CHARTER

SYNTHESIS ON THE EFFECT OF GRAZING AND TRAMPLING ON PLANT BIODIVERSITY

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CHARTER Synthesis on the effect of grazing and trampling on plant biodiversity. A case study of northernmost Fennoscandia.

Final Version

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1 Introduction

The objective of this literature synthesis is to summarize existing evidence on how reindeer (*Rangifer tarandus*) shape vegetation, soil carbon and nutrient cycles in the boreal and subarctic ecosystems. We use an approach where we link the role of the reindeer in ecosystems with the historical developments of reindeer herding practices. Despite often regarded as natural rather than cultural landscapes, the structure of Arctic ecosystems is closely connected with cultural activities that have shaped the intensity and the spatial distribution of herbivores. In particular, those relating to semi-domestic reindeer herding involve a vast region in the Eurasian Arctic. Grazing intensity and the spatial distribution of semi-domestic reindeer at different time-scales derive from particular historical events, such as land-border agreements, and other socio-political processes that modify the patterns of resource use. Land-use patterns deriving from complex socio-environmental circumstances, built infrastructures (e.g., roads, powerlines), predator abundances and social settings have an important role. General knowledge among stakeholders, scientists and general public on how the ecological effect of the reindeer relates with these historical and socio-political processes is currently not very strong. We present an analysis on how reindeer affect vegetation at different habitats, and how these impacts in turn govern the soil carbon and nutrient cycles, eventually soil carbon storage, and quality of the reindeer ranges for the livelihood. By doing this, we provide tools for predicting what types of ecosystems we may expect to see in the future, and how any potential changes in reindeer herding practices and numbers could alter the ecosystem trajectories.

Reindeer (*Rangifer tarandus* L.) are resident in northern Europe, Asia and North America across boreal, sub-Arctic and Arctic vegetation zones (Uboni et al. 2016). In vast areas of northern Eurasia, the semi-domesticated nature of this ungulate makes it a distinct case among the world's herbivores. Reindeer husbandry relies on freely ranging semi-domesticated reindeer on natural pastures, to which they have access to irrespective of land ownership. The natural behavior and forage selection of reindeer during the different seasons drive spatial and temporal grazing patterns across the landscapes, thus resembling their wild ancestors (Vorren 1980). Another feature that resembles wild rather than domesticated grazers is that the reindeer are exposed to predation, mainly by lynx (*Lynx lynx*), wolverines (*Gulo gulo*), bears (*Ursus arctos*), golden eagle (*Aquila chrysaetos*) and wolves (*Canis lupus*) (Rasmus et al. 2020). Yet, to a very large extent, the influence of reindeer on vegetation and soils depends on not only the ecological interactions between the reindeer and its natural surroundings, but on human management that was shaped by the socio-political history and essentially determines today's reindeer movements in space and time (e.g. Lundmark 2006). Reindeer numbers are jointly driven by human and state control (Uboni et al. 2016), abiotic environmental factors (e.g. extreme winter weather events; Helle and Kojola 2006, Uboni et al. 2016), and biotic interactions (e.g. interactions

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of reindeer herds with pasture quality, diseases and predation; Åhman et al. 2014, Rasmus et al. 2020, Riseth et al. 2020).

A substantial pool of scientific evidence of the role of reindeer in shaping ecosystem structure and function has accumulated regarding northern Fennoscandia (see Suominen and Olofsson 2000, Bernes et al. 2015 for earlier reviews). However, literature on other parts of the Arctic is very scarce. Few studies have been conducted where the effects of herbivores would have been experimentally studied. For this particular reason, one important target of CHARTER was to identify and fill in geographical gaps on data regarding herbivore effects by analyzing vegetation in some recently established reindeer exclosures and building up new experimental setups in the Russian Arctic. In this literature review, we decide to focus on northernmost Fennoscandia, because it presents the only area where the effects of reindeer have been experimentally studied over a wide range of habitats and reindeer herding management systems. Through revealing the complex interactions between the reindeer and the ecosystem functioning under currently ongoing global warming, the case study of northernmost Fennoscandia helps understanding the variability of reindeer impacts over different habitats and management regimes – a framework applicable also for other areas.

Within the discipline of ecology, reindeer grazing in northernmost Fennoscandia has been discussed in the context of ecological theories, such as whether habitat fertility dictates the direction of the effect of herbivory on soil nutrient cycling (e.g. Stark et al. 2002, 2015a, Sitters et al. 2017) and the concept of alternative ecosystem states (van der Wal 2006, Egelkraut et al. 2018, Stark et al. 2019). 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 Björklund 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. A very important part of our literature review is therefore that we bridge the ecosystem effects of reindeer, with the historical contexts that have shaped them. By this way, we provide a deeper understanding of the fundamental role of herbivory in ecosystems as well as on predictions regarding ecosystem trajectories under a warming climate.

