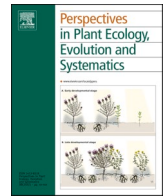




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The ecosystem effects of reindeer (*Rangifer tarandus*) in northern Fennoscandia: Past, present and future

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ABSTRACT

The semi-domesticated nature of the reindeer (*Rangifer tarandus* L.) makes it a distinct case among the world's herbivores. Here, we review the literature on how reindeer shape vegetation and soil carbon and nitrogen cycles in northernmost Fennoscandia. We first describe main historical events that shaped the present-day grazing patterns in the different countries, then discuss the methodological considerations needed for interpreting evidence from grazer enclosures in ecological and environmental contexts. We argue that it is critical to be aware that these experiments do not measure the effect of grazing per se, but rather, they measure the responses of existing ecosystem structure and function to the sudden cessation of grazing in an environment, which was to a large degree shaped by it. Studies show that the direction and the magnitude of the effects of reindeer on vegetation and soil processes vary across habitats and depend on both the current land-uses and the historically formed grazing regimes; knowledge of the history is thus a key prerequisite for understanding the role of reindeer in ecosystems. As a general trend, reindeer affect soil nutrient cycles to a stronger extent in subarctic than in boreal ecosystems. In sites where reindeer have changed soil nutrient availability, they indirectly modify vegetation and productivity even after the cessation of grazing. We reason that the concepts of cultural and natural landscapes are not mutually exclusive in the case of reindeer ranges. Understanding how the intensity and seasonal timing of both past and present grazing direct ecosystem changes under climate warming is crucial for predicting future ecosystem structures and functioning in northern Fennoscandia as well as ecosystems in general.

1. Introduction

The semi-domesticated nature of the reindeer (*Rangifer tarandus* L.) makes it a distinct case among the world's herbivores. This large ungulate has a circumpolar distribution across North Eurasia and America. Reindeer husbandry was formed as a livelihood several centuries ago in the Eurasian continent (Uboni et al., 2016). Reindeer husbandry relies on freely ranging animals in natural ecosystems to which they have access, irrespective of land ownership. Species-specific behavior and forage selection of reindeer during different seasons drive spatial and temporal grazing patterns across landscapes, thus resembling their wild ancestors. Like wild grazers, their numbers are regulated by large predators, extreme winter weather events, disease and forage

availability in their resident ecosystems (Åhman et al., 2014; Helle and Kojola, 2008; Rasmus et al., 2020; Riseth et al., 2020; Uboni et al., 2016). However, to a large extent, the grazing patterns and number of reindeer depends on not only the ecological interactions between the reindeer and its natural surroundings, but on human management regimes – formed by the socio-political history and socio-economic factors – that essentially determine contemporary reindeer movements and abundance in space and time (e.g. Helle and Jaakkola, 2008; Lundmark, 2006; Holand et al., 2022).

So far, a substantial pool of literature has accumulated on the role of reindeer in shaping ecosystem structure and functioning in northernmost Fennoscandia. Within the discipline of ecology, reindeer grazing has been discussed, e.g., in the contexts of alternative ecosystem states

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(van der Wal, 2006; Egelkraut et al., 2018; Stark et al., 2019), and the theory that habitat fertility dictates the direction of the effect of herbivory on soil nutrient cycles (e.g. Stark et al., 2002; Sitters et al., 2017). As forage availability for reindeer is important for body condition, reproduction rate and mortality, ecological evidence also informs pasture management and the sustainable use of natural resources (e.g., Riseth et al., 2002). Winter forage availability is especially used for defining the upper limits of reindeer numbers (Kumpula et al., 2014; Marin and Bjørklund, 2015; Marin et al., 2020). Yet, for ecological and reindeer management contexts, a central point is how the historical development of reindeer herding regimes have modified their role in ecosystems. Here, we review the existing literature on Fennoscandia to bridge the effects of reindeer on vegetation with the historical contexts of reindeer herding and other land use regimes. We then discuss direct and indirect mechanisms by which reindeer modify soil carbon and nitrogen cycles, and how these in turn contribute to the ecosystem effect of the reindeer. Finally, we outline some future prospects of reindeer herding under the cumulative effects of other land uses and climate change, and reflect them against the concepts of cultural and natural landscapes. We create this linkage between ecology and history as to provide a deeper understanding of the fundamental role of herbivory in ecosystems as well as on predictions regarding ecosystem trajectories under a warming climate. By doing this, we hope to contribute to creating a generalized model in how scientists should see and study large grazers in ecosystems.

2. Vegetation and history in the Fennoscandian reindeer herding area

The distribution of reindeer in Fennoscandia extends across several vegetation zones along latitudinal and altitudinal gradients (Fig. 1). Boreal forests are dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) intermixed with deciduous trees such as birch (*Betula* sp.) and are bordered by a vegetation zone composed primarily of multi-stemmed mountain birch (*Betula pubescens* ssp. *czerepanovii*). The border between the mountain birch forests and open tundra depends on a combination of climatic and edaphic conditions and land-use history (Oksanen and Virtanen, 1995; Tømmervik et al., 2019; Virtanen et al., 2015). Dwarf shrubs such as *Vaccinium* sp., *Betula nana* and *Empetrum nigrum* together with mosses, ground lichens, forbs and graminoids form the dominant ground vegetation.

Seasonal movements between different habitats and landscapes are a key behavioral feature of reindeer across all climatic vegetation zones (Fig. 2). Reindeer consume a wide range of plant species, which vary by season depending on plant phenology and the accessibility of plants in the landscape. Reindeer have a special ability to digest lichens, a symbiosis between algal and fungal partners, and they form an important part of the winter diet, supplemented by evergreen dwarf shrubs, grasses, and arboreal lichens (Storeheier et al., 2003; Kojola et al., 1995; Jaakkola et al., 2006). During summer and autumn, reindeer rely on grasses, herbs, birch foliage and mushrooms to build up body reserves for the winter. Mires are an important habitat during summer, in particular in areas where reindeer are not able to move above the tree line during summer.

