RESEARCH ARTICLE

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

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Abstract

Questions: Vegetation in the forest–tundra ecotone faces changes in both climate and land-use. While climate warming is an important driver of vegetation growth and composition, herbivory may have opposing effects. In the present study, we experimentally test how removal of sheep herbivory affects the vegetation in an alpine forest–tundra ecotone, and how responses are manifested at higher temperatures.
Location: Dovre Mountains, Central Norway.
Methods: Shrub growth (height and cover) and ground layer composition were analysed each third year over an 18-year period in a nested, three-factorial experiment (ambient temperature and herbivory; ambient temperature and no herbivory; increased temperature and no herbivory). Fencing and open-top-chambers were used as expedients. Treatment effects and interactions over time were analysed using linear mixed effects models and ordination.
Results: Shrub height and cover increased over time due to reduced herbivory, but without additional warming effect. Lichen cover declined in all treatments over time, but more rapidly and earlier under warming treatment (significant after three years). Contrary to expectations, there was no statistically significant increase in woody species due to warming, although evergreen woody species displayed a trend shift after six years, comprising a sharp decline towards year twelve. Litter accumulated in all treatments, but at higher rates under warming (significant after nine years).
Conclusions: Our results disclose removal of sheep herbivory as a prominent driver of shrub growth, with warming as a subordinate driver in the studied alpine vegetation. The warming-driven increased litter abundance may, however, be caused by the decrease of wind inside chambers and the subsequent absence of wind-driven removal of litter. This chamber effect and the displayed timing differences in vegetation responses call for the critical use of short-term experimental data in predictions of long-term consequences of environmental change.

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

1 | INTRODUCTION

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

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

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

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

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

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

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

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

2 | METHODS

2.1 | Study area

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

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

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

2.2 | Study design and experimental set-up

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

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

2.3 | Data collection

In the present study, we randomly selected ten out of the 25 plots per treatment to analyse shrub height, shrub cover and ground

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

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

2.4 | Data treatment and statistical analyses

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

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

To investigate the consistency effect of warming and herbivory on shrub cover and height, and ground layer composition over time, we used separate linear mixed effect models with shrub height, and shrub layer and component groups cover as response variables, respectively. The response variables were square-root transformed to attain normality and equal variances. Treatment

(AGA, NGA and NGW), year (0–18, categorical variable) and the interaction between treatment and year were used as fixed factors. As sub-plots were nested in plots (spatial autocorrelation) and were repeatedly analysed (temporal autocorrelation) we used plot as a random factor and an autocorrelation factor of 1 (corAR1()) to account for this (cf. Crawley, 2008). In models where a significant interaction between treatment and time was found, we used a Tukey HSD test to investigate the contrast between year 0 and the subsequent years to identify when the responses turned significant, and to identify pairwise differences between treatments in each of the years.

