Ecosystems
https://doi.org/10.1007/s10021-023-00865-x

ECOSYSTEMS

Rewilding Risks for Peatland Permafrost

Milena Holmgren,* Finn Groten, Manuel Rodríguez Carracedo, Sverre Vink, and Juul Limpens

Department of Environmental Sciences, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands

Abstract

Permafrost thaw is projected to reinforce climate warming by releasing large stocks of stored carbon. Rewilding northern high latitude regions with large herbivores has been proposed as a climate mitigation strategy to protect frozen soils and increase ecosystem resilience to climate warming. We explored the impact of summer reindeer density on subarctic peatlands by comparing 17 peatlands differing in reindeer density in Fennoscandia. We used a combination of high-resolution image analyses and field assessments along 50 transects to assess microtopography, surface water cover, vegetation, summer albedo, permafrost presence, soil temperature, soil nutrients and snow depth. Our results show that high summer reindeer densities fragment the characteristic bumpy topography of the peatlands, reducing the insulating soil properties and the probability of keeping permafrost in elevated hummocks. As a result, waterlogged lawns with surface water increase in size and reduce summer albedo. Furthermore, high reindeer density peatlands were associated with an increase in tall inedible shrubs and thicker snow layers. These changes may favor summer warming and reduce winter cooling of the soil thus accelerating permafrost loss. Our results suggest that high reindeer densities may reduce resilience of the peatland permafrost to climate warming. High densities of large herbivores will likely have different effects in well-drained uplands, but in the lowlands we studied, the complex cascading effects of summer trampling may well offset any climate-protection gained by browsing. Optimal use of wildlife management to mitigate global warming will thus require tuning herbivore densities to different ecosystem types across high northern landscapes.

Key words: arctic; climate warming; climate change adaptation; herbivore; mitigation; nature-based solutions; reindeer; resilience; subarctic.

Highlights

- We assessed subarctic peatlands under contrasting levels of summer reindeer density.
- Peatlands with high reindeer density have fragmented topography and less permafrost.
- High reindeer density may accelerate climate warming impacts on subarctic peatlands.

Received 10 February 2023; accepted 20 June 2023

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-023-00865-x.

Author Contributions: The project was conceived, performed and supervised equally by MH and JL. All authors contributed to data collection, data analysis, and result interpretation. MH wrote the first version and all authors revised the manuscript.

**Corresponding author; e-mail:* Milena.Holmgren@wur.nl

Published online: 31 August 2023

Introduction

Today, about 24% of the exposed land in the northern hemisphere has permanently frozen soils, mostly located in subarctic and arctic regions (Brown 1998; Zhang and others 2008). However, these high latitude landscapes are warming up to four times faster than the global average resulting in rapid permafrost thaw (Rantanen and others 2022). This has profound implications for the functioning of landscapes including changes in hydrology, soil processes, vegetation composition and ecological interactions (Schuur and Mack 2018; Meredith and others 2019). Some of these changes can potentially trigger substantial positive feedbacks to the climate system, accelerating warming. For instance, permafrost is the largest reservoir of global soil carbon (C) which can be released to the atmosphere as permafrost thaws and organic matter decomposes in warmer soils (Strauss and others 2017; Schuur and Mack 2018). This feedback to the atmosphere is expected to be most pronounced for poorly drained permafrost peatlands where stored carbon may be released as methane (Schuur and Mack 2018; Hugelius and others 2020) and expanding surface water may further boost local warming by increasing vegetation browning (Li and others 2021) and decreasing summer albedo (Schuur and Mack 2018). Permafrost peatlands make up about half of the 3.7 ± 0.5 million km^2 covered by northern peatlands and store approximately 185 ± 66 Pg of soil C (Hugelius and others 2020). Being situated at the southern edge of the permafrost distribution, subarctic permafrost peatlands are particularly sensitive to climate-change induced degradation (Hugelius and others 2020; Olvmo and others 2020).

Subarctic permafrost peatlands are also within the main distribution range of wild and semi-domesticated reindeer (*Rangifer tarandus*). The animals roam actively in the peatlands during spring and early summer in search for sedges, herbs and deciduous shrubs (Skjenneberg and Slagsvold 1979; Suominen and Olofsson 2000; Kitti and others 2009). Although much attention has been given to the potential cascading effects of permafrost degradation on reindeer populations and the livelihoods of indigenous herding communities that have traditionally depended on them (Vuojala-Magga and Turunen 2015; Istomin and Habeck 2016), very little is known about the effects that reindeer have on the processes that influence permafrost degradation itself. Research from well-drained upland sites in the arctic tundra suggests that high reindeer densities may offset climate-induced permafrost degradation by enhancing winter soil cooling (Olofsson and Post 2018). Reindeer may limit the build-up of an insulating snow blanket by trampling and compacting the snow itself and also by browsing on snow-capturing and albedo-reducing shrubs. Both mechanisms can enable deeper soil freezing that delays thaw and increases albedo resulting in negative feedbacks that prevent further climate warming (Cohen and others 2013; Te Beest and others 2016; Beer and others 2020). However, reindeer effects on vegetation and soil may drive climate in opposite ways too. For instance, while heavily browsed sites in arctic upland tundra have lower shrub cover and higher albedo, the loss of the insulating layer of mosses and shrubs caused by reindeer also results in warmer summer soil temperatures (Te Beest and others 2016). Experimental evidence on the effects of large herbivores in permafrost peatlands is very scarce but field enclosures in an arctic peatland of Greenland showed that trampling by muskoxen (*Ovibos moschatus*) strongly reduced moss cover and litter accumulation and increased soil temperature and methane emissions (Falk and others 2015). Higher summer soil temperatures have also been recorded in grazed wet tussock tundra influenced by seasonal flooding in arctic Siberia. Here grazing promoted topsoil warming and drying and decreased methane emissions during summer (Fischer and others 2022). These contrasting results highlight the need to assess the ways large herbivores may influence permafrost in different types of northern ecosystems. How reindeer habitat use affects the balance between winter cooling and summer warming and the implications for permafrost condition and the carbon balance remain puzzling, and seem to vary across landscapes (Windirsch and others 2022). Most studies on the role of large herbivores have been conducted in uplands of Scandinavia and Siberia (Metcalfe and others 2018), but the few studies in wetlands, suggest that northern uplands and peatlands may respond differently to high densities of large herbivores. Northern landscapes often combine uplands and peatlands. Tailoring herbivore management to these different local environmental conditions could potentially build ecosystem resilience to climate warming (Scheffer and others 2015) and prevent shifts to undesired alternative ecosystem states in boreal systems (Scheffer and others 2012).

To explore reindeer effects on subarctic peatlands, we studied the structure and permafrost condition in peatlands under contrasting levels of reindeer densities near the northern border between Finland and Norway (Fennoscandia). These peatlands are within the region of sporadic permafrost (Seppälä 1988; Johansson and others 2006). We hypothesized that locally high reindeer densities could change the peatland microtopography, fragmenting the elevated frozen hummocks, where most permafrost and seasonal frost is kept, and unfolding a series of ecological changes that could speed up permafrost loss. We compared how peatlands under low and high reindeer densities differ in micro-topography, vegetation and soil characteristics and assessed the implications for permafrost condition, summer albedo and winter snow accumulation.

