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Experimental evidence of the long-term effects of reindeer on Arctic vegetation greenness and species richness at a larger landscape scale

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Abstract

1. Large herbivores influence plant community structure and ecosystem processes in many ecosystems. In large parts of the Arctic, reindeer (or caribou) are the only large herbivores present. Recent studies show that reindeer have the potential to mitigate recent warming-induced shrub encroachment in the Arctic and the associated greening of high-latitude ecosystems. This will potentially have large scale consequences for ecosystem productivity and carbon cycling.

2. To date, information on variation in the interactions between reindeer and plants across Arctic landscapes has been scarce. We utilized a network of experimental sites across a latitudinal gradient in the Scandinavian mountains where reindeer have been excluded from 59 study plots for at least 15 years. We used this study system to test the effect of long-term exclusion of reindeer on the abundance of major plant functional groups, the greenness indexes Leaf Area Index (LAI) and Normalized Difference Vegetation Index (NDVI), soil mineral nitrogen (N) and phosphorous (P), and species richness, and to determine whether the effect of reindeer exclusion is dependent on reindeer density, productivity, soil fertility or climate.

3. We found that NDVI and LAI, lichen and deciduous shrub abundances were largely reduced while soil mineral N was enhanced by reindeer. The direction and amplitude of other plant functional group responses to reindeer exclusion differed between forest and tundra as well as shrub and herbaceous dominated vegetation. Higher reindeer densities were related to decreased plant species richness in low productive sites and to increased species richness in productive sites.

4. The relative reduction in LAI and associated absolute reductions of deciduous shrubs in response to reindeer were positively related to reindeer density, while the relative reduction in NDVI was not. Further, relative reductions in LAI and NDVI in response to reindeer was unrelated to climate and soil fertility.

5. *Synthesis.* Our results provide long-term experimental evidence highlighting the role of reindeer density in regulating plant species richness, global climate change induced greenness patterns and shrub encroachment at regional scales in the Arctic. These findings emphasize the need to consider reindeer in models predicting vegetation patterns and changes in high-latitude ecosystems.

Keywords: plant-herbivore interactions, large mammalian herbivores, grazing, climate change, soil nutrients, tundra, forest, plant community composition

Introduction

Herbivores are major regulators of plant biomass, and the interactions that occur between herbivores and plants are essential for determining vegetation patterns and ecosystem functioning worldwide (e.g. Côté, Rooney, Tremblay, Dussault, & Walker, 2004; Estes et al., 2011; Tanentzap & Coomes, 2012; Jia et al., 2018). In the high-latitude ecosystems of Eurasia and North America, reindeer and caribou (*Rangifer tarandus* L.) are well known to influence plant community structure (Jefferies, Klein, & Shaver, 1994; Suominen & Olofsson, 2000; Bernes, Bråthen, Forbes, Speed, & Moen, 2015), and ecosystem processes and functions (Väisänen et al., 2014; Christie, Bryant, Gough, Ravolainen, Ruess, & Tape, 2015; Vowles et al., 2018), particularly at the local scale. Hence, a recent systematic review

of the current literature on reindeer effects on vegetation patterns across high-latitude ecosystems found strong local responses to reindeer grazing in a wide array of plant functional groups (Bernes et al., 2015). However, vegetation responses to reindeer grazing across all studies were either weak or non-significant, with the strong negative effect of reindeer on ground lichens across locations being the only exception (Bernes et al., 2015). This lack of response could reflect that effects of reindeer on vegetation are not particularly strong in many locations. But since local statistically significant effects were detected in most studies included in the review, more likely explanations are that the lack of a common protocol made it difficult to summarize results among studies, or that responses are context dependent and vary even qualitatively depending on grazing regime and environmental conditions (Bernes et al., 2015).

Ongoing climate change influences numerous ecosystem properties and processes in the Arctic, including plant community composition, plant biomass, productivity, nutrient cycling, and carbon storage and flux (Wookey et al., 2009; Elmendorf et al., 2012a; Bjorkman et al., 2018). It is becoming increasingly recognized that reindeer can influence plant responses to climatic changes by altering ecosystem properties, processes and functions such as plant biomass, community composition (Olofsson et al., 2009; Post & Pedersen, 2008; Eskelinen, Kaarlejärvi, & Olofsson, 2017; Kaarlejärvi, Eskelinen, & Olofsson, 2017), and carbon storage and flux (Cahoon, Sullivan, Post, & Welker 2012a; Metcalfe & Olofsson 2015; Väisänen et al., 2014; Yläne, Stark, Tolvanen, 2015). For example, recent greening of northern ecosystems (Mao et al., 2016) is associated with an increased dominance of shrubs in the Arctic (e.g. Forbes, Macias-Fauria, & Zetterberg, 2010; Myers-Smith et al., 2011; Ju & Masek 2016), and deciduous arctic shrub expansion can, at least locally, be suppressed by grazing (Olofsson et al., 2009; Ims & Henden 2012; Vowles et al., 2017a; Vowles, Lovehav,

Molau, & Björk, 2017b). Further, relationships between temporal and spatial patterns of caribou and reindeer populations and greening, measured by remotely sensed Normalized Difference Vegetation Index (NDVI), have been found at regional scales (Cohen et al., 2013; Newton, Pond, Brown, Abraham, & Schafer, 2014; Fauchald, Park, Tømmervik, Myneni, & Hausner, 2017). However, the causality of these effects is not always clear, since it is difficult to separate the direct effect of caribou and reindeer from other factors that vary in time or space (Newton et al., 2014; Fauchald et al., 2017). Modelling efforts are now starting to address the effect of reindeer on plant biomass and production in response to future warming at a pan-Arctic scale (Yu, Epstein, Engstrom, & Walker, 2017). Therefore, better quantitative data on the effect of reindeer on vegetation across large spatial scales are needed to build and validate such models. The availability of such data would further improve both the interpretation of remote sensing results and help with assessing whether differences in reindeer densities would influence observed environmental changes at large scales, such as the greening of the Arctic (Mao et al., 2016).

The effects that reindeer have on arctic vegetation depend on direct effects via grazing, for example the defoliation of plants, as well as indirect effects, such as via influences on soil nutrient availability (Olofsson, Stark, & Oksanen, 2004). Reindeer have commonly been shown to increase nitrogen (N) turnover and availability in heavily grazed areas by providing easily available N in urine and faeces (e.g. Barthelemy, Stark, Kytöviita, & Olofsson, 2017; Barthelemy, Stark, Michelsen, & Olofsson, 2018) and when changing the plant community composition towards a greater abundance of species that produce litter of higher quality and with higher decomposition rates (Olofsson & Oksanen, 2002). In contrast to the positive effect of reindeer on N cycling, the effect of reindeer on soil phosphorus (P) availability appears to be small or even negative (Sitters, te Beest, Cherif, Giesler, & Olofsson, 2017).

Hence, it has been proposed that positive effects of reindeer on plant growth via increases in soil mineral N availability may be associated with a long-term shift towards increasing P limitation in these ecosystems (Sitters et al., 2017). However, as current studies of reindeer effects on soil mineral N and P concentrations are from a few sites with high reindeer densities, general effects of reindeer on soil nutrient availability across arctic ecosystems are still unknown.

While reindeer are projected to influence plant species richness and diversity in the Arctic, the effect is expected to depend on climatic conditions and productivity, where more positive effects are expected at warmer climates and higher productivity (Post & Pedersen 2008; Kaarlejärvi et al., 2017; Bernes et al., 2015). The underlying mechanism of stronger positive effects of grazing on species richness in more productive environments has mainly been found to result from nutrients and herbivores serving as counteracting forces in controlling local plant diversity through light limitation; nutrients have a negative effect on species richness via increased light limitation for shorter-statured plants while herbivores have a positive effect on species richness by browsing taller-statured plants (Borer et al., 2014; Kaarlejärvi et al., 2017). This pattern is further supported by experimental data on plant trait responses to excluding reindeer, where the species that are disfavoured under exclusion of reindeer are predominantly short-statured with a low specific leaf area, i.e. species that are expected to be weak competitors for light (Kaarlejärvi et al., 2017; Olofsson & Oksanen 2005). Since multisite studies utilizing the same methodology to measure plant diversity under reindeer exclusion are still lacking, it is still not known how current grazing pressures affect plant species richness at the larger landscape scale.

Long-term experiments along natural gradients are valuable for assessing the isolated role of a factor in driving patterns of ecosystem properties and processes at larger landscape scales (Dunne, Saleska, Fischer, & Harte, 2004; Fukami & Wardle 2005; De Frenne et al., 2013).

