

Impacts of Reindeer on Soil Carbon Storage in the Seasonally Frozen Ground of Northern Finland: A Pilot Study

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To test the effect of reindeer husbandry on soil carbon storage of seasonally frozen ground, we analysed soil and vegetation properties in peatlands and mixed pine and mountain birch forests. We analysed sites with no grazing and contrasting intensities of grazing, and associated trampling, in Northern Finland. With a pilot study approach, we optimised the study design to include several grazing class sites including grazing seasonality but omitting sample replication at one site. Soils were analysed for water content, bulk density, total organic carbon (TOC), total nitrogen, stable carbon isotopes and radiocarbon ages. We found that there was no significant difference between grazing intensities in terms of TOC, but that TOC mainly depended on the soils' TOC content present prior to intensive herbivory introduction. In contrast, understory vegetation was visibly transformed from dwarf shrub to graminoid-dominated vegetation with increasing grazing and trampling intensity. Also, we found a decrease in bulk density with increasing animal activity on soil sites, which most likely results from named vegetation changes and therefore different peat structures.

Introduction

Due to global warming, high-latitude regions are experiencing rapid warming, which has the potential to emit substantial amounts of carbon

from previously frozen organic material (OM) stored underground, either seasonally or perennially. (Hugelius *et al.* 2014, Schuur *et al.* 2015). With rising soil temperatures, microbial decomposition of OM accelerates (Davidson and

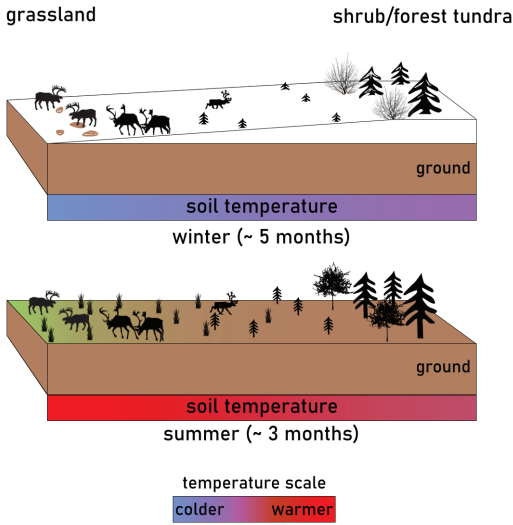


Fig 1. Schematic overview of our hypothesis stating that increased herbivore activity reduces snow height by trampling, and induces vegetation changes towards grasslands, overall reducing snow trap mechanisms; this promotes cooling of the ground in winter and reduces OM degradation, leading to higher carbon levels stored in pasture substrates; approximate season length taken from Ruosteenoja *et al.* (2011).

Janssens 2006, Walz *et al.* 2017). Also, following recent global climate modelling approaches, high-latitude soil temperatures will further increase, thus shortening the freezing season as well as reducing permafrost extent, with more subarctic and low Arctic areas losing perennially frozen ground conditions (IPCC 2021). In seasonally frozen soils, the frozen season is also shortened due to climate warming and increasing snowfall (Venäläinen *et al.* 2001).

Large grazing herbivores exert two important effects on soil temperatures both during and outside the growing season. First, large herbivores are assumed to have stabilised cold ground conditions during the late Pleistocene (Zimov *et al.* 1995) by altering the vegetation structure both via grazing and trampling (Tuomi *et al.* 2021). Especially a reduction in vegetation height has been shown to alter the temperature regime (Olofsson *et al.* 2004, Zimov 2005). At very high intensities, grazing by large herbivores may reduce shrub growth in favour of grasslands, which increases albedo hence reducing heat fluxes and overall energy input (te Beest

et al. 2016). A similar effect on vegetation is known from anthropogenic disturbances (Forbes *et al.* 2001). Second, large herbivores compress and partially remove the snow cover in winter. In this way, large herbivores again promote ground cooling, since this reduction of insulation allows for cold winter air temperatures to reach the ground (Beer *et al.* 2020).

Adding to this, pasture areas have been shown to act as a carbon sink in temperate climate (Mudge *et al.* 2011), which is most likely a result of increased vegetation productivity linked to grassland establishment by intensive grazing, compared to former tundra vegetation.

With herbivores promoting lower ground temperatures by above-named processes, in permafrost areas, OM degradation is slowed down by maintaining a perennially or at least seasonally frozen state of soil OM (Macias-Fauria *et al.* 2020, Windirsch *et al.* 2022a). Yet, the mechanisms by which herbivores influence soil carbon storage are likely different in non-permafrost areas, where soil temperatures are lower under grazing during winter, but higher under grazing during summer (Fig. 1) (Olofsson *et al.* 2004, Macias-Fauria *et al.* 2008, Stark *et al.* 2015). In permafrost areas, this effect is mainly observed in the seasonal thaw layer on top of the permafrost called active layer. However, in Fennoscandia this seasonal thaw layer is most often not present, simply due to the absence of permafrost. Instead, unfrozen or seasonally frozen peat soils make up approximately 18.1% of the land surface of Finland (Tanneberger *et al.* 2017), where this study was carried out, and are preferred by reindeer for pasture sites. This allows us to assume that the pasture effects proposed by Mudge *et al.* (2011) take place here as well. Especially changes in vegetation by reindeer grazing are present in Fennoscandia (Maliniemi *et al.* 2018).

For this study, we hypothesise that more intense animal activity leads to snow compaction and vegetation changes, which both reduce ground insulation, promoting winter cooling of the ground and hence reducing OM decomposition, hence increasing soil carbon storage with grazing intensity in a similar way as for perennially frozen soils (Windirsch *et al.* 2022a) (Fig. 1). In detail, we aim to assess the effects of

reindeer presence on soil organic carbon storage in a northern boreal landscape with seasonally frozen ground. We aim to answer whether combined reindeer grazing and trampling increase soil carbon storage in a cold region. Further we aim to decipher under which grazing intensity (from exclosures to pastures) the shifts in carbon storage occur. For this, we sampled as many sites as possible, spanning over five different grazing intensities and two grazing seasons, as a first assessment of possibly detectable changes.

Study area

We conducted this pilot study in Inari municipality in Northern Finland. The study area varies between 185 and 370 m above sea level (Paoli *et al.* 2018). The landscape was shaped by glaciation during the last ice age and became ice-free approximately 9000 years ago. Glacial features such as eskers and moraines provide relief in the valley areas between mountain ranges. As a result of former glaciation, the ground consists of sandy sediments and gravel deposits which are typical glacial remnants at ground level. Fine material (silt, loess) is washed out during, or removed by, aeolian processes after glacial melt (Derbyshire and Owen 2018). The area is characterised by vast pine (*Pinus sylvestris*) and mountain birch (*Betula pubescens* ssp. *czerepanovii*) forests, interspersed with lakes and peat mires characterised by graminoids and shrubby vegetation. Mountain birch consists of short-statured, shrub-like multi-stemmed growth forms. Evergreen dwarf shrubs dominate the understorey vegetation (e.g. *Empetrum nigrum* ssp. *hermaphroditum*, *Vaccinium vitis-idaea*, *Calluna vulgaris* and *Linnaea borealis*) (Oksanen and Virtanen 1995, Maliniemi *et al.* 2018). The deciduous dwarf shrubs *Vaccinium myrtillus* and *Betula nana* are also common. *Deschampsia flexuosa* is the most common graminoid species. The ground layer is dominated by the bryophytes *Pleurozium schreberi* and *Dicranum* spp. and ground lichens *Cladonia rangiferina*, *Cladonia arbuscula* and *Cladonia* spp. (Oksanen and Virtanen 1995). The climate in our study area is typically subarctic and continental, with January as the coldest month (mean air temperature of -13.1°C) and

July as the warmest (mean air temperature of 13.9°C). Mean annual air temperature was 0.1°C from 2008 to 2020 (monthly observation data of the weather station at Inari Kaamanen, Finnish Meteorological Institute, 2021). Annual precipitation sums up to 458.4 mm, based on monthly averages, and is highest in July with 69.2 mm (Finnish Meteorological Institute, 2021).

