological Research 31:569–578.

Oerlander, G., and C. Karlsson. 2000. Influence of shelterwood density on survival and height increment of *Picea abies* advance growth. Scandinavian Journal of Forest Research 15:20–29.

Oliveras, I., and Y. Malhi. 2016. Many shades of green: the dynamic tropical forest–savannah transition zones. Philosophical Transactions of the Royal Society B 371:20150308.

Olofsson, J., and E. Post. 2018. Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. Philosophical Transactions of the Royal Society B 373:20170437.

Ossi, F., J.-M. Gaillard, M. Hebblewhite, and F. Cagnacci. 2015. Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer. European Journal of Wildlife Research 61:111–124.

Patterson, G., D. Nelson, P. Robertson, and J. Tullis 2014. Scotland's native woodlands. Results from the native woodland survey of Scotland. Forestry Commission Scotland, Stirling, UK.

Putman, R. 2003. An analysis of trends in deer populations and in the vegetation of Creag Meagaidh National Nature Reserve, 1986–2001. Scottish Natural Heritage, Inverness, UK.

Rao, S. J. 2017. Effect of reducing red deer *Cervus elaphus* density on browsing impact and growth of Scots pine *Pinus sylvestris* seedlings in semi-natural woodland in the Cairngorms, UK. Conservation Evidence 14:22–26.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, and M. P. Nelson. 2014. Status and ecological effects of the world's largest carnivores. Science 343:1241484.

Ripple, W. J., T. M. Newsome, C. Wolf, R. Dirzo, K. T. Everatt, M. Galetti, M. W. Hayward, G. I. Kerley, T. Levi, and P. A. Lindsey. 2015. Collapse of the world's largest herbivores. Science Advances 1:e1400103.

Ross, L. C., G. Austrheim, L.-J. Asheim, G. Bjarnason, J. Feilberg, A. M. Fosaa, A. J. Hester, Ø. Holand, I. S. Jónsdóttir, and L. E. Mortensen. 2016. Sheep grazing in the North Atlantic region: a long-term perspective on environmental sustainability. Ambio 45:551–566.

Saunders, M. R., and K. J. Puettmann. 1999. Effects of overstory and understory competition and simulated herbivory on growth and survival of white pine seedlings. Canadian Journal of Forest Research 29:536–546.

Scott, D., D. Welch, M. Thurlow, and D. A. Elston. 2000. Regeneration of *Pinus sylvestris* in a natural pinewood in NE Scotland following reduction in grazing by *Cervus elaphus*. Forest Ecology and Management 130:199–211.

Scottish Natural Heritage. 2016. Deer management in Scotland: report to the Scottish Government from Scottish Natural Heritage. SNH, Battleby, Inverness, UK.

Speed, J. D., G. Austrheim, A. J. Hester, and A. Mysterud. 2011. Browsing interacts with climate to determine tree-ring increment. Functional Ecology 25:1018–1023.

Speed, J. D. M., G. Austrheim, A. J. Hester, and A. Mysterud. 2012. Elevational advance of alpine plant communities is buffered by herbivory. Journal of Vegetation Science 23:617–625.

Speed, J. D., G. Austrheim, A. L. Kolstad, and E. J. Solberg. 2019. Long-term changes in northern large-herbivore communities reveal differential rewilding rates in space and time. PLoS ONE 14:e0217166.

Stark, S., M. Väisänen, H. Ylänne, R. Julkunen-Tiitto, and F. Martz. 2015. Decreased phenolic defence in dwarf birch

(*Betula nana*) after warming in subarctic tundra. Polar Biology 38:1993–2005.

Staver, A. C., and W. J. Bond. 2014. Is there a ‘browse trap’? Dynamics of herbivore impacts on trees and grasses in an African savanna. Journal of Ecology 102:595–602.

Staver, A. C., W. J. Bond, W. D. Stock, S. J. Van Rensburg, and M. S. Waldram. 2009. Browsing and fire interact to suppress tree density in an African savanna. Ecological Applications 19:1909–1919.

Stevens, N., B. Erasmus, S. Archibald, and W. Bond. 2016. Woody encroachment over 70 years in South African savannahs: overgrazing, global change or extinction aftershock? Philosophical Transactions of the Royal Society B 371:20150437.

Sturm, M., C. Racine, and K. Tape. 2001. Climate change: increasing shrub abundance in the Arctic. Nature 411: 546.

Svenning, J.-C., P. B. Pedersen, C. J. Donlan, R. Ejrnæs, S. Faurby, M. Galetti, D. M. Hansen, B. Sandel, C. J. Sandom, and J. W. Terborgh. 2016. Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. Proceedings of the National Academy of Sciences USA 113:898–906.

Tanentzap, A. J., J. Zou, and D. A. Coomes. 2013. Getting the biggest birch for the bang: restoring and expanding upland birchwoods in the Scottish Highlands by managing red deer. Ecology Evolution 3:1890–1901.

Tardif, J. C., and F. Conciatori. 2015. Microscopic examination of wood: sample preparation and techniques for light microscopy. Pages 373–415 *in* E. C. T. Yeung, C. Stasolla, M. J. Sumner, and B. Q. Huang, editor. Plant microtechniques and protocols. Springer, Cham, Switzerland.

The National Trust for Scotland. 2012. Mar Lodge Estate Forest Plan 2012–2032. The National Trust for Scotland, Edinburgh, UK.

Tremblay, G. D., and S. Boudreau. 2011. Black spruce regeneration at the treeline ecotone: synergistic impacts of climate change and caribou activity. Canadian Journal of Forest Research 41:460–468.

Treml, V., M. Šenfeldr, T. Chuman, T. Ponocná, and K. Demková. 2016. Twentieth century treeline ecotone advance in the Sudetes Mountains (Central Europe) was induced by agricultural land abandonment rather than climate change. Journal of Vegetation Science 27:1209–1221.

Ueda, H., S. Takatsuki, and Y. Takahashi. 2002. Bark stripping of hinoki cypress by sika deer in relation to snow cover and food availability on Mt Takahara, central Japan. Ecological Research 17:545–551.

Van Langevelde, F., C. A. Van De Vijver, L. Kumar, J. Van De Koppel, N. De Ridder, J. Van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, and W. J. Bond. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84:337–350.

Vazquez-Cooz, I., and R. Meyer. 2002. A differential staining method to identify lignified and unlignified tissues. Biotechnic & Histochemistry 77:277–282.

Vuorinen, K. E., L. Oksanen, T. Oksanen, A. Pyykönen, J. Olofsson, and R. Virtanen. 2017. Open tundra persist, but arctic features decline—Vegetation changes in the warming Fennoscandian tundra. Global Change Biology 23:3794–3807.

White, K. S., G. W. Pendleton, and E. Hood. 2009. Effects of snow on Sitka black-tailed deer browse availability and nutritional carrying capacity in southeastern Alaska. Journal of Wildlife Management 73:481–487.

SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2119/full

DATA AVAILABILITY

Date are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.ghx3ffbk2

Supporting Information. Vuorinen, K.E.M., S.J. Rao, A.J. Hester, and J.D.M. Speed. 2020. Herbivory and climate as drivers of woody plant growth: Do deer decrease the impacts of warming? Ecological Applications.

Appendix S1

Figures

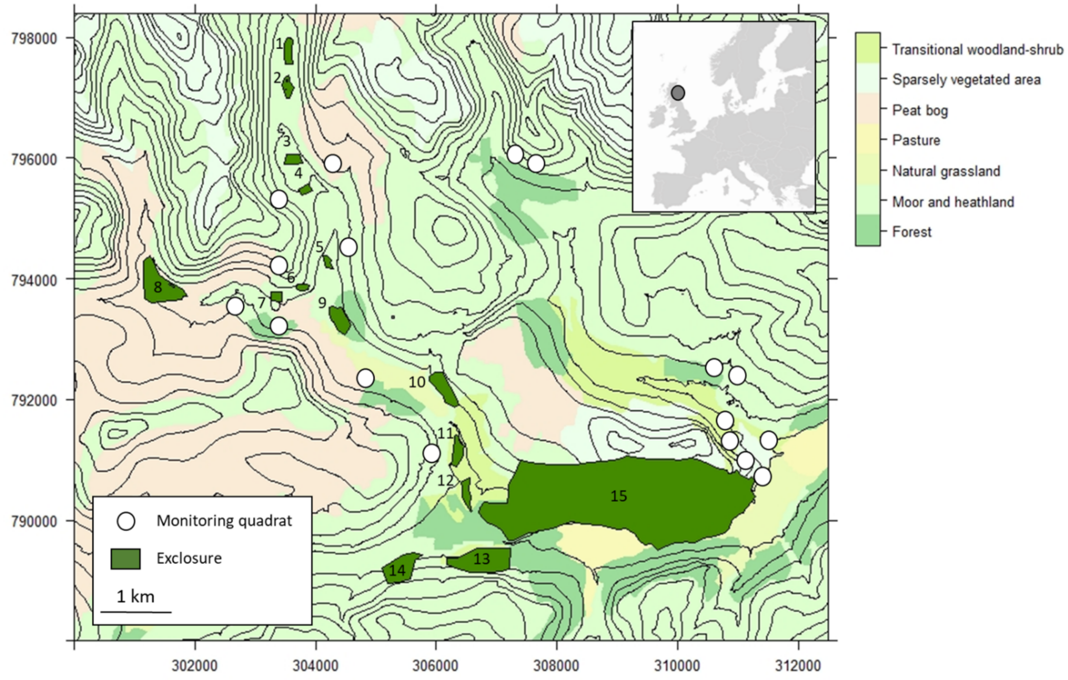
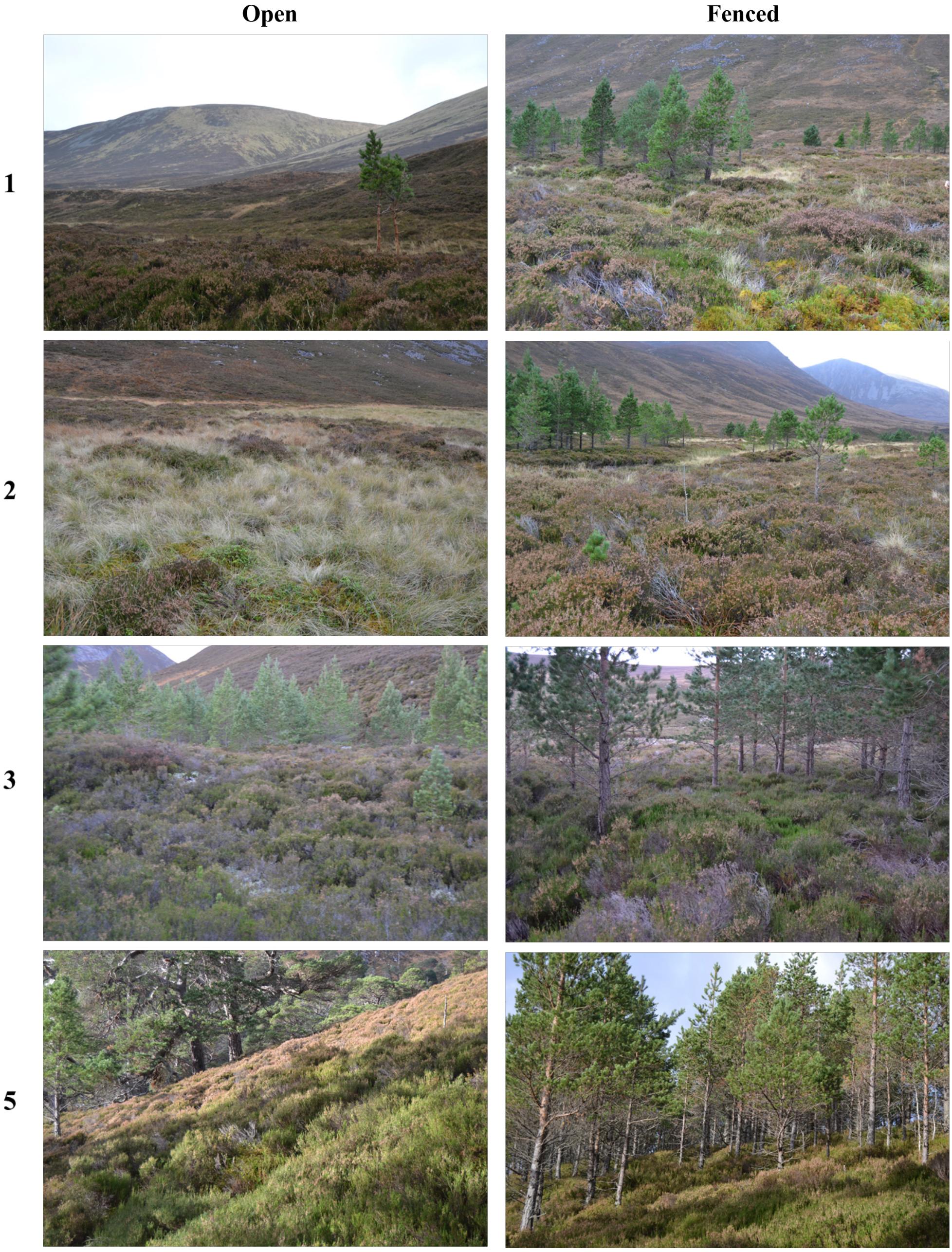


Figure S1. Exclosure sites and tree growth and deer pellet monitoring quadrats in the regeneration zone of Mar Lodge Estate. See Table S1 for site descriptions. Background elevational map is based on OS Terrain 50 open data, elevational contours with 50 m intervals (© OS (Ordnance Survey, 2018)). Background land cover map is based on Corine land cover map of 2012 for the UK, Jersey and Guernsey (Cole B., 2015).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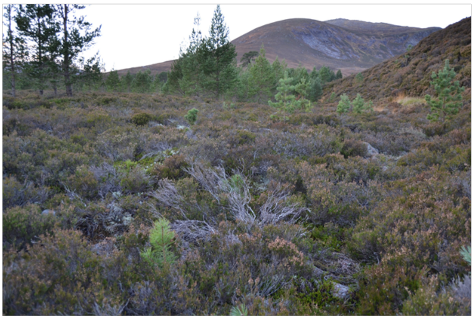

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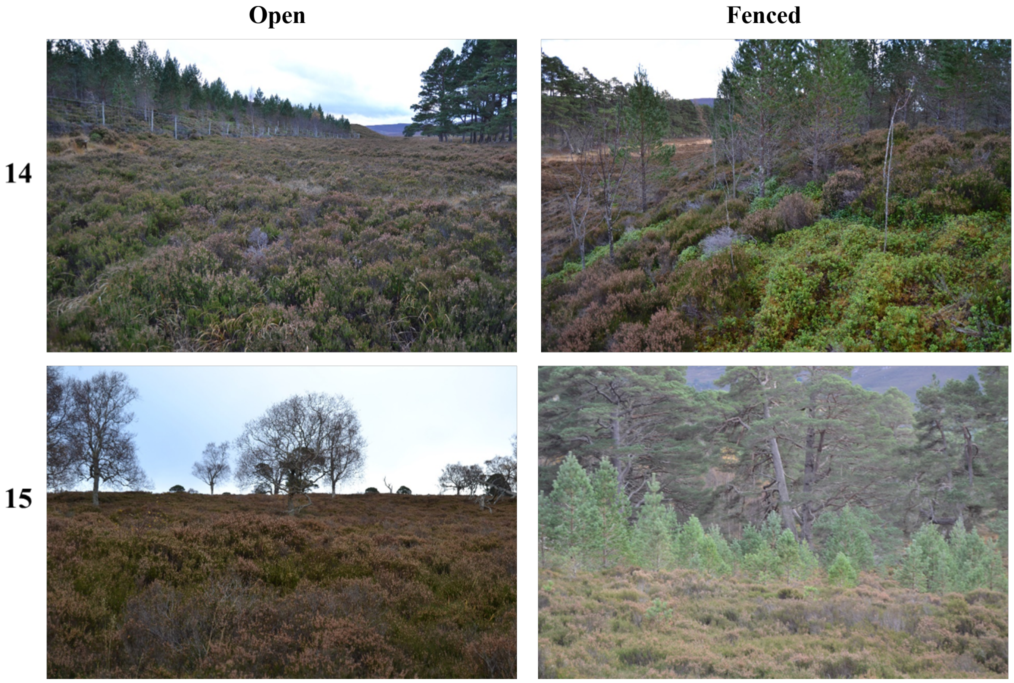

Figure S2. Pictures of sampling sites inside and outside the exclosures from each sampled fence (fence 4 was not sampled and thus not photographed).

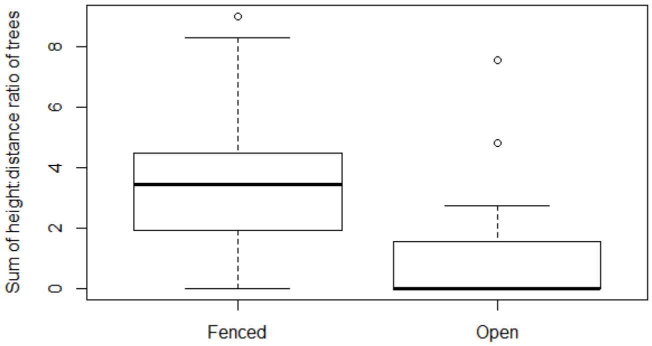

Figure S3. Tree shading, measured as a sum of the height:distance ratio of the trees growing within a 10 m radius circle around each sampled individual, on open and fenced sites. The difference between treatments is significant (linear mixed model with fence as random factor and slope, aspect, elevation and treatment as explanatory factors; df=20, t=-3.4, p=0.0028)

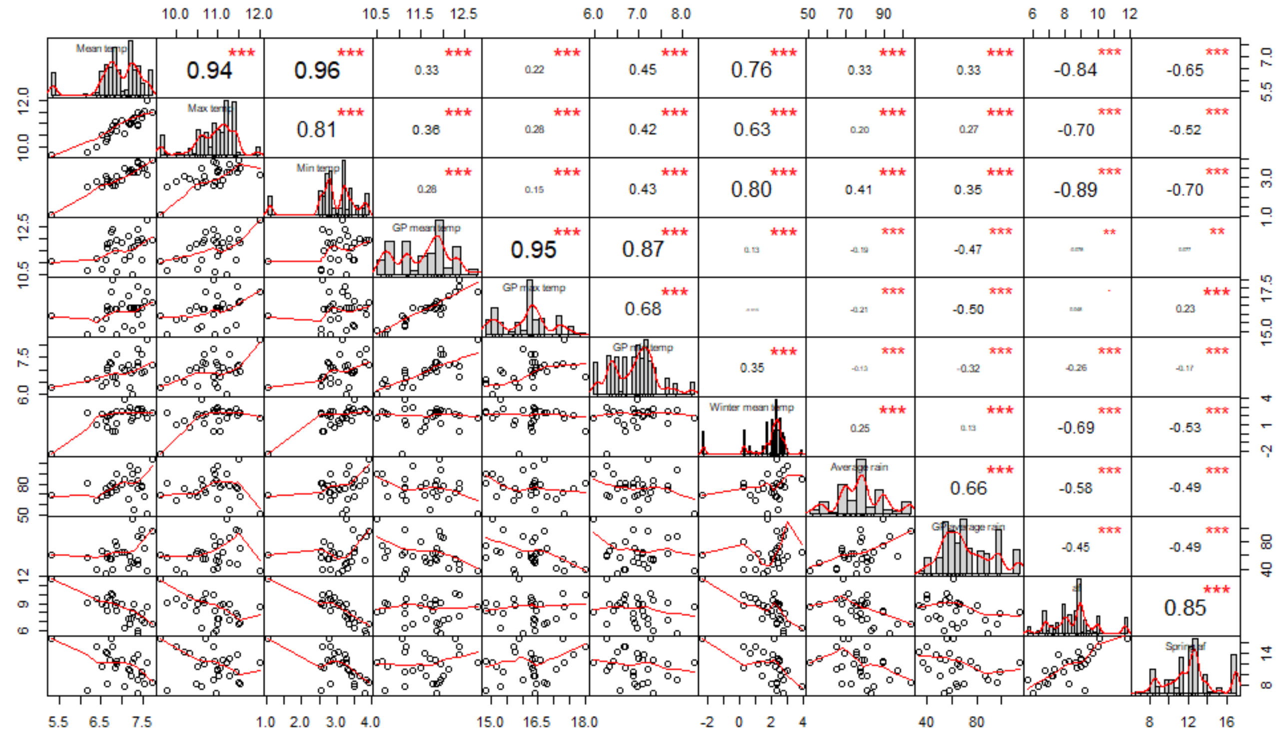

Figure S4. Correlation chart of correlation matrix of all climate variables examined before the main analysis. We obtained data on yearly mean, maximum and mininum temperature, growth period mean, maximum and minimum temperature, winter mean temperature, precipitation, growth period precipitation, total days of air frost and spring days of air frost, and tested correlations between them: Right upper half presents the absolute values of the correlations and the results of the correlation tests with as stars, and left lower half bivariate scatterplots with a fitted lines. As most of the variables were highly correlated, we selected only one variable, mean temperature, for the main analysis. Out of all variables winter temperature, mean temperature and min temperature had highest correlation with growth, and we decided to use mean temperature as it is also the most conservative approach and commonly used. Figure has been drawn with chart.Correlation function from PerformanceAnalytics-package (Peterson et al 2018).

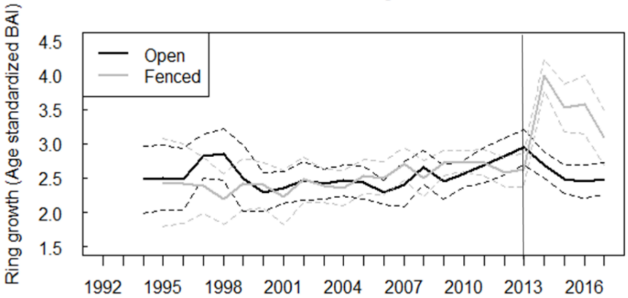

Figure S5. Heather growth trends 1992-2017 inside and outside the exclosures based on dendroecological measurements (average ± SE with dashed lines). Data points of years with less than three individuals have been excluded. Note that even though most of the fences were taken down 2012-2014 (vertical lines), they are depicted here as exclosures.

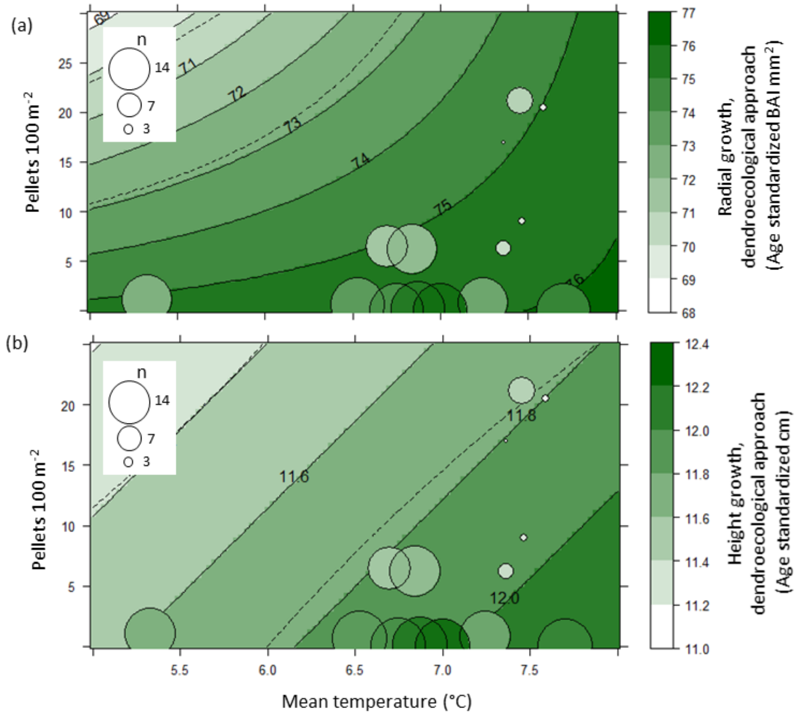

Figure S6. Pine radial (a) and height (b) growth along temperature and deer pellet density gradients as predicted by the respective models. SEs are plotted for contour lines 72 (radial growth), 11.6 (height growth) with dashed lines. See model results in Supplementary Table 4. Observation points are depicted as circles with size representing sample size on each point. The highest pellet vales (>30) have been excluded to avoid unnecessary extrapolation. Note that model predictions get less reliable when moving further away from the data points.

Tables

Table S1. Exclosure site data. Exclosure numbers refer to those in Figure S1. Pine, birch and heather 'n' refer to the number of individuals, sampled as pairs at each exclosure.

Exclosure number	Establishment year	Exclosure removal year	Area (ha)	Elevation	Pine n	Birch n	Heather n
1	1999	2012-2013	5.6	518	-	-	2
2	1999	2012-2013	0.02	513	-	-	2
3	1996-98	2012-2013	4.4	498	2	-	2
4	1968-77	2012-2013	2.4	492	-	-	-
5	1959	2012-2013	2.1	458	-	-	2
6	1980	2012-2013	1.9	509	2	-	2
7	1991	2012-2013	2.6	460	2	-	2
8	1989	2012-2013	29.4	458	2	-	4
9	1992	2012-2013	10.3	441	2	-	2
10	1992	2012-2013	12.3	415	4	2	2
11	1986	2012-2013	6.8	396	4	4	4
12	1986	2012-2013	5.5	402	2	2	2
13	1992	still up	33.5	372	2	-	4
14	1992	still up	20.1	377	-	-	2
15	1994	2012-2014	478.8	416	4	4	4

Table S2. Observed and expected Moran Indexes for residuals from each model, and test statistics for differences between them. Values were calculated with Moran.I function from ape-package (Paradis et al 2019), based on Gittleman and Kot (1990).

Model *Response*	*deer factor*	Moran I observed	Moran I expected	SD	p
Pine radial growth	deer density	-0.012	-0.0027	0.0082	0.25
Pine height growth	deer density	-0.0103	-0.0091	0.0045	0.11
Birch radial growth	deer density	-0.032	-0.0023	0.0023	0.43
Birch height growth	deer density	-0.067	-0.0202	0.0043	0.33
Heather radial growth	deer density	-0.009	-0.013	0.0034	0.42
Pine height growth	Browsing	-0.023	-0.013	0.0092	0.09
Birch height growth	Browsing	-0.026	-0.0054	0.0012	0.45
Pine radial growth	Treatment	-0.07	-0.0056	0.0101	0.43
Pine height growth	Treatment	-0.034	-0.0092	0.0032	0.17
Birch radial growth	Treatment	-0.012	-0.0023	0.0054	0.15
Birch height growth	Treatment	-0.028	-0.0033	0.0054	0.65
Heather radial growth	Treatment	-0.03	-0.0065	0.0075	0.72
Pine radial growth	Pellet number	-0.011	-0.0021	0.0055	0.12
Pine height growth	Pellet number	-0.0062	-0.0096	0.0073	0.32
Birch radial growth	Pellet number	-0.023	-0.01	0.002	0.32
Birch height growth	Pellet number	-0.013	0.0067	0.0086	0.29
Heather radial growth	Pellet number	-0.0089	-0.0021	0.0093	0.19

Table S3. Goodness of fit of the models, indicated as R^2 of the best model and mean R^2 of all the models in model averaging.

Model *Response*	 *deer factor*	Max R^2	Mean R^2	SD R^2
Pine radial growth	deer density	0.50	0.37	0.109
Pine height growth	deer density	0.59	0.54	0.022
Birch radial growth	deer density	0.29	0.22	0.033
Birch height growth	deer density	0.23	0.21	0.009
Heather radial growth	deer density	0.38	0.35	0.013
Pine height growth	Browsing	0.12	0.07	0.003
Birch height growth	Browsing	0.02	0.01	0.003
Pine radial growth	Treatment	0.46	0.45	0.005
Pine height growth	Treatment	0.60	0.57	0.010
Birch radial growth	Treatment	0.34	0.32	0.009
Birch height growth	Treatment	0.40	0.38	0.009
Heather radial growth	Treatment	0.40	0.40	0.003
Pine radial growth	Pellet number	0.46	0.35	0.077
Pine height growth	Pellet number	0.60	0.54	0.027
Birch radial growth	Pellet number	0.33	0.23	0.041
Birch height growth	Pellet number	0.28	0.21	0.027
Heather radial growth	Pellet number	0.56	0.48	0.080

Table S4. Coefficients for the model with the effects of exclosing deer, mean temperature and covariates on tree and shrub growth by analysis, conducted separately for each growth measurement type. Sample numbers given for each analysis refer to the number of growth observations. The relative importance of each variable reflects the sum of the Akaike weights over all of the models in which the term appears, SEs are averaged square roots of variance estimators (based on Burnham and Anderson, 2004 equations), z-values regression coefficients divided by SEs and Pr(>|z|)-values probabilities of calculated z > tabulated z. Significant p-values in bold.

			Importance	**Estimate**	**SE**	**z**	**Pr(>|z|)**
Pine							
n=363	Radial growth	Intercept		75.12	2.61	28.72	<2e-16
		Mean temperature x Treatment: exclosed	0.33	-0.27	0.19	2.07	**0.038**
		Mean temperature	0.73	0.26	0.16	1.62	0.106
		Treatment: exclosed	0.51	1.75	1.74	0.97	0.333
		Tree shading	0.29	-0.02	0.03	0.50	0.619
		Slope	0.27	0.00	0.03	0.08	0.940
		Aspect	0.64	0.01	0.00	1.76	0.078
		Elevation	0.41	-0.01	0.01	1.11	0.266
	Height growth	Intercept		10.70	1.28	8.33	< 2e-16
		Mean temperature x Treatment: exclosed	0.97	-0.29	0.09	3.37	**0.001**
		Mean temperature	1.00	0.27	0.07	3.92	**0.000**
		Treatment: exclosed	0.98	2.17	0.65	3.08	**0.002**
		Tree shading	0.39	-0.02	0.01	1.06	0.291
		Slope	0.31	-0.01	0.01	0.64	0.521
		Aspect	0.41	0.00	0.00	1.18	0.237
		Elevation	0.37	0.00	0.00	1.01	0.311
		Intercept		43.786	5.59	7.8	<0.001
Birch							
n=156	Radial growth	Mean Temperature x Treatment: exclosed	0.10	-0.527	0.30	1.7	0.08
		Mean Temperature	0.34	0.138	0.20	0.7	0.50
		Treatment: exclosed	0.34	1.272	2.09	0.5	0.58
		Tree shading	0.32	0.024	0.03	0.6	0.54
		Slope	0.28	-0.006	0.05	0.1	0.92
		Aspect	0.30	-0.004	0.01	0.5	0.60
		Elevation	0.56	-0.020	0.01	1.3	0.19
	Height growth	Intercept		17.643	2.55	6.9	<0.001
		Mean Temperature x Treatment: exclosed	0.03	0.039	0.13	0.3	0.77
		Mean temperature	0.28	0.011	0.07	0.2	0.88
		Treatment: exclosed	0.42	0.250	0.36	0.5	0.59
		Tree shading	0.39	-0.015	0.01	0.8	0.40
		Slope	0.32	-0.011	0.02	0.4	0.67
		Aspect	0.41	-0.003	0.00	0.9	0.36
		Elevation	0.55	-0.009	0.01	1.3	0.21
Heather							
n=430	Radial growth	Intercept		4.17	1.76	2.37	0.018
		Mean temperature x Treatment: exclosed	0.02	-0.02	0.13	0.16	0.875
		Mean temperature	0.28	-0.01	0.07	0.10	0.921
		Treatment: exclosed	0.28	-0.01	0.37	0.02	0.984
		Tree shading	0.52	-0.03	0.02	1.39	0.166
		Slope	0.28	0.00	0.02	0.27	0.790
		Aspect	0.29	0.00	0.00	0.34	0.730
		Elevation	0.56	-0.01	0.00	1.46	0.144

Table S5. Coefficients for the model with effects of pellet density, mean temperature and covariates on growth by analysis, conducted separately for each growth measurement type. Sample numbers given for each analysis refer to the number of growth observations. The relative importance of each variable reflects the sum of the Akaike weights over all of the models in which the term appears, SEs are averaged square roots of variance estimators (based on Burnham and Anderson, 2004 equations), z-values regression coefficients divided by SEs and Pr(>|z|)-values probabilities of calculated z > tabulated z. Significant p-values in bold.

			Importance	Estimate	SE	z	Pr(>|z|)
Pine							
(n=138)	Radial growth	Intercept		74.02	2.47	29.81	<0.001
		Mean temperature x Pellet density	0.66	0.07	0.04	1.94	**0.042**
		Mean temperature	0.95	0.33	0.17	1.88	0.061
		Pellet density	1	-0.4	0.32	1.24	0.214
		Tree shading	0.24	0	0.02	0.01	0.994
		Slope	0.6	-0.05	0.02	0.44	0.662
		Aspect	0.83	0.01	0.01	0.66	0.51
		Elevation	0.44	-0.01	0.01	0.29	0.77
	Height growth	Intercept		10.24	0.96	10.55	<0.001
		Mean temperature x Pellet density	0.84	0.02	0.02	1.38	0.168
		Mean temperature	0.96	0.21	0.07	2.88	**0.004**
		Pellet density	0.97	-0.02	0.01	2.99	**0.003**
		Tree shading	0.56	-0.01	0.01	0.3	0.768
		Slope	0.82	-0.04	0.02	0.57	0.571
		Aspect	0.8	0.01	0	0.52	0.601
		Elevation	0.26	0	0	0.05	0.959
Birch							
(n=74)	Radial growth	Intercept		43.943	6.46	6.7	<0.001
		Mean temperatures x Pellet density	0.07	0.038	0.04	1	0.34
		Mean temperature	0.37	0.231	0.25	0.9	0.36
		Pellet density	0.5	-0.054	0.15	0.4	0.71
		Tree shading	0.53	0.044	0.02	0.5	0.65
		Slope	0.56	-0.122	0.07	0.4	0.69
		Aspect	0.6	-0.055	0.03	0.3	0.75
		Elevation	0.24	-0.003	0.01	0	0.97
	Height growth	Intercept		15.623	1.46	10.5	<0.001
		Mean temperature x Pellet density	0.08	0.023	0.02	1.5	0.13
		Mean temperature	0.31	-0.047	0.1	0.5	0.64
		Pellet density	0.47	-0.036	0.08	0.4	0.66
		Tree shading	0.24	-0.002	0.01	0	0.96
		Slope	0.24	-0.012	0.03	0.1	0.95
		Aspect	0.28	-0.008	0.01	0.1	0.89
		Elevation	0.24	0.002	0	0.1	0.95
Heather							
(n=148)	Radial growth	Intercept		3.37	2.09	1.61	0.108
		Mean temperature x Pellet density	0.11	0	0.02	0.2	0.843
		Mean temperature	0.44	0.11	0.11	1.05	0.296
		Pellet density	1	-0.04	0.05	0.71	0.479
		Tree shading	0.66	-0.02	0.01	0.46	0.644
		Slope	0.28	-0.02	0.04	0.11	0.916
		Aspect	0.33	0.01	0.01	0.15	0.879
		Elevation	0.4	-0.01	0.01	0.16	0.876

Supplementary references

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC in model selection. Sociological methods research, 33(2), 261-304.

Cole B., K. S., Ogutu B.; Palmer D., Smith G., Balzter H. . (2015). Corine land cover 2012 for the UK, Jersey and Guernsey. *NERC Environmental Information Data Centre,*

Gittleman, J. L. and Kot, M. (1990) Adaptation: statistics and a null model for estimating phylogenetic effects. *Systematic Zoology*, **39**, 227--241.

Paradis, E., Blomberg, S., Bolker, B., Brown, J., Claude, J., Cuong, H. S., & Desper, R. (2019). Package 'ape'. *Analyses of phylogenetics and evolution, version*, *2*(4).

Peterson BG, Carl P, Boudt K, Bennett R, Ulrich J, Zivot E, Cornilly D, Hung E, Lestel M, Balkissoon K, Wuertz D. Package 'PerformanceAnalytics'. R Team Cooperation. 2018.

Ordnance Survey. (2018). OS Terrain 50 - GB. Retrieved from https://www.ordnancesurvey.co.uk/business-and-government/products/terrain-50.html.

Paper II

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Ecology, 101(11), 2020, e03159

Cool as a moose: How can browsing counteract climate warming effects across boreal forest ecosystems?

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Abstract. Herbivory has potential to modify vegetation responses to climatic changes. However, climate and herbivory also affect each other, and rarely work in isolation from other ecological factors, such as plant–plant competition. Thus, it is challenging to predict the extent to which herbivory can counteract, amplify, or interact with climate impacts on ecosystems. Here, we investigate how moose modify climatic responses of boreal trees by using experimental exclosures on two continents and modeling complex causal pathways including several climatic factors, multiple tree species, competition, tree height, time, food availability, and herbivore presence, density, and browsing intensity. We show that moose can counteract, that is, "cool down" positive temperature responses of trees, but that this effect varies between species depending on moose foraging preferences. Growth of preferred deciduous trees was strongly affected by moose, whereas growth of less preferred conifers was mostly driven by climate and tree height. In addition, moose changed temperature responses of rowan in Norway and balsam fir in Canada, by making fir more responsive to temperature but decreasing the strength of the temperature response of rowan. Snow protected trees from browsing, and therefore moose "cooling power" might increase should a warming climate result in decreased snow cover. Furthermore, we found evidence of indirect effects of moose via plant–plant competition: By constraining growth of competing trees, moose can contribute positively to the growth of other trees. Our study shows that in boreal forests, herbivory cooling power is highly context dependent, and in order to understand its potential to prevent changes induced by warming climate, species differences, snow, competition, and climate effects on browsing need to be considered.

Key words: birch; boreal forest; browsing; climate changes; fir; moose; pine; rowan; spruce; structural equation modeling.

INTRODUCTION

As herbivores control multiple ecosystem properties that affect climate, including albedo, carbon cycling, and forest fire prevalence, it has been suggested that herbivory management can play a crucial role in mitigating global warming (Schmitz et al. 2014, Cromsigt et al. 2018, Schmitz et al. 2018). Large vertebrate herbivores can also act as a buffer of the impacts of climate change by counteracting potential vegetation changes induced by warming climate, also referred to as a "cooling" effect (Fisichelli et al. 2012). Empirical studies have shown support on the cooling effect in arctic and alpine contexts (Olofsson et al. 2009, Speed et al. 2011, 2012, Bråthen et al. 2017, Vuorinen et al. 2017), but its applicability in other regions is poorly understood. As plant species vary in their herbivory resistance and responses, it is also not clear how cooling works at the plant community level and how it shapes plant–plant competition. To complicate the story even further, climatic changes might affect herbivory pressure by changing forage amount and composition, herbivore population dynamics, or browsing intensity (Niemelä et al. 2001, Turunen et al. 2009, Rempel 2011).

As climate plays a major role for tree growth, its changes are expected to have pronounced effects on boreal forests (Ruckstuhl et al. 2007, Soja et al. 2007, Brecka et al. 2018). Some studies predict increased

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biomass production (Boisvenue and Running 2006, D’orangeville et al. 2016), whereas others highlight the increasing frequency of stress events (Brecka et al. 2018), such as drought (Peng et al. 2011), loss of protective snow layer (Blume-Werry et al. 2016), and forest fires (Soja et al. 2007, de Groot et al. 2013), making overall effects challenging to model. In addition, plant growth is rarely only driven by abiotic factors: herbivory shapes boreal forests by affecting the growth rate, successional pathways, plant competition, and community composition (Hidding et al. 2013, Bernes et al. 2018, Kolstad et al. 2018*a*, *b*, Vuorinen et al. 2020). Boreal forest ecosystems are networks of biotic and abiotic factors that cannot be regarded in isolation (Fig. 1), and it is increasingly important to understand these networks for providing predictions on future forestry and forest carbon storage potential under a warmer climate (Soja et al. 2007, Brecka et al. 2018).

Here, we use replicated exclosure experiments to investigate the cooling potential of moose on boreal tree growth at early successional stages on two continents, while considering the ecological pathways regulating this potential. Early succession determines the composition of mature forests (Birch et al. 2019), and it is the phase where ungulate herbivory has most potential to affect climate responses as trees are at reachable heights (Kolstad et al. 2018*a*). Thus, it is a key stage for understanding additive, counteracting and interactive effects of climate and herbivory on boreal forest tree growth, composition, and structure. To capture the complexity of the system, we modeled networks including several climate variables, multiple tree species, time effects, tree height, and plant–plant competition, as well as herbivore presence, density, and browsing intensity. We hypothesize that moose cooling power (1) exists for preferred species but not for less preferred species, (2) is, at least partly, realized indirectly via moose effect on tree height (moose keep tree height low and the low height keeps growth rates low), and (3) is weakened or counteracted by decreased plant–plant competition. In addition, we hypothesize that (4) increased snow precipitation decreases browsing pressure, whereas (5) temperature increases it for preferred species (that respond strongly to temperature) but decreases it for less preferred species.

METHODS

Study sites were located in Trøndelag, Vestfold & Telemark, Viken, and Innlandet counties in Norway (59–64° N, 8–12° E), and in Matane, Chic-Chocs, and ZEC Casault wildlife areas in Québec, Canada (48–49° N, 67–66° W; Appendix S1: Fig. S1). The main ungulate

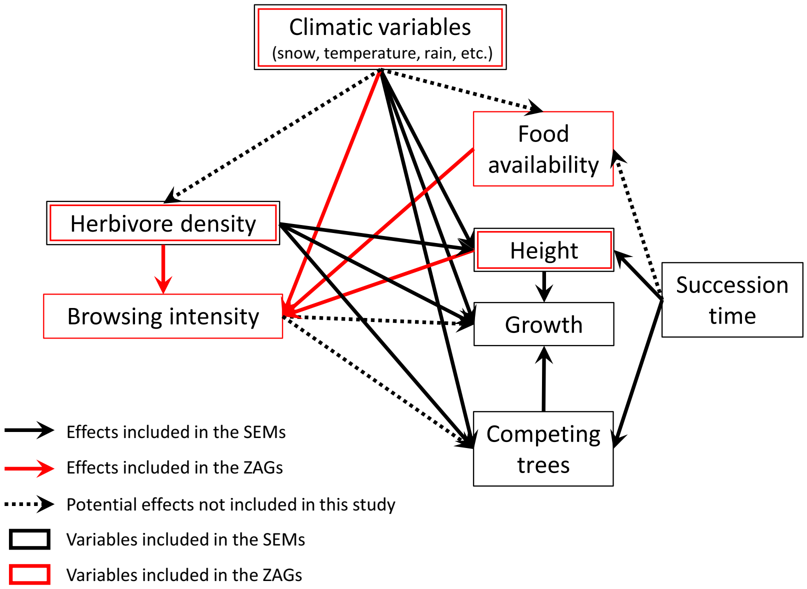

FIG. 1. Schematic illustration of potential effects in the study system, separated by two analysis types applied; structural equation models (SEMs) in black and zero-inflated models (ZAGs) in red. Note that moose density refers to binomial 0 and >0 moose density for SEMs, but to continuous density estimates for ZAGs. Food availability refers to the amount of edible forage available for moose. Browsing intensity refers to the proportion of twigs browsed. Height refers to the height of the target trees. Succession time refers to the number of years since clear-cut. Competing trees refer to interspecific competition, represented by sum of heights of the tree individuals potentially competing with the target trees. Climatic variables, herbivore density, succession time, and food availability are explanatory variables; browsing intensity and growth response variables; and height and competition are serving as both response and explanatory variables.

browser in the study sites in both countries is moose (*Alces alces*, Norway; *Alces americanus*, Canada), but roe deer (*Capreolus capreolus*; Norway), red deer (*Cervus elaphus*; Norway), and white-tailed deer (*Odocoileus virginianus*; Canada) are also present.

Tree growth was followed at 47 clear-cut sites over 11 yr in Norway and at 15 sites over 7 yr in Canada (Appendix S1: Table S1). Study designs were conducted independently of each other and applied somewhat different field methods. Each site consisted of an ungulate exclusion plot, protected by 3- and 2.5-m-tall fences in Canada and Norway, respectively, and an open, browsed plot. Plots were 20 × 20 m in Norway and 14 × 28.5 m in Canada. Each plot included four circular subplots with a radius of 2 m in Norway and 12 circular subplots with a radius of 1.13 m in Canada. (For details on the fence designs, see Appendix S1: Supplementary Methods.) Within these subplots, tree heights were measured late spring each year after the snowmelt. At the same time, browsing intensity on each measured tree was estimated by assessing the proportion of twigs browsed on both continents. In this study, we excluded data from trees >3 m, as these have started to escape moose browsing.

In Norway, up to four individuals of each tree species were randomly selected from each subplot for measurements. These individuals were followed across years and thus individual growth rates could be calculated. In addition, all tree individuals present within subplots were counted in 50-cm height classes for each species. In Canada, all individuals of all species were measured within each subplot, but individuals were not followed across years and thus calculated growth values represent average growth rate across individuals at the subplot level. Here, we studied four species (or species groups) in each country: *Sorbus aucuparia* L., *Betula pubescens* Ehrh., *Pinus sylvestris* L., and *Picea abies* (L.) H. Karst. in Norway, and *Sorbus americana* Marshall, *Betula* spp. (mostly *B. papyrifera* Marshall and some *B. alleghaniensis* Britton), *Abies balsamea* (L.) Mill and *Picea* spp. (mostly *P. glauca* (Moench) Voss and some *P. mariana* (Miller) Britton, Sterns & Poggenburgh) in Canada. These species and species groups (rowans, birches, pine/fir, spruces) correspond to each other functionally across continents, and moose prefer them as forage in descending order as presented above. Tree measurements resulted in 2,109 height-increment observations in Canada and 14,489 in Norway (Appendix S1: Table S1). In addition to the individuals of the target species (and species groups), data allowed for calculating the sum of heights of individuals of all other tree species in each plot to account for potential interspecific plant–plant competition and facilitation.

Daily temperature and precipitation data were obtained from the Norwegian Meteorological Institute's MET database (Lussana et al. 2016, 2018) for Norway, and the climate monitoring program (PSC) of the Ministry of Sustainable Development, Environment and Climate Change (MDDELCC 2018) for Canada. MET data are based on modified optimal interpolation from weather stations with 1 × 1 km grid cells. PSC data are based on ordinary Kriging interpolation from manned and unmanned weather stations with a 0.1° resolution. Temporally, the data sets cover the whole study period. Based on the temperature and precipitation values, growth period mean temperature (June–September), growth period precipitation and winter snow–water equivalent were calculated for each year. For minimum, maximum, and average values for these variables, see Appendix S1: Table S1.

Moose densities in 2009 and 2015 for each Norwegian municipality were taken from (Speed et al. 2019), and the reports of Ministère des Ressources naturelles et de la Faune provided estimates from aerial surveys for 2010 (Chic-Chocs; Dorais and Lavergne 2010) and 2012 (Matane, ZEC Casault; Lamoureux et al. 2012) in Canada. We estimated the available moose forage amount by ranking all tree species present in subplot into moose forage preference classes, based on the literature (Belovsky 1981, Hörnberg 2001, Månsson et al. 2007) and our own experience from the study sites (Appendix S1: Table S2). Then, by multiplying the number of individuals of each species with given rank number, we obtained a food availability index (FAI) for each subplot (see also Månsson et al. 2007).

