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Moose, trees, and ground-living invertebrates: indirect interactions in Swedish pine forests

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The role of moose in structuring the boreal forest ecosystem has been studied extensively in recent years. This research has focused mainly on the effects of moose on vegetation and soil dynamics. However, the extent to which these effects influence animal communities has received little attention. We studied how invertebrate assemblages on the forest floor of two Swedish pine forests were affected by the presence of moose. Our approach was to trap invertebrates using pitfall traps in unbrowsed exclosures and browsed reference plots, estimate the percentage cover of herb-layer plants, measure the height and density of tree species, and measure the accumulation of leaf litter. The effect of moose on tree strata differed between the two areas. In Sunnäs, where the stand was a mixture of deciduous trees and pines, the main effect of moose was to eliminate most of the deciduous trees from the canopy. Here the amount of deciduous leaf litter was ten times higher in unbrowsed exclosures compared with browsed plots. The stands on the dry sites in the other area, Furudal, were almost pure pine. Here, moose browsing reduced the density of taller pines, but increased the number of pine saplings. At Sunnäs, the herb-layer plant cover did not differ between browsed and unbrowsed plots. However, there was a difference between exclosures and browsed plots in terms of the ground-dwelling invertebrate assemblage. Number of individuals of most invertebrate groups that differed between exclosures and browsed plots were higher in unbrowsed plots and the total number of invertebrates was also higher in unbrowsed plots, but diversity of invertebrate fauna was higher in browsed plots. At Furudal both the vegetation and invertebrate assemblages differed between browsed and unbrowsed plots. Browsed plots had a higher cover of ground lichens, while unbrowsed plots had more mosses. Among the invertebrate taxa that differed between treatments, the number favored by browsing and the number disfavored by browsing were roughly equal, and diversity was not affected by moose. We suggest that by affecting the density and composition of tree species, moose indirectly influenced the structure of invertebrate communities. At Sunnäs, the reduction in the amount of deciduous leaf litter was probably the key effect. Vegetation was not affected much, but the differences in litter layer composition had affected the microclimate on the forest floor while also providing an important additional trophic resource and habitat for ground-dwelling invertebrates. At Furudal the main effect of moose was to reduce the density of the pine canopy, thus increasing the amount of light penetrating to the forest floor. As a consequence, the floral composition and microclimate was altered which, in turn, affected the invertebrate fauna.

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Selective foraging of large mammalian herbivores, like moose (*Alces alces*), in boreal forests, can affect the structure of their habitat. Moose can influence tree species composition (e.g. Naiman 1988, Bryant et al.

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1991, Pastor et al. 1993, Kielland and Bryant 1998), herb-layer vegetation (McInnes et al. 1992, Suominen, Danell, and Bryant unpubl.), leaf litter accumulation and decomposition (Pastor et al. 1993, Kielland et al. 1997), mycorrhizal colonization of tree roots (Rossow et al. 1997), and the rate of succession (Pastor and Naiman 1992, Kielland and Bryant 1998) in boreal forests. There is also some evidence that cervid foraging can influence insect abundances. Herbivorous insects are more numerous on twigs and leaves of browsed deciduous trees than on those that have not been browsed by moose earlier (Danell and Huss-Danell 1985, Roininen et al. 1997). Red deer (*Cervus elaphus*) in Scotland have a negative influence on the invertebrates living on its food plant bilberry (*Vaccinium myrtillus*) (Baines et al. 1994). Changes caused by moose in an early successional floodplain ecosystem affected ground-living beetle assemblages in Alaska (Suominen, Danell, and Bryant unpubl.). Most beetle families that responded to the presence of moose were more abundant in browsed areas, but there were exceptions.

The ecosystems studied here are very different from the habitat investigated in the Alaskan study (Suominen, Danell, and Bryant unpubl.), which is the only other case that we know of where the influence of moose on ground-living invertebrates has been studied. In Alaska, moose changed early successional willow thickets to alder thickets. In Fennoscandian forests moose prefer to browse on a variety of deciduous trees (willow *Salix* spp., birch *Betula* spp., aspen *Populus tremula*, mountain ash *Sorbus aucuparia*), and Scots pine (*Pinus sylvestris*) but avoid Norway spruce (*Picea abies*) (Bergström and Hjeljord 1987). Moose also avoid alder (*Alnus* spp.), deciduous trees that are fairly uncommon in Fennoscandia except in some early successional habitats. Thus, moose could be expected to decrease the abundance of many deciduous tree species and pine, and by reducing the amount of competition from these tree species, enhance the growth of spruce and alder in the secondary succession of Fennoscandian forests.

It has been suggested that selective foraging by cervids in boreal forest will lead to slower nutrient turnover and a reduction in nutrient availability compared with unbrowsed forest (Pastor et al. 1993, Pastor and Cohen 1997). These effects can be attributed to the fact that the same chemical compounds that make conifer trees unpalatable also render these plant tissues somewhat recalcitrant to decomposition (Bryant et al. 1991, Pastor and Cohen 1997). Scots pine in Fennoscandia, however, can be viewed as an exception. This slowly growing and decomposing conifer is an important part of the moose diet (Bergström and Hjeljord 1987). Since this dominant conifer in Fennoscandian pine forests is readily

eaten by moose in addition to deciduous trees, the situation in Fennoscandia differs in principle from those forests in North America where this theory has been formed (e.g. Pastor et al. 1993). If the accumulation of deciduous leaf litter is substantially lower in browsed forests than in unbrowsed ones, then one could expect that the amount of resources available for invertebrates on the forest floor would be lower in the former. Consumption of pine can also reduce litter accumulation on the forest floor if browsing reduces pine density. Thus, we predict that if moose browsing substantially reduces leaf litter accumulation, invertebrates that feed on decomposing litter or use it as shelter will be more abundant in unbrowsed forests. At least in some cases the addition of deciduous leaf litter has increased the total abundance of ground-living invertebrates (e.g. Facelli 1994). On the other hand, by keeping the canopy more open (at the early stages of succession) browsing can increase the amount of light reaching the forest floor and thus support a more luxuriant herb-layer vegetation, which in turn might support more invertebrates. Thus, we predict that if browsing enriches the herb-layer vegetation, it should increase the abundance of invertebrates that feed on these herbs as well as predators in food chains depending on them.

In this study we compared unbrowsed exclosures and browsed reference plots at two locations in central Sweden in terms of tree species composition, leaf litter accumulation, vegetation, and the abundance of ground-dwelling invertebrates. One of the sites contained dry, unproductive sedimentary soil with an almost pure pine forest where lichens dominated the ground flora, while at the other site there was a stony, more moist till on which a pine forest mixed with spruce and deciduous trees had developed. Since the effects of moose browsing on deciduous trees are considered to contribute greatly to the overall influence that the moose has on the ecosystem, we expected that the two locations might differ from each other in terms of how invertebrate assemblages responded to browsing.

