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Semi-domesticated Reindeer Inhibit the Recruitment and Expansion of Mountain Birch at the Fennoscandian Treeline

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Abstract

Herbivory may offset climate change-driven treeline expansion into the tundra, but the strength of this effect is rarely quantified. This study leverages a unique semi-natural experiment involving Malla Strict Nature Reserve in northernmost Finland, where the reindeer herding regime shifted from being nearly ungrazed for several decades to being heavily grazed for the past two decades. This is contrasted by low grazing pressure in the adjacent herding district in Norway, which is separated by the border fence preventing free reindeer movement between the two countries. We aimed to quantify the effects of reindeer browsing and grazing on mountain birch treeline position and structure on both sides. We measured seedling numbers and the allometry of trees, vegetation composition, nutrient concentrations in soils and birch leaves, and radial tree growth. We found higher numbers of seedlings and saplings in the area with lower reindeer density, indicating that the treeline may be responding to climatic forcing by expanding into the tundra. Contrastingly, we observed almost no recruitment and treeline expansion in the area with high reindeer density. Furthermore, while birch leaves showed signs of nitrogen enrichment under high reindeer density, we found no differences in soil chemical composition or birch tree growth rates. Our results suggest that the high density of reindeer in Malla Strict Nature Reserve keeps the treeline in a browsing trap, thereby preventing climate change-driven forest expansion. These results are highly relevant for land management decisions that aim to preserve mountain tundra.

Key words: grazing and browsing; *Rangifer tarandus*; treeline; *Betula pubescens* ssp. *czerepanovii*; tundra; Fennoscandia.

Introduction

The subarctic treeline ecotone is defined as the transition zone between the boreal forest and the treeless tundra. It is a spatially and ecologically complex ecosystem with its position governed by

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abiotic drivers such as climate and topography, and biotic drivers such as herbivory and human impacts (Callaghan and others 2002; Ranson and others 2011; Körner 2021). Over the past decades, average temperatures around the globe have increased dramatically, particularly in the Arctic where temperatures have risen at four times the global average rate (Rantanen and others 2022). These temperature increases have the most pronounced effects at high elevations and latitudes, where short growing seasons limit plant growth (IPCC 2023). As climatic limitations to tree growth are alleviated in a warmer climate, treelines are expected to expand into alpine and tundra ecosystems (Lagergren and others 2024).

The scientific consensus on the future dynamics of the treeline is still largely dominated by climatic determinism. Modeling studies of the Arctic suggest that climatic warming will lead to rapid expansion of boreal forest into tundra ecosystems (Moen and others 2004; Pearson and others 2013; Kruse and others 2023; Lagergren and others 2024). However, projected treeline position and change tend to not match observed rates of treeline advance (Harsch and others 2009; Rees and others 2020; Vitasse and others 2021). Studies incorporating herbivory as a factor reach varying conclusions but all agree that herbivory can constrain treeline expansion, though the strength of this effect varies (Herrero and others 2016; Lagergren and others 2024). In sum, climate change and herbivory exert opposing forces on the treeline ecotone, which raises questions about its future dynamics under differing herbivory intensities.

The treeline ecotone in northern Fennoscandia is dominated by mountain birch (*Betula pubescens* ssp. *czerepanovii*). These birch forests are important habitats for semi-domesticated and wild reindeer (*Rangifer tarandus tarandus*), which are by far the most widespread large herbivores in the Eurasian Arctic (Olofsson and Post 2018). Owing to their sheer numbers, reindeer have a dominant ecological role in arctic ecology. As intermediate feeders between browsing and grazing, reindeer regularly browse on mountain birch leaves at the treeline, particularly in spring (Tenow 1996; Moen and others 2008). Browsing can be intense and can hamper recruitment as reindeer can consume up to 90% of leaf biomass below browsing height (< 2 m), thereby keeping birch seedlings in a ''browsing trap'' (Helle 2001; Bråthen and others 2017; Olofsson and Post 2018). This intense browsing has the potential to both hinder forest regeneration after disturbance, as well as prevent colonization of the open tundra in otherwise not climatically limited treelines (Herder and Niemelä 2003; Cairns and Moen 2004; Neuvonen and others 2005; Holtmeier 2012). On the other hand, intermediate levels of reindeer herbivory may favor birch seedling establishment by opening up the field layer canopy and reducing light limitation (Helle 2001; Moen and others 2008; Tømmervik and others 2009). Additionally, long-term grazing can significantly alter soil processes related to nitrogen and phosphorus cycling which may have implications for tree growth (Egelkraut and others 2018; Sitters and others 2019). Thus, the presence of reindeer at the treeline may substantially influence its structure, position, and dynamics at a local scale through several distinct mechanisms (Suominen and Olofsson 2000; Cairns and Moen 2004).

The main objective of this study was to investigate the role of reindeer in stabilizing treeline dynamics, and their potential to offset the projected effects of climate change on treeline advance. Furthermore, we investigate alternative pathways through which reindeer may influence birch tree growth besides herbivory. We hypothesize that high reindeer density stabilizes treeline position by keeping it in a browsing trap, while simultaneously promoting birch tree growth for individuals that escaped the browsing trap through increased nutrient input. Conversely, we hypothesize that the treeline is expanding in response to a warmer climate in the area with low reindeer densities. This study takes advantage of a unique natural experiment in Malla Strict Nature Reserve northernmost Finland, where the reindeer management regime shifted from being almost ungrazed to heavily grazed two decades ago. We conducted a field campaign in Malla Strict Nature Reserve and a neighboring area across the Finnish-Norwegian border separated by a fence. In contrast to Malla, the reference area in Norway has been grazed by reindeer in low densities during autumn and winter in a similar way for several decades. This natural experiment allows us to investigate the effects of herbivory at a landscape scale. By leveraging the shift in reindeer density in Malla Strict Nature Reserve, we can quantify the effects of reindeer on mountain birch treeline position and structure of the ecotone.