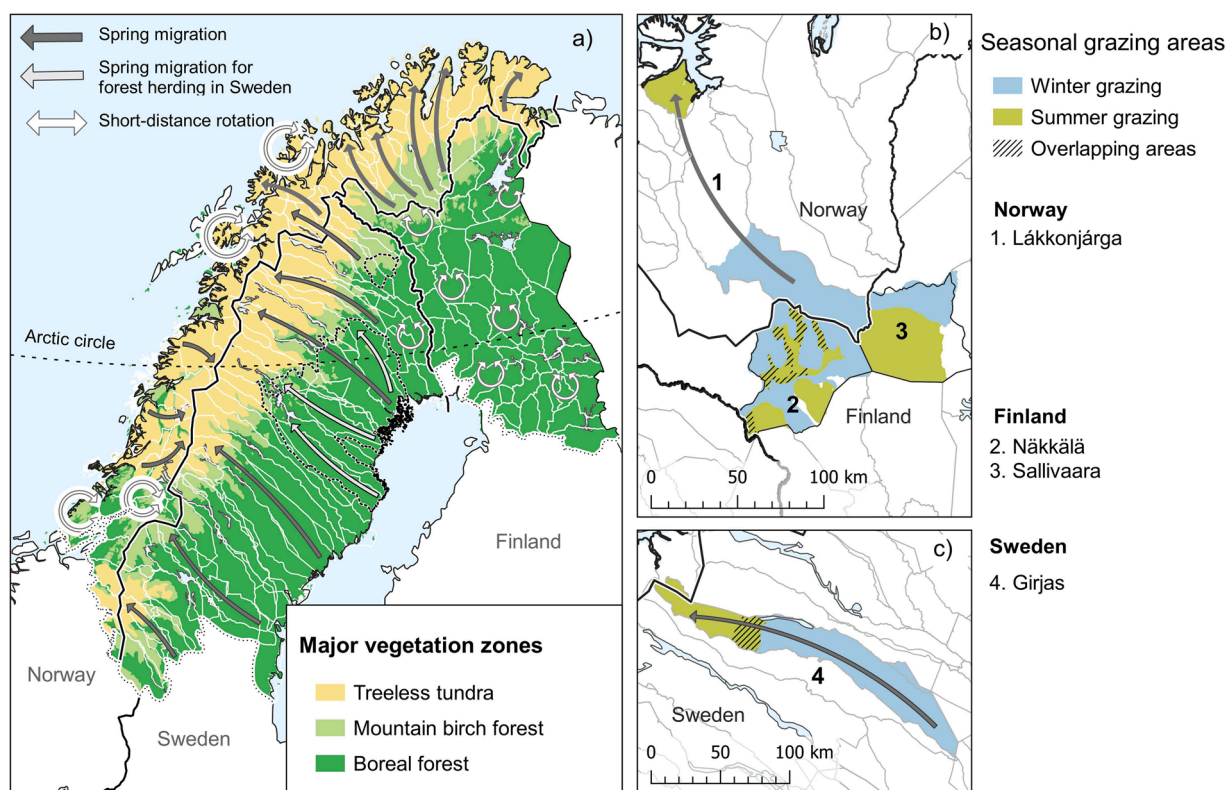


Fig. 1. a. Climatic vegetation zones (adapted from Olson et al., 2001) and reindeer management regimes (www.sametinget.se for Sweden, <https://kilden.nibio.no> for Norway, Finnish Reindeer Herders Association for Finland) in northern Fennoscandia. Arrows drawn in the map do not depict precise migration routes, but rather the general direction of the movement. Straight arrows describe the direction of the movement during spring, whereas circular arrows describe more stationary herding that involves migration within short distances. Due to the combined effects of climatic and environmental conditions and historical developments, seasonal range rotations are within shorter distances in Finland compared to many districts in Norway and Sweden. b. Examples of seasonal range rotations in some Finnish and Norwegian herding districts. The illustrated winter grazing area in Norway is shared by several districts based on customary rules. In Finland, seasonal areas overlap in Näkkälä, while they are separated by a pasture rotation fence in Sallivaara. c. An example of seasonal range rotation in a Swedish district. In all districts, the use of each area can vary substantially between years depending on environmental factors.

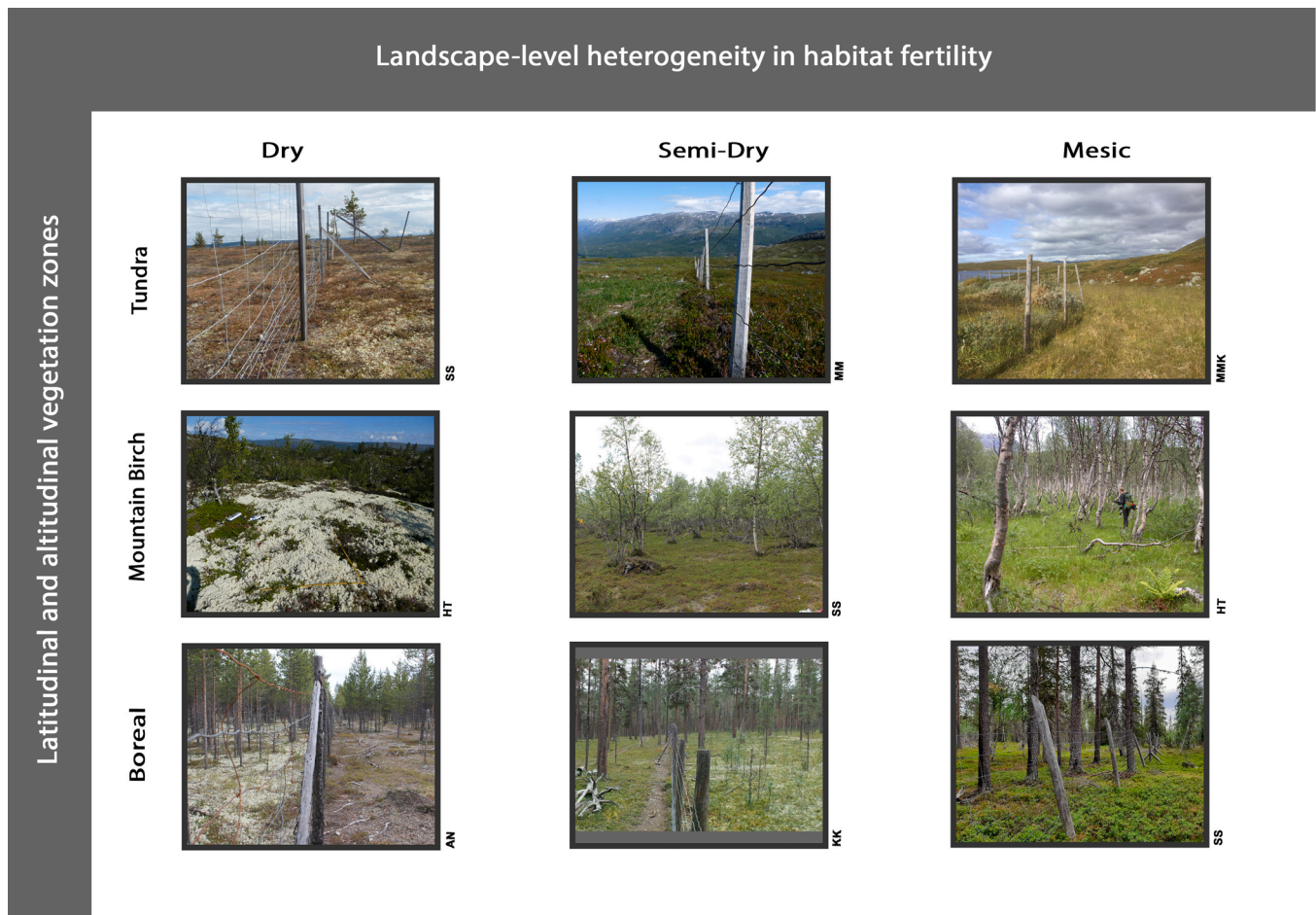


Fig. 2. Dry, semidry and mesic sites in boreal forests, mountain birch forests, treeless arctic-alpine tundra heaths. While vegetation in dry habitats is dominated by lichens, more mesic habitats become increasingly dominated by dwarf and tall shrubs, herbs and graminoids across all climatic vegetation zones. Following their nutritional needs and the availability of forage plants during different seasons, added by insect avoidance, reindeer seasonally move between different habitat types. The Authors of the photographs: AN = Aarno Niva, KK = Kajar Köster, MM = Minna Männistö, MK = Minna-Maarit Kytöviita, HT = Hans Tømmervik, SS = Sari Stark.