The herding of semi-domesticated reindeer (*Rangifer tarandus tarandus*) has been the prevailing form of land-use in the study area for centuries (Löf *et al.* 2022). The livelihood originally adapted to long seasonal migrations between nutrient-rich coastal areas in Norway during summer and continental lichen-rich mountain areas in Finland, Sweden and Norway during winter (Oksanen and Virtanen 1995). Since the 1880's, reindeer herding has been practised within separate reindeer herding cooperatives, many of which have established a pasture rotation system separating winter and summer ranges with fences (Kumpula *et al.* 2011). Reindeer select their feeding sites based on forage availability and insect avoidance, and favour peatlands for foraging during summer (Bezard *et al.* 2015, Horstkotte *et al.* 2022). Semi-dry and dry mountain birch forests are used for foraging especially in early and late summer (Bezard *et al.* 2015).

In this study, we selected a total of 21 sites from the Kutuharju Field Research Station and the Muotkatunturi reindeer herding cooperative. Out of these sites, 18 were located on the premises of the Kutuharju Field Research Station, and three in the reindeer summer ranges of the Muotkatunturi herding co-operative (Fig. 2) (Windirsch *et al.* 2021).

The Kutuharju Field Research Station spans across 44.6 km² (Fig. 2) and consists of peatlands (16.9%, 7.5 km²) and mineral soil deposits (77.0%, 34.4 km²), interspersed with lakes (4.6%, 2.1 km²) and rocky terrain without soil formation (1.5%, 0.7 km²) (coverage based on National Land Survey of Finland (2021)). Approximately 170–200 animals are kept at the station after autumn slaughter, resulting in an average reindeer density of 4.4 reindeer/km². The area is separated into four fenced areas where the animals roam during different seasons (early summer, all summer, late summer, winter). The

surrounding area outside the station's fences is part of the reindeer summer ranges of the Muotkatunturi reindeer herding co-operative, which has an area of 2580 km² with a reindeer stock of maximum 6800 individuals, leading to an average density of approximately 2.6 animals per km² (Finnish Reindeer Herders' Association 2022).

Methods

Field work

In order to detect the long-term effects of reindeer grazing on soil carbon storage, we applied a space-for-time approach, in which we selected presumably similar sites, in terms of soil type, influenced by different grazing intensities, instead of monitoring one site for a longer time period while gradually introducing herbivory. We did so in a pilot study design that aimed at sampling a high number of individual sites to gain a detailed overview over a large area.

We selected sites to cover all five grazing intensities that we were able to identify: control sites entirely without grazing, sites along reindeer migration routes (i.e., sites that the reindeer use for passage and which then experience occasional grazing pulses), and sites in the reindeer pastures (i.e., sites where the reindeer stay for long periods and which then experience long-term grazing and trampling). We selected our sites according to observed grazing intensity via animal numbers and visiting frequency over several days, as well as long-term observations made by the station and identified five different grazing intensities:

- 1) no grazing (exclosure; intensity 1; 2 sites)
- 2) occasional migration route (seasonal; intensity 2; 2 sites)
- 3) daily migration route (seasonal; intensity 3; 4 sites)
- 4) high-frequency daily migration route (seasonal; intensity 4; 4 sites)
- 5) pasture or supplementary feeding site (seasonal; intensity 5; 6 sites) (Table 1)

In addition, we sampled sites from the overall state present outside the research station premises (intensity 3; 3 sites) — which visually

matched the migration route sites within the station premises. We accounted for this as the natural grazing state, where 'natural' refers to the common grazing intensity in the context of reindeer herding in Fennoscandia throughout history.

If there were several vegetation types present within one grazing intensity, we sampled each type. This resulted in 21 sites, out of which 18 were located on the premises of the Kutuharju Field Research station (Fig. 2).

In the site labels, the letters M (mineral soil), P (peat), and F (forest) are used to identify the individual sites by main characteristics. In this naming scheme, forest sites are also peat soils but covered by trees instead of open peatlands. The letter S marks sites from the Kutuharju station summer ranges, while W marks sites from winter ranges. R marks reference sites outside the station, E indicates exclosure sites. M and P are describing the soil type as either mineral soil or peat. At peat sites, we tried capturing the complete peat column and the first few cm of underlying mineral soil (Figs. S2 and S3 in Supplementary Information). Winter ranges were sampled in June 2022, while summer ranges and reference sites were sampled in September 2020.

To avoid confounding factors such as soil erosion effects and soil moisture differences, we chose our sampling sites neither on hill tops nor steep slopes or valley bottoms, and avoided sites with ponding water or dried-up vegetation to make them as comparable as possible.

We retrieved peat cores with a Russian peat corer (50 cm sampling length, 530 cm³). For mineral soil sites, soil profiles were excavated and sampled using fixed volume cylinders. Peat cores were subsampled in the field in 5 cm increments, while at mineral soil sites samples were collected according to all visible soil horizons. Sampling with the peat sampler and fixed volume cylinders allowed us to determine the volume of each sub-sample, which later allowed us to calculate bulk densities. All samples were stored in Whirlpak sampling bags and kept cool throughout the transport to the laboratory.

On each site, we first visually assessed the main vegetation types (grassland, tundra, forest) by identifying the predominant species as well as the average height of each predominant species, both in the field and on pictures later on. We did

Table 1. Description of the sampling sites, including location, sampling depth, soil, relief and vegetation type description; E marks enclosure sites, S marks reindeer summer ranges, W marks reindeer winter ranges

Site	Latitude (°N)	Longitude (°E)	Grazing intensity (during season)	Sampling depth (cm bs)	Soil type	Relief	Vegetation type
E-1M-A	69.159500	26.991278	no grazing (~50 yrs)	40	mineral	flat, dry	mixed forest, mosses
E-1M-B	69.154113	26.971089	no grazing (~50 yrs)	17.5	mineral	slight slope, dry	open mixed forest, mosses
S-2M	69.159861	26.991250	seldom	67	mineral	flat, dry	mixed forest, mosses
S-2P	69.152357	26.971650	seldom	50	peat, bedrock below	slope, wet	mixed forest / bog edge
S-3M	69.139250	26.984000	regularly	42	mineral	valley edge, dry	heath / grassland
S-3P	69.139944	26.983778	regularly	100	peat (0–92 cm), mineral (92–100 cm)	valley, wet	heath / grassland
S-4P	69.143500	26.990000	frequently	143	peat	valley, wet	heath / grassland
S-5F	69.145806	26.994306	very often	112	peat (0–92 cm), mineral	valley, wet	birch forest, grassy
S-5P	69.146722	26.993306	very often	150	peat (0–135 cm), mineral	valley, semi-dry	grassland
S-5M	69.147222	26.991528	very often	22	mineral	mineral (135–150 cm)	grassland
W-3M	69.107441	27.015753	regularly	22	mineral	valley edge, dry	grassland
W-3P	69.103456	27.019161	regularly	25	peat, bedrock below	slope plateau	shrubby understorey
W-4M-A	69.109031	27.013619	frequently	11	mineral	valley, wet (meltwater run)	heath/grassland
W-4M-B	69.109079	27.013550	frequently	26.5	mineral	bog edge, dry	birch forest
W-4P	69.119953	27.030306	frequently	88	peat (0–66 cm), mineral content (66–88 cm)	bog edge, dry	birch forest
W-5M	69.120851	27.026792	very often	22.5	mineral	slight slope	bog in a mixed forest clearing
W-5P-A	69.109076	27.012831	very often	135	mineral	dry, flat	forest edge
W-5P-B	69.120867	27.026270	very often	176	peat (0–133 cm), mineral (133–135 cm)	valley, wet	fenn/grassland
MR	69.229750	26.795806	regularly	35	peat	valley, wet	fenn / grassland
PR	69.226778	26.810111	regularly	125	mineral	flat, dry	mixed forest, shrubby understorey
FR	69.226000	26.833417	regularly	50	peat (0–115 cm), mineral (115–125 cm)	lakeside peatland, wet	heath/grassland, mosses
					peat (0–30 cm), mineral (30–50 cm)	valley, semi-dry	birch forest, grassy understorey

