

Impact of cervid browsing and grazing on the terrestrial gastropod fauna in the boreal forests of Fennoscandia

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Selective foraging by cervids can affect vegetation, and that in turn can have far-reaching effects on various components of the boreal forest ecosystem. Since terrestrial gastropods are sensitive to habitat alterations, they can be expected to respond to changes caused by grazing. This study is based on gastropod specimens from two data sets that were collected with pitfall traps in order to study the effects of moose and reindeer on ground-layer invertebrates. Invertebrates were trapped from 23 pairs of plots, where one plot was open to all animals while the other one was fenced to exclude large mammals. Half of the sites were in Finnish Lapland, where reindeer grazing was the main cause of differences between the plots; the rest were located in central Sweden and southern Finland, where moose was the most important cervid grazer. The composition of the gastropod fauna differed between grazed and ungrazed plots in both areas, and the abundance of gastropods in general and that of many species was higher in ungrazed plots (the number of gastropods caught was 17% lower in grazed than in ungrazed plots in moose sites, and 24% smaller in reindeer sites). Species richness differed significantly between grazed and ungrazed plots in the combined data of both site types, and was 15% higher in ungrazed plots. In moose sites the relative diversity (H'/H'_{\max}) of gastropods was 17% higher in grazed plots. In reindeer sites, the means of richness and diversity (H') were considerably higher in ungrazed plots (35% and 40% respectively) but the differences were only marginally significant. By indirectly modifying the microclimate within the forest, cervids fulfil the criteria for a 'physical ecosystem engineer'. Since the population density and distribution of terrestrial gastropods depend largely on the physical conditions of the microhabitat, the engineering effects of cervids are the most likely cause of the changes observed in the density and composition of the gastropod fauna in the boreal forest.

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Cervids can have a far-reaching indirect impact on ecosystems through changes in vegetation caused by their foraging. In most of Fennoscandia, moose population densities have been high during the latter half of this century (Nygrén 1987, Østgård 1987, Cederlund and Markgren 1987). In the northern parts of Finland, Norway, and Sweden, the densities of semi-domesticated reindeer, which range freely in the forest, have been extremely high in recent decades (Kojola and Helle 1993), and reindeer grazing is an important factor affecting vegetation in northern Finland (Oksanen et al. 1995, Väre et al. 1995, 1996).

It has been shown that selective browsing by moose on preferred deciduous trees can have a direct impact on tree species composition (Pastor et al. 1993, Kielland and Bryant 1998, Suominen et al. 1999) and a further indirect impact on the rate of succession (Kielland and Bryant 1998), on the composition of the herb-layer vegetation (McInnes et al. 1992, Suominen et al. 1999), on leaf litter accumulation (Pastor et al. 1993, Kielland and Bryant 1998, Suominen et al. 1999), on litter decomposition and soil productivity (Pastor et al. 1993, Kielland et al. 1997), and on the ground-living invertebrate fauna (Suominen et al. 1999). The effect of moose

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on the tree, herb and litter layers will also affect the microclimate inside the forest.

Reindeer grazing is a natural part of the ecosystem in northern Fennoscandia, but the population densities of semi-domesticated reindeer in Finnish Lapland have grown extremely high during the last two decades (1974–1990) (Kojola and Helle 1993).

Certain changes in the practices of reindeer husbandry have also amplified the grazing pressure in many areas in Lapland. One change has been that the traditional migrations between winter and summer ranges that were part of reindeer husbandry up to the 20th century no longer take place. Another important difference from wild reindeer populations is that supplementary feeding in winter, started in 1974 (Helle and Kojola 1993), keeps densities constantly high. In a natural system, reindeer populations crash during exceptionally hard winters and/or when they have depleted their food resources, giving the vegetation an opportunity to recover. Trampling and grazing by reindeer have been considered to be major factors controlling forest ground vegetation in northern Finland, especially in lichen-rich oligotrophic forests (Väre et al. 1995, 1996). These changes in vegetation have led to indirect effects of reindeer on the microclimate, soil respiration, soil nutrients, fine root biomass and invertebrate assemblage (Väre et al. 1996, Suominen et al. unpubl.). Thus the high density of reindeer has been named as one of the most important threats to forest ecosystems in northern Finland (Anon. 1997).

