

Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: a review

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Received 2 May 2000, accepted 26 October 2000

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

Grazing and trampling by semi-domesticated reindeer are important factors controlling vegetation in northern Fennoscandia. In this article we review Nordic studies on the effects of reindeer on vegetation and animal communities. The studies have shown clear effects on vegetation, especially on *Cladina* lichen dominated sites. *Cladina* is the main forage of reindeer during winter and dominates climax vegetation in dry site types in the absence of reindeer. Reindeer can even affect galling and ground-dwelling invertebrates. Due to the special relationship between reindeer and *Cladina* majority of the research has concentrated on winter grazing on *Cladina*, but there are some studies of summer grazing which have also shown substantial changes in vegetation. Reindeer grazing increases richness and diversity of vegetation and invertebrate assemblages in most cases, but this influence depends on site type and grazing intensity. The enriching effect seems to be strongest at moderate grazing intensity.

Introduction

Effects of mammalian herbivores on ecosystems

The effects of mammalian herbivory can have far-reaching consequences. For example, it has

been proposed that vegetation changes caused by the elimination of megaherbivores explain the extinction of about half of the medium sized mammalian genera in the late Pleistocene (Owen-Smith 1987). Several herbivore species have been called keystone species (keystone herbivores) due to their relatively disproportionate im-

pact on their habitat, e.g. beaver (Naiman *et al.* 1986), pocket gophers (Cantor & Whitham 1989), and bison (Collins *et al.* 1998). In particular, ungulate herbivory has been found to be important in maintaining and regulating grassland ecosystems, such as the African savannas (e.g. McNaughton 1985, McNaughton *et al.* 1988) and the American prairies (Milchunas *et al.* 1998, Frank & Groffman 1998).

There are several models predicting the impact of grazing on the diversity of a plant community (e.g. Paine 1966, Grime 1973), such as the 'intermediate disturbance hypothesis' (IDH) (Connell 1978, Fox 1979). According to this hypothesis diversity is low in the absence of disturbance due to competitive exclusion, high at the intermediate level of disturbance, and low during extreme disturbance due to stress. However, the generality and applicability of IDH has been questioned recently by modelling the relationship between disturbance and diversity or species richness in different situations (Wootton 1998, Mackey & Currie 2000). It is also not clear when and to what extent grazing by natural herbivores should be considered a disturbance. Milchunas *et al.* (1988) presented a generalized model of the effects of grazing on grassland community structure, and suggested that grazing can be considered to be a disturbance for a plant community depending on its evolutionary history. Thus, the plant community's reaction to different grazing pressures depends on its history of grazing and mode of competition (competition for light vs. water and nutrients; above and below ground resources). In a community that has been adapted to moderate grazing pressure, both very high grazing pressure and total absence of grazing can be considered as disturbances.

The majority of the studies of ungulate grazing and plant species diversity/richness have found higher diversity or richness in grazed areas when compared to ungrazed ones. In their review of the effects of herbivores on grassland plant diversity Olf & Ritchie (1998) demonstrated that herbivores can have either positive or negative effects on plant species diversity depending on the type and abundance of the herbivore. They found that large vertebrate herbivores quite consistently increase the plant species diversity. One possible reason for this is that they can use abun-

dant low-quality food, such as competitively dominant grasses in grassland ecosystems. At very high densities, however, even large grazers reduce plant diversity (Olf & Ritchie 1998). Such high densities are usually only reached as a result of human activities (i.e. livestock grazing, predator extirpation). Some examples of the enriching effects of mammalian herbivores on plant diversity have come from the grassland ecosystems of Africa (e.g. Belsky 1992) and North American prairies (e.g. Collins *et al.* 1998). In arctic ecosystems vole (Fox 1985) and lemming (Virtanen *et al.* 1997), and in the boreal zone reindeer (Helle & Aspi 1983, Oksanen & Virtanen 1995, Väre *et al.* 1995) grazing have been shown to increase plant species diversity.

Mammalian herbivores can affect soil nutrients and nutrient cycling through their defecation, trampling and through the changes in plant individuals and species composition. Augustine and McNaughton (1998) listed four mechanisms by which herbivory can affect the energy and nutrient flow in an ecosystem: (1) by changing plant species composition, and hence litter input from uneaten plants; (2) by altering the chemical composition of plant tissues during digestion; (3) by altering inputs from eaten plants to the soil due to changes in the root system or leaf-litter quality; and (4) by altering plant and soil micro-environments. The effects on productivity and rate of nutrient cycling can be the opposite, depending on the strengths of these mechanisms. The plants that are the preferred forage of herbivores are often fast-growing and decomposing species, and selective foraging by herbivores can thereby increase the proportion of highly defended, slowly growing and decomposing species. This in turn decreases soil nutrient availability and slows the rate of energy and nutrient flow (Pastor *et al.* 1993, Pastor & Cohen 1997, Augustine & McNaughton 1998). On the other hand, the feces and urine of herbivores provide soil with easily utilized nutrients, and increased solar radiation due to the more open canopy of grazed vegetation tends to quicken decomposition (Augustine & McNaughton 1998).

In grassland ecosystems ungulate grazing is often important for sustaining efficient nutrient cycling (McNaughton *et al.* 1997, Frank & Groffman 1998). In forests the impact of herbivores on

tree density and canopy species composition is the most important determinant of the net influence of ungulates on productivity (Augustine & McNaughton 1998). It has been suggested that selective foraging by cervids in boreal forest can lead to slower nutrient turnover and a reduction in soil nutrient availability compared with un-browsed forest (Pastor & Naiman 1992, Pastor *et al.* 1993, Pastor & Cohen 1997).

