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RESEARCH ARTICLE

Long-term herbivore removal experiments reveal how geese and reindeer shape vegetation and ecosystem CO_2-fluxes in high-Arctic tundra

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Abstract

1. Given the current rates of climate change, with associated shifts in herbivore population densities, understanding the role of different herbivores in ecosystem functioning is critical for predicting ecosystem responses. Here, we examined how migratory geese and resident, non-migratory reindeer—two dominating yet functionally contrasting herbivores—control vegetation and ecosystem processes in rapidly warming Arctic tundra.
2. We collected vegetation and ecosystem carbon (C) flux data at peak plant growing season in the two longest running, fully replicated herbivore removal experiments found in high-Arctic Svalbard. Experiments had been set up independently in wet habitat utilised by barnacle geese *Branta leucopsis* in summer and in moist-to-dry habitat utilised by wild reindeer *Rangifer tarandus platyrhynchus* year-round.
3. Excluding geese induced vegetation state transitions from heavily grazed, moss-dominated (only $4\,g\,m^{-2}$ of live above-ground vascular plant biomass) to ungrazed, graminoid-dominated ($60\,g\,m^{-2}$ after 4-year exclusion) and horsetail-dominated ($150\,g\,m^{-2}$ after 15-year exclusion) tundra. This caused large increases in vegetation C and nitrogen (N) pools, dead biomass and moss-layer depth. Alterations in plant N concentration and CN ratio suggest overall slower plant community nutrient dynamics in the short-term (4-year) absence of geese. Long-term (15-year)

goose removal quadrupled net ecosystem C sequestration (NEE) by increasing ecosystem photosynthesis more than ecosystem respiration (ER).

4. Excluding reindeer for 21 years also produced detectable increases in live aboveground vascular plant biomass (from 50 to 80 $g m^{-2}$; without promoting vegetation state shifts), as well as in vegetation C and N pools, dead biomass, moss-layer depth and ER. Yet, reindeer removal did not alter the chemistry of plants and soil or NEE.
5. *Synthesis*. Although both herbivores were key drivers of ecosystem structure and function, the control exerted by geese in their main habitat (wet tundra) was much more pronounced than that exerted by reindeer in their main habitat (moist-to-dry tundra). Importantly, these herbivore effects are scale dependent, because geese are more spatially concentrated and thereby affect a smaller portion of the tundra landscape compared to reindeer. Our results highlight the substantial heterogeneity in how herbivores shape tundra vegetation and ecosystem processes, with implications for ongoing environmental change.

KEYWORDS
carbon (C) and nitrogen (N), ecosystem respiration (ER), gross ecosystem photosynthesis (GEP), habitats, mosses, net ecosystem exchange (NEE), plant–herbivore interactions, Svalbard

1 | INTRODUCTION

Vertebrate herbivores are found in most terrestrial ecosystems, and their key role in shaping ecosystem structure and function has been recognised for decades in systems as diverse as savannas (McNaughton, 1985), temperate grasslands (Frank & Groffman, 1998), boreal forests (Pastor & Naiman, 1992) and Arctic tundra (Jefferies et al., 1994). In the latter, partly due to a mixture of anthropogenic factors, densities of herbivore populations are undergoing drastic changes (Fox & Madsen, 2017; Uboni et al., 2016). With the Arctic experiencing the fastest rate of climate warming on Earth (IPCC, 2021), together with the potential for herbivory to modulate warming effects on vegetation and ecosystem processes (Leffler et al., 2019; Post & Pedersen, 2008; Sjögersten et al., 2008), interest in how herbivores affect tundra ecosystems is high (Barrio et al., 2016; Koltz et al., 2022). A growing body of studies has shown that herbivore impacts are far from homogeneous and often depend on both the species and the ecological context (Bernes et al., 2015; Lara et al., 2017; Petit Bon, Inga, et al., 2020; Sjögersten et al., 2008; Speed et al., 2010; Sundqvist et al., 2019). However, these insights mainly emerge when synthesising outcomes from different single-species studies conducted in different systems (Forbes et al., 2019; Soininen et al., 2021). Herein, by sampling two independent sets of long-term herbivore exclosures in the same Arctic system, we investigate the role of geese and *Rangifer* (reindeer/caribou), two circumpolar-distributed herbivores, in shaping tundra vegetation and ecosystem carbon (C) exchange rates.

Herbivores influence standing biomass and composition of tundra vegetation via direct and indirect mechanisms. By directly consuming plant tissue, herbivores generally reduce plant biomass, although no effects or even increases in biomass have also been reported (Olofsson et al., 2004). This latter effect results from shortcutting the litter decomposition pathway through the deposition of soluble nutrients (mainly nitrogen [N]) in animal excreta (Barthelemy et al., 2017; Van der Wal et al., 2004) and from reducing the depth of the moss layer through trampling (Tuomi et al., 2021), in turn raising soil temperatures (Gornall et al., 2009). Herbivores can thereby hasten nutrient cycling rates and indirectly enhance plant productivity. This is also how herbivores can promote a graminoid-dominated vegetation state in the tundra (Van der Wal, 2006) and modify the quality (N concentration and CN ratio) of forage plants (Olofsson et al., 2001; Petit Bon et al., 2022). Yet, if herbivore pressure exceeds certain thresholds, resultant alterations to the plant–soil system can spark feedback loops leading to degraded vegetation states, which can be temporarily (Ravolainen et al., 2020) or near-irreversible (Jefferies et al., 2006).

By affecting vegetation and soil, Arctic herbivores can alter CO_2 emissions from the tundra. An herbivore-induced decrease in plant biomass can directly reduce the potential for C uptake of the ecosystem (Metcalfe & Olofsson, 2015; Plein et al., 2022; Sjögersten et al., 2008; Van der Wal et al., 2007). However, reduced biomass inherently translates to lower plant respiration, potentially levelling out the net loss of C at the ecosystem level. Herbivores can also indirectly enhance C emission by stimulating soil respiration through reducing moss-layer depth, thereby increasing soil temperatures (Gornall et al., 2009). Yet, this effect might also be levelled out if herbivores concurrently limit soil respiration by reducing the amount of plant C returned to microbes (Stark & Grellmann, 2002), or if they enhance plant productivity, and hence ecosystem C sequestration, by accelerating nutrient cycling rates (Ylänne & Stark, 2019). Although pathways are complex, investigating how herbivores modify CO_2-fluxes of tundra ecosystems can provide essential information to predict alterations in the C balance of Arctic regions under ongoing climate change. This is critical, considering that approximately one-third of the world's soil C is stored in permafrost regions (Tarnocai et al., 2009), with potential for climate feedbacks if released (IPCC, 2021; Schuur et al., 2015).

Arctic ecosystems host a range of vertebrate herbivores (Speed et al., 2019). The influence on ecosystem functioning likely varies across taxonomic and functional herbivore groups, and their pattern of resource utilisation. For example, spatially co-occurring mammalian herbivores with contrasting size, such as reindeer and small rodents, have been repeatedly shown to differentially affect tundra vegetation (Petit Bon, Inga, et al., 2020; Ravolainen et al., 2011) and ecosystem CO_2-fluxes (Metcalfe & Olofsson, 2015). Analogously, herbivores that are spatially more separated may differentially alter ecosystem structure and function in their respective habitats (Jefferies et al., 1994). Migratory geese are known to exert a strong pressure on the Arctic tundra, notably during spring and while rearing goslings throughout the summer (Gauthier et al., 1995). Yet, the intensity of goose herbivory varies among habitats (Kellett & Alisauskas, 2022), and is greatest in wet tundra (Speed et al., 2009), indicating that the effects of geese are likely to be spatially concentrated. Contrastingly, reindeer roam the tundra year-round, ranging widely and utilising both relatively moist and dry habitat (Hansen et al., 2010; Iversen et al., 2014). Perhaps also for this reason, at a circumpolar scale, reindeer impacts on tundra vegetation are generally weak (Bernes et al., 2015).

