



# Impacts of winter climate change on northern forest understory carbon dioxide exchange determined by reindeer grazing

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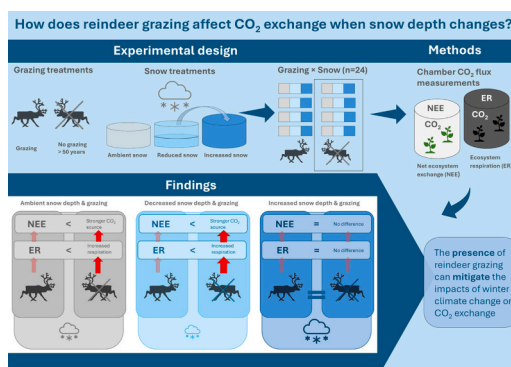
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## HIGHLIGHTS

- Snow depth and grazing had complex interactive effects on understory CO<sub>2</sub> fluxes
- Reduced snow depth increased understory CO<sub>2</sub> release with 55 years of reindeer exclusion
- Increased snow depth offset the CO<sub>2</sub> gap between grazed and excluded areas
- Presence of reindeer enhanced stability of CO<sub>2</sub> exchange to snow depth changes

## GRAPHICAL ABSTRACT



## ARTICLE INFO

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## ABSTRACT

In northern regions, the ongoing climate change is altering snow depth with complex consequences for carbon dioxide (CO<sub>2</sub>) exchange and thus, global carbon (C) balance. In addition, ungulate grazers such as reindeer and caribou often alter plant and soil properties that may lead to modifications in the magnitudes and patterns of CO<sub>2</sub> exchange. To understand how reindeer grazing, coupled with changes in snow depth affects CO<sub>2</sub> exchange, we used recent snow treatments (ambient, reduced, and increased snow depth) combined with 25- and 55-year-old reindeer exclusions and the adjacent grazed areas in boreal and subarctic Scots pine forests that are main winter pastures for reindeer/caribou and cover a significant portion of boreal and subarctic landscapes. At both study sites, we measured understory net ecosystem exchange (i.e., NEE), ecosystem respiration (i.e., ER), and gross ecosystem production (i.e., GEP) over two snow-free seasons. We found that 55 years of reindeer exclusion

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increased C source strength by 136 % under ambient snow depth and 205 % under reduced snow depth in comparison to the grazed area with respective snow conditions. On the contrary, increased snow depth decreased C source strength inside the exclusion offsetting the difference between reindeer grazing treatments. Our results show that grazing may enhance ecosystem stability to winter climate change in comparison to long-term absence of grazing. This highlights the complexity of climate-grazer interactions in functioning of northern ecosystems which are experiencing variations in snow depth.

## 1. Introduction

Climate change is altering the depth and duration of snow cover in northern ecosystems (Luomaranta et al., 2019; Bogerd et al., 2020; Rantanen et al., 2022; Thoman et al., 2023) and, for Northern Europe, variable snow conditions are expected as snow cover may become either shallower and shorter in duration (Räsänen et al., 2025) or deeper (Bailey et al., 2021). Snow depth, in turn, affects ecosystem processes in winter (Welker et al., 2000; Natali et al., 2019; Liu et al., 2024) but also during the subsequent snow-free season with consequences for annual carbon dioxide (CO<sub>2</sub>) exchange (Leffler et al., 2016; Rixen et al., 2022; Hermesdorf et al., 2024; Yang et al., 2024). Boreal and subarctic forests are globally important atmospheric CO<sub>2</sub> sinks (Ciais et al., 2019; Watts et al., 2023) and their understory vegetation can account for half of total forest CO<sub>2</sub> uptake (Goulden and Crill, 1997; Nilsson and Wardle, 2005; Ikawa et al., 2015). Understory vegetation is, however, sensitive to fluctuations in snowpack (Wipf and Rixen, 2010; Kreyling et al., 2012; Bokhorst et al., 2023) and in boreal and subarctic forests, is also affected by ungulate grazers such as reindeer (*Rangifer tarandus* L.; caribou in North America, Egelkraut et al., 2020; Lindén et al., 2021). In Northern Eurasia and North America reindeer are among the main large grazers (Holand et al., 2022; Bjerke et al., 2024) but during the past decades, abundance in the reindeer/caribou herds has been declining (Hervieux et al., 2013; Russell et al., 2018). Coupled shifts in snow conditions and grazing may thus affect understory vegetation and thereby understory CO<sub>2</sub> exchange (Johnson et al., 2022; Kantola et al., 2023) but these responses have seldom been quantified and remain uncertain. Studying the snow-grazing interactions can reveal how changing winters affect the carbon (C) cycle and if these responses are indeed dependent on ungulate grazing regimes.

Snow depth regulates winter soil temperature and availability of water that can directly affect CO<sub>2</sub> release in winter and summer (Fahnestock et al., 1999; Jones et al., 1999; Leffler et al., 2016; Rogers et al., 2011). More precisely, in comparison to shallow snow, deeper snow results in warmer and often wetter soils (Pattison and Welker, 2014; Liu et al., 2023; Mavrovic et al., 2023, but see Cooper, 2014). Warmer and wetter conditions allow soil microbial activity to continue under the snowpack and thus increase ecosystem CO<sub>2</sub> release (ecosystem respiration, ER) during winter in tundra (Welker et al., 2000; Lupascu et al., 2018; Natali et al., 2019; Pedron et al., 2023; Hua et al., 2024; Yin et al., 2024). Additionally, deeper snow protects vegetation and roots from frost damage and wind abrasion in comparison to shallower/absent snow during winter and during the late spring frosts (Kreyling et al., 2012; Blume-Werry et al., 2016; Martz et al., 2016; Sanders-DeMott et al., 2018).

Snow depth may also affect CO<sub>2</sub> exchange during the snow-free season through its wintertime effects on soil microbes and vegetation (Schimel et al., 2004; Pedron et al., 2023). Deeper snow can enhance microbial activity such as nitrogen (N) mineralization, by insulating soil and increasing soil temperatures (Schimel et al., 2004; Yin et al., 2024), which in turn can increase soil N availability and plant N contents (Welker et al., 2000; Leffler et al., 2016) potentially enhancing plant CO<sub>2</sub> uptake. In contrast, shallower snow, via reduction in stomatal conductance in response to colder soil temperatures, can reduce photosynthesis even 40 % (Pattison and Welker, 2014). Variations in snow depth may also affect net ecosystem CO<sub>2</sub> exchange (NEE) by altering the onset of growing season and soil moisture. Deeper snow

delays the onset of plant photosynthesis (Cooper et al., 2011) decreasing productivity by 13 % (Wipf and Rixen, 2010) while shallower snow and earlier snowmelt can advance it (Pulliainen et al., 2017; Slatyer et al., 2022). In water-limited systems extended snowmelt and increased moisture can temporarily enhance gross ecosystem production (GEP) (Jespersen et al., 2021) but also may allow high rates of microbial respiration (Arndt et al., 2020; Hua et al., 2024) thus affecting the patterns and magnitudes of CO<sub>2</sub> exchange across ecosystem types.

Changes in snow depth may have consequences on understory vegetation such as lichens that are an important component of northern forests' vegetation. Lichens contribute to C, nutrient, and water cycling via photosynthesis, affecting soil microclimate, and microbial activity, as well as via intercepting precipitation and increasing surface albedo (Cornelissen et al., 2007; Porada et al., 2018; Mallen-Cooper et al., 2021; Finne et al., 2023; Ghiloufi et al., 2023). Deeper snow may reduce the survival of lichens (Bidussi et al., 2016) but shallow snow can decrease lichen growth (Benedict, 1990; Bokhorst et al., 2012).