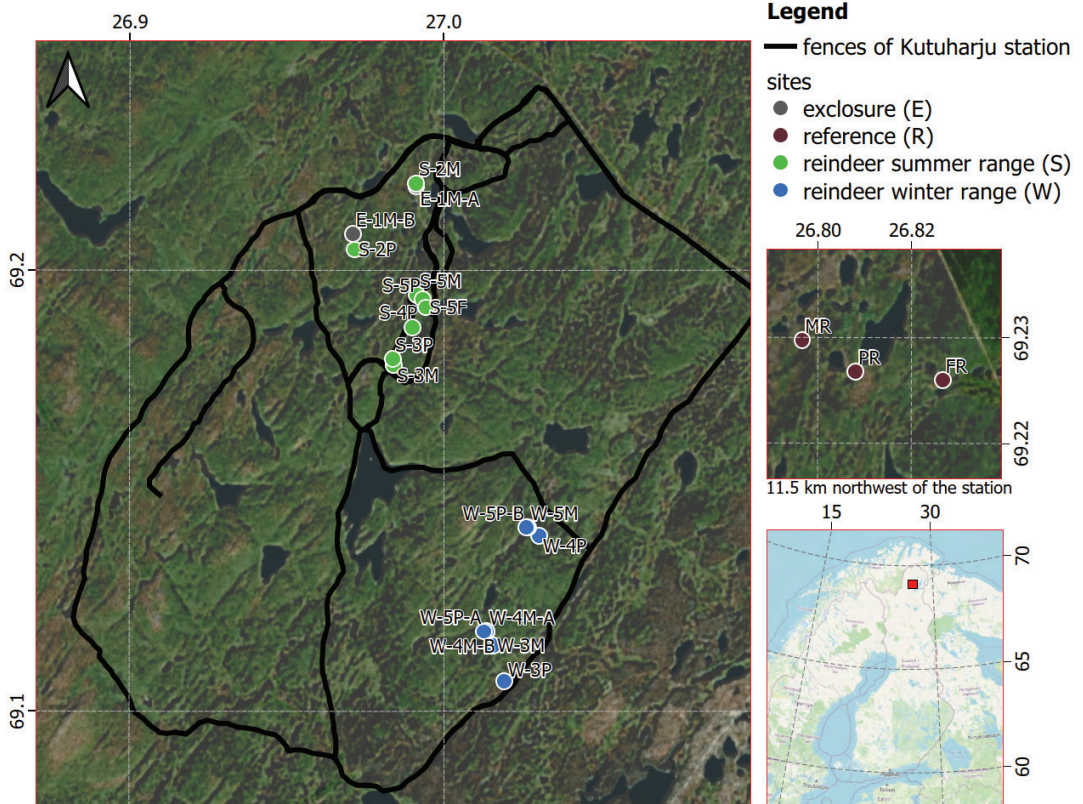


Fig 2. Satellite imagery and topographic map of the study sites; left: satellite image of the sampling locations on the Kutuharju station premises; right top: satellite image of the sampling locations outside the research station in the Muotkatunturi herding district; right bottom: study area location map (red square); basemap provided by ESRI and OSM.

this on 1 m² plots, in which centre we collected soil samples in the form of one soil core or soil profile afterwards. The plots were selected for not having trees, as tree roots would obstruct the soil sampling. However, we accounted for trees being present in the wider surrounding (approximately 10 m × 10 m) to identify a site as either forest or open landscape. The dominance of vegetation species was estimated by the approximate area covered on the 1 m² plots. At many sites, we found one species each to cover more than 50% of the plot. We did not aim to account for all species present, but the most abundant ones, to identify the main differences between plots.

Laboratory analysis

We determined the absolute water content of all samples by weighing (Mettler Toledo KERN

FCB 8K0.1, accuracy 0.1 g) them pre- and post-freeze drying (Zirbus Sublimator 15) and related this to wet weight. Using the sample volumes calculated by the peat corer volume and sample thickness, we calculated the bulk density. Afterwards, samples were split into subsamples for biogeochemical and sedimentological analysis.

Using a planetary mill (Fritsch Pulverisette 5), samples for biogeochemical analysis were homogenised and weighed into steel crucibles for elemental analysis. Total organic carbon (TOC) and total nitrogen (TN) were determined by combustion, using a soliTOC cube and a rapidMAX N elemental analyser (both Elementar Analysensysteme). These parameters are reported in percentage by weight (wt%).

Carbon to nitrogen ratio (TOC/TN) was calculated from TOC and TN, used as a proxy for OM decomposition state by assuming a stable source (Strauss *et al.* 2015).

In order to have an indication on the quality and source of the organic matter, we analysed stable carbon isotope ratios ($\delta^{13}\text{C}$). For this, the previously homogenised samples were treated with hydrochloric acid at 50°C for three hours to remove carbonates. After washing the sample acid free, we used a Delta V Advantage Isotope Ratio MS supplement equipped with a Flash 2000 Organic elemental analyser for isotope measurement. The resulting values are given in ‰ in relation to the Vienna Pee Dee Belemnite (‰ vs.VPDB) standard (Coplen *et al.* 2006).

In addition, we took OM for radiocarbon dating from selected samples from the dried original samples, and used the Mini Carbon Dating System (MICADAS) at Alfred Wegener Institute

Bremerhaven (Mollenhauer *et al.* 2021). Results were calculated in calibrated years before present (cal yr BP, meaning before 1950) using the calibration software Calib ver. 8.2 and applying the IntCal20 calibration curve (Reimer *et al.* 2020, Stuiver *et al.* 2021).

For sample reference, the mean sample depth is used for all soil parameters throughout this manuscript. Depth is given in cm below surface (cm bs).

Data analysis and calculations

We used a principal component analysis (PCA) comparing the top 30 cm of all our sites in terms of bulk density, TOC, $\delta^{13}\text{C}$ ratios, TOC/TN ratios and water content, categorised by grazing intensity, soil type (mineral soil or peat) and season of animal activity (summer, winter or no seasonality) to assess which measured parameters have the strongest effects within our dataset. For this, data were normalised between zero and one, using the following function: $\text{function}(x) \{ (x - \min(x)) / \max(x) - \min(x) \}$, where x is the dataset and $\min(x)$ and $\max(x)$ mark the minimum and maximum value of dataset x .

For the PCA we used 'prcomp' on the normalised data. We chose the top 30 cm as grazing effects are usually most visible in the upper parts of a soil column. All calculations were done in the R environment using the 'stats' package (R Core Team 2021).

We further calculated weighted mean TOC values in wt% for the samples of the top 30 cm of each site, using Eq. 1:

$$\text{meanTOC} = \left[\begin{array}{l} (h(\text{sample } A) \times \\ \text{TOC}(\text{sample } A)) + \\ (h(\text{sample } B) \times \\ \text{TOC}(\text{sample } B)) + \dots \end{array} \right] / 30, \quad (1)$$

where h is the height as the vertical sample dimension in cm, TOC is the total organic carbon measurement value in percentage by weight, and 30 is the total depth that samples used in this calculation originate from, given in cm below surface.

Sampling gaps were interpolated from the adjacent sample. We did this for a more readable comparison across grazing intensities, soil types and seasonality.

For better comparability of our study sites, we also calculated soil organic carbon (SOC) stocks in kg m^{-2} , restricted to the top 30 cm due to large differences in sampling depth between sites. SOC was calculated using Eq. 2.

$$\text{SOC} [\text{kg m}^{-2}] = \left[\begin{array}{l} \frac{\text{TOC}[\text{wt}\%]}{100} \times \\ \text{bulk density} [\text{g cm}^{-3}] \times \\ \text{sample height} [\text{cm}] \times 10 \end{array} \right]. \quad (2)$$

Due to small sample numbers within each grazing intensity, especially when differentiating between soil types, our dataset does not allow for significance testing of differences in soil parameters.

Results

Core descriptions

Almost all mineral soil profiles featured similar horizons, although with varying horizon thickness (Fig. 3, Fig. S2 in Supplementary Information). They consist of an organic layer on top, followed by an organic-rich soil layer in E-1M-B, MR, S-3M and W-3M. In W-5M, the organic top layer was compressed into the underlying

