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Lemming Grazing on Snowbed Vegetation during a Population Peak, Northern Norway

Jon Moen,
Peter A. Lundberg,
and Lauri Oksanen

Department of Ecological Botany, University of Umeå, S-901 87 Umeå, Sweden.

Abstract

The impact of a lemming population on a snowbed in northern Fennoscandia was examined during a population peak. Twelve exclosures and 12 open plots were established on a moderately early snowbed. The plots were photographed in autumn 1988, spring 1989, autumn 1989, and autumn 1990, and the cover of graminoids, woody plants, lichens, litter, lemming feces, and mosses were measured. The changes in cover were analyzed with repeated measures ANOVAs. The lemmings significantly decreased cover of graminoids by 33% and mosses by 66% during the peak winter. Our results show that grazing needs to be considered when discussing the development of snowbed vegetation.

Introduction

The Norwegian lemming (*Lemmus lemmus* L.) is well known in Fennoscandia for its appearance in large numbers some years and its virtual absence other years (Kalela et al., 1971; Henttonen et al., 1977, 1987; Henttonen and Järvinen, 1981; Oksanen and Oksanen, 1981, 1992). In the period between 1977 and 1989, lemmings have had two outbreaks in northernmost Fennoscandia: 1978 and 1988 (Oksanen and Oksanen, 1992). A typical lemming population peak is characterized by a rapid increase in numbers followed by a steep decline to very low numbers. Several explanations for the cause of the declines have been proposed, including food shortage (Henttonen and Järvinen, 1981; Oksanen and Oksanen, 1981, 1992) and predation (Andersson and Jonasson, 1986; Henttonen et al. 1987).

The preferred winter habitats for the lemmings are dwarf shrub heaths and snowbeds above the treeline. Only in years of mass occurrence are lemmings found in the birch forest and in the taiga due to migration (Kalela et al., 1961, 1971; Henttonen and Järvinen, 1981; T. Oksanen, 1992). The lemmings feed mainly on graminoids and mosses (Hansson, 1969; Kalela and Koponen, 1971; Tast 1991), and large amounts of the available food may be consumed during peak years (Kalela et al., 1971; Henttonen and Järvinen, 1981; Oksanen and Oksanen, 1981). However, very little quantitative data showing significant effects of lemmings on the vegetation exist.

The aim of this study is to examine the effect of a lemming population on the vegetation of a snowbed during a peak winter, and the subsequent recovery of the vegetation in the 2 yr after the peak. As the population peaks seem to be separated by about 10 yr, and the lemmings are more or less absent in the years between the peaks (Oksanen and Oksanen, 1992), a short-term study is sufficient to capture the effects of the lemmings during an outbreak.

Methods

The study was carried out in the Joatka research area 25 km southeast of Alta, northern Norway (69°46′N, 23°58′E). The research area consists of a lowland plateau (about 400 m a.s.l.) dominated by barren lichen–dwarf birch tundra, a south-facing slope with an abundance of luxuriant habitats (herb-rich mountain birch forest, willow thickets, and meadows), and a highland plateau (500–650 m a.s.l.) dominated by dwarf shrub heaths and snowbed vegetation. The main vertebrate herbivores in the area are microtine rodents, two species of grouse (*Lagopus lagopus* and *L. mutus*), and reindeer (*Rangifer tarandus*) which move through the area during spring and autumn migrations (Moen, 1993).

Twenty-four permanent plots (50 × 80 cm) were marked on a typical snowbed (area of snowbed ca. 400 × 100 m; 600 m a.s.l.) on the highland plateau ca. 1 km from the slope. The vegetation had a fairly low diversity with *Carex bigelowii* and *Salix herbacea* as the by far most common vascular plants (see Appendix for a species list of vascular plants, mosses, and lichens, together with frequencies of occurrence on the plots).

The 24 plots were randomly positioned in a 30 × 30 m area on the snowbed, and then randomly allocated to 12 open plots and 12 lemming-proof exclosures. The exclosures were about 80 × 120 cm and were constructed of galvanized net, with a 1.27 × 1.27 cm mesh size and with a height of 60 cm. The exclosures were dug down into the mineral soil to a depth of ca. 15 cm. Snap-traps were put inside the exclosures, but no animals were caught during the experiment.

