

Impact of reindeer grazing on ground-dwelling Carabidae and Curculionidae assemblages in Lapland

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Reindeer *Rangifer tarandus* L. grazing shapes forest vegetation, microclimate, and soil respiration in Lapland, especially due to grazing on lichens (*Cladina*). We studied how these changes and their magnitude affect ground-dwelling species of beetle families Carabidae (predators) and Curculionidae (herbivores), by using pitfall traps to collect invertebrates from pairs of grazed and ungrazed study plots over a wide range of site types. Changes in abundance, composition, richness and diversity of beetle assemblage were tested in relation to magnitude of the impacts on vegetation. The species compositions of Carabidae and Curculionidae differed between grazed and ungrazed plots in all sites. The relative difference between grazed and ungrazed plots in the number of individuals increased linearly with the impact of reindeer on vegetation cover. Carabid beetles, as a family, were more common in grazed plots in all sites. Curculionid beetles were more common in ungrazed plots in the birch dominated sites. This difference was mainly due to the species that feeds on deciduous leaves. In the pine dominated sites with high *Cladina* cover and more changes in ground vegetation, the number of curculionids feeding on conifers was higher in grazed plots. Species richness and diversity (H') of both families were higher in grazed plots. Of the total 27 species, 11 were found only in grazed plots, while not a single species was found only in ungrazed plots. The relative difference between plots in diversity and evenness (H'/H'_{max}) had humped response to the difference in *Cladina* cover. The diversity values were greater in grazed plots at the intermediate levels of grazing impact, and only in sites with very low or extremely high *Cladina* cover difference was the diversity higher in ungrazed plots. The response of beetle diversity resembled the hypotheses suggested for the relationship between grazing and vegetation diversity: greatest positive effect at intermediate grazing intensity and negative effects at unproductive sites.

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Large mammalian herbivores can be important modifiers of ecosystem structure and function (Bryant et al. 1991, Hobbs 1996, Augustine and McNaughton 1998). For instance, in boreal ecosystems, browsing and grazing cervids, such as moose *Alces alces* (McInnes et al. 1992, Suominen et al. 1999a, b) and reindeer (Helle and Aspi 1983, Lehtonen and Heikkinen 1995, Oksanen

et al. 1995, Väre et al. 1995, 1996, Suominen 1999a) can alter the species composition and structure of vegetation by selective foraging. These changes in vegetation cover can affect physical properties of the environment, such as microclimate and soil chemistry (Väre et al. 1996, Kielland and Bryant 1998, Wardle et al. 2001). Changes in vegetation and physical properties of the

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environment can indirectly affect animals in other trophic levels (DeCalesta 1994, Baines et al. 1994, Bromham et al. 1999, Suominen et al. 1999a, b, Wardle et al. 2001).

Reindeer grazing is a natural part of ecosystem functioning in northern Fennoscandia, but populations of semidomesticated reindeer have grown to reach extremely high densities during the last two decades in Finnish Lapland (Kojola and Helle 1993, Suominen and Olofsson 2000). This high population density has been maintained by supplemental feeding since the 1970s (Helle and Kojola 1993). The ecosystem impacts of reindeer and the underlying processes that generate these changes are quite different in the typical winter and summer habitats of reindeer. In winter the main food sources are ground and arboreal lichens, while in summer reindeer feed on a variety of herbs, grasses, lichens and leaves of deciduous trees. Before 20th century, wild herds and the traditionally herded reindeer migrated long distances between summer and winter ranges, but at present the herds remain in the area of the local reindeer herding cooperation throughout the year so that the seasonal habitats are no longer so distinct geographically. The disappearance of thick reindeer lichen (*Cladina* spp.) carpets from dry forests in Lapland (i.e. typical winter ranges of reindeer) has received considerable public and scientific attention (e.g. Anon. 1997). The negative impacts of reindeer foraging on regeneration of deciduous trees (Oksanen et al. 1995, Mäkitalo et al. 1998) in more moist and productive habitats have also aroused attention, especially due to the harmful effects on forestry. Trampling and grazing by reindeer have been considered major factors in controlling forest ground vegetation in northern Finland, especially in lichen rich oligotrophic forests (Väre et al. 1995, 1996, Suominen and Olofsson 2000). These changes in vegetation have led to indirect effects of reindeer on microclimate, soil moisture and temperature, soil respiration, soil nutrients, and fine root biomass (Väre et al. 1996, Stark et al. 2000, Olofsson and Oksanen 2002). Distinction between trophic effects and physical habitat modification (engineering sensu Jones et al. 1994, 1997) is not clear because part of the modification of the habitat results, directly or indirectly, from the food consumption of reindeer. Nevertheless, reindeer affect directly or indirectly several processes and components of forest ecosystems in Lapland.

Majority of studies on the effects of grazing on plant communities have shown that grazers tend to increase species diversity of vegetation according to intermediate disturbance hypothesis (Connell 1978, Fox 1979) and this has been shown also for reindeer (Helle and Aspi 1983). Milchunas et al. (1988) suggested that the plant community's response to different grazing pressures depends on its evolutionary history of grazing. Proulx and Mazumder (1998) analyzed large number of

studies on the relationship between grazing, plant species richness, and productivity, and found out that in nutrient-poor ecosystems high grazing pressure decreased richness, while in nutrient-rich ecosystems high grazing pressure tended to increase plant species.