Methods

Study System

We studied the structure and permafrost condition in 17 subarctic peatlands (between 69°N and 70°N latitude) under contrasting levels of reindeer density in Fennoscandia (Supplementary Figure S1; Supplementary Table S1). Subarctic permafrost peatlands are characterized by elevated microsites (hummocks) within an overall flat and waterlogged environment (lawns). Within the discontinuous and sporadic permafrost zones of the subarctic, all hummocks have a frozen core in winter but some of them thaw during summer (Seppälä 1988). The peatlands have soft organic (peaty) top soils of 40 cm or deeper, covered by a continuous layer of mosses or litter. Drying out in summer, this layer insulates the underlying soil effectively. Consequently, frozen conditions (seasonal frost) may persist through summer, resulting in elevated landforms with a frozen core in summer, locally known as pounu's. In some locations ice may aggregate, resulting in elevated landforms with a core of pure ice, known as palsa's. In our study, we did not separate between these landforms, focusing instead on the presence or absence of a frost table, referred to as permafrost.

Northern Finland is divided into grazing districts that restrict reindeer movement. The herding cooperatives in this region manage between 5000 and 8000 semi-domesticated reindeer livestock units (Reindeer Herding Cooperatives; https://paliskunnat.fi/reindeer/reindeer-herding/cooperatives/). Reindeer densities range between 2.2 and 2.6 reindeer/km^2 (Kumpula and others 2009). Reindeer densities can be locally high in northern Finland as reindeer herding has become more stationary with country borders closing the historical paths between summer and winter grounds and fences separating cooperative herding districts (Vuojala-Magga and Turunen 2015; Stark and others 2022). As a result, reindeer tend to concentrate at the northern edges near the fences separating cooperative herding districts when the animals want to migrate toward their former summer grazing grounds. Norway is also divided into grazing districts with reindeer densities estimated around 1.6–2.0 reindeer/km^2 close to the border with northern Finland.

Sampling Design

To assess the effects of reindeer, we made use of the local contrasts in reindeer densities artificially imposed by the fences, taking a "natural" experimental approach. The presence of fences allows assessing the effects of low and high reindeer density as a "natural" experiment because within each herding district, reindeer herds concentrate at the northern edges near the fences during summer resulting in strong local contrasts in animal densities. We selected 17 peatlands under relatively low or high reindeer density based on the experience of scientists at the Kevo Subarctic Research Station and the information they received from local Sami herders.

We sampled a total of 50 transects in the 17 peatlands selected: 25 transects in peatlands with low reindeer density and 25 transects in peatlands with high reindeer density. The transects were established at locations representative for the local microtopography and peatland vegetation with a peat depth of at least 40 cm. Peatlands were sampled with one to four 50 m-long transects keeping a distance of at least 50 m between transects within a same peatland. To explore vegetation and soil condition in more detail, we selected four out of the 17 peatlands, two pairs at either end of our study region, one with low and one with high reindeer density (Figure S1). The peatlands within each pair were less than 2 km apart and were separated from each other by a reindeer fence, resulting in a local contrast of reindeer density. Within these four peatlands, we selected 24 hummocks per peatland where we performed more detailed measurements on both vegetation and soil characteristics. One of the soil samples was lost in processing, leading to 95 samples for this detailed study.

Reindeer Abundance

To verify reindeer abundance at the level of a peatland, we recorded the occurrence of reindeer fecal pellet groups and assessed browsing signs on tree architecture along 50 transects along the peatland edge on mineral soil (Supplementary Information S2). These edge transects ran roughly parallel to the transects in the peatland, with a minimum distance of 50 m between them. We counted all summer and winter fecal pellet groups (Alves and others 2013) within a 2 m wide area along the 50 m edge-transect. We decided against counting pellet groups along the peatland transects as pellet groups could dissolve in the moist environment and therefore underestimate reindeer densities.

Browsing-induced changes on tree architecture are a more indirect proxy of reindeer densities than fecal pellet groups but may give a more stable signal as they persist longer in a landscape than reindeer fecal pellets do. Along the same edge transects, we measured the height of the lowest leaf in all birch trees (*Betula* sp., mostly *Betula pubescens*) as reindeer browse preferentially on the lowest branches, modifying birch stem architecture strikingly (Vuojala-Magga and Turunen 2015) (and citations therein). We selected leaves sprouting from branches aged at least 1 year old to have a more conservative estimate of the level of reindeer browsing (Supplementary Information S2).

Peatland Structure and Micro-Topography

To assess peatland structure, we used a combination of field-based and drone-based data. For all 143 hummocks encountered along the 50 peatland transects, we measured width and maximum height above the local water table with measurement tape. In addition, we determined the number and size of hummocks as well as the presence of standing water on the lawns in a roughly 3500 m^2 area, centered around each of the peatland transects, using high resolution drone images taken between June and July 2019. We used a Parrot ANAFI UAV drone equipped with a 4 K resolution, high dynamic range (HDR) camera. We took four images, at 25 m altitude, around the marked peatland transect. We stitched the images carefully and scaled using the meter line indicating the peatland transect on the ground. We processed the images using Image J software (www.imagej.net) to manually outline the perimeter of every hummock based on their color contrast with the surrounding lawns and calculate the surface area covered by hummocks and lawns. We validated the image-analyses results using the field-based measurements of hummock-width (143 hummocks) and the surface condition of the lawns (standing water or moss-cover) along the field transect placed at the center of each drone image (Supplementary Information S3).

Permafrost and Soil Data

Permafrost condition was monitored on all (143) transect-hummocks encountered along the 50 m long peatland transects (n = 25 transects in low reindeer peatlands, n = 25 transects in high reindeer peatlands). Presence of a frost table was recorded in four points on the top of every hummock using a standard metal T-shaped rod: if a frost table was hit at either of the four points, this was counted as 'present,' resulting into one reading per hummock. Recordings were done in early July 2019. For the additional 95 hummocks of the detailed study we recorded the depth of the frost table both at the beginning and end of July as a proxy for the maximum thaw depth, i.e., the active layer (Supplementary Information S9), giving some insight into seasonal thaw progression.

We took soil samples from the 95 hummocks (see set-up) extracting a 100 cm^3 volume from the upper 0–10 cm layer at the center of each hummock (Supplementary Information S6). Soil samples were cleaned from plant material and dried at 70 °C following standard protocols (Holmgren and others 2015). Soil carbon (C) and nitrogen (N) concentrations were measured using an elemental analyzer (Fisions Instruments EA 1108, Milan, Italy).

Vegetation Data

Vegetation composition was recorded using a 50 × 50 cm grid with 36 intersecting points placed on top of the 143 hummocks encountered along the peatland transects and an additional 95 hummocks where we performed more detailed measurements. Species were recorded at the grid interception points. In the case of layered vegetation, multiple species were recorded and cover scaled to 100%. Vegetation responses to reindeer browsing and permafrost condition were explored at plant functional type level (Supplementary Information S4: 143 transect hummocks only) and species level (Supplementary Information S5: all 238 hummocks).