Reindeer and caribou reduce lichen abundance and biomass (Joly et al., 2009; Köster et al., 2013; Väisänen et al., 2021; Stark et al., 2023; Maliniemi et al., 2025) in boreal and subarctic pine forest. After cessation of grazing, recovery of lichens is gradual and usually takes decades even though, in some cases, recovery may occur faster (Kumpula et al., 2000; Saikkonen et al., 2019; Greuel et al., 2021). Besides impacts on lichens, reindeer grazing can reduce plant biomass (Köster et al., 2013), either increase or decrease soil nutrient content (Stark et al., 2002; Väisänen et al., 2021), affect faunal and microbial communities (Suominen et al., 2003; Santalahti et al., 2018; Väisänen and Markkula, 2025) and cause physical disturbances such as soil compaction (Tuomi et al., 2021). All these reindeer/caribou effects may have consequences for CO<sub>2</sub> exchange, but the effects often depend on the ecological context (Soininen et al., 2021; Stark et al., 2023) and, for example, in boreal forest understory, lichen recovery due to decadal exclusion of reindeer has been linked with decreased net CO<sub>2</sub> release (Kantola et al., 2023). Currently, it remains unclear how grazing and the associated changes in lichen abundance in concert with changing snow depths influence CO<sub>2</sub> exchange under varying context, such as differences in the duration of reindeer absence and climatic conditions.

To understand the impacts of changing snow depth and multi-decadal exclusion of reindeer grazing on CO<sub>2</sub> exchange, we measured understory CO<sub>2</sub> fluxes in two oligotrophic Scots pine (*Pinus sylvestris* L.) forests in northern boreal and subarctic Fennoscandia. We used recent experimental snow treatments (i.e., ambient, reduced, and increased snow depth) that were crossed with reindeer grazing treatments: in the boreal study site, grazing treatment consisted of a 25-year-old reindeer exclusion and the adjacent grazed area whereas in the subarctic site, grazing treatment consisted of a 55-year-old reindeer exclusion and the adjacent grazed area. We measured CO<sub>2</sub> fluxes during two snow-free seasons following the snow treatments: 2019 and 2020 at the boreal site, and 2022 and 2023 at the subarctic site. We asked (1) How does recently altered snow depth affect understory CO<sub>2</sub> fluxes (i.e., NEE, ER, GEP)? (2) Does absence of reindeer grazing interact with the recent changes in snow depth in terms of understory CO<sub>2</sub> exchange? (3) Does the interaction of grazing with snow depth changes on understory CO<sub>2</sub> exchange depend on the duration of reindeer absence? We discuss the findings in the light of lichens and their recovery after reindeer exclusion as well as in relation to other contextual factors.

## 2. Methods

### 2.1. Study area

As study sites, we used two, oligotrophic non-permafrost, pine forests: one situated in boreal zone in northeastern Finland, close to Oulanka research station (66°22'N, 29°19'E, 165 m a.s.l., hereafter referred as 'boreal site'), and one situated in subarctic zone in northernmost Finland, close to Kevo subarctic research institute (69°46'N, 26°57'E, 90 m a.s.l., hereafter referred as 'subarctic site', Fig. S1). The densities of semi-domesticated reindeer and moose (*Alces alces* L.) are 1.4 and 0.2 individuals per km<sup>2</sup> at the boreal site, and 2.2 and 0.1 individuals per km<sup>2</sup> at the subarctic site, respectively (Natural Resources Institute Finland, 2025).

At the boreal site, the long-term (1966–2020) mean annual temperatures in January and July are −14.4 and 15.0 °C, respectively and mean annual precipitation is 552 mm; the rainiest month is July (Finnish Meteorological Institute, 2023). The length of the growing season (years 1991–2020) is 125–135 days and snow cover persists (years 1991–2020) for 180–190 days year<sup>-1</sup> with the snow depth being the highest in March (max 116 cm, Finnish Meteorological Institute, 2023, Table S1). The study years 2019 and 2020 followed the long-term meteorological averages, except January 2020 was 6.5 °C warmer and maximum snow depth was 30 cm lower in March 2019 compared to long-term averages (Tables S1 & S2). The canopy layer is at 16–20 m, and the trunk density is 4607 ± 318 trees ha<sup>-1</sup> (mean ± SE, tree diameter > 1 cm at 1.3 m height) consisting of non-cultivated *P. sylvestris* L. The understory consists of shaded and sunlit habitats. Shaded habitats are dominated by lingonberry (*Vaccinium vitis-idaea* L.), bilberry (*V. myrtillus* L.), crowberry (*Empetrum nigrum* L.) and feather mosses (*Pleurozium schreberi* L.). In sunlit habitats, to which this study focuses on, vascular vegetation is low and mainly composed of common heather (*Calluna vulgaris* (L.) Hull) and the ground floor has reindeer lichens (*Cladonia* spp.) that grow on top of a shallower carpet of feather moss species (Väisänen et al., 2021). Soil is classified as haplic podzol with the 0.5–5 cm deep organic horizon comprising of litter and humus (Väisänen et al., 2021).

At the subarctic site, the long-term (1962–2023) mean temperatures in January and July are −14.4 and 13.1 °C, respectively and mean annual precipitation is 417 mm; the rainiest month is July (Finnish Meteorological Institute, 2023, Table S1). The length of the growing season (years 1991–2020) is 115–125 days and snow cover persists (years 1991–2020) for over 190 days year<sup>-1</sup> with the snow depth being the highest in April (max 100 cm, Finnish Meteorological Institute, 2023). The study years 2022 and 2023 followed the long-term meteorological averages, except the maximum snow depth in April was 30–40 cm lower in both years compared to long-term averages (Tables S1 & S2). The canopy layer is at 7–14 m (den Herder et al., 2003; Sewerniak, 2020), and the trunk density is 1253 ± 325 trees ha<sup>-1</sup> (mean ± SE, tree diameter > 1 cm at 1.3 m height) consisting of *P. sylvestris* L. and polycormic mountain birch (*Betula pubescens* ssp. *czerepanovii* N. I. Orlova). The understory is dominated by sunlit habitats where vascular vegetation is low and composed of dwarf shrubs (mainly *Empetrum nigrum* ssp. *hermaphroditum* Hagerub, *Vaccinium vitis-idaea* L.) and the ground floor has reindeer lichens (Heikkinen and Kalliola, 1989). Soil is classified as podzol (Hinneri, 1974) with shallow organic layer (*pers. obs.*).

### 2.2. Grazing and snow treatments

To test the impacts of reindeer grazing on CO<sub>2</sub> exchange, a reindeer exclusion (2 m high fence, mesh size 100 mm × 200 mm) was compared with an adjacent grazed area at both the boreal and subarctic study sites. At the boreal site, the experiment consisted of grazed area and a reindeer exclusion (100 m × 120 m) built in 1994 (hereafter referred as '25-year-old exclusion'). At the subarctic site, the experiment consisted of a grazed area and a reindeer exclusion (80 m × 80 m) built in 1968 (den Herder et al., 2003, hereafter referred as '55-year-old exclusion'). The

exclusions have been maintained reindeer-free at both study sites since their establishment. At the boreal site, lichen mat is 83 % higher in the exclusion compared to the grazed area (Kantola et al., 2023) while at the subarctic site, lichen coverage and biomass are approx. 50 % higher in the exclusion than in the grazed area (den Herder et al., 2003).

To test the impacts of recent changes in snow depth and reindeer grazing on CO<sub>2</sub> exchange, 18 study plots were established at the boreal site and 24 at the subarctic site which vegetation (and microtopography) were alike and representative of the sunlit habitats (Fig. S1). The study plots were organized in three blocks (size of a block 3.5 m × 7–10 m) in the exclusion and in the grazed area at the boreal site (six blocks in total) and in four blocks in the exclusion and in the grazed area at the subarctic site (eight blocks in total). All blocks were located >10 m from the fence. Each block contained three experimental plots assigned to three snow depth treatments including ambient, reduced, and increased snow depths. The size of an experimental plot was 2 m × 3.5 m including a 0.5 m buffer zone whereas the distance between the plots was 0.5 m. Experimental plots were not trenched to cut roots and fungal hyphae as has been done in previous studies (Ryhti et al., 2021). Due to logistics, the reduced and increased snow plots were always located next to each other, and their order was randomly selected and dictated the location of the ambient snow depth treatment (either one of the outermost plots). The snow treatments consisted of manually removing snow from the reduced snow plots to maintain a 25 cm snow depth throughout the winter, and the removed snow was added over the increased snow plots. Monthly mean snow depth was calculated for each study plot (Fig. S2). Recording of snow depth varied between the sites: at the boreal site, snow depth was measured approx. once a week and always immediately after snow treatments, and at the subarctic site 1–2 times a month and always before snow treatments. The snow treatments were carried out in 2018–2020 at the boreal site and in 2021–2023 at the subarctic site and the snow treatment effect on snow depth was statistically significant (Table S3).