There are very few studies on the impacts of wild ungulates on ground dwelling invertebrates (but see: Putman et al. 1989, Suominen et al. 1999a, b, Wardle et al. 2001) or invertebrates living in the field layer vegetation (Baines et al. 1994, Rambo and Faeth 1999). However, it is better known that grazing or browsing by large herbivores usually improves the quality of the grazed plants for invertebrate herbivores (e.g. Danell and Huss-Danell 1985, Roininen et al. 1997, Olofsson and Strengbom 2000). Wardle et al. (2001) compared the impacts of browsing in different types of habitats in New Zealand and they did not find connection between the magnitude of the impact on vegetation and on invertebrates, but otherwise there are no studies about the relationship between grazing intensity and responses of invertebrate communities in forests. It has been found that reindeer grazing can modify the numbers and richness of forest floor invertebrates including herbivores, detritivores and their associate predators (Suominen 1999a, b) and soil nematodes (Stark et al. 2000).

In this paper, we examine how the hypothesis suggested to explain the relationship between grazers and vegetation diversity fit to the relationship between reindeer grazing and ground-dwelling beetles. The predictions were 1) that grazing at intermediate level would increase diversity and 2) that high grazing intensity, especially at unproductive sites, would lead to lower diversity. We expected the effects of reindeer on beetle assemblages to be different and greater in lichen-dominated sites than in more productive habitats. To test these predictions, we examined the effects of reindeer grazing on ground-dwelling carabid beetles (predators) and weevils (herbivores) at enclosure sites in Finnish Lapland.

Methods

Study sites

We sampled six enclosure/control pairs in the vicinity of the Kevo Subarctic Research Station (Table 1), where the most important large mammalian herbivore is reindeer (moose visit the area only occasionally). Microtine rodents (voles *Clethrionomys* spp., *Microtus* spp. and lemming *Lemmus lemmus*) can also be important during the high density periods of their population cycles, but our enclosures did not prevent herbivory by small mammals. Rodent numbers were not particularly high during our study or the previous winter. Mountain hare (*Lepus timidus*) could enter most of the enclosures. The

Table 1. Study sites. Each site consists of one grazed plot (reindeer had free access to the plot) and one ungrazed plot (access of reindeer prevented by a fence). On national borders grazed plot was on the Finnish side of a reindeer fence and ungrazed on Russian or Norwegian side of the fence. Number codes of sites are used in the text and in Fig. 1 and 2. More information in the text.

Areas	Location	Year exclosed	Size of enclosure ¹	Dominant tree species	Age of forest in 1995 (successional state)
Number codes for sites					
Kevo	69°N, 27°E				
241, 242, 243		1970	20 × 20 m	Birch	Partly recovered from 1965 <i>Epirrita</i> damage ²
250		1968	35 × 30 m	Pine	Mature forest
271, 272		1989	20 × 30 m	Meadow	Succession from bare soil in 1988
Finnish/Russian border					
310, 320, 330	68°N, 28°E	1940's ³	30 × 30 m	Pine	Mature forest
340	67° N, 30°E	1960	30 × 30 m	Birch	35 yr since forest fire
Finnish/Norwegian border					
410, 420, 430, 440	68°N, 24°E	1953	30 × 30 m	Birch	Mature forest
Pomokaira					
500	67°N, 26°E	1987	50 × 50 m	Birch, spruce	13 yr since clear-cut ⁴

¹ Size of the study plot on the national borders. ² More information in Lehtonen and Heikkinen 1995.

³ Has been fenced since the 1940s but the present fence was erected in 1975. ⁴ More information in Mäkitalo et al. 1998.

area is situated in the subarctic mountain birch zone, where pine forests exist only in river valleys. Three of our study sites were located in mountain birch forests which had been defoliated and partly killed by the geometrid moth *Epirrita autumnata* in 1965, which has affected vegetation at these sites (sites 241, 242, 243) (Lehtonen and Yli-Rekola 1979, Lehtonen 1987, Lehtonen and Heikkinen 1995). Site 250 was an old IBP enclosure site in a pine forest near Lake Kevo. Two of the sites were established in an abandoned meadow, where the fence also excluded hares (sites 271, 272). It was treated with herbicide (1986, 1987) and the moss layer was removed (1988) so that succession began from bare ground in 1988 (Zobel et al. 1997).

In Pomokaira, central Lapland, the enclosure (site 500) was in Norway spruce forest (*Hylocomium*-*Myrtillus* type) that was clear-cut in 1972 and after that allowed to regenerate naturally, mainly by birch (*Betula pubescens*) (Table 1). Moose density is low and most of the treatment effect is due to summer foraging of reindeer. In 1997, the height of birch saplings inside the enclosures was 160 cm compared to 40 cm in the grazed plots, and the above ground biomass of birch inside the enclosures was four times higher than in the grazed plots (Mäkitalo et al. 1998).

Finnish reindeer are prevented from entering Norwegian and Russian territory by a fence on the borders between the countries. There are no reindeer on the Russian side of the fence near the border. Clear signs of moose browsing can be seen on both sides of the fence, at least on the Russian border. Reindeer forage in our study area on the Norwegian side only in winter during periods when the thick snow cover prevents them from digging to reach the ground vegetation, thus the influence of reindeer on vegetation is weak. Later in this text

the plots on the Norwegian side will be referred to as ungrazed plots. We had eight study sites (pairs of plots on both sides of the fence) in three different areas (Table 1). The fence on the Russian border is on the Finnish side and all our ungrazed study plots there were on Finnish territory on a strip of land between the reindeer fence and the actual border, thus forest management and land use history are similar on both sides of the reindeer fence.

Invertebrate sampling

The plots, used as replicates in this study, had an area of 16 × 16 m–30 × 30 m (depending on the size of the enclosure). We placed pitfall traps (5 × 5 m quadrates, a trap in each corner and one in the middle point of the quadrate) inside each ungrazed and grazed plot. There were 4–6 of these quadrates in each plot (20–30 traps per plot) depending on the size of the enclosure. Traps were not situated closer than two meters from the fence to minimize edge effects. Plots (30 × 30 m) along the national borders were positioned so that the closest traps were at a 10-m distance from the reindeer fence.

