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Reindeer trampling promotes vegetation changes in tundra heathlands: Results from a simulation experiment

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Abstract

Question: Herbivores exert strong influences on vegetation through activities such as trampling, defoliation, and fertilization. The combined effect of these activities on plant performance may cause dramatic vegetation shifts. Because herbivore pressures and the relative importance of their different activities are not equally distributed across the landscape, it is important to understand their isolated effect. One example of an herbivore-induced vegetation shift is the reindeer-driven transition from a subarctic tundra vegetation dominated by dwarf shrubs into a more productive, graminoid-dominated state. Here, we asked how each of the grazing activities by reindeer separately and combined shape vegetation composition.

Location: Nordreisa, Norway.

Methods: We used a field experiment over six summers to study the separate and interacting effects of reindeer trampling, defoliation, addition of faeces and removal of moss on tundra heath vegetation, and to identify which of these factors were most important in driving the plant community towards a graminoid-dominated state.

Results: The combination of all treatments resulted in the strongest changes in vegetation, but trampling was the single most important factor altering the vegetation composition by reducing the abundance of both evergreen and deciduous dwarf shrubs. In contrast to what was expected, none of our treatments, separate or combined, resulted in an increased abundance of graminoids in 5 years, although such rapid vegetation changes have been observed in the field in similar environmental conditions.

Conclusions: Trampling is the key process by which reindeer influence the abundance of functional groups, but only many processes combined result in strong changes in community composition. Moreover, additional factors not included in this experiment, such as urine, may be important in causing a state shift to a graminoid-dominated community.

KEYWORDS

defoliation, fertilization, grazing simulation, herbivory, *Rangifer tarandus*, shrubification, trampling, vegetation shifts

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1 | INTRODUCTION

Herbivores can strongly influence the functioning and composition of plant communities (Borer et al., 2014; Schmitz, 2008), and may cause dramatic shifts in terms of community composition and ecosystem functioning (Estes et al., 2011; Rietkerk & van de Koppel, 1997). Most studies of herbivore effects focus on the integral effect of herbivore presence in a system; however, their effect is the sum of a number of activities that can generate highly contrasting responses such as defoliation, trampling, and addition of urine and faeces (Olf & Ritchie, 1998). Moreover, the intensity of these activities is not uniform across landscapes and depends on the movement patterns and foraging behaviour of the herbivores. Herbivores will primarily forage on plants in patches where preferred food plants are abundant (Owen-Smith, Fryxell, & Merrill, 2010). Herbivore movements are not only determined by the distribution of food resources in a landscape, but also by other landscape characteristics such as the distribution of suitable resting places, or predator-free spaces (Laundré, Hernández, & Ripple, 2010; McArthur, Banks, Boonstra, & Forbey, 2014). Whether corridors exist between such places also influences movement patterns, and thus trampling intensity in the landscape (Coughenour, 1991). Dung deposition is, on the other hand, closely linked to suitable resting places for many herbivores (Pouvelle, Feer, & Ponge, 2008). The relative impact of foraging, trampling and dung and urine deposition on the vegetation will thus vary in heterogeneous landscapes. Understanding the specific and interactive impacts of these activities is vital to the understanding of how different movement patterns of wild herbivores and herding practices of livestock affect ecosystems.

Foraging herbivores remove photosynthetically active plant tissue (i.e. defoliation) and thereby compromise plant growth (Crawley, 1997). Defoliation is always to some degree selective because herbivores will prefer some plants to others depending on their nutritional content, and structural and chemical defence (Bryant et al., 1983; Mattson, 1980). Excluding herbivores has therefore often been reported to favour palatable vegetation (Christie et al., 2015; Maron & Crone, 2006). However, as plants are rarely completely consumed by herbivores, differences among plants in tolerance to defoliation in terms of survival, growth and competitive ability might be vital for the effects of defoliation on plant community composition (Hermes & Mattson, 2010; Strauss & Agrawal, 1999). Generally, plants need to balance tolerance and resistance to defoliation and, as a result, fast-growing, palatable species such as graminoids are often better suited to tolerate defoliation compared with slower growing and better defended plants. Herbivores can thus, at least in the long-term, also increase the abundance of palatable species (Augustine & McNaughton, 1998; Del-Val & Crawley, 2005).

All large herbivores influence the ecosystem through trampling, but the effects differ depending on herbivore size, anatomy and movement patterns (Cumming & Cumming, 2003). Unlike defoliation, trampling exerts a non-selective physical impact on plants, but different species and communities will vary both in their ability to resist being damaged by trampling and in their ability to recover from

trampling damage (Cole, 1995a). The overall resistance and tolerance to trampling is primarily determined by vegetation stature, growth form, and location of growth and storage organs. Various mountain vegetation types (Cole, 1995b), graminoids were more resistant than forbs and shrubs in their response to simulated trampling, and caespitose (turf-forming) plants were more resistant than plants with a matted or erect growth form. One important mechanism explaining this difference is that graminoids usually have well-protected basal meristems and thin, disturbance-resistant roots (Jonasson & Callaghan, 1992; Mulder, 1999). Trampling does harm vegetation, but it also creates gaps suitable for seedling establishment (Olf & Ritchie, 1998). In addition to its direct impact on plants, trampling can also alter soil physical properties by compacting the soil, which affects its water holding capacity and oxygen availability (Veldhuis, Howison, Fokkema, Tielens, & Olf, 2014), and it can increase soil moisture by reducing plant evapotranspiration (Schrama et al., 2013).