2 Vegetation and history in the Fennoscandian reindeer herding area

2.1 Vegetation and habitat use of the reindeer during different seasons

The distribution of reindeer extends across several vegetation zones in all Fennoscandian countries (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*) (Fig. 2). Dwarf shrubs such as *Vaccinium* sp., *Betula nana* and *Empetrun nigrum* ssp. *hermaphroditum* together with mosses, ground lichens, forbs and graminoids form the dominant ground vegetation with dwarf shrubs species such as *Loiseleuria procumbens* and *Phyllodoce caerulea* appearing further north. Arctic-alpine tundra heaths dominate the landscapes above the mountain birch tree line, and the location of the tundra-forest ecotone depends on both climatic and edaphic conditions, and land-use history (Oksanen and Virtanen 1995, Östlund et al. 2015, Kuuluvainen et al. 2017).

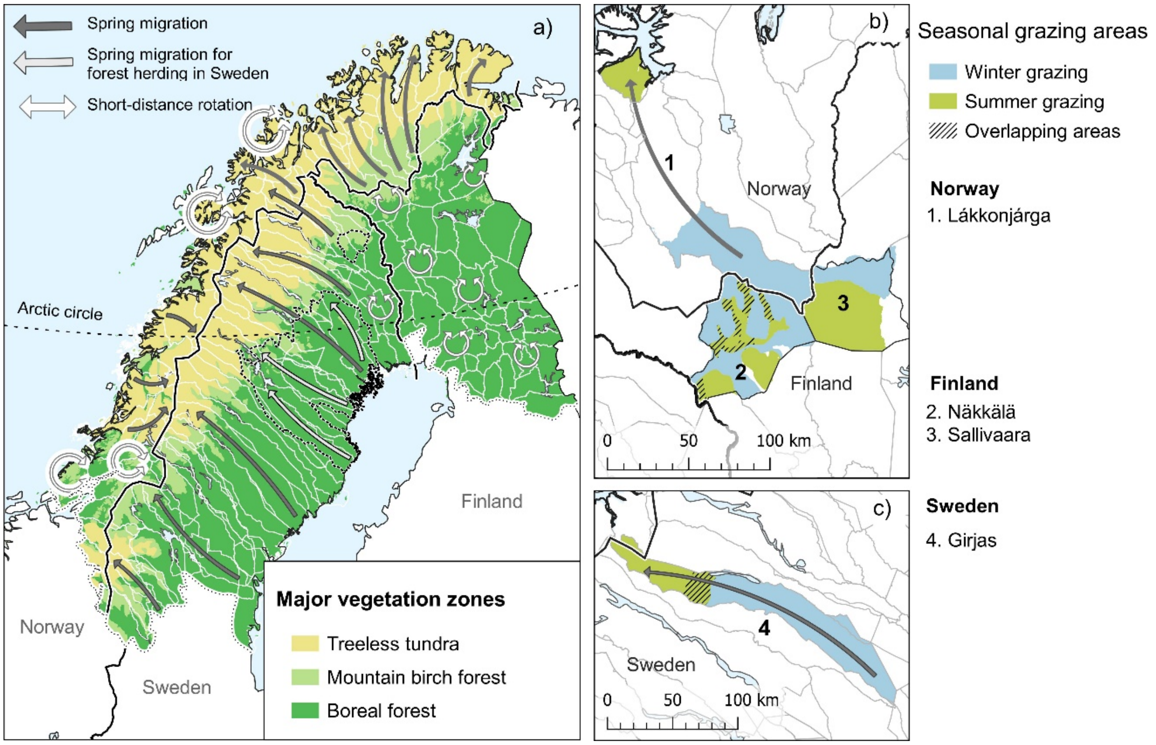

Figure 1a. Climatic vegetation zones and reindeer management regimes in northern Fennoscandia. Due to the combined effects of climatic and environmental conditions and historical developments, reindeer management regimes differ between countries. Seasonal range rotations are within shorter distances in Finland compared to many districts in Norway and Sweden. **Figure 1b.** 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. **Figure 1c.** 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.

Seasonal movements between different habitats and landscapes is a key behavioral feature of reindeer across all climatic vegetation zones (Fig. 2). Reindeer consume over 200 different plant species, but the most common forage plants vary by season (Warenberg et al. 1997). Reindeer have a special ability to digest lichens, a symbiosis between algal and fungal partners, which form an important part of the winter diet. Ground lichens are by no