Traps (170 ml plastic cups, height 70 mm, diameter at top 70 mm) were filled with 50% ethylene glycol with detergent added and covered by metal roofs (12 × 12 cm, 3–5 cm above ground) to prevent dilution of the glycol and flooding of the traps by rain water. The traps were operated continuously from late June to early August 1995 and checked only at the end of trapping period. After retrieval of the traps all invertebrates were transferred to vials containing ethanol (70%). Individuals of beetle families Carabidae and Curculionidae from 18–20 randomly selected traps (due to limited resources for the time consuming task) in

each plot were later identified to species (Carabidae: by J. Niemelä; Curculionidae: by P. Martikainen). The percentage cover of ground vegetation was estimated from the same plots at each site in summer 1996 (Suominen 1999a).

Data analysis

The analyses of the whole beetle assemblage were conducted both for the entire data, and for a group of sites with a lichen cover on the ungrazed side of the fence >40%, and for those with a lichen cover of <40% (the two meadow sites were omitted since they represent such a different type of community – i.e. early successional phase). The limit was set at 40% *Cladina* cover because it divided the sites into two almost equal sized groups, and separated all pine forest sites into the same group (43% was the lowest *Cladina* cover for an ungrazed pine forest plot). Thus, in this classification sites in the high *Cladina* coverage group are either pine or birch forests, while the low *Cladina* coverage class sites are all birch-dominated forests.

The beetle assemblage was studied with detrended correspondence analysis (DCA) using CANOCO 3.15 software (ter Braak 1988). The mean number of individuals (X) of each species per trap in a plot was used as a test variable in the analyses. Values were $\ln(X + 0.1)$ transformed before the analyses, and we used detrending by segments (number of segments 26) and nonlinear rescaling of axes. Since species present in less than four plots in a data set were omitted from the analyses, down weighing of rare species was not needed. We restricted the interpretation to the ordination space determined by the first two dimensions. At first, we ran unconstrained DCA ordination with the data, in which differences among sites were the main source of variation. Thereafter, partial ordination was used, where the effect of site differences was partialled out by using sites as covariables.

Differences in the number of individuals of the various beetle species were tested with G^2 tests and the null hypothesis that the number of individuals of a species does not differ between grazed and ungrazed plots. Tests were conducted on the pooled data from all sites, on sites with >40% lichen cover, and on sites with <40% lichen cover in the ungrazed plots. Because of multiple testing, the p -values were corrected with the sequential Bonferroni technique (Rice 1989). We calculated species richness standardized to similar sample size with rarefaction, the Shannon-Wiener diversity index (H'), and relative diversity (“evenness”, $H'/H'max$) for each plot. Paired t -tests were used to test whether these values differed between grazed and ungrazed plots (for species richness we used rarefaction estimation for a sample size of the plot with a lower

number of individuals – i.e. the maximum sample size that could be used for both plots at a site).

The influence of reindeer grazing on lichen cover is the most important direct effect of reindeer on the ecosystem (Oksanen and Virtanen 1995) and we expected that the effect of reindeer on insect fauna is related to the extent of change in vegetation caused by grazing. A study on the effects of reindeer on vegetation in these same sites (Suominen 1999b) showed that %-similarity of vegetation between grazed and ungrazed plot had a strong linear relationship ($r^2 = 0.77$) to difference in *Cladina* cover between the grazed and ungrazed plots in percentage units (%-cover ungrazed – %-cover grazed). We used this difference between %-units as a measure of the magnitude of reindeer impact on vegetation.

The relative differences between the grazed and ungrazed plots at each site ($[\text{grazed} - \text{ungrazed}] / \text{grazed}$) in terms of the number of individuals of both beetle families, species richness (standardized to similar sample size with rarefaction), diversity (H'), and relative diversity (“evenness” $H'/H'max$) of both families combined were related to the difference in lichen cover between the grazed and ungrazed plot. We tested for both linear regression and curvilinear relationship (second and third order polynomial function). The results of higher order regression analyses are presented when the p -value for the significance of adding the higher order term was <0.20. Littell et al. (1991) recommend using $p < 0.20$ or $p < 0.25$ as a limit for including a higher order term in a regression model. All statistical analyses except ordination with CANOCO were performed with SAS statistical software (Anon. 1990).

Results

Beetle species composition

Unconstrained DCA with all sites included reflected differences in beetle assemblage among sites (Fig. 1a). When the analysis was repeated with sites as covariables, the scores of grazed and ungrazed plots differed clearly from each other on axes 1 and 2 of partial DCA (Fig. 1b). These axes explained 21.4% (eigenvalue 0.097) and 15.8% (eigenvalue 0.071), respectively, of residual variation in the species data after the effect of site differences was partialled out. At “lichen rich sites” (both pine and birch forests) the first two axes of partial DCA separated grazed and ungrazed plots from each other without any overlap and explained 32.0% (eigenvalue 0.161) and 20.2% (eigenvalue 0.102) of the residual variation respectively (Fig. 2a). At sites with <40% lichen cover the partial DCA axes 1 and 2 were also connected to the effects of reindeer and separated grazed and ungrazed plots from each other without overlap (Fig. 2b). Axes 1 and 2 explained

