Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone

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Both theoretical arguments and empirical evidence suggests that herbivory in general and mammalian winter herbivory in particular is important in arctic–alpine ecosystems. Although knowledge of the effect of herbivores on specific plants and communities is quite extensive, little is known about the relative impact of large and small vertebrate herbivores and how it might vary among different habitats. To address this key issue, we established exclosures with two different mesh sizes in forest and nearby tundra at three different sites in four contrasting locations in the forest–tundra ecotone in northernmost Sweden and Norway. Plant community composition was recorded annually in three permanent plots within each exclosure and an unfenced control. Local densities of vertebrate herbivores were estimated in spring and autumn from 1998 to 2002.

Reindeer (*Rangifer tarandus*) were the most abundant large vertebrate while Norwegian lemmings (*Lemmus lemmus*) and grey-sided voles (*Clethrionomys rufocanus*) were the most common small vertebrates. The study reveals that voles and lemmings have larger effects on the vegetation than reindeer in both habitats in all four locations, even though densities of reindeer differ between locations and only two locations experienced lemming peaks during the period of the experiment. The relative abundance of five of the fifteen most common species was significantly influenced by voles and lemmings whereas only a single species was significantly influenced by reindeer. Different analyses give contrasting results on the importance of herbivory in forest versus open heathlands. A principal component analyses revealed that herbivory influenced the vegetation more in open heathlands than in forests. However, an importance index of herbivores did not differ between forest and open heathlands. Moreover, none of the plant species responded differently in the two habitats, when herbivores were removed. Our results suggest that intense and localised selective foraging by small mammals may have a more marked effect on vegetation than transient feeding by reindeer.

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Numerous studies have shown that herbivores influence vegetation patterns in tundra communities (Jefferies et al. 1994, Mulder 1999). Herbivores have substantial impacts on the structure and diversity of plant communities by decreasing the abundance of preferred species (Bazely and Jefferies 1986, Virtanen et al. 1997, Brathen and Oksanen 2001, Olofsson 2001, Grellmann 2002) and by changing competitive interactions between plants (Mulder and Ruess 1998, Virtanen 1998, Olofsson et al. 2002). Moreover, herbivores might also increase

(Bazely and Jefferies 1985, 1989, Olofsson et al. 2001, 2004, Olofsson and Oksanen 2002) or decrease (Stark and Grellmann 2002) nutrient availability for plants. Such impacts are surprising since herbivores, on average, only remove between 5–10% of the primary production in arctic areas (reviewed by Jefferies et al. 1994 and Mulder 1999). However, such averages mask considerable variation among habitats and herbivores. For example, lemmings and geese may remove up to 90% of the primary production (Shultz 1968, Cargill and Jefferies 1984), while muskoxen only remove 1–2% (Bliss 1986). Clearly different guilds of herbivores have markedly different impacts and it is essential to tease apart their relative contribution in order to understand their role in plant community structure.

The relative impact of herbivores may be a function of body size which, at least for mammals, may affect their capacity to use diets differing in fibre content and other secondary metabolites (Demment and Van Soest 1985, Freeland 1989, Olff and Ritchie 1999). Overall, within the same vegetation stands, large bodied cervids appear to feed less selectively than hares and hares less selectively than small rodents (Davidson 1993). With comparatively high metabolic demands and small gut capacities, small rodents have to feed selectively on plants with high concentration of nutrients and low levels of secondary metabolites (reviewed by Lindroth 1988 and Tahvanainen et al. 1991). Larger mammalian herbivores, with larger stomachs and relatively lower metabolic demands, have evolved a higher capacity to tolerate secondary metabolites and low nutrient concentrations (reviewed by Bryant et al. 1991).

Besides differing in their ability to digest food, large and small vertebrate herbivores differ in their mobility and thus opportunities to exploit a range of feeding areas. A relationship between body mass and daily distances travelled is well established for mammalian herbivores (Garland 1983, Altman 1987, Cumming and Cumming 2003). In arctic and subarctic areas, the largest contrast is how different animals survive the winter. Small animals, such as voles and lemmings, do not have the possibility to migrate to more favourable winter conditions or enough stored energy to hibernate. Hence, they remain in the same locality throughout the year and have to remain active during winter. However, their small size allows them to move under an insulating layer of snow, where they can consume plants, and find protection from most predators (Kalela 1957). Larger herbivores either have to feed above the snow like hares and moose, or dig down through the snow to reach the food on the ground like reindeer. This can potentially reduce their ability to consume field layer plants.

The long-term effect of herbivory is dependent not only on the foraging pattern of the herbivore but also on the regrowth capacity of the vegetation. Opportunities for regrowth appear linked to habitat productivity. For

example, basal meristem monocots regrow faster after herbivory at high resources levels, while dicots respond better at low resource levels (Hawkes and Sullivan 2001). In the forest–tundra ecotone of Scandinavia, more productive areas are covered by discrete patches of fairly dense birch forest interspersed with treeless tundra areas of lower productivity. Such a habitat matrix provides an ideal opportunity to assess the relative impact of large and small mammalian herbivores in neighbouring habitats of contrasting productivity.