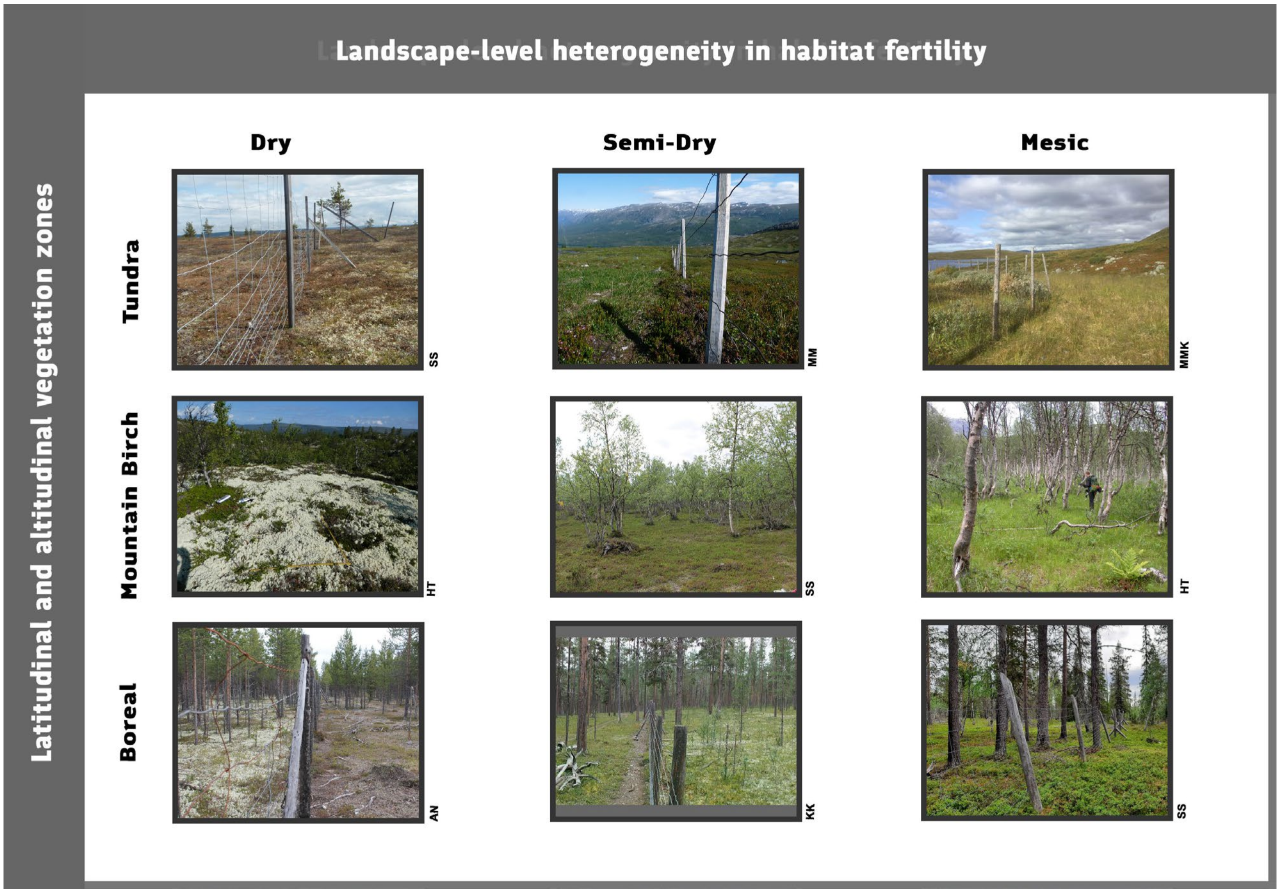

Figure 2. Dry, semidry and mesic sites in boreal forests, mountain birch forests, treeless arctic-alpine tundra heaths. While vegetation in dry habitats is dominated by lichens, more mesic habitats become increasingly dominated by dwarf and tall shrubs, herbs and graminoids across all vegetation zones. Reindeer change habitat types in different seasons due to different nutritional needs and the associated changes on the availability of different food plants in different seasons. Insect avoidance also contributes to habitat selection. Authors of the photographs: AN = Aarno Niva, KK = Kajar Köster, MM = Minna Männistö, MK = Minna-Maarit Kytöviita, HT = Hans Tømmervik, SS = Sari Stark.

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means the only food resource for the reindeer even during the winter, as also evergreen dwarf shrubs, grasses, and epiphytic lichens are important components of reindeer diet (Storeheier et al. 2002, 2003, Kojola et al. 1995, Jaakkola et al. 2006). During the snow-free period, reindeer rely on grasses, herbs, leaves and mushrooms to build up body reserves for the winter. In mountain birch forests, birch foliage and tree seedlings are also a favored food resource (Kumpula et al. 2011). Mires are an important habitat during summer, in particular where reindeer do not move above the treeline during summer. Seasonal movements between different habitats and landscapes depending on the availability of forage plants is thus a key behavioral feature of the reindeer.

2.2 The history of reindeer herding

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 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 livelihoods of the indigenous Sámi were primarily based on a mixed subsistence strategy including hunting, fishing and gathering. Some domesticated reindeer were used as draft and pack animals or decoys for hunting, for providing meat and milk for the households, and for transport (Itkonen 1948, Kortesalmi 2008, Björklund 2013, Salmi et al. 2021). Reindeer domestication took place gradually and in a non-synchronous manner in the different regions of northern Fennoscandia, when at the same time, wild reindeer hunting still continued (Lundmark 2006, Pelletier et al. 2021). The gradual transition towards reindeer husbandry was driven by a combination of economic, social, and ecosystem processes (Bergman et al. 2013). After Northern Fennoscandia was claimed by competing nation states (Norway-Denmark, Sweden-Finland and Novgorod/Russia) during mid-1600's, 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). Increasingly these taxes were paid in meat and hides of domesticated reindeer. Domesticated herds increased and led to adoption of long seasonal migrations between summer ranges at the Norwegian coastal areas and forested areas in Sweden-Finland during winter (Vorren 1980).