The exclosures were put in and the first sampling of the vegetation was carried out just before the onset of winter 1988. The plots were photographed on color slide film from a height of 1.5 m at the start of the experiment (11 September 1988), immediately after the snowmelt (25 June 1989), on 19 August 1989, and on 25 August 1990. The camera, equipped with a 50-mm macro lens, was centred over the plot, and the film plane was kept parallel to the ground. The slide positives (24 × 36 mm) were magnified to 20 × 30 cm (i.e. 15% of life size) and printed on photographic paper. Two hundred and fifty needle-point-sized points were randomly chosen and marked on a transparent plastic template. The same point template was used for all photographs. The template was put on top of each photograph and anything under the points was registered. All plants were identified to the lowest taxonomic category that the resolution of the photographs allowed (species for the majority of vascular plants and genera for the majority of lichens; see Appendix).

Photo quadrat estimates of abundances and cover are commonly used in studies of sessile marine organisms, and they have been shown to be accurate and comparable to cover-pin methods performed in the field especially in monolayered assemblages (Foster et al., 1991). We regard the photographic method as reliable for obtaining a measure of shoot abundance for vascular plants and fruticose lichens that were easily visible. The visibility of the moss shoots, however, changed seasonally due to color variations, and they also grew under areas covered by vascular plants. Thus, instead of trying to directly estimate the coverage of mosses, we estimated the areas that could be identified as being devoid of an intact moss cover (bare ground, stones, areas covered by crustose lichens or cup lichens, and continuous *Stereocaulon* mats). The outlines of these moss-free areas were copied on a transparency, and their extent was measured by a planimeter. The proportion of the plots covered with mosses was then calculated as $1 - a$, where a is the cover of moss-free areas. To prevent bias, the photographs were analyzed in random order and without knowledge of when and where each photograph were taken. We will present data on the pooled number of sample points covered by graminoids, woody plants, and lichens (herbs were only a minor component of the vegetation), litter, and lemming feces, along with moss cover.

The treatment effects were tested with repeated measures analysis of variance on the scores for the different categories (graminoids, woody plants, lichens, litter, lemming feces, and moss-free areas). Each category was analyzed separately for the period autumn 1988 to autumn 1989 to examine the grazing effect, and for the period autumn 1988 to autumn 1990 to examine the recovery of the vegetation. In the cases where a Mauchley sphericity test showed that assumptions of symmetry were violated, the degrees of freedom were adjusted using the Huyn-Feldt Epsilon (Milliken and Johnson, 1984; Norusis, 1988). However, in no case did the adjusted degrees of freedom change a significant *F*-ratio to a nonsignificant ratio. The significance probabilities reported in Table 1 are thus from the nonadjusted tests.

At the end of August 1992, i.e. 4 yr after the population peak of lemmings (see below), the species composition and the relative abundances of the species were analyzed in the field with a point frequency method. A plastic square of 50 × 40 cm with 120 holes (ø 4 mm) was placed on each plot, and species covering 50% or more of each hole were recorded. The relative abundance of each species or genera in the exclosures were tested against the open plots with Mann-Whitney tests.

Microtine densities in the research area have been surveyed by index trapping using the small quadrat method of Myllymäki et al. (1971) twice a year since 1986 by L. Oksanen and P. Ekerholm (unpubl.). Here we will only present data on lemmings and on voles (*Clethrionomys rufocanus* and *Microtus agrestis*) from the upper plateau. The method is briefly as follows: on the upper plateau three habitats were defined (snowbed, heath, and bog). In each habitat, five to six permanent quadrats of 15 × 15 m were laid out with three snap-traps in each corner. The traps were baited with black rye bread and were set for two days and nights in the spring and autumn each year giving a total of 24 trap nights per quadrat and trapping occasion. The traps were inspected daily during these periods. One of the snowbed quadrats was placed on the same snowbed as the one on which the exclosure experiment was performed. We will present the numbers of animals caught per 24 trap nights in this snowbed quadrat, together with a weighted capture index for the upper plateau. The weighted indexes were calculated as follows: the capture indices for each habitat (individuals caught per 100 trap nights) were combined by multiplying them with the fraction that the habitat covers of the total area, and summing these products. This weighted capture index corrects for the fact that trapping effort was not distributed according to the abundance relationships of different habitats. The index corresponds roughly to density per hectare of average type terrain (Oksanen and Oksanen, 1981).