The exclusion of moose and reindeer from the boreal forest can bring about changes in ground-dwelling invertebrate assemblage (Suominen et al. 1999, Suominen et al. unpubl.). In these studies, all terrestrial gastropods were dealt with as a single combined group (class Gastropoda). This was the taxonomic group that was most consistently more common in areas from which cervids had been excluded. Terrestrial gastropods are a specially important invertebrate taxon for cervids since they are the intermediate hosts of nematode parasites of them; in fact, the only studies, to my knowledge, where gastropods have been studied in relation to cervids deal with the transmission of these parasites to cervids (e.g. Lankester and Peterson 1996, Whitlaw et al. 1996). If cervid foraging reduces substantially gastropod density, it may lower the prevalence of these parasites in cervids.

In this paper, the gastropod specimens of pitfall trap catches from 23 sites in Finland and Sweden have been identified to species (or genus) level. The population density of gastropods depends largely on the physical conditions of the microhabitat. In the present study, I test the hypothesis that most terrestrial gastropod species are more abundant in ungrazed areas, which are more humid and cooler than grazed forests that are exposed to more intense solar radiation. Further, the distributions of many gastropod species in Fennoscandia

are closely tied to specific deciduous tree species, such as the aspen *Populus tremula* (Hutri and Mattila 1991), which form the highly preferred winter forage of cervids (Bergström and Hjeljord 1987). It might be expected that those snail species whose habitat requirements include the presence of certain deciduous trees or deciduous leaf litter would be less common in browsed areas. One purpose of this study was to determine whether the enriching effect of ungulate grazing on various plant and animal taxa observed in other studies (e.g. Olff and Ritchie 1998, Milchunas et al. 1998) also affects terrestrial gastropods, a group on which grazing can so clearly be expected to have harmful effects.

Study sites

The data were collected from 23 pairs of sampling plots in Finnish Lapland, central Sweden and southern Finland; in each pair, access by large mammals to one plot had been prevented with fencing, while the other gave free access to all animals (Table 1). In the following, the fenced plots are called 'ungrazed plots' and the open plots 'grazed' or 'reference' plots (in the case of moose also 'unbrowsed' and 'browsed' plots respectively; in this text, browsing refers to feeding on twigs, mainly by moose, and grazing refers to feeding on ground vegetation, mainly by reindeer, and grazing is also used when referring to both types of foraging). At the border between Finland and Russia, ungrazed plots mean plots on the Russian side of the reindeer fence between the countries, while grazed plots mean plots on the Finnish side (the fence along the border is on the Finnish side and all the ungrazed study plots were on Finnish territory within a strip of land between the reindeer fence and the actual border, thus, there are no differences in the forest management). Here the term 'grazing' refers only to reindeer grazing, while moose were present on both sides of the fence. The gastropod material was extracted from the pitfall trapping data of Suominen et al. (1999, Suominen et al. unpubl.). I have included data from five additional sites that were not used in the earlier studies. Four of these sites were used for forest breeding experiments by the Finnish Forest Research Inst., where the saplings planted within and outside of the enclosure belong to different tree species; thus mammalian herbivory is not the only difference between 'grazed' and 'ungrazed' plots in these sites. The fifth additional site is an enclosure in central Sweden in a pine sapling stand, where moose had broken into the enclosure in the winter before invertebrate trapping and was thus omitted from the study of Suominen et al. (1999). These locations were included in this study because they represent interesting early successional site types and gastropod species that could not otherwise have been studied.

Table 1. Study sites. Each site consists of one grazed plot (with free cervid access to the site) and one ungrazed plot (cervid access prevented with a fence). 'Fin/Rus border' refers to the reindeer fence between Finland and Russia (no reindeer on Russian side). All other sites are enclosures built to exclude all large mammals.

