

Indirect effects of mammalian browsers on vegetation and ground-dwelling insects in an Alaskan floodplain¹

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Abstract: Several studies in recent years have shown that large mammalian herbivores can have a substantial effect on boreal forest vegetation and soil dynamics. We studied the potential indirect effects of moose and snowshoe hare browsing on ground-living Orthoptera and Coleoptera and herb-layer vegetation in seven long-term exclosures and adjacent browsed plots. Insect and plant assemblages of exclosures and browsed plots differed from each other. Higher biomass of mosses, grass, and forbs characterized browsed plots, whereas *Equisetum spp.* and *Pyrola asarifolia* were more common in unbrowsed plots. Insect abundance was generally higher in browsed plots. Curculionidae was the only insect family that tended to be more abundant inside the exclosures. An enhanced food supply, in the form of feces and carrion of mammalian herbivores, and the direct and indirect effects of browsing on tree species composition, field-layer vegetation, litter, and microclimate are the probable causes of differences in the studied insect assemblages.

Keywords: browsing, Coleoptera, ecosystem effects, moose, Orthoptera, snowshoe hare.

Résumé : Au cours des dernières années, plusieurs études ont montré que les grands mammifères herbivores ont un impact substantiel sur la végétation forestière boréale et sur la dynamique des sols. Nous avons étudié les impacts potentiels indirects du broutement par l'orignal et le lièvre sur les orthoptères et les coléoptères et sur la végétation herbacée. L'étude a été effectuée grâce au suivi à long terme de sept exclos et de milieux broutés adjacents. Les assemblages d'insectes et de plantes des exclos diffèrent de ceux des milieux broutés. Ces derniers renferment une plus grande biomasse de mousses, de graminées et d'herbacées. Par contre, les *Equisetum spp.* et *Pyrola asarifolia* sont plus communs dans les exclos. Les insectes sont en général plus abondants dans les sites broutés. Une seule famille d'insectes (Curculionidae) compte davantage d'individus au sein des exclos qu'en dehors de ceux-ci. Les causes probables des différences au niveau des assemblages d'insectes sont la plus grande quantité de nourriture disponible hors des exclos (fèces des mammifères herbivores), ainsi que les répercussions directes et indirectes du broutement sur la composition des espèces de la strate arborescente, la composition des espèces de la strate herbacée, la litière et le microclimat.

Mots-clés : broutement, coléoptères, effets sur l'écosystème, orignal, orthoptères, lièvre d'Amérique.

Introduction

In boreal forests, herbivores such as moose (*Alces alces*) have the potential to affect many ecosystem processes, including their own habitat, through selective foraging (Naiman, 1988; Bryant *et al.*, 1991; Pastor *et al.*, 1993). North American moose generally prefer to feed on deciduous tree species rather than conifers. Thus they can influence both tree species composition and the rate of forest succession (Naiman, 1988; Pastor & Naiman, 1992). This in turn can change the light and moisture conditions on the forest floor, leaf-litter quality and quantity, soil nutrients, and field-layer herb communities (McInnes *et al.*, 1992; Pastor *et al.*, 1993).

In Alaska, moose avoid thinleaf alder (*Alnus tenuifolia*) and prefer to browse on willow (*Salix spp.*; Wolf & Zasada, 1979; McAviney, 1991). This facilitates the successional transition from willow to alder which has a lower and more open canopy (Wolf & Zasada, 1979; Bryant & Chapin,

1986; McAviney, 1991). It has been found that in unbrowsed exclosures, litter production, relative humidity, and soil moisture are higher than in browsed plots, whereas light intensity and soil temperature are lower in unbrowsed than in browsed plots (Kielland & Bryant, 1998). We expected that the modification of tree strata by browsers may influence herb-layer vegetation and ground-living invertebrates through changes in litter, soil, and microclimate.

We studied the potential indirect effects of excluding moose and snowshoe hare (*Lepus americanus*) on ground-living insects at seven sites along the Tanana River in Alaska. The coleopteran and orthopteran assemblages in plots where moose and hare browsing was excluded by fences were compared with the corresponding assemblages in adjacent plots where moose and snowshoe hare had free access. The order Orthoptera was selected because interactions between grasshoppers, which are phytophagous, and mammalian herbivores have been suggested to occur in grazing systems (Belovsky, 1986). The order Coleoptera was chosen because of its high taxonomic and biological diversity, including predators, herbivores, and fungivores that can be found in nearly all types of habitats.

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Material and methods

The study area was located on the Tanana River floodplain at Bonanza Creek Experimental Forest Long-Term Ecological Research (LTER) site, about 32 km southwest of Fairbanks, Alaska, U.S.A. (64° 40' N, 148° 15' W; for further information see Van Cleve, Viereck & Marin, 1993; Viereck, Dyrness & Foote, 1993; and Rossow, Bryant & Kielland, 1997).