As complex ecological systems cannot readily be described by simple (univariate) models (Grace et al. 2010), we applied structural equation models (piecewise SEMs), that can combine multiple predictors and response variables into one model network (Lefcheck 2016). Separate models were developed for each country and each target species/species group. The following a priori (linear mixed effects) full submodels were defined: (1) annual tree growth of the target species explained by growth period temperature, precipitation, and snow–water equivalent, ungulate exclusion, tree height of the target species, and competition with other trees, represented by the sum of the heights of the all other tree individuals but the individuals of the target species in each subplot (for full species list, see Appendix S1: Table S2); (2) tree height of the target species in a given year explained by the number of years since clear-cutting (called "succession time" from now on), long-term average growth-period temperature, precipitation and snow–water equivalent across all years, and ungulate exclusion; and (3) competition explained by succession time, long-term average growth period temperature, precipitation, and snow–water equivalent across all years, and ungulate exclusion. These effects are illustrated in Fig. 1 with black arrows.

To account for typical optima in species' responses, each full submodel included potential quadratic terms of temperature, snow and tree height, and interactions between ungulate exclusion and temperature and ungulate exclusion and snow. Predetermined correlations for these models can be seen in Appendix S1: Supplementary Methods, and correlations for all explanatory variables in Appendix S1: Fig. S2. Nonsignificant effects were dropped, starting from the least significant until only significant variables remained (exploratory SEM approach; see final model structures in Appendix S1: Table S4). Models were run separately for each species and country. Continuous first-order autoregressive correlation structures AR(1) were built in every model to account for temporal autocorrelation, and trees nested within subplots and within sites were accounted for as random factors (three-way nested term in a priori linear mixed-effects models).

For all SEMs, model assumptions were fulfilled (see Appendix S1: Table S3 for model R^2-values and Fisher's test results for global goodness of fit). To visualize the strength of effects in SEMs (Fig. 2), we used R^2 differences between the full final model and a model without the variable in question, thus quantifying amount of variation explained by each variable (as we detected quadratic effects and interactions, model coefficient estimates could not be used to describe the response strength; Fairchild et al. 2009).

Ideally, all factors presented in Fig. 1 could be analyzed in one SEM. However, as browsing was zero inflated (most trees were not browsed), we cannot use it as a response variable in piecewise SEM. Furthermore, it cannot be used as a simple explanatory variable because it was collinear with climate variables. Instead, we constructed zero-inflation hurdle models with separate gamma and Bernoulli parts (zero-altered gamma, ZAG; Zuur and Leno 2016) to test the effects of temperature, rain, snow, moose density, tree height, and food availability on browsing intensity. These effects are visualized in Fig. 1 as red arrows. In Canada, we only had moose density estimates from one year for each region, with no temporal variation, whereas in Norway we used linear interpolation to estimate moose density in each year.

All analyses were carried out within the R environment (R version 3.5.1, R Core Team, R Foundation for Statistical Computing, Vienna, Austria). For SEMS, we used the piecewiseSEM-package that admits random factors (Lefcheck et al. 2016). As we ran eight SEMs and eight ZAG models, an alpha level of 0.01 was applied.

RESULTS

For four species, growth increased linearly with temperature: a warming of 1°C resulted in a 7.3 cm (±1.4 SE) increase of annual growth for rowan, 7.5 cm (±1.6 SE) for birch and 6.4 cm (±1.4 SE) for spruce in Canada, and 1.1 cm (±0.3 SE) for birch in Norway (Figs. 2, 3; Tables 1, 2). However, decreasing and quadratic trends were also observed: pine in Norway responded negatively to temperature as a warming of 1°C resulted in a 1.5 cm (±0.3 SE) decrease of annual growth. Spruce in Norway responded quadratically, with highest growth rates at high and low temperatures. Observed snow responses were positive or quadratic (Appendix S1: Fig. S3; Tables 1, 2): a 100-mm/yr increase in snow–water equivalent resulted in an annual growth increase of 2.1 cm (±0.5 SE) and 2.7 cm (±0.6 SE) for pine and spruce in Norway, respectively, whereas fir in Canada and birch in Norway responded quadratically, expressing highest growth rates at intermediate snow–water equivalent values. Only one significant effect of annual rain on growth was observed (for pine in Norway), but long-term rain in Norway negatively affected the height of three species (Fig. 2, Tables 1, 2).

Herbivore presence lowered the annual growth of rowan and birch in Canada, and birch and pine in Norway by 12.0 cm (±2.0 SE), 12.5 cm (±2.1 SE), 7.9 cm (±0.8 SE), and 3.3 cm (±0.6 SE), respectively. In addition, we observed interactive effects of herbivore presence and temperature on rowan growth in Norway, and on fir growth in Canada (Figs. 2, 3; Tables 1, 2), and an interactive effect of herbivore presence and snow on rowan growth in Norway (Appendix S1: Fig. S3; Tables 1, 2). There were no herbivore effects on spruce growth in either country.

In Norway, herbivore presence limited the height of rowan, birch, and pine, which reflected on growth as an additional, indirect negative effect (because height had a direct positive effect on growth; Fig. 2). However, in the cases of rowan and fir in Canada and birch and pine in Norway, herbivore presence also lowered the growth of competing trees, resulting in a positive indirect, cascading effect on growth (because competition had a direct negative effect on growth).

Along with moose density, tree height, and food availability, browsing pressure was affected by climatic variables in several cases (Appendix S1: Fig. S4, S5; Appendix S1: Table S5). In general, increasing snow lowered both the likelihood and intensity of browsing (Appendix S1: Fig. S5), whereas increasing temperatures increased browsing on rowans, but for coniferous species, results were mixed (Appendix S1: Fig. S4).

DISCUSSION

By modeling multiple ecological pathways in boreal ecosystems on two continents, we have shown evidence of a cooling effect of moose. However, this effect is highly dependent on other ecosystem factors and the tree species in question. In comparison to climatic factors, herbivore presence explained more variation in growth of preferred forage species than in less preferred species in both continents. Herbivore presence also lowered the growth of preferred species more than that of less preferred species. In addition, indirect herbivore effects, operating via plant–plant competition and tree height, were observed, as were climatic effects mediating browsing. Our results thus show how the ability of browsing to cool the growth of trees in a warmer climate (Fisichelli et al. 2012) varies with ecological context.

Fast-growing deciduous species may be more responsive to climatic factors than trees with conservative growth strategies, such as conifers (Way and Oren 2010), and thus climate change might have pronounced effects

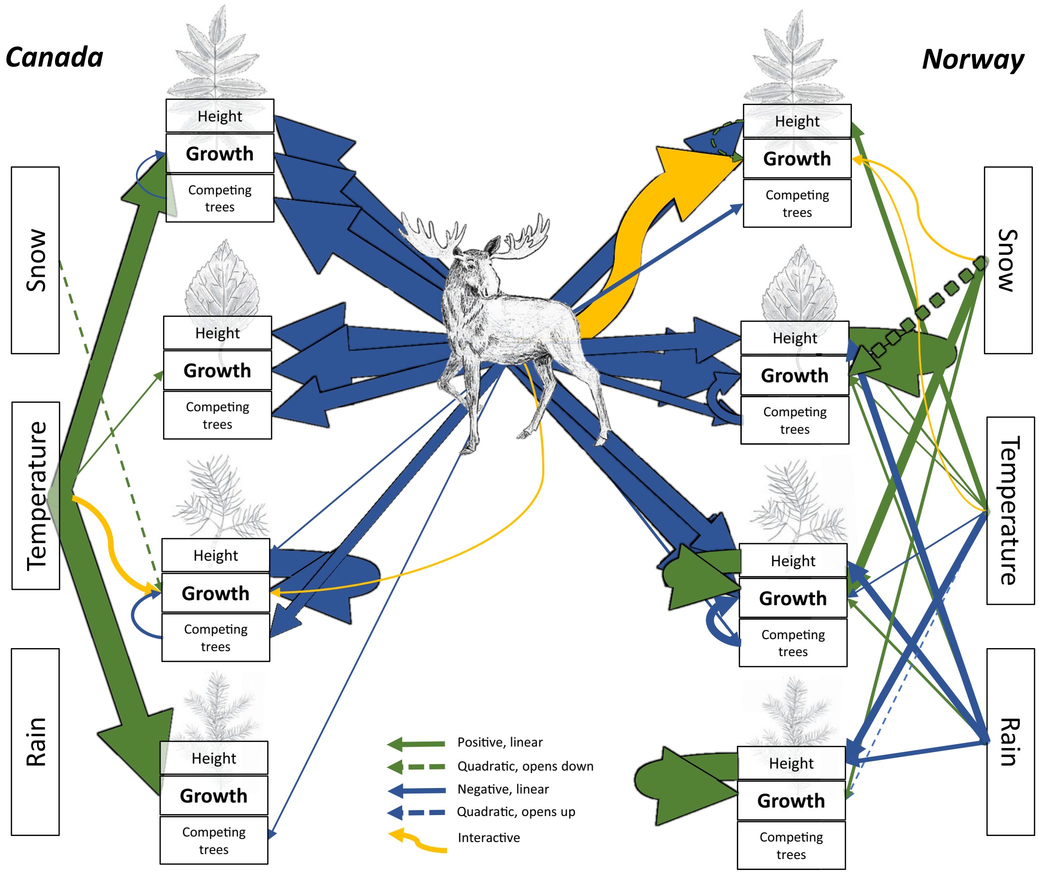

FIG. 2. Visualization of SEMs with significant effects presented as arrows. Arrow size represents *R*-squared contribution of the variable in question (for interactions, *R*-square contribution was defined separately for both terms). Sizes were scaled within species by giving the significant explanatory variable that explained least variation a set minimum size and by giving the significant explanatory variable that explained most variation a set maximum size. Thus, individual arrow sizes are comparable within species, but not between species. Species are indicated as background images (from top to bottom: rowan, birch, fir/pine, spruce). Quadratic effects are separated based on response curve ($y = ax^2$) shape: When a is positive, the parabola opens up; when a is negative, the parabola opens down. Competing trees refer to interspecific competition, represented by sum of heights of the tree individuals potentially competing with the target trees.

on boreal forest composition (Ruckstuhl et al. 2007, Fisichelli et al. 2012). In our study, the strongest positive temperature effects were also observed for deciduous species in Canada. However, as we hypothesized (Hypothesis 1), deciduous trees were also the species with higher sensitivity to moose cooling (Fig. 3), likely because of higher browsing intensity and likelihood (Appendix S1: Fig. S5). Taking into account moose forage preferences (Belovsky 1981, Pastor and Naiman 1992, Hörnberg 2001, Månsson et al. 2007), it is possible that herbivory could balance the competitive advances brought to deciduous species by global warming, preventing them from taking over in succession. Benefits from higher temperatures for preferred forage species are likely to be lower if browsing is affected by other climatic factors: we showed that browsing pressure increased with temperature for rowan, and decreased with snow cover for rowan and birch (see also Nordengren et al. 2003), whereas trends for coniferous species were weaker or nonexistent (Appendix S1: Figs. S4, S5; note, however, that if climate change results in increased snow cover, exposition effect will not realize). These results give some support to our Hypotheses 4 (on the protective effect of snow) and 5 (on the varying effects of temperature), but show that the effects are species dependent.

We expected that moose would change competitive dynamics by directly decreasing competition between trees (Hypothesis 3). For birch and pine in Norway, and for fir and rowan in Canada, we found that herbivory

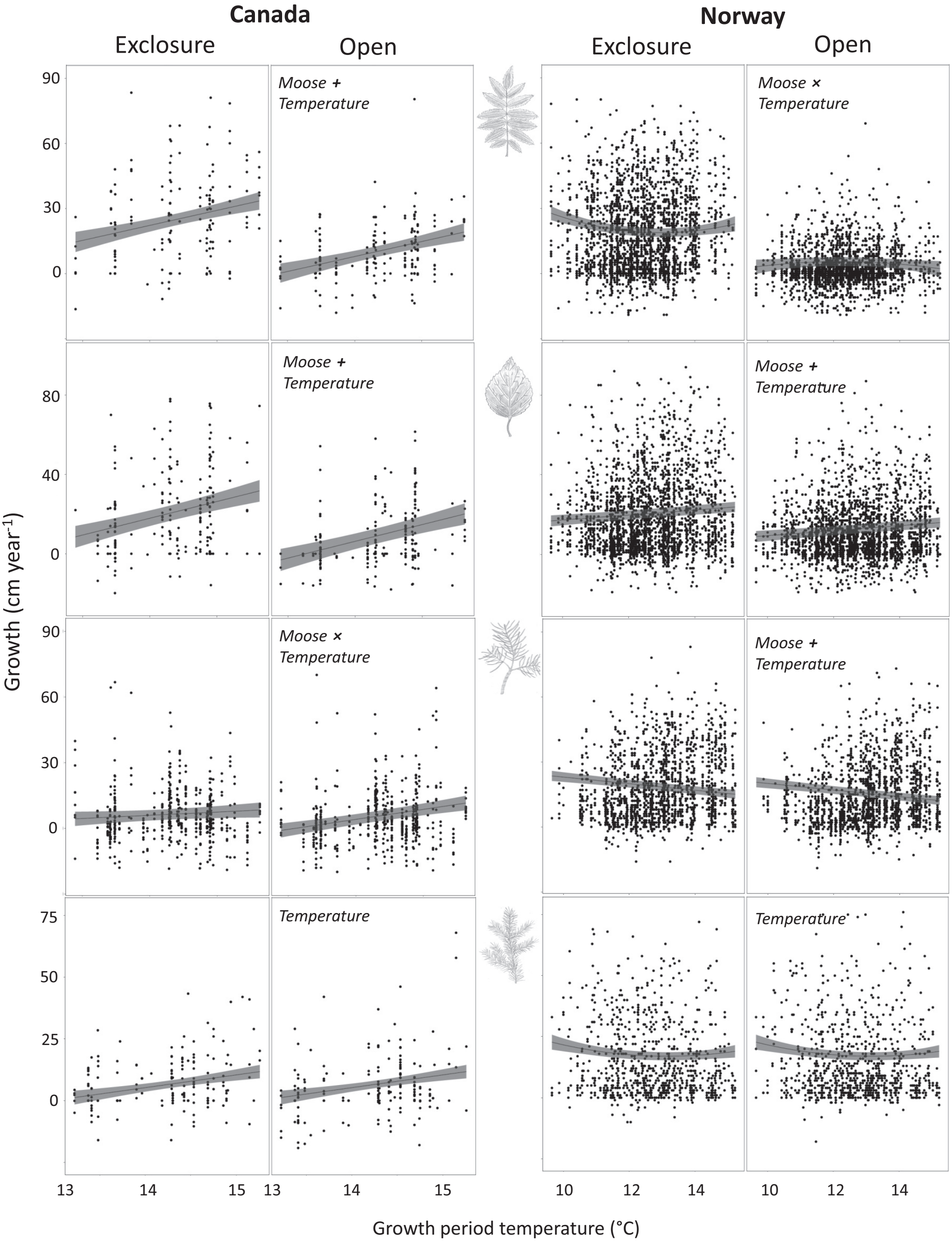

FIG. 3. Tree growth response to temperature at exclosed and open sites, presented separately for each species. Species are indicated as background images (from top to bottom: rowan, birch, fir/pine, spruce). Significant herbivore and temperature effects are written on the right panels with italics.

Table 1. Model coefficients (estimates [Est.], SEs, dfs, critical values [Crit. val.], P values, and standard estimates [Std. est.]) for significant effects that were retained in the SEMs for Canada, presented for each species and species groups.

	Resp	Pred	Est.	SE	df	Crit. val.	P	Std. est.
Rowan	G	Exclosure	−12	2.0	94	−5.9	<0.0001	−0.3
	G	Temperature	7.3	1.4	225	5.2	<0.0001	0.3
	G	Competition	−0.47	0.15	225	3.1	0.0023	0.2
	H	Succession	15.5	1.1	226	14	<0.0001	0.5
	H	Exclosure	−20.3	4.2	94	−4.9	<0.0001	−0.3
	C	Succession	277.2	21.5	226	12.9	<0.0001	0.4
	C	Exclosure	−399.5	87.7	94	−4.6	<0.0001	−0.3
Birch	G	Exclosure	−12.5	2.1	153	−5.9	<0.0001	−0.3
	G	Temperature	7.5	1.6	243	4.7	<0.0001	0.2
	H	Succession	12.5	1.3	245	9.9	<0.0001	0.3
	H	Exclosure	−26.4	4.8	153	−5.5	<0.0001	−0.3
	C	Succession	241.4	19.7	245	12.2	<0.0001	0.3
	C	Exclosure	−422.4	102	153	−4.1	0.0001	−0.3
Pine/fir	G	Exclosure	−62.5	18.8	313	−3.3	0.001	−2.1
	G	Temperature	0.6	1.1	790	0.6	0.569	0
	G	Snow	28.23	8.32	790	3.4	0.0007	1.1
	G	Height	−16.32	1.86	790	−8.8	<0.0001	−0.3
	G	Competition	0.28	0.09	790	3.3	0.001	0.1
	G	Snow^2	−0.04	0.01	790	−3.6	0.0004	−1.2
	G	Exclosure:Temperature	4.3	1.3	790	3.3	0.0011	2
	H	Succession	1.4	0.4	795	3.3	0.0012	0.1
	H	Exclosure	−5.5	2.4	313	−2.3	0.0029	−0.1
	C	Succession	158.1	10.1	795	15.6	<0.0001	0.3
	C	Exclosure	−229.2	44.2	313	−5.2	<0.0001	−0.2
Spruce	G	Temperature	6.4	1.4	212	4.7	<0.0001	0.2
	H	Succession	3.8	0.9	214	4.1	0.0001	0.1
	C	Succession	154.4	17.4	214	8.9	<0.0001	0.3
	C	Exclosure	−304.2	90.2	113	−3.4	0.001	−0.2

Notes: Response codes G, H, and C stand for growth, height, and competition. Temperature_av and Rain_av represent averages across years, used to explain tree height and competition instead of annual averages. For full model output, see Appendix S1: Table S5.

presence indeed decreased the height of competing trees, which, in turn, positively affected the growth of individual trees. Interestingly, these indirect positive effects were not strongest for less preferred species, as could be expected (Pastor and Naiman 1992). Moose effects on plant–plant interactions might also explain why temperature response of fir in Canada was stronger in the presence of moose: firs in browsed plots might respond to temperature more strongly than firs in exclosures, where growth is constrained by plant–plant competition and shelter provided by other trees protects firs from extreme cold events. This effect may be amplified by selective moose browsing: during the warm years, moose prefer deciduous species that grow faster in relation to conifers, and avoid fir, whereas in cold years, fir is more preferred as deciduous species suffer more from low temperatures than conifers (this interpretation is also partly supported by ZAGs; Appendix S1: Fig. S4).

Competition effects were found to explain only a small part of variation in growth in comparison to other factors (Fig. 2), although this might be partly caused by our methods: by measuring competition as sum of tree heights, we account for both density and height effects of competing trees, but not, for example, for the density of branches and leaves that might determine shading effects (Canham et al. 2004, Stadt et al. 2007). We suggest that observed negative temperature trends could be caused by this neglected competition effect: In Norway, the growth of rowan and spruce individuals was lowest at intermediate temperatures and pine growth at high temperatures, which might be caused by increased shading under these conditions.

Tree height was found to be a crucial component mediating moose cooling effect: tall trees have a different growth rate compared to lower trees, browsing pressure is different on them and their height is differently mediated by moose. Our results show that the cooling effect of moose is only apparent when trees are at browsable heights (Appendix S1: Table S6; Kolstad et al. 2018*a*). However, by acting at the crucial early stage of succession, moose effect can reflect to the climax stage of boreal forests. Even when mediated by herbivory, height itself is an important factor affecting growth. For example, for less preferred species in Norway, height explained a considerable amount of growth variation in comparison to herbivore presence. However, as we

Table 2. Model coefficients (estimates [Est.], SEs, dfs, critical values [Crit. val.], *P* values, and standard estimates [Std. est.]) for significant effects that were retained in the SEMs for Norway, presented for each species and species groups.

	Resp	Pred	Est.	SE	df	Crit. Val.	*P*	Std. Est.
Rowan	G	Exclosure	−195.2	41	185	−4.8	<0.0001	−5.8
	G	Temperature	−21.4	4.7	3,623	−4.6	<0.0001	−1.4
	G	Snow	0.45	0.53	3,623	0.8	0.3967	0.1
	G	Height	3.15	1.7	3,623	2	0.0436	0.1
	G	Height^2	−0.01	0.01	3,623	−2.3	0.0098	−0.1
	G	Temperature^2	0.8	0.2	3,623	4.4	<0.0001	1.4
	G	Exclosure:Temperature	28.4	6.7	3,623	4.3	<0.0001	10.5
	G	Exclosure:Temperature^2	−1.1	0.3	3,623	−4.2	<0.0001	−5.3
	G	Exclosure:Snow	2.84	0.75	3,623	3.8	0.0002	0.1
	H	Succession	10.6	0.2	3,630	42.6	<0.0001	0.4
	H	Exclosure	−46.1	3.6	185	−12.9	<0.0001	−0.4
	H	Temperature_av	14.9	3	42	5	<0.0001	0.2
	C	Succession	310	10.3	3,630	30.2	<0.0001	0.2
	C	Exclosure	−1,033	299	185	−3.4	0.0007	−0.2
Birch	G	Exclosure	−7.9	0.8	253	−9.3	<0.0001	−0.2
	G	Temperature	1.1	0.3	3,943	3.9	0.0001	0.1
	G	Rain	70.78	23.04	3,943	3.1	0.0021	0.1
	G	Snow	8.27	1.14	3,943	7.3	<0.0001	0.3
	G	Height	7.13	0.52	3,943	13.7	<0.0001	0.2
	G	Competition	−0.06	0.01	3,943	−4.9	<0.0001	−0.1
	G	Snow^2	−0.02	0.0	3,943	−4.7	<0.0001	−0.2
	H	Succession	13.3	0.2	3,948	53.6	<0.0001	0.5
	H	Exclosure	−24.1	3.7	253	−6.5	<0.0001	−0.2
	H	Temperature_av	11.7	4.1	44	2.8	0.0067	0.2
	H	Rain_av	−20.8	6	44	−3.5	0.0012	−0.2
	C	Succession	340	10	3,948	33.9	<0.0001	0.2
	C	Exclosure	−933	284	253	−3.3	0.0012	−0.1
Pine/fir	G	Exclosure	−3.3	0.6	180	−5.4	<0.0001	−0.1
	G	Temperature	−1.5	0.3	2,702	−5.7	<0.0001	−0.1
	G	Snow	2.06	0.47	2,702	4.4	<0.0001	0.1
	G	Height	24.92	1.25	2,702	20	<0.0001	0.9
	G	Competition	−0.03	0.01	2,702	−2.9	0.0034	−0.1
	G	Height^2	−0.05	0.01	2,702	−8.1	<0.0001	−0.3
	G	Rain	51.11	19.72	2,702	2.6	0.0096	0.1
	H	Succession	14.2	0.3	2,707	56	<0.0001	0.6
	H	Exclosure	−11.7	4.4	180	−2.7	0.0086	−0.1
	H	Rain_av	−31.2	8.4	40	−3.7	0.0006	−0.4
	C	Succession	303.5	10.7	2,707	28.4	<0.0001	0.2
	C	Exclosure	−822.1	349	180	−2.4	0.0097	−0.1
Spruce	G	Temperature	−11.3	4	1,392	−2.8	0.0048	−0.9
	G	Snow	2.71	0.55	1,392	4.9	<0.0001	0.1
	G	Height	29.5	1.92	1,392	15.4	<0.0001	1.2
	G	Temperature^2	0.4	0.2	1,392	2.7	0.0069	0.9
	G	Height^2	−0.07	0.01	1,392	−9.7	<0.0001	−0.7
	H	Succession	13.1	0.4	1,396	35.8	<0.0001	0.4
	H	Temperature_av	−16.3	5.8	44	−2.8	0.0073	−0.3
	H	Rain_av	−25.4	8.7	44	−2.9	0.0052	−0.3
	C	Succession	298.2	18.7	1,396	15.9	<0.0001	0.2

Notes: Response codes G, H, and C stand for growth, height, and competition. Temperature_av and Rain_av represent averages across years, used to explain tree height and competition instead of annual averages. For full model output, see Appendix S1: Table S5.

expected (Hypothesis 2), indirect negative moose effects via reduced height also play a role. For preferred forage species, it is possible that moose herbivory creates "browsing traps" (Staver and Bond 2014, Faison et al. 2016, Churski et al. 2017, Olofsson and Post 2018), from which trees are unable to escape (Kolstad et al. 2018*a*) and thus the growth rates are permanently low, as smaller trees grow slower than taller ones.

Qualitatively, the results were fairly similar between the two continents, suggesting broad applicability of our study across the boreal forest biome. However, there are some apparent differences that are likely to be explained rather by differing methods than differences in study systems. The number of growth observations from Canada was lower, and as expected, we observed fewer significant results than in Norway. Furthermore, we observed no positive effects of height on growth in Canada, likely because growth rates and height measures were average values across subplots, as individual trees were not followed between years. Average tree height may not increase average tree growth at the subplot level, or it might even have a negative impact via competition effects, as in the case of fir. An additional constraint in our study is that even though we accounted for several ecosystem properties, some neglected factors, such as soil properties and branching structure, might be crucial in mediating herbivory effect (Augustine and McNaughton 2006).

Herbivory has been suggested to have various mediating effects on climate-driven vegetation changes by inhibiting shrubification and constraining tree growth. Our findings show support for cooling effects of moose on growth of trees in different boreal forest ecosystems. However, these effects are highly context-dependent. If we are to place hope on herbivory as a cooler of climate change impacts, constraints imposed by species differences, snow, and competition, as well as climate effects on browsing, must be acknowledged.

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LITERATURE CITED

Augustine, D. J., and S. J. McNaughton. 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. Ecosystems 9:1242–1256.

Belovsky, G. E. 1981. Food plant selection by a generalist herbivore: the moose. Ecology 62:1020–1030.

Bernes, C., B. Macura, B. G. Jonsson, K. Junninen, J. Müller, J. Sandström, A. Lõhmus, and E. Macdonald. 2018. Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates. A systematic review. Environmental Evidence 7:13.

Birch, J. D., J. A. Lutz, E. Hogg, S. W. Simard, R. Pelletier, G. H. LaRoi, and J. Karst. 2019. Decline of an ecotone forest: 50 years of demography in the southern boreal forest. Ecosphere 10:e02698.

Blume-Werry, G., J. Kreyling, H. Laudon, and A. Milbau. 2016. Short-term climate change manipulation effects do not scale up to long-term legacies: effects of an absent snow cover on boreal forest plants. Journal of Ecology 104:1638–1648.

Boisvenue, C., and S. W. Running. 2006. Impacts of climate change on natural forest productivity—evidence since the middle of the 20th century. Global Change Biology 12: 862–882.

Bråthen, K. A., V. T. Ravolainen, A. Stien, T. Tveraa, and R. A. Ims. 2017. Rangifer management controls a climate-sensitive tundra state transition. Ecological Applications 27: 2416–2427.

Brecka, A. F., C. Shahi, and H. Y. Chen. 2018. Climate change impacts on boreal forest timber supply. Forest Policy and Economics 92:11–21.

Canham, C. D., P. T. LePage, and K. D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Canadian Journal of Forest Research 34:778–787.

Churski, M., J. W. Bubnicki, B. Jędrzejewska, D. P. Kuijper, and J. P. Cromsigt. 2017. Brown world forests: increased ungulate browsing keeps temperate trees in recruitment bottlenecks in resource hotspots. New Phytologist 214:158–168.

Cromsigt, J. P., M. te Beest, G. I. Kerley, M. Landman, E. le Roux, and F. A. Smith. 2018. Trophic rewilding as a climate change mitigation strategy? Philosophical Transactions of the Royal Society B 373:20170440.

de Groot, W. J., M. D. Flannigan, and A. S. Cantin. 2013. Climate change impacts on future boreal fire regimes. Forest Ecology and Management 294:35–44.

Dorais, M., and D. Lavergne. 2010. Inventaire aérien de l'orignal dans la réserve faunique des Chic-Chocs à l'hiver 2010. Ministère des Ressources naturelles et de la Faune, Québec, Canada.

D'orangeville, L., L. Duchesne, D. Houle, D. Kneeshaw, B. Cote, and N. Pederson. 2016. Northeastern North America as a potential refugium for boreal forests in a warming climate. Science 352:1452–1455.

Fairchild, A. J., D. P. MacKinnon, M. P. Taborga, and A. B. Taylor. 2009. R^2 effect-size measures for mediation analysis. Behavior Research Methods 41:486–498.

Faison, E. K., S. DeStefano, D. R. Foster, J. M. Rapp, and J. A. Compton. 2016. Multiple browsers structure tree recruitment in logged temperate forests. PLoS ONE 11:e0166783.

Fisichelli, N., L. E. Frelich, and P. B. Reich. 2012. Sapling growth responses to warmer temperatures "cooled" by browse pressure. Global Change Biology 18:3455–3463.

Grace, J. B., T. M. Anderson, H. Olff, and S. M. Scheiner. 2010. On the specification of structural equation models for ecological systems. Ecological Monographs 80:67–87.

Hidding, B., J.-P. Tremblay, and S. D. Côté. 2013. A large herbivore triggers alternative successional trajectories in the boreal forest. Ecology 94:2852–2860.

Hörnberg, S. 2001. The relationship between moose (*Alces alces*) browsing utilisation and the occurrence of different forage species in Sweden. Forest Ecology and Management 149:91–102.

Kolstad, A. L., G. Austrheim, E. J. Solberg, L. De Vriendt, and J. D. Speed. 2018*a*. Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species. Ecosphere 9:e02458.

Kolstad, A. L., G. Austrheim, E. J. Solberg, A. M. Venete, S. J. Woodin, and J. D. Speed. 2018*b*. Cervid exclusion alters boreal forest properties with little cascading impacts on soils. Ecosystems 21:1027–1041.

Lamoureux, J., M. Bélanger, and C. Larocque. 2012. Inventaire aérien de l'orignal dans les réserves fauniques de Matane et Dunière à l'hiver 2012. Page 40. Ministère des Ressources Naturelles et de la Faune, Direction de l'Aménagement de la Faune du Bas-St-Laurent, Rimouski, Québec, Canada.

Lefcheck, J., J. Byrnes, and J. Grace. 2016. Package 'piecewiseSEM'. R package version 1. https://CRAN.R-project.org/package=piecewiseSEM

Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

Lussana, C., E. Ole, and U. Francesco. 2016. seNorge v2. 0: an observational gridded dataset of temperature for Norway. Met. no report 14. Norwegian Meteorological Institute, Norway.

Lussana, C., T. Saloranta, T. Skaugen, J. Magnusson, O. E. Tveito, and J. Andersen. 2018. seNorge2 daily precipitation, an observational gridded dataset over Norway from 1957 to the present day. Earth System Science Data 10:235–249.

Månsson, J., H. Andrén, Å. Pehrson, and R. Bergström. 2007. Moose browsing and forage availability: A scale-dependent relationship? Canadian Journal of Zoology 85:372–380.

Ministry of Sustainable Development, Environment and Climate Change (MDDELCC). 2018. Data from Climate Monitoring Program. MDCC, State of the Environment Monitoring Branch, Quebec City, Quebec, Canada.

Niemelä, P., F. S. Chapin, K. Danell, and J. P. Bryant. 2001. Herbivory-mediated responses of selected boreal forests to climatic change. Climatic Change 48:427–440.

Nordengren, C., A. Hofgaard, and J. P. Ball. 2003. Availability and quality of herbivore winter browse in relation to tree height and snow depth. Annales Zoologici Fennici 40:305–314.

Olofsson, J., L. Oksanen, T. Callaghan, P. E. Hulme, T. Oksanen, and O. Suominen. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. Global Change Biology 15:2681–2693.

Olofsson, J., and E. Post. 2018. Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. Philosophical Transactions of the Royal Society B 373:20170437.

Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist 139:690–705.

Peng, C., Z. Ma, X. Lei, Q. Zhu, H. Chen, W. Wang, S. Liu, W. Li, X. Fang, and X. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nature Climate Change 1:467–471.

Rempel, R. S. 2011. Effects of climate change on moose populations: exploring the response horizon through biometric and systems models. Ecological Modelling 222:3355–3365.

Ruckstuhl, K., E. Johnson, and K. Miyanishi. 2007. Introduction. The boreal forest and global change. Philosophical Transactions of the Royal Society B 363:2243–2247.

Schmitz, O. J., P. A. Raymond, J. A. Estes, W. A. Kurz, G. W. Holtgrieve, M. E. Ritchie, D. E. Schindler, A. C. Spivak, R. W. Wilson, and M. A. Bradford. 2014. Animating the carbon cycle. Ecosystems 17:344–359.

Schmitz, O. J., C. C. Wilmers, S. J. Leroux, C. E. Doughty, T. B. Atwood, M. Galetti, A. B. Davies, and S. J. Goetz. 2018. Animals and the zoogeochemistry of the carbon cycle. Science 362:eaar3213.

Soja, A. J., N. M. Tchebakova, N. H. French, M. D. Flannigan, H. H. Shugart, B. J. Stocks, A. I. Sukhinin, E. Parfenova, F. S. Chapin III, and P. W. Stackhouse Jr. 2007. Climate-induced boreal forest change: predictions versus current observations. Global and Planetary Change 56:274–296.

Speed, J. D., G. Austrheim, A. J. Hester, and A. Mysterud. 2011. Browsing interacts with climate to determine tree-ring increment. Functional Ecology 25:1018–1023.

Speed, J. D., G. Austrheim, A. J. Hester, and A. Mysterud. 2012. Elevational advance of alpine plant communities is buffered by herbivory. Journal of Vegetation Science 23: 617–625.

Speed, J. D., G. Austrheim, A. L. Kolstad, and E. J. Solberg. 2019. Long-term changes in northern large-herbivore communities reveal differential rewilding rates in space and time. PLoS ONE 14:e0217166.

Stadt, K. J., C. Huston, K. D. Coates, Z. Feng, M. R. Dale, and V. J. Lieffers. 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. Annals of Forest Science 64:477–490.

Staver, A. C., and W. J. Bond. 2014. Is there a 'browse trap'? Dynamics of herbivore impacts on trees and grasses in an African savanna. Journal of Ecology 102:595–602.

Turunen, M., P. Soppela, H. Kinnunen, M.-L. Sutinen, and F. Martz. 2009. Does climate change influence the availability and quality of reindeer forage plants? Polar Biology 32:813–832.

Vuorinen, K. E., L. Oksanen, T. Oksanen, A. Pyykönen, J. Olofsson, and R. Virtanen. 2017. Open tundra persist, but arctic features decline—vegetation changes in the warming Fennoscandian tundra. Global Change Biology 23:3794–3807.

Vuorinen, K. E., S. J. Rao, A. J. Hester, and J. D. Speed. 2020. Herbivory and climate as drivers of woody plant growth: Do deer decrease the impacts of warming? Ecological Applications.30:e02119.

Way, D. A., and R. Oren. 2010. Differential responses to changes in growsth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiology 30:669–688.

Zuur, A. F., and E. N. Ieno. 2016. Chapter 7, Beginner's guide to zero-inflated models with R. Highland Statistics Limited, Newburgh, UK.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3159/suppinfo

Appendix S1

Cool as a moose: How can browsing counteract climate warming effects across boreal forest ecosystems?

Ecology

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Supplementary Methods

Exclosure fence design

Norwegian fences were established as described by Kolstad et al., 2018, see also https://www.ntnu.edu/museum/sustherb/study-sites. All Canadian exclosures were located in CPRS (cut with protection of regeneration and soils) sites in wildlife reserve forests (Reserve Matane 1275 km^2; Chic-Choc 1130 km^2; and Zec Casault 838 km^2), and management determined by PEFC standards. Clear cut size was < 10 ha. The exclosures in Canada were build the next spring following the clear-cut, and in Norway as described by Kolstad et al., 2018. Subplots were placed in a stratified systematic layout: In Canada, minimum distance from a subplot edge to fence was 1.5 m, and plots were located 2.2 m from each other in width of the exclosure, and 5.6 m in length of the exclosure. For the subplot design in Norway, see Kolstad et al., 2018.

PiecewiseSEM

In piecewiseSEM, it is possible to define known correlative, non-causal relationships before modeling. Our model network included multiple such relationships, defined as follows:

1) Quadratic terms (Temperature^2, Temperature_av^2, Snow^2, Snow_av^2, Rain^2, Rain_av^2, Height^2), are correlated to their linear equivalents; these were included as paired correlations;

2) Competition is correlated to tree height that was used to calculate it; this was included as correlation between Competition and Height, and Competition and Height^2;

3) Growth is correlated with time since exclusion (Succession time), but we can expect that this pattern is driven by indirect effects via competition and height, rather than time itself; this was included as correlation between tree growth and time.

4) We used two types of climate variables: annual values to explain annual growth, and averages across multiple years to explain tree height and competition. To avoid unnecessary complexity, we assumed that annual tree growth is not driven by climate averages across several years, and that competition and height are not driven by annual climate variables. Thus, we defined all possible correlations between growth and average climate variables, as well as between competition and annual climate variables, including quadratic effects.

For correlations between explanatory variables, see Fig S2. Model coefficients for the relationships that were retained in the models after model reduction are presented in Table S5.

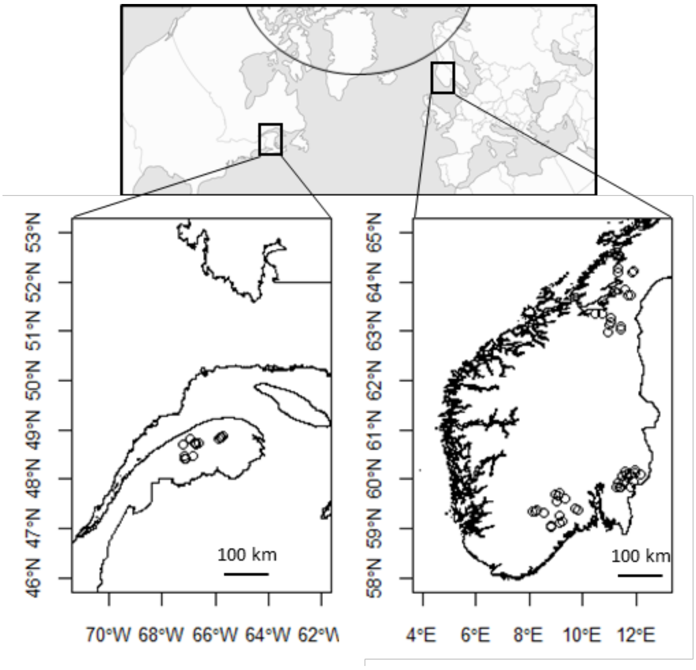
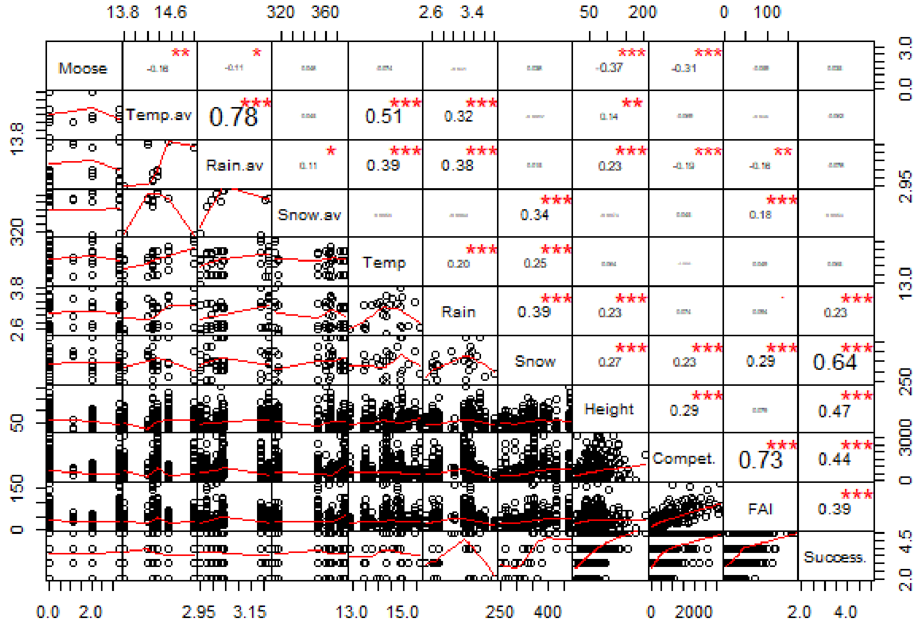
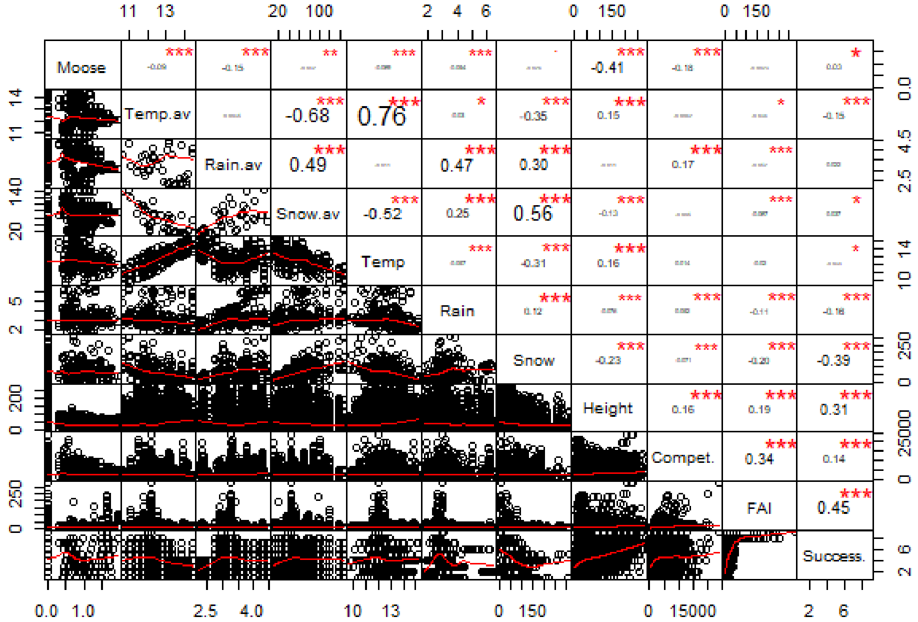


Figure S1. Map of the study areas. Country lines based on GADM version 2.8. Study sites marked with open circles.

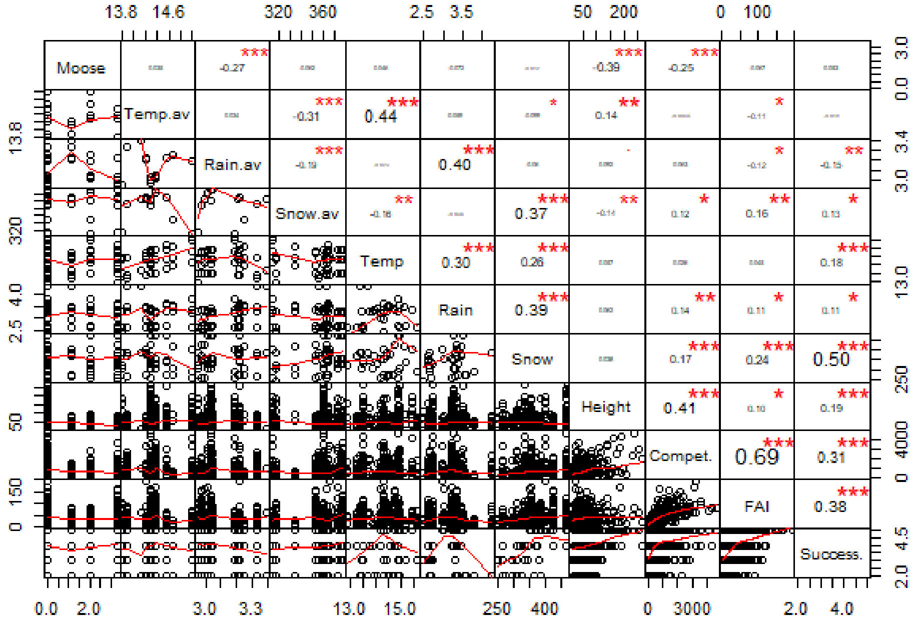
Canada: *Sorbus americana*



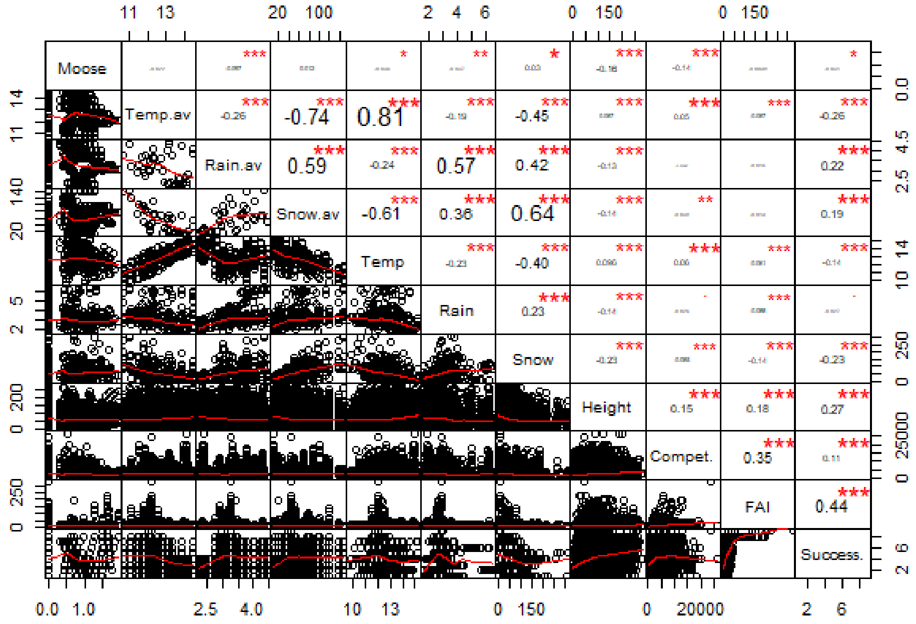
Norway: *Sorbus aucuparia*



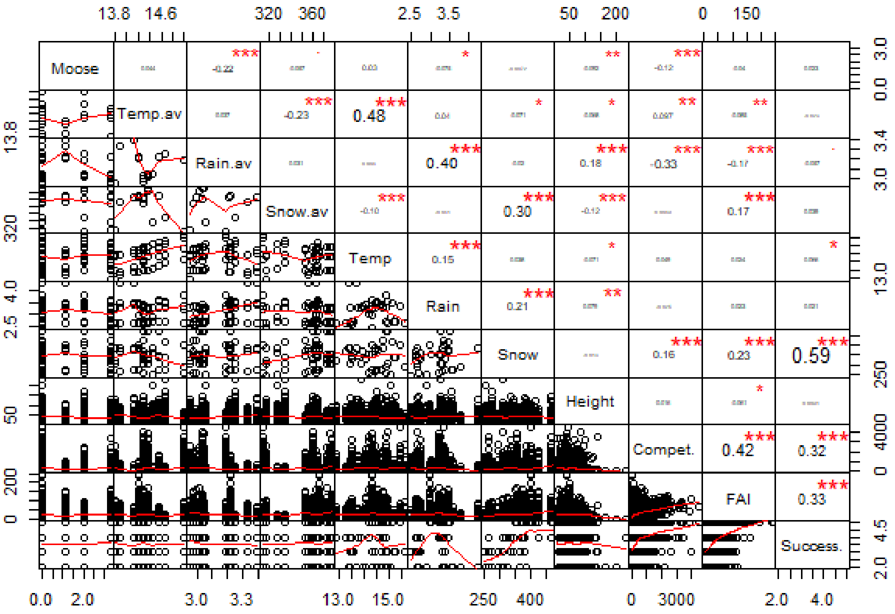
Canada: *Betula* spp.



