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Effects of reindeer density on vascular plant diversity on North Scandinavian mountains

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Abstract: We studied the effects of reindeer grazing on species richness and diversity of vascular plants on dolomite influenced low alpine sites in the species rich northern part of the Scandes using 8 sites with different reindeer densities. Two sites were situated inside Malla Strict Nature Reserve, where reindeer grazing have been totally prohibited since 1981, and strongly restricted since 1950s. The six other sites were located in other species rich hotspot sites standardized to be as similar to the dolomite-influenced sites in Malla Strict Reserve as possible but varying in reindeer densities commonly found in the Fennoscandian mountain chain. Each site with a habitat complex especially rich in rare vascular plants (the *Dryas* heath – low herb meadow complex) was systematically sampled in four plots of 2 m x 10 m. The plots were divided to 20 squares of 1 m x 1 m, and complete species lists of vascular plants were compiled for each of the squares. The first DCA (detrended correspondence analysis) axis was strongly related to an index of reindeer grazing, indicating that grazing has a strong impact on the composition of the vegetation. None of the characteristics indices of biodiversity (species richness, evenness or Shannon-Wiener H') was correlated with reindeer density. The local abundances of categories consisting of relatively rare plants (Ca favored plants and red listed plants of Finland) showed significant, positive correlation with the intensity of reindeer grazing. We conclude that even though the density of reindeer has no influence on the total species richness or diversity of vascular plants, reindeer may still be important for regional biodiversity as it seems to favour rare and threatened plants. Moreover, our results imply that standard diversity indices may have limited value in the context of conservation biology, as these indices are equally influenced by rarities and by trivial species.

Key words: arctic, alpine, diversity, disturbance, grazing, *Rangifer tarandus*, vascular plants.

Rangifer, 25 (1): 5-18

Introduction

One of the established ecological principles is the Intermediate Disturbance Hypothesis (IDH), stating that for each habitat, there is an optimum level of disturbance, leading to highest plant species diversity by allowing the coexistence of both disturbance-adapted plants and plants adapted to various durations of transient dynamics initiated by the disturbance (Grime, 1973; 1979; Connell, 1978). As the optimum level supposedly depends on the intensity of environmental stresses, the dominating impact of disturbance on local species diversity changes from positive to negative along gradients of decreasing primary productivity (Grime, 1979; Proulx & Mazumder, 1998; Austrheim & Eriksson,, 2001).

Among the forms of disturbance where humans play a role, reindeer grazing is the most extensive form in northern Fennoscandia, influencing practically all parts of the area save some islands and coastal areas of northern Norway (especially in Nordland, see Bernes, 1996; Suominen & Olofsson, 2000). Given the prevailing view that arctic-alpine plants live in a stressful environment, where the intensity of disturbance that maximize diversity should be low, reindeer grazing have often been regarded as a negative factor that overexploits arctic-alpine habitats, decreases biodiversity and causes erosion (see Moen & Danell, 2003).

Studies on the impact of reindeer on Fennoscandian arctic-alpine nature have improved our knowledge on the impact of reindeer on the coverage of lichens (Johansen *et al.*, 1995; Ihse & Allard, 1995; Johansen & Karlsen, 1996; 1998; Allard *et al.*, 1998), on nutrient mineralization rate and primary production (Stark *et al.*, 2000; Olofsson *et al.*, 2001; Olofsson & Oksanen, 2002; Stark & Grellmann, 2002), on ground temperatures (Olofsson *et al.*, 2003) and on abundances of ground-dwelling (Suominen *et al.*, 1999a; Suominen *et al.*, 1999b) and galling (Olofsson & Strengbom, 2000; Herder *et al.*, 2004) invertebrates. Vegetation studies have corroborated the predictions of IDH in the context of lichen rich heathlands, which become overwhelmingly dominated by *Cladina stellaris* in the absence of reindeer, whereas only crustose lichens survive on the most grazed and trampled sites along reindeer fences. Highest diversity is found under intermediate grazing conditions, *e.g.* on fairly intensely used winter ranges, characterized by a species-rich mixture of fruticose lichens, cup lichens, crustose lichens and bryophytes (Du Rietz, 1925; Dahl, 1957; Helle & Aspi, 1983; Oksanen, 1978; Oksanen & Virtanen, 1995; Olofsson *et al.*, 2001; Väre *et al.*, 1995; Suominen *et al.*, 1999a).

However, there are few studies focusing on the effects of reindeer grazing on the diversity of vascular vegetation and on the flourishing of rare arctic-alpine plants, even though sustainable reindeer grazing, which promotes a high biodiversity, is an environmental quality objective of the Swedish Government for mountain areas (Swedish Environmental Protection Agency, 1999). Recall also that reindeer is a native herbivore in Fennoscandia, and that wild ungulates in arctic areas in North America often have been found to be resource limited and thus pronouncedly influenced the vegetation (Caughly & Gunn, 1993; Crête & Manseau, 1996). Moreover, grazing pressure in the arctic may have been even higher in the evolutionary past than today (Zimov *et al.*, 1995). Thus, another view of the tundra is that it is an ecosystem where grazing has always been intense and where the survival of many currently rare plants may be critically dependent on the actions of the last arctic ungulate that has survived in Eurasia – the reindeer (see Oksanen, 1990; Oksanen & Ranta, 1992; Oksanen & Virtanen, 1997; Oksanen & Oksanen, 2000).