The objectives of the present study were (1) to quantify the relative role of large herbivores (reindeer, *Rangifer tarandus*, and moose, *Alces alces*) and small herbivores (grey-sided vole, *Clethrionumus rufocanus*, and Norwegian lemming, *Lemmus lemmus*), and (2) to evaluate whether the importance of herbivory varies between contrasting habitats. We therefore established exclosures of two different mesh sizes to exclude only large or both small and large herbivores in forest and adjacent tundra at three different sites in four contrasting locations in northernmost Sweden and Norway. The present paper describes changes in vegetation and herbivore abundance over five years.

Methods

Study area

The study sites are situated at the mountain birch (*Betula pubescens* spp. *czerepanovii*) forest–tundra ecotone in the Fennoscandian mountain range. Four study locations are used: Abisko and Vássijávri in northernmost Sweden and Joatka and Seiland in northernmost Norway (Fig. 1). The locations were chosen to include one more oceanic and one more continental site at the two different latitudes. All study sites occur on nutrient poor bedrock.

Abisko

The study sites in Abisko, the more continental of the two locations in northernmost Sweden, are located between 550 and 600 m a.s.l. at 68°19′23″N, 18°51′57″E on a gentle north-west slope. The mean annual precipitation at the nearest climatic station (Abisko Scientific Research Station at 385 m.a.s.l.) is only 304 mm (Alexandersson et al. 1991). The forest–tundra ecotone is a wide zone with a mosaic of forested patches and open heathlands between 500 m and 800 m.a.s.l. Average birch density in the forest sites was 746.5±67.8 trees per hectare. The location is used by reindeer mainly in late spring and autumn but summer grazing also occurs.
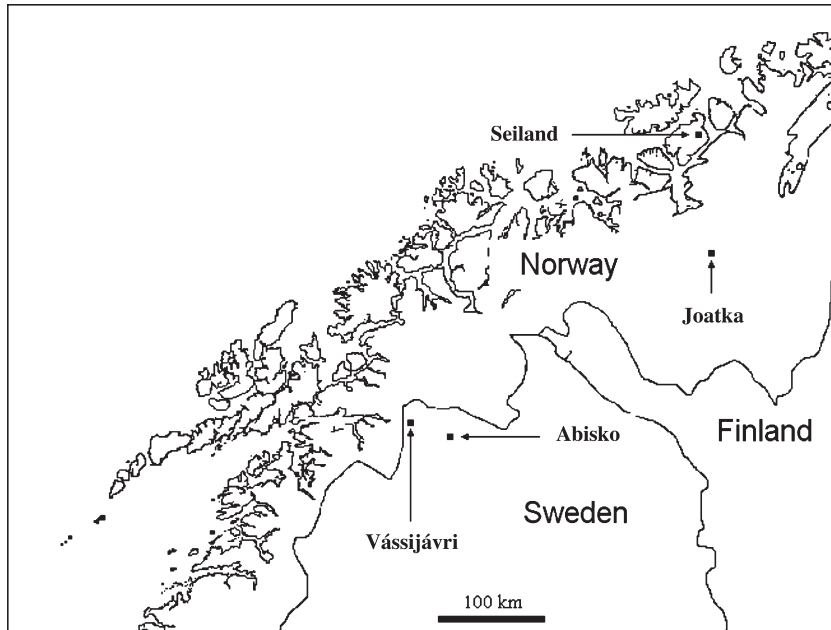
Fig. 1. Map of northern Scandinavia showing the locations of the four research locations: 1. Abisko (Sweden), 2. Vássijávri (Sweden), 3. Joatka (Norway) and 4. Seiland (Norway).

Vássijávri

The study sites in Vássijávri, the more oceanic of the two locations in northernmost Sweden, are located between 460 and 500 m.a.s.l. at 68°26′26″N, 18°16′29″E on a flat area east of a large lake. The mean annual precipitation at the nearest climatic station, Katterjåk, is 848 mm. The location consists of a mosaic of patches with forest, open heathland and mire. Average birch density in the forest sites is almost three times that in Abisko at 1996.5±340.3 trees per hectare. The area is used for winter-grazing by reindeer, but low numbers of reindeer are found in the area throughout the summer.