Herbivore removal experiments have proved a powerful tool to address the effects of herbivores on ecosystem functioning (Forbes et al., 2019; Soininen et al., 2021), especially in the long term, after sufficient time for the system to adjust (e.g. Sundqvist et al., 2019). However, due to the paucity of long-term removal experiments in the Arctic, and even more so in the high Arctic (Forbes et al., 2019), studies on how herbivores influence ecosystem structure and function across the tundra landscape are scarce. With the Arctic rapidly changing, there is an urgent need for experiments testing the role of different herbivores in shaping tundra ecosystems (Koltz et al., 2022).

In this study, we examine grazing impacts of barnacle geese *Branta leucopsis* and wild Svalbard reindeer *Rangifer tarandus platyrhynchus*, whose populations in high-Arctic Svalbard have increased considerably in size and spatial extent during the last decades (Fox & Madsen, 2017; Le Moullec et al., 2019). We took advantage of two long-term (≥15 years) herbivore removal experiments, one set up in wet habitat largely utilised by post-breeding and moulting migratory geese and one set up in moist-to-dry habitat largely utilised by resident, non-migratory reindeer. Our aim was to investigate the role of each herbivore in shaping tundra vegetation and associated ecosystem processes in its respective main habitat. We focused on herbivore-induced changes in (i) live plant biomass and vegetation composition, (ii) concentrations and pools of C and N in vegetation and (iii) instantaneous ecosystem CO_2-fluxes. Changes in standing-dead biomass and moss-layer depth, as well as in soil C and N concentrations, were also assessed to draw a more complete picture of how these functionally different herbivores affect the Arctic tundra over the long term. We expected geese to exert a strong control on the functioning of wet habitat, and for reindeer to exert a less pronounced, yet detectable, influence on the functioning of moist-to-dry habitat.

2 | MATERIALS AND METHODS

2.1 | Study systems

The high-Arctic archipelago of Svalbard (Norway)—one of the most rapidly warming regions on Earth (Isaksen et al., 2022)—hosts only two resident vertebrate herbivores: the wild Svalbard reindeer *Rangifer tarandus platyrhynchus* and the Svalbard rock ptarmigan *Lagopus muta hyperborea*. In summer, however, several species of migratory birds dwell and breed in Svalbard, among which two geese, the barnacle goose *Branta leucopsis* and the pink-footed goose *Anser brachyrhynchus*, extensively utilise wet tundra across the archipelago.

This study utilised the two longest running, fully replicated herbivore removal experiments found in Svalbard. The two study sites, found near the settlement of Ny-Ålesund and in the valley named Semmeldalen, are ~130 km apart, yet both are located on the largest island of the archipelago, Spitsbergen (Figure 1a). The Ny-Ålesund site is a tundra wetland (Thiisbukta) near the shore of Kongsfjorden, while the Semmeldalen site is moist-to dry tundra situated in the inner part of the ~8-km long, U-shaped valley in a more central part of Spitsbergen. Table 1a provides study site characteristics.

The two long-term experiments were independently set up to study the influence of, respectively, migratory barnacle geese (Ny-Ålesund) and resident, non-migratory reindeer (Semmeldalen) on Svalbard's terrestrial ecosystems. Yet, owing to their comparable design and duration (Section 2.2), they also provide a unique opportunity to conduct a side-by-side assessment of the extent to which these two circumpolar-distributed herbivores influence the habitat they most extensively utilise.

The Ny-Ålesund area has since the early 1980s had an increasing population of barnacle geese (Table 1b), which largely utilises wet habitats. Reindeer are now also fairly abundant on Brøggerhalvøya (the peninsula of which Ny-Ålesund is part), but very infrequently use wet tundra in the vicinity of Ny-Ålesund; rather, they more commonly graze within drier habitats (as confirmed by GPS collar data; Hansen et al., *data unpublished*). This renders our study site in Ny-Ålesund an example of a system intensively grazed by geese, but only for a limited period of 3–5 weeks when vascular plant growth is greatest. During this period, adult geese undergo full wing moult and goslings grow up, conditions which limit their spatial range. By the time adults and young geese can fly, they leave the area.

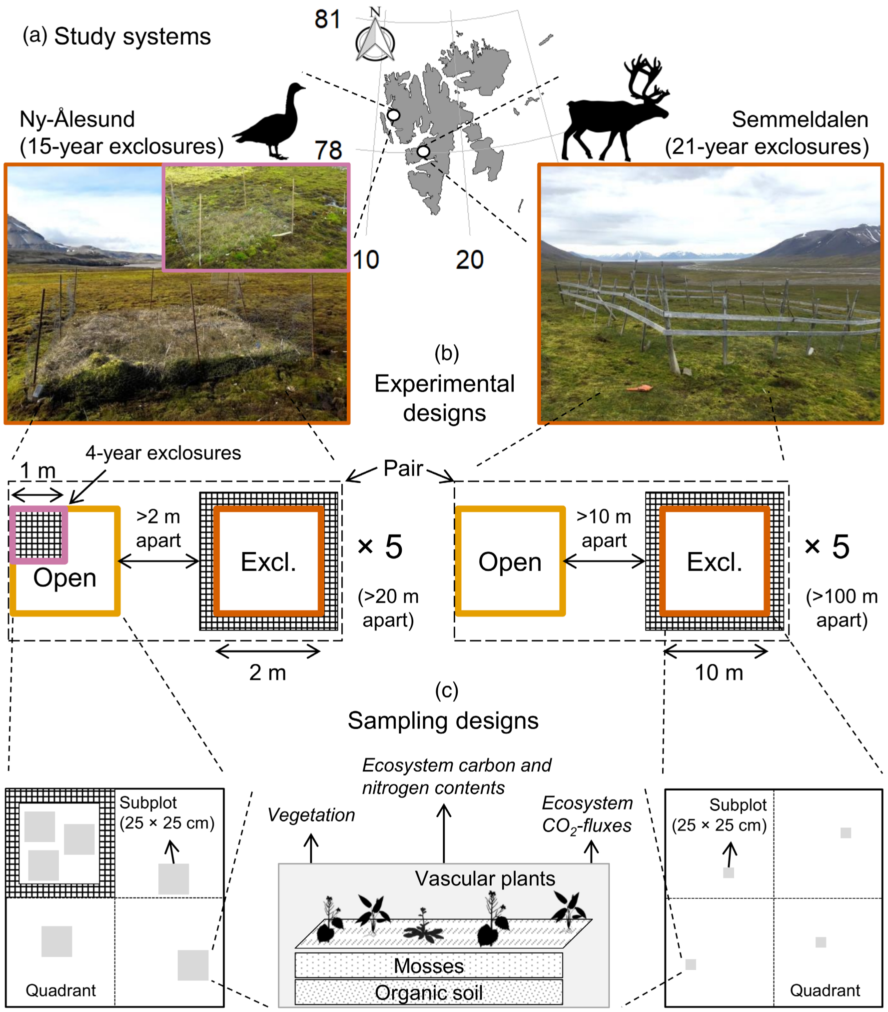

FIGURE 1 Schematic of the experiments at the two study sites. (a) Study systems, (b) details on the spatial structure of the experimental designs (photographs show examples of the long-term exclosures at the two experimental sites in the sampling year 2018; the inset for Ny-Ålesund shows a short-term exclosure) and (c) sampling designs. The drawing in (c) summarises the ecosystem properties considered in this study.

The Semmeldalen study site is grazed year-round by reindeer, a 'mixed grazer/browser' that is less spatially restricted (home-range size of a few km^2; Tyler & Øritsland, 1989) and consumes a much wider range of plant species compared to barnacle geese. The local reindeer population (Colesdalen–Semmeldalen–Reindalen valley system) has tripled in size during the last 20 years (Table 1b), and extensively utilises moist-to-dry habitat. Pink-footed geese, and to a lesser extent barnacle geese, have locally increased in numbers, as in the rest of the archipelago (Madsen et al., 2017). However, they are generally confined to wet tundra (Speed et al., 2009), and only sporadic signs of goose activity were observed at the reindeer exclosure locations (Van der Wal & Petit Bon, *personal observations*).