Materials and Methods

Study Area

The study area is located at the border between Norway and Finland (69°04′ N, 20°35′ E) (Fig-

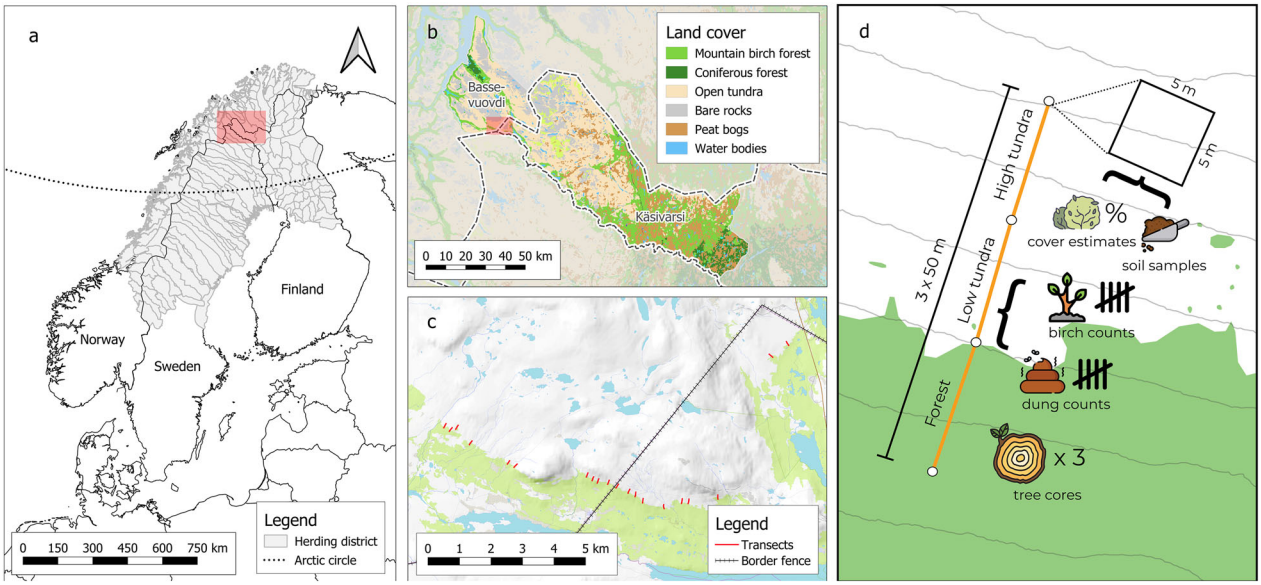

Figure 1. **a** Reindeer herding districts in Fennoscandia, **b** the two herding districts in which the study area is situated, **c** the locations of transects within both study areas separated by a fence following the border between Finland and Norway, and **d** the sampling design along the transects and in the vegetation plots.

ure 1a), where the mean annual temperature is −1.0 °C and the mean annual precipitation is 377 mm (Finnish Meteorological Institute, 2024). No substantial difference in climate between the two areas is expected. Local land use is dominated by reindeer husbandry, tourism, and scientific research. The treeline in the area is found at elevations between 530 and 660 m a.s.l. The forest and treeline ecotone are dominated by mountain birch (*Betula pubescens ssp. czerepanovii*), and the field layer is dominated by dwarf shrubs, herbs, and grasses. The vegetation in the tundra consists of heaths dominated by shrubs such as *Betula nana*, *Empetrum nigrum*, and *Juniperus communis*. Geologically, the area is part of the eastern thrust front of the Scandinavian Caledonide nappes (Kauhanen 2013). The bedrock on the Norwegian slope consists of mainly arkose quartzite (Geological Survey of Norway), while the Finnish slope consists of a mix of arkose quartzite, Silicate sandstone, and silicate claystone (Geological Survey of Finland).

Our study area encompassed a stark difference in reindeer density between two adjacent herding districts separated by the Finnish-Norwegian border fence (Figure 1b). The area with ''low reindeer density'' is part of the Bassevuovdi herding district (Norway), and the area with ''high reindeer density'' is part of and Käsivarsi herding district (Finland). On the Norwegian side, the area of Bassevuovdi is subject to browsing and grazing at low reindeer densities during late autumn. On the Finnish side, the study area lies within Malla Strict Nature Reserve, established in 1938. A fence was constructed in 1955 along the border between Norway and Finland, preventing reindeer from moving across the national border (Heikkinen and others 2010). With the establishment of the border fence, reindeer management became restricted in Malla Strict Nature Reserve and prohibited in 1981. The restriction on reindeer was formally included in the Reserve's regulations in 1993 (Jokinen 2005). Although a few sparse reindeer entered the park during that time, densities were still extremely low (personal observation, Johan Olofsson; Jokinen 2005). Reindeer are known to have entered the park in the summers of 1998–1999, but densities were still low in the parts used in this study in 2003 (Olofsson and Oksanen 2005). Thereafter, an informal agreement to ease collaboration between reserve management and reindeer herders was made that would tolerate reindeer to graze in the reserve, but without permitting deliberate herding activities within the Reserve (Jokinen 2005). Since then, high densities of reindeer have moved into the Malla Reserve especially during summer. The reindeer density of the Bassevuovdi district has fluctuated between 0.8 and 1.6 reindeer per km^2 from 2000 to 2022 (Landbruksdirektoratet), while the reindeer density in Käsivarsi district has fluctuated between 1.9 and 2.8 reindeer per km^2 from 2000 to 2022 (Finnish Reindeer Herders Association) (see Figure S1). Malla Strict Nature Reserve is

likely grazed at higher intensity than the rest of Käsivarsi herding district (personal observation Johan Olofsson). Although we do not have similar numbers for the specific parts of the districts used in this study, the difference in reindeer density between these specific parts of the districts is far larger than the differences between the whole districts.