Summer Albedo and Snow Depth

Summer albedo was measured using two SR05-A1 pyranometers (Hukseflux Thermal Sensors, 2012), one facing up and one facing down, sustained on a hand-held device 1.5 m above the soil surface. The upper sensor measured incoming shortwave radiation and the lower sensor measured shortwave radiation reflected from below. The pyranometers were kept in position for 18 s before recording their output on the multimeters. We measured albedo on a subset of three hummocks and three lawns along every 50 m long peatland transect. All measurements were done between 11:00 and 15:00 in July. To upscale the albedo measurements to all hummocks where we recorded vegetation, we followed a two-step approach. First, for a separate subset of 95 additional hummocks of our detailed study, we expressed the vegetation composition as function of the summer albedo measured at these hummocks, using a redundancy analysis (RDA, CANOCO 5.0). Scores of each plant species along the albedo-axis were derived. Second, we applied the species-specific albedo scores to the vegetation sampled in all the 143 hummocks assessed along the peatland transects, weighting the albedo scores for each species depending on their cover (Supplementary Information S7).

Snow depth was recorded between 3 and 6 February 2020. We sampled a subset of 12 peatlands monitored the previous summer where winter access was feasible with ski's or snow scooter. In every site, we ran two parallel 100 m long transects (one transect on the peatland and one along the peatland edge on mineral soil) and recorded snow depth every 10 m by inserting a standard yard stick in 3–4 points. Data were averaged to 10 snow depth values per transect.

Statistical Analysis

To assess the relationship between peatland microtopography (i.e., abundance and size of hummocks) and reindeer density, we used general linear models (GLM) relating the features of the hummocks as response variables with reindeer density (low vs. high) as fixed factor and peatland site as random factor. We used Chi-square analysis to compare the frequency of reindeer fecal pellet groups, hummocks with vs. without permafrost and the frequency of lawns with vs. without standing surface water in peatlands with low and high reindeer density.

We also used general linear models to assess the cover of plant functional types (i.e., cover ratio of shrubs to herbs, evergreen shrubs, deciduous shrubs, herbs, mosses) and vegetation height in response to reindeer density (low vs. high) and permafrost condition (present vs. absent) including their two-way interaction as fixed factors and peatland site as a random factor. In this model, Type I error sums of squares (not the standard Type III in SPSS 25) were used because of the varying number of hummocks per peatland.

General linear models were also used to assess soil characteristics (soil C:N ratio, soil bulk density and total soil N), with reindeer density (low vs. high) and permafrost condition (present vs. absent) including their two-way interaction as fixed factors and peatland pair as a random factor. Peatland pair was included to control for potential differences in soil conditions between the two peatland pairs (low vs high reindeer density) selected for detailed analyses on opposite ends of our study region (Figure S1). Type I error sums of squares were used because of the varying number of hummocks per peatland.

To compare summer albedo of hummocks and lawns, we used paired t-tests, pairing field measurements within a same peatland in order to account for local differences in environmental conditions. The derived summer albedo estimations for all hummocks (Supplementary Information S7) were analyzed using the same type of general linear models as described earlier for plant functional types.

The impact of reindeer density on snow depth in peatlands and surrounding mineral edge was analyzed with a GLM, using snow depth as dependent variable, transect location (peatland vs. upland) and reindeer density (low vs high) as fixed factors and peatland and region (north vs south) as random factors. Region was added to correct for regional differences in snow depth because at the time of the snow measurement there had been more snow south of the Kevo Research Station.

Results

Reindeer Abundance

We found on average twice as many summer fecal pellet groups (0.06 vs 0.03 pellets/m^2) and three times less winter fecal pellet groups (0.01 vs 0.03 pellets/m^2) in areas identified by locals as having high reindeer abundance in summer, but due to large spatial variability those differences in pellet abundance were not significant (Supplementary Figure S2-1). In addition, we found that in areas defined as having relatively high reindeer by locals, birch trunks were practically free from lower leaves and branches up to roughly 60 cm high, as also observed by others in this region (Vuojala-Magga and Turunen 2015). In contrast, birch trees growing in low reindeer areas had lower branches with leaves occurring closer to the ground (Figure 1a vs. 1b). Although reindeer can browse higher, the bimodality of this browsing effect on the architecture of birch trees (Supplementary Figure S2-2) allows a fairly good distinction of peatland sites with relatively low versus high reindeer densities consistent with the local knowledge (Supplementary Figure S2-3). These results also suggest that contrasts in reindeer densities between our study sites are mostly associated to summer browsing.

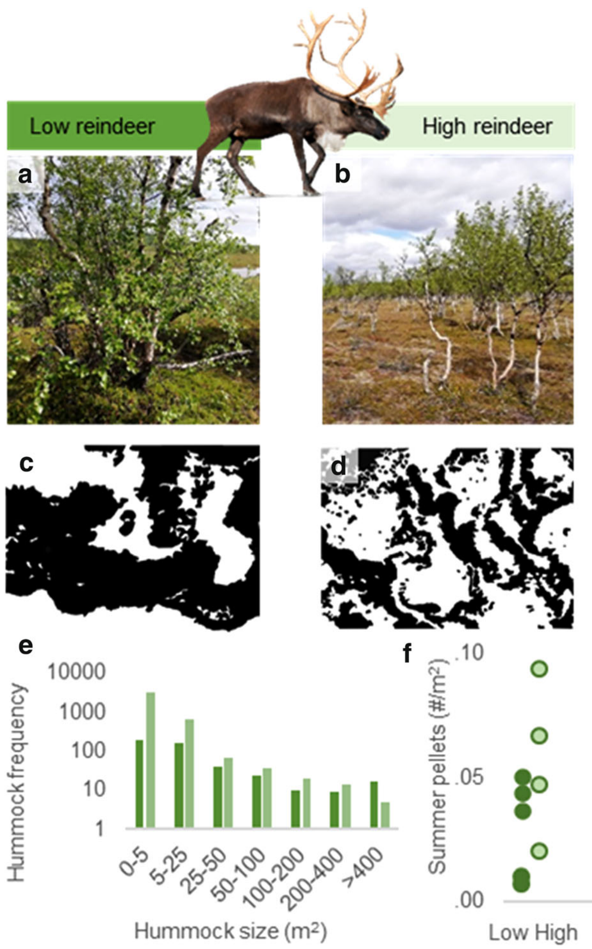


Figure 1. Structure of subarctic permafrost peatlands under low and high reindeer levels. **a-b** Architecture of birch trees surrounding two typical peatlands under low and high reindeer density. Reindeer browsing removes lower leaves and branches resulting in striking savanna-like trees. **c-d** Hummock surface (black) and lawn surface (white) derived from drone images show that hummock surface is less fragmented in peatlands under low **c** as compared to high **d** reindeer levels. **e** Peatlands under high reindeer levels (light green) have a high abundance of small hummocks as compared to peatlands with low reindeer levels (dark green). **f.** Hummock size is significantly larger in peatlands under low reindeer (65 m^2 ± 1 s.e.) than in peatlands under high reindeer levels (2 m^2 ± 1 s.e.) (GLM, reindeer factor $p = 0.031$); $n = 25$ transects in high reindeer sites; $n = 24$ transects in low reindeer sites.