Materials and methods

Study sites

Sunnäs Research Area (founded and managed by the Swedish Hunters' Association) is situated in the southern boreal vegetation zone (Ahti et al. 1968) near the coast of the Gulf of Bothnia in the province of Hälsingland in eastern mid-Sweden (61° 10′ N, 17° 05′ E, 35 m alt.). Five pairs of study plots were established, and one randomly chosen plot in each pair was fenced off during 1979–80, in order to exclude large mammals. The other plot in each pair was not fenced off and

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served as a reference. Each plot was 40 × 40 m, and the distance between the exclosure and the reference was 10–20 m. The fence, which was 3 m high, excluded moose and roe deer (*Capreolus capreolus*), but not mountain hare (*Lepus timidus*). The sites were located in *Vaccinium-Myrtillus* type coniferous forest dominated by Scots pine. The pines were 8–9 years old at the time of fencing and had been planted on clear-cuttings established between 1969 and 1973. The other tree and shrub species were Norway spruce, juniper (*Juniperus communis*), birch (*Betula pendula* and *B. pubescens*), aspen, mountain ash, and willow. Apart from pine, only spruce and birches were relatively common. Moose browsing has prevented almost all aspens, mountain ashes, and willow as well as most birch from forming part of the canopy outside the exclosures.

Moose population densities in the Sunnäs area remained above the average for Sweden during the exclosure period. However, moose densities in winter concentration areas can be higher than at Sunnäs. Winter densities were 0.8–5.5 moose/km^2, giving a mean density for the period of about 3.4 moose/km^2. Roe deer density was estimated to be about 4–5 deer/km^2, which is normal or below the average for coniferous forests in central Sweden.

Furudal study area is situated in the province of Dalarna in middle Sweden (61° 11′ N 15° 10′ E, 220 m alt.) and represents the middle boreal vegetation zone (Ahti et al. 1968). It consisted of four pairs of study plots. One plot in each pair was randomly chosen to serve as the exclosure plot, while all animals had free access to the other. Exclosures were established in 1979, using 2.8-m-high fencing that excluded moose and roe deer. Each plot was 25 × 25 m, and the distance between exclosure and reference was 10–70 m. The mean height of the pines at time of fencing was 2.4–3.1 m (final cutting took place in 1962–63, whereafter the areas were naturally regenerated). All sites support fairly unproductive, pine-dominated forest with a variable tree species composition. Three of the sites are of *Cladina-Vaccinium* site type, and one contains *Sphagnum*-dominated bog vegetation. Exact figures on moose density for the study period were not available. Furudal is a winter concentration area, where densities of about 7 moose/km^2 were recorded during the 1980's. Although exact roe deer densities in the Furudal area are not known, the overall density is low.

Herb-layer plant cover and tree strata

In August 1995 we estimated the percentage covers of herb- and bottom-layer plant species within a 1-m^2 circular plot around 15 randomly chosen invertebrate trapping points out of the 30 points laid out systematically in a grid in each plot. Grasses, herbs, and dwarf-shrubs were identified to species or genus. The identity of the most common mosses and lichens was determined to species or genus, and the less common ones were combined to form a single group. The percentage covers of bare ground, stones, and dead wood were also estimated. For the statistical analysis the cover values were grouped into 10 classes (Table 1). Trees (higher than 30 cm) were classified as small (shorter than 3 m) or large (3 m or taller), and the number of each size class was determined for each species within a 10-m^2 circle around the same trapping points. Three meters is about the height limit for moose browsing; thus trees shorter than 3 m can be considered available for moose, whereas the taller ones can be considered to be part of the forest canopy, no longer susceptible to browsing (however, moose can break off taller trees to reach the canopy; thus, this is not an exact limit).

Leaf litter

We collected leaf litter from the study plots in Sunnäs from June through November 1996 (traps were collected after deciduous trees had dropped their leaves). Litter traps were placed on the ground in each plot at ten randomly chosen pitfall-trapping points. Traps were 50 × 100-cm wooden frames with a wire gauze bottom (mesh size < 1 mm). After collection, litter from each trap was sorted into deciduous, coniferous, and miscellaneous material. The litter was then dried for 48 h at 60°C and weighed (to the nearest 0.01 g).

Invertebrates

In late August 1995, 30 pitfall traps were set out in a systematic fashion (distance between traps 5 m at Sunnäs, and 3 m at Furudal) in each plot in both study areas and collected one month later. The traps were made of plastic (170-ml volume, 70-mm high, 70-mm top diameter), half-filled with 50% polypropylene glycol (with detergent added) and covered with small metal roofs to prevent dilution of the glycol (12 × 12 cm; 3–5 cm above ground). After collecting the traps the

Table 1. Vegetation cover classes used in the analysis and corresponding percentage-cover values.

Class	% cover
0	0
1	0–<1
2	1–<5
3	5–<10
4	10–<16
5	16–<25
6	25–<36
7	36–<51
8	51–<76
9	≥76

invertebrates were transferred to containers filled with 70% ethanol for storage. During the following winter all macroinvertebrates (Insecta, Araneae, Opiliones, large Acari [large individuals of Gamasina and Trombidia], Isopoda, Chilopoda, Diplopoda, and Gastropoda) from 15 randomly chosen traps (trapping points were the same as those used in plant cover estimations) were determined at least to order. Beetles, spiders, and harvestmen were identified to family level. Family Formicidae was separated from the rest of the order Hymenoptera, and later in this text 'Hymenoptera' refers to Hymenoptera excluding Formicidae. The only common gastropod in both areas was the slug *Arion subfuscus*.

We are aware that biases inherent in pitfall trapping could have contributed to the observed differences. The catchability of pitfall traps depends on the activity and behavior of the animals, which in turn are affected by habitat differences (Adis 1979). It is possible that the movements of insects in our study were influenced by differences in vegetation and microclimate. Since there were no significant differences in herb-layer vegetation between unbrowsed and browsed plots in Sunnäs, it is unlikely that differences in vegetation could have caused differences in the trap performance there. Furthermore, we do not believe that the changes in habitat were so severe as to invalidate comparisons of pitfall trap catches between unbrowsed and browsed plots. However, our trap count data should not be considered to reflect actual abundance values. We have used them, instead, as a relative measure of abundance in the different plots.