Joatka

The study sites in Joatka, the more continental of the two locations in northernmost Norway, are located between 550 and 600 m.a.s.l. at 69°45′11″N, 24°00′10″E at about 450 m.a.s.l. The mean annual precipitation at Joatka is 354 mm. The location consists mainly of open heathlands, with patches of forests in more favourable sites, such as south or west slopes. The forest at the study sites is sparse with the lowest average birch density of all four sites (399.3±78.6 trees per hectare) comprising low trees with a shrubby growth form. The location is used for migration between summer and winter ranges by reindeer in early spring and late autumn, but low numbers of reindeer are commonly found throughout the summer.

Seiland

The study sites on Seiland, the more oceanic of the two locations in northernmost Norway, are located at 70°30′22″N, 23°31′41″E at about 100 m.a.s.l. Seiland is an island of the Arctic Ocean. The mean annual precipitation at the nearest climatic station (Hammerfest) is 734 mm. The study sites are located on gentle slopes with either south or north aspects, in an east-facing valley, in the north-eastern part of the Island. The forest-tundra ecotone is narrower here, than it is at the other study locations. Average birch density in the forest sites is the highest of all four locations (3072.9±746.6 trees per hectare) and consists of tall trees. The location is used as summer-grazing for reindeer, but is mainly used in late spring and autumn.

Experimental design

In July 1998, we chose three sites along the forest–tundra ecotone in each of the four locations. The distances between the sites varied between 0.2 km and 2 km. Each site comprises an adjacent pair of birch forest and open heathland, selected to minimize the differences between tundra and forest except for the presence of trees. The vegetation consists of dwarf shrub heath in all tundra sites in all locations, and in the forest the field vegetation is dominated by dwarf shrubs, grasses or herbs depending on local conditions.

Three 8 × 8 m experimental plots were established in both the forest and in the tundra at each site, and these

plots were randomly chosen to become either the unfenced plot, an exclosure with a large mesh size or an exclosure with a small mesh size. The exclosures with the smaller mesh size was constructed from galvanized net with a mesh size of 1.2×1.2 cm. The net is 1 m high and was dug down into the mineral soil, between 10 and 30 cm deep, to exclude digging animals. These exclosures should exclude all mammalian herbivores, however to ensure this was the case snap-traps were set in the exclosures throughout the study to catch microtine rodents that might have entered. The exclosures with a large mesh size were constructed from standard sheep fencing. The net is 1.2 m high and was fastened on wooden poles about 10 to 20 cm off the ground. Voles and lemmings will easily enter these exclosures, but large herbivores will be excluded. Moose could potentially enter the exclosures as they can jump over the fence, but as the exclosures are quite small this is unlikely to have happened and no signs of moose entering the exclosures were found. Hares can enter these exclosures but it is possibly that they will partly avoid them, as they cannot freely move in and out of them. In total, 24 exclosures with a large mesh size and 24 exclosures with a small mesh size were built in the northernmost part of the Fennoscandian mountain range. The two small mesh size exclosures in site 3 in Vássijávri were broken in the winter 2000–2001 and are thus excluded from all analyses.

Herbivore densities census

Microtine rodent densities were studied by means of twice-a-year snap-trapping from 1998 to 2002, using the small quadrate method (SQM) of Myllymäki et al. (1971). A quadrate of 15×15 m was marked, and 12 traps of galvanized steel were placed as clusters of three in each corner. Traps were baited with small pieces of Finnish rye bread, set for 48 h and checked twice (after 24 h and 48 h). Each quadrate thus represents 24 trap nights. We used 5 small quadrates in a forest and 5 small quadrates in an open heathland close to the sites where exclosures were built in all locations. The abundance of all other vertebrate herbivores was estimated by collecting droppings (reindeer, moose, hare and ptarmigans). In each habitat in each site, a 20×1 m transect, close to the exclosures, was cleared of all droppings in autumn 1998. In Joatka, only 10×1 m transects were used for some years. New droppings were collected twice a year, as soon as possible after snowmelt and in the second half of August.

Vegetation recording

Plant community composition was recorded annually in permanent plots between 1998 and 2002. Within each exclosure plot and control, vegetation was recorded from three 0.5×0.5 m sub-plots. We quantified the abundance of plant species with a point intercept method (Jonasson 1986). A transparent Perspex board (0.25 m^2) with 100 randomly placed holes ($\varnothing$ 4 mm) was fixed over the subplots. A pin ($\varnothing$ 4 mm) was passed vertically through each hole. All living plant parts touched by the pin were recorded as a hit. The total abundance of each species was estimated as total number of hits on that species. Nomenclature follows Mossberg et al. (1995) for vascular plants, Moberg and Holmåsen (1992) for lichens and Hallingbäck and Holmåsen (1981) for mosses.

The relative change in abundance of plants was calculated as:

$$Ra_i = \ln\left(\frac{X_{i2002}}{X_{i1998}}\right)$$

where: R_{ai} is the relative change in abundance of species I, X_{i2002} is the abundance of species i 2002, X_{i1998} is the abundance of species i 1998.