### 2.3. Soil temperature and meteorological data

To record soil temperature, all study plots were instrumented with sensors (T107 temperature probe, Campbell Scientific Inc., Logan, UT, USA) that were set to record soil temperature (°C) with 10-min interval (CR1000x data logger, Campbell Scientific Inc.) at 5 cm depth. At both sites, soil temperature was recorded during the (respective) study years. Due to instrument malfunctions, there are gaps in the soil temperature data of the subarctic site; data of the grazed area is not available for June in 2022 and for June to August in 2023. Air temperature and precipitation data were obtained from the meteorological stations (Finnish Meteorological Institute) at Oulanka and Kevo research stations (Table S2).

### 2.4. Vegetation recording

To map the impacts of reindeer exclusion on plant abundance, vegetation composition was recorded in July 2018 at the boreal site and in August 2020 at the subarctic site. At each study plot, the abundances of (reindeer) lichens, feather mosses (bryophytes), and vascular plants were recorded from 50 cm × 40 cm sized areas using a modified point-frequency method (Jonasson, 1988) with ten pins and five rows (50 pins in total). All hits were recorded, and abundances normalized for 100 pins.

### 2.5. CO<sub>2</sub> exchange

To study the impacts of reindeer grazing and snow depth on CO<sub>2</sub> exchange during snow-free season, permanent CO<sub>2</sub> study subplots were established within each study plot. The subplots represented the vegetation composition of the entire plot. A portable manual chamber system was used for CO<sub>2</sub> measurements. The system consisted of a custom-made

chamber (2-mm thick transparent polycarbonate, diameter 30 cm, height 39 cm) equipped with a battery driven fan and sensors for CO<sub>2</sub> (model GMP343, Vaisala Inc., Vantaa, Finland), air temperature, and humidity (model HMP75, Vaisala Inc.). At the boreal site, a plastic skirt and a chain were used to secure an airtight seal during the measurement, while at the subarctic site, permanently installed soil collars (5 cm depth in soil) were used for the same purpose.

At each CO<sub>2</sub> subplot, first, NEE was measured and after venting the chamber to restore the atmospheric CO<sub>2</sub> concentration, the chamber was covered with an opaque shroud for ER measurement. During each measurement, CO<sub>2</sub> concentration (ppm), relative humidity (%), and temperature (°C) were logged every 5 s for 2 min with a handheld logger (model MI70, Vaisala Inc.). To capture daytime variation in CO<sub>2</sub> fluxes, the measurements were taken between 8 am and 6 pm. At the boreal site, CO<sub>2</sub> fluxes were measured during the snow-free season (June–October) in 2019 (1. study year) and 2020 (2. study year) approx. two to three times a week during June, July, and August, and once a week in September and October. At the subarctic site, CO<sub>2</sub> fluxes were measured during snow-free seasons in 2022 (1. year) and 2023 (2. year) approx. two to three times a week from June to September (Table S4).

Here, the CO<sub>2</sub> fluxes are presented from an ecosystem perspective; positive values indicate that understory ecosystem is a net CO<sub>2</sub> sink while negative values indicate a net CO<sub>2</sub> source to the atmosphere. NEE and ER rates were calculated from the linear change of the CO<sub>2</sub> concentration in the chamber and the first 15 s at minimum were excluded as a ‘deadband’ from each measurement. GEP was obtained by subtracting ER from NEE.

## 2.6. Statistics

For soil temperature, monthly average values per study plot were used in separate tests for both study sites. First, the data were split into snow-covered (December to May, i.e., the months when snow treatments were carried out) and snow-free seasons (June to November, i.e., the months without snow treatments). For both seasons, the data were split by year and a linear mixed effect model was employed, with soil temperature as a response variable, snow treatment, grazing, and month as fixed factors, and plot identity as a random factor. In case of significant interactions, a Tukey post hoc test was used.

For vegetation abundance, mean values per plot were calculated for lichens, bryophytes, and vascular plants separately at both study sites. A linear mixed effect model was used with an abundance of lichens, bryophytes, and vascular plants (in separate tests) as a response variable with grazing as a fixed factor and spatial block as a random factor.

For CO<sub>2</sub> fluxes (i.e., NEE, ER, GEP), weekly mean values were calculated per plot and the impacts of snow treatments and grazing on snow-free season weekly CO<sub>2</sub> fluxes were tested separately for both study sites. A linear mixed effect model was used for both study years separately with NEE, ER, and GEP (in separate tests) as a response variable, and grazing and snow treatment as fixed factors with plot identity as a random factor. In cases of significant interactions among the variables, a Tukey post hoc test was applied.

All the statistical analyses were performed in R (version 4.1.0, R Core Team). The significance level of  $P < 0.05$  is used as a threshold for statistical significance. Linear mixed effect models were tested with the *lme* function (‘nlme’-package, Pinheiro et al., 2021) followed by ANOVA. No data transformations were applied and the fit of all models was quantified visually through residual plots (Zuur et al., 2009). For post hoc tests, pairwise comparisons of estimated marginal means were used with *emmeans* function (‘emmeans’-package, Lenth, 2022) and ‘ggplot2’-package (Wickham, 2016) was used for data visualization.

## 3. Results

### 3.1. Soil temperature

At the boreal site, during the snow-covered season, snow treatment had a significant main effect on soil temperature, but this effect also varied depending on month (Fig. 1, Table 1). In the first year, reduced snow plots were 1.6–1.7 °C colder than ambient and increased snow plots in February and 1.2 °C colder than ambient in March. In the second year, reduced snow plots were 0.6–1.1 °C colder than ambient and increased snow plots from February to April, while increased snow plots were 0.6–0.8 °C colder than ambient and reduced snow plots in May. Grazing did not affect soil temperature during the snow-covered season. During the snow-free season, snow treatments and grazing had no statistically significant effect on soil temperature and soil temperature varied only due to month (Table 1).

At the subarctic site, during the snow-covered season, soil temperature varied depending on snow treatment, grazing, and month (Fig. 1, Table 1). In the first year, reduced snow plots were 1.6 °C colder than ambient and increased snow plots in February. In the second year, reduced snow plots were 2.5–2.6 °C colder than ambient and increased snow plots in March. In the first year, soil temperature was 1.3–2.1 °C colder in the grazed area compared to 55-year-old reindeer exclusion in December and January. In the second year, soil temperature was 0.9–2.0 °C colder in the grazed area compared to the exclusion from December to March. During the snow-free season, soil temperature varied depending on grazing and month. In the first year, soil temperature was 1.1 °C warmer in the grazed area than in the exclusion in July but the exclusion was 0.9 °C and 1.1 °C warmer than grazed area in October and November, respectively. In the second year, soil in the exclusion was 1.3–2.1 °C warmer than in the grazed area from September to November.