Statistical methods

The composition of tree strata, collected leaf litter, vegetation, and ground-dwelling fauna were studied with correspondence analysis (CA) (CANOCO 3.12 software, ter Braak 1988). Correspondence analysis has been recommended over principal component analysis (PCA) for handling species data because a unimodal response model is usually more appropriate for species data, and the gradient length was more than 2 SD units (ter Braak 1988, Jongman et al. 1995). This version of CANOCO is not corrected for the observed sources of instability, but since this instability should affect the results in cases when eigenvalues of axes are close to each other, our results should not be affected (Oksanen and Minchin 1997, Cajo ter Braak technical information[1]). We used CA

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[1] Information concerning an upgraded CANOCO program, CANOCO 3.15, can presently be found at http:// ww1.microcomputerpower.com/webpages/mcp/canoco315/

to demonstrate separation of browsed and unbrowsed plots. Plot means of tree and invertebrate numbers, leaf-litter dry mass, and plant cover in a sampled circle or a trap were used as test variables in the analyses. At first, we ran unconstrained CA ordination with plant, litter and invertebrate data. Thereafter, partial ordination was used where the effect of site differences was partialed out using sites as covariables. *T*-tests were used to test whether the site scores for unbrowsed and browsed plots on CA axes differed significantly from each other. We only tested those axes that appeared most likely to be connected to a treatment effect based on a brief visual inspection.

Between-treatment differences in plant-species cover, number of invertebrate individuals, taxa richness (corrected with rarefaction), and diversity (Shannon-Wiener index H') in the pooled data for two areas were tested with a paired *t*-test using plot means (rarefaction and H' were calculated according to Krebs 1989). A G^2 test was used to indicate which invertebrate groups differed in their abundance within each area. Apart from the ordination with CANOCO, SAS statistical software was used for all statistical analyses (SAS Institute 1990).

Results

Tree strata

Sunnäs

At Sunnäs the main source of variation in the tree data was clearly the exclosure treatment. The first unconstrained CA axis divided the sites into exclosures (negative site score) and browsed plots (positive site score) (Fig. 1A). The first axis explained 52.9% of the total variation (eigenvalue = 0.304) (there is a clear arch effect in the second axis [eigenvalue = 0.173]), Fig. 1A, but that is irrelevant since browsed and unbrowsed plots are separated by the first axis). Site scores for unbrowsed and browsed plots on this axis were significantly different (DF = 8, $t = 2.84$, $R^2 = 0.50$, $P = 0.0219$). Since the unconstrained CA explained variation between treatments so well, we did not run a partial CA with Sunnäs tree data. Exclosures were characterized by higher abundances of tall spruce, birch, and mountain ash as well as saplings of spruce, pine, and mountain ash, whereas tall pines and birch saplings were more common in browsed plots than in exclosures (Table 2).

Deciduous tree species preferred as browse by moose, i.e. mountain ash and aspen, were absent from the canopy of browsed plots. For birch (height ≥ 3 m), which is moderately preferred, numbers in browsed plots were only about 20% as high as numbers in the unbrowsed plots.
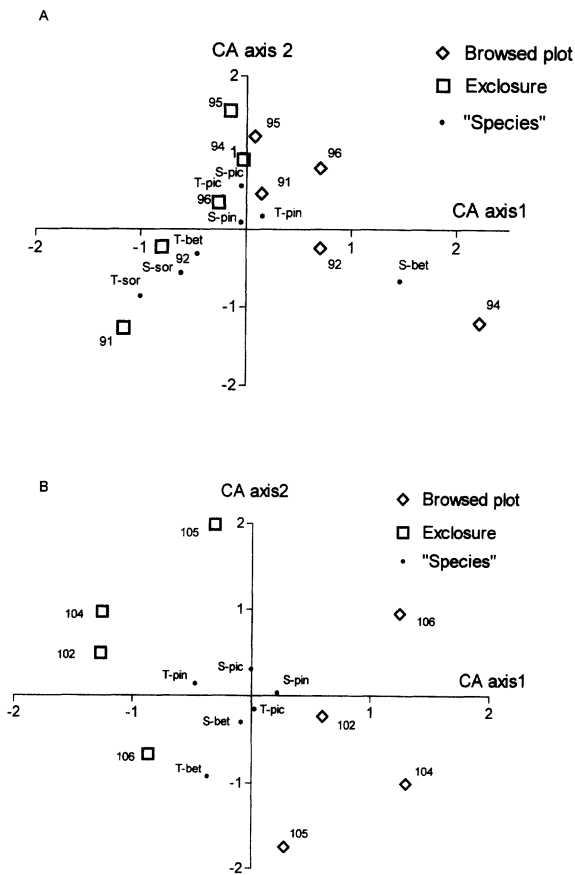
A

B

Fig. 1. Joint plot of ordination scores of trees species and sites. A) Unconstrained CA axes 1 and 2 with plot values of Sunnäs tree abundance data. B) Axes 1 and 2 of partial CA of Furudal tree data (effect of site differences partialed out). In both areas exclosure and browsed reference plots differ significantly from each other. Tree "species" are: T-pin = tall pines (height > 3 m), S-pin = small pines (height < 3 m), T-pic = tall spruces, S-pic = small spruces, T-bet = tall birches, S-bet = small birches, T-sor = tall mountain ashes, S-sor = small mountain ashes.

Furudal

At Furudal, the boggy site (no. 105) received high scores on the first unconstrained CA axis of tree data, and is thus separated from all the other plots (results of this unconstrained CA are not shown). This axis explained 50% of the total variation in the tree data from Furudal. The exclosure plots at the other three sites received lower, but still positive, scores, and the browsed plots at these three sites received negative scores on axis 1. This is quite logical since no. 105 was the only site with tall Norway spruce and several tall birches in both un-browsed and browsed plots. On the other sites, tall birches were found only in exclosure plots. Site scores for exclosures and references did not differ significantly from each other on CA axis 1 or axis 2 (axis 1: eigenvalue = 0.154, DF = 6, $t = 1.071$, $R^2 = 0.16$, $P = 0.325$; axis 2: eigenvalue = 0.118, $t = 1.58$, $R^2 = 0.294$, $P = 0.165$). Thus, we ran partial CA's (sites as covari-

ables) with the Furudal tree data. The first axis of this partial CA separated unbrowsed and browsed plots from each other (eigenvalue = 0.085, DF = 6, $t = 5.31$, $R^2 = 0.82$, $P = 0.0018$) and explained 66% of the residual variation after using sites as covariables (Fig. 1B).

At Furudal there were twice as many tall pines in unbrowsed plots compared with in the browsed plots, and the number of birches over 3 m high was three times higher inside the exclosures (Table 2). Pine saplings were more numerous in the browsed plot at every site. Birches were only present at two sites, and the other two were almost pure pine stands. The most preferred deciduous trees were not growing on the dry sandy soils of Furudal.

Leaf litter

The first axis of the correspondence analysis of plot means of litter data (only studied in Sunnäs) separated unbrowsed and browsed plots from each other (Fig. 2) (eigenvalue = 0.217, DF = 8, $t = 3.71$, $R^2 = 0.632$, $P = 0.0060$). This axis explained 97.8% of the total variation in the litter data. Thus, the exclosure treatment was the main source of variation in litter accumulation at Sunnäs.