Most of the reported effects of reindeer grazing are from winter-grazed or year-around grazed areas, but reindeer also influences the vegetation in summer-grazed areas (Oksanen, 1978; Bråthen & Oksanen, 2001; Olofsson *et al.*, 2001; Moen *et al.*, 2003). In the context of protecting rare vascular plants, the impacts of summer grazing are focal, since our arctic-alpine rarities are found in the mountain chain, which is primarily used for summer grazing. The effect of summer grazing on biodiversity can be studied by constructing exclosures (Oksanen & Moen, 1994; Virtanen *et al.*, 1997; Moen & Oksanen, 1998; Virtanen, 1998; 2000; Bråthen & Oksanen, 2001) but this approach is so slow that impacts on biodiversity can only be inferred by extrapolation, based on initial stages of transient dynamics.

Old large-scale fences, constructed for non-scientific purposes, provide another opportunity. Results obtained by using them as makeshift experiments indicated that the diversity of vascular plants and bryophytes increases in some locations in response to moderate and sometimes even in response to extremely intense grazing by reindeer, while it in other locations species diversity does not differ between grazing regimes (Olofsson *et al.*, 2001). Unfortunately, such studies are burdened by design problems (*e.g.* fixed directions of grazing gradients). In this study, we have thus used a comparative approach in the context of the species-rich habitats of North Scandinavian mountains by treating the varying grazing intensity in the area as independent variable and patterns in plant species diversity as dependent variable.

The study area and outlines of our approach

Northernmost Fennoscandia is characterized by large variations in species richness, which is especially pronounced for arctic-alpine plants and for

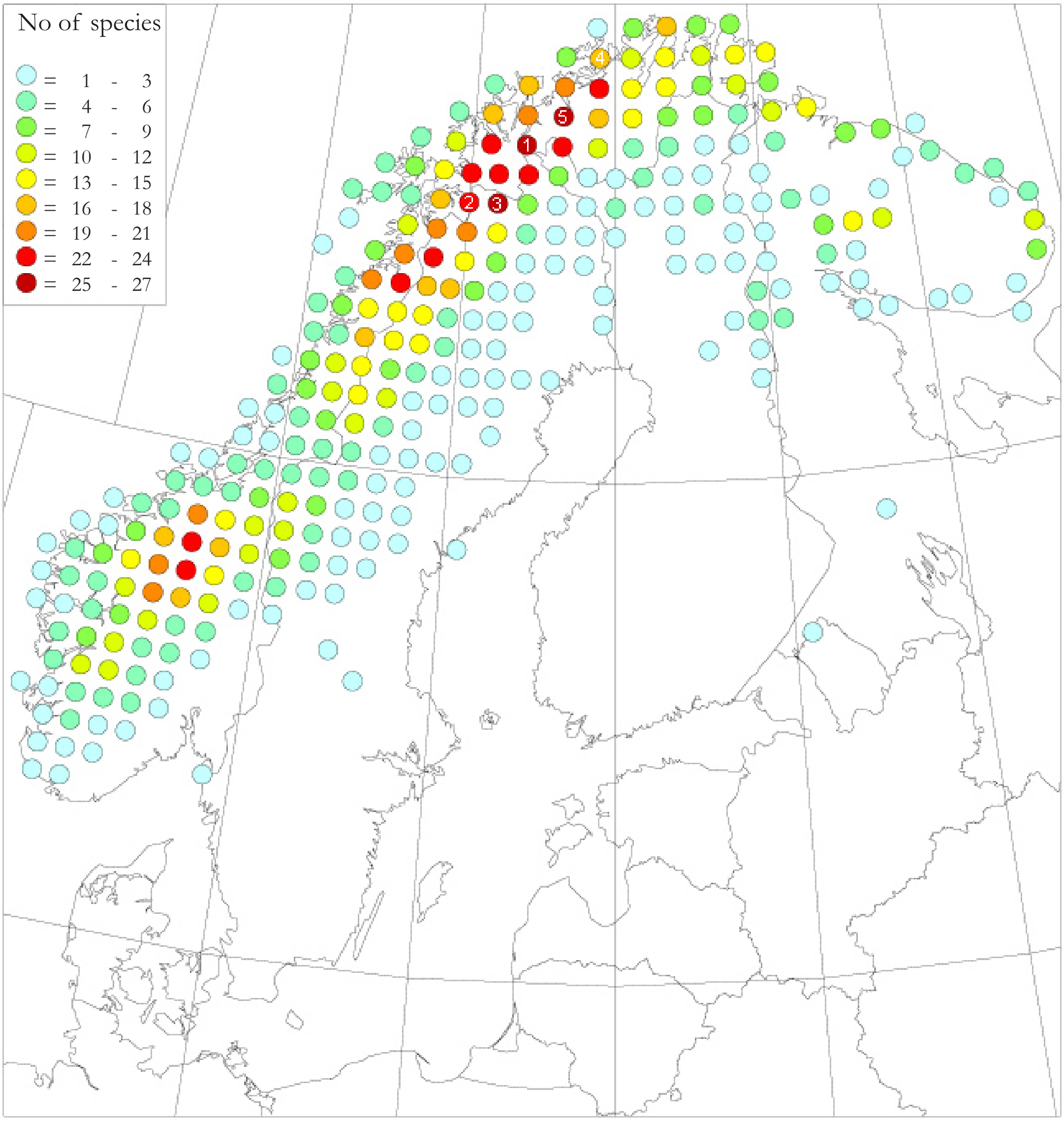

Fig. 1. Occurrence of lime favored arctic-alpine species in different northern grids of Atlas Florae Europaea (Jalas *et al.* 1972-99). The number on the maps refer to the following sites: 1. Pikku-Malla, Iso-Malla and Saana, 2. Geadgečorro and Boazuvárri, 3. Vággečohkka, 4. Jeahkkir, 5. Jávrioaivit.