In the boreal forest regions of today's Sweden and Finland, seasonal migrations were shorter and Sámi reindeer herders have led a more sedentary way of living. Starting from the 1600's, Finnish settlers started migrating to the area and adopted reindeer herding

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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. This reindeer herding system then formed the ground for present-day herding districts in Finland, especially in the middle and southern parts of the present reindeer herding area. 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.

When national borders in northernmost Fennoscandia between the kingdoms Norway-Denmark and Sweden-Finland were settled, the Lapp Codicil (1751) granted Sámi reindeer herders the free crossing of these borders due to the need to access the different seasonal grazing grounds, now situated in two different kingdoms. Border establishment also coincided with the increased economic importance of reindeer husbandry for the household and increased herd sizes. This led to extended migration patterns across the newly drawn borders and longer grazing periods on winter areas in Sweden-Finland compared to earlier seasonal migrations (Aarseth 1989). 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 late 19th century, country border agreements formed barriers to earlier seasonal migration routes. Finland was annexed by Russia from Sweden in 1809, and Russia closed the border to Norway in 1852. The reason was to protect the stationary and small-scale reindeer husbandry practices in Finland from the large migratory herds that entered from Northern Norway and spent the winter in Finland and caused damage to local farms, reduced grazing resources and swallowed the local herds (Cramér and Ryd 2012). For migratory reindeer herders, the border closure entailed a loss either of summer grazing areas at the Norwegian coast or of winter grazing areas in Finland and thus strongly reduced the length of seasonal migrations. Migration between Norway and Finland via northern Sweden was still possible until a second border closure between Russia-Finland and Sweden in 1889.

Border closures between the countries induced new practices of how the seasonal ranges of the reindeer were arranged and utilized (Fig. 1b, 1c). Norway had issued regulations already in 1853 to prevent summer grazing in Inner Finnmark to protect winter grazing resources, and to assign particular summer grazing areas to the different herding groups in 1888 (Aarseth 1989). The high concentration of reindeer herds at the border areas between northern Norway and northern Sweden, caused by the border closures, lead to a severe shortage of grazing resources (Riseth et al. 2016). These events led to relocations of reindeer herding families from the north to the southern parts of Fennoscandian mountains, further east into Finland or as far as the Kola peninsula (Aarseth 1989).

In 1898, the Finnish Senate ordered reindeer owners to establish geographically defined herding districts, based on the sedentary herding practices in order to arrange and organize the reindeer herding system as c co-operative based organization. As a result, there are no long-ranging seasonal migrations in Finland as in Sweden and Norway (Fig. 1a & b). However, some herding districts in Finland have established seasonal range rotation through fences during the late 1980's (Fig. 1b,c). In Sweden, the Reindeer Husbandry Act of 1886 established herding districts (lappby, today sameby), that partly corresponded to the previous areas used by different herding groups (siida). Migration by reindeer herders from Sweden to their customary summer grazing areas at the Norwegian coast increasingly became restricted in the Reindeer Grazing Conventions (1883, 1919, 1972) between the two nations, both in the time and number of herders from Sweden who were allowed to spend the summer in Norway (Lantto and Mörkenstam 2008). In 1957, a border fence between Norway and Finland was erected, preventing any cross-border activities. The building of the borders fence was not pushed only by the states, but also reindeer herders themselves saw border fences between the states as necessary for supporting, protecting and helping reindeer herders in each country (Lähteenmäki 2006).

Historical events have thus shaped the current grazing regimes, which define when and where the reindeer reside in each particular location and which kinds of seasonal rotation systems of pastures exist at present. The seasonal timing and the intensity of grazing varies within and between countries depending on landscape types, vegetation, history and the different institutions that regulate access to grazing areas. Within these boundaries, the semi-domesticated reindeer can freely graze across the landscape. The present-day ecosystem structure and functioning must therefore be looked at in the light of these historical events and drivers of reindeer herding and grazing systems. The total 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

A common way of analyzing the role of herbivores across ecosystems is to exclude them from the system, after which various parameters on ecosystem structure and function are analyzed with and without herbivory (see e.g. Andriuzzi and Hall 2017). In studies on the

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effects of reindeer on vegetation, this has become a core experimental method. Areas that have excluded reindeer have not always been built 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. 2001, 2004, Stark et al. 2007, 2008, 2021; Kumpula et al. 2011). Because of differing national management regimes, many have also compared the opposing sides of the Finnish-Norwegian border (e.g., Biuw et al. 2014, Ylänne et al. 2021, Meyer et al. 2022, 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 important trampling is as a mechanism by which reindeer impact vegetation (Oksanen 1978, Kumpula et al. 2011). During summer, trampling is a key factor that affects lichens in particular (Heggenes et al. 2017), whereas during winter, a thick snowpack buffers the ground vegetation from trampling.