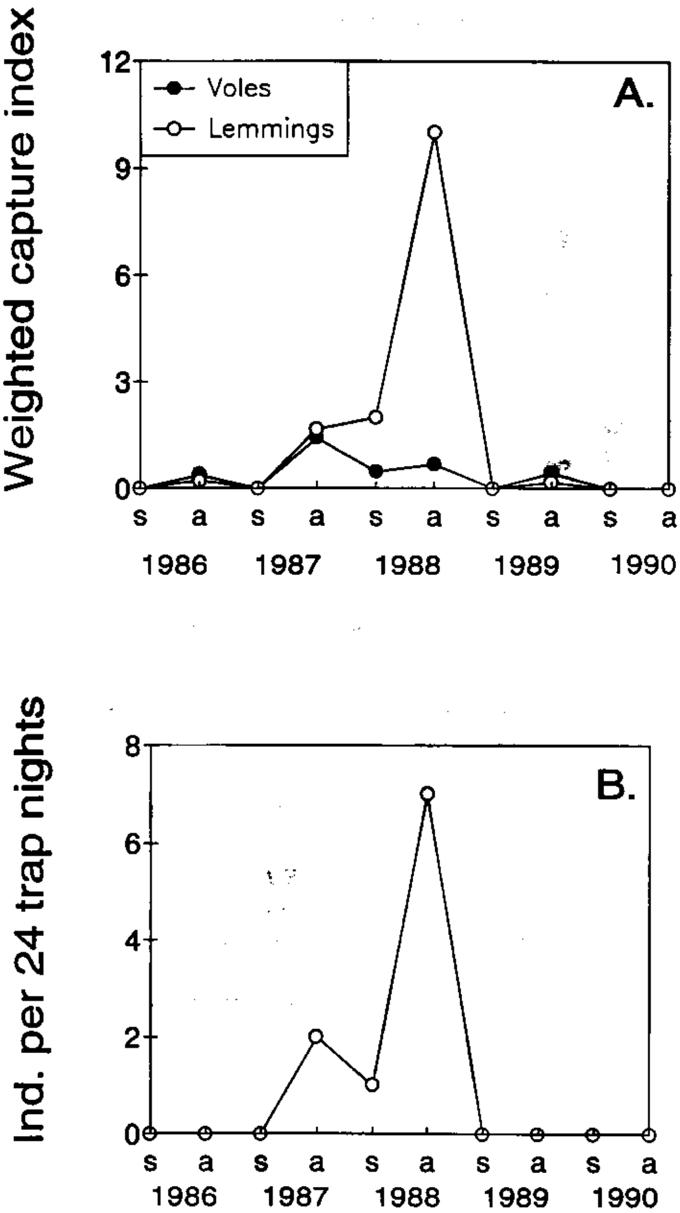

FIGURE 1. Capture indices for voles and lemmings (s stands for spring, a stands for autumn). A. Weighted capture indices for the upper plateau based on three habitat complexes (snowbed, heath and bog). B. Number of caught animals per 24 trap nights (i.e. numbers caught per trapping occasion) on the snowbed. (Data from L. Oksanen and P. Ekerholm unpubl.).

Results

The lemmings peaked on the entire plateau in the autumn of 1988 with a subsequent crash during the winter (Fig. 1). No lemmings were caught on the snowbed from spring 1989 to autumn 1992 (Fig. 1b and P. Ekerholm pers. comm.). The voles in the area did only reach moderate densities on the plateau (Fig. 1a), and no voles were caught on the snow-bed (Fig. 1b), making it unlikely that vole grazing was an important factor for the vegetation during the study.