Area	Site number(s)	Location	Fenced in year	Size of enclosure ¹	Dominant tree species	Age of forest in 1995 (successional state)
Holm	80	62° N 17° E	1986	50 × 50 m	Pine	Pines planted on clear-cut 1970
Sunnäs	91–96	61° N 17° E	1979	40 × 40 m	Pine	Pines planted on clear-cuts in ca 1970 ²
Furudal	102–106	61° N 15° E	1979	25 × 25 m	Pine	Clear-cut in 1963, naturally regenerated ²
Solbåle	200	60° N 23° E	1985	1.9 ha	Birch, pine	Sapling stand, clear-cut 1983, planted 1985
Konttikivalo	210	66° N 26° E	1987	12.6 ha	Pine	Sapling stand, planted 1987
Siperia	220	66° N 27° E	1983	0.8 ha	Spruce, birch	Sapling stand, planted 1983
Lammassuoma	230	66° N 27° E	1982	3.7 ha	Spruce, birch	Sapling stand, clear-cut 1979, planted 1982
Kevo	241, 242, 243	69° N 27° E	1970	20 × 20 m	Birch	Partly recovered from 1965 <i>Epirrita</i> damage ³
	250		1968	35 × 30 m	Pine	Mature forest
Fin/Rus border	310, 320, 330	68° N 28° E	1940s	30 × 30 m	Pine	Mature forest
	340	67° N 30° E	1960	30 × 30 m	Birch	35 years from forest fire
Pomokaira	500	67° N 26° E	1987	50 × 50 m	Birch, spruce	13 years from clear-cut ⁴

¹ Size of a study plot in Fin/Rus border. ² More information in Suominen et al. (1999). ³ More information in Lehtonen and Heikkinen (1995). ⁴ More information in Mäkitalo et al. (1998).

Materials and methods

Field data

A plot is an area of 16 × 16 m–30 × 30 m, with 18–30 traps, and it is used as a replication in this study. Pitfall traps were placed inside each ungrazed and grazed plot. The traps were not situated closer than 2 m from the fence, to minimize the edge effect. At the border the plots (30 × 30 m) were situated so that the closest traps were at a distance of 10 m from the reindeer fence. The traps (170 ml plastic vials, height 70 mm, diameter at top 70 mm) were filled with 50% ethylene glycol or polypropylene 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 traps by rain water. The traps were active for about one month in summer 1995. After retrieval of the traps, all invertebrates were transferred to vials containing ethanol (70%). All gastropods (Stylommatophora: Pulmonata) were identified to the level of genus or species, using the manuals of Hutri and Mattila (1991) and Kerney et al. (1979), and counted.

The pitfall traps were established mainly for the sampling of arthropods (Suominen et al. 1999, Suominen et al. unpubl.). Pitfall trapping is not the optimal method for sampling terrestrial gastropods. However, since cardboard sheets have been found to be a good method for estimating the relative densities of terrestrial gastropods and the species composition of the species that are active on the surface of the forest floor (Hawkins et al. 1998), and since pitfall trapping is similarly based on the activity of the animals, I consider that these data can be used to compare relative numbers of individuals between grazed and ungrazed plots.

Data analyses

Differences in gastropod assemblage between grazed and ungrazed plots were analyzed with partial principal components analysis (PCA, centered by species) using the CANOCO 3.15 software. Ter Braak (1988) and Jongman et al. (1995) recommend that PCA should be used instead of correspondence analysis when the gradient length is less than two SD units. A preliminary DCA indicated that this was the case in the gastropod data. Site differences were partialled out by using them as covariables. The plot means of the number of individuals of each gastropod species in a trap were used as variables in the analyses (log transformed values). Since rare species tend to dominate in the ordination solution, only species that were present in at least four plots were included in the analyses. The PCA was run separately for southern sites, where the most important herbivore was the moose (roe deer and white-tailed deer were also present in some sites), and for northern sites, where the most important herbivore was the reindeer (although moose were also present).

After the partial PCA had indicated that the gastropod assemblage differed between grazed and ungrazed plots, I used the G^2 -test to test whether the number of individuals of a species also differed between grazed and ungrazed plots (tests were conducted with SAS statistical software, Anon. 1990). This test was applied to the data for all sites pooled and to the data for moose sites and reindeer sites separately and p-values within each of these categories were corrected with sequential Bonferroni test for multiple testing (Rice 1989).