The importance of herbivores for plant community structure was calculated as:

$$I = \sum Z_{i1998} \times \left(\ln\left(\frac{X_{i2002}}{X_{i1998}}\right)\right) - \left(\ln\left(\frac{Y_{i2002}}{Y_{i1998}}\right)\right)$$

where: I is the importance index (reflecting the extent of herbivore impact), X_{i2002} is the abundance of species i in 2002 when the herbivore is absent, X_{i1998} is the abundance of species i in 1998 when the herbivore is absent, Y_{i2002} is the abundance of species i in 2002 when the herbivore is present, Y_{i1998} is the abundance of species i in 1998 when the herbivore is present, Z_{i1998} is the proportion of species i in 1998 of the total abundance of plants in 1998.

This measure calculates the effect of herbivores on the relative abundance of each plant, as the difference in the change in abundance of that species between 1998 and 2002, with and without the herbivore. The effect of the herbivore on each species was then multiplied by the relative abundance of that species as a proportion of the total plant community. Finally, these products were summarised for all available plants. This measure is as equally sensitive to increases as to decreases in abundance of plants, but results in higher values for altered abundances of common rather than of rare species.

Bray–Curtis Measure of dissimilarity was calculated as:

$$B = \frac{\sum |X_{ij} - X_{ik}|}{\sum (X_{ij} + X_{ik})}$$

where: B = Bray–Curtis measure of dissimilarity, X_{ij} = Abundance of species i in sample j, X_{ik} = Abundance of species i in sample k.

The Bray–Curtis measure ignores cases in which species are absent in both community samples and it is strongly

influenced by the abundant species, so rare species add very little to the value of the coefficient (Krebs 1989).

Statistical analyses

A principal component analyses (PCA) was performed to reduce the large number of correlated variables (i.e. abundance of the 78 different species), down to a smaller number of components. We chose to base the PCA on a correlation matrix as this is the most appropriate association matrix to use when the values of the components are used in linear model analyses (Quinn and Keough 2002). The change in the component scores between 1998 and 2002 from axes explaining a large proportion of the variance were then analysed with a univariate ANOVA. By this approach, we avoid type 1 error problems due to multiple testing. We used a PCA followed by an univariate ANOVA instead of an MANOVA as this combination of methods copes better with the large number of zeros, which is typical of species abundance data and post hoc comparisons of groups are more straightforward under a univariate ANOVA framework than under a MANOVA framwork (Quinn and Keough 2002). Repeated measure analyses were avoided as the data did not fulfil the assumptions of circularity and equal variance among years.

The components from the PCA, the importance index (I), Bray–Curtis similarity measure (B) as well as the abundance of the 15 most common species, species richness and Shannon–Wieners diversity index and were all analysed as a split-plot design experiment, as the design involves different treatments with different number of replicates and hence require separate error terms for each treatment (Crawley 2002). Least significant difference (LSD)/2 or Tukey's test for honesty of significance were used in post hoc comparisons where appropriate. Suitable transformations were used on data from a few species to achieve equal variance.

Results

The abundance of all species for all plots in 1998 and 2002 was used in a PCA analyses (Fig. 2). The two first axes in the PCA described most of the variance (axis 1, eigen value = 4.1, explained variance = 27.3%; axis 2, eigen value = 3.0, explained variance = 19.9%) and as the eigenvalue of the third axis was smaller than the broken-stick eigenvalue, the other axes were not considered for further analyses. A highly significant main effect of exclosures (F = 12.49, p = 0.001) and a significant exclosure × habitat interaction (F = 5.65, p = 0.021) was found on the change of component scores for each plot between 1998 and 2002 on the first axis and a significant effect of excluding herbivores was
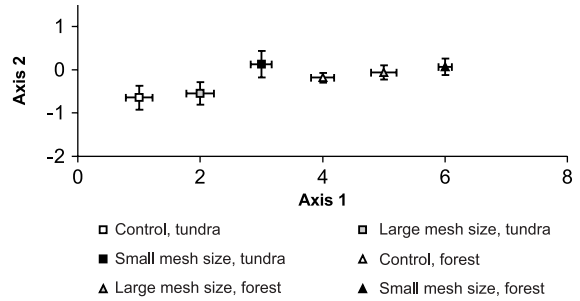
Fig. 2. The change of the principal component scores for each plot between 1998 and 2002 in different treatments and habitats on the first two axes of a principal component analyses. Mean $\pm\frac{1}{2}$ LSD (least significant difference) is used as non-overlapping bars then indicate that treatments are significantly different.

found in the change of thecomponent scores on the second axis (F = 4.63, p = 0.035). Post hoc comparisons reveal that the exclosure × habitat interaction is caused by a stronger effect of the small mesh size exclosure in the tundra than in the forest. The importance of small and large herbivores, calculated as the importance index, differed significantly (Fig. 3, F = 6.27, p = 0.017), but no effect of location or habitat, or any second or third order interactions were found.

