

## Research

### Interactions between winter and summer herbivory affect spatial and temporal plant nutrient dynamics in tundra grassland communities

Matteo Petit Bon, Katarina Gunnarsdotter Inga, Ingibjörg Svala Jónsdóttir, Tove Aagnes Utsi, Eeva Marjatta Soininen and Kari Anne Bråthen

M. Petit Bon (<https://orcid.org/0000-0001-9829-8324>) ✉ ([matteo.petitbon@gmail.com](mailto:matteo.petitbon@gmail.com)), Dept of Arctic Biology, Univ. Centre in Svalbard (UNIS), PO Box 156, NO-9171 Longyearbyen, Norway. – MPB, K. Gunnarsdotter Inga, T. A. Utsi (<https://orcid.org/0000-0003-0776-2369>), E. M. Soininen (<https://orcid.org/0000-0003-4280-8350>), K. A. Bråthen (<https://orcid.org/0000-0003-0942-1074>), Dept of Arctic and Marine Biology, Faculty of Biosciences, Fisheries, and Economics, Arctic Univ. of Norway (UiT), Tromsø, Norway. – I. S. Jónsdóttir (<https://orcid.org/0000-0003-3804-7077>), Inst. of Life and Environmental Sciences, Univ. of Iceland, Reykjavik, Iceland.

#### Oikos

129: 1229–1242, 2020

doi: 10.1111/oik.07074

Subject Editor: Eric Seablom

Editor-in-Chief: Dries Bonte

Accepted 18 April 2020



[www.oikosjournal.org](http://www.oikosjournal.org)

In the long-term, herbivores can alter nutrient dynamics in terrestrial ecosystems by changing the functional composition of plant communities. Here, we ask to what extent herbivores can affect plant-community nutrient dynamics in the short-term. We provide theoretical expectations for immediate effects of herbivores on tundra-grassland plant-community nutrient levels throughout a single growing season and empirically evaluate these predictions. We established an experiment within two forb-dominated and two grass-dominated tundra-grassland communities. We selected tundra-patches disturbed by small rodents during the previous winter, and neighbouring undisturbed tundra-patches. Within each tundra-patch, we set up a reindeer-open and a reindeer-exclusion plot. Throughout the summer, we randomly collected over 2800 leaf samples from 34 vascular plant species/genera and analysed their nitrogen and phosphorus contents. Plant-community nutrient levels were consistently higher in tundra-patches affected by small rodents, both across tundra-grassland types and throughout the growing season. Forbs and grasses growing in small-rodent disturbed tundra-patches had 11% and 25% higher nutrient content, respectively, compared to undisturbed tundra-patches. Reindeer affected only grasses growing in grass-dominated tundra-grasslands and the outcome was dependent on small-rodent winter disturbance. Reindeer increased grass nitrogen content in undisturbed tundra-patches (+7%) and weakened the positive effects of small rodents in disturbed tundra-patches (from 25% to 15% higher nutrient content [both nitrogen and phosphorus]). By enhancing plant nutrient levels throughout a single growing season, herbivores were key, immediate modifiers of plant-community nutrient dynamics in tundra-grasslands. Higher nutrient contents still detected in senescent leaves at the end of the summer in herbivore-affected tundra suggest that herbivory is accelerating short-term tundra-grassland nutrient cycling rates. Our findings from tundra-grassland communities align with theoretical expectations of positive herbivore effects on nutrient cycling in relatively productive ecosystems.

© 2020 The Authors. Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos  
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Keywords: near infrared reflectance spectroscopy (NIRS), nitrogen (N), phosphorus (P), plant functional types (PFTs), *Rangifer* (reindeer/caribou), small rodents

---

## Introduction

Mammalian herbivores have long been recognized as fundamental drivers of the nutrient cycling in terrestrial ecosystems worldwide (reviewed by Pastor et al. 2006, Harrison and Bardgett 2008, Sitters and Olde Venterink 2015). In the long-term, herbivores modify the rate of nutrient cycling through several pathways, such as altering plant species composition and thus the quantity and quality of resources returned to the soil, affecting soil physical/chemical properties and/or influencing the movement of nutrients between habitats (McNaughton et al. 1997, Olofsson and Oksanen 2002, Schrama et al. 2013, Stark et al. 2015). The plant nutrient-related traits that contribute to the palatability of foliage can also govern the decomposability of plant litter (Grime et al. 1996, Cornelissen et al. 2004). Perhaps for this reason long-term herbivore-driven changes in ecosystem nutrient cycling of cold, nutrient-limited environments, such as (sub-)Arctic and alpine tundra, can be contingent on herbivore-induced changes in the functional composition of plant communities (reviewed by Stark 2007). Here, long-term herbivory can promote higher abundance of either palatable, nutrient-rich plant species (e.g. forbs and grasses) or less palatable, nutrient-poor plant species (e.g. shrubs), thus either accelerating (Olofsson et al. 2004a, Tuomi et al. 2018) or retarding (Pastor et al. 1993, Grellmann 2002) nutrient-cycling rates. However, it remains an open question whether herbivores can also cause immediate changes in tundra plant-community nutrient levels, indicative of accelerating, neutral or retarding effects on nutrient cycling rates.

There is a set of mechanisms through which herbivores may provoke immediate changes in tundra plant-community nutrient levels. Herbivores may select leaves in early phenological stages and/or more nutritious plants and plant parts (Bråthen and Oksanen 2001, Iversen et al. 2014), thus reducing the overall nutrient status of plant communities. Conversely, herbivores can increase plant-community nutrient levels by returning readily available nutrients to soil through faeces and urine (Bazely and Jefferies 1985). The latter process shortcuts the slower litter-decomposition pathway and enhances soil microbial activity and plant nutrient availability (Stark et al. 2002, Van der Wal et al. 2004). Further, herbivory may induce rapid re-growth of highly-nutritious plant tissue, i.e. keep leaves in younger phenological stages (Chapin 1980, McNaughton 1983, Mysterud et al. 2011). Consequently, one may expect herbivores to either accelerate or retard short-term nutrient-cycling rates in tundra ecosystems depending on the relative strength of these opposing mechanisms, which operate simultaneously in all ecosystems (Bardgett and Wardle 2003).

Phenological development of plants causes plant nutrient levels to change over a growing season. Because newly

emergent leaves in early summer have higher nutrient contents than older, senescing leaves in late summer (Aerts and Chapin 1999), food quality for herbivores declines throughout the growing season (Albon and Langvatn 1992, Mysterud et al. 2011). However, a large variety of plant species, belonging to several plant functional types (PFTs), co-exist in plant communities (sensu Chapin et al. 1996). Nutrient levels vary among PFTs from nutrient-rich forbs, through grasses to the less nutritious shrubs (Cornelissen et al. 2004). Moreover, PFTs at high latitudes are characterized by diverse patterns in phenological development (Iversen et al. 2009), which dictate tundra plant-community nutrient status at a given time. Thus, plant-community nutrient levels vary according to plant-species composition and time of the year, which in turn are likely to mediate the interactions between tundra herbivores and their food sources (Ims and Fuglei 2005, Iversen et al. 2014). In addition, within- and between-season herbivore attraction to a given plant community, i.e. tundra-patch, is likely to be either intensified or diminished if herbivores can increase or decrease, respectively, nutrient contents of dominant plant species (Hik and Jefferies 1990). Therefore, through immediate impacts on plant-community nutrient levels, herbivores may drive spatial and temporal nutrient dynamics of tundra plant communities and manipulate their own food supply, potentially influencing habitat selection of other herbivores.

Tundra ecosystems harbour a range of different-sized mammalian herbivores, which differ in their temporal and spatial displacement (Ims and Fuglei 2005, Ims et al. 2007). Small rodents, such as voles and lemmings, strongly disturb tundra vegetation during their population density peaks, both in summer and winter (Olofsson et al. 2004b, Ims and Fuglei 2005). However, observations conducted during their population heights reveal extreme heterogeneity in small-rodent activity, with some tundra-patches experiencing a much higher disturbance level compared to nearby ones (Hambäck et al. 1998). In contrast, large vertebrates, such as *Rangifer* (reindeer/caribou), may impact the vegetation on a larger spatial and temporal scale through a migratory behaviour (Bernes et al. 2015). The conspicuous mobility of reindeer enable them to locate and utilise highly nutritious vegetation-patches distributed in space and time (Iversen et al. 2014). Studies on how different-sized mammalian herbivores affect the functional composition of tundra plant communities indicate that herbivory may have mixed effects on ecosystem nutrient cycling. Either alone or in combination, small and large herbivores have been shown to benefit sometimes species that accelerate (Olofsson et al. 2001, Van der Wal 2006, Tuomi et al. 2018) and sometimes species that retard (Bråthen and Oksanen 2001, Grellmann 2002, Bråthen et al. 2007, Ravolainen et al. 2011) tundra-ecosystem nutrient dynamics in the long-term. Yet, how do tundra-herbivores modify plant-community nutrient dynamics in the short-term? Here, we assess to what extent herbivore interactions affect tundra plant-community nutrient levels during the short duration of an alpine/sub-Arctic summer.