Dry masses of deciduous litter, miscellaneous material (mainly *Vaccinium myrtillus* leaves) and all litter combined were higher inside the exclosures (Table 2). On average, there were ten times more deciduous litter inside the exclosures than in the browsed references. The dry mass of coniferous litter (mainly pine needles) was slightly higher in browsed plots.

Plant cover

The influence of browsers on the cover of different plant species (combined data for the areas) was tested with paired t-tests using means from each unbrowsed and browsed plot. None of the plant species showed a consistent response to browser exclusion in this data set (mean % covers of plant species in both areas are given in Appendix 1). No significant differences between treatments were found in plant species richness or diversity (H') in the herb- or bottom-layer or both combined when site means were tested (paired t-test: DF = 8, $t < 1.63$, $P > 0.14$, for all groups).

Sunnäs

The unconstrained CA with plot means of vegetation cover mainly reflected differences in vegetation among sites. Even after the effect of site differences had been partialed out, none of the CA axes was clearly linked to the exclosure treatment (Fig. 3A) (t-test: DF = 8, $t < 1.05$, $P > 0.32$). Thus, we conclude that moose browsing did not have a major impact on the composi-

Table 2. Mean number of trees per hectare in each of the study areas and accumulation of leaf litter (g/m^2) at Sunnäs (leaf litter accumulation was not measured in Furudal).

Variable	Sunnäs E[1] mean (SE)	Sunnäs B[2] mean (SE)	Furudal E[1] mean (SE)	Furudal B[2] mean (SE)
Tree density				
Tall *Pinus*	207 (14.5)	185 (18.4)	372 (72.5)	155 (48.2)
Tall *Picea*	88 (10.4)	40 (16.6)	15 (15.0)	7 (7)
Tall *Betula*	76 (23.8)	15 (6.1)	30 (25.8)	20 (20)
Tall *Sorbus*	44 (29.8)	0	0	0
Small *Pinus*	31 (15.4)	17 (4.9)	562 (272)	810 (270)
Small *Picea*	41 (11.4)	32 (12.2)	17 (9.6)	12 (7)
Small *Betula*	7 (3.0)	33 (8.4)	165 (120)	115 (37.9)
Small *Sorbus*	67 (42.9)	21 (9.3)	0	0
Leaf litter				
Coniferous	90.3 (6.52)	103 (6.17)		
Deciduous	49.1 (6.54)	4.9 (1.13)		
Miscellaneous	1.75 (0.09)	0.75 (0.03)		

[1] Exclosure, unbrowsed.
[2] Browsed reference.

tion of field- or bottom-layer vegetation at Sunnäs. Or, if the exclusion of browsers did affect the vegetation, this effect did not have similar features at all sites.

Furudal

At Furudal the unconstrained CA axes were mainly related to differences in vegetation among sites. After partialing out the effect of site differences the CA axes 1 and 2 (eigenvalues 0.049 and 0.036, explained 40.0% and 29.7%, respectively, of the residual variation after variation among sites was partialed out) clearly separated the exclosures and browsed plots of the three sites with substantial ground lichen cover (Fig. 3B). The fourth site (no. 105) was very different, with boggy *Sphagnum*-dominated vegetation and no lichens. Thus, the effect of browsing on vegetation at site 105 could not have been similar to its effect at the lichen-dominated sites. Even with site 105 included, site scores for exclosures and reference plots on partial CA axis 2 differed from each other nearly significantly (DF = 6, $t = 2.020$, $R^2 = 0.405$, $P = 0.0899$). When the t-test was repeated without site 105 the difference was statistically significant (DF = 4, $t = 2.96$, $R^2 = 0.69$, $P = 0.0413$). This suggests that at Furudal the herb-layer vegetation differed between the browsed and unbrowsed plots and that browsing had similar effects on the vegetation at the three *Cladina-Vaccinium* type sites.

At the three "lichen sites" higher covers of bare ground, dead wood, mushrooms, birch seedlings, *Vaccinium uliginosum*, *Calluna vulgaris*, *Hylocomium splendens*, and all lichen species (*Cetraria islandica*, *Cladina arbuscula*, *C. rangiferina*, *C. stellaria*, and *Cladonia* spp.) characterized the browsed plots. *Vaccinium myrtillus*, *Empetrum nigrum*, *Deschampsia flexuosa*, *Dicranum* spp., and *Pleurozium schreberi* were more typical inside the exclosures. In summary, lichens and *Calluna* were more common in browsed plots, and mosses, *Vaccinium myrtillus*, and *Empetrum* were more abundant in unbrowsed plots (see Appendix 1).

Invertebrates

The influence of browsers on the number of individuals of different invertebrate taxa (data from both areas combined) was tested with paired t-test using means for each exclosure and reference plot. We used the mean number of individuals per trap in each plot as a test variable. Due to differences between the two areas and the low number of replications there were only a few taxa that showed a consistent response to browser exclusion. And even these results could have occurred by chance due to multiple testing. The number of individuals of Phalangiidae (harvestmen, DF = 8, $t = 2.57$, $P = 0.0331$) and the only common slug, *Arion subfuscus* (DF = 8, $t = 2.82$, $P = 0.0224$), differed significantly between treatments. Both were more common
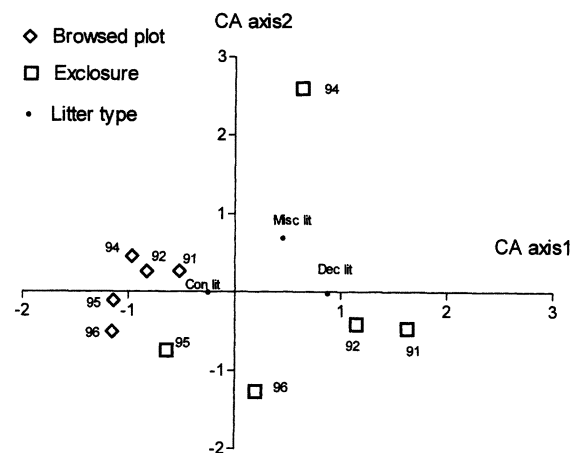