The deposition of reindeer faeces did not differ significantly between the two habitats (Fig. 4). Faeces of moose and grouse were only found sporadically. The mountain hare pellets were also relatively uncommon, except for Seiland where relatively high densities of pellets were found in some years. Moreover, vole and lemming densities appear to be higher in the forests than in the open heathlands but the difference cannot be tested statistically due to a lack of replication. For the same reason the differences between the four locations cannot be tested either. Nevertheless, some differences appear apparent (Fig. 4, 5). Reindeer densities were lower in Vássijávri than in the other three locations and Vássijávri and Abisko experienced a vole and lemming peak in 2001 while Seiland and Joatka had high densities of voles in 1998, but low densities of rodents during the
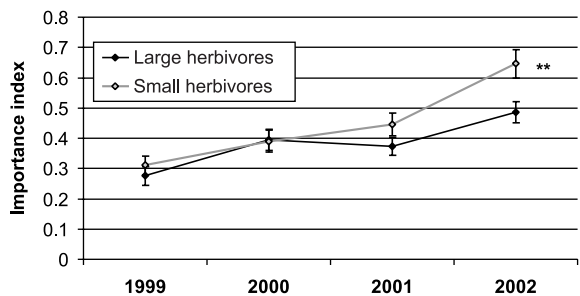
Fig. 3. Importance of large and small herbivores, calculated as a product of the relative change of species multiplied with their abundance (mean ± SE). As no significant effects of location or biotop was found, only the two types of herbivores are plotted in the figure. * p < 0.05, ** p < 0.01, ***p < 0.001.
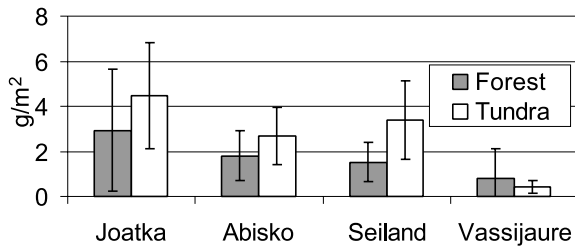
Fig. 4. Accumulated deposition of reindeer faeces from 1998 to 2002. No statistically significant differences between locations or habitats were found (mean ± SE).

rest of the study. Some voles and lemmings were caught inside the exclosures in Abisko and Vássijávri, especially in the forest.

The relative change in plant species abundance was calculated for the 15 most common species or species groups. On the basis of coverages, these species together represent about 89.7% of the total plant community (Table 1). To avoid too many empty cells in the analyses, only the sites or habitats where the plant occurred frequently were included in the analyses, and thus effects of locations or habitats could not be included in the analyses for some species. Significant effects of excluding

herbivores were found for the following six species (Fig. 6); *Vaccinium myrtillus* (F = 8.053, p = 0.008), *Vaccinium vitis-idaea* (F = 7.272, p = 0.009), *Dicranum* spp. (F = 26.44, p < 0.001), *Polytrichum* spp. (F = 5.5359, p = 0.027), *Ptilidium ciliare* (F = 19.52, p < 0.001) and *Cladina mitis* (F = 21.12, p < 0.001). With the exception of *P. ciliare* herbivore exclosure led to an increase in species abundance. Post-hoc comparisons with Tukey's test for honesty of significance showed that the small mesh size exclosures were significantly different from the other two treatments for five species; *V. myrtillus*, *V. vitis-idaea*, *Dicranum* spp., *Polytrichum* spp. and *P. ciliare*, while the controls were significant different from the two exclosure types for *Cladina mitis*. Two species, *Betula nana* (F = 3.124, p = 0.084) and *Empertum nigrum* (F = 2.144, p = 0.1484) had p-values just slightly above 0.05 and are thus included in Fig. 6. No significant effects were found for the other 7 species and no significant differences between habitats and locations, or second or third order interactions were found for any of the species. Species richness and Shannon–Wiener's diversity index were not significantly influenced by exclosure type. The dissimilarity in plant community structure between forests and open heathlands was not affected by excluding herbivores (Fig. 7).
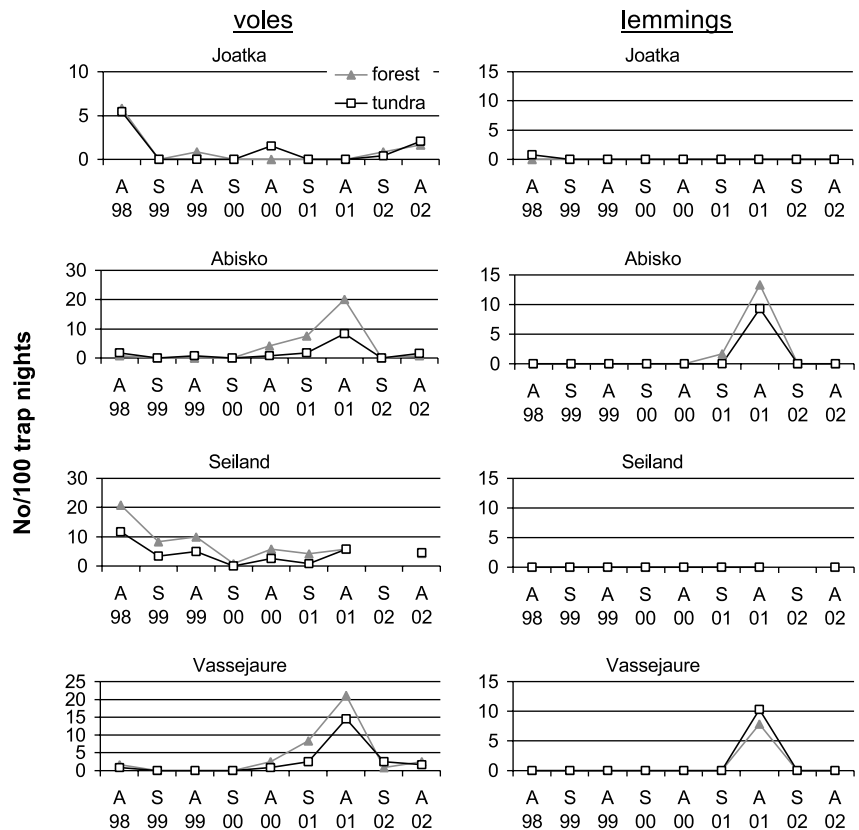