In most ecosystems including tundra systems, the growth of plants is often limited by nutrient availability (Aerts & Chapin, 1999). Herbivores can influence the growth of plants by providing readily available nutrients in the form of faeces and urine (Bardgett & Wardle, 2003; Hobbs, 1996; Pastor, Cohen, & Thompson Hobbs, 2006). The ability to exploit these resources, however, is expected to differ among plant species and functional groups, depending on factors such as differences in root depth, root architecture or association with different types of mycorrhiza (Aerts & Chapin, 1999; Mulder, 1999). Graminoids are often suggested to be especially efficient in using readily available nutrients from urine and faeces (Barthelemy, Stark, & Olofsson, 2015; Mulder, 1999), but this is not always the case (Mulder, 1999). Most other plants seem to efficiently utilize this nutrient source, at least in strongly nutrient limited systems, (Barthelemy, Stark, Kytöviita, Stark, Kytöviita, & Olofsson, 2017; Barthelemy, Stark, Michelsen, & Olofsson, 2017), although graminoids are often the plant functional group responding strongest to experimentally added faeces (Barthelemy et al., 2015; van der Wal, Bardgett, Harrison, & Stien, 2004). The faeces could also facilitate the spreading of plants by providing seeds at a site to germinate (Bräthen et al., 2007).

By competing for light and nutrients with the vascular plant species (Sjögersten et al., 2010), and because they mediate soil processes, bryophytes (i.e. mosses and liverworts) are important components of arctic ecosystems. For example, a dense insulating moss layer reduced soil temperatures in summer in high arctic Svalbard (Gornall, Jónsdóttir, Woodin, & Wal, 2007). By trampling and the addition of faeces (Olofsson, Kitti, Rautiainen, Stark, & Oksanen, 2001; van der Wal et al., 2004), herbivores can substantially reduce the moss layer, which may result in higher soil temperatures during the growing season, higher soil microbial activity and higher nutrient availability (Gornall et al., 2007; Olofsson, Stark, & Oksanen, 2004).

Herbivores can cause dramatic transitions of the vegetation between different vegetation states (Brown & Heske, 1990; Côté, Rooney, Tremblay, Dussault, & Waller, 2004; Estes et al., 2011; van de Koppel, Rietkerk, & Weissing, 1997; Rietkerk & van de Koppel, 1997). Yet, the specific contributions of trampling, defoliation and

addition of faeces are not well understood, neither for such vegetation transitions in general nor for heathland to grassland transitions in the tundra specifically. Here, we performed a herbivore simulation experiment in a tundra heathland to investigate the specific role of each of these activities for the observed vegetation changes. We conducted the experiment close to a reindeer (*Rangifer tarandus*) management fence in northern Norway, on the side of the fence that is only lightly grazed by reindeer and is dominated by heath vegetation. Decades of high densities of reindeer on the heavily grazed side of the fence have resulted in a dramatic decrease in dwarf shrubs, forbs and mosses, and a strong increase in graminoids, as well as higher nutrient availability and soil temperatures (te Beest, Sitters, Ménard, & Olofsson, 2016; Olofsson et al., 2001, 2004; Stark & Väisänen, 2014). These vegetation shifts can occur fairly rapidly, at least at small spatial scales, as demonstrated by a transplantation study recording a dramatic vegetation change in only 3 years (Olofsson, 2006). Moreover, repeated inventories show that changes at the landscape scale can occur in <14 years (Ylänne, Olofsson, Oksanen, & Stark, 2018). In this unique setting, we performed a field-based experiment in order to study the isolated and combined effects of defoliation, trampling, addition of faeces, and moss removal on tundra vegetation, with special focus on how these activities drive the vegetation transition from heathland to grassland. Because species of all functional groups are present in the local species pool, we proposed the following hypotheses. H1: Trampling will decrease the abundance of trampling-sensitive functional groups such as lichens, bryophytes, deciduous and evergreen dwarf shrubs and forbs, and increase the abundance of trampling-tolerant caespitose graminoids. H2: Defoliation will decrease the abundance of palatable plants such deciduous dwarf shrubs, graminoids and forbs, and will increase the abundance of unpalatable plants such as evergreen dwarf shrubs. H3: Adding faeces will favour graminoids most, because they have a high capacity to exploit the occasional pulses of easy available nutrients. H4: Removal of the moss layer will increase growth of the vascular plants. H5: A combination of all the herbivore activities is needed to trigger a transition from a moss and dwarf shrub-dominated vegetation to a graminoid-dominated vegetation.