2.2 | Experimental sites and set-up

Detailed experimental site and study design descriptions are given elsewhere (Ny-Ålesund: Sjögersten et al., 2011; Semmeldalen: Van der Wal & Brooker, 2004), but a summary is provided here. Plant names follow the Svalbard Flora (https://www.svalbardflora.no).

The Ny-Ålesund experimental site was established in 2003 in a wet habitat (Van der Wal & Hessen, 2009) dominated by grasses (mainly *Poa arctica*), forbs (e.g. *Saxifraga* spp. and *Cardamine* spp.) and the horsetail *Equisetum arvense*. *Calliergon* spp. are the dominant mosses. Five pairs of exclosure and open-grazed plots (2 m × 2 m) were set up within the wetland (1-km^2 area; Figure 1b). Exclosures were built with 50-cm high poultry netting and metal strings across the top. Five additional exclosures were built in 2015 by fencing off a randomly selected corner (quarter; 1 m × 1 m) of each open-grazed plot.

The Semmeldalen experimental site was established in 1997 in two different moss-dominated habitats: moist grass-rich meadow and dry *Luzula* heath. Across the two habitats, common vascular plant species are the grasses *P. arctica* and *Alopecurus ovatus*; the woodrush *Luzula confusa*; the forbs *Bistorta vivipara* and *Stellaria longipes*; the deciduous dwarf shrub *Salix polaris*; and the horsetail *E. arvense*. Dominant mosses are *Sanionia uncinata*, *Tomentypnum nitens* and *Aulacomnium* spp. Five pairs of exclosure and open-grazed

TABLE 1 Characteristics of the study sites.

	Ny-Ålesund	Semmeldalen
(a)		
Location	78°55′ N, 11°55′ E	77°59′ N, 15°22′ E
Altitude	5–10 m a.s.l.	150–165 m a.s.l.
Mean annual temperature	−4.3 [−2.1]°C	−4.0 [−1.8]°C
Mean July temperature	5.6 [6.2]°C	6.8 [7.2]°C
Annual precipitation	465 [749] mm	204 [293] mm
(b)		
Main herbivore at the exclosure locations	Geese (June–July)	Reindeer (year-round)
Trend in main herbivore population	$\lambda = 1.02$ (geese) (a)	$\lambda = 1.09$ (reindeer) (b)
Mean main herbivore biomass in summer (June–July)(c)	560 kg geese km^{-2}	154 kg reindeer km^{-2}
Mean main herbivore biomass throughout the year(d)	93 kg geese km^{-2}	154 kg reindeer km^{-2}

Note: (a) Climate data are for the 30-year period 1989–2018 from the climate stations in Ny-Ålesund (for Ny-Ålesund site) and at Svalbard airport (for Semmeldalen site); in brackets, data for the sampling year 2018 (www.met.no). (b) Estimated mean annual population growth rate (λ) for (a) barnacle geese for the period 2004–2017 (Layton-Matthews et al., 2019) and (b) reindeer for the period 1998–2018 (Solberg et al., 2022). Estimated biomass of geese (Ny-Ålesund, period 2004–2017; mean population size $n = 693$, mean body mass = 1.6 kg, area = 2 km^2) and reindeer (Semmeldalen, period 1998–2018; mean population size $n = 898$, mean body mass = 52 kg, area = 300 km^2), separately for (c) summer only and (d) whole year (data from references above).

plots (10 m × 10 m) were established within a 10-km^2 area (Figure 1b). Three pairs were set up in moist grass-rich meadows and two pairs in dry *Luzula* heaths. Exclosures were built with 150-cm high timber.

We did not observe signs of herbivore activity inside the exclosures during the sampling season of 2018. Reindeer could step over the wooden fences during winter when snow reaches sufficient depth; however, no over-winter cratering (sensu Hansen et al., 2010) took place. Hence, the exclosures remove effectively the herbivory pressure on the vegetation and the underlying soil system. Three independent visits (February 2010; March and April 2018) to the study sites suggest that snow cover during winter does not differ between open-grazed and exclosure plots (Van der Wal & Petit Bon, *personal observations*). Yet, as a control area to evaluate the effect of fences on snow accumulation, and hence vegetation and soil, was not available, we cannot rule out the possibility of slightly different snowmelt patterns across plots in spring.

2.3 | Sample collection and processing

2.3.1 | Sampling design

Around the peak of the growing season in 2018 (Ny-Ålesund: 15–21 July; Semmeldalen: 25–31 July), an intense sampling campaign was undertaken to investigate how Svalbard tundra ecosystems respond to the long-term removal of geese (Ny-Ålesund; 15-year exclusion) and reindeer (Semmeldalen; 21-year exclusion). In Ny-Ålesund, short-term exclosures (4-year-old) were also sampled to help interpret long-term responses.

To account for some of the spatial variation within plots, measurements of focal ecosystem properties were taken in three (Ny-Ålesund) or four (Semmeldalen) subplots (25 cm × 25 cm) per plot (Figure 1c). Plots were divided into quadrants and one subplot was determined at random within each quadrant.

2.3.2 | Vegetation: Vascular plants and mosses

We assessed above-ground vascular plant biomass using point intercept frequency methodology (PIM; Bråthen & Hagberg, 2004). PIM was performed at each subplot using a sampling frame (25 cm × 25 cm) with 15 points. A pin (3 mm diameter) was lowered from above onto the moss or soil at each point and the number of contacts (intercepts) between the pin and each live vascular plant species was counted. Standing-dead graminoid material was also a possible intercept and recorded as additional category. We converted the number of intercepts for each species (live) and category (standing-dead graminoids) into plant biomass (g m^{-2}, as dry weight [dw]) following Bråthen and Hagberg (2004) and by using correlation coefficients in Petit Bon et al. (2021). We grouped vascular plant species into five broadly classified plant functional types (PFTs): forbs, grasses, horsetails, rushes and deciduous dwarf shrubs (species data are given in Table S1).

We measured moss-layer depth (separately for the photosynthetically active green part and the nearly decomposed brown part) in two randomly selected, yet opposing, corners of each subplot.

2.3.3 | Ecosystem C and N contents

We assessed leaf C and N concentrations (%dw) in five focal vascular plant species belonging to the five PFTs: *B. vivipara* (forb), *P. arctica* (grass), *E. arvense* (horsetail), *L. confusa* (woodrush) and *S. polaris* (deciduous dwarf shrub). Together, these species made up on average

84% and 94% of the live above-ground vascular plant biomass at the Ny-Ålesund and Semmeldalen sites respectively. Total leaf C and N pools (g m^{-2} dw) were calculated by combining elemental concentrations and biomass data (Section 2.3.2). Finally, we assessed C and N concentrations of mosses and soil.

Vascular plant leaf sampling was conducted randomly while performing PIM. The closest live-leaf to each pin and belonging to one of the five focal species was collected (2–4 leaves per species per subplot). In open-grazed plots in Ny-Ålesund, where vascular plant biomass was very low (Section 3), leaves were collected at the plot level. Leaves from each species and subplot were stored in a separate tea-filter bag, pressed dry between filter papers for 72 h, and then oven-dried at 60°C for 48 h, following Petit Bon, Böhner, et al. (2020). In Semmeldalen, where we did not have access to oven facilities, leaves were kept as dry as possible by regularly substituting filter papers and oven-dried within 5 days.

Each leaf was analysed for C and N concentration with near-infrared reflectance spectroscopy (NIRS FieldSpec 3; ASD Inc.®) in 350–2500 nm range and using a 4-mm light-adapter for full-leaf analysis (Petit Bon, Böhner, et al., 2020). For each leaf, three to six NIR measurements were taken, depending on leaf size. Each measurement was converted to C and N concentration using prediction models developed for ground leaf samples (Ancin-Murguzur et al., 2019) and correcting for measures on intact leaves (Petit Bon, Böhner, et al., 2020). We computed the median of the measurements of each leaf and then averaged the medians to obtain mean C and N concentration for each focal species within a subplot (for a similar approach, see Petit Bon, Inga, et al., 2020). This led to a total of 66 and 120 leaf nutrient samples from Ny-Ålesund and Semmeldalen respectively (Table S2).