However, reindeer management regimes – and consequently, seasonal migrations and habitat use – differ substantially across Fennoscandia due to a combination of environmental conditions and historical developments (Fig. 1a–c). An awareness and understanding of these differences is central to understanding the ecosystem effects of reindeer in Fennoscandia, because besides of vegetation and landscape factors, the differences in socio-political history over time shaped when and where reindeer graze and move in particular locations and seasons. Until the early medieval period, the indigenous Sámi followed a mixed subsistence strategy including fishing, hunting and gathering, and some domesticated reindeer were used as transport, draft and pack animals, decoys for hunting and for providing meat and milk (Bergman et al., 2013; Salmi et al., 2021). Reindeer domestication took place gradually and in a non-synchronous manner across the different regions in parallel with wild reindeer hunting (Lundmark, 2006; Pelletier et al., 2021). When Northern Fennoscandia was claimed by competing nation states (Norway-Denmark, Sweden-Finland and Novgorod/Russia) during mid-1600's, the indigenous Sámi paid taxes for their lands and waters sometimes to several kingdoms at the same time, which over time were increasingly paid by the meat and hides of domesticated reindeer (Bergman et al., 2013). This increased the sizes of domesticated herds and, in the north and north-west, led to an adoption of long seasonal migrations between summer ranges on the Norwegian coast and forested areas in Sweden-Finland during winter. This was because the oceanic Atlantic coast is rich in graminoids, forbs and mountain birch foliage

and thus provided good summer nutrition, whereas the lichen-rich continental interior provided good winter grazing grounds (Oksanen and Virtanen, 1995).

In the boreal forest regions of today's Sweden and Finland, differences between vegetation and landscape types are less pronounced. Therefore, seasonal migrations were shorter and Sámi reindeer herders have led a more sedentary way of living. Starting from the 1600's, Finnish settlers started moving to the area and adopted reindeer herding practices to supplement their mixed subsistence livelihoods which included farming, fishing, and hunting. Meanwhile, local forest Sámi adopted farming practices (Heikkinen, 2006; Lähteenmäki, 2006). Migratory reindeer husbandry with larger herd sizes spread into northern Finland from the western parts of Fennoscandia during the 1600's. However, stationary communities with gradually mixed Sámi and Finnish populations still relied on nature-based livelihoods and small-scale farming. For these historical reasons, in Finland both Sámi and Finns are engaged in reindeer husbandry, whereas in Sweden and Norway, the livelihood is almost exclusively practiced by Sámi.

Originally, an agreement called the Lapp Codicil in 1751 granted Sámi reindeer herders free passage across the borders of different kingdoms due to a recognition of their need for seasonal range migrations (Lantto, 2010). However, in the late 1800's, country borders began to form barriers to migration routes. Finland was annexed by Russia from Sweden in 1809, and Russia closed the border to Norway in 1852 to protect the stationary and small-scale reindeer husbandry practices in

Finland from large migratory herds from Northern Norway that damaged farms, reduced grazing resources and mixed with the local reindeer herds (Lantto, 2010). For the migratory reindeer herders, these border closures entailed a loss of either summer grazing areas on the Norwegian coast, or of winter grazing areas in Finland. A second border closure in 1889 cut off remaining migration routes between Norway and Finland that had remained open through Sweden (between Troms county and Norrbotten; Lundmark, 2006; Lantto, 2010). Border closures induced new practices of seasonal range rotation in all countries (Fig. 1b, c). Norway assigned specific summer grazing areas to different *siidas*, i.e. groups often based on kinship that share the work of reindeer herding, in 1888 (Aarseth, 1989). Increased reindeer numbers near national borders led to a severe shortage of grazing resources (Riseth et al., 2016) and the partly forced, partly voluntary relocations of reindeer herding families to more southerly Fennoscandian mountains, to north-east Finland or to the Kola peninsula (Aarseth, 1989). In Finland, the state authorities ordered the establishment of geographically defined herding districts as a co-operative based organization in 1898 that were based on the sedentary herding practices (Lähteenmäki, 2006). There are no long-ranging seasonal migrations between winter and summer areas in Finland as in Sweden and Norway (Fig. 1a, b) Long seasonal migrations between summer and winter grazing areas are still continued for the vast majority of reindeer herding districts in Norway and Sweden. In Finland, northern herding districts at in the started to fence their borders from 1960 to 1970's and later, during the 1980's, many of them also built pasture rotation fences between different seasonal ranges (Fig. 1b, c). In Sweden, the Reindeer Husbandry Act of 1886 established herding districts (then *lappby*, today *sameby*) that partly corresponded to earlier *siidas*. The migration of reindeer herders from Sweden to their customary summer ranges on the Norwegian coast became increasingly restricted in successive Reindeer Grazing Conventions (1883, 1919, 1972; Lantto and Mörkenstam, 2008). In 1957, a border fence between Norway and Finland was erected, preventing most cross-border reindeer movements. However, many districts in Sweden have their summer grazing areas in Norway, and some few herding districts from Norway spend the winter in Sweden, often based on agreements with herders in Sweden.

Reindeer numbers fluctuated substantially during the last century throughout the whole region. In Finland, the total reindeer number reached a historical maximum in the early 1990's, whereas the southern reindeer herding districts in Sweden and Norway have retained stable overall trend over the last 50 years. Today, the number of semi-domesticated reindeer after the customary autumn slaughter is approximately 250,000 in Norway and Sweden, and 200,000 in Finland (Holand et al., 2022).

3. Effects of grazing, and grazing exclusion: methods for unraveling how reindeer shape ecosystems

3.1. The decadal history of studies on reindeer effects

A common way of analyzing the role of herbivores across ecosystems is to exclude them from the system, after which ecosystem structure and function are analyzed with and without herbivory (see e.g. Andriuzzi and Hall, 2017). In studies on the effects of reindeer on vegetation, this has become a core experimental method. Areas that have excluded reindeer have not always been established for scientific purposes. For instance, many studies have used sites located on the Finnish-Russian border zone where access by reindeer has been prevented for over a century (e.g. Stark et al., 2003; Susiluoto et al., 2008; Akujärvi et al., 2014; Köster et al., 2015).