plants favoured by lime rich bedrock. To illustrate the general pattern in an objective way, we have compiled data on the occurrence of arctic-alpine phanerogams (criterion: Fennoscandian localities presented by Hultén (1971) are primarily above the timberline) and phanerogams noted as lime favored by Mossberg *et al.* (1992) in different parts of the northern parts of Fennoscandia and Kola, in accordance to the currently available part of Atlas Florae Europeae (Jalas *et al.*, 1972-1999), now covering the phanerogams of in the beginning of the customary systematic rank order (including families Brassicaceae, Papaveraceae, Crassulaceae and Saxifragaceae; species without known localities north of 68°N were excluded).

The pattern emerging from this data set is clear indeed. The occurrence of arctic-alpine plants that are lime-favored (Fig. 1) is strongly concentrated to a relatively small 'hot spot area' in the eastern and interior part of the mountain chain, stretching from the Abisko area in northernmost Swedish Lapland to Altafjord in Finnmark, Norway. The highest species richness is found on the grid encompassing the surroundings of Lake Kilpisjärvi (Gilbbisjávri), but values obtained for surroundings of Torneträsk (Duortnosjávri) and Reisadalen (Raisávžži) are only marginally lower. The underlying reason for the floristic richness of the area is the rich occurrence of dolomite in the lowermost and oldest overthrust plate of the Scandinavian mountain chain (Du Rietz, 1924), and the relatively continental climate, which counteracts leaching.

The use of this hot spot area for reindeer grazing is variable (Bernes, 1996). In Sweden and in northernmost Norway, the migratory herding system allows relatively high reindeer densities, as the lichen grounds are saved from unnecessary trampling. Densities on summer ranges are thus typically of the order of 5 to 10 reindeer per km^2. On the Finnish side, where grazing is stationary, reindeer densities are only 1 to 2 animals per km^2. Moreover, the Finnish side harbors the Malla Strict Nature Reserve, located right in the 'hottest' part of the hot spot – on the western shores of Lake Kilpisjärvi. One of the main scopes of the reserve was to protect the rich flora against the supposedly negative impacts of reindeer husbandry (Montell, 1914). Hence, reindeer grazing in the reserve has been restricted since early, 1900s, though the ambition to reduce reindeer grazing and associated human activities was not especially successful before the late, 1950s (Itkonen, 1948; Kokko, 1969). In, 1981, reindeer grazing in the reserve became totally forbidden, but even afterwards, some grazing has occurred in the western part of the reserve (Iso-Malla, see below).

The northern hot spot area thus provides unique opportunities for studying the impact of reindeer grazing on the rare elements of the North Fennoscandian flora. Unfortunately, however, the 'Malla experiment' has major design problems, which had to be solved before this opportunity could be exploited. The point of departure for establishing the Malla Reserve was Montell's personal excitement about the rich flora and fascinating vegetation of this mountain. To translate this into a random sampling process and to define the statistical population, from which the reserve could be regarded to be drawn, is not easy. Yet, this is vital for the obtainance of replicated controls, without which the 'Malla experiment' would be scientifically worthless. To obtain this replication, we overlooked current national borders, which are of no relevance to the distributions of plants, and tried to imagine what mountains would been likely to fascinate Montell chosen any if he had got acquainted with some other part of North Fennoscandian hot spot. From the general areas thus defined, we searched for sites geologically and topographically maximally similar to Malla, with exposed dolomite rock belonging to the oldest overthrust plate being exposed above but no more than 350 meters above the treeline. To avoid pseudoreplication, we did not allow for selection of two sites from the same side of the same valley formation, unless one represented the edge of the mountain chain, while then other was located along the perimeter of a 'window' (outcropping granite area), where the dolomite-rich geological formation became exposed again. As precipitation, altitude from the timberline and latitude differed between the sites anyhow; the sites were chosen so that the sites inside Malla Reserve, with the lowest grazing pressure, were in the middle of the environmental gradients. When the Malla sites lost their average position along some of these gradients, the next grazed site was selected from the underrepresented parts of the gradient. By these criteria, we found one 'Malla replicate' from the Finnish part of the Kilpisjärvi Basin, three from the Swedish Torneträsk area and one from Reisadalen in Norway. As we had decided to have at least six areas with reindeer grazing, we had to extend our sampling area and to include one site from the outer parts of Altafjord in Norway, in the periphery of the hot spot.

