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ORIGINAL ARTICLE

# Long-Term Reindeer Exclusion Leads to Higher Carbon Storage and Less Recalcitrant Carbon Compounds in Boreal Forest Soils

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## Abstract

Dry and unproductive Scots pine forests in the northern boreal forest zone provide conditions where ground-dwelling lichens can thrive. These lichens are a crucial winter forage for reindeer. Reindeer reduce lichen biomass both by consumption and trampling, leading to cascading effects on microclimate, litter inputs, and soil carbon dynamics. To investigate long-term impacts of reindeer exclusion, we assessed the plant biomass, soil nutrients, and soil organic carbon (SOC) quantity and quality in three dry pine forest sites in northern Finland, where reindeer have been excluded for over 50 years. Within exclosures, lichen biomass was 4.5 times higher and dwarf shrub biomass nearly doubled compared to grazed controls. These vegetation changes were associated with a 33% higher soil moisture and 0.8 °C lower summer soil temperatures at 10 cm depth beneath the thicker lichen mats. The organic layer SOC stock was 28% higher in exclosures. Spectroscopic analysis using $^{13}$C NMR spectroscopy revealed 9.5% higher O-alkyl carbon (carbohydrates) content and lower methoxy (−5.1%), alkyl (−6.9%), and carbonyl (−8.7%) content, reflecting a younger, more labile carbon pool in the exclosures. Despite these changes, soil nutrient concentrations and C:N ratios remained unchanged between treatments, suggesting that altered SOC storage and composition result primarily from increased litter inputs and microclimatic changes. We conclude that in lichen-rich boreal forests, long-term reindeer exclusion enhances SOC stocks and promotes a shift toward more decomposable soil organic matter, with potential implications for carbon stability under changing grazing regimes.

**Key words:** Reindeer; soil organic carbon; $^{13}$C NMR spectroscopy; boreal forest; lichen; grazing.

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## Highlights

- Long-term reindeer exclusion strongly increases lichens and vascular plant biomass.
- Long-term reindeer exclusion increases soil carbon storage.
- Changes in vegetation and microclimate shifts soil carbon toward younger, more easily decomposed forms.

## Introduction

Boreal forests store approximately one-third of the global terrestrial carbon (C) stock (Pan and others 2011; Bradshaw and Warkentin 2015), with a large portion sequestered in soil organic matter (SOM) (Lehmann and Kleber 2015). As such, SOM in boreal forests is a key component of the global C cycle (Adamczyk 2021). This SOM originates from organic materials such as roots, leaves, and fungal hyphae (Clemmensen and others 2013; Adamczyk 2021), and its stability is influenced by both abiotic and biotic factors, including microclimate, microbial activity, and soil organisms. Further, the quality and chemical composition of organic inputs also affect SOM persistence (Audette and others 2021; Lehmann and Kleber 2015; Sun and others 2018). The chemical composition of plant biomass varies both among species and among tissue types, reflecting differences in structural and metabolic functions, which shape decomposition rates and the long-term storage of C. In particular, the resistance of SOM to microbial breakdown depends in part on the composition of its C compounds (He and others 2018). Large herbivores, such as deer and reindeer, are widespread across boreal forests and can significantly alter soil carbon inputs, decomposition, and stabilization processes through their impacts on vegetation structure, microbial communities, and soil microclimate (Côté and others 2004; Felton and others 2024), but their effects on soil carbon storage and quality are still relatively poorly understood.

In oligotrophic boreal forests, ground-dwelling mat-forming lichens such as *Cladonia* spp. are an important component of the forest floor (Ahti 1977), and could potentially play a key role in the accumulation and long-term stabilization of SOM, with consequences for predicting how SOM will respond to future climate and land-use change. However, relatively little is known about how lichens influence the SOM in boreal soils. Lichens are rich in phenolic compounds such as usnic and perlatolic acid (Stark and others 2007), and their litter decomposes slower than litter from other understorey vegetation (Moore 1984). In undisturbed, nutrient-poor, late-successional forests, they can outcompete vascular plants and form a continuous ground layer (Ahti 1977; Oksanen & Ahti 1982).

Because *Cladonia* lichens are a key wintertime forage resource for the semi-domesticated reindeer (*Rangifer tarandus* L.) in northern Fennoscandia, large portions of the northern boreal forest in this region are intensively grazed (Kumpula and others 2014; Stark and others 2023). Lichen cover has declined sharply in recent decades due to the combined effects of reindeer grazing, forestry, and climate change (Jaakkola and others, 2012; Kumpula and others 2014; Roos and others 2025; Sandström and others 2016; Stark and others 2026; Tonteri and others 2016). Today, thick lichen mats are mostly restricted to late-successional forests that remain undisturbed by logging and have been protected from reindeer for several decades. Such conditions occur, for example, in long-term grazing exclosures—areas that were previously grazed but later protected for experimental purposes (Stark and others 2000; Olofsson and others 2010; Köster and others 2013)—and along fenced land borders that restrict reindeer movement between countries (Akujärvi and others 2014; Köster and others 2015).

Reindeer reduce the abundance and alter the species composition of mat-forming lichens by trampling and feeding (Väre and others 1995; den Herder and others 2003; Olofsson and others 2010; Akujärvi and others 2014; Bernes and others 2015; Stark and others 2026). These changes in the lichen layer alter soil insulation and moisture dynamics, thereby influencing soil microclimatic conditions (van Zuijlen and others 2020). In addition, some studies have shown that reindeer reduce dwarf shrubs in the understorey vegetation (Kumpula 2001), whereas other studies have found no effects (Stark and others 2000; Väisänen and others 2021).

Reductions in lichen cover and changes to understorey composition can directly influence key soil processes governing C and nutrient cycling. In boreal forests, the presence of reindeer is associated with warmer and drier soils, decreased litter accumulation and decomposition, and lower microbial respiration in the organic soil layer (Väre and others 1995; Ohtonen & Väre, 1998; Stark and others 2000, 2010; Santalahti and others 2018). These changes suggest that reindeer can significantly influence C and nutrient dynamics and potentially soil C storage, although previous studies have

found similar C stocks in grazed areas and ungrazed exclosures (Stark and others 2000; Köster and others 2013, 2015). While many studies have examined total soil C stocks, the quality of SOM remains poorly understood. Given the critical role of SOM chemical composition in long-term carbon stability, its response to grazing may provide valuable insights into the mechanisms regulating soil carbon persistence. Understanding these shifts is essential for assessing the broader ecological impacts of herbivory and predicting future C storage in grazed boreal forest systems.

$^{13}$C NMR spectroscopy has been a commonly used method for the characterization of SOM for decades (Kögel-Knabner, 1997). It can provide detailed insights into the chemical composition and structure of organic C groups in soils, allowing the identification of functional groups, the assessment of decomposition stages, and the characterization of carbon cycling dynamics. O-alkyl C, which mainly comprises carbohydrates such as cellulose and hemicellulose, typically is the most abundant C functional group in soils and represents labile and readily decomposable material (He and others 2018). In contrast, alkyl C, often derived from waxes, lipids, or partially degraded lignin, is generally resistant to microbial breakdown (Baldock and others 1997). Accordingly, alkyl C has been associated with greater stability. Of the different compounds in this fraction, lignin does not appear to accumulate during decomposition or contribute strongly to stable soil C pools (Baldock and others 1992; Preston and others 2009; Fekete and others 2023), whereas complex lipophilic compounds and condensed tannins are recalcitrant to microbial decomposition and accumulate in boreal forest soils (Stark and others 2010; Adamczyk 2021). Since the abundance of different C functional groups changes with soil age, the alkyl/O-alkyl C ratio has been proposed as a relative indicator of SOM decomposition, with higher ratios reflecting more advanced decomposition due to the preferential use of O-alkyl C by soil microbiota (Baldock and others 1997). Differences in the composition C groups of SOM can therefore offer valuable insight into soil C stability.

The aim of this study is thus to assess whether reindeer influence (i) vegetation composition, soil microclimate, and soil nutrient conditions, (ii) soil C storage and C composition in lichen-rich forests, and (iii) the mechanisms linking vegetation and environmental changes to soil C composition and storage. We hypothesise that: (1) reindeer exclusion increases lichen and dwarf shrub abundance, which will alter soil microclimate (cooler, moister conditions), resulting in lower soil C recalcitrance and a higher proportion of labile soil C compounds in exclosures compared to grazed controls; and (2) despite these changes in soil C composition, total soil C storage may not differ between treatments because higher carbon inputs in exclosures may be offset by accelerated decomposition.

To address these objectives, we combined measurements of vegetation biomass and chemistry, soil carbon stocks and composition, soil nutrients, and microclimatic conditions, analysed using mixed-effects models and multivariate ordination approaches.

## Methods

### Study Design

Reindeer herding in Finland spans a land area of approximately 122,936 km$^2$, covering more than one third of the country's land surface. In the boreal forest zone, reindeer husbandry began in the 1600 s and has historically been relatively sedentary, organized within geographically defined herding cooperatives with fenced borders since the late nineteenth century (Stark and others 2023). Nowadays, reindeer herding area in northern Finland is divided into 54 reindeer herding districts that govern the herding in their area. The reindeer within these districts are semi-domesticated and managed, where grazing areas, seasonal movements, and population densities are actively regulated rather than occurring as free-ranging wildlife. Reindeer numbers increased markedly during the late twentieth century, accompanied by changes in management practices such as supplementary winter feeding and intensified herd regulation (Kumpula and others 2002).