Fences that separate seasonal pastures both in Norway and in Finland have formed another method of analyzing reindeer effects on vegetation and ecosystem functions (e.g. Oksanen, 1979; Olofsson et al., 2004; Stark et al., 2007, 2021; Kumpula et al., 2011). Due to different national management regimes, many studies have also compared the opposing

sides of the Finnish-Norwegian border fence in areas where the Finnish side is grazed throughout the year, and the Norwegian side only during parts of the winter (e.g., Biuw et al., 2014; Yläne et al., 2021, see Fig. 1). The season during which reindeer forage in an area is a major determinant of reindeer impacts on vegetation, because it determines which plant species are consumed, and how strongly grazing and trampling impact vegetation (Oksanen, 1979; Kumpula et al., 2011). Especially during summer, trampling is a key factor that affects lichens in particular (Heggenes et al., 2017), whereas during winter, a thick snowpack can limit the grazing area and buffers the ground vegetation from trampling.

Early studies compared plant communities under differing grazing intensities (e.g., Pegau, 1970; Oksanen, 1979; Helle and Aspi, 1983) and in reindeer exclosures (e.g., Väre et al., 1995, 1996). More recent studies have often combined this with other approaches, such as re-analyzing exclosures (Tømmervik et al., 2012; Vowles et al., 2017; Sundqvist et al., 2019) or pasture rotation fences (Yläne et al., 2018; Stark et al., 2021) after one or more decades, which has revealed how current vegetation trends vary under differing grazing regimes. Pasture rotation fences have been used for analyzing the roles of long-term grazing history vs. short-term grazer exclusions (Olofsson, 2006; Väisänen et al., 2014; Yläne et al., 2020), plant nutrient uptake strategies (Barthelemy et al., 2017), or the temperature acclimation of soil microbial functions (Stark et al., 2015a).

3.2. Methodological considerations of exclosure effects

When translating experimental evidence from exclosures into ecological and environmental contexts, it is critical to remember that exclosures represent an artificially created state where all activities and processes related to large grazers and many other have been eliminated. However, large herbivores have been grazing northern ecosystems throughout their evolutionary history. Exclosures represent small pieces of an ecosystem, where a natural component of the ecosystem has been excluded, which - besides reindeer - involves also wild large herbivores such as moose. We do not have information on how the wild ancestors of the present, semi-domestic reindeer modified Fennoscandian ecosystems. However, studies in other areas have shown that wild herbivores such as caribou (Manseau et al., 1996; Gough et al., 2007; Zamin and Grogan, 2013), moose (Pastor and Naiman, 1992), and wild reindeer herds in southern Norway (Skogland, 1984; Vistnes and Nellemann, 2008) have a strong influence on vegetation. Furthermore, within areas of reindeer herding, microtine rodents exert an effect on vegetation in arctic-alpine or arctic tundra heaths comparable to, or even exceeding that of reindeer (Virtanen et al., 1997; Grellmann, 2002; Olofsson et al., 2014; Tuomi et al., 2019). As reindeer have been present in Fennoscandia since the end of the last Ice Age, plant communities are composed of grazing-tolerant species, i.e., plants that withstand or thrive under grazing (Olofsson and Post, 2018). By creating conditions entirely without grazing, exclosures will trigger a slow succession towards more grazing-sensitive plant species that are competitive in undisturbed conditions. It has been observed that a short-term grazer exclusion (i.e., a duration of a couple of years) does not predict vegetation responses in the long run (i.e., over decades), as very different plant species become dominant inside exclosures in the long-term compared to what could be predicted based on the short-term responses (Olofsson, 2006; Saccone and Virtanen, 2015). The difference in vegetation and ecosystem processes between the grazed area and the exclosure is one 'snapshot' of a continuous transition where the grazed vegetation changes in response to the variations in grazing pressure, whereas the vegetation inside the exclosure changes along a succession that started when the area was fenced.

For a correct interpretation of evidence from exclosures, it is necessary to know what has happened in the area at the larger geographical and temporal scale. Past land-uses exert important legacies on northern ecosystem structure and function, involving vegetation and soil nutrient

cycling alike (Josefsson et al., 2009; Egelkraut et al., 2018). An experiment in subarctic tundra in northern Norway demonstrated that short-term exclosures in an area that had been heavily grazed for the past 50 years did not shift the system to resemble a system that had been only lightly grazed, but rather, amplified the difference between the heavily and the lightly grazed tundra (Yläne et al., 2020). Similar results have also been found in alpine ecosystems (Haynes et al., 2014).

Another important consideration are current land-use pressures that can greatly affect vegetation directly, but also modify and strengthen reindeer grazing pressure in the remaining areas (Kumpula et al., 2014). When exclosure experiments in boreal forests, for example, demonstrate an increase in lichens with decreasing grazing intensity, the observed difference between grazed areas and exclosures does not mean that lichen abundances could be explained solely by the grazing pressure from present or past reindeer density on the studied area. The reason is that exclosures do not provide information on how ongoing processes and mechanisms and their interactions work alone or with reindeer grazing and affect vegetation and reindeer behavior at a larger spatial scale. For instance, it creates a fundamental difference if the forest where the exclosure is built, is surrounded by a nature conservation area, or by commercial forest subjected to multiple land-use pressures.

4. Effects of reindeer on boreal forests

4.1. Lichens, mosses and dwarf shrubs

The effect of reindeer grazing on lichens is perhaps the best documented component of vegetation studies. In dry boreal forests, reindeer change the lichen vegetation towards two alternative directions (Helle and Aspi, 1983; Väre et al., 1995, 1996; Kumpula et al., 2000; Stark et al., 2000; den Herder et al., 2003; Olofsson et al., 2011; Köster et al., 2013; Akujärvi et al., 2014; Väisänen et al., 2021). Where reindeer lichen species *Cladonia stellaris*, *C. rangiferina* and *C. mitis* dominate areas that have been ungrazed for a long time, grazing usually shifts species composition cup lichens (e.g., *C. uncialis*, *C. coccifera*) and tin lichens (*Stereocaulon* sp.), or increases amount of mosses at the expense of lichens. Grazing in semi-dry forests may also decrease the moss layer thickness (Väisänen et al., 2021).

Interestingly, the effect of reindeer grazing on ungrazed lichens resembles an opposite vegetation succession after forest fires, where early stages are composed of cup lichens, the middle stages of *C. rangiferina* and *C. mitis* sp., and – in undisturbed conditions - late stages of *C. stellaris* (Ahti, 1977; Kumpula et al., 2000). However, in very old-growth forests that are not grazed by reindeer, the lichen layer becomes increasingly mixed with evergreen dwarf shrubs (Haapasaari, 1988; Miina et al., 2020) or mosses (Coxson and Marsh, 2001). Historically, in northern Sweden, herders may even have used fire to promote the proportion of lichen heaths in the landscape (Hörnberg et al., 1999). In contrast to lichens, the effects of reindeer grazing on dwarf shrubs seem to be rather weak (Stark et al., 2000; Väisänen et al., 2021), but they may sometimes decrease due to grazing (Kumpula, 2001).