The locations of the study sites are presented in Fig. 2. The general characteristics of these eight sites, ranked in accordance to the intensity of reindeer grazing (pellet group index), are summarized in Table 1. As an index of species pool, we used the numbers for the Atlas grid in question (Jalas *et al.*, 1972-99), except for sites less than 5 km from a grid boundary, whose pools were computed by averaging the numbers of species for both grids, rounded integers to the direction of the values on the grid where the site was located.

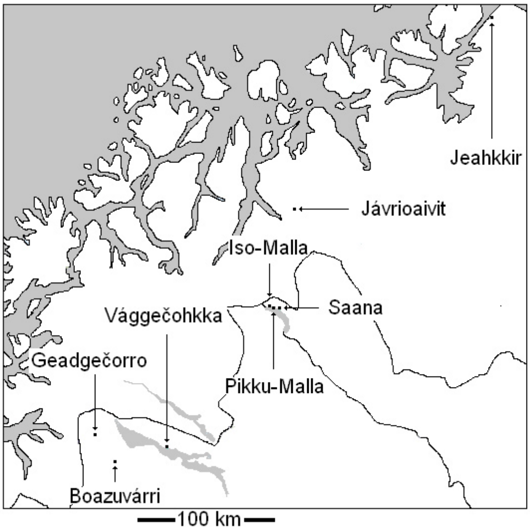

Fig. 2. Map over the study area, showing the locations of the study sites in northernmost Fennoscandia (Boazuvárri, Geadgečorro and Vággečohkka in Sweden; Pikku-Malla, Iso-Malla and Saana in Finland; Jávrioaivit and Jeahkkir in Norway).

Methods

In these eight areas, we have quantified the intensities of reindeer grazing and studied the composition of the vascular vegetation within the pivotal habitat for the majority of the rare vascular plants – the *Dryas* heath - low herb meadow complex, created by the impact of base rich bedrocks, especially dolomite (Du Rietz, 1924). Data on vascular plant species richness were collected between 10th July and 12th August, 2001. In each site, sampling started by identification of exposed dolomite rocks, which in northern Scandinavia occur primarily as discontinuous horizontal strands, outcropping from the softer shales. Sampling started from the midpoint of the first encountered dolomite strand and proceeded as follows. A grid of 10 m x 2 m was laid out 2 m to 12 m below the edge of the exposed dolomite rock, the long side of the grid pointing straight down the slope. The grid was divided into, 20 plots on 1 m x 1 m. This sampling method ensured that the grid became located within the *Dryas* heath - low herb meadow complex and included a fair amount of habitat variation. When the first grid had been located, three more grids were sampled from the same area moving horizontally along the dolomite rich part of the slope and choosing the nearest exposed rocks which were at least 100 m from the first sampling site and from each other. For each of the 80 (1 m x 1 m) subplots at each of the 8 sites, a complete list of all vascular plant species was compiled. Abundances of vascular plants within a grid were calculated as the % of subplots within each grid, with the plant present.

Since the reindeer data compiled by Bernes (1996) and those obtainable from national authorities refer to entire districts, their representativeness for local areas is imperfect at its best. We thus used a pellets group abundance index as our primary estimate of reindeer density. Normally, this technique is applied so that the numbers of dropping groups are counted along long transects (Van der Wal *et al.*, 2001; Moen *et al.*, 2003). While appropriate for studies focusing on widespread habitats, this technique is less suitable for our study, focusing on patchily occurring lime-rich habitats. Instead, presence/absence of reindeer pellets was recorded for each of the 1 m x 1 m plots, used in the vascular plant study and the natural logarithm of the number of plots with reindeer pellets was used as an index of reindeer density. The natural logarithm of 1+ the number of plots with pellets was used to down-weight the importance of the sites with the highest reindeer density, which would otherwise dominate in the computations of regressions. Reindeer pellets decompose slowly and remain visible for several years. The abundance of reindeer pellets is thus indicative of the reindeer density over, at least, the last 10 years.

To describe over-all species diversity of the grids, we used the exponential form of the Shannon-Wiener function. We used the Shannon-Wiener function, as it is sensitive to rare species, and presented it in the exponential form, as this is a unit more understandable to ecologists (Krebs, 1998). We used Smith and Wilson's index of evenness, as this is robust to differences in quality of the abundance estimates of common and rare species (Krebs, 1998). Plants were defined as calcium favored respectively arctic and alpine according to Mossberg *et al.* (1992), Hultén (1971) and Nilsson (1986). To obtain a set of rare plants, which definitely belonged to the species pool of the Finnish sites, we even focused on the occurrence of vascular plants belonging to the Finish red-list (Ryttäri & Kettunen, 1997), excluding species not encountered in the 'Finnish wedge' (*Gymnocarpium robertianum, Gentianella campestris* ssp. *campestris*

Table 1. Position, altitude, precipitation (climate stations: 1 = Kilpisjärvi, 2 = Katterjokk, 3 = Abisko, 4 = Ankerlien, 5 = Porsa Gruber), number of arctic-alpine and lime favoured phanerogams species in the Atlas Florae Europae (Jalas *et al.*, 1972-99) grid to which the site belongs within the taxa for which the Atlas work has been completed, and reindeer grazing pressure in accordance to official statistics (reindeer per km^2, Bernes, 1996) and reindeer pellet counts. The reindeer densities of Jávrioarvit are adjusted for the real size of the summer range and are thus different to the number presented by Bernes (1996).