Graminoids covered a significantly higher percentage of the sample points in the exclosures than in the open plots in autumn

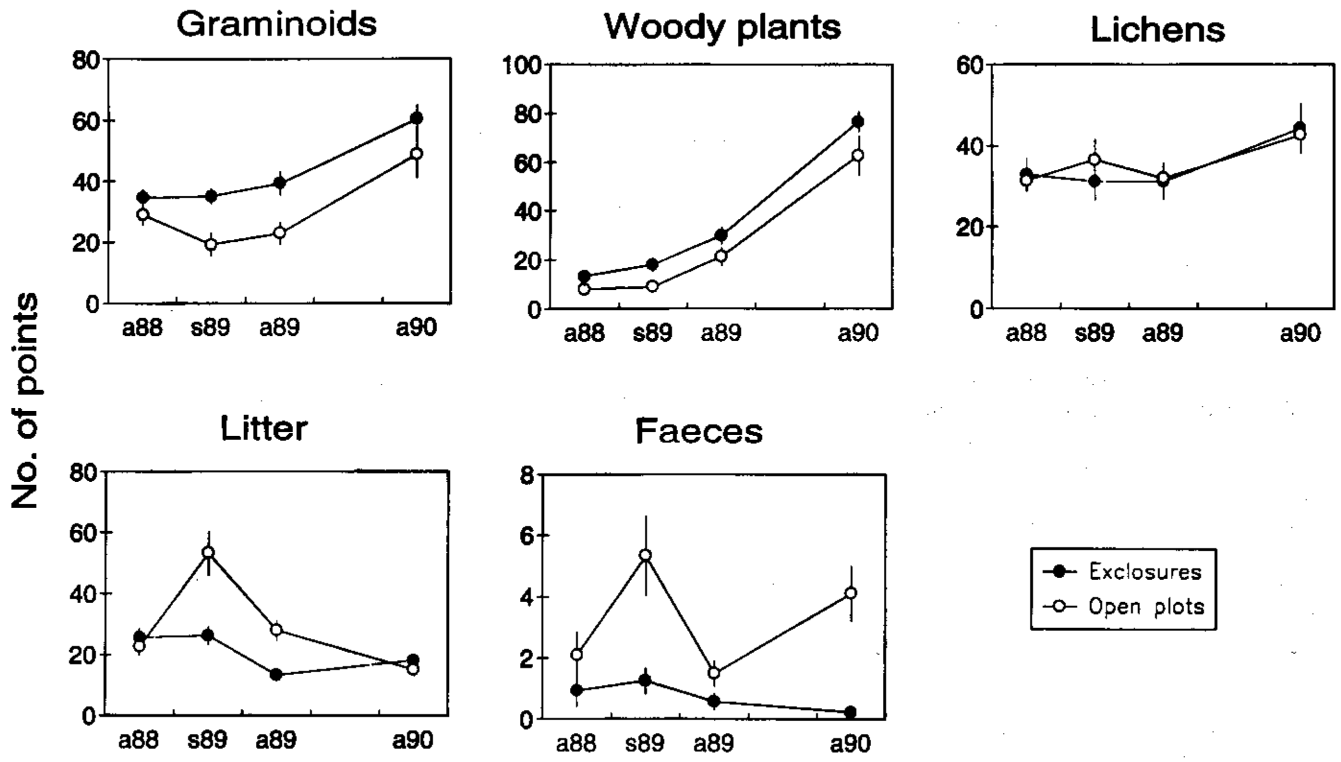

FIGURE 2. Number of points (mean ± SE) covered by graminoids, woody plants, lichens, litter, and lemming feces. a88 means autumn 1988, s89 spring 1989, etc.

TABLE 1

F-values from repeated measures ANOVAs. A. Data from autumn 1988 to autumn 1989. B. Data from autumn 1988 to autumn 1990.

	Fence	Time	Interaction
A. 1988–1989			
Graminoids	10.05*	2.71	4.08*
Woody plants	8.28*	23.66***	0.39
Lichens	0.10	0.46	1.02
Litter	11.23*	17.08***	9.51***
Feces	6.05*	13.06***	7.16*
Moss cover	13.11*	26.18***	13.93***
B. 1988–1990			
Graminoids	6.21*	46.80***	2.13
Woody plants	4.60*	140.80***	0.92
Lichens	0.05	6.86**	0.51
Litter	7.43*	16.59***	7.76**
Feces	16.01**	5.23*	3.61*
Moss cover	15.86**	36.36***	19.86***

* Significant at the 0.05 level; ** significant at the 0.001 level; *** significant at the 0.0001 level.