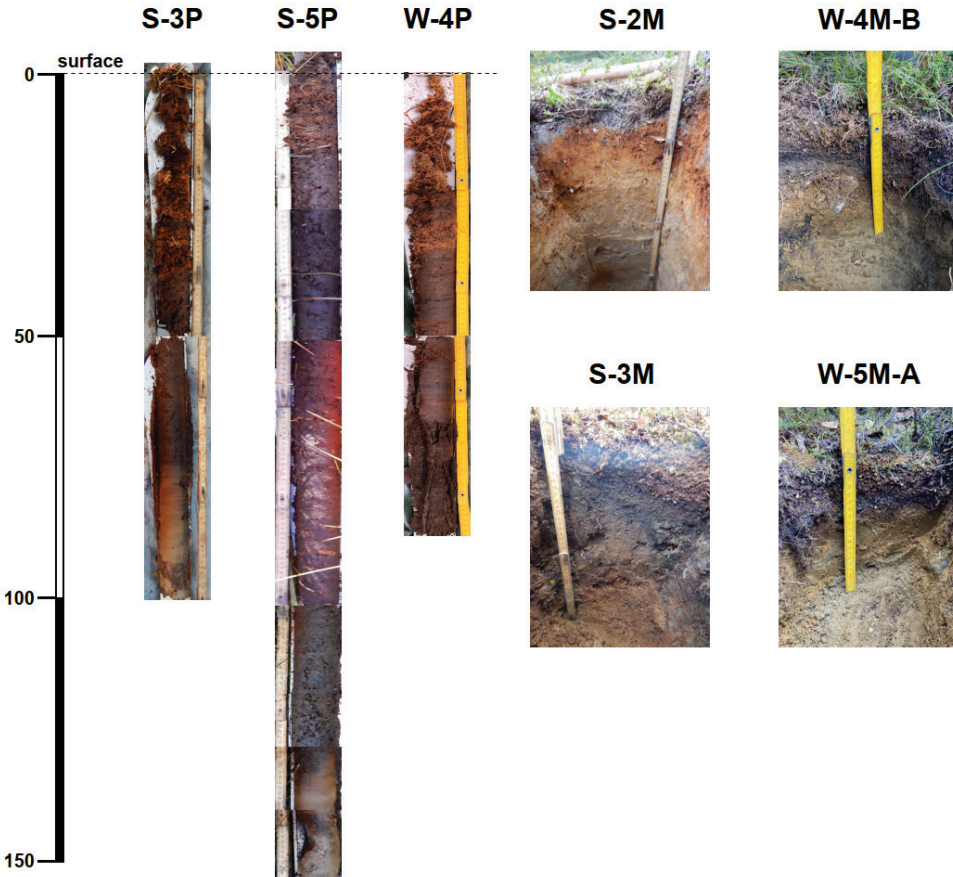


Fig 3. Representative field photos of the peat cores obtained at S-3P, S-5P and W- 4P, as well as soil profiles excavated at S-2M, S-3M, W-4M-B and W-5M-A; for field photos of all sites please see Figs S2 and S3 in Supplementary Information.

soil (Table 2). The organic-rich soil layer is followed by a pale, sandy eluvial horizon and an orange-reddish illuvial horizon (7.5YR ~ 5/8 on Munsell colour chart). At sites E-1M-A and W-4M-A and -B, the organic-rich soil layer was not found. Instead, the organic layer on top of the soil was directly followed by an eluvial horizon. Underneath, the eluvial horizon is followed by a yellowish (2.5Y 5/4) sand horizon down to the end of the profile. However, this layer was not reached at all mineral soil sites.

At the peat sites, the peat column (between 25 cm (W-3P) and 143 cm (S-4P)) was underlain by sandy material (Fig. 3). The peat column was divisible by the degradation state (Table 2). There were differences in peat source material, which was (*Sphagnum*) moss in S-2P, PR, W- 4P, W-5P-A and W-5P-B, while at the other sites the

material was more heterogeneous, darker and often more decomposed. However, similar moss peat appeared deeper in the profiles at S-3P and S-5F.

Vegetation

We encountered four main vegetation types at our sampling locations. The first is a mixed forest mainly consisting of *Pinus sylvestris* and *Betula pubescens* ssp. *czerepanovii* trees, which was found at sites E-1M-A, S-2M, W-3M, W-4M-A and -B, W-5M and MR. There were differences in the understorey vegetation, though (Table 2).

The second vegetation type we found is best described as a wet birch forest, consisting mainly of *B. czerepanovii*. This type, found at sites S-5F,

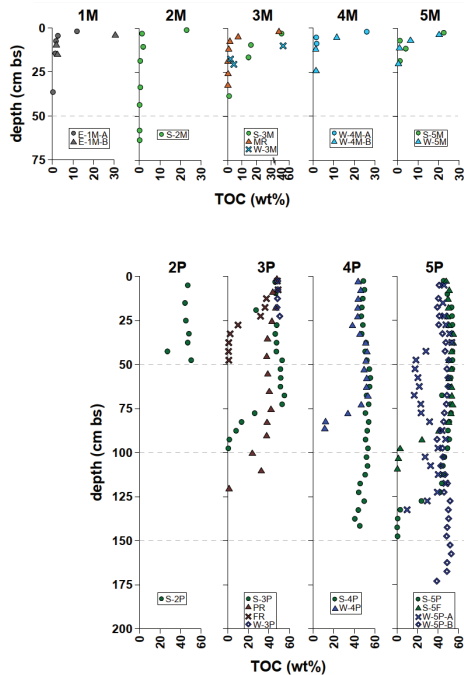


Fig 4. TOC for all sites, plotted over depth; grazing intensity increases from left to right; a) mineral soil sites; b) peat sites; different symbols are for different sites within one plot; green indicates summer sites, blue winter sites, grey enclosure sites, and brown colours mark reference sites with natural grazing regime outside the reindeer fences. Note the differently scaled x-axes for mineral soil and peat sites as well as the axis break in 3M.

W-4P and FR, featured a ground layer holding *Vaccinium*, and some *Sphagnum* spp. underneath (Table 2).

The third vegetation type, found in non-forest areas, was a tundra-like mix of heath and grassland vegetation. It is predominantly covered by *Salix* sp., *Vaccinium* sp. and *Empetrum nigrum* and was found at S-2P, S-3M, S-3P, W-3P, S-4P and PR (Table 2).

The fourth vegetation type, found only at grazing-intensive sites S-5P, W-5P-A and -B and S-5M, was a grassland with no significant shrub layer and very few species. Summer sites were strongly dominated (> 90% coverage) by *D. cespitosa*, which grew nest- or tussock-like and reached up to 120 cm in height at S-5P and up to 70 cm in height at S-5M, while on winter sites *Eriophorum* made up the vast majority of graminoid vegetation (Table 2). For detailed vegetation records per site, please see Table 2.

Carbon parameters

(a) Total organic carbon (TOC)

At mineral soil sites, the maximum sampling depth was reached at S-2M with 67 cm bs (Fig. 4a). For all mineral soil sites, TOC was highest in the uppermost sample, representing the organic top layer, and declined with depth. The highest value across mineral soil sites was found in W-3M (51.30 wt% at 10 cm bs), while the lowest value occurred in W-5M (0.44 wt% at 19.75 cm bs).

At peat sites, TOC was high and homogeneous in the peat column, with a sharp drop in the underlying mineral soil (Fig. 4b). Within the peat columns, the TOC ranged between 17.62 wt% (W-5P-A at 52.5 cm bs) and 55.67 wt% (S-4P at 57.5 cm bs). In the underlying mineral soil, excluding the visible mineral soil–peat mix phase, TOC ranged between 0.24 wt% (S-5P at 142.5 cm bs) and 1.58 wt% (S-3P at 92.5 cm bs). In general, TOC was higher in the upper core parts, in which S-4P marks an exception.

TOC/TN and $\delta^{13}\text{C}$ ratios

We calculated the TOC/TN ratio for 221 out of 255 samples. For the remaining samples (often the lowermost samples of a core, and only mineral soil samples) the TN was below the detection limit of 0.1 wt%. As excluding these samples would cause a systematic bias we decided to set the TN values to 0.05 wt% (half the detection limit). This was the case for 34 samples. For four samples (E-1M-5, S-2M-6, -7, and -8), $\delta^{13}\text{C}$ measurement was not successful, as a result of low TOC content. Therefore, we excluded these four samples from TOC/TN– $\delta^{13}\text{C}$ analysis (Fig. S4 in Supplementary Information).

For the mineral soil sites, we found highest TOC/TN values at intensity 3 with 43.76 (S-3M; 3 cm bs), with similar values occurring in intensities 1 and 2 (summer) as well as 5 (winter) (Fig. S4 in Supplementary Information). The lowest TOC/TN value in mineral soils is found in S-5M (11.28 at 7 cm bs), indicating a less decomposed state of the OM. With $\delta^{13}\text{C}$, all values range between -29.99 (S-3M; 3 cm bs)

Table 2. Detailed soil and vegetation descriptions of the sampling sites; vegetation coverage identifies only the most abundant species; soil horizons given as "eh" mark eluvial horizons. "ih" marks illuvial horizons.