Within this managed landscape, our study was conducted in three ombrotrophic, dry Scots pine (*Pinus sylvestris* L.) forests (Angeli, Kätkäsuvanto, and Raja-Jooseppi) in northern Finland (Figure 1; Stark and others 2003). All sites are actively grazed by reindeer and have a long history of grazing. Each site also contains fenced areas that have excluded reindeer for several decades. These long-term exclosures provide a unique opportunity to examine ecosystem responses to the cessation of reindeer herbivory under otherwise comparable environmental conditions.

Kätkäsuvanto is situated in northwestern Finland near the Swedish border (68°07′N, 23°25′E); the ungrazed plot is in an exclosure built around the 1970s. The site belongs to Muonio herding cooperative (the total area is 2 666 km$^2$, the area

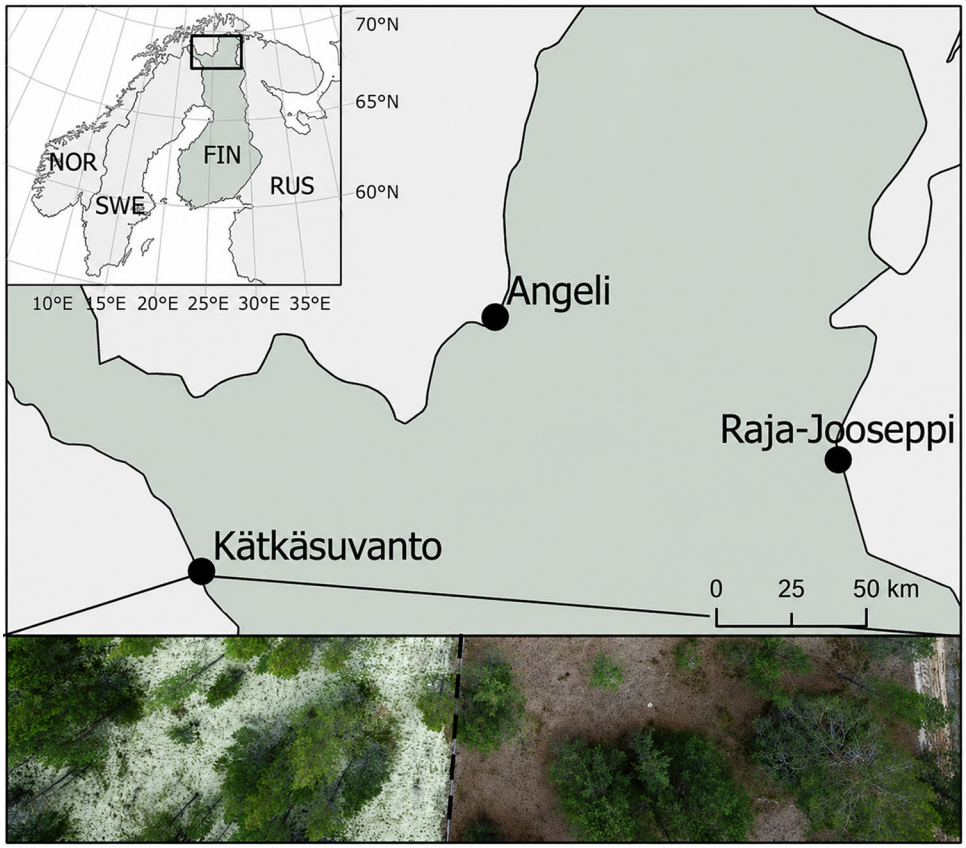


**Figure 1.** Location of the three boreal forest study sites in northern Finland: Kätkäsuvanto, Angeli, and Raja-Jooseppi. The insert map shows the location of the study region within Fennoscandia. The aerial photograph (bottom) shows a sharp contrast in ground vegetation between a reindeer-excluded plot (left) and a grazed plot (right) at the Kätkäsuvanto site. Dashed black line indicates the exclosure fence.

dominated by lichen is around 433 km$^2$), and earlier was grazed only during the winter, but since the 1990s, grazing has been present year-round (Teresa Komu, personal communication). Angeli is located on the border between Norway and Finland (69°05′N, 25°45′E), and here the fence was erected in the 1960s to prevent the Finnish reindeer from going into the Norwegian side of the border. The area belongs to Muotkatunturi herding co-operative (the total area is 2 580 km$^2$, the area dominated by lichen is around 915 km$^2$) and is grazed during the winter (TOKAT database, Reindeer Herders Association of Finland). The site in Raja-Jooseppi is bordering the Finnish-Russian land border (68°28′21″N, 28°28′40″E). The fence was built around the 1920s to prevent Finnish reindeer from entering Russia. Raja-Jooseppi belongs to Ivalo herding co-operative (the total area is 2 826 km$^2$, the area dominated by lichen is around 737 km$^2$) and is grazed throughout the year (TOKAT database, Reindeer Herders Association of Finland). Average reindeer densities for the herding co-operatives during the past decades are presented in Supplementary Figure B. All herding districts experienced a peak in reindeer densities during early 1990s, after which the densities decreased. The field and ground layer of all three study sites are dominated by mats of lichens from the genus *Cladonia*, interspersed with patches of evergreen dwarf shrubs such as *Empetrum nigrum* and *Vaccinium vitis-idaea*. The exclosure areas support a continuous, thick lichen mat, whereas grazed areas have a much thinner lichen layer that is locally sparse or absent due to ongoing reindeer herbivory.

To study the effect of reindeer exclusion on soil and vegetation, we established two paired lines of 10 sub-plots (1 × 1 m) across an area of 10 × 25 m on each side of the fence at Kätkäsuvanto and Angeli, and 24 sub-plots (1 × 1 m) covering 10 × 60 m on each side at Raja-Jooseppi (Figure 1, Supplementary Figure A), positioned at least 2.5 m away from the fence. Within these plots, we measured all relevant soil and vegetation variables. A similar sampling design along a continuous line has

been used in all earlier studies within the exclosures (Stark and others 2000, 2003, 2010). This design was originally adopted to ensure that grazed and ungrazed samples are taken from a topographically and edaphically uniform area, which ensures that any differences along the transect are caused by grazing and not by changes in abiotic conditions. The larger study area at Raja-Jooseppi was chosen due to its lower tree density, which was an important consideration for another study that was conducted at the same time.

## Vegetation Biomass and Quality

Vegetation biomass and chemical composition were quantified to characterise potential mechanisms through which reindeer exclusion could influence soil carbon storage and composition (objective iii). In August 2022, we clipped vegetation of a 25 × 25 cm square within each sub-plot and collected the remaining lichen and litter. We sorted the vascular plants to the species level before drying (65 °C, > 5 days). Subsequently, all sub-plots were pooled and categorized based on species, site, and treatment. All pooled plant samples were homogenized before analyses by grinding them in a coffee grinder followed by ball milling. We analysed the C and N concentration in the aboveground plant pools using elemental analyser (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany; Werner and others 1999).

To provide a general characterization of plant carbon chemistry, we analysed pooled samples of the two most common vegetation groups—lichens and *E. nigrum*—using solid-state $^{13}C$ nuclear magnetic resonance ($^{13}C$ CP-MAS NMR). For each vegetation group, material was pooled across all sites and treatments, as assessing variation among treatments was not an aim of this study; instead, the analysis serves as a general indicator of carbon composition to support interpretation of subsequent results.

We identified seven C functional groups in the NMR spectra for each vegetation class, corresponding to the following chemical shift regions: carbonyl C (from 190 to 160 ppm), O-aromatic C (from 160 to 140 ppm), aromatic C (from 140 to 112 ppm), di-O-alkyl C (112–93 ppm), O-alkyl C (93–60 ppm), methoxy C (60–50 ppm), and alkyl C (50–0 ppm). The analysis was performed on a Bruker Avance III 500 MHz spectrometer with a 4 mm HX CP MAS probe and a SamplePro HR-MAS sample changer. To increase the measurement speed and obtain stronger signals, we used the semi-quantitative method of proton ($^{1}H$) cross polarisation (CP) instead of the orders of magnitude slower quantitative direct polarisation (DP) solid-state $^{13}C$ NMR.

The cross-polarization (CP) experiments started with a 3 µs proton excitation pulse corresponding to a 90° angle followed by a simultaneous static $^{13}C$ spinlock at 60 kHz and a ramped $^{1}H$ spinlock from 45 to 90 kHz with a contact time of 1.5 ms. During this time, the cross-polarization occurred between the proton and the $^{13}C$. At $^{13}C$ signal acquisition, the proton was decoupled with a ''spinal64'' decoupling scheme at 83 kHz (Fung and others 2000). The relaxation time between scans was 2 s and each sample was scanned at least 4000 times. All measurements were taken with magic-angle spinning (MAS) at 10 kHz and at a temperature of 298 K. The chemical shift was externally calibrated to the adamantane $CH_2$ signal at 38.48 ppm (Morcombe and Zilm 2003).

We measured the total tree biomass in blocks on either side of the fences (10 × 60 m in Raja-Jooseppi and 10 × 25 m in Kätkäsuvanto and Angeli). We recorded the height and tree diameter at 1.3 m height to calculate the tree biomass according to Repola and others (2009). Further, we measured the average distance to the three closest trees from each plot as a proxy of forest openness.

## Soil Analysis

We collected 5 soil cores (Ø2.5 cm) in each sub-plot to study the organic soil layer in August 2021. In order to collect only the organic layer, we separated the organic and mineral layers in the field, and sampled the full depth of the former. The samples were kept frozen at −19 °C until analysis. To homogenize the samples for analyses we thawed and pooled 5 cores from each sub-plot together, which resulted in 48 soil samples in Raja-Jooseppi and 20 soil samples in Angeli and Kätkäsuvanto each.