Peatland Structure and Permafrost Condition

Our results indicate that high reindeer density is associated with profound changes in the micro-topography of subarctic peatlands and degraded permafrost condition within the hummocks. High resolution drone image analysis showed that subarctic peatlands in areas with high reindeer density have a fragmented structure composed by smaller hummocks (Figure 1). The proportion of hummocks with permafrost is lower in peatlands under high reindeer density (Figure 2a, and 2b) as smaller hummocks have a lower probability of holding permafrost (Figure 2c). Also, the proportion of hummocks thawing during the summer was highest and the frost table deepest in peatlands with high reindeer density (Supplementary Table S2). The reduction in hummock sizes tends to increase the ratio of lawn to hummock surface in peatlands under high reindeer density (Figure 3a). Despite the large geographical variability across the studied peatlands, the fragmentation patterns are consistent with the spatial patterns of reindeer abundance observed by locals. In general, we find within a same grazing district, larger lawn to hummock ratios toward the north where reindeer tend to concentrate in the summer (Supplementary Figure S8a). Moreover, adjacent peatlands separated by a reindeer fence show larger hummock fragmentation on the side defining the northern end of a cooperative herding district (Supplementary Figure S8b), making it unlikely that the effects are a result of reindeer selecting peatlands with large lawns. High reindeer peatlands also tend to have a larger proportion of surface standing water in the lawns (Figure 3b). These changes in hummock sizes and surface water cover are most likely the result of trampling, as reindeer step on hummock edges and compact the moss layer of the surrounding lawns.

Summer Albedo

The fragmentation of the hummocks and the increase in standing water in peatlands under high reindeer density have profound implications for summer albedo. Our summer albedo measurements were lower in lawns than on hummocks (Figure 3c) and decreased even further as the proportion of open water increased in the lawns

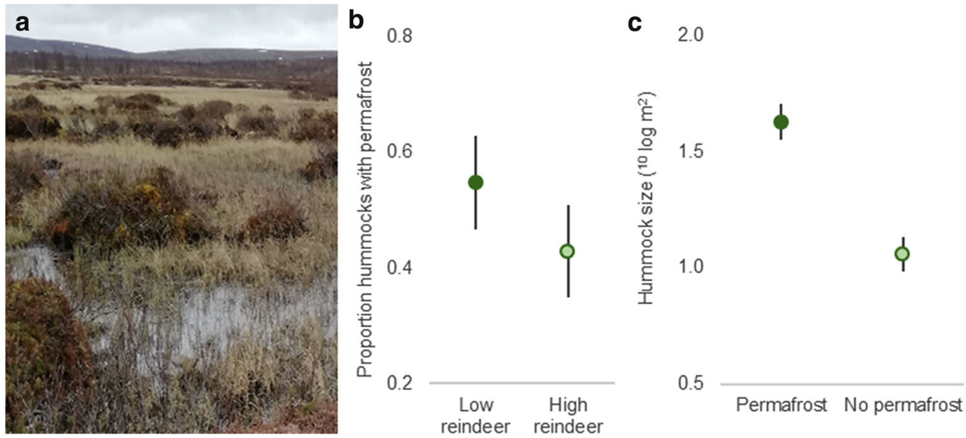


Figure 2. Permafrost presence in peatlands under low and high reindeer levels. **a** Micro-elevations (hummocks) within a surrounding lower matrix (lawn). **b** Proportion of hummocks with permafrost is smaller in peatlands with high reindeer levels (GLM, reindeer factor $p = 0.019$; $n = 25$ transects in high reindeer sites; $n = 25$ transects in low reindeer sites). **c** Hummocks with permafrost are significantly larger than hummocks with no permafrost (T-test, $p < 0.001$; $n = 58$ hummocks with no permafrost; $n = 38$ hummocks with permafrost, from detailed study sites).

(Figure 3d). Although the increases in the proportion of water cover and the lowering of the albedo as a result, suggest that high reindeer density could contribute locally to intensification of climate warming effects, their net effect would also depend on how reindeer change vegetation characteristics.

Vegetation and Soil Patterns

We found that subarctic peatlands under high reindeer density tended to have more shrubby hummocks dominated by unpalatable evergreen shrubs such as the relatively tall *Rhododendron tomentosum* (Supplementary Information Figs. S4 and S5). The increases in unpalatable shrubs found in peatlands under high reindeer density were concentrated on hummocks that had retained the permafrost. In contrast, hummocks without permafrost shifted from a dominance of evergreen shrubs toward a larger abundance of herbs and mosses as reindeer density increased (Supplementary Information Figure S5). Hummocks with no permafrost had lower soil N and higher C:N ratios (Supplementary Figure S6).

We further explored how changes in vegetation could influence summer albedo by deriving plant species-specific albedo values. Our derived summer albedo estimations were lower on hummocks with permafrost than on hummocks without permafrost (Figure 3e and f) which could be explained by the larger proportion of shrubs than herbs in frozen hummocks (Supplementary Information Figure S4). We found that reindeer abundance had no significant direct effects on the estimated hummock summer albedo (Supplementary Information S7).

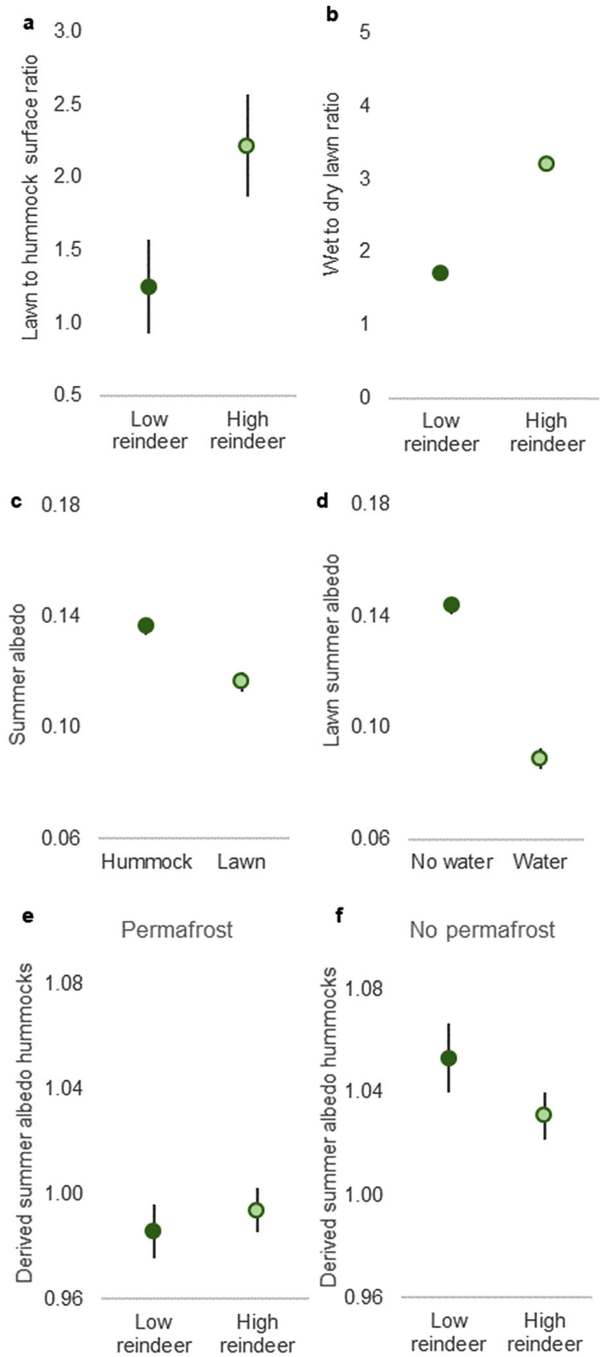
Snow Thickness

We found that subarctic peatlands under high reindeer density tended to have deeper snow packs in winter, particularly along the mineral peatland edge (Figure 4), where the snow pack was very loose in structure. On the open peatlands differences between low and high reindeer density sites were less pronounced.