While 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 (Ylänne 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, Ylänne et al. 2020), plant nutrient uptake strategies (Barthelemy et al. 2016, 2017), or the temperature acclimation of soil microbial functions (Stark et al. 2015b).

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 have been eliminated. However, large herbivores have been grazing northern ecosystems throughout their evolutionary history, and exclosures therefore do not represent a "natural" ecosystem state. Wild grazers 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 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 does not predict vegetation responses in the long run, as very different plant species become dominant inside exclosures in the long-term compared to what could be predicted based on the virshort-term responses (Olofsson 2006, Saccone et al. 2014, 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, 2010, Egelkraut et al. 2018). In an experiment that combined long-term difference in grazing intensity with short-term exclosures demonstrated that a sudden cessation of grazing in a previously heavily grazed site did not return the system to a previous state of light or no grazing, but rather, amplified the changes caused by the decadal difference in grazing intensity (Ylänne et al. 2020). It is possible that instead of bringing the system back to a state prior to grazing, grazer exclusion induces a further directional shift of an ecosystem, a phenomenon found in other alpine ecosystems (Haynes et al. 2014). Another important consideration are current land-use pressures that greatly affect directly vegetation but also modify and strengthen reindeer grazing pressure (Kumpula et al. 2014). 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-uses. Reindeer exclosures thus do not measure the effect of grazing *per se*, but the responses of ecosystem structure and function to a sudden cessation of grazing – and all other disturbances that end with fencing - in a situation, where the previously existing ecosystem was jointly shaped by long-term land-uses and abiotic conditions (Olofsson and Post 2018, Ylänne et al. 2020). A documented difference between the ungrazed and the grazed area always represents a transitional phase where the grazed vegetation changes along with grazing intensity and patterns, and the ungrazed vegetation along a vegetation succession that started when the area was fenced.

4 Effects of grazing on ground vegetation and tree species composition in boreal forests

The high importance of reindeer grazing for the ground vegetation in dry boreal forests is well-documented, because these ecosystems constitute important winter ranges for the reindeer. As a summary, these studies have shown that reindeer change the lichen vegetation towards two alternative directions: a shift from reindeer lichens (*Cladonia stellaris*, *C. rangiferina* and *C. mitis*) towards cup and tin lichens (e.g. *Cladonia uncialis*

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and *Stereocaulon* sp.), or an increase in mosses at the expense of lichens (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, 2015, Akujärvi et al. 2014, Väisänen et al., 2021). Grazing in semi-dry forests may also decrease the moss layer thickness (Väisänen et al. 2021). Interestingly, the effect of reindeer grazing on lichens resembles a characteristic 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, 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 with 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 be affected (Kumpula 2001).

When exclosure experiments in boreal forests 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 number of reindeer. Exclosures do not provide information on ongoing processes affecting vegetation and reindeer behaviour at a larger spatial scale. Forestry activities cause fragmentation and reduction in lichen-rich old-growth forests, changing the use of different habitats by reindeer and increasing grazing pressures on the remaining pastures even if reindeer numbers remain unchanged (Kumpula et al. 2014, Sandström et al. 2016). 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) reveal a strong interactive effect of forestry activities and reindeer husbandry. In Sweden, historically formed seasonal migration routes also appear to be important, 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 are able to migrate to the mountains during the summer months (Horstkotte and Moen 2019, Uboni et al. 2019). However, the size of these forest districts and their spatial flexibility between seasonal areas is still larger compared to many districts in the reindeer herding area in Finland. Pasture rotation to protect lichens during the snow-free period is therefore less a topic of debate in Sweden compared to Finland.

Relatively few publications exist on the effects of reindeer on mesic forests. Old-growth mesic forests are not preferred grazing grounds for reindeer, as they prefer lichen-rich forests during winter, and wetlands during summer (Kitti et al. 2009). However, they have importance if their preferred habitats are not available. Mesic old-growth forests also contain epiphytic lichens which are important winter forage for reindeer (Jaakkola et al. 2006). A recent study in mesic, herb-rich forests in Finland, however, showed that higher reindeer densities were associated with increased species diversity, because they regulated the abundance of tall forbs (Happonen et al. 2021).

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, Pastor et al. 1993) – could promote conifers over deciduous trees, but this requires experimental verification.

5 Effects on vegetation and mountain birches in subarctic ecosystems

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, Eskelinen et al. 2012, Francini et al. 2014, Kaarlejärvi et al. 2018, Stark et al. 2021 for Finland, e.g. Olofsson et al. 2001, 2004, Grellmann 2002, Bråthen et al. 2007, 2017, Odland et al. 2018, Ylänne et al. 2018 for Norway, e.g. Vowles et al. 2017, for Sweden; Bernes et al. 2015, Sundqvist et al. 2019 for all countries). Considering variation along climatic gradients, landscape heterogeneity, and reindeer grazing histories (Fig. 1), this is not surprising. A decrease in lichen biomass and coverage with increasing grazing intensity seems to be the only consistent trend (Bernes et al. 2015), which agrees with the evidence from boreal forests.