It is evident that the pronounced changes caused by large herbivores in both soil and vegetation will also affect other animals in these communities. Merrill *et al.* (1994) showed that native ungulate grazing increased densities of both microbial-feeding and root-feeding nematodes in the grasslands of Yellowstone National Park. At the level of an individual plant it has been shown that herbivorous insects are more numerous on twigs and leaves of browsed deciduous trees than on those that have not been browsed by mammalian herbivores earlier (Danell & Huss-Danell 1985, Roininen *et al.* 1997, Martinsen *et al.* 1998). In these cases, responses of invertebrates have been attributed to changes in the chemistry, morphology and growth rate of the plant tissues. Baines *et al.* (1994) found that red deer had a substantial negative effect on invertebrate abundance on bilberry on the floor of pine forests in Scotland. The effects were due to grazing on bilberry, which, for instance, decreased the number of Lepidoptera larvae that feed on bilberry. Keesing (1998) showed that the exclusion of ungulates from a savanna in East Africa increased both the number and diversity of small mammals. In these cases exploitation competition is proposed as the most important mechanism for the observed indirect interactions between large ungulates and other herbivores. In the coniferous forests of southern Sweden, domestic cattle grazing increased the diversity and numbers of herbs, fungi, and ground-living beetles, as well as the number of ant hills (Andersson *et al.* 1993).

History of wild reindeer and reindeer herding

Reindeer (*Rangifer tarandus*) grazing is a natural component of northern Fennoscandian ecosystems (Oksanen *et al.* 1995). Reindeer grazing and

trampling have been shaping the ecosystems during their development since the last glacial epoch. The winter and summer diet of reindeer are markedly different from each other, leading to correspondingly diverse impact on winter and summer pastures. In winter their main source of food are ground and arboreal lichens, while in summer they feed on herbs, grasses, and leaves of deciduous trees (Danell *et al.* 1994).

In the Nordic countries it is probably of little use to discuss previous reindeer counts or how the vegetation looked like before humans influenced the reindeer densities, as reindeer and humans have interacted continuously since the last ice age. Humans arrived immediately after the inland ice melted, at approximately the same time as the wild reindeer. They were hunting reindeer, and thus probably decreased the population size. As the number of wild reindeer decreased, large-scale nomadic reindeer herding begun during the 17th century through expansion of small intensively managed herds that the Sami people had kept even earlier. The previous management-intensive reindeer husbandry has now developed into a more extensive form during the 20th century (Emanuelsson 1985, Danell *et al.* 1999).

Reindeer management in Norway and Sweden

Reindeer herding in northern Sweden and Norway is restricted by law to the Sami people. Most of the Swedish reindeer migrate from winter grazing areas in the forest to summer grazing areas in the alpine tundra close to the Norwegian border (Fig. 1). However, in some areas close to Finland, the reindeer stay in the forest year-round, grazing different plants at different times of the year. The migration patterns in Norway are more complex. The reindeer in Finnmark (northernmost Norway) migrate from winter grazing areas on the lichen heaths of inner Finnmark, to summer grazing areas near the coast. In Nordland and Nord-Trøndelag reindeer have their winter grazing at snow-free areas near the coast and the summer grazing in the mountains (Danell *et al.* 1999) (Fig. 1). In Gudbrandsdalen and Valdres in southern Norway, four companies practice non-

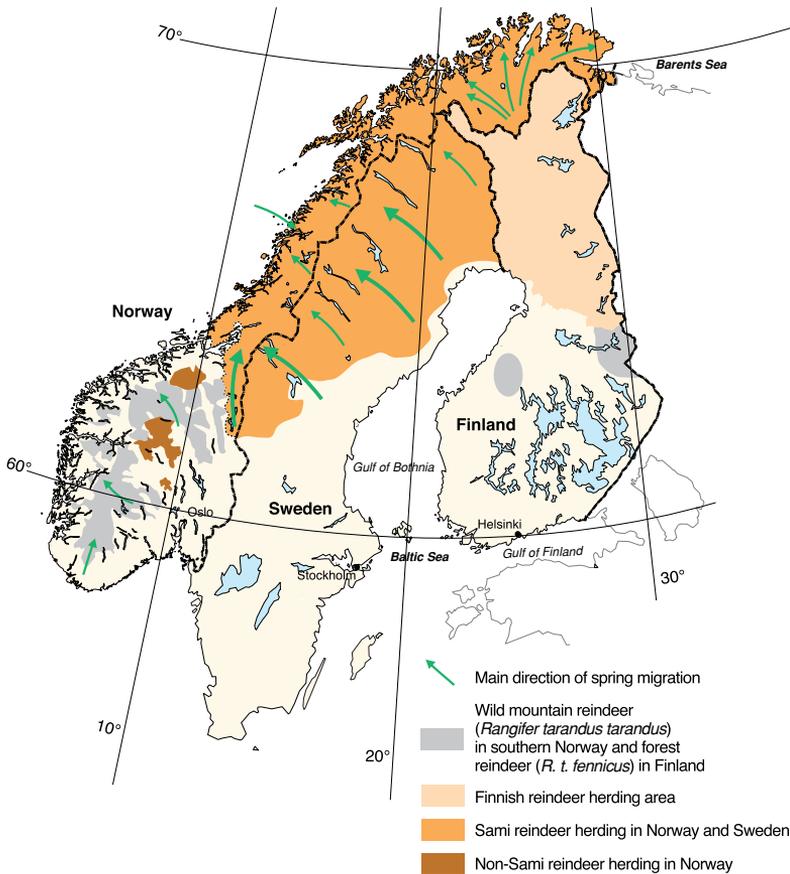


Fig 1. Map showing the distribution of wild reindeer subspecies and areas used for management of semi-domesticated reindeer (domesticated from *Rangifer tarandus tarandus*) in Fennoscandia. Major spring migration directions are also illustrated. Modified from Gaare and Danell (1999) with the permission of the publisher and authors.

Sami reindeer management. The number of reindeer in Sweden has fluctuated between 175 000 and 300 000 reindeer during the 20th century. In 1998, the number of reindeer was about 225 000 animals. This is somewhere in the range of the mean number of reindeer during the last century (Fig. 2). Reindeer densities in Finnmark have increased substantially during the last 50 years (Fig. 2), with the number of reindeer increasing from about 50 000 animals in 1950 to almost 200 000 animals in 1990. Thereafter, the number of reindeer decreased to about 130 000 animals in 1997 (Danell *et al.* 1999).

Reindeer management in Finland

There are two major differences in the Finnish reindeer herding system compared with the neighboring countries. Firstly, the right to reindeer herding is not restricted to the Sami people alone.