Tundra-grasslands are suitable systems to test short-term effects of herbivores on plant-community nutrient

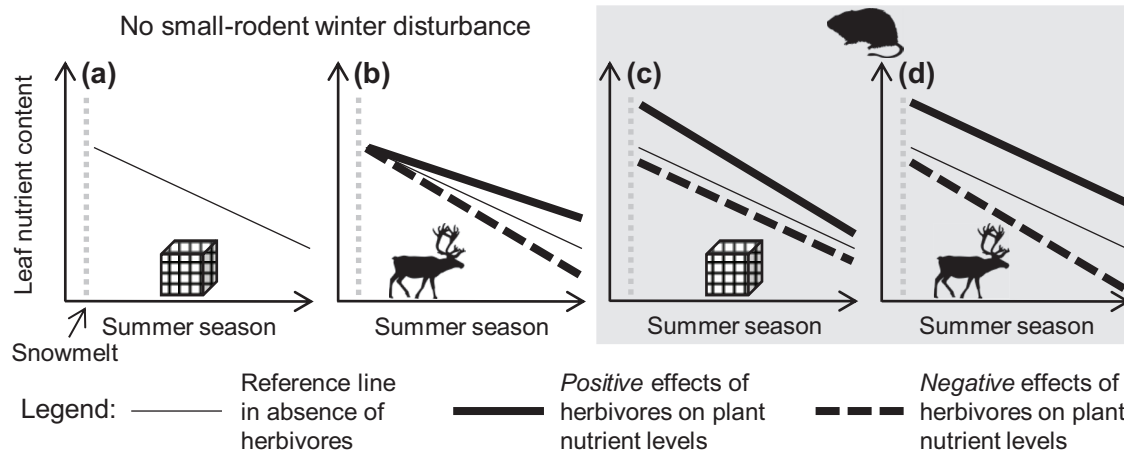


Figure 1. Schematic presentation of the two competing hypotheses addressed in this study. (a) Reference line in absence of herbivores, with plant nutrient levels decreasing along the summer. (b–d) Positive (thick solid lines) or negative (dashed lines) effects of (b) reindeer summer herbivory alone, (c) small-rodent winter disturbance alone and (d) both herbivores together on plant nutrient levels (see main text for details). The reference line in absence of herbivores (thin solid line) is maintained in each panel for an easier comparison with our competing hypotheses.

levels. First, they are characterized by plant species with high nutrient contents (i.e. forbs and grasses), and thus are key hotspots for plant–herbivore interactions (Skarin et al. 2008, Soininen et al. 2013b). Second, tundra-grasslands are characterized by both a long reindeer-grazing history (Hætta et al. 1994) and the ubiquitous presence of small rodents (Ims and Fuglei 2005). We performed an herbivore-interaction experiment during summer in two forb-dominated and two grass-dominated tundra-grasslands in northern Fennoscandia. We excluded reindeer summer herbivory both within and outside tundra-patches that had been disturbed by small rodents during the previous winter. Higher plant-community nutrient levels in the presence of herbivores would suggest that herbivory is accelerating short-term nutrient cycling rates in these tundra-grasslands. Conversely, lower plant-community nutrient levels in the presence of herbivores would indicate that herbivory is retarding short-term tundra-grassland nutrient cycling rates. Given the strong inter- and intra-specific variability of nutrient-related plant traits (Siefert et al. 2015), we sampled all the main species found within tundra-grasslands in our experiment. Moreover, to account for the high intra-specific phenological variation of nutrient-related plant traits (Fajardo and Siefert 2016), we encompassed the whole range of plant-leaf developmental stages by repeatedly sampling throughout the whole growing season.

Given the seasonal component in plant nutrient contents (Aerts and Chapin 1999), we expected that, in absence of herbivores, plant-community nutrient levels will be highest at the beginning of the season and that they will decrease as the summer progresses (Fig. 1a). Based on current theoretical and empirical evidence, we formulated two competing hypotheses for immediate effects of herbivores on tundra-grassland plant-community nutrient levels. By returning nutrients through faeces and urine (Bazely and Jefferies 1985) or by keeping leaves in young phenological stages (Chapin 1980), small-rodent winter disturbance or reindeer summer

herbivory alone will enhance plant-community nutrient levels (Fig. 1b–c – thick solid lines). Alternatively, by removing more nutrient-rich plant species or by selecting more nutritious plant parts (Pastor et al. 1993), either herbivore alone will cause negative plant-community nutrient responses (Fig. 1b–c – dashed lines). Both herbivores together will cause either positive (Fig. 1d – thick solid line) or negative (Fig. 1d – dashed line) plant-community nutrient responses depending on magnitude and direction of their main effects. We expected plant-community nutrient responses to herbivores to be paralleled by responses of the dominant PFTs, i.e. forbs and grasses. The effects of reindeer on plant nutrient levels will grow stronger as the season proceeds, reflecting repeated events of herbivory. Effects of small-rodent winter disturbance, if positive, will instead be mainly visible at the beginning of the summer due to a sudden release of nutrients in the system soon after snowmelt, after which plant-community nutrient dynamics will converge towards those of plant communities not affected by herbivores.

## Methods

### Study area

The study was conducted in the low alpine zone at 300–400 m a.s.l. at Ifjordfjellet (70°27'N, 27°08'E), Finnmark, northern Norway (Fig. 2a) during the summer season of 2015. The annual temperature of the study area in the warmest month (July) ranges from 8.2 to 13.6°C (period 1986–2015), with a mean of 8.6°C in July 2015. Total annual precipitation for the same period ranges from 429 to 704 mm, with 564 mm fallen in 2015 (Norwegian Meteorological Institute, <<http://met.no>>). The bedrock consists of sedimentary rocks, mainly sandstone and mudstone (Geological Survey of Norway, <<http://ngu.no>>). Date of snowmelt varies from early to

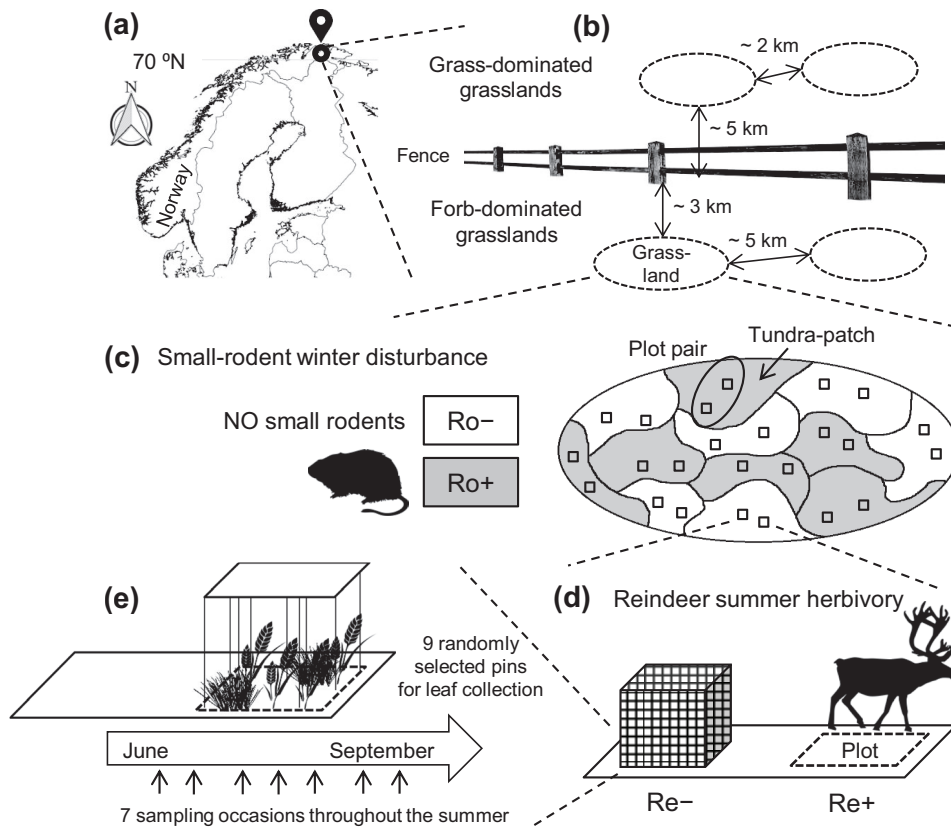


Figure 2. Study and sampling design. (a) Study location, (b–d) hierarchical spatial structure of the study design (four grassland sites [two sites in each of the two grassland types], for a total of 48 plot pairs) and (e) temporal structure of the sampling design adopted for plant leaf collection.

late June. In 2015, our study area was snow-free by the end of June.

The region is mainly characterized by dwarf-shrub heaths (Walker et al. 2005), whereas grasslands typically dominate river plains. A fence was built in 1950s and divided Ifjordfjellet in spring/fall migratory and summer pasture ranges for semi-domesticated reindeer *Rangifer tarandus tarandus* (Hætta et al. 1994). Historical differences in reindeer herbivory pressure on the two sides of the fence caused a divergence in plant-community composition of grassland communities. Grasslands found in the spring/fall migratory range are forb-dominated, whereas grasslands found in the summer range are grass-dominated. Reindeer faeces counts in permanent plots during the last five years showed that reindeer also utilize forb-dominated grasslands in summer. Yet, a higher reindeer grazing pressure in grass-dominated grasslands was evident throughout the summer season of 2015 (Supplementary material Appendix 1 Fig. A1a). Common plant species across these grasslands are forbs, such as *Alchemilla* spp., *Bistorta vivipara*, *Geranium sylvaticum*, *Rumex acetosa*, *Solidago virgaurea*, *Trollius* spp. and *Viola* spp. along with grasses, such as *Poa* spp., *Calamagrostis phragmitoides*, *Deschampsia cespitosa* and *Nardus stricta*. Plant names follow the Pan-Arctic Flora (<<http://nhm2.uio.no/paf>>).

The semi-domesticated reindeer is the main large herbivorous mammal in the study area, which is encompassed by the

Lågesduotter reindeer herding district, where a density of 4.8 reindeer  $\text{km}^{-2}$  was estimated in summer 2015 (<<https://landbruksdirektoratet.no>>). Along with semi-domesticated reindeer, other wild large herbivores occasionally found in these areas are moose *Alces alces*. The community of medium-sized vertebrate herbivores consists of ptarmigan *Lagopus lagopus* and *L. muta* and hare *Lepus timidus*. Three species of small rodents (tundra vole *Microtus oeconomus*, grey-sided vole *Myodes rufocanus* and Norwegian lemming *Lemmus lemmus*) are active year-round; tundra vole is the species dominating the small-rodent guild in tundra-grasslands (Killengreen et al. 2007).