1989 (Fig. 2, Table 1). This difference was caused by a decline in the open plots during the winter by about 33%, while no such trend was seen in the exclosures. Positive net changes were seen in both exclosures and open plots from spring 1989 to autumn 1990. Overall there were significant differences between the treatments for both analyses, although the interaction between treatment and time were only significant for the first part of the period (Table 1) due to the general increase between 1989 and 1990. Woody plants increased in both exclosures and open plots (Fig. 2) giving a significant time trend but no significant interaction (Table 1). Lichens showed no net changes between 1988 and 1989 and a positive trend in both treatments between 1989 and 1990 (Fig. 2, Table 1).

Both litter and lemming feces increased significantly in the open plots as compared with the exclosures from autumn 1988 to spring 1989 (Fig. 2, Table 1). Litter decreased in the open plots to roughly the same value in autumn 1990 as it had in 1988, while the exclosures showed no net change. The lemming feces decreased in the open plots during the summer of 1989 and then increased again between 1989 and 1990. This increase is difficult to explain since no lemmings were caught in 1990. However, the number of points covered by feces were very low (note the differences in scale in Fig. 2), and the increase could be due to random factors.

The moss cover decreased significantly in the open plots in the spring of 1989 by 66% as compared to the exclosures (Fig. 3 and Table 1). The moss cover then increased over the summer as the moss shoots recovered.

The relative abundances of the species in 1992 of hepatics, *Pohlia* spp. (*P. nutans* and *P. drummondii*), *Ochrolechia* spp., and fungi were significantly higher in the open plots than in the exclosures (Table 2). No other significant differences were found.

Discussion

The lemmings caused a marked decline in their two preferred food plant groups: graminoids and mosses. Graminoids decreased by about 33% in the open plots in the spring, while no decrease was seen in the exclosures (Fig. 2). The graminoids in the exclosures in the spring consisted mostly of standing dead leaves, and the increase during the summer was probably due to the growth of new leaves. The graminoids in the open plots were to a large extent cut down close to the ground in the spring, and the increase over the summer reflected regrowth from the basal meristems. The recovery continued during the next year,

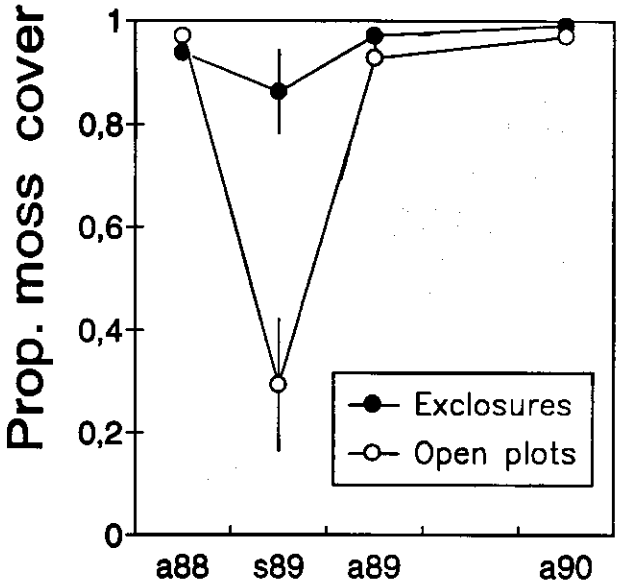

FIGURE 3. Proportion of plot areas covered with mosses (mean±SE). a88 means autumn 1988, s89 spring 1989, etc.

TABLE 2

Mean (±SE) number of points covered in exclosures and open plots in 1992 (n = 12).

