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Higher plant species richness has been proposed to increase the resilience of plant communities to disturbance. The purpose of this study was to test whether this is true for reindeer grazed arctic tundra vegetation. Plant biomass, plant community structure, and species richness were measured along four fences that separated areas grazed by reindeer from ungrazed areas in northern Norway. I found a negative relationship between plant species richness and the change in species richness and biomass due to grazing. These results indicate diversity did not confer greater resilience to increased reindeer grazing intensity. No support for higher grazing pressure in diverse habitats were recorded, thus, these results suggest lower resilience to grazing in species-rich arctic tundra vegetation.

Abstract

Methods

The study was carried out along fences at four different locations in northernmost Norway: (1) Čearro (69°40’N, 24°40’E); (2) Lagisduoddar (70°30’N, 27°30’E); (3) Raisduoddar (69°30’N, 21°10’E); and (4) Sicˇcˇaja´vri (68°50’N, 23°50’E). See Olofsson et al. (2001) for a more detailed description of the study locations. At all four locations, the fences were established in the 1960s to reduce the risk that reindeer illegally enter winter ranges during the summer. The fences are built of wire between 1- to 2-m-high posts, and stretch for several kilometers across the tundra. In all areas, winter ranges near the fences are little used, and almost no signs of reindeer are found there. The grazed side of the fences is heavily grazed in all four areas. Reindeer concentrate close to the fences, and the grazing pressure and trampling close to the fences are higher than in other parts of the summer pastures (Oksanen, 1978; Olofsson et al., 2001; Olofsson et al., 2004a).

The fences cross through a mosaic of patches of different vegetation types. The three main types are dwarf shrub heath, low herb meadow, and tall herb meadow. Evergreen and deciduous dwarf shrubs dominate dwarf shrub heath vegetation, but graminoids and forbs are present. Low herb meadows are dominated by low-growing graminoids and forbs. Tall forbs, graminoids, and willow shrubs dominate tall herb meadows. Stress-tolerant plants dominate the dwarf shrub heath, competitors dominate the tall-herb meadow, and the low-herb meadow contains stress-tolerators, competitors, and ruderals, according to the classification by Grime (2001).

To study the effect of grazing in different habitats, I marked a number of study sites at random positions along the fences at the end of June 2000. The number of sites at each fence varied between 6 and 11 depending on length of the fence and number of vegetation types along the fence. In total, 35 study sites were used along the four fences. Distances between sites were at least 100 m. I studied the effect of grazing and trampling on the plant community composition 2 m from each side of the fence in five 0.5 m × 0.5 m plots. I estimated the plant diversity of these fences using these fences have shown that reindeer grazing and trampling influence plant species richness, plant community composition, nutrient cycling, and primary production (Olofsson and Strengbom, 2000; Olofsson et al., 2001, 2004a; Olofsson and Oksanen, 2002). To study how the resilience and resistance to herbivory are affected by species richness and vegetation type, I measured plant biomass, community composition, and species richness in grazed and ungrazed plant communities with contrasting species richness along four of these fences.
cover in the plots with a modified point intercept method (Jonasson, 1988). I used a transparent Plexiglas table, 0.5 m × 0.5 m, with 100 randomly distributed holes. The holes had a diameter of 4 mm. At each hole, a pin with the same diameter was lowered through the vegetation, and I recorded the number of contacts of the pin to each species. The biomass of each species was then estimated with regressions between number of contacts and biomass for each species (Olofsson, 2001). Because the relationship between number of contacts and biomass did not differ between controls and exclosures in that study, similar functions were used for grazed and ungrazed vegetation. Reindeer densities were estimated once, by counting droppings in each plot where a vegetation survey was carried out. This method is commonly used for comparing herbivore densities between areas (Neff, 1968; Putman, 1984; van der Wal et al., 2001). There are several weaknesses in this method. The decomposition rate of feces can differ between areas, and at the small scale used in this study, different activities of the reindeer can be concentrated in different habitats. Local feces densities are thus not necessarily directly related to either grazing or trampling intensity. I still used this method in this study as it was the best method that was logistically possible. The results on reindeer densities are, however, interpreted with caution.

The effects of grazing on plant biomass and plant species richness were analyzed as ln (grazed/ungrazed) because this measure is symmetric around 0 (responds equally strong to an increase or to a decrease caused by grazing). The dissimilarity of the vegetation was analyzed with a Bray-Curtis Measure because it should be robust against different species richness and mainly is affected by changes in abundance of common species (Krebs, 1999). An assumption for these calculations is that vegetation was similar on both sides, before the fences were constructed. As there are no systematic vegetation recordings from these locations at that time, I have no data showing that this is actually true. However, all comparisons across the fences used in this study were in sites where the fences were crossing through places with homogeneous topography. Moreover, discussions with the reindeer herders who constructed the fences confirm that they were not built along any natural vegetation borders that should confound this comparison.