### Study design

We implemented a full-factorial semi-randomized pair design in which small-rodent winter disturbance was used as a quasi-experimental factor (Shadish et al. 2002) and reindeer summer herbivory as a fully experimental factor. Immediately after snowmelt, we selected two relatively homogeneous grassland sites of about 1  $\text{km}^2$  within each of the two grassland-types (Fig. 2b). Twelve pairs of plots were laid within each grassland site. Six plot-pairs were located in tundra-patches disturbed by small rodents during the previous winter (disturbed tundra-patches: Ro+), whereas the other six plot-pairs were arranged in tundra-patches with no evident signs of

small-rodent disturbance (undisturbed tundra-patches: Ro−) (Fig. 2c). Finally, plots within a pair were randomly assigned to be either reindeer-open (Re+) or reindeer-exclusion (Re−) plots (Fig. 2d). In total, 96 plots were established. The area of each plot was 60 × 60 cm. To exclude reindeer, we used cages made of metal net (70 × 70 cm area × 50 cm height, mesh-size 1.3 × 1.3 cm).

Distance between plots within a pair was maximum 3 m, whilst distance between neighbouring plot-pairs was at least 3 m. Suitability of tundra-patches was evaluated following two criteria: 1) plots within a pair were characterized by similar plant species composition and micro-topographical features, and 2) for Ro+ plot-pairs at least 80% of the plot surface should show signs of winter disturbance by small rodents, whereas for Ro− plot-pairs there should be no visible signs of small-rodent disturbance. Small-rodent winter activity had visibly altered the vegetation in disturbed tundra-patches, where most aboveground plant parts were cut down and found in the form of a litter layer often mixed with soil particles and rodent waste products (Supplementary material Appendix 1 Fig. A2a–b). The extreme heterogeneity in small-rodent winter disturbance observed within our relatively homogeneous grassland sites suggests a rather random fine-scale spatial variation in winter herbivory (Hambäck et al. 1998). Gaps between cages and the ground allowed small rodents to have free access into Re− plots. Small-rodent faeces counts in the permanent plots indicated that the number of small rodents within the study area in early summer 2015 was low, but it increased throughout the growing season at both grassland-types (Supplementary material Appendix 1 Fig. A1b). Small-rodent effects throughout the summer are assumed to be equal in all plots.

### Sampling design, sample analyses and data processing

Leaf sampling was performed within the 96 plots at seven instances (hereafter sampling occasions) from the start to the end of the growing season; on average every  $12 \pm 1.3$  days, between 29 June and 9 September (Supplementary material Appendix 1 Table A1). This sampling design allowed us to encompass the whole range of leaf developmental stages, i.e. from newly emergent leaves soon after snowmelt to old senescent leaves before the first snowfall. Leaf sampling was conducted randomly by using nine pins attached to a metal frame (42 × 46 cm area × 40 cm height) consisting of 50 regularly-distributed pin placements (Fig. 2e, Supplementary material Appendix 1 Fig. A2c). We used a sampling frame smaller than the plot size to minimize possible edge effects. The position of the pins was changed at each sampling occasion, but not the position of the metal frame, and pin placements used in the previous two sampling occasions were excluded from the random selection in order to minimize the possibility of sampling repeatedly the same ramets. The uppermost plant leaf touching each pin was collected. Additional leaves touching the pin were collected whenever the first leaf was not considered to be large enough for nutrient content analyses (a

minimum leaf area of 4 mm in diameter). Since grasses intercept pins more easily than other PFTs (Bråthen and Hagberg 2004) and the aim of the sampling was to obtain a complete spectrum of the plant community composition in our plots, a correction for the Poaceae family was introduced. When Poaceae species were hit by more than two pins, the second uppermost plant leaf was sampled for the consecutive pins as long as it belonged to a species (or genera when the species were not further identified) of a different PFT. The final number of species sampled within a plot at each sampling occasion ranged between a minimum of three and a maximum of nine; on average  $4.3 \pm 1.5$  species. We assume the number of samples collected for a given species or PFT to reflect its relative abundance within our grasslands.

We collected in total 2831 plant leaf samples from 34 species/genera belonging to seven broadly-classified PFTs, i.e. (number of species in brackets) forbs (21), grasses (5), sedges (1), deciduous (2) and evergreen (3) shrubs, rushes (1) and horsetails (1). As a consequence of the random sampling and/or the development of our tundra-grassland communities throughout the summer, the frequency of occurrence of different plant species/genera varied between sampling occasions (Supplementary material Appendix 1 Table A2). During fieldwork, each sample was placed in a tea-filter bag and pressed within 1–10 h after collection by using a plant press. In the lab, all leaf samples were oven-dried flat at 60°C for 48 h within four days of collection and subsequently stored in their original tea-filter bags in a dry and dark place at room temperature.

All samples were analysed for nitrogen (N) and phosphorus (P) contents (% of dry weight – %DW) using near infrared reflectance spectroscopy (NIRS) with a FieldSpec 3 in 350–2500 nm range and equipped with a 4 mm light-adapter for full-leaf scanning. Prior to analysis, plant samples were cleaned from dust particles. Because traces of water can cause distortion in the light absorbance and undermine predictions of leaf elemental contents, samples were oven-dried again at 60°C for 2 h following Smis et al. (2014). Subsequently, samples were cooled down in a desiccator until scanning by NIRS. For species with leaves narrower than 4 mm, leaves were cut and stacked together in order to cover the minimum area needed for analyses. For each plant sample, between 4 and 32 measurements (i.e. scans) were taken (on average  $7 \pm 3.1$  scans), leading to a total of 19 834 spectra. The high variability in the number of scans per sample reflects the variability of both number and size of the leaves constituting that sample. Each sample spectrum was converted to N- and P-content by applying the prediction models based on milled and tableted plant samples (Murguzur et al. 2019) and with correction factors for full leaves (Petit Bon et al. 2020). For each sample, we finally used the median of the replicate scans for data analyses. In total, 63 (2.23% of the data) predicted median values for leaf P-content fell outside the calibration range of our prediction model (range for leaf P-content: 0.04–0.70 %DW; Murguzur et al. 2019). To avoid possible statistical artefacts, these data were excluded from the analyses.

In sampling occasion four (3–5 of August, peak of the growing season), point intercept frequency method (PIM – Bråthen and Hagberg 2004) was performed to assess differences in plant-community composition between forb- and grass-dominated tundra-grasslands. Within each plot, all intercepts between the nine randomly selected pins for leaf sampling and each vascular plant species were counted. Point intercepts for each species were finally converted into above-ground plant biomass ( $\text{g m}^{-2}$ ) following Bråthen and Hagberg (2004) and by using the correlation coefficients in Ravolainen et al. (2010) and Tuomi et al. (2018). A pin density of nine pins per  $0.25 \text{ m}^{-2}$  area (our sampling frame covered  $0.19 \text{ m}^{-2}$  area) is within the recommendations for efficient estimation of plant biomass (Bråthen and Hagberg 2004) and has been utilized in previous studies quantifying tundra-grassland plant-community responses to herbivory (Ravolainen et al. 2011). Soil environmental variables were also measured to characterize forb- and grass-dominated tundra-grasslands. We measured soil moisture within plots throughout the summer. In sampling occasion five (13–15 August), we collected samples of organic soil within plots and assessed their pH and N- and P-content. Plant-species composition, PFT above-ground biomass and soil environmental characteristics for forb- and grass-dominated grasslands are presented in Supplementary material Appendix 1 Table A3, Fig. A3.

### Statistical analysis

Prior to model fitting, data exploration was conducted following standardized protocols (Zuur et al. 2010). In particular, we explored possibly introduced non-random trends in missing observations for leaf P-content. No patterns were identified that could affect the estimates of the models and hence modify our biological conclusions.

### Plant communities

The effect of herbivores on plant-community nutrient levels was evaluated by using linear mixed-effects models (LMMs). We fitted a separate LMM for the two response variables of interest (plant leaf nitrogen [N] and phosphorus [P] contents – %DW), in which the initial full fixed-effects structure included the three-way interaction between ‘small-rodent winter disturbance’ (two-level factor: undisturbed [Ro–] and disturbed [Ro+] tundra-patches), ‘reindeer summer herbivory’ (two-level factor: reindeer-exclusion [Re–] and reindeer-open [Re+] plots), and ‘seasonality’ (continuous variable: seven sampling occasions throughout the summer). Given the hierarchical spatial structure of the study design and the fact that the same plant species could be sampled across all plots, both nested and crossed random-effects had to be specified (Baayen et al. 2008). In both LMMs, the study design was entered as nested random factors, with ‘plots’ nested within ‘tundra-patch’, and subsequently nested within ‘grassland site’. ‘Plots’ accounted for both the hierarchical nested design of our study and the repeated measures over the summer. ‘Plant species’ was entered as a crossed random-effect

with the hierarchical nested design. We fitted full random-intercept LMMs and avoided random-slope LMMs to prevent over-parameterization and convergence problems, as suggested by Bates et al. (2015a).

### Plant functional types (PFTs)

Plant-community composition significantly differed between forb- and grass-dominated tundra-grasslands (Supplementary material Appendix 1 Fig. A3 and Supplementary material Appendix 3), and thus the effects of herbivores on PFT nutrient levels were evaluated separately for the two grassland-types. We analysed the data obtained for forbs and grasses (over 91% of the collected plant leaf samples). Results for sedges and deciduous shrubs (6.7% of the samples), for which sample sizes did not allow full model fitting, are presented in Supplementary material Appendix 1 Table A4, A5, Fig. A4, A5. Evergreen shrubs, rushes and horsetails (2% of the samples) were not analysed statistically because of too small sample sizes for model fitting (summary statistics for these PFTs are given in Supplementary material Appendix 1 Table A6). We fitted a separate LMM for forb- and grass-dominated grasslands and for the two response variables of interest (leaf N and P – %DW). We avoided a direct statistical comparison between forb- and grass-dominated grasslands given only two grassland sites within each grassland-type. We first created full LMMs with a basic fixed-effects structure including the four-way interaction between ‘PFT’ (two-level factor: forbs and grasses), ‘small-rodent winter disturbance’, ‘reindeer summer herbivory’ and ‘seasonality’. ‘Site’ (two-level factor) was technically considered as random-effect, but incorporated as additive fixed-effect in the models since too few levels were available to properly determine its variance component (Bolker et al. 2009). In all full LMMs, which were fitted with random-intercepts only (see above), the study design was entered as nested random factors, with ‘plots’ nested within ‘tundra-patch’. ‘Plant species’ was entered as a crossed random-effect with the hierarchical nested design.