Discussion

Direct and Indirect Reindeer Effects on Peatland Permafrost

Our results suggest that reindeer affect the characteristic micro-topography of the peatlands and change vegetation in ways that favor summer warming and reduce winter cooling resulting in permafrost degradation (Figure 5). Reindeer trampling is the most plausible mechanism explaining the changes in peatland structure observed in high summer reindeer sites. Reindeer at high densities fragment hummocks, reducing their sizes and their insulating capacity to maintain a frozen core. Trampling also increases the area of open water in the lawns, reducing summer albedo. On frozen hummocks, selective browsing may further favor the dominance of evergreen unpalatable shrubs (Supplementary Figure S4). The shrubby structure of hummocks in high reindeer sites can also act as a snow trap. Indeed, we found deeper snow packs in sites under locally high reindeer density in summer (Figure 4). Because snow insulates soils effectively, thicker snow layers may slow down winter freezing



◀**Figure 3.** Summer albedo in hummocks and lawns of subarctic peatlands. **a** Ratio of lawns to hummocks surface tends to increase with high reindeer pressure as hummocks fragment but spatial variability is high and differences are not statistically significant (GLM reindeer effect, $p = 0.319$). **b** Standing water, expressed as wet: dry lawn ratio, tends to increase in lawns of peatlands with high reindeer density (Chi-square Test, $p = 0.07$). **c** Summer albedo of lawns is lower than albedo of hummocks (Paired T-test, $p < 0.001$). **d** Summer albedo of lawns decreases as standing water increases (T-test, $p = 0.001$). **e** Derived summer albedo on hummocks with permafrost is unaffected by reindeer density (GLM reindeer effect, $p = 0.823$). **f** Derived summer albedo in hummocks with no permafrost is unaffected by reindeer density (GLM reindeer effect, $p = 0.374$). Sample sizes: **a**, **b** $n = 25$ transects in high reindeer sites; $n = 24$ transects in low reindeer sites, **c**, **d** $n = 75$ in high reindeer sites; 72 in low reindeer sites, (e, f) $n = 145$ hummocks along the 49 transects as $n = 51$ high reindeer no permafrost, $n = 35$ high reindeer with permafrost; $n = 23$ low reindeer no permafrost, $n = 34$ low reindeer with permafrost.

and contribute to permafrost degradation (Johansson and others 2006, Devoie and others 2019). Modeling studies support the possibility of shrub-induced permafrost melt as a result of snow accumulation and lower albedo (Lawrence and Swenson 2011, Beer and others 2020). The deeper snow layers in the sites under high reindeer densities could potentially have increased the sensitivity of the peatlands to summer trampling as permafrost integrity is lower under thick snow packs. The thicker snow packs could also be explained by seasonal differences in reindeer habitat use between our low and high reindeer sites. We found less winter reindeer pellet groups in high reindeer sites suggesting that a thicker snow pack could also result from less reindeer snow compaction during winter (Supplementary Figure S2.1). Winter trampling is likely limited in peatlands as reindeer preferentially seek out the forest to forage mostly on ground and arboreal lichens in winter (Skjenneberg and Slagsvold 1979; Suominen and Olofsson 2000, Kitti and others 2009).

At the ecosystem-scale, the direct effects of reindeer browsing on plant species composition seem to be much smaller than the indirect effects of reindeer through hummock fragmentation and permafrost loss. Peatlands under high reindeer densities show a larger proportion of small hummocks without a frozen core. Vegetation in unfrozen hummocks is dominated by mosses and sedges, indicating a transition toward moister conditions (Holmgren and others 2015, Limpens and others 2020), which is comparable to the vegetation succession reported for arctic tundra after permafrost thaw (Magnússon and others 2020, Heijmans and others 2022). The interactive effects of permafrost condition and reindeer density on vegetation, that we have described here, echo earlier conclusions about the complexity and context-dependency of reindeer effects on vegetation (Bernes and others 2015). The transition from