All people living in the reindeer herding area (demarcated by law; *see* Fig. 1), have a legal right to own reindeer. The reindeer herding area is divided into 56 reindeer herding districts with a cooperative of reindeer owners (*paliskunta*) and geographical limits defined by legislation. All reindeer owners within this area are members of the herding cooperative and their reindeer form in principle a single stock, which is herded and managed together.

A second major difference to the herding system in the other Nordic countries is that in Finland the reindeer of each *paliskunta* stay within the area of the *paliskunta* throughout the year and the traditional long seasonal migrations between winter and summer ranges that were part of reindeer husbandry up to the 20th century no longer take place. Reindeer within each *paliskunta* do tend to forage in different type of habitats within the *paliskunta* borders in different seasons (Kumpulainen *et al.* 1999a) and are herded to prevent

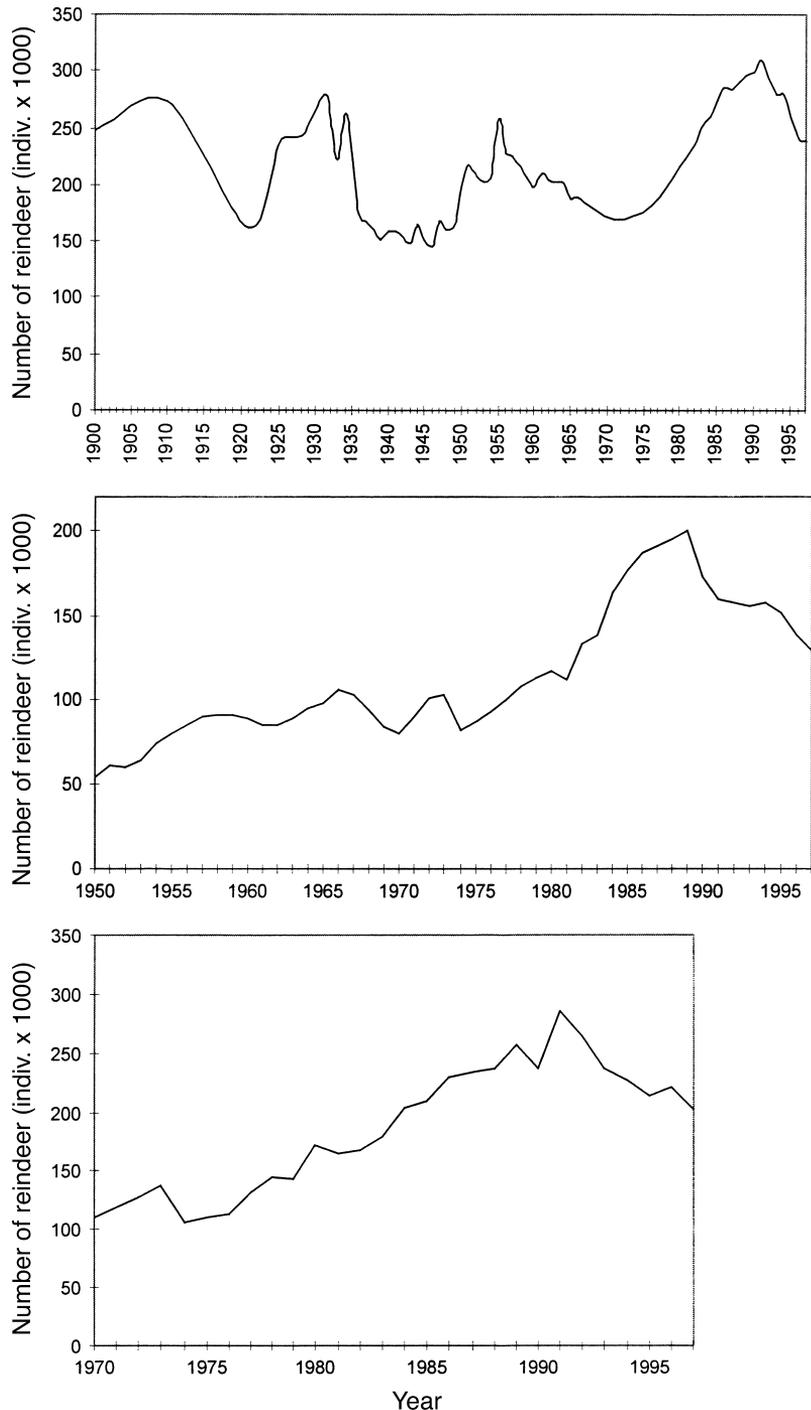


Fig 2. The development of numbers of managed reindeer (number in winter after culling) in A. Sweden (before 1925 based only on three points: 1900, 1910, 1921), B. Finmark, northern Norway, and C. Finland. Reproduced from Danell *et al.* (1999) with the permission of the publisher.

overgrazing of especially the best winter ranges. However, compared to reindeer herds of Norway and Sweden the herds in Finland live in the same area throughout the year.

The long term trend in reindeer number and grazing intensity in Finland has been increasing since the Second World War, peaking in the early 1990's and slightly diminishing thereafter (Fig. 2).

In the shorter term, reindeer numbers varied between years and the mortality due to exceptionally hard winters occasionally lowered reindeer densities before supplemental feeding was started in 1974 (Helle & Kojola 1993), and before modern veterinary practices were implemented. During the last two decades the absence of high mortality years has kept the population densities of reindeer in Finnish Lapland at constantly high levels (Kojola & Helle 1993). The disappearance of thick reindeer lichen (*Cladina* spp.) carpets from dry forests in Lapland due to these high reindeer densities has received a lot of public and scientific attention. The Organization for Economic Co-operation and Development (OECD) has named high reindeer density as the “single greatest threat to forest ecosystems in Lapland” (Anonymous 1997).