Site	Position	Altitude m.a.s.l. (and m above treeline)	Precipitation mm/yr (climate stations)	Arctic alpine plants (pool)	Lime favored plants (pool)	Lime favored alpine plants (pool)	Reindeer density per km^2	Reindeer pellet count	
								raw	ln trans-fm
Pikku-Malla	69°05'N, 20°45'E	640 (90)	450 (1)	49	32	27	0	0	0
Iso-Malla	69°05'N, 20°40'E	700 (150)	450 (1)	49	32	27	0	0.75	0.56
Saana	69°00'N, 20°50'E	720 (170)	450 (1)	48	30	25	1-2	2	1.10
Geadgečorro	68°24'N, 18°20'E	700 (200)	848 (2)	47	30	24	5-10	2	1.10
Boazuvárri	68°16'N, 18°32'E	780 (130)	330 (3)	47	31	25	5-10	2.5	1.25
Vággečohkka	68°24'N, 19°05'E	760 (160)	330 (3)	47	31	25	3-5	4.5	1.70
Jeahkkir	70°27'N, 23°47'E	200 (-50(1))	748 (4)	40	21	18	5-10	4.0	1.61
Jávrioaivit	69°31'N, 21°15'E	860 (360)	455 (5)	47	31	25	>10(2	15	2.77

1) The site is treeless due to long-lasting intense grazing, but in sites inaccessible to reindeer, tree-sized birches are encountered up to 250 m.a.s.l.

2) Size of summer range erroneosly marked 4 times larger than it is by including most of the autumn-spring range; reindeer density corrected accordingly.

and *Allium schoenoprasum* var. *sibiricum*). In this part of the study, we used the red list concept both in narrow sense (categories 1-3, *i.e.* extinct, critically endangered and threatened species), and broad sense (categories 1-4, including even species considered as near to be threatened). Comparisons focusing on these categories of plants are thus biased in the favor of finding highest numbers of occurrences in the Finnish sites, everything else being equal.

The structure of the data set was described with a DCA (detrended correspondence analyzes) and the correlation of the axis with grazing was tested. All ordination analyses were performed with the software package CANOCO (ter Braak, 1998). We tested the effect of reindeer density on species richness with linear regression, with sites as sampling units.

Results

The reindeer pellet abundance indices reveal that there is a clear gradient of grazing pressure between the eight study sites, with the lowest reindeer density, as expected, on Pikku-Malla and Iso-Malla, and the highest grazing pressure on Jávrioaivit (Table 1). The local indices of grazing pressure are, by and large, consistent with the district level data on reindeer densities. The DCA was able to detect 4 significant gradients (Table 2). The first axis describes most of the variation and is mainly related to reindeer density (Fig. 3). The second and third axes are of fairly similar importance and seem to be mainly related to altitude and moisture respectively.

There was no significant correlation between reindeer density and any of the conventional indices of biodiversity (species richness, the Shannon-Wiener index of species diversity or the Smith and Wilson index of evenness, Fig. 4, Table 3). On the other hand, reindeer density was significantly and positive correlated with the richness of Ca-favored species and Finnish red-listed species in narrow sense (1-3) (Fig. 5). Moreover, there were a tendency for a positive relationship between reindeer density and species richness of arctic and alpine species and Finnish red-listed species in broad sense (1-4). Notice that these correlations emerged in spite of the fact that the area with the third highest grazing intensity – Jeahkkir – harbored considerably fewer arctic alpine species and lime-favored species than the other study sites (Table 1).

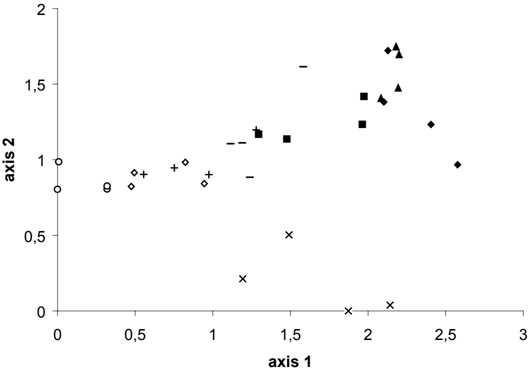

Fig. 3. Ordination plot from the DCA (detrended correspondence analysis), based on sample grids (32 grids in 8 sites). ■ Pikku-Malla, ▲ Iso-Malla, ◆ Saana, + Geadgečorro, – Boazuvárri, ◇ Vággečohkka, O Jeahkkir, × Jávrioaivit.

The occurrence of individual species was too variable between the various study sites to allow statistically established inferences concerning their relation to grazing pressure. To allow for tentative conclusions and to provide background for inter-

Table 2. Eigenvalues and variance explained by the first four axes in the DCA analyses and regression coefficients between environmental variables and the 4 axes.

Axis	1	2	3	4
Eigenvalue	0.347	0.188	0.114	0.062
Community composition:				
Variance explained (%)	15.8	8.5	5.2	2.8
Cumulative variance (%)	15.8	24.3	29.5	32.3
Species-environment relation:				
Variance explained (%)	31.5	15.7	-	-
Cumulative variance (%)	31.5	47.2	-	-
Regression coefficients:				
Reindeer density	-0.4291	-0.2349	0.1152	0.1056
Precipitation	-0.1489	-0.0152	-0.2242	-0.1752
Altitude	-0.2382	0.3408	-0.0867	-0.1002
Inclination	0.0642	0.0126	0.1558	0.027

Table 3. Linear and quadratic regressions between the reindeer density index and the various measurements of richness and diversity.