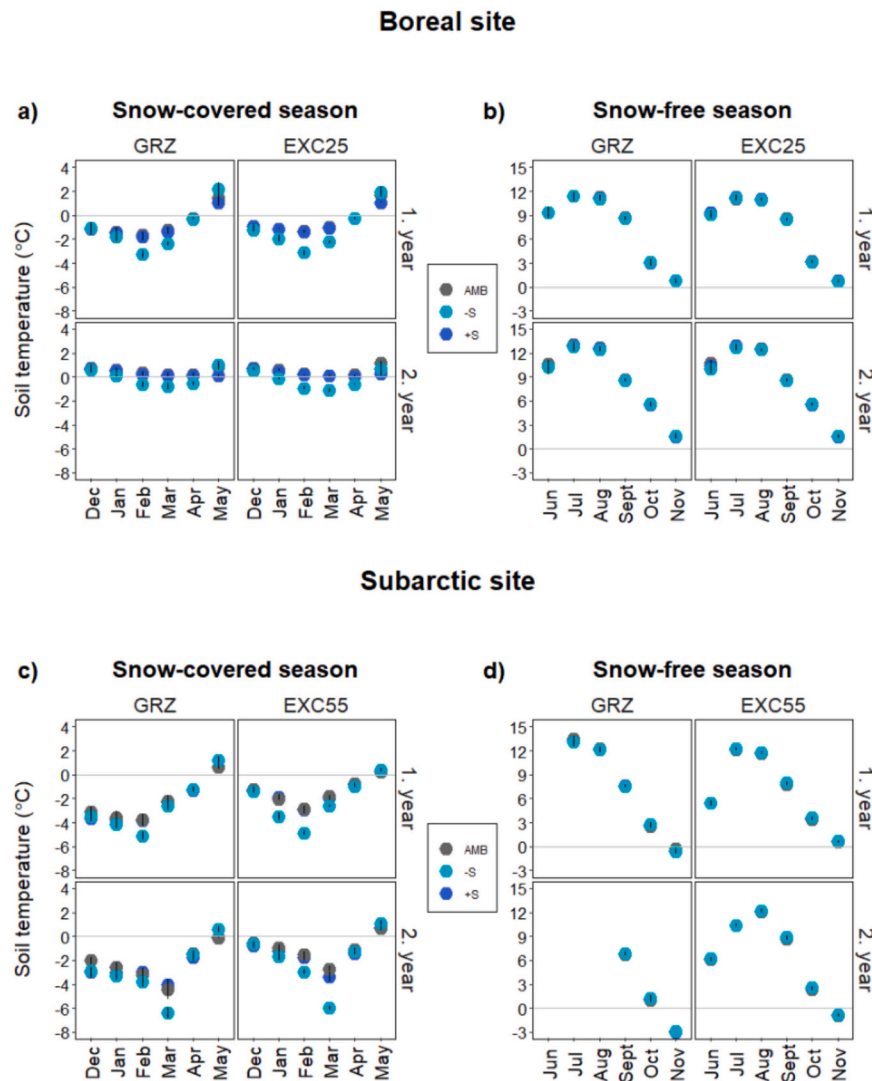
### 3.2. Vegetation abundance

At the boreal site, lichens were 125 % more abundant in the exclusion than in the grazed area although the difference was only marginally significant. The abundance of bryophytes and vascular plants did not differ between the exclusion and the grazed area (Table 2, Fig. 2). At the subarctic site, lichens were 51 % more abundant in the exclusion than in the grazed area while the abundance of bryophytes and vascular plants did not differ between the exclusion and the grazed area (Table 2, Fig. 2).

### 3.3. CO<sub>2</sub> fluxes

At the boreal site, in neither the first nor second year, grazing and snow treatments had statistically significant main or interactive effects on CO<sub>2</sub> fluxes (Table 3, Fig. 3). At the subarctic site, in the first year, grazing treatment affected NEE ( $P = 0.008$ ) and ER ( $P = 0.049$ ); these were 115 % (i.e., stronger CO<sub>2</sub> source) and 71 % more negative (i.e., stronger CO<sub>2</sub> release) in the exclusion compared to the grazed area, respectively (Table 3, Fig. 4). In the first year, there were no other statistically significant effects on CO<sub>2</sub> fluxes (Table 3).

In the second year, grazing also had a main effect on NEE ( $P < 0.001$ ) and ER ( $P = 0.004$ ); these were 136 % and 82 % more negative in the exclusion than in the grazed area with ambient snow, respectively, while grazing and snow treatments did not affect GEP ( $P = 0.102$  and  $P = 0.655$ , respectively). The snow treatments had a main effect on NEE ( $P = 0.049$ ) that was 36 % and 62 % more negative with reduced snow compared to ambient and increased snow, respectively. The snow treatments affected NEE ( $P = 0.017$ ) and ER ( $P = 0.028$ ) depending on grazing (Grazing × Snow, Table 3, Fig. 4). In general, in the exclusion, NEE and ER were 46 % and 31 %, respectively, more negative in reduced snow plots than in ambient snow plots and 134 % and 112 %, respectively, more negative in reduced than in increased snow plots. These



**Fig. 1.** Monthly mean soil temperature during the snow-covered (December–May) and snow-free (June–November) seasons across snow treatments; ambient (i.e., AMB, grey), reduced (i.e., –S, light blue), and increased snow (i.e., +S, dark blue) depths. Soil temperature was measured at 5 cm depth in grazed areas and in the exclusions that had been excluding reindeer for 25 years (Boreal) and 55 years (Subarctic). Panels a) and b) represent soil temperature at the boreal site and panels c) and d) at the subarctic site during and after the first and second winters of snow treatments. Values are presented as mean  $\pm$  standard error. Note data gaps at the subarctic site during snow-free seasons.

differences in NEE and ER were statistically significant between reduced and increased snow plots ( $P = 0.002$  and  $P = 0.005$ , respectively, Table 4). In the grazed area, NEE and ER did not differ significantly between the snow treatments (Table 4). Consequently, with reduced snow depth, NEE ( $P < 0.001$ ) and ER ( $P = 0.002$ ) were 205 % and 119 % more negative, respectively, in the exclusion than in the grazed area (Table 4, Fig. 4). On the other hand, with increased snow depth, NEE and ER did not differ anymore between grazing treatments.

#### 4. Discussion

The impact of snow depth on understory NEE was dependent on site and reindeer grazing highlighting a critical complexity in understanding global climate changes in the north on C processes and feedbacks. More precisely, at the boreal site, neither excluding reindeer grazing for 25 years nor changes in snow depth affected NEE. On the contrary, at the subarctic site, excluding reindeer grazing for 55 years turned NEE more negative (i.e., the understory became a stronger CO<sub>2</sub> source) in comparison to the grazed area under ambient snow conditions. In addition, at the subarctic site, reduced snow depth intensified CO<sub>2</sub> source while

increased snow depth turned NEE less negative (i.e., a weaker CO<sub>2</sub> source) inside the exclusion. Snow treatments had no effects on CO<sub>2</sub> source strength in the adjoining grazed area (Fig. 5). These findings suggest that the impacts of snow cover (Lundquist et al., 2013; Sun et al., 2022) and grazing are landscape- and context-dependent, even though the vegetation type was consistent between the boreal and subarctic sites (Soininen et al., 2021; Lindén et al., 2021). Here, we propose that in northern pine forests, the duration of reindeer exclusion (over 50 years) with associated changes in lichens and soil microclimate may affect the responses of understory CO<sub>2</sub> exchange to the changing winter climates that are underway.

##### 4.1. Snow depth and reindeer grazing affect soil temperature

Reduced snow depth (25 cm depth) resulted in lower soil temperatures compared to ambient conditions during mid and late winter at both study sites, aligning with snow depth studies in tundra (Cooper, 2014; Zhao et al., 2022) and boreal ecosystems (Blume-Werry et al., 2016; Martz et al., 2016; Zhao et al., 2022). Conversely, increased snow depth (mean 45–88 cm) did not elevate soil temperature compared to