Because ground lichens are very sensitive to trampling, seasonal pasture rotation is an effective tool to promote higher lichen abundances (e.g., Kumpula et al., 2011). In Sweden, historically formed seasonal pasture rotation also appears to be important for keeping lichen pasture areas in good condition, as the cover and biomass of lichens is lower in areas where reindeer stay in the forests year-round compared to those areas where reindeer migrate to the mountains during the summer months (Horstkotte and Moen, 2019; Uboni et al., 2019). A system of rotation (annual shift of winter grazing areas) existed traditionally in South Sápmi in order to have always fresh and good lichen pastures (Drake, 1918; Vorren, 1998) also found other places in Sápmi (Vorren, 1980).

Relatively few publications exist on the effects of reindeer on mesic forests. Old-growth mesic forests are not preferred cratering grounds for reindeer, as they prefer lichen-rich forests during winter, and wetlands

during summer (Kitti et al., 2009). However, these forests have importance if their preferred habitats are not available. Mesic old-growth forests, often dominated by spruce, also contain epiphytic lichens which are important winter forage for reindeer, in particular when deep or hard snow hinders reindeer in digging for ground lichens (Jaakkola et al., 2006). A recent study in mesic, herb-rich forests in Finland showed that higher reindeer densities were associated with increased species diversity, because they reduced the abundance of tall forbs (Happonen et al., 2021), demonstrating that reindeer modify the ground vegetation of also in more nutrient-rich forests.

4.2. Tree growth and regeneration

The question how reindeer husbandry might influence boreal forest growth and regeneration has attracted public interest even as early as the late 1800's (Turunen et al., 2020). Nonetheless, few international publications exist on the topic. Some studies reported a 20 % faster growth of Scots pine in grazed over ungrazed areas in Finland (Helle and Moilanen, 1993; Macias Fauria et al., 2008). Evidence regarding forest regeneration is mixed: reindeer can cause indirect frost damage to seedlings or increase the likelihood of fungal infections when digging for lichens through the snow (Helle and Moilanen, 1993; Roturier and Bergsten, 2006; Akujärvi et al., 2014), but by opening gaps in the lichen layer, grazing may also promote tree seedling establishment (Macias Fauria et al., 2008). In young forests, reindeer browsing may decrease deciduous seedlings, such as birch (*Betula pubescens*) and – similar to what has been found for moose browsing (Pastor and Naiman, 1992) – could promote conifers over deciduous trees, but this requires experimental verification.

4.3. Interactions between reindeer and forestry

Decadal trends in lichen biomass in a nature conservation area vs. commercial forests in Finland (Jaakkola et al., 2013); and south and within the reindeer herding area in Sweden (Sandström et al., 2016) and Finland (Tonteri et al., 2022) reveal a strong interactive effect of forestry activities and reindeer husbandry. Forestry causes fragmentation and reduction in old-growth forests rich in ground and arboreal lichens (Kumpula et al., 2014; Sandström et al., 2016; Tonteri et al., 2022). Arboreal lichens disappear immediately in forest clear-cutting, where all trees are removed in a single harvest, and due to their low dispersal rates, require a long time to colonize young forests and re-establish in sufficient abundance (Dettki and Esseen, 2003; Horstkotte et al., 2011). The current rotation times of 90–120 years between harvests does not permit good arboreal lichen recovery (Esseen et al., 2022).

While clear-cutting creates open areas with high light availability that promote the growth of ground lichens, mechanical site preparation to enhance seedling growth damages tstry change the use of different habitats by reindeer ahem (Kivinen et al., 2010). The structure of the regenerating forest also affects the ground lichens. As increased tree density limits light availability at the forest floor, the ground lichens become outcompeted by mosses or vascular plants (Jonsson Čabrajčić et al., 2010; Sandström et al., 2016; Horstkotte and Moen, 2019). The direct effects of forend increase grazing pressures on the remaining pastures even if reindeer numbers remain unchanged (Kumpula et al., 2014; Sandström et al., 2016).

5. Effects of reindeer on subarctic ecosystems

5.1. Mountain birch forest structure and the location of tree-line

In the Finnish subarctic, reindeer reside in the interior also during the summer season due to historical reasons. Therefore, they exert a strong effect on the mountain birch forest structure, and make birch forests more open with a lower tree density (Biuw et al., 2014) and biomass (Oksanen et al., 1995; Lempa et al., 2005; Kumpula et al., 2011;

Stark et al., 2021). Browsed birches typically have fewer and thicker trunks when compared with a more multi-stemmed structure with thinner trunks in the absence of browsing (Kumpula et al., 2011; Stark et al., 2021). In addition to mountain birches, also other tall shrubs/-deciduous trees in the subarctic zone are affected. Willows are particularly strongly affected by browsing, because they constitute a palatable and favored food resource for reindeer during summer (den Herder et al., 2008; Pajunen et al., 2008; Kitti et al., 2009; Ravolainen et al., 2011; Kolari et al., 2019).

Habitats close to the forest distribution limit are usually sensitive to shifts between forested and treeless states (Scheffer et al., 2012). Reindeer seem to influence the location of the tree line, i.e., the border between mountain birch forest and open tundra (e.g., Oksanen et al., 1995; Moen et al., 2008), but this interaction is ambiguous. Reindeer grazing may increase germination of tree seeds, both conifers and mountain birch, as well as emergence and growth of seedlings by breaking the soil surface and removing the “lichen barrier” leading to a formation of tree clusters (Tømmervik et al., 2004, 2009; Aakala et al., 2014). On the other hand, reindeer also contribute to maintaining the current tundra landscape by keeping tall shrubs in a “browsing trap” by preventing tree seedlings from growing above browsing height or encroaching on open tundra (Bråthen et al., 2017; Olofsson and Post, 2018). Mass outbreaks of autumnal moths (*Epirrita autumnalis*) and winter moths (*Operophtera brumata*) are of major importance, as in reindeer summer ranges, defoliated mountain birch forests can gradually change into “secondary mountain heaths”, because reindeer grazing prevents the establishment of new trees (Chapin et al., 2004; Biuw et al., 2014).