I calculated species richness (standardized with rarefaction), the Shannon-Wiener index of diversity (H'), and diversity relative to the maximum possible (H'/H'_{max} , 'evenness') according to Krebs (1989) for each plot. Rarefaction curves were created for the pooled data of moose and reindeer sites. Differences between grazed and ungrazed plots were tested with paired t-tests. For species richness I used for each site the rarefaction estimate calculated for a sample size equal to the number of gastropods in the plot with a lower number of individuals (i.e. the maximum sample size that could be used for both the grazed and the ungrazed plot in the site).

Results

Assemblages

In moose sites, partial PCA axes 1 and 2 separated browsed and unbrowsed sites from each other (Fig. 1). These axes explained 52.2% and 19.3% (eigenvalues 0.081 and 0.030), respectively, of the residual variance in the species data after site differences were partialled out. In reindeer sites, axis 1 was closely related to the gradient of grazing effect and separated grazed and ungrazed sites from each other (Fig. 1). Axes 1 and 2 explained 45.3% and 34.6% (eigenvalues 0.046 and 0.035), respectively, of the residual variance in species data after site differences were partialled out. Thus the gastropod assemblage of the study sites was clearly affected by both moose browsing and reindeer grazing.

Individual species

In southern moose sites, both the total number of gastropods and the numbers of individuals of five out of ten species tested (G^2 -test, Bonferroni correction) differed at least marginally significantly between grazed and ungrazed plots (Table 2). *Zoogenetes harpa* was the only species that was more common in grazed plots. *Cochlicopa*, present only in site 80, and *D. reticulatum*, present only in site 200, were also more common in grazed plots but their numbers were so low that they were not tested. The numbers of individuals of all