## Soil Carbon Quantity and Quality

We analysed the total C and nitrogen (N) concentrations of dried (65 °C, > 5 days) soil sub-samples using elemental analyser (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany; Werner and others 1999). Using these concentrations and the soil volume and weight, we calculated the total soil organic layer C and N pools on an area basis. We studied the soil's C composition to address objective (ii) using solid-state $^{13}C$ CP-MAS NMR with the same chemical shift regions and instrument settings as for the vegetation C composition samples.

## Soil Nutrient Concentration

We analysed the organic soil to investigate the effect of reindeer on plant-available nutrients, specifically measuring the concentration of nitrate ($NO_3$), ammonium ($NH_4$), and phosphate ($PO_4$) using water soluble soil extractions. We extracted a sub-sample of 5 g which we diluted with 30 ml distilled water. The solutions were shaken for 2 h before being filtered using Munktell filters (grade 3, particle retention $< 10$ µm). The extracts were analysed by measuring colour on a photometer in a segmented flow analyser. Nitrate was measured after reagents and samples passed a copperized Cd reduction coil to form an azo dye [method: MT3B Q-126-12 Rev 1]. Ammonium concentration was determined with the salicylate method [method: Q-033-04 Rev. 8] and phosphate with the molybdenum blue method [method: MT3A Q-125-12 Rev 1].

## Soil pH, Density, Moisture and Temperature

We measured the soil pH in a soil:water suspension, using 1 g of fresh soil. The volume of deionized water added was adjusted based on the soil's C content, maintaining a ratio of 1 g soil C to 20 ml water. The mixture was shaken for 24 h and allowed to settle for 2 h before pH measurement. The remaining soil was oven dried (65 °C, $> 5$ days) to calculate the moisture and bulk density of the soil. The soil temperature was measured for 3 consecutive summers at 10 cm depth using Tomst™ loggers (Wild and others 2019), with summer being defined from day 172 to 266. Loggers were installed 7 m from the fence, with one logger in each treatment area per site.

## Statistical Analysis

Linear mixed-effects models were used to test treatment effects on vegetation, soil carbon stocks, nutrients, and microclimate (objective I and ii), while soil carbon composition metrics were analysed separately to address objective (ii). Multivariate ordination (NMDS) and vector fitting were used to explore relationships between vegetation, microclimate, and soil properties as potential mechanisms underlying observed SOC patterns (objective iii).

We explored the effect of reindeer exclusion on all environmental variables (total C, total N, C concentration, N concentration, $PO_4$, $NO_3$, $NH_4$, C:N ratio, pH, bulk density, moisture, plot distance to closest tree, lichen biomass, litter biomass and vascular plant biomass) as well as C groups (*carbonyl, O-aromatic, aromatic, di-O-alkyl, O-alkyl, methoxy, and alkyl*) using linear mixed-effects models from the R package lme4 (Bates and others 2015). We included treatment as a fixed effect and site as a random effect to account for the nesting of subplots within plots and to avoid pseudo replication. All variables were normally distributed except for total C and *methoxy C*, which were square root transformed.

We explored the (dis)similarities in soil C groups across grazed and non-grazed plots using non-metric multidimensional scaling (NMDS) analysis (Minchin 1987), implemented through the 'vegan' package (Oksanen and others 2025). The NMDS was based on a Bray–Curtis dissimilarity matrix and the best ordination solution was sought using 20 random starts. To assess the relationship between soil C groups and environmental variables, we fitted all environmental variables to the NMDS ordination using the envfit function in the 'vegan' package. This allowed us to identify which environmental factors were significantly associated with the observed ordination patterns in soil C groups. All statistical analyses were conducted using the R statistical environment (version 4.3.2, R Core Team 2022) and RStudio (version 2023.12.1, RStudio Team 2020). We used ChatGPT for grammar and spelling check in the manuscript.

# Results

To address objective (i), we first quantified how reindeer exclusion influenced vegetation biomass, vegetation chemistry, and soil microclimatic conditions. These variables were subsequently used to explore potential mechanisms underlying treatment effects on soil carbon (objective iii). The exclusion of reindeer for over 50 years had a substantial impact on various soil and vegetation variables, except for extractable nutrients and total soil nitrogen, which remained unchanged (Table 1). Lichen biomass was 4.5-fold higher within the reindeer exclosures compared to grazed controls ($p = 0.007$). This substantial increase in lichen biomass likely contributed to the 33% higher soil moisture observed in the exclosures. Additionally, the absence of reindeer in the exclosures resulted in a doubling of vascular plant biomass—primarily dwarf shrubs ($p = 0.025$)—and reduced the distance between trees and study plots from 2.7 to 1.9 m ($p = 0.045$), indicating a denser forest. The soil pH was 0.2 units lower in the grazed plots ($p = 0.037$). Litter mass was 20% higher in the exclosures ($p = 0.082$). Although moss biomass

**Table 1.** Effects of Reindeer Exclusion on Soil Environmental Variables Based on Linear Mixed-effects Models

| Response variable | Effect | $\beta \pm$ SE | df | t | p | Marginal $R^2$ | Conditional $R^2$ |
|---|---|---|---|---|---|---|---|
| sqrt(Total C) | Intercept | 34.86 ± 1.38 | 3.0 | 25.31 | < **0.001** | 0.091 | 0.109 |
| | Treatment (NG) | 5.02 ± 1.95 | 3.0 | 2.58 | 0.081 | | |
| Total N (g $m^{-2}$) | Intercept | 26.00 ± 2.37 | 3.9 | 10.96 | < **0.001** | 0.008 | 0.102 |
| | Treatment (NG) | 1.79 ± 3.36 | 3.9 | 0.53 | 0.622 | | |
| C concentration (%) | Intercept | 27.65 ± 1.40 | 2.4 | 19.79 | **0.001** | 0.025 | 0.025 |
| | Treatment (NG) | 2.97 ± 1.98 | 2.4 | 1.50 | 0.253 | | |
| N concentration (%) | Intercept | 0.61 ± 0.08 | 4.1 | 8.04 | **0.001** | 0.027 | 0.35 |
| | Treatment (NG) | − | | | | | 0.07 ± 0.11 |
| 4.1 | − 0.66 | 0.548 | | | | | |
| $PO_4$(μg $L^{-1}$) | Intercept | 1042 ± 337 | 4.2 | 3.09 | **0.035** | 0.005 | 0.317 |
| | Treatment (NG) | 141 ± 476 | 4.1 | 0.30 | 0.780 | | |
| $NO_3$ (μg $L^{-1}$) | Intercept | 19.2 ± 5.0 | 3.6 | 3.84 | **0.022** | 0.005 | 0.113 |
| | Treatment (NG) | 2.7 ± 7.1 | 3.6 | 0.39 | 0.719 | | |
| $NH_4$ (μg $L^{-1}$) | Intercept | 177.8 ± 37.8 | 4.4 | 4.70 | **0.007** | 0.052 | 0.206 |
| | Treatment (NG) | 64.0 ± 53.4 | 4.4 | 1.20 | 0.291 | | |
| C:N ratio | Intercept | 47.3 ± 4.7 | 4.0 | 10.11 | < **0.001** | 0.247 | 0.68 |
| | Treatment (NG) | 11.8 ± 6.6 | 4.0 | 1.79 | 0.148 | | |
| pH | Intercept | 4.3 ± 0.1 | 4.2 | 64.70 | < **0.001** | 0.31 | 0.46 |
| | Treatment (NG) | − 0.3 ± 0.1 | 4.0 | − 3.06 | **0.037** | | |
| Soil bulk density (g $cm^{-3}$) | Intercept | 0.27 ± 0.02 | 4.4 | 11.07 | < **0.001** | 0.066 | 0.203 |
| | Treatment (NG) | − | | | | | 0.05 ± 0.04 |
| 4.4 | − 1.40 | 0.229 | | | | | |
| Summer soil T (°C) | Treatment (G) | 11.2 | Ø | Ø | Ø | Ø | Ø |
| | Treatment (NG) | 10.4 | Ø | Ø | Ø | | |
| Soil moisture (%) | Intercept | 43 ± 4 | 3.7 | 10.52 | < **0.001** | 0.281 | 0.514 |
| | Treatment (NG) | 14 ± 6 | 3.7 | 2.48 | **0.073** | | |
| Lichen biomass (gC $m^{-2}$) | Intercept | 224 ± 106 | 3.8 | 2.11 | 0.106 | 0.515 | 0.584 |
| | Treatment (NG) | 794 ± 151 | 3.9 | 5.25 | **0.007** | | |
| Moss biomass (gC $m^{-2}$) | Intercept | 37 ± 15 | 3.8 | 2.48 | 0.073 | 0.046 | 0.135 |
| | Treatment (NG) | − 27 ± 21 | 3.9 | − 1.25 | 0.281 | | |
| Vascular plant biomass (gC $m^{-2}$) | Intercept | 65 ± 18 | 3.9 | 3.55 | **0.025** | 0.227 | 0.335 |
| | Treatment (NG) | 73 ± 26 | 4.0 | 2.78 | **0.050** | | |

**Table 1.** continued

| Response variable | Effect | $\beta \pm$ SE | df | t | p | Marginal $R^2$ | Conditional $R^2$ |
|---|---|---|---|---|---|---|---|
| Litter biomass (gC $m^{-2}$) | Intercept | 689 ± 58 | 59.0 | 11.97 | < **0.001** | 0.049 | 0.049 |
| | Treatment (NG) | 148 ± 84 | 59.0 | 1.77 | 0.082 | | |
| Tree biomass (kgC $m^{-2}$) | Treatment (G) | 2.74 | Ø | Ø | Ø | Ø | Ø |
| | Treatment (NG) | 3.48 | Ø | Ø | Ø | | |
| Forest openness (m)[a] | Intercept | 2.7 ± 0.2 | 3.3 | 13.40 | < **0.001** | 0.118 | 0.133 |
| | Treatment (NG) | − 0.9 ± 0.3 | 3.7 | − 2.98 | **0.045** | | |