Besides reindeer population densities, reindeer management regimes also differ between Norway and Finland (Stark and others 2023). Historically, Sámi reindeer herders in Norway practiced seasonal migration, moving their herds between summer pastures at the Atlantic coast and the lichen-rich continental interior, which provides good winter grazing grounds. Geopolitical conflicts in the late nineteenth century led to border closures between countries, forcing Sámi reindeer herders in the boreal forest regions of Finland to adopt shorter seasonal migrations within their districts. With the establishment of the border fence between Norway and Finland, migration routes have been altered. While long-ranging seasonal migrations within Norway have been largely preserved, herding practices in Finland have become more sedentary (Lähteenmäki 2006; Stark and others 2023). For our study area, this means that reindeer in Bassevuovdi (Norway) are mostly present in the area during autumn and winter, whereas in Käsivarsi (Finland) the reindeer are likely present during summer and autumn (Jokinen 2005). However, it should be noted that despite these overall differences in herding regimes it remains difficult to say with certainty exactly how reindeer herds utilize the area without further supporting data on reindeer movement within their respective areas.

Sampling Design & Site Selection

During a field campaign in August 2023, we conducted measurements and sample collection along and around designated transects across the treeline on each side of the Finnish-Norwegian border. A total of 10 transects were placed in the upslope direction within the Malla reserve and the Norwegian reference area (Figure 1c). To be able to clearly observe how far from the forest edge birch recruitment occurred, transects were placed where the forest edge was discrete, specifically avoiding parts of the treeline where the forest edge was fragmented or patchy. We tried to select locations with similar slope and aspect. Microclimatic conditions were not taken into account while placing the transects; however, fens and mires were specifically avoided as these are generally unsuitable habitats for mountain birch establishments. Beyond the exclusion of wet habitats, we did not specifically select locations based on vegetation type. Some areas were avoided at the request of the management of Malla Strict Nature Reserve. Transects were 150 m long, extending 50 m down into the forest and 100 m up into the tundra, thus consisting of three 50 m long sections hereafter referred to as ''forest,'' ''low tundra,'' and ''high tundra.'' Four 25 m^2 vegetation plots were placed at 50 m intervals along each transect, representing four habitat types, hereafter referred to as ''forest,'' ''forest edge,'' ''low tundra,'' and ''high tundra'' (Figure 1d).

Field Measurements

All mountain birch trees within 2 m distance from either side of each transect were recorded and inventoried. Live trees were grouped into three size classes: seedlings (< 0.5 m tall), saplings (0.5—2 m tall), and adult trees (> 2 m tall). In particular in the treeline ecotone, mountain birch often grows with multiple stems (polycormism). In such cases, the number of stems suspected to originate from the root of same individual were counted. Dead trees along the transect were counted but not measured. The height of the highest photosynthetic part and stem diameter of each tree were recorded. The main stem diameter was measured at the base of the stem if the individual was shorter than 2 m, and at breast height (1.3 m) if the individual was taller than 2 m. We also recorded leaf presence below 2 m along the length of the stem divided into 10 cm sections. Tree cores were collected to measure ring width as an estimate of yearly growth rate. Cores were collected from three trees in the continuous forest along each transect. Selected trees were at least 10 cm in diameter at breast height and were standing within 2 m from either side of the transect. We made sure that one tree matching these criteria was cored close to the midpoint and both ends of the forest section of the transects. Leaf samples were also collected from the same trees for which core samples were collected. Lastly, piles of reindeer dung were counted within 1 m on either side of the transect as proxy for reindeer density.

In each vegetation plot, the percentage covers of plant functional groups (that is, shrubs, forbs, and graminoids), cryptogams (that is, lichens and bryophytes), as well as other ground cover types (that is, rock and bare ground) were visually estimated. The organic layer was sampled by taking four soil cores (Ø 5 cm) from the corners of each

vegetation plot and pooled into one composite sample per plot. We measured the depth of the organic layer in each soil core before pooling them. Soil samples were stored at ambient temperatures (~ 10 °C in the field) before being frozen within two days of collection. Composite samples were later chemically analyzed (Chemical analyses).

Chemical Analyses

The effect of reindeer density on soil nutrient availability was assessed by analyzing the chemical composition of leaf and soil samples. Leaf samples were dried for 72 h at 65 °C, ground, and weighed into tin capsules for further analysis. Prior to analysis, each composite soil sample was thawed, sieved through a 2 mm sieve, and homogenized. Subsamples of 6 g fresh soil were extracted with 50 ml of distilled water and subsequently analyzed for ammonium (NH_4), nitrate (NO_3), and phosphate (PO_4) using a segmented flow analyzer (QuAAtro 39, Seal Analytical). The remaining fresh soil was analyzed for soil moisture by measuring gravimetric weight loss after drying for 72 h at 65 °C. Dried leaf and soil samples were analyzed for total carbon and total nitrogen using an elemental analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany), and stable isotopes (that is, $\delta^{15}N$ and $\delta^{13}C$) using an isotope ratio mass spectrometer (DeltaV, Thermo Fisher Scientific, Bremen, Germany).

Birch Tree Radial Growth

To investigate whether reindeer presence is associated with changes in birch tree growth rates, we conducted dendrochronological analysis of birch tree cores. Tree cores were prepared following standard dendrochronological procedures (Fritts 1976). The samples were air-dried and sanded with progressively finer sandpaper (240 to 1000 grit) before being scanned at a resolution of 3200 dpi using a flatbed scanner. The resulting scans were used to measure tree-ring widths to a precision of 0.01 mm using CooRecorder (Larsson 2022). Prior to further statistical analysis, ring width series for each tree were detrended by implementing age-dependent smoothing spline using the *dplR* package (Bunn 2008). The last 20 rings of each core were used as a proxy for the last 20 years during statistical analysis, which covers the period after the shift in reindeer grazing regimes in Malla Strict Nature Reserve.

Environmental Variables

Environmental variables were extracted prior to fieldwork and later used as environmental variables in the multivariate statistical analysis. Two point-cloud datasets with a resolution of 2 points/m^2 for Norway (source: Kartverket), and 1.3 points/m2 for Finland (source: National Land Survey of Finland) were used to generate a digital elevation model with a resolution of 1 m for the entire study area. This digital elevation model was used to calculate slope and aspect, using the *terra* package (Hijmans and others 2025), and topographic wetness (TWI) using SAGA GIS (Conrad and others 2015). Slope, aspect, and TWI were extracted as averages within a 10 m radius of plots and transect.