2 | METHODS

2.1 | Field site and experimental design

This study took place in Raisduoddar (69°31'N, 21°19'E; altitude 600 m a.s.l.). The study site is above the current local treeline and average yearly temperature was 0.2°C during the experiment (2011–2015, see Appendix S1a). The area has a sub-oceanic climate, and reindeer husbandry is common practice. In addition to reindeer, other common herbivores include ptarmigan (*Lagopus muta*), lemmings (*Lemmus lemmus*) and voles (*Myodes rufocanus*). The dominant vegetation type is tundra heath, dominated by deciduous dwarf shrubs such as *Betula nana*, *Vaccinium vitis-idaea* and *Vaccinium uliginosum*

and evergreen dwarf shrubs such as *Empetrum nigrum* ssp. *hermaphroditum* (hereafter, *E. nigrum*) and *Vaccinium vitis-idaea*, but also includes graminoids such as *Deschampsia flexuosa*, *Carex bigelowii* and *Festuca ovina*, and forbs such as *Rubus chamaemorus*, *Linna borealis* and *Pedicularis lapponica*. We located the experiment on the eastern side of a reindeer fence, which was established in the 1960s. The fence runs for several kilometres and separates the area into a side that is grazed heavily by reindeer during several weeks every summer (hereafter: grazed), and a lightly grazed side that is only occasionally visited by reindeer (hereafter: ungrazed). Importantly, the vegetation on the heavily grazed side of the fence has shifted to a graminoid-dominated vegetation type (Figure 1), (Olofsson et al., 2001), and is dominated by graminoid species such as *F. ovina*, *D. caespitosa*, *Poa alpina* and multiple *Carex* species, and forbs such as *Bistorta vivipara* and *Viola biflora* (Sitters, te Beest, Cherif, Giesler, & Olofsson, 2017; Ylänne et al., 2018). At the ungrazed side of the fence, we selected five blocks with homogenous vegetation. We ensured the blocks were similar with regards to topography (as flat as possible) and distance to the fence (approximately 10–25 m). In each block, we established seven plots of 1 m² and randomly assigned one of seven treatments to each of those plots. Distance between plots was at least 50 cm, and distance between blocks was 10–50 m, depending on terrain. The experiment was started on 28 July 2011 and all treatments were applied once a year in August for six consecutive years, which is the season when the area is used by reindeer.

2.2 | Treatments

The seven treatments applied were control (C), defoliation (D), addition of faeces (F), trampling (T), removal of moss (M), F+D+T (FDT) and F+D+T+M (FDTM). We aimed for the intensity of each of the treatments to mimic the intensity of the activities observed at the heavily grazed side of the fence. In the defoliation treatment, we removed 50% of the leaves for every shoot of *B. nana*, 50% of all young and green shoots of *Vaccinium myrtillus*, and cut down all graminoids and forbs to 3 cm from the moss layer. Evergreen shrubs such as *E. nigrum* and *V. vitis-idaea* were not defoliated because they are less palatable for reindeer. The treatment is roughly similar to the level of defoliation on the different functional groups at the heavily grazed side of the fence.

Trampling was simulated using a 5 kg pointy wooden pole that we dropped from knee-height to mimic reindeer trampling (Olofsson, 2006). The pole was dropped 100 times, distributed evenly over the plot. The number of hits mimics the intensity of trampling on the heavily grazed side of the fence according to trampling indicators (Olofsson et al., 2004). However, later data showed that those measurements were taken during a temporal decline in reindeer densities in the area, and a more realistic trampling intensity in the area is thus probably substantially higher (Appendix S1b).

In the faeces treatment, we added 500 g of fresh reindeer faeces (approximately 100 g dry faeces) to each plot, spread evenly over the whole surface. Although we intended to mimic the deposition

on the heavily grazed side of the fence, our treatment resulted in five times more faeces being added compared with what has been recorded there (~20 g dry faeces/m², Sitters et al. (2017)). In the plots with combined treatments (FDT and FDTM), we dropped the pole 80–90 times, then added faeces, and then added the remaining hits to mimic the natural mixing that occurs in the field.

In the moss removal treatment, we removed as much of the top layer of bryophytes as possible, focusing mostly on the green parts and taking care not to damage small plant shoots growing between them. This approximates the dramatic decline of moss biomass by 80%–90% in the heavily grazed side of the fence (Yläne et al., 2018).

2.3 | Field measurements

Each year in August, we recorded the vegetation composition, soil temperature and moisture, before adding the treatments to the plots. Vegetation and soil properties were measured in a subplot of 50 cm × 50 cm to avoid edge effects, while each treatment was added to the full square metre plot. For the vegetation survey using point frequency recording, we used a point frame with 10 pins (pin diameter 2.5 mm and distance between pins 5.5 cm) which we placed in the subplot at 10 evenly spaced intervals, resulting in a grid of 100 points per plot. We recorded the living leaves and stems of all vascular plants touching each pin. In the bottom layer (mosses and lichens), we counted only one hit per species, but more than one moss or lichen species could be recorded. Nomenclature follows Mossberg and Stenberg (2008) for vascular plants, and Hallingbäck and Holmåsén (1985); Moberg (1990) for mosses and lichens,

respectively. We measured soil temperature using a rugged thermometer (10 cm depth) with a HI-765BL probe with a resolution of 0.1°C (Hanna Instruments) and soil moisture (10 cm depth) using a ML3-ThetaProbe soil moisture sensor connected to a HH2 moisture meter. The ThetaProbe sensor measures volumetric soil moisture content in the topsoil, and the thermometer measured soil temperatures at 12 cm depth. We recorded three readings per plot for both these methods, aiming for an overcast but dry day to achieve stable values.