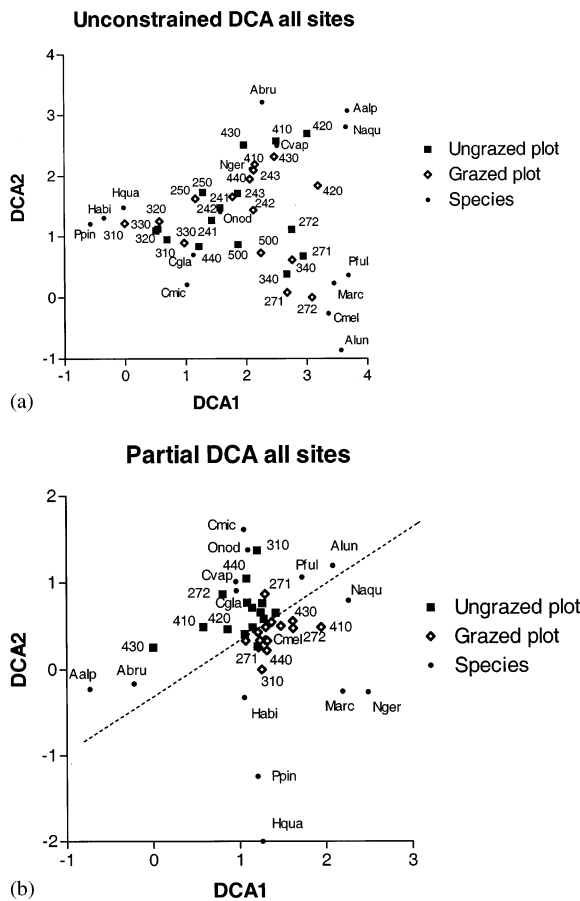


Fig. 1. Joint plot of (a) Unconstrained DCA results of the whole species data. (b) Partial DCA of the same data (site differences partialled out by using them as covariables). Sites scores (one grazed and one ungrazed plot) marked with numbers (see Table 1). Species scores marked with abbreviations of Latin names. Species are: Cgla = *Carabus glabratus*, Cmic = *Calathus micropterus*, Cmel = *C. melanocephalus*, Marc = *Miscodera arctica*, Hqua = *Harpalus quadripunctatus*, Abru = *Amara brunnea*, Aalp = *A. alpina*, Alun = *A. lunicollis*, Nger = *Notiophilus germinyi*, Naqu = *N. aquaticus*, Cvap = *Cymindis vaporariorum*, Onod = *Otiorhynchus nodosus*, Pful = *Polydrusus fulvicornis*, Habi = *Hylobius abietis*, Ppin = *Pissodes pini*.

43.9% (eigenvalue 0.124) and 14.6% (eigenvalue 0.041) of the residual variation after site differences were partialled out. Thus, the main source of variation in the beetle assemblage in our data is the difference among sites. However, when the effect of site differences was excluded, reindeer grazing stood out as an important factor affecting the beetle fauna. Some species responded differentially numerically to grazing at the two site type categories.

Number of individuals

The number of all Carabidae individuals combined was higher in grazed plots at both high and low *Cladina*

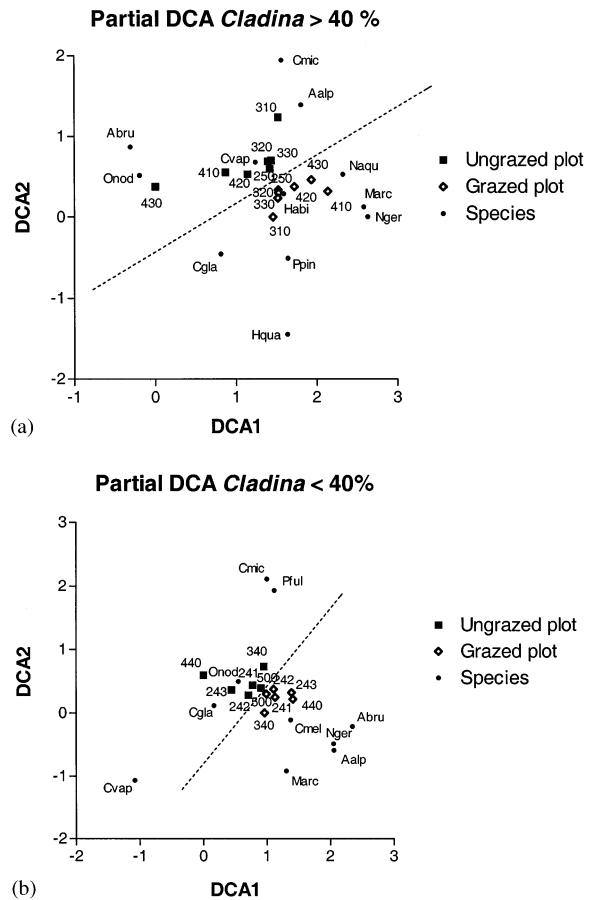


Fig. 2. Joint plot of (a) Partial DCA of the species data from sites with >40% cover of *Cladina* lichens in ungrazed plots (site differences partialled out by using them as covariables). (b) Partial DCA of the species data from sites with <40% cover of *Cladina* lichens in ungrazed plots. Site scores (one grazed and one ungrazed plot) marked with numbers (see Table 1). Species scores marked with abbreviations of Latin names (see Fig. 1).

cover sites (Table 2). The number of all Curculionidae individuals combined was higher in ungrazed plots at low lichen cover sites, but at high lichen cover sites they were more common in grazed plots. This may be due to the feeding ecology of the curculionids. Species that eat pine were found only at high lichen cover sites (all pine forests belong to this vegetation group) and were more common in grazed plots, while curculionids that forage on deciduous trees were more common in ungrazed plots in both vegetation groups.