Fig. 2. Joint plot of litter types and site scores of unconstrained CA ordination axes 1 and 2 of leaf litter-fall data. Exclosure and browsed reference plots differ significantly from each other. Litter types are: Con lit = coniferous litter (mainly pine needles), Dec lit = leaves of deciduous trees, Misc lit = miscellaneous litter (mainly *Vaccinium myrtillus* leaves).
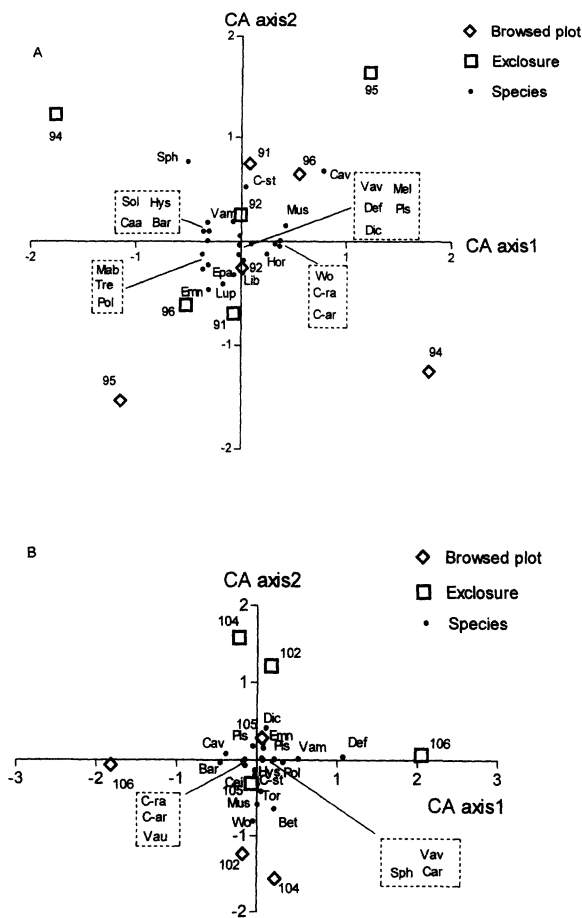
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Fig. 3. Joint plot of plant species and site scores of partial CA ordination (effect of site differences partialed out) of vegetation cover data. CA axes 1 and 2 for A) Sunnäs and B) Furudal vegetation data. Exclosure and browsed reference plots do not differ from each other at Sunnäs. At Furudal exclosures and references at three lichen-dominated sites differ from each other, but no such difference was indicated for the boggy site 105. Plant species are: Pis = *Pinus sylvestris* seedlings, Bet = *Betula* spp. seedlings, Cav = *Calluna vulgaris*, Emn = *Empetrum nigrum*, Vav = *Vaccinium vitis-idaea*, Vam = *V. myrtillus*, Vau = *V. uliginosum*, Lib = *Linnaea borealis*, Tre = *Trientalis europea*, Epa = *Epilobium angustifolium*, Mel = *Melampyrum* spp., Sol = *Solidago virgaurea*, Mab = *Maianthemum bifolium*, Lup = *Luzula pilosa*, Caa = *Calamagrostis arundinacea*, Def = *Deschampsia flexuosa*, Car = *Carex* spp., Hys = *Hylocomium splendens*, Pls = *Pleurozium schreberi*, Dic = *Dicranum* spp., Pol = *Polytrichum* spp., Sph = *Sphagnum* spp., C-ra = *Cladina rangiferina*, C-ar = *C. arbuscula*, C-st = *C. stellaris*, Hor = horn lichens *Cladonia* spp., Cei = *Cetraria islandica*, Mus = mushrooms, Bar = bare ground, Wo = dead wood.

inside the exclosures (mean of plot means ± SE: Phalangiidae inside 18.7 ± 7.40, outside 12.2 ± 5.38, *Arion* inside 1.64 ± 0.308, outside 1.28 ± 0.227). Lycosidae (wolf spiders) were slightly more common outside the exclosures in both areas, but the difference was only marginally significant (DF = 8, $t = 1.91$, $P = 0.0929$). Taxa richness did not differ significantly between treatments in any of the tested groups (mean number of taxa

per trap for all taxa, insect orders, beetle, and spider families) (paired t-test: DF = 8, $t < 1.8$, $P > 0.11$, for all groups). Diversity of invertebrate taxa at plot level measured with Shannon-Wiener index (H') was slightly higher in browsed plots (paired t-test: DF = 8, $t = 2.08$, $P = 0.0709$). In Sunnäs diversity was higher in browsed plot at every site (t-test: DF = 8, $t = 4.19$, $P = 0.0031$).

Sunnäs

The unconstrained correspondence analysis (CA) of invertebrate data mainly separated the different sites at Sunnäs from each other. Thus, the main source of variation in the invertebrate assemblages was related to site differences. But when the influence of site was partialed out by using sites as covariables the partial CA axis 2 separated unbrowsed and browsed plots from each other (eigenvalues of axes 1 and 2 were 0.077 and 0.010; these axes explained 79.7% and 10.1% of the residual variation in the invertebrate data after the site differences had been partialed out) (Fig. 4A). Site scores for unbrowsed and browsed plots on this axis differed significantly from each other (t-test DF = 8, $t = 4.91$, $R^2 = 0.75$, $P = 0.0012$). Thus, we conclude that ground-dwelling invertebrate assemblages at Sunnäs differed between the browsed and unbrowsed plots and that there were similarities in the effects of browsing on invertebrates at all five sites.

According to G^2 tests of pooled Sunnäs data (Table 3) the number of individuals of all invertebrates combined, all insects combined, Homoptera, Diptera, Hymenoptera, Formicidae, Coleoptera, Staphylinidae, Phalangiidae, Gastropoda, and *Arion subfuscus* differed significantly between the two treatments (Table 2). Among these taxa, numbers of individuals of Homoptera and Formicidae were higher in browsed areas, while those of all other taxa were higher in unbrowsed exclosures. Thus, unbrowsed plots in Sunnäs seemed to sustain higher abundance of invertebrate individuals in general compared with browsed forest areas.

Furudal

At Furudal the first two axes of unconstrained CA seemed to reflect differences in invertebrate assemblages among sites, but the third unconstrained axis was clearly linked to the difference between exclosures and reference plots (eigenvalues of axes 1, 2, 3, and 4 were 0.545, 0.267, 0.052, and 0.036, respectively). All exclosure plots received lower scores on axis 3 compared with all of the browsed plots (Fig. 4B). The third CA axis explained 10.6% of the total variation in the invertebrate data. Site scores for exclosure and reference plots differed marginally significantly from each other on this axis according to a t-test (DF = 6, $t = 2.10$, $R^2 = 0.424$, $P = 0.0802$). Although we also ran a partial CA (sites as covariables) with the Furudal data, it did not give any more information on the treatment effects. Thus here the results refer only to the unconstrained

CA. We suggest that at Furudal ground-dwelling invertebrate assemblages also differed between browsed and unbrowsed plots and that the character of the difference was similar at all four sites.