Statistical Analysis

We tested for differences in individual numbers of three tree size classes (that is, seedling, sapling, tree) and dead trees, as well as dung counts along the transects between areas with different reindeer densities. To do this, we used generalized linear mixed-effect models (GLMM) with a negative-binomial family error distribution. We defined ''reindeer density'' with two levels (high and low) and ''habitat'' with three levels (forest, low tundra, high tundra) as fixed categorical factors, and ''transect'' as a categorical random factor. We used models with the beta family error distribution (Damgaard and Irvine 2019) using ''reindeer density'' with two levels and ''habitat'' with four levels (forest, forest edge, low tundra, high tundra) as fixed factors and ''transect'' as a random factor to model cover of different plant groups. A similar model structure with a Gaussian error distribution using ''reindeer density'' as a fixed factor and ''transect'' as a random factor was used to analyze soil total nutrient contents (that is, total nitrogen and total carbon), soil mineralized nutrients (that is, ammonium, nitrate, and phosphate), soil isotopes (that is, $\delta^{15}N$ and $\delta^{13}C$), leaf chemical composition (that is, total nitrogen, total carbon, $\delta^{15}N$ and $\delta^{13}C$), and mean tree-ring width of the last 20 rings as a proxy for tree radial growth during the last 20 years. The random intercept was excluded in cases where the model failed to converge (see Table S1-3). All mixed-effect models were formulated using the *glmmTMB* package (Brooks and others 2024). We subsequently performed multiple comparisons among the three levels of habitat (that is, forest, low tundra, and high tundra) adjusted according to Tukey's method, using the *emmeans*

package (Lenth 2024). All models were checked for overdispersion an collinearity using the *DHARMa* package (Hartig and others 2024). We analyzed vegetation composition using constrained correspondence analysis (CCA), using the Sørensen (Bray–Curtis) distance measure in the *vegan* package (Oksanen and others 2019). The effect of ''reindeer density'' on plant community composition while correcting for ''habitat'' was tested using a PERMANOVA. Additionally, a CCA with forward selection was employed to determine which environmental variables besides ''reindeer density'' and ''habitat'' were significantly related to community composition. Data handling and all subsequent analyses were performed using R version 4.4.3 (R Core Team 2024).

Results

Reindeer Dung Counts and Signs Of Browsing

Reindeer dung counts were on average six times higher in Malla Strict Nature Reserve (46.4 ± 4.5) than on the Norwegian side (7.6 ± 1.9) across all habitats (GLMM, $\chi^2_1 = 60.339$, $p < 0.0001$), confirming higher reindeer densities in that area (Figure 2a). The proportion of the trunk where leaves were present on trees was lower under high reindeer densities (0.389 ± 0.038) than under low reindeer densities (0.780 ± 0.041) (GLM, $\chi^2_1 = 45.75$, $p < 0.0001$) (Figure 2b). Furthermore, the numbers of basal root shoots of mountain birch individuals were lower in the area with high reindeer densities (GLMM, $\chi^2_1 = 32.11$, $p < 0.0001$). This difference was statistically significant for saplings ($p = 0.0443$) and trees ($p < 0.0001$), but not for seedlings (Figure 2c).

Tree Counts & Recruitment

Abundances of mountain birch trees of the three different size classes differed between the two grazing regimes (Figure 3, Table S1). More seedlings and saplings were found in the area with low reindeer densities than in the area with high densities, though for seedlings the difference is only significant in the forest. The effect of reindeer density on adult tree numbers was dependent on habitat type. A higher number of adult trees was recorded in the high tundra in the area with low reindeer densities than in the area with high reindeer densities ($p = 0.0133$). More dead trees were recorded in the area with high reindeer densities than with low reindeer densities, but this was only significant in the forest section. Differences in