5.2. Vegetation in mountain birch forests and tundra heaths

The effects of reindeer on vegetation in arctic-alpine tundra heaths show high spatial variability among regions and habitat types (e.g. den Herder et al., 2003; Lempa et al., 2005; Eskelinen and Oksanen, 2006; Kumpula et al., 2011; Francini et al., 2014; Stark et al., 2021 for Finland, e.g. Olofsson et al., 2004; Grellmann, 2002; Bråthen et al., 2007, 2017, Odland et al., 2018, Yläne et al., 2018 for Norway, e.g. Vowles et al., 2017, for Sweden; Bernes et al., 2015; Sundqvist et al., 2019 for all countries). To detect general patterns at a larger landscape-level, Sundqvist et al. (2019) analyzed most existing reindeer exclosures across the Fennoscandian subarctic and concluded that reindeer generally maintain vegetation in a low-biomass state with decreased lichen

and deciduous tall shrub abundances (Fig. 3). Yet, the direction and amplitude of the responses of other plant groups depended on habitat. For example, in mountain birch forests, reindeer increased deciduous dwarf shrubs in semi-dry habitats but decreased them in mesic habitats. Evergreen dwarf shrub abundances decreased in response to grazing in mountain birch forests, whereas there was no effect in tundra heaths. Changes in the vegetation may yield higher or lower plant diversity depending on the habitat (Sundqvist et al., 2019). In fertile tundra heaths, moderate grazing increases species diversity by promoting graminoid and forb seed germination and seedling emergence (Eskelinen and Virtanen, 2005; Eskelinen and Oksanen, 2006) and by favoring small and light-demanding species over tall ones (Eskelinen et al., 2016; Kaarlejärvi et al., 2017). In dry habitats the effect may however be the opposite (Kontula and Raunio, 2019; Sundqvist et al., 2019).

It raises an interesting question as to which extent the historically formed reindeer herding regimes influence the vegetation responses to reindeer exclusion, and by this way, the high spatial variation in the findings. Tømmervik et al. (2012) found that ground lichens in mountain birch sites in Norway recovered very rapidly after reindeer population reduction, facilitated by increased precipitation. They hypothesized that lichen recovery is faster in areas with a history of only winter grazing compared with areas that have a history of summer or year-around grazing. These findings agree with observations from boreal forests - that lichen growth is at highest during a certain phase of the lichen vegetation, showing a bell-shaped function with its biomass (Kumpula et al., 2000). In both the Norwegian and Finnish subarctic, dwarf shrub cover seems to increase in parallel with lichens (Tømmervik et al., 2012; Stark et al., 2021).

6. How do reindeer modify soil and ecosystem carbon and nutrient cycles?

Herbivores around the world affect soil carbon and nutrient cycles through a variety of mechanisms (Fig. 4), and through these effects, have an indirect feedback on plant production and soil carbon sequestration (Andriuzzi and Hall, 2017; Schmitz et al., 2014). Soil feedbacks on vegetation through herbivory are of particular importance in northern ecosystems, because soils store a major proportion of the total ecosystem carbon stock, and plant species composition and productivity are strongly limited by nutrient availability.

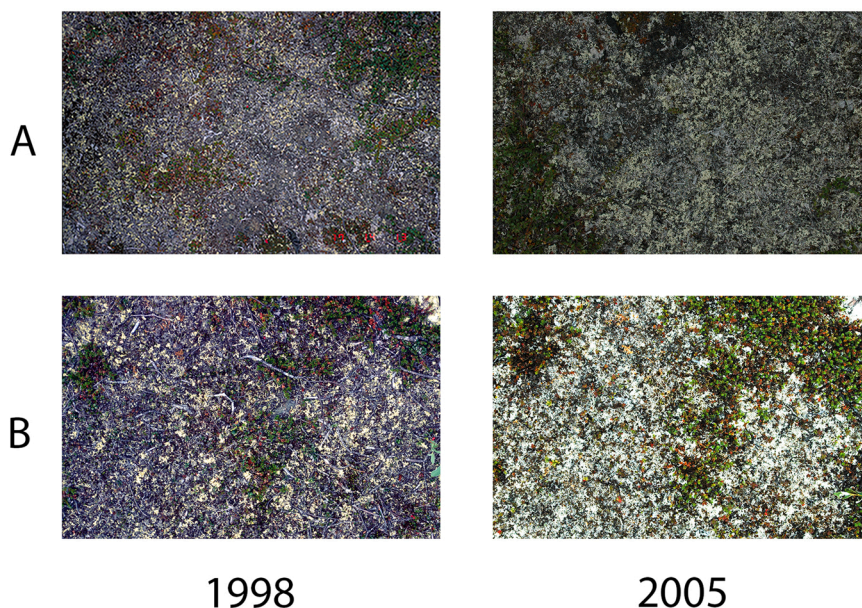
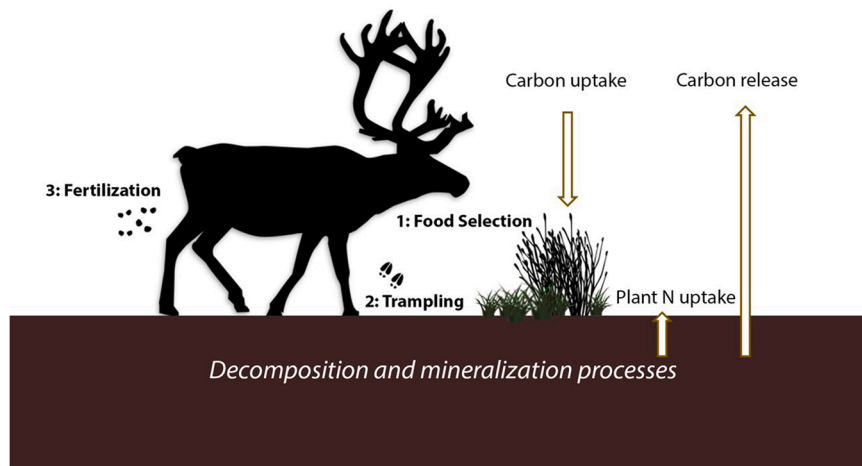


Fig. 3. a. Ridge dominated by *Betula nana* and *Loiseleuria procumbens* with lichens, and b. *Empetrum nigrum* and lichen tundra heath in inland Finnmark, northern Norway. Same plots were photographed in 1998 and 2005. In 1998, the lichen layer composed mainly of *Flavocetraria nivalis* fragments, whereas in 2005, a mixture of *Flavocetraria nivalis* and *Cladonia arbuscula* dominated. Increase in lichen cover was mainly due to reduced reindeer density between 1998 and 2005. The Author of the photographs: Hans Tømmervik.