Site	Soil layers (depth, given in cm bs)	Vegetation composition and coverage (% of 1 m ²)
E-1M-A	podsol; organic layer (0–4); eh (4–5); ih (5–10); transition (10–19); pale sand with gravel (19–41)	<i>Cladonia rangiferina</i> (76%); <i>Vaccinium uliginosum</i> (12%); <i>Empetrum nigrum</i> (6%); <i>Vaccinium myrtillus</i> (2%); <i>Vaccinium vitis-idaea</i> (1%)
E-1M-B	podsol; organic layer (0–4); organic-rich soil (4–7); eh (7–10); ih (10–25); gravel/bedrock	<i>Cladonia rangiferina</i> (36%); <i>Empetrum nigrum</i> (28%); <i>Vaccinium myrtillus</i> (6%); <i>Vaccinium uliginosum</i> (4%); <i>Ledum palustre</i> (3%); brown moss
S-2M	podsol; organic layer (0–2); eh (2–4); ih (4–15); transition (15–25); pale sand (25–70)	<i>Cladonia arbuscula</i> (38%); <i>Vaccinium vitis-idaea</i> (17%); <i>Vaccinium uliginosum</i> (16%); mossy understorey
S-2P	fresh moss peat (0–30); light-brown moss peat, hardly decomposed (30–41); brown, decomposed peat (41–50)	<i>Eriophorum</i> (43%); <i>Vaccinium uliginosum</i> (14%); <i>Rubus chamaemorus</i> (11%); <i>Ledum palustre</i> (10%); <i>Betula nana</i> (8%); <i>Empetrum nigrum</i> (8%); <i>Vaccinium myrtillus</i> (2%); <i>Vaccinium vitis-idaea</i> (2%); <i>Calluna vulgaris</i> (1%); <i>Andromeda polifolia</i> (1%); mossy understorey
S-3M	podsol; organic layer (0–6); organic-rich soil (6–13); greyish silty sand with gravel (13–23); brownish sand (23–40); gravel/bedrock	<i>Salix</i> (shrubs) (46%); <i>Betula nana</i> (24%); <i>Empetrum nigrum</i> (13%); <i>Vaccinium uliginosum</i> (9%); <i>Vaccinium myrtillus</i> (8%); <i>Ledum palustre</i> (4%); mossy understorey
S-3P	organic layer (0–6); dark, undecomposed peat (6–13); light-brown moss peat, hardly decomposed (13–37); dark, sandy peat (37–92); greyish sand with gravel (92–100)	<i>Eriophorum</i> (52%); <i>Empetrum nigrum</i> (28%); <i>Vaccinium uliginosum</i> (18%); <i>Rubus chamaemorus</i> (6%); <i>Ledum palustre</i> (3%); other grasses (2–3%)
S-4P	organic layer (0–2); dark, undecomposed peat (2–19); light-brown moss peat (19–33); dark peat (33–81); dark peat with macro organics (81–133); dark, compact peat (133–143)	<i>Sphagnum</i> (33%); <i>Empetrum nigrum</i> (32%); <i>Vaccinium myrtillus</i> (17%); <i>Vaccinium uliginosum</i> (9%); <i>Betula nana</i> (4%)
S-5F	organic layer (0–4); dark, undecomposed peat (4–19); light-brown moss peat (19–22); dark peat (22–45); dark peat, hardly decomposed (45–57); dark peat (57–82); sandy transition (82–92); organic-rich sand (92–101); grey sand (101–112)	<i>Eriophorum</i> (57%); <i>Vaccinium uliginosum</i> (22%); <i>Rubus chamaemorus</i> (6%); <i>Vaccinium vitis-idaea</i> (5%); <i>Equisetum arvense</i> (1%); mossy understorey
S-5P	peat, hardly decomposed (0–15); peat (15–60); peat with macro organics (60–125); sandy transition (125–135); grey sand (135–150)	<i>Deschampsia cespitosa</i> (> 95%)
S-5M	podsol; organic layer (0–5); eh (5–6); ih (6–15); pale sand with gravel (15–25); gravel/bedrock	<i>Deschampsia cespitosa</i> (> 95%)

Table 2. ...continued

Site	Soil layers (depth, given in cm bs)	Vegetation composition and coverage (% of 1 m ²)
W-3M	podsol; organic layer (0–4); organic-rich soil (4–16); eh (16–19); ih (19–22); gravel/bedrock	<i>Vaccinium myrtillus</i> (48%); <i>Vaccinium uliginosum</i> (23%); <i>Eriophorum</i> (6%); <i>Empetrum nigrum</i> (12%); <i>Vaccinium vitis-idaea</i> (9%); other grasses (1–2%); mossy understorey
W-3P	dark peat (0–25); gravel/bedrock	<i>Eriophorum</i> (72%); <i>Sphagnum</i> (19%); <i>Equisetum</i> (3%); <i>Carex appendiculata</i> (2%); <i>Andromeda polifolia</i> (1%); <i>Potentilla palustris</i> (1%); <i>Vaccinium uliginosum</i> (1%)
W-4M-A	podsol; organic layer (0–4); eh (4–6.5); ih (6.5–12); gravell/bedrock	<i>Empetrum nigrum</i> (49%); <i>Vaccinium uliginosum</i> (34%); <i>Vaccinium myrtillus</i> (11%); <i>Eriophorum</i> (5%); <i>Cladonia rangiferina</i> (3%); <i>Vaccinium vitis-idaea</i> (2%); mossy understorey
W-4M-B	podsol; organic layer (0–8); eh (8–9); ih (9–14); yellowish sand (14–28); gravel/bedrock	<i>Eriophorum</i> (previous year) (51%); <i>Empetrum nigrum</i> (31%); <i>Vaccinium myrtillus</i> (11%); <i>Vaccinium vitis-idaea</i> (6%)
W-4P	moss peat (0–33); dark, compact, decomposed peat (33–52); moss peat (52–55); dark, brown peat (55–66); dark, sandy peat (66–88)	<i>Eriophorum</i> (17%); <i>Empetrum nigrum</i> (16%); <i>Vaccinium uliginosum</i> (11%); <i>Betula nana</i> (5%); <i>Rubus chamaemorus</i> (4%); <i>Ledum palustre</i> (1%); <i>Vaccinium macrocarpon</i> (1%); mossy understorey
W-5M	podsol; organic-rich soil (0–6); eh (6–7); ih (7–17); pale sand with gravel (17–22.5)	<i>Empetrum nigrum</i> (47%); <i>Phyllodoce caerulea</i> (9%); <i>Vaccinium myrtillus</i> (8%); <i>Cladonia rangiferina</i> (7%); <i>Vaccinium uliginosum</i> (5%); <i>Ledum palustre</i> (4%); <i>Vaccinium vitis-idaea</i> (2%); mossy understorey
W-5P-A	fresh peat (0–20); brown, decomposed peat (20–133); grey silty sand (133–135)	<i>Eriophorum</i> (previous year) (63%); <i>Vaccinium uliginosum</i> (11%); <i>Betula nana</i> (9%); <i>Empetrum nigrum</i> (8%); <i>Rubus chamaemorus</i> (2%); mossy understorey
W-5P-B	fresh peat (0–10); dark, decomposed peat (10–145); dark, very fine peat (145–165); light-brown peat (165–176)	<i>Eriophorum</i> (20%); <i>Potentilla palustris</i> (8%); <i>Andromeda polifolia</i> (1%); <i>Eriophorum</i> (previous year) (60%); <i>Equisetum arvense</i> L. (1%); <i>Viola epipsila</i> (1%); mossy understorey
MR	podsol; organic layer (0–3); organic-rich, sandy soil (3–6); eh (6–8); ih (8–18); pale sand (18–35); gravel/bedrock	<i>Cladonia stellaris</i> (21%); <i>Vaccinium vitis-idaea</i> (13%); mosses
PR	organic layer (0–2); moss peat, hardly decomposed (2–15); dark peat (15–115); yellowish sand (115–125)	<i>Empetrum nigrum</i> (27%); <i>Cladonia stellaris</i> (16%); <i>Salix</i> (shrubs) (14%); <i>Vaccinium uliginosum</i> (8%); <i>Ledum palustre</i> (7%); <i>Vaccinium vitis-idaea</i> (3%); mossy understorey
FR	organic layer (0–5); dark peat with roots (5–25); sandy peat (25–30); grey sand with gravel (30–50)	<i>Vaccinium uliginosum</i> (43%); <i>Empetrum nigrum</i> (22%); <i>Vaccinium vitis-idaea</i> (16%); <i>Salix</i> (13%); <i>Betula nana</i> (11%); <i>Eriophorum</i> (10%); <i>Ledum palustre</i> (2 %); mossy understorey

and -25.99% vs. VPDB (W-5M at 19.75 cm bs). At the peat sites, we found much higher TOC/TN values, with a maximum value of 109.37 at intensity 2 (S-2P; 15 cm bs) (Fig. S4 in Supplementary Information). The lowest value occurred in FR (intensity 3; 4.88 at 32.5 cm bs). The TOC/TN maximum found in PR also features the highest $\delta^{13}\text{C}$ values with -25.44% vs. VPDB. In general, values for all peat cores lie between -29.87% vs. VPDB (W-5P-B at 173 cm bs) and -26.33% vs. VPDB (PR at 17.5 cm bs). Grazing intensity 3 shows the greatest range $\delta^{13}\text{C}$ values, while the strongest spread in TOC/TN ratios is found in summer peat sites at intensity 2.