For each LMM, we first selected the better random-effects structure by removing from the models those random terms for which the variance was estimated as zero. We then selected the better fixed-effects structure using likelihood ratio test (model parameters estimated using maximum likelihood – ML). We here only present the results from the most parsimonious LMMs (fitted by restricted ML), for which statistically significant effects were defined by 95% confidence intervals not encompassing 0. We proceeded to model validation by assessing homogeneity of variances in the residuals for the fixed-effects retained in each model and checking for approximate linearity between observed and fitted values. We estimated the significance of the fixed-effects using parametric bootstrapping with 10 000 replicates.

Additional details on statistical analyses are provided in Supplementary material Appendix 3. All statistical analyses were conducted in the R environment ver. 3.6.1 (<www.r-project.org>) with the packages ‘lme4’ (Bates et al. 2015b), ‘emmeans’ (Lenth et al. 2018) and ‘ggplot2’ (Wickham 2016).

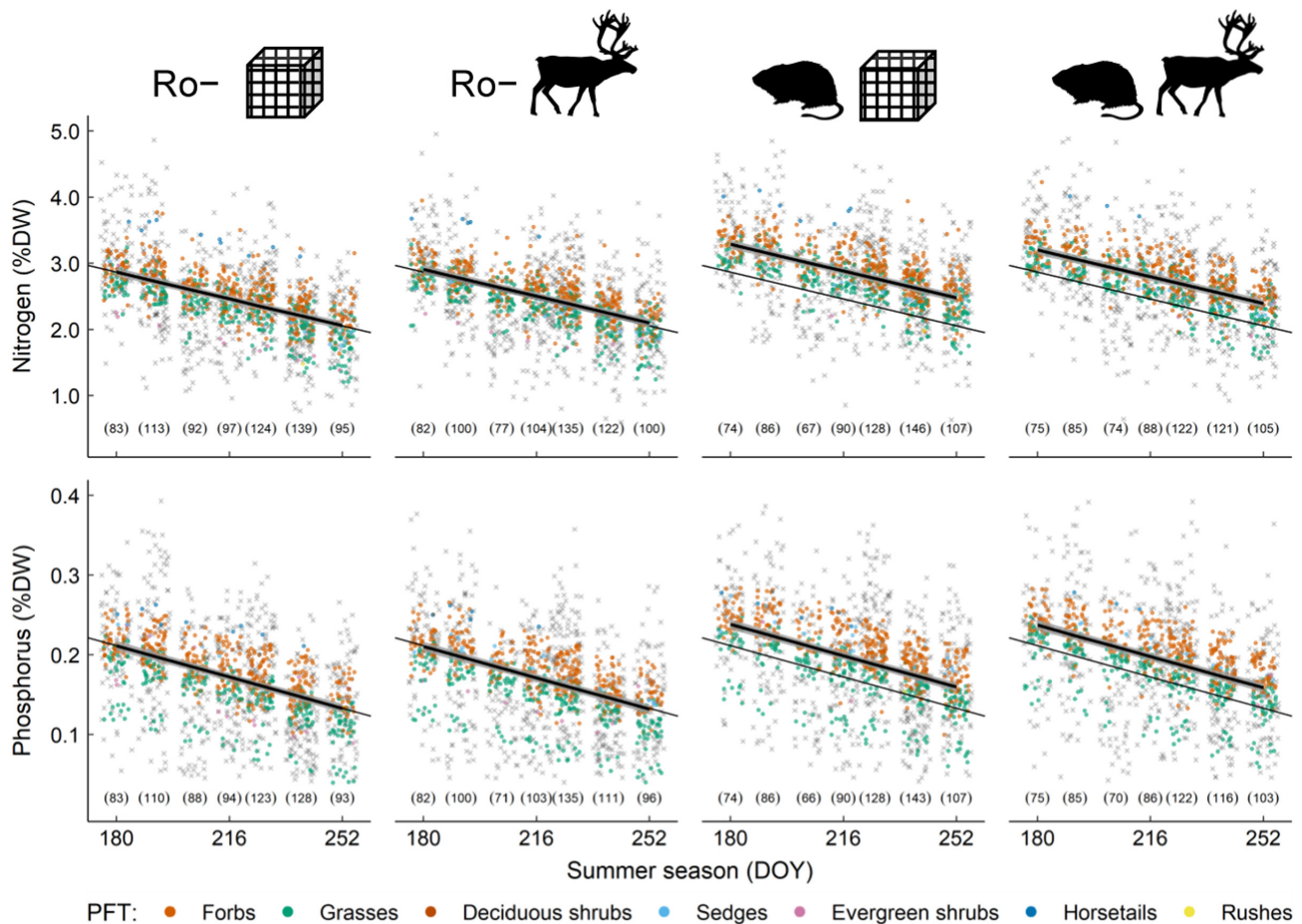


Figure 3. Effects of herbivores on overall tundra-grassland plant-community nutrient levels. Effects of small-rodent winter disturbance, reindeer summer herbivory and seasonality on leaf nitrogen [N] content (upper panel) and leaf phosphorus [P] content (lower panel) (% of dry weight – %DW) in plant communities of tundra-grasslands. Thick lines and bands represent regression lines for the fitted values and their 95% confidence intervals (CIs). Fitted values were acquired from the prediction models on plant-community N- and P-content. The reference line (thin line) in absence of herbivores [Ro-/Re-] is maintained in each panel to facilitate the visualization of the effects of herbivores on plant-community nutrient levels. Coloured dots represent fitted values for each plant leaf sample, whereas grey dots represent raw values. All dots were spaced apart within each of the seven sampling occasions to reduce overlapping. Numbers in parentheses represent the number of plant leaf samples collected at each sampling occasion in each herbivore–treatment combination. Parameter estimates and their CI are provided in Table 1.

## Results

### Plant-community and PFT leaf nutrient levels in absence of herbivores

Plant-community nutrient levels peaked in early summer soon after snowmelt and significantly decreased by the end of the growing season (N-content:  $-28\%$ ; P-content:  $-37\%$ ) (Fig. 3 [Ro-/Re-], Table 1). Forbs and grasses differed in their nutrient contents and dynamics throughout the summer, although a seasonal decrease in nutrient levels characterized both PFTs (Fig. 4, 5 [Ro-/Re-], Table 2, 3). Soon after snowmelt, forbs in forb-dominated grasslands had on average 22% higher N- and P-content compared to grasses (Fig. 4 [Ro-/Re-], Table 2). In grass-dominated grasslands, the difference was similar for N-content, but forbs had 52% higher P-content than grasses (Fig. 5 [Ro-/Re-], Table 3). Although nutrient levels were

consistently higher in forbs, the relative difference in PFT nutrient contents decreased throughout the growing season (significant two-way ‘PFT  $\times$  seasonality’ interactions – Table 2, 3). At the end of the summer, forbs and grasses in forb-dominated grasslands did not significantly differ in their nutrient levels (Fig. 4 [Ro-/Re-]), whereas in grass-dominated grasslands, forbs still had higher nutrient contents (14% and 25% higher N and P, respectively) compared to grasses (Fig. 5 [Ro-/Re-]). Nutrient levels of sedges and deciduous shrubs also significantly decreased throughout the summer (Supplementary material Appendix 1 Table A4, A5, Fig. A4, A5).

### Plant-community leaf-nutrient levels in presence of herbivores

Small-rodent winter disturbance alone significantly increased plant-community N- and P-content of about 16% and this

Table 1. Parameter estimates for linear mixed-effects models for the effects of herbivores on overall tundra-grassland plant-community nutrient levels. Parameter estimates of fixed-effects (Estimates) and their 95% confidence interval (CI – lower and upper bounds) for the most parsimonious models in which predictors are ‘small-rodent winter disturbance’, ‘reindeer summer herbivory’ and ‘seasonality’ and responses are (a) leaf nitrogen [N] content and (b) leaf phosphorus [P] content (% of dry weight – %DW) in plant communities of tundra-grasslands. Intercept is calculated for undisturbed tundra-patches (Ro–), reindeer-exclusion plots (Re–) and first sampling occasion (DOY 180, 29 June). Estimates with bold indicate that their 95% CI does not include 0. Random-effects retained in the final models are presented as standard deviations. Empty cells indicate that a predictor was not statistically significant, thus it was removed from the model. Observations refer to the number of plant leaf samples used in each model. Marginal R<sup>2</sup> represents the variance explained by the model when only fixed-effects are considered, whereas the conditional R<sup>2</sup> represents the variance explained by the model when both fixed- and random-effects are considered.