2.4 | Data handling and statistical analyses

We used a non-metric multidimensional scaling (NMDS; the meta-MDS function, (Oksanen et al., 2017. vegan: Community ecology package)) in the statistical package R (R Core Team, 2017) to analyse the development of vegetation composition in each treatment over the years, based on the point frequency species counts in each individual plot (n = five replicates per treatment) in 2011 and 2016. We made several adjustments to the dataset before analysing. First, all species with a total of one or two counts in the whole dataset were discarded to make the analyses more robust. Furthermore, a number of species were merged in the collective taxa 'Cladina' (*C. mitis*, *C. rangiferina*, *C. spp.*), 'Cladonia' (*Cladonia gracilis*, *C. spp.*), 'Barbilophozia' (*Barbilophozia spp.*, *Lophozia spp.* and other liverworts) and 'PleuHylo' (*Pleurozium schreberi* and *Hylocomium splendens*) to remove inconsistencies in species identification among years. Appendix S2 provides an overview of the recorded species grouped per functional type, and their range of abundance in 2011.

(a) Site location

(b) Research site and example of plot layout



FIGURE 1 (a) Location and (b) overview of the research site with example of the plot layout in Reisadalen, northern Norway. The photo shows the reindeer fence, separating the vegetation in a grazed side dominated by graminoids (right), and an ungrazed side (left), dominated by dwarf shrubs. The experiment was located at the ungrazed side of the fence, in homogenous patches of *Betula nana* and *Empetrum nigrum*-dominated heath. We established five blocks, each containing seven plots (1 m²), to which we randomly assigned one of the treatments. Vegetation responses were measured in 50 cm × 50 cm subplots. Treatments were control (C), defoliation (D), addition of faeces (F), trampling (T), moss removal (M), F+D+T (FDT) and F+D+T+M (FDTM). Photo credit: L. Muurinen

In order to better understand the changes in vegetation composition over time, we grouped all recorded species into plant functional types (bryophytes, deciduous dwarf shrubs, evergreen dwarf shrubs, forbs, graminoids, lichens, see Appendix S2). We then calculated the percentage change (% change) over time per functional type, based on the total number of hits of all species per functional type per treatment per year. The percentage change of species counts was calculated as follows:

$$F1. \% \text{ change} = \left(\frac{\text{count 2011} - \text{count xx}}{\text{count 2011}} \right) \times 100\%$$

This allowed us to express the change in abundance relative to the start of the experiment (2011) in each of the treatments, per functional type, throughout the experiment. The resulting values for 2016 were analysed using one-way ANOVA, testing for differences among treatments per functional type ($n = 5$). Block was not included in analyse because of missing values that would have made tests less robust. The data for forbs, graminoids and lichens were log-transformed to avoid heteroscedasticity. Because each dataset contained positive and negative values, absolute values were logged, after which we added a minus to originally negative values. Lastly, we used repeated measures ANOVAs to test the effect of treatment on soil temperature and soil moisture (three repeated measurements per plot per year), comparing the years 2011 and 2016. All tests were carried out in the statistical package R (R Core Team, 2013).

3 | RESULTS

The plant community composition at the end of the experiment in 2016 did not differ between control (C) plots and plots receiving the defoliation (D), addition of faeces (F) or trampling (T) treatments, as the ranges of the plots receiving these treatments had overlapping confidence intervals in the NMDS (Figure 2). However, the Mm and FDT and FDTM treatments resulted in clearly different plant community composition with non-overlapping confidence intervals (Figure 2). The vegetation responded similarly to each of these three treatments, by changing towards a community with lower density of the dominant dwarf shrubs (*E. nigrum*, *B. nana* and *V. myrtillus*), forbs (*Linnea borealis*, *Cornus suecica* and *Pedicularis lapponica*) and large bryophytes (*P. schreberi* and *H. splendens*). Instead, these three treatments were associated with higher densities of *Lycopodium annotinum*, graminoids such as *C. bigelowii* and small bryophytes and lichens of the genera *Dicranum*, *Ptilidium* and *Cladonia*. The plant community receiving all four treatments combined (i.e. FDTM), differed the most from the controls by the end of the experiment. There was no difference in plant community composition between the treatments at the start of the experiment (Appendix S3).

Grouping the species into functional types revealed significant effects of the treatments on the density of bryophytes ($F = 15.67$; $p < 0.001$), deciduous dwarf shrubs ($F = 6.89$; $p < 0.001$) and evergreen dwarf shrubs ($F = 6.18$; $p < 0.001$) by the end of the experiment (Figure 3). Bryophytes decreased in both moss removal treatments