	Exclosures		Open plots
Vascular plants			
Anthoxanthum odoratum	1.2 ± 0.7		0.0
Carex bigelowii	12.2 ± 2.6		7.2 ± 1.3
Carex lachenalii	0.0		0.2 ± 0.1
Luzula multiflora ssp. *frigida*	0.2 ± 0.2		0.3 ± 0.2
Luzula spicata	0.1 ± 0.1		0.0
Polygonum viviparum	1.1 ± 0.5		0.7 ± 0.2
Salix herbacea	12.9 ± 1.7		11.0 ± 1.8
Vaccinium vitis-idaea	0.1 ± 0.1		0.0
Mosses			
Conostomum tetragonum	0.2 ± 0.1		0.2 ± 0.1
Dicranum spp. + *Kiaeria* spp.	25.3 ± 5.5		29.1 ± 2.5
Hepaticae	16.8 ± 4.9	*	25.4 ± 3.1
Pohlia spp.	2.3 ± 0.7	*	12.4 ± 2.2
Polytrichum alpinum	3.8 ± 1.7		3.8 ± 1.3
P. juniperinum	8.2 ± 4.3		4.0 ± 1.4
P. norvegicum	0.8 ± 0.7		0.7 ± 0.6
Lichens			
Cetraria delisei	0.9 ± 0.5		0.2 ± 0.1
C. islandica	12.8 ± 3.8		5.9 ± 1.9
Cladina mitis	0.1 ± 0.1		0.0
Cladonia spp.	3.8 ± 0.8		7.8 ± 1.8
Lecidea spp.	0.1 ± 0.1		1.2 ± 1.0
Nephroma arcticum	0.2 ± 0.2		0.0
Ochrolechia spp.	0.3 ± 0.2	*	1.9 ± 0.6
Peltigera rufocanus	0.1 ± 0.1		0.0
Stereocaulon spp.	7.2 ± 1.6		4.3 ± 1.1
Fungi	0.0	*	2.4 ± 0.7

* Significant difference from a Mann-Whitney test ($p < 0.05$).

and the coverage of graminoids in both exclosures and open plots reached higher values than at the start of the experiment. However, the lemming population had begun to increase in 1987 (Fig. 3), so the coverages in 1988 represents a plant community that was already grazed to some extent.

The moss cover decreased from 97 to 29% in the open plots in the spring (Fig. 3). A slight decrease from 94 to 86% in the exclosures is probably due to changes in the color of the moss shoots which influenced their visibility on the photographs. However, even when adjusted for that factor, there were still ca. 4.5 times larger area without any visible moss shoots in the open plots than in the exclosures in the spring, and the lemmings had removed 66% of the moss cover. The apparent strong regrowth of mosses in the following summer (Fig. 3) is in part an artifact as areas where no moss was visible on the photographs were considered moss free. In spring 1989 large areas of the open plots looked completely devoid of aboveground moss shoots. However, once the grazed moss shoots began to be replaced, probably by branches arising from subapical positions close to the ground (Longton, 1988), areas with protruding moss shoots were no longer included in moss-free areas. This gave the impression of an almost total recover of mosses during the summer while in fact the actual cover was a lot less than in the exclosures (pers. observations). The difference in moss cover between the open plots and the exclosures in spring 1989, however, reflects the activity of the lemmings and is not an artifact of the method. It thus seems that the photographic method used in this study is less suitable for ground layer plants without clearly defined shoots or divergent colors, although a coarse measure of changes in abundance or cover can still be obtained.

The general increase in both exclosures and open plots of woody plants (mainly *Salix herbacea*) is somewhat puzzling. Grazing effects by the lemmings seem unlikely since woody plants are not eaten by them, and the increase is seen in both treatments. However, it is possible that the exclosures have caused reindeers to move round this part of the snowbed during migration, and that the increase is an effect of relaxed trampling, but we have no data on that.

The relative abundances of hepatics and the *Pohlia* species differed between the treatments 4 yr after the lemming peak (Table 2). Taken together, these species represented 48% of the total number of points covered by mosses in the exclosures, and 50% in the open plots, and were thus a major component in the moss community. These bryophytes are favored by disturbance (Schuster, 1966; Oksanen and Ranta, 1992) and the difference could have been caused by the lemming grazing. It is thus possible that the grazing has a long-term effect on the relative abundances of the species in the community.

The lemming population peaked in autumn 1988, both on the snowbed and in the upper plateau as a whole (Fig. 1), followed by a sharp decline. No lemmings were caught at all on the upper plateau in the following spring. The population peak is also seen in the increase in lemming feces and litter in the open plots over the winter (Fig. 2). The three-fold increase in litter in the open plots in the spring reflects the cutting of mainly graminoids and mosses by the lemmings. The litter and the lemming feces are either washed away by spring meltwater or blown away from the plots as the ground dries up in the summer.