Here, we utilize a network of sites across a large latitudinal and climatic gradient encompassing forests and tundra as well as herbaceous and shrub dominated vegetation in the Scandinavian mountains where reindeer have been experimentally excluded from a total of 59 study plots for at least 15 years. Across this study system, we applied a standardized sampling protocol for in-field measurements of plant abundance, soil abiotic properties, reindeer density, and two vegetation indices shown to be strong predictors of gross primary productivity and net ecosystem CO₂ exchange in arctic systems (Leaf Area Index (LAI) and NDVI; Street, Shaver, Williams, & Van Wijk, 2007; Shaver, Street, Rastetter, Van Wijk, & Williams, 2007; Cahoon, Sullivan, Shaver, Welker, & Post, 2012b).

Together with climate data from each location, we used this study system to test four hypotheses: 1) Reindeer increase soil mineral N, but not P, availability and reduce LAI and NDVI. 2) The overall reduction in LAI and NDVI is driven by a reduction in palatable plants, but 3) will depend on reindeer density, vegetation productivity, soil fertility and climate (with a greater reduction per unit of reindeer density at lower productivity, soil fertility and in a harsher climate). 4) Reindeer decrease plant species richness in low productive sites and under harsher climatic conditions but increase species richness in sites with high productivity and under more favourable climatic conditions, and these effects will be strongest at higher reindeer densities. Since all exclosures were of similar age, we specifically tested how exclusion of reindeer for two decades influenced the vegetation compared to areas exposed to the current grazing regime. By testing these hypotheses, we aim to advance the understanding

of how reindeer determine vegetation patterns across the different environmental conditions that occur in the Scandinavian mountains.

Materials and methods

Study area and experimental design

This study was conducted at 12 study locations across the Scandinavian mountains where reindeer exclosures have existed for ≥ 15 years (Fig. 1, Table S1, Olofsson et al., 2009; Eriksson, Niva, & Caruso, 2007; Francini, Liiri, Männistö, Stark, & Kytöviita, 2014). These locations represent a wide range in latitude and climatic conditions, and encompass common vegetation types in treeless tundra and Mountain birch forest (*Betula pubescens* ssp.

czerepanovii). All plots were installed for 15-25 years prior to our measurements and included 59 exclosures (ungrazed) and their paired control plots (grazed), resulting in a total of 118 plots (Fig. 1, Table S1). Treeless tundra is found at 11 of the study locations, where vegetation dominated by graminoids and forbs occur at three, and vegetation dominated by evergreen and deciduous shrubs and dwarf shrubs occur at nine locations (Table S1).

Mountain birch forest is found at eight of the study locations, where understory plant communities include vegetation dominated by dwarf shrubs and mosses or lichens, vegetation dominated by lower statured forbs, graminoids and dwarf shrubs, and herbaceous vegetation dominated by tall forbs and graminoids (Table S1). Hence, our study system enables comparison of how long term (≥ 15 years) exclusion of reindeer and other wild large mammals that occur in this region (e.g. moose) influence vegetation properties across a wide range of conditions in the Scandinavian mountain landscape.

Within each vegetation type at the Swedish locations Långfjället, Fulufjället, Sånfjället, Ritsem and Pulsuvuoma, three pairs of 25 × 25 m plots were installed in 1995 as part of a World Wildlife Foundation (WWF) project aiming to document vegetation changes over time in the Scandinavian mountains (Eriksson et al., 2007, Table S1, Figure 1); exclosures were installed following vegetation recording at each location and plots were paired by similarity of plant community composition. In the exclosure plot of each pair, grazing by large mammals was prevented by a 1.7 m tall fence surrounding the plot, generating three pairs of grazed and ungrazed plots within each vegetation type at each location (Eriksson et al. 2007). At each of these locations, the three pairs of plots within each vegetation type had been maintained until the time of sampling in our study, except in Pulsuvuoma where only three exclosures in total were intact (Table S1). In Ammarnäs, Sweden, we utilized two pairs of grazed control plots and ungrazed exclosure plots (100 × 100 m; ~3 m tall fences around ungrazed exclosure plots) in tundra and one pair of plots in the Mountain birch forest that were installed in 1996 by the County Administrative Board of Västerbotten and Umeå University, Sweden. In Kilpisjärvi, two pairs of grazed control plots and ungrazed exclosure plots (10 × 30 m; ~1.3-1.4 m tall fences around ungrazed exclosure plots) were installed in 1999 (Francini et al., 2014). In Raisduoddar, two pairs of grazed and ungrazed exclosure plots (12 × 12 m; 1.5 m tall fences around ungrazed exclosure plots) were installed in 1989. In Abisko, Vassijaure, Seiland and Joatka all plots were installed in 1998 and consist of three pairs of 8 x 8 m plots within each vegetation type at each location; large mammals have been excluded from one plot of each pair by a 1.2 m high fence (Olofsson et al., 2009, Table S1).

Vegetation recording

Across all locations, vegetation types and plots (ungrazed and grazed), we performed all our vegetation recordings on several subplots within each plot, and used the measurements at the subplot level to calculate one value for each measurement at the entire plot-level. No subplots were placed closer than 1 m from the edge of the plot in any location. Generally, a total of 20 subplots (1 × 1 m) were used for all vegetation recordings in Långfjället, Fulufjället, Sånfjället, Ritsem and Pulsuvuoma, a total of 30 subplots (0.3 × 0.7 m) situated in one half of the plots (50 × 100 m) were used in Ammarnäs, and a total of eight 0.5 × 0.5 m subplots were used in Vassijaure, Abisko, Joatka, Seiland, Kilpisjärvi and Raisduoddar (see Table S1 for more details on the number of subplots inventoried within each plot at each location).

In July-August 2014, a vegetation survey was conducted by point intercept method (Goodall 1952) on subplots within all exclosures and their paired controls across our study system except in Fulufjället, where the vegetation survey was conducted in July 2015 (Table S1). We used 50 cm wide rows of ten vertical pins at every 10 cm and counted the total number of times each species was intercepted by 50 pins within a 0.5 × 0.5 m area in each subplot across all locations, except for in the shrub dominated tundra vegetation in Ammarnäs where 100 pins within a 0.3 × 0.7 m subplot area was used. The total number of hits was normalized to hits per 100 pins in each subplot (Väisänen et al., 2014). This data was further used to calculate the abundance of plant functional groups (graminoids, forbs, evergreen and deciduous shrubs, deciduous dwarf shrubs, mosses and lichens), total plant species richness, and species richness for vascular plants, mosses and lichens (in a few cases using taxa including more than one species) at the plot level. For each subplot within each plot, LAI (m⁻² m⁻²) of ground and field layer vegetation was estimated non-destructively using an AccuPAR

LP-80, Decagon Devices, Pullman, USA (Wilhelm, Ruwe, & Schlemmer, 2000). Three measurements were taken below the vegetation and two above to encompass the spatial heterogeneity within subplots. For each subplot, we also measured NDVI from 2 m above each plot using a hand-held pole and 2 channel sensors (SKR 1800D/SS2, SKL925 logger, SpectroSense2, Sky Instruments, Llandrindod Wells, Wales UK). These measurements at the subplot level were used to calculate mean LAI and NDVI at the plot level.

Reindeer pellet counts

Outside each ungrazed plot, we established a 50 m × 1 m transect in which we counted the number of reindeer pellet groups as an estimate of reindeer density, hereafter referred to as reindeer density index. In fragmented landscapes, transects was sometimes divided into smaller sections, but the total length was always 50 m. Since the reindeer activity might vary substantially between different parts of a district we used this faeces-based reindeer index as it is probably the most accurate description of local reindeer densities.

Climate, soil mineral nitrogen and phosphorus

Within each plot, ten randomly selected soil samples were taken of the whole humus layer using a 2.5 cm diameter corer. All soil samples collected in each plot were bulked into one sample and each soil sample was passed through a 4 mm sieve. To determine soil mineral N (NH_4^+ -N and NO_3^- -N) and P (PO_4^- -P) concentrations in each sample, a subsample of 5 g fresh weight was extracted in 80 ml 1 M KCl. The KCl extractable concentrations of NH_4^+ -N, NO_3^- -N and PO_4^- -P were determined by colorimetry, and concentrations were calculated as mg g^{-1} dry soil weight. We used coordinates from each location and gridded data of long-term records of annual climate data from senorge.no and luftwebb.smhi.se to calculate mean annual temperature (MAT), mean growing season temperature (June, July and August) and

mean annual precipitation (MAP) for each location between 1995 and 2013. Since there were no qualitative differences between results using mean annual or mean growing season temperature, only results using MAT is presented in the manuscript.