Fig. 5. Seasonal and annual variation in densities of voles and lemmings at the four study locations.

Table 1. Percent of total vegetation and percent of plots containing the species for the 15 most common species. These 15 plants do together represent 89.7% of the total vegetation. Forest (F) and tundra (T) shows which habitats the plants were abundant enough to include in the analysis and 1 (Joatka), 2 (Abisko), 3 (Seiland) and 4 (Vássijávri) show which locations the plant were abundant enough to include in the analysis.

Species	Abundance		Analysed for	
	% of total plants	% of plots	habitats	location
Empetrum nigrum	25.8	98.6	F,T	1,2,3,4
Vaccinium myrtillus	19.4	75.7	F	1,2,3,4
Betula nana	8.5	68.6	F,T	1,2,4
Deschampsia flexuosa	6.0	61.4	F	2,3,4
Dicranum spp.	5.7	100	F,T	1,2,3,4
Vaccinum vitis-idaea	4.7	88.6	F,T	1,2,3,4
Vaccinium uliginosum	3.2	62.9	F,T	2,3
Cornus suecica	3.2	31.4	F	4
Cladina mitis	2.7	67.1	T	1,2,3,4
Pleurozium schreberi	2.7	61.4	F,T	2,3,4
Ptilidium ciliare	1.9	34.3	T	2,3
Barbilophozia spp.	1.7	60	F,T	1,4
Cladonia uncialis	1.5	72.9	T	1,2,3,4
Polytrichum spp.	1.4	70	F,T	1,4
Cladonia gracilis	1.3	72.9	T	1,2,3,4