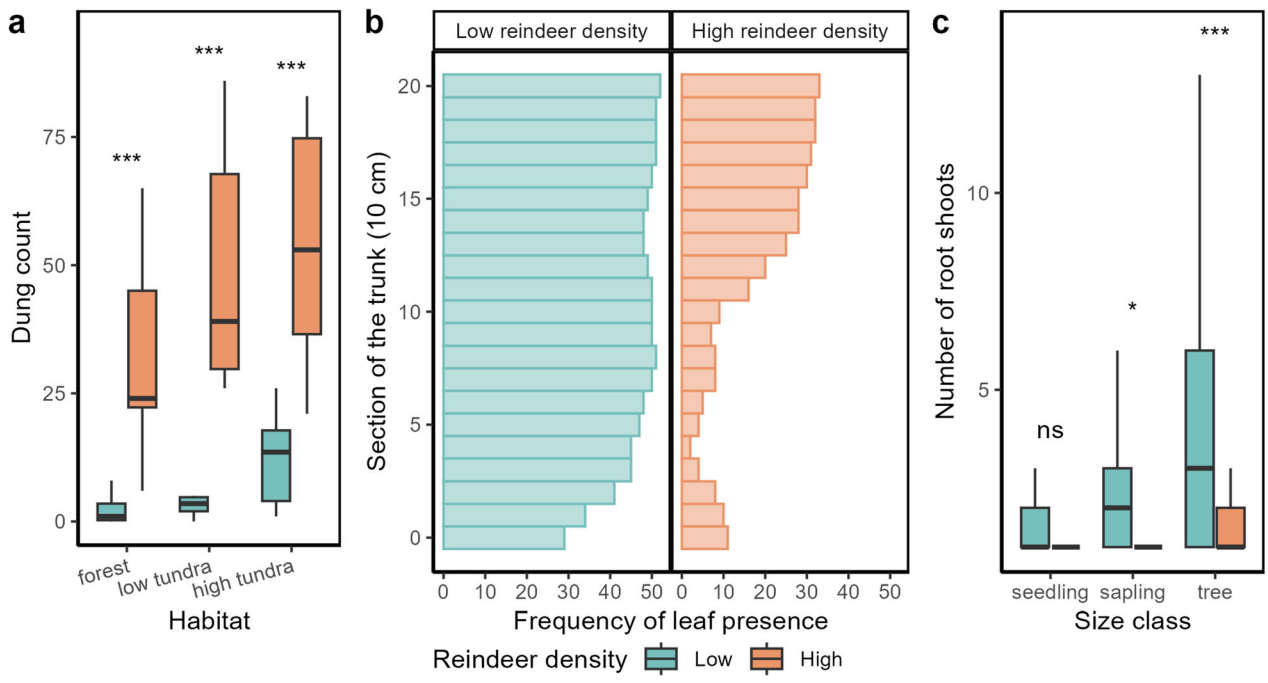

Figure 2. **a** Counts of reindeer dung along the transects, **b** counts of recorded leaf presence along tree trunks divided in 10-cm sections from the base of the tree trunk to 2 m above the base (low reindeer density, n = 58; high reindeer density, n = 43), **c** and numbers of root shoots growing at the base of the main stem. Significance level is indicated by ns = non-significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ (generalized linear mixed-effect model [GLMM], Tukey's HSD).

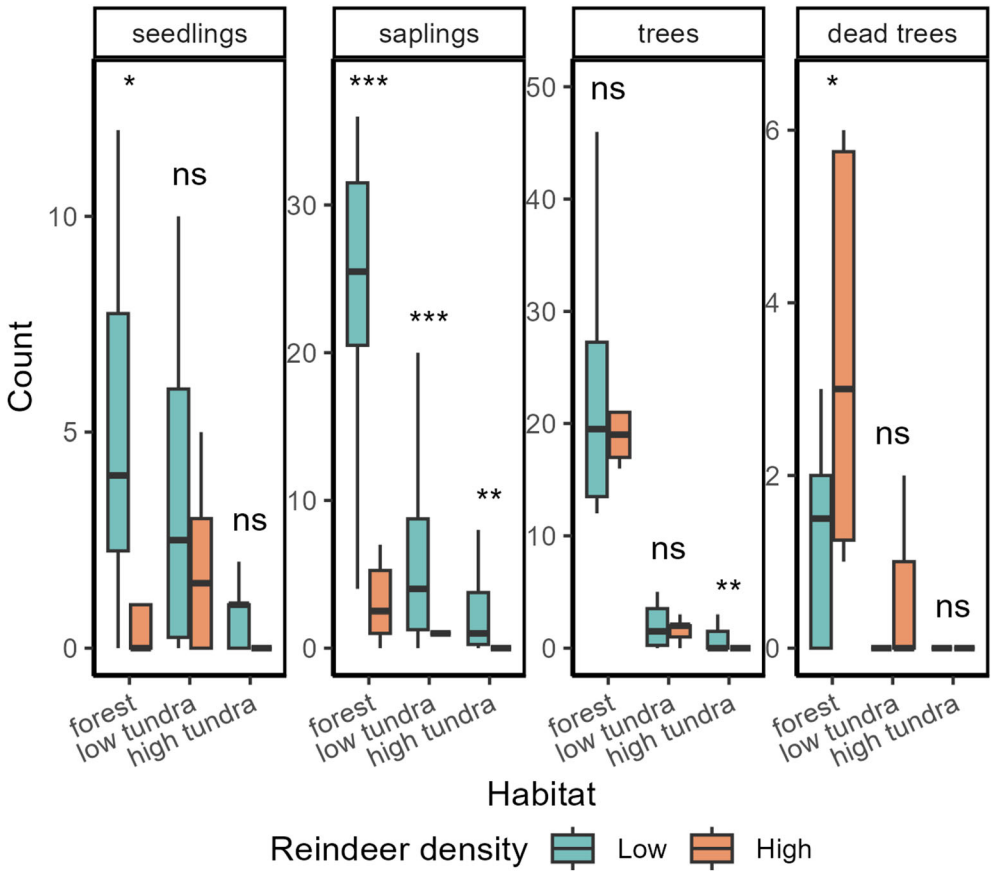

Figure 3. Counts of trees of different size classes (i.e., seedling < 0.5 m, sapling 0.5—2 m, tree > 2 m) and dead trees across the different sections of the transects. Significance level is indicated by ns = non-significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ (generalized linear mixed-effect model [GLMM], Tukey's HSD).

seedling, sapling, tree, and dead tree counts did not depend on variation in other environmental factors such as slope, aspect, or topographic wetness (TWI) (Table S2).

Field Layer Vegetation

A CCA of the field layer vegetation shows that community composition differed significantly between the areas with different reindeer densities when correcting for the effect of habitat (PERMANOVA, $F_1 = 4.504$, $p < 0.001$; Figure 4a). A CCA with forward selection showed that community composition was correlated with habitat ($p = 0.015$), soil ammonium ($p = 0.015$), soil C:N ratio ($p = 0.026$), and reindeer density ($p = 0.036$; Figure S2). The cover of some plant functional groups and ground cover types differed between reindeer densities (Figure S3, Table S3). Specifically, graminoid cover was higher across all habitats under high reindeer density (24.6% ± 4.3) compared to low reindeer density (8.2% ± 1.8). Differences in graminoid cover were especially pronounced in the forest and at the forest edge. On the other hand, forbs and *Salix* shrubs were less abundant under high reindeer densities (0.8% ± 0.3) than under low reindeer densities (5.6% ± 1.2). The field layer canopy was more open under high reindeer densities, with more bare ground observed (1.8% ± 0.4) than in the low reindeer density plots (0% ± 0). No differences were observed in cover of the tall shrubs *Betula nana* and *Juniperus communis*, deciduous and evergreen dwarf shrubs, lichens, and bryophytes.