Statistical analysis

We used a linear mixed effect model with paired plots (exclosure + controls) as a random factor to explore the main and interactive effect of our treatment reindeer exclusion (T), forest versus tundra (F), and herbaceous versus shrub dominated vegetation (H) on the density of plant functional groups, LAI and NDVI, as well as soil mineral N and P. We used Spearman's rank correlation to explore the relationship between the density of each plant functional group and NDVI and LAI, and explored the role of reindeer density index for absolute reductions in the density of plant functional groups by linear regression. We calculated the relative effect of reindeer exclusion on LAI and NDVI for all plots as the percent difference in these indices between ungrazed exclosures and grazed controls. We used ANOVA to test for the main and interactive effect of forest versus tundra (F), herbaceous versus shrub vegetation (H), reindeer density index, MAT 1995-2013, MAP 1995-2015 and soil mineral N in the control plots on the relative effect of exclosures on LAI and NDVI. No significant interactions among factors were detected in any of the two analyses, and the final models were therefore run without interaction terms. We further tested the effect of reindeer density, productivity (NDVI), MAP and MAT on the effect of excluding reindeer on species richness using a linear mixed effect model. The model was simplified to a model including only statistically significant factors. To explore the relationship between LAI and NDVI in our dataset we compared linear and asymptotic exponential non-linear regression models by AIC scores comparison. We used Spearman's rank correlation to explore the relationship between MAT, MAP, mean summer temperature,

reindeer density index, LAI, NDVI and soil mineral nutrients across the study system. All statistical analyses were performed in the statistical package R (R Core Team 2016), except for correlations which were performed in IBM SPSS Statistics 24.

Results

Effects of excluding reindeer on LAI and NDVI

Overall, both LAI and NDVI were higher inside ungrazed exclosures than in grazed controls (Table 1, Fig. 2a-b). Specifically, mean LAI was overall 0.15 units higher inside the ungrazed exclosures compared to the grazed controls. However, the effect differed among vegetation types (T×H, Table 1, Fig. 2a) with 0.42 units higher mean LAI in exclosures than in grazed controls in the herbaceous tundra, 0.15 and 0.13 units higher in the shrub dominated tundra and herbaceous forest exclosures, respectively, and 0.04 units lower in the forest exclosures with an understory dominated by shrubs (Table 1, Fig. 2a). Mean NDVI was 0.013 units higher in ungrazed exclosures compared to grazed controls, and there were no interactive effects of any of the main factors on NDVI (Table 1, Fig. 2b). The relative difference in LAI between ungrazed exclosures and grazed controls was significantly and positively related to reindeer density index ($F_{1,49}=15.0$, $P<0.001$, Fig. 2c): LAI was almost twice as high in ungrazed exclosures compared to in grazed controls at the highest reindeer density index, but there was no difference at the lowest reindeer densities. There was no significant effect of MAT, MAP or soil mineral N, or any statistically significant interactive effects among any factors on the relative difference in LAI between grazed exclosures and ungrazed controls. Further, there was no relationship between the relative difference in NDVI between ungrazed exclosures and grazed controls and any other biotic or abiotic factor, nor were there any significant interactive effects among any factors on the relative difference in NDVI between

grazed exclosures and ungrazed controls. Overall patterns of LAI and NDVI among vegetation types are given in Appendix S1.

Relationship between NDVI and LAI

There was a strong relationship between the two indices NDVI and LAI, but as NDVI values cannot get higher than 1, NDVI saturated at high LAI. Hence, a non-linear relationship between these indices with an asymptote of 1 had a better fit than a linear model (lower AIC, modelled $r^2=0.66$) across the study system.

Effects of excluding reindeer on soil mineral nutrient concentrations

Soil mineral N concentrations were almost twice as high in the grazed controls as in the exclosures (Table 1, Fig. 3a). Soil mineral N concentrations were also overall higher in forests compared to open tundra, and in herbaceous vegetation compared to vegetation dominated by shrubs (Table 1, Fig. 3a). There was no difference in soil mineral P concentrations between ungrazed exclosures and grazed controls, but soil mineral P concentrations were almost ten times higher in the forest compared to the tundra (Table 1, Fig. 3b). The effect of reindeer exclusion on soil N or P availability was not related to reindeer density ($P>0.2$).

Effects of excluding reindeer on plant functional groups

Deciduous shrub and lichen densities were overall lower in grazed controls than in ungrazed exclosures (main effect; Table 1, Fig. 4). Graminoids, deciduous dwarf shrubs, evergreen

shrubs and mosses had also responded to the exclusion of reindeer, but these effects differed between vegetation types (statistically significant two or three way interaction terms, Table 1, Fig. 4). The average graminoid density was higher in the grazed than in the ungrazed forests, while the opposite was found in the tundra (F×T, Fig. 4a). The average deciduous dwarf-shrub density was higher in grazed than in ungrazed forest with understory vegetation dominated by shrubs, while it was lower in grazed than in ungrazed shrub and herbaceous dominated tundra (F×H×T; Table 1, Fig. 4). The average evergreen shrub density was, on the other hand, lower in grazed than in ungrazed forests, while it was higher in grazed than ungrazed herbaceous tundra (F×H×T; Table 1, Fig. 4). The cover of mosses was lower in grazed compared to ungrazed forests, and higher in grazed compared to ungrazed tundra (Fig. 4). Forb abundance was unresponsive to the exclusion of reindeer (Table 1, Fig. S1). Only absolute changes in deciduous shrub and forb abundance following exclusion of reindeer were positively related to reindeer density index ($R^2 = 0.1$, $P = 0.03$, d.f. = 1, 58 and $R^2 = 0.1$, $P = 0.028$, d.f. = 1, 58, respectively). Overall patterns of plant functional group densities in forest versus tundra and shrub versus herbaceous vegetation are described in Appendix S1, and a list of vascular plant, moss and lichen species with a density of ≥ 1 in one or more treatments are found in Table S2. Across all plots the densities of graminoids and forbs were positively correlated to LAI and NDVI, the density of evergreen shrubs was positively correlated to LAI while the density of lichens was negatively correlated to both indexes (Table S3).

Effects of excluding reindeer on plant species richness

Reindeer density index ($t = 4.7$, d.f. = 55, $P < 0.001$) and the interaction between site productivity (NDVI) and reindeer density index ($t = -4.8$, d.f. = 55, $P < 0.001$), influenced the

response of total species richness to excluding reindeer, while MAT, MAP and their interactions with reindeer density index did not. Excluding reindeer had a positive effect on total species richness in sites with NDVI < 0.75, a negative effect at sites with NDVI > 0.75 and the strength of the effect of excluding reindeer increased with increasing reindeer density (Fig. 5). The effects of NDVI and reindeer density index on the response of species richness for vascular plants, mosses and lichens to excluding reindeer was largely similar to the response of total species richness (Appendix S2, Fig. S2).

Climate

Mean annual temperature over 1995-2013 across the study sites ranged between -1.94 °C and 2.44 °C, with the coldest temperatures measured in Raisduoddar and the warmest temperatures on Seiland (Fig. 1, Fig. S3). Mean annual precipitation during the same period ranged between 487 and 1031 mm, with Joatka receiving the lowest and Vassijaure the highest amount of precipitation (Fig. 1, Fig. S3). There was a positive relationship between MAT and MAP across the study locations (Fig. 1, Fig. S3). Further, MAT was positively correlated with LAI, while MAT and MAP were both negatively correlated with reindeer density index (Table S4). Mean annual summer temperatures (June, July and August) were negatively correlated with reindeer density index and positively correlated with LAI, NDVI, soil mineral N and P concentrations (Table S4).

Discussion

In line with our first hypothesis, we found that reindeer contributed to keeping the Fennoscandian tundra in a low biomass state, since both indices related to vegetation density,

NDVI and LAI, were in general higher after excluding reindeer for about two decades. This is the first experimental evidence of reindeer grazing reducing plant density consistently across multiple locations and vegetation types along the Scandinavian mountains. The differences between grazed and ungrazed plots were small compared to the range in vegetation density across the reindeer grazed tundra that we have studied (NDVI: 0.588-0.925, LAI: 0.034-2.316), and our findings thus also show that reindeer alone are not, at least at decadal time scales, the major driver of the variation in plant density across the Scandinavian mountains. The effect of reindeer on NDVI following two decades was also low compared to the reduction in NDVI recorded in a single year from vole and lemming outbreaks (Olofsson, Tømmervik, & Callaghan, 2012) or insect outbreaks (Jepsen et al., 2009). However, the pan-Arctic changes in LAI (Mao et al., 2016) and NDVI (Xu et al., 2013) that have been recorded from satellites during the last decades in the circumpolar Arctic, which are considered large enough to have feedbacks on the global climate (Zeng et al., 2017), are of similar amplitude as our recorded differences in LAI and NDVI between exclosures and grazed controls.

The overall differences in NDVI between the ungrazed exclosures and grazed vegetation are consistent with the strength of the effect of reindeer projected from arctic tundra vegetation dynamics models (Yu et al., 2017). They are also in line with some remote sensing results from Arctic regions aiming at assessing the direct effect of reindeer on peak growing season NDVI. For example, a density peak of the wild Pen Islands caribou herd in Ontario and Manitoba, Canada, resulted in a 0.04 unit reduction of NDVI (Newton et al., 2014). Further, NDVI was up to 0.08 units lower (Cohen et al., 2013) in year-round reindeer grazed Finnish sites where all plants were influenced by reindeer, compared to winter grazed Norwegian sites (Olofsson, Kitti, Rautiainen, Stark, & Oksanen, 2001; Kitti, Forbes, & Oksanen, 2009).