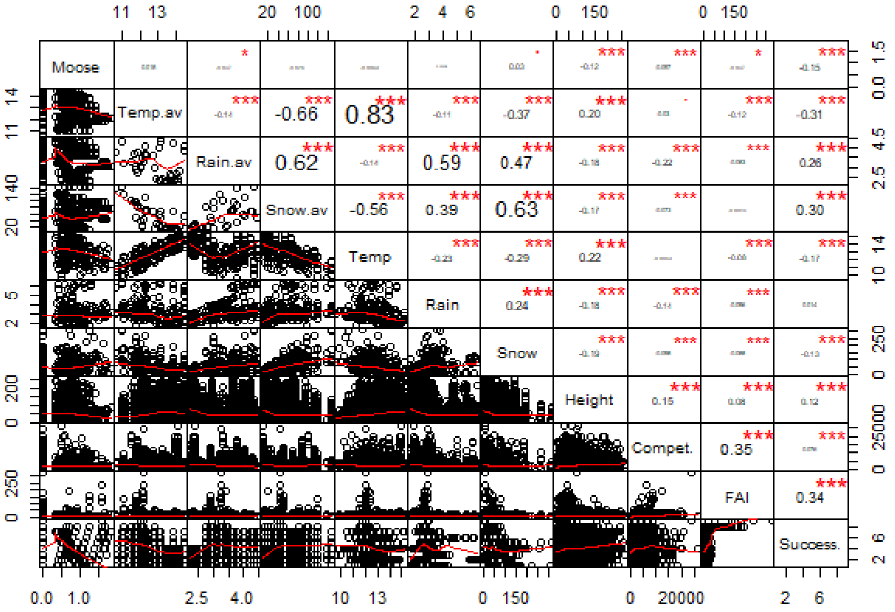
Norway: *Betula pubescens*



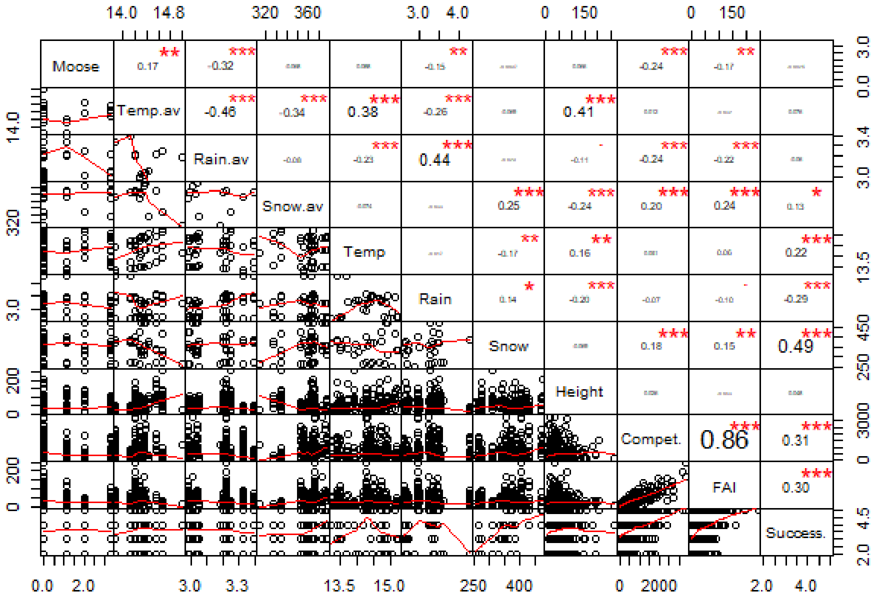
Canada: *Abies balsamea*



Norway: *Pinus sylvestris*



Canada: *Picea* spp.



Norway: *Picea abies*

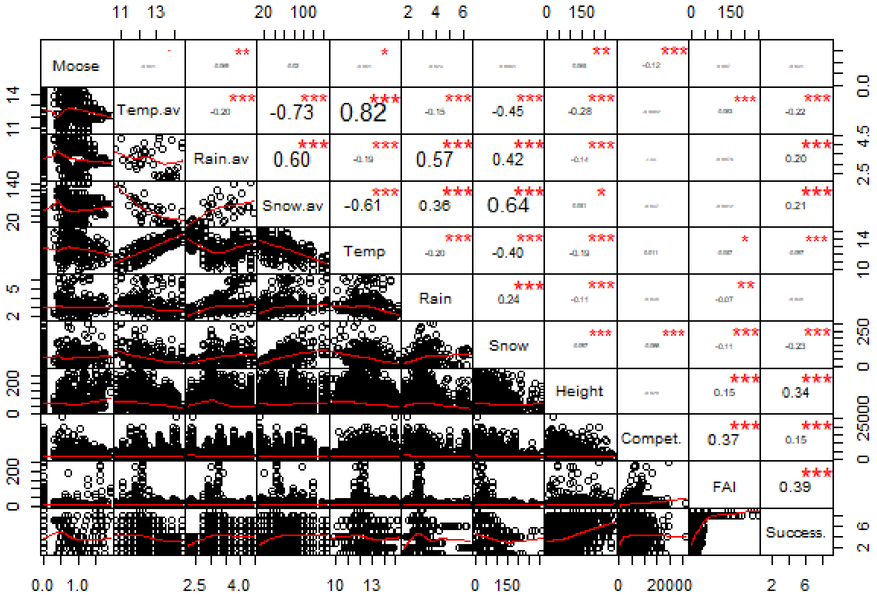


Figure S2. Correlation charts of correlation matrix of SEM explanatory variables and moose density. Right upper half presents the absolute values of the correlations and the results of the correlation tests (Pearson) indicated with stars, and left lower half bivariate scatterplots with a fitted lines. Figures have been drawn with chart. Correlation function from PerformanceAnalytics-package (Peterson et al. 2018). Note that in some cases, there seems to be potential for problematic collinearity between average snow, temperature and rain values; however, VIF values did not indicate issues.

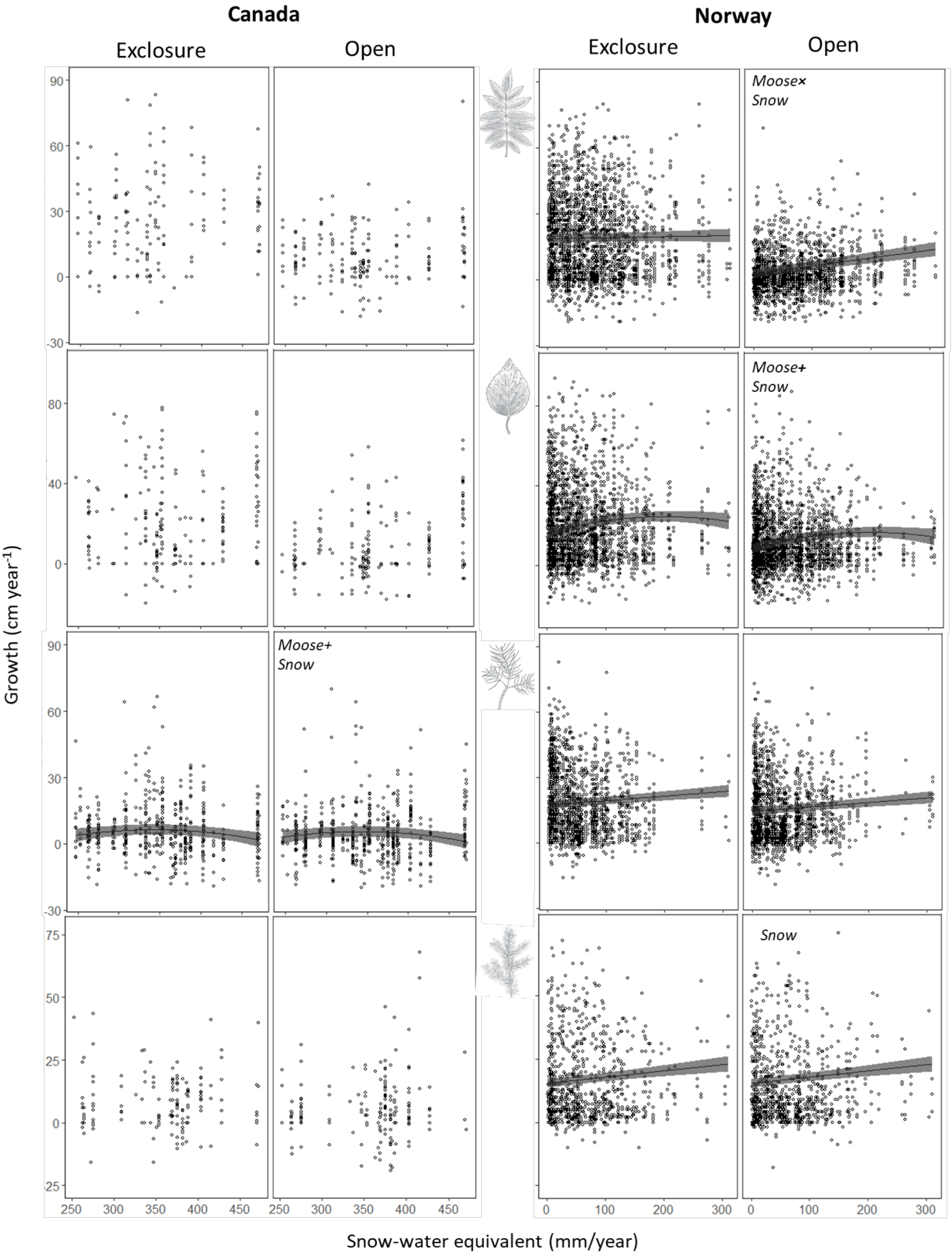


Figure S3. Tree growth response to snow in fenced and open sites, presented separately for each species, ±SE. Species indicated as background images (from top to bottom: rowan, birch, fir/pine, spruce). Significant herbivore and temperature effects are written on the right panels with italics.

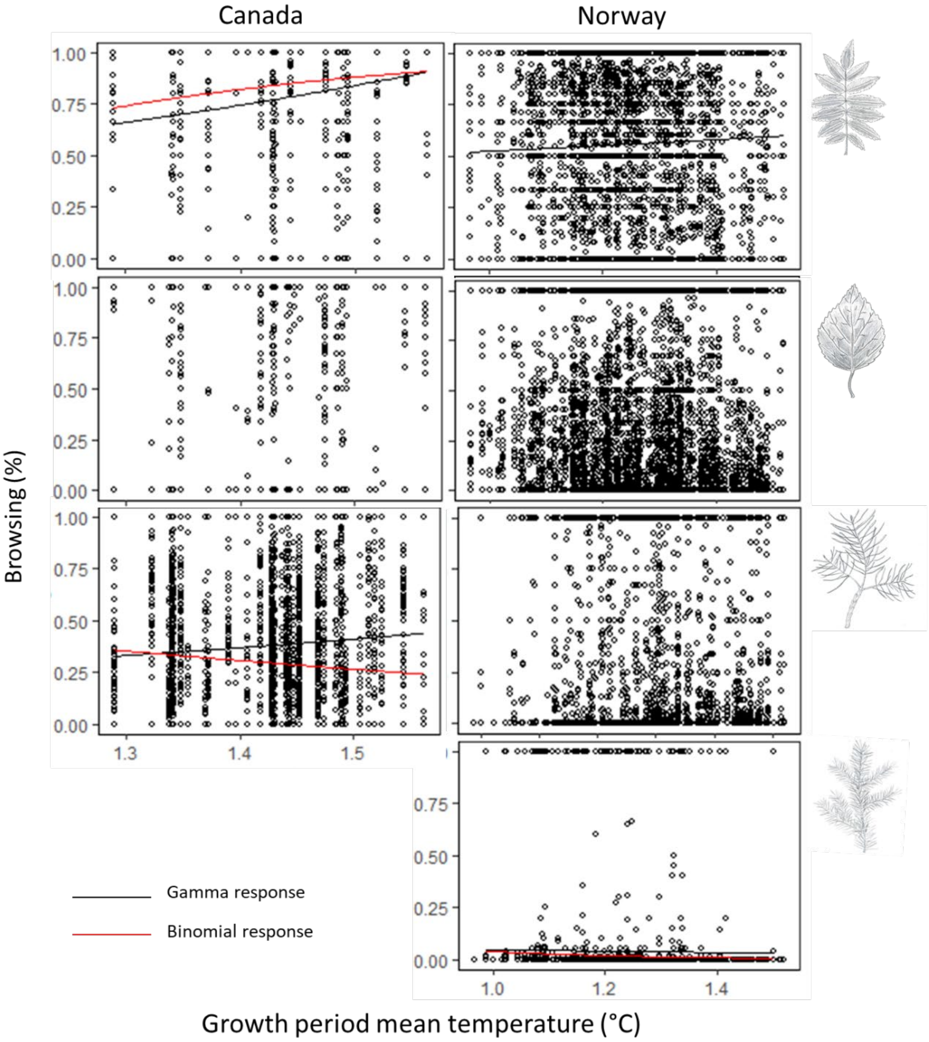


Figure S4. Temperature effect on browsing intensity and likelihood presented separately for each species. Species indicated as images on the right side of the figure (from top to bottom: rowan, birch, fir/pine, spruce). Red Bernoulli model lines are based on binomial data (browsed, unbrowsed) and black gamma model lines on positive, continuous data. Note that data points are presented as both continuous and binomial (all positive values marked as 1) versions. Thus, y-scale represents both continuous browsing (0-1) and binomial browsing (0 or 1). Furthermore, note that in Canada, spruce is not browsed and it was therefore excluded from browsing analyses.

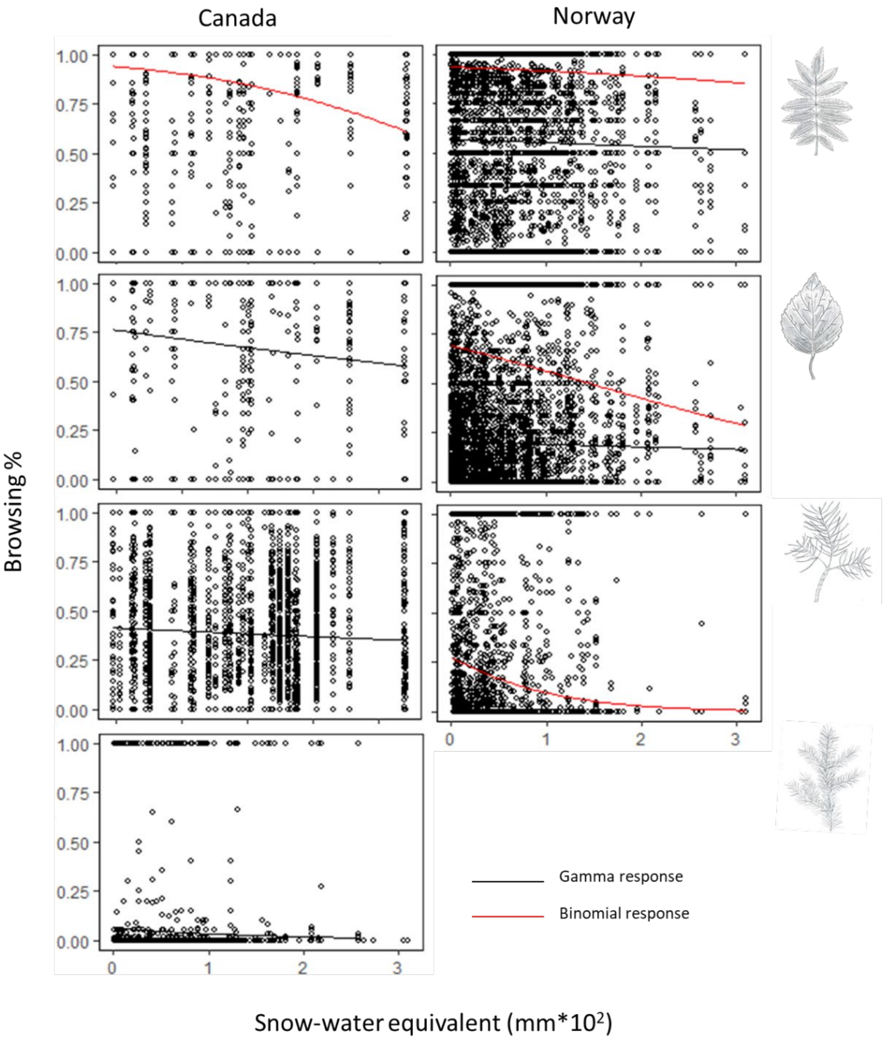


Figure S5. Snow effect on browsing intensity and likelihood presented separately for each species. Species indicated as images on the right side of the figure (from top to bottom: rowan, birch, fir/pine, spruce). Black gamma model line is based on positive, continuous data, and red Bernoulli model lines on binomial data (browsed, unbrowsed). Note that data points are presented as both continuous and binomial (all positive values marked as 1) versions. Thus, y-scale represents both continuous browsing (0-1) and binomial browsing (0 or 1). Furthermore, note that in Canada, spruce is not browsed and it was therefore excluded from browsing analyses.

Table S1. Metadata for study design and sample sizes in Canada and Norway.

	Canada	Norway
Growth data period	2011-2015	2009-2017
Exclosure size	14×28.5 m	20×20 m
Subplot diameter	1.13 m	2 m
Moose density variation	1.1-3.3 km^{-2}	0.21-2.0 km^{-2}
Number of exclosure sites	15	47
Number of plots	347	373
Number of individuals	-	2928
Number of observations	2109	14489
Rowan	323	4432
Birch	396	4923
Pine/Fir	1061	3402
Spruce	329	1732
Growth period temperature (min/mean/max)	15.6/14.3/12.9 °C	15.2/12.6/9.7 °C
Growth period precipitation (min/mean/max)	514/376/295 mm	780/388/200 mm
Winter precipitation (min/mean/max)	412/323/216 mm	698/301/115 mm

Table S2. Moose forage preference ranks for all species present in study circles; the higher the rank, the more preferred is the species. Based on literature (Belovsky, 1981; Hörnberg, 2001; Månsson et al., 2007) and the authors' experience from the study sites.

Rank value	**Canada**	**Norway**
3	*Sorbus americana*	*Sorbus aucuparia*
3	*Abies balsamea*	*Salix caprea*
3	*Acer spicatum*	*Populus tremula*
3	*Cornus stolonifera*	
3	*Salix* spp.	*Corylus avellana*
2	*Betula* spp.	*Betula pendula*
2	*Amelanchier canadensis*	*Betula pubescens*
2	*Corylus cornuta*	*Juniperus communis*
2	*Populus tremuloides*	
2	*Populus balsamifera*	
2	*Viburnum edule*	
1	*Acer rubrum*	*Pinus sylvestris*
1	*Prunus pensylvanica*	
1	*Lonicera canadensis*	
1	*Alnus incana* subsp. *rugosa*	
0	*Sambucus racemosa*	*Sambucus racemosa*
0	*Picea* spp.	*Picea abies*

Table S3. R^2-values for each response variable in each SEM, and Fisher's test results for global goodness-of-fit for each SEM.

		Individual R-squared:			Global goodness-of-fit:		
		Response	Marginal	Conditional	Fisher's C	df	p
Norway	*Sorbus aucuparia*	Growth	0.23	0.49	2.44	4.00	0.66
		Height	0.33	0.44			
		Competition	0.07	0.87			
	Betula pubescens	Growth	0.12	0.38	5.35	4.00	0.25
		Height	0.24	0.43			
		Competition	0.06	0.9			
	Pinus sylvestris	Growth	0.34	0.5	4.00	2.00	0.14
		Height	0.22	0.54			
		Competition	0.04	0.93			
	Picea abies	Growth	0.35	0.53	7.02	6.00	0.32
		Height	0.25	0.46			
		Competition	0.03	0.86			
Canada	*Sorbus americana*	Growth	0.21	0.21	0.395	2	0.821
		Height	0.29	0.51			
		Competition	0.27	0.44			
	Betula sp.	Growth	0.13	0.18	0	0	1
		Height	0.18	0.39			
		Competition	0.15	0.3			
	Abies balsamea	Growth	0.11	0.2	0	0	1
		Height	0.01	0.64			
		Competition	0.11	0.46			
	Picea sp.	Growth	0.07	0.07	3.548	4	0.471
		Height	0.01	0.49			
		Competition	0.1	0.47			

Table S4. Final model structures within SEMs for each species. Effects included to explain each response factor are marked with x, dropped factors with 0 and irrelevant factors (see Supplementary Methods for explanation) with -. Temperature_av and Rain_av represent averages across years, used to explain tree height and competition instead of annual averages.

			Exclosure	Temperature	Temperature^2	Snow	Snow^2	Rain	Height	Height^2	Competition	Succession time	Temperature_av	Rain_av	Temperature *Exclosure	Temperature^2 *Exclosure	Snow *Exclosure
Norway	*Sorbus aucuparia*	Growth	x	x	x	x	0	0	x	x	0	-	-	-	x	x	x
		Height	x	-	-	-	-	-	-	-	-	x	x	0	-	-	-
		Competition	x	-	-	-	-	-	-	-	-	x	0	0	-	-	-
	Betula pubescens	Growth	x	x	0	x	x	x	x	0	x	-	-	-	0	0	0
		Height	x	-	-	-	-	-	-	-	-	x	x	x	-	-	-
		Competition	x	-	-	-	-	-	-	-	-	x	0	0	-	-	-
	Pinus sylvestris	Growth	x	x	0	x	0	x	x	x	x	-	-	-	0	0	0
		Height	x	-	-	-	-	-	-	-	-	x	0	x	-	-	-
		Competition	x	-	-	-	-	-	-	-	-	x	0	0	-	-	-
	Picea abies	Growth	0	x	x	x	0	0	x	x	0	-	-	-	0	0	0
		Height	0	-	-	-	-	-	-	-	-	x	x	x	-	-	-
		Competition	0	-	-	-	-	-	-	-	-	x	0	0	-	-	-
Canada	*Sorbus americana*	Growth	x	x	0	0	0	0	0	0	x	-	-	-	0	0	0
		Height	x	-	-	-	-	-	-	-	-	x	0	0	-	-	-
		Competition	x	-	-	-	-	-	-	-	-	x	0	0	-	-	-
	Betula sp.	Growth	x	x	0	0	0	0	0	0	0	-	-	-	0	0	0
		Height	x	-	-	-	-	-	-	-	-	x	0	0	-	-	-
		Competition	x	-	-	-	-	-	-	-	-	x	0	0	-	-	-
	Abies balsamea	Growth	x	x	0	x	x	0	x	0	x	-	-	-	x	0	0
		Height	x	-	-	-	-	-	-	-	-	x	0	0	-	-	-
		Competition	x	-	-	-	-	-	-	-	-	x	0	0	-	-	-
	Picea sp.	Growth	0	x	0	0	0	0	0	0	0	-	-	-	0	0	0
		Height	0	-	-	-	-	-	-	-	-	x	0	0	-	-	-
		Competition	x	-	-	-	-	-	-	-	-	x	0	0	-	-	-

Table S5. Model coefficients (estimates, SEs, dfs, critical values, p-values and std. Estimates) for SEMs, including pre-defined correlations and independence claims. Temperature_av and Rain_av represent averages across years, used to explain tree height and competition instead of annual averages. Asterisk in the last column indicate significant response on the alpha level <0.01.

			Est.	SE	df	Crit. Val.	p	Std. Est.	
	Coefficients								
	Response	**Predictor**							
Sorbus aucuparia	Growth	Exclosure	-195.2	41.0	185	-4.8	<0.05	-5.8	*
	Growth	Temperature	-21.4	4.7	362	-4.6	<0.05	-1.4	*
	Growth	Snow	0.45	0.53	362	0.8	0.4	0.0	
	Growth	Height	3.15	1.7	362	2.0	<0.05	0.1	
	Growth	Height^2	-0.01	0.01	362	-2.3	<0.05	-0.1	*
	Growth	Temperature^2	0.8	0.2	362	4.4	<0.05	1.4	*
	Growth	Exclosure:Temperature	28.4	6.7	362	4.3	<0.05	10.5	*
	Growth	Exclosure:Temperature^2	-1.1	0.3	362	-4.2	<0.05	-5.3	*
	Growth	Exclosure:Snow	2.84	0.75	362	3.8	<0.05	0.1	*
	Height	Exclosure	-46.1	3.6	185	-12.9	<0.05	-0.4	*
	Height	Succession time	10.6	0.2	363	42.6	<0.05	0.4	*
	Height	Temperature_av	14.9	3.0	42	5.0	<0.05	0.2	*
	Competition	Exclosure	-1032.9	299.9	185	-3.4	<0.05	-0.2	*
	Competition	Succession time	309.6	10.3	363	30.2	<0.05	0.2	*
	Pre-defined correlations								
	Temperature	Temperature^2	1.0	NA	448	1173.5	<0.05	1.0	*
	Height	Height^2	0.7	NA	448	71.8	<0.05	0.7	*
	Height	Competition	0.1	NA	448	8.0	<0.05	0.1	*
	Height^2	Competition	0.1	NA	448	5.7	<0.05	0.1	*
	Height	Temperature	0.0	NA	448	0.8	0.2	0.0	
	Height^2	Temperature	0.1	NA	448	9.4	<0.05	0.1	*
	Height	Temperature^2	0.0	NA	448	1.0	0.2	0.0	
	Height	Snow	0.0	NA	448	-0.4	0.4	0.0	
	Competition	Temperature	0.0	NA	448	-0.5	0.3	0.0	
	Competition	Temperature^2	0.0	NA	448	-0.4	0.3	0.0	
	Height^2	Temperature^2	0.1	NA	448	9.5	<0.05	0.1	*
	Height^2	Snow	-0.2	NA	448	-13.8	<0.05	-0.2	*
	Competition	Snow	0.0	NA	448	1.6	0.1	0.0	
	Succession t.	Growth	-0.1	NA	448	-3.8	<0.05	-0.1	*
	Growth	Temperature_av	0.0	NA	448	1.3	0.1	0.0	
	Tests of directed separation								
	Independence claims:								
	Competition ~ Temperature_av		172.3	367.9	42	0.5	0.6	NA	
	Growth ~ Competition		0.0	0.0	362	-0.7	0.5	NA	

			Est.	SE	df	Crit. Val.	p	Std. Est.	
	Coefficients								
	Response	**Predictor**							
Betula pubescens	Growth	Exclosure	-7.9	0.8	253	-9.3	<0.05	-0.2	*
	Growth	Temperature	1.1	0.3	394	3.9	<0.05	0.1	*
	Growth	Rain	70.78	23.04	394	3.1	<0.05	0.0	*
	Growth	Snow	8.27	1.14	394	7.3	<0.05	0.3	*
	Growth	Height	7.13	0.52	394	13.7	<0.05	0.2	*
	Growth	Competition	-0.06	0.01	394	-4.9	<0.05	-0.1	*
	Growth	Snow^2	-0.02	0.0	394	-4.7	<0.05	-0.2	*
	Height	Exclosure	-24.1	3.7	253	-6.5	<0.05	-0.2	*
	Height	Succession time	13.3	0.2	394	53.6	<0.05	0.5	*
	Height	Temperature_av	11.7	4.1	44	2.8	<0.05	0.2	*

	Height	Rain_av	-20.8	6.0	44	-3.5	<0.05	-0.2	*
	Competition	Exclosure	-933.0	284.4	253	-3.3	<0.05	-0.1	*
	Competition	Succession time	339.6	10.0	394	33.9	<0.05	0.2	*
	Pre-defined correlations								
	Snow	Snow^2	0.9	NA	497	165.8	<0.05	0.9	*
	Height	Competition	0.1	NA	497	3.9	<0.05	0.1	*
	Height	Temperature	-0.1	NA	497	-3.8	<0.05	-0.1	*
	Height	Rain	0.1	NA	497	3.7	<0.05	0.1	*
	Height	Snow	0.1	NA	497	4.9	<0.05	0.1	*
	Height	Snow^2	0.0	NA	497	3.3	<0.05	0.0	*
	Competition	Temperature	0.0	NA	497	-0.4	0.4	0.0	
	Competition	Rain	0.1	NA	497	4.2	<0.05	0.1	*
	Competition	Snow	0.0	NA	497	2.4	<0.05	0.0	*
	Competition	Snow^2	0.0	NA	497	1.8	<0.05	0.0	
	Succession t.	Growth	-0.1	NA	497	-6.0	<0.05	-0.1	*
	Growth	Temperature_av	0.0	NA	497	0.5	0.3	0.0	
	Growth	Rain_av	0.0	NA	497	-0.7	0.3	0.0	
	Tests of directed separation								
	Independence claims:								
	Competition ~ Temperature_av		405.3	384.5	45	1.1	0.3	NA	
	Competition ~ Rain_av		-676.7	558.3	45	-1.2	0.2	NA	

			Est.	SE	df	Crit. Val.	p	Std. Est.	
	Coefficients								
	Response	**Predictor**							
Pinus sylvestris	Growth	Exclosure	-3.3	0.6	180	-5.4	<0.05	-0.1	*
	Growth	Temperature	-1.5	0.3	270	-5.7	<0.05	-0.1	*
	Growth	Rain	51.11	19.72	270	2.6	<0.05	0.0	*
	Growth	Snow	2.06	0.47	270	4.4	<0.05	0.1	*
	Growth	Height	24.92	1.25	270	2<0.0	<0.05	0.9	*
	Growth	Competition	-0.03	0.01	270	-2.9	<0.05	-0.1	*
	Growth	Height^2	-0.05	0.01	270	-8.1	<0.05	-0.3	*
	Height	Exclosure	-11.7	4.4	180	-2.7	<0.05	-0.1	*
	Height	Succession time	14.2	0.3	270	56.0	<0.05	0.6	*
	Height	Rain_av	-31.2	8.4	40	-3.7	<0.05	-0.4	*
	Competition	Succession time	303.5	10.7	270	28.4	<0.05	0.2	*
	Competition	Exclosure	-822.1	349.3	180	-2.4	<0.05	-0.1	*
	Pre-defined correlations								
	Height	Height^2	0.7	NA	341	57.5	<0.05	0.7	*
	Temperature	Temperature^2	1.0	NA	341	1096.8	<0.05	1.0	*
	Height	Competition	0.1	NA	341	3.9	<0.05	0.1	*
	Height^2	Competition	0.0	NA	341	1.9	<0.05	0.0	
	Height	Temperature	0.0	NA	341	0.7	0.3	0.0	
	Height^2	Temperature	0.2	NA	341	11.7	<0.05	0.2	*
	Height	Temperature^2	0.0	NA	341	0.7	0.2	0.0	
	Height^2	Temperature^2	0.2	NA	341	11.6	<0.05	0.2	*
	Height	Rain	0.0	NA	341	1.7	<0.05	0.0	
	Height^2	Rain	-0.1	NA	341	-8.7	<0.05	-0.1	*
	Height	Snow	0.1	NA	341	4.0	<0.05	0.1	*
	Height^2	Snow	-0.2	NA	341	-9.8	<0.05	-0.2	*
	Competition	Temperature	0.0	NA	341	-1.4	0.1	0.0	
	Competition	Temperature^2	0.0	NA	341	-1.2	0.1	0.0	
	Competition	Rain	0.0	NA	341	2.1	<0.05	0.0	
	Competition	Snow	0.0	NA	341	1.0	0.2	0.0	
	Succession t.	Growth	-0.1	NA	341	-6.4	<0.05	-0.1	*
	Growth	Rain_av	0.0	NA	341	-0.6	0.3	0.0	
	Tests of directed separation								
	Independence claims:								
	Competition ~ Rain_av		-927.7	608.5	40	-1.5	0.1	NA	

			Est.	SE	df	Crit. Val.	p	Std. Est.	
	Coefficients								
	Response	**Predictor**							
Picea abies	Growth	Temperature	-11.3	4.0	139	-2.8	<0.05	-0.9	*
	Growth	Snow	2.71	0.55	139	4.9	<0.05	0.1	*
	Growth	Height	29.5	1.92	139	15.4	<0.05	1.2	*
	Growth	Height^2	-0.07	0.01	139	-9.7	<0.05	-0.7	*
	Growth	Temperature^2	0.4	0.2	139	2.7	<0.05	0.9	*
	Height	Succession time	13.1	0.4	139	35.8	<0.05	0.4	*
	Height	Temperature_av	-16.3	5.8	44	-2.8	<0.05	-0.3	*
	Height	Rain_av	-25.4	8.7	44	-2.9	<0.05	-0.3	*
	Competition	Succession time	298.2	18.7	139	15.9	<0.05	0.2	*
	Pre-defined correlations								
	Height	Height^2	0.7	NA	173	43.7	<0.05	0.7	*
	Temperature	Temperature^2	1.0	NA	173	735.1	<0.05	1.0	*
	Height	Competition	0.0	NA	173	0.5	0.3	0.0	
	Height^2	Competition	0.0	NA	173	-1.2	0.1	0.0	
	Height	Temperature	0.0	NA	173	0.5	0.3	0.0	
	Height^2	Temperature	-0.2	NA	173	-7.8	<0.05	-0.2	*
	Height	Temperature^2	0.0	NA	173	0.5	0.3	0.0	
	Height^2	Temperature^2	-0.2	NA	173	-7.9	<0.05	-0.2	*
	Height	Snow	0.0	NA	173	0.9	0.2	0.0	
	Height^2	Snow	-0.1	NA	173	-3.6	<0.05	-0.1	*
	Competition	Temperature	0.0	NA	173	0.1	0.4	0.0	
	Competition	Temperature^2	0.0	NA	173	0.2	0.4	0.0	
	Competition	Snow	0.0	NA	173	1.9	<0.05	0.0	
	Succession t.	Growth	-0.1	NA	173	-3.3	<0.05	-0.1	*
	Growth	Temperature_av	0.0	NA	173	0.8	0.2	0.0	
	Growth	Rain_av	0.0	NA	173	-0.7	0.3	0.0	
	Tests of directed separation								
	Independence claims:								
	Competition ~ Temperature_av		285.3	342.9	45	0.8	0.4	NA	
	Competition ~ Rain_av		-603.9	504.2	45	-1.2	0.2	NA	
	Growth ~ Competition		0.0	0.0	139	-1.0	0.3	NA	

			Est.	SE	df	Crit. Val.	p	Std. Est.	
	Coefficients								
	Response	**Predictor**							
Sorbus americana	Growth	Exclosure	-12.0	2.0	94	-5.9	<0.05	-0.3	*
	Growth	Temperature	7.3	1.4	225	5.2	<0.05	0.3	*
	Growth	Competition	-0.47	0.15	225	3.1	<0.05	0.2	*
	Height	Succession time	15.5	1.1	226	14.0	<0.05	0.5	*
	Height	Exclosure	-20.3	4.2	94	-4.9	<0.05	-0.3	*
	Competition	Succession time	277.2	21.5	226	12.9	<0.05	0.4	*
	Competition	Exclosure	-399.5	87.7	94	-4.6	<0.05	-0.3	*
	Pre-defined correlations								
	Height	Height^2	0.3	NA	333	6.6	<0.05	0.3	*
	Height	Competition	0.0	NA	333	0.1	0.5	0.0	
	Height^2	Competition	0.0	NA	333	-0.5	0.3	0.0	
	Height	Temperature	-0.1	NA	333	-2.0	<0.05	-0.1	
	Height^2	Temperature	0.1	NA	331	1.0	0.3	0.1	
	Competition	Temperature	0.0	NA	333	<0.05	0.5	0.0	
	Succession t.	Growth	0.0	NA	333	-0.2	0.4	0.0	
	Tests of directed separation:								
	Independence claims								
	Growth ~ Height		0.0	0.0	223	0.2	0.8	NA	

			Est.	SE	df	Crit. Val.	p	Std. Est.	

	Coefficients								
	Response	**Predictor**							
Betula sp.	Growth	Exclosure	-12.5	2.1	153	-5.9	<0.05	-0.3	*
	Growth	Temperature	7.5	1.6	243	4.7	<0.05	0.2	*
	Height	Succession time	12.5	1.3	245	9.9	<0.05	0.3	*
	Height	Exclosure	-26.4	4.8	153	-5.5	<0.05	-0.3	*
	Competition	Succession time	241.4	19.7	245	12.2	<0.05	0.3	*
	Competition	Exclosure	-422.4	102.0	153	-4.1	<0.05	-0.3	*
	Pre-defined correlations								*
	Height	Competition	0.2	NA	414	4.3	<0.05	0.2	*
	Height	Temperature	0.0	NA	414	-0.9	0.2	0.0	
	Competition	Temperature	0.0	NA	414	-0.2	0.4	0.0	
	Succession t.	Growth	0.0	NA	414	0.6	0.3	0.0	
	Tests of directed separation:								
	No independence claims present.								

			Est.	SE	df	Crit. Val.	p	Std. Est.	
	Coefficients								
	Response	**Predictor**							
Abies balsamea	Growth	Exclosure	-62.5	18.8	313	-3.3	<0.05	-2.1	*
	Growth	Temperature	0.6	1.1	790	0.6	0.6	0.0	
	Growth	Snow	28.23	8.32	790	3.4	<0.05	1.1	*
	Growth	Height	-16.32	1.86	790	-8.8	<0.05	-0.3	*
	Growth	Competition	0.28	0.09	790	3.3	<0.05	0.1	*
	Growth	Snow^2	-0.04	0.01	790	-3.6	<0.05	-1.2	*
	Growth	Exclosure:Temperature	4.3	1.3	790	3.3	<0.05	2.0	*
	Height	Succession time	1.4	0.4	795	3.3	<0.05	0.1	*
	Height	Exclosure	-5.5	2.4	313	-2.3	<0.05	-0.1	*
	Competition	Succession time	158.1	10.1	795	15.6	<0.05	0.3	*
	Competition	Exclosure	-229.2	44.2	313	-5.2	<0.05	-0.2	*
	Pre-defined correlations								
	Snow	Snow^2	1.0	NA	112	345.1	<0.05	1.0	*
	Height	Competition	0.1	NA	112	2.4	<0.05	0.1	*
	Height	Temperature	-0.1	NA	112	-1.8	<0.05	-0.1	
	Height	Snow	0.0	NA	112	1.0	0.2	0.0	
	Height	Snow^2	0.0	NA	112	1.3	0.1	0.0	
	Competition	Temperature	0.0	NA	112	-0.7	0.3	0.0	
	Competition	Snow	0.0	NA	112	-1.0	0.2	0.0	
	Competition	Snow^2	0.0	NA	112	-0.7	0.2	0.0	
	Succession t.	Growth	0.1	NA	112	2.5	<0.05	0.1	*
	Tests of directed separation:								
	No independence claims present								

			Est.	SE	df	Crit. Val.	p	Std. Est.	
	Coefficients								
	Response	**Predictor**							
Picea sp.	Growth	Temperature	6.4	1.4	212	4.7	<0.05	0.2	*
	Height	Succession time	3.8	0.9	214	4.1	<0.05	0.1	*
	Competition	Succession time	154.4	17.4	214	8.9	<0.05	0.3	*
	Competition	Exclosure	-304.2	90.2	113	-3.4	<0.05	-0.2	*
	Pre-defined correlations								
	Height	Competition	0.1	NA	343	1.3	0.1	0.1	
	Height	Temperature	0.0	NA	343	-0.8	0.2	0.0	
	Competition	Temperature	0.0	NA	343	-0.4	0.3	0.0	
	Succession t.	Growth	0.0	NA	343	-0.2	0.4	0.0	
	Tests of directed separation:								
	Independence claims								
	Height ~ Exclosure		1.8	6.0	113	0.3	0.8	NA	
	Growth ~ Exclosure		-2.0	1.6	113	-1.2	0.2	NA	

Table S6. Model coefficients (estimates, standard errors, t- and p-values) for ZAG-models for each species, presented separately for continuous gamma and binomial Bernoulli parts.

			Gamma					Bernoulli				
			Est.	Std. Err.	t	Pr(>|z|)		Est.	Std. Err.	t	Pr(>|z|)	
Sorbus aucuparia	Intercept		4.1	0.1	37.8	< 2e-16	*	3.2	0.9	3.5	0.001	*
	Moose		0.1	0.0	3.9	0.000	*	1.4	0.3	5.7	<0.001	*
	Height		-0.8	0.0	-38.9	< 2e-16	*	-0.8	0.2	-5.1	<0.001	*
	FAI	.	0.0	0.0	1.7	0.082		0.0	0.0	-3.5	<0.001	*
	Temperature		0.3	0.1	3.4	0.001	*	-0.4	0.7	-0.7	0.502	
	Rain		-0.1	0.1	-0.9	0.357		-0.8	0.6	-1.5	0.144	
	Snow		0.0	0.0	-2.7	0.008	*	-0.3	0.1	-2.8	0.005	*
Betula pubescens	Intercept		3.7	0.2	17.8	< 2e-16	*	-0.6	0.8	-0.8	0.439	
	Moose		0.4	0.1	7.5	0.000	*	1.9	0.2	9.4	< 2e-16	*
	Height		-1.1	0.0	-28.7	< 2e-16	*	0.8	0.1	6.7	<0.001	*
	FAI	.	0.0	0.0	4.6	0.000	*	0.0	0.0	0.7	0.486	
	Temperature		-0.1	0.1	-0.5	0.621		-0.3	0.6	-0.5	0.632	
	Rain		0.1	0.1	0.8	0.413		-0.4	0.5	-0.8	0.424	
	Snow		-0.1	0.0	-2.8	0.006	*	-0.6	0.1	-5.4	<0.001	*
Pinus sylvestris	Intercept		4.1	0.5	8.3	< 2e-16	*	-1.9	1.3	-1.5	0.139	
	Moose		0.4	0.1	3.0	0.003	*	2.4	0.3	7.8	<0.001	*
	Height		-0.8	0.1	-9.5	< 2e-16	*	1.7	0.2	8.7	< 2e-16	*
	FAI	.	0.0	0.0	3.4	0.001	*	0.0	0.0	3.0	0.003	*
	Temperature		-0.5	0.3	-1.4	0.154		-1.3	0.9	-1.4	0.157	
	Rain		-0.8	0.3	-2.7	0.006	*	-2.0	0.8	-2.4	0.014	
	Snow		-0.1	0.1	-1.7	0.096		-1.3	0.2	-6.1	<0.001	*
Picea abies	Intercept		3.3	0.0	1143.5	<2e-16	*	-2.0	1.9	-1.1	0.294	
	Moose		0.1	0.0	29.5	<2e-16	*	1.1	0.3	4.1	<0.001	*
	Height		-0.9	0.0	-323.2	<2e-16	*	0.7	0.2	3.1	0.002	*
	FAI	.	0.0	0.0	1.8	0.066		0.0	0.0	-1.2	0.213	
	Temperature		-0.8	0.0	-277.3	<2e-16	*	-3.7	1.4	-2.6	0.008	*
	Rain		1.5	0.0	524.3	<2e-16	*	2.0	1.8	1.1	0.273	
	Snow		-0.6	0.0	-207.0	<2e-16	*	0.4	0.3	1.5	0.144	
Sorbus americana	Intercept		2.6	0.5	5.0	0.000	*	-	2.1	-5.2	<0.001	*
	Moose		1.1	0.1	7.9	0.000	*	1.7	0.2	10.8	< 2e-16	*
	Height		0.1	0.1	1.3	0.187		0.4	0.2	1.7	0.089	
	FAI	.	0.0	0.0	1.0	0.299		0.0	0.0	-1.1	0.278	
	Temperature		1.2	0.3	4.7	0.000	*	4.8	1.4	3.5	<0.001	*
	Rain		0.0	0.0	0.6	0.548		1.6	0.2	6.8	<0.001	*
	Snow		0.0	0.0	0.2	0.806		-1.1	0.1	-7.7	<0.001	*
Betula sp.	Intercept		3.4	0.4	9.0	< 2e-16	*	-6.8	1.8	-3.7	<0.001	*
	Moose		0.2	0.0	6.9	0.000	*	2.2	0.2	10.2	< 2e-16	*
	Height		-0.4	0.1	-5.2	0.000	*	0.6	0.2	2.4	0.014	
	FAI	.	0.0	0.0	-1.4	0.150		0.0	0.0	-3.0	0.003	*
	Temperature		-0.1	0.3	-0.5	0.636		-2.4	1.3	-1.8	0.067	
	Rain		0.4	0.1	7.6	0.000	*	1.7	0.3	6.6	<0.001	*
	Snow		-0.1	0.0	-3.6	0.000	*	0.1	0.1	0.4	0.710	
Abies balsamea	Intercept		2.7	0.3	8.3	< 2e-16	*	-2.5	0.9	-2.8	0.005	*
	Moose		0.2	0.1	3.3	0.001	*	2.0	0.1	17.8	< 2e-16	*
	Height		-0.3	0.0	-7.8	0.000	*	3.5	0.1	27.3	< 2e-16	*
	FAI	.	0.0	0.0	-4.0	0.000	*	0.0	0.0	-3.4	0.001	*
	Temperature		1.1	0.2	5.4	0.000	*	-2.0	0.5	-3.8	<0.001	*
	Rain		-0.1	0.0	-5.0	0.000	*	-0.3	0.1	-3.5	<0.001	*
	Snow		-0.1	0.0	-3.6	0.000	*	0.0	0.1	-0.2	0.847	

Supplementary references

Peterson BG, Carl P, Boudt K, Bennett R, Ulrich J, Zivot E, Cornilly D, Hung E, Lestel M, Balkissoon K, Wuertz D. Package ‘PerformanceAnalytics’. R Team Cooperation. 2018.

Kolstad AL, Austrheim G, Solberg EJ, De Vriendt L, Speed JD. Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species. Ecosphere. 2018 Oct;9(10):e02458.

Paper III

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Herbivores counteract the effects of warming on Arctic shrub growth at intermediate temperatures

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Abstract

Global warming has pronounced impacts on tundra vegetation, and increasing mean temperatures may increase plant growth potential across the Arctic tundra biome. However, herbivores can modify and counteract the warming impacts by lowering plant growth. Yet, the strength of this herbivore buffer may depend in prevailing climatic conditions. To study how ungulates interact with temperature to shape growth of tundra shrubs across the Arctic tundra biome, we assembled dendroecological data from 20 sites, comprising 1,388 individual shrubs and 25,017 annual growth rings. Our analysis showed that the negative effect of herbivore density on shrub radial growth was at its highest at intermediate summer temperatures (~7.5°C), and the effect diminished towards colder and warmer conditions. Multiple factors, including landscape use and forage preferences of the herbivores, as well as mediating effect of precipitation, may explain these findings. Our results demonstrate that herbivores are able to counteract the effects of warming on arctic shrub growth under certain conditions, and identify potential climatic limits to this effect.

Main

Tundra plants are known to be sensitive to climatic changes (Björkman et al., 2020; Chapin III et al., 1992; Myers-Smith et al., 2020). During the past decades, the warming Arctic has experienced increases in vegetation cover, height, biomass and abundance, resulting in greening (Berner et al., 2020; Björkman et al., 2018; Björkman et al., 2020; Bolton et al., 2018; Carlson et al., 2017). Along this continuing transition, changes in species diversity (Boscutti et al., 2018; Niskanen et al., 2017), phenology (Prevéy et al., 2019), and ecosystem functioning (Bret-Harte et al., 2019; Jespersen et al., 2018; Yu et al., 2017) are expected and observed. Increased shrub abundance (García Criado et al., 2020; Myers-Smith and Hik, 2018; Naito and Cairns, 2011; Vowles and Björk, 2019) may even change albedo and soil carbon storage, reflecting back to climate (Bonfils et al., 2012; DeFranco et al., 2020).