The relative difference between grazed and ungrazed plots in the number of individuals of Curculionidae had a significant positive linear relationship with the difference in *Cladina* cover between grazed and ungrazed plots (Table 3, Fig. 3). For Carabidae individuals this regression was marginally significant (Table 3, Fig. 3). Since these relationships could also be interpreted to mean that changes in *Cladina* cover affected catchabil-

Table 2. Differences in numbers of individuals of different species in pooled data, >40% lichen cover sites (in ungrazed plots) (7 sites), and <40% lichen cover sites (8 sites). P-values of G² tests (DF = 1) corrected for multiple testing with sequential Bonferroni technique. UG = ungrazed plots; Gr = grazed plots.

Species	All sites			Lichen <40%			Lichen >40%		
	UG	Gr	p <	UG	Gr	p <	UG	Gr	p <
Total Carabidae ¹	271	451	0.0001	197	281	0.001	74	170	0.0001
<i>Carabus glabratus</i>	69	105	0.05	65	82	ns	4	23	0.0001
Males	31	57	0.05	30	47	ns	1	11	0.005
Females	38	48	ns	35	36	ns	3	12	0.07
<i>Calathus micropterus</i>	48	35	ns	37	28	ns	11	7	ns
<i>C. melanocephalus</i>	22	34	ns	22	34	ns	0	0	–
<i>Miscodera arctica</i>	15	57	0.0001	15	30	ns	0	27	0.0001
<i>Harpalus quadrip.</i>	9	36	0.001	1	0	–	8	36	0.0001
<i>Amara brunnea</i>	19	19	ns	4	10	ns	15	9	ns
<i>A. alpina</i>	24	14	ns	6	8	ns	18	6	0.07
<i>A. lunicollis</i>	10	22	ns	10	21	ns	0	1	–
<i>Notiophilus germinyi</i>	11	53	0.0001	8	27	0.01	3	26	0.0001
<i>N. aquaticus</i>	14	31	0.1	3	4	–	11	27	0.05
<i>Cymindis vaporariorum</i>	8	9	ns	4	2	–	4	7	ns
<i>Pterostichus adstrictus</i>	22	27	ns	22	27	ns	0	0	–
Total Curculionidae ²	193	202	ns	115	65	0.0002	78	137	0.0001
<i>Otiorhynchus nodosus</i>	91	72	ns	38	28	ns	53	44	ns
<i>Polydrusus fulvicornis</i>	77	39	0.001	77	35	0.0001	0	4	–
<i>Hylobius abietis</i>	23	78	0.0001	0	0	–	23	78	0.0001
<i>Pissodes pini</i>	2	7	–	0	0	–	2	7	–

¹ Includes rare species (*Harpalus fuliginosus*, *Carabus nitens*, *Amara fulva*, *Trichocellus cognatus*, *Patrobus assimilis*, *Patrobus atrorufus*).

² Includes rare species (*Magdalis duplicata*, *Hylobius piceus*, *Pissodes piniphilus*, *Pissodes gyllenhalii*, *Rhyncolus ater*).

Table 3. Results of regression analysis where the difference in *Cladina* cover (%-units) between the grazed and ungrazed plots is the explanatory variable and the relative difference between plots [(value in grazed plot–value in ungrazed plot)/value in grazed plot] in the number of Curculionidae and Carabidae individuals, species richness (standardized with rarefaction), Shannon-Wiener diversity index (H'), and relative diversity (H'/H'max) of both families combined are the explained variables. A third order term was not significant in any case. A second order model is presented only when the p-value for the second order term is <0.20 (Littell et al. 1991).

	r ²	DF	F	p
Number of Curculionidae individuals				
linear model	0.48	1,13	12.1	0.004
second order term	1,13	1.30	0.279	
Number of Carabidae individuals				
linear model	0.20	1,13	3.21	0.097
second order term	1,13	0.28	0.607	
Richness				
linear model	0.03	1,13	0.46	0.509
second order model	0.23	2,12	1.79	0.209
second order term	1,13	3.04	0.107	
H'				
linear model	0.02	1,13	0.27	0.612
second order model	0.40	2,12	4.02	0.046
second order term	1,13	7.62	0.017	
H'/H'max				
linear model	0.13	1,13	1.89	0.193
second order model	0.48	2,12	5.57	0.019
second order term	1,13	8.21	0.014	

ity of pitfall traps (i.e. the results would be artifacts due to sampling bias), we tested how *Cladina* cover as such affected the number of specimens of Carabidae and Curculionidae per trap. The mean number of specimens of Carabidae or Curculionidae did not correlate significantly with *Cladina* cover in either grazed or ungrazed plots (Pearson correlation, p > 0.1 in all cases). Thus, at least the differences between sites were not explained by the extent of *Cladina* cover.

Partial DCA and G² test (Table 2) results (DCA emphasizes rare species [Jongman et al. 1995] while G² is better for the species present in all plots) indicate that the carabids *Carabus glabratus* (males), *Miscodera arctica*, *Notiophilus germinyi*, and *N. aquaticus* were more common in grazed plots, while the curculionid *Otiorhynchus nodosus* characterized the fauna of ungrazed plots in both vegetation groups. The carabids *Amara brunnea* and *A. alpina* were more common in grazed plots at low lichen cover sites, but they were more common in ungrazed plots at high lichen cover sites. The carabid *Harpalus quadripunctatus*, and the curculionids *Hylobius abietis*, and *Pissodes pini* were common only at high lichen cover sites and in there more abundant in grazed plots. The carabids *Calathus melanocephalus*, *Amara lunicollis*, and curculionids *Polydrusus fulvicornis* were common only in low lichen cover sites, and there *A. lunicollis* was more abundant in grazed plots and *P. fulvicornis* in ungrazed plots.