Although the effects of reindeer on NDVI in these remote sensing studies are stronger than the average differences we recorded between grazed vegetation and exclosures, they are well within the range of responses recorded in our study. One potential reason for these remote sensing studies showing recorded values in the higher range of what we found is that they are conducted during peak densities (Newton et al., 2014) or in areas where high reindeer densities were known to have strong effects on vegetation (Cohen et al., 2013). In the forest, our values may also be slightly underestimated, since we measured only ground and field level vegetation and not trees.

Our results, which for the first time quantify the effect of reindeer across arctic landscapes, revealed a strong positive effect of reindeer on soil mineral N availability across the entire study system. Hence, these findings are further consistent with our first hypothesis as well as previous detailed local scale studies at high reindeer densities (e.g. Olofsson et al., 2004; Sitters et al., 2017). In combination with the increase in LAI and NDVI following exclusion of reindeer, these results clearly show that the effect of reindeer on soil N availability is strong enough to affect the ability of these ecosystems to recover and maintain a high productivity under decades of defoliation and trampling. In contrast to soil mineral N concentrations, we found no corresponding positive effect of reindeer on soil P availability.

One underlying reason for the different responses of soil mineral N and P concentrations across this study system may be contrasting interactive effects of reindeer and vegetation type on these two nutrients (Sitters et al., 2017). Specifically, Sitters et al. (2017) found unidirectional and positive effects of reindeer grazing on soil mineral N that were particularly strong in less fertile vegetation. In contrast, they found negative effects of reindeer on soil mineral P concentrations to occur in more fertile vegetation while neutral, or a tendency towards positive effects, in less fertile vegetation (Sitters et al., 2017). The underlying

mechanisms for these contrasting effects of reindeer grazing on soil mineral N and P concentrations are yet to be unravelled, but they may be related to the stronger responsiveness of soil mineral N relative to soil mineral P concentrations we observe at the larger landscape scale. Therefore, our results further indicate that, in the long-term, reindeer may push arctic systems towards an increase in the relative importance of P versus N limitation even at larger landscape scales, as proposed by Sitters et al. (2017).

As we hypothesised, excluding reindeer did not only result in changes in vegetation density, but also in vegetation composition. However, in contrast to our second hypothesis, the effect of excluding reindeer on the abundance of plant functional groups was not based only on their palatability. The highly palatable deciduous shrubs were indeed less abundant in grazed vegetation than in ungrazed exclosures, consistent with results in many previous studies (Post & Pedersen 2008; Olofsson et al., 2009; Ims & Henden 2012; Vowles et al., 2017a,b). While lichen responses to reindeer exclusion can be highly site specific (e.g. Saccone et al., 2014) lichen abundances were also higher in the ungrazed exclosures compared to grazed vegetation, providing additional support for reindeer to generally reduce the abundance of ground lichens (e.g. Bernes et al., 2015). Responses of other functional groups varied between forest and tundra, as well as between herbaceous versus shrub dominated vegetation, and were not directly linked to their palatability. For example, graminoids were promoted by reindeer, but only in the forest and not in the tundra. Further, unpalatable evergreens were unresponsive to reindeer in shrub dominated tundra, in line with previous findings (Olofsson et al., 2009; Bråthen, Gonzalez, & Yoccoz 2018; Vowles et al., 2017a,b). However, evergreens were favoured by excluding reindeer in forests, while favoured by reindeer in grazed herbaceous tundra, further in line with previous findings (Vowles et al. 2017b). These multidirectional responses of plant functional groups to excluding reindeer could be caused

by their competitive interactions with surrounding plants and depend heavily on the underlying plant community composition (Oksanen & Moen, 1994; Olofsson, Moen, & Oksanen, 2002; Vowles et al., 2017b). Alternatively, large variation in resilience to grazing among plants (Dahlgren, Oksanen, Olofsson, & Oksanen, 2009) could be the reason why palatability does not fully explain plant responses to excluding reindeer.

Reindeer density alone was, as predicted, positively related to the increased LAI in exclosures across vegetation types, and the greatest impact per unit of reindeer density occurred in herbaceous tundra. However, these effects were independent of climate and soil fertility, in contrast to our third hypothesis. This is not to be taken to suggest that climate is not an important factor for plant productivity. It is well known that climate, and especially temperature, drive vegetation density and composition in Arctic ecosystems (e.g. Elmendorf et al., 2012a; Bjorkman et al., 2018), and we found a positive relationship between LAI and both MAT and MAP, as well as positive relationships between mean summer temperatures and LAI, NDVI, soil mineral N and P concentrations across our study system. Instead, our findings may suggest additive effects of reindeer density, productivity and climate on relative changes in LAI following reindeer exclusion, and show a stronger effect of reindeer density and vegetation type than climate on such changes in LAI. Further, any interacting effects of climate and reindeer on the vegetation is likely to be influenced by the negative correlation between reindeer density index and both MAT and MAP in our data. This pattern hardly reflects a causal effect of climate on reindeer across the study system, but rather show that the highest reindeer densities are found in remote northern cold and dry areas for various reasons. Further in contrast to our third hypothesis, the increased NDVI in exclosures was not significantly positively related to reindeer density. One reason for this discrepancy in responses between LAI and NDVI may be that NDVI is close to saturation in more

productive vegetation, as suggested by the non-linear relationship between LAI and NDVI across our study system, and therefore effects of reindeer on vegetation density in productive habitats only result in small effects on NDVI.

In line with our fourth hypothesis, reindeer decreased plant species richness in low productive sites (e.g. environments with low NDVI) and increased plant species richness in productive sites. These results are coherent with previous single site experiments that show a stronger positive effect of reindeer on plant richness and diversity with increased productivity through experimental warming (Post & Pedersen 2008; Kaarlejärvi et al., 2017). In further support of our hypothesis, reindeer impact on species richness was highest at high reindeer densities. In their meta-analyses Bernes et al. (2015) found that the effects of reindeer on vascular plant species richness depended on temperature, ranging from negative at low temperature to positive at high temperature. Although a measure of productivity could not be included in the meta-analyses these findings largely corroborate our results as productivity and temperature were positively correlated across the study system we used. While we did not study the underlying mechanism of these patterns, they are consistent with previous studies showing that reindeer can promote species richness in productive sites by preventing light limitation for short-statured plants (Olofsson & Oksanen 2005; Borer et al., 2014; Kaarlejärvi et al., 2017). In low productive environments, competition among plants may be weak while facilitative interactions may be more common (Brooker et al., 2008). Thus, one plausible mechanism underlying the pattern we found in lower productive environments is that reindeer may reduce species richness by removing grazing intolerant species, yet without this removal having any positive effects on neighbouring plants through reduced competition.

While large scale vegetation patterns in Fennoscandian forests have been rather small in response to global change drivers over the last decades (Hedwall & Brunet 2016), our results highlight that such patterns would likely be different if these forests were not grazed by reindeer. Further, under ongoing greening and an increase of predominantly deciduous shrubs in the Arctic (Myers-Smith et al., 2011; Elmendorf et al., 2012a,b; Ju & Masek 2016), our results not only reveal the first experimental evidence of the important individual role of reindeer in driving significant reductions in the vegetation greenness indexes (LAI and NDVI) at regional scales, but also a uniform effect on deciduous shrubs across multiple locations and plant community types. Recent local scale studies have found that particularly one common deciduous shrub across our study system, *Betula nana*, can play a central role in community CO₂ flux, even when suppressed by reindeer (Metcalf & Olofsson 2015). More specifically, due to a greater gross primary productivity and lower ecosystem respiration, communities dominated by *B. nana* have shown to be stronger carbon sinks than communities dominated by graminoids (Cahoon et al., 2016). Together with the strong positive relationships found between NDVI, LAI and gross primary productivity (Street et al., 2007; Shaver et al., 2007; Cahoon et al., 2012b), our results thus highlight the need to account for reindeer as an important driver of arctic vegetation carbon flux across large spatial scales. Most of the Arctic is grazed by reindeer (Uboni et al., 2016). If these effects of reindeer on vegetation found in Fennoscandia are applicable to other regions, consideration of reindeer densities in climate and vegetation models should improve predictions of plant biomass, productivity and carbon cycling patterns in a future climate (e.g. Cahoon et al., 2012a; Väisänen et al., 2014; Yu et al., 2017). Although other factors, such as a warmer climate, may play a more central role in driving vegetation patterns in some regions (Fauchalt et al., 2017), our findings further reinforce the importance of considering the effects of

reindeer in models predicting future vegetation patterns in high-latitude ecosystems (Yu et al., 2017).