6.1. Effects of reindeer on soil nutrient status and carbon storage

Reindeer seem to have a relatively minor effect on nitrogen availability in boreal forests (Stark et al., 2003, 2010; Köster et al., 2015; Santalahti et al., 2018; Väisänen et al., 2021) although soil nitrogen concentrations may increase at the vicinity of the reindeer feeding sites (Turunen et al., 2013). Studies in subarctic ecosystems have shown substantial but highly variable effects, others have shown higher levels (Olofsson et al., 2004; Stark et al., 2007; Stark and Väisänen, 2014), lower levels (Stark and Grellmann, 2002), or no difference (Virtanen et al., 2008; Francini et al., 2014) between grazed and ungrazed areas. Reindeer may increase soil nitrogen availability via fertilization through urine and faeces (Stark and Väisänen, 2014; Barthelemy et al., 2015). It has therefore been suggested that nutrient transport from foraging areas to areas where waste products are deposited could largely influence whether reindeer increase or decrease soil nutrient availability in each site (Stark and Grellmann, 2002; Stark et al., 2015b). However, at the landscape level, reindeer seem to induce higher soil nitrogen levels, which has an ecosystem-level importance, because it may sustain higher plant productivity and thus counterbalance the effects of plant consumption and trampling (Olofsson et al., 2004; Sundqvist et al., 2019). Interestingly, the impact of high reindeer densities on soil nutrient status can still be visible even after a century without grazing, because a transition of the dominant shrub-dominated vegetation into a community dominated by more rapidly decomposable species leads to a self-reinforcing feedback loop, which creates a sustained historical legacy on vegetation and soil processes (Josefsson et al., 2009; Tømmervik et al., 2010; Egelkraut et al., 2018; Stark et al., 2019).

The loss of vegetation cover due to herbivory may expose the soil organic layer to erosion through wind, running water or landslides, which in arctic regions is found in connection with, e.g., cattle husbandry (Normand et al., 2017). Erosion could be detected as lower nutrient contents or as a thinner or absent organic soil layer. However, studies have generally not found differences in the amount of carbon stored in the organic soil layer (e.g. Stark et al., 2000; Köster et al., 2013, 2015; Väisänen et al., 2021; Yläne et al., 2018, 2021). The organic soil layer is often drier and thinner under grazing, but also more compact (Tuomi et al., 2021). Lichens store only a small fraction of the ecosystem carbon. As carbon storage is dominated by trees, mosses and understorey dwarf shrubs (Stark et al., 2000; Köster et al., 2015), lichen removal does not affect the ecosystem net carbon sink (Susiluoto et al., 2008). In turn, observations from mesic habitats indicate that even substantial shifts in the vegetation may result in equivalent soil carbon stocks. For example, a vegetation shift from dwarf shrubs and mosses to graminoids increases root litter production, leading to a similar (Yläne et al., 2020) or a higher soil carbon stock (Yläne et al., 2018). Erosion

Fig. 4. By structuring the plant community composition through three major mechanisms, (1) food selection (i.e., favoring some plant species over others), (2) trampling and (3) fertilization, grazers modify both the quantity and quality of plant litter that forms the soil organic matter. Through this mechanism, grazers exhibit a major impact on microbially mediated decomposition and mineralization processes in the soil, which in turn feedbacks to plant nutrient availability and uptake as well as carbon release. The eventual effect of grazing on the ecosystem carbon storage is determined by the balance between carbon uptake and release. Due to the complexity of mechanisms by which herbivores influence soil processes, the direction of the effect on both nitrogen availability and carbon storage vary substantially among ecosystems.

due to a high trampling intensity has been detected along reindeer fences, but is often local (Moen and Danell, 2003). In northernmost Fennoscandia, deflation landforms formed by wind erosion started to appear on sandy moraines thousands of years ago and are thus geologically much older than reindeer domestication, but it has been suggested that reindeer may increase susceptibility to wind erosion in these areas (Holtmeier and Broll, 2006).

6.2. Effects of reindeer on soil community composition and function

Reindeer induce several types of effects on the soil communities, many of which are mediated by the changes in the quantity and the quality of the plant biomass that eventually is deposited onto the ground as plant litter. In boreal forests, microbial activity of carbon dioxide release (i.e., microbial respiration) is generally lower in grazed than ungrazed areas both in dry and mesic habitats (Väre et al., 1996; Stark et al., 2003). This could explain the 'neutral' effect of grazing on soil carbon stocks, as increased CO₂ release may result from the plant biomass that was protected from grazing undergoing microbial decomposition. Studies on litter decomposition in dry forests have shown either lower rates under grazing (Stark et al., 2010) or no effects (Santalahti et al., 2018). Some fungal taxa change in abundances in response to grazing, but the dominant taxa remain the same (Santalahti et al., 2018).

In subarctic ecosystems, leaf litter seems to decompose more rapidly in areas with summer grazing compared to areas with winter grazing in both mountain birch forests (Stark et al., 2007) and arctic-alpine tundra heaths (Olofsson and Oksanen, 2002; Olofsson et al., 2004). Interestingly, the more rapid rates of litter decomposition in both habitats seem to derive from both a higher litter quality and improved conditions for decomposition in terms of soil nutrient availability and microclimate. At the Finnish-Norwegian border, mountain birch forest sites grazed throughout the year showed higher fungal abundance but lower fungal diversity compared to areas with only winter grazing (Yläne et al., 2021). In a subarctic tundra heath, however, fungal communities were more diverse under heavy than light grazing, and also responded more rapidly to increasing nutrients (Ahonen et al., 2021). The density and community composition of nematodes, a major component of soil microfauna, seem surprisingly tolerant to reindeer grazing and trampling in both mountain birch forests and tundra (Stark et al., 2008; Francini et al., 2014; Sørensen et al., 2009).

7. The future of Fennoscandian northern ecosystems – and reindeer in it

7.1. Interactions between climate change and reindeer

Climate warming is shifting northern boreal forests and subarctic areas into a new state with increasing abundances of tall and dwarf shrubs and declining lichen abundances (Elmendorf et al., 2012). Reindeer interact with the ecosystem response to climate warming in complex and multiple ways. Reindeer seem to dampen or slow down climate-induced increases in deciduous shrub encroachment (Horstkotte et al., 2017; Maliniemi et al., 2018; Olofsson et al., 2009; Vowles et al., 2017; Vuorinen et al., 2017), while having less influence on evergreen shrubs (Bråthen et al., 2017; Vowles et al., 2017; Stark et al., 2021). Contrastingly, reindeer grazing may reinforce the climate-driven decline in lichens (Tømmervik et al., 2004; Odland et al., 2018).

In the long-term, a biome shift from treeless to forested areas will likely take place, but whether reindeer promote or counteract a warming-induced advance in the tree line may vary between tree species and areas (Callaghan et al., 2013). Reindeer can have a surprisingly strong impact also on less palatable evergreen seedlings in the timberline (Bognounou et al., 2018). Yet, the individual roles of climate and reindeer is difficult to separate from ecosystem trends. For example, historical time series from northern Norway indicated that current increase in the biomass and distribution of mountain birch in northern Norway may be more strongly related to discontinued forms of land-use, such as wood cutting for fuel, than to summer warming (Horstkotte et al., 2017; Tømmervik et al., 2019). Interestingly, release from browsing pressure due to declining caribou populations, rather than climate warming seem to drive increases in dwarf birch growth in interior Canada (Andruko et al., 2020). Where it occurs, the dampening of 'shrubification' or delaying the advance of the treeline has several consequences that may be considered beneficial. By controlling the growth of tall species through grazing, reindeer may mitigate a warming-induced reduction in plant diversity (Kaarlejärvi et al., 2015, 2017; Happonen et al., 2021), increase albedo and therefore have a cooling effect on climate (Cohen et al., 2013; te Beest et al., 2016).