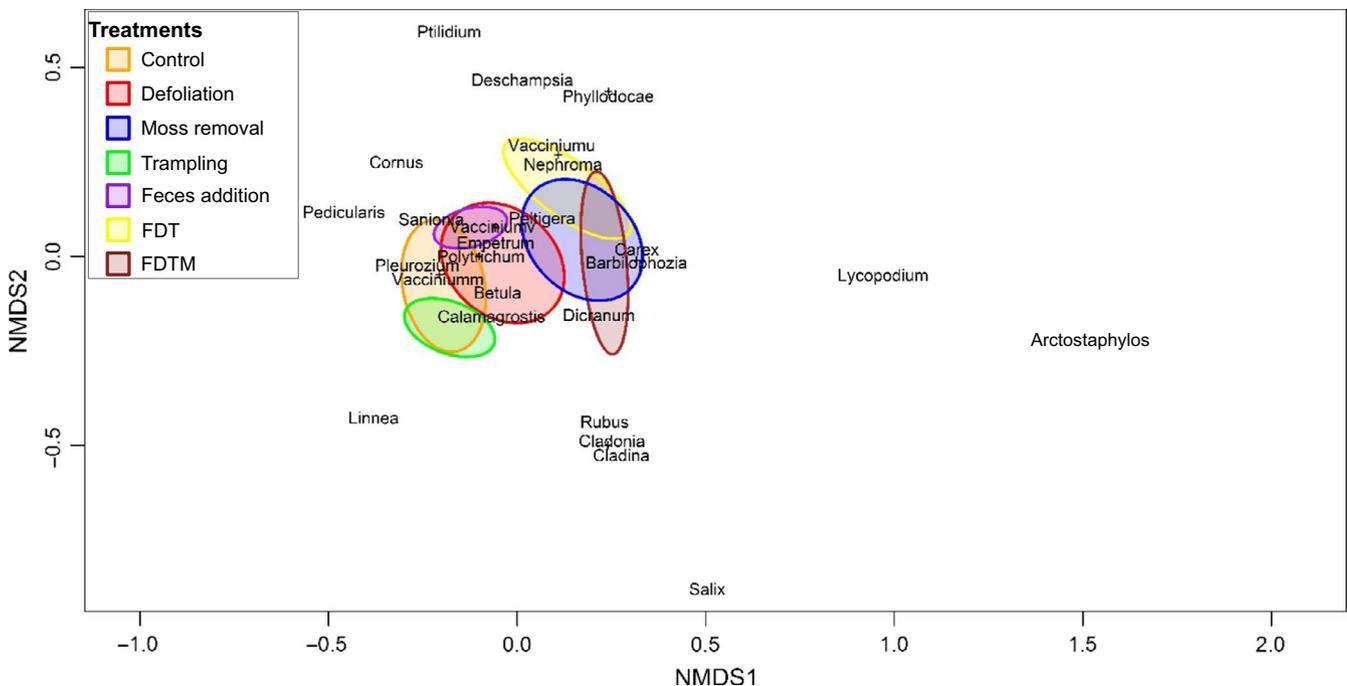


FIGURE 2 NMDS plot of the vegetation composition at the end of the experiment in 2016. The oval shapes represent the 95% confidence intervals of the mapped location of all plots ($n = 5$) per treatment. The location of the species names indicate where they have the highest relative impact on the species composition. Because there was only one species per genus we used genus names only here, except for 'Vaccinium' and 'Vacciniumm' (*Vaccinium uliginosum* and *Vaccinium myrtillus*, respectively). An overview of the full species names and the functional group they belong to is provided in Appendix S2