Fixed-effects (Predictors)	(a) Nitrogen (%DW)		(b) Phosphorus (%DW)	
	Estimates	CI (95%)	Estimates	CI (95%)
(Intercept) [Ro–/Re–/DOY = 180]	<b>2.86***</b>	<b>2.65; 3.07</b>	<b>0.212***</b>	<b>0.193; 0.231</b>
Small-rodent winter disturbance [Ro+]	<b>0.42***</b>	<b>0.34; 0.50</b>	<b>0.0267***</b>	<b>0.020; 0.033</b>
Reindeer summer herbivory [Re+]	0.04	–0.01; 0.10	–0.001	–0.005; 0.003
Seasonality [+1 DOY]	<b>–0.011***</b>	<b>–0.012; –0.010</b>	<b>–0.0011***</b>	<b>–0.0012; –0.0010</b>
Herbivore interaction [Ro+ × Re+]	<b>–0.13**</b>	<b>–0.21; –0.04</b>		
<b>Random-effects</b>		SD		SD
Grassland site		0.12		0.012
Grassland site: Tundra-patch		0.09		0.009
Plant species		0.41		0.029
Residual		0.55		0.056
Observations	2831		2768	
Marginal R <sup>2</sup> /Conditional R <sup>2</sup>	0.162/0.483		0.157/0.373	

\* p < 0.05, \*\* p < 0.01, \*\*\* p < 0.001.

effect was consistent throughout the summer (Fig. 3 [Ro+/Re–], Table 1). Reindeer summer herbivory alone did not significantly affect plant-community nutrient levels. However, reindeer significantly weakened the positive effects of small rodents on plant-community N-content (significant two-way ‘Ro+ × Re+’ interaction – Table 1a). Indeed, both herbivores together significantly increased plant-community N-content of about 13%, i.e. less than small rodents alone (Fig. 3 [cf. Ro+/Re+ and Ro+/Re–]). Such counteractive effect of reindeer on positive plant-nutrient responses induced by small rodents only characterized grass-dominated grasslands, but not forb-dominated grasslands, when the two grassland-types were analysed separately (see below and cf. Fig. 4, 5).

### PFT leaf-nutrient levels in presence of herbivores

Small-rodent winter disturbance had clear effects on PFT nutrient contents. Small rodents alone significantly increased nutrient levels in forbs (about 11% increase in N- and P-content) and even more in grasses (about 25% increase in N- and P-content) (significant two-way ‘PFT × Ro+’ interactions – Table 2, 3). This diminished partially (in grass-dominated grasslands) and completely (in forb-dominated grasslands) the nutrient-level gap between the two PFTs observed in absence of herbivores (Fig. 4, 5 [Ro+/Re–]). Forbs and grasses in small-rodent disturbed tundra-patches of forb-dominated grasslands did not significantly differ in their nutrient levels at any time during the summer (Fig. 4 [Ro+/Re–]). Furthermore, nutrient levels in plants affected by small rodents alone remained consistently higher compared to those in absence of herbivores throughout the entire summer season (Fig. 4, 5 [Ro+/Re–], Table 2, 3). Grasses

in small-rodent disturbed tundra-patches at the end of the summer had on average only a non-significant 5% lower N- and P-content compared to those not affected by herbivores in early summer soon after snowmelt (Fig. 4, 5 [Ro+/Re–]). Similar nutrient responses also characterized forbs and grasses affected by both herbivores in forb-dominated grasslands (Fig. 4 [cf. Ro+/Re+ and Ro+/Re–], Table 2). N-content in sedges and N- and P-content in deciduous shrubs were also significantly increased by small rodents alone (Supplementary material Appendix 1 Table A4, A5, Fig. A4, A5).

Reindeer summer herbivory had weaker and more variable effects than small-rodent winter disturbance. Reindeer did not significantly affect nutrient levels in forbs, but consistently affected those of grasses throughout the entire summer season. However, such effects were only detected in grass-dominated grasslands and were found to be dependent on small-rodent winter disturbance (significant three-way ‘PFT × Ro+ × Re+’ interactions – Table 3). In undisturbed tundra-patches, reindeer significantly increased grass N-content by 7% (Fig. 5 [Ro–/Re+], Table 3a). In contrast, in disturbed tundra-patches, reindeer significantly weakened the positive effects of small rodents by reducing grass N- and P-content of about 10% compared to small-rodent disturbed/reindeer-exclusion plots (Fig. 5 [cf. Ro+/Re+ and Ro+/Re–], Table 3). Yet, grasses affected by both herbivores still had a significant 15% higher N- and P-content than grasses not affected by herbivores (Fig. 5 [Ro+/Re+]). A similar counteractive effect of reindeer summer herbivory when acting in small-rodent disturbed tundra-patches was also observed for leaf N-content in deciduous shrubs, whereas reindeer alone did not affect nutrient levels in either deciduous shrubs or sedges (Supplementary material Appendix 1 Table A4, A5, Fig. A4, A5).



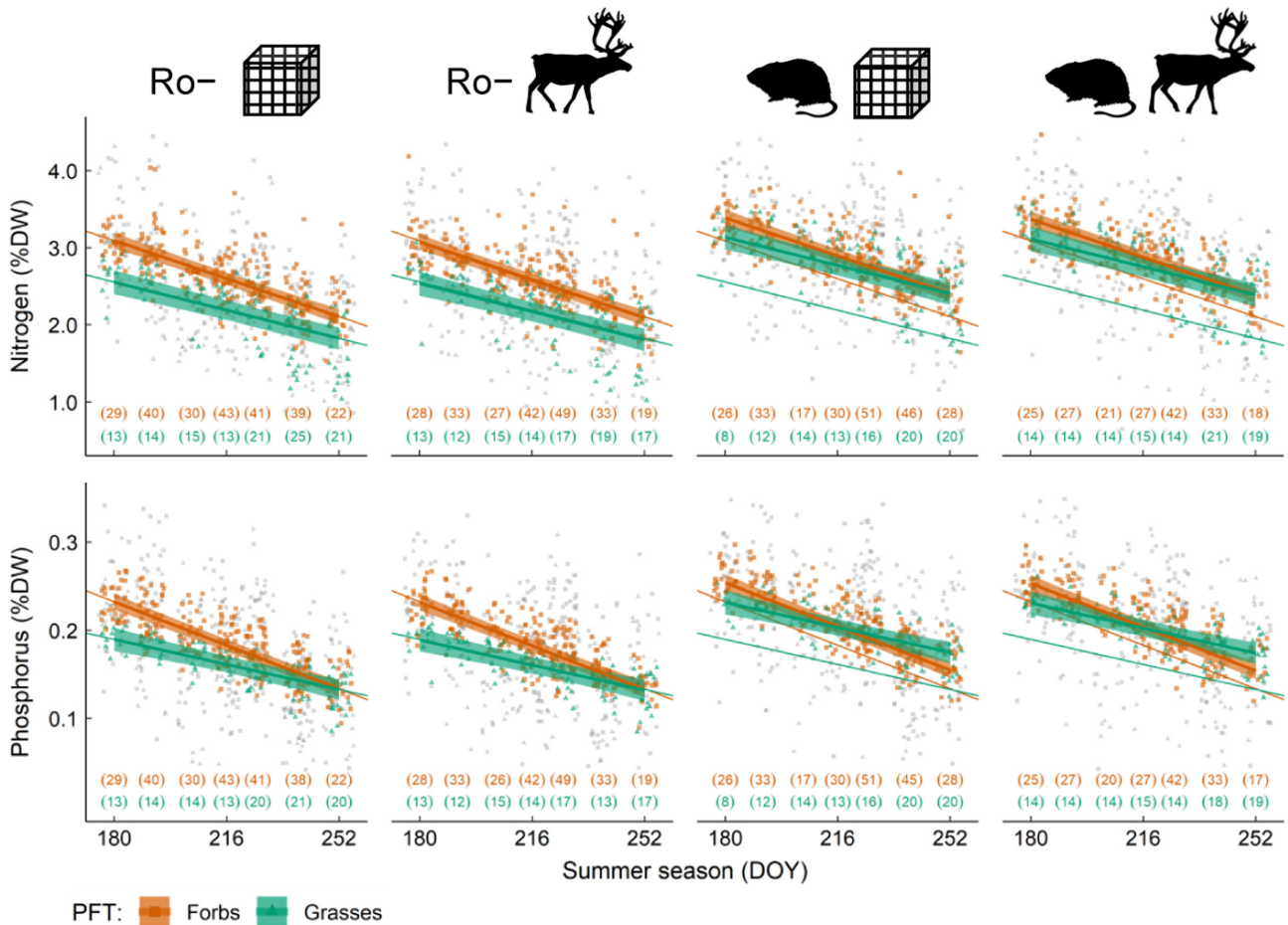


Figure 4. Effects of herbivores on plant functional type (PFT) nutrient levels in forb-dominated tundra-grasslands. Effects of small-rodent winter disturbance, reindeer summer herbivory and seasonality on leaf nitrogen [N] content (upper panel) and leaf phosphorus [P] content (lower panel) (% of dry weight – %DW) in forbs and grasses. Fitted values were acquired from the prediction models on PFT N- and P-content in forb-dominated grasslands. The reference lines (thin lines) are given separately for forbs and grasses. Description of graph content is provided in Fig. 3. Parameter estimates and their CI are provided in Table 2.

## Discussion

Based on current theoretical/empirical evidence, we hypothesized that mammalian herbivores could have either positive or negative short-term effects on tundra-grassland plant-community nutrient levels. The key result of this study is that tundra-grassland communities responded to herbivores with an increase in their N and P levels. Contrary to our predictions, we found that these positive effects of herbivores were temporally consistent throughout the summer and higher nutrient levels were still detected in senescent leaves at the onset of the winter period. This demonstrates that herbivores act as positive, short-term modifiers of tundra-grassland plant-community nutrient dynamics, potentially accelerating short-term nutrient cycling rates by enhancing plant nutrient levels. As expected, these immediate, positive plant-community nutrient responses to herbivores paralleled those of the dominant, nutrient-rich PFTs, i.e. forbs and grasses. Overall, our findings from tundra-grasslands align with theoretical

expectations of positive herbivore effects on nutrient cycling in relatively productive ecosystems.