We calculated total live-leaf C and N pools (cf. Petit Bon, Bråthen, et al., 2023):

$$\sum_{(i=1)}^{n}\left(\frac{b_i \times (\text{elemental concentration})_i}{100}\right),$$

where n equals the focal vascular plant species (see above), b_i is the absolute live above-ground biomass (g m^{-2} dw) contributed by species i and (elemental concentration)$_i$ represents either C or N concentration (%dw) of species i.

Moss shoots (5–10) were collected at each interception of the 15 pins (see above) with the moss mat, and these were pooled for each subplot. For each resultant moss sample, we separated green and brown parts. Moreover, two samples of organic soil (0–5 cm below the brown moss parts) were collected from the two corners of each subplot and pooled. Soil samples were mixed, homogenised and sieved at 2 mm mesh size.

Moss (green and brown parts separately) and soil samples were analysed with NIRS for C and N concentrations using prediction models developed specifically for mosses (Figure S1) and soil (Petit Bon, Inga, et al., 2020). We took three to eight NIR measurements for each moss sample and six NIR measurements for each soil sample. After converting each measurement to C and N concentration, we computed the average C and N concentrations for mosses and organic soil in each subplot (Table S2).

2.3.4 | Instantaneous ecosystem CO_2-fluxes

A set of CO_2-flux measurements was taken twice in each subplot, resulting in a total of 90 and 80 sets from Ny-Ålesund and Semmeldalen respectively. Each set consisted of a light and a dark measurement, from which we calculated net ecosystem exchange (NEE) and ecosystem respiration (ER). In the short-term exclosures in Ny-Ålesund, only ER was measured. Estimates of gross ecosystem photosynthesis (GEP) were obtained by subtracting ER from NEE. The two sets of measurements at each subplot were taken on separate days. To minimise differences in environmental conditions among measurements across treatments, each pair of exclosure and open-grazed plot was measured consecutively.

CO_2-flux measurements were taken using a closed static/non-steady state system composed of a clear chamber (25 cm × 25 cm area × 35 cm height, made of LEXAN© polycarbonate; >90% light transmittance), connected to a CO_2 infrared gas analyser (LI-840A; LICOR Inc.®) through an air pump with 0.9–1.0 L min^{-1} flow rate (L052C-11; Parker Corp.®). To prevent disturbance to the tundra, mattress-foam fabric (1.5 cm thick) was attached to the bottom of the chamber. To minimise air exchange with the external environment, a plastic skirt (30 cm wide) was attached to the bottom of the chamber and held down (i.e. sealing) during measurements by a 2-m long draped around steel chain weighing 4 kg. A fan mixed the air inside the chamber continuously (cf. Sundqvist et al., 2020).

Measurements at each subplot took place within 3 h either side of solar noon, started 15–20 s after sealing (acclimation period), and lasted 120–150 s. Air CO_2 concentration inside the chamber was registered every 5 s. During ER measurements, a completely dark hood was placed over the chamber to stop light and temporarily halt photosynthesis. Photosynthetically active radiation (PAR) and air temperature (~20 cm above the vegetation) were recorded simultaneously with the CO_2-fluxes within the chamber every 5 and 10 s, respectively, using a PAR sensor and datalogger (LI-190SA and LI-1400; LICOR Inc.) and a temperature logger (DS1922L-F5; Maxim Integrated®). CO_2 data were collected under a wide range of light and temperature conditions: PAR during NEE measures was on average 525 ± 256 SD μmol m^{-2} s^{-1} (range: 129–1131 μmol m^{-2} s^{-1}), whereas air temperature during both NEE and ER measures was on average 11.4 ± 5.0°C (range: 5.4–22.1°C). No appreciable differences in average PAR and air temperature were detected between treatments (Table S3).

Because small-scale spatial variations in hydrological conditions affect tundra CO_2-fluxes (Sjögersten et al., 2006), soil volumetric water content across 0–5 cm depth was measured in two corners of each subplot after each set of flux measurements using a hand-held moisture logger (ML3 Theta Probe and HH2 Meter; Delta-T Ltd.®). We concurrently measured soil temperature (5 cm depth) in the same two corners using a temperature probe (TFX 410-1 Handheld Thermometer; Ebro®).

We used linear regression models to obtain ecosystem CO_2-fluxes (NEE and ER) at each subplot (cf. Sundqvist et al., 2020):

$$CO_2 - \text{flux} = \frac{V \times P}{R \times T_{\text{air}} \times S} \times \frac{\Delta C}{\Delta t},$$

where V is the volume of the chamber (0.021875 m^3), P is the average air pressure (standard atm, registered at Adventdalen weather station [~10 m a.s.l.; ~110 km from Ny-Ålesund and ~30 km from Semmeldalen] every 1 s), R is the ideal gas constant (8.314 J mol^{-1} K^{-1}), T_{air} is the average air temperature (K), S is the surface area of the chamber (0.0625 m^2) and $\Delta C/\Delta t$ is the slope of the linear regression, that is, the change in CO_2 concentration (ΔC) within the chamber during the measurement period (Δt). The protocol used for checking and cleaning raw CO_2-flux data and its associated R-script is provided in Data S1. Fluxes are shown as μmol CO_2 m^{-2} s^{-1} and presented from an atmospheric perspective, that is, positive and negative values signify ecosystem CO_2 release (C source) and CO_2 uptake (C sink) respectively.

2.4 | Statistical analyses

Because our aim was to assess the impacts of each herbivore independently on its main habitat, the two experiments were analysed separately. In Ny-Ålesund, there were three levels of the 'herbivory' treatment (open-grazed [Open], 4-year-old exclosures [Short-excl], and 15-year-old exclosures [Long-excl]), while in Semmeldalen there were two levels (open-grazed [Open] and 21-year-old exclosures [Long-excl]). Pairs of exclosure and open-grazed plots were considered the inferential units (i.e. true replicates; $N=5$ in both experiments), while subplots within plots were considered the experimental units (per treatment: Ny-Ålesund, $n=15$; Semmeldalen, $n=20$). Therefore, if not otherwise specified, whenever multiple measures for a given variable were taken in a subplot (e.g. moss-layer depth recorded in the two corners), data were averaged prior to analyses.

We employed a variety of statistical models within a linear mixed-effects model (LMM) framework to account for the spatial structure of the study design, whereby we consistently specified 'plot' nested in 'pair' as random effects. 'Herbivory' treatment was used as a fixed effect in all models. Data were either *log*- or *arcsine*-transformed when necessary to improve normality and homoscedasticity of model residuals.

2.4.1 | Vegetation

Differences in vascular plant community structure were assessed on both absolute (actual biomass changes) and relative (plant community compositional changes) PFT biomass. For relative differences, we determined proportional biomass by summing the biomass of all PFTs and then calculating the relative contribution of each PFT. First, we assessed the effect of herbivory on absolute total biomass and relative PFT biomass using LMMs and permutational multivariate analysis of variance respectively. Then, to test for the effects of herbivory on absolute biomass of each PFT, we used LMMs fitted separately for each PFT (cf. Sitters et al., 2019).

LMMs were also built to assess the effects of herbivory on standing-dead graminoid biomass and moss-layer depth (total and green and brown parts separately).

2.4.2 | Ecosystem C and N contents

To investigate how herbivory affects plant and soil chemistry, we used LMMs with either N concentration or CN ratio as response variable. We fitted separate models for the five focal vascular plant species belonging to the five PFTs, different moss parts and organic soil. Similarly, LMMs were built to assess the effects of herbivory on live-leaf C and N pools. We refrained from fitting a single 'herbivory × species' interaction model because, due to the relatively low number of replicates ($N=5$), several interaction coefficients could not be interpreted with confidence.