Reindeer and vegetation

Tundra vegetation, Norway and Sweden

Most studies about the impact of reindeer grazing on tundra vegetation in Fennoscandia concern the coverage of lichens in heathlands (Johansen *et al.* 1995, Ihse & Allard 1995, Johansen & Karlsen 1996, 1998, Allard *et al.* 1998). A comparison of satellite pictures over Finnmarksvidda in northern Norway, from 1973 to 1988, shows that lichens have severely decreased in the studied area. In 1973, 85.1% of the area was covered with thick lichen carpets and 14.9% was covered with a moderate lichen cover. In 1987/1988, thick lichen carpets covered only 15.1% of the area, while 56.2% had a moderate lichen cover and 28.7% of the area had almost no lichens at all (Johansen & Tømmervik 1993). A follow-up report in 1996 recorded that the lichens had decreased even further and only 7%–8% of the research area was covered with thick lichen carpets, while about 40% had a moderate lichen cover and as much as 50% of the area had no lichen cover at all (Johansen & Karlsen 1996). The only reasonable explanation for this decrease of lichens is intensive reindeer grazing. The severe decline of lichens in these areas might be a serious problem for reindeer management, as most of the investigated areas in Finnmark are

utilized for winter grazing in which lichens are the most important food resource. The poor condition of the lichen in the winter ranges might be one reason for the decrease in reindeer densities in Finnmark during the last few years.

Changes in lichen cover have also been observed in five summer grazing areas spread over the Swedish alpine tundra by comparing CIR photos from 1979 to 1986 with photos from 1996 (Ihse & Allard 1995, Allard *et al.* 1998). The cover of lichens had decreased severely in two of the locations but no clear changes were detected in the other three areas. The coverage of substrate patches without vegetation had increased in two of the areas but decreased in the other three areas. Decreased lichen cover in summer grazing areas has also been observed in Lövhögsområdet (Höglund & Eriksson 1972) and Sånfjället (Kullman 1989) in Härjedalen, central Sweden. Even if reindeer do not consume large amount of lichens during summer, trampling easily destroys dry lichens.

In a thirty year-long reindeer exclusion experiment in northern Sweden, vegetation changes were recorded from two tundra heath sites and two mountain birch sites (Eriksson *et al.* 1998). Lichens increased and *Dicranum* mosses decreased in the heath enclosures, while graminoids and lichens increased and *Polytrichum* mosses decreased in the forest enclosures. These observations support the view that the presence of reindeer, both in summer and winter grazing areas, decreases the amount of lichens and may thus give room for other plants like bryophytes and graminoids to establish. The most pronounced effect of reindeer grazing on vegetation is reported from fences separating areas with different grazing regimes in Finnmark, northern Norway. Along these fences bare ground and even local patches of soil erosion have been found (Evans 1994, Evans 1996). Generally, *Salix* shrubs, tall herbs and ericoids decreased in heavily grazed areas, while graminoids increased and bryophytes responded inconsistently to grazing (Olofsson *et al.* 2001).

In northern Norway, nearly 35 year-old reindeer fences in tundra areas separate summer ranges from lightly grazed spring and autumn ranges thus offering an experimental situation where the long-term impacts of intense summer

grazing on Fennoscandian arctic-alpine vegetation can be studied. Along these fences, vegetation-mediated changes of primary production have been found, which would not have been detected in short-term enclosure experiments (Olofsson *et al.* 2001). Moderate grazing pressure appears to decrease primary production, due to the fact that herbivores select the most preferred plant species such as nutrient rich herbs and graminoids, the plants that produce easily decomposed litter (Hobbie 1996). Thus, nutrient cycling and primary production decreased in moderately grazed tundra heath (Olofsson *et al.* 2001). Intensive grazing pressure increased the primary production in some areas, with productive grassland replacing the ericoid-dominated heathland. Still, little is known about the grazing regimes and climatic conditions required to form a grassland stage, as intensive grazing in other areas creates only bare ground and sparse remnants of heath vegetation (Evans 1996, Olofsson *et al.* 2001).

The effects of wild reindeer and caribou on tundra vegetation in many ways resemble the effects of the semi-domesticated reindeer. The wild reindeer on Hardangervidda reduced the cover of lichens by 67% between 1958 and 1968 (Tveitnes 1980). The high grazing pressure on Hardangervidda, with its corresponding food limitation, led to a lower-quality diet (Skogland 1988). A pronounced effect of wild reindeer has also been recorded in Dovre in central Norway, where lichens and ericoids decreased between 1951 and 1987 (Gaare 1995). It is important to note that even if reindeer in these areas are not domesticated, human activities such as hunting reindeer or their predators still influence the densities of these reindeer. Similar influences of wild caribou herds on vegetation have been reported in North America — i.e. grazing reduces the lichen cover and growth of deciduous shrubs and bryophytes, while non-forage lichens and bare soil have higher coverage in areas grazed by wild caribou (*Rangifer tarandus caribou*) (Manseau *et al.* 1996). Among the most dramatic effects reported is the almost complete elimination of lichen mats following the introduction of reindeer on St Matthew, Alaska. A population crash eventually eliminated the population of reindeer, but the vegetation still recovered slowly (Klein 1987).

Forest vegetation, Finland

The disappearance of reindeer lichen (*Cladina*) carpets due to reindeer grazing was reported already in the early 20th century (Du Rietz 1925, Söyrinki 1939). People began to worry about the carrying capacity and the state of the pastures in Finland already in the 1960s and several investigations were performed to estimate these parameters (e.g. Helle 1966). In the 1990s, both winter and summer pasture resources have been inventoried and mapped using Landsat images (Kumpula *et al.* 1997, 1999b).

The inventory showed that in large portions of the Finnish reindeer herding area winter (lichen) pastures are in poor condition and the amount of lichen available per reindeer is low (Kumpula *et al.* 1997). One attempt to analyze the state of the forage resources was an investigation of reindeer winter pastures as a part of the Finnish National Forest Inventory (1976–1978, 1982–1984, 1992–1993) (Mattila 1981, 1988, 1996). During this period the availability of natural winter forage decreased. In particular, the cover of reindeer lichens (*Cladina*) and the most common graminoid species (*Dechampsia flexuosa*) diminished. The amount of arboreal lichens used by reindeer also decreased, probably as a result of a lower proportion of old forest. In general, it seems that the proportion of dry lichen-type forest sites has decreased and the proportion of more productive forest types has increased (Mattila 1998).