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Author contributions

JO, JM, RGB, MKS, TV and M-MK conceived the ideas and designed methodology; MKS, JO, MAP collected the data; MKS and JO analysed the data; MKS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data is available in the Figshare repository: <https://doi.org/10.6084/m9.figshare.7981829.v1> (Sundqvist & Olofsson, 2019)

References

Barthelemy, H., Stark, S., Kytöviita, M.M. & Olofsson, J. (2017). Grazing decrease N partitioning among coexisting plant species. *Functional Ecology*, 31, 2051-2060.

<https://doi.org/10.1111/1365-2435.12917>

Barthelemy, H., Stark, S., Michelsen, A. & Olofsson, J. (2018). Urea is an important nitrogen source for plants irrespectively of vegetation composition in an Arctic tundra: insights from a N-15-enriched urea tracer experiment. *Journal of Ecology*, 106, 367-378.

<https://doi.org/10.1111/1365-2745.12820>.

Bernes, C., Bråthen, K. A., Forbes, B. C., Speed, J. D. M. & Moen, J. (2015). What are the impacts of reindeer/caribou (*Rangifer tarandus* L.) on arctic and alpine vegetation? A systematic review. *Environmental Evidence*, 4, 4. <https://doi.org/10.1186/s13750-014-0030-3>.

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

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., ... Michalet, R. (2008). Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, 96, 18-34. <https://doi.org/10.1111/j.1365-2745.2007.01295.x>

Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., ... Yang, L. H. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508, 517-520. <https://doi.org/10.1038/nature13144>.

Bråthen, K. A., Gonzalez, V. T. & Yoccoz, N. G. (2018). Gatekeepers to the effects of climate warming? Niche construction restricts plant community changes along a temperature

gradient. *Perspectives in Plant Ecology, Evolution and Systematics*, 30, 71-81.

<https://doi.org/10.1016/j.ppees.2017.06.005>.

Cahoon, S. M. P., Sullivan, P. F., Post, E. & Welker, J.M. (2012a). Large herbivores limit CO₂ uptake and suppress carbon cycle responses to warming in West Greenland. *Global Change Biology*, 18, 469-479. <https://doi.org/10.1111/j.1365-2486.2011.02528.x>.

Cahoon, S. M. P., Sullivan, P. F., Shaver, G. R., Welker, J. M. & Post, E. (2012b). Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. *Ecology Letters*, 15, 1415-1422. <https://doi.org/10.1111/j.1461-0248.2012.01865.x>

Cahoon, S. M. P., Sullivan, P. F. & Post, E. (2016). Greater abundance of *Betula nana* and early onset of the growing season increase ecosystem CO₂ uptake in west Greenland. *Ecosystems*, 19, 1149-1163. <https://doi.org/10.1007/s10021-016-9997-7>.

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. <https://doi.org/10.1093/biosci/biv137>

Cohen, J., Pulliainen, J., Ménard, C. B., Johansen, B., Oksanen, L., Luojus, K. & Ikonen, J. (2013). Effect of reindeer grazing on snowmelt, albedo and energy balance based on satellite data analyses. *Remote Sensing of Environment*, 135, 107-117. <https://doi.org/10.1016/j.rse.2013.03.029>

Côté, S. D., Rooney, T.P., Tremblay, J.P., Dussault, C. & Walker, D.M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, 35, 111-147. <https://doi.org/10.1146/annurev.ecolsys.35.021103.105725>

Dahlgren, J., Oksanen, L., Olofsson, J. & Oksanen, T. (2009). Plant defences at no cost? The recovery of tundra scrubland following heavy grazing by grey-sided voles, *Myodes rufocanus*. *Evolutionary Ecology Research*, *11*, 1205-1216.

De Frenne, P., Graae, B.,J., Rodríguez-Sánchez, F., Kolb, A., Chabrierie, O., Decocq, G., ... Verheyen K. (2013). Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology*, *101*, 784-795. doi: 10.1111/1365-2745.12074

Dunne, J. A., Saleska, S.R., Fischer, M.L. & Harte, J. (2004). Integrating experimental and gradient methods in ecological climate change research. *Ecology*, *85*, 904-916.
<https://doi.org/10.1890/03-8003>

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., ... Wipf, S. (2012a). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, *2*, 453-457. doi: 10.1038/NCLIMATE1465.

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

Eriksson, O., Niva, M. & Caruso, A. (2007). Use and abuse of reindeer range. *Acta Phytogeographica Suecica*, *87*.

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

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, 333, 301-306. doi: 10.1126/science.1205106.

EuroGeographics. (2016). Administrative boundaries. Retrieved from ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-statistical-units/nuts#nuts16

Fauchald, P., Park, T., Tømmervik, H., Myneni, R. & Hausner, V. H. (2017). Arctic greening from warming promotes declines in caribou populations. *Science advances*, 3, e1601365. DOI: 10.1126/sciadv.1601365.

Forbes, B. C., Macias-Fauria, M. & Zetterberg, P. (2010). Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology*, 16, 1542-1554. <https://doi.org/10.1111/j.1365-2486.2009.02047.x>.

Francini, G., Liiri, M., Männistö, M., Stark, S. & Kytöviita, M-M. (2014). Response to reindeer grazing removal depends on soil characteristics in low Arctic meadows. *Applied Soil Ecology*, 76, 14-25. <https://doi.org/10.1016/j.apsoil.2013.12.003>.

Fukami, T. & Wardle, D. A. (2005). Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society – B*, 272, 2105-2115. doi: 10.1098/rspb.2005.3277.

Goodall, D. W. (1952). Some considerations in the use of point quadrats for the analysis of vegetation. *Australian Journal of Scientific Research, Series B*, 5, 1 – 41. doi: 10.1071/BI9520001.

Hedwall, P. & Brunet, J. (2016) Trait variations of ground flora species disentangle the effects of global change and altered land-use in Swedish forests during 20 years. *Global Change Biology*, 22, 4038-4047.

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.

<https://doi.org/10.1016/j.biocon.2012.02.008>.

Jefferies, R. L., Klein, D. R. & Shaver, G.R. (1994). Vertebrate herbivores and northern plant communities – reciprocal influences and responses. *Oikos*, 71, 193-206. doi:

10.2307/3546267.

Jepsen, J. U., Hagen, S. B., Hogda, K. A., Ims, R. A., Karlsen, S. R., Tommervik, H. & Yoccoz, N. G. (2009). Monitoring the spatio-temporal dynamics of geometrid moth

outbreaks in birch forest using MODIS-NDVI data. *Remote Sensing of Environment*, 113, 1939-1947. doi: 10.1016/j.rse.2009.05.006.

Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Hao, Z. & Luskin, M.S. (2018). Global signal of top-down control of terrestrial plant communities by herbivores. *Proceedings on the National*

Academy of Sciences of the United States of America, 115, 6237-6264.

<https://doi.org/10.1073/pnas.1707984115>.

Ju, J. & Masek, J. G. (2016). The vegetation greenness trend in Canada and US Alaska from 1984-2012 Landsat data. *Remote Sensing of Environment*, 176, 1-16.

<https://doi.org/10.1016/j.rse.2016.01.001>.

Kaarlejärvi, E., Eskelinen, A. & Olofsson, J. (2017). Herbivores rescue diversity in warming tundra by modulating trait-dependent species losses and gains. *Nature Communications*, 8, 419, DOI: 10.1038/s41467-017-00554-z.

Kitti, H., Forbes, B. & Oksanen, L. (2009). Long- and short term effects of reindeer grazing on tundra wetland vegetation. *Polar Biology*, 32, 253-361. <https://doi.org/10.1007/s00300-008-0526-9>.

Mao, J., Ribes, A., Yan, B., Shi, X., Thornton, P. E., Séférian, R., ... Lian, X. (2016). Human-induced greening of the northern extratropical land surface. *Nature Climate Change*, 6, 959-963. Doi: 10.1038/NCLIMATE3056.

Metcalf, D. B. & Olofsson, J. (2015). Distinct impacts of different mammalian herbivore assemblages on arctic tundra CO₂ exchange during the peak of the growing season. *Oikos*, 124, 1632-1638. <https://doi.org/10.1111/oik.02085>.

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

Natural Earth. (2019). Arctic circle [Data file]. Retrieved from naturalearthdata.com/downloads/10m-physical-vectors/10m-geographic-lines/

Newton, E. J., Pond, E.A., Brown, G. S., Abraham, K. F. & Schafer, J. A. (2014). Remote sensing reveals long-term effects of caribou on tundra vegetation. *Polar Biology*, 37, 715-725. <https://doi.org/10.1007/s00300-014-1472-3>.

Oksanen, L. & Moen, J. (1994). Species-specific plant responses to exclusion of grazers in three Fennoscandian tundra habitats. *EcoScience*, 1, 31-39.

<https://doi.org/10.1080/11956860.1994.11682225>.

Olofsson, J. & Oksanen, L. (2002). Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. *Journal of Ecology*, 96, 507-515. <https://doi.org/10.1034/j.1600-0706.2002.960312.x>.

Olofsson, J., Kitti, H., Rautiainen, P., Stark, S. & Oksanen, L. (2001). Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, 24, 13-24. DOI: 10.1034/j.1600-0587.2001.240103.x.