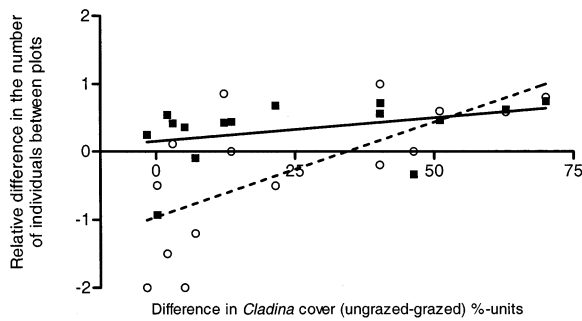


Fig. 3. Relationship between difference in *Cladina* cover between grazed and ungrazed plots at a site and relative difference [(number in grazed plot–number in ungrazed plot)/number in grazed plot] in the number of individuals of Carabidae (black squares and solid line) and Curculionidae (open circles and dotted line). Values above x-axis mean higher abundance in grazed plot and below x-axis higher abundance in ungrazed plot. Results of linear regression analysis are shown in Table 3.

Species richness and diversity

Of the total 18 carabid species found in our sample, six (33%) were found only in grazed plots (*Harpalus fuliginosus*, *Carabus nitens*, *Amara fulva*, *Trichocellus cognatus*, *Patrobus assimilis*, and *P. atrorufus*), while none were found only in ungrazed plots. Five of the total nine (56%) curculionid species were found only in grazed plots (*Magdalis duplicata*, *Hylobius piceus*, *Pissodes piniphilus*, *Pissodes gyllenhali*, *Rhyncolus ater*), but none only in ungrazed plots.

The combined species richness of Carabidae and Curculionidae was higher in grazed plots in both lichen cover classes after standardization by rarefaction (Fig. 4) (mean value in ungrazed plots was 4.7 and in grazed plots 5.7, paired t-test: DF = 14, $t = 2.414$, $p = 0.0300$). Diversity (H') of grazed and ungrazed plots differed from each other (paired t-test, DF = 14, $t = 2.364$, $p = 0.0331$) but relative diversity (H'/H'_{\max}) did not (paired t-test, DF = 14, $t = 0.3315$, $p = 0.7452$). Diversity was higher in grazed plots (mean \pm SE of H' : 1.966 ± 0.1089) than in ungrazed plots (mean \pm SE of H' : 1.624 ± 0.1549).

The relative differences between grazed and ungrazed plots in species richness, diversity (H'), or relative diversity (evenness, H'/H'_{\max}) [(value in grazed plot–value in ungrazed plot)/value in grazed plot] were not significantly related to the difference in lichen cover tested with linear regression (Table 3). However, there was a statistically significant curvilinear relationship between the difference in lichen cover and relative differences in diversity and relative diversity (Fig. 5, Table 3). There was a similar trend in species richness even though the model was not statistically significant. The difference in *Cladina* lichen cover explained a substantial proportion of the variation in the relative difference of H' , $H'/$

H'_{\max} , and species richness between grazed and ungrazed plots (Table 3). In every case the coefficient of the second order term was negative and the maximum point of the curve ($-b/(2c)$) was within the range of variation of the data (Fig. 5). Thus we can conclude that the relative difference between plots in these diversity/richness values was highest (and higher in grazed plots) at the intermediate levels of difference in lichen cover.

Discussion

Our results show that the exclusion of reindeer affected species composition, the number of individuals, species richness, and diversity of Carabidae and Curculionidae assemblages at ground level and litter-layer. It has not been demonstrated earlier that reindeer grazing has such impacts. The effect of reindeer on beetle assemblage was modified by the extent of *Cladina* lichen cover and the effect of reindeer on vegetation so that the effect of reindeer on both Carabidae and Curculionidae abundance at the family level (number of individuals trapped) increased linearly in relation to the effect of grazing on the lichen cover. Contrary to our results Wardle et al. (2001) failed to find any significant relationship between the magnitude of the effect of ungulate browsing on vegetation and the abundance of soil and litter dwelling fauna in 30 enclosure sites in New Zealand. Differences between grazed and ungrazed plots in the number of individuals of the family Carabidae and most of the carabid species in our study were greater at high *Cladina* cover sites (at low *Cladina* sites 59% of the carabid individuals were trapped in grazed plots and 70% at high *Cladina* cover sites). This may be because carabids are sensitive to changes in microclimate (e.g. Niemelä 1996) and many of the collected species are favored by the warmer and dryer conditions in grazed plots where both tree and herb layer vegetation are more open (Lindroth 1985, 1986). The generally higher invertebrate numbers in grazed plots (Suominen 1999a) also indicates that there was more prey in grazed plots for invertebrate predators such as carabid beetles. The relationship between total invertebrate catch and *Cladina* difference was, however, bell shaped (Suominen 1999a) not linear as the same relationship for carabids. Two carabid species, *Calathus melanocephalus* and *Pterostichus adstrictus*, were relatively abundant in low *Cladina* cover sites, but were absent from high *Cladina* cover sites. Both of these species favor open habitats and are more common at early successional sites, which belong to low *Cladina* vegetation class in our data.