At Furudal numbers of individuals of all invertebrates combined, all insects combined (both with and without Formicidae included), Dictyoptera, Diptera, Hymenoptera excluding Formicidae, Formicidae, Phalangiidae, Nemastomatidae, Acari, Thomisidae, Lycosidae, Linyphiidae, Gastropoda, and *Arion subfuscus*

(*Arion* was the only common gastropod in Furudal) differed significantly between unbrowsed and browsed plots (G^2 tests, Table 3). Number of individuals of Hymenoptera, Phalangiidae, Nemastomatidae, Linyphiidae, and *Arion* were higher inside exclosures, and the other taxa were more numerous in browsed plots. The situation at Furudal was quite different from the one at Sunnäs. Even though the combined number of all invertebrates was slightly higher in browsed plots, which was opposite to the case at Sunnäs, this difference was not consistent. The number of taxa more numerous in exclosures was about equal to the number more numerous in browsed plots.

Discussion

The effects of moose on vegetation and invertebrates differed between the two locations. At the more productive and moist location, Sunnäs, the main direct influence of moose seemed to have been a browsing-induced change in stand composition from mixed conifer/deciduous forest to more pure conifer forest. This caused a 90% drop in the amount of deciduous leaf litter-fall. Pine density did not differ significantly between treatments; in fact, there was 12% more pine needle litter in the browsed plots than in unbrowsed plots. At Furudal's unproductive sandy sites the forests were almost pure pine stands, even in the absence of moose, but density of tall pines was 31% lower in browsed plots than in unbrowsed exclosures. In addition, the density of the birch that was present in two sites was 33% lower in browsed plots than in exclosures, and there must have been more deciduous litter in these unbrowsed plots, but amounts were low even inside the exclosures. The unbrowsed plots were more shaded at both locations, but the difference was more pronounced at Furudal (judging by the density of over three meter tall trees). Shading affected light intensity, temperatures, and humidity at ground level. At Sunnäs the thicker deciduous litter layer in unbrowsed plots had similar effects, i.e. decreasing the light intensity and maximum temperature at the soil surface, and increasing the humidity of the soil and air.

Bilberry (*Vaccinium myrtillus*) is readily eaten by moose (Cederlund et al. 1980), and the exclosure-related differences in its cover, height, and leaf litter production can be direct effects of moose foraging. It is also an important food of roe deer (Cederlund et al. 1980); thus the observed differences can be partly attributed to the effects of roe deer activities. Roe deer and moose also feed on heather (*Calluna vulgaris*) (Cederlund et al. 1980), but at Furudal it was more common in browsed plots, probably owing to the more open canopy and intense solar radiation. Apart from the possible effects on *Calluna* and *Vaccinium* species,
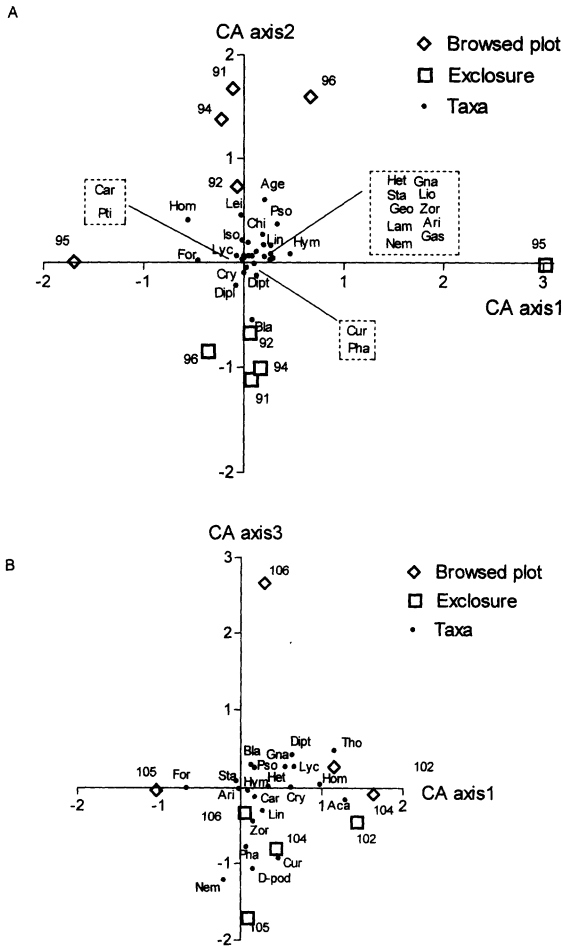

Fig. 4. Joint plot of ordination scores of invertebrate taxa and sites scores. A) partial CA axes 1 and 2 (effect of site differences partialed out) of Sunnäs invertebrate data, and B) unconstrained CA axes 1 and 3 of Furudal invertebrate data. Exclosure and browsed reference plots differ from each other in both areas. Invertebrate taxa are: Bla = Blattodea (Dictyoptera), Pso = Psocoptera, Het = Heteroptera, Hom = Homoptera, Dipt = Diptera, Hym = Hymenoptera (without family Formicidae), For = Formicidae, Car = Carabidae, Lei = Leiodidae, Sta = Staphylinidae, Pti = Ptilidae, Geo = Geotrupinae, Lam = Lampyridae, Cry = Cryptophagidae, Cur = Curculionidae, Pha = Phalangiidae, Nem = Nemastomatidae, Aca = Acari (large indivuals of Gamasina and Trombidia), Gna = Gnaphosidae, Lio = Liocranidae, Zor = Zoridae, Lyc = Lycosidae, Age = Agelionidae, Tho = Thomisidae, Lin = Linyphiidae, Iso = Isopoda, Dipl = Diplopoda, Chi = Chilopoda, Gas = Gastropoda (excluding *Arion*), Ari = *Arion subfuscus*.

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Table 3. Mean number (and SE) of invertebrate individuals per trap in exclosure (unbrowsed) and reference (browsed) plots in the two areas. G^2 results obtained when testing whether the abundance of the invertebrates differed between unbrowsed and browsed plots at Sunnäs and Furudal (DF = 1 for all tests).