Soil and Birch Leaf Chemical Composition, and Birch Radial Growth

Chemical composition of soil samples did not differ between reindeer densities, while leaf samples indicated differences in carbon contents and nitrogen isotopic composition (Figure 5, Table S3). Differences in reindeer density did not significantly affect soil C:N ratios, total carbon, or total nitrogen contents. Soil $\delta^{15}N$ and C:N ratio did not differ among habitats either. Soil $\delta^{13}C$ differed among

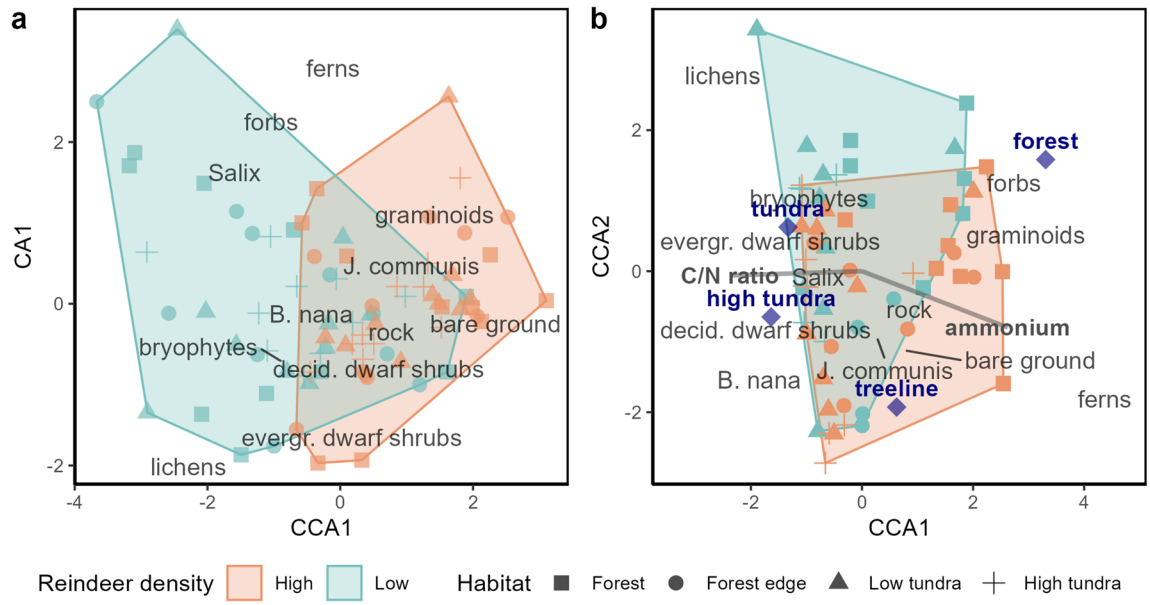

Figure 4. Canonical correspondence analyses (CCAs) of field layer vegetation composition **a** with ''reindeer density'' as an explanatory variable while correcting for ''habitat,'' and **b** an ordination including significant explanatory variables according to forward selection. The polygons represent convex hulls enclosing the plots recorded for the different reindeer densities. Field layer composition is based on cover estimates of functional types (that is, forbs, graminoids, deciduous dwarf shrubs, evergreen dwarf shrubs, lichens, bryophytes), tall shrubs (that is, *Betula nana*, *Juniperus communis*), and other ground cover types (that is, rock, bare ground).

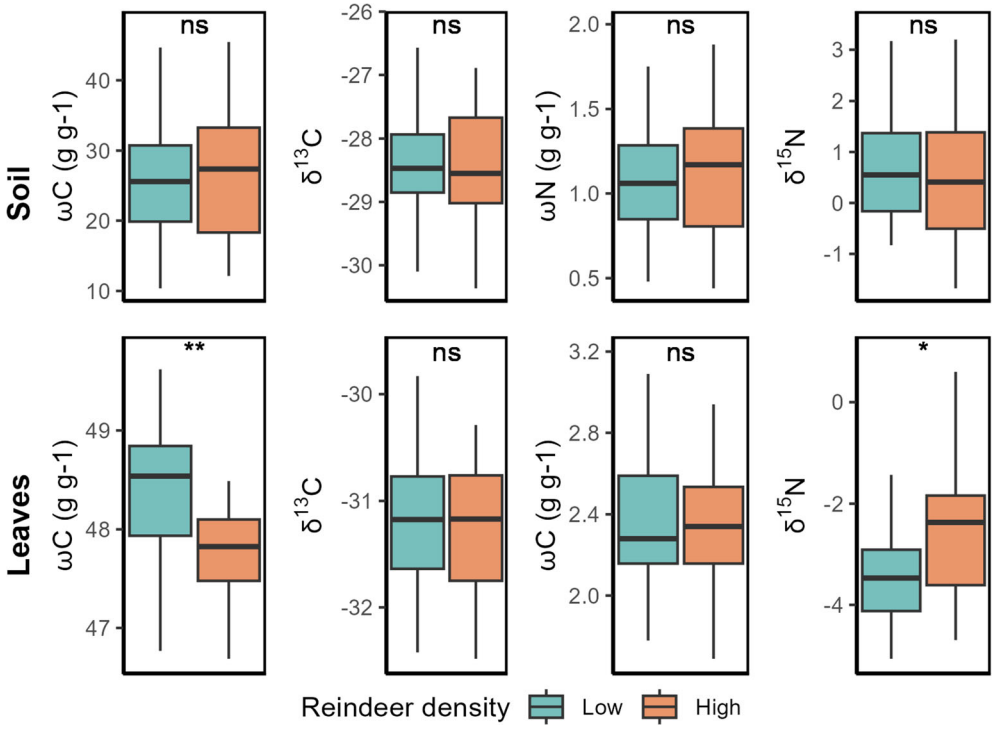

Figure 5. Observed mass fraction (ω) of nitrogen and carbon (g g-1 dry mass), δ13C, and δ15N of mountain birch leaves and soil samples. Significance level is indicated by ns = non-significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ (generalized linear mixed-effect model [GLMM], Tukey's HSD).

habitats but did not differ between reindeer densities. Soil $\delta^{13}C$ was higher in the low tundra and high tundra plots compared to the forest and treeline plots. While concentrations of soil phosphate and ammonium differed among habitats, they did not depend on reindeer density. Nitrate concentrations were consistent irrespective of reindeer density or habitat. However, leaves from trees under high reindeer density had lower carbon contents and enriched $\delta^{15}N$ values compared to leaves from trees from the area with low reindeer density. Yet, leaves from the two areas did not differ in C:N ratio, $\delta^{13}C$, or total nitrogen content. Similarly, birch tree radial growth during the last 20 years did not differ between the two reindeer densities (LMM, $\chi^2_1 = 1.27$, $p = 0.2597$).