**Table 1**

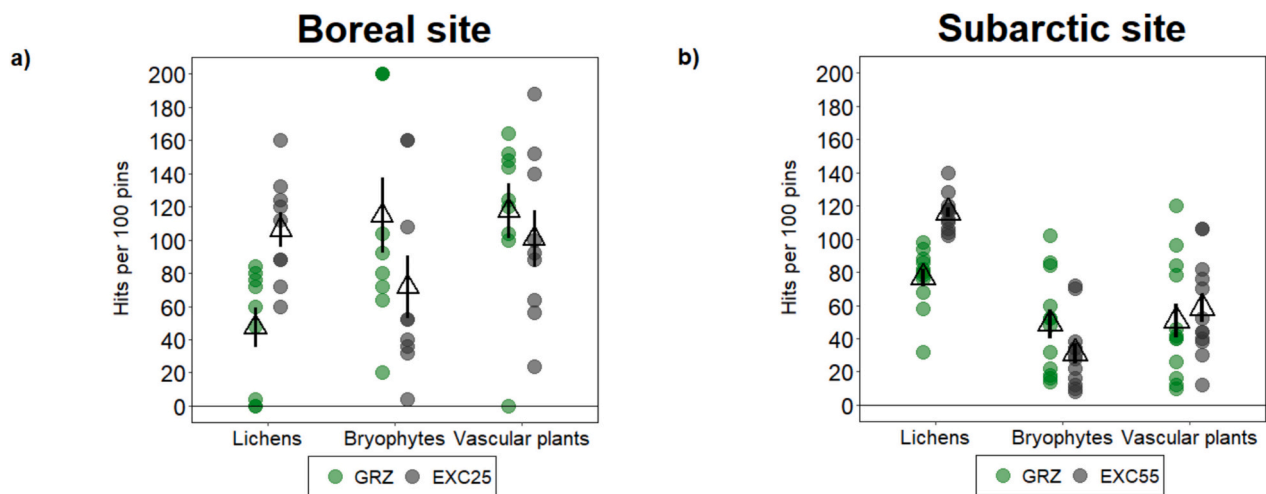
The main and interaction effects of grazing, snow treatment, and month on snow-covered (i.e., season of snow treatments; December–May) and snow-free season (i.e., off-season of snow treatments; June–November) soil temperature at the boreal (snow-covered seasons of 2018–2019 & 2019–2020, snow-free seasons of 2019 & 2020) and subarctic (snow-covered seasons of 2021–2022 & 2022–2023, snow-free seasons of 2022 & 2023) study sites. The effects were tested with linear mixed models followed by ANOVA using grazing, snow treatment (i.e., ambient, reduced, increased snow depth), and month as fixed factors, and plot identity as a random factor. Superscript values indicate numerator and denominator degrees of freedom, respectively. Bold indicates significant effects ( $P < 0.05$ ). Note that the snow-free season at the subarctic site includes the months of July–November in 2022 and September–November in 2023.

Site	Fixed effects	Snow-covered season				Snow-free season			
		1. Year		2. Year		1. Year		2. Year	
		F value	P value	F value	P value	F value	P value	F value	P value
Boreal	Grazing (G)	1.560 <sup>1, 12</sup>	0.236	0.690 <sup>1, 12</sup>	0.422	0.926 <sup>1, 12</sup>	0.356	0.125 <sup>1, 12</sup>	0.730
	Snow (S)	8.228 <sup>2, 12</sup>	<b>0.006</b>	22.01 <sup>2, 12</sup>	<b>&lt;0.001</b>	0.175 <sup>2, 12</sup>	0.842	1.055 <sup>2, 12</sup>	0.378
	Month (M)	157.4 <sup>5, 60</sup>	<b>&lt;0.001</b>	66.84 <sup>5, 60</sup>	<b>&lt;0.001</b>	1114 <sup>5, 60</sup>	<b>&lt;0.001</b>	1294 <sup>5, 60</sup>	<b>&lt;0.001</b>
	G × S	0.530 <sup>2, 12</sup>	0.602	0.819 <sup>2, 12</sup>	0.464	0.065 <sup>2, 12</sup>	0.937	0.017 <sup>2, 12</sup>	0.983
	G × M	0.305 <sup>5, 60</sup>	0.908	0.685 <sup>5, 60</sup>	0.637	0.252 <sup>5, 60</sup>	0.937	0.077 <sup>5, 60</sup>	0.996
	S × M	7.636 <sup>10, 60</sup>	<b>&lt;0.001</b>	15.21 <sup>10, 60</sup>	<b>&lt;0.001</b>	0.037 <sup>10, 60</sup>	1.000	0.363 <sup>10, 60</sup>	0.958
	G × S × M	0.092 <sup>10, 60</sup>	1.000	0.417 <sup>10, 60</sup>	0.933	0.043 <sup>10, 60</sup>	1.000	0.049 <sup>10, 60</sup>	1.000
Subarctic	Grazing	19.12 <sup>1, 18</sup>	<b>&lt;0.001</b>	41.86 <sup>1, 18</sup>	<b>&lt;0.001</b>	1.970 <sup>1, 18</sup>	0.177	95.08 <sup>1, 18</sup>	<b>&lt;0.001</b>
	Snow	4.281 <sup>2, 18</sup>	<b>0.030</b>	6.047 <sup>2, 18</sup>	<b>0.010</b>	0.080 <sup>2, 18</sup>	0.925	0.290 <sup>2, 18</sup>	0.752
	Month	419.6 <sup>5, 90</sup>	<b>&lt;0.001</b>	313.5 <sup>5, 90</sup>	<b>&lt;0.001</b>	4101 <sup>4, 72</sup>	<b>&lt;0.001</b>	4270 <sup>2, 36</sup>	<b>&lt;0.001</b>
	G × S	0.833 <sup>2, 18</sup>	0.451	0.230 <sup>2, 18</sup>	0.797	1.330 <sup>2, 18</sup>	0.289	0.036 <sup>2, 18</sup>	0.965
	G × M	34.69 <sup>5, 90</sup>	<b>&lt;0.001</b>	12.16 <sup>5, 90</sup>	<b>&lt;0.001</b>	29.63 <sup>4, 72</sup>	<b>&lt;0.001</b>	7.407 <sup>2, 36</sup>	<b>0.002</b>
	S × M	9.638 <sup>10, 90</sup>	<b>&lt;0.001</b>	15.65 <sup>10, 90</sup>	<b>&lt;0.001</b>	0.380 <sup>8, 72</sup>	0.929	0.111 <sup>4, 36</sup>	0.978
	G × S × M	0.767 <sup>10, 90</sup>	0.660	1.474 <sup>10, 90</sup>	0.162	0.140 <sup>8, 72</sup>	0.997	0.067 <sup>4, 36</sup>	0.991

**Table 2**

The main effects of grazing on lichen, bryophyte, and vascular plant abundance in boreal and subarctic oligotrophic Scots pine forests. The effects were tested with linear mixed models followed by ANOVA using grazing as a fixed factor, and spatial block as a random factor. Superscript values indicate numerator and denominator degrees of freedom, respectively. Bold indicates significant ( $P < 0.05$ ) and italics marginal ( $P < 0.1$ ) effects.

	Fixed effect	Lichens		Bryophytes		Vascular plants	
		F value	P value	F value	P value	F value	P value
Boreal	Grazing	4.986 <sup>1, 4</sup>	<i>0.089</i>	0.805 <sup>1, 4</sup>	0.420	0.506 <sup>1, 4</sup>	0.516
Subarctic	Grazing	43.61 <sup>1, 6</sup>	<b>&lt;0.001</b>	1.049 <sup>1, 6</sup>	0.345	0.313 <sup>1, 6</sup>	0.596



**Fig. 2.** Total abundance of lichens, bryophytes, and vascular plants in grazed areas (GRZ) and in the exclusions that had been excluding reindeer for a) 25 years (EXC25, Boreal) and b) 55 years (EXC55, Subarctic) in oligotrophic Scots pine forests. Dots represent vegetation abundances at individual study plots (boreal:  $n = 18$ , subarctic:  $n = 24$ ) in grazed (green) and exclusion (grey) areas while triangles represent mean values  $\pm$  standard error. At the boreal site, vegetation abundances were recorded in July 2018 and at the subarctic site in August 2020.

ambient (mean 43–60 cm). This demonstrates that c. 40 cm of snow depth is required to insulate soil from cold air temperatures while further deepening provides no additional insulation (Zhang, 2005). However, the increased snow depth cooled soil during spring thaw (at the boreal site), consistent with observations in tundra (Cooper, 2014) whereas reduced snow depth did not affect spring soil temperatures.

Besides snow conditions, changes in reindeer grazing may also affect

soil temperatures during both snow-covered and snow-free seasons (Fauria et al., 2008; Zhao et al., 2011; Saikkonen et al., 2019). In the 55-year-old exclusion at the subarctic site, soils were warmer from early fall until mid-winter and cooler during the peak growing season. In this study, we found that at the boreal site, lichens were approx. 125 % and, at subarctic site, approx. 51 % more abundant inside the exclusions than in the adjacent grazed areas. In addition, at the same boreal site, lichens

**Table 3**

The main and interaction effects of grazing and snow treatment on net ecosystem exchange (i.e., NEE), ecosystem respiration (i.e., ER), and gross ecosystem production (i.e., GEP) in boreal and subarctic oligotrophic Scots pine forests during the first and second snow-free seasons following the snow treatments. The effects were tested with linear mixed models followed by ANOVA using grazing and snow treatment (i.e., ambient, reduced, increased snow depth) as fixed factors, and plot identity as a random factor. Superscript values indicate numerator and denominator degrees of freedom, respectively. Bold indicates significant ( $P < 0.05$ ) effects.