Olofsson, J., Moen, J. & Oksanen, L. (2002). Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity. *Oikos*, 96, 265-272.

<https://doi.org/10.1034/j.1600-0706.2002.960208.x>.

Olofsson, J., Stark, S. & Oksanen, L. (2004). Reindeer influence ecosystem processes in the tundra. *Oikos*, 105, 386-396. <https://doi.org/10.1111/j.0030-1299.2004.13048.x>.

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

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

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

R Core Team, (2016). R: A language and Environment for statistical computing. R Foundation for statistical computing, Vienna, Austria. URL <https://www.R-project.org/>.

Saccone, P., Pyykkonen, T., Eskelinen, A. & Virtanen, R. (2014) Environmental perturbation, grazing pressure and soil wetness jointly drive mountain tundra toward divergent alternative states. *Journal of Ecology*, *102*, 1161-1672. doi: 10.1111/1365-2745.12316

Shaver, G. R., Street, L. E., Rastetter, E. B., Van Wijk, M. T. & Williams, M. (2007). Functional convergence in regulation of net CO₂ flux in heterogeneous tundra landscapes in Alaska and Sweden. *Journal of Ecology*, *95*, 802-817. <https://doi.org/10.1111/j.1365-2745.2007.01259.x>.

Sitters, J., te Beest, M., Cherif, M., Giesler, R. & Olofsson, J. (2017). Interactive effects between reindeer and habitat fertility drive soil nutrient availabilities in arctic tundra. *Ecosystems*, *20*, 1266-1277. <https://doi.org/10.1007/s10021-017-0108-1>.

Street, L. E., Shaver, G. R., Williams, M. & Van Wijk, M. T. (2007). What is the relationship between changes in canopy leaf area and changes in photosynthetic CO₂ flux in arctic ecosystems? *Journal of Ecology*, *95*, 139-150. <https://doi.org/10.1111/j.1365-2745.2006.01187.x>.

Sundqvist, M.K. & Olofsson, J. (2019) Data from: Experimental evidence of the long-term effects of reindeer on Arctic vegetation greenness and species richness at a larger landscape scale. Figshare. <https://doi.org/10.6084/m9.figshare.7981829.v1>

Suominen, O. & Olofsson, J. (2000). Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: a review. *Annales Zoologici Fennici*, *37*, 233-249.

Tanentzap, A. J. & Coomes, D. A. (2012). Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? *Biological Reviews*, 87, 72-94.

<https://doi.org/10.1111/j.1469-185X.2011.00185.x>.

Uboni, A., Horstkotte, T., Kaarlejärvi, E., Sévêque, A. Stammer, F., Olofsson, J., Forbes, B. & Moen, J. (2016). Long-term trends and role of climate in the population dynamics of Eurasian reindeer. *PLoS ONE*, 11(6):e0158359.

<https://doi.org/10.1371/journal.pone.0158359>.

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

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

<https://doi.org/10.1088/1748-9326/aa62af>.

Vowles, T., Lindwall, F., Ekblad, A., Bahram, M., Furneaux, B. R., Ryberg, M. & Björk, R. G. (2018). Complex effects of mammalian grazing on extramatrical mycelial biomass in the Scandes forest-tundra ecotone. *Ecology and Evolution*, 8, 1019–1030.

doi:10.1002/ece3.3657.

Väisänen, M., Yläne, H., Kaarlejärvi, E., Sjögren, S., Olofsson, J., Crout, N. & Stark, S. (2014). Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nature Climate Change*, 4, 384-388. doi:10.1038/NCLIMATE2147.

Wilhelm, W. W., Ruwe, K. & Schlemmer, M. R. (2000). Comparison of three leaf area index meters in a corn canopy. *Crop Science*, 40, 1179-1183.

Wookey, P. A., Aerts, R., Bardgett, R. D., Baptist, F., Bråthen, K. A., Cornelissen, J. H. C., ... Shaver, G. R. (2009). Ecosystem feedbacks and cascade processes: understanding their

role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology*, 15, 1153-1172. <https://doi.org/10.1111/j.1365-2486.2008.01801.x>.

Xu, L., Myneni, R. B., Chapin, F. S., Callaghan, T. V., Pinzon, J. E., Tucker, C. J., ...

Stroeve, J. C. (2013) Temperature and vegetation seasonality diminishment over northern lands. *Nature Climate Change*, 3, 581-586. doi: 10.1038/NCLIMATE1836.

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. doi: 10.1111/gcb.13632.

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

Zeng, Z. Z., Piao, S. L., Li, L. Z. X., Zhou, L., Ciais, P., Wang, T., ... Wang, Y. (2017). Climate mitigation from vegetation biophysical feedbacks during the past three decades. *Nature Climate Change*, 7, 432-436. doi: 10.1038/NCLIMATE3299.

Table 1. Results from a linear mixed effect model (F-values) testing for the effect of excluding reindeer (Treatment; T) on LAI, NDVI and plant functional groups in forests versus tundra (F) and herbaceous versus shrub (H) dominated vegetation. Values in boldface indicate statistical significance at $p \leq 0.05$. (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

	Forest versus tundra (F)	Herbaceous versus Shrub (H)	Treatment (T)	F*H	F*T	H*T	F*H*T
df	1,55	1,55	1,55	1,55	1,55	1,55	1,55
LAI	4.3*	1.2	8.9**	0.0	2.4	4.4*	0.2
NDVI	8.1**	7.6**	4.9*	0.0	0.3	0.5	0.4
Forbs	0.0	34.9**	0.3	8.8**	0.7	2.1	0.0
Graminoids	9.1**	40.4***	3.1	9.3**	8.8**	1.6	2.6
Deciduous shrubs	9.9**	2.5	5.7*	7.1	0.3	2.7	0.1
Deciduous dwarf shrubs	7.5**	0.0	0.0	5.1*	0.6	0.1	4.9*
Evergreen shrubs ^a	0.1	25.0***	0.3	5.4*	3.7	2.3	4.4*
Mosses	5.6*	0.4	0.0	2.1	8.2**	0.7	1.3
Lichens	9.6**	30.3***	7.2**	24.5***	1.0	2.9	0.0
Mineral N	5.3*	16.5***	9.7**	8.7**	3.7	0.0	0.6
Mineral P	54.9***	0.8	0.1	1.5	0.2	1.7	0.5

^aIncludes both shrubs and dwarf shrubs.

Figure 1. Photographs of reindeer exclosures at each study location a-l, and map depicting each of the 12 study locations utilized in this study and where reindeer exclosures have been installed since 1995-1999. a) Seiland, b) Joatka, c) Raisduoddar, d) Vassijaure, e) Kilpisjärvi f) Abisko, g) Pulsuvuoma h) Ammarnäs i) Ritsem j) Sånfjället, k) Långfjället, l) Fulufjället. See Appendix 1 for more details on the study system and experimental setup. Photo credits: Jonas Gustafsson (a-g, l), Maja Sundqvist (h-i), Mikael Marberg (j-k). The map was created in Esri Inc. (2019). ArcMap 10.5.1. Redlands, CA: Esri Inc; data from EuroGeographics (2016) and Natural Earth (2019).

Figure 2. LAI (a) and NDVI (b) in grazed vegetation (red bars) and vegetation where reindeer have been excluded (blue bars); error bars are \pm SE. F=Forest versus tundra, H=Herbaceous versus Shrub, T=Treatment (exclosures versus grazed controls); whenever significant main or interactive effects between factors occurred, these are indicated within each panel; results from a linear mixed effect model are found in Table 1. (c-d) The relationship between relative percent difference between ungrazed exclosures and grazed controls in vegetation indexes (c: LAI, $F_{1,49}=15.0$, $P<0.001$; d: NDVI $F_{1,57}=1.7$, $P=0.2$) and reindeer density index. No trendline is included in (d) as this is not a significant relationship. Black circles = shrub dominated tundra vegetation, pink circles = forest with understory dominated by shrubs, orange circles = herbaceous dominated tundra vegetation, blue circles = forest with understory dominated by herbaceous plants.