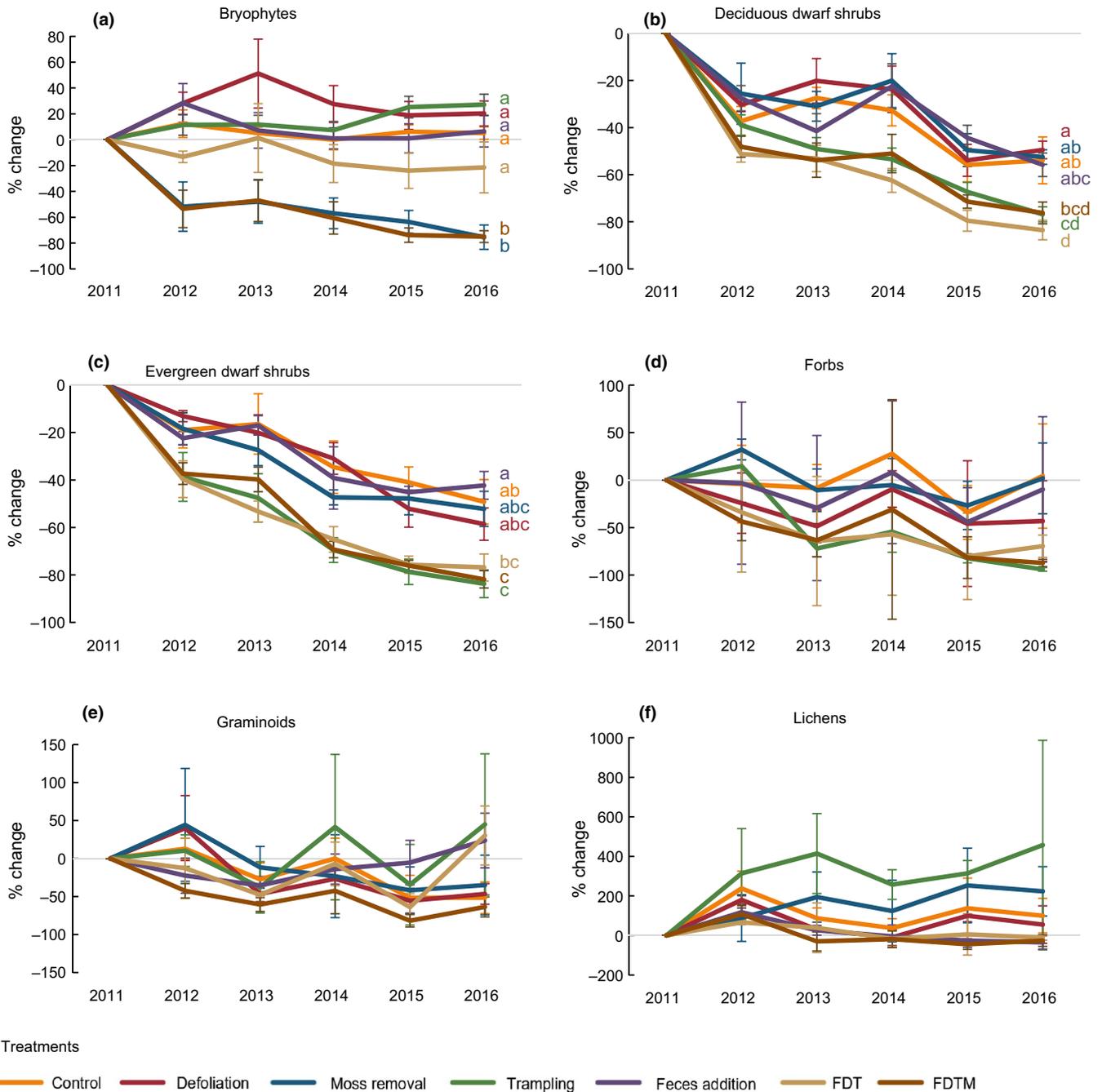


FIGURE 3 Percentage change over time for the total counts of each plant functional type, compared with starting year (2011). Each line represents a treatment and error bars indicate \pm SE, $n = 5$. The coloured numbers to the right of graphs a, b and c (Bryophytes, Deciduous dwarf shrubs and Evergreen dwarf shrubs, respectively) indicate the outcomes of post-hoc testing (Tukey-test) when there was a significant difference between treatments in 2016 (one-way ANOVA, $p < 0.05$). There are no significant differences between treatments in graphs d, e and f (Forbs, Graminoids and Lichens, respectively)

(M and FDTM), while other treatments were not different from the control (Figure 3a). Deciduous and evergreen dwarf shrub density decreased in all treatments, including the control, resulting in sparser vegetation cover. Pronounced decreases were recorded in the trampling (T), FDT and FDTM treatments, but only T and FDT were statistically different from the control for deciduous dwarf shrubs, and T and FDTM for the evergreen dwarf shrubs. There was no effect of the treatments on forbs, graminoids or lichens (Figure 3d-f), and

there were no differences in soil temperature ($F = 0.31$; $p = 0.933$) or soil moisture ($F = 1.77$; $p = 0.109$) among treatments (Figure 4).

4 | DISCUSSION

The aim of this study was to gain a better mechanistic understanding of herbivory-induced vegetation changes in tundra, by simulating

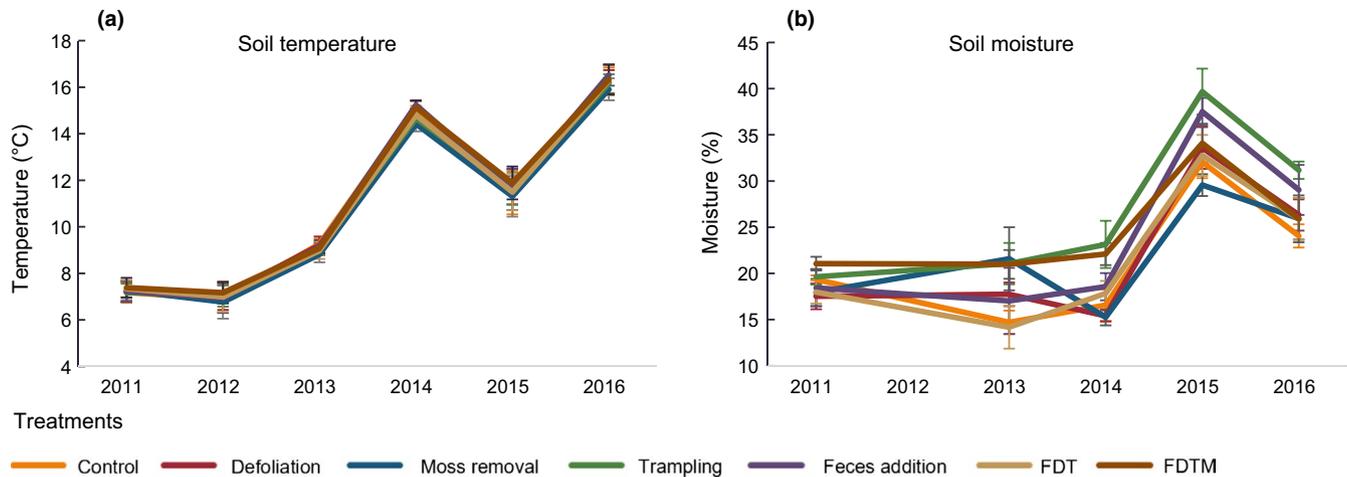


FIGURE 4 (a) Average soil temperature in °C and (b) moisture in % per treatment per year, measured in August, each year of the experiment. Each line represents a treatment and error bars indicate \pm SE, $n = 5$. Repeated measures ANOVA indicated no difference between plots when comparing values for 2011–2016; $p = 0.933$ and 0.109 for temperature and moisture, respectively