Taxa	Sunnäs exclosure	Sunnäs reference	P	Furudal exclosure	Furudal reference	P
Blattodea	0.09 (0.04)	0.02 (0.02)	0.0863	0.83 (0.14)	1.47 (0.28)	0.0011
Psocoptera	0.30 (0.08)	0.32 (0.09)	ns	0.67 (0.14)	0.58 (0.13)	ns
Heteroptera	1.95 (0.21)	1.68 (0.24)	ns	1.77 (0.27)	1.75 (0.27)	ns
Homoptera	0.22 (0.06)	0.85 (0.16)	0.0001	1.73 (0.35)	1.58 (0.27)	ns
Diptera	33.3 (3.50)	18.6 (2.08)	0.0001	7.00 (1.00)	10.0 (2.79)	0.0001
Hymenoptera[1]	11.3 (0.97)	8.54 (0.53)	0.0001	5.32 (0.92)	4.32 (0.53)	0.0125
Formicidae	17.7 (2.38)	29.3 (9.27)	0.0001	12.4 (1.45)	68.0 (21.5)	0.0001
Carabidae	0.54 (0.09)	0.47 (0.09)	ns	0.10 (0.04)	0.07 (0.03)	ns
Leiodidae	0.11 (0.05)	0.23 (0.07)	0.0560	0	0	–
Staphylinidae	5.60 (0.63)	4.37 (0.44)	0.0004	1.05 (0.20)	1.37 (0.53)	ns
Ptilidae	1.09 (0.21)	0.84 (0.18)	ns	0.10 (0.05)	0	–
Cryptophagidae	0.05 (0.02)	0.02 (0.02)	ns	0.03 (0.02)	0.03 (0.02)	–
Curculionidae	0.12 (0.04)	0.16 (0.06)	ns	0.07 (0.03)	0.02 (0.02)	ns
Coleoptera	7.69 (0.74)	6.21 (0.54)	0.0003	1.35 (0.23)	1.48 (0.53)	ns
Insecta	72.6 (4.47)	65.5 (9.64)	0.0001	31.0 (2.01)	89.5 (21.6)	0.0001
Insecta excluding Formicidae	–	–	–	18.7 (1.79)	21.5 (3.38)	0.0006
Isopoda	0.17 (0.06)	0.22 (0.08)	ns	0	0	–
Chilopoda	0.23 (0.06)	0.22 (0.06)	ns	0.03 (0.02)	0.02 (0.02)	–
Diplopoda	0.22 (0.07)	0.12 (0.04)	ns	0.22 (0.08)	0.13 (0.04)	ns
Arion subfuscus	1.84 (0.12)	1.46 (0.11)	0.0128	1.38 (0.18)	1.07 (0.13)	0.0265
Gastropoda	3.90 (0.21)	3.26 (0.18)	0.0047	1.40 (0.18)	1.11 (0.14)	0.0434
Acari[2]	0	0	–	11.1 (2.13)	13.9 (2.15)	0.0001
Phalangiidae	33.8 (3.69)	22.4 (2.35)	0.0001	2.17 (0.46)	0.42 (0.14)	0.0001
Nemastomatidae	2.73 (0.29)	2.31 (0.33)	0.0921	0.60 (0.25)	0.22 (0.10)	0.0008
Gnaphosidae	0.15 (0.04)	0.14 (0.05)	ns	0.13 (0.04)	0.28 (0.10)	0.0687
Liocranidae	0.09 (0.04)	0.07 (0.03)	ns	0.02 (0.02)	0	–
Zoridae	0.10 (0.04)	0.07 (0.03)	ns	0.13 (0.06)	0.05 (0.03)	ns
Thomisidae	0.01 (0.01)	0.05 (0.03)	ns	0.02 (0.02)	0.13 (0.04)	0.0128
Lycosidae	1.12 (0.16)	1.22 (0.17)	ns	1.20 (0.17)	2.22 (0.26)	0.0001
Linyphiidae	7.07 (0.67)	7.22 (0.67)	ns	6.03 (0.68)	3.98 (0.39)	0.0001
Araneae	8.65 (0.70)	8.86 (0.65)	ns	7.55 (0.71)	6.67 (0.44)	0.0695
Arthropoda	118.4 (6.57)	99.6 (9.89)	0.0001	52.7 (2.61)	110.9 (21.1)	0.0001
Arthropoda excluding Formicidae	–	–	–	40.3 (2.60)	42.9 (4.04)	0.0292

[1] excluding Formicidae.
[2] large species of Gamasina and Trombidia.

moose probably did not have any significant direct effects on the herb- and bottom-layer vegetation. The other observed differences in the vegetation at Furudal, particularly with regard to mosses and lichens, and possibly also with regard to *Calluna* and *Vaccinium*, were most likely indirect effects of moose resulting from the differences in light intensity, moisture, and litter-layer characteristics. Thus, we suggest that, ultimately, the effects on forest-floor vegetation were indirect consequences of browsing on trees by moose. At Furudal, as in an Alaskan exclosure study (Suominen, Danell, and Bryant unpubl.) and at Isle Royale (McInnes et al. 1992), the canopy was more open in browsed plots, and there were species differences in the herb-layer vegetation. The difference in the moss and lichen cover at Furudal could be interpreted as reflecting a difference in the amount of light reaching the forest floor between browsed and unbrowsed plots. In browsed plots the light-demanding and drought-resistant lichens were able to outcompete the more shade-tolerant mosses, which were more common inside the exclosures.

Pastor et al. (1993) showed that moose browsing can reduce both the amount and nutritional quality of the leaf litter. As a result, leaf litter in the plots protected from moose may decompose faster. Thus, soil nutrient resources and productivity in coniferous forest could be lower in the presence of moose. Although feces and urine of moose can affect the nutrient status of the soil, Pastor et al. (1993) reported that defecation did not compensate for the reduction in leaf litter accumulation. We do not know what the overall effect of defecation and browsing was at our study sites. Still, it seems likely that the net effect was a decrease in soil nutrients, at least at Sunnäs where browsed plots only contained about one-tenth as much deciduous litter as unbrowsed exclosures. At Furudal, the effects of browsing on deciduous litter accumulation must have been smaller due to low density of deciduous trees. On the other hand, sites with mosses are generally regarded to be more productive than sites covered with lichens (Cajander 1949, Carleton 1990; but see Väre et al. 1995). Thus, it seems likely that the unbrowsed plots were also more productive at Furudal.

In both of our study areas, results of (partial) correspondence analysis indicate that there was a difference in the ground-dwelling invertebrate assemblage between unbrowsed exclosures and browsed plots. However, the effect of browsers seemed to differ between the two areas. If we look at the results of paired *t*-tests of the combined data, only phalangiid harvestmen and slug *Arion subfuscus* showed a consistent numerical response to browsing. Numbers of many other taxa, as well as the number of all invertebrates, were significantly affected by the exclusion of browsers in both areas, but in opposite directions. At Sunnäs, the total number of invertebrate individuals trapped was higher in the exclosures. Also, for most of the taxa that differed significantly between the treatments number of individuals was higher inside the exclosures. At Sunnäs, diversity, but not taxa richness, of the invertebrate assemblage was significantly higher in browsed plots. In Furudal's pooled data, the total abundance of invertebrates was slightly higher in browsed plots, but this was not consistent among sites. Of those taxa that differed in their abundance at Furudal, six were more abundant in exclosures, and five were more abundant in browsed plots. At Furudal the diversity or richness of browsed and unbrowsed plots did not differ significantly between treatments.

It is likely that the two taxa that were more common in browsed plots in the pooled data, phalangiid harvestmen and the slug *Arion subfuscus*, were both favored by the effects of leaf litter and more moist microclimate. Both taxa are sensitive to low air humidity and seek shade. Furthermore, at Furudal harvestmen were almost completely absent from the plots without deciduous species (83% of all phalangiids at Furudal were caught inside the two exclosures, which contained some birches). Decomposing deciduous leaves and the fungal hyphae on them are important foods of slugs (Jennings and Barkham 1975). Facelli (1994) reported that the addition of deciduous leaf litter increased the total abundance of invertebrates and invertebrate damage to seedling cotyledons in an old-field community.