*For Each Response Variable, Models Included Treatment (Grazed vs. Not Grazed) as a Fixed Effect. Site-Level Grouping Was Initially Included as a Random Intercept But Excluded When It Did Not Explain Additional Variance. Reported Coefficients ($\beta \pm$ SE) Correspond to the Model Intercept and the Effect of the Not-Grazed Treatment (NG). Degrees of Freedom (df), t-values, and p values Are Shown for Fixed Effects. Marginal $R^2$ Represents Variance Explained by Fixed Effects Only, and Conditional $R^2$ Represents Variance Explained by the Full Model. Ø Indicates that No Statistical Test Was Performed, Typically Due to Variables Not Being Measured at the Plot Level.*
[a]*Plot distance to nearest tree as a proxy for forest openness.*

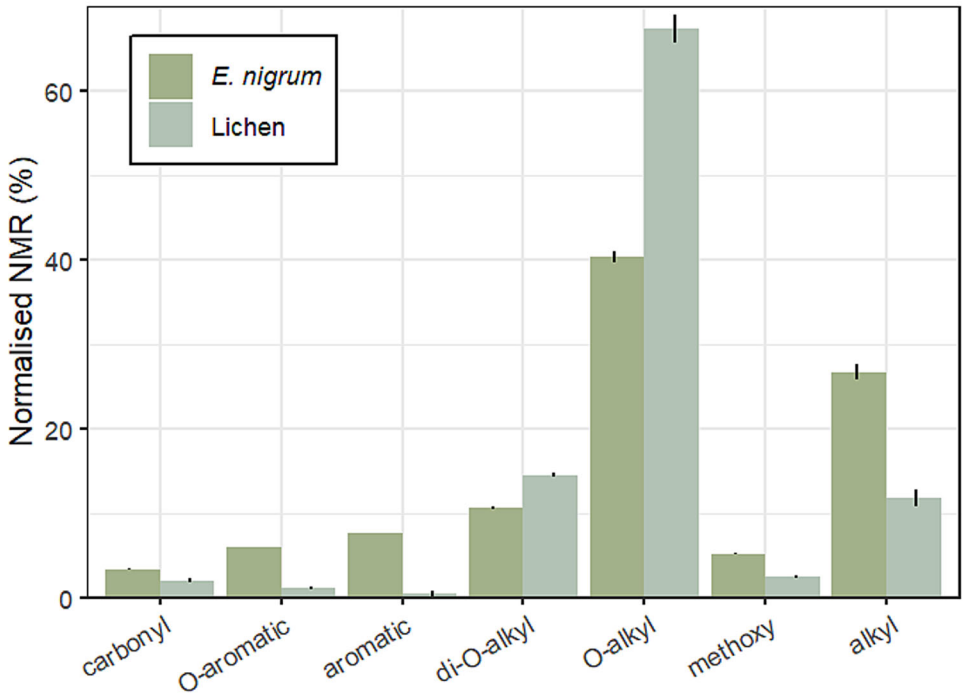


**Figure 2.** Relative abundance of carbon functional groups (% of total NMR signal) in E. nigrum and Lichen, averaged across the three study sites. Error bars represent standard errors (n = 6).

appeared higher in exclosures (approximately four-fold), this effect was not statistically significant and was based on very low and spatially restricted biomass, suggesting no consistent treatment effect.

The carbon composition of lichen and the dominant dwarf shrub *Empetrum nigrum* differed noticeably (Figure 2). Lichens were clearly dominated by carbohydrate polymers, with a pronounced peak in the O-alkyl region (67.4%). In contrast, the NMR spectra of *E. nigrum* were more complex (Supplementary Figure E). Although the O-alkyl region was also the most abundant in *E. nigrum* (40.4%), the peak was much smaller compared to lichen. Additionally, *E. nigrum contained* higher proportions of lignin-derived C and fatty acid chains, reflected in the alkyl, aromatic, and methoxy regions.

Multivariate ordination was used to evaluate how vegetation characteristics and environmental variables covaried with soil carbon properties, providing insight into potential mechanisms linking reindeer exclusion to SOC patterns (objective iii). Vegetation and soil changes were accompanied by changes in soil organic carbon (SOC) composition. A clear separation in C functional groups was observed between grazed and ungrazed plots

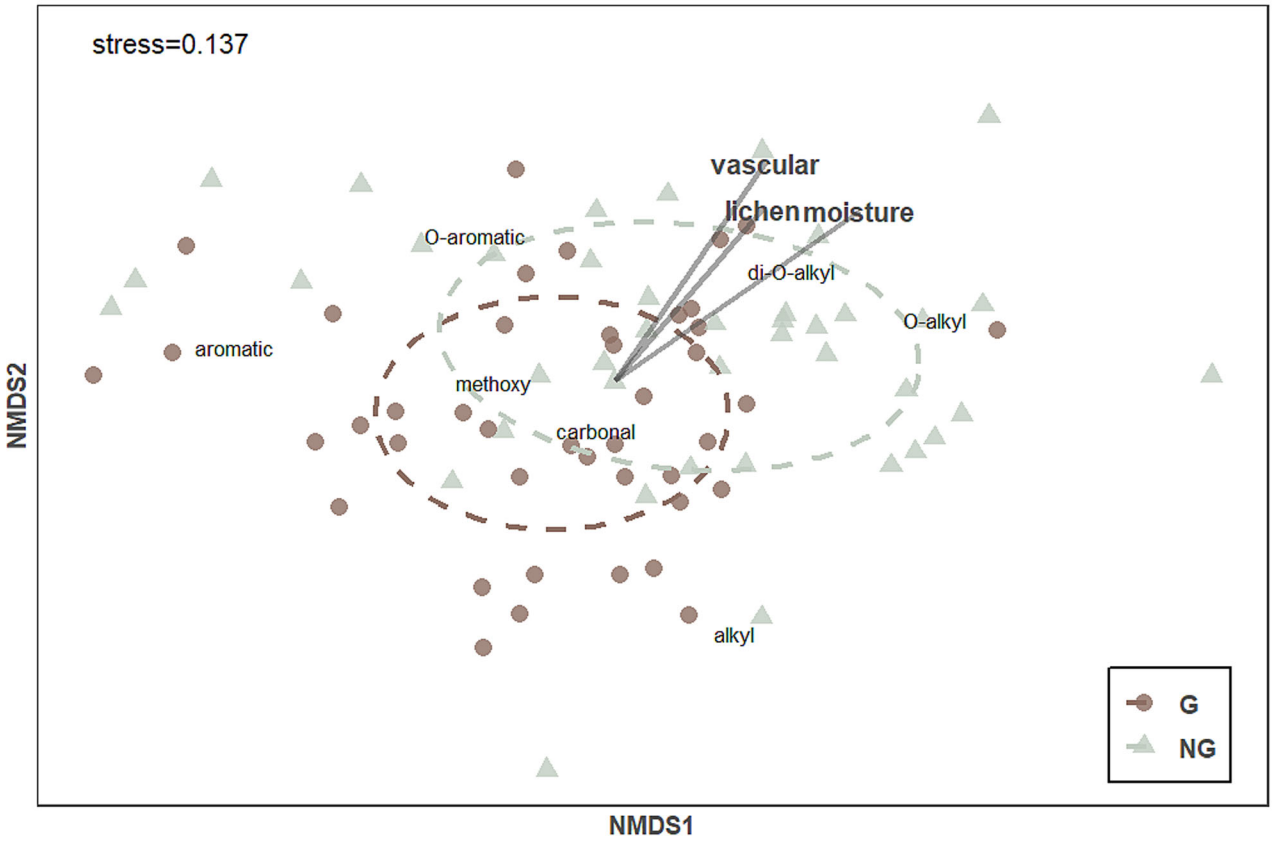


**Figure 3.** NMDS ordination of soil organic matter composition across grazed (G, brown) and reindeer-excluded (NG, grey) plots. Vectors indicate significant environmental variables (based on envfit, $p < 0.05$) associated with variation in SOM composition. Carbon functional groups (based on NMR) are also displayed and marked with a black dot.

(NMDS, stress value: 0.137, Figure 3). Exclosures were characterized by a relatively higher proportion of O-alkyl and di-O-alkyl C groups and clustered towards the right end of NMDS axis 1 and upper end of axis 2. In contrast, grazed plots exhibited a higher proportion of methoxy C groups and were positioned at the left end of NMDS axis 1 and lower end of axis 2. Soil moisture, lichen biomass, and vascular plant biomass emerged as the primary correlates of the observed shifts in SOC composition (Supplementary Figure C). Their envfit-vectors pointed towards the exclosures, aligning with the distribution of O-alkyl and di-O-alkyl C, and highlighting the role of vegetation structure and microclimate in shaping SOC quality.

The shifts in C composition were accompanied by an increase in total SOC storage in the exclosures (objective ii). Across all three sites, we observed a 28% higher organic C stock in the topsoil of reindeer exclosures compared to grazed plots ($p = 0.081$; Figure 4A, Table 1). Alongside this increase in total C, the chemical composition of SOC also differed between grazing regimes (Figure 4B, Supplementary Figure D, objective ii). Specifically, the exclosures contained 9.5% more O-alkyl C ($p = 0.008$), while concentrations of alkyl C (− 6.9%, $p = 0.004$), carbonyl C (− 8.7%, $p < 0.001$), and methoxy C (− 5.1%, $p = 0.010$) were lower. However, aromatic and O-aromatic C fractions did not vary statistically significantly between treatments ($p = 0.564$ and $p = 0.320$, respectively), suggesting that only specific components of the SOC pool responded to the exclusion of herbivory.