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

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

3 | RESULTS

3.1 | Shrub layer

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

Shrub cover decreased from 3.8% to 2.2% in the AGA treatment, but increased from 3.6% to 16.4% in the NGA treatment and from 2.7% to 26.3% in the NGW treatment during the 18-year experiment, with a significant main effect of treatment (p = 0.028) and a significant treatment × year effect (p < 0.001). The shrub cover showed negligible changes in all three treatments in the first six years, but a strong significant increase was seen after this initial period in both the NGA and the NGW treatments (Figure 1b). For the NGW treatment, the increase in cover turned significant in year 9 (p < 0.01) and for the NGA treatment in year 12 (p < 0.001). There were no significant changes in the AGA over time. NGW became significantly larger than AGA in year 18 (p < 0.01). There was no significant difference between any of the other treatments.
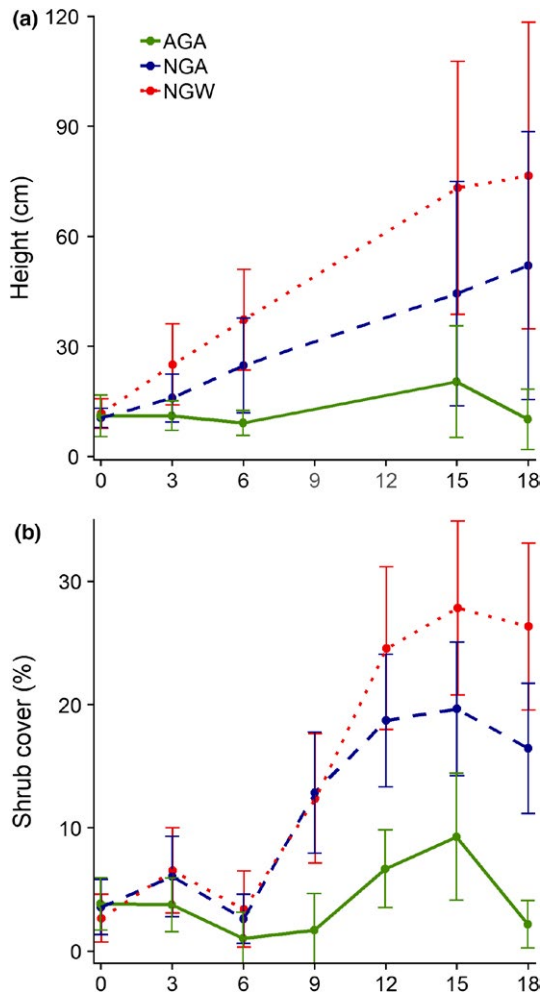
FIGURE 1 Change in shrub layer height (a), and shrub layer cover (b) for the three treatments over the 18-year experimental period. Treatment abbreviations: AGA, ambient grazing and ambient temperature; NGA, no grazing and ambient temperature; and NGW, no grazing and experimentally increased temperature. Points show the mean measured values and error bars the 95% confidence interval. Grey font for *x*-axis values in panel (a) marks years where height recordings are lacking
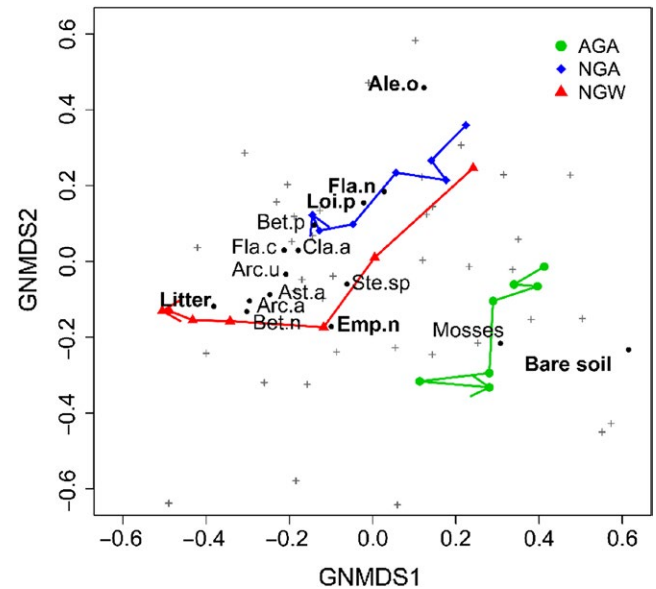

FIGURE 2 Change in ground layer composition over the 18-year experimental period shown by trajectories of mean plot values in a global nonmetric multidimensional scaling (GNMDS) ordination in the treatments AGA, NGA and NGW (see Figure 1 for an explanation of the acronyms). Crosses represent ground layer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