These changes are most likely the result of the impacts of forestry, but higher reindeer densities can also shift the ground vegetation towards stages with more mosses and less reindeer lichens. This shift is important because mosses are regarded as indicators of more productive forest site types (Väre *et al.* 1995). Thus, a combination of increased reindeer densities and more intense commercial forestry and other human land use forms have led to a situation where the amount of natural winter forage per reindeer has substantially decreased. As supplemental winter-feeding is compensating for the poor condition of winter pastures in Finland, the role of summer forage is becoming more important as a limiting factor for productivity of reindeer herds. Thus, summer pastures are becoming more heavily exploited

(e.g. Helle *et al.* 1998).

Trampling and grazing by reindeer are considered to be major factors controlling forest ground vegetation in northern Finland, especially in lichen rich oligotrophic forests (Väre *et al.* 1995, 1996), in which ground layer vegetation is dominated by *Cladina* lichens (especially the climax species *Cladina stellaris*), the main winter forage of reindeer (e.g. Mattila & Helle 1978). Several studies conducted at this type of site in Finland have demonstrated that exclusion of reindeer substantially influences the plant and lichen assemblage at ground level. While reindeer grazing reduces *Cladina* cover, many other plant or lichen species simultaneously increase their abundance in these grazed areas (Helle & Aspi 1983, Väre *et al.* 1995, Suominen *et al.* 1999a). Many of these species (*Dicranum*, *Polytrichum*, *Cladonia*) are bottom-layer species that benefit from the removal of the competitively dominant *Cladina* (Helle & Aspi 1983, Väre *et al.* 1995, Suominen *et al.* 1999a). In some cases other early-successional *Cladina* species benefit from the reduction of *C. stellaris* cover (Väre *et al.* 1995).

The direct effects of reindeer grazing on *Cladina* thus seem to explain most of the impacts of reindeer on the ground vegetation in dry oligotrophic *Cladina*-dominated forest sites. Interestingly the other dominant ungulate in boreal Fennoscandia, the moose, can have an opposite effect on the competition between bryophytes and lichens. Moose browsing can increase *Cladina* cover at the expense of bryophytes, probably by opening the canopy and thus increasing light intensity and drought at ground level (Suominen *et al.* 1999b).

These changes in vegetation caused by reindeer have indirect effects on microclimate, soil respiration, soil nutrients, and fine root biomass (Väre *et al.* 1996). It has been shown that the *Cladina stellaris* carpets of late-successional dry forests can have a substantial effect on many physical features at ground level and in the soil. Reduction in lichen height and cover raise the temperature both at ground level and upper soil layers in the daytime and lower them at night; with an overall increase in daily and seasonal variation in temperature (Sandbacka 1974, Kershaw & Field 1975, Jalkanen 1998). This *Cladi-*

na grazing also decreases soil moisture and increases rainwater run-off (Sandbacka 1974). In areas covered by thick *Cladina* carpet the soil does not freeze as deeply and the extreme winter temperatures in the soil do not drop as low as in grazed areas without a lichen carpet (Väre *et al.* 1996, Sutinen *et al.* 1998). This protecting impact of a *Cladina* carpet can be important for tree roots, especially in late fall and early winter when air temperatures can be below freezing, but the protective snow cover is missing (Jalkanen 1998, Sutinen *et al.* 1998). Brown and Mikola (1974) have shown that *Cladina* lichens produce allelopathic extracts that inhibit the development of the mycorrhizae of Scots pine (*Pinus sylvestris*) and thus recruitment of pine seedlings can benefit from reindeer grazing. *Cladina* lichens are important ecosystem engineers (organisms that affect the physical features of their environment, Jones *et al.* 1994, 1997) that control many abiotic factors on the forest floor. By having a great impact on the lichen carpet, reindeer thus have an indirect effect on these habitat features.

Although the ecosystem impacts of reindeer are most evident in winter ranges, their feeding ecology in summer has also caused notable changes in ecosystems. The effects of reindeer on the regeneration of deciduous trees (Oksanen *et al.* 1995, Mäkitalo *et al.* 1998) in moister and more productive summer ranges have also aroused attention, mainly because forestry is negatively affected. Leaves of deciduous trees, mainly birch and willow, are important summer forage for reindeer (Haukioja & Heino 1974). By feeding on young birches and willows reindeer have an adverse effect on the regeneration of these trees and they can thus prevent the recruitment of deciduous trees into the canopy. For example, in northern Fennoscandia, where larvae of outbreaking autumnal moth (*Epirrita autumnata*) can defoliate and kill vast areas of mountain birch forest, reindeer grazing has been one factor that has prevented the development of new forest in some areas (Lehtonen & Heikkinen 1995, Oksanen *et al.* 1995, Helle *et al.* 1998). Thus, these two herbivorous animals have together created extensive areas of open savanna-like woodlands, or have even changed the treeline forest habitat into an open mountainous tundra (Oksanen *et al.* 1995).

On the other hand, the disturbance of ground vegetation through grazing and trampling by reindeer improves establishment of birch seedlings. Helle *et al.* (1998) compared a heavily grazed summer range in mountain birch forest to an area which had been avoided by reindeer during the past 20 years in northern Finland. In the grazed area, the number of newly-germinated birches (size class < 0.5 m) was about four times higher than in the ungrazed area, while in the size class 0.5–1.0 m the situation was reversed in that the number of saplings was five times higher in the ungrazed area. The substantial changes in the density and species composition of tree stratum will inevitably have an impact on both biotic and abiotic factors at ground level.

It has been found that even in sites with low *Cladina* cover and birch dominated tree layer, ground vegetation differs between grazed and ungrazed plots, but the picture is not as clear as in *Cladina* dominated sites (Suominen *et al.* 1999a). Even here *Polytrichum* mosses, non-forage lichens, and soil devoid of vegetation were more common in grazed plots while *Cladina* was more common in ungrazed plots. However, *Cladina* lichens were not the only species that covered more ground in ungrazed plots; some dwarf shrubs, graminoids, and bryophytes were also more common in ungrazed plots. Many of the sites with low *Cladina* cover were birch-dominated summer ranges, and therefore the indirect effects of feeding on deciduous trees most likely affected the vegetation in addition to the direct effects of trampling, defecating, and feeding on the herb-layer plants themselves.