Yet, recent studies have shown that tundra vegetation changes are anything but uniform (Berner et al., 2020; Björkman et al., 2020; Myers-Smith et al., 2020). Heterogeneity in plant growth responses to climatic variation suggests that factors other than abiotic conditions also play a role, counteracting or modifying climatic effects. The circumpolar tundra is characterized by strong interactions between herbivores and seasonally available plants (Oksanen et al., 2020), and a key role in these interactions is played by ungulates, such as reindeer/caribou (*Rangifer tarandus*; Cohen et al., 2013; Kaarlejärvi et al., 2015; Olofsson et al., 2004a; Olofsson et al., 2009; Plante et al., 2014; Vowles et al., 2017; Ylänne et al., 2018), muskoxen (*Ovibos moschatus*; Mosbacher et al., 2019; Post and Pedersen, 2008) and sheep (*Ovis aries*; Speed et al., 2012; Speed et al., 2013). Ungulate herbivores can, for example, slow down, stop or even reverse woody plant increases caused by warming (Cahoon et al., 2012; Christie et al., 2015; Olofsson et al., 2009; Plante et al., 2014; Speed et al., 2013; Vowles et al., 2017). Rodents, such as collared lemmings (*Dicrostonyx* spp.) and grey-sided voles (*Myodes rufocanus*) may play similar roles (Legagneux et al., 2014), but they appear to interact primarily with dwarf shrubs rather than with shrubs with erect or semi-erect shoots (Olofsson et al., 2004b).

The potential of ungulates to control woody plant growth is especially strikingly demonstrated in northern Fennoscandia, where ungulates have stabilized tree lines (Aune et al., 2011; Vuorinen et al., 2017) and suppressed shrubs (den Herder et al., 2008; Ims and

Henden, 2012; Pajunen et al., 2012), in spite of a warming climate. It is, however, unclear whether and how this potential of ungulates to buffer warming induced changes in growth varies throughout the tundra. Precipitation, snow and moisture conditions may change shrubs' response both to warming and to ungulates. Furthermore, different climatic regimes of the Arctic harbour different shrub and ungulate species, likely leading to different buffer strengths. For example, it has been suggested that browsing is likely to retard birch expansion in Fennoscandia and western Siberia as these areas are dominated by less effectively defended non-resin birches, whereas in the North-American mainland, browsing is less likely to retard birch expansion as the prevailing birch species are more effectively defended through resins (Bryant et al., 2014). Overall, interactions between ungulates and climate remain understudied (Andruko et al., 2020; García Criado et al., 2020; Olofsson and Post, 2018). Climatic factors and ungulates are rarely simultaneously quantified in studies of tundra ecosystems (Christie et al., 2015; Plante et al., 2014; Vuorinen et al., 2017), and the existing studies are usually undertaken at local scale with differing methods (Kaarlejärvi et al., 2015; Olofsson et al., 2009; Speed et al., 2013), making it challenging to scale up effects to a pan-Arctic level. Thus, while it is clear that ungulates can, in principle, modify climate effects, the question remains: under which conditions do ungulates change and override climatic responses of plants across the Arctic?

During the past decades, the tundra biome has experienced simultaneous changes in climate (Björkman et al., 2020; Myers-Smith et al., 2020), and in herbivore densities (Andruko et al., 2020; Cuyler et al., 2020; Speed et al., 2019; Vors and Boyce, 2009), and the concurrent nature of these changes has made it hard to disentangle their effects on vegetation dynamics. In this study, we overcome this challenge by examining the radial growth of deciduous shrubs, woody plants that play a central part in tundra vegetation change by driving the vegetation structure, albedo, carbon balance and other ecosystem properties (García Criado et al., 2020; Myers-Smith and Hik, 2018; Naito and Cairns, 2011; Vowles and Björk, 2019). The growth rings of these shrubs provide a standardized basis for assessment of radial growth variation over decades and large spatial scales (Myers-Smith et al., 2015b), enabling analysis across the tundra biome. We compiled dendroecological data from 20 sites (Fig. 1) to quantify the effect sizes of summer temperature and ungulates on shrub growth under different conditions, and to answer the question: Does the shrub radial growth response to ungulates depend on summer temperature conditions across the Arctic? In addition, we relate the results to summer precipitation, winter precipitation, local soil moisture and ungulate and shrub species in question to identify whether they could be linked to the shrub growth patterns observed under different ungulate and summer temperature conditions.

Results & Discussion

By modelling shrub radial growth as a response to annual climatic factors and annual ungulate density, we found that ungulate density decreased shrub radial growth strongest at summer temperature ~7.5°C. When moving to higher and lower summer temperatures, the effect of ungulate density on shrub radial growth decreased, and the effect of summer temperature increased. This can be seen in Fig. 2 where predicted shrub radial growth is presented as green colour at different ungulate densities and summer temperatures: the closer we are the summer temperature 7.5°C, the more horizontal the shrub radial growth isoclines are, indicating high relative ungulate density effect, but when moving towards higher or lower summer temperatures, the isoclines turn vertical, indicating high relative summer temperature effect. When the ungulate effect was at its highest, an increase of around 4 kg km^{-2} in ungulate density was linked to a decrease in shrub radial growth of 0.1 mm^2, but for most of the observed ungulate density and temperature conditions, ungulate density effect was moderate (Fig. 2; Table 1).

These results suggest that ungulates may have best chances to counteract warming effects on shrub radial growth at intermediate summer temperatures (~7.5°C; Fig. 2; see also Appendix S1: Fig. S1), typical for sites in northern Sweden (Ritsem), eastern Canada (Deception Bay, Boniface), western Canada (Qikiqtaruk), and southern Alaska (Dalton Highway; Fig. 3; see also Appendix S1: Fig. S2 for each site's position on summer temperature – ungulate density plane). It is possible that when moving towards the warm and cold ends of the observed temperature gradient, temperature becomes a more critical determinant of shrub radial growth so that it eventually overrides potential ungulate effects.

However, these results should not be interpreted separate from the other abiotic and biotic factors. At the warmer end of the observed summer temperature gradient (>8°), high ungulate densities were associated with high summer precipitation (Appendix S1: Fig. S3a) and high winter precipitation (Appendix S1: Fig. S3b). It is possible that ungulate effects were not detected under high summer temperatures because they were counteracted by precipitation: summer rain and a longer snow-cover period can be hypothesized to increase shrubs' potential for compensatory growth and decrease shrubs' vulnerability to herbivory (Jespersen et al., 2018; Ossi et al., 2015; Ueda et al., 2002; White et al., 2009; also, our analysis showed a positive shrub radial growth response to summer precipitation, see Table 1). Furthermore, snow may modify biogeochemical and hydrological conditions to be more favourable for shrub growth (Jespersen et al., 2018; Pattison and Welker, 2014). This may explain why our model predicted a low ungulate effect at high summer temperatures, typical for sites in southern Sweden (Långfjället), eastern Russia (Chokurdakh), northern Alaska (Toolik), central northern Canada (Daring Lake), and western Greenland (Kangerlussuaq; Fig. 3; Appendix S1: Fig. S2). Local soil moisture conditions did not have apparent connection to the observed trends (Fig. S3c).

Furthermore, sites with high summer temperature, high precipitation, and high ungulate density were typically dominated by sheep (Appendix S1: Fig. S4a). As grazers (Hofmann, 1989; Kausrud et al., 2006), sheep may be less efficient in moderating shrub radial growth than reindeer and muskox, especially if the landscape harbours abundant forage that is more preferred than shrubs. In addition, sheep are present at the sites only during the summer season. These connections may be an additional factor explaining why our model predicted no negative ungulate density effect for conditions typical for sample sites in northern Norway and Iceland (Fig. 3). Interestingly, for the conditions typical for mild, moist, sheep-dominated southern Norway, the model predicted a moderate positive ungulate density effect (shown by isoclines inclined to the left at temperatures above ~10°C and at ungulate densities above ~100 kg km^{-2} in Fig. 2; these are the conditions typical for sites in southern Norway, as shown in Appendix S1: Fig. S2). This is possibly driven by suppression of competing plants by sheep (Bråthen and Lortie, 2016; Speed et al., 2013).

At the colder end of the observed summer temperature gradient (<7°), our data captured less variation in ungulate densities compared to the captured variation in ungulate densities under warmer conditions (shown by narrow ungulate density coverage under summer temperatures below 7°C in Fig. 2). This may explain why ungulate density appeared to be lacking in High Arctic (Svalbard and eastern Greenland; Fig. 3). It may be that high-Arctic shrubs are responsive to changes in ungulate densities, but our model failed to detect this effect. Another explanation for the lack of herbivore response in the high Arctic is that the shrubs from this area were small, prostrate species (Table S1), not necessarily damaged by ungulates to the same extent as taller, erect shrub species (Vowles and Björk, 2019).

Summer temperature affected shrub radial growth positively at summer temperatures 1.5-7.5°C, but negatively at higher summer temperatures (7.5-14°C; Fig. 2; see also Appendix S1: Fig. S5). This may be due to extreme climatic events associated to high average summer temperatures, such as drought events, spring stress (Welker et al., 2005; Welker et al., 1993), or icing events related to winter precipitation (Le Moullec et al., 2020), but also simply due low shrub growth at the warmest sites driven by some other factor than temperature (Fig. S5b). Summer temperatures lower than ~5°C were generally accompanied by low summer and winter precipitation, whereas at higher temperatures, we observed a wider range of precipitation values (Fig. 2a, Appendix S1: Fig. S3a,b). Water availability may also increase shrubs' potential to respond positively to warming (Ackerman et al., 2017; Myers-Smith et al., 2015a; Naito and Cairns, 2011). These precipitation patterns could potentially contribute to low shrub radial growth at low temperatures. However, according to variance inflation factors (Table 1), collinearity was low, so precipitation is not expected to distort the temperature coefficients. Nevertheless, shrub growth in the high Arctic may be constrained by factors not accounted for in this study, such as available sunlight.

It is possible that the observed ungulate density and summer temperature effects were partly a result of shrub species turnover across the ungulate density and summer temperature gradients. At cold temperatures, only small *Salix* species were present, whereas at higher temperatures, the shrub species pool consisted of tall *Salix* species and *Betula nana*/*glandulosa* (Appendix S1: Fig. S1c, Fig. S4b, Fig. S5c, Table S1). This reflects the natural abundances of different species under different climatic conditions. However, the most prevalent genus, *Betula*, showed the above-described patterns when analysed separately from other shrubs (Appendix S1: Fig. S6), suggesting that the observed general patterns cannot be accounted solely to shrub species turnover. Interestingly, we also did not found any apparent support for shrub responses begin different between North-America and north-western Eurasia, despite differences in shrub palatability (Bryant et al., 2014).

The potential of ungulates to affect local shrub responses may also be dependent on how ungulate individuals are dispersed in space and time (Schmidt et al., 2016; Skarin et al., 2020). Migratory ungulates may affect tundra vegetation at different times of the year, with varying intensities within different time frames, possibly leading to different effect strengths on shrub growth. For example, the Riviere-aux-Feuilles caribou herd migrates frequently through the easternmost shrub sampling site in the Canadian Arctic (Morrissette-Boileau et al., 2018; Nicholson et al., 2016), whereas northern summer grazing sites are exposed to more constant grazing pressure. On the other hand, sheep (Speed et al., 2014), much like muskox in Greenland (Beumer et al., 2020; Schmidt et al., 2016), are more sedentary, imposing a more constant summer browsing pressure. When present, ungulates may also use the landscape unevenly: It is possible that we did not observe ungulate effects under certain summer temperature conditions because under these conditions, ungulates did not trample or forage at the exact shrub sampling spots. Thus, our results should not be taken as evidence of lack of shrubs' responses to ungulate on the landscape level. Furthermore, ungulate effects on sampled shrubs may depend on the forage preferences of the ungulates (Welker et al., 2005), and on the prevalence of potentially more preferred forage species, such as graminoids and forbs, in the landscape

Ungulate density, mean summer temperature, summer precipitation, winter precipitation, shrub age, and the interaction between annual ungulate density and mean summer temperature explained 32% of the variation in shrub radial growth, suggesting that there are likely to be also other important environmental variables that define shrub growth rates. This needs to be kept in mind when evaluating the role of temperature and ungulates. In our analysis, age, summer temperature and precipitation, and the interaction of summer temperature and ungulate density scored highest in the variable importance (Appendix S1: Fig. S7a), but it is known that for example rodents and insect outbreaks can modify shrub growth, potentially exceeding the effect sizes of ungulate herbivores (Post and Pedersen, 2008; Prendin et al., 2020).

As our dataset included some ungulate exclosure studies (Fig. 1), we also ran an additional analysis to see whether experimental ungulate exclusion and summer temperature interacted in determining shrub radial growth. However, we did not find summer temperature or ungulate density effects (Appendix S1: Table S2), likely due to low amount of data and short chronologies from the majority of the exclosure sites, reflecting the relatively short experimental ungulate exclusion periods (Appendix S1: Table S3).

Conclusions

Our results are in line with previous studies that have suggested that ungulates can counteract warming effects on shrubs (Christie et al., 2015; Olofsson et al., 2009; Post and Pedersen, 2008; Speed et al., 2010; Vowles et al., 2017). However, we showed that under the observed densities of ungulates, the negative effect of ungulates on shrub radial growth appeared to be at its highest at intermediate summer temperatures of the Arctic (~7.5 C). Consequently, under the colder (summer temperature <7°) and the warmer (summer temperature >8°) conditions, shrub radial growth appeared to be predominantly responsive to summer temperature rather than to ungulate density. Even though exact mechanisms behind these patterns are hard to prove, our results suggest that climatic factors may interact with ungulate density in determining shrub radial growth. This needs to be acknowledged when evaluating the potential of current herbivore densities to counteract the effects of warming.

There are several potential factors for why shrub growth dynamics across the Arctic do not necessarily fit the simple story where warming increases shrub growth and ungulates decrease it equally everywhere. Firstly, ungulates may use different plant species (Welker et al., 2005) and different parts of the landscape unevenly (Schmidt et al., 2016; Skarin et al., 2020), depending on both plant and ungulate characteristics, which leads to varying herbivore buffer strengths. Secondly, there are also other abiotic factors in addition to temperature that are likely to complicate the picture. It is possible that at the sites where we observed the highest ungulate densities, high precipitation values led to high moisture availability that increased shrub growth potential, and thus counteracted the effect of high ungulate densities. Similarly, winter precipitation may lead to higher snow cover protection against ungulates. Yet, naturally, our results only apply within the observed ungulate density range. Sufficiently high densities of ungulates – above the densities studied here – can be expected to be able to counteract warming effects on shrub growth regardless of other biotic conditions and climate.

It has been suggested that herbivore management could be used to mitigate the effects of climatic changes on ecosystems across the globe (Cromsigt et al., 2018; Macias-Fauria et al., 2020; Olofsson and Post, 2018; Verma et al., 2020). However, only recently have we started to unravel the complicated relationships between climate and herbivore effects on vegetation. It has been shown, for example, that African browsers and fire can interact to affect tree density (Staver and Bond, 2014; Staver et al., 2009), and that moose and deer can "cool down" boreal tree growth responses to warming (Fisichelli et al., 2012; Vuorinen et al., 2020a; Vuorinen et al., 2020b). However, overall knowledge of biotic buffers to climate change effects is still sparse. Our study has shed light on under which conditions ungulates are most likely to mediate tundra shrub radial growth, yet, further studies on other crucial shrub characters, such as shrub cover, height and stem establishment rate (Myers-Smith et al., 2011), are needed to understand how climate and herbivores interact in shaping arctic shrubification trends.

Methods

We assembled a database that comprised published and unpublished shrub radial growth and ungulate data from 20 sites across the Arctic tundra biome, including the oroarctic tundra *sensu* (Virtanen et al., 2016). We included studies where both shrub growth and ungulate abundance data were available, irrespective of their study design. The data included 1,388 individual shrubs and 28,228 ring measurements (Fig. 1; Appendix S1: Table S1, S4).

Ungulate abundance data

Large ungulate species (i.e. body mass >50kg) occurring at the study sites were reindeer/caribou (*Rangifer tarandus*), muskox (*Ovibos moschatus*) and sheep (*Ovis aries*). Different types of abundance data available for these species (Appendix S1: Table S5) were converted to approximation of metabolic biomass per square kilometre (i.e. biomass$^{0.75}$; kg km^{-2}) per year, based on literature and local expert knowledge (Appendix S1: Table S5). Data on body size variation within ungulate populations was not available in most cases, and thus we used average male weight (Appendix S1: Table S5) to acquire the potential maximum metabolic biomass density; even when not precise on the absolute biomass scale, we expect this measure to capture the interannual variation and approximate site differences in ungulate density. The size of the area over which ungulate numbers were estimated differed among studies (Appendix S1: Table S5), and therefore the metabolic biomass estimates should be regarded as approximations that vary in spatial precision. Biomass values were log-transformed before analyses to homogenize the residual variance.

Climate data

We used climate data from the Climatic Research Unit Time-Series version 4.03 of high-resolution gridded data of month-by-month variation in climate (CRU TS 4.03; Harris, 2019), a global climate model on a 0.5° latitude by 0.5° longitude grid that covers the time period of 1901-2018 and thus all our shrub chronologies (Appendix S1: Table S1). This data correlates highly with climate data from meteorological stations (Myers-Smith et al., 2015a). For each of the shrub sampling sites, we extracted monthly mean temperature and precipitation data covering the available shrub growth chronology periods. The repeated site mean values that are used to gap fill CRU data (Macias-Fauria et al., 2014) were removed. For data from Svalbard and the Dalton Highway (Fig. 1), this resulted in considerable drop in available precipitation data (values not available for >30% of shrub chronology data points), and thus we substituted CRU data with local climate station data in these two cases (Appendix S1: Supplementary Methods 1). Annual averages for mean summer temperature (June-August), summer precipitation and winter precipitation (October-April) were then calculated for each shrub sampling site. As precipitation does not necessarily describe the local soil moisture conditions, each data contributor was asked to assess the moisture class of the site based on three classes: 1) Dry: soil is dry to the touch throughout the summer, apart from just after rain; 2) Moist: soil is wet to the touch throughout most of the summer apart from particularly dry spells; 3) Wet: standing water is present and the soil is saturated throughout the summer (Myers-Smith et al., 2015a). All sites were described as either Dry or Moist on average, i.e. there were no Wet sites in our data.

Shrub data

Shrub data series came from three functionally distinct groups: dwarf birch (*Betula nana*, *B. glandulosa*), two small, prostrate *Salix* species (*S. arctica*, *S. polaris*) and five large, erect *Salix* species (*S. pulchra*, *S. glauca*, *S. richardsonii*, *S. lapponum*, *S. lanata*; Appendix S1: Table S1). The majority of data originated from randomly sampled shrubs with chronologies established at the stem base; however, a portion of the data came from selectively chosen large individuals (stratified sampling involving only one part of the population) and chronologies that were measured at the root collar (Fig. 1; Appendix S1: Table S1). In most cases, one cross-section with four measured radii was sampled for each shrub, and these four radii measurements were averaged for each shrub. If multiple sections were acquired from the same shrub individual, measurements were again averaged to acquire one chronology for each shrub. We accepted shrubs from ungulate exclosure experiments, but not shrubs subjected to any other experimental treatments. Ring widths were converted to basal area increment (BAI) by using the dplR-package (Bunn et al., 2019) to account for geometrical growth trends, assuming that ring circumference can be approximated by a circle (Biondi and Qeadan, 2008). Prior to the analysis, we excluded ring measurements of younger than 5 years of shrub age to account for typical irregular growth patterns of young individuals (Myers-Smith et al., 2015b). To meet the assumption of normality, BAI was log-transformed prior to analyses. After applying the constrains described above, and excluding years with no ungulate data, we had 25,017 ring measurements from 1,388 shrubs, covering the time period of 1973-2018.

Statistical Analyses

Our ungulate data consisted of non-experimental annual densities of natural and managed ungulate populations, and on annual experimental zero-ungulate densities within exclosures (Fig. 1). To be able to test for ungulate interactions reliably, data needed to be balanced across the captured ungulate density range. To achieve this, we ran two separate analysis: 1) one to test the effects of variation in observational ungulate density, and 2) one to test the effects of experimental presence-absence of ungulates. In the first analysis, we included only the data points outside of the experimental exclosures; in the second analysis, we only included data from within exclosures and from corresponding open control plots including only shrub rings grown after the exclosure fence installation. The analysis looking into the effects of variation in observed ungulate density included 18,327 BAI values from 1,078 shrub individuals from 20 sites (see Appendix S1: Fig. S8 for distribution of data in time, and shrub ages). As the number of ungulate exclusion studies was limited and exclusion times typically short, the analysis looking into the effects of experimental presence-absence of ungulates only included 2,936 BAI values from 247 shrub individuals from 8 sites (see Appendix S1: Table S3 for details on this dataset).

In the analysis looking into the effects of variation in observed ungulate density, we modelled log-transformed BAI as a response to annual ungulate metabolic biomass density, summer temperature, summer precipitation, winter precipitation and interaction of summer temperature and ungulate metabolic biomass density in a linear mixed-effects model, by using lme-function of the nlme-package (Pinheiro et al., 2017). Shrub age was used as a log-transformed covariate as we found a non-linear relationship between age and BAI (Appendix S1: Fig. S9). We also fitted a quadratic term for summer temperature, as we expected that the shrub growth response to temperature may turn negative at high temperatures, especially if warm summer conditions are associated with longer snowy period or drying events in spring (Phoenix and Bjerke, 2016). Values of summer temperature, summer precipitation and ungulate density were values from the same shrub growth year, whereas values of winter precipitation were from the previous winter (i.e. including winter months of the previous year). Spatial and temporal dependencies were accounted for by nesting shrub individuals within sites and sites within years as random factors. VIF-values of linear effects were checked for potential collinearity issues, and remained acceptable (Table 1; Graham, 2003). Soil moisture classification was not included into the model as its primary purpose was to ensure that soil moisture was not collinear with temperature conditions (Appendix S1: Fig. S3c). We also did not include shrub or ungulate species into the model as we knew that these variables would necessarily be collinear with summer temperature; the potential underlying effects of ungulate and shrub species are discussed in the Results section.

The model structure of the analysis looking into the effects of experimental presence-absence of ungulates was similar to that of the analysis looking into the effects of observed ungulate density, but annual ungulate density was replaced with annual ungulate presence-absence. In addition, we had to exclude winter precipitation as it was collinear with summer precipitation in this dataset, and thus these two variables could not be disentangled. Summer precipitation was selected as it was deemed to be more likely driver for shrub growth than winter precipitation.

We applied model averaging for both analyses to avoid model selection uncertainty, and to avoid potentially unimportant variables from gaining unreasonably much weight in the models (Cade, 2015; Dormann et al., 2018; Johnson and Omland, 2004). Averaging was done by using MuMIn package (Barton, 2016). We first build all possible models between null model and a full model with all explanatory variables and the interaction of summer temperature and ungulate factors by using the dredge-function. Coefficient estimates were then acquired by averaging the estimates across these models weighted by model AIC, by using the model.avg-function.

In the first model, we were dealing with two continuous variables (summer temperature and annual ungulate density) and a continuous response variable (BAI). To visualise this three-dimensional data, we created heat maps where y-axis represented annual ungulate density, x-axis represented summer temperature, and the predicted BAI-values were presented as colour on this summer temperature – ungulate density plain. This also allowed us to visualize potential interactive collinearities with other climatic variables that cannot be detected by VIFs.

All analyses were carried out within the R environment (R version 3.5.1, R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

Data availability

Climatic Research Unit Time-Series version 4.03 of high-resolution gridded data of month-by-month variation in climate (CRU TS 4.03; Harris, 2019) is available at CRU repository (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.03/; see also https://catalogue.ceda.ac.uk/uuid/10d3e3640f004c578403419aac167d82). Ungulate data sources are given in Appendix S1: Table S5.

Shrub datasets (as specified in Appendix S1: Table S1) are available at following repositories:

Chronologies from Dalton Highway, Toolik, Deception Bay, Zackenberg, Audkuluheidi, Theistareykir, Ritsem, Långfjället, Setesdal, Hol (Speed et al., 2013), Rakkonjarga, Varjjatnjarga, Erkuta and Chokurdakh (Li et al., 2016) on Dryad.

Chronologies from Semmeldalen and Ny-Ålesund (Le Moullec et al., 2019a; Le Moullec et al., 2020) on Dryad (http://dx.doi.org/10.5061/dryad.k3j9kd54c, and http://datadryad.org/resource/doi:10.5061/dryad.d7p3b40).

Chronologies from Kangerlussuaq (Sullivan, 2012) on the NSF Arctic Data Center (https://arcticdata.io/catalog/#view/urn:uuid:3dc91064-7b8b-4308-b949-a361b7146baa).

Chronologies from Boniface (Ropars, 2015) on Dryad (doi: 10.5061/dryad.n812k).

Chronologies from Daring lake (Andruko et al., 2020) on the Polar Data Catalogue (http://link.springer.com/article/10.1007/s10021-019-00474-7).

Chronologies from Qikiqtaruk on GitHub repository for the ShrubHub growth ring database (https://github.com/ShrubHub/ShrubringHub; Myers-Smith et al., 2015) and on Qikiqtaruk Ecological Monitoring Database (DOI 10.5281/zenodo.2397996; https://zenodo.org/record/2397996#.X2scO2gzZaQ)

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Table 1. Model-averaged coefficients for the main model with ungulate metabolic biomass density: estimates, standardized estimates, standard errors, adjusted standard errors, z-values and Wald-test based p-values. Variance inflation factors (VIF-values) are given for the main effects. Marginal R^2 of the model was 0.32.

	VIF	Est.	Std. Est.	SE	Adj. SE	z	Pr(>|z|)
Intercept		8.31	14.30	0.43	0.43	19	<0.0001
Ungulate density	1.1	0.36	-0.23	0.28	0.28	1.3	0.199
Summer temperature	1.1	1.12	0.04	0.11	0.11	10	<0.0001
Summer temperature ^{2}		-0.07	-0.60	0.01	0.01	9.8	<0.0001
Ungulate density : Summer temperature		-0.18	0.21	0.06	0.06	3.0	0.00245
Ungulate density : Summer temperature ^{2}		0.01	0.17	0.00	0.00	3.6	0.000302
Summer precipitation	1.6	0.57	0.41	0.07	0.07	8.0	<0.0001
Winter precipitation	1.5	0.04	0.05	0.03	0.03	1.2	0.236
Age	1.0	0.48	0.32	0.01	0.01	34	<0.0001

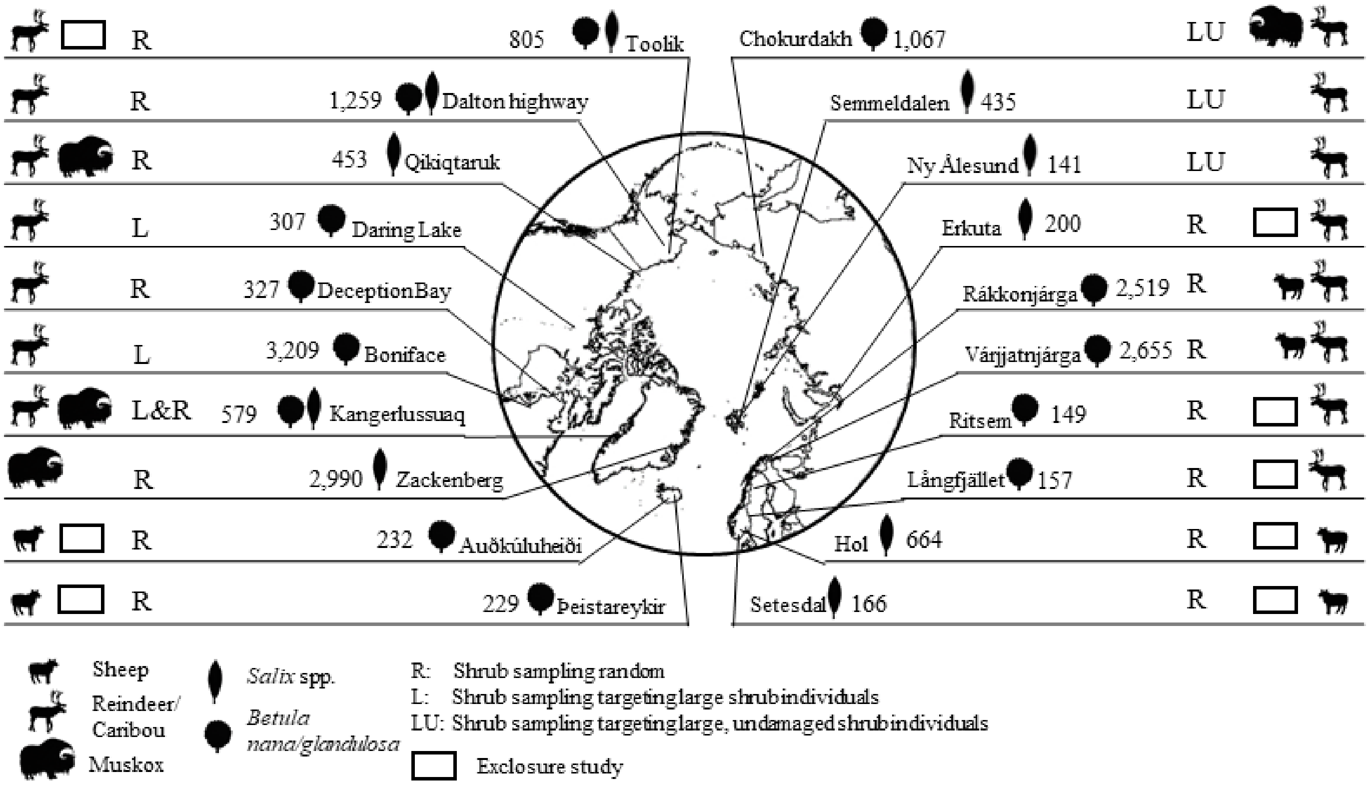

Figure 1. Locations of sampling sites with indications of ungulate species, shrub genus, sampling method, and sample size (numbers represent observation points from each site after excluding individuals younger than 5 years). Study designs including shrubs from herbivore exclosures are marked with quadrangles. For more site-specific information on each dataset, see Appendix S1: Tables S1, S4-S5.

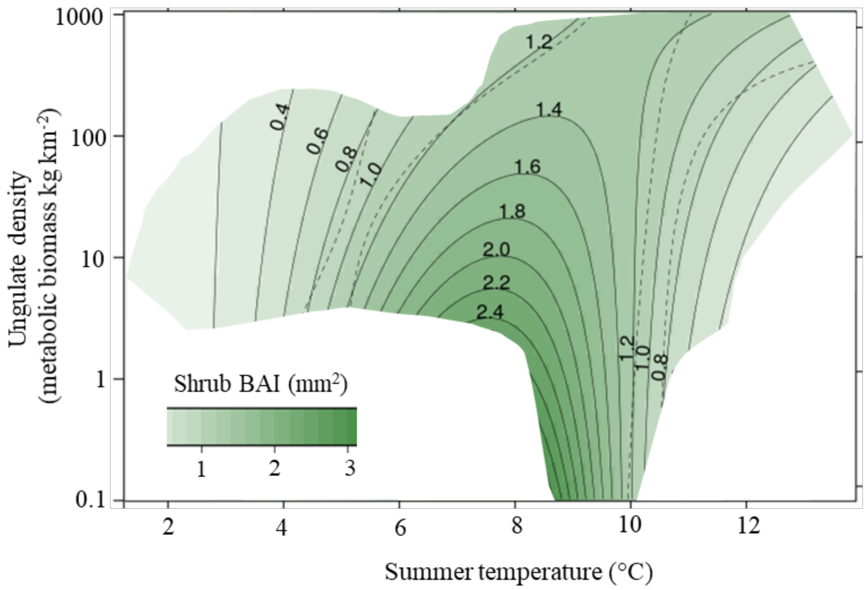

Figure 2. Predicted shrub basal area increment (BAI) shown as green colour at different ungulate densities and summer (June-August) temperatures. The darker the green colour, the higher the BAI. White sections are contexts we did not have data from, i.e. combinations of ungulate density and summer temperature values that did not exist in our data. Dashed lines are SEs illustrated for the isoclines where BAI is predicted to be 1.0 mm^2. When temperature increases from 1.8 to 7.5°C, BAI increases, but when temperatures go above 7.5°C, BAI starts decreasing. There is no clear negative ungulate density effect at temperatures <5°C or >10°C (where isoclines are primarily vertical), but at temperatures 5-10°C, increasing ungulate pressure results to lower BAI, i.e. to lighter green (isoclines bend to be more horizontal). The ungulate effect is at its highest at ~7.5°C.

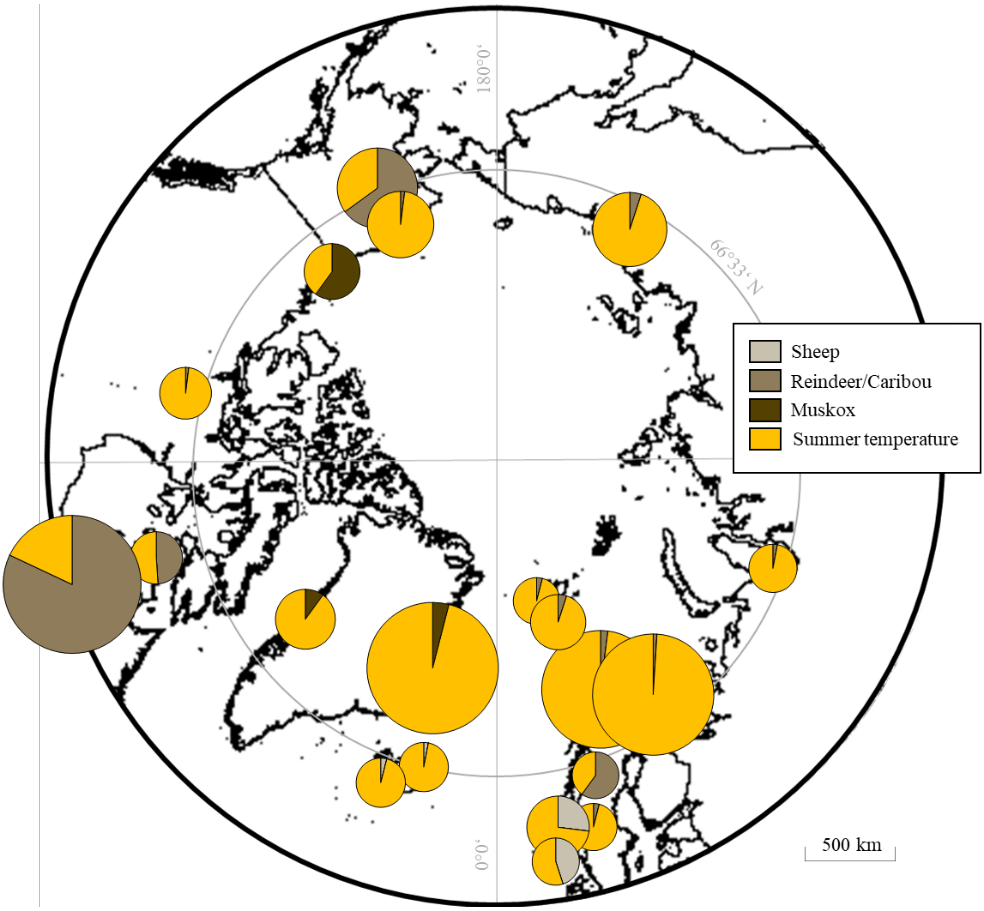

Figure 3. Relative effect size of summer temperature and ungulate density under average summer temperature and ungulate density conditions observed at each site (note that as we did not include site-interactions in the model, the predictions are based on the *average* site-specific environmental variables only). Pie charts have been standardized so that when temperature and ungulate density sectors are of equal size, the shrub radial growth prediction isocline is cutting the prediction point in 45° angle in Fig. 2. Thus, any temperature density sector larger than half of the pie chart area in question indicates higher slope inclination (and consequently, lower ungulate effect), whereas smaller indicates lower inclination (and consequently, higher ungulate effect). Pie chart sizes are proportional to the sample size of each site (Fig. 1).

References

Ackerman, D., Griffin, D., Hobbie, S. E., Finlay, J. C., 2017. Arctic shrub growth trajectories differ across soil moisture levels. Global Change Biology 23, 4294-4302.

Andruko, R., Danby, R., Grogan, P., 2020. Recent Growth and Expansion of Birch Shrubs Across a Low Arctic Landscape in Continental Canada: Are These Responses More a Consequence of the Severely Declining Caribou Herd than of Climate Warming? Ecosystems, 1-18.

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.

Barton, K., 2016. Multi-model inference. R package version 1.15. 6.; 2016.

Berner, L. T., Massey, R., Jantz, P., Forbes, B. C., Macias-Fauria, M., Myers-Smith, I., Kumpula, T., Gauthier, G., Andreu-Hayles, L., Gaglioti, B. V., 2020. Summer warming explains widespread but not uniform greening in the Arctic tundra biome. Nature communications 11, 1-12.

Beumer, L. T., Pohle, J., Schmidt, N. M., Chimienti, M., Desforges, J.-P., Hansen, L. H., Langrock, R., Pedersen, S. H., Stelvig, M., van Beest, F. M., 2020. An application of upscaled optimal foraging theory using hidden Markov modelling: year-round behavioural variation in a large arctic herbivore. Movement Ecology 8, 1-16.

Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. Tree-Ring Research 64, 81-96.

Björkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., 2018. Plant functional trait change across a warming tundra biome. Nature 562, 57-62.

Björkman, A. D., Criado, M. G., Myers-Smith, I. H., Ravolainen, V., Jónsdóttir, I. S., Westergaard, K. B., Lawler, J. P., Aronsson, M., Bennett, B., Gardfjell, H., 2020. Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring. Ambio 49, 678-692.

Bolton, D. K., Coops, N. C., Hermosilla, T., Wulder, M. A., White, J. C., 2018. Evidence of vegetation greening at alpine treeline ecotones: three decades of Landsat spectral trends informed by lidar-derived vertical structure. Environmental Research Letters 13, 084022.

Bonfils, C., Phillips, T., Lawrence, D., Cameron-Smith, P., Riley, W., Subin, Z., 2012. On the influence of shrub height and expansion on northern high latitude climate. Environmental Research Letters 7, 015503.

Boscutti, F., Casolo, V., Beraldo, P., Braidot, E., Zancani, M., Rixen, C., 2018. Shrub growth and plant diversity along an elevation gradient: Evidence of indirect effects of climate on alpine ecosystems. PloS one 13, e0196653.

Bråthen, K. A., Lortie, C., 2016. A portfolio effect of shrub canopy height on species richness in both stressful and competitive environments. Functional ecology 30, 60-69.

Bret-Harte, M. S., Mack, M. C., Euskirchen, E. S., Edgar, C., 2019. Comparison of the Effects of Ten Years of Warming and Twenty Years of Altered Plant Species Composition on Ecosystem Carbon Storage in Alaskan Arctic Tundra. AGUFM 2019, B11A-07.

Bryant, J. P., Joly, K., Chapin III, F. S., DeAngelis, D. L., Kielland, K., 2014. Can antibrowsing defense regulate the spread of woody vegetation in arctic tundra? Ecography 37, 204-211.

Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., Buras, A., Cecile, J., Mudelsee, M., 2019. Package 'dplR'.

Cade, B. S., 2015. Model averaging and muddled multimodel inferences. J Ecology 96, 2370-2382.

Cahoon, S. M., Sullivan, P. F., Post, E., Welker, J. M., 2012. Large herbivores limit CO 2 uptake and suppress carbon cycle responses to warming in W est G reenland. Global Change Biology 18, 469-479.

Carlson, B. Z., Corona, M. C., Dentant, C., Bonet, R., Thuiller, W., Choler, P., 2017. Observed long-term greening of alpine vegetation—a case study in the French Alps. Environmental Research Letters 12, 114006.

Chapin III, F. S., Jefferies, R. L., Reynolds, J. F., Shaver, G. R., Svoboda, J., Chu, E. W., 1992. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press.

Christie, K. S., Bryant, J. P., Gough, L., Ravolainen, V. T., Ruess, R. W., Tape, K. D., 2015. The role of vertebrate herbivores in regulating shrub expansion in the Arctic: a synthesis. BioScience 65, 1123-1133.

Cohen, J., Pulliainen, J., Menard, C., Johansen, B., Oksanen, L., Luojus, K., Ikonen, J., 2013. Effect of summer reindeer grazing on spring snowmelt, albedo and energy balance. Remote Sens. Environ 135, 107-117.

Cromsigt, J. P., te Beest, M., Kerley, G. I., Landman, M., le Roux, E., Smith, F. A., 2018. Trophic rewilding as a climate change mitigation strategy? Philosophical Transactions of the Royal Society B 373, 20170440.

Cuyler, C., Rowell, J., Adamczewski, J., Anderson, M., Blake, J., Bretten, T., Brodeur, V., Campbell, M., Checkley, S. L., Cluff, H. D., 2020. Muskox status, recent variation, and uncertain future. Ambio 49, 805-819.

DeFranco, K. C., Ricketts, M. P., Blanc-Betes, E., Welker, J. M., Gonzalez-Meler, M. A., Sturchio, N. C., 2020. Deeper snow increases the net soil organic carbon accrual rate in moist acidic tussock tundra: 210Pb evidence from Arctic Alaska. Arctic, Antarctic, and Alpine Research 52, 461-475.

den Herder, M., Virtanen, R., Roininen, H., 2008. Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone. Basic and Applied Ecology 9, 324-331.

Dormann, C. F., Calabrese, J. M., Guillera-Arroita, G., Matechou, E., Bahn, V., Bartoń, K., Beale, C. M., Ciuti, S., Elith, J., Gerstner, K., 2018. Model averaging in ecology: a review of Bayesian, information-theoretic, and tactical approaches for predictive inference. Ecological Monographs 88, 485-504.

Fisichelli, N., Frelich, L. E., Reich, P. B. J. G. C. B., 2012. Sapling growth responses to warmer temperatures 'cooled' by browse pressure 18, 3455-3463.

García Criado, M., Myers-Smith, I. H., Bjorkman, A. D., Lehmann, C. E., Stevens, N., 2020. Woody plant encroachment intensifies under climate change across tundra and savanna biomes. Global Ecology and Biogeography 29, 925-943.

Graham, M. H., 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84, 2809-2815.

Harris, I. C., Jones, P.D. , 2019. CRU TS4.03: Climatic Research Unit (CRU) Time-Series (TS) version 4.03 of high-resolution gridded data of month-by-month variation in climate (Jan. 1901- Dec. 2018). Centre for Environmental Data Analysis, 22 January 2020. doi:10.5285/10d3e3640f004c578403419aac167d82.

Hofmann, R. R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78, 443-457.

Ims, R. A., Henden, J.-A., 2012. Collapse of an arctic bird community resulting from ungulate-induced loss of erect shrubs. Biological conservation 149, 2-5.

Jespersen, R. G., Leffler, A. J., Oberbauer, S. F., Welker, J. M., 2018. Arctic plant ecophysiology and water source utilization in response to altered snow: isotopic (δ 18 O and δ 2 H) evidence for meltwater subsidies to deciduous shrubs. Oecologia 187, 1009-1023.

Johnson, J. B., Omland, K. S., 2004. Model selection in ecology and evolution. Trends in ecology & evolution 19, 101-108.

Kaarlejärvi, E., Hoset, K. S., Olofsson, J., 2015. Mammalian herbivores confer resilience of Arctic shrub-dominated ecosystems to changing climate. Global Change Biology 21, 3379-3388.

Kausrud, K., Mysterud, A., Rekdal, Y., Holand, Ø., Austrheim, G., 2006. Density-dependent foraging behaviour of sheep on alpine pastures: effects of scale. Journal of Zoology 270, 63-71.

Le Moullec, M., Sandal, L., Grøtan, V., Buchwal, A., Hansen, B. B., 2020. Climate synchronises shrub growth across a high-arctic archipelago: contrasting implications of summer and winter warming. Oikos.

Legagneux, P., Gauthier, G., Lecomte, N., Schmidt, N. M., Reid, D., Cadieux, M.-c. C., Berteaux, D., Bety, J., Krebs, C., Ims, R., 2014. Arctic ecosystem structure and functioning shaped by climate and herbivore body size. Nature Climate Change 4, 379-383.

Li, B., Heijmans, M. M., Berendse, F., Blok, D., Maximov, T., Sass-Klaassen, U., 2016. The role of summer precipitation and summer temperature in establishment and growth of dwarf shrub Betula nana in northeast Siberian tundra. Polar Biology 39, 1245-1255.

Macias-Fauria, M., Jepson, P., Zimov, N., Malhi, Y., 2020. Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? Philosophical Transactions of the Royal Society B 375, 20190122.

Macias-Fauria, M., Seddon, A. W., Benz, D., Long, P. R., Willis, K., 2014. Spatiotemporal patterns of warming. Nature Climate Change 4, 845-846.

Morrissette-Boileau, C., Boudreau, S., Tremblay, J.-P., Côté, S. D., 2018. Revisiting the role of migratory caribou in the control of shrub expansion in northern Nunavik (Québec, Canada). Polar Biology 41, 1845-1853.

Mosbacher, J. B., Michelsen, A., Stelvig, M., Hjermstad-Sollerud, H., Schmidt, N. M., 2019. Muskoxen modify plant abundance, phenology, and nitrogen dynamics in a High Arctic fen. Ecosystems 22, 1095-1107.

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S., Wilmking, M., Hallinger, M., Blok, D., Tape, K. D., Rayback, S. A., Macias-Fauria, M., Forbes, B. C., 2015a. Climate sensitivity of shrub growth across the tundra biome. Nature Climate Change 5, 887-891.

Myers-Smith, I. H., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S. A., Weijers, S., Trant, A. J., Tape, K. D., Naito, A. T., Wipf, S., 2015b. Methods for measuring arctic and alpine shrub growth: a review. Earth-Science Reviews 140, 1-13.

Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P. S., 2020. Complexity revealed in the greening of the Arctic. Nature Climate Change 10, 106-117.

Myers-Smith, I. H., Hik, D. S., 2018. Climate warming as a driver of tundra shrubline advance. Journal of Ecology 106, 547-560.

Naito, A. T., Cairns, D. M., 2011. Patterns and processes of global shrub expansion. Progress in Physical Geography 35, 423-442.

Nicholson, K. L., Arthur, S. M., Horne, J. S., Garton, E. O., Del Vecchio, P. A., 2016. Modeling caribou movements: seasonal ranges and migration routes of the Central Arctic herd. PLoS One 11, e0150333.

Niskanen, A. K., Heikkinen, R. K., Väre, H., Luoto, M., 2017. Drivers of high-latitude plant diversity hotspots and their congruence. Biological Conservation 212, 288-299.

Oksanen, T., Oksanen, L., Vuorinen, K. E., Wolf, C., Mäkynen, A., Olofsson, J., Ripple, W. J., Virtanen, R., Utsi, T. A., 2020. The impact of thermal seasonality on terrestrial endotherm food web dynamics: a revision of the Exploitation Ecosystem Hypothesis. Ecography.

Olofsson, J., Post, E., 2018. Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. Philosophical Transactions of the Royal Society B: Biological Sciences 373, 20170437.

Olofsson, J., Stark, S., Oksanen, L., 2004a. Reindeer influence on ecosystem processes in the tundra. Oikos 105, 386-396.

Olofsson, J., E. Hulme, P., Oksanen, L., Suominen, O., 2004b. Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. Oikos 106, 324-334.