It is difficult to speculate as to the reasons behind the patterns observed for most of the invertebrate taxa since they are so diverse taxonomically and ecologically. Thus the only general statement that we can make concerning the number of individuals of these taxa is that at Sunnäs the microclimate was probably more favorable inside the exclosures (more moist and shaded), and the richer deciduous litter layer provided additional resources and substrate. At Furudal, the effects of large browsers on the vegetation and on the openness of the canopy probably contributed most to the observed differences in the composition of the ground-dwelling fauna.

At Furudal, the number of wood ants (*Formica* spp.) was extremely high at some sites, making them the most numerous taxon in the area. Wood ants are known to affect the abundance of other invertebrates (e.g. Way and Khoo 1992) and, thus, might have contributed to variation in the abundances of other taxa in our results. It is likely that responses to changes in the environment within each invertebrate family vary depending on the species concerned. Thus opposite changes at the species level would tend to counteract one another in this kind of order/family-level study. Thus, we would have found more significant differences if we had extended our analyses to the species level. The main point of our work was, however, to show that it is possible for moose to affect the ground-dwelling insect fauna, and we had no a priori knowledge of which invertebrate groups would be most affected by browsing. For this purpose, family-level identification appeared to suffice, as indicated by differences found in the structure of invertebrate assemblages between exclosures and references. For the same reason, we believe that trapping during only part of the active season for invertebrates was sufficient for our purpose.

At Sunnäs the number of individuals of most of the invertebrate taxa on the forest floor was higher in unbrowsed, litter-rich plots. By contrast, in the early successional floodplains in Alaska most of the beetle families were more common in browsed plots (Suominen, Danell, and Bryant unpubl.), and at Furudal the taxa that differed showed no consistent direction in their response to browsing. This inconsistency could, of course, be due in part to any difference between the areas. Still, our findings suggest that the direction and magnitude of the effects of browsing on the forest floor can depend, among other things, on the effects of moose on leaf litter quality and quantity, and on the openness of canopy. The important point in all of these tree cases is that fauna and flora at ground level were different when moose was excluded, and that this resulted most likely from indirect effects of changes in habitat quality. Thus, moose is acting as an allogenic ecosystem engineer as defined by Jones et al. (1994) or a keystone modifier as defined by Mills et al. (1993). Changes in tree species composition are of central importance in boreal forest succession and affect the succession of flora and fauna at the forest floor. Thus, by affecting the density and species composition of tree strata in boreal forest during the course of succession moose can indirectly affect the invertebrate communities on the forest floor.

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Appendix 1: Mean % cover of field- and bottom-layer plant species in both study areas.

Plant species	Sunnäs E[1] mean (SE)	Sunnäs B[2] mean (SE)	Furudal E[1] mean (SE)	Furudal B[2] mean (SE)
Pinus seedlings	0	0.09 (0.03)	0.61 (0.12)	0.47 (0.11)
Betula seedlings	0.03 (0.03)	0.03 (0.03)	0.13 (0.07)	0.28 (0.19)
Vaccinium vitis-idaea	16.1 (1.60)	16.9 (1.60)	14.8 (1.28)	11.6 (1.97)
V. myrtillus	16.0 (1.90)	10.0 (0.98)	3.62 (0.95)	1.67 (0.49)
V. uliginosum	0.20 (0.20)	0	4.03 (1.22)	3.38 (1.28)
Empetrum nigrum	0.07 (0.07)	0.17 (0.10)	4.57 (1.01)	2.75 (0.59)
Calluna vulgaris	2.79 (0.82)	1.23 (0.68)	4.57 (0.88)	11.3 (1.97)
Linnaea borealis	2.34 (0.59)	3.32 (0.46)	0	0
Trientalis europea	0.33 (0.09)	0.47 (0.13)	0	0
Epilobium angustifolium	0.27 (0.14)	0.10 (0.03)	0	0
Melampyrum spp.	1.55 (0.25)	2.04 (0.28)	0	0
Solidago virgaurea	0.30 (0.10)	0.20 (0.08)	0	0
Maianthemum bifolium	0.19 (0.07)	0.32 (0.12)	0	0
Convallaria majalis	0.08 (0.07)	0	0	0
Orthilia secunda	0.17 (0.08)	0.41 (0.25)	0	0
Calamagrostis arundinacea	0.79 (0.28)	1.73 (0.48)	0	0
Deschampsia flexuosa	11.2 (1.60)	12.6 (1.43)	0.38 (0.15)	0.44 (0.24)

Appendix 1. (continued)

Plant species	Sunnäs E[1] mean (SE)	Sunnäs B[2] mean (SE)	Furudal E[1] mean (SE)	Furudal B[2] mean (SE)
Carex spp.	0	0	1.20 (0.40)	1.28 (0.41)
Hylocomium splendens	7.97 (0.96)	6.13 (0.88)	2.05 (1.01)	0.48 (0.27)
Pleurozium schreberi	42.0 (2.83)	46.4 (2.51)	20.1 (3.07)	16.8 (2.60)
Polytrichum spp.	0.37 (0.17)	0.65 (0.27)	15.3 (3.19)	9.15 (2.21)
Dicranum spp.	12.3 (1.02)	13.7 (1.11)	3.87 (0.68)	1.97 (0.47)
Sphagnum spp.	0.93 (0.81)	0.80 (0.67)	13.5 (3.37)	11.2 (2.90)
Cladina arbuscula	0.95 (0.33)	0.96 (0.18)	10.6 (1.59)	13.5 (1.64)
C. rangiferina	2.15 (0.52)	1.68 (0.24)	18.9 (2.38)	21.3 (2.40)
C. stellaris	0	0.15 (0.08)	6.00 (1.79)	9.50 (2.35)
Cladonia uncialis	0	0	0.08 (0.08)	0.17 (0.17)
Cladonia spp.	3.88 (1.01)	5.53 (0.80)	1.02 (0.35)	2.15 (0.57)
Cetraria islandica	0	0	5.12 (1.34)	8.85 (1.63)
Mushroom	0.54 (0.10)	0.53 (0.11)	0.20 (0.07)	0.53 (0.13)
Bare ground	16.2 (2.51)	6.87 (1.51)	1.12 (0.42)	2.17 (0.76)
Dead wood	2.41 (0.47)	3.05 (0.53)	0.17 (0.10)	0.80 (0.25)
Stone	6.71 (0.91)	8.32 (1.12)	0.58 (0.45)	0

[1] Exclosure, unbrowsed.
[2] Browsed reference.