Manseau *et al.* (1996), studying caribou in the Canadian tundra, proposed that migratory ungulates can have a significant impact on vegetation when the food resources of summer and winter ranges are not balanced and vegetation does not recover rapidly from the impacts of grazers. Further requirements in this scenario are that the ungulate population must be potentially regulated by the food resource and that the animals must return to the same area each year. In the Finnish Lapland, the area of lichen-dominated winter ranges is small (Helle & Aspi 1983) and the recovery of lichens is much slower than the recovery of the vascular plants in the summer pastures. Human impact has removed most natural

predators and the herds are kept within the area belonging to the local reindeer herding cooperative. Thus, all the prerequisites for substantial impacts on vegetation mentioned by Manseau *et al.* (1996) are fulfilled. With the introduction of supplemental winter-feeding of reindeer in the beginning of the 1970s (Kojola *et al.* 1991) the situation has changed. If the supplemental feeding only supplements the natural pastures when the reindeer are starting to show signs of starvation, it does not release the winter ranges from high grazing pressure, whilst it will increase winter survival and thus grazing pressure in summer ranges. It will thus lead to high grazing pressure over the whole range of the reindeer herds.

Vegetation diversity

Several studies in the Finnish Lapland have shown that plant species richness and diversity are higher in areas grazed by reindeer than in ungrazed areas. Most of these studies have concentrated on dry pine forests with a *Cladina*-dominated ground-layer (Helle & Aspi 1983, Väre *et al.* 1995) concluding that reindeer grazing on *Cladina* has released other plants from competition with these dominant lichens. Helle and Aspi (1983) showed that the species richness of the flora of *Calluna*–*Cladina* -type heaths in Finnish Lapland was highest under moderate grazing pressure, and lower both in heavily- and lightly-grazed sites. While diversity (inverse of Simpson) was about equally high in moderately and heavily grazed sites, it was lower in ungrazed sites.

Suominen *et al.* (1999a) tested the relationship between the effect of reindeer on *Cladina* cover and the relative difference of vegetation richness parameters between pairs of grazed and ungrazed plots over a wider range of forest site types. Richness and diversity of vegetation were found to be generally higher in grazed plots. The relative difference in plant species richness was not related to *Cladina* cover difference, but the relative difference between plots in the Shannon-Wiener diversity index (H') increased linearly in relation to increase in *Cladina* cover difference. Furthermore, the relative difference between plots in relative diversity (H'/H'_{\max} , evenness)

increased with increasing difference in *Cladina* cover until it leveled off when the *Cladina* difference exceeded about 40%–50%-units. The percentage similarity of vegetation between grazed and ungrazed plot responded in a very similar way; similarity decreased (difference in composition increased) when difference in *Cladina* cover increased until the *Cladina* difference exceeded about 40%–50%-units.

These results demonstrate that reindeer grazing has an enriching effect on ground vegetation even in non-lichen type sites, as has been suggested by Oksanen and Virtanen (1995), even though the effect is strongest in *Cladina*-type habitats. The influence of reindeer on vegetation diversity thus seems to be related to more general phenomena than just the role of *Cladina* lichens. One general mechanism seems to be that by feeding on competitively dominant plant species, herbivores can indirectly enhance the growth of other species by reducing competition (Olf & Ritchie 1998). In the case of reindeer in Lapland this phenomenon is most clear in dry *Cladina*-type sites since these slow-growing lichens dominate both in reindeer diet (Danell *et al.* 1994, Kojola *et al.* 1995) and in late successional ground vegetation.

Despite those results, relatively little is known about the impact of reindeer grazing on plant diversity in tundra environments. To our knowledge, only four reports about the impact of reindeer grazing on species richness have been completed, and three of them refer to unnatural situations near fences (Olofsson *et al.* 2001) or inside enclosures (Näsman 1994), while the fourth study lacks replication (Eriksson *et al.* 1998). The studies from the fences separating areas with different grazing regimes support the studies from the Finnish pine forest vegetation suggesting that diversity will increase when reindeer grazing on *Cladina* releases other plants from competition. In general, at least moderate grazing seems to increase diversity in heathlands, while diversity remains unaltered or is slightly lower in moderately grazed grass- and herb-dominated meadows. However, diversity only decreased substantially when the grazing pressure was so severe that a large proportion of the ground had lost the vegetation cover. Therefore, the diversity of mosses seems to be more favored by grazing than

that of vascular plants and lichens. This is interesting, as most of the red-listed alpine plants are mosses (Hallingbäck 1998). However, Eriksson *et al.* (1998), found no influence at all on species diversity after excluding reindeer, neither on the tundra heath nor in the mountain birch forest. Inside a large enclosure at Mittåkläppen, which is utilized three weeks per year during calf marking, no changes in species richness were found between 1984 and 1993. However, the number of species increased substantially inside a small enclosure, indicating that species richness could still be lowered by the high grazing and trampling pressure inside the enclosure (Näsman 1994).

Reindeer and animal assemblages

Studies on the effects of reindeer grazing on other animals in northern communities are very scarce, as are similar studies of any ungulates. Nevertheless, Suominen *et al.* (1999c, 1999d) have studied how reindeer affect ground-dwelling invertebrate assemblages by comparing pitfall trap catches of pairs of grazed and ungrazed plots in a wide range of forest site types and successional stages in the Finnish Lapland. The assemblages differed both in high and low *Cladina* coverage sites. In both classes, the number of individuals of most of the invertebrate taxa was higher in the grazed plots. In the high *Cladina* cover sites cockroaches, linyphiid spiders, mites and terrestrial gastropods were more abundant in ungrazed plots, while most of the other taxa were more abundant in the grazed plots. When the *Cladina* coverage was low, only the individuals of the beetle family Curculionidae were significantly more abundant in ungrazed plots while most of the other taxa were more abundant in grazed plots. There was a curvilinear relationship between the relative difference in invertebrate abundance between grazed and ungrazed plots and *Cladina* cover difference between the plots. The difference in invertebrate abundance between plots was highest at an intermediate level of *Cladina* grazing intensity. The only exceptions to the total number of invertebrates being higher in grazed plots occurred at sites where the grazed plots had more than 60%-units less *Cladi-*

na cover than the ungrazed plot — i.e. at most intensively grazed *Cladina* type sites (Suominen *et al.* 1999c).