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.

Ossi, F., Gaillard, J.-M., Hebblewhite, M., Cagnacci, F. J. E. j. o. w. r., 2015. Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer 61, 111-124.

Pajunen, A., Virtanen, R., Roininen, H., 2012. Browsing-mediated shrub canopy changes drive composition and species richness in forest-tundra ecosystems. Oikos 121, 1544-1552.

Pattison, R. R., Welker, J. M., 2014. Differential ecophysiological response of deciduous shrubs and a graminoid to long-term experimental snow reductions and additions in moist acidic tundra, Northern Alaska. Oecologia 174, 339-350.

Phoenix, G. K., Bjerke, J. W., 2016. Arctic browning: extreme events and trends reversing arctic greening. Global change biology 22, 2960-2962.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., Maintainer, R., 2017. Package 'nlme'. Linear and nonlinear mixed effects models, version 3.

Plante, S., Champagne, E., Ropars, P., Boudreau, S., Lévesque, E., Tremblay, B., Tremblay, J.-P., 2014. Shrub cover in northern Nunavik: can herbivores limit shrub expansion? Polar biology 37, 611-619.

Post, E., Pedersen, C., 2008. Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences 105, 12353-12358.

Prendin, A. L., Carrer, M., Karami, M., Hollesen, J., Bjerregaard Pedersen, N., Pividori, M., Treier, U. A., Westergaard-Nielsen, A., Elberling, B., Normand, S., 2020. Immediate and carry-over effects of insect outbreaks on vegetation growth in West Greenland assessed from cells to satellite. Journal of Biogeography 47, 87-100.

Prevéy, J. S., Rixen, C., Rüger, N., Høye, T. T., Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Ashton, I. W., Cannone, N., Chisholm, C. L., 2019. Warming shortens flowering seasons of tundra plant communities. Nature ecology & evolution 3, 45-52.

Schmidt, N. M., van Beest, F. M., Mosbacher, J. B., Stelvig, M., Hansen, L. H., Nabe-Nielsen, J., Grøndahl, C., 2016. Ungulate movement in an extreme seasonal environment: year-round movement patterns of high-arctic muskoxen. Wildlife Biology 22, 253-267.

Skarin, A., Verdonen, M., Kumpula, T., Macias-Fauria, M., Alam, M., Kerby, J. T., Forbes, B. C., 2020. Reindeer use of low Arctic tundra correlates with landscape structure. Environmental Research Letters.

Speed, J. D., Austrheim, G., Hester, A. J., Mysterud, A., 2010. Experimental evidence for herbivore limitation of the treeline. Ecology 91, 3414-3420.

Speed, J. D., Austrheim, G., Hester, A. J., Mysterud, A. J. J. o. V. S., 2012. Elevational advance of alpine plant communities is buffered by herbivory 23, 617-625.

Speed, J. D., Austrheim, G., Hester, A. J., Mysterud, A., 2013. The response of alpine Salix shrubs to long-term browsing varies with elevation and herbivore density. Arctic, Antarctic, and Alpine Research 45, 584-593.

Speed, J. D., Austrheim, G., Kolstad, A. L., Solberg, E. J., 2019. Long-term changes in northern large-herbivore communities reveal differential rewilding rates in space and time. PloS one 14, e0217166.

Speed, J. D., Martinsen, V., Mysterud, A., Mulder, J., Holand, Ø., Austrheim, G., 2014. Long-term increase in aboveground carbon stocks following exclusion of grazers and forest establishment in an alpine ecosystem. Ecosystems 17, 1138-1150.

Staver, A. C., Bond, W. J., 2014. Is there a 'browse trap'? Dynamics of herbivore impacts on trees and grasses in an African savanna. Journal of Ecology 102, 595-602.

Staver, A. C., Bond, W. J., Stock, W. D., Van Rensburg, S. J., Waldram, M. S., 2009. Browsing and fire interact to suppress tree density in an African savanna. Ecological applications 19, 1909-1919.

Ueda, H., Takatsuki, S., Takahashi, Y., 2002. Bark stripping of hinoki cypress by sika deer in relation to snow cover and food availability on Mt Takahara, central Japan. Ecological Research 17, 545-551.

Verma, M., to Bühne, H. S., Lopes, M., Ehrich, D., Sokovnina, S., Hofhuis, S. P., Pettorelli, N., 2020. Can reindeer husbandry management slow down the shrubification of the Arctic? Journal of Environmental Management 267, 110636.

Virtanen, R., Oksanen, L., Oksanen, T., Cohen, J., Forbes, B. C., Johansen, B., Käyhkö, J., Olofsson, J., Pulliainen, J., Tømmervik, H., 2016. Where do the treeless tundra areas of northern highlands fit in the global biome system: toward an ecologically natural subdivision of the tundra biome. Ecology and evolution 6, 143-158.

Vors, L. S., Boyce, M. S., 2009. Global declines of caribou and reindeer. Global change biology 15, 2626-2633.

Vowles, T., Björk, R. G., 2019. Implications of evergreen shrub expansion in the Arctic. Journal of Ecology 107, 650-655.

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.

Vuorinen, K. E., Rao, S. J., Hester, A. J., Speed, J. D., 2020a. Herbivory and climate as drivers of woody plant growth: Do deer decrease the impacts of warming? Ecological Applications.

Vuorinen, K. E., 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.

Vuorinen, K. E., Kolstad, A. L., De Vriendt, L., Austrheim, G., Tremblay, J. P., Solberg, E. J., Speed, J. D., 2020b. Cool as a moose: How can browsing counteract climate warming effects across boreal forest ecosystems? Ecology, e03159.

Welker, J., Fahnestock, J., Sullivan, P., Chimner, R., 2005. Leaf mineral nutrition of Arctic plants in response to warming and deeper snow in northern Alaska. Oikos 109, 167-177.

Welker, J. M., Wookey, P., Parsons, A. N., Press, M. C., Callaghan, T. V., Lee, J. A., 1993. Leaf carbon isotope discrimination and vegetative responses of Dryas octopetala to temperature and water manipulations in a High Arctic polar semi-desert, Svalbard. Oecologia 95, 463-469.

White, K. S., Pendleton, G. W., Hood, E., 2009. Effects of snow on Sitka black-tailed deer browse availability and nutritional carrying capacity in southeastern Alaska. The Journal of Wildlife Management 73, 481-487.

Ylänne, H., Olofsson, J., Oksanen, L., Stark, S., 2018. Consequences of grazer-induced vegetation transitions on ecosystem carbon storage in the tundra. Functional Ecology 32, 1091-1102.

Yu, Q., Epstein, H., Engstrom, R., Walker, D., 2017. Circumpolar arctic tundra biomass and productivity dynamics in response to projected climate change and herbivory. Global change biology 23, 3895-3907.

Appendix S1

Herbivores counteract the effects of warming on Arctic shrub growth at intermediate temperatures

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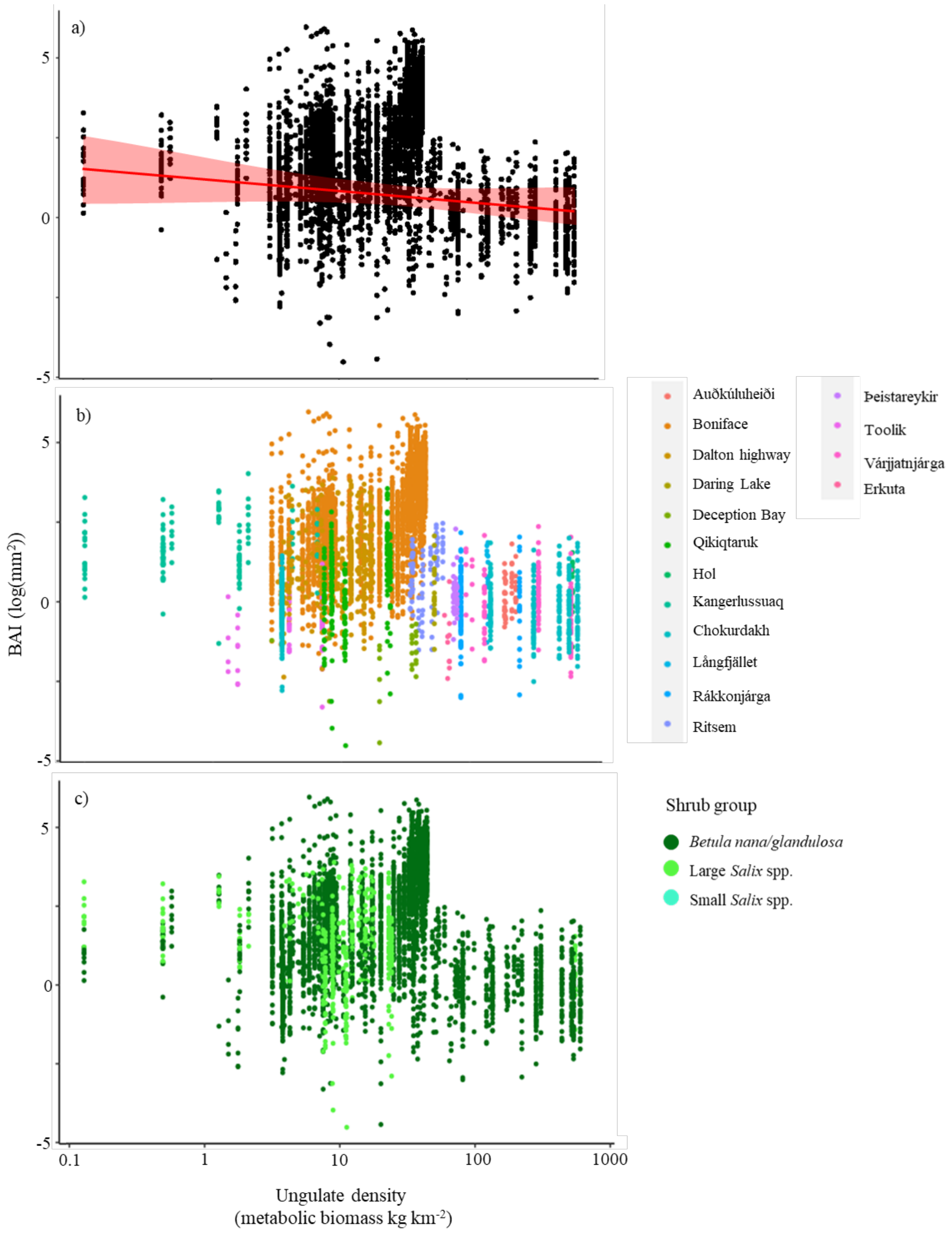
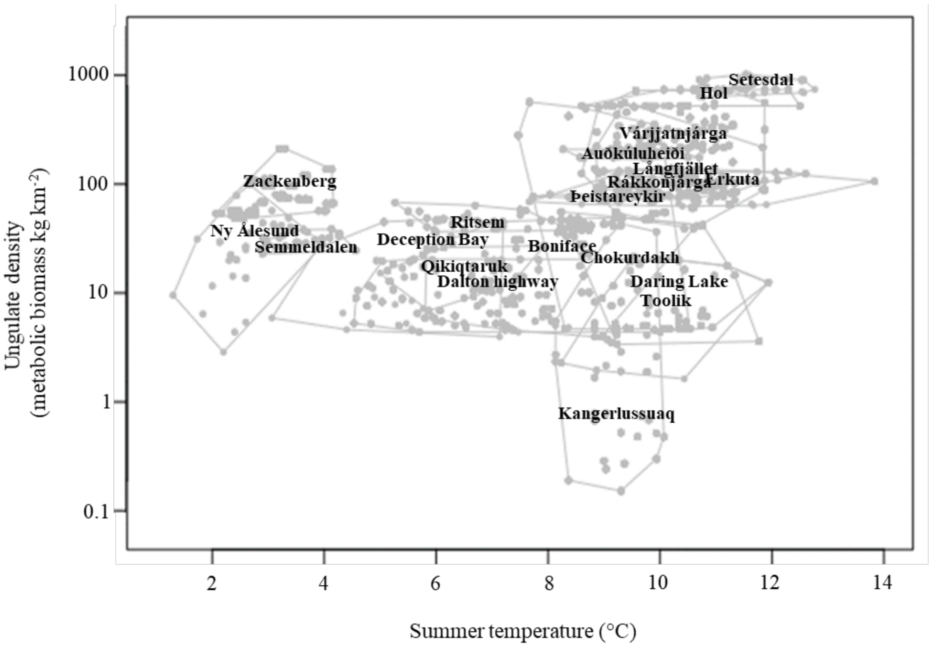
Supplementary Methods 1: Precipitation data for Dalton Highway and Svalbard

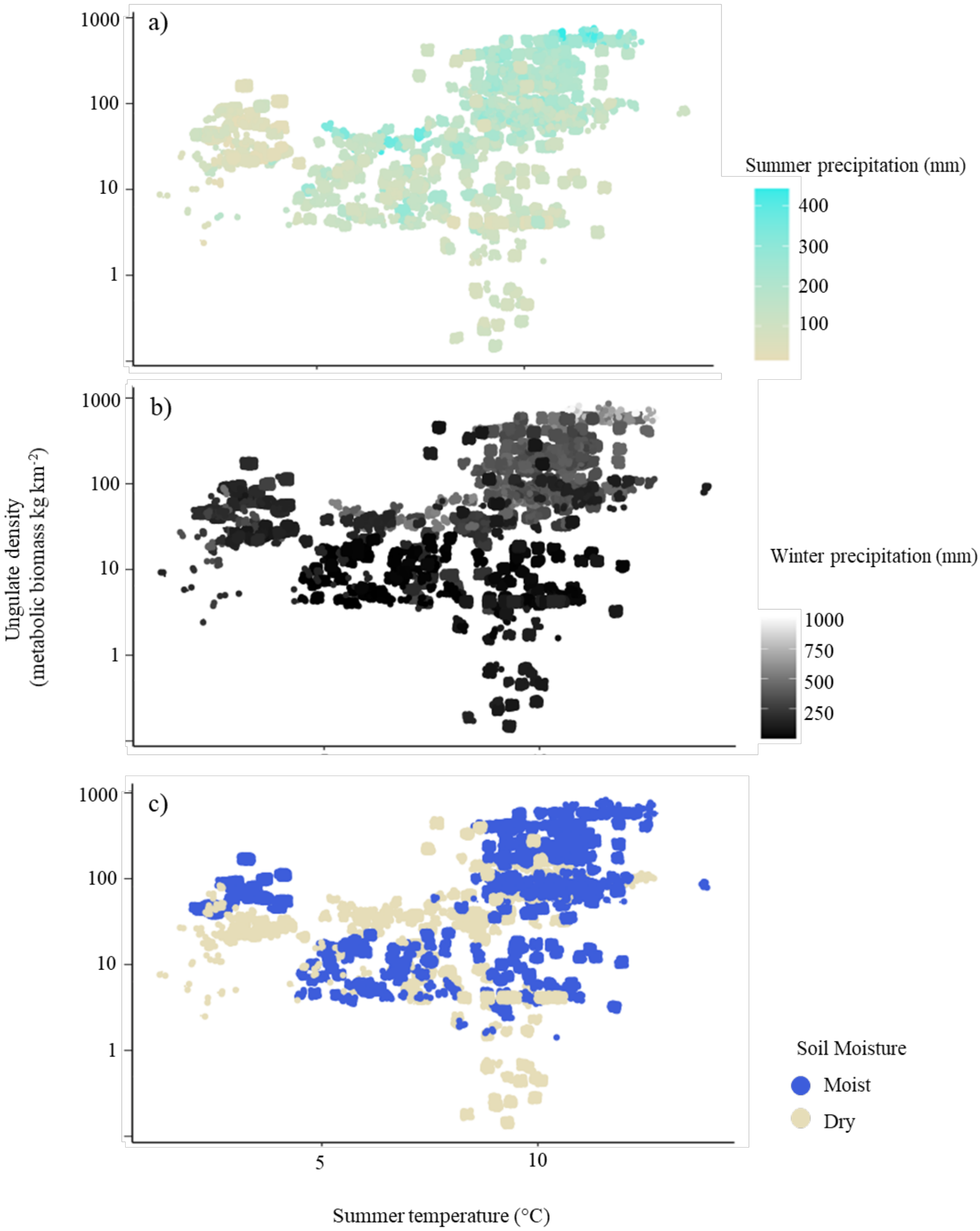
Monthly precipitation data for Dalton highway sampling locations was obtained from the Scenarios Network for Alaska & Arctic Planning group (SNAP, 2019). This data is downscaled from the global Climate Research Unit time series v. 4.0 (Harris et al., 2014; Walsh et al., 2018) to spatial resolution of 1 km^2, and spans the time period from 1901 to 2015. Daily precipitation data for Semmeldalen and Adventdalen (Svalbard) were obtained from the eKlima service of the Norwegian Meteorological Institute (Meteorologisk institute, MET). This is observational data from the nearest weather stations at Svalbard Lufthavn and Ny-Ålesund, located 28 and 6 km from the shrub sampling sites, respectively.



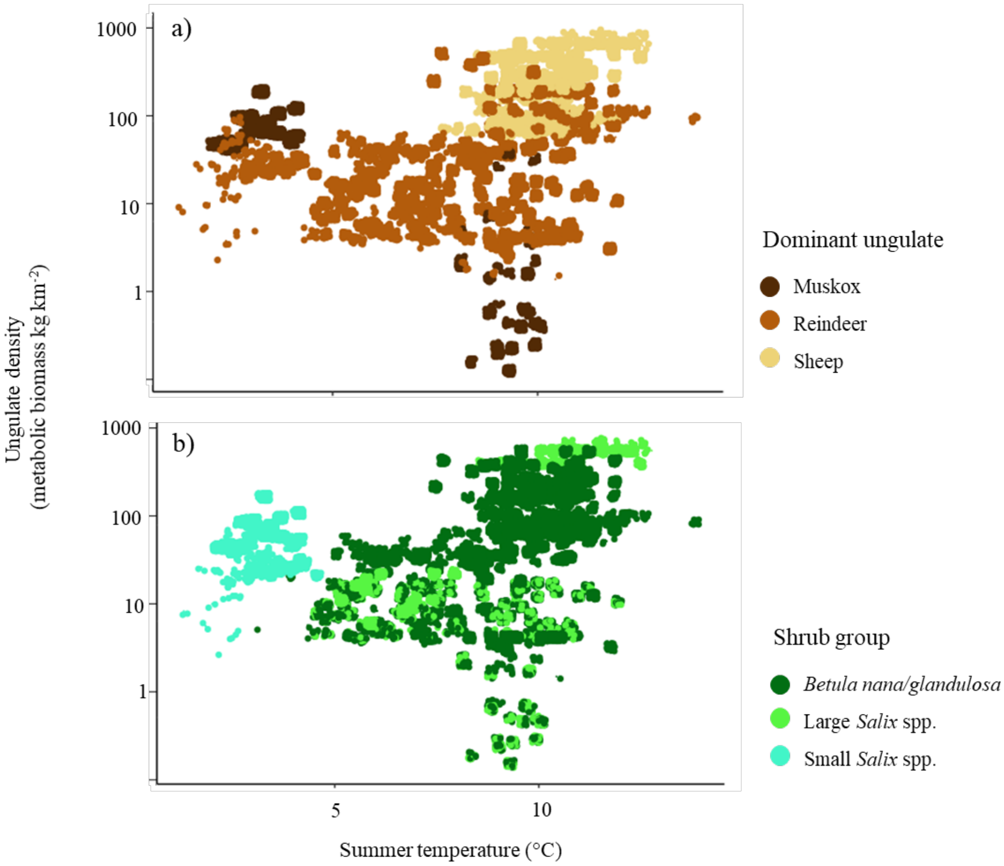
Supplementary Figure 1. Shrub basal area increment (BAI) as a response to ungulate density at intermediate temperatures 6.5-9 °C (a), where the ungulate effect was predicted to be at its highest (Fig. 2), with points coloured for sites (b) and for the group of the shrubs (c). The prediction line (±SE) in panel a is based on the model prediction under average climatic conditions across the data. Note that as we detected summer temperature × ungulate density interaction (Fig. 2, Table 1), the ungulate effect presented here should not be interpreted separately from the summer temperature effect; this figure simply illustrates the ungulate effect at intermediate summer temperatures under average climatic conditions.



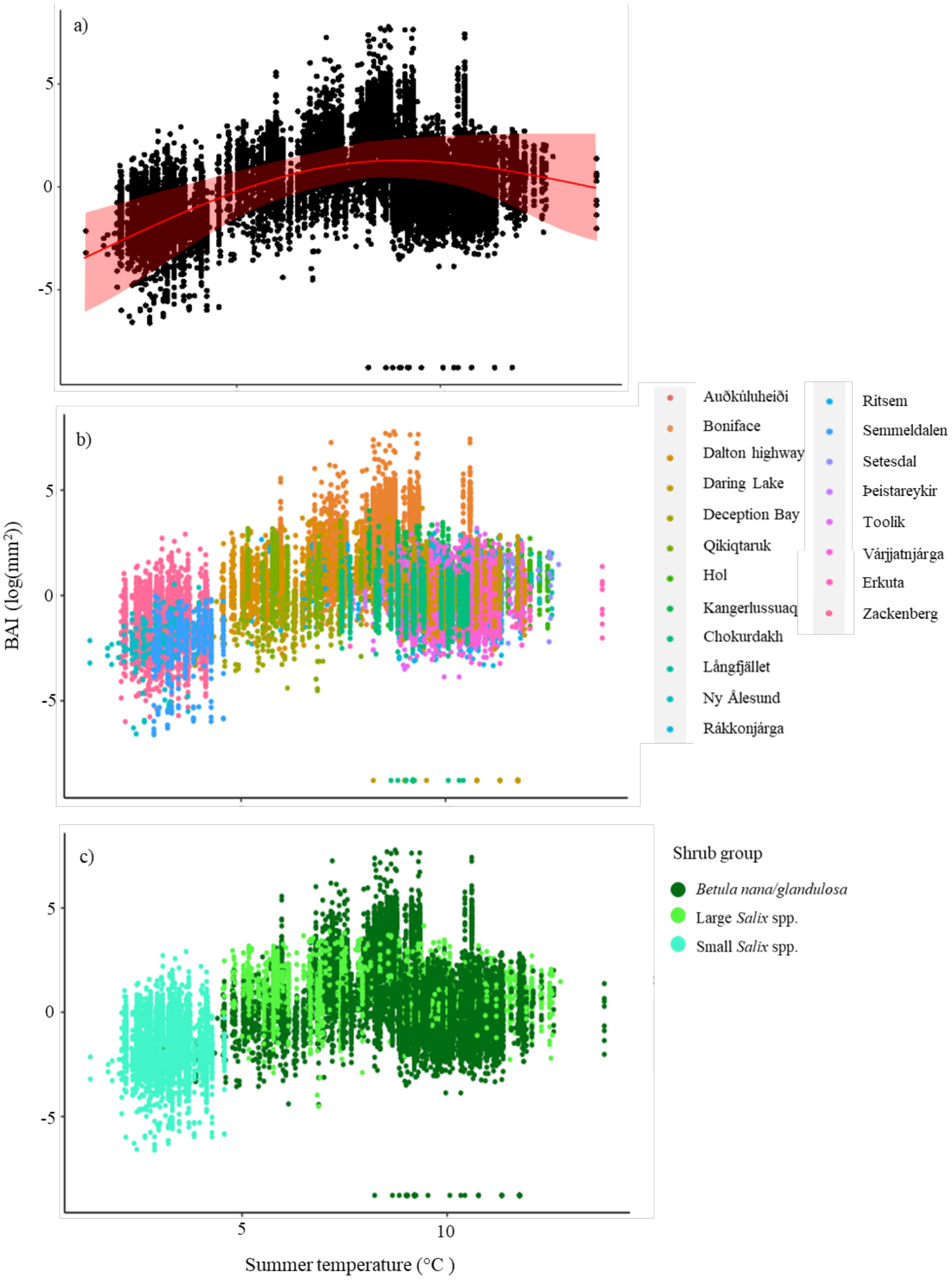
Supplementary Figure 2. Observation points in the ungulate metabolic biomass density and summer temperature (June-August) plane, divided by convex hulls for each site. Site names indicate the centroid points for the sites.



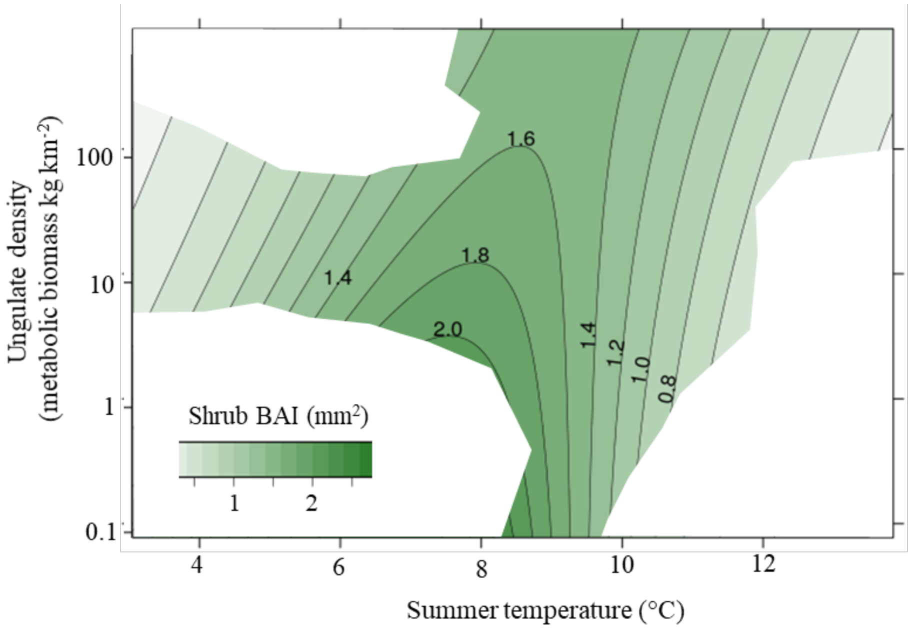
Supplementary Figure 3. Shrub ring measurement points on the ungulate metabolic biomass density and summer (June-August) temperature plane, coloured by summer (June-August) precipitation (a), winter (October-April) precipitation (b), and soil moisture class (c). This three-dimensional presentation enables comparison with Fig. 2 to see the connections between all studied variables. The points have been jittered for better visibility (0.1 units on both axes).



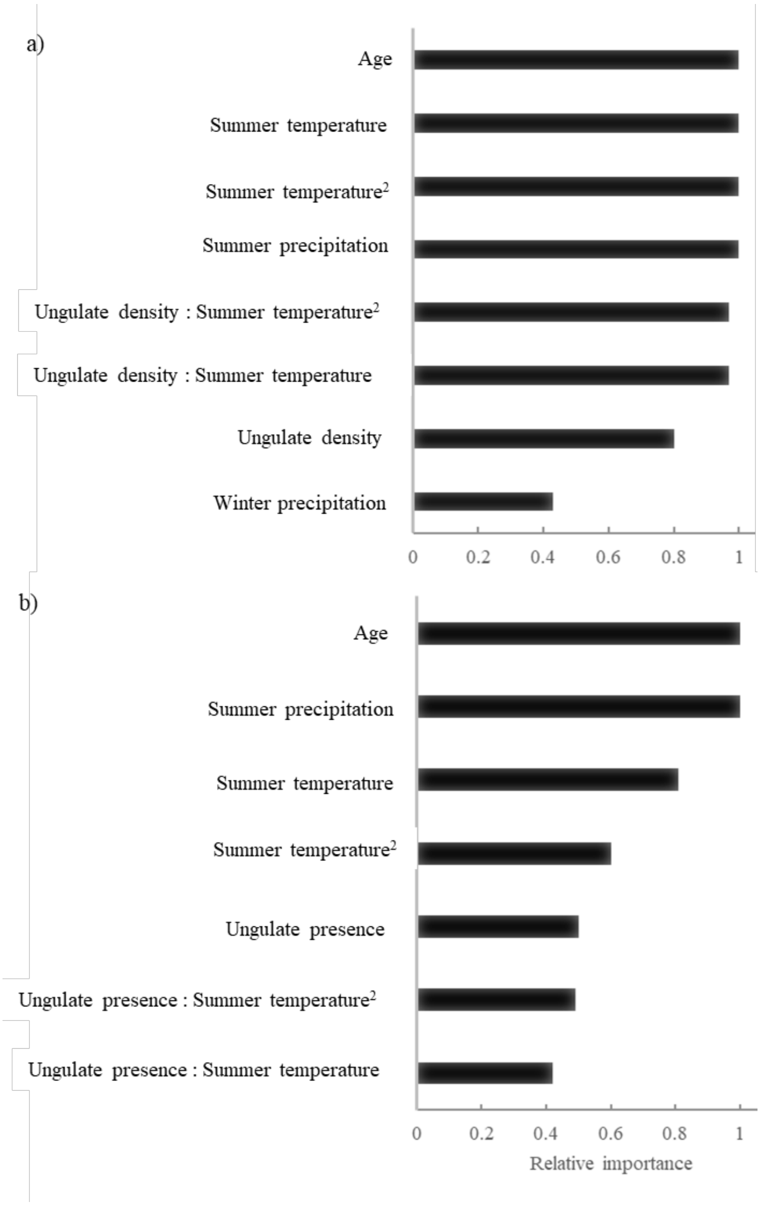
Supplementary Figure 4. Shrub ring measurement points on the ungulate metabolic biomass density and summer (June-August) temperature plane, coloured by dominant ungulate species (a), and functional type of the shrub (b). This three-dimensional presentation enables comparison with Fig. 2 to visualise connections between all studied variables. The points have been jittered for better visibility (0.1 units on both axes).



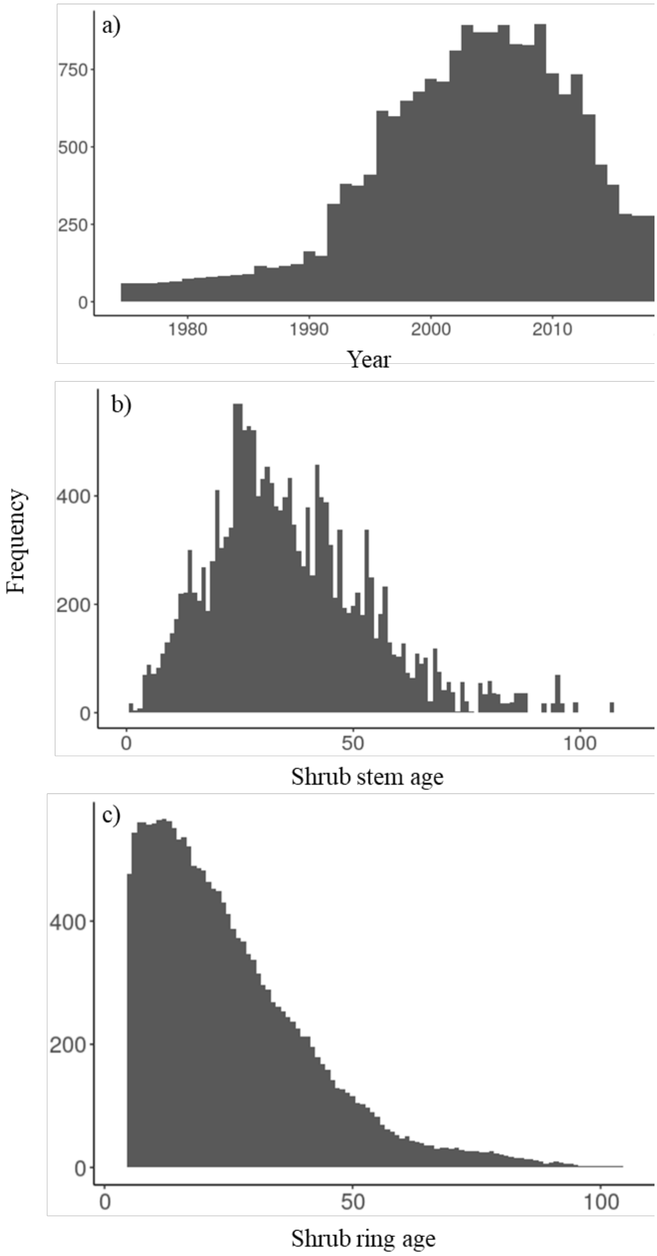
Supplementary Figure 5. Shrub basal area increment (BAI) as a response to summer temperature (June-August) at average ungulate densities (a), with points coloured for sites (b) and for the functional group of the shrubs (c). The prediction line (±SE) in panel a is based on the model prediction under average ungulate densities across the data. Note that as we detected an interaction of summer temperature and ungulate density (Fig. 2, Table 1), the summer temperature effect presented here should not be interpreted separately from the ungulate density effect.



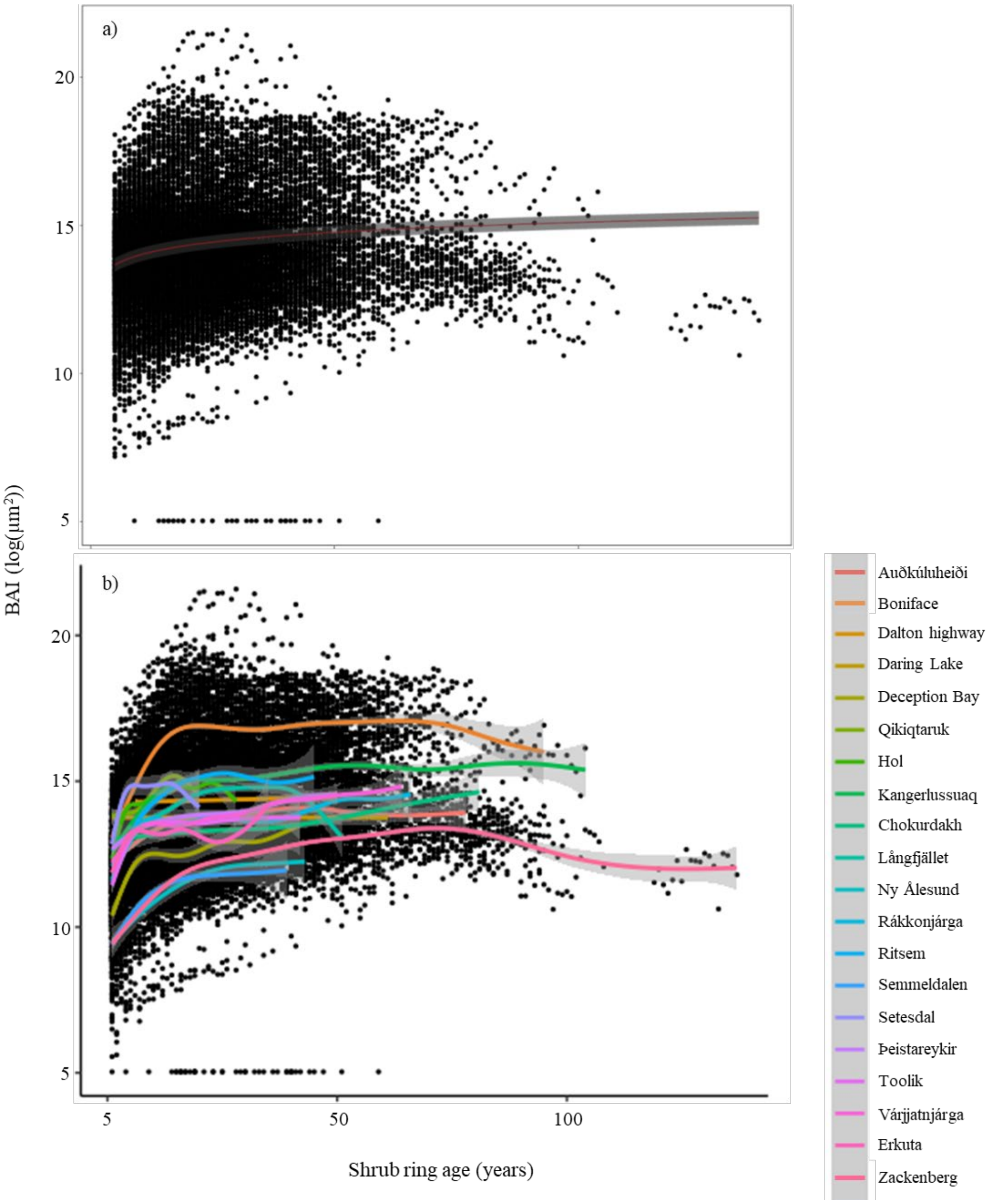
Supplementary Figure 6. Predicted *Betula nana*/*glandulosa* basal area increment (BAI) shown as green colour at different ungulate densities and summer (June-August) temperatures. The darker the green colour, the higher the BAI. White sections are contexts we did not have data from, i.e. combinations of ungulate density and summer temperature values that did not exist in our data. The underlying model was constructed similar to what is described for the analysis on whole data in the Methods section. When temperature increases from 3 to ~8°C, BAI increases, but when temperatures go above ~8°C, BAI starts decreasing. Ungulate density affects growth negatively strongest at ~8°C (isoclines bend more horizontal), but summer temperature becomes more important towards colder and warmer ends of the summer temperature gradient (isoclines more vertical). This patter is close to prediction for whole dataset (Fig. 2).



Supplementary Figure 7. Relative variable importance of the explanatory factors in the analysis looking into the effects of variation in observed ungulate density (a), and in the analysis looking into the effects of experimental presence-absence of ungulates (b), calculated as a sum of the Akaike weights over all of the models in which the parameter in question appears.



Supplementary Figure 8. Distribution of data in the analysis looking into the effects observed ungulate density, for each year (a), shrub stem age (b), and shrub ring age (c).



Supplementary Figure 9. Remaining age pattern in shrub basal area increment (BAI) after removing the first 5 years of growth as predicted from the model ±SE (a), and for each site as smoothed conditional means produced by the geom_smooth-function of ggplot2-package with gam-method (Wickham, 2011).

Table S1. Site-genus specific shrub metadata, ordered along longitude. Selection criteria refer to randomly sampled shrub individuals (R), selective sampling targeting large shrub individuals (L), and selective sampling targeting large, undamaged shrub individuals (LU). Shrub species canopy heights are based on (Myers-Smith et al., 2015).

Site	**Shrub species (max canopy height cm)**	**Data contributors**	**Chronology period**	**Reference**	**Mean stem age**	**Selection criteria**	**Part of the shrub sampled**	**Exclosures**	**Dominant ungulate**	**Observations**	**Individuals**	**Number of subsites**	**Longitude**	**Latitude**
Toolik	*Betula nana* (100)	Peter Frank, Ruby An, Jeffrey Welker, Agata Buchwal, Laura Gough	1975-2018	Unpublished	31	R	Base	yes	Caribou	1030	39	5	-149.608	68.626
Toolik	*Salix pulchra* (450)	Peter Frank, Ruby An, Laura Gough	1991-2018	Unpublished	27	R	Base	yes	Caribou	188	12	3	-149.612	68.624
Dalton highway	*Betula nana* (100)	Peter Frank	1975-2018	Unpublished	36	R	Base	no	Caribou	1051	38	20	-149.439	68.313
Dalton highway	*Salix glauca* (600)*, Salix pulchra* (450)	Peter Frank	1975-2018	Unpublished	28	R	Base	no	Caribou	868	40	20	-149.448	68.323
Qikiqtaruk	*Salix richardsonii (650), Salix pulchra* (450)*, Salix glauca* (600)	Isla Myers-Smith, Sandra Angers-Blondin	1986-2015	(Myers-Smith et al., 2011)	7	R	Root collar	no	Caribou	1347	66	3	-138.905	68.575
Daring Lake	*Betula glandulosa* (300)	Paul Grogan, Rhett Andruko	1952-2016	Unpublished	35	L	Base	no	Caribou	387	55	5	-111.583	64.867
Boniface river	*Betula glandulosa* (300)	Pascale Ropars, Stéphane Boudreau	1915-2009	(Ropars, 2015)	43	L	Root collar	no	Caribou	3426	115	9	-76.033	57.982
Deception Bay	*Betula glandulosa* (300)	Jean-Pierre Tremblay, Clara Morrissette-Boileau	1966-2013	(Morrissette-Boileau et al., 2018; Morrissette-Boileau et al., 2018)	11	R	Base	no	Caribou	364	202	5	-74.692	62.140
Kangerlussuaq	*Betula nana* (100)	Eric Post, Paddy Sullivan	1903-2013	(Gamm et al., 2018)	26	L	Base	no	Muskox	2001	42	5	-50.318	67.112
Kangerlussuaq	*Salix glauca* (600),	Eric Post, Paddy Sullivan	1935-2013	(Gamm et al., 2018)	19	L	Base	no	Muskox	960	32	5	-50.315	67.100
Zackenberg	*Salix arctica* (25)	Signe Normand, Sigrid Nielsen	1996-2014	Unpublished	46	R	Root collar	no	Muskox	3111	176	6	-20.559	74.510
Audkuluheidi	*Betula nana* (100)	Isabel C. Barrio, Katariina E. M. Vuorinen	1941-2018	(Mulloy et al., 2019)	31	R	Base	yes	Sheep	582	12	12	-19.674	65.133
Theistareykir	*Betula nana* (100)	Isabel C. Barrio, Katariina E. M. Vuorinen	1969-2018	(Mulloy et al., 2019)	39	R	Base	yes	Sheep	446	12	12	-17.087	65.901
Setesdal	*Salix glauca* (600),	Katariina E. M. Vuorinen, Gunnar Austrheim	2000-2018	Unpublished	15	R	Base	no	Sheep	166	12	4	7.218	59.026

Hol	*Salix glauca* (600), *Salix lapponum* (120), *Salix lanata* (700)	James D. M. Speed, Gunnar Austrheim	1979-2010	(Speed et al., 2013)	16	R	Base	yes	Sheep	2062	159	9	7.936	60.698
Långfjället	*Betula nana* (100)	Fredrik Dalerum, Katariina E. M. Vuorinen	1966-2016	Unpublished	36	R	Base	yes	Reindeer	547	16	3	12.272	62.115
Ny Ålesund	*Salix polaris* (9)	Mathilde Le Moullec, Lisa Sandal, Brage B. Hansen	1972-2014	Unpublished	15	LU	Base	no	Reindeer	163	5	1	11.693	78.959
Semmeldalen	*Salix polaris* (9)	Mathilde Le Moullec, Lisa Sandal, Brage B. Hansen	1979-2014	(Le Moullec et al., 2019)	11	LU	Base	no	Reindeer	711	30	10	15.343	77.992
Ritsem	*Betula nana* (100)	Mats Björkman, Robert Björk, Katariina E. M. Vuorinen	1972-2016	Unpublished	26	R	Base	yes	Reindeer	513	21	3	17.536	67.773
Rákkonjárga	*Betula nana* (100)	Hans Ivar Hortman	1992-2018	Unpublished	35	R	Base	no	Reindeer	2772	118	5	28.925	70.756
Várjjatnjárga	*Betula nana* (100)	Hans Ivar Hortman	1992-2018	Unpublished	34	R	Base	no	Reindeer	2902	119	5	29.558	70.310
Erkuta	*Betula nana* (100)	Katariina E. M. Vuorinen, Dorothee Ehrich, Aleksandr Sokolov, Natalya Sokolova	1984-2018	Unpublished	22	R	Base	yes	Reindeer	304	16	4	69.184	68.206
Chokurdakh	*Betula nana* (100)	Rúna Íris Magnússon, Monique Heijmans, Bingxi Li, Ute Sass-Klaassen	1933-2013	(Li et al., 2016)	42	LU	Base	no	Reindeer	1070	51	10	147.467	71.000

Table S2. Model-averaged coefficients for the analysis looking into the effects of experimental presence-absence of ungulates: estimates, standardized estimates, standard errors, adjusted standard errors, z-values and Wald-test based p-values. Variance inflation factors (VIF-values) are given for the main effects. Marginal R^2 of the model was 0.17.

	VIF	Estimate	Std. Estimate	SE	Adj. SE	z-value	Pr(>|z|)
Intercept		15.07	13.91	1.42	1.42	10.64	<0.0001
Ungulates present	1.0	-1.03	0.19	0.90	0.90	1.15	0.25
Summer temperature	1.1	-0.44	0.03	0.29	0.29	1.50	0.13
Summer temperature^2		0.02	0.08	0.01	0.02	1.58	0.11
Ungulates present : Summer temperature		0.22	0.10	0.20	0.20	1.13	0.26
Herbivores present : Summer temperature^2		-0.01	-0.06	0.01	0.01	0.79	0.43
Summer precipitation	1.1	0.39	0.35	0.05	0.05	7.23	<0.0001
Age	1.0	0.40	0.33	0.03	0.03	15.47	<0.0001

Table S3. Number of shrub ring measurements (n), number of shrub individuals, start and end year of the used chronologies, and chronology length for each site entering the additional the analysis looking into the effects of experimental presence-absence of ungulates.

Site	n	Number of shrub individuals	Chronology start year	Chronology end year	Number of exclusion years
Toolik	898	51	1997	2018	22
Auðkúluheiði	36	12	2016	2018	3
Þeistareykir	36	12	2016	2018	3
Setesdal	165	12	2001	2018	18
Hol	971	107	2001	2010	10
Långfjället	333	16	1996	2016	21
Ritsem	417	21	1996	2016	21
Erkuta	80	16	2014	2018	5

Table S4. Site-genus specific climate and herbivory values averaged over the study periods at each site, ordered along longitude.

		Summer temperature (°C)			Summer precipitation (mm)			Winter precipitation (mm)			NPP	Average metabolic biomass kg km^{-2}		
Site	**Shrub species**	**min**	**average**	**max**	**min**	**average**	**max**	**min**	**average**	**max**		**Sheep**	**Reindeer/ Caribou**	**Muskox**
Toolik	*Betula nana*	8.2	10.0	11.9	68	104	191	12	25	44	3.69	0.0	8.7	0.0
Toolik	*Salix pulchra*	8.8	10.1	11.9	68	109	191	14	26	44	3.69	0.0	6.6	0.0
Dalton highway	*Betula nana*	3.8	6.8	11.9	68	123	270	2	10	44	0.89	0.0	11.3	0.0
Dalton highway	*Salix glauca, Salix pulchra*	3.8	7.1	11.9	68	124	270	2	11	44	0.89	0.0	12.5	0.0
Qikiqtaruk	*Salix richardsonii, Salix pulchra, Salix glauca*	5.0	6.5	7.9	55	86	124	9	18	29	3.19	0.0	12.1	6.5
Daring Lake	*Betula glandulosa*	6.4	9.9	12.0	63	103	131	79	94	121	4.02	0.0	20.4	0.0
Boniface river	*Betula glandulosa*	5.4	7.9	10.6	66	183	285	92	218	341	2.51	0.0	23.5	0.0
Deception Bay	*Betula glandulosa*	2.6	6.1	8.1	121	135	153	145	156	175	2.90	0.0	36.6	0.0
Kangerlussuaq	*Betula nana*	6.7	8.7	10.1	29	86	129	40	88	142	1.57	0.0	0.6	0.1
Kangerlussuaq	*Salix glauca*	6.7	8.8	10.1	29	90	129	40	95	142	1.57	0.0	0.1	0.1
Zackenberg	*Salix arctica*	2.1	3.2	4.2	19	57	113	86	171	290	0.54	0.0	0.0	89.8
Audkuluheidi	*Betula nana*	7.4	9.1	10.7	63	149	271	165	334	493	0.86	74.4	0.0	0.0
Theistareykir	*Betula nana*	6.8	9.2	10.7	71	172	305	311	486	675	1.51	40.6	0.0	0.0
Setesdal	*Salix* sp.	10.2	11.7	12.8	214	324	444	501	797	1043	2.66	382.5	0.0	0.0
Hol	*Salix glauca, Salix lapponum, Salix lanata*	8.6	10.9	12.5	150	237	300	297	496	658	2.31	831.2	0.0	0.0
Langfjallet	*Betula nana*	8.2	10.4	12.6	126	253	356	210	294	412	2.84	0.0	35.9	0.0
Ny Ålesund	*Salix polaris*	1.3	2.8	4.0	84	129	211	165	334	478	0.42	0.0	36.7	0.0
Semmeldalen	*Salix polaris*	1.7	3.6	4.7	79	120	187	180	305	402	1.24	0.0	34.4	0.0
Ritsem	*Betula nana*	4.0	6.7	8.4	178	299	456	314	499	685	2.81	0.0	16.4	0.0
Rákkonjárga	*Betula nana*	8.9	10.3	11.9	102	191	257	237	352	440	1.69	25.8	79.0	0.0
Várjjatnjárga	*Betula nana*	8.6	10.2	11.9	104	203	294	221	350	455	1.98	210.6	102.9	0.0
Erkuta	*Betula nana*	7.7	10.8	13.8	79	123	161	100	129	163	3.72	0.0	88.7	0.0
Chokurdakh	*Betula nana*	6.5	8.9	10.6	37	85	157	32	75	162	1.66	0.0	245.1	0.0

Table S5. Ungulate datasets included in the study, ordered along longitude. Area size refers to the area over which herbivory number or density has been estimated (i.e. spatial accuracy). Herbivory density was interpolated for missing years, unless the column “Covered years” states otherwise.