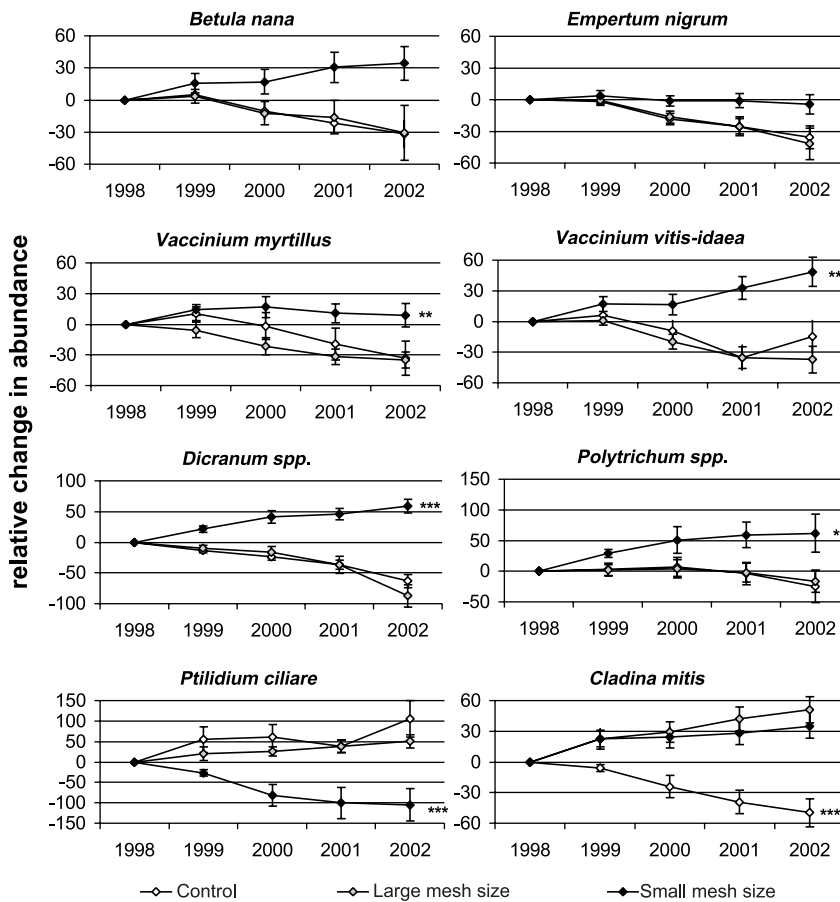Fig. 6. Relative change in abundance of plants in the controls, large mesh size exclosures and small mesh size exclosures (mean±SE). * p < 0.05, ** p < 0.01, ***p < 0.001. The stars indicate which treatment that is significantly different from the other two treatments.
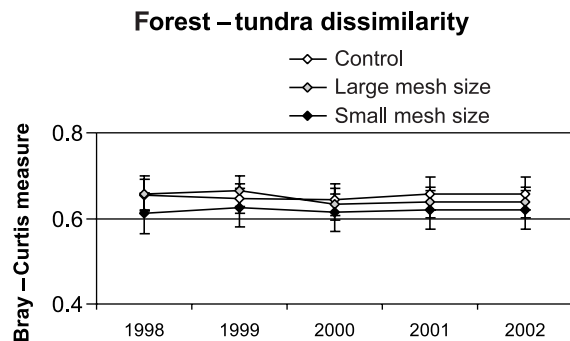
Forest – tundra dissimilarity

Fig. 7. Difference between the forest and tundra vegetation, in the control, large mesh size exclosure and small mesh size exclosure (mean ± SE). No significant differences was found between the tree different treatments.

Discussion

Our results indicate that small herbivores are more important than large herbivores for the predominating plant communities at the timberline in northernmost Fennoscandia, both in the forest and in the open heathlands. The herbivore census data shows that the major small herbivores are grey-sided voles and lemmings and that reindeer are the major large herbivore. The higher importance of small herbivores contrast with general ecological theories, as large herbivores are often found to have a more profound impact on ecosystem processes (Owen-Smith 1988, Zimov et al. 1995). In addition, based on scaling relationships between body mass and daily ranging, the impact of trampling should be greater for larger herbivores (Cumming and Cumming 2003). However, in the few studies where vertebrates of different sizes have been excluded separately, small herbivores are found to have as large or even larger effect on the plant community than large herbivores (Cid et al. 1991, Bowers 1993, Ritchie and Olff 1999, Grellmann 2002). Moreover, reindeer are semi-domesticated in northern Fennoscandia and managed for meat production. Supplemental feeding and protection from predators and parasites have been claimed to create artificially high reindeer densities (Suominen and Olofsson 2000, Moen and Danell 2003). Reindeer grazing has indeed been found to alter plant species composition (Väre et al. 1995, Olofsson et al. 2001), change nutrient availability and primary production (Stark et al. 2000, Olofsson et al. 2001, Olofsson and Oksanen 2002) and influence the abundance's of ground-dwelling (Suominen 1999, Suominen et al. 2003) and galling (Olofsson and Strengbom 2000) invertebrates. Moreover, caribou in North America (Caughly and Gunn 1993, Crête and Manseau 1996) and reindeer on Svalbard (van der Wal et al. 2001, 2004) markedly influenced the vegetation.

However, numerous studies have also revealed substantial effects of voles and lemmings on tundra vegetation (reviewed by Jefferies et al. 1994 and Mulder 1999).

During peak years, lemmings have been reported to consume up to 90% of the primary production in North America (Schultz 1968) and 66% of the mosses and 33% of the graminoids in Scandinavia (Moen et al. 1993). The primary reason that voles and lemmings had a larger effect on the plant community composition than reindeer in our study is probably that voles and lemmings are present year-around, while reindeer are migratory and only present in our study locations for a shorter period of time. Moreover, reindeer had indeed a clear impact on their main winter forage plant present in our exclosures – *Cladina mitis*. An alterative interpretation of our results is thus that in the timberline region, winter grazing by herbivorous mammals has a major impact on the abundance of their winter forage plants.