All statistical analyses were calculated using the R statistical package (Ihaka and Gentleman, 1996). The relationship between each of the three response variables and species richness in the two contrasting grazing treatments was estimated with a three-factor ANCOVA with location of the fence and vegetation type as a categorical explanatory variable, and species richness as a continuous explanatory variable. The models are then simplified by removing all terms that did not significantly increase the fit of the model, until minimal adequate models, with only significant terms, are found (Crawley, 2002).

**Results**

There was no statistical support for including different vegetation types in the model ($F = 1.7, P = 0.158$), and they were thus lumped together. After model simplification, the minimal adequate model for the effect of grazing and species richness on the relative change in plant biomass had two intercepts and one common slope. The common negative slope for all four locations ($t = -4.40, P < 0.001$; Fig. 1) indicated that reindeer reduced the biomass more in species-rich plant communities. The intercept for Cearro, Raisduoddar, and Šiččajávri combined areas was not significantly different from 0 ($t = -1.71, P = 0.096$). Reindeer reduced plant biomass more in Lagisduoddar than in the other areas as the intercept for Lagidouddar is significantly lower than the intercept for the other locations ($t = -3.97, P < 0.001$).

There were no statistical support for including different vegetation types in the model ($F = 1.6, P = 0.169$) and they were thus lumped together. The minimal adequate model of the effect of reindeer and species richness on compositional stability, calculated with Bray-Curtis
dissimilarity measure, had one intercept and slope for Síččajávri and one intercept and slope for the other three areas combined (Fig. 2). Reindeer influenced species-rich plant communities more in Síččajávri, as the slope was positive \((t = 2.63, P = 0.013)\). However, plant species richness did not influence the effect of reindeer on plant community structure in the other three areas \((t = -0.79, P = 0.438)\).

There were no statistical support for including different vegetation types in the model \((F = 0.1, P = 0.999)\) and they were thus lumped together. The minimal adequate model for the effect of reindeer and species richness on the change in species richness had one common slope and two intercepts (Fig. 3). Positive intercepts and a negative slope \((t = -5.57, P < 0.001)\) indicated that reindeer grazing and trampling increased species richness in species-poor communities and decreased species richness in species-rich communities. The intercept for Lagisdouddar was positive \((t = 2.95, P = 0.006)\). The combined intercept for the other three areas was greater than the intercept for Lagisdouddar \((T = 3.41, P = 0.002)\).

Including vegetation type did not improve the models for plant biomass \((F = 1.7, P = 0.158)\), compositional stability \((F = 1.6, P = 0.169)\), or species richness \((F = 0.121, P = 0.999)\) and was thus not incorporated in the models described above. There was no relationship between the number of reindeer droppings in the grazed areas and biomass or species richness in the ungrazed plant communities. The number of reindeer droppings was significantly higher in Lagisdouddar \((3.0 \pm 0.5 \text{ droppings m}^{-2} \text{mean} \pm \text{SE})\) than in the other areas \((1.6 \pm 0.3 \text{ droppings m}^{-2})\) \((F = 38.2, P < 0.001)\). The change in species richness was negatively correlated with reduction in plant biomass \((r^2 = 0.34, t = 4.5, P < 0.001)\).

### Discussion

Contrary to previous findings from Serengeti National Park (McNaughton, 1985), species-rich plant communities were more affected by grazing than areas in species-poor communities. Herbivory consistently reduced plant biomass and species richness more in species-rich habitats at all four locations. The effects of reindeer were more severe in Lagisdouddar, where also the reindeer densities were higher, than in the other three areas. There was no consistent pattern in the relationship between species richness and change in plant community composition due to reindeer. Even though the dwarf shrub heath, the tall herb meadow, and the low-herb meadow are highly contrasting vegetation types and dominated by plants that could be expected to respond differently to grazing (Grime, 2001), there was no statistical support that they responded differently to grazing, in respect to the general measurements that we analyzed here. This means that, surprisingly, all vegetation types responded to grazing in the same way and the vegetation types could thus be lumped together. I cannot explain the similar response in all vegetation types, but one reason might be that the grazing is so severe in these locations that it more or less creates new vegetation types. The composition of these new vegetation types is not necessarily determined by the strategy of the plants that dominated the ungrazed vegetation.