The effect of reindeer foraging in summer on the abundance of birch and is a logical explanation for the higher number of *Polydrusus fulvicornis*, and thus all curculionids, in ungrazed plots of low *Cladina* cover

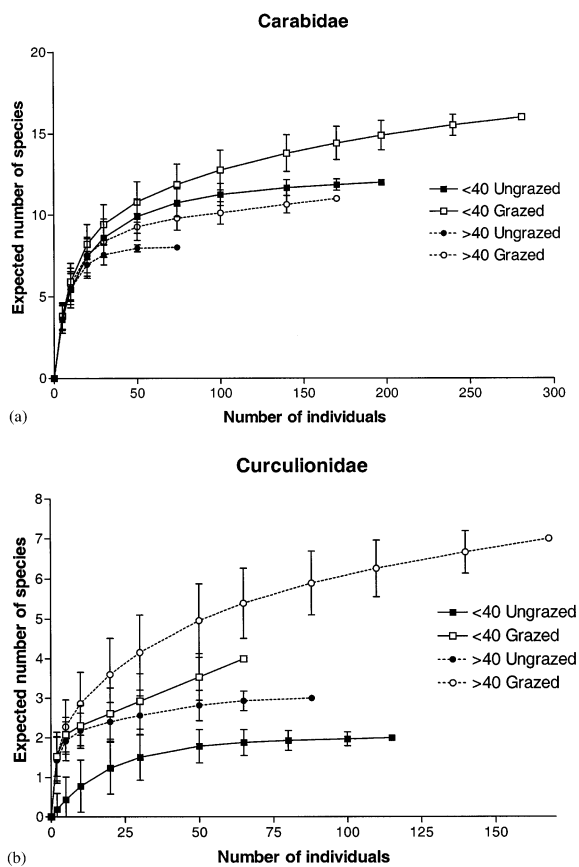


Fig. 4. Rarefaction curves (with standard error bars) estimating species richness of (a) Carabidae and (b) Curculionidae. Sites with <40% *Cladina* cover and sites with >40% *Cladina* cover in ungrazed plot analyzed separately.

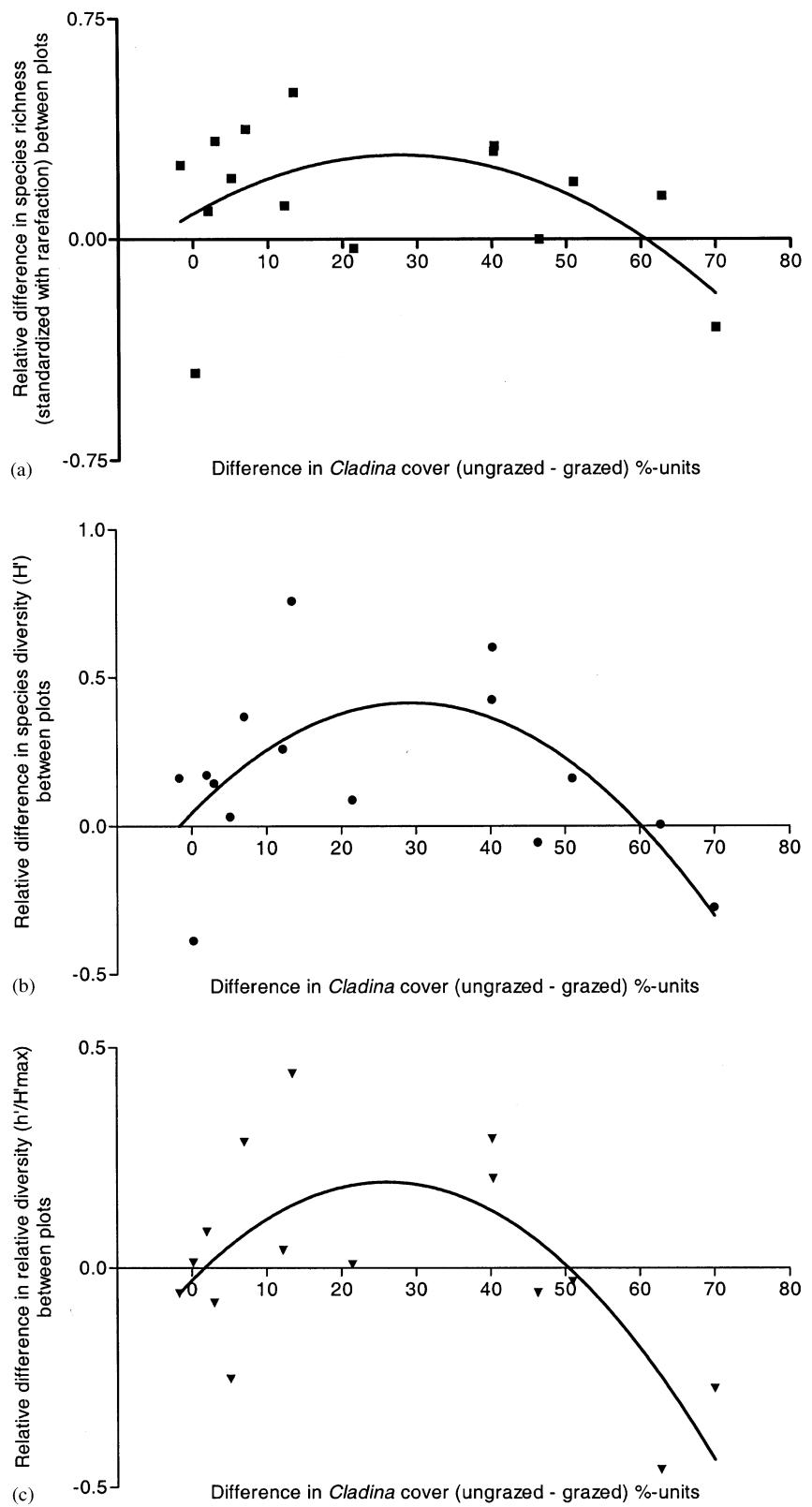
sites, since the adult beetles feed on leaves of deciduous trees. On the other hand grazing by cervids including reindeer has been shown to induce such changes in chemistry and growth of deciduous trees that herbivorous invertebrates are more abundant on earlier grazed trees (Danell and Huss-Danell 1985, Bardgett et al. 1998, Olofsson and Strengbom 2000). Obviously this effect could not compensate for the lower leaf biomass in grazed areas in our study sites. It is not as clear, however, why the curculionids feeding on conifers were more abundant in grazed areas. Consequently, curculionids were generally more common in grazed plots at high *Cladina* coverage sites (all pine forests belong to this *Cladina* cover class). Larvae of *Pissodes* and *Hylobius* forage on dying and recently dead conifers and the adults on conifer seedlings. Thus, one could expect that either pine seedlings are more common in grazed plots or that there are more dying pines in grazed areas. Although reindeer grazing has been shown to enhance establishment of pine seedlings by exposing unvegetated topsoil (Helle and Moilanen 1993) we did not find any evidence for that at our sites. On the other hand,