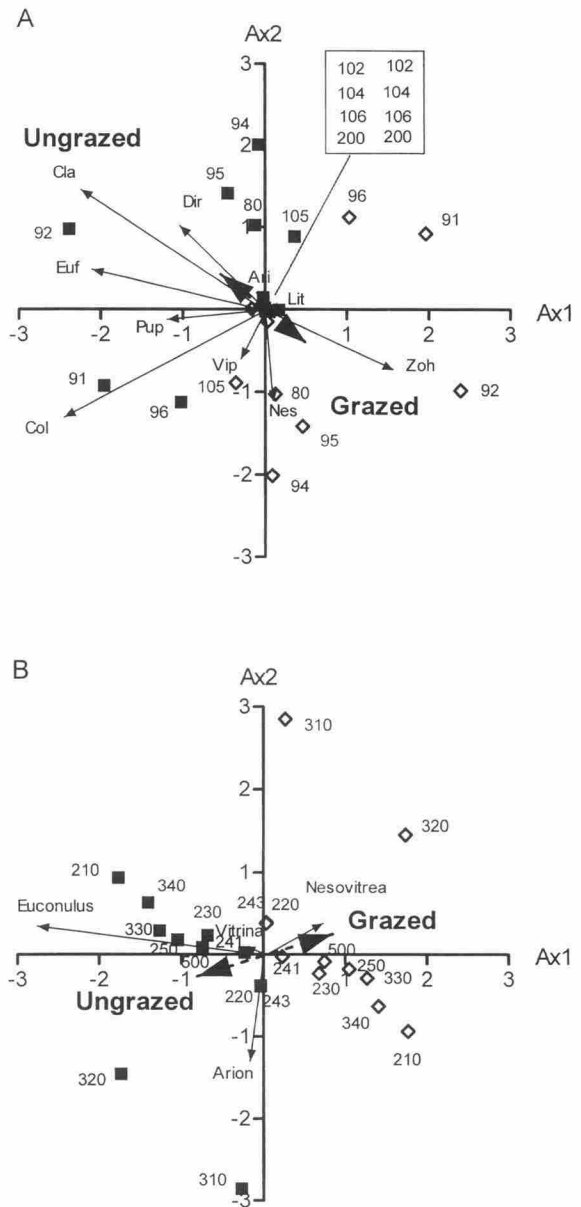


Fig. 1. Biplot of partial PCA results from A) moose and B) reindeer sites. Differences between sites partialled out using sites as covariables. Sites (one grazed and one ungrazed plot) are marked with numbers (see Table 1 for explanation). Scales marked on the axes apply to plot scores, while the scales for species scores are 3: 0.6 in Fig. 1A and 3: 0.7 in Fig. 1B. The bold arrows show the direction of grazed-ungrazed gradient and point to the means of grazed and ungrazed plots. Species scores for gastropods are marked with vectors: Col = *Columella* sp., Zoh = *Zoogenetes harpa*, Pup = *Punctum pygmaeum*, Dir = *Discus ruderatus*, Ari = *Arion subfuscus*, Vip = *Vitrina pellucida*, Nes = *Nesovitrea hammonis*, Lit = *Limax tenellus*, Euf = *Euconulus fulvus*, Cla = *Clausilia* sp.

gastropod species combined and those of five species in particular (*Columella* sp., *Arion subfuscus*, *Vitrina pellucida*, *Euconulus fulvus*, and *Arianta arbustorum*) were more common in ungrazed enclosure plots. Of these

species, *A. arbustorum* was present only in site 80, while the others were found in several sites. In the biplot of partial PCA results (Fig. 1) of moose sites, *Clausilia* sp., *E. fulvus*, and *Discus ruderatus* were most strongly linked to unbrowsed plots; *Columella* sp. and *Punctum pygmaeum* were also somewhat more common in unbrowsed plots. Browsed plots were characterized by higher numbers of *Z. harpa* and *Nesovitrea hammonis*. The explanation for the minor differences between the results of the G²-test and the PCA is that in PCA, rare species that are present only in a few plots, such as *Clausilia* sp., are highly influential, while species that are present in all plots, such as *A. subfuscus*, have less effect on the PCA results. The G²-test, on the other hand, is more suitable for common species.

In the reindeer sites of Finnish Lapland, the numbers of individuals of two out of four species tested, as well as the number of all gastropod individuals, differed significantly between grazed and ungrazed plots (Table 2). Gastropods in general and these two species, *Arion subfuscus* and *Euconulus fulvus*, were more common in ungrazed plots. In the partial PCA results for reindeer sites, ungrazed plots are characterized by a higher abundance of *E. fulvus* and *A. subfuscus*, while *Nesovitrea hammonis* is more common in grazed plots (Fig. 1).

Richness and diversity

Diversity (H') and relative diversity (H'/H'_{max}) did not differ significantly between grazed and ungrazed plots in the combined data for all sites, but the rarefaction estimation of species richness for maximum possible sample size differed and was higher in ungrazed plots (Table 3). In moose sites, species richness and diversity did not differ between grazed and ungrazed plots but relative diversity was higher in grazed plots (Fig. 2, Table 3). In reindeer sites, the Shannon-Wiener diver-

sity index and the rarefaction estimation of species richness for the maximum sample size differed marginally significantly (p < 0.10) between grazed and ungrazed plots, and were higher in ungrazed plots, while relative diversity did not differ between treatments (Table 3). Rarefaction curves for pooled data of grazed and ungrazed plots of reindeer sites segregate quite clearly (Fig. 2). The curve for grazed plots levels off at a sample size of about 200 individuals in grazed plots.

Discussion

Species responses

The results show that there were generally more snails and slugs active in those plots where cervid access was prevented than in the reference plots where cervids had grazed or browsed. Likewise most of the forest generalist species that showed a numerical response to grazing (*Columella* spp., *Arion subfuscus*, *Vitrina pellucida*, and *Euconulus fulvus*) were more common in ungrazed plots. Terrestrial gastropods in general and slugs in particular are sensitive to moisture, and their population density is thus related to the soil moisture in the area (Godan 1983). It has been suggested that the physical properties of the habitat, such as humidity, shelter, and temperature, are more important determinants of the distribution of terrestrial gastropods than the availability of food resources (e.g. Boag 1985). They are more likely to be found in shaded, moist and cool places than in open, dry and warm habitats.