2.4.3 | Ecosystem CO_2-fluxes

To examine how herbivory affects ecosystem CO_2-fluxes, we used separate LMMs with NEE, ER and GEP as response variable. Abiotic covariates known to influence NEE and GEP (i.e. PAR and soil moisture) and ER (i.e. soil moisture and soil temperature) were initially incorporated to improve model fit and allow for more meaningful ecological interpretations of herbivore effects (cf. Leffler et al., 2019; Sjögersten et al., 2008). Because in Ny-Ålesund the open-grazed tundra was by-and-large moss (Section 3), and mosses have lower light requirements than vascular plants (Douma et al., 2007), we added an 'herbivory × PAR' interaction to NEE and GEP models built on data from there. Moreover, as soil moisture was high (88% ± 15%; Table S3) and often found to be ~100% (Figures S2 and S3), we did not include soil moisture in models from Ny-Ålesund. In Semmeldalen, soil moisture and soil temperature were correlated (Figure S2); as the former influences the latter, we excluded soil temperature from the ER model to avoid spurious results. Ultimately, we only kept abiotic covariates in the final models that explained a significant portion of the variance. Because two sets of CO_2-flux measurements were taken at each subplot, we here specified 'subplot' as an additional nested random effect in all models to account for the repeated measures.

To gain a better mechanistic understanding of how herbivores affect ecosystem CO_2-fluxes, we explored the relationships between

CO_2-flux data (NEE, ER and GEP as separate response variables in LMMs) and either live vascular plant biomass or moss-layer depth (used as predictor). In these models, we did not include 'herbivory' as a fixed-effect as it would be highly correlated with both these predictors (Section 3). The random structure of these models was as specified above.

Statistically significant differences between 'herbivory' treatments were defined as having their 95% confidence interval (CI) not crossing zero. Analogously, significant relationships were also defined as having the 95% CI of their slope not crossing zero. Model summaries are presented in Tables S4–S11. We performed data analyses in R ver. 4.2.1 (https://www.r-project.org) using the packages *vegan* (Oksanen et al., 2020), *nlme* (Pinheiro et al., 2015) and *emmeans* (Lenth, 2021).

3 | RESULTS

3.1 | Vegetation: Vascular plants and mosses

In Ny-Ålesund, the short-term (4-year) and long-term (15-year) experimental exclusion of geese from their main habitat (i.e. wet tundra) resulted in 16-fold and 39-fold greater, respectively, live above-ground vascular plant biomass compared to open-grazed tundra (Figure 2a). While both long- and short-term exclosures had higher biomass of grasses and horsetails compared to goose-grazed tundra, only the latter had higher forb biomass. Live biomass was twice as high in long-term than short-term exclosures, largely due to an eightfold increase in horsetail biomass. Herbivory treatments also differed in plant community composition (Figure 2b). Forbs, grasses

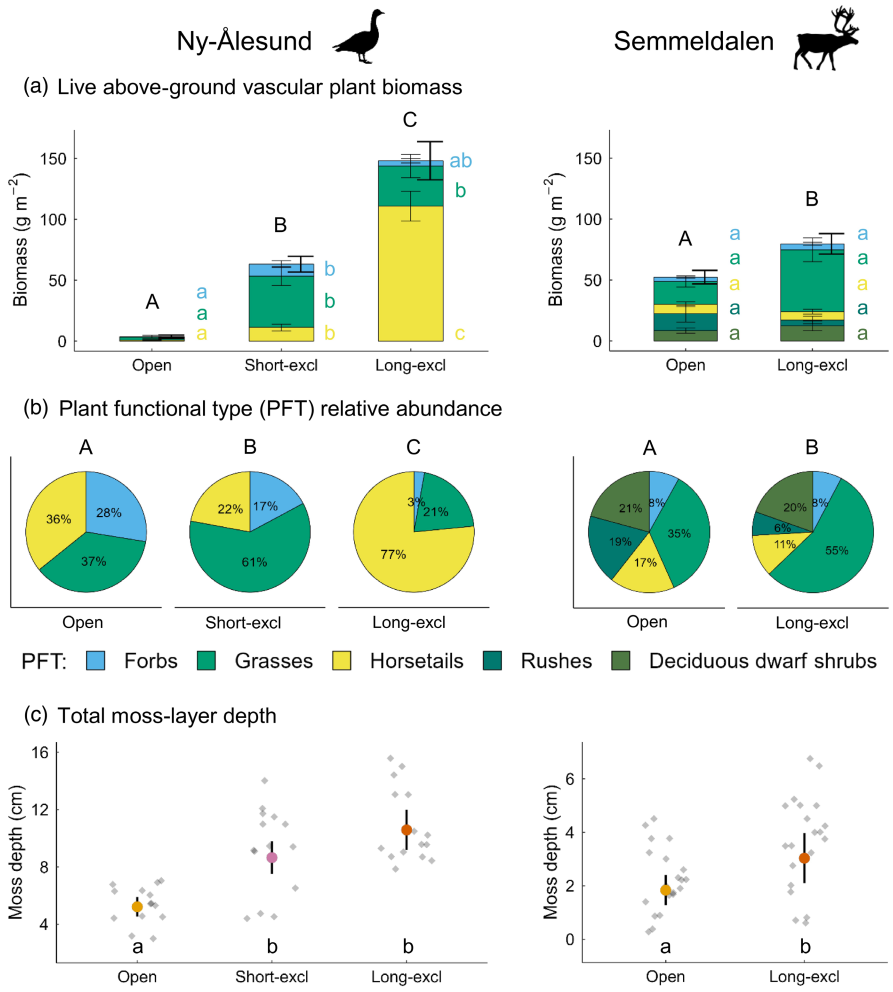

FIGURE 2 Effects of herbivore removal on vegetation in Ny-Ålesund (left panels) and Semmeldalen (right panels). (a) Live above-ground vascular plant biomass (dry weight) in each herbivory treatment (Open: open-grazed; Short-excl: short-term exclosures; Long-excl: long-term exclosures), sorted according to plant functional types (PFTs). Thick and thin bars are the standard error (SE) of the mean for total biomass and biomass of each PFT respectively. (b) Above-ground PFT relative abundance within each herbivory treatment. (c) Model predictions ± SE for total moss-layer depth within each herbivory treatment. Grey dots show raw values; note the different scale of *y*-axes. Treatments connected by different letters indicate a statistically significant difference.

and horsetails contributed overall equally to the little vascular plant biomass found in goose-grazed tundra. Conversely, long-term and short-term exclosures were in two different vegetation states, dominated by horsetails and grasses respectively. Goose exclosures also had 120–200-fold higher dead graminoid biomass than open-grazed tundra (0.12 ± 0.52 SE g m^2), without a significant difference between long-term (31 ± 15 g m^2) and short-term (22 ± 11 g m^2) exclosures (Table S4).

In Semmeldalen, the long-term (21-year) experimental exclusion of reindeer from their main habitat (i.e. moist-to-dry tundra) resulted in 45% greater live above-ground vascular plant biomass compared to open-grazed tundra (Figure 2a). Here, however, the biomass of each individual PFT did not differ between herbivory treatments. Despite the two treatments differing in plant community composition due to a higher relative abundance of grasses and a lower relative abundance of rushes in exclosures compared to reindeer-grazed tundra (Figure 2b), this difference disappeared when these two PFTs were combined into graminoids (Table S5). Reindeer exclosures also had 3× higher biomass of dead graminoids (31 ± 17 g m^2) than open-grazed tundra (10 ± 6 g m^2) (Table S4).

In Ny-Ålesund, the total moss layer was almost twice as deep in exclosures than in goose-grazed tundra (Figure 2c). This difference was due to contributions from photosynthetically active green and nearly decomposed brown parts of mosses, both of which were deeper in short-term (green: 2.1 ± 0.3 cm; brown: 6.3 ± 1.1 cm) and long-term (green: 1.8 ± 0.3 cm; brown: 8.6 ± 1.5 cm) exclosures than in goose-grazed tundra (green: 1.0 ± 0.2 cm; brown: 4.0 ± 0.7 cm) (Table S6). In Semmeldalen, exclosures had about 60% deeper total moss-layer than reindeer-grazed tundra (Figure 2c). This was due to the depth of the green part being greater within exclosures (1.2 ± 0.3 cm vs. 0.6 ± 0.1 cm), as that of the brown part did not differ (Table S6).