Discussion

We found a clear difference in reindeer density between the two studied areas as indicated by substantially higher dung counts in the ''high reindeer density'' area compared to the ''low reindeer density'' area. We also found that trees under high reindeer density had fewer vegetative root shoots and had fewer leaves along the trunk below browsing height, which are likely signs of the direct effects of reindeer browsing (Kumpula and others 2011). These findings confirm our a priori expectation that the ''high reindeer density'' area is more heavily grazed than the ''low reindeer density'' site.

It has been suggested that herbivory may offset climate change-driven treeline expansion (Cairns and Moen 2004; Hofgaard and others 2010; Van Bogaert and others 2011; Stark and others 2021). We found a lower abundance of mountain birch saplings and adult trees across all transects within of Malla Strict Nature Reserve compared to the adjacent area across the border in Norway with lower reindeer densities. The observed contrast in mountain birch recruitment across the ecotone could not be explained by local environmental factors, suggesting that reindeer browsing is the main limiting factor for seedling and sapling recruitment. Furthermore, we observed birch trees gradually encroaching into the tundra under low reindeer density, while they were virtually absent beyond the forest edge in areas with high reindeer density. Seedlings and saplings establishing in the tundra at lower reindeer densities will likely contribute to forest expansion and treeline advance, unlike in the adjacent area with higher reindeer density. This signals the capacity of large herbivores to decouple treeline advance from climate change by keeping the treeline in a browsing trap when present at sufficient densities (Hofgaard and others 2010; Bråthen and others 2017). This locally conflicts with modeling studies that predict the expansion of the boreal zone into the tundra (Speed and others 2010; Mienna and others 2024).

Seedling establishment does not appear to be as limited by seed viability and availability of suitable microhabitats in either of the two studies areas, as is evident from the lack of clear difference found in seedling densities in the tundra in both areas. Even though seedlings are more vulnerable during their first years after establishment and are therefore more ephemeral, slow growth rates of seedlings approaching the edge of their climatic range suggests that the ''saplings'' found intact during our survey would have thus needed to remain relatively undisturbed for several years to be able to escape the field layer (Loehle 1998; Scharn and others 2022). Trees growing at the treeline are at or near the edge of their climatic range resulting in slow growth (Grace 2002; Wielgolaski and others 2005). When climatic conditions already limit growth, even little and infrequent browsing by reindeer could set back years of growth and impact recruitment. Once escaping the field layer to grow into what we classify as ''saplings,'' birch trees become even more vulnerable to herbivory by reindeer, which leads to a browsing trap when reindeer cause adequate degrees of disturbance (Helle 2001; Olofsson and Post 2018). Furthermore, persistence of saplings in the ''high tundra'' sections of the transects suggests that birch tree recruitment may not be strictly climatically limited, as this would have been apparent from a distinct clustering of younger trees near the treeline where snow accumulation during winter ameliorates the harsh winter conditions they would otherwise experience in the wind-swept open tundra (Frei and others 2018; Sigdel and others 2020). The presence of saplings in the area with lower reindeer density compared to their absence under higher reindeer densities thus suggests that herbivory in this area is likely the main factor limiting birch recruitment.

We also observed substantial impacts on the composition of the field layer vegetation by grazing. The observed differences in plant community composition between the areas align with both direct and indirect effects associated with reindeer. Under high reindeer density, we found plant communities to be more graminoid dominated, a finding that is widely echoed in other studies where it is generally attributed to nutrient inputs from fecal matter (Olofsson and others 2001, 2004; van der Wal and others 2003; Van Der Wal and

others 2004; Te Beest and others 2016). While high reindeer density may yield positive results for inhibiting treeline expansion, shifts in field layer vegetation toward becoming increasingly graminoid dominated may have consequences for the functioning and integrity of tundra habitats (Van Der Wal and others 2004, 2006). Additionally, *Salix* shrubs were more common under low reindeer density, but virtually absent under high reindeer density. This is likely because *Salix* species are a preferred forage species by reindeer during the growing season (Christie and others 2015). Higher reindeer density was related to a more open field layer canopy, which has been shown to have potential competitive benefits for low statured species, and their diversity (Kaarlejärvi and others 2017).

Two decades of high reindeer densities might be too short to change the soil conditions. Although the effects of high reindeer density were clearly distinguishable aboveground, we found no significant evidence of altered carbon and nitrogen content in the soil. How reindeer affect soil nitrogen contents tends to depend on the habitat, but the effect is often minor when the vegetation has not been changed dramatically for decades (Stark and others 2023). Yet, we found enriched δ^{15}N values in leaves at high reindeer densities, which could be an indication of a contribution of reindeer derived nitrogen to the plant available nitrogen pool. This is consistent with findings from Barthelemy and others (2015, 2018, 2024), who showed that reindeer derived nitrogen deposited by reindeer quickly gets immobilized and incorporated in cryptogams and aboveground tissues of vascular plants, thereby contributing to plant growth without affecting soil nitrogen contents. This may also explain why δ^{15}N values, inorganic nitrogen, and total nitrogen contents in the soil did not differ between reindeer densities. We found lower total carbon contents in birch leaves under high reindeer densities which may be related to an increased nitrogen availability which has been suggested to decrease carbohydrate contents of birch leaves (McDonald and others 1986; Zhang and others 2021). This decrease in carbohydrate content may be a result of increases in carbon assimilation rate with increased growth in response to higher N availability (Iivonen and others 2001; Zhang and others 2021). Nonetheless, this increase in nitrogen availability did not affect observed birch tree growth rates derived from tree rings. The contribution of reindeer fecal deposition to soil nutrient availability is thus likely not substantial enough. Inorganic nitrogen or phosphorus concentrations in the soil also did not show consistent patterns related to reindeer density.