and monitoring the most important reindeer-associated activities on heath vegetation for 5 years. Importantly, a dramatic vegetation shift towards productive grassland can, and has, occurred because of high reindeer grazing pressures in just a few years, as could be observed at a distance <50 m from our experiment (Olofsson, 2006; Olofsson et al., 2001, 2004; Yläne, Stark, & Tolvanen, 2015), even though this is a habitat with nutrient-poor soils and cold temperatures. In line with our hypothesis (H5), defoliation, trampling, addition of faeces and removal of moss combined, resulted in a substantially altered vegetation, with lower abundance of dwarf shrubs, forbs and large bryophytes. However, graminoids had not expanded into the available gaps in the vegetation. Instead, the combination of all simulated activities resulted in a sparser vegetation.

Trampling had the strongest effect on the abundance of functional groups of the separate simulated herbivore activities. As expected (H1) based on previous trampling simulation experiments (Cole, 1995 a, b), both deciduous and evergreen dwarf shrubs suffered severely from the trampling treatment and decreased in 5 years by 30%–40% compared with control plots. This strong non-selective effect might explain why the response of plants to reindeer is not directly linked to plant palatability (Bernes et al., 2013; Manseau, Huot, & Crete, 1996; Olofsson et al., 2001). The shrubs most likely suffer from trampling because their growth points are exposed and growth rates are relatively slow (Mulder, 1999), and their roots may be more sensitive to mechanical damage compared with graminoid and forb roots (Jonasson & Callaghan, 1992). However, contrary to what we had expected in H1 (Cole, 1995a, 1995b; Olofsson, 2006), trampling had no significant effects on bryophytes, lichens, forbs or graminoids. This contrasts with findings from previous studies that have recorded strong negative effects of summer grazing by reindeer on lichens and attributed this to trampling (Olofsson, 2006; Olofsson et al., 2001; Sundqvist et al., 2019). The lack of response in lichens, mosses and forbs might be explained by the fact that these are heterogeneous functional groups, and include species with contrasting responses

at our sites. Another possible explanation for the lack of clear responses of mosses and lichens could be that we only recorded cover of bryophytes and lichens, whereas data on thickness or biomass might have provided further insight. Finally, lichens appear to show a slight increase in abundance in response to trampling (Figure 3f). This may indicate that lichen species favoured by disturbance can benefit from the gaps created in the moss layer, likely owing to an increased availability of light.

Interestingly, our results suggest that trampling is the reindeer activity that exerts the strongest impact on abundance of plant functional groups, even though the intensity of the trampling treatment ended up being slightly lower than the trampling intensity in the field. The strength of the treatment was based on trampling intensities measured during a temporary decline in the reindeer population in the area (Appendix S1b and Figure 1, Olofsson et al., 2004), which was much lower than what was recorded in 2014 (te Beest et al., 2016). Even though the pole we used does not exactly mimic the impact of reindeer hooves, we are confident that our experimental design was realistic enough and thus demonstrates the importance of reindeer trampling on plant functional type abundance.

Contrary to our expectations (H2) and findings in previous studies (Olofsson, 2006), we could not detect any vegetation response to our rather severe defoliation treatment, or to adding a substantial amount of reindeer faeces, or removal of moss alone. In contrast to the trampling treatments, the defoliation treatment was comparable in effect to that observed at the heavily grazed side of the fence, and the removal moss and addition of faeces were both applied at a higher rate than observed in the field. Hence, the lack of response is clearly not the result of too-weak treatments. One explanation for the lack of response might be that the most palatable species are also tolerant to defoliation (Augustine & McNaughton, 1998; Herms & Mattson, 2010). The weak effect of the defoliation treatment in our study site is also potentially linked to the timing of reindeer activity. Previous defoliation studies have found that the effect of

defoliation is strongest in spring and weaker in autumn, when plants have had more time to build up reserves through photosynthesis (Bergstrom & Danell, 1995). Our treatments were applied once per year in August, because this mimics how the area naturally is grazed by reindeer, with big herds moving through the area during that part of the season.