In our study, tundra-plant N- and P-content were assessed within one growing season and significant community-level nutrient responses to herbivores were readily detected. By using near infrared reflectance spectroscopy (NIRS) methodology, we were able to assess plant nutrient contents at the bite-size level of the herbivores, ultimately providing precise estimates of herbivore-induced nutrient-level changes at the plant-community level. We are not aware of other studies from tundra ecosystems that report such fine-scale estimates for plant nutrient responses to herbivores at the level of the whole plant community. However, previous field-based studies focusing on the most abundant plant species and/or PFTs within tundra-grasslands have typically found little or no effects of herbivore activities on plant nutrient contents (Van der Wal et al. 2004, Mysterud et al. 2011, Barthelemy et al. 2015). These studies used methods that required merging several leaves together in order to obtain enough plant

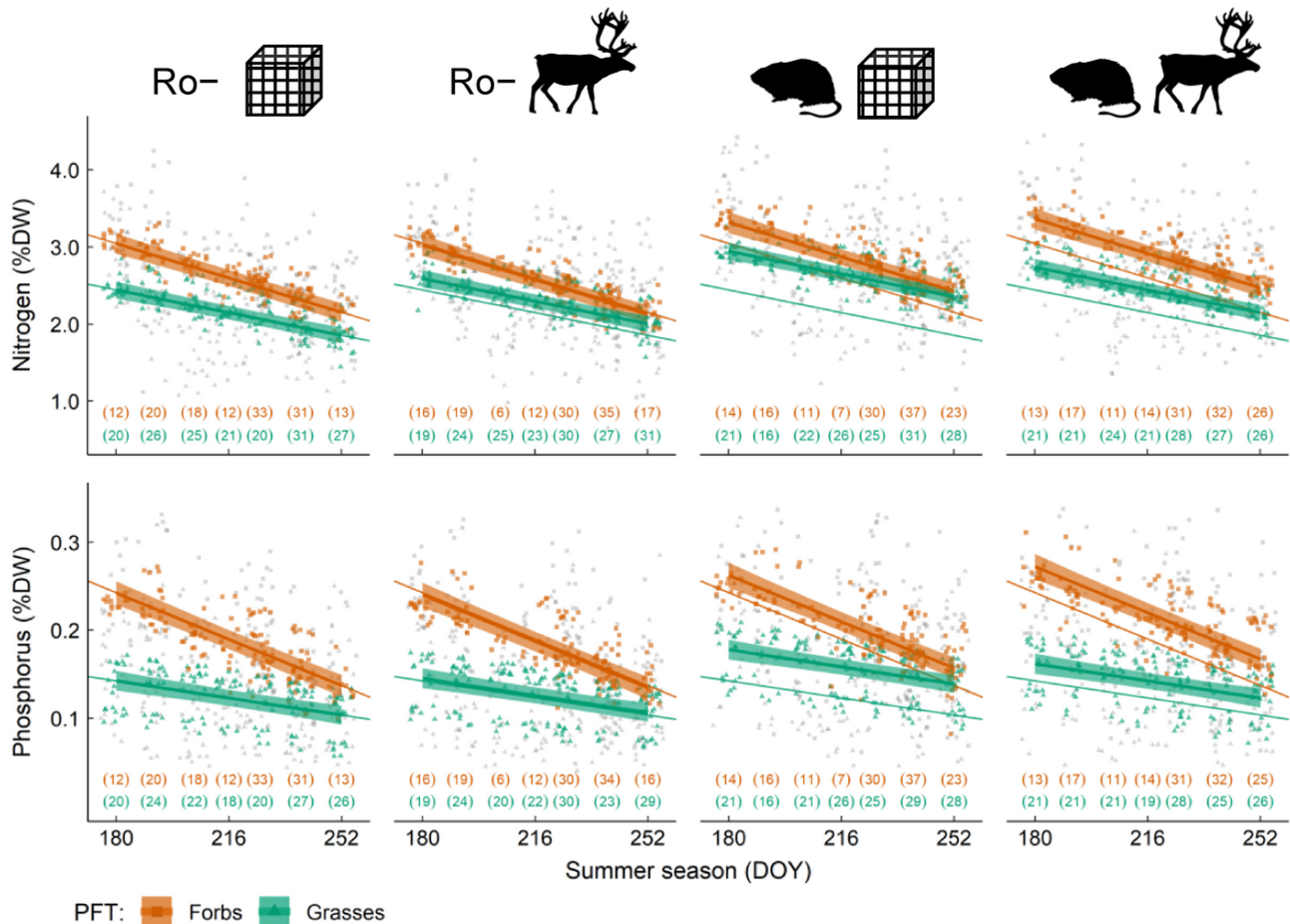


Figure 5. Effects of herbivores on plant functional type (PFT) nutrient levels in grass-dominated tundra-grasslands. Effects of small-rodent winter disturbance, reindeer summer herbivory and seasonality on leaf nitrogen [N] content (upper panel) and leaf phosphorus [P] content (lower panel) (% of dry weight – %DW) in forbs and grasses. Fitted values were acquired from the prediction models on PFT N- and P-content in grass-dominated grasslands. The reference lines (thin lines) are given separately for forbs and grasses. Description of graph content is provided in Fig. 3. Parameter estimates and their CI are provided in Table 3.

material for analyses. Given the high variability in plant nutrient-related traits within and among plant individuals (Siefert et al. 2015), pooling leaves together may thus have hampered the detection of plant nutrient responses to herbivores. NIRS methodology allowed us to quantify nutrient contents of single leaves (Petit Bon et al. 2020) for all the main species found in our grasslands and to properly incorporate such level of detail into our analyses. For the first time, we show that tundra-grassland nutrient dynamics are considerably modified by mammalian herbivores and that this can occur at a much shorter time-scale than previously revealed.

Effects of small-rodent winter disturbance were greater than effects of reindeer summer herbivory. Small-rodent activity in winter may have increased nutrient availability for soil and plant compartments in spring by providing animal-excreta, which are rich in labile nutrients (Bazely and Jefferies 1985). Soon after snowmelt, higher nutrient availability in disturbed tundra-patches may have stimulated soil microbial activity (Van der Wal et al. 2004), nutrient mineralization (Olofsson et al. 2004a) and ultimately plant nutrient acquisition (Hik and

Jefferies 1990, Olofsson et al. 2004a). Yet, contrary to our expectation that a positive effect of small-rodent winter disturbance would dampen as the summer proceeded, plant-community nutrient levels in disturbed tundra-patches were consistently higher than in undisturbed ones across the entire growing season. Tundra-grasslands have a prominent accumulation of snow during winter and a large amount of water is released into the system in spring during snowmelt. Large inputs of water early in the season, combined with high soil moisture levels throughout the summer, may have promoted both a gradual release of nutrients from small-rodent waste products (Van der Wal et al. 2004) and the maintenance of high microbial activity throughout the growing season (Illeris et al. 2003). These findings show that, within tundra-grasslands, intense and localised small-rodent activities occurring outside the growing season can induce immediate, positive plant-community nutrient responses lasting an entire summer season. This, in turn, could accelerate litter decay rate via change in litter quality (Quested et al. 2003), eventually enhancing soil process rates and nutrient turnover in tundra-grasslands.

Table 2. Parameter estimates for linear mixed-effects models for the effects of herbivores on plant functional type (PFT) nutrient levels in forb-dominated tundra-grasslands. Parameter estimates of fixed-effects (Estimates) and their 95% confidence interval (CI – lower and upper bounds) for the most parsimonious models in which predictors are ‘PFT’, ‘small-rodent winter disturbance’, ‘reindeer summer herbivory’ and ‘seasonality’ and responses are (a) leaf nitrogen [N] content and (b) leaf phosphorus [P] content (% of dry weight – %DW). Intercepts are calculated for forbs, undisturbed tundra-patches (Ro–), reindeer-exclusion plots (Re–) and first sampling occasion (DOY 180, 29 June), separately for the two forb-dominated grassland sites (conventionally named site A and B) since site (technically considered as random-effect) was retained in the final model (see ‘Statistical analysis’ for details). Estimates with bold indicate that their 95% CI does not include 0. Random-effects retained in the final models are presented as SD. Empty cells indicate that a predictor was not statistically significant, thus it was removed from the model. Observations refer to the number of plant leaf samples used in each model. Marginal R<sup>2</sup> represents the variance explained by the model when only fixed-effects are considered, whereas the conditional R<sup>2</sup> represents the variance explained by the model when both fixed- and random-effects are considered.

Fixed-effects (Predictors)	(a) Nitrogen (%DW)		(b) Phosphorus (%DW)	
	Estimates	CI (95%)	Estimates	CI (95%)
(Intercept site A) [Forbs/Ro–/Re–/DOY = 180]	<b>2.99***</b>	<b>2.75; 3.23</b>	<b>0.223***</b>	<b>0.208; 0.239</b>
(Intercept site B) [Forbs/Ro–/Re–/DOY = 180]	<b>3.24***</b>	<b>2.99; 3.48</b>	<b>0.242***</b>	<b>0.226; 0.257</b>
Plant functional type (PFT) [grasses]	<b>–0.60*</b>	<b>–1.10; –0.10</b>	<b>–0.047***</b>	<b>–0.073; –0.020</b>
Small-rodent winter disturbance [Ro+]	<b>0.30***</b>	<b>0.18; 0.42</b>	<b>0.021***</b>	<b>0.009; 0.032</b>
Reindeer summer herbivory [Re+]	–0.02	–0.08; 0.04	–0.001	–0.007; 0.005
Seasonality [+1 DOY]	<b>–0.014***</b>	<b>–0.015; –0.012</b>	<b>–0.0014***</b>	<b>–0.0015; –0.0012</b>
PFT and Small rodents interaction [Grasses×Ro+]	<b>0.28***</b>	<b>0.15; 0.41</b>	<b>0.022***</b>	<b>0.009; 0.035</b>
PFT and Seasonality interaction [Grasses×DOY]	<b>0.004*</b>	<b>0.001; 0.006</b>	<b>0.0006***</b>	<b>0.0003; 0.0009</b>
<b>Random-effects</b>		SD		SD
Grassland site: Tundra-patch		0.11		0.011
PFT: Plant species		0.44		0.018
Residual		0.55		0.055
Observations		1342		1321
Marginal R <sup>2</sup> /Conditional R <sup>2</sup>		0.236/0.543		0.229/0.329

\* p<0.05, \*\* p<0.01, \*\*\* p<0.001.