3.2 | Ecosystem C and N contents

Overall, N concentration and CN ratio of the three ecosystem compartments (vascular plant leaves, green and brown moss parts, organic soil) displayed relatively few responses to herbivore exclusion, and where then only in Ny-Ålesund. *Poa arctica* grass leaves in short-term exclosures had about 20% lower N concentration and 30% higher CN ratio than in either goose-grazed tundra or long-term exclosures (Figure 3a,b). Similarly, green moss parts in short-term exclosures had about 13% lower N concentration (1.19% ± 0.09%) and 17% higher CN ratio (38.5 ± 3.1) compared to goose-grazed tundra (N: 1.38% ± 0.11%; CN ratio: 31.8 ± 2.5), and tended to have lower N concentration and higher CN ratio than in long-term exclosures (N: 1.38% ± 0.12%; CN ratio: 33.2 ± 2.9). Soil N concentration in long-term exclosures (0.87% ± 0.03%) also tended to be lower than in goose-grazed tundra (0.96% ± 0.03%) (Table S8).

Overall, live-leaf C and N pool responses to herbivore removal were of similar magnitude as vascular plant biomass responses, reflecting their tight positive correlations (Figure 3c). In Ny-Ålesund, the exclusion of geese for 4 and 15 years resulted in 13-fold and 40-fold greater, respectively, leaf C and N pools compared to open-grazed tundra. C and N pools also differed between exclosures, with long-term ones holding 3× higher leaf C and N pools than short-term exclosures. In Semmeldalen, reindeer exclusion for 21 years resulted in 60% and 80% greater leaf C and N pools, respectively, compared to open-grazed tundra.

3.3 | Instantaneous ecosystem CO_2-fluxes

In Ny-Ålesund, 15 years of goose exclusion resulted in threefold higher GEP and ER compared to open-grazed tundra (Figure 4a,b). Because of GEP being greater than ER, net CO_2 exchange of the ecosystem (NEE) was also greater (4×), that is, more negative (i.e. higher C sequestration), in long-term exclosures than in goose-grazed tundra (Figure 4c). ER in short-term exclosures was 90% higher than in goose-grazed tundra, but only 30% lower than in long-term exclosures (Figure 4b).

In Semmeldalen, the exclusion of reindeer for 21 years increased ER by 50% compared to open-grazed tundra (Figure 4b), but had no effect on either GEP or NEE (Figure 4a,c).

Overall, PAR was related to both GEP and NEE in Ny-Ålesund and GEP in Semmeldalen (Figure 5a). However, in Ny-Ålesund, the explanatory power of PAR depended on herbivory treatment, being strongest in long-term exclosures. In Semmeldalen, soil moisture was a significant predictor of NEE, with the ecosystem switching from net loss to net uptake of CO_2 above about 50% soil moisture content (Figure 5a).

GEP, ER and NEE were mostly linked to both live above-ground vascular plant biomass (Figure 5b) and total moss-layer depth (Figure 5c) at both the Ny-Ålesund and Semmeldalen sites. Exceptions were the absence of any relationship with NEE in Semmeldalen and between moss-layer depth and GEP in Ny-Ålesund. Soil temperature decreased with increasing total moss-layer depth in Semmeldalen, but not in Ny-Ålesund, whereas soil moisture was not related to moss depth at either site (Figure S3).

4 | DISCUSSION

We investigated how Svalbard tundra responds to long-term removal of either migratory geese or resident, non-migratory reindeer, two of its most abundant Arctic herbivores. Standardised data from two independent experiments revealed how herbivores that differ in spatio-temporal distribution and feeding ecology also differ in the extent to which they shape vegetation and ecosystem CO_2-fluxes in their respective main habitats. While the effects of geese in wet habitat (wetland) were considerably greater than those of reindeer in moist-to-dry habitat (meadow/heath), impacts are scale dependent, with geese being more spatially concentrated and thus influencing a smaller portion of the tundra landscape compared to the more widely dispersed reindeer. Our findings highlight the conspicuous heterogeneity in how key tundra herbivores control ecosystem

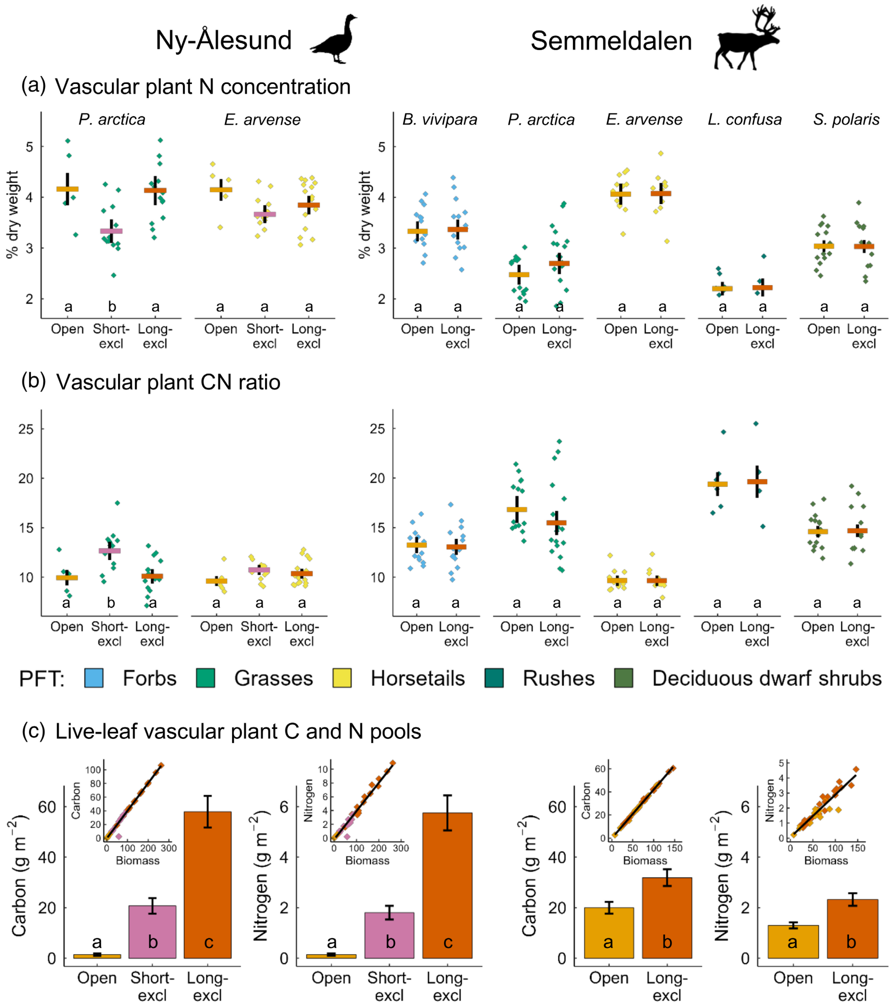

FIGURE 3 Effects of herbivore removal on vascular plant chemistry in Ny-Ålesund (left panels) and Semmeldalen (right panels). Model predictions ± SE for leaf (a) N concentration and (b) CN ratio in each herbivory treatment (Open: open-grazed; Short-excl: short-term exclosures; Long-excl: long-term exclosures) for the five focal vascular plant species representing plant functional types (PFTs). Dots show raw values. (c) Live-leaf vascular plant C and N pools (dry weight) in each herbivory treatment. Bars are the SE of the mean. Insets show the correlation between live above-ground vascular plant biomass and leaf C and N pools. Treatments connected by different letters indicate a statistically significant difference.

structure and function, with implications for a rapidly changing Arctic.

In the wet habitat in Ny-Ålesund, live above-ground vascular plant biomass in 4-year and 15-year goose exclosures was 16-fold and 39-fold greater, respectively, than that in open-grazed tundra (only 4 g m^{-2}). This shows that, when highly aggregated in space, even for relatively short period of times, geese exert large control over tundra wetlands by maintaining very low levels of vascular plant biomass (Kuijper et al., 2009; Van der Wal & Hessen, 2009), which greatly reduces vegetation C and N pools (this study; Sjögersten et al., 2011; Petit Bon, Bråthen, et al., 2023). Concurrently, the presence of geese and their exclusion for 4 and 15 years led to three distinct vegetation states: moss-, graminoid- and horsetail-dominated tundra respectively. By using the same experimental plots, Sjögersten et al. (2011) found that removing geese for 4 years largely increased grass abundance. We extend those results by showing that the successional trajectory of the vegetation in the longer-term absence of geese currently concerns the replacement of grasses by horsetails, and thus that the ecosystem had not reached an equilibrium after 4 years of goose removal.