Despite the large amounts of reindeer pellets added to our faeces treatment plots, and contrary to our expectations (H3), none of the plant functional types showed a change in abundance compared with the control treatment. This is a surprising finding because this system is nutrient limited (Sitters, Cherif, Egelkraut, Giesler, & Olofsson, 2019) and several studies in comparable field sites have reported increased plant growth in response to the addition of dung (Barthelemy et al., 2015; van der Wal et al., 2004). We believe that the most parsimonious explanation is that the response of vegetation to the addition of faeces is slow at this site simply because the decomposition of the faeces is slow (Barthelemy, Dorrepaal, & Olofsson, 2019). Many pellets were still found intact in subsequent years in our plots (personal observation, DE). Clear responses of the added faeces were observed after 3 years on Svalbard (van der Wal et al., 2004) and after 6 years in a similar vegetation type in Abisko, Sweden (Barthelemy et al., 2015). One potential reason for the slower decomposition at this site is that soils are drier in this habitat, and that it is rather dry with precipitation of 639 mm/year (gridded data, klima, Norway) compared with over 800 mm in the Abisko site (Barthelemy et al., 2015). The decomposition rate of reindeer faeces is well known to increase with increasing soil moisture (Barthelemy et al., 2015; Skarin, 2008). Moreover, the numbers of graminoids appear to show a slight increase in abundance in response to the addition of faeces after 5 years of treatment, suggesting that a few additional years could potentially have resulted in a graminoid-dominated vegetation.

The moss removal treatment substantially reduced the overall presence of bryophytes, but in contrast to H4, this did not result in any other vegetation responses or changes in soil properties measured in summer. In similar studies, bryophyte removal mediated vegetation responses to herbivory through competing for resources (Sjögersten et al., 2010) and by insulating soils (Gornall et al., 2007; van der Wal & Brooker, 2004). Importantly, these studies were conducted in High Arctic sites, where bryophytes make up roughly 30–40% of the total (above- and below-ground) biomass (Gornall et al., 2007), whereas they only contribute 10–20% of the biomass in our study site (Barthelemy, Stark, Michelsen, et al., 2017), depending on the phase of the vole and lemming cycles. It is thus likely that bryophytes are a less important insulator in our study system.

The question remains why none of the simulated treatments, isolated or combined, caused a transition into grassland as observed at the other side of the reindeer management fence. As clarified above, it is not likely that the intensity of the treatments is too low. Yet our treatments may still promote a transition to graminoid-dominated vegetation in the long run. Our data show a tendency of graminoid cover starting to increase in response to trampling and addition of faeces, but the low initial graminoid cover, combined with a remaining

allelopathic effect of *E. nigrum* (Bråthen, Gonzalez, & Yoccoz, 2018), may have limited their ability to rapidly become dominant. However, rapid transitions have been recorded in the same area, when turfs of vegetation were moved from the ungrazed to the grazed side of the fence and showed clear conversion in just 3 years (Olofsson, 2006; Ylänne et al., 2015); yet, our experiment still cannot repeat that. This indicates that some vital way in which reindeer influence the vegetation was not included in our study; the most likely candidate being urine deposition. Approximately 50% of the N returned to the ecosystems by reindeer is expected to be in the form of faeces, and 50% as urine (Hobbs, 1996). Moreover, the most dominant form of N in urine is urea, which is rapidly taken up by plants (Barthelemy, Stark, Kytöviita, et al., 2017; Barthelemy, Stark, Michelsen, et al., 2017). Although all tundra plants seem to take up urea successfully, graminoids are likely the functional group that benefits most from the added N (Aerts & Chapin, 1999). This hypothesis is further strengthened by a significant increase in graminoid cover following N fertilization as ammonium nitrate (NH_4NO_3) in liquid form, in the same habitat type (Sitters et al., 2019, Figure 4a).

In general, we conclude that separate effects of each treatment explained most of the results, and that combined effects were weak, with some important exceptions. The combined effect of defoliation, faeces and trampling pushed the vegetation towards a dominance of disturbance-favoured mosses and graminoids in a way that could not be expected based on their separate effects. Finally, our findings suggest that trampling is an important mechanism to consider when assessing the impact of reindeer on tundra vegetation, and has a much stronger negative effect than defoliation on reindeer-sensitive species such as dwarf shrubs. This could be particularly important for reindeer compared with other grazers because they move long distances (Skarin, Danell, Bergström, & Moen, 2010) and dwarf shrubs dominate much of their summer grazing range (Moen, Boogerd, & Skarin, 2009). The combination of widespread trampling on trampling-sensitive dwarf shrubs may be an important way that reindeer influence vegetation (Bernes et al., 2013; Manseau et al., 1996; Moen et al., 2009; Olofsson et al., 2001). Moreover, it may be one of the mechanisms by which arctic grazers counteract shrub expansion in tundra habitats (Myers-Smith et al., 2011; Olofsson et al., 2009; Plante et al., 2014).

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AUTHOR CONTRIBUTIONS

HB and JO conceived the ideas and designed methodology; HB and DE collected the field data. DE analysed the data and wrote the manuscript, with contribution from both coauthors.

DATA AVAILABILITY STATEMENT

The raw vegetation and soil data are accessible in the Dryad Digital Repository: Egelkraut, Barthelemy, and Olofsson (2020).

Vegetation and soil data are available in the paper: 'Reindeer trampling promotes vegetation changes in tundra heathlands: results from a simulation experiment.' <https://doi.org/10.5061/dryad.jm63xsj6v>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Mean annual temperature and reindeer numbers in the study area

Appendix S2. Range of species counts per treatment in the first year of the experiment

Appendix S3. NMDS plot of the vegetation composition at the start of the experiment

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