In this case, the seasonal timing of browsing and herd migration may also be important factors in determining the impact on treeline position and structure (Kumpula and others 2011; Biuw and others 2014; Stark and others 2021). At the ''high density'' area, reindeer are likely mainly affecting the vegetation during summer, whereas the ''low density'' area is predominantly used by reindeer during late autumn and winter. As young birch leaves have the highest nutritional value in early summer (Helle 2001), the effect of reindeer browsing on birch trees is most pronounced during this time. Additionally, large herbivores and invertebrate herbivores interact to amplify their influence over the treeline. By browsing on young birch seedlings and sprouts, reindeer can slow or even prevent regeneration of birch stands after naturally occurring defoliation events caused by outbreaks of geometrid moths (*Epirrita autumnata, Operophtera brumata*), potentially contributing to forest thinning and treeline retreat following such events (Neuvonen and others 2005; Tenow and others 2005; Biuw and others 2014). Besides reindeer, mountain hares (*Lepus timidus*) and moose (*Alces alces*) are two of the sympatric herbivores of reindeer that are known to browse on mountain birch. Mountain hares mainly browse on birch during winter, mostly affecting taller saplings reaching out of the snowpack (Rao and others 2003). In our study area, mountain hares would have found most of their available forage in the area with lower reindeer densities. Moose display similar browsing behavior that is similar to that of reindeer, thus mainly browsing on juvenile birches that have most of their twigs within reach (Danell and others 1985). Nonetheless, moose population densities are likely much lower than reindeer population densities in both areas (Jensen and others 2020). While it is possible that mountain hares and moose are responsible for some herbivory on mountain birch, their impact is unlikely to overshadow that of browsing reindeer.

Mountain birch is a browsing tolerant species as it regenerates vegetatively through basal shoots from the root as opposed to coniferous species that are heavily reliant on their apical meristems for vertical growth (Herrero and others 2012; Biuw and others 2014). As a result, coniferous species may be more negatively impacted by browsing than birch. For instance, moose (Alces alces) is known to browse on coniferous species such as Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) and has been reported to cause damages

to coniferous forest plantations (Milligan and Koricheva 2013; Nichols and Spong 2014), although moose still prefer birch over coniferous species (Niemelä and others 2001). Similarly, reindeer do not browse on coniferous species, even though they have been reported to reduce regeneration in coniferous forests (Köster and others 2015). This difference in palatability may favor the establishment of coniferous species over mountain birch in heavily grazed areas throughout Fennoscandia, potentially contributing to the gradual spread of coniferous tree species into the more mountain birch dominated boreal zones of Fennoscandia (Seppä and others 2009; Lindbladh and others 2014). Nonetheless, the extent of this influence is still relatively unknown and is likely confounded by changes in forestry practices over the last century (Berg and others 2008; Bognounou and others 2018). Otherwise, in the European alps where treelines are dominated by coniferous species, a part (5 to 23%) of the diets of ungulates such as chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and mouflon (*Ovis musimon*) consists of coniferous tree species (Mussa and others 2003; Bertolino and others 2009; Rayé and others 2011; Andreoli and others 2016). Yet, also in these systems the capability of herbivores to impede treeline advance will likely depend on the intensity and timing of herbivory and will need to be studied more extensively.

Wild and semi-domesticated reindeer and caribou are the most abundant large herbivores across the circumpolar tundra. Browsing and grazing by reindeer likely have far reaching effects on birch treelines across Fennoscandia, which we suggest are at times unappreciated and need to be taken into consideration by decision makers (Barrio and others 2025). The most recent comprehensive inventory of reindeer and caribou populations across the circumarctic in 2016 showed an overall decline in population size of 40%, from 4.9 million to 2.9 million individuals over the preceding three generations (Gunn 2016). Since then a continuation of this declining has been reported by CircumArctic Rangifer Monitoring and Assessment network (Gunn and Russell 2022). While population trends are highly variable across the Eurasian continent (Uboni and others 2016), reindeer herding practices continue being challenged by the cumulative impacts of natural resource exploitation, tourism, and climate change (Riseth and others 2011; Horstkotte and others 2017; Rosqvist and others 2022; Ward Jones and others 2024). This could have consequences for treelines that are being kept in a browsing trap by reindeer as is the case in our study. Therefore, if reindeer browsing is to continue to be able to halt treeline encroachment of the tundra, it is important to protect wild reindeer populations and to promote the continuation of pastoral practices by securing access to grazing grounds and facilitating the participation of reindeer herders in decision-making (Blind 2022; Laptander and others 2024).

Conclusions

Despite recent climate change, treelines across the globe have been reported to remain stable in about 48% of recorded cases (Harsch and others 2009; Rees and others 2020). Studies have attributed this stability to species specific limitations to dispersal or recruitment/establishment (Dullinger and others 2004; Harsch and others 2012), edaphic, topographic, or microclimatic factors (Harsch and others 2012; Beloiu and others 2022; Fetzer and others 2024), climatic factors other than temperature (McIntire and others 2016; Sigdel and others 2018; Rees and others 2020), winter conditions (Rees and others 2020), and tree-to-tree interactions (Dullinger and others 2005; Sigdel and others 2020; Zheng and others 2024). Our study shows that high reindeer densities can reduce or prevent the expansion of the treeline under current and likely also projected climate change by keeping the treeline in a browsing trap. We highlight the potential of reindeer herding practices to aid in the preservation of threatened tundra habitats and the importance of facilitating the continuation of these practices. We thus stress the importance of integrating sources of disturbance, and the impacts of large herbivores in particular, into perspectives on current and future treeline dynamics under climate change.

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AUTHOR CONTRIBUTIONS

JO, TH, MS, LH, and FP conceived of or designed study. LH, TH, FP, BA, JO, and MS performed research. LH analyzed data. LH, TH, JO, MS, BA, and FP contributed new methods or models and wrote the paper.

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DATA AVAILABILITY

The data associated with the manuscript have been published on Zenodo: https://doi.org/10.5281/zenodo.10512662.

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