Goose impacts in this wetland appear to increase over time: in 2008, peak summer grass biomass in grazed tundra was ~20 g m^{-2} (Sjögersten et al., 2011), 5× higher than we found in 2018. Likewise, grass biomass in our 4-year-old exclosures was about half of what Sjögersten and colleagues found 11 years earlier in their 4-year-old exclosures (i.e. our long-term exclosures). Furthermore, moss biomass did not differ between herbivory treatments in 2008, while we observed a moss layer in open-grazed tundra about half the depth of that in 4- and 15-year-old exclosures, suggesting that trampling intensity (Tuomi et al., 2021) and grazing on mosses (Soininen et al., 2010) have also increased. Although these findings align with the notion that goose impacts in wetlands—unlike in saltmarshes,

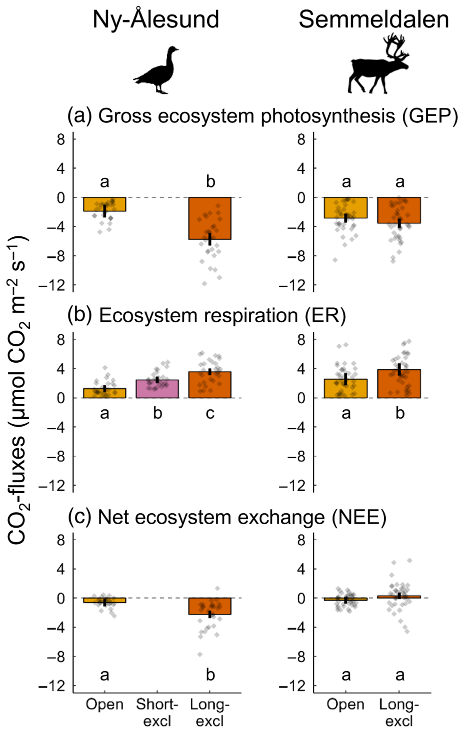

FIGURE 4 Effects of herbivore removal on ecosystem CO$_2$-fluxes in Ny-Ålesund (left panels) and Semmeldalen (right panels). Model predictions ± SE for (a) GEP, (b) ER and (c) NEE in each herbivory treatment (Open: open-grazed; Short-excl: short-term exclosures; Long-excl: long-term exclosures); final models included the abiotic covariates that explained a significant proportion of the variance (Figure 5a; Section 2.4). Dots show raw values. Treatments connected by different letters indicate a statistically significant difference.

where they may lead to near-irreversible, degraded states (Jefferies et al., 2006)—seem generally reversible (cf. Kellett & Alisauskas, 2022; Speed et al., 2010), the overall system's potential for recovery may have decreased.

In moist-to-dry habitat in Semmeldalen, 21 years of reindeer removal resulted in 45% higher live above-ground vascular plant biomass in exclosures compared to open-grazed tundra. Yet, when considering PFTs separately, no significant treatment effects could be detected, suggesting that the observed overall response was likely driven by weak responses by several PFTs. Although the Colesdalen–Semmeldalen–Reindalen valley system hosts one of the densest reindeer populations in Svalbard (Le Moullec et al., 2019), grazing pressure on vascular plants remains low (Van der Wal et al., 2004). At the landscape scale, low offtake rates by non-migratory, large herbivores may be the rule rather than exception in high-Arctic systems; for example, muskoxen, while at high densities in northeast Greenland, remove a very low amount of plant biomass (Mosbacher et al., 2016). Our results are in line with that overall effects of reindeer on vegetation in circumpolar regions are typically weak (Bernes et al., 2015). This contrasts with studies from low/sub-Arctic Scandinavia, where migratory, semi-domesticated reindeer gathering in the proximity of rotational pasture fences in summer exert strong controls on both vegetation (Olofsson et al., 2001; Sitters et al., 2019) and ecosystem processes (Olofsson et al., 2004; Ylänne & Stark, 2019).

Differences in ecosystem C and N contents among open-grazed tundra and exclosures were only detected in the Ny-Ålesund wetland. Here, N concentration of *Poa arctica*, which accounted for ~40% of the total live above-ground vascular plant biomass across treatments, was lowest (and CN ratio highest) in short-term exclosures. The same pattern held for green moss parts, indicating that vegetation N levels (and the quality of goose forage) decrease following short-term goose removal (Beard et al., 2019; Gauthier et al., 1995). Rapid nutrient return via animal excreta and keeping leaves in early phenological stages through grazing (Bazely & Jefferies, 1985; Petit Bon, Inga, et al., 2020) are the likely short-term mechanisms (i.e. the fast herbivore-mediated pathway) that maintain N concentration in grazed tundra plants high (and CN ratio low) relative to plants subject to short-term exclusion. Conversely, in the protracted absence of geese, it is the build-up of a large vascular plant N pool that eventually regulates the return rate of N to the system (i.e. the slow vegetation-mediated pathway), as vascular plant litter is more nutrient rich and releases nutrients more promptly than moss litter (Fivez, 2014; Hobbie, 1996). This likely allowed for plant N concentration in long-term exclosures to increase (and CN ratio to decrease), reaching levels like those of plants in grazed tundra. Overall, our results suggest that plant community nutrient dynamics are generally slower in the short-term absence of geese.

The fourfold increase in peak summer net CO$_2$ uptake rate of the ecosystem (NEE) due to 15 years of goose exclusion in Ny-Ålesund aligns with findings from other studies showing that intense herbivory by either geese (Leffler et al., 2019; Sjögersten et al., 2011; Van der Wal et al., 2007) or mammals (Metcalfe & Olofsson, 2015; Plein et al., 2022) can greatly reduce C sink strength of tundra ecosystems (but see Lara et al., 2017). Larger GEP than ER, together with their tight connection to live vascular plant biomass, and to a lesser extent moss-layer depth, indicates that the goose-induced changes in ecosystem CO$_2$-fluxes of this high-Arctic wetland are predominantly driven by changes in vegetation as opposed to soil (Sjögersten et al., 2011). In line with this, soil temperature did not influence ER, likely because microbial respiration was constrained by high soil moisture content (Sjögersten et al., 2006). The fact that ER in short-term exclosures was 90% higher than ER in open-grazed tundra, but only 30% lower than ER in long-term exclosures (despite 11 additional years of goose removal), indicates that following herbivore exclusion CO$_2$ exchange rates of wet habitat change rapidly, but thereafter rates of change slow down. Interestingly, this also suggests that the large differences in vegetation composition observed between short-term and long-term exclosures (as discussed above) do not transpose in major alterations of ER (cf. Sistla et al., 2013).

Notable insights also emerge when comparing our findings to those obtained by Sjögersten et al. (2008), who used captive barnacle geese to investigate the effects of short-term (3-year) goose