## Discussion

Our results show that long-term reindeer exclusion increased SOC storage and altered its chemical composition, with these changes closely associated with shifts in vegetation structure and soil microclimatic conditions. Specifically, exclosures were characterized by greater plant biomass and litter inputs, higher soil moisture, and increased SOC stocks, alongside a shift towards a greater relative abundance of O-alkyl C, indicative of less decom-

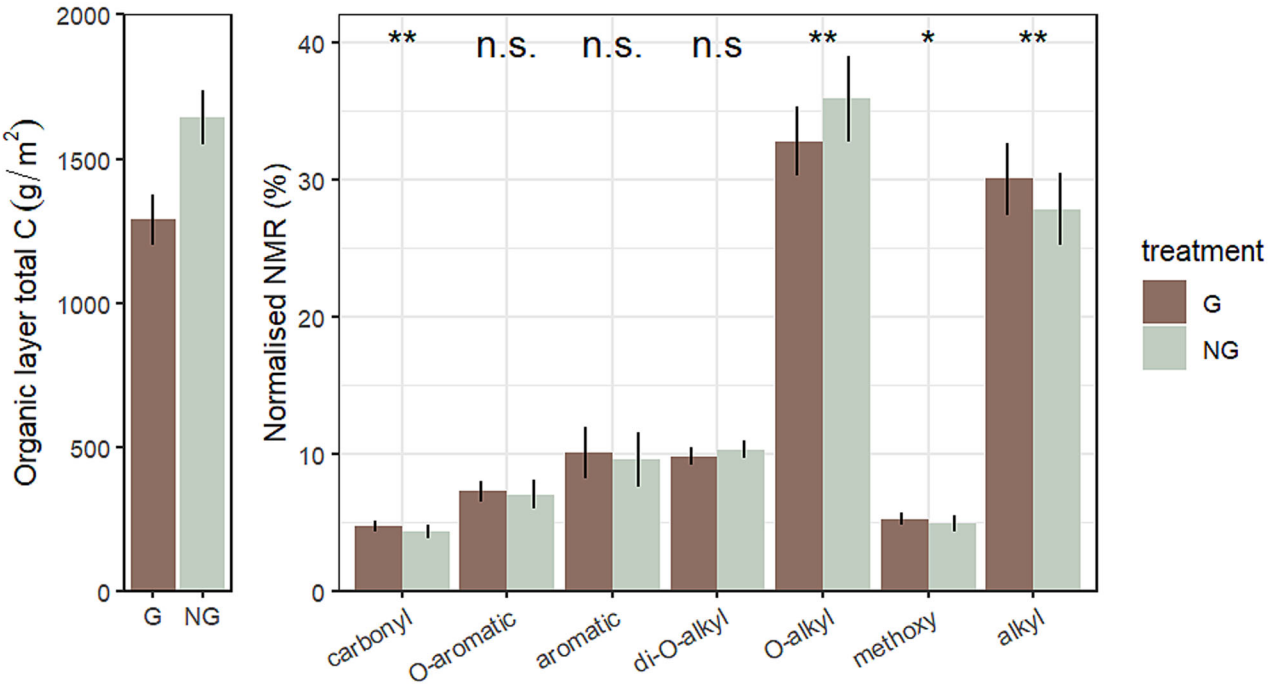


**Figure 4.** (A) Total organic layer carbon storage (g C $m^{-2}$) and (B) relative abundance of carbon functional groups (% of total NMR signal) in grazed (G) and reindeer-excluded (NG) plots, averaged across the three study sites. Asterisks indicate statistically significant differences between treatments (*p < 0.05, **p < 0.01). Error bars represent standard errors (n = 40).

posed organic matter. In contrast, grazed areas exhibited lower SOC stocks but relatively higher proportions of more processed carbon compounds.

Together, these findings suggest that reindeer influence both the quantity and quality of soil carbon. Herbivory reduces carbon inputs and promotes more processed soil organic matter, whereas long-term exclusion increases soil carbon stocks but shifts the pool toward more labile, less decomposed carbon that is potentially more vulnerable to decomposition. This nuanced pattern aligns partly with broader evidence that large herbivores regulate ecosystem carbon dynamics through their effects on vegetation, litter inputs, microclimate, and decomposition processes (Leroux and others 2020; Trepel and others 2024), but also highlights that the direction of change in carbon persistence may depend on ecosystem context and the balance between inputs and decomposition.

## Herbivore Exclusion Increases Plant and Soil Carbon Storage

Following prediction 1, the exclusion of reindeer at these sites led to substantial increases in lichen, dwarf shrubs, vascular plant, and tree biomass—but a decrease in moss biomass. A strong effect of reindeer grazing on lichen biomass has been well documented for decades and consistently reported in northern ecosystems (Väre and others 1995, 1996; Olofsson and others 2010; Bernes and others 2015; Stark and others 2023). Reindeer have been shown to reduce lichen biomass by 68 to 93% (Stark and others 2000; Akujärvi and others 2014) and decrease field layer vegetation by 60 to 94% in boreal forests (Stark and others 2000; Köster and others 2013), when at the same time, moss biomass is often increased (Väre and others 1996). Our study sites, which are dry and nutrient-poor, are dominated by *Cladonia stellaris*, accounting for 88% of the field layer biomass in exclosures, but only 69% in the grazed areas.

We found higher C storage in the organic layer over 50 years of reindeer exclusion, which contrasts our prediction 2 and previous studies in boreal forests, which have reported little to no effects of excluding reindeer on C storage (Köster and others 2013, 2015; Stark and others 2023). The outcome in our study, however, may be expected given a higher litter input from the increased ground and field layer vegetation that had continued for multiple decades, combined with altered microclimate. An explanation for these contrasting results could be that the response of SOM to the changes in lichen vegetation in response to rein-

deer exclusion is a slow and possibly nonlinear relationship that was not captured in previous studies. Stark and others (2000) analysed plant, litter and soil C pools in the Kätkäsuvanto site, one of the sites used in this study, after 25 years of exclusion, and found no changes in soil C storage. However, lichens are very slow-growing organisms, and it takes up to 20 years to reach their peak growth rate and up to 100 years to reach maximum height and biomass along primary succession after forest fire (Kumpula and others 2000). *Cladonia* lichens begin to contribute significantly to litter input only once their thalli reach their maximum height and start to die back, forming necromass (Hale 1983). Under reindeer grazing, lichen height is unlikely to ever reach that stage of maturity (Ahti 1977, Helle and Aspi 1982, Kumpula and others 2000). In our study, this idea is supported by the absence of dead bases in the lichen layer in the grazed area (Stark and others 2007). Therefore, since the lichen layer must increase in cover and thickness before it can influence the microclimate and litter input to the soil, the effects on C storage may lag decades behind the above-ground effects. In another type of northern boreal forest, Köster and others (2015) found no effect of reindeer exclusion on soil C storage even after a century, but this study was carried out in a semi-dry forest with a higher cover of mosses in the ground layer. The reported increase in soil C storage following long-term reindeer exclusion in our study may therefore be specific to particularly dry oligotrophic boreal forests, where lichen necromass can constitute a major component of total litter input. More broadly, these results highlight how herbivore impacts on soil carbon dynamics vary across forest types, and how site conditions mediate the balance between vegetation change, litter inputs, and soil carbon storage.

Although we observed a clear increase in SOC with reindeer exclusion, there were no reindeer effects on soil nutrient concentrations such as total nitrogen, nitrate, ammonium, or phosphate. This result differs from studies in low arctic tundra that generally show greater nitrogen availability in grazed than ungrazed areas (Sundqvist and others 2019) but is consistent with earlier studies from oligotrophic boreal forests that have found weak or spatially variable effects of reindeer on nitrogen mineralization or immobilization (Stark and others 2000, 2003, 2010). This suggests that the accumulation of SOC in oligotrophic boreal forests appears to occur independently of changes in nutrient availability and is likely driven by altered plant inputs and decomposition rather than shifts in soil nitrogen cycling.

In addition to changes in litter inputs, excluding reindeer substantially changes the conditions for litter decomposition. Decomposition of litter and organic matter is primarily influenced by temperature and moisture, with warmer and wetter conditions generally accelerating microbial activity (Bond-Lamberty and others 2016). As the lichen layer thickens in ungrazed sites, it provides greater insulation to the soil and increases the albedo, resulting in lower summer soil temperatures, reduced daily temperature fluctuations, and increased soil moisture retention (e.g. Gaare 1997; Stark and others 2010). Lichen species with high water-holding capacities, such as those from the *Cladonia* genus, play a key role in buffering the soil from extreme temperature and moisture changes. Thick lichen layers also reduce the frequency of freeze–thaw cycles, thereby stabilizing soil conditions (Nystuen and others 2019; van Zuijlen and others 2020). An earlier litter decomposition experiment using the same study sites showed higher rates of litter decomposition inside exclosures both during winter and summer (Stark and others 2010). Thus, although the thick lichen layer in the exclosures results in cooler soils during summer, the importance of more stable moisture conditions seems to outweigh this impact. Greater insulation also reduces the temperature sensitivity of organic matter decomposition (Tomczyk and others 2020). A substantial part of the litter decomposition usually takes place during winter, when the soils in the exclosures are warmer and more stable than in the grazed plots. Taken together, higher litter inputs and faster decomposition rates are also expected to lead to higher soil microbial $CO_2$ respiration in soil organic layer inside the exclosures (Väre and others 1996; Stark and others 2003).