The development of snowbed vegetation has generally been attributed to the duration of the snow cover. There is usually a well-developed zonation which is related to the time of snowmelt in the summer. The growing season is thus more or less shortened. However, the plants in the snowbed are also protected against low temperatures in the winter, and meltwater may provide moisture for most or all of the growing season (Dahl, 1956; Gjaerevoll, 1956; Wijk, 1986). Our results suggest that the plants of snowbeds must also tolerate recurrent severe grazing by lemmings and accompanying physical disturbance. The dominating snowbed plants, i.e. acrocarpic mosses and graminoids, seem to manage the situation by having resources and meristematic tissues in the ground or at the ground surface.

In the absence of lemmings, the mosses of northern Fennoscandian snowbeds increases linearly at a rate of about 10 g m^{-2} yr^{-1} dry weight (Kyllönen and Laine, 1980; L. Oksanen, 1983). A continuous thick moss carpet is strongly inhibitory for the generative reproduction of vascular plants (Söyrinki, 1939). Thus, the recurrent disturbance by lemmings might contribute to the persistence of plants dependent on generative reproduction or reproduction by bulbils (in our material: *Luzula spicata*, *Festuca ovina*, and *Polygonum viviparum*) in snowbed vegetation. In the longer run, the buildup of moss biomass would probably be detrimental to all vascular plants, as indicated by the long-term exclosure experiments at Barrow, Alaska (Batzli, 1975; Batzli et al., 1980) and the heavily moss-dominated communities on the lemming-free islands of Jan Mayen and Bear Island (Summerhayes and Elton, 1923; Warren Wilson, 1952).

Our observations are consistent with the predictions of the hypothesis of exploitation ecosystems (Fretwell, 1977; L. Oksanen et al., 1981; L. Oksanen, 1988, 1990; T. Oksanen, 1990) stating that large tracts of relatively barren land (annual primary productivity of 30–700 g $m^{-2}yr^{-1}$ dry matter; L. Oksanen, 1983) are characterized by intense natural grazing pressure. In our case, a seven-fold increase of the local lemming population caused a decrease of at least 33% of the graminoids and 66% of the mosses during a winter of peak densities. These estimates must be seen as conservative since some grazing had already taken place before the exclosures were put up.

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APPENDIX

Species list from the snowbed. Species are grouped according to the classification used (see Methods). The number of plots that species were registered in are given after the taxonomic level identifiable in the photographs, except for mosses which were analyzed as a group. Species that were identified in the field, but not in the photographs, are given under the respective collective taxa. Nomenclature follows Nilsson (1986) for vascular plants, Hallingbäck and Söderström (1987) for mosses, and Santesson (1984) for lichens.

Species	No. of Plots
Graminoids	
Agrostis mertensii	3
Anthoxanthum odoratum	1
Calamagrostis lapponica	1
Carex bigelowii	24
C. canescens	1
C. lachenalii	13
Festuca ovina	1
Luzula multiflora ssp. *frigida*	1
L. confusa	9
L. spicata	1
Vahlodea atropurpurea	3
Herbs	
Polygonum viviparum	10
Sibbaldia procumbens	3
Woody plants	
Empetrum hermaphroditum	1
Salix herbacea	24
Vaccinium vitis-idaea	3
Lichens	
Cladonia spp.	24
C. amaurocraea	
C. coccifera	
C. uncialis	
C. bellidiflora	
Cetraria spp.	20
C. delisei	
C. ericetorum	
C. nivalis	
Nephroma arcticum	2
Stereocaulon spp.	24
Crustose lichens	24
Ochrolechia spp.	
Mosses	
Conostomum tetragonum	
Dicranum spp.	
Kiaeria starkei	
Pogonatum urnigerum	
Pohlia nutans	
P. drummondii	
Polytrichum alpinum	
Polytrichum juniperinum	
Polytrichum piliferum	
Polytrichum sexangulare	
Tetraplodon mnioides	
Hepaticae	