Zoogenetes harpa was exceptional in being the only typical boreal forest species that was far more common in browsed plots. Both *Z. harpa* and *Nesovitrea hammonis*, which were characterized as being more common in browsed plots by PCA, are adapted to acidic conditions of coniferous litter (Kerney et al. 1979). Thus they

Table 2. Species abundances in all sites combined, moose sites, and reindeer sites. Difference between grazed and ungrazed plots tested with G²-tests (DF = 1) for species with more than ten individuals. p-values are corrected with a sequential Bonferroni technique. UG = ungrazed plots, GR = grazed plots.

Species	All sites			Moose			Reindeer		
	UG	GR	p <	UG	GR	p <	UG	GR	p <
<i>Cochlicopa</i> spp.	1	6	—	1	6	—			
<i>Columella</i> spp.	27	12	0.1	25	12	ns	2	0	—
<i>Zoogenetes harpa</i>	5	25	0.01	3	21	0.001	2	3	—
<i>Punctum pygmaeum</i>	5	7	ns	5	7	ns			
<i>Discus ruderatus</i>	8	4	ns	8	4	ns			
<i>Arion subfuscus</i>	904	706	0.0001	491	378	0.001	413	328	0.01
<i>Vitrina pellucida</i>	76	46	0.05	56	32	0.1	20	14	ns
<i>Nesovitrea</i> sp.	45	58	ns	34	45	ns	11	13	ns
<i>Limax tenellus</i>	219	213	ns	219	213	ns			
<i>Deroceras reticulatum</i>	0	5	—	0	5	—			
<i>Euconulus</i> sp.	52	14	0.0001	28	9	0.02	24	5	0.001
<i>Clausilia</i> sp.	6	2	—	6	2	—			
<i>Arianta arbustorum</i>	11	2	0.06	11	2	0.07			
All species ¹	1361	1097	0.0001	889	737	0.005	472	360	0.001

¹ Includes rare species *Limax cinereoniger*, *L. marginatus* in moose sites.

Table 3. Means of rarefaction estimations of species richness for maximum possible sample size calculatable for both plots in a pair, Shannon-Wiener diversity index (H'), and relative diversity (H'/H'_{\max}) values for all sites, moose sites, and reindeer sites. p-values of paired t test.

Variable	Mean grazed	Of ungrazed	DF	t	p
All sites					
Richness max	3.099	3.567	22	2.130	0.044
H'	1.282	1.348	13	0.672	0.513
H'/H'_{\max}	0.575	0.570	13	0.094	0.927
Moose sites					
Richness max	4.713	5.078	10	1.017	0.333
H'	1.737	1.650	7	0.719	0.495
H'/H'_{\max}	0.661	0.564	7	3.213	0.015
Reindeer sites					
Richness max	1.619	2.182	11	2.045	0.066
H'	0.675	0.945	5	2.128	0.087
H'/H'_{\max}	0.461	0.577	5	0.958	0.382

might have benefitted by the reduction in the abundance of deciduous trees in browsed forests. The gastropod species in the data represent quite closely the species typical of boreal forest habitats in Fennoscandia, according to the habitat characterizations given in Hutri and Mattila (1991) and Kerney et al. (1979). The species pool of terrestrial gastropods in northern Lapland is much smaller than in the mid- and hemiboreal zone of the moose sites, and the habitat requirements of the species are usually narrower in the northernmost areas. The low number of species in reindeer sites is thus not surprising.

Moose browsing can substantially reduce the number of aspens in the forest canopy. Aspen is also readily eaten by other mammalian herbivores, such as mountain hare, beaver, white-tailed deer and roe deer. There are several gastropod species that in the boreal zone of Fennoscandia have been found exclusively in habitats with old aspens. Of the gastropod taxa in my data, the snail genus *Clausilia* is restricted to habitats with aspen, *Populus tremula* or linden *Tilia cordata* leaf litter (Hutri and Mattila 1991). Six out of eight of the *Clausilia* sp. individuals in my data were caught in the enclosure plots of Sunnäs (sites 91–96); here the unbrowsed plots contained some large aspens, while none of the browsed plots of any site contained any. As a consequence, *Clausilia* was the taxon that most clearly characterized unbrowsed plots in the partial PCA results for moose sites.