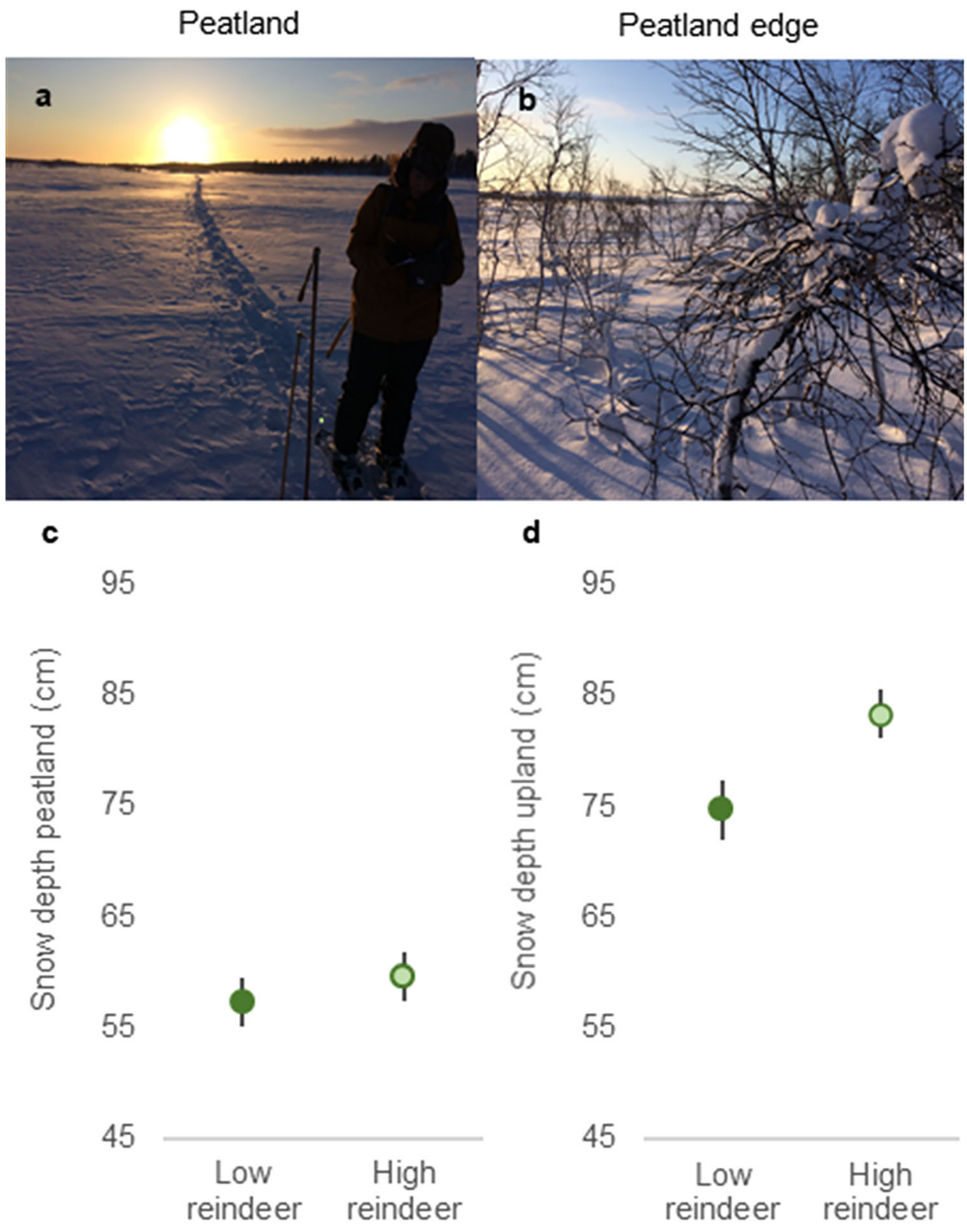


Figure 4. Snow depth in peatlands and adjacent edges with mineral soil under low and high reindeer levels. Snow accumulation tends to be higher in peatlands (a and c) and mineral surroundings (**b** and **d**) with high reindeer density (GLM reindeer effect; $p = 0.079$. Data shows mean ± 1 s.e. ($n = 6$ sites with high reindeer density and $n = 6$ sites with low reindeer density).

permafrost peatlands with large frozen hummocks toward wetter peatlands with fragmented hummocks without permafrost may increase the emission of the strong greenhouse gases methane and nitrous oxide (N_2O) (Voigt and others 2017, Hugelius and others 2020, Shan and others 2020). We found that hummocks with no permafrost had lower soil N and higher C:N ratios, suggesting N is being lost from the soil as permafrost thaws. Some of this N may have been emitted to the atmosphere while part may have been sequestered by sedges and herbs.

A Hypothetical Successional Model

It might well be that the patterns we observe reflect only part of a long-term, perhaps cyclic successional pattern. Consider the following hypothetical scenario: Browsing initially promotes the relative abundance of unpalatable large shrubs in hummocks that still retain their frozen core. However,

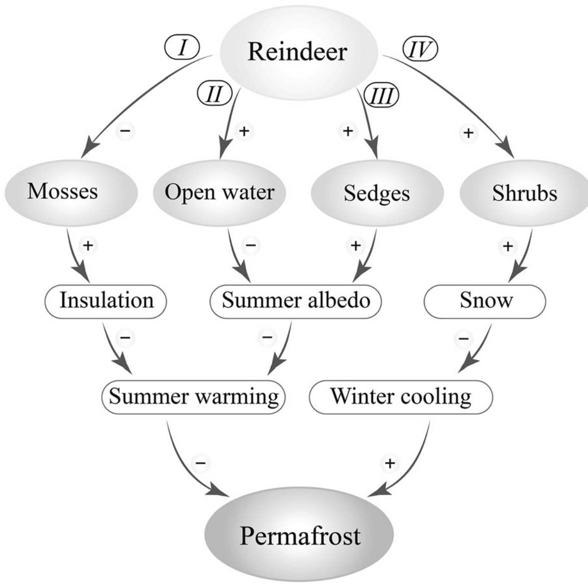


Figure 5. Schematic representation of reindeer effects on subarctic permafrost peatlands. This conceptual model shows the mechanisms by which reindeer may affect permafrost condition. Signs are used to indicate positive or negative relationships between variables. Multiplying the signs along each pathway describes the direction of the net effects reindeer have for that mechanisms. Net effects of reindeer on permafrost are all negative with the exception of their impact on sedges (III) which implies a protective effect. **(I)** Reindeer trample on mosses reducing thermal insulation, increasing summer soil temperatures and degrading permafrost. (**II)** Reindeer trampling increases the lawn to hummock surface ratio and the water cover in lawns, reducing summer albedo and facilitating permafrost loss. **(III)** Reindeer favor sedges by increasing the surface of moist lawns. The high summer albedo of the sedges slows down local warming, protecting the permafrost. (**IV**) Reindeer promote the relative abundance of tall unpalatable shrubs on hummocks which retain thicker snow packs, increasing winter temperature and facilitating permafrost degradation.

as the reindeer return annually to forage on the sedges in the surrounding lawns, the persistent trampling, damages and fragments the hummocks. Smaller hummocks lose their insulating capacity and permafrost eventually thaws. During this stage shrubs are replaced by sedges which can increase the hummock albedo, but as trampling reduces the area covered by hummocks and increases the area covered by lawns with surface water, the overall albedo of the peatland decreases. During this stage, peatlands may amplify climate warming due to a combination of decreased albedo and increase methane emission. Eventually, as peatlands become too wet, this may hinder the access of reindeer and facilitate the regrowth of moss. Such recovery of the moss layer could potentially reduce methane emissions by creating an aerated layer where methane can be oxidized and also increase the soil capacity to retain seasonal frost as open water is replaced by insulating moss. The possibility of peatlands ultimately recovering some of their microtopography and ecosystem functions remains speculative. Also, long-term outcomes likely depend on reindeer densities and habitat use, the ratio of hummocks to lawns and the overall climate and topographic features of the peatland.

The ''natural'' experiment approach we used allows assessing only the short-term effects of contrasting reindeer densities at those landscape scales. Long-term observations are needed to assess the mechanisms that explain the broader successional trajectories of peatlands under low and high reindeer densities. Also, future experimental studies, under more controlled conditions, could help assessing the relative importance of the different pathways that may affect permafrost condition of subarctic peatlands (Figure 5), and how this compares to reindeer effects in other high latitude ecosystems. Such a combination of approaches has proven a successful strategy to understand complex phenomena in ecological systems at relevant spatial and temporal scales (Schindler 1998, Underwood and others 2000).