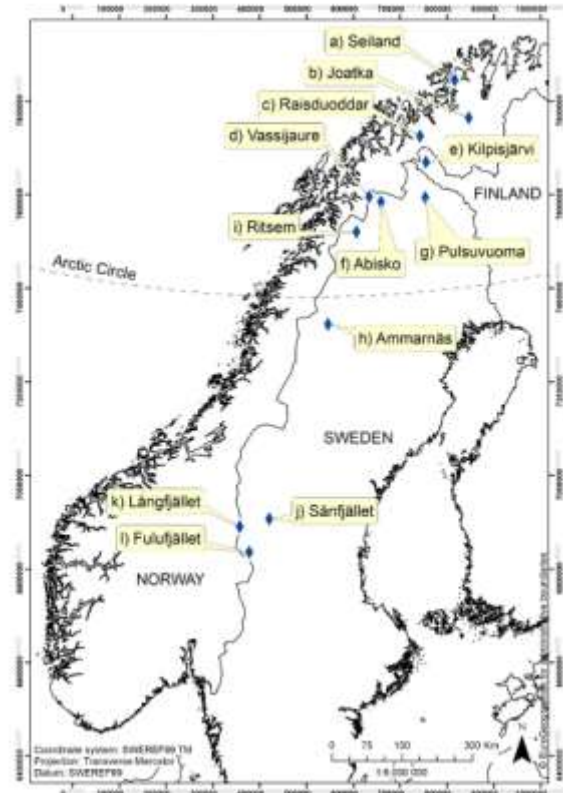
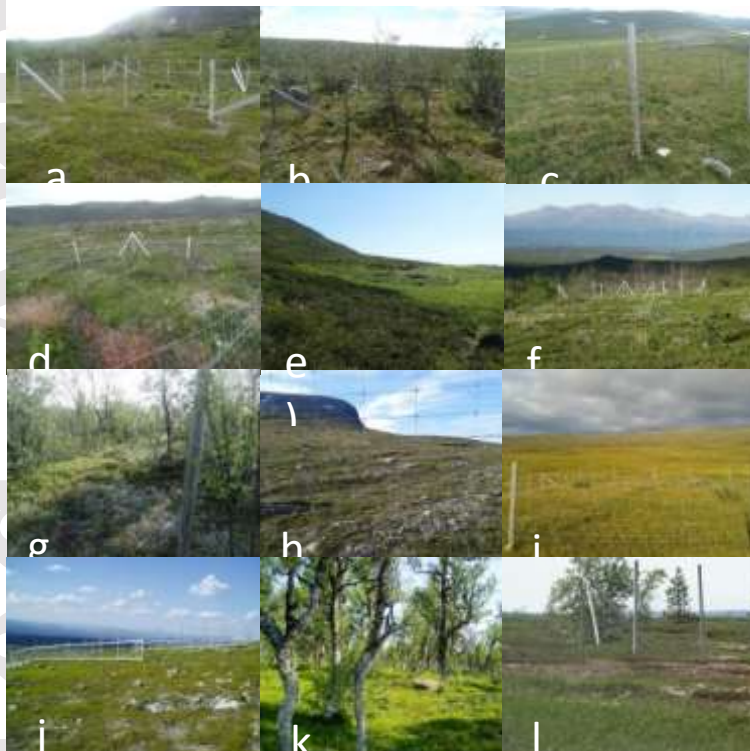
Figure 3. Concentrations (mg g^{-1} soil dry weight) of soil mineral N (NH_4^+ -N and NO_3^- -N) (a) and soil mineral P (PO_4 -P) (b) in grazed vegetation (red bars) and vegetation where reindeer have been excluded (blue bars); error bars are \pm SE. F=Forest versus tundra, H=

Herbaceous versus Shrubs (S), T=Treatment (exclosures versus grazed controls); whenever significant main or interactive effects between factors occurred, these are indicated within each panel. Results from a linear mixed effect model are found in Table 1.

Figure 4. Abundance of graminoids (a), deciduous shrubs (b), deciduous dwarf shrubs (c), evergreen shrubs (d), mosses (e), and lichens (f) in grazed vegetation (red bars) and vegetation where reindeer have been excluded (blue bars); error bars are \pm SE. F=Forest versus tundra, H= Herbaceous versus Shrubs (S), T=Treatment (exclosures versus grazed controls); whenever significant main or interactive effects between factors occurred, these are indicated within each panel. Results from a linear mixed effect model are found in Table 1.

Figure 5. Levelplot showing how reindeer density index and the interaction between NDVI and reindeer density index significantly influences the response of total species richness (including mosses, lichens and vascular plants) to excluding reindeer. Red colour indicates a higher species richness in ungrazed exclosures and a blue colour indicates a lower species richness in ungrazed exclosures. Number of species within the gradients of red and blue are according to the coloured bar (right).

Figure 1



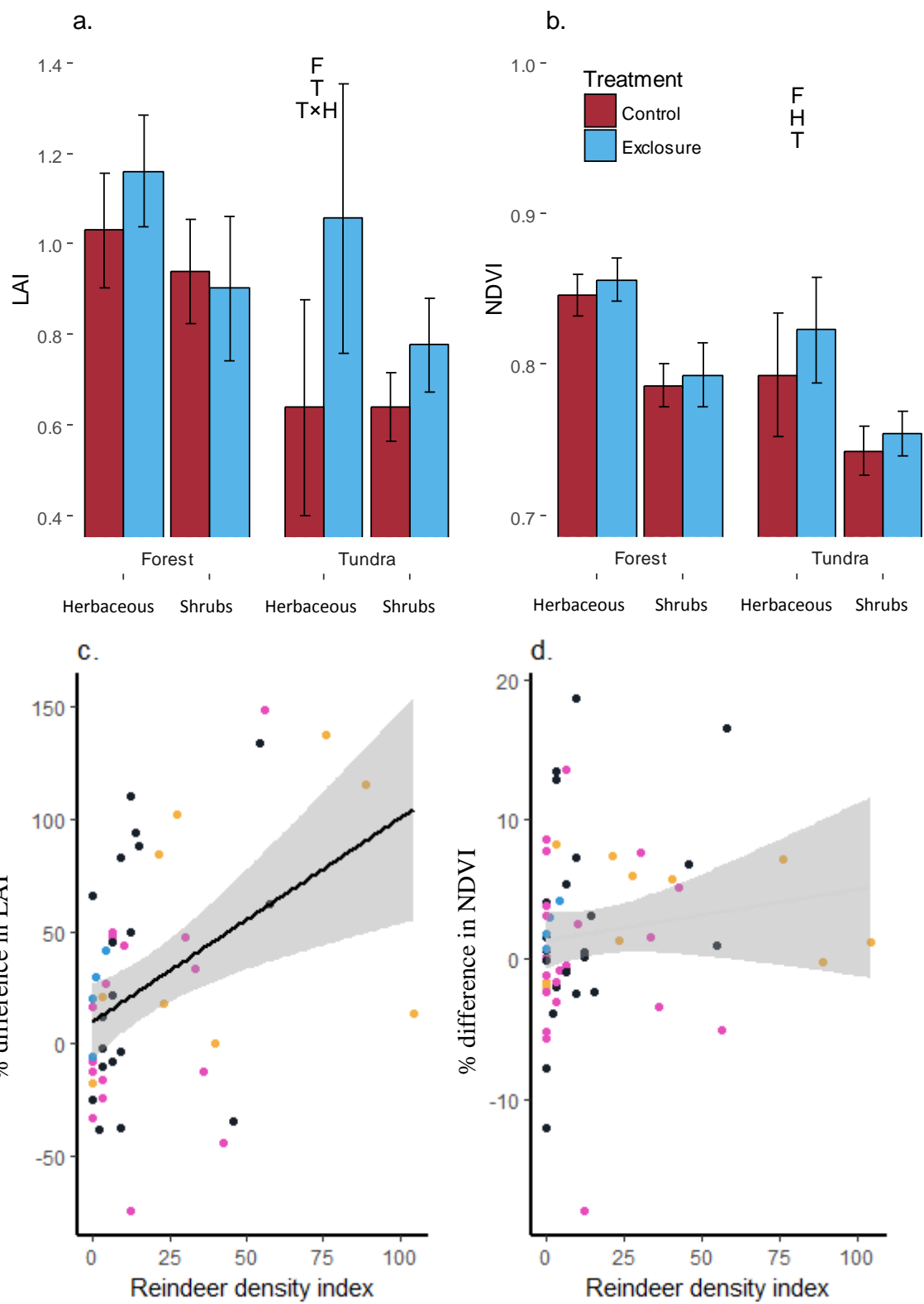


Figure 2.