To detect general patterns at a larger landscape-level, Sundqvist et al. (2019) analysed 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. 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

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ones (Eskelinen et al. 2016a, Kaarlejärvi et al. 2017). In dry habitats the effect may however be the opposite (Kontuila and Raunio 2019, Sundqvist et al. 2019).

Reindeer also 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). 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). The question of the position of the tree line links strongly with other natural disturbances. In regions which have been exposed to the destruction by mass outbreaks of autumnal moths (*Epirrita autumnalis*) and winter moths (*Operophtera brumata*), summer grazing and browsing may make regeneration of mountain birches difficult and as a result, defoliated mountain birch forest can gradually change into a treeless tundra that are also referred to as secondary mountain heaths (Chapin et al. 2004, Jepsen et al. 2008, Biuw et al. 2014, Meyer et al. 2021).

There is evidence to support that historically formed reindeer herding regimes influence the vegetation responses to grazer exclusion. Tømmervik et al. (2012) found that in Norway ground lichens in mountain birch sites 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 under lower grazing intensities (Tømmervik et al. 2012, Stark et al. 2021).

Because – due to historical reasons – reindeer in the Finnish subarctic reside in the interior also during the summer season, they exert a strong effect on the mountain birch forest structure. Browsing modifies the morphology of the birch individuals, as 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). Browsing makes the birch forests more open with lower tree density (Jepsen et al. 2008, Biuw et al 2014), biomass (Oksanen et al. 1995, Helle 2002, Den Herder and Niemelä 2003, Lempa et al. 2005, Kumpula et al. 2011, Stark et al. 2021), and concentration of phenolic secondary compounds (Stark et al. 2007). Browsing decreases the height and the abundance of tall shrubs, such as willows, as they are highly palatable and a preferred summer food resource (Herder et al. 2004, 2008, Pajunen et al. 2008, Kitti et al. 2009, Ravolainen et al. 2011, Kolari et al. 2019).

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

Ungulates across the world have an effect on carbon and nutrient cycles through a variety of mechanisms that constitute important drivers of ecosystem function such as plant production (Wardle et al. 2004, Andriuzzi and Wall 2017) and soil carbon storage (Schmidt et al. 2018). It is thus not surprising that also reindeer influence soils and their diverse belowground faunal and microbial communities (Fig. 3). 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.

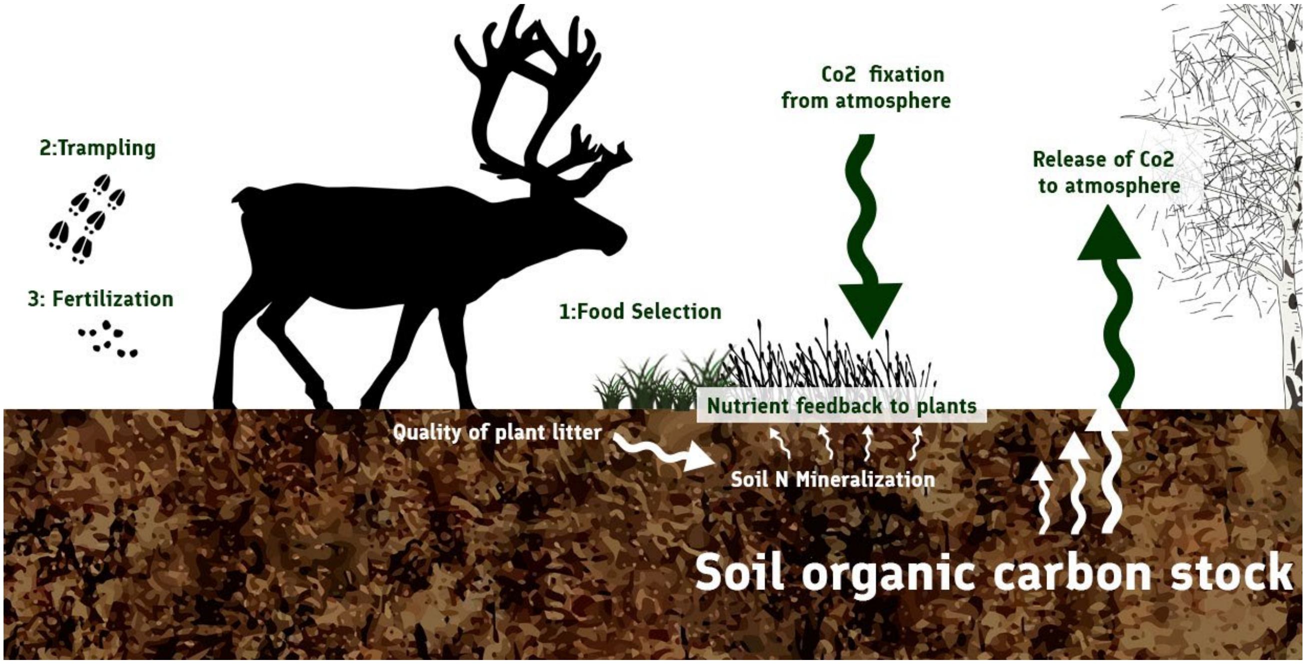

Figure 3. By structuring plant community composition through food selection, trampling and fertilization, large grazers alter both the quantity and quality of plant litter that eventually forms the long-term soil organic carbon stock. Through this mechanism, grazers exhibit a major impact on soil nitrogen mineralization and release of carbon dioxide to atmosphere. Due to the complexity of mechanisms by which herbivores influence soil processes, the effect of herbivory on decomposition and nutrient cycling varies substantially among ecosystems.