Site	Data type	Estimation area(s)	Area size(s) km^2	Covered years	Animal weight (kg)	Reference for density/number data	Reference for biomass data
Toolik and Dalton highway	Caribou number	Central Arctic Herd area	136 000	1978, 1981, 1983, 1991, 1992, 1995, 1997, 2000, 2002, 2008, 2010, 2013, 2016 and 2019	150	(Alaska Department of Fish and Game, 2017; Healy, 2003) The most recent estimate (2019) was obtained in communication with Beth Lenart, Northeast Alaska Wildlife Area Biologist, Alaska Department of Fish and Game, Division of Wildlife Conservation, 1300 College Rd, Fairbanks, AK 99708.	
Qikiqtaruk	Caribou and muskox number	Qikiqtaruk – Herschel Island	116	1986-2015	300 150	Qikiqtaruk Ecological Monitoring Database (DOI 10.5281/zenodo.2397996; https://zenodo.org/record/2397996#.X2scO2gzZa)	
Daring Lake	Caribou number	Bathurst Herd area	350 000	1986, 1990, 1996, 2003, 2006, 2009 2012 and 2015,	150	(Adamczewski, 2018)	
Deception Bay and Boniface	Caribou number	Riviere-aux-Feuilles Herd area	524 300	1975, 1983, 1987, 1991, 2001, 2011 and 2016	150	(Morrissette-Boileau et al., 2018; Morrissette-Boileau et al., 2018)	
Kangerlussuaq	Muskox and reindeer number	Kangerlussuaq census area	100	1993 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014; Extrapolation between 1993 and 2002 was deemed unreasonable and was thus not applied.	300 150	Unpublished data by Post E., Kerby J. and John C.: daily animal observations for May and June	(Olesen et al., 1994)
Zackenberg	Muskox number	Zackenberg muskox census area	47	1996-2017	300	(Schmidt et al., 2015; Tomassini et al., 2019)	(Olesen et al., 1994)
Audkuluheidi and Theistareykir	Sheep number	Norðurland Vestra and Norðurland Eystra	12 737 and 21 968	1998-2018	65	(Statistics Iceland, 2019) In addition, sheep exclosures provided zero herbivory years.	(Ross et al., 2016)
Setesdal	Sheep number	Suleskar and Nomeland	205 and 247	2000-2019	85	Data from local sheep farmers and (Rekdal and Angeloff, 2007) In addition, sheep exclosures (Speed et al., 2014) provided zero herbivory years.	(Ross et al., 2016)
Hol	Sheep density	Study fence of (Austrheim et al., 2014)	0.3 (for each fence section)	1975-2010	85	(Austrheim et al., 2014)	(Ross et al., 2016)
Långfjället and Ritsem	Reindeer density	Idre and Baste herding areas	5 477 and 3 355	1995-2013	150	(Vowles et al., 2017)	
Semmeldalen and Ny-Ålesund	Reindeer number	Colesdalen-Reindalen and Brøgger Peninsula	940 and 188	1972-2015	90	Data for Semmeldalen was extracted from (Lee et al., 2015). Data for Brøgger Peninsula was provided by Norwegian Polar Institute, acquired in communication with Åshild Ønvik Pedersen (Hansen et al., 2019).	

Rákkonjárga and Várjjatnjárga	Reindeer number	Rákkonjárga and Várjjatnjárga herding areas	2 185 and 2 228	1992-2018	150	Data was provided first-hand by Trade The Norwegian Agriculture Agency (Landbruksdirektoratet). See also (Landbruksdirektoratet, 2019) and	
	Sheep number	Nesseby, Vadsø and Berlevåg	210 and 294	1992-2018	85	(Norsk institutt for bioøkonomi, 2019).	(Ross et al., 2016)
Erkuta	Reindeer number	Yamal Peninsula	122 000	1985, 1990, 1995, 1998, 2000, 2006, 2010, 2014-2018	126,5	(Golovatin et al., 2012); local expert knowledge of Alexander Volkovitskiy and Alexandra Terekhina (Yuzhakov, 2003; Южаков, 2003). In addition, reindeer exclosures (Baubin et al., 2016) provided zero herbivory years.	
Chokurdakh	Reindeer number	Kytalyk Nature Reserve	16 000	1992 2012	150	Communication with Kytalyk Nature Reserve manager Tatyana Stryukova, Ministry of Nature Protection of the Allaikhovsky Region, Naberezhnaya 9, Chokurdakh	
	Muskox number	Allaikha district	107 300	2000, 2009 and 2011	300	(Kirillin, 2012)	(Olesen et al., 1994)

Supplementary References

Adamczewski, J., Garner, K., Croft, B., and Van Der Wielen, S. , 2018. Project Caribou - An Educator's Guide to Wild Caribou of North America; Case Study: Bathurst Herd. Environmental Education and Youth Programs Government of Yukon, Department of Environment Conservation Officer Services, http://www.env.gov.yk.ca/publications-maps/documents/ProjectCaribou-BathurstHerd.pdf.

Alaska Department of Fish and Game, 2017. Central Arctic Caribou Herd News, Alaska Department of Fish and Game, Winter 2016–17. Alaska Department of Fish and Game, Division of Wildlife Conservation, 1300 College Road, Fairbanks, AK 99701, http://www.cookinletarchers.com/central_arctic_caribou_herd_news_winter_2016_2017.pdf.

Austrheim, G., Speed, J. D., Martinsen, V., Mulder, J., Mysterud, A., 2014. Experimental effects of herbivore density on aboveground plant biomass in an alpine grassland ecosystem. Arctic, Antarctic, and Alpine Research 46, 535-541.

Baubin, C., Ehrich, D., Ravolainen, V., Sokovina, S., Ektova, S., Sokolova, N., Ims, R. A., Sokolov, A., 2016. First results from an experiment excluding three sizes classes of herbivores from tundra vegetation in southern Yamal, Russia. Czech Polar Reports 6, 132-140.

Gamm, C. M., Sullivan, P. F., Buchwal, A., Dial, R. J., Young, A. B., Watts, D. A., Cahoon, S. M., Welker, J. M., Post, E., 2018. Declining growth of deciduous shrubs in the warming climate of continental western Greenland. journal of ecology 106, 640-654.

Golovatin, M. G., Morozova, L. M., Ektova, S. N., 2012. Effect of reindeer overgrazing on vegetation and animals of tundra ecosystems of the Yamal peninsula. Czech Polar Reports 2, 80-91.

Hansen, B. B., Pedersen, Å. Ø., Peeters, B., Le Moullec, M., Albon, S. D., Herfindal, I., Sæther, B. E., Grøtan, V., Aanes, R., 2019. Spatial heterogeneity in climate change effects decouples the long-term dynamics of wild reindeer populations in the high Arctic. Global change biology 25, 3656-3668.

Harris, I., Jones, P. D., Osborn, T. J., Lister, D. H., 2014. Updated high‐resolution grids of monthly climatic observations–the CRU TS3. 10 Dataset. International journal of climatology 34, 623-642.

Healy, C., 2003. Caribou Management Report of Survey-inventory Activities, 1 July 2000-30 June 2002. Alaska Department of Fish and Game, Division of Wildlife Conservation.

Kirillin, E. V., Okhlopkov, I. M., Tatsuzawa, S., Nikolaev, E. A. , 2012. Reacclimatization of the muskox in the arctic zone of Yakutia: results and prospects for further research. . Global Warming and the Human-Nature Dimension in Siberia: Social Adaptation to Changes in the Terrestrial Ecosystem, with an Emphasis on Water Environments" in Kyoto, Japan, on 7-10 March, https://www.chikyu.ac.jp/siberia/2012_Siberia_International_workshop@RIHN1.pdf.

Landbruksdirektoratet, 2019. Ressursregnskap for reindriftsnæringen - For reindriftsåret 1. april 2018 – 31. mars 2019. Landbruksdirektoratet , Rapport nr. 34/2019, 19.12.2019.

Le Moullec, M., Buchwal, A., van der Wal, R., Sandal, L., Hansen, B. B., 2019. Annual ring growth of a widespread high arctic shrub reflects past fluctuations in community‐level plant biomass. Journal of Ecology 107, 436-451.

Lee, A. M., Bjørkvoll, E. M., Hansen, B. B., Albon, S. D., Stien, A., Sæther, B. E., Engen, S., Veiberg, V., Loe, L. E., Grøtan, V., 2015. An integrated population model for a long‐lived ungulate: more efficient data use with Bayesian methods. Oikos 124, 806-816.

Li, B., Heijmans, M. M., Berendse, F., Blok, D., Maximov, T., Sass-Klaassen, U., 2016. The role of summer precipitation and summer temperature in establishment and growth of dwarf shrub Betula nana in northeast Siberian tundra. Polar Biology 39, 1245-1255.

Morrissette-Boileau, C., Boudreau, S., Tremblay, J.-P., Côté, S. D., 2018. Revisiting the role of migratory caribou in the control of shrub expansion in northern Nunavik (Québec, Canada). Polar Biology 41, 1845-1853.

Morrissette‐Boileau, C., Boudreau, S., Tremblay, J. P., Côté, S. D., 2018. Simulated caribou browsing limits the effect of nutrient addition on the growth of Betula glandulosa, an expanding shrub species in Eastern Canada. Journal of Ecology 106, 1256-1265.

Mulloy, T. A., Barrio, I. C., Björnsdóttir, K., Jónsdóttir, I. S., Hik, D. S., 2019. Fertilisers mediate the short-term effects of sheep grazing in the Icelandic highlands. Icelandic Agricultural Sciences 32, 75-85.

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6, 045509.

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S., Wilmking, M., Hallinger, M., Blok, D., Tape, K. D., Rayback, S. A., Macias-Fauria, M., Forbes, B. C., 2015. Climate sensitivity of shrub growth across the tundra biome. Nature Climate Change 5, 887-891.

Norsk institutt for bioøkonomi, 2019. Statistikk for beitelag for heile Noreg og for kvart fylke frå 2013 - 2018, og fylkesstatistikk for organisert beitebruk frå 1970 - 2018. https://www.nibio.no/tema/landskap/kart-over-beitebruk-og-seterdrift/beitestatistikk, retrieved 9/2019.

Olesen, C. R., Thing, H., Aastrup, P., 1994. Growth of wild muskoxen under two nutritional regimes in Greenland. Rangifer 14, 3-10.

Rekdal, Y., Angeloff, M., 2007. Vegetasjon og beite i Setesdal Vesthei. Oppdragsrapport fra Skog og landskap.

Ropars, P., Lévesque, E., Boudreau, S., 2015. Data from: How do climate and topography influence the greening of the forest tundra ecotone in northern Québec? A dendrochronological analysis of Betula glandulosa. . Dryad Digital Repository, doi: 10.5061/dryad.n812k.

Ross, L. C., Austrheim, G., Asheim, L.-J., Bjarnason, G., Feilberg, J., Fosaa, A. M., Hester, A. J., Holand, Ø., Jónsdóttir, I. S., Mortensen, L. E., 2016. Sheep grazing in the North Atlantic region: A long-term perspective on environmental sustainability. Ambio 45, 551-566.

Schmidt, N. M., Pedersen, S. H., Mosbacher, J. B., Hansen, L. H., 2015. Long-term patterns of muskox (Ovibos moschatus) demographics in high arctic Greenland. Polar Biology 38, 1667-1675.

SNAP, 2019. Scenarios Network for Alaska and Arctic Planning: Historical monthly temperature and precipitation products, University of Alaska. https://www.snap.uaf.edu/ (Accessed: 2 December 2019). .

Speed, J. D., Austrheim, G., Hester, A. J., Mysterud, A., 2013. The response of alpine Salix shrubs to long-term browsing varies with elevation and herbivore density. Arctic, Antarctic, and Alpine Research 45, 584-593.

Speed, J. D., Martinsen, V., Mysterud, A., Mulder, J., Holand, Ø., Austrheim, G., 2014. Long-term increase in aboveground carbon stocks following exclusion of grazers and forest establishment in an alpine ecosystem. Ecosystems 17, 1138-1150.

Statistics Iceland, 2019. Livestock by region from 1980. Statistics Iceland, Borgartún 21A, 105 Reykjavík, https://px.hagstofa.is/pxis/pxweb/is/?rxid=c732bcf5-1a87-4f42-b564-509cb50558d6. .

Tomassini, O., van Beest, F. M., Schmidt, N. M., 2019. Density, snow, and seasonality lead to variation in muskox (Ovibos moschatus) habitat selection during summer. Canadian Journal of Zoology 97, 997-1003.

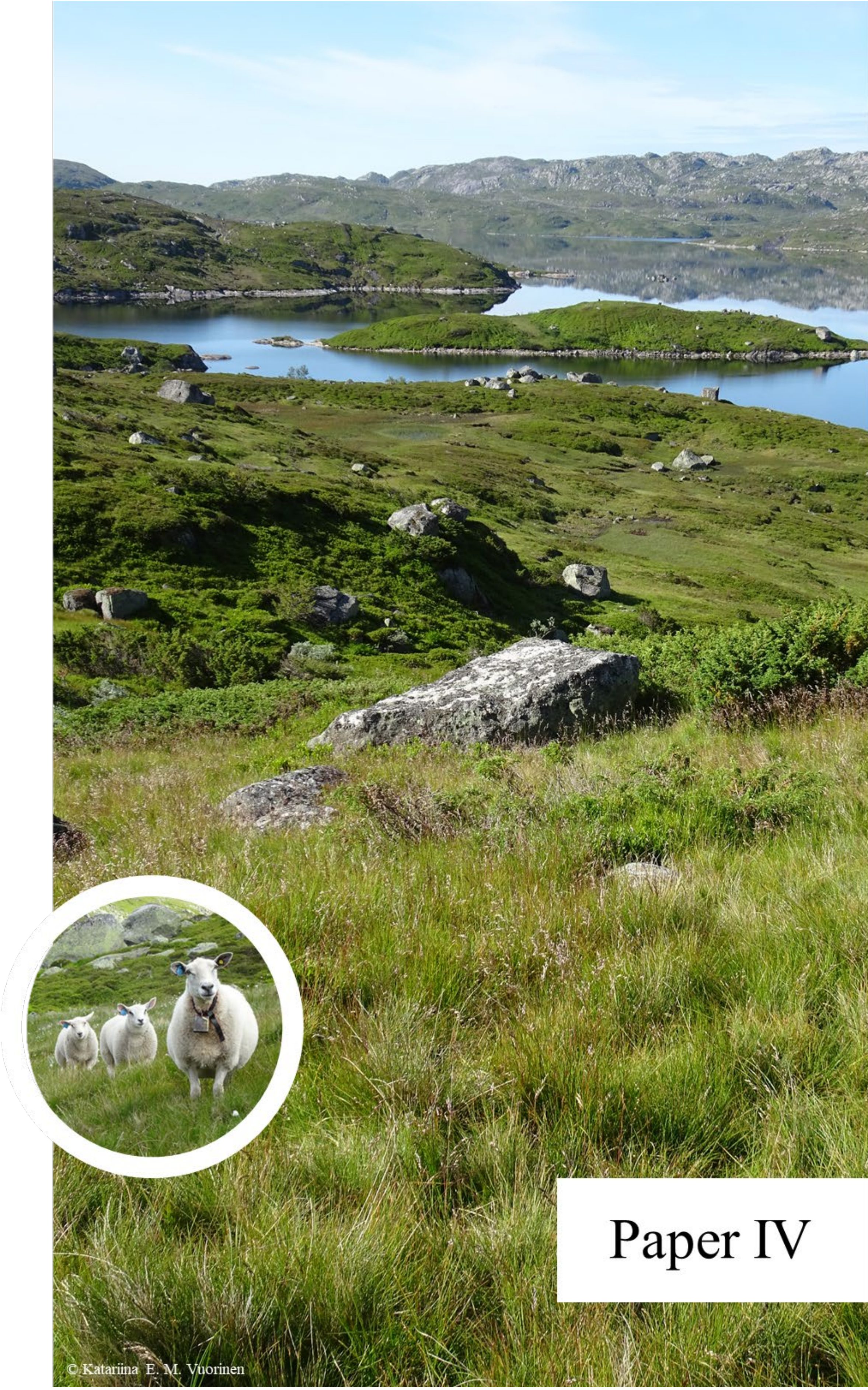
Vowles, T., Lovehav, C., Molau, U., Björk, R. G., 2017. Contrasting impacts of reindeer grazing in two tundra grasslands. Environmental Research Letters 12, 034018.

Walsh, J. E., Bhatt, U. S., Littell, J. S., Leonawicz, M., Lindgren, M., Kurkowski, T. A., Bieniek, P. A., Thoman, R., Gray, S., Rupp, T. S., 2018. Downscaling of climate model output for Alaskan stakeholders. Environmental Modelling & Software 110, 38-51.

Wickham, H., 2011. ggplot2. Wiley Interdisciplinary Reviews: Computational Statistics 3, 180-185.

Yuzhakov, A. A., 2003. Nenetskaya aborigennaya poroda severnykh olenej./ The Nenets aboriginal reindeer breed. . Dissertation for the Doctor of agriculture degree, Salekhard.

Южаков, А. А., 2003. Ненецкая аборигенная порода северных оленей. Диссертация … доктора сельскохозяйственных наук.



Paper IV

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Alpine plant community traits show long-term resistance to changing sheep densities across elevational gradients

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Alpine, climate changes, elevation, grazing, plants, sheep, traits

Abstract

Climatic factors are known to affect plant size, reproduction, and resource economics, and thus global warming is expected to lead to fundamental changes in vegetation characteristics, especially in northern and high-elevation ecosystems. Changes in plant community traits, in turn, affect key ecosystem functions such as albedo, biotic interactions and carbon storage. However, cold environments harbor herbivores that affect plant communities simultaneously with climate. Currently, we know little about the interactive effects of herbivores and climate on plant traits, but this information is crucial if we are to adapt herbivore management to the changing climatic conditions. In our study, we looked into the effects of sheep on the plant community traits at different elevations in intensively grazed Norwegian alpine tundra that has experienced temperature and precipitation changes over the past decades. We combined data from two long-term (13 and 19 years) sheep fence experiments with differing productivity levels, and showed that the site with low productivity had gone through trait composition changes in time, potentially driven by increased temperature and precipitation, while the trait composition at the site with higher productivity remained stable. However, the stability at the high-productivity site and the temporal change at the low-productivity site were consistent across different sheep densities and elevations. We also did not find evidence for interaction of elevation and sheep density affecting the trait composition changes. These results suggest that the plant trait communities were highly resistant to differing sheep pressures regardless of the elevation. However, when conducting an additional analysis to compare the plant trait composition on grazed mainland and the plant trait composition on historically non-grazed islands, we found that the islands had drastically different trait composition. We conclude that community trait compositions that have been shaped under intensive grazing pressure over thousands of years may not necessarily respond to changing grazer densities over time periods of <20 years, but historical timescales, likely several decades to centuries, are needed for these changes to manifest. Climatic effects on trait composition, in contrasts, may be visible in time scales <20 years.

Introduction

Climate shapes plant species community composition both in time and in space (Björkman et al., 2018a; Franklin et al., 2016; Walker et al., 2005; Walker et al., 2006), resulting in species turnover with changing climate and along elevational gradients. This turnover affects plant community traits, which, in turn, changes the functional properties of the ecosystem (Björkman et al., 2018a; Ma et al., 2017). Thus, climatic factors that shape plant species communities can have far-reaching consequences. Climatic effects are pronounced especially at high latitudes and elevations, as these areas have high elevational variation and are experiencing the most drastic temporal climate changes (Pachauri et al., 2014).

Warm habitats typically harbour a higher proportion of species adapted to southern, low-elevation conditions compared to cold habitats. These species are often taller and larger in leaf area than northern, high-elevation species, resulting in higher levels of shading, plant-plant competition, and carbon content of vegetation, and they are likely to become more abundant when climate warms (Björkman et al., 2018a; Gottfried et al., 2012; Stewart et al., 2018; Walker et al., 2006). Large, fast-growing plants also modify ecosystem hydrology, decrease albedo, and speed up the soil processes resulting in carbon release, reinforcing climatic warming (Zhang et al., 2013). These dynamics are crucial, particularly with rising global temperatures driving the advancement of treelines (Harsch et al., 2009), expansion of woody plants (García Criado et al., 2020; Myers-Smith and Hik, 2018), and poleward and upward shifts of plant species and communities (Lenoir et al., 2008; Pauli et al., 2012; Steinbauer et al., 2018; Stewart et al., 2018; van Vuuren et al., 2006). Even if species range shifts were modest, climate-driven changes in abundances of local species may drastically transform plant communities (Rumpf et al., 2018; Stewart et al., 2018; Vuorinen et al., 2017).

Warm conditions are likely to favour different plant resource economies, compared to cold conditions. If nutrient availability is high under warm temperatures, plants are more likely to have low leaf dry matter content and high specific leaf area (area of a fresh leaf divided by its dry mass) that are connected to high photosynthetic rates (Lavorel and Garnier, 2002). However, if plant growth is limited by water availability, warmer conditions may lead to higher leaf dry matter content and lower specific leaf area, allowing better water conservation (Björkman et al., 2018a). These resource-economic traits affect, for example, vegetation productivity and decompositions rates (Cornwell et al., 2008; Lavorel and Garnier, 2002). Furthermore, climatic factors may shape plant dynamics by changing the relative fitness of different reproduction strategies (Gray and Brady, 2016), leading to changes in seed size (Leishman et al., 2000) and number (Gray and Brady, 2016).

Despite the drastic effects of warming, plant species turnover does not always follow the patterns that would be expected if it was driven solely by climate, neither in space nor time (Bond, 2005; Lenoir and Svenning, 2015; Lenoir et al., 2010; Myers-Smith et al., 2020). One potential explanation for these discrepancies are biotic drivers, such as herbivory by large vertebrates (Diaz et al., 2007). Ungulates often favour highly palatable, fast-growing species with high specific leaf area and low dry matter content (Diaz et al., 2007; Pastor and Naiman, 1992; Skarpe and Hester, 2008), and thus they can decrease the advantages of traits favoured by high temperatures, and forage off the biomass increase driven by warming. Herbivores may also modify carbon cycling *via* effects on plants with differing traits (Schmitz and Leroux, 2020), lower the growth of woody species in boreal forests (Vuorinen et al., 2020a; Vuorinen et al., 2020b) and prevent climate-driven shrub expansion in the arctic and alpine tundra (Kaarlejärvi, 2014; Kolari et al., 2019; Speed et al., 2010; Speed et al., 2011; Verma et al., 2020). Furthermore, herbivores affect the success of different plant reproduction strategies – both by acting as browsers or grazers and as seed-dispersal agents – reflecting to plant traits such as life span, seed number and seed mass, and role of asexual dispersal (Austrheim et al., 2005; Hendrix, 1988; Maron and Vilà, 2001; Pellerin et al., 2016). Herbivores can also potentially affect plant trait diversity when affecting plant species diversity (Speed and Austrheim, 2017; Speed et al., 2013; Speed et al., 2020). Thus, herbivory is an important factor in shaping plant community trait composition (Diaz et al., 2007), and may drive the vegetation to different directions than climate.

The ungulate populations in northern and high-elevation tundra ecosystems are often controlled by humans, and it has been suggested that herbivore management could preserve desired vegetation characteristics, even under changing climatic conditions. For example, reindeer might be used to keep tundra as an open habitat (Kolari et al., 2019; Verma et al., 2020), and sheep to conserve semi-natural environments (Green and Vos, 2003). Megafauna could even act as a mean for climate change mitigation by changing ecosystem properties (Cromsigt et al., 2018). Yet, herbivore effects on plant community traits may differ depending on abiotic conditions (Cingolani et al., 2005; Milchunas et al., 1988), making the consequences of potential management acts hard to predict. Identifying potential interactive effects of herbivory and other ecosystem properties is thus of vital importance. Furthermore, we know that the short-term effects of abiotic factors and herbivory may differ considerably from longer-term effects (Alexander et al., 2018; Blume-Werry et al., 2016), highlighting the importance of acknowledging the role of time scale.

In this study, we investigate the long-term effects of sheep on alpine vegetation communities at different elevations of Southern-Norwegian mountains. Livestock farming has been practiced in this area for 3500-4000 years (Olsson et al., 2000; Speed et al., 2012b). Since the 16th century, an intensive transhumance farming system has been widespread, within which livestock are kept in the main farm settlements during winter, but released to the mountain pastures to range and forage over the summer (Daugstad et al., 2014; Hayward, 1948). This practice continues today, mainly involving domestic sheep *(Ovis aries*; Speed et al., 2019). Earlier studies from this region suggest that sheep could prevent climate-driven treeline advancement (Speed et al., 2010; Speed et al., 2011) and plant species community changes (Speed et al., 2012a). However, we do not know whether sheep modify the functional trait composition of these plant communities. Grazing may, for example, push plant communities towards lower height, lower leaf area, and higher leaf dry matter content, but these effects can vary depending on climatic conditions. At low elevations with high temperatures, plants may have high compensatory growth potential and thus the communities may have more resistance to sheep than communities at higher, colder elevations. On the other hand, plant adaptations to cold, windy conditions typical for high elevations, such as low stature and high leaf dry matter content, are often in line with adaptations for tolerating herbivore pressure, meaning that sheep effects could decrease towards higher elevations. By utilizing two long-term (13 and 19 years) sheep fence experiments with differing productivity levels, we studied the combined effects of sheep and elevation on plant community traits to answer the question: Does the effect of sheep density on plant community trait composition change depend on elevation? As we expect that sheep effects could be different in longer time periods than our experimental set-up, we also compared the vegetation of the grazed mainland with the vegetation of historically non-grazed islands to answer the question: Does the historical absence of sheep lead to different trait composition than historical intensive grazing pressure?

Methods

Study sites

The study was conducted at two sites in alpine Southern-Norway: Hol (7° 55′–8° 00′ E, 60° 40′–60° 45′ N; 1091-1311 masl), and Setesdal (7° 0′–7° 20′ E, 59° 0′–59° 5′ N; 852-1014 masl), located in Viken and Agder counties respectively (Appendix S1: Fig. S1). The climate is sub-continental in Hol and oceanic in Setesdal (Moen and Lillethun, 1999). The sites have experienced moderate summer warming and precipitation increases over the past decades (Appendix S1: Fig. S2). Both sites are located in regions with a long history of transhumance-type livestock production, mainly involving sheep. The typical sheep densities have been ~25 sheep km^{-2} in Hol and ~55 sheep km^{-2} in Setesdal (sheep densities presented in this paper are excluding ungrazeable land such as bare rock and boulder fields; for details, see Rekdal, 2001; Rekdal and Angeloff, 2007). Both sites also have low densities of wild reindeer (*Rangifer tarandus*; 0.15–0.25 reindeer km^{-2}).

To test the effects of different grazing pressures, sheep densities were modified with fences at both study sites. This was done with 6 sheep enclosure fences and 3 sheep exclosure fences in Hol 2002-2015, and with 10 sheep exclosure fences in Setesdal 2000-2019 (Appendix S1: Fig. S1). In Hol, the fences were located next to each other, and encompassed a total area of 2.7 km^2. In Setesdal, the fences were 20x50 m in size and spread over a considerably larger area of ~250 km^2 (Appendix S1: Fig S1). In Hol, three of the fences had no sheep, three sections had the pre-experiment sheep density typical for the area (25 sheep km^{-2}), and three sections had sheep density elevated to 80 sheep km^{-2}. In Setesdal, the exclosures were accompanied by equivalent, grazed sections located ~30 m from the exclosures. These grazed sections experienced sheep pressure of ~55 sheep km^{-2} over the study period (see Appendix S1: Fig. S3 for details).

Hol has a bedrock of meta-arkose, resulting in moderately base-rich soils, whereas Setesdal has a bedrock of granite, resulting in acidic mineral soil low in nutrients (Austrheim et al., 2005). These differences are associated to the plant species pools and productivity: Hol is more productive and diverse, providing more and higher quality forage for the sheep, whereas Setesdal is less productive and has lower number of species, providing less and lower quality forage. The enclosures and exclosures in Hol encompass diverse vegetation types, most common ones being dwarf-shrub and lichen heaths, but also willow thickets, productive meadows, snowbeds and wetlands are present (Speed et al., 2012a). In Setesdal, the exclosure locations were within habitats preferred by grazing sheep, mostly in humid, grassy heathlands (Speed et al., 2014). In Hol, the enclosures and exclosures spanned the treeline ecotone (Speed et al., 2013), whereas in Setesdal, the exclosures were are at least 5 km from the forest line, historically decreased by human impact 1500–2000 years ago (Eide et al., 2006).

All exclosure and enclosure fences were constructed out of wire mesh supported on wooden posts, placed on south-facing slopes, and taken down every winter (outside of the grazing season) where necessary to avoid snow damage. Small mammals, such as rodents and mountain hare, could access the fenced sections year-round. In addition, wild reindeer could access the fenced sections in spring before the fence installation and in autumn after fence removal, but due to low reindeer population density, we expect this effect to be negligible.

Plant community surveys

We followed plant community composition over time under different sheep treatments and at different elevations with permanent vegetation plots, 0.5x0.5 m in size. In Hol, 20 plots were placed in each enclosure and exclosure section by a stratified balanced procedure among elevational levels and habitats (for details, see Austrheim et al., 2008), summing up to 180 plots. In Setesdal, each exclosure and grazed section had 10 randomly placed plots (for details, see Austrheim et al., 2005), summing up to 200 plots. At neither of the sites were plots placed in wet depressions or on rocks.

Over the two sites the plots covered an elevational gradient from 852 to 1311 masl (1091-1311 masl for Hol and 852-1014 mals for Setesdal; Appendix S1: Fig. S1, Fig. S4). Each plot was divided into 16 sub-squares, and each survey year we recorded all vascular plant species occurring in each subsquare. The survey years were 2001, 2003, 2005, 2007, 2009, 2011, 2013 and 2015 for Hol, and 2000, 2002, 2004, 2006, 2008, 2010, 2012, 2014 and 2019 for the Setesdal exclosures. At both sites, the survey of the first year was done before sheep density manipulation to capture the initial plant community composition structure.

Plant trait data

Data on plant functional traits for the species occurring at the study plots was retrieved from open trait data sources. To ensure data retrieval across species synonyms, species names were standardized using tnrs-function in taxize-package that utilizes the Taxonomic Name Resolution Service from the iPlant Collaborative (Chamberlain and Szöcs, 2013). All potential accepted synonyms were retrieved from the Integrated Taxonomic Information System and Catalogue of Life with the synonyms-function of the same package. When multiple synonyms appeared, each synonym was used in turn until a match was found in the functional trait databases.

We used tr8-function of the TR8-package to access multiple databases simultaneously on R (Bocci, 2015). To achieve as full trait data coverage as possible, we requested data on all leaf, height, seed and chemical traits available from Ecoflora (Fitter and Peat, 1994), LEDA (Kleyer et al., 2008), BiolFlor (Klotz et al., 2002), Eflora_cal and PLANTS (Green, 2009). In addition, we included data from Tundra Trait Team (Björkman et al., 2018b), from SeedClim (Gya, 2017), and from TRY database (download number 4659; Kattge et al., 2011), covering all datasets containing data on leaf, height, seed and chemical traits. See Appendix S1: Table S1 for trait details from each database. Trait data with uncertain or deficient unit information were excluded.

We included data on all traits that had data for at least 70% of species observed in the plant survey plots in each study site. After this process, eight traits remained: vegetative height (height of highest photosynthetic part), generative height (height of the highest reproductive part), leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), leaf fresh mass, seed dry mass and seed number per plant. These traits capture the central functional dimensions of size, resource economics, and reproduction. When there were multiple observations of the same trait for a species from different data sources, the mean was calculated to acquire one value for each species for each trait.

To fill in data gaps for species without trait values, we used phyEstimate-function of the Picante-package. This function allows predicting species trait data based on the existing traits data and phylogenetic relationships between species (Kembel and Kembel, 2020). For these predictions, we used a published phylogeny of the Norwegian flora (Mienna et al., 2020) and existing trait data of all vascular plants native for Norway (retrieved from the databases as described above). In addition to the eight selected traits, we determined a binary variable of woodiness for each species based on literature, as this trait may play a key role in ecosystem functioning (García Criado et al., 2020; Myers-Smith et al., 2011; Weintraub and Schimel, 2005).

After achieving full data coverage for nine traits for all species occurring in Hol and Setesdal, we used the functcomp-function of the FD-package to acquire the community-weighted mean for each trait for each plot for each survey year (Laliberté et al., 2014), based on the plant occurrence in the 16 sub-squares. This gave us a matrix where each plot had one community-weighted mean value for each trait.

Statistical analyses

To create a measure of trait composition across the time, we constructed a principal components analysis for the community-weighted mean traits, by using the rda-function from the vegan-package (Oksanen et al., 2013). This was done for both study sites separately. For both sites, the two first PC-axis were significant, and explained 61% (Hol) and 77% (Setesdal) of the variation in the trait composition (Appendix S1: Table S2). The further analysis was constrained to these two axes.

To acquire an indicator of the trait composition change under different sheep densities at different elevations over the study periods, we built a linear model where PC-scores were explained by number of years since exclusion for each plot. Thus, we could extract model slope values, describing the trait composition change over time for each plot. These models were built separately for PC1 and PC2. This method was chosen to capture the overall plot-specific change over the study period, not distorted by potential anomalies of individual years. Extracted plot-specific slopes were then modelled as a response to sheep treatment, elevation and their interaction in linear regression, for both sites separately, and for both PC-axes separately, resulting in four final models.

Enclosure and exclosure sections (Hol) and sites (Setesdal; site consisting of an exclosure and a paired grazed section) were included into the model as random factors. To check whether these random factors were sufficient to account for the spatial structure of the data, we tested whether there was spatial autocorrelation left in the model residuals by using Moran's I autocorrelation coefficients. No differences between expected and observed Moran's I values were detected, suggesting that the used random structures were sufficient (Appendix S1: Table S3).

To visualize which species were driving the trait composition trends, we constructed principal components analyses also for species community data for both sites. This was done in a same way as described for the trait composition above, except that we did not test for statistical changes in PC-score trends.

All analyses were carried out within the R environment (R version 3.5.1, RCore Team, R Foundation for Statistical Computing, Vienna, Austria).

Island-mainland comparison

Setesdal harbours multiple lakes with islands that have experienced low or zero grazing pressure in history. These islands support stunted birch forests (Appendix S1: Fig. S1; Fig. S5) that are not present in the surrounding mainland, likely because sheep are preventing the re-establishment of trees. To gain perspective on the effects of sheep grazing on longer time scales, we conducted an additional vegetation survey and compared the trait composition at grazed and exclosed sections to trait composition of the islands. This survey was a snapshot in time, conducted only in 2012, after 12 years of sheep exclusion on the mainland. Three islands, located on three separate lakes, approximately 0.06, 0.16 and 0.15 km^2 in size, were included in this survey. These islands showed similar levels of topographic heterogeneity to the mainland (Speed et al., 2014).

In this part of the study, plant species were recorded on 0.5x0.5m plots by using point intercept method. At each plot, 16 regularly spaced pins were lowered into the plot, and every intercept with each plant species was recorded. Each exclosure and grazed section on the mainland had three plots stratified by the upper, mid and lower part of the section’s slope. Each of the three islands had six plots placed randomly on the south-facing slope of the island (to be comparable to the south-facing exclosures on the mainland), out of which three plots were placed directly under the birch canopy and three outside the birch canopy. Plots were not placed in wet depressions or on rocks. (For details and justifications for the island methods, see Speed et al., 2014).

We used point intercept community data to calculate community weighted means for each trait for each plot, as described above for the main analysis. To create a measure of trait composition in exclosed, grazed and island plots, we again constructed a principal components analysis. The first PC-axis was significant (df=1, Variance=1.2, F=11.9, Pr(>F)=0.001), and explained 89% of the variation in the data. Plot scores on this axis were modelled as a response to treatment (grazed, exclosed, island) in a mixed linear model where location (island number and exclosure number) were used as a random factor to account for the potential spatial dependencies. To check whether these random factors were sufficient to account for the potential spatial structure of the data, we tested whether there was spatial autocorrelation left in the model residuals by using Moran's I autocorrelation coefficients. No differences between expected and observed Moran's I values were detected, suggesting that the random structure used in our models was sufficient (Appendix S1: Table S3). Elevation was not included into the model as the islands were at low elevations in comparison to the mainland plots; the potential effects of this constrain are discussed below.

To visualize which species were driving the trait composition differences, we constructed a principal components analysis also for species community data for island and mainland plots. This was done in a same way as described for the trait composition above, except that we did not test for statistical significances of PC-score differences.

Results

We observed 126 vascular plant species in Hol and 64 in Setesdal over the study period. In Hol, elevation appeared to be weakly linked to trait composition across the study period (Fig. 1a): high vegetative height, SLA, leaf area, and leaf fresh mass being associated to lower elevations, and LDMC and woodiness associated to middle and high elevations (Fig 1e). In Setesdal, elevation did not appear to be linked to trait composition across the study period (Fig. 2a,d).

In Hol, there were no apparent directional changes in plant community trait composition over the study period. This is shown by the ordination visualizations where we can see that the plot locations in ordination did not change over time (red arrows in Fig. 1b-d); consequently we did not find evidence for sheep treatment, elevation or their interaction affecting the trait change in time (Table 1; Appendix S1: Fig. S6). In Setesdal, however, there seemed to be a moderate trait change over the study period (red arrows in Fig. 2b-c). This temporal change seems to be accounted for by changes in generative height (+0.3cm ± 1.8SE), vegetative height (+0.3cm ± 1.7SE), SLA (+7.7 mm^2/mg ± 5.1SE), leaf area (+53mm^2 ± 49SE), leaf fresh mass (+9.9 mg ± 8.5SE) and LDMC (-20 g/g ± 3.4SE); see Appendix S1: Fig. S7-8 for the temporal trends in the traits, and Fig. 2d for their role in the ordination. Yet, also in Setesdal, we did not find evidence for sheep treatment, elevation or their interaction affecting the trait change in time (Table 1; Appendix S1: Fig. S9), implying that the observed temporal change was unidirectional in different sheep treatments and at different elevations (Fig. 2b-c; see also Appendix S1: Fig. S10).

Trait stability in Hol appeared to be accompanied by species community stability of equal degree: there were no visible differences between the centroids of the first and the last survey year in any sheep treatment (red arrows in Appendix S1: Fig. S11b-d; see Fig. S12 for the underlying species). Moderate temporal trait community change in Setesdal was accompanied by moderate species community change, again similar across the sheep treatments (red arrows in Appendix S1: Fig. S13b-c; see Fig. S14 for the underlying species).

Contrasts from the island-mainland comparison model showed that the island trait composition differed from the trait composition at exclosed and grazed plots, but the trait composition at the exclosed plots did not differ from the trait composition at the grazed plots (Table 2). Ordination visualization shows that even though there is an overlap between the trait composition in mainland and on the islands, island vegetation under the birch canopy showed distinct trait composition in comparison to the mainland (Fig. 3a). Islands were, on average, at lower elevations (884masl ± 41SD) than mainland plots (961masl ± 59SD), but even the mainland plots at low elevations appeared to be distinct from most of the island plots (Fig. 3b).

Island plots were associated with higher vegetative and generative height, seed dry mass and woodiness, and, to a lower degree, with higher SLA, whereas the mainland plots were associated with higher LDMC (Fig. 3c; for absolute differences in traits between mainland and islands, see Appendix S1: Fig. S15). The species most implicated in driving these differences appeared to be *Solidago virgaurea*, *Gentiana purpurea*, *Cornus suecica*, *Descampsia flexuosa*, and *Betula pubescens*, associated with island plots, and *Nardus stricta*, associated with mainland (Appendix S1: Fig. S16-17).

Discussion

Livestock have become a keystone species group in many ecosystems by affecting vegetation properties (Gillson and Hoffman, 2007; Öllerer et al., 2019; Wang and Wesche, 2016; Yayneshet and Treydte, 2015). Sheep grazing is known to change plant communities and traits in many different types of habitats (Bouchard et al., 2003; Løkken et al., 2019; Louhaichi et al., 2012; Marteinsdóttir et al., 2017; Navarro et al., 2006; Ross et al., 2016; Scohier and Dumont, 2012). We showed, however, that historically intensively grazed alpine vegetation communities at two study sites had high resistance to changing sheep densities over 13- and 19-year study periods, regardless of elevation. However, our analyses also indicate that longer-term grazing history on the mainland had resulted to a different trait composition compared zero-to-low sheep grazing on the islands of the region. Thus, the results suggest that sheep can have effects on alpine plant community trait composition, but these effects may take historical timescales, from several decades to centuries, to manifest.

Earlier studies have shown moderate changes in some grazing-sensitive and grazing-resistant species at our experimental sites (Austrheim et al., 2007; Austrheim et al., 2008; Speed et al., 2014), but the community-level resistance to changes in sheep densities documented here was remarkable. Similar stability under sheep exclusion has been reported from a chenopod shrubland in the arid South Australia, where a decade of sheep exclusion was insufficient to change vegetation shaped under over a century of intensive grazing (Meissner and Facelli, 1999). Also in historically overgrazed Iceland, mere sheep exclusion is rarely considered to be a sufficient method for ecosystem restoration (Mulloy, 2020; Mulloy et al., 2019).

Furthermore, there is evidence of slow and partial vegetation recoveries in relation to cervid herbivory (Collard et al., 2010; Wright et al., 2012).

Potential explanations for slow vegetation recovery are numerous, and likely to vary depending on prevailing abiotic conditions. If productivity is low and plant growth rates slow, as they often are in northern and high-elevation ecosystems, vegetation structure changes are likely to take time. When plant community consists of long-lived (Cotto et al., 2017) species and low-stature species that keep the lower field layer closed, free establishment space for new plant individuals is limited. Thus, strong imbalances in plant-plant competition abilities of the species are needed to cause changes in species composition (Choler et al., 2001). All of these factors are likely to result in slow species turnover, reflecting to slow community trait turnover. This is may explain the lack of community change in Setesdal after sheep removal: This site had low productivity, and most of the plant species we recorded were perennials. Many prevalent species were long-lived shrubs or grasses with strongly rooted, thick tufts. The lack of sheep disturbance also decreased the available open soil surface in exclosures (Austrheim et al., 2008), further diminishing open growth space for new plant individuals. In Hol, we could expect to have potential for faster species turnover capacity due to higher productivity, but this may be counteracted by closed vegetation and lack of establishment space in the exclosures (Choler et al., 2001).

Moreover, it can be asked whether the vegetation transformed by historical sheep grazing is particularly resistant to community changes, i.e. whether grazing has tipped the vegetation into an alternative state from which it is hard to transform back. Vegetation with long grazing history may be more resilient to changes in grazing when compared to vegetation with no grazing history, as it harbours plants that are likely to have evolved avoidance and tolerance to grazing (Cingolani et al., 2005; Lemaire, 2001; Milchunas et al., 1988). As our island-mainland comparison at the less-productive site showed, island vegetation tended to be taller (both in vegetative and generative height) and had higher specific leaf area, due to herbs such as *Solidago virgaurea*, *Gentiana purpurea* and *Cornus suecica*, grazing-sensitive grass *Descampsia flexuosa*, and birch *Betula pubescens*. The grazed mainland, in contrast, had higher leaf dry matter content due to dwarf shrubs and low, grazing-resistant grasses, especially *Nardus stricta*. Thick grass tufts and prostrate shrubs in the mainland could lower the establishment chances of new plant individuals (Lemaire, 2001; Milchunas et al., 1988), possibly explaining the lack of vegetation changes in the exclosures. Furthermore, grazing may lead to plant acclimation towards low growth forms rather than erect ones (Lemaire, 2001), further closing low field layer. Under more productive conditions in Hol, grazing tolerance rather than avoidance (Coley et al., 1985) seems likely reason for the community stability after sheep removal: when nutrients are not limiting growth, even relatively grazing-sensitive species have potential for compensatory growth, and thus the plant community under no sheep grazing did not develop to different direction compared to the plant community under maintained sheep density. Taking into account that high grazing pressure has affected our study region over thousands of years (Speed et al., 2012b), it is also possible that there has been evolutionary pressure towards high grazing resistance and tolerance (Cingolani et al., 2005; Lemaire, 2001). Even long before human impact, ungulates have been present in European landscape, possibly sustaining a natural mosaic of open patches and closed vegetation (Sandom et al., 2014; Svenning, 2002), promoting the evolution of herbivore resistance and tolerance in plants.

The lack of birch establishment may be one reason why the trait composition did not change in the exclosures in Setesdal, whereas we observed clear trait composition difference between the mainland and the birch-growing islands. It appears that most of the island survey plots located under birch trees were functionally distinct from the plots on the mainland where sheep prevent tree establishment, whereas most of the island plots located outside the birch canopy were closer to the plots on the mainland. If birch shading and potential facilitation effects (Choler et al., 2001) are crucial for field vegetation to develop into the direction of the trait composition we observed in the islands, the exclosure vegetation may not change considerably before birch canopy has established, which, in this environment, will take longer than our 19 year experiment period. In Hol, birch growth has been shown to be higher when sheep are excluded (Speed et al., 2011), but this effect appears to have been too sparse to affect field layer vegetation.

Drastic vegetation changes are often reported following increases in herbivore pressure, exceeding the turnover rates observed in herbivore exclusion experiments (Estes et al., 2011). This is understandable, as grazing and browsing may devastate plant species with low herbivore resistance or tolerance in short time scales, and create empty establishment space for new plant individuals. However, we did not observe vegetation stability only in the sheep exclosures, but also under the increased sheep densities applied in Hol. We hypothesize that this may be because the increased sheep density was still within most species' compensatory growth potential, backed up by high productivity (Cingolani et al., 2005).