7.2. Sustainable use of reindeer ranges under changing conditions

Although the present reindeer grazing pressure slows down many undesired effects of climate change, such as the shrubification of open tundra (Virtanen et al., 2010; Bråthen et al., 2017) and declining diversity (Kaarlejärvi et al., 2017), areas where ground lichens have been depleted due to reindeer grazing or combined pressures of reindeer grazing, forestry and other forms of land use would likely benefit from reduced reindeer numbers or changed grazing patterns. In the present herding systems with supplementary feeding and treating reindeer against parasites, reindeer populations can be kept relatively stable, which does not allow lichen recovery in the same way as earlier in the history. Earlier stronger population fluctuations due to harsh winter conditions, predation, disease and parasitic outbreaks were common and caused alternating of high and low grazing pressures (Riseth et al., 2016, 2020). Such fluctuations cannot, however, be implemented both for the reasons of animal welfare and stable income requirements.

Reducing the reindeer numbers to enable lichen recovery would likely be echoed in mesic habitats where tall shrubs and forbs would increase, with negative consequences on diversity as well as the quality of summer pastures for the reindeer. For example, a reduction in reindeer density in mid-Norway from 10 reindeer/km² to 2–3 reindeer/km² led to an increase of lichen abundance in dry areas, but at the same time also to increased shrubification, which reduced the proportion of good herb- and graminoid-rich summer pastures (Tømmervik et al., 2010). Thresholds that would prevent willows, dwarf birch and mountain birch from invading tundra areas have been estimated to range between 3 and 4 reindeer per km² (den Herder et al., 2004; Tømmervik et al., 2010).

Importantly, there is a considerable difference in the timeframe over which plants respond to changes in grazing intensity or herding regimes in different habitats. On fertile habitats, vegetation appears to recover rapidly even after very intensive grazing (Ravolainen et al., 2011), indicating that reduced reindeer numbers could quickly result in a reduction in the diversity and quality of summer ranges. By contrast, lichen recovery in exposed winter pastures like ridges and heaths might be slow. In Finnmark, northern Norway, for example a reduced winter grazing density (from 19 to 10 reindeer per km²) in concert with higher precipitation during summer led to a rapid lichen recovery between 1998 and 2005 (Tømmervik et al., 2009, 2012). Models concerning Finnish commercial boreal forests suggest that even after a very substantial reduction in reindeer numbers implemented together with increased protection of old-growth forests, lichen recovery would require several decades (Pekkarinen et al., 2015).

From the perspective of science, commonly used concepts such as 'ecological state' or 'overgrazing' are problematic, and depend on how their concepts and meanings are understood and valued (Mysterud, 2006; Landauer et al., 2021). When the impacts of reindeer husbandry and the ecological state of reindeer ranges are assessed, one has to ask which stages or changes in ecosystems are seen as positive, negative or neutral, and from whose perspective. For example, the formation of a secondary tundra heath by combined summer grazing and moth outbreaks may either be interpreted as overgrazing, or as preserving open tundra habitats (Oksanen et al., 1995; Horstkotte et al., 2017), which are better winter pastures with improved visibility and higher availability of winter forage due to a thinner wintertime snow cover. Similarly, while moderate grazing by reindeer and sheep is considered a key process for maintaining biodiversity in the Scandinavian mountains ((Austrheim and Eriksson, 2001) Austrheim and Eriksson, 2001; Olofsson and Oksanen, 2005), climate change and constant high grazing pressure may threaten dry Finnish fell habitat types (Kontula and Raunio, 2019). Practices such as pasture rotation should be promoted, together with diminishing the detrimental impact by other land-uses that contribute to lichen decline (Kumpula et al., 2014; Sandström et al., 2016; Horstkotte and Moen, 2019). Pasture rotation would mean both extending pasture rotation between 'strict' summer- and winter ranges to prevent damages to lichens by trampling during summer, and establishing rotation between grazing sites during winter. Collaboration with reindeer herders should be promoted in regional land-use planning, in particular regarding the effects on reindeer forage availability (Forbes et al., 2020; Sandström et al., 2012; Turunen et al., 2020; Tyler et al., 2007; Miina et al., 2021). Increased rotation times, harder thinning in young forests to promote ground lichens (Horstkotte et al., 2016) and implementation of alternative forest management, such as continuous cover forestry (Boudreault et al., 2013; Rikkonen et al., 2023) could reduce the impact of forest management on both arboreal and ground lichens and increase landscape connectivity for lichen dispersal and reindeer movements (St John et al., 2016).

8. Conclusions: how to integrate ecology with history in understanding the effects of ungulates on present-day ecosystems

Wild and/or domesticated herbivores modify almost every terrestrial ecosystem, including both aboveground and below ground components, and northern Fennoscandian ecosystems are no exception. Reindeer husbandry in Fennoscandia has a long history and the gradual replacement of wild reindeer by semi-domesticated reindeer has modified the environment over centuries. Exclosure experiments and pasture rotation fences give an overview of trends and patterns in vegetation dynamics induced and developed by excluding reindeer grazing. However, they fail to capture all the interacting processes and mechanisms acting in real pasture ecosystems. The study site, and its experimental set-up to study the effect of grazing, needs to be located into a larger context that takes into consideration both the historical developments and the

modern-day infrastructures (Stoessel et al., 2022). In scientific publications addressing the effects of herbivores adding a specific section to the methods describing what is known on historical land-uses and mechanisms driving the habitat use would contribute to this goal. In the case of reindeer, the differences in socio-political history over time shaped when and where reindeer graze and move in particular locations and seasons. Present-day ecosystem structures and functioning must be looked at in the light of historical events and current drivers of reindeer herding and grazing systems.

It has been suggested that northern boreal forests, subarctic mountain birch forests and tundra habitats should be seen as cultural landscapes despite the fact that they are not structured by humans to the same extent as agrarian landscapes (Josefsson et al., 2009; Staland et al., 2010; Egelkraut et al., 2018). Wild reindeer have existed in northern Fennoscandia since the last Ice Age, and since then they were hunted and later domesticated by humans. For this reason, Fennoscandia has never experienced a state without any human impact at all. We argue that the concepts of natural and cultural landscapes may not be mutually exclusive in the case landscapes shaped by reindeer husbandry. However, reindeer grazing is just one factor behind vegetation trajectories, as these often are induced in combination with other land-uses and climate change. Questions still remain as to what Fennoscandian ecosystems will look like in the long-term, when climate warming advances tree-lines, to which extent large-scale vegetation trajectories in different habitat types under climate warming depend on the long-term land-use history, and how future changes in reindeer numbers and herding methods might alter these trajectories.

Declaration of Competing Interest

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

Data Availability

No data was used for the research described in the article.

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