Cervid browsing and grazing also affect the abundance of potential gastropod predators (Suominen et al. 1999). This provides another link whereby cervid browsing can have an indirect impact on gastropod populations. Of the invertebrates that are known to hunt slugs and snails (Godan 1983), in the Swedish sites harvestmen (Phalangidae) and *Carabus* beetles were more common in unbrowsed plots and ants (Formicidae) more common in browsed plots (Suominen et al. 1999, Suominen and Niemelä unpubl.). In Lapland both ants and ground beetles (Carabidae) were more

abundant in grazed plots (Suominen et al. unpubl.). Thus, in the Swedish moose sites two important predator groups were more abundant, similarly to the gastropods, in unbrowsed plots; this suggests that invertebrate predation is probably not the explanation of the observed patterns of gastropod density in relation to moose browsing. In Lapland, gastropods were

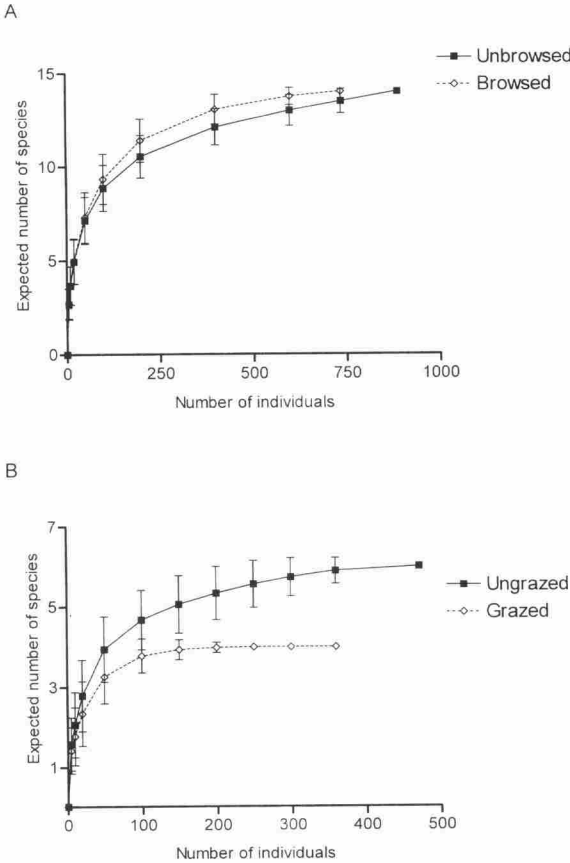


Fig. 2. Rarefaction curves estimating species richness of terrestrial gastropods for grazed and ungrazed plots from pooled data of A moose and B reindeer sites.

one of the few groups that were more abundant in ungrazed plots, while most of their invertebrate predators were more common in grazed plots. Here invertebrate predation may have contributed to the observed difference in gastropod density caused by reindeer grazing.

Richness and diversity

Gastropod species richness and diversity were not affected by moose browsing, but there were more gastropods in the traps of unbrowsed exclosures than in those of browsed plots, and the individuals caught were more evenly distributed among different species in browsed plots (higher relative diversity H'/H'_{\max}). Thus the higher number of gastropod individuals in exclosures resulted mainly from the increase in numbers of individuals of a few of the most common species. In reindeer sites, the rarefaction estimations of species richness and the diversity index were higher in ungrazed plots (marginally significant difference), as was population density. In reindeer sites, the differences in the rarefaction curves of grazed and ungrazed plots clearly indicate both a higher population density and a greater species richness of gastropod fauna in ungrazed plots than in grazed plots. Moose browsing reduced the population density of generalist species without affecting species richness, and there were some species that were more common in browsed plots. The stronger effect of reindeer may be due to the higher grazer densities (caused by reindeer husbandry) and more severe habitat changes at ground level, or to the harsher and less productive environment, where gastropod species live close to the limits of their distribution.