		R^2	*d.f.*	*F*	*P*
Species richness	Linear	0.073	6	0.47	0.518
Diversity (N')	Linear	0.006	6	0.038	0.851
Evenness (E-var)	Linear	0.022	6	0.14	0.723
Ca favored species	Linear	0.510	6	6.3	0.047
Arctic-alpine species	Linear	0.310	6	5.17	0.151
Red listed (1-4) species	Linear	0.287	6	2.214	0.171
Red listed (1-3) species	Linear	0.512	6	6.3	0.046

preting the observed correlations, we nevertheless summarize the occurrences of Finnish; Swedish or Norwegian red listed species or genera including many such species represented by at least ten records (Table 4). We see that all the taxa showing any clear relationship to grazing were more abundant on the most grazed mountains.

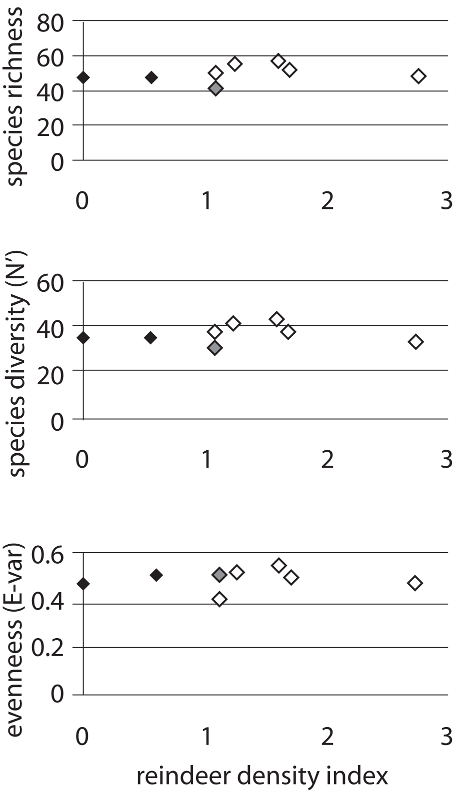

Fig. 4. Relationship between reindeer density and species richness, species diversity and species evenness. The two sites inside Malla Reserve are marked with black squares and Saana is marked with gray squares.

Discussion

Reindeer grazing is clearly related to plant community composition, as the first axis of the ordination, which explained a large part of the variance, mainly correlates with reindeer density. By itself, this relation does not tell what the cause is and what is the consequence. For the Swedish and Norwegian data points, the relation could even be interpreted so that rich occurrences of lime are both favorable for certain groups of plants and make the mountains attractive for reindeer. However, this explanation does not apply to the Finnish data points, since the stationary grazing practices account for the low grazing pressure on the Finnish mountains and the virtual absence of reindeer from the Malla reserve is a consequence of administrative decisions.

In spite of the clear relation between plant community structure and grazing pressure, reindeer-grazing pressure is totally unrelated to the standard measures of biodiversity - species richness, the Shannon-Wiener diversity index and the index of evenness. Correspondingly, Moen *et al.* (2003) have not found any differences in diversity between summer grazed heathlands and heathlands with relaxed grazing pressure in the summer. However, the numbers of calcium favored species and Finnish red listed (1-3) species is positively correlated with reindeer density and even the number of arctic-alpine species showed a similar tendency. This indicates that even though reindeer has no detectable effect on the local species richness of all vascular plants, reindeer grazing increases the number of those species, which make the largest contribution to γ-diversity (biodiversity in northern Europe).

While correlative data have their inherent weaknesses, we cannot see any reasonable alternative explanation but regard differences in reindeer densities as causal for the pattern observed here, except for random variation in site conditions. This explanation can be rejected by standard statistical criteria ($P < 0.05$). The four most intensely grazed sites include the southernmost and northernmost sites, the sites with the most oceanic and most continental climates, and the sites with lowest and highest altitudes, both from the sea level and from the timberline. Geological conditions were standardized by the sampling method. It seems thus implausible that any shared physical attributes of these sites would account for the rich occurrence of calcium-favored species and Finnish red listed species in the strict sense (categories 1-3) in the intensely grazed sites. Differences in species pool cannot possibly account for the pattern, since the pool of calcium favored species in the Kilpisjärvi area is at least equally large as around Torneträsk (Boazuvárri, Vággečohkka, Geađgečorro) and Reisadalen (Jávrioaivit) and larger than in outer Altafjord (Jeahkkir).

The discrepancy between the results concerning over-all diversity and flourishing of rare and threatened plants indicates that collective indices like the number of species present or the Shannon-Wiener *H'* have limited value in the context of nature protection. It is at least equally important to look at the identity of the species, their local abundances and at their protection status.

Although the species level data must be treated with caution, as the lack of replication prevents us from testing these patterns statistically, they can be used to clarify how grazing might influence the dynamics of arctic-alpine plant populations. All the taxa for which the grazing favouredness index was higher than +80 consisted of relatively small plants with low-lying foliage and primarily or exclusively sexual reproduction, a combination of traits typical for red-listed arctic alpine plants. (Ryttäri & Kettunen, 1997). That herbivory can increase the abundance of such plants by preventing competitive exclusion is not especially surprising (Grime, 1973; 1979; Connell, 1978; Oksanen & Virtanen, 1997; Olff & Ritchie, 1998; Pärtel *et al.*, 1999).