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

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highly variable effects, others have shown higher (Olofsson et al. 2001, 2004, Stark et al. 2007, Stark and Väisänen 2014), lower (Stark and Grellmann 2002), or no difference (Virtanen et al. 2008, Stark et al. 2008, Francini et al. 2014) in grazed over ungrazed areas. 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). Reindeer increase soil nitrogen availability via fertilization through urine and faeces (Stark and Väisänen 2014, Barthelemy et al. 2015). Nutrient transport from foraging areas to areas where waste products are deposited could largely decide whether reindeer increase or decrease soil nutrient availability in each site (Stark and Grellmann 2002, Stark et al. 2015a).

On the other hand, 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, published 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, Ylänne et al. 2018, 2021). The organic soil layer is often drier and thinner under grazing, but also more compact (Tuomi et al. 2020). Studies have shown that lichens store only a small fraction of the ecosystem carbon, which is dominated by trees, mosses and understorey dwarf shrubs (Stark et al. 2000, Köster et al. 2015) and their removal does not affect the ecosystem net carbon sink (Susiluoto et al. 2008). In boreal forests, reindeer grazing seems to have a negligible effect on the soil CO_2 efflux in the field (Köster et al. 2016). Yet, at the soil microbial level, carbon dioxide release from boreal forest soils is lower in grazed rather than ungrazed dry and mesic forests (Väre et al. 1996, Stark et al. 2003), which may indicate that the plant biomass that was protected from grazing undergoes microbial decomposition and therefore does not add to long-term soil carbon storage.

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 similar (Ylänne et al. 2020) or higher soil carbon (Ylänne et al. 2018). Local erosion due to a high trampling intensity has been detected along reindeer fences (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 promote wind erosion on these areas (Holtmeier and Broll 2006).

Although grazed and ungrazed areas would eventually store a similar amount of soil carbon, many changes still take place in soil microbial processes and community structure. Microbial activity of carbon dioxide release (i.e., microbial respiration) in boreal forests is

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generally lower in grazed than ungrazed areas both in dry and mesic habitats (Väre et al. 1996, Stark et al. 2003). Studies on litter decomposition in dry forests have shown either lower rates under grazing (Stark et al. 2010) or unaffected (Santalahti et al. 2018) rates. Some fungal taxa change in abundances in response to grazing, but the dominant taxa remain the same (Santalahti et al. 2018). In mountain birch forests, leaf litter decomposed more rapidly in the summer than winter range side of reindeer herding districts in Finland (Stark et al. 2007). In 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 and higher abundances of mountain birches (Ylänne et al. 2021). In arctic-alpine tundra, graminoid litter decomposed more rapidly in heavily than lightly grazed side of the pasture rotation fence at the same site (Olofsson and Oksanen 2002, Olofsson et al. 2004). At the same site, it was also found that bacterial and fungal communities were highly different depending on grazing intensity, showing a higher diversity and stronger responses to nutrient increment under heavy than light grazing (Ahonen et al. 2020).

Some studies have also analysed the connections between reindeer and insect herbivores. In dry boreal forests, the response of beetle diversity resembled the hypotheses suggested for the relationship between grazing and vegetation diversity: greatest positive effect at intermediate grazing intensity and negative effects at unproductive sites (Suominen et al. 2003). In a mesic tundra heath, however, intensive reindeer grazing led to higher densities of insect herbivores on willows (Olofsson and Strengbom 2000).

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

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). Yet, reindeer interact with the ecosystem response to climate warming in complex and multiple ways that depend on the habitat. Changes in the vegetation in response to climate warming may be in general slower in nutrient-poor than nutrient-rich tundra ecosystems (Virtanen et al. 2010, Ylänne et al. 2015). Reindeer seem to dampen or slow down climate-induced increases in deciduous shrub encroachment (Horstkotte et al. 2017, Vowles et al. 2017, Vuorinen et al. 2017, Maliniemi et al. 2018), 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). The observed decline in lichens has raised the concern of the availability of winter forage for the reindeer in the future (Turunen et al. 2009).