Ecosystem engineering

Both moose and reindeer browsing and grazing tend to create habitats that are warmer and drier in summer than they would be without grazing (Väre et al. 1996, Kielland and Bryant 1998). One reason for this is that their foraging on trees prevents height growth and thereby recruitment into the overstorey, thereby increasing the amount of radiation penetrating to the forest floor and possibly the wind velocity under the canopy. Grazing on field- and bottom-layer vegetation by cervids will also increase solar radiation and raise the temperature, thus reducing the level of moisture at the ground level and in the top soil. The decrease in the density of deciduous trees also reduces the amount of deciduous leaf litter falling to the ground (Pastor et al. 1993, Kielland and Bryant 1998, Suominen et al. 1999). A thick deciduous litter layer means that the microclimate will be more shaded and humid, and thus more suitable for gastropods; at the same time it creates additional shelter for them. Decom-

posing leaf litter and the fungal hyphae on it are also a source of food for gastropods. For example, the most common species in the present data, the slug *Arion subfuscus*, which was more common in ungrazed plots, is particularly sensitive to warmth and dryness (Godan 1983) and feeds largely on dead plant material and fungal material (Jennings and Barkham 1975). In the Swedish moose sites, the density of canopy trees, especially deciduous ones, was lower in browsed plots, and the yearly accumulation of leaf litter in the browsed plots at Sunnäs was only 10% of that in unbrowsed plots (Suominen et al. 1999). In young stands of both moose and reindeer sites, grazed plots had far fewer deciduous saplings; the plots were more open, and had more grasses in the herb-layer vegetation (Suominen unpubl.). In the mature forests of reindeer sites the most evident effects of grazing were a reduction in the lichen cover (*Cladonia* lichens) and in birch density (Suominen et al. unpubl.).

Jones et al. (1994, 1997) define a 'physical ecosystem engineer' as a species that "directly or indirectly control[s] the availability of resources to other organisms by causing a physical state changes in biotic or abiotic materials". A related concept is that of the 'keystone modifier' (Mills et al. 1993), but Power et al. (1996) define a keystone species as "one whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance". Since moose and reindeer are so abundant in Fennoscandia, it can be argued that they are dominant rather than keystone species. I therefore prefer the term 'ecosystem engineer', which can be used to describe ecosystem modification by either a dominant or a keystone species. In any case, whatever the term used, it is evident that moose and reindeer have a strong impact on various biotic and abiotic components of the boreal forest ecosystems in Fennoscandia, and that many of these impacts are not direct trophic effects of their foraging.

Parasite transmission

Parasitic nematodes that use gastropods as intermediate hosts create a potential link between the ecosystem effects of grazing and browsing and the cervids themselves. If the observed decrease of ca 20% (24% in reindeer sites; 17% in moose sites) in the density of gastropods active at the ground level in grazed compared to ungrazed plots reduces the prevalence of nematode infection in cervids, there will be a positive feedback effect of grazing on the engineering cervids themselves. Jones et al. (1994) call such positive feedbacks of engineering, where engineering affects the fitness of the engineer itself, 'extended phenotype engineering', as opposed to 'accidental engineering'. Whether this change in gastropod density actually affects the fitness of moose and reindeer in boreal forests is not known, but the effects of minor changes in gastropod densities on the prevalence of infection in cervids are probably negligible (Lankester pers. comm.).

Even if the links described above indirectly reduce the prevalence of nematode parasites in cervids, it should probably still be categorized as an accidental consequence of engineering.

Conclusions

Since the physical properties of microhabitats are so important for the distribution and density of terrestrial gastropods (Godan 1983, Boag 1985), the way in which cervid foraging modifies the humidity, temperature, and shelter (leaf litter accumulation and herb-layer vegetation) is more important than the possible trophic effects that may reduce food availability for gastropods (i.e. cervids eating the same plants as gastropods). I thus conclude that allogenic physical engineering of boreal forests by moose and reindeer may change the species composition and reduce the population densities of the terrestrial gastropod assemblage in Fennoscandia, and that in Finnish Lapland gastropod species richness too was lower in areas grazed by reindeer.

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