3.2 | Ground layer

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

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

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

Litter cover increased in all treatments, but with apparent differences between treatments (*p* < 0.001). The largest increase over time was seen in the NGW treatment (Figure 3g), with a significant increase after three years (*p* = 0.028), and with a cover peak in year 12 after a strong increase in year 9 (*p* < 0.001). The cover of litter was consistently higher in NGW than in the other treatments from year
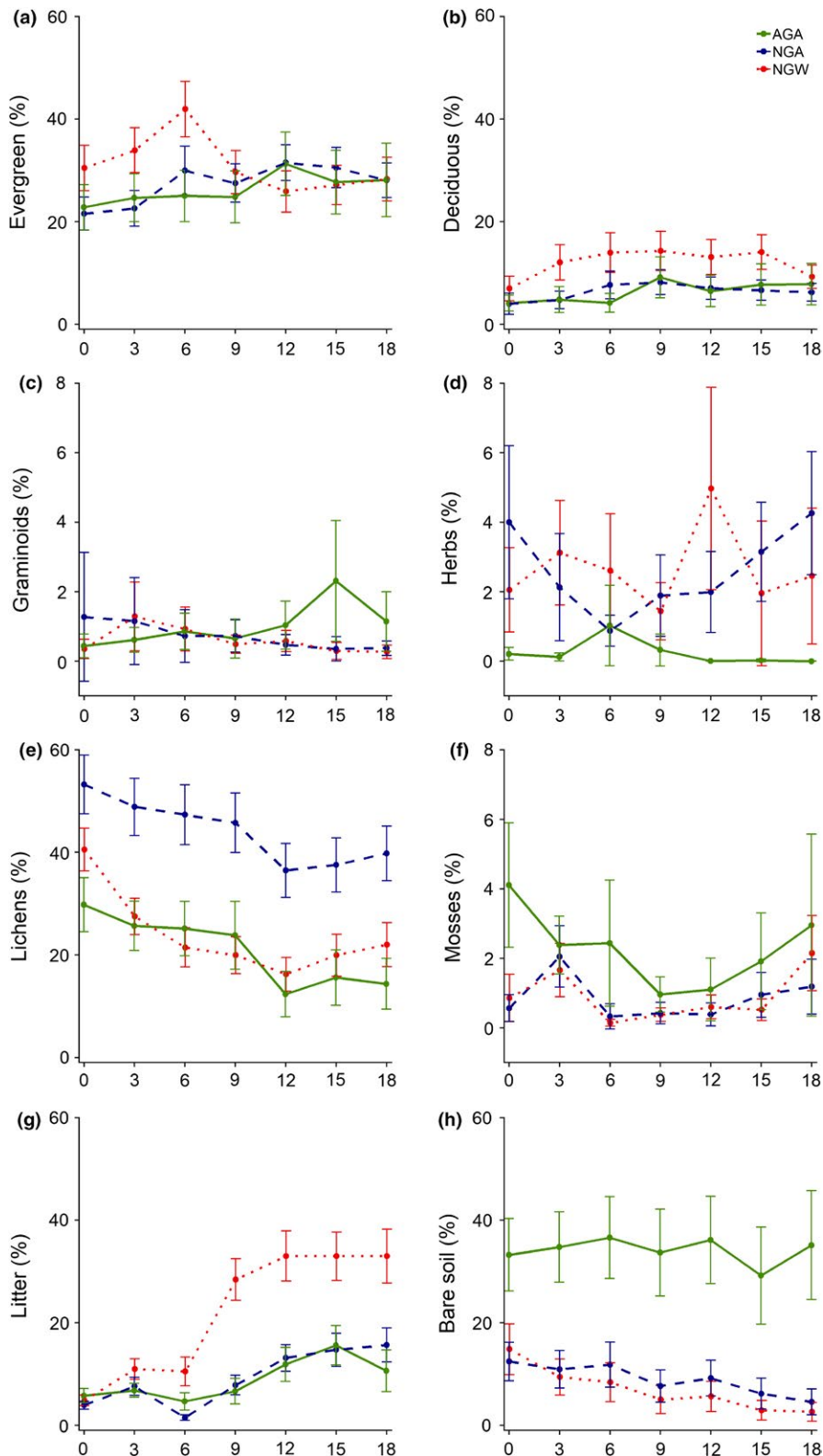
FIGURE 3 Change in mean cover (%) of ground layer component groups over the 18-year experimental period, for the treatments AGA, NGA and NGW (see Figure 1 for an explanation of the acronyms). (a) Evergreen woody species, (b) deciduous woody species, (c) graminoids, (d) herbs, (e) lichens, (f) mosses, (g) litter, and (h) bare soil. Points show the mean measured values and error bars the 95% confidence interval. Note different y-axis scales

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

The cover of ground layer deciduous woody species varied through time ($p < 0.001$, Figure 3a), but the change was not different between treatments ($p = 0.562$). For herbs, on the other hand, there were significant cover differences between treatments ($p < 0.001$), but no significant variation over time ($p = 0.606$, Figure 3d). Mosses varied in cover over time with a close to significant difference

between treatments ($p = 0.080$), but with no treatment × year interaction ($p = 0.140$, Figure 3f). Finally, the cover of bare soil was generally higher in the AGA treatment than in the two other treatments and varied over time ($p < 0.001$), but with no treatment × year interaction ($p = 0.249$, Figure 3h).

4 | DISCUSSION

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

4.1 | Effects of herbivore removal

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

4.2 | Effects of warming combined with herbivore removal

The reduction in the cover of lichens with added warming in our experiment is in line with results from other warming experiments (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Lang

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

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

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

The increased litter accumulation in warmed plots, mainly consisting of shrub leaves, corresponds to findings in similar experiments (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Jónsdóttir,

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

4.3 | Short- and long-term effects

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

5 | CONCLUDING REMARKS

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

DATA ACCESSIBILITY

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

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SUPPORTING INFORMATION

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

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

Appendix S2 List of components.

Appendix S3 Linear mixed effects model statistics.

Appendix S4 Tukey HSD post-hoc test statistics.

Appendix S5 CCA test statistics.

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