Implications for Rewilding of Northern Landscapes in a Warming World

It has been hypothesized that the widespread extinction of mega herbivores at the end of the Pleistocene caused a major ecosystem shift from drier grass-dominated steppes to moister moss-shrub-dominated tundra with patchy deciduous forests. If true, rewilding the Arctic with high densities of large herbivores could help re-establish a lost top-down control on woody plants and facilitate the expansion of grasslands (Zimov and others 1995). The paleo-ecological evidence on the cause-effect relationship between the extinction of mega herbivores and the shrub expansion of the Arctic remains controversial (Monteath and others 2021, Murchie and others 2021). Nevertheless, increasing the density of large herbivores in northern landscapes has been proposed as a nature-based solution to mitigate current climate warming. The proposed mechanism is two-fold. Intense browsing and nutrient addition may facilitate grass expansion leading to higher albedo and evapotranspiration resulting in soil cooling and drying. Meanwhile, trampling in winter may compact the snowpack allowing deeper winter freezing and protection of the permafrost (Macias-Fauria and others 2020, Malhi and others 2022). Although rewilding projects aim to actively reintroduce or facilitate the dispersal of large herbivores in order to restore ecosystem functions and resilience (Perino and others 2019), our results with a semi-domesticated large herbivore can contribute to anticipating the implications of high densities of large herbivores on the functioning of permafrost peatlands.

Our results suggest that even moderate densities of reindeer may profoundly affect the functioning of subarctic permafrost peatlands in ways that could amplify climate warming. Those different results could be explained by a difference in the response of uplands and peatlands to high densities of large herbivores, especially in the summer. Indeed, opposite effects have been found for upland tundra at very high reindeer densities (Beer and others 2020). The different outcomes may be mediated by hydrology. Peatlands are found in poorly drained terrain, with permafrost kept closer to the surface, or stored in small dry micro-elevations surrounded by waterlogged conditions. In peatlands, summer trampling by large herbivores enhances permafrost thaw by reducing thermal insulation of the top soil. Indeed, trampling may also lead to deeper thaw in wet tussock tundra of Siberia as suggested by a deeper thawing depth in experimental areas under high density of herbivores compared to areas under lower herbivore densities (Fischer and others 2022).

Understanding how different types of northern landscapes respond to large herbivores in a warming world is urgently needed to improve the adaptive capacity of local herding communities as well as to anticipate potential feedbacks to the climate system. Reindeer-people interactions have shaped northern socio-ecological systems for millennia, evolving and adapting to changing natural and social conditions (Vuojala-Magga and Turunen 2015). Clearly, reindeer management can have major effects on the capacity of northern ecosystems to maintain permafrost for a longer period of time under climate warming. Understanding this better will be important if we are to optimize reindeer management for climate control. Our results indicate that in subarctic peatlands, reindeer densities much smaller than those proposed for rewilding the arctic tundra may already have negative effects on permafrost (Beer and others 2020). Here, reducing reindeer densities may slow down permafrost thaw in peatlands and may build ecosystem resilience to climate warming, sensu (Scheffer and others 2015) preventing transitions to alternative ecosystem states in these northern latitude landscapes (Scheffer and others 2012). The sensitivity of peatlands to high reindeer densities may be larger in the southern end of the arctic region already exposed to warmer temperatures and a discontinuous permafrost layer. Our findings in those subarctic peatlands may help anticipate how the colder arctic peatlands may respond to high reindeer densities as climate warming progresses. Rewilding projects in northern high latitude peatlands should carefully monitor the effects of increasing densities of large herbivores on ecosystem functions that may cause permafrost degradation.

ACKNOWLEDGEMENTS

Kevo Subarctic Station provided logistical support: Otso Suominen and Elina Vainio facilitated information on reindeer distribution and the communication with local Sami reindeer herders, Ilkka Syvänperä facilitated winter access to sampling sites. Victor van Dijk assisted in the field. Bert Heusinkveld advised on albedo measurements. We thank Marten Scheffer for insightful discussions. Financial support was provided by an INTERACT grant (EU-H2020, No. 730938).

FUNDING

INTERACT grant (EU-H2020), 730938.

DATA AVAILABILITY

Data are accessible through this public repository link: https://doi.org/10.17026/dans-xg5-drnc.

REFERENCES

Alves J, da Silva AA, Soares AM, Fonseca C. 2013. Pellet group count methods to estimate red deer densities: precision, potential accuracy and efficiency. Mammalian Biology 78:134–141.

Beer C, Zimov N, Olofsson J, Porada P, Zimov S. 2020. Protection of permafrost soils from thawing by increasing herbivore density. Scientific Reports 10:1–10.

Bernes C, Bråthen KA, Forbes BC, Speed JD, Moen J. 2015. What are the impacts of reindeer/caribou (*Rangifer tarandus* L.) on arctic and alpine vegetation? A Systematic Review. Environmental Evidence 4:1–26.

Brown, J. 1998. National Snow and Ice Data Center. World Data Center for Glaciology.

Cohen J, Pulliainen J, Ménard CB, Johansen B, Oksanen L, Luojus K, Ikonen J. 2013. Effect of reindeer grazing on snowmelt, albedo and energy balance based on satellite data analyses. Remote Sensing of Environment 135:107–117.

Devoie ÉG, Craig JR, Connon RF, Quinton WL. 2019. Taliks: A tipping point in discontinuous permafrost degradation in peatlands. Water Resources Research 55:9838–9857.

Falk JM, Schmidt NM, Christensen TR, Ström L. 2015. Large herbivore grazing affects the vegetation structure and greenhouse gas balance in a high arctic mire. Environmental Research Letters 10:045001.

Fischer W, Thomas CK, Zimov N, Göckede M. 2022. Grazing enhances carbon cycling but reduces methane emission during peak growing season in the Siberian Pleistocene Park tundra site. Biogeosciences 19:1611–1633.

Heijmans MM, Magnússon RÍ, Lara MJ, Frost GV, Myers-Smith IH, van Huissteden J, Jorgenson MT, Fedorov AN, Epstein HE, Lawrence DM. 2022. Tundra vegetation change and impacts on permafrost. Nature Reviews Earth & Environment 3:68–84.

Holmgren M, Lin CY, Murillo JE, Nieuwenhuis A, Penninkhof J, Sanders N, van Bart T, van Veen H, Vasander H, Vollebregt ME. 2015. Positive shrub–tree interactions facilitate woody encroachment in boreal peatlands. Journal of Ecology 103:58–66.

Hugelius G, Loisel J, Chadburn S, Jackson RB, Jones M, MacDonald G, Marushchak M, Olefeldt D, Packalen M, Siewert MB. 2020. Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. Proceedings of the National Academy of Sciences 117:20438–20446.

Istomin KV, Habeck JO. 2016. Permafrost and indigenous land use in the northern Urals: Komi and Nenets reindeer husbandry. Polar Science 10:278–287.

Johansson M, Christensen TR, Akerman HJ, Callaghan TV. 2006. What determines the current presence or absence of permafrost in the Torneträsk region, a sub-arctic landscape in northern Sweden? AMBIO A Journal of the Human Environment 35:190–197.

Kitti H, Forbes BC, Oksanen J. 2009. Long-and short-term effects of reindeer grazing on tundra wetland vegetation. Polar Biology 32:253–261.

Kumpula, J., A. Tanskanen, A. Colpaert, M. Anttonen, H. Törmänen, J. Siitari, and S. Siitari. 2009. Winter pastures in the northern part of the reindeer management area in Finland during 2005–2008–changes in the state of pastures after the mid-1990s. Riista ja kalatalous–Tutkimuksia.

Lawrence DM, Swenson SC. 2011. Permafrost response to increasing Arctic shrub abundance depends on the relative influence of shrubs on local soil cooling versus large-scale climate warming. Environmental Research Letters 6:045504.