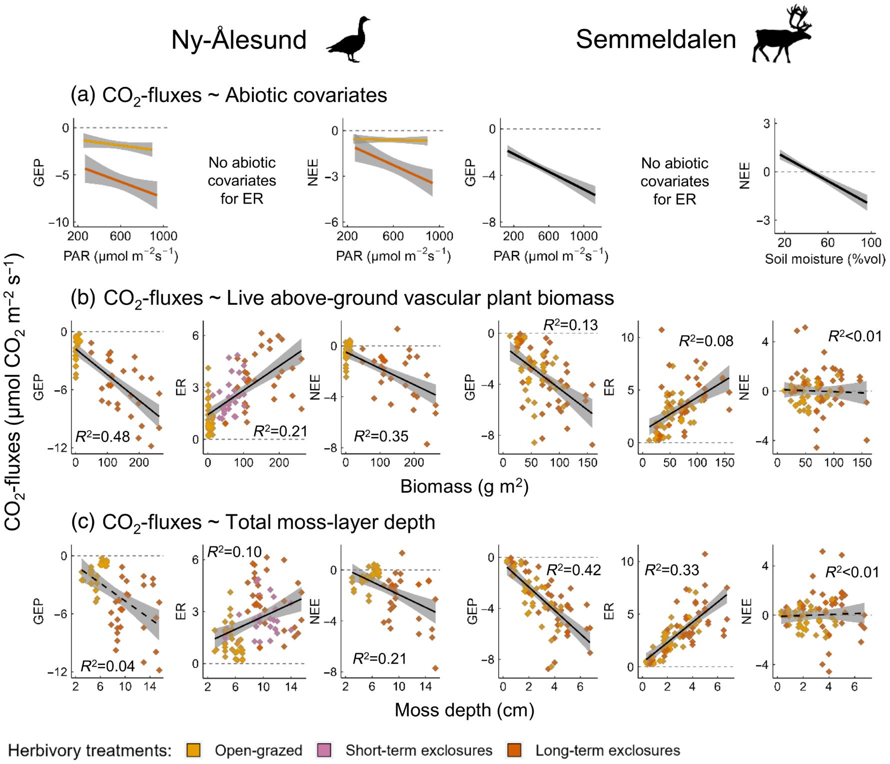

FIGURE 5 Relationships between ecosystem CO_2-fluxes and environmental variables in Ny-Ålesund (left panels) and Semmeldalen (right panels). (a) CO_2-fluxes (GEP, ER and NEE) in relation to changes in abiotic covariates that explained a significant proportion of the variance and were thus included in the final models of herbivore removal effects on CO_2-fluxes (Figure 4; Section 2.4). Relationships between GEP or NEE and PAR in Ny-Ålesund are displayed separately for each herbivory treatment (coloured lines), as the 'herbivory × PAR' interaction was retained in the final model. CO_2-fluxes as predicted by (b) live above-ground vascular plant biomass (dry weight) and (c) total moss-layer depth. Dots show raw values, coloured according to treatments. Statistically significant and non-significant relationships are displayed with solid and dashed lines respectively (marginal R^2 are shown in each panel). Lines and bands represent regression lines and their 95% CI. Note the different scale of *y*- and *x*-axes.

grazing on CO_2-fluxes in previously ungrazed wet and mesic habitats in Adventdalen, a valley in central Svalbard. First, CO_2-fluxes in our exclosures were 2–6× greater than those observed in the ungrazed wet habitat in Adventdalen, which highlight how high-Arctic wetlands may vary considerably in ecosystem process rates. Second, the fact that experimentally induced goose grazing in previously ungrazed tundra strongly reduced C sink strength of the wet habitat—as in our study—but not that of the mesic habitat (Sjögersten et al., 2008), highlights that the impacts of geese depend upon habitat type (Speed et al., 2010) and reflects that they naturally graze more intensively in wet habitat (Madsen et al., 2011; Speed et al., 2009).

Long-term reindeer removal in Semmeldalen had little effect on ecosystem CO_2-fluxes. Yet, ER was higher in exclosures than in open-grazed tundra. Because GEP did not increase concurrently, it is likely that the exclosure-induced change in ER was predominantly soil driven. By decreasing plant biomass and thereby the plant C pool, reindeer herbivory may limit the C available for soil microbes, hence decreasing microbial biomass C and respiration (Stark & Grellmann, 2002). We found both GEP and ER tightly related to moss-layer depth, and to a lesser extent live vascular plant biomass, which highlights the contribution of mosses to instantaneous CO_2 exchange rates of moist-to-dry high-Arctic tundra (cf. Douma et al., 2007). Yet, because GEP and ER concurrently (and similarly) increased with moss-layer depth, and so balanced each other out, mosses did not exert a detectable influence on NEE. Instead, we found NEE to be controlled by soil moisture (cf. Sjögersten et al., 2006; Zona et al., 2023). Together, these observations lead to two important considerations for the C dynamics of high-Arctic meadows and heaths utilised by non-migratory, large herbivores. If their populations continue to increase (Le Moullec et al., 2019; Schmidt et al., 2015; Solberg et al., 2022), further lowering moss-layer depth and vascular plant biomass, alterations in GEP and ER should be expected, although NEE might remain relatively uninfluenced. Nevertheless, should an additional decrease in moss-layer depth translate into higher soil evaporation rates (Blok et al., 2011), grazed moist-to-dry tundra could eventually turn into a C source. This may be exacerbated if reduced moss-layer depth and reduced soil moisture content are accompanied by increased soil temperatures (our study; Blok et al., 2011; Gornall et al., 2009), and thus higher soil respiration rates, providing the resulting lower plant C pool does not become limiting for soil microbes.

5 | CONCLUSIONS

We set out to assess the role of geese and reindeer, two circumpolar-distributed herbivores, in shaping high-Arctic vegetation and ecosystem CO_2-fluxes in their respective main habitat. Our investigation—conducted at the peak of the plant growing season, when process rates are likely most discernible—indicates that geese, highly aggregated in space, exert a stronger control on their main habitat (wet tundra) compared to the control exerted by more widely dispersed reindeer on their main habitat (moist-to-dry tundra). This likely reflects inherent differences in both habitat sensitivity and habitat use, as well as herbivores' characteristics and grazing pressure. As recently argued by Koltz et al. (2022), addressing the role of herbivores in the habitat in which they operate can help us understand how herbivory influences ecosystem structure and function across the heterogeneous tundra landscape. This, in turn, will provide important information to project the effects of shifting herbivore population densities on ecosystem functioning, and refine predictions on whether and where these shifts are likely to mitigate or further amplify the impact of climate change on Arctic ecosystems.

AUTHOR CONTRIBUTIONS

Matteo Petit Bon, Brage B. Hansen, René van der Wal and Maarten J. J. E. Loonen had the initial idea, which was discussed with all authors. René van der Wal and Maarten J. J. E. Loonen originally designed the long-term experiments. Matteo Petit Bon, René van der Wal, Maarten J. J. E. Loonen and Alessandro Petraglia planned the methodology. Matteo Petit Bon, Alessandro Petraglia and Kate Layton-Matthews collected the data. Hanna Böhner and Matteo Petit Bon wrote the R-script for CO_2 data processing. Kari Anne Bråthen and Hanna Böhner developed NIRS models for mosses. Matteo Petit Bon processed the samples, analysed the data and wrote the manuscript, to which René van der Wal and Brage B. Hansen provided key contributions. All authors commented on previous drafts and approved the final version for publication.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14200.

DATA AVAILABILITY STATEMENT

Data are available via DataverseNO UiT Open Research Data Repository https://doi.org/10.18710/ETR83N (Petit Bon, Hansen, et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Vascular plant species and corresponding plant functional types.

Table S2. Overview of the plant and soil samples analysed for carbon and nitrogen concentrations.

Table S3. Overview of the environmental conditions during CO_2-flux measurements and quality of these measurements.

Table S4. Results from linear mixed-effects models on the effects of herbivore removal on absolute aboveground vascular plant biomass.

Table S5. Results from permutational multivariate analysis of variance on the effects of herbivore removal on overall plant-community composition.

Table S6. Results from linear mixed-effects models on the effects of herbivore removal on moss-layer depth.

Table S7. Results from linear mixed-effects models on the effects of herbivore removal on vascular plant chemistry.

Table S8. Results from linear mixed-effects models on the effects of herbivore removal on moss and soil chemistry.

Table S9. Results from linear mixed-effects models on the effects of herbivore removal on CO_2-fluxes.

Table S10. Results from linear mixed-effects models on the relationships between CO_2-fluxes and either vascular plant biomass or moss-layer depth.

Table S11. Results from linear mixed-effects models on the relationships between either soil temperature or soil moisture and moss-layer depth.

Figure S1. Correlations between moss carbon and nitrogen concentrations obtained using wet chemistry and using Near Infrared Reflectance Spectroscopy methodology.

Figure S2. Correlations between soil moisture and soil temperature in Ny-Ålesund and Semmeldalen.

Figure S3. Relationships between either soil temperature or soil moisture and total moss-layer depth in Ny-Ålesund and Semmeldalen.

Data S1. Protocol and R-script used for cleaning and processing raw CO_2-flux data.

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