From the same data the individuals of beetle families Carabidae and Curculionidae and terrestrial gastropods were identified to species level and their species richness and diversity patterns were examined. The numbers of individuals of two gastropod species out of the four species abundant enough to be tested, as well as the number of all gastropod individuals, differed significantly between grazed and ungrazed plots (Suominen 1999). In the partial ordination results for gastropods, ungrazed plots were characterized by a higher abundance of *Euconulus fulvus* and *Arion subfuscus*, while *Nesovitrea hammonis* was more common in grazed plots. Most of the invertebrate predators of gastropods were more common in grazed plots (Suominen 1999), and invertebrate predation may have contributed to the observed differences in gastropod density coupled with the effects of changes in microhabitats caused by reindeer grazing. However, gastropods are extremely sensitive to the physical conditions of their habitats (Godan 1983, Boag 1985), and the warmer and dryer microclimate and soil in the grazed plots probably explain most of the observed differences. The differences in the rarefaction curves of gastropod fauna of grazed and ungrazed plots (Suominen 1999) clearly indicate a greater species richness of gastropod fauna in ungrazed plots compared with the grazed plots.

The exclusion of reindeer affected species composition, number of individuals, species richness, and diversity of the Carabidae and Curculionidae assemblage at ground level and litter-layer (Suominen *et al.* 1999d). The effect of reindeer on the beetle assemblage was modified by the extent of *Cladina* lichen cover, so that the increasing effect of reindeer grazing on number of individuals of both Carabidae and Curculionidae at family level grew linearly in relation to the effect of grazing on lichen cover. For carabids, this may be because they are sensitive to changes in microclimate, and many of the collected species are favored by the warm and dry conditions (Lindroth 1985, 1986) in grazed plots where both tree and herb layer vegetation were more open. The generally higher invertebrate numbers in

grazed plots (Suominen *et al.* 1999c) also indicate that there was more prey for invertebrate predators such as carabid beetles.

In low *Cladina* cover sites curculionids in general were more common in ungrazed plots due to the species *Polydrusus fulvicornis*, which was nearly twice as numerous in ungrazed plots as in grazed ones (Suominen *et al.* 1999d). In high *Cladina* cover sites curculionids were more common in grazed plots due to the higher abundance of species that feed on coniferous trees (all pine forests belong to this *Cladina* cover class). The effect of summer grazing on the abundance and growth of deciduous trees (especially birch) is the likely explanation for the higher number of *P. fulvicornis* in ungrazed plots since the adult beetles feed on the leaves of deciduous trees. It is not clear, however, why the curculionids that feed on conifers are more abundant in grazed areas.

The species richness and diversity (H') of Carabidae and Curculionidae were generally higher in grazed plots, while relative diversity did not differ between plots in the pooled data (Suominen *et al.* 1999d). Six (33%) of the carabid species and nine (56%) of the curculionid species were found only in grazed plots while none were found only in ungrazed plots. The difference between grazed and ungrazed plots in diversity and relative diversity (evenness) had a curvilinear response to the difference in *Cladina* cover. Both were higher in grazed plots at the intermediate values of difference in *Cladina* cover. Diversity and relative diversity were higher in ungrazed plot only in sites with a very low or extremely high *Cladina* cover difference. This indicates that even quite high grazing pressure may increase the diversity of these beetle assemblages, but also that in areas with the most severe effects of reindeer on the lichen carpet (and probably on other vegetation as well) the diversity of beetles has decreased. The mechanisms through which reindeer grazing affects these beetles are probably indirect and result from the changes in vegetation caused by their foraging, which creates partly trophic effects and partly physical changes in the habitat.

Reindeer grazing has also been shown to increase the number of a gall-forming insect (*Pontania glabrifrons*) and gall-forming mites on *Salix*

lanata shrubs (Olofsson & Strengbom 2000). *P. glabrifrons* was ten times more abundant on heavily grazed than on lightly grazed shrubs. The ultimate reason for this increase of invertebrate herbivores is unknown, but the increase was not associated with the typical plant response characters found in moose browsed shrubs (Danell & Huss-Danell 1985, Roininen *et al.* 1997), such as longer shoots or lower C:N ratio. It is quite probable that long-term grazing has reduced plant defences against herbivores.

Kojola *et al.* (I. Kojola, O. Suominen, T. Helle, E. Huhta, S. Kankaanpää, P. Niemelä, M. Niskanen & A. Niva unpubl. data) compared densities of songbirds in mountain birch forests grazed by reindeer to densities in ungrazed forests separated by fences in northern Finland and Norway. They found that densities of two common bird species, Meadow Pipit (*Anthus pratensis*) and Lapland Bunting (*Calcarius lapponicus*), were higher in the nearly ungrazed forests. The densities were about twice as high in these areas as in the grazed forests on the other side of the fence, but small sample size produced only marginally significant results. They suggest that the substantially lower birch leaf biomass and thus lower availability of insect prey is the cause behind the difference in bird density.

For other ungulates, it has been shown that high white-tailed deer densities have a negative effect on the species richness and density of songbirds nesting in the intermediate canopy in Pennsylvania (deCalesta 1994). deCalesta (1994) simply refers to habitat alterations in general, but many of these bird species are insectivorous, and thus indirect effects of deer grazing on insects are a possible cause. It has been suggested that one reason for the increase in the number of breeding birds in Finnish forests during the 20th century has been the end of cattle grazing in forests and its impact on the amount of deciduous trees (von Haartman 1978, Järvinen & Väisänen 1978).

Conclusions

Moderate mammalian herbivory has been observed to increase plant species richness or diversity of many grassland communities (Olf & Ritchie 1998). Reindeer grazing increases the

richness and diversity of flora and invertebrate fauna in most of the studied cases, excluding terrestrial gastropods. For plants the most obvious explanation for higher diversity in grazed plots is a release from competition with the successional dominant *Cladina* lichens. The richness was, however, higher in grazed areas even in sites with no *Cladina*. For invertebrates the increased floral diversity and general microhabitat heterogeneity are probably important. The effect of reindeer on diversity in the Finnish Lapland is related to the effect of reindeer on *Cladina* cover, but the nature of this relationship varies among different taxa.