## Herbivores Influence the Chemical Composition of Soil Organic Matter

Total SOC provides a snapshot of C storage but does not reflect how stable or vulnerable that C is to loss. To better understand the ecological consequences of reindeer exclusion, we also examined the chemical composition of SOC (Audette and others 2021). Using $^{13}C$ NMR spectroscopy, we found that the relative abundance of four out of seven C groups differed between reindeer exclosures and grazed controls, indicating a shift in SOC quality despite the slow turnover typical of these cold, nutrient-poor soils. In particular, the enrichment of

labile carbon fractions within exclosures suggests a shift toward a more dynamic, fast-cycling organic matter pool. This observation validates previous reports of accelerated carbon turnover and heightened microbial respiration following large herbivore exclusion.

O-alkyl and alkyl C were the dominant groups, comprising ~ 34% and ~ 29% of total SOC, respectively. O-alkyl C, typically derived from carbohydrates such as cellulose and hemicellulose (Baldock and others 1997), was more abundant in the exclosures and indicates greater input of labile plant material. In contrast, alkyl, carbonyl, and methoxy C were relatively more abundant in the grazed sites. These carbon compounds are derived from lipids, waxes, and lignin and are generally more resistant to decomposition (Baldock and others 1997). The resulting lower alkyl/O-alkyl ratio in the exclosures suggests a younger, less decomposed C pool, potentially shaped by increased litter input and cooler, wetter microclimate in ungrazed sites. This shift in C composition highlights that while long-term reindeer exclusion increases total SOC, it also alters its chemical nature, potentially making the C pool more susceptible to microbial decomposition under future environmental changes.

Although the observed differences in SOC composition were modest, similar shifts in functional group abundances have been linked to changes in decomposition dynamics in Arctic and boreal ecosystems (DeMarco and others 2014; Parker and others 2018). However, the extent to which SOC chemical composition influences decomposition rates is strongly contingent on biophysical controls such as temperature, moisture, and soil insulation, which can modulate or even override biochemical litter quality effects (DeMarco and others 2014; Parker and others 2018). In this context, our results suggest that reindeer exclusion alters the potential vulnerability of SOC to loss by promoting less-processed carbon pools, without directly implying faster decomposition under current microclimatic conditions.

To further understand what drives the observed changes in SOC composition, we explored how environmental, and vegetation variables relate to the distribution of C functional groups (Figure 3). We found that soil moisture, lichen biomass, and dwarf shrub biomass were the main factors structuring SOC composition, all of which were enhanced in the exclosures. Notably, lichen biomass was significantly higher than any other litter input source and was also characterised by a high proportion of O-alkyl C, suggesting that increased lichen cover may be a major source of carbohydrate-rich material entering the soil (Figure 2). Further, continuous litter input from lichen thalli, dwarf shrubs, and tree needles, combined with a moister microclimate likely reinforces the build-up of fresh, early-stage SOM and can explain the higher relative abundance of O-alkyl C and the lower alkyl/O-alkyl ratio. Interestingly, Stark and others (2010) found, using *B. pubescens* and *P. sylvestris* litter, at the interface between the lichen layer and the soil surface that litter decomposition dynamics varied at the different stages of decomposition. During the initial six weeks, which usually reflects the leaching phase in decomposition (Berg and Staaf 1981), litter mass loss was greater in grazed areas, after which the mass loss was higher in the ungrazed exclosures, suggesting that easily degradable compounds may leach or break down more rapidly under grazed conditions, whereas more complex organic material decomposes more effectively in the exclosures. Although these changes in fresh litter are not directly applicable for the whole SOM pool, this proposes a mechanism that promotes a higher proportion of recalcitrant C fractions in grazed than ungrazed areas.

Taken together, our findings reveal that excluding reindeer resulted in a higher input of organic material from lichens, dwarf shrubs, and trees. This fresh litter accumulation promotes the presence of younger, less-decomposed SOC in the exclosures, which is reflected in lower alkyl-to-O-alkyl C ratios—indicative of an earlier decomposition stage. In contrast, grazed sites exhibit reduced litter inputs due to lower plant biomass consumption, vegetation removal, and trampling, leading to older and more processed SOC. This is supported by higher alkyl-to-O-alkyl ratios and lower carbonyl C abundance in the soil carbon pool. Importantly, this contrast between carbon accumulation under exclusion and carbon persistence under grazing mirrors patterns observed across ecosystems dominated by large mammalian herbivores. Comparative studies of large herbivores indicate that herbivore-driven shifts toward more chemically processed or physically protected soil carbon are common across ecosystems, even when total SOC stocks decline (Naidu and others 2022; Trepel and others 2024). Our finding of lower SOC stocks but relatively more processed carbon in grazed plots is thus consistent with global patterns showing that herbivory can shift soil carbon composition toward more processed forms, particularly in systems where plant regrowth and litter inputs are strongly constrained by nutrient availability or disturbance.

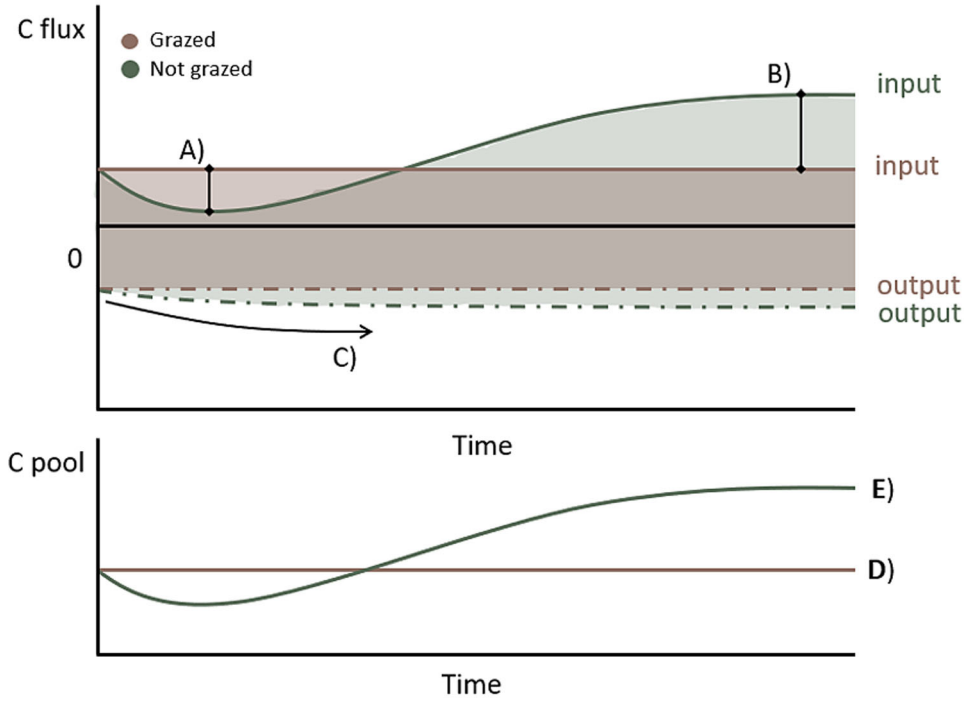


**Figure 5.** Conceptual model of soil organic carbon (SOC) accumulation under grazed and non-grazed (reindeer exclusion) conditions. (A) Shortly after the establishment of exclosures, carbon input decreases due to reduced plant biomass, as nutrient inputs from reindeer dung and urine are removed. (B) Over time, carbon input in exclusion areas increases as field-layer vegetation remains ungrazed and biomass accumulates. (C) Litter decomposition dynamics shift with seasonal conditions. During winter, thick lichen mats insulate the soil, resulting in warmer and moister conditions that promote decomposition. During summer, the lichen mats provide more stable moisture conditions that also promote litter decomposition. However, in spring and autumn, the same lichen cover can reduce soil temperatures by buffering the soil against air temperatures, potentially enhancing microbial activity during spring. (D) SOC pool development under long-term grazing, where vegetation and carbon inputs remain low. (E) SOC pool development under long-term grazing exclusion, where increased carbon inputs and seasonal changes in decomposition lead to SOC accumulation. Dashed lines represent carbon inputs; dotted lines represent carbon losses per area through decomposition.

## Conclusion

*Rangifer tarandus*, which includes reindeer and various caribou subspecies, has a circumpolar distribution throughout northern Eurasia and North America. Domestication of this species for reindeer husbandry several centuries ago in the Eurasian continent makes it a distinct case among the world's herbivores (Uboni and others 2016; Stark and others 2023). While in North America, the migratory behaviour and predator–prey dynamics of wild caribou populations result in more heterogeneous grazing pressure (Leroux and others 2020), in the managed reindeer ranges of northern Fennoscandia, grazing pressure is more stable over time especially under current climatic conditions and land-use regimes (Stark and others 2023, 2026, Roos and others 2025). The ecosystem responses observed here are the consequence of semi-domesticated reindeer and may potentially differ from the effects of wild reindeer. To summarize the long-term dynamics of SOC under different grazing regimes, Figure 5 illustrates a conceptual model of grazed and ungrazed (exclosure) conditions. Following exclosure establishment, C input may initially decline due to reduced plant growth associated with the loss of nutrient inputs from reindeer dung and urine (Figure 5A). Over time, however, C input is expected to increase steadily as vegetation remains ungrazed and plant biomass accumulates (Figure 5B). At the same time, decomposition dynamics may shift in both directions: resulting from warmer soils during winter and more stable moisture conditions during summer, litter decomposition during winter is higher when reindeer are excluded, but this outcome may be the opposite during spring when the dense lichen layer in exclosures delays the warming of the soil (Figure 5C). The combined effect of increasing C inputs and seasonally variable decomposition leads to a gradual but substantial increase in the

SOC pool in exclosures (Figure 5E), in contrast to grazed areas where plant biomass remains low (Figure 5D) and SOC is relatively more chemically processed.