In the long-term, a biome shift from treeless to forested areas will likely take place, and whether reindeer promote or counteract treeline advancements may vary between tree species and areas (Callaghan et al. 2013). However, historical time series indicate that

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current increase in biomass and the distribution of the mountain birch in northern Norway may be even more strongly related to changes in land-use than to summer warming (Tømmervik et al. 2019). The relationship between reindeer and climate-induced changes in the timberline is thus very complex. Reindeer can have a surprisingly strong impact also on less palatable evergreen seedlings in the timberline (Bognounou et al. 2018), and delay the north-ward expansion of the pine treeline also through browsing on mountain birches that provide protections to pine seedlings (Juntunen and Neuvonen 2006).

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). Present reindeer grazing pressure thus slows down many undesired effects of climate change, such as shrubification of open tundra landscapes (Bråthen et al. 2017) and declining diversity (Kaarlejärvi et al. 2017). On the other hand, some habitats would likely benefit from reduced reindeer numbers or changed grazing patterns, especially those where ground lichens have been depleted due to the combined pressures of reindeer grazing, forestry and other forms of land use. Current relatively stable reindeer populations do not allow lichen recovery in the same way as earlier in history which featured stronger population fluctuations and alternating high and low grazing pressures due to harsh winter conditions, predation, disease and parasitic outbreaks (Riseth et al. 2016, 2020). Such fluctuations cannot be implemented both for the reasons of animal welfare and stable income requirements.

A major question regarding the effects of reindeer on diversity at different habitats is that if the reindeer numbers were reduced to enable lichen recovery, this would 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/km^2 to 2-3 reindeer/km^2 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 3-4 reindeer per km^2 (den Herder et al. 2004, Tømmervik et al. 2010). Importantly, there is a considerable difference in the timeframe over which the changes would occur between 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 although a reduced winter grazing density (19 to 10 reindeer per km2) in concert with higher precipitation during summer led to a rapid lichen recovery in large parts of northern Norway between 1998-2005 (Tømmervik et al. 2009, 2012). Models concerning Finnish

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boreal forests suggest that even after a very substantial reduction in reindeer numbers, lichen recovery would require several decades, provided that there was also an increase in the proportion of old-growth forests (Pekkarinen et al. 2015, 2017). Governance of reindeer numbers therefore needs to consider different targets with their ecological consequences on ecosystem structure and function in different habitats. With a controlled and accepted reduction of the reindeer density done by herders themselves combined with a winter rotation system for each siida/district (3year rotation system which provides fresh lichen pastures each third year) - improved lichen pastures could be accomplished without huge loss of reindeer incomes.

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). The impacts of reindeer husbandry on biodiversity vary among sites: intensive grazing pressure increases biodiversity in productive arctic-alpine tundra heaths, but decreases vegetation diversity in nutrient-poor, lichen-rich habitats (Sundqvist et al. 2019). Yet, there is no evidence of reindeer decreasing biodiversity at large spatial or temporal scale or any species being extinct by too high grazing pressure. When the impacts of reindeer husbandry and the ecological state of reindeer ranges are assessed, one has to ask which changes 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 outbreak may either be interpreted as overgrazing, or as preserving open tundra habitats (Oksanen et al. 1995, Horstkotte et al. 2017), which make 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, Olofsson and Oksanen 2005), climate change and constant high grazing pressure in combination are likely the most significant threat for dry Finnish fell habitat types (Kontuila 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, 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 (Sandström et al. 2012, Turunen et al. 2020, Forbes et al. 2020, Miina et al. 2021).

8 Conclusions

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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 centuries ago has modified the environment over centuries. Exclosure experiments and pasture rotation fences give an overview of trends and patterns in vegetation dynamics induced by reindeer grazing, yet fail to capture all the interacting mechanisms on pasture ecosystems. We highlight that when interpreting evidence from grazer exclosures in ecological and environmental contexts, it is critical to be aware that these experiments do not measure the effect of grazing per se. Rather, they measure the responses of ecosystem structure and function to the sudden cessation of grazing in a situation, where the existing ecosystem was to a large degree shaped by the presence of herbivory. As a general trend, lichens decrease with increased grazing intensity, but the magnitude of the impact on lichens and the responses of other plant groups vary depending on both habitat and historically formed management regimes. Reindeer affect soil nutrient cycles to a stronger extent in subarctic than in boreal ecosystems.

Because 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, including other land-uses. Northern boreal forests, subarctic mountain birch forests and tundra habitats should be seen as cultural biotopes 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). This is supported by several studies showing that the impact of high reindeer densities on soil nutrient status can still be visible even after a century without grazing, thereby creating a sustaining historical legacy on vegetation and soil processes (Josefsson et al. 2009, 2010, Tømmervik et al. 2010, Egelkraut et al. 2018, Stark et al. 2019). Wild reindeer have existed in northern Fennoscandia since the last Ice Age, and through this time, were hunted and later domesticated by humans. For this reason, Fennoscandia has never experienced a state that could be referred to as "natural" in terms of reindeer numbers, if defined as existing without any human impact at all. We reason that the concepts of "natural state" and "cultural landscape" may not be mutually exclusive in the case of reindeer ranges. However, reindeer grazing is just one factor behind vegetation trajectories 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 might future changes in reindeer numbers alter these trajectories. 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.

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