Elevation appeared to shape species and community trait composition moderately in Hol, high size traits being associated to low-elevation sites, but not in Setesdal. It seems likely that in Setesdal, where exclosed and grazed sections were spread over a larger and more heterogenous area, plot location could play more important role for local climatic conditions than elevation *per se*. Naturally, elevation does not necessarily reflect to climatic differences, as local topography and microclimate may override its effect (Opedal et al., 2015). The result difference of elevation responses between the sites may also be due to shorter elevational gradient in Setesdal (162m), compared to Hol (220m). However, Setesdal community trait structure seemed to have gone through a moderate temporal change towards taller stature, larger leaf size and lower leaf dry matter content, at the same time when the area has experienced increased temperatures and precipitation. The climatic change was not linear, and we cannot show causality between the climatic change and trait composition change, but increased size, typical for low-elevation and southern species, and lowered leaf dry matter content, typical for prostrate arctic-alpine plants, could be expected from warmer and wetter conditions (Björkman et al., 2018a).

Livestock may play an important role in altering the vegetation composition under future climatic conditions (Gillson and Hoffman, 2007; Öllerer et al., 2019; Wang and Wesche, 2016; Yayneshet and Treydte, 2015), especially if vegetation has not experienced intensive herbivory before. However, as we showed here, long grazing history may dampen the role of herbivory (Cingolani et al., 2005; Milchunas et al., 1988). Our results suggest that plant communities may have resistance to lowered herbivory pressure even at different productivities, although likely through different mechanisms: under low-productivity, vegetation community may resist changes due to slow growth rates and community turnover, whereas under high productivity, intensive plant-plant competition appears to be more likely reason to explain the stability (Choler et al., 2001). Furthermore, we showed that under high productivity, increased sheep densities may not result to community change if there are ample resources for compensatory growth. We conclude that the grazing history needs to be acknowledged when evaluating herbivores' potential to shape plant community trait composition under different climatic conditions.

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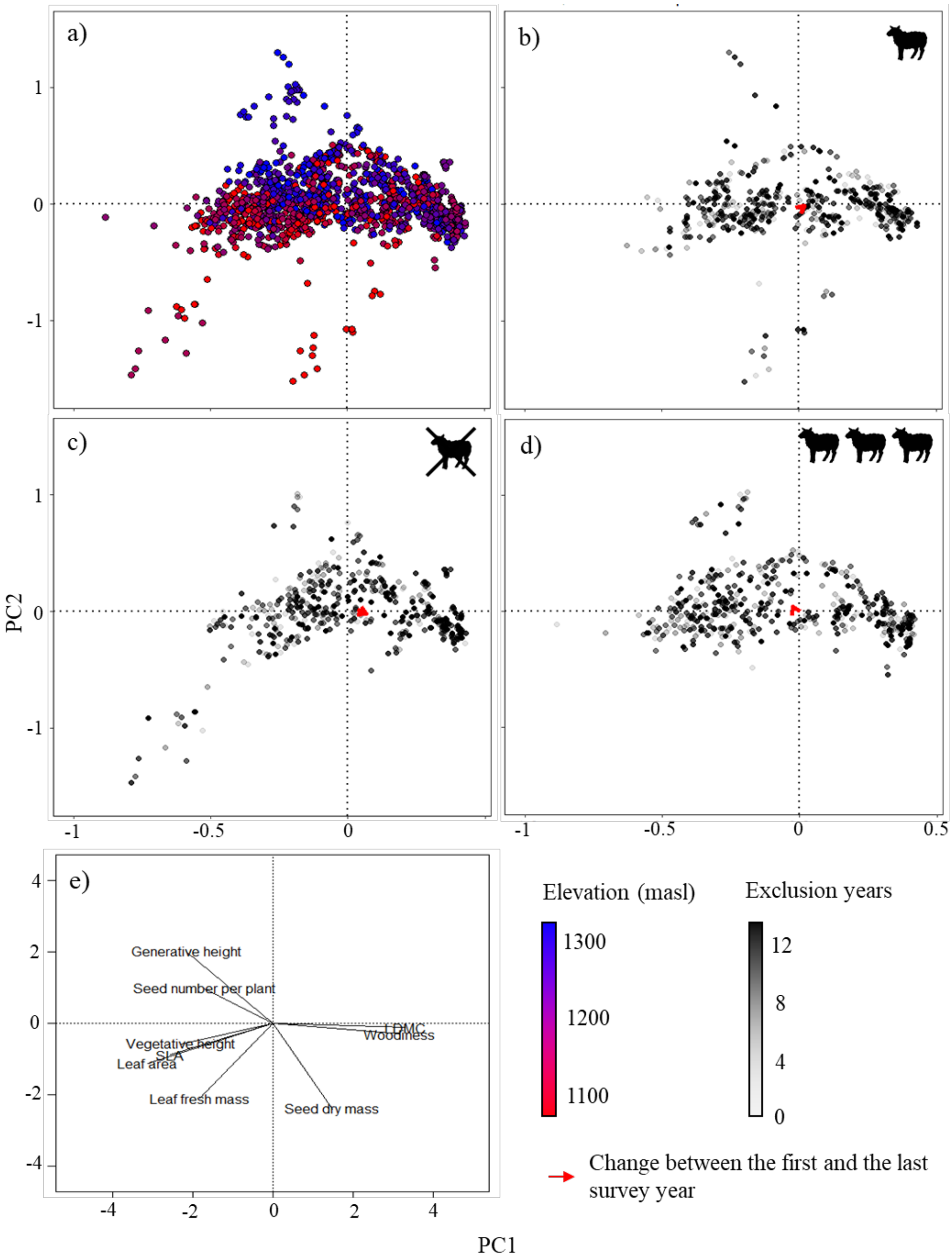

Figure 1. Trait composition of plots on PC1 and PC2 in Hol over the study period, colored by elevation (a), and by year at different sheep treatments (b-d). The arrows in the panels b, c and d represent the centroid change from the baseline vegetation survey year to the last vegetation survey year; Note that the arrows are barely visible due to overlap of the centroids. Panel e shows the underlying trait vectors (note different axis scales compared to panels a-d).

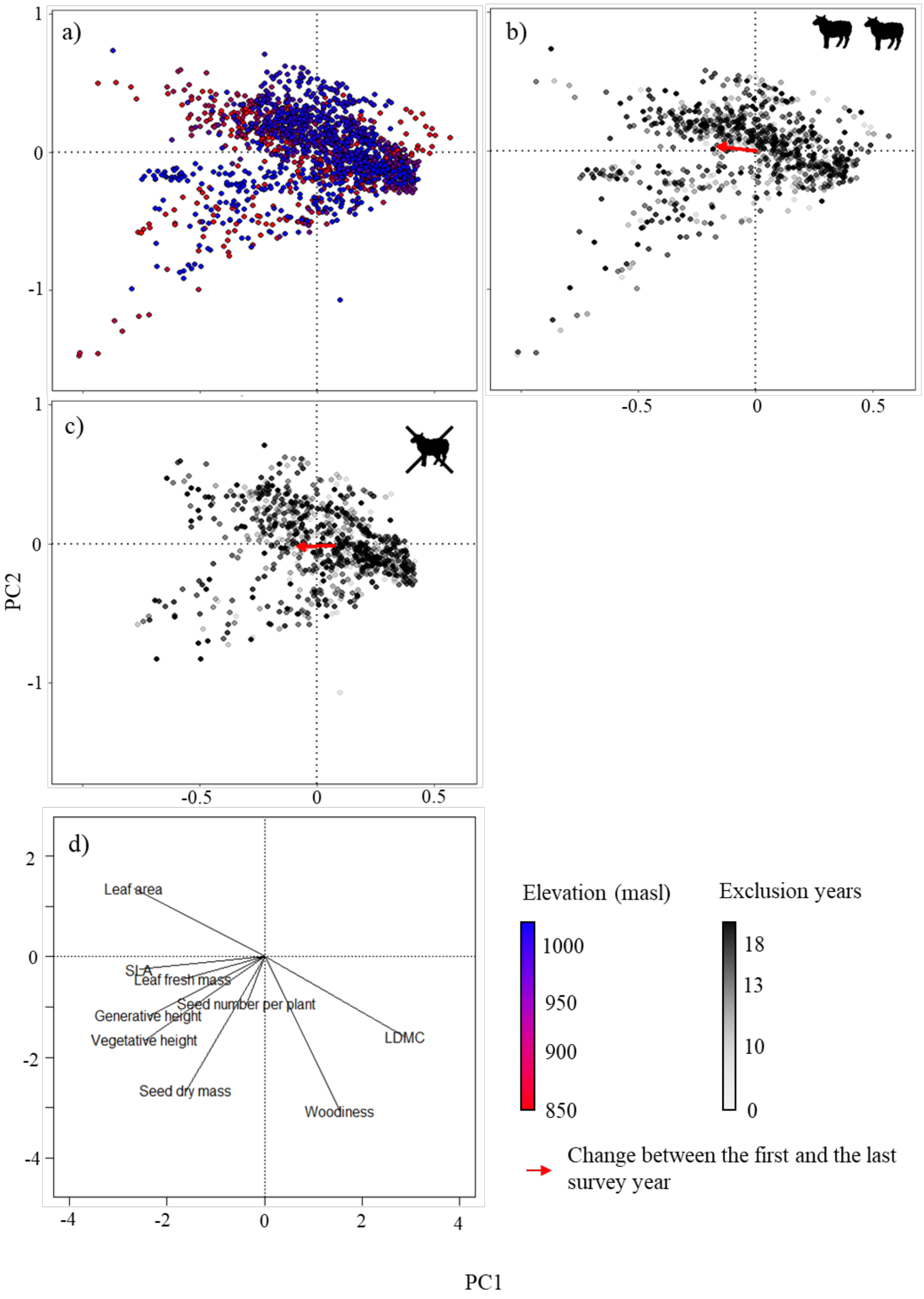

Figure 2. Trait composition of plots on PC1 and PC2 in Setesdal over the study period, colored by elevation (a), and by year at different sheep treatments (b-c). The arrows in the panels b and c represent the centroid change from the baseline vegetation survey year to the last vegetation survey year. Panel d shows the underlying trait vectors (note different axis scales compared to panels a-c).

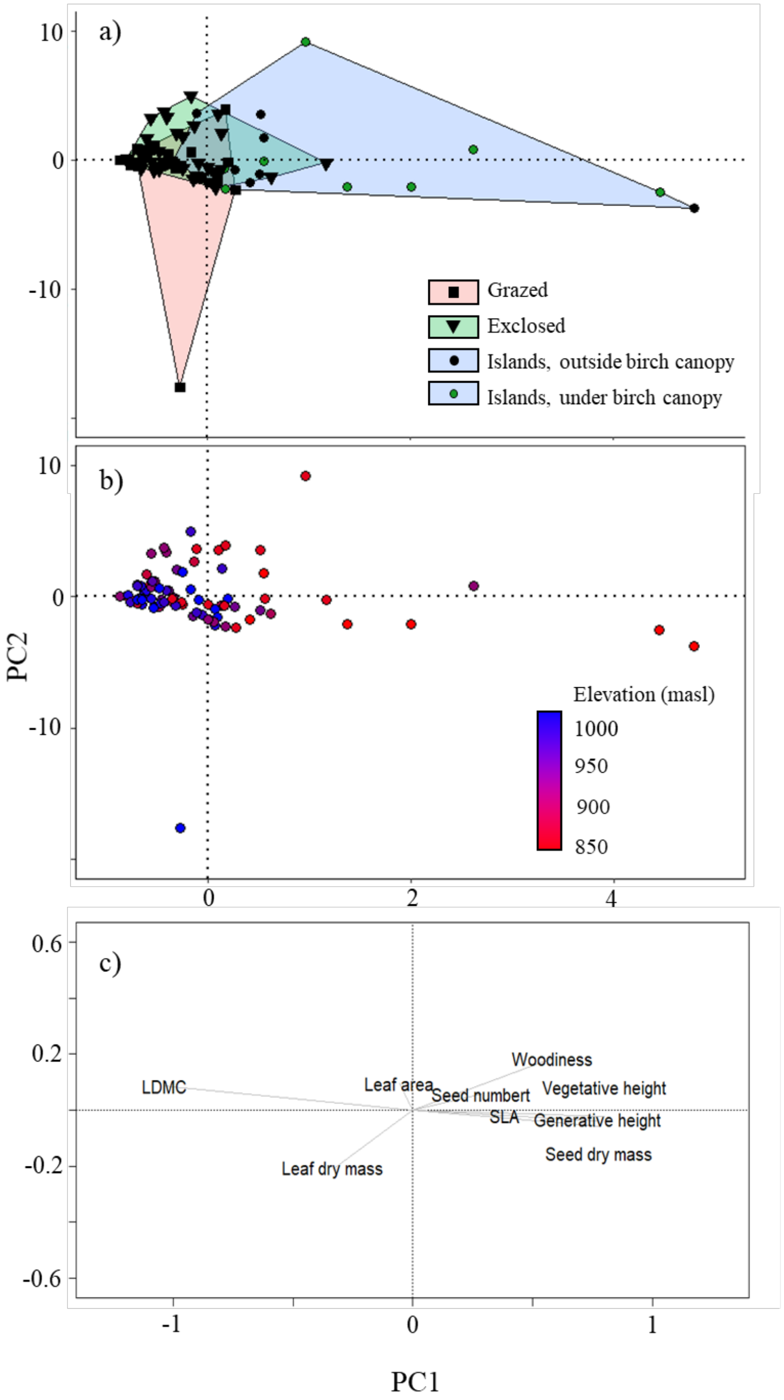

Figure 3. Trait composition of plots on PC1 and PC2 for the island-mainland comparison in Setesdal, colored by elevation (a), and treatment (b). Panel c shows the underlying trait vectors (note different axis scales compared to panels a-b).

Table 1. Model estimates, standard errors, t-values and p-values for the PC-slope models.

		Value	SE	df	t	p
Hol PC1	Intercept	-0.012	0.019	168	-0.65	0.52
	Increased Grazing	0.016	0.025	6	0.62	0.56
	Zero Grazing	0.007	0.026	6	0.27	0.80
	Elevation	0.000	0.000	168	0.70	0.48
	Increased Grazing : Elevation	0.000	0.000	168	-0.64	0.52
	Zero Grazing : Elevation	0.000	0.000	168	-0.28	0.78
Hol PC1	Intercept	0.019	0.033	168	0.59	0.56
	Increased Grazing	0.035	0.043	6	0.82	0.45
	Zero Grazing	0.006	0.044	6	0.14	0.89
	Elevation	0.000	0.000	168	-0.70	0.49
	Increased Grazing : Elevation	0.000	0.000	168	-0.73	0.47
	Zero Grazing : Elevation	0.000	0.000	168	-0.05	0.96
Setesdal PC1	Intercept	-0.017	0.034	187	-0.49	0.63
	Grazed	0.032	0.032	187	1.00	0.32
	Elevation	0.000	0.000	187	0.31	0.76
	Grazed : Elevation	0.000	0.000	187	-0.93	0.35
Setesdal PC2	Intercept	-0.007	0.023	187	-0.32	0.75
	Grazed	0.030	0.023	187	1.29	0.20
	Elevation	0.000	0.000	187	0.28	0.78
	Grazed : Elevation	0.000	0.000	187	-1.21	0.23

Table 2. Post-hoc contrast estimates, standard errors, degrees of freedom, t-ratios and p-values of the island-mainland comparison in Setesdal, acquired by emmeans-function in emmeans-package (Lenth et al., 2018). Tukey method for comparing a family of 3 estimates was used for p-value adjustment.

	Estimate	SE	df	t-ratio	p-value
Exclosure-Grazed	0.12	0.18	64	0.70	0.76
Exclosure-Island	-1.31	0.34	11	-3.89	0.0066
Grazed-Island	-1.44	0.34	11	-4.26	0.0035

References

Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., 2018. Lags in the response of mountain plant communities to climate change. Global change biology 24, 563-579.

Austrheim, G., Evju, M., Mysterud, A., 2005. Herb abundance and life-history traits in two contrasting alpine habitats in southern Norway. Plant Ecology 179, 217-229.

Austrheim, G., Mysterud, A., Hassel, K., Evju, M., Økland, R. H., 2007. Interactions between sheep, rodents, graminoids, and bryophytes in an oceanic alpine ecosystem of low productivity. Ecoscience 14, 178-187.

Austrheim, G., Mysterud, A., Pedersen, B., Halvorsen, R., Hassel, K., Evju, M., 2008. Large scale experimental effects of three levels of sheep densities on an alpine ecosystem. Oikos 117, 837-846.

Björkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., 2018a. Plant functional trait change across a warming tundra biome. Nature 562, 57-62.

Björkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Thomas, H. J., Alatalo, J. M., Alexander, H., Anadon-Rosell, A., Angers-Blondin, S., Bai, Y., 2018b. Tundra Trait Team: A database of plant traits spanning the tundra biome. Global Ecology and Biogeography 27, 1402-1411.

Blume-Werry, G., Kreyling, J., Laudon, H., Milbau, A., 2016. Short-term climate change manipulation effects do not scale up to long-term legacies: Effects of an absent snow cover on boreal forest plants. Journal of Ecology 104, 1638-1648.

Bocci, G., 2015. TR8: an R package for easily retrieving plant species traits. Methods in Ecology and Evolution 6, 347-350.

Bond, W. J., 2005. Large parts of the world are brown or black: a different view on the 'Green World'hypothesis. Journal of Vegetation Science 16, 261-266.

Bouchard, V., Tessier, M., Digaire, F., Vivier, J.-P., Valery, L. c., Gloaguen, J.-C., Lefeuvre, J.-C., 2003. Sheep grazing as management tool in Western European saltmarshes. Comptes Rendus Biologies 326, 148-157.

Chamberlain, S. A., Szöcs, E., 2013. taxize: taxonomic search and retrieval in R. F1000Research 2.

Choler, P., Michalet, R., Callaway, R. M., 2001. Facilitation and competition on gradients in alpine plant communities. Ecology 82, 3295-3308.

Cingolani, A. M., Noy-Meir, I., Díaz, S., 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. Ecological applications 15, 757-773.

Coley, P. D., Bryant, J. P., Chapin, F. S., 1985. Resource availability and plant antiherbivore defense. Science 230, 895-899.

Collard, A., Lapointe, L., Ouellet, J.-P., Crête, M., Lussier, A., Daigle, C., Côté, S. D., 2010. Slow responses of understory plants of maple-dominated forests to white-tailed deer experimental exclusion. Forest Ecology and Management 260, 649-662.

Cornwell, W. K., Cornelissen, J. H., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology letters 11, 1065-1071.

Cotto, O., Wessely, J., Georges, D., Klonner, G., Schmid, M., Dullinger, S., Thuiller, W., Guillaume, F., 2017. A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. Nature Communications 8, 1-9.

Cromsigt, J. P., te Beest, M., Kerley, G. I., Landman, M., le Roux, E., Smith, F. A., 2018. Trophic rewilding as a climate change mitigation strategy? Philosophical Transactions of the Royal Society B: Biological Sciences 373, 20170440.

Daugstad, K., Mier, M. F., Peña-Chocarro, L., 2014. Landscapes of transhumance in Norway and Spain: Farmers' practices, perceptions, and value orientations. Norsk Geografisk Tidsskrift-Norwegian Journal of Geography 68, 248-258.

Diaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., NOY-MEIR, I., 2007. Plant trait responses to grazing–a global synthesis. Global Change Biology 13, 313-341.

Eide, W., Birks, H. H., Bigelow, N. H., Peglar, S. M., Birks, H. J. B., 2006. Holocene forest development along the Setesdal valley, southern Norway, reconstructed from macrofossil and pollen evidence. Vegetation History and Archaeobotany 15, 65-85.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B., 2011. Trophic downgrading of planet Earth. Science 333, 301-306.

Fitter, A. H., Peat, H. J., 1994. The ecological flora database. Journal of Ecology 82, 415-425.

Franklin, J., Serra-Diaz, J. M., Syphard, A. D., Regan, H. M., 2016. Global change and terrestrial plant community dynamics. Proceedings of the National Academy of Sciences 113, 3725-3734.

García Criado, M., Myers-Smith, I. H., Bjorkman, A. D., Lehmann, C. E., Stevens, N., 2020. Woody plant encroachment intensifies under climate change across tundra and savanna biomes. Global Ecology and Biogeography 29, 925-943.

Gillson, L., Hoffman, M. T., 2007. Ecology: Rangeland ecology in a changing world. science 315, 53-54.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, J. L. B., Coldea, G., Dick, J., Erschbamer, B., Kazakis, G., 2012. Continent-wide response of mountain vegetation to climate change. Nature climate change 2, 111-115.

Gray, S. B., Brady, S. M., 2016. Plant developmental responses to climate change. Developmental Biology 419, 64-77.

Green, B., Vos, W., 2003. Threatened landscapes: conserving cultural environments. Taylor & Francis.

Green, W., 2009. USDA PLANTS Compilation, version 1, 09-02-02. WWW document] URL http://bricol. net/downloads/data/PLANTSdatabase.

Gya, R., 2017. The role of intraspecific variability in driving community trait shifts along temperature and precipitation gradients in alpine and boreal semi-natural grasslands. Master's thesis, The University of Bergen, https://bora.uib.no/bora-xmlui/handle/1956/17229.

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.

Hayward, D., 1948. Transhumance in southern Norway. Scottish Geographical Magazine 64, 71-80.

Hendrix, S. D., 1988. Herbivory and its impact on plant reproduction. Plant reproductive ecology: patterns and strategies, 246-263.

Kaarlejärvi, E., 2014. The role of herbivores in mediating responses of tundra ecosystems to climate change. Umeå universitet.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., 2011. TRY–a global database of plant traits. Global change biology 17, 2905-2935.

Kembel, S. W., Kembel, M. S. W., 2020. Package ‘picante’.

Kleyer, M., Bekker, R., Knevel, I., Bakker, J., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J., Klimeš, L., Klimešová, J., 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of ecology 96, 1266-1274.

Klotz, S., Kühn, I., Durka, W., Briemle, G., 2002. BIOLFLOR: Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Bundesamt für Naturschutz Bonn.

Kolari, T. H., Kumpula, T., Verdonen, M., Forbes, B. C., Tahvanainen, T., 2019. Reindeer grazing controls willows but has only minor effects on plant communities in Fennoscandian oroarctic mires. Arctic, Antarctic, and Alpine Research 51, 506-520.

Laliberté, E., Legendre, P., Shipley, B., Laliberté, M. E., 2014. Package ‘FD’. Measuring functional diversity from multiple traits, and other tools for functional ecology.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional ecology 16, 545-556.

Leishman, M. R., Wright, I. J., Moles, A. T., Westoby, M., 2000. The evolutionary ecology of seed size. Seeds: the ecology of regeneration in plant communities 2, 31-57.

Lemaire, G., 2001. Ecophysiology of grasslands: dynamic aspects of forage plant populations in grazed swards. International Grassland Congress, Vol. 19, pp. 29-37.

Lenoir, J., Svenning, J. C., 2015. Climate-related range shifts–a global multidimensional synthesis and new research directions. Ecography 38, 15-28.

Lenoir, J., Gégout, J.-C., Marquet, P., De Ruffray, P., Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. science 320, 1768-1771.

Lenoir, J., Gégout, J. C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W., Svenning, J. C., 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography 33, 295-303.

Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M., 2018. Emmeans: Estimated marginal means, aka least-squares means. R package version 1, 3.

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, 698-708.

Louhaichi, M., Ghassali, F., Salkini, A., Petersen, S., 2012. Effect of sheep grazing on rangeland plant communities: case study of landscape depressions within Syrian arid steppes. Journal of Arid Environments 79, 101-106.

Ma, Z., Liu, H., Mi, Z., Zhang, Z., Wang, Y., Xu, W., Jiang, L., He, J.-S., 2017. Climate warming reduces the temporal stability of plant community biomass production. Nature Communications 8, 1-7.

Maron, J. L., Vilà, M., 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95, 361-373.

Marteinsdóttir, B., Barrio, I. C., Jónsdóttir, I. S., 2017. Assessing the ecological impacts of extensive sheep grazing in Iceland. Icelandic Agricultural Sciences 30, 55-72.

Meissner, R. A., Facelli, J. M., 1999. Effects of sheep exclusion on the soil seed bank and annual vegetation in chenopod shrublands of South Australia. Journal of Arid Environments 42, 117-128.

Mienna, I. M., Speed, J. D., Bendiksby, M., Thornhill, A. H., Mishler, B. D., Martin, M. D., 2020. Differential patterns of floristic phylogenetic diversity across a post-glacial landscape. Journal of Biogeography 47, 915-926.

Milchunas, D., Sala, O., Lauenroth, W. K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist 132, 87-106.

Moen, A., Lillethun, A., 1999. National atlas of Norway: vegetation. Norwegian Mapping Authority.

Mulloy, T., 2020. Effects of nutrient addition and sheep grazing on tundra rangelands in the Icelandic highlands. Science: Biological Sciences Department.

Mulloy, T. A., Barrio, I. C., Björnsdóttir, K., Jónsdóttir, I. S., Hik, D. S., 2019. Fertilisers mediate the short-term effects of sheep grazing in the Icelandic highlands. Icelandic Agricultural Sciences 32, 75-85.

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6, 045509.

Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P. S., 2020. Complexity revealed in the greening of the Arctic. Nature Climate Change 10, 106-117.

Myers-Smith, I. H., Hik, D. S., 2018. Climate warming as a driver of tundra shrubline advance. Journal of Ecology 106, 547-560.

Navarro, T., Alados, C. L., Cabezudo, B., 2006. Changes in plant functional types in response to goat and sheep grazing in two semi-arid shrublands of SE Spain. Journal of Arid Environments 64, 298-322.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R., Simpson, G. L., Solymos, P., Stevens, M. H. H., Wagner, H., 2013. Package 'vegan'. Community ecology package, version 2, 1-295.

Öllerer, K., Varga, A., Kirby, K., Demeter, L., Biró, M., Bölöni, J., Molnár, Z., 2019. Beyond the obvious impact of domestic livestock grazing on temperate forest vegetation–A global review. Biological Conservation 237, 209-219.

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.

Opedal, Ø. H., Armbruster, W. S., Graae, B. J., 2015. Linking small-scale topography with microclimate, plant species diversity and intra-specific trait variation in an alpine landscape. Plant Ecology & Diversity 8, 305-315.

Pachauri, R. K., Allen, M. R., Barros, V. R., Broome, J., Cramer, W., Christ, R., Church, J. A., Clarke, L., Dahe, Q., Dasgupta, P., 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. Ipcc.

Pastor, J., Naiman, R. J., 1992. Selective foraging and ecosystem processes in boreal forests. The American Naturalist 139, 690-705.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J. L. B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R. F., 2012. Recent plant diversity changes on Europe's mountain summits. Science 336, 353-355.

Pellerin, M., Picard, M., Saïd, S., Baubet, E., Baltzinger, C., 2016. Complementary endozoochorous long-distance seed dispersal by three native herbivorous ungulates in Europe. Basic and Applied Ecology 17, 321-332.

Rekdal, Y., 2001. Vegetasjon og beite ved Minnestølen. NIJOS dokument.

Rekdal, Y., Angeloff, M., 2007. Vegetasjon og beite i Setesdal Vesthei. Oppdragsrapport fra Skog og landskap.

Ross, L. C., Austrheim, G., Asheim, L.-J., Bjarnason, G., Feilberg, J., Fosaa, A. M., Hester, A. J., Holand, Ø., Jónsdóttir, I. S., Mortensen, L. E., 2016. Sheep grazing in the North Atlantic region: A long-term perspective on environmental sustainability. Ambio 45, 551-566.

Rumpf, S. B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J., Willner, W., Zimmermann, N. E., Dullinger, S., 2018. Range dynamics of mountain plants decrease with elevation. Proceedings of the National Academy of Sciences 115, 1848-1853.

Sandom, C. J., Ejrnæs, R., Hansen, M. D., Svenning, J.-C., 2014. High herbivore density associated with vegetation diversity in interglacial ecosystems. Proceedings of the National Academy of Sciences 111, 4162-4167.

Schmitz, O. J., Leroux, S. J., 2020. Food Webs and Ecosystems: Linking Species Interactions to the Carbon Cycle. Annual Review of Ecology, Evolution, and Systematics 51, 271-295.

Scohier, A., Dumont, B., 2012. How do sheep affect plant communities and arthropod populations in temperate grasslands? Animal: an international journal of animal bioscience 6, 1129.

Skarpe, C., Hester, A. J., 2008. Plant traits, browsing and gazing herbivores, and vegetation dynamics. The ecology of browsing and grazing. Springer, pp. 217-261.

Speed, J. D., Austrheim, G., 2017. The importance of herbivore density and management as determinants of the distribution of rare plant species. Biological Conservation 205, 77-84.

Speed, J. D., Austrheim, G., Mysterud, A., 2013. The response of plant diversity to grazing varies along an elevational gradient. Journal of Ecology 101, 1225-1236.

Speed, J. D., Austrheim, G., Hester, A. J., Mysterud, A., 2010. Experimental evidence for herbivore limitation of the treeline. Ecology 91, 3414-3420.

Speed, J. D., 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.

Speed, J. D., Austrheim, G., Hester, A. J., Mysterud, A., 2012a. Elevational advance of alpine plant communities is buffered by herbivory. Journal of Vegetation Science 23, 617-625.

Speed, J. D., Austrheim, G., Kolstad, A. L., Solberg, E. J., 2019. Long-term changes in northern large-herbivore communities reveal differential rewilding rates in space and time. PloS one 14, e0217166.

Speed, J. D., Austrheim, G., Bendiksby, M., Kolstad, A. L., Vuorinen, K. E., 2020. Increasing Cervidae populations have variable impacts on habitat suitability for threatened forest plant and lichen species. Forest Ecology and Management 473, 118286.

Speed, J. D., Martinsen, V., Mysterud, A., Mulder, J., Holand, Ø., Austrheim, G., 2014. Long-term increase in aboveground carbon stocks following exclusion of grazers and forest establishment in an alpine ecosystem. Ecosystems 17, 1138-1150.

Speed, J. D., Austrheim, G., Birks, H. J. B., Johnson, S., Kvamme, M., Nagy, L., Sjögren, P., Skar, B., Stone, D., Svensson, E., 2012b. Natural and cultural heritage in mountain landscapes: towards an integrated valuation. International Journal of Biodiversity Science, Ecosystem Services & Management 8, 313-320.

Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. Nature 556, 231-234.

Stewart, L., Simonsen, C. E., Svenning, J. C., Schmidt, N. M., Pellissier, L., 2018. Forecasted homogenization of high Arctic vegetation communities under climate change. Journal of Biogeography 45, 2576-2587.

Svenning, J.-C., 2002. A review of natural vegetation openness in north-western Europe. Biological Conservation 104, 133-148.

van Vuuren, D. P., Sala, O. E., Pereira, H. M., 2006. The future of vascular plant diversity under four global scenarios. Ecology and Society 11.

Verma, M., to Bühne, H. S., Lopes, M., Ehrich, D., Sokovnina, S., Hofhuis, S. P., Pettorelli, N., 2020. Can reindeer husbandry management slow down the shrubification of the Arctic? Journal of Environmental Management 267, 110636.

Vuorinen, K. E., Rao, S. J., Hester, A. J., Speed, J. D., 2020a. Herbivory and climate as drivers of woody plant growth: Do deer decrease the impacts of warming? Ecological Applications.

Vuorinen, K. E., 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.

Vuorinen, K. E., Kolstad, A. L., De Vriendt, L., Austrheim, G., Tremblay, J. P., Solberg, E. J., Speed, J. D., 2020b. Cool as a moose: How can browsing counteract climate warming effects across boreal forest ecosystems? Ecology, e03159.

Walker, D. A., Raynolds, M. K., Daniëls, F. J., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., 2005. The circumpolar Arctic vegetation map. Journal of Vegetation Science 16, 267-282.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences 103, 1342-1346.

Wang, Y., Wesche, K., 2016. Vegetation and soil responses to livestock grazing in Central Asian grasslands: a review of Chinese literature. Biodiversity and Conservation 25, 2401-2420.

Weintraub, M. N., Schimel, J. P., 2005. Nitrogen cycling and the spread of shrubs control changes in the carbon balance of arctic tundra ecosystems. Bioscience 55, 408-415.

Wright, D. M., Tanentzap, A. J., Flores, O., Husheer, S. W., Duncan, R. P., Wiser, S. K., Coomes, D. A., 2012. Impacts of culling and exclusion of browsers on vegetation recovery across New Zealand forests. Biological Conservation 153, 64-71.

Yayneshet, T., Treydte, A., 2015. A meta-analysis of the effects of communal livestock grazing on vegetation and soils in sub-Saharan Africa. Journal of Arid Environments 116, 18-24.

Zhang, W., Miller, P. A., Smith, B., Wania, R., Koenigk, T., Döscher, R., 2013. Tundra shrubification and tree-line advance amplify arctic climate warming: results from an individual-based dynamic vegetation model. Environmental Research Letters 8, 034023.

Appendix S1

Alpine plant community traits show long-term resistance to changing sheep densities across elevational gradients

Katariina E. M. Vuorinen[1], Gunnar Austrheim[1], Atle Mysterud[2], Ragnhild Gya[3], Vigdis Vandvik[3,4], John-Arvid Grytnes[3] & James D. M. Speed[1]

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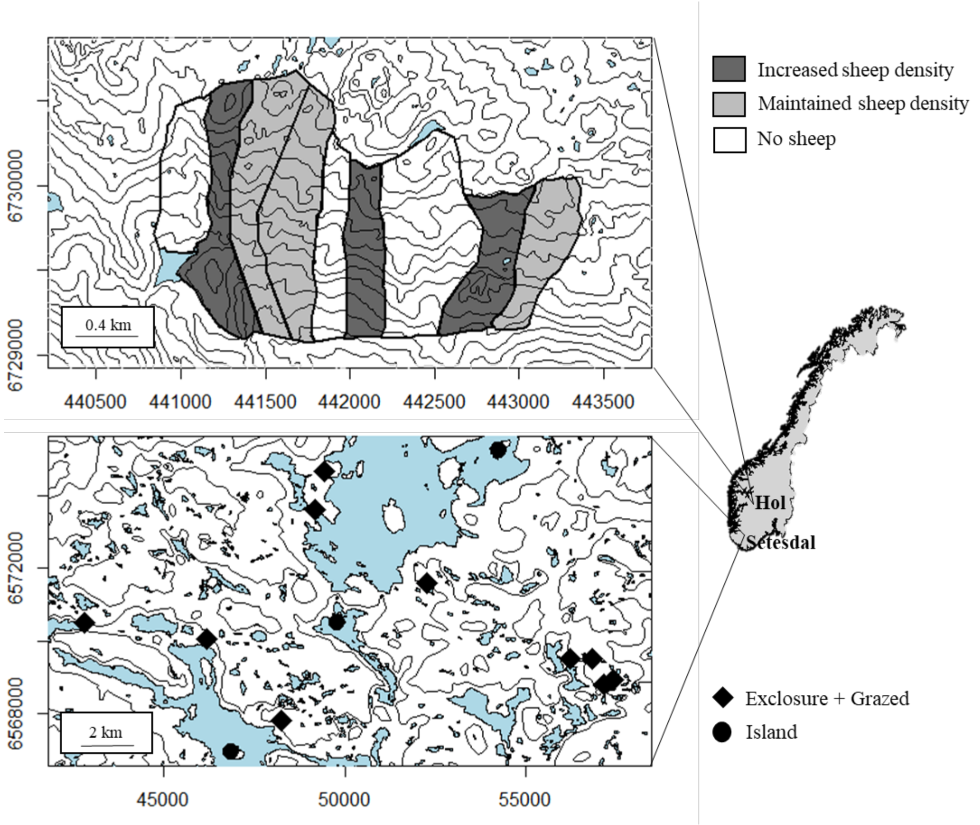


Figure S1. Map of the study areas. Hol had 6 enclosure and 3 exclosure sections with three different sheep density levels. Setesdal had 10 sheep exclosures, each accompanied by a grazed section. In addition, Setesdal had three island sites. Note different spatial resolution between the maps.

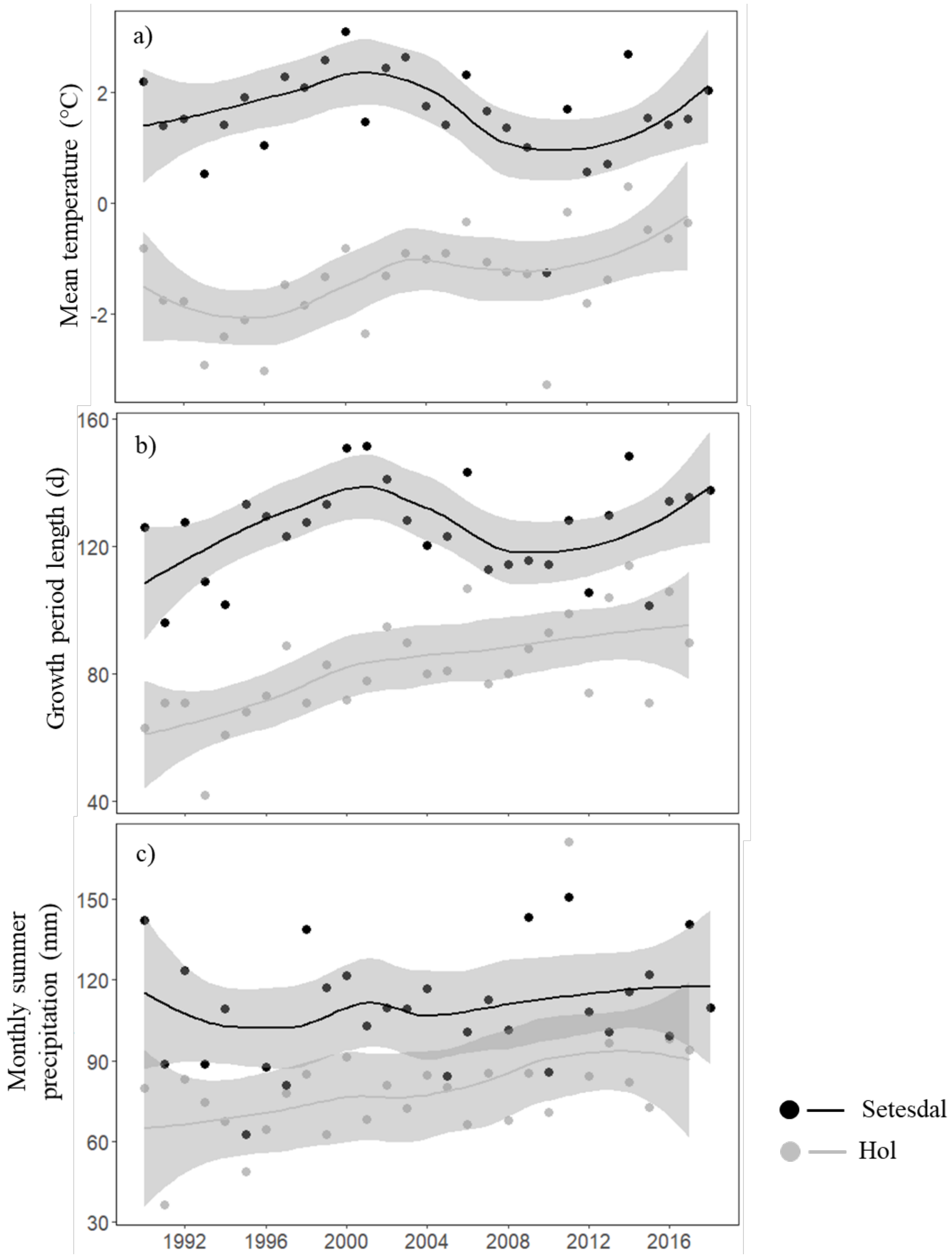


Figure S2. Annual mean temperature (a), growth period length (b) and summer precipitation (c) at the study sites (Lussana et al., 2016; Lussana et al., 2018).

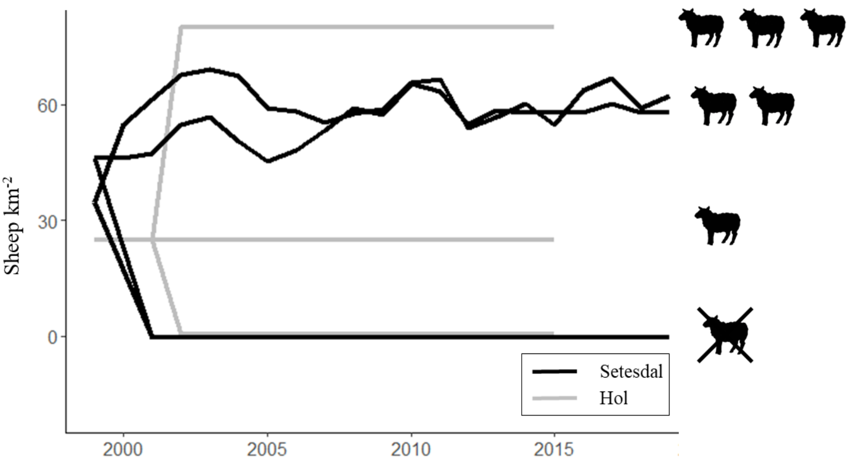


Figure S3. Annual sheep densities over the study period at different sheep treatments. The sheep density data in the grazed areas of Setesdal is from the two sheep management areas where the plots were located (Suleskar and Nomeland; Rekdal and Angeloff, 2007).

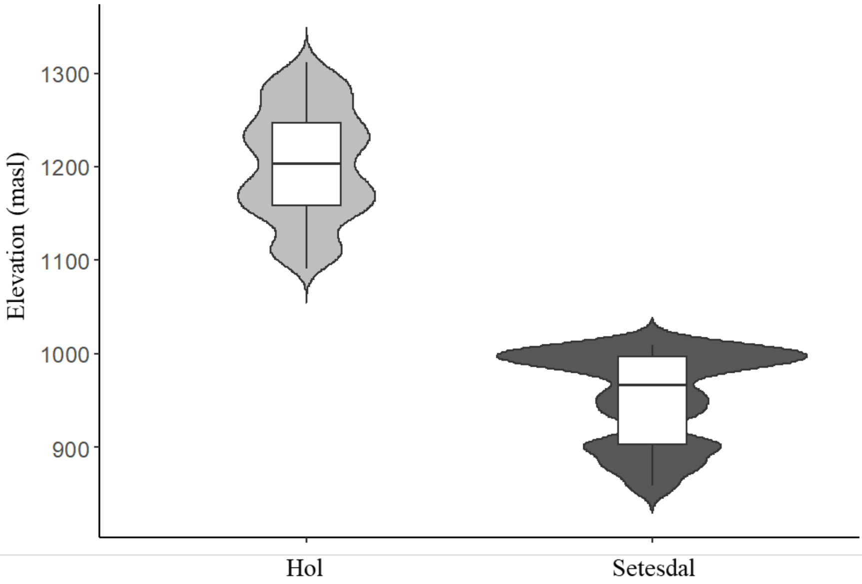
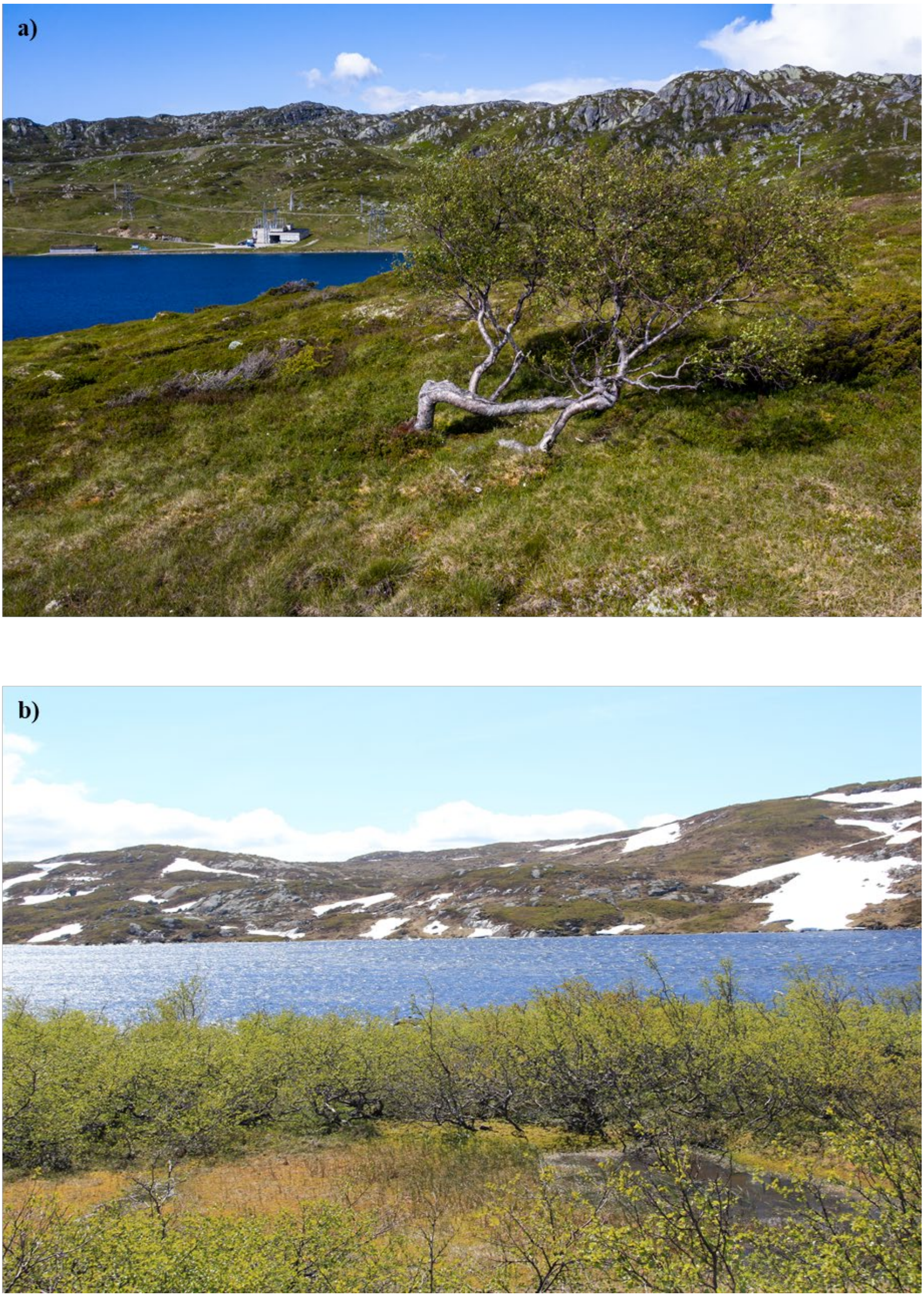


Figure S4. Relative distribution of plant survey plot data at elevational gradient.

Figure S5. Island landscape in Setesdal. The front of the picture depicts island vegetation, whereas land across the water body is mainland. (Photos by Sylvain Fleur (a) and James D. M. Speed (b)).