To summarize, excluding reindeer for half a century led to dramatically higher ground-dwelling lichen biomass, which in turn increased soil moisture and lowered summer soil temperatures. The changes in vegetation composition, combined with the changes in soil microclimate, contributed to a 28% increase in soil C storage in the exclosures compared to grazed plots—a pattern that contrasts with findings from many earlier studies. The chemical composition of the soil C indicates that this increase was likely driven by greater C inputs particularly from lichens. However, despite the lower total soil C pool in the grazed plots, the C present there was relatively more chemically processed, suggesting a more decomposed SOC pool under continued reindeer grazing. These findings underscore a critical distinction: while excluding reindeer enhances soil carbon stocks, continued grazing appears to promote a relatively more processed and potentially more stable soil carbon pool. Nevertheless, changes in soil C stocks in lichen-rich boreal forests remain slow, and even under highly contrasting grazing regimes, decades may be required before shifts in total C storage become detectable.

From a management perspective, our results highlight a trade-off between soil carbon quantity and quality. While long-term reindeer exclusion increases total soil carbon stocks, it also shifts the soil carbon pool toward a more labile and potentially more climate-sensitive composition. In contrast, grazed systems store less carbon but maintain a relatively more processed carbon pool. Under future warming and changes in soil moisture, these differences in carbon quality may become increasingly important, as more labile carbon fractions are generally more responsive to changes in decomposition conditions. However, the long-term net effect on soil carbon storage under changing climate remains uncertain. Because lichen recovery was a key driver of the higher SOC stocks observed in exclosures, management practices that promote the persistence of lichen-rich ground layers may also influence ecosystem carbon storage. In northern Fennoscandia, seasonal range rotation has been proposed as an important strategy for maintaining lichen resources under increasing grazing pressure and climate change (Stark and others 2026). Our results suggest that such practices could have implications not only for forage availability and reindeer husbandry, but also for soil carbon sequestration, although direct tests of these links are still needed.

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## DATA AVAILABILITY

Data used in this study are available at: https://doi.org/10.5061/dryad.jwstqjqrg.

## Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

## OPEN ACCESS



## REFERENCES

Adamczyk B. 2021. How do boreal forest soils store carbon? BioEssays 43:202100010. https://doi.org/10.1002/bies.202100010.

Ahti T. 1977. Lichens of the boreal coniferous zone. In: Seaward MRD, Ed. Lichen ecology, . Academic Press. pp 145–181.

Akujärvi A, Hallikainen V, Hyppönen M, Mattila E, Mikkola K, Rautio P. 2014. Effects of reindeer grazing and forestry on ground lichens in Finnish Lapland. Silva Fennica 48:1153. https://doi.org/10.14214/sf.1153.

Audette Y, Congreves KA, Schneider K, Zaro GC, Nunes ALP, Zhang H, Voroney RP. 2021. The effect of agroecosystem management on the distribution of C functional groups in soil organic matter: A review. Biology and Fertility of Soils 57:881–894. https://doi.org/10.1007/s00374-021-01546-4.

Baldock JA, Oades JM, Waters AG, Peng X, Vassallo AM, Wilson MA. 1992. Aspects of the chemical structure of soil organic materials as revealed by solid-STATE13C NMR spectroscopy. Biogeochemistry 16(1):1–42. https://doi.org/10.1007/bf02402261.

Baldock JA, Oades JM, Nelson PN, Skene TM, Golchin A, Clarke P. 1997. Assessing the extent of decomposition of natural organic materials using solid-state 13C NMR spectroscopy. Australian Journal of Soil Research 35:1061–1083. https://doi.org/10.1071/S97004.

Bardgett RD, Wardle DA. 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84:2258–2268. https://doi.org/10.1890/02-0274.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48. https://doi.org/10.18637/jss.v067.i01.

Berg B, Staaf H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. In: Clark RE, Rosswall T (eds) Terrestrial nitrogen cycles. Ecological Bulletins 33:163–178.

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

Blok D, Heijmans MMPD, Schaepman-Strub G, Van Ruijven J, Parmentier FJW, Maximov TC, Berendse F. 2011. The cooling capacity of mosses: Controls on water and energy fluxes in a Siberian tundra site. Ecosystems 14:1055–1065. https://doi.org/10.1007/s10021-011-9463-5.

Bond-Lamberty B, Smith AP, Bailey V. 2016. Temperature and moisture effects on greenhouse gas emissions from deep active-layer boreal soils. Biogeosciences 13:6669–6681. https://doi.org/10.5194/bg-13-6669-2016.

Bradshaw CJ, Warkentin IG. 2015. Global estimates of boreal forest carbon stocks and flux. Global and Planetary Change 128:24–30. https://doi.org/10.1016/j.gloplacha.2015.02.004.

Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl BD. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339:1615–1618. https://doi.org/10.1126/science.1231923.

Côté SD, Rooney TP, Tremblay J, Dussault C, Waller DM. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725.

DeMarco J, Mack MC, Bret-Harte MS. 2014. Effects of arctic shrub expansion on biophysical vs. biogeochemical drivers of litter decomposition. Ecology 95:1861–1875. https://doi.org/10.1890/13-2221.1.

den Herder MD, Kytöviita M, Niemelä P. 2003. Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and a subarctic heathland in Finnish Lapland. Ecography 26:3–12. https://doi.org/10.1034/j.1600-0587.2003.03211.x.

Fekete I, Francioso O, Simpson MJ, Gioacchini P, Montecchio D, Berki I, Móricz N, Juhos K, Béni Á, Kotroczó Z. 2023. Qualitative and quantitative changes in soil organic compounds in Central European oak forests with different annual average precipitation. Environments 10:48. https://doi.org/10.3390/environments10030048.

Felton AM, Wam HK, Borowski Z, Granhus A, Juvany L, Matala J, Melin M, Wallgren M, Mårell A. 2024. Climate change and deer in boreal and temperate regions: From physiology to population dynamics and species distributions. Global Change Biology 30:e17505. https://doi.org/10.1111/gcb.17505.

Fung B, Khitrin A, Ermolaev K. 2000. An improved broadband decoupling sequence for liquid crystals and solids. Journal of Magnetic Resonance 142:97–101. https://doi.org/10.1006/jmre.1999.1896.

Gornall JL, Jónsdóttir IS, Woodin SJ, Van der Wal R. 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia 153:931–941. https://doi.org/10.1007/s00442-007-0785-0.

Hale ME Jr. 1983. The biology of lichens, 3rd edn. Edward Arnold.

He Y, He X, Xu M, Zhang W, Yang X, Huang S. 2018. Long-term fertilization increases soil organic carbon and alters its chemical composition in three wheat-maize cropping sites across central and south China. Soil and Tillage Research 177:79–87. https://doi.org/10.1016/j.still.2017.11.018.

Jaakkola LM, Heiskanen MM, Lensu AM, Kuitunen MT. 2012. Consequences of forest landscape changes for the availability of winter pastures to reindeer (Rangifer tarandus tarandus) from 1953 to 2003 in Kuusamo northeast Finland. Jyväskylä University Digital Archive 18:6. https://doi.org/10.60910/8vfa-5h5m.

Kögel-Knabner I. 1997. 13C and 15N NMR spectroscopy as a tool in soil organic matter studies. Geoderma 80:243–270. https://doi.org/10.1016/S0016-7061(97)00055-4.

Köster K, Köster E, Kulmala L, Berninger F, Pumpanen J. 2016. Are the climatic factors combined with reindeer grazing affecting the soil $CO_2$ emissions in subarctic boreal pine forest? CATENA 149:616–622. https://doi.org/10.1016/j.catena.2016.06.011.

Köster E, Köster K, Aurela M, Laurila T, Berninger F, Lohila A, Pumpanen J. 2013. Impact of reindeer herding on vegetation biomass and soil carbon content: A case study from Sodankylä, Finland. Boreal Environment Research 18:35–42.

Köster K, Berninger F, Köster E, Pumpanen J. 2015. Influences of reindeer grazing on above- and belowground biomass and soil carbon dynamics. Arctic, Antarctic, and Alpine Research 47:495–503. https://doi.org/10.1657/AAAR0014-062.

Kumpula J. 2001. Winter grazing of reindeer in woodland lichen pasture: Effect of lichen availability on the condition of reindeer. Small Ruminant Research 39:121–130. https://doi.org/10.1016/S0921-4488(00)00179-6.

Kumpula J, Colpaert A, Nieminen M. 2002. Productivity factors of the Finnish semi-domesticated reindeer (Rangifer tarandus tarandus) stock during the 1990s. Rangifer 22:1. https://doi.org/10.7557/2.22.1.387.

Kumpula J, Colpaert A, Nieminen M. 2000. Condition, potential recovery rate, and productivity of lichen (Cladonia spp) ranges

in the Finnish Reindeer Management Area. Arctic 53:152–160. https://doi.org/10.14430/arctic845.

Kumpula J, Kurkilahti M, Helle T, Colpaert A. 2014. Both reindeer management and several other land use factors explain the reduction in ground lichens (Cladonia spp.) in pastures grazed by semi-domesticated reindeer in Finland. Regional Environmental Change 14:541–559. https://doi.org/10.1007/s10113-013-0508-5.