Even abundance of lime favored plants correlated positively with grazing pressure. Moreover, R. Virtanen (pers. comm.) pointed out that the species showing clearest positive relation to grazing are relatively drought-adapted. Intense reindeer grazing may indeed make the sites drier as reindeer paths even work as drainage channels in rainy weather. Moreover, grazing-inflicted erosion may spread lime and nutrients from exposed rocks to their surroundings and grazing even speeds up nutrient mineralization (Olofsson *et al.*, 2004). However, the causal factors responsible for these correlations can be indirect. The lime-favored plants occurring in our material are, in practice, a subset of arctic and alpine plants and contain many red-listed species. Moreover, the characteristic features of drought-adapted plants - low stature and small or narrow leaves – increase grazing-tolerance while making the plants weak competitors in closed vegetation. The most parsimonious interpretation of our results is thus that in the habitats sampled by us (heaths and meadows close to dolomite outcrops), grazing and associated mechanical disturbance favors small plants, which are weak competitors and require disturbed ground for successful reproduction, as even shown in the experiments conducted in the other alpine habitats in the Kilpisjärvi area (Virtanen, 1998; 2000; Virtanen *et al.*, 1997) and in northernmost Norway (Moen & Oksanen, 1998; Olofsson *et al.*, 2002).

Management perspectives

The present study was motivated by the need of a scientific basis for the future management of the Malla Strict Reserve. The results reported here pertain to one of the goals of these preserves: to protect rare and threatened species. Even a maximally conservative interpretation of our results implies that reindeer densities prevailing in northwestern Finnish Lapland cannot be regarded as harmful for the survival of Fennoscandian arctic-alpine rarities. To the contrary, our results indicate that the majority of these species thrive best on maximally intensely grazed mountains. Scientifically, this indication is hardly surprising. The arctic and its subarctic-alpine extensions are characterized by intense grazer-plant interactions, with lemmings and reindeer/caribou in main roles (Tihomirov, 1958; Wielgolaski, 1975; Baztli *et al.*, 1981; Crête & Manseau, 1996, Oksanen & Oksanen, 2000), and elimination of a strong interactor tends to reduce biodiversity (Paine, 1974; 2000).

Table 4. Occurrences of plants red listed plants in Finland, Sweden or Norway on the grids representing the four least intensely grazed areas (Pikku-Malla, Iso-Malla, Saana, Geađgečorro) and in the four most intensely grazed areas (Boazuvárri, Vággečohkka, Jeahkkir, Jávrioaivit). Numbers refer to the total number of subplots where the taxon was encountered. The index of grazing favouredness is computed as $100(N_i\text{-}N_w)/max(N_i, N_w)$, where N_i is the number of subplots in the intensely grazed areas where the taxon in question was encounters and N_w is the corresponding number for the weakly grazed areas.

Taxon	Weak Grazing	Intense Grazing	Grazing Favoredness
Viola rupestris ssp. *relicta*	0	20	+100
Armeria maritima ssp. *sibirica*	0	14	+100
Veronica fruticans	2	19	+89
Euphrasia salisburgensis	7	58	+88
Rhododendron lapponicum	4	26	+85
Minuartia spp.	6	35	+83
Chamorchis alpina	4	7	+57
Antennaria spp.	31	48	+35
Erigeron spp.	36	55	+35
Bothrychium spp.	10	10	0
Campanula uniflora	67	42	-37