Summer grazing by microtine rodents has been reported to be low, even during peak years (Andersson and Jonasson 1986, Bergeron and Jodoin 1987). On islands with extremely high vole densities, voles consumed between 10–100% of shoots from preferred species in the winter, and only a few percent of available shoots from preferred species in the summer (Hambäck and Ekerholm 1998). The dominating role of winter herbivory in arctic locations is obvious, where the growing season only lasts for three months, and snow covers the ground for more than eight months each year. During the short summer, resident herbivores are easily saturated by the relative abundance of food. In winter, the resident endothermic herbivores consume plant parts that are available under or above the snow, and this resource is not renewed in wintertime. Consequently, the strong effect of herbivores on their winter food plants is not surprising. While it might be expected that voles and lemmings would have substantial impact on the vegetation in our two southern sites that experienced lemming peaks during the period of this study, their impact was greater than reindeer in the two northern sites even in the absence of peak population density of lemmings. Moreover, even vole densities were low during the study period in Joatka, while fairly high vole densities were found in Seiland in 1999. This finding is consistent with previously reported impacts of microtines in non-peak years (Oksanen and Moen 1994, Virtanen et al. 1997, Virtanen 2000, Grellmann 2002).

Five out of the fifteen most common species of heathlands and oligotrophic forests are significantly influenced by microtine rodents. Four of these species increase following herbivore exclosure while only one declined. Two of the species most responsive to herbivore exclosure, *Vaccinium myrtillus* and *Vaccinium vitis-idaea*, are the most preferred winter forage plants for grey-sided voles (Kalela 1957), and the other two, *Dicranum* spp. and *Polytrichum* spp., are preferred winter forage for lemmings (Kalela 1961). The only species to decrease when herbivores are excluded was the hepatic *Ptilidium ciliare*. Hepatics have been reported to

be weak competitors that only can persist in grazed or disturbed patches (Gjaerevoll 1956, Moen et al. 1993, Virtanen et al. 1997).

Only *Cladina mitis* increased in response to the exclosure of large herbivores. Fruticose lichens are known to be particularly sensitive to reindeer and caribou as they suffer from both trampling (mainly in summer) and selective grazing (mainly in winter, Pegau 1969, Wielgolaski 1975). Numerous studies have reported that reindeer or caribou decrease the abundance of lichens (Pegau 1969, Väre et al. 1995, 1996, Manseau et al. 1996, Arseneault et al. 1997, Olofsson et al. 2001, van der Wal et al. 2001). Even though only *Cladina* lichens were significantly influenced by excluding reindeer, we should not conclude that reindeer are unimportant in these areas. Four years should be regarded as a short term experiment compared to the long life span of these plants (Yodzis 1988, Jeffries et al. 1994). *Cladina* lichens can in the long term, in the absence of reindeer, form thick carpets that out-compete vascular plants and mosses in suitable habitats (Du Rietz 1925, Söyrinki 1938, Nordhagen 1943, Väre et al. 1995, Olofsson et al. 2001, van der Wal et al. 2001). Short-term effects of reindeer on grasses and herbs have only been recorded in northern Fennoscandia in areas with particularly high grazing pressure (Brathen and Oksanen 2001). The indirect effects of reindeer on the plant community, through changes in nutrient availability and soil temperature, might take long time before they can be observed (Olofsson et al. 2004).

Our analysis gives conflicting results on the importance of herbivory in the two different habitats. The PCA showed a larger effect of excluding herbivores in the open heathlands than in the forest. However, the importance index (I) revealed that small herbivores were indeed more important than large herbivores but no interaction between herbivore and habitat was found. The difference between these two measurements is that PCA is much more sensitive to rare species than the importance index. The importance index is mainly affected by the changes in abundance of a few dominant species. Thus the interaction between herbivory and habitat in the ANOVA, based on the principal components in the ordination analyses is totally dependent upon a few species such as *Cladina mitis* and *Ptilidium ciliare*, which are more common in the tundra and respond dramatically to an altered grazing regime. A few voles and lemmings were caught inside the exclosures at Abisko and Vássijávri. It is possible that the effect of the small mesh size would have been larger, if no microrodent would have entered the exclosures.

In a review on vertebrate herbivores in northern plant communities (Jefferies et al. 1994), one of the stated research priorities for the future were to established exclosures of different mesh sizes to exclude different herbivores, in a variety of plant communities across the circumpolar region and record short-term (5 yr) and long-term (25 yr) changes in vegetation. In this study, we did indeed establish exclosures with different mesh sizes in two different habitats. Even though we could not work across the whole circumpolar region, we did replicate the experiment in four different landscapes in northern Fennoscandia. The main conclusions are that (1). Herbivores influence plant communities in northern Fennoscandia. (2). Small herbivores (e.g. voles and lemmings) have a larger impact on the plant community than large herbivores (e.g. reindeer). (3). All winter food plants were influenced by their consumers. (4) Herbivores did not increase the difference in plant community composition between forests and open heathlands. The continuation of these studies over the next 10–20 years will provide excellent opportunities to understand the role of herbivores in northern plant communities.

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