Fixed effects		NEE		ER		GEP	
		F value	P value	F value	P value	F value	P value
Boreal 1st year	Grazing	1.613 <sup>1, 12</sup>	0.228	1.314 <sup>1, 12</sup>	0.274	0.340 <sup>1, 12</sup>	0.570
	Snow	0.464 <sup>2, 12</sup>	0.640	0.511 <sup>2, 12</sup>	0.613	0.035 <sup>2, 12</sup>	0.966
	Grazing × Snow	0.120 <sup>2, 12</sup>	0.888	0.151 <sup>2, 12</sup>	0.862	0.021 <sup>2, 12</sup>	0.979
Boreal 2nd year	Grazing	1.342 <sup>1, 12</sup>	0.269	1.061 <sup>1, 12</sup>	0.323	0.894 <sup>1, 12</sup>	0.363
	Snow	0.234 <sup>2, 12</sup>	0.795	0.554 <sup>2, 12</sup>	0.589	0.383 <sup>2, 12</sup>	0.690
	Grazing × Snow	0.023 <sup>2, 12</sup>	0.977	0.023 <sup>2, 12</sup>	0.977	0.444 <sup>2, 12</sup>	0.652
Subarctic 1st year	Grazing	9.031 <sup>1, 18</sup>	<b>0.008</b>	4.459 <sup>1, 18</sup>	<b>0.049</b>	0.004 <sup>1, 18</sup>	0.950
	Snow	0.438 <sup>2, 18</sup>	0.652	0.413 <sup>2, 18</sup>	0.668	0.658 <sup>2, 18</sup>	0.530
	Grazing × Snow	2.438 <sup>2, 18</sup>	0.116	2.025 <sup>2, 18</sup>	0.161	0.166 <sup>2, 18</sup>	0.848
Subarctic 2nd year	Grazing	21.43 <sup>1, 18</sup>	<b>&lt;0.001</b>	10.75 <sup>1, 18</sup>	<b>0.004</b>	2.976 <sup>1, 18</sup>	0.102
	Snow	3.584 <sup>2, 18</sup>	<b>0.049</b>	2.449 <sup>2, 18</sup>	0.115	0.433 <sup>2, 18</sup>	0.655
	Grazing × Snow	5.324 <sup>2, 18</sup>	<b>0.017</b>	4.406 <sup>2, 18</sup>	<b>0.028</b>	1.090 <sup>2, 18</sup>	0.357

inside the exclusion formed a discontinuous mat and were c. 5 cm tall while in the grazed area were sporadic and c. 2 cm tall (Kantola et al., 2023). At the subarctic site, lichens inside the exclusion formed a more continuous mat (den Herder et al., 2003) and were over 12 cm deep, while in the grazed area were sporadic and c. 2 cm tall (*pers. obs.*). The impacts of lichens on soil microclimate are driven by lichen mat morphology, and therefore, the varying microclimatic effects of reindeer exclusion on soil temperature (observed only at the subarctic site) may highlight the role of lichen mat continuity and thickness in controlling soil insulation (van Zuijlen et al., 2020; Mallen-Cooper et al., 2021). In addition, the albedo effect of lichens (Finne et al., 2023) may contribute to cooler soil during the peak growing season especially at the subarctic site with relatively open canopy structure. We propose that a continuous and thick lichen mat may contribute to soil temperature during the snow-free season and in early winter until the time when the insulative effect of snow becomes dominant.

#### 4.2. Recent changes in snow depth affect subarctic understory NEE when grazing is absent

At the subarctic site, reduced snow depth increased CO<sub>2</sub> source strength while increased snow depth dampened it inside the 55-year-old exclusion compared to the grazed area, where NEE remained stable regardless of snow depth changes. Since grazing also affected NEE, which was a 136 % more negative inside the exclusion than in the grazed area under ambient snow depth, differences between grazing treatments further depended on snow depth: under reduced snow depth NEE inside the exclusion was 205 % more negative than in the grazed area whereas under increased snow depth NEE did not differ between the exclusion and the grazed area. Previous work from tundra suggests that the presence of reindeer grazing can mitigate the effects of summer warming on ecosystem C balance (Väisänen et al., 2014). Our findings demonstrate that A) reindeer can curtail the effects of both reduced and increased snow depth on the C balance in forested ecosystems and B) increased snow depth can curtail the effects of reindeer absence on C balance.

In our study, ER was less negative (i.e., less CO<sub>2</sub> release) with increased snow depth, similar to previous work covering tundra ecosystems (Welker et al., 2000; Blankinship and Hart, 2012; Semenchuk et al., 2016), while ER became more negative (i.e., more CO<sub>2</sub> release) with reduced snow depth. To our knowledge, no previous study has reported similar effects of reduced snow depth on ER. The effects of increased snow depth on ER could be associated, at least ephemerally, with greater inputs of snow melt water that may flush away organic matter in freely draining soils (Mavrovic et al., 2023) and thereby also limit microbial respiration throughout the growing season (Rogers et al., 2011; Lupascu et al., 2014; Zhao et al., 2022). On the other hand, the

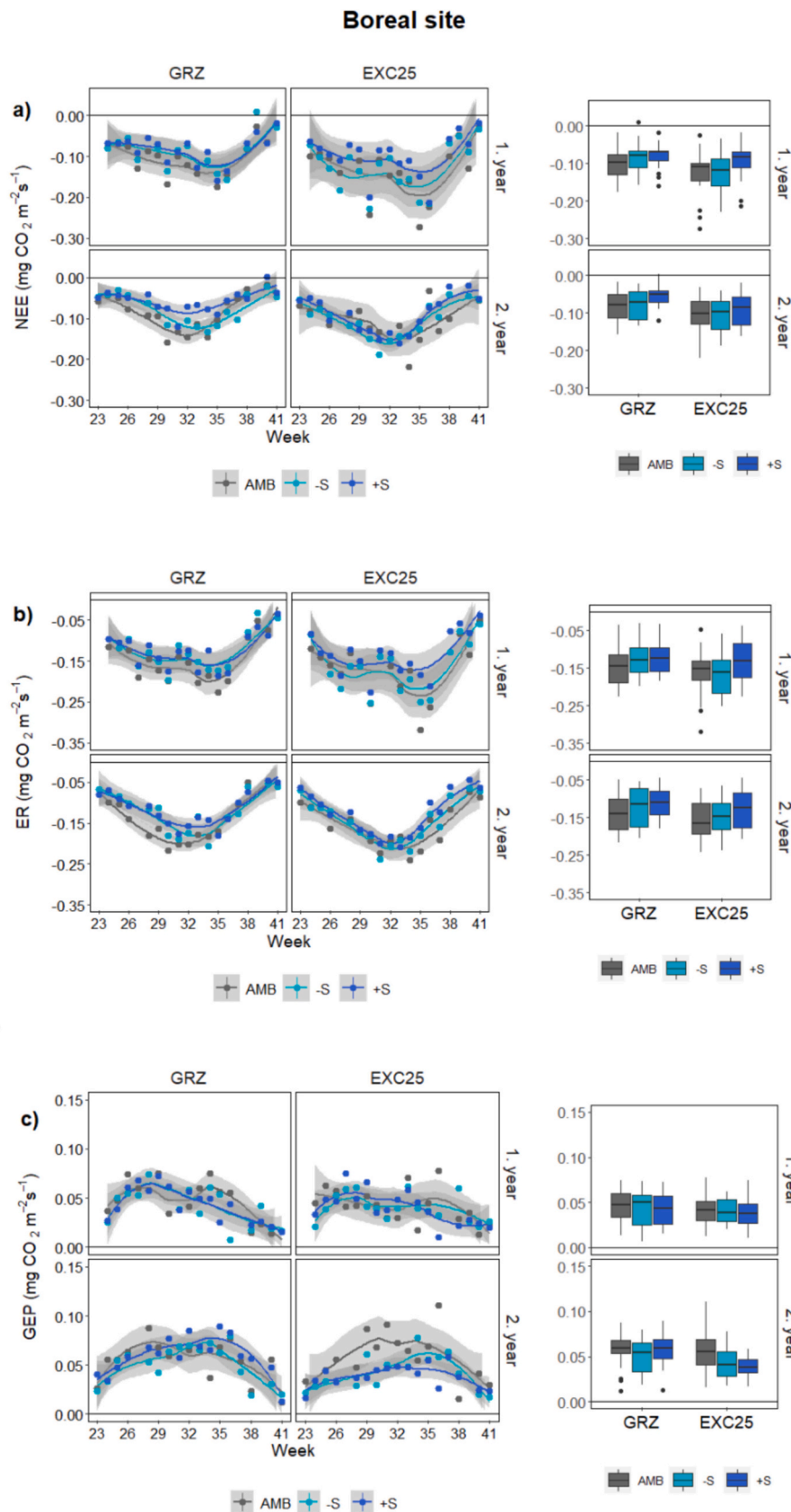
effects of reduced snow depth on ER could be associated with increased wintertime plant and root mortality and decreased winter decomposition (Martz et al., 2016; Sanders-DeMott et al., 2018; Du et al., 2024) that together could provide more decomposable material for microbes during summer, and thus greater CO<sub>2</sub> release.