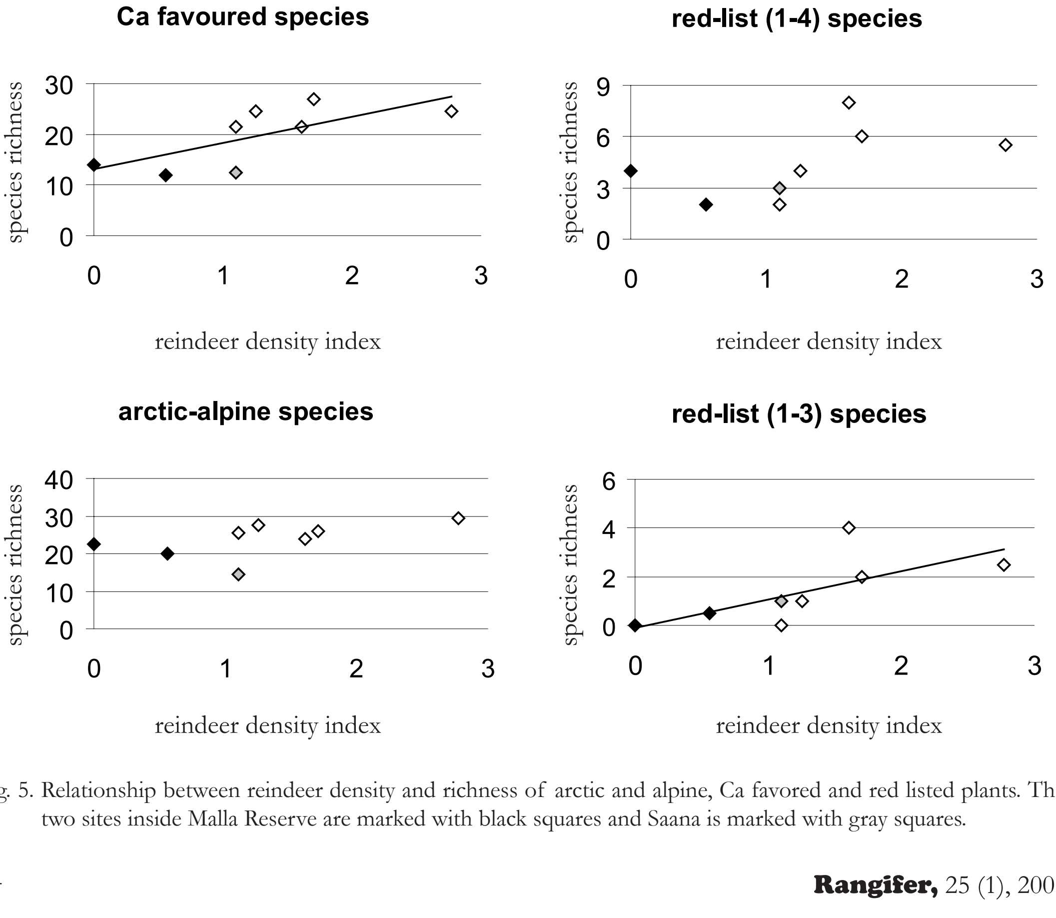

Fig. 5. Relationship between reindeer density and richness of arctic and alpine, Ca favored and red listed plants. The two sites inside Malla Reserve are marked with black squares and Saana is marked with gray squares.

Whether and in which time scale the current lack of reindeer grazing on Malla can be regarded as perilous for our arctic-alpine plants is nevertheless a complicated issue. The rare species found on our plots on the intensely grazed mountains, are present on Malla, too, but have more restricted habitat range. On Malla, they occur primarily in habitats, where the density of taller plants is low for reasons other than grazing, such as rock outcrops and wind-deflated gravel fields (own observations, and personal communication with H. Väre, R. Virtanen and H. Kauhanen). In these habitats, the majority of the rarities seem to be doing quite well on Malla, too. However, small, local populations face the risk of extinction and the rate recolonization depends on the abundance of the species in the area (Hanski & Gyllenberg, 1993). In a longer time perspective, habitat loss and reduced abundance can thus threaten the persistence of arctic-alpine rarities on Malla via impacts on metapopulation dynamics, even if their current populations were not in immediate peril.

While the risks outlined above should be taken seriously, the current situation gives no reason to panic. As for the future of arctic-alpine rarities on Malla, there is time to test the interpretations presented above by studies conducted along local gradients of grazing intensity and by manipulative experiments. Recall that our results concerning the relation between reindeer grazing and abundance of arctic-alpine rarities depend on the assumption that, with respect to abiotic factors, the reference areas and Malla can be regarded as random samples, drawn from a single statistical population. The premise that such a statistical population can be defined *a posteriori* is central for the whole idea that Malla is scientifically valuable as a reindeer-free reference area. Unfortunately, however, there is no totally dependable way to mimic random sampling, if the treatment has not been drawn randomly from an *a priori* defined statistical population. This is indeed a major weakness for the entire 'Malla experiment', which must be taken in account when evaluating the messages of comparisons between Malla and grazed mountains.

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Abstract in Swedish / Sammandrag:

Vi studerade hur renbete påverkar kärlväxtflorans artrikedom och diversitet på dolomitpåverkade lågalpina lokaler i de artrikaste delarna av norra Fennoskandien. Vi inventerade 8 lokaler med olika rentätheter. Två lokaler ligger inom Malla Nationalpark, där renar har varit förbjudna sedan 1981 och starkt begränsade sedan 1950-talet. De sex andra lokalerna ligger i andra artrika områden med samma dolomitdominerade berggrund, men är betade av renar. Rentätheterna vid de studerade lokalerna varierar från helt obefintligt till bland de högsta rentätheter man kan finna i Fennoskandien. Inventeringen utfördes genom att systematiskt undersöka fyra 2 m x 10 m stora ytor i varje lokal i en habitattyp som är speciellt rik i ovanliga kärlväxter (fjällsippehed-lågörtsäng komplex). Varje yta delades upp i 20 småytor (1m x 1m), och en total artlista upprättades för var och en av dessa småytor. Den första axeln i DCA (detrended correspondence analyses) analysen korrelerade med rentätheten. Det visar att renar påverkar sammansättningen av växtsamhället. Ingen av de vanliga måtten på biodiversitet (artrikedom eller Shannon-Wiener diversitetsindex) var korrelerade med rentätheten. Trots detta, var tätheterna av Ca-gynnade växter och arter rödlistade i Finland positivt korrelerade med rentätheten. Trots att renarna inte påverkade totala artrikedommen, kan de vara betydelsefulla för regionala biodiversiteten eftersom de gynnar ovanliga och hotade arter. De vanliga måtten på biodiversitet har begränsat värde för bevarandebiologiska frågeställningar, eftersom de är lika känsliga för ovanliga och vanliga arter.