For some taxa the relationship between grazing, diversity and lichen cover is consistent with the intermediate disturbance hypothesis (IDH). Wootton (1998) and Mackey and Currie (2000) have modeled IDH and shown that disturbance does not always produce humped response of diversity or species richness and that the impact of disturbance is often quite small. Wootton (1998) concludes that IDH works best at single (and low) trophic level situations, but that disturbance can affect real multitrophic communities in different ways. In the reindeer studies reviewed in this article, the closest resemblance to an IDH curve and the biggest effect on richness was with the carabid and curculionid species i.e. high trophic levels in a multitrophic system.

However, it is debatable whether reindeer grazing should be considered a disturbance. Milchunas *et al.* (1998) claim that grazing by a herbivore that is a natural to the system should not be regarded as a disturbance. On the other hand, it has been suggested that the ecological effects of herbivory, like traditional animal husbandry, are similar to fires and other natural disturbances (Pykälä 2000). Semi-domesticated reindeer are neither purely wild animals nor domestic animals, and their role in the ecosystems of northern Fennoscandia varies between these two extremes in time and space. It is evident that in some areas the present densities are so high that reindeer are a disturbance to natural ecosystems. This can be said, for example, in cases where bare ground and even local patches of soil erosion have been found (Evans 1994, Evans 1996). In addition, the aim of biodiversity conservation is not to maximize the number of species in all habitats, but to

maintain the existence of viable populations of naturally existing species in their habitats (Myk-rä *et al.* 2000). Thus, even if the number of plant or animal species is high in grazed habitats, there can be special species and habitats that are more sensitive to grazing and suffer from the present grazing pressure. There exist, of course, also situations where reindeer grazing can be seen as a tool for conservation similar to the use of domestic cattle as a tool for maintaining certain habitat types (Pykälä 2000). For example, the disturbance caused by the natural fire regime in the dry oligotrophic pine heaths has diminished due to efficient fire control during last century (Angel-stam 1998). Thus, the importance of reindeer as controller of climax *Cladina* carpets might have increased.

Succession and its interaction with the impacts of selective foraging are important factors in the whole system of the ecosystem effects of mammalian herbivores (e.g. Pastor and Naiman 1992). Reindeer affect deciduous sapling stands mainly at the early phases of succession, but lichen grazing in winter concentrates on climax vegetation. Thus, reindeer have a bipartite effect with different consequences for the communities in different site types and successional phases even within the range of a single herd. The successional dynamics have not been explicitly studied in relation to the effects of reindeer on forest floor communities, but there is no doubt that the effects of mammalian herbivores vary during the course of succession. Engelmark *et al.* (1998) have shown that succession of a pine forest is still going on more than 200 years after a forest fire and that reindeer grazing in this area is affecting the dynamics of tree species composition.

The effects of reindeer can be seen as partly direct trophic top-down effects on vegetation. However, the animals also modify the physical features of the habitats of other species through changes in vegetation structure and thereby influence their abundance and the whole ecosystem functioning. Thus, they can be considered to be ecosystem engineers, as defined by Jones *et al.* (1994, 1997). It is evident that in terms of the responses of many invertebrate taxa to the exclusion of the reindeer the indirect effects of reindeer foraging on microhabitats are the likely explanations.

The effects of reindeer grazing are in many ways very similar to the effects of many other large ungulate grazers e.g. it increases diversity of vegetation, changes successional development that would take place in the absence of grazing and prevents forestation of some habitats. Thus, even with the special relationship between reindeer and *Cladina* lichens the huge geographical range of the different subspecies of *Rangifer tarandus* (reindeer/caribou) seems to be, in some ways, comparable to grasslands in which ungulate grazers are important regulators of plant communities.

The severity of the effects of reindeer on the forest floor depends on reindeer population density, season of grazing, site type, and successional state. Of these, all except the site type are at least partly controlled by humans in Fennoscandia. Historically, grazing pressure has had more variation both spatially and temporally so that there have been sites and periods of high grazing pressure followed by low reindeer densities when pastures have had a chance to recover. However, sites suitable for the development of the preferred winter ranges with thick *Cladina* carpets cover only about 10% of the total land area of the Finnish Lapland (Sutinen *et al.* 1998). Thus, it is likely that many of the *Cladina*-type sites have a long history of grazing, even before modern reindeer herding. We do not know of any data on prehistoric grazing pressure in northern Fennoscandia, but the wild Rivière George caribou herd in Québec, Canada, had substantial effect on the vegetation of the summer ranges, which are the limiting resource there (Manseau *et al.* 1996). At this site, the difference in the cover of lichens between grazed and ungrazed plots was 38%-units (Manseau *et al.* 1996). This corresponds to the 30%–50%-units which was the turning point in the response curves of diversity of both vegetation and invertebrate assemblages to reindeer-induced *Cladina* cover difference in Finnish Lapland (Suominen *et al.* 1999a, 1999c, 1999d).

It has been argued that the response of a community to grazing depends on the evolutionary history of grazing in the given community (Milchunas *et al.* 1988), and that grazing can be considered to be a disturbance if it deviates from the conditions under which the community has developed. Both plant and invertebrate commu-

nities of *Cladina*-heaths could be expected to have a well-developed capacity to utilize even quite heavily grazed sites. In this situation, totally ungrazed *Cladina* carpet would be an “unnatural” condition. But the studies also suggest that at sites showing the greatest effects on *Cladina* cover the current grazing pressure seems to be harmful for a majority of the species in these communities.

Acknowledgements

Comments of Pekka Helle, Genaro Lopez, Sakari Mykrä, Mikko Mönkkönen, Pekka Niemelä and John Pastor on the manuscript have greatly improved it. We greatly appreciate the financial support from the Maj and Tor Nessling Foundation (to O. Suominen) and SJFR (to J. Olofsson).

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