Li J, Holmgren M, Xu C. 2021. Greening vs browning? Surface water cover mediates how tundra and boreal ecosystems respond to climate warming. Environmental Research Letters 16:104004.

Limpens, J., T. P. Fijen, I. Keizer, J. Meijer, F. Olsthoorn, A. Pereira, R. Postma, M. Suyker, H. Vasander, and M. Holmgren. 2020. Shrubs and Degraded Permafrost Pave the Way for Tree Establishment in Subarctic Peatlands. Ecosystems:1–14.

Macias-Fauria M, Jepson P, Zimov N, Malhi Y. 2020. Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? Philosophical Transactions of the Royal Society B 375:20190122.

Magnússon RÍ, Limpens J, van Huissteden J, Kleijn D, Maximov TC, Rotbarth R, Sass-Klaassen U, Heijmans MM. 2020. Rapid vegetation succession and coupled permafrost dynamics in Arctic thaw ponds in the Siberian lowland tundra. Journal of Geophysical Research Biogeosciences 125:e2019JG005618.

Malhi Y, Lander T, le Roux E, Stevens N, Macias-Fauria M, Wedding L, Girardin C, Kristensen JÅ, Sandom CJ, Evans TD. 2022. The role of large wild animals in climate change mitigation and adaptation. Current Biology 32:R181–R196.

Meredith, M., M. Sommerkorn, S. Cassotta, C. Derksen, A. Ekaykin, A. Hollowed, G. Kofinas, A. Mackintosh, J. Melbourne-Thomas, and M. Muelbert. 2019. Polar Regions. Chapter 3, IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.

Metcalfe DB, Hermans TD, Ahlstrand J, Becker M, Berggren M, Björk RG, Björkman MP, Blok D, Chaudhary N, Chisholm C. 2018. Patchy field sampling biases understanding of climate change impacts across the Arctic. Nature Ecology & Evolution 2:1443–1448.

Monteath AJ, Gaglioti BV, Edwards ME, Froese D. 2021. Late Pleistocene shrub expansion preceded megafauna turnover and extinctions in eastern Beringia. Proceedings of the National Academy of Sciences 118:e2107977118.

Murchie TJ, Monteath AJ, Mahony ME, Long GS, Cocker S, Sadoway T, Karpinski E, Zazula G, MacPhee RD, Froese D. 2021. Collapse of the mammoth-steppe in central Yukon as revealed by ancient environmental DNA. Nature Communications 12:7120.

Olofsson J, Post E. 2018. Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. Philosophical Transactions of the Royal Society b: Biological Sciences 373:20170437.

Olvmo M, Holmer B, Thorsson S, Reese H, Lindberg F. 2020. Sub-arctic palsa degradation and the role of climatic drivers in the largest coherent palsa mire complex in Sweden (Vissátvuopmi), 1955–2016. Scientific Reports 10:1–10.

Perino A, Pereira HM, Navarro LM, Fernández N, Bullock JM, Ceausu S, Cortés-Avizanda A, van Klink R, Kuemmerle T, Lomba A. 2019. Rewilding complex ecosystems. Science 364:eaav5570.

Rantanen M, Karpechko AY, Lipponen A, Nordling K, Hyvärinen O, Ruosteenoja K, Vihma T, Laaksonen A. 2022. The Arctic has warmed nearly four times faster than the globe since 1979. Communications Earth & Environment 3:168.

Scheffer M, Hirota M, Holmgren M, Van Nes EH, Chapin FS. 2012. Thresholds for boreal biome transitions. Proceedings of the National Academy of Sciences 109:21384–21389.

Scheffer M, Barrett S, Carpenter S, Folke C, Green AJ, Holmgren M, Hughes T, Kosten S, Van de Leemput I, Nepstad D. 2015. Creating a safe operating space for iconic ecosystems. Science 347:1317–1319.

Schindler DW. 1998. Whole-ecosystem experiments: replication versus realism: the need for ecosystem-scale experiments. Ecosystems 1:323–334.

Schuur EA, Mack MC. 2018. Ecological response to permafrost thaw and consequences for local and global ecosystem services. Annual Review of Ecology, Evolution, and Systematics 49:279–301.

Seppälä M. 1988. Palsas and related forms. In: Clark MJ, Ed. Advances in periglacial geomorphology, . Chichester: Wiley. pp 247–277.

Shan W, Xu Z, Guo Y, Zhang C, Hu Z, Wang Y. 2020. Geological methane emissions and wildfire risk in the degraded permafrost area of the Xiao Xing'an Mountains, China. Scientific Reports 10:1–21.

Skjenneberg, S., and L. Slagsvold. 1979. Reindeer husbandry and its ecological principles. US Department of the Interior, Bureau of Indian Affairs.

Stark, S., T. Horstkotte, J. Kumpula, J. Olofsson, H. Tømmervik, and M. Turunen. 2022. The ecosystem effects of reindeer (Rangifer tarandus) in northern Fennoscandia: Past, present and future. Perspectives in Plant Ecology, Evolution and Systematics:125716.

Strauss J, Schirrmeister L, Grosse G, Fortier D, Hugelius G, Knoblauch C, Romanovsky V, Schädel C, von Deimling TS, Schuur EA. 2017. Deep Yedoma permafrost: A synthesis of depositional characteristics and carbon vulnerability. Earth-Science Reviews 172:75–86.

Suominen O, Olofsson J. 2000. Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: a review. Annales Zoologici Fennici 37:233–249.

Te Beest M, Sitters J, Ménard CB, Olofsson J. 2016. Reindeer grazing increases summer albedo by reducing shrub abundance in Arctic tundra. Environmental Research Letters 11:125013.

Underwood A, Chapman M, Connell S. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. Journal of Experimental Marine Biology and Ecology 250:97–115.

Voigt C, Marushchak ME, Lamprecht RE, Jackowicz-Korczyński M, Lindgren A, Mastepanov M, Granlund L, Christensen TR, Tahvanainen T, Martikainen PJ. 2017. Increased nitrous oxide emissions from Arctic peatlands after permafrost thaw. Proceedings of the National Academy of Sciences 114:6238–6243.

Vuojala-Magga T, Turunen MT. 2015. Sámi reindeer herders' perspective on herbivory of subarctic mountain birch forests by geometrid moths and reindeer: a case study from northernmost Finland. SpringerPlus 4:1–13.

Windirsch, T., G. Grosse, M. Ulrich, B. C. Forbes, M. Göckede, J. Wolter, M. Macias-Fauria, J. Olofsson, N. Zimov10, and J. Strauss. 2022. Large herbivores on permafrost—a pilot study of grazing impacts on permafrost soil carbon storage in northeastern Siberia. Frontiers in Environmental Science **10**.

Zhang T, Barry R, Knowles K, Heginbottom J, Brown J. 2008. Statistics and characteristics of permafrost and ground-ice distribution in the Northern Hemisphere. Polar Geography 31:47–68.

Zimov SA, Chuprynin V, Oreshko A, Chapin Iii F, Reynolds J, Chapin M. 1995. Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. The American Naturalist 146:765–794.