The mechanisms behind this pattern could either be that species-poor plant communities are more resistant to grazing or that reindeer graze more in species-rich plant communities. McNaughton (1985, 1993) recorded a higher grazing pressure in species-rich habitats in African savannas. If reindeer grazing intensity were higher in species-rich plant communities, this could explain the higher reduction in biomass. Moreover, because reduction in biomass was negatively correlated with the change in species richness, differential utilization between habitats could explain effects on species richness as well. However, feces abundance recordings do not support any differences between sites in abundance of herbivores. The small-scale densities of droppings are a weak indicator of reindeer activity, especially as differences in decomposition rates between sites were not accounted for. Moreover, these fences crossed through a mosaic of habitats with high and low species richness. Because reindeer move long distances along these fences, across numerous different habitats, trampling intensity and feces density is expected to be fairly similar even if the grazing intensity should differ.

Sankaran and McNaughton (1999) recorded greater species turnover in species-poor communities when experimentally disturbed. However, as this pattern disappeared when each habitat was analyzed separately, they argued that their results are best explained by the ecological history and species characteristics of communities, rather than by species diversity in itself. In this study, the correlation between diversity and resistance was not an effect of differences between plant community types. However, as species richness was not manipulated experimentally, this study cannot separate between effects of species richness per se and effects of species identity.

Negative correlations between species richness and resistance to grazing in these natural communities should not be interpreted as evidence that increased species richness per se decrease resistance to grazing. In natural communities, a negative relationship between diversity and productivity have been found within the range of productivities considered in most ecological studies, i.e., the descending section of the humped-back model (Grime, 2001), and a positive relationship between species richness and invasibility have been found (Levine, 2000). The opposite pattern has, however, been found in experiments where the number of species is manipulated experimentally under otherwise constant condition (Tilman et al., 1996; Hector et al., 1999; Levine, 2000). The reason for these contradictory results is probably that the same environmental condition that causes a high species richness (moderate nutrient availability and moderate disturbance) also results in a low productivity and low resistance to invasive plants (Levine, 2000; Huston and McBridge, 2002). Low nutrient availability and disturbance are two factors that both increase plant

![FIGURE 3. Effect of reindeer grazing on plant species richness in habitats with different plant species richness. The different symbols represent the four different locations: ○ = Lagisdouddar, ■ = Cearro, ● = Raisduddar, and ▲ = Síččajávri. The least adequate model contained one common slope and two intercepts.](Image)

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species richness (Austerheim and Eriksson, 2001) and decrease regrowth ability of plants (Mulder, 1999) in tundra vegetation. Species richness and regrowth ability might thus be negatively correlated and cause the negative correlation between species richness and resistance to grazing.

It is intriguing that this study and the study by McNaughton (1985) found contradictory results, because natural gradients in species richness were used in both studies. McNaughton (1985) points out the role of coevolution for the positive relationship between species richness and resistance to grazing. However, as reindeer also have coevolved with the tundra vegetation (Suominen and Olofsson, 2001), this is not a likely explanation for the contradictory results. However, different mechanisms might determine species richness in nutrient limited arctic tundra and water limited African savannas (McNaughton, 1985) and thus, in turn, the resistance to grazing.

Reindeer grazing decreased plant biomass in all plant communities, but the decrease was even larger in species-rich communities. In contrast, plant species richness was enhanced by reindeer grazing in inherited species-poor communities and reduced in inherited species-rich plant communities. Herbivory has been found to increase local species richness in most ecosystems, by reducing plant biomass and thus the competition between plants (Olff and Ritchie, 1998). However, reindeer grazing in tundra areas do not often influence the species richness at all, even though they influence plant community composition (Olofsson et al., 2004b; Olofsson and Oksanen, 2005). This might indicate that competition between plants was low in species-rich plant communities, even in the absence of reindeer, and one possible explanation for the results in this study could thus be that the natural biotic and abiotic disturbance regimes are high enough to maintain low competition intensities and thus high local species richness. The dramatic effects of reindeer grazing and trampling on plant biomass, community composition, and species richness reported here should not be interpreted as indications of overabundance of reindeer. The grazing and trampling intensities close to these fences are higher than in most other areas in the Fennoscandian mountain chain (Oksanen, 1978; Olofsson et al., 2004a). Moreover, even in the intensively grazed and trampled zone close to the fences where plant biomass were severely reduced, previous studies have reported an increased nutrient availability and primary production at some locations (Olofsson et al., 2004a). The increased nutrient turnover rate in grazed areas enhances the resilience of the vegetation to grazing. It is not clear how that affects the relationship between species richness and resilience. To separate between effects of reindeer consumption patterns and resistance of vegetation, as well as separating between effects of species richness per se and species identity, are research priorities for the future.

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