Interestingly, the responses in ER to snow depth variations, which ultimately drove the response in NEE, occurred only within the 55-year-old reindeer exclusion whereas no effects occurred with present grazing at the subarctic site or at the boreal site regardless of grazing. We suggest that these responses could be explained, at least partly, by lichens (subarctic site) and tree density (boreal site). Lichens' water-holding capacity may be up to ten times higher than that of bare soil (Porada et al., 2018; van Zuijlen et al., 2020; Ghiloufi et al., 2023) and, together with lower summer soil temperature with potentially decreased evapotranspiration, and well-drained soil, lichens could provide more stable soil moisture and enhance decomposition in the exclusion (Stark et al., 2010), while drier conditions in general may limit decomposition (Schimel et al., 2007). Lichens can also serve as an energy source for microbes and enhance microbial activity (Stark et al., 2003, 2010; Ghiloufi et al., 2023). Thus, the deeper and continuous lichen mat with the absence of grazing at the subarctic site (see 4.1) may support microbial decomposition of surplus litter following a winter with reduced snow depth (van Zuijlen et al., 2020). The reason why increased snow depth resulted in decreased CO<sub>2</sub> release only with absence of grazing remains unknown but requires further attention given its role in dampening grazing effects on CO<sub>2</sub> exchange.

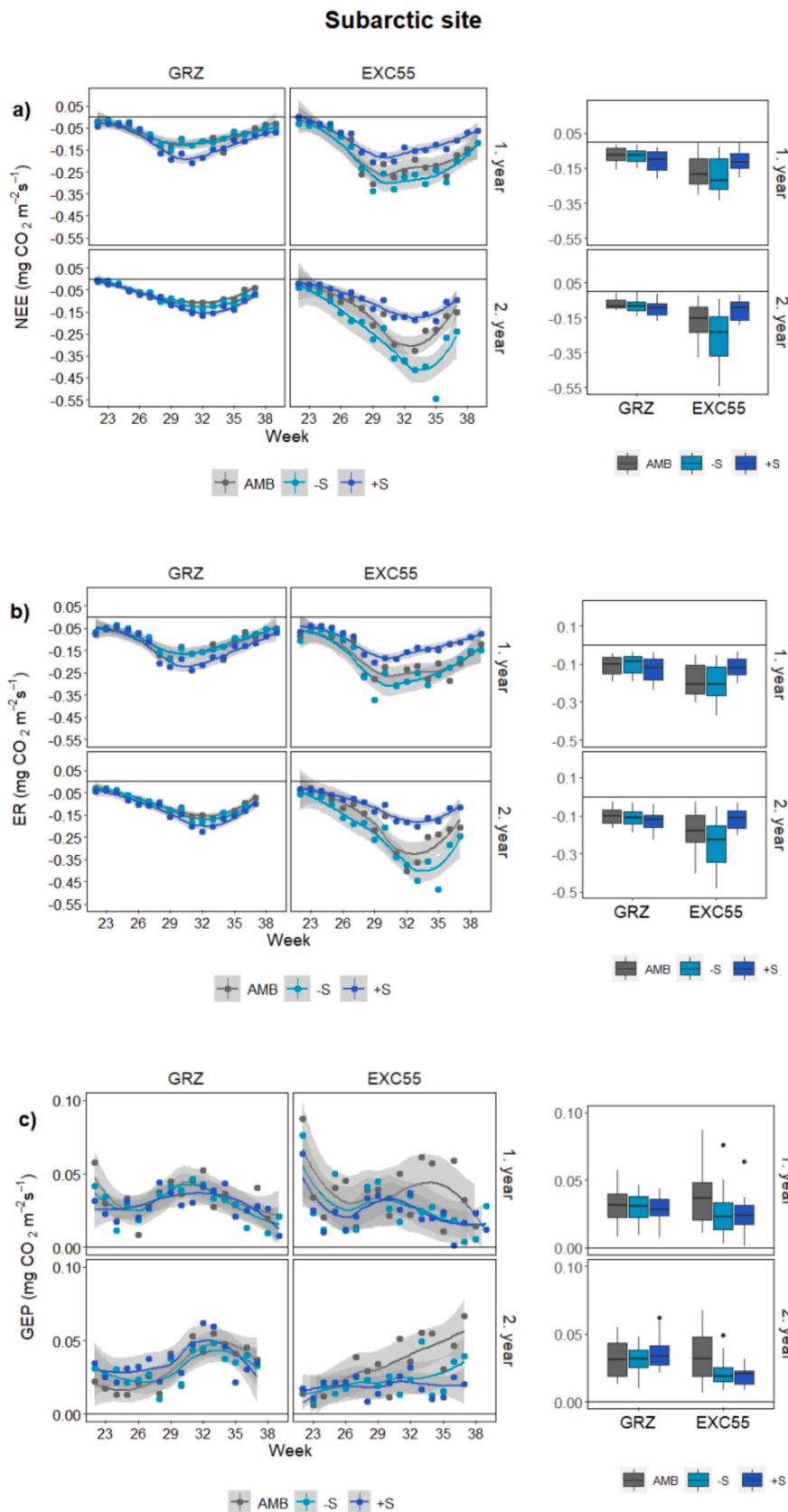
The boreal site, due to its high tree density in comparison to the subarctic site, may be less susceptible to snow depth impacts (*sensu lato*, Varhola et al., 2010; Lundquist et al., 2013; Sun et al., 2022) as high tree root density may regulate CO<sub>2</sub> release via root respiration (Högberg et al., 2002; Bhanja et al., 2022) regardless of snow depth changes at least in short term. Furthermore, sporadically growing and lower lichens with potentially lower water-holding capacity (van Zuijlen et al., 2020) combined with well-drained soil (*pers. obs.*, Mavrovic et al., 2023) may play a role in offsetting any impacts of altered snow depth and thereby potentially altered C supply on microbial activity. Further, the lack of any main effects of grazing on CO<sub>2</sub> exchange similar to recent work (Köster et al., 2015; Kantola et al., 2023) supports the idea that the succession/full recovery of lichens with their potential effects on ecosystem processing is still underway.

#### 4.3. Conclusions

Reduced and increased snow depth affected understory net CO<sub>2</sub> release with 55 years of reindeer exclusion, but not in the presence of reindeer grazing or at the boreal site, regardless of grazing. This suggests that A) reindeer grazed boreal/subarctic forests may show stable CO<sub>2</sub>



**Fig. 3.** Snow-free season CO<sub>2</sub> flux rates including a) net ecosystem exchange (i.e., NEE), b) ecosystem respiration (i.e., ER), and c) gross ecosystem production (i.e., GEP) after the first and second winter of snow treatments; ambient (i.e., AMB, grey), reduced (i.e., -S, light blue), and increased snow (i.e., +S, dark blue) depths in the grazed area (GRZ) and in the exclusion that has excluded reindeer grazing for 25 years (EXC25) in an oligotrophic boreal Scots pine forest. Dots represent weekly averages of CO<sub>2</sub> fluxes with mean curves (loess smoothing, span 0.6) while boxplots represent the overall snow-free season mean values. Negative NEE values indicate a net CO<sub>2</sub> source to the atmosphere and positive values indicate a net CO<sub>2</sub> sink.