SOC density

SOC stocks in total as well as in the upper 30 cm show no trend across either seasonality or grazing intensity (Table 3). However, using their mean values across soil types and seasonality or soil type and grazing intensity allows for easier comparison between sites. Highest SOC value was found at site PR (26.47 kg m^{-2}), lowest value occurred in W-4M-A (3.45 kg m^{-2}) with values ranging between 4.95 and 26.47 kg m^{-2} for peat, and 3.45 and 19.4 kg m^{-2} for mineral soils. Due to missing bulk density values for site W-3M, we did not calculate SOC density here.

Based on the station premises' coverage with peatlands (16.9%, 7.5 km^2) and mineral soil (77.0%, 34.4 km^2) we calculated 83.08 ± 37.92 kilotons (kt) of carbon for the top 30 cm of peat sites across the station area, and 256.21 ± 177.11 kt for mineral soil sites, omitting areas covered by lakes and rock. This gives us a total SOC stock of 339.29 ± 215.03 kt for the uppermost 30 cm of soil for the 44.6 km^2 station area ($7.61 \pm 4.82\text{ kt km}^{-2}$).

Bulk density

At all mineral soil sites, dry bulk density shows a converse behaviour in relation to TOC, resulting in highest bulk density values for those samples with the lowest TOC (Fig. S5a). Bulk density was lowest in the organic top layer with values between 0.09 g cm^{-3} (MR, 1.5 cm bs) and

0.39 g cm^{-3} (W-4M-B, 4.75 cm bs). The maximum bulk density was found in W-4M-A with 1.77 g cm^{-3} (8.75 cm bs). Bulk density could not be measured for site W-3M due to equipment restraints in the field.

Sampling also did not allow for bulk density measurement in samples S-4P-7 (32.5 cm bs) and W-3P-5 (22.5 cm bs). At peat sites, bulk density values within the peat column ranged between 0.004 g cm^{-3} (W-5P-B, 12.5 cm bs) and 0.54 g cm^{-3} (W-5P-A, 67.5 cm bs) and reached a maximum of 2.49 g cm^{-3} in the underlying mineral soil at S-5P (147.5 cm bs) (Fig. S5b in Supplementary Information).

Radiocarbon ages

For radiocarbon ages, we used macro-organic remains, especially moss and grass root remains for 42 samples. However, due to low content of such remains in the mineral soils sampled, we also used bulk TOC of 12 additional samples for dating mineral sediments. In the dated samples closest to the surface, we found modern material (younger than 1950 AD) at some sites. This was the case, in mineral soils, for E-1M-A (7.5 cm bs), E-1M-B (9.25 cm bs and 14.75 cm bs), S-3M (9.5 cm bs), S-5M (11.5 cm bs), W-3M (20.5 cm bs), W-4M-A (8.75 cm bs) and W-4M-B (23.75 cm bs), and W-5M (6.5 cm bs and 19.75 cm bs). Age-depth relations show similar radiocarbon ages at similar depth, giving 3239 cal yr BP in E-1M (36.5 cm bs), 3283 cal yr BP in MR (32 cm bs) and 3853 cal yr BP in S-3M (38.5 cm bs). The oldest material in mineral soil sites was found in S-2M with 4738 cal yr BP (63.5 cm bs). For full radiocarbon dating details, please see Table S1 in Supplementary Information.

For peat sites, modern material was encountered at site FR for samples at 7.5 cm bs and 22.5 cm bs as well as at site S-2P (25 cm bs). In general, we found older ages at peat sites. Again, age-depth relations are similar across some sites with 7650 cal yr BP in S-4P (57.5 cm bs), 7589 cal yr BP in S-5F (52.5 cm bs) and 7698 cal yr BP in S-5P (82.5 cm bs) and 7397 cal yr BP in W-5P-A (82.5 cm bs). W-5P-B held much younger material, reaching

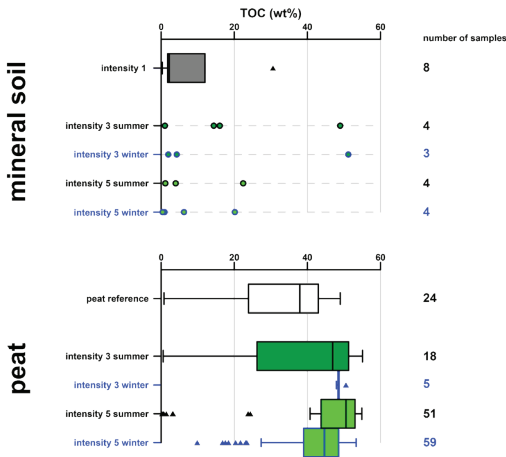


Fig 5. Boxplots of TOC concentration of all non-grazed (E-1M-A, E-1M-B; grey), summer migration route (grazing intensity 3: S-3M, S-3P; dark green, black line), winter migration route (grazing intensity 3: W-3M, W-3P; dark green, blue line), summer pasture (grazing intensity 5: S-5F, S-5P, S-5M; light green, black line) and winter pasture (grazing intensity 5: W-5P-A, W-5P-B, W-5M; light green, blue line) sites, differentiated by soil type; peat reference sites (PR, FR) were additionally added; for mineral soils, intensity 1 (exclosures) are used as reference; median indicated by vertical line in the boxes; box margins show the upper and lower quartile; whiskers mark the range of the data; outliers (outside 1.5 time the interquartile range) are marked by black triangles; the number of samples per plot is given in each box; if less than 5 samples are in one group, no boxplot was created but the individual samples were plotted instead, using a dashed line for orientation.

6332 cal yr BP at 173 cm bs. The maximum ages within the peat column are also similar across some cores, with 8650 cal yr BP in W-5P-A (132.5 cm bs), 8714 cal yr BP in PR (110 cm bs), 9815 cal yr BP in S-4P (141.5 cm bs), 9643 cal yr BP in S-5F (92.5 cm bs) and 9147 cal yr BP in S-5P (127.5 cm bs). In S-5P, an age inversion is found between the peat column and the underlying sand, which was dated to 5584 cal yr BP at 147.5 cm bs.

Comparative data analysis

When visualising the data, the differences in TOC concentration range and median between migration route sites and pasture sites is clearly visible (Fig. 5). The range of these TOC data

is similar for grazing intensity-corresponding summer and winter sites. For mineral soil sites, the uppermost and organic-rich sample shows much higher TOC values compared to the underlying samples, increasing the range. For mineral soils, we found a range from 1.06 to 49.01 wt% TOC in summer migration route (intensity 3 summer; $n = 4$ samples, median of 15.25 wt%), and a range from 1.98 to 51.23 wt% TOC in winter migration route (intensity 3 winter; $n = 3$ samples, median of 4.29 wt%) (Fig. 5 mineral soil). For pasture sites on mineral soil, we found a range of 1.17 to 22.47 wt% TOC for summer (intensity 5 summer; $n = 4$ samples, median of 2.59 wt%) and a range of 0.44 to 20.19 wt% TOC for winter (intensity 5 winter; $n = 4$ samples, median of 3.61 wt%).

The median for non-grazed mineral soil sites (intensity 1, $n = 8$ samples) is 6.7 wt%. Comparing the samples from peat sites, we found a range of 0.56 to 52.91 wt% TOC for summer migration route (intensity 3 summer; $n = 18$ samples, median of 46.92 wt%) and a range of 47.98 to 50.59 wt% TOC for winter migration route (intensity 3 winter; $n = 5$ samples, median of 48.60 wt%) (Fig. 5: peat). On pasture / feeding peat sites, we found a range of 0.24 to 54.90 wt% TOC for summer pastures (intensity 5 summer; $n = 51$ samples, median of 50.57 wt%), and a range of 9.91 to 53.38 wt% TOC for winter feeding sites (intensity 5 winter; $n = 59$ samples, median of 44.70 wt%). For the peat reference sites outside the station area, we found a range from 0.78 to 49.00 wt% TOC ($n = 24$ samples, median of 37.94 wt%).