mechanical damage caused by dense reindeer population by trampling and/or indirect effects of removing lichen cover on soil and tree roots (Väre et al. 1996) might be harmful for pines and make them more susceptible to insect damage.

It has been shown that vertebrate herbivores can maintain or restore plant species diversity in various types of habitats (Virtanen et al. 1997, Gough and Grace 1998, Olf and Ritchie 1998, Collins et al. 1998) by consuming competitively dominant species. Reindeer grazing increases the diversity of vegetation by decreasing the dominance of *Cladina* lichens (Helle and Aspi 1983, Väre et al. 1995) and reverting the succession of forest floor vegetation in areas where *Cladina* would otherwise dominate the climax vegetation (Väre et al. 1995). A general increase in plant species richness in grazed plots could also be seen at our study sites (Suominen 1999a), and the relative difference in plant species diversity (H') and dissimilarity of vegetation composition increased with increasing difference in *Cladina* (Suominen 1999a). Thus, the difference between *Cladina* cover of the grazed and ungrazed plots seemed to act as an indirect measure of the cumulative influence of reindeer on the forest floor vegetation.

The relative differences in species richness, diversity, and evenness of the beetles were highest at intermediate levels of reindeer influence on *Cladina* cover and lowest (and negative) either at very low *Cladina* cover difference (also low %-cover in general) or at sites with the highest difference in *Cladina* cover (and high *Cladina* cover in ungrazed plot). Again, our results differ from those of Wardle et al. (2001) in New Zealand. At their sites magnitude of the browser effect on vegetation was not related to the diversity of most of the invertebrate groups (humus-dwelling nematods were the only exception). But, similarly to our results, the diversity of macroarthropods in shortgrass steppe had a bell shaped response to cattle grazing intensity (Milchunas et al. 1998). A confounding factor in our study is that sites with high *Cladina* cover, and difference, are also drier and less productive than sites with low *Cladina* cover. Unfortunately, we cannot disentangle the effects of grazing intensity and site type in our data. Reindeer densities were high in all studied areas and thus the differences in the response of the communities are most likely predominantly due to differences in vegetation type. The fact that most severely harmful effects of reindeer were at dry unproductive sites with slowly growing lichens dominating vegetation fits into our prediction that the effect on diversity will most likely be negative at unproductive sites. The prediction was based on Proulx and Mazumder's (1998) finding concerning the effects of grazing on plant communities. At our study sites the effect of reindeer on vegetation (dissimilarity and diversity) grew almost linearly until it leveled off at very high *Cladina* difference i.e. at most heavily grazed unproductive sites (Suominen 1999a). It

Fig. 5. Relationship between difference in *Cladina* cover between grazed and ungrazed plots and relative difference in (a) species richness (standardized with rarefaction), (b) Shannon-Wiener diversity index (H'), and (c) relative diversity (H'/H'_{max}) of Carabidae and Curculionidae ([value in grazed plot - value in ungrazed plot]/value in grazed plot). Points above x-axis mean higher value in grazed plot and below x-axis higher value in ungrazed plot. Results of regression analyses are shown in Table 3.



seems that beetle diversity (but not abundance) was more sensitive to grazing than plant diversity. Thus the effect of reindeer turned clearly harmful at unproductive heavily grazed sites. The linear relationship between vegetation effects and beetle abundance also means that there were great differences among beetle species in the response to grazing at heavily grazed unproductive sites. Some species could not tolerate grazing but the tolerant species could numerically compensate for the loss of the sensitive species.

Reindeer densities in Finnish Lapland are constantly higher than natural densities of wild reindeer (Gaare and Skogland 1980, Helle and Kojola 1993), and reindeer grazing might be considered to be a disturbance to the ecosystem in some areas. On the other hand, the preferred reindeer wintering areas with *Cladina* dominated ground vegetation have probably experienced high grazing pressure since the last glaciation (Oksanen and Virtanen 1995). Thus, reindeer are an intrinsic part of the ecosystem in Lapland, and the effects of grazing could be considered as part of the normal functioning of the ecosystem. The long evolutionary history of reindeer grazing impact in Fennoscandia might be one major difference and reason for opposite results between our study system and that of Wardle et al. (2001) in New Zealand where all large mammalian herbivores are introduced species.

Reindeer had a strong impact on the ground-dwelling assemblage of predatory carabid and herbivorous curculionid beetles. Both the number of individuals and number of beetle species were higher in grazed plots. As we expected, the differences between grazed and ungrazed plots were greater in areas with low site productivity and great grazing induced differences in vegetation than at more productive sites with less vegetation changes. Our results indicate that even fairly high grazing pressure may increase the diversity and richness of these beetle assemblages, but also that in areas with the most severe effects of reindeer on lichen carpet (and the whole vegetation), usually at unproductive sites, grazing at the present level reduces beetle diversity. The mechanisms through which reindeer grazing affects these beetles are probably indirect and result from the changes in vegetation caused by their foraging and trampling, which create partly trophic effects and partly physical changes in the habitat.

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