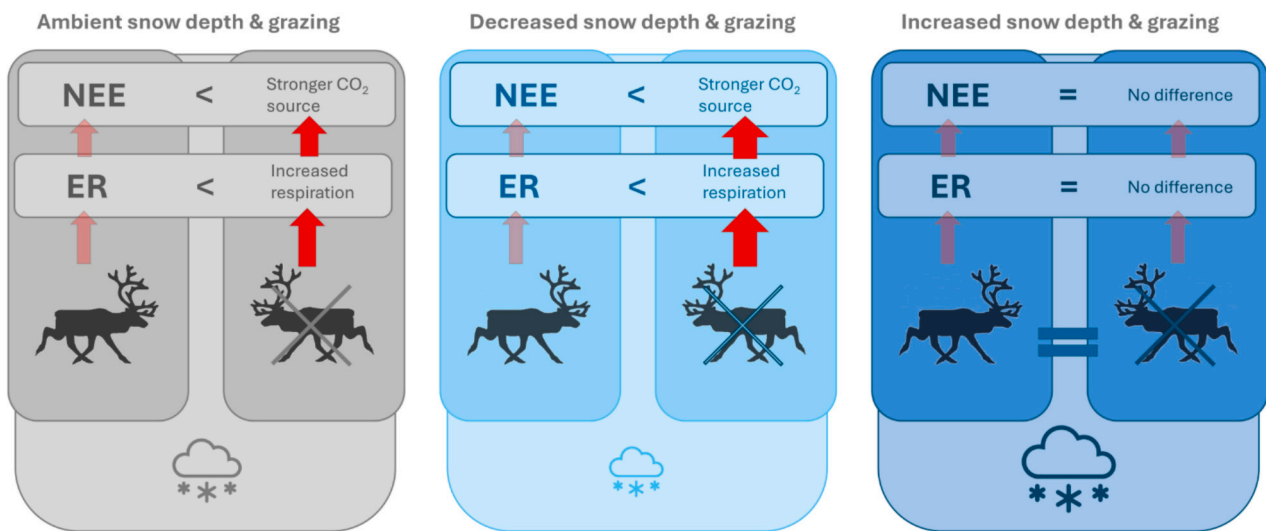


**Fig. 4.** Snow-free season  $\text{CO}_2$  flux rates including a) net ecosystem exchange (i.e., NEE), b) ecosystem respiration (i.e., ER), and c) gross ecosystem production (i.e., GEP) after the first and second winter of snow treatments; ambient (i.e., AMB, grey), reduced (i.e., –S, light blue), and increased snow (i.e., +S, dark blue) depths in the grazed area (GRZ) and in the exclusion that has excluded reindeer grazing for 55 years (EXC55) in an oligotrophic subarctic Scots pine forest. Dots represent weekly averages of  $\text{CO}_2$  fluxes with mean curves (loess smoothing, span 0.6) while boxplots represent the overall snow-free season mean values. Negative NEE values indicate a net  $\text{CO}_2$  source to the atmosphere and positive values indicate a net  $\text{CO}_2$  sink.

**Table 4**

The results of post hoc test (i.e., Tukey) on net ecosystem exchange (i.e., NEE) and ecosystem respiration (i.e., ER) across snow treatments in the 55-year-old exclusion and in the grazed area in the subarctic Scots pine forest during snow-free season of the second study year (i.e., 2023). Abbreviations are: -S = reduced snow depth, AMB = ambient snow depth, +S = increased snow depth, EXC = 55-year-old reindeer exclusion, GRZ = grazed area. Bold indicates significant ( $P < 0.05$ ) and italics marginally significant ( $P < 0.1$ ) effects.

		NEE				ER						
		Est.	SE	df	t ratio	P value	Est.	SE	df	t ratio	P value	
EXC	-S vs. AMB	0.076	0.034	18	2.281	<i>0.085</i>	0.056	0.035	18	1.603	0.270	
	-S vs. +S	0.139	0.034	18	4.150	<b>0.002</b>	0.127	0.035	18	3.616	<b>0.005</b>	
	AMB vs. +S	-0.062	0.034	18	-1.869	0.177	-0.071	0.035	18	-2.013	0.138	
GRZ	-S vs. AMB	0.010	0.034	18	0.275	0.959	0.008	0.035	18	0.241	0.969	
	-S vs. +S	-0.015	0.034	18	-0.452	0.894	-0.018	0.035	18	-0.504	0.870	
	AMB vs. +S	0.024	0.034	18	0.727	0.751	0.026	0.035	18	0.745	0.740	
AMB	EXC vs. GR	-0.096	0.034	18	-2.870	<b>0.010</b>	-0.083	0.035	18	-2.359	<b>0.030</b>	
	-S	EXC vs. GR	-0.163	0.034	18	-4.875	<b>&lt;0.001</b>	-0.130	0.035	18	-3.720	<b>0.002</b>
	+S	EXC vs. GR	-0.010	0.034	18	-0.273	0.787	0.014	0.035	18	0.399	0.694



**Fig. 5.** Conceptual Diagram of carbon dioxide ( $\text{CO}_2$ ) flux responses under different snow depth conditions (i.e., ambient, reduced, increased) coupled with 55 years of reindeer exclusion and ongoing reindeer grazing in a subarctic Scots pine forest. Bright red arrows indicate statistically significant ( $P > 0.05$ ) effects of snow depth and grazing treatments on ecosystem respiration (i.e., ER) and net ecosystem exchange (i.e., NEE). The understory acts as a net  $\text{CO}_2$  source to the atmosphere in both grazed and exclusion areas. The exclusion increases  $\text{CO}_2$  release (ER) and  $\text{CO}_2$  source strength (NEE) in comparison to the grazed area under ambient and reduced snow depth while increased snow offsets the differences in ER and NEE between grazing treatments.

exchange in the face of winter climate changes at least in short term and B) the duration of grazer absence with accompanied recovery in lichens may determine the impacts of changing snow depth on  $\text{CO}_2$  fluxes. In addition, these results suggest that the role of context (Lindén et al., 2021; Soininen et al., 2021) such as differences in tree density between the subarctic and boreal sites could dictate the role of grazing and, consequently, its interactions with other environmental factors including future climate.

Since the strongest  $\text{CO}_2$  exchange response to snow depth changes occurred in the 55-year-old exclusion at the subarctic site, these  $\text{CO}_2$  exchange processes might be more sensitive to snow depth changes when reindeer grazing is ceased for extended periods, over five decades in this case. We propose that the presence of reindeer and/or other herbivores with similar impacts on ecosystem functions at high latitudes (Lindén et al., 2021) may enhance ecosystem  $\text{CO}_2$  exchange stability to changing snow conditions. Among the many important roles of grazers on ecosystem functions (Ramirez et al., 2024) our results emphasize their significance in maintaining ecosystem stability under changing winter climate. This is particularly important as regional variations in snowfall (both decreases and increases) are expected across the grazing ranges of reindeer and caribou (Kapnick and Delworth, 2013; Krasting et al., 2013; Bailey et al., 2021; Quante et al., 2021; Räisänen et al., 2025) with potential consequences for  $\text{CO}_2$  exchange depending on

grazing intensity.

**CRediT authorship contribution statement**

**Noora Kantola:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jeffrey M. Welker:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **A. Joshua Leffler:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Juho Lämsä:** Writing – review & editing, Validation, Investigation, Data curation. **Riku Paavola:** Writing – review & editing, Validation, Resources, Funding acquisition, Conceptualization. **Otso Suominen:** Writing – review & editing, Validation, Resources, Funding acquisition, Conceptualization. **Maria Väisänen:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT (OpenAI) in order to improve readability and language of the work. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2025.180089>.

## Data availability

### Figshare

Impacts of winter climate change on northern forest understory carbon dioxide exchange determined by reindeer grazing (Original data) (Kantola et al., 2025)

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