Comparing the mean TOC values of the top 30 cm across grazing intensities, soil types and seasonalities, we see an increase for summer peat sites with increasing grazing intensity (Fig. 6). Contrary to this, values decrease for summer mineral soil, winter mineral soil and winter peat sites. Under grazing intensities 2, 4 and 5, we see similar values as found at the exclosure sites, with the mineral soil at intensity 3 which was not affected by a clear grazing seasonality (MR) showing a similar mean TOC. The peat reference sites PR and FR (intensity 3, no seasonality) is in line with the value for intensity 3 summer peat, justifying our understanding of these sites as intensity 3 (migration route).

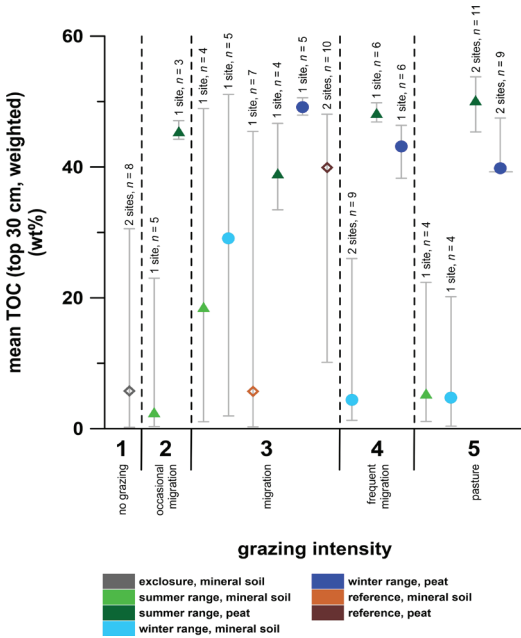


Fig 6. Mean TOC for the top 30 cm, summarised for sites with identical grazing intensity, soil type and seasonality; triangles indicate summer sites, dots indicate winter sites, rhombuses indicate sites with no seasonality; the TOC value range of the samples used in these mean values is given as grey error bars.

PCA revealed a stretch along bulk density among samples of the top 30 cm of all sites (Fig. 7). TOC and water content are correlating. The combination of $\delta^{13}C$ ratios and TOC/TN ratios as markers of OM degradation shows a spread on the Y-axis.

Discussion

Reindeer impact on soil carbon storage

For this study, seasonality at the sites was expected to be crucial. On the one hand in summer, grazing effects including trampling, fertilisation via faeces, and browsing in summer affect mainly vegetation. On the other hand, in winter the animal effects on the snow cover are more important. High grazing intensity in summer shifts vegetation towards graminoid-dominated and mainly light-coloured vegetation, increasing albedo and hence leading to a relatively lower heat transfer into the ground as

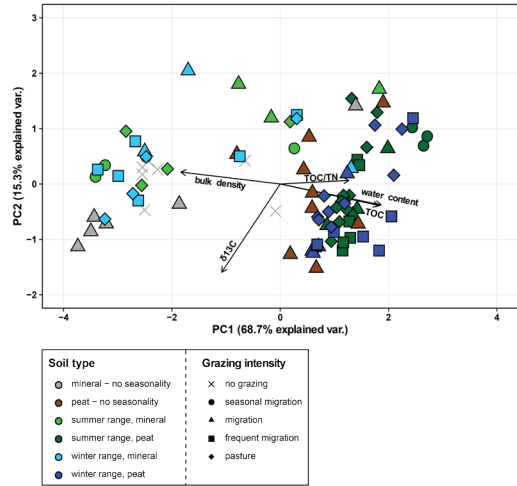


Fig 7. Principal component analysis of the top 30 cm of all sites across the parameters bulk density, $\delta^{13}C$ ratios, TOC/TN ratio, soil type, water content and TOC; shapes encode different grazing intensities; colours indicate seasonality and soil type.

with short tundra-like vegetation (te Beest *et al.* 2016). In contrast, winter grazing reduces snow cover, baring the ground to cold air, inducing a cooling effect on the soil (Beer *et al.* 2020).

Looking at our data, like TOC, all median values are close together when comparing peat sites across grazing intensities. We found the interquartile ranges of migration and pasture sites overlapping largely, regardless of seasonality (Fig. 5 peat). For mineral soils, the median differences are much larger, but since this is a comparison of individual sites (1 site per grazing intensity and seasonality, except for the enclosures), this difference is mainly due to the TOC content in the uppermost sample, taken from organic-rich soil horizons, and therefore most likely depending on the vegetation growing on top. No clear trend along grazing intensity was found. Also, SOC densities of the top 30 cm show no clear trend along grazing intensity or grazing seasonality (Table 3). Thus, following our research question if reindeer grazing increases soil carbon storage, and under which grazing intensity and seasonality this effect is greatest, we found no clear evidence for strong differences in TOC between grazing intensities. As TOC is slightly higher on summer pastures compared to summer migration route sites, artifi-

cially intensified grazing appears to increase soil carbon storage in comparison to natural grazing intensities (Fig. 4-3M and -3P). In winter sites, this effect is not visible, but the animal impact on snow might be relevant here: At the feeding sites (intensity 5) on the winter ranges, supplementary feeding is practiced, so there is less need for the animals to dig through snow. Instead, the animals will compact the snow, while snow removal and breakup is more likely along migration tracks in this case. The proposed effect of ground cooling via snow removal would therefore not be in place at our study sites, but might occur at winter pastures without supplementary feeding.

The small differences in TOC we observed are likely related to the pre-existing and general soil conditions, resulting in similar TOC values across mineral soil sites as well as across peat sites (Fig. 4). The differences in TOC range between migration route sites versus pasture sites in peat (Fig. 5 peat) are likely originating from the presence of underlying TOC-poor min-

eral soil in some of the sampled cores, lowering the median value. Other options are that the differences in grazing intensity or frequency, reindeer stock size or grazing duration were not strong enough to see differences in SOC in our study area. Opposing to this, findings from a similar study in a permafrost area with only 25 years of intensive grazing history already show differences in soil TOC storage (Windirsch *et al.* 2022a). Yet, our results agree with findings from other studies conducted on boreal forest sites in northern Fennoscandia that also found no effect of reindeer presence on soil carbon storage (Stark *et al.* 2008, Köster *et al.* 2015). This leads to the assumption that frozen ground would have a major impact and the increased carbon storage under grazing pressure observed in permafrost is linked to the animals maintaining a frozen ground state, hence reducing OM degradation. Therefore, our hypothesis of intensive grazing leading to higher soil carbon storage was not proven for this study site on seasonally frozen ground. We state that an increase of soil carbon storage as a result of intensive animal grazing occurs only in permafrost-affected landscapes, where the ground underneath the active layer can be kept frozen by animal activity, hence reducing OM degradation (Windirsch *et al.* 2022a).

Table 3. SOC stocks calculated for the top 30 cm of each site, given in kg m⁻², SOC density range per cm depth of the samples used for SOC stock calculation, given in g cm⁻³, and the number of samples in the top 30 cm (*n*)

Site	SOC 0–30 cm (kg m ⁻²)	SOC density range (g cm ⁻³)	<i>n</i>
E-1M-A	4.39	0.06–2.98	5
E-1M-B	11.32	0.36–1.86	3
S-2M	3.60	0.09–2.18	5
S-2P	4.95	0.13–0.19	3
S-3M	19.40	0.24–1.86	4
S-3P	10.25	0.21–1.71	4
S-4P	7.56	0.63–1.39	6
S-5M	7.43	0.16–1.14	4
S-5P	22.66	0.76–2.77	5
S-5F	11.36	0.71–2.18	6
W-3M	n/a	n/a	n/a
W-3P	15.92	1.19–1.46	5
W-4M-A	3.45	0.66–0.82	3
W-4M-B	6.14	0.23–0.81	3
W-4P	10.19	0.23–1.17	6
W-5M	3.88	0.09–10.17	4
W-5P-A	8.99	0.15–1.22	4
W-5P-B	7.32	0.03–0.98	5
MR	4.51	0.04–1.93	7
PR	26.47	0.51–2.20	4
FR	19.21	0.73–4.19	6