Table 3. Parameter estimates for linear mixed-effects models for the effects of herbivores on plant functional type (PFT) nutrient levels in grass-dominated tundra-grasslands. Parameter estimates of fixed-effects (Estimates) and their 95% confidence interval (CI – lower and upper bounds) for the most parsimonious models in which predictors are ‘PFT’, ‘small-rodent winter disturbance’, ‘reindeer summer herbivory’ and ‘seasonality’ and responses are (a) leaf nitrogen [N] content and (b) leaf phosphorus [P] content (% of dry weight – %DW). Intercept is calculated for forbs, undisturbed tundra-patches (Ro–), reindeer-exclusion plots (Re–) and first sampling occasion (DOY 180, 29 June). Estimates with bold indicate that their 95% CI does not include 0. Random-effects retained in the final models are presented as standard deviations. Empty cells indicate that a predictor was not statistically significant, thus it was removed from the model. Observations refer to the number of plant leaf samples used in each model. Marginal R<sup>2</sup> represents the variance explained by the model when only fixed-effects are considered, whereas the conditional R<sup>2</sup> represents the variance explained by the model when both fixed- and random-effects are considered.

Fixed-effects (Predictors)	(a) Nitrogen (%DW)		(b) Phosphorus (%DW)	
	Estimates	CI (95%)	Estimates	CI (95%)
(Intercept) [Forbs/Ro–/Re–/DOY = 180]	<b>3.01***</b>	<b>2.83; 3.20</b>	<b>0.241***</b>	<b>0.220; 0.262</b>
Plant functional type (PFT) [Grasses]	<b>–0.58***</b>	<b>–0.88; –0.29</b>	<b>–0.099***</b>	<b>–0.135; –0.062</b>
Small-rodent winter disturbance [Ro+]	<b>0.29***</b>	<b>0.14; 0.43</b>	<b>0.021**</b>	<b>0.006; 0.036</b>
Reindeer summer herbivory [Re+]	–0.02	–0.14; 0.11	–0.002	–0.015; 0.010
Seasonality [+1 DOY]	<b>–0.013***</b>	<b>–0.015; –0.010</b>	<b>–0.0015***</b>	<b>–0.0017; –0.0013</b>
PFT and Small rodents interaction [Grasses×Ro+]	<b>0.21*</b>	<b>0.04; 0.39</b>		
PFT and Reindeer interaction [Grasses×Re+]	<b>0.16*</b>	<b>0.0001; 0.33</b>		
PFT and Seasonality interaction [Grasses×DOY]	<b>0.004**</b>	<b>0.002; 0.007</b>	<b>0.0010***</b>	<b>0.0007; 0.0012</b>
PFT, Small rodents and Reindeer interaction [Grasses×Ro+×Re+]	<b>–0.41***</b>	<b>–0.65; –0.17</b>	<b>–0.031*</b>	<b>–0.055; –0.006</b>
<b>Random-effects</b>		SD		SD
Grassland site: Tundra-patch		0.09		0.009
PFT: Plant species		0.22		0.029
Residual		0.53		0.053
Observations		1242		1204
Marginal R <sup>2</sup> /Conditional R <sup>2</sup>		0.236/0.362		0.294/0.470

\* p<0.05, \*\* p<0.01, \*\*\* p<0.001.

Grasses responded more strongly than forbs to small-rodent winter disturbance in both grassland-types. Notably, in forb-dominated tundra-grasslands, small-rodent winter disturbance increased N- and P-content of grasses to the level of forbs. In grass-dominated grasslands, grasses, but not forbs, responded to reindeer summer herbivory, although here nutrient levels of grasses never reached those of forbs. Forbs and grasses are fast-growing and productive PFTs (Aerts and Chapin 1999) and the fact that both would show short-term nutrient responses to herbivores could be expected. However, graminoids can have higher nutrient absorption rates compared to forbs (Hong et al. 2018) and they have been found to respond more rapidly than other PFTs in nutrient amendment and mammalian excreta-addition experiments from the tundra (Grellmann 2002, Barthelemy et al. 2015). Thus, grasses may have been able to absorb a relatively higher proportion of nutrients released from herbivore waste products compared to forbs. Moreover, graminoids, but not forbs, have basal meristems in their leaves causing leaf rejuvenation following herbivory (McNaughton 1983). This mechanism is likely to affect nutrient dynamics within grass individuals, and could have contributed to the higher responsiveness of grasses compared to forbs. Yet, despite grasses had a relatively higher increase in N- and P-content compared to forbs in response to herbivory, nutrient levels in grasses never exceeded those of forbs. Overall, the nourishing state of our tundra-grassland communities was consistently increased by short-term herbivore activities.

Reindeer summer herbivory affected only grasses growing in grass-dominated tundra-grasslands. We see two main reasons for this. First, reindeer grazing pressure throughout the summer in forb-dominated grasslands may have not been high enough to cause immediate nutrient responses of grasses. Second, different species composition of the community of grasses in the two grassland-types could have resulted in these different responses. Grass-dominated grasslands were dominated by grass species that are high in silica content (i.e. silica-rich grasses), whereas silica-poor grasses were the most abundant in forb-dominated grasslands. Reindeer select for palatable, silica-poor grass species, thus reducing their abundance in tundra plant communities (Bråthen and Oksanen 2001, Bråthen et al. 2007). On the other hand, plant communities dominated by unpalatable, silica-rich grasses are maintained by reindeer summer herbivory (Bråthen et al. 2007, Ravolainen et al. 2011), suggesting that high silica levels may confer a competitive advantage to these grass species in the presence of herbivores (Soininen et al. 2013a). Here, we show that grass communities with dominance of silica-rich grass species can increase their nutrient levels in response to reindeer summer herbivory. This could be another potential mechanism under which these communities thrive.

As part of our theoretical/empirical framework, we hypothesised that the impact of both herbivores together on plant-community nutrient levels would reflect the magnitude and direction of the effects of either herbivore alone. In contrast to this prediction, reindeer herbivory in grass-dominated tundra-grasslands partly counteracted the positive effects

of small rodents on grass nutrient levels, but it increased grass N-content in undisturbed tundra-patches. Although grass nutrient levels were still largely higher in the presence of both herbivores than in their absence, these results suggest that diverse plant–reindeer interactions can arise in tundra-patches that differ in their initial nutrient status. The mechanisms behind these opposing grass nutrient responses could not be identified directly in our study, and manipulative experiments able to disentangle under which conditions either negative or positive effects of reindeer prevail would be needed. However, one possible explanation might lie in that the net effect of herbivores on plant-community nutrient levels is often determined by the subtle balance between selective grazing and nutrient return to forage species through animal-excreta (Pastor et al. 2006, Harrison and Bardgett 2008). Ruminants are highly selective towards plant individuals with high nutrient contents (White 1983), and reindeer show preferences for nutrient-rich vegetation-patches across the tundra landscape (Iversen et al. 2014). Higher plant-community nutrient levels promoted by small rodents may have intensified reindeer grazing in disturbed tundra-patches relatively to undisturbed ones, causing the removal of highly-nutritious grass parts. Here, more intense and selective grazing may have outbalanced the immediate return of nutrients to the system through faeces and urine (Pastor et al. 1993), thus lowering grass nutrient contents. In undisturbed tundra-patches, conversely, a lower grazing intensity may have promoted a larger nutrient investment in leaf re-growth (Chapin 1980, McNaughton 1983), thus enhancing grass nutrient contents. As disturbed and undisturbed tundra-patches alternate within a few meters, and reindeer actively move across their feeding landscape (Iversen et al. 2014), a reindeer-mediated transfer of nutrients was likely to be maintained across tundra-patches throughout the growing season, as has already been suggested (Stark et al. 2015). Irrespective of the underlying mechanisms, our results clearly show that, within grass-dominated tundra-grasslands, interactions between winter and summer herbivory can lead to the formation of a mosaic of tundra-patches that differ in their nutrient-level states and that persist till the end of the summer season. In turn, such patchiness in landscape nutrient distribution could have important consequences for the spatial heterogeneity of ecosystem process rates within tundra-grasslands.

## Conclusions

Nutrient limitation of terrestrial ecosystems is globally distributed (Elser et al. 2007, LeBauer and Treseder 2008). Hence, any factors that modify nutrient cycling rates may have significant effects on processes and functions of terrestrial environments. Insights into the drivers of tundra nutrient cycling are of particular concern given the fast changes high-latitude ecosystems are experiencing, both in their biotic and abiotic components. However, N- and P-content in plants are costly measures to attain and they are seldom reported in ecological studies with sufficient resolution to be useful explanatory

variables of underlying ecological processes. By using NIRS, which allowed us to process a large amount of samples, thus working at the plant-community level, this study demonstrated a breakthrough in the assessment of short-term effects of plant–herbivore interactions on tundra-grassland nutrient dynamics.

Overall, we show that herbivores cause immediate, positive changes in tundra-grassland plant-community N and P levels by enhancing leaf nutrient contents of the dominant, nutrient-rich PFTs, i.e. forbs and grasses. Considering the long-term grazing history characterizing our tundra-grassland communities, these PFTs are also the ones that have been promoted here by several decades of herbivory. Thus, our short-term findings indicate that forbs and grasses are currently having positive nutrient-level responses to herbivore activities in these tundra-grasslands, which align with theoretical expectations of positive herbivore effects on nutrient cycling in relatively productive ecosystems, when dominant, nutrient-rich PFTs benefit from herbivory (Bardgett and Wardle 2003).

### Data accessibility

Data and R script are available via DataVerseNO UiT Open Research Data Repository <<https://doi.org/10.18710/XCEXJ1>>.

*Acknowledgements* – We are grateful to Freja Fagerholm, Victor Toscani, Torunn Moe and Francisco Murguzur for help with field assistance and Hanna Böhner for providing continuous updates on NIRS calibration models. We are also grateful to Michele Carbognani and Nigel Yoccoz for precious advice during the preliminary data analyses and Alessandro Petraglia for useful discussions during the preparation of this manuscript. Finally, we thank the leader of the reindeer herding district for being positive to the study. This work is part of the Tall Shrub Tundra module of the Climate ecological Observatory in the Arctic Tundra (COAT, <<http://coat.no>>).