Lehmann J, Kleber M. 2015. The contentious nature of soil organic matter. Nature 528:60–68. https://doi.org/10.1038/nature16069.

Leroux SJ, Wiersma YF, Van der Wal E. 2020. Herbivore impacts on carbon cycling in boreal forests. Trends in Ecology & Evolution 35:1001–1010. https://doi.org/10.1016/j.tree.2020.07.009.

Minchin PR. 1987. An evaluation of the relative robustness of techniques for ecological ordinations. Vegetatio 69:89–107.

Moore TR. 1984. Litter decomposition in a subarctic spruce–lichen woodland, eastern Canada. Ecology 65:299–308. https://doi.org/10.2307/1939482.

Morcombe CR, Zilm KW. 2003. Chemical shift referencing in MAS solid-state NMR. Journal of Magnetic Resonance 162:479–486. https://doi.org/10.1016/S1090-7807(03)00082-X.

Naidu DGT, Roy S, Bagchi S. 2022. Loss of grazing by large mammalian herbivores can destabilize the soil carbon pool. Proceedings of the National Academy of Sciences 119:e2211317119. https://doi.org/10.1073/pnas.2211317119.

Nystuen KO, Bakkestuen V, Aarrestad PA. 2019. Lichens facilitate seedling recruitment in alpine heath. Journal of Vegetation Science 30:868–880. https://doi.org/10.1111/jvs.12773.

Ohtonen R, Väre H. 1998. Vegetation composition determines microbial activities in a boreal forest soil. Microbial Ecology 36:328–335. https://doi.org/10.1007/s002489900119.

Oksanen J, Ahti T. 1982. Lichen-rich pine forest vegetation in Finland. Annales Botanici Fennici 19:275–301.

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szöcs E, Wagner H, and others 2025. vegan: Community Ecology Package (Version 2.7-0). https://vegandevs.github.io/vegan/

Olofsson J, Stark S, Oksanen L. 2004. Reindeer influence on ecosystem processes in the tundra. Oikos 105:386–396. https://doi.org/10.1111/j.0030-1299.2004.13048.x.

Olofsson J, Moen J, Östlund L. 2010. Effects of reindeer on boreal forest floor vegetation: Does grazing cause vegetation state transitions? Basic and Applied Ecology 11:550–557. https://doi.org/10.1016/j.baae.2010.03.004.

Ono K, Hiradate S, Morita S, Ohse K, Hirai K. 2011. Humification processes of needle litters on forest floors in Japanese cedar (Cryptomeria japonica) and Hinoki cypress (Chamaecyparis obtusa) plantations in Japan. Plant and Soil 338:171–181. https://doi.org/10.1007/s11104-010-0397-z.

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, and others 2011. A large and persistent carbon sink in the world's forests. Science 333:988–993. https://doi.org/10.1126/science.1201609.

Parker TC, Sanderman J, Holden RD, Blume-Werry G, Sjögersten S, Large D, Castro-Díaz M, Street LE, Subke J, Wookey PA. 2018. Exploring drivers of litter decomposition in a greening Arctic: Results from a transplant experiment across a treeline. Ecology 99:2284–2294. https://doi.org/10.1002/ecy.2442.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Repola J. 2009. Biomass equations for Scots pine and Norway spruce in Finland. Silva Fennica 43:184. https://doi.org/10.14214/sf.184.

Roos U, Adler S, Lind T, Sandström P. 2025. Ground lichen cover and response in relation to forest characteristics in Sweden 1993–2023. Global Ecology and Conservation 64:e03946. https://doi.org/10.1016/j.gecco.2025.e03946.

RStudio Team. 2020. RStudio: Integrated development for R. RStudio, PBC. http://www.rstudio.com/

Sandström P, Cory N, Svensson J, Hedenås H, Jougda L, Borchert N. 2016. On the decline of ground lichen forests in the Swedish boreal landscape: Implications for reindeer husbandry and sustainable forest management. AMBIO 45:415–429. https://doi.org/10.1007/s13280-015-0759-0.

Santalahti M, Sun H, Sietiö O, Köster K, Berninger F, Laurila T, Pumpanen J, Heinonsalo J. 2018. Reindeer grazing alter soil fungal community structure and litter decomposition related enzyme activities in boreal coniferous forests in Finnish Lapland. Applied Soil Ecology 132:74–82. https://doi.org/10.1016/j.apsoil.2018.08.013.

Stark S, Horstkotte T, Kumpula J, Olofsson J, Tømmervik H, Turunen M. 2023. The ecosystem effects of reindeer (Rangifer tarandus) in northern Fennoscandia: Past, present and future. Perspectives in Plant Ecology, Evolution and Systematics 58:125716. https://doi.org/10.1016/j.ppees.2022.125716.

Stark S, Wardle DA, Ohtonen R, Helle T, Yeates GW. 2000. The effect of reindeer grazing on decomposition, mineralization and soil biota in a dry oligotrophic Scots pine forest. Oikos 90:301–310. https://doi.org/10.1034/j.1600-0706.2000.900210.x.

Stark S, Tuomi J, Strömmer R, Helle T. 2003. Non-parallel changes in soil microbial carbon and nitrogen dynamics due to reindeer grazing in northern boreal forests. Ecography 26:51–59. https://doi.org/10.1034/j.1600-0587.2003.03336.x.

Stark S, Kytöviita MM, Neumann AB. 2007. The phenolic compounds in Cladina lichens are not antimicrobial in soils. Oecologia 152:299–306. https://doi.org/10.1007/s00442-006-0644-4.

Stark S, Männistö MK, Smolander A. 2010. Multiple effects of reindeer grazing on the soil processes in nutrient-poor northern boreal forests. Soil Biology and Biochemistry 42:2068–2077. https://doi.org/10.1016/j.soilbio.2010.08.001.

Stark S, Wallén H, Kurkilahti M, Pekkarinen AJ, Kumpula J. 2026. Plant interactions, climate and the reindeer (Rangifer tarandus) interdependently shape vegetation in northern Finland. Ecological Applications, in press.

Sun T, Hobbie SE, Berg B, Zhang H, Wang Q, Wang Z, Hättenschwiler S. 2018. Contrasting dynamics and trait controls in first-order root compared with leaf litter decomposition. Proceedings of the National Academy of Sciences 115:10392–10397. https://doi.org/10.1073/pnas.1716595115.

te Beest M, Sitters J, Ménard CB, Olofsson J. 2016. Reindeer grazing increases summer albedo by reducing shrub abundance in Arctic tundra. Environmental Research Letters 11:125013. https://doi.org/10.1088/1748-9326/aa5128.

Tomczyk NJ, Rosemond AD, Bumpers PM, Cummins CS, Wenger SJ, Benstead JP. 2020. Ignoring temperature variation leads to underestimation of the temperature sensitivity of plant litter decomposition. Ecosphere 11:e03050. https://doi.org/10.1002/ecs2.3050.

Tonteri T, Salemaa M, Rautio P, Hallikainen V, Korpela L, Merilä P. 2016. Forest management regulates temporal change in the cover of boreal plant species. Forest Ecology and Management 381:115–124. https://doi.org/10.1016/j.foreco.2016.09.015.

Trepel J, Roux EL, Abraham AJ, Buitenwerf R, Kamp J, Kristensen JA, Tietje M, Lundgren EJ, Svenning JC. 2024. Meta-analysis shows that wild large herbivores shape ecosystem properties and promote spatial heterogeneity. Nature Ecology & Evolution 8:705–716. https://doi.org/10.1038/s41559-024-02327-6.

Uboni A, Horstkotte T, Kaarlejärvi E, Sévéque A, Stammler F, Olofsson J, Forbes BC, Moen J. 2016. Long-term trends and role of climate in the population dynamics of Eurasian reindeer. PLoS One 11:e0158359.

Van der Wal R, Bardgett RD, Harrison KA, Stien A. 2004. Vertebrate herbivores and ecosystem control: Cascading effects of faeces on tundra ecosystems. Ecography 27:242–252. https://doi.org/10.1111/j.0906-7590.2004.03688.x.

Van Zuijlen K, Roos RE, Klanderud K, Lang SI, Asplund J. 2020. Mat-forming lichens affect microclimate and litter decomposition by different mechanisms. Fungal Ecology 44:100905. https://doi.org/10.1016/j.funeco.2019.100905.

Väre H, Ohtonen R, Oksanen J. 1995. Effects of reindeer grazing on understorey vegetation in dry Pinus sylvestris forests. Journal of Vegetation Science 6:523–530. https://doi.org/10.2307/3236351.

Väre H, Ohtonen R, Mikkola K. 1996. The effects and extent of heavy grazing by reindeer in oligotrophic pine heaths in northeastern Fennoscandia. Ecography 19:245–253.

Väisänen M, Tuomi M, Bailey H, Welker JM. 2021. Plant and soil nitrogen in oligotrophic boreal forest habitats with varying moss depths: Does exclusion of large grazers matter? Oecologia 196:839–849. https://doi.org/10.1007/s00442-021-04957-0.

Werner R, Bruch B, Brand W. 1999. ConFlo III – An interface for high precision $\delta$13C and $\delta$15N analysis with an extended dynamic range. Rapid Communications in Mass Spectrometry 13:1237–1241. https://doi.org/10.1002/(SICI)1097-0231(19990715)13:13%3c1237::AID-RCM633%3e3.0.CO;2-C.

Wild J, Kopecký M, Macek M, Šanda M, Jankovec J, Haase T. 2019. Climate at ecologically relevant scales: A new temperature and soil moisture logger for long-term microclimate measurement. Agricultural and Forest Meteorology 268:40–47. https://doi.org/10.1016/j.agrformet.2018.12.018.