Reindeer impact on vegetation

We found strong contrasts in vegetation cover between grazing intensities. While the exclusion of reindeer promotes an increase or rather preservation of *Cladonia rangiferina* (Inga 2009), summer pasture sites are more likely to be transformed into grasslands dominated by *Deschampsia cespitosa* (Rosef *et al.* 2004), with a reduced or missing shrub layer. On winter pastures where the animals trample down the snow cover but hardly feed on the local vegetation due to supplementary feeding, vegetation is also graminoid-dominated but still features common tundra vegetation such as *Vaccinium* ssp. and *Empetrum nigrum*. Studies conducted in the same study area have shown that the biomass of *Empetrum nigrum* has increased substantially over the recent decades (Stark *et al.* 2021). The gradual transformation from tundra

vegetation towards graminoid-dominated vegetation as a result of animal impacts is best seen by comparing the shrubby vegetation found at migration route sites of this study, the tundra-like vegetation at sites with high revisiting frequency (intensity 4) featuring some *D. cespitosa* (summer; S-4P) or *Eriophorum* (W-4P) and the vast grasslands found at the pasture sites. The x-axis spread in TOC/TN- $\delta^{13}\text{C}$ analysis (Fig. S4 in Supplementary Information) is therefore most likely not an indicator of different degrees of OM decomposition, but a source signal produced by different vegetation communities found at the different sites. The very high TOC/TN values at S-2P, W-4P and W-5M are likely a result of the presence of mosses and lichen that would disappear under more intensive animal impact.

Vegetation change effects with increasing grazing intensity are less visible at winter sites. Thermal aspects of the animals' physical impacts on winter sites (snow removal, snow compaction), resulting in a proposed cooling effect on the ground and hence increased carbon storage (Sturm *et al.* 2005, Falk *et al.* 2015) or rather reduced OM decomposition (Davidson and Janssens 2006, Walz *et al.* 2017) could not be confirmed in this study.

However, the vegetation composition and structure shows no signs of shrubification on the studied pasture sites. In contrast to this, shrub expansion is a prominent process in many high-latitude non-forest ecosystems (Mekonnen *et al.* 2021). Intensive herbivory might slow down this process, thereby reducing two main effects of shrub expansion: (1) increased localised snow trapping and warming of the ground underneath (Beer *et al.* 2020), and (2) increased carbon uptake from the soil, which adds carbon to the more active part of the carbon cycle by biomass increase, litter production and above-ground litter decomposition (Vowles and Björk 2019, Verma *et al.* 2020, Parker *et al.* 2021).

Reindeer impact on ground characteristics

The shallow peat and relatively young basal peat age (Table S1 in Supplementary Information) at migration sites (sites S-3P and W-3P)

indicate that peat formation started later than at the other peat sites. The older ages found at the pasture sites indicate a difference in peat accumulation, compared to S-3P. The age inversion at the bottom of the pasture (site S-5P) shows that there was rearrangement of organic carbon at approximately 130 cm bs. However, this rearrangement must have taken place after peat formation started on top. An option would be relocation of carbon inside the soil column caused by lateral water flow (Kramer *et al.* 2004). The bottom ages of most peat columns (Table S1 in Supplementary Information) match the beginning of peat formation after the deglaciation of northern Fennoscandia around 9700 cal yr BP (Stroeven *et al.* 2016).

The organic top layer of the mineral soil sites indicates two things: undisturbed growth of moss and lichen at the exclusion sites (E-1M-A and -B) on the one hand and animal action such as trampling and therefore turbation as well as the soil structure, consisting of an eluvial and an illuvial horizon, at mineral sites (S-3M, S-5M, W-3M, W-4M-A and W-4M-B) on the other hand bring newly formed organic material into the ground (Table S1 in Supplementary Information). This is most likely enhanced by the formation of roots. This might be a result of grassland formation featuring plants that tend to develop deeper roots than tundra vegetation, as a result of high grazing pressure.

Bulk density of the peatland sites slightly decreases with increasing grazing intensity (Fig. S5b in Supplementary Information), especially from intensities 3 to 5. While this is not a common result, as animal trampling usually compresses the ground (Tuomi *et al.* 2021), we reckon that the previously mentioned vegetation shift towards graminoid-dominated vegetation produced a less compressible peat compared to peat produced by mosses and shrubby tundra vegetation. This lower compressibility is likely caused by larger and more stable vegetation pieces in the peat, such as roots and grass stalks compared to mosses, as can be seen in root-intervened peat in other locations (Carlton 1974, van Asselen *et al.* 2010). This less-dense peat on intensity 5-sites means more spaces inside the ground, that would insulate underlying material from intruding air temperature and reduce

cooling effects on the soil in winter, if air-filled. Taking that into account, our hypothesis suggests colder ground temperatures and therefore less carbon decomposition in intensity 3-sites, where bulk density is higher. As we do not see any clear trend in the carbon data pointing towards this hypothesis, we assume that, independent of bulk density, all examined peats feature high water contents throughout the year, allowing for temperature exchanges between air and deeper soil layers, eliminating the insulation effects that air-filled spaces would cause.

SOC density and stocks across the Kutuharju station area

While we did not find obvious correlations between reindeer grazing intensity and soil TOC storage, we used our dataset to calculate mean SOC stocks for the premises of the Kutuharju Field Research Station. We calculated mean SOC stocks for peatlands and mineral soil areas separately, as well as for summer and winter ranges, again classified by soil type. While there was only little difference for uppermost 30 cm of the peatlands (summer mean: $11.36 \pm 6.07 \text{ kg m}^{-2}$; winter mean: $10.61 \pm 3.23 \text{ kg m}^{-2}$; overall mean: $11.02 \pm 5.03 \text{ kg m}^{-2}$), mineral soils showed a larger difference between reindeer ranges (summer mean: $10.14 \pm 6.73 \text{ kg m}^{-2}$; winter mean: $4.49 \pm 1.18 \text{ kg m}^{-2}$; overall mean: $7.45 \pm 5.15 \text{ kg m}^{-2}$) (Table 3). Separate calculations grouped by grazing intensity revealed highest mean SOC values for regular migration route sites (intensity 3) for both mineral ($19.40 \pm 0.00 \text{ kg m}^{-2}$) and peat ($13.09 \pm 2.84 \text{ kg m}^{-2}$) sites, but no clear trend across grazing intensities. These values are likely a result of vegetation composition at these sites, keeping in mind that for mineral soils only one site (S-3M) was available for SOC stock calculation.

Methodological limitations of the pilot study design

Our pilot study design mainly aimed at identifying if there are TOC differences between grazing intensities that need to be investigated further.

For this reason, we did not collect multiple replicates of our samples. This leaves us with an extendable dataset that does not allow for significance testing, as e.g. in unfrozen soil conditions samples from different depths within a core are not independent in terms of TOC, due to seeping water possibly relocating carbon, which would require using every core as a single sample.

While summer is the best sampling period to allow for full area access, ensuring fully unfrozen conditions in seasonally frozen ground, the limitation to separate summer and winter pastures does not provide direct insights into animal effects year-round.

Implications of the pilot study for future research

Due to only seasonally frozen soil conditions and soil parts staying unfrozen during the whole year, carbon relocation via seeping water as well as year-round decomposition processes are likely to take place in our study area. Contrary to a similar study on permafrost (Windirsch *et al.* 2022a), this might be the reason for non-visible trends found in this study. However, to record the full impact of grazing on seasonally frozen soils, sampling a year-round reindeer enclosure that has been grazed by large numbers of animals for several decades is needed.

A key element for estimating animal-induced effects on both vegetation and soil is also a sufficient availability of reference sites where animals are excluded. In this study, there was no enclosure site featuring peat soils available. These enclosures would also be vital for creating a baseline for all parameters, measured repeatedly throughout the duration of the experiment.

Conclusion

In conclusion, we found no clear evidence that reindeer alter the soil organic carbon storage capacities in seasonally frozen ground in the studied setting. However, while putting no detectable effects on mineral soils, they do affect bulk density in peat under heavy grazing influence. This is most likely a result of their effect on

vegetation communities, increasing root production by transforming tundra into species-poor grasslands.

Thus, we found no analogue effects of herbivores like in permafrost-affected landscapes, where intensive animal grazing likely promotes an increase of soil carbon storage. If these results for our studied seasonally frozen Arctic soils is caused by lower herbivory pressure, higher winter temperatures or other aspects could not be answered in our pilot study.

Increasing the number of reference sites for also covering peat soils and analysing soils of year-round reindeer pastures needs to be addressed in order to assess the potential for long-term carbon storage in high-latitude soils by changing grazing regimes.

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