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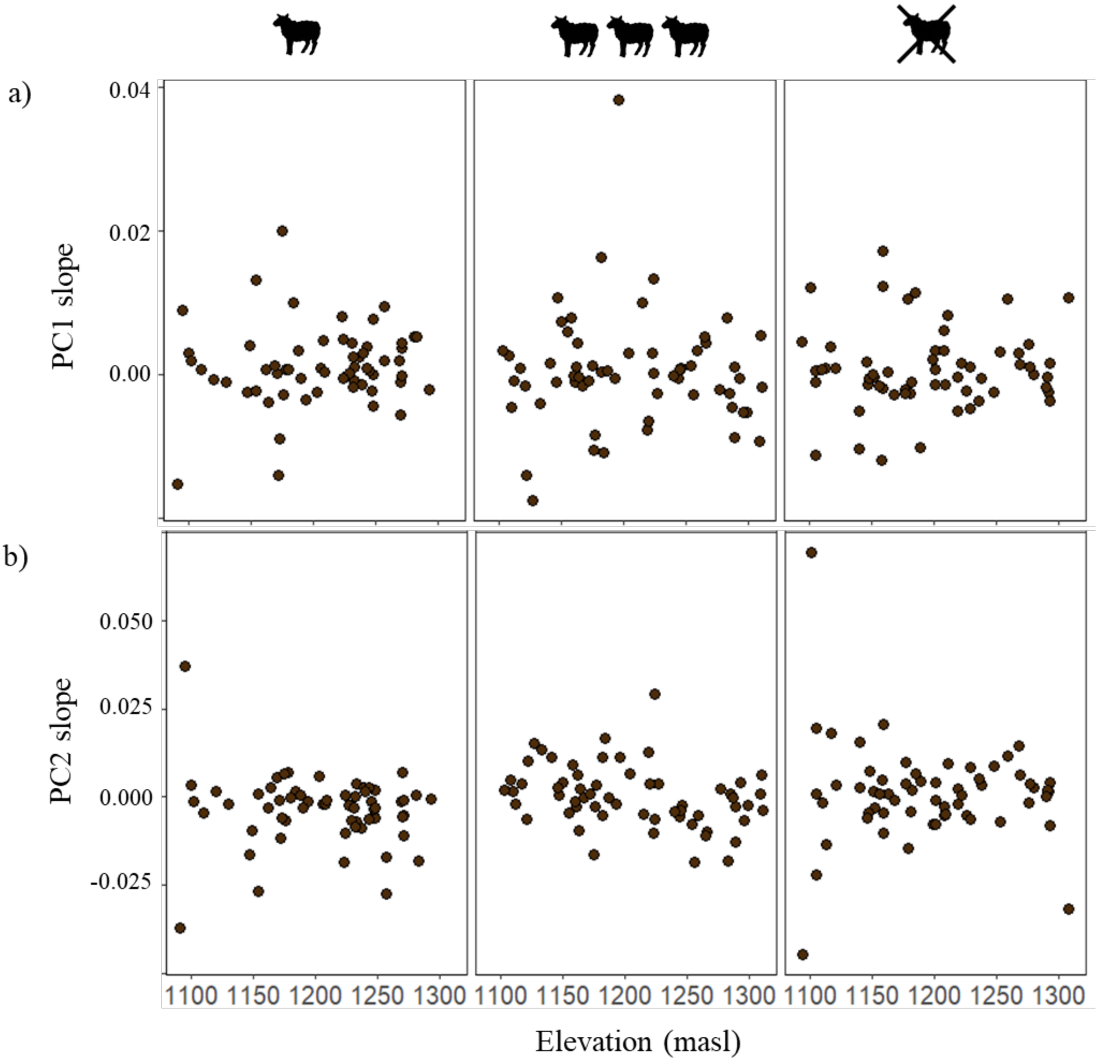

Figure S6. Change on PC1 (a) and PC2 (b) over the study period at different elevations and sheep treatments in Hol, indicated with plot-specific time slope for change over the study period. Neither sheep, elevation, nor their interaction affected the slopes (Table 1).

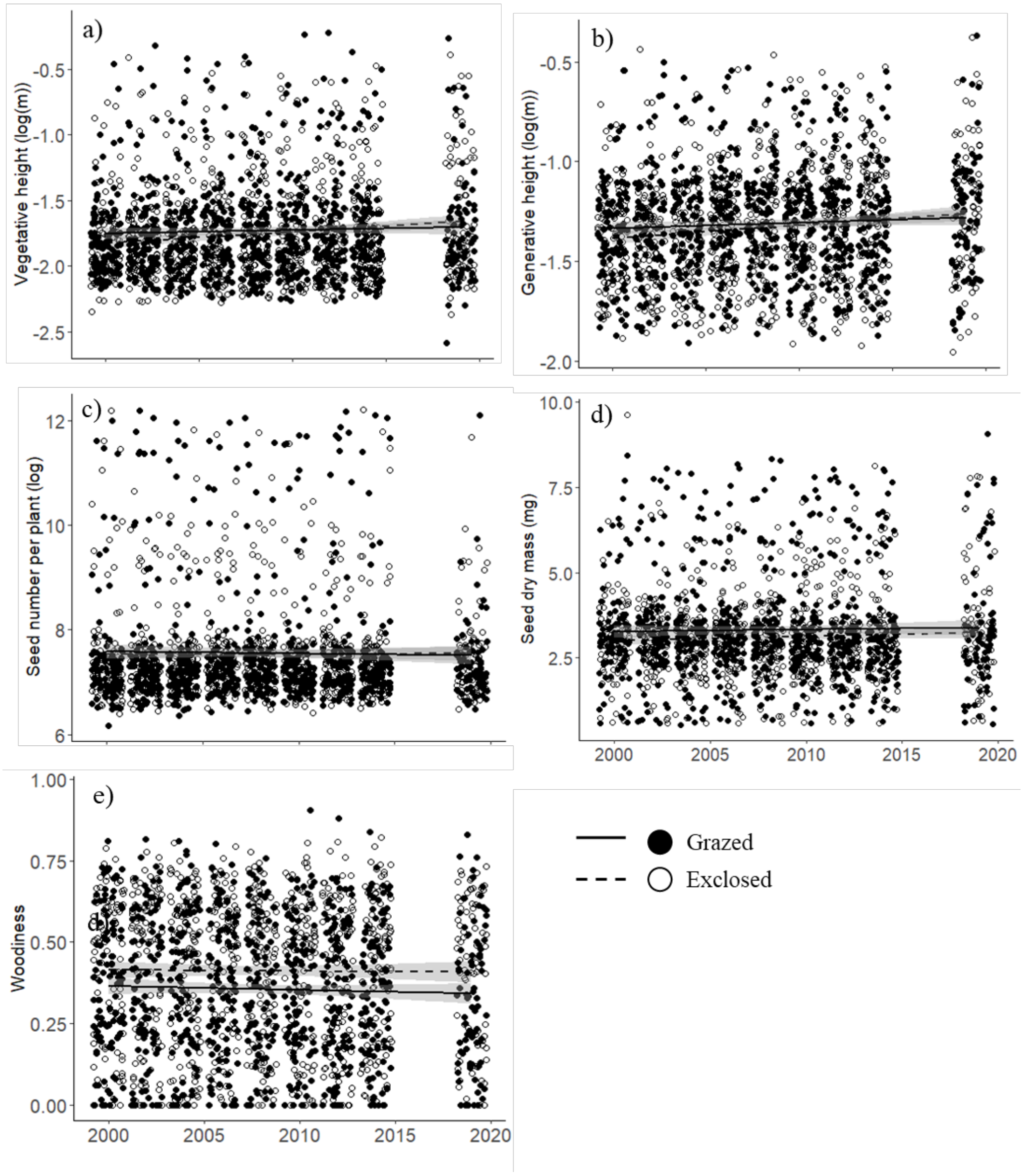

Fig S7. Changes in vegetative height (a), generative height (b), seed number (c), seed dry mass (d), and woodiness (e) in Setesdal over the study period. Trend lines are linear regressions with 0.95 confidence intervals, presented for both treatments separately. The significances of each trend was not statistically tested.

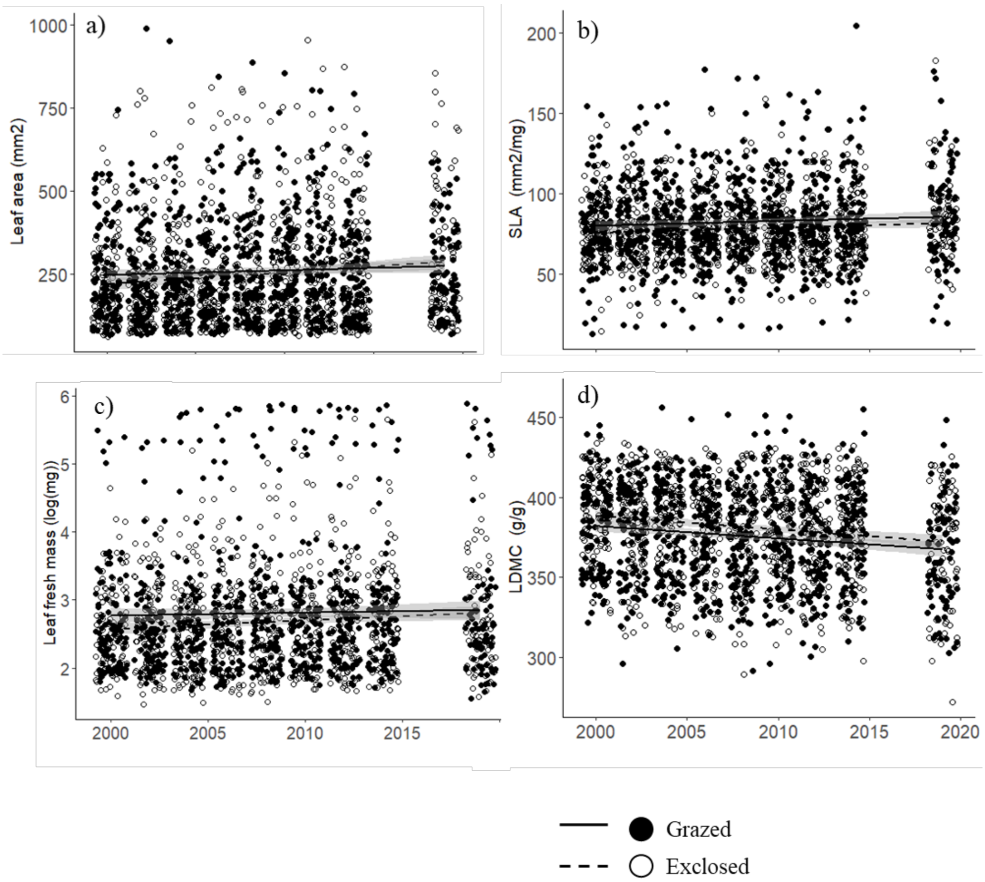

Fig S8. Changes in leaf area (a), specific leaf area (b), leaf fresh mass (c), and leaf dry matter content (d) in Setesdal over the study period. Trend lines are linear regressions with 0.95 confidence intervals, presented for both treatments separately. The significances of each trend was not statistically tested.

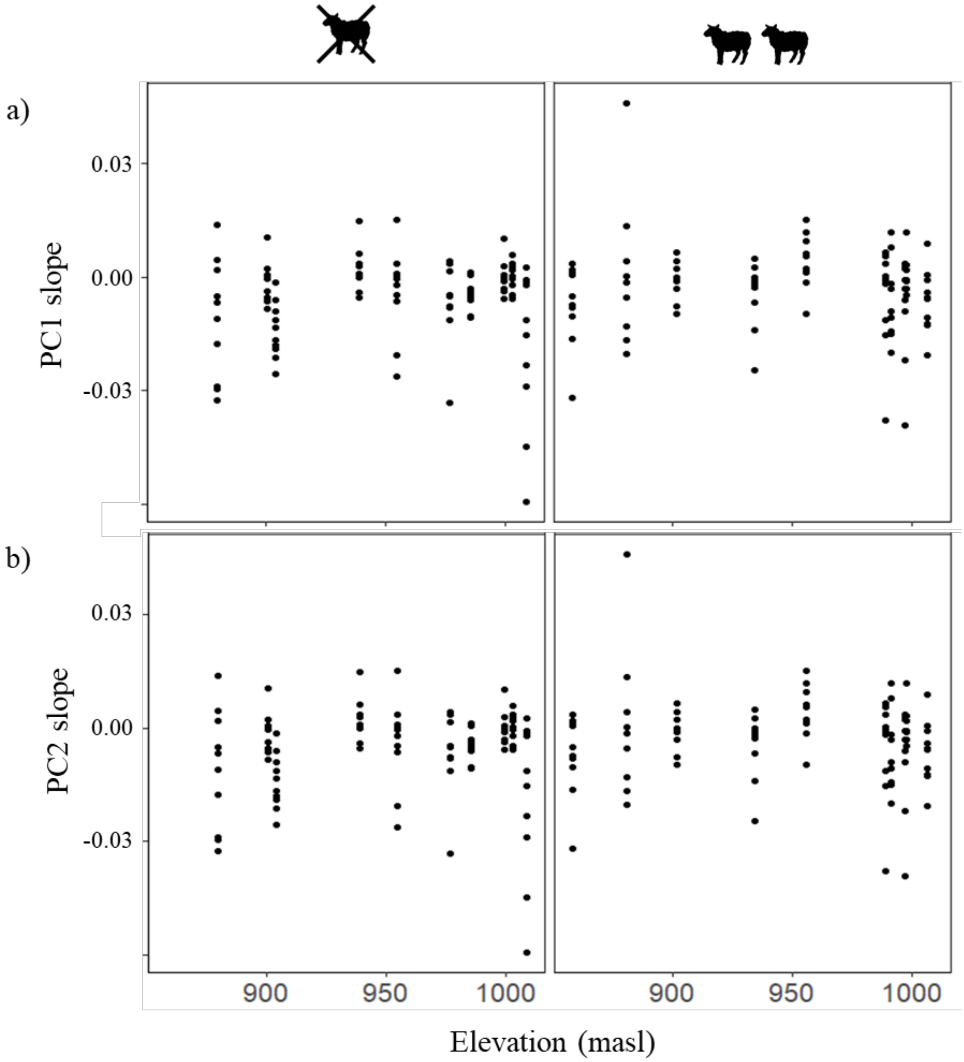

Figure S9. Change on PC1 (a) and PC2 (b) over the study period at different elevations and sheep treatments in Setesdal, indicated with plot-specific time slope for change over the study period. Neither sheep, elevation, nor their interaction affected the slopes (Table 1).

Figure S10. Drone images of two of the exclosures in Setesdal (a-b). Fence lines are enhanced with red lining. No apparent differences between exclosed and unexclosed area can be seen. (Photos by Sylvain Fleur).

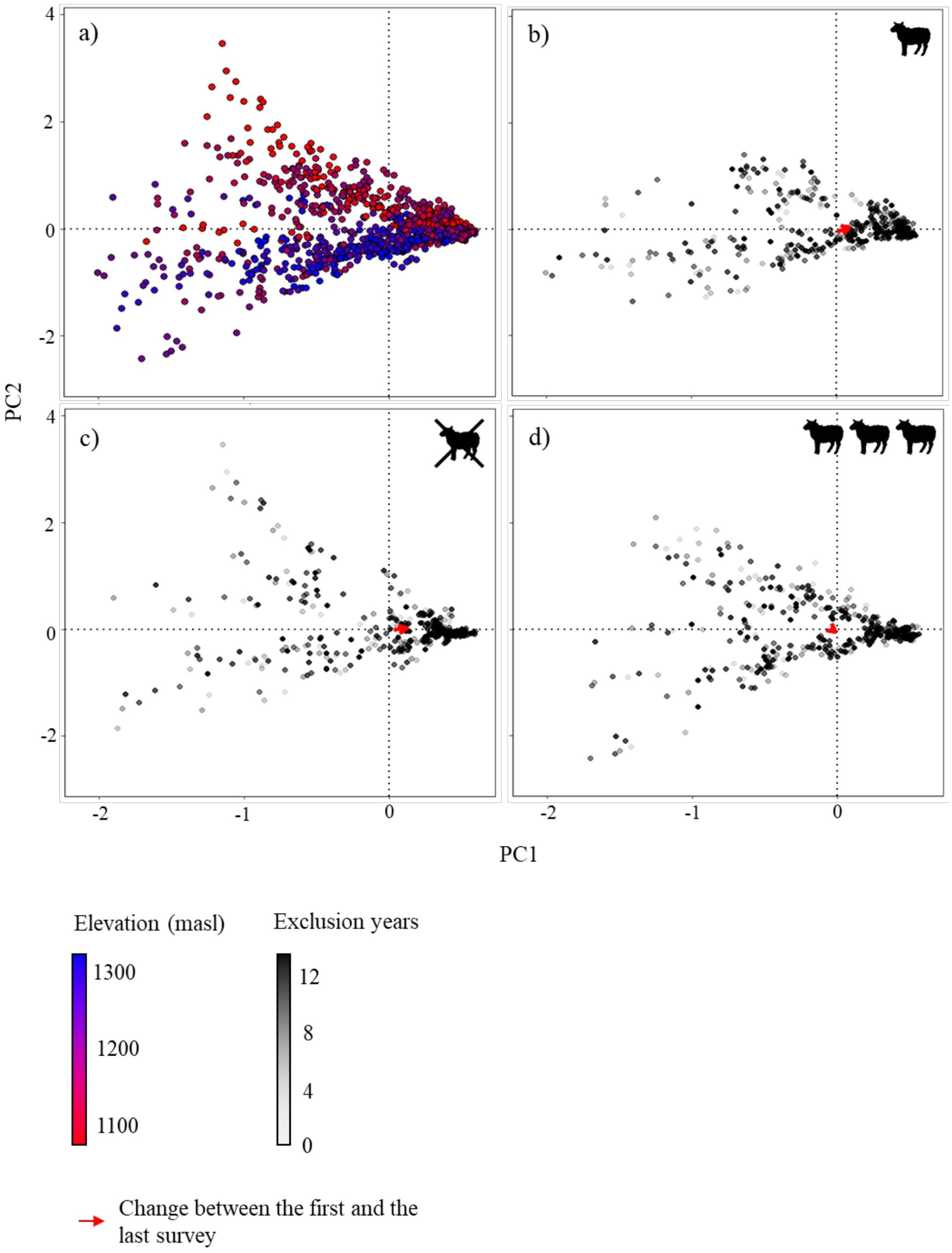

Figure S11. Species composition of plots on PC1 and PC2 in Hol over the study period, colored by elevation (a), and by year at different sheep treatments (b-d). The arrows in the panels b, c and d represent the centroid change from the baseline vegetation survey year to the last vegetation survey year (note that the arrows are barely visible due to overlap of the centroids). The underlying species PCA was constructed in the same way as the PCA for traits in the main analysis, described in the methods.

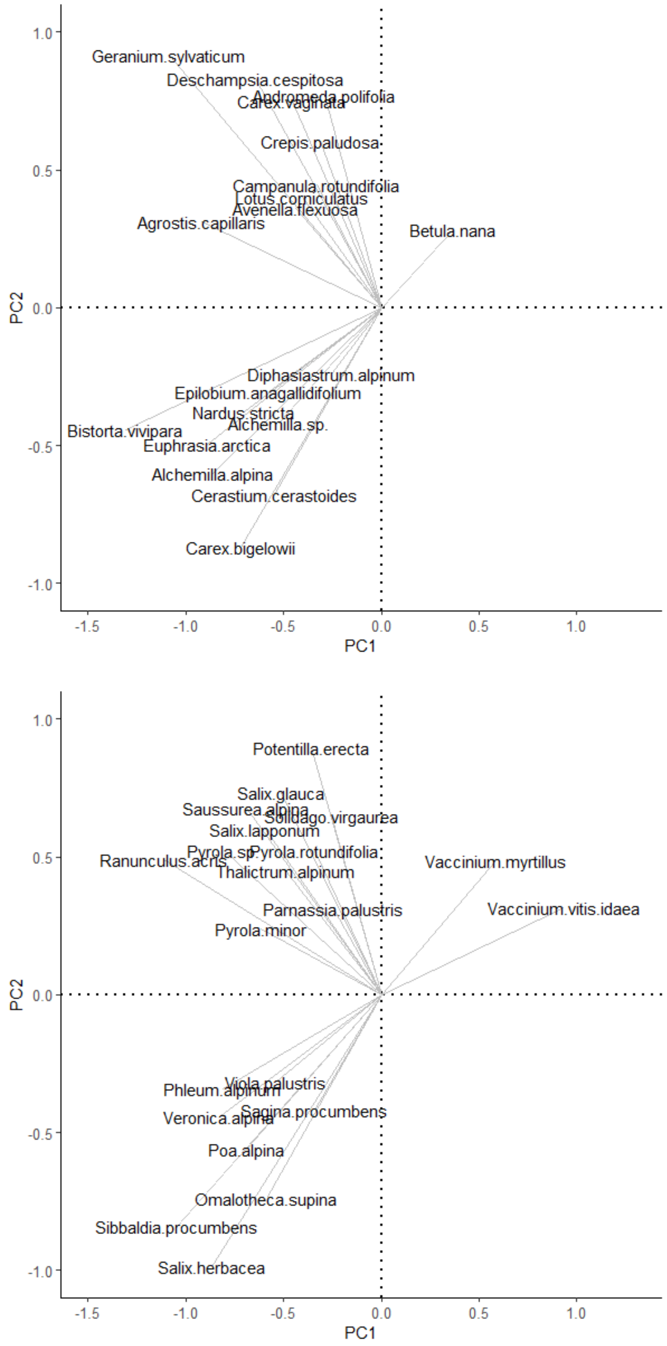

Figure S12. Species vectors corresponding to PCA for Hol, presented in Fig. S11. For easier readability, plotting is done in two panels with species that did not overlap (a-b), and for the 45 most influential species only.

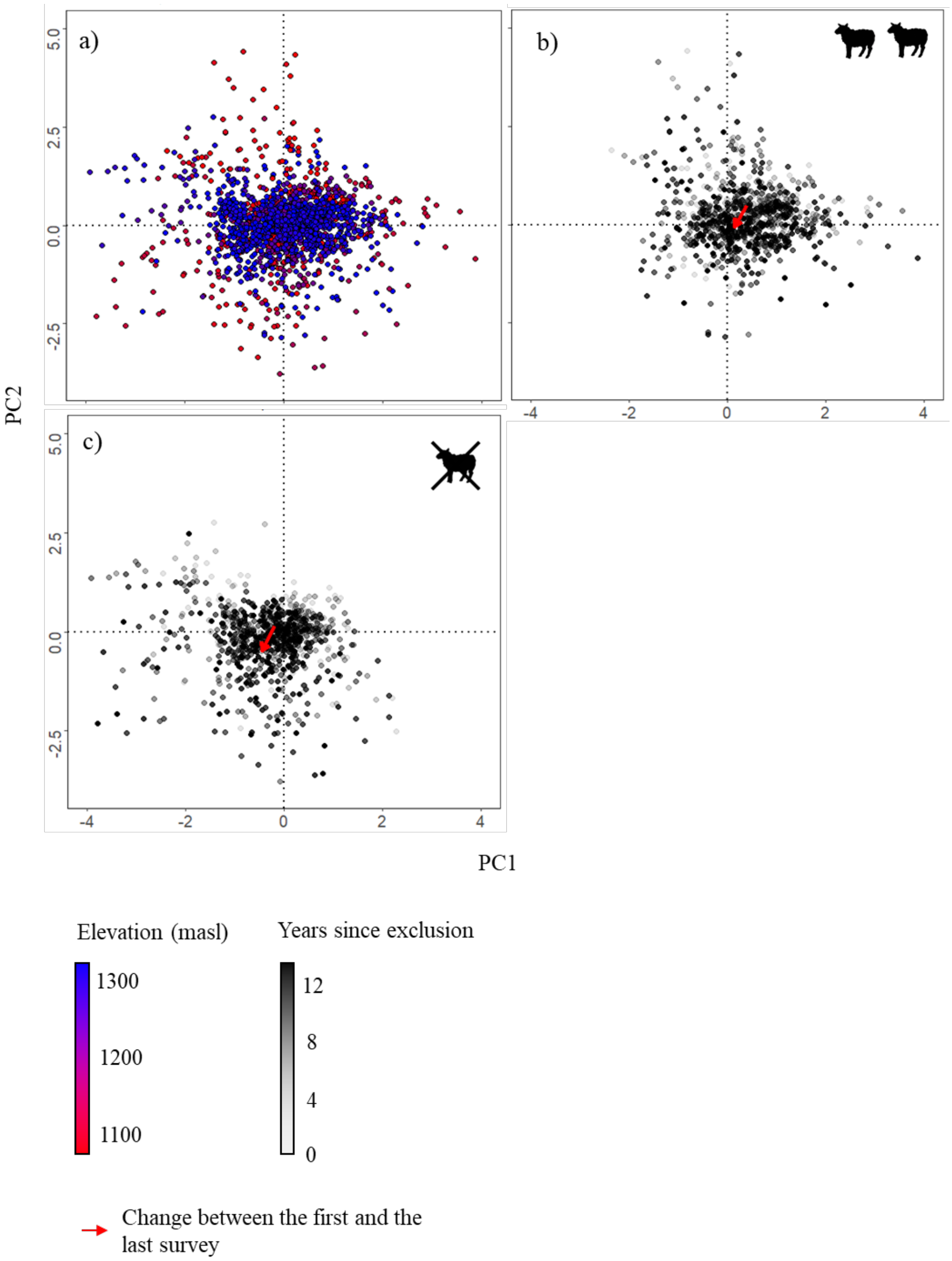

Figure S13. Species composition of plots on PC1 and PC2 in Setesdal over the study period, colored by elevation (a), and by year at different sheep treatments (b-c). The arrows in the panels b and c represent the centroid change from the baseline vegetation survey year to the last vegetation survey year. The underlying species PCA was constructed in the same way as the PCA for traits in the main analysis, described in the methods.

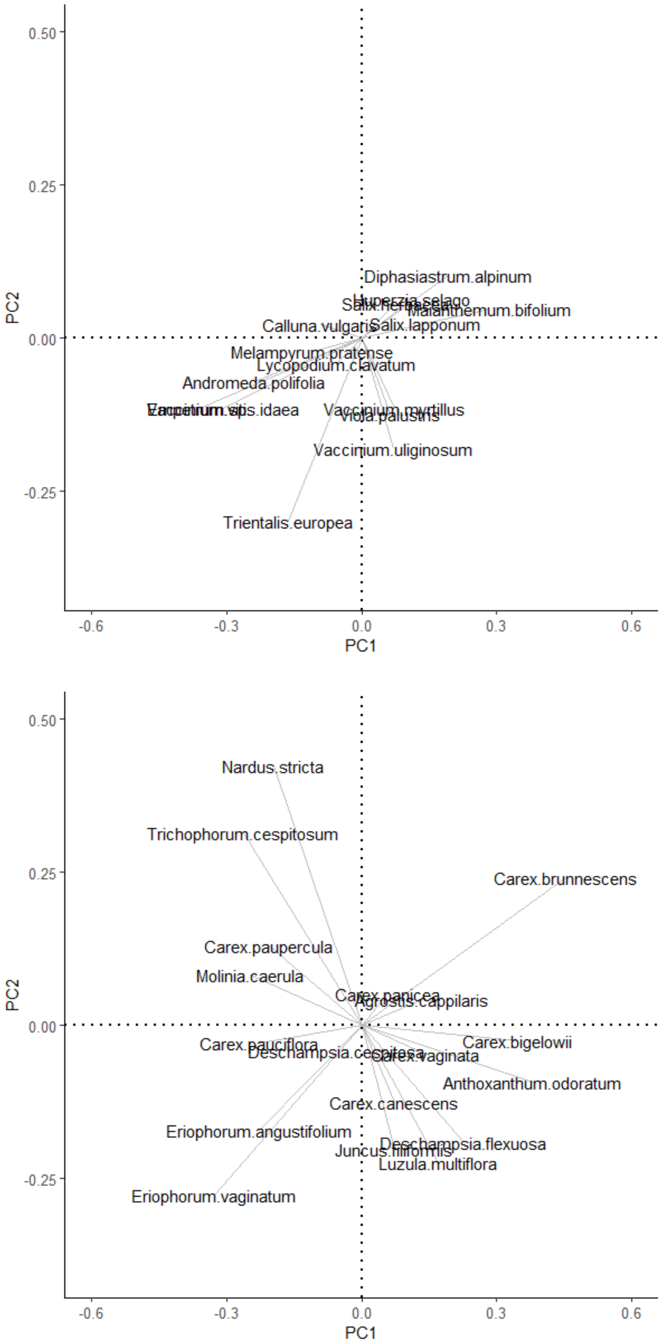

Figure S14. Species vectors corresponding to PCA for Setesdal, presented in Fig. S13. For easier readability, plotting is done in two panels with species that did not overlap (a-b), and for the 34 most influential species only.

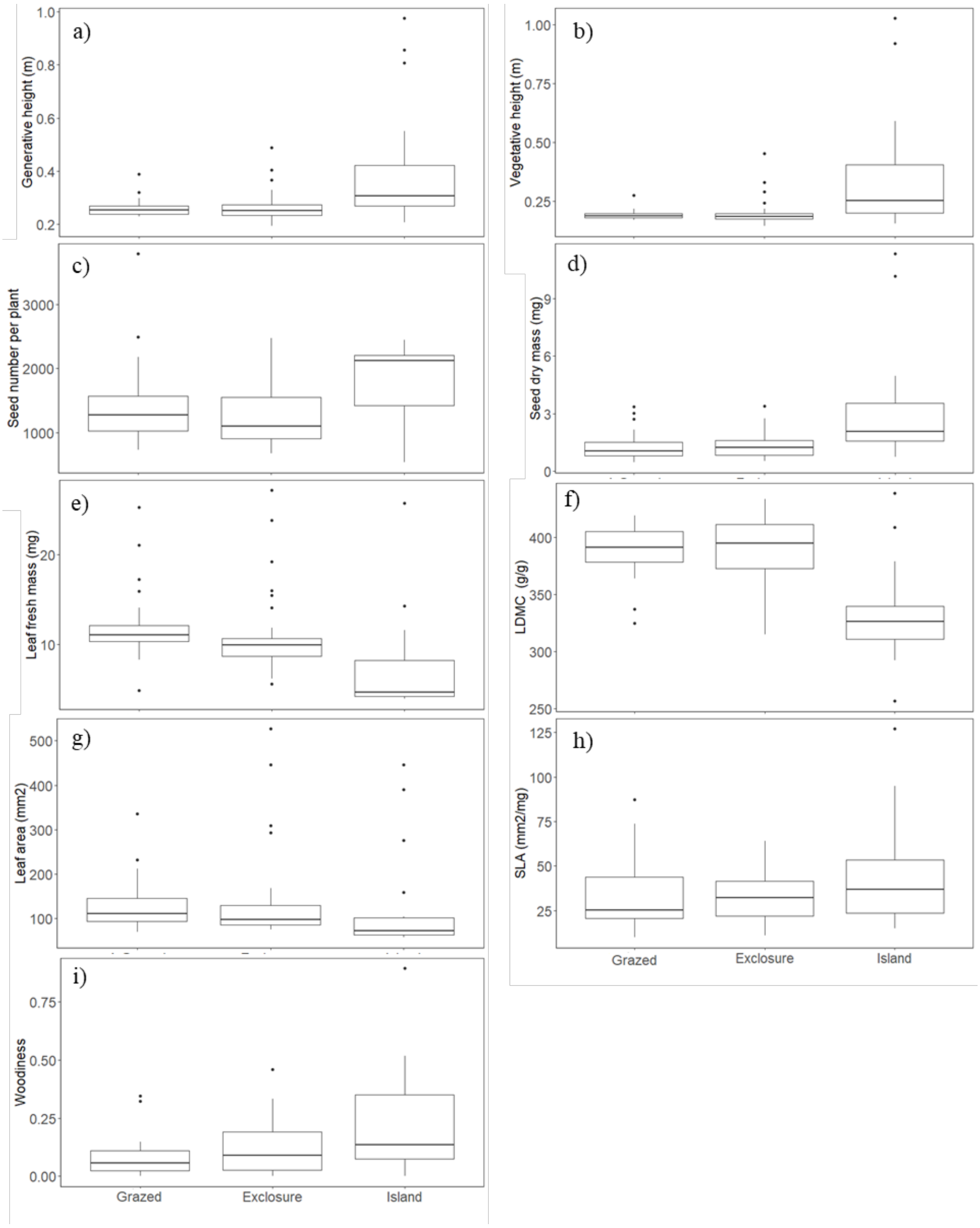

Figure S15. Generative height (a), vegetative height (b), seed number (c), seed dry mass (d), leaf fresh mass (e), leaf dry matter content (f), leaf area (g), specific leaf area (h), and woodiness (i) in grazed, exclosed and island plots for Setesdal island-mainland comparison.

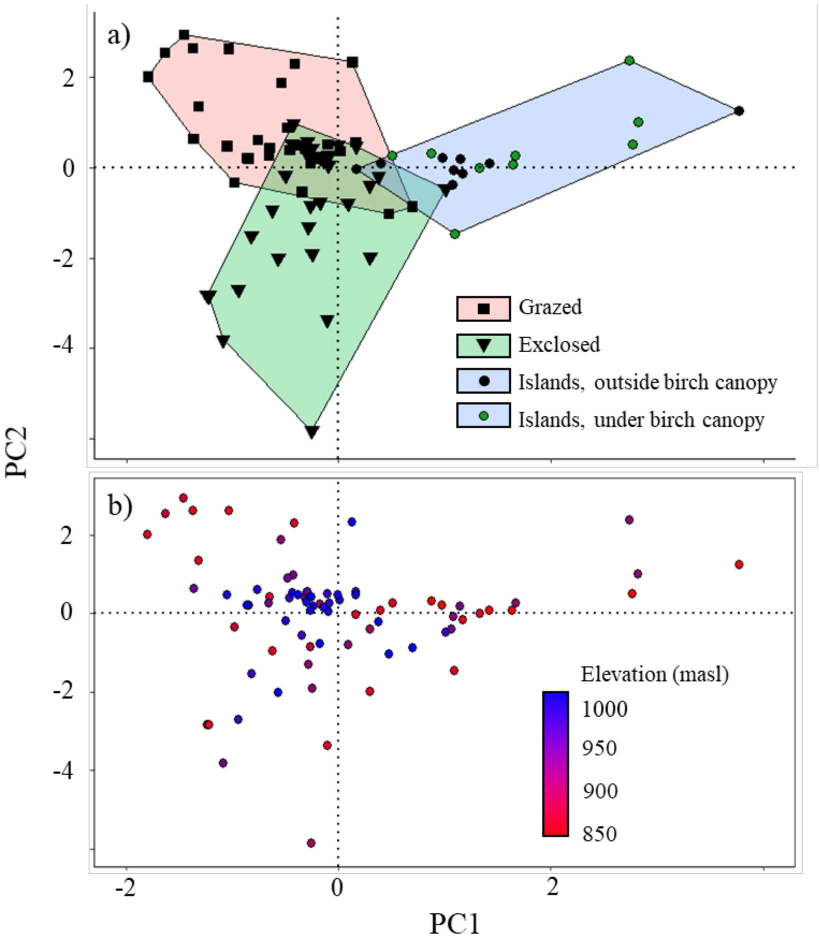

Fig S16. Species composition of plots on PC1 and PC2 for island-mainland comparison in Setesdal, by treatment (a) and elevation (b). Note that this dataset is a snapshot in time (from year 2012 only), and the differences in grazed and exclosed plots reflect species composition differences that were present already at the start of the experiment.

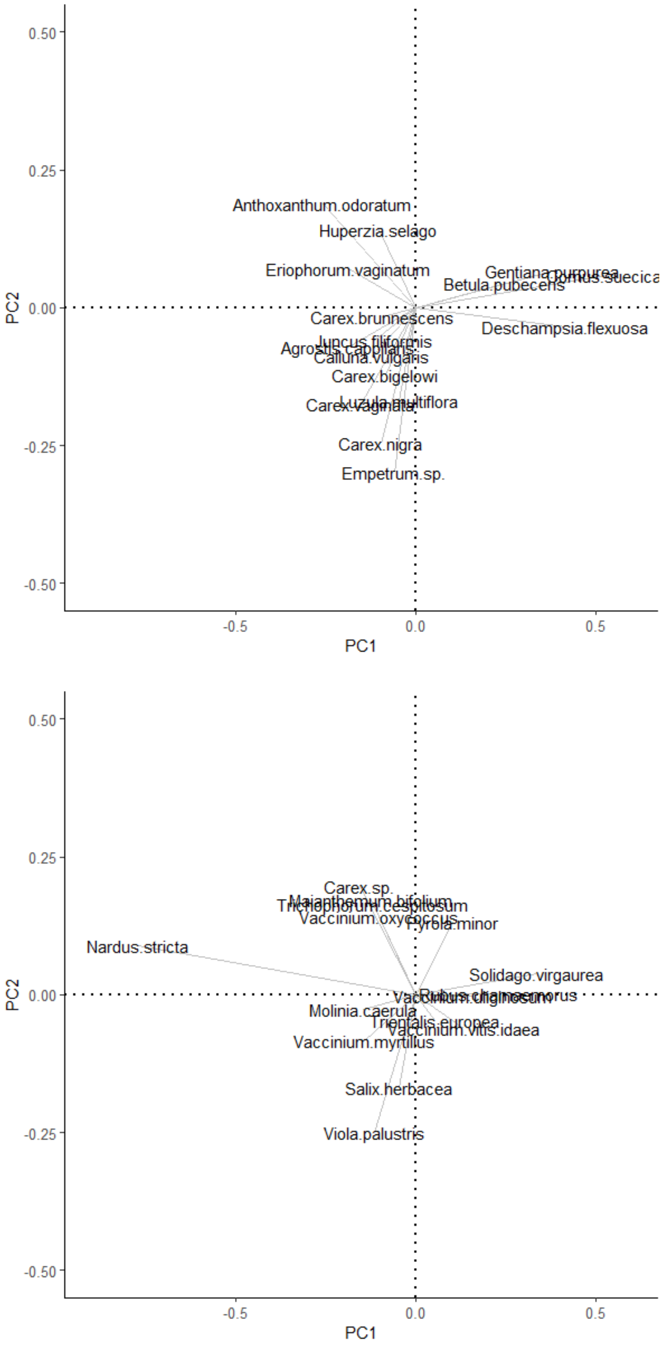

Figure S17. Species vectors corresponding to principle component analysis for Setesdal Island-mainland comparison, presented in Fig. S16. For easier readability, plotting is done in two panels with species that did not overlap (a-b), and only for 35 most influential species.

Table S1. Traits acquired from different databases, their database-specific codes, and references.

Database	Trait	Trait code	Reference
Ecoflora	maximum height	h_max	(Fitter and Peat, 1994)
	minimum height	h_min	(Fitter and Peat, 1994)
	leaf area	le_area	(Fitter and Peat, 1994)
	leaf longevity	le_long	(Fitter and Peat, 1994)
	seed weight	seed_wght	(Fitter and Peat, 1994)
LEDA	canopy height	canopy_height	(Kleyer et al., 2008)
	leaf dry matter content	leaf_dmc	(Kleyer et al., 2008)
	leaf mass	leaf_mass	(Kleyer et al., 2008)
	leaf size	leaf_size	(Kleyer et al., 2008)
	life span	life_span	(Kleyer et al., 2008)
	seed mass	seed_mass	(Kleyer et al., 2008)
	seed number per shoot	seed_number_per_sh	(Kleyer et al., 2008)
BiolFlor	life span	li_span	(Kleyer et al., 2008)
Eflora_cal	annual seed production per plant	annual seed production per plant	(Green, 2009)
Eflora_cal	seed mass	seed mass	(Green, 2009)
PLANTS	c-n ratio	C.N.Ratio	(Green, 2009)
	mature height	Height..Mature	(Green, 2009)
	life span	Lifespan;	(Green, 2009)
TRY	Plant height vegetative	3106	(Kattge et al., 2011)
	Plant height generative	3107	(Kattge et al., 2011)
	Leaf life span	12	(Kattge et al., 2011)
	Seed dry mass	26	(Kattge et al., 2011)
	Canopy height	889, 773	(Kattge et al., 2011)
	Leaf dry mass	55	(Kattge et al., 2011)
	Leaf fresh mass	163	(Kattge et al., 2011)
	Leaf volume	120	(Kattge et al., 2011)
	Leaf length	144	(Kattge et al., 2011)
	Leaf width	145	(Kattge et al., 2011)
	Seed number per flower	1103	(Kattge et al., 2011)
	Seed number per florescence	1104	(Kattge et al., 2011)
	Seed number per plant	131	(Kattge et al., 2011)
	Seed number per ramet	336	(Kattge et al., 2011)
	Seed number per reproduction unit	138	(Kattge et al., 2011)
	Leaf nitrogen content per leaf area	50	(Kattge et al., 2011)
	Leaf nitrogen content per leaf dry mass	14	(Kattge et al., 2011)
	Specific leaf area	125	(Kattge et al., 2011)
	Leaf carbon nitrogen-ratio	146	(Kattge et al., 2011)
	Plant carbon nitrogen-ratio	1021	(Kattge et al., 2011)
	plant lifespan	59	(Kattge et al., 2011)
TTT	Leaf area	Leaf area	(Björkman et al., 2018)
	Spefic leaf area	Leaf area per leaf dry mass (specific leaf area, SLA)	(Björkman et al., 2018)
	Leaf carbon content per leaf dry mass	Leaf carbon (C) content per leaf dry mass	(Björkman et al., 2018)
	Leaf carbon isotope discrimination	Leaf carbon (C) isotope discrimination (delta 13C)	(Björkman et al., 2018)

	Leaf carbon/nitrogen ratio	Leaf carbon/nitrogen (C/N) ratio	(Björkman et al., 2018)
	Leaf dry mass	Leaf dry mass	(Björkman et al., 2018)
	Leaf dry matter content	Leaf dry mass per leaf fresh mass (Leaf dry matter content, LDMC)	(Björkman et al., 2018)
	Leaf fresh mass	Leaf fresh mass	(Björkman et al., 2018)
	Leaf nitrogen content per leaf dry mass	Leaf nitrogen (N) content per leaf dry mass	(Björkman et al., 2018)
	Leaf nitrogen isotope signature	Leaf nitrogen (N) isotope signature (delta 15N)	(Björkman et al., 2018)
	Leaf nitrogen/phosphorus ratio	Leaf nitrogen/phosphorus (N/P) ratio	(Björkman et al., 2018)
	Leaf phosphorus content per leaf dry mass	Leaf phosphorus (P) content per leaf dry mass	(Björkman et al., 2018)
	Plant height, reproductive	Plant height, reproductive	(Björkman et al., 2018)
	Plant height, vegetative	Plant height, vegetative	(Björkman et al., 2018)
	Rooting depth	Rooting depth	(Björkman et al., 2018)
	Seed dry mass	Seed dry mass	(Björkman et al., 2018)
	Stem diameter	Stem diameter	(Björkman et al., 2018)
	Stem dry mass per stem fresh volume	Stem dry mass per stem fresh volume (stem specific density, SSD)	(Björkman et al., 2018)
SeedClim	leaf area	leaf area	(Gya, 2017)
	wet mass	wet mass	(Gya, 2017)
	dry mass	dry mass	(Gya, 2017)
	SLA	SLA	(Gya, 2017)
	LDMC	LDMC	(Gya, 2017)
	leaf thickness	leaf thickness	(Gya, 2017)
	C% in leaf	C% in leaf	(Gya, 2017)
	N% in leaf	N% in leaf	(Gya, 2017)
	C/N ratio	C/N ratio	(Gya, 2017)
	vegetative height	vegetative height	(Gya, 2017)

Table S2. Variation explained by each PC-axis, and their variance, F-values, and p-values based on permutation test under reduced model, with 999 permutations.

		Variation explained (%)	Df	Variance	F	Pr(>F)
Hol	PC1	0.48	1	0.31	51.14	0.001
	PC2	0.13	1	0.06	9.67	0.001
	PC3	0.12	1	0.00	0.81	0.493
Setesdal	PC1	0.42	1	0.22	44.65	0.001
	PC2	0.35	1	0.10	20.88	0.001
	PC3	0.17	1	0.01	1.90	0.12

Table S3. Observed and expected Moran Indexes for residuals from each model, and test statistics for differences between them. Values were calculated with Moran.I function from ape-package (Paradis et al., 2015) based on (Gittleman and Kot, 1990).

Model	Expected Moran I	Observed Moran I	SD	p
Hol PC1	-0.0056	-0.0028	0.020	0.19
Hol PC2	-0.0056	-0.0141	0.012	0.48
Setesdal PC1	-0.0050	0.0023	0.034	0.83
Setesdal PC2	-0.0050	0.0022	0.034	0.42
Setesdal island-mainland comparison PC1	-0.0130	-0.0776	0.052	0.12

Supplementary References

Björkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., 2018. Plant functional trait change across a warming tundra biome. Nature 562, 57-62.

Fitter, A. H., Peat, H. J., 1994. The ecological flora database. Journal of Ecology 82, 415-425.

Gittleman, J. L., Kot, M., 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. Systematic Zoology 39, 227-241.

Green, W., 2009. USDA PLANTS Compilation, version 1, 09-02-02. WWW document] URL http://bricol.net/downloads/data/PLANTSdatabase.

Gya, R., 2017. The role of intraspecific variability in driving community trait shifts along temperature and precipitation gradients in alpine and boreal semi-natural grasslands. Master's thesis, The University of Bergen, https://bora.uib.no/bora-xmlui/handle/1956/17229.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., 2011. TRY–a global database of plant traits. Global change biology 17, 2905-2935.

Kleyer, M., Bekker, R., Knevel, I., Bakker, J., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J., Klimeš, L., Klimešová, J., 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of ecology 96, 1266-1274.

Lussana, C., Ole, E., Francesco, U., 2016. seNorge v2. 0: an observational gridded dataset of temperature for Norway. Met. no report 14.

Lussana, C., Saloranta, T., Skaugen, T., Magnusson, J., Tveito, O. E., Andersen, J., 2018. seNorge2 daily precipitation, an observational gridded dataset over Norway from 1957 to the present day. Earth System Science Data 10, 235.

Paradis, E., Blomberg, S., Bolker, B., Brown, J., Claude, J., Cuong, H. S., Desper, R., Didier, G., 2015. Package ‘ape’. Analyses of phylogenetics and evolution, version 2, 4-1.

Rekdal, Y., Angeloff, M., 2007. Vegetasjon og beite i Setesdal Vesthei. Oppdragsrapport fra Skog og landskap.

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; impact 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 phospholiphase 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 value adding 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	Ph Biology	Improving the FAIRness of causal interactions in systems biology: data curation and standardisation to support systems modelling applications
2020	Silje Forbord	Phd Biology	Cultivation of *Saccharina latissima* (Phaeophyceae) in temperate marine waters; nitrogen uptake kinetics, growth characteristics and chemical composition
2020	Jørn Olav Løkken	Phd Biology	Change in vegetation composition and growth in the forest-tundra ecotone – effects of climate warming and herbivory
2020	Kristin Odden Nystuen	Phd Biology	Drivers of plant recruitment in alpine vegetation
2021	Sam Perrin	Phd Biology	Freshwater Fish Community Responses to Climate Change and Invasive Species
2021	Lara Veylit	Phd Biology	Causes and consequences of body growth variation in hunted wild boar populations
2021	Semona Issa	Phd Biology	Combined effects of environmental variation and pollution on zooplankton life history and population dynamics
2021	Monica Shilereyo	Phd Biology	Small Mammal Population Ecology and Ectoparasite Load: Assessing Impacts of Land Use and Rainfall Seasonality in the Serengeti Ecosystem, Tanzania
2021	Vanessa Bieker	Phd Biology	Using historical herbarium specimens to elucidate the evolutionary genomics of plant invasion
2021	Håkon Austad Langberg	Phd Biology	Fate and transport of forever chemicals in the aquatic environment: Partitioning and biotransformation of mixtures of Per- and Polyfluoroalkyl Substances (PFAS) from different point sources and resulting concentrations in biota
2021	Julie Renberg	Phd Biology	Muscular and metabolic load and manual function when working in the cold
2021	Olena Meleshko	Phd Biology	Gene flow and genome evolution on peatmosses (S*phagnum*)