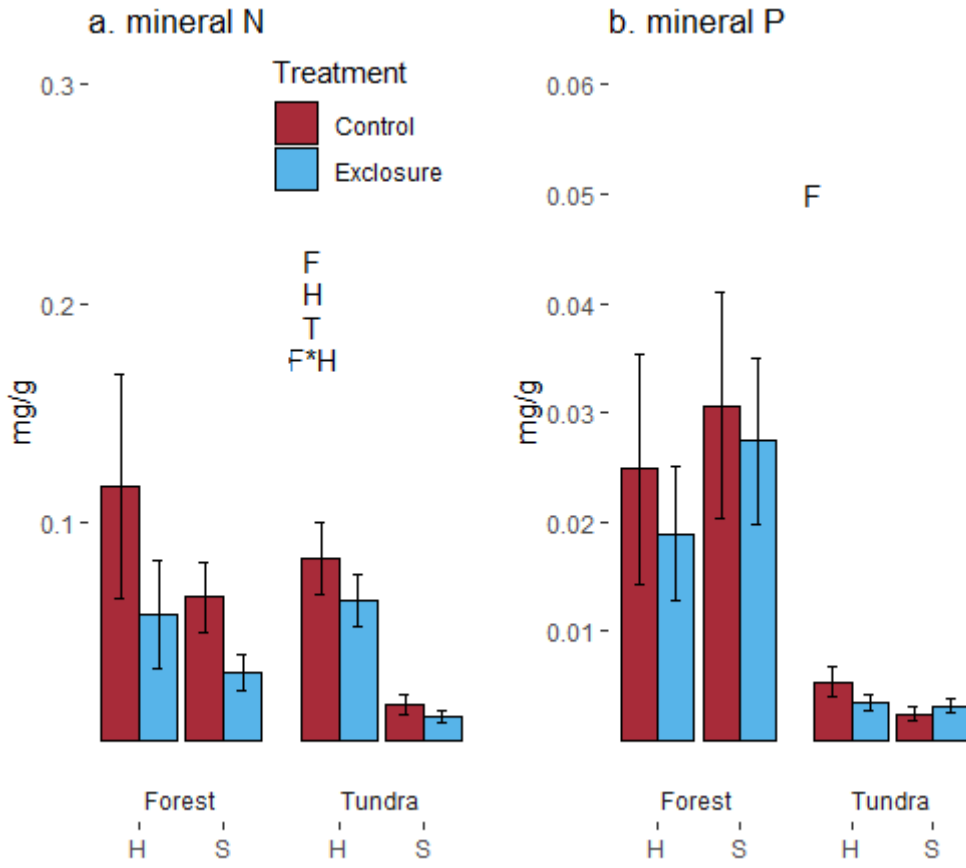


Figure 3.

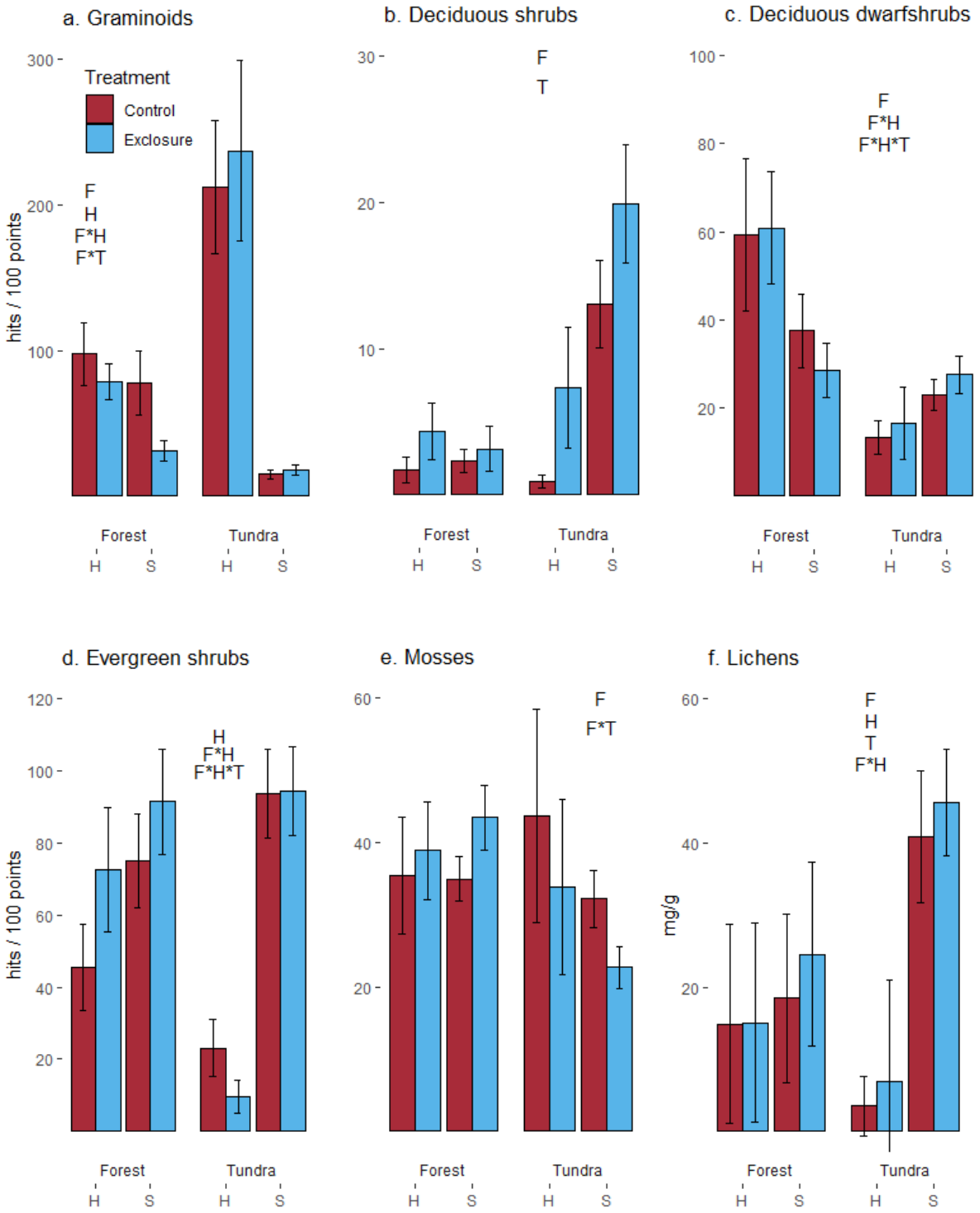


Figure 4.

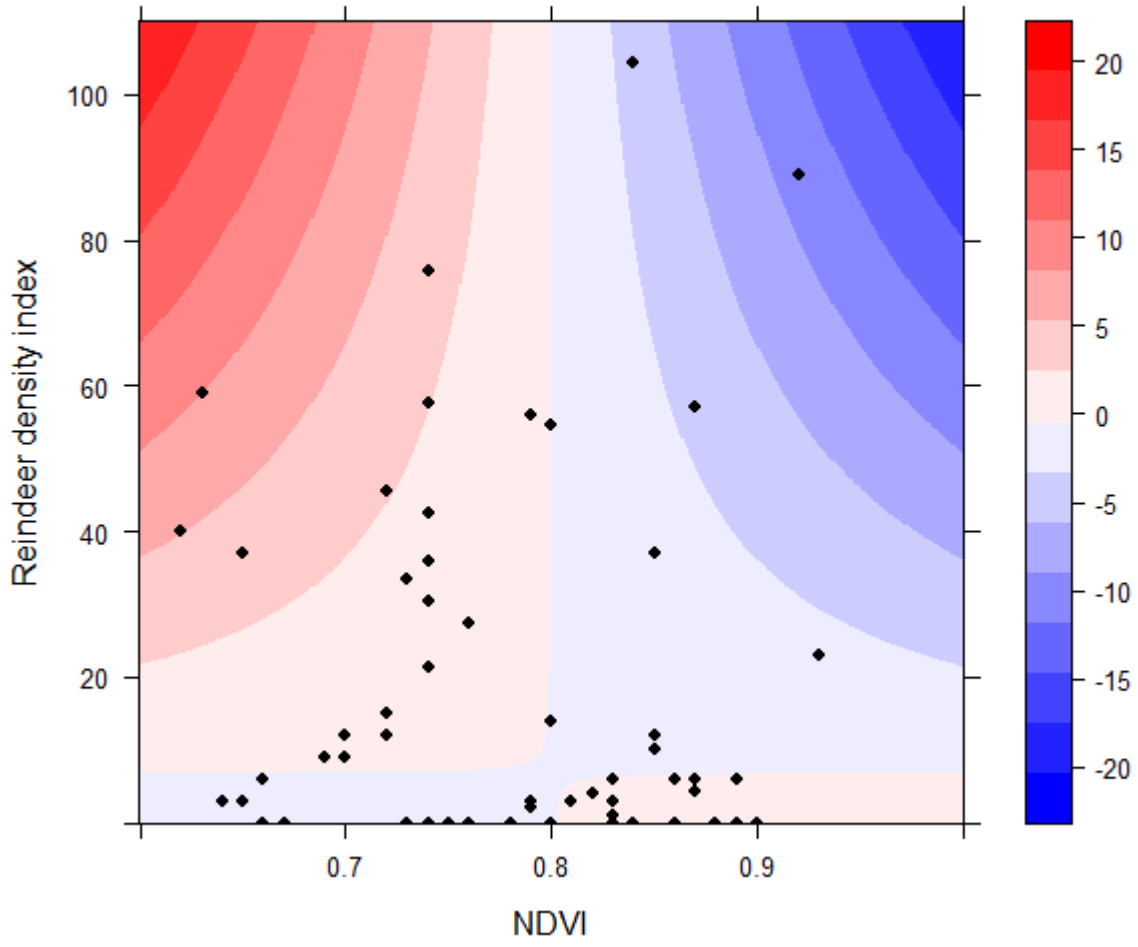


Figure 5