*Conflicts of interest* – There are no conflicts of interest to declare.

*Author contributions* – KAB conceived the idea with contributions from MPB, KGI and TAU, and all four collected the data. MPB analysed the data and wrote the manuscript with contributions from KAB, ISJ, TAU and KGI. EMS provided and interpreted data concerning small-rodent and reindeer dynamics at our study area. ISJ and KAB financed the study through their research grants. All authors read the manuscript and approved the final version for publication.

### References

- Aerts, R. and Chapin, F. S. 1999. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. – *Adv. Ecol. Res.* 30: 1–67.
- Albon, S. D. and Langvatn, R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. – *Oikos* 65: 502–513.
- Baayen, R. H. et al. 2008. Mixed-effects modeling with crossed random effects for subjects and items. – *J. Mem. Lang.* 59: 390–412.
- Bardgett, R. D. and Wardle, D. A. 2003. Herbivore-mediated linkages between aboveground and belowground communities. – *Ecology* 84: 2258–2268.
- Barthelemy, H. et al. 2015. Strong responses of subarctic plant communities to long-term reindeer feces manipulation. – *Ecosystems* 18: 740–751.
- Bates, D. et al. 2015a. Parsimonious mixed models. – arXiv:1506.04967v2 [stat.ME].
- Bates, D. et al. 2015b. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Bazely, D. R. and Jefferies, R. L. 1985. Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. – *J. Appl. Ecol.* 22: 693–703.
- Bernes, C. et al. 2015. What are the impacts of reindeer/caribou (*Rangifer tarandus* L.) on arctic and alpine vegetation? A systematic review. – *Environ. Evid.* 4: 4.
- Bolker, B. M. et al. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. – *Trends Ecol. Evol.* 24: 127–135.
- Bråthen, K. A. and Oksanen, J. 2001. Reindeer reduce biomass of preferred plant species. – *J. Veg. Sci.* 12: 473–480.
- Bråthen, K. A. and Hagberg, O. 2004. More efficient estimation of plant biomass. – *J. Veg. Sci.* 15: 653–660.
- Bråthen, K. A. et al. 2007. Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. – *Ecosystems* 10: 773–789.
- Chapin, F. S. 1980. Nutrient allocation and responses to defoliation in tundra plants. – *Arct. Alp. Res.* 12: 553–563.
- Chapin, F. S. et al. 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. – *J. Veg. Sci.* 7: 347–358.
- Cornelissen, J. H. C. et al. 2004. Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. – *Funct. Ecol.* 18: 779–786.
- Elser, J. J. et al. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. – *Ecol. Lett.* 10: 1135–1142.
- Fajardo, A. and Siefert, A. 2016. Phenological variation of leaf functional traits within species. – *Oecologia* 180: 951–959.
- Grellmann, D. 2002. Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. – *Oikos* 98: 190–204.
- Grime, J. P. et al. 1996. Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. – *Oikos* 77: 489–494.
- Hætta, J. I. et al. 1994. Reindriften i Finnmark: lovgivning og distriktsinndeling. – Reindriftsadministrasjonen, Alta, in Norwegian.
- Hambäck, P. A. et al. 1998. Winter herbivory by voles during a population peak: the relative importance of local factors and landscape pattern. – *J. Anim. Ecol.* 67: 544–553.
- Harrison, K. A. and Bardgett, R. D. 2008. Impacts of grazing and browsing by large herbivores on soils and soil biological properties. – In: Gordon, I. J. and Prins, H. H. T. (eds), *The ecology of browsing and grazing*. Springer, pp. 201–216.
- Hik, D. S. and Jefferies, R. L. 1990. Increases in the net aboveground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. – *J. Ecol.* 78: 180–195.
- Hong, J. et al. 2018. Which root traits determine nitrogen uptake by alpine plant species on the Tibetan Plateau? – *Plant Soil* 424: 63–72.

- Illeris, L. et al. 2003. Soil plus root respiration and microbial biomass following water, nitrogen and phosphorus application at a high arctic semi desert. – *Biogeochemistry* 65: 15–29.
- Ims, R. A. and Fuglei, E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. – *BioScience* 55: 311–322.
- Ims, R. A. et al. 2007. Can reindeer overabundance cause a trophic cascade? – *Ecosystems* 10: 607–622.
- Iversen, M. et al. 2009. Predictors of plant phenology in a diverse high-latitude alpine landscape: growth forms and topography. – *J. Veg. Sci.* 20: 903–915.
- Iversen, M. et al. 2014. Phenology and cover of plant growth forms predict herbivore habitat selection in a high latitude ecosystem. – *PLoS One* 9: e100780.
- Killengreen, S. T. et al. 2007. Structural characteristics of a low Arctic tundra ecosystem and the retreat of the Arctic fox. – *Biol. Conserv.* 135: 459–472.
- LeBauer, D. S. and Treseder, K. K. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. – *Ecology* 89: 371–379.
- Lenth, R. et al. 2018. emmeans: estimated marginal means, aka least-squares means. – R package ver. 1.4.5. <<https://cran.r-project.org/web/packages/emmeans/index.html>>.
- McNaughton, S. 1983. Compensatory plant growth as a response to herbivory. – *Oikos* 40: 329–336.
- McNaughton, S. J. et al. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. – *Science* 278: 1798–1800.
- Murguzur, F. J. A. et al. 2019. Towards a global arctic-alpine model for near-infrared reflectance spectroscopy (NIRS) predictions of foliar nitrogen, phosphorus and carbon content. – *Sci. Rep.* 9: 8259.
- Mysterud, A. et al. 2011. Plant quality, seasonality and sheep grazing in an alpine ecosystem. – *Basic Appl. Ecol.* 12: 195–206.
- Olofsson, J. and Oksanen, L. 2002. Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. – *Oikos* 96: 507–515.
- Olofsson, J. et al. 2001. Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. – *Ecography* 24: 13–24.
- Olofsson, J. et al. 2004a. Reindeer influence on ecosystem processes in the tundra. – *Oikos* 105: 386–396.
- Olofsson, J. et al. 2004b. Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. – *Oikos* 106: 324–334.
- Pastor, J. et al. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. – *Ecology* 74: 467–480.
- Pastor, J. et al. 2006. The roles of large herbivores in ecosystem nutrient cycles. – In: Danell, K. et al. (eds), *Large herbivore ecology: ecosystem dynamics and conservation*. Cambridge Univ. Press, pp. 289–325.
- Petit Bon, M. et al. 2020. One leaf for all: chemical traits of single leaves measured at the leaf surface using near infrared-reflectance spectroscopy (NIRS). – *Methods Ecol. Evol.* <<https://doi.org/10.1111/2041-210X.13432>>
- Quested, H. M. et al. 2003. Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasite. – *Ecology* 84: 3209–3221.
- Ravolainen, V. T. et al. 2010. Additive partitioning of diversity reveals no scale-dependent impacts of large ungulates on the structure of tundra plant communities. – *Ecosystems* 13: 157–170.
- Ravolainen, V. T. et al. 2011. Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. – *Basic Appl. Ecol.* 12: 643–653.
- Schrama, M. et al. 2013. An integrated perspective to explain nitrogen mineralization in grazed ecosystems. – *Perspect. Plant Ecol. Evol. Syst.* 15: 32–44.
- Shadish, W. R. et al. 2002. *Experimental and quasi-experimental designs for generalized causal inference*. – Cengage Learning.
- Siefert, A. et al. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. – *Ecol. Lett.* 18: 1406–1419.
- Sitters, J. and Olde Venterink, H. O. 2015. The need for a novel integrative theory on feedbacks between herbivores, plants and soil nutrient cycling. – *Plant Soil* 396: 421–426.
- Skarin, A. et al. 2008. Summer habitat preferences of GPS-collared reindeer *Rangifer tarandus tarandus*. – *Wildl. Biol.* 14: 1–15.
- Smis, A. et al. 2014. Determination of plant silicon content with near infrared reflectance spectroscopy. – *Front. Plant Sci.* 5: 496.
- Soininen, E. M. et al. 2013a. More than herbivory: levels of silica-based defences in grasses vary with plant species, genotype and location. – *Oikos* 122: 30–41.
- Soininen, E. M. et al. 2013b. Arctic small rodents have diverse diets and flexible food selection. – *PLoS One* 8: e68128.
- Stark, S. 2007. Nutrient cycling in the tundra. – In: Marschner, P. and Rengel, Z. (eds), *Nutrient cycling in terrestrial ecosystems*. Springer, pp. 309–331.
- Stark, S. et al. 2002. Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. – *Oikos* 97: 69–78.
- Stark, S. et al. 2015. When do grazers accelerate or decelerate soil carbon and nitrogen cycling in tundra? A test of theory on grazing effects in fertile and infertile habitats. – *Oikos* 124: 593–602.
- Tuomi, M. et al. 2018. Herbivore effects on ecosystem process rates in a low-productive system. – *Ecosystems* 22: 1–17.
- Van der Wal, R. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. – *Oikos* 114: 177–186.
- Van der Wal, R. et al. 2004. Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. – *Ecography* 27: 242–252.
- Walker, D. A. et al. 2005. The circumpolar arctic vegetation map. – *J. Veg. Sci.* 16: 267–282.
- White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. – *Oikos* 40: 377–384.
- Wickham, H. 2016. *ggplot2: elegant graphics for data analysis*. – Springer.
- Zuur, A. F. et al. 2010. A protocol for data exploration to avoid common statistical problems. – *Methods Ecol. Evol.* 1: 3–14.

Supplementary material (available online as Appendix oik-07074 at <[www.oikosjournal.org/appendix/oik-07074](http://www.oikosjournal.org/appendix/oik-07074)>). Appendix 1.