We used seven pairs of permanent exclosures and their respective browsed reference plots (10 m from the exclosure) located in willow and thinleaf alder stands on both shores of the 17 km segment of the Tanana River floodplain (Table I). Exclosures were established with fencing in 1988 to prevent moose and snowshoe hare browsing. Hare densities had been so low during the period after the exclosures were built that most treatment effects were due to consistent winter browsing by moose (Kielland & Bryant, 1998).

At each site we placed 30 pitfall traps inside and 30 traps outside each exclosure in the respective reference plot (Table I). Within each exclosure, no traps were placed within 2 m of the fence. Over the remaining area the traps were placed using a grid system. In the reference area the traps were set out according to a similar pattern. The trapping period lasted about two weeks in July 1995 (Table I). It was a short period, due to practical reasons, but we consider it long enough to compare the ground-dwelling fauna of exclosures and browsed plots. However, we admit that the situation might differ during the growing season and between seasons. Since our aim was to demonstrate that mammalian browsers can have an effect on ground-dwelling insects, rather than to describe the composition of the insect fauna in browsed and unbrowsed areas, we feel that even this short period was sufficient for our purpose.

The traps (170-ml plastic vials; height = 70 mm; diameter at top = 70 mm; diameter at bottom = 50 mm) contained polypropyleneglycol (50%; with detergent added). All specimens belonging to the insect orders Coleoptera and Orthoptera were stored in vials containing ethanol (70%), and the adult insects were classified to family and counted.

Herbs and mosses were sampled at six of the sites from five randomly selected 0.5 m × 1 m quadrats in the exclosure and five from the reference plot (site C3 was not sampled since it was flooded during the sampling period). Above-ground parts of herbs were clipped off and mosses were pulled from the soil surface and all soil washed off.

Dicotyledonous forbs and horsetails (*Equisetum*) were determined to species; *Calamagrostis canadensis* was the only grass species, and mosses formed a pooled group. The plant material was dried for 48 hours at 80°C and weighed.

Differences in the composition of the assemblages were studied with principal components analysis (PCA, centered by species; PCA was chosen due to the short gradients; see Jongman, ter Braak & van Tongeren, 1995) using means of each unbrowsed and browsed plot as test variables (mean drymass of plant species per quadrat and mean number of insect individuals of each taxa per trap, log transformed values). First we ran an unconstrained PCA, which separated different sites from one another (the results are not presented here). We then ran a constrained PCA by partialing out the site differences by using sites as covariates. Correlation between insect and plant ordination scores was used to indicate a relationship between insect and plant assemblages.

After running the partial PCA and detecting differences in the assemblages, masses of plant species were tested for differences between exclosure and reference plots with paired *t*-test using plot means (only the taxa that were present in all of the sites were tested). G^2 test (with sequential Bonferroni correction) applied to pooled data was used to test whether the individuals of different insect families were equally numerous in the traps of exclosure and reference plots (families that were present in less than three sites were not tested owing to their low abundance).

Differences in insect and plant species richness and diversity were also tested with paired *t*-test. At trap level, mean number of taxa per trap or quadrat used for plant sampling in a plot were used as test variables. At the whole-plot level we used number of different taxa found in an exclosure or reference plot. The influence of differences in sample size in insect taxa richness at plot level was corrected with the use of rarefaction, and we used the expected number of taxa in a sample size of 100 individuals as a test variable. We also calculated Shannon-Wiener diversity index (H') for vegetation and insects at plot level. Rarefaction and the Shannon-Wiener index were calculated according to Krebs (1989). Linear regression using number of insect individuals and vegetation masses as explanatory variable was conducted to explain the variation in number of insect individuals as well as insect and vegetation richness and diversity. Statistical analyses were conducted with SAS statistical software (SAS Institute, 1990) or with CANOCO 3.15 software (PCA; ter Braak, 1988).

TABLE I. Ground-living invertebrates were collected by pitfall trapping on seven sites along the Tanana River, Alaska, in the summer of 1995. Each site consists of one unbrowsed exclosure and one browsed reference plot. Thirty traps were located in each exclosure and reference plot, but the final number of intact, undisturbed traps was lower in some cases owing to disturbances of one kind or another (*e.g.*, a rise in the groundwater level lifted up some traps, and others were disturbed by snowshoe hares)

Site	Geographical position (N; W)	Size of exclosure (m × m)	Trapping period		Number of insect traps	
			Start	End	Exclosure	Reference
A1	64° 42' 148° 15'	20 × 65	12 July	29 July	28	18
A2	64° 42' 148° 15'	20 × 80	11 July	29 July	25	25
B1	64° 44' 148° 09'	20 × 40	16 July	29 July	28	29
B2	64° 44' 148° 09'	20 × 20	16 July	29 July	28	30
C1	64° 41' 148° 16'	25 × 60	14 July	29 July	30	29
C2	64° 41' 148° 16'	25 × 25	14 July	29 July	30	28
C3	64° 41' 148° 16'	20 × 20	14 July	29 July	30	30

Height of fence about 3 m.

Results

Both plant and insect assemblages of different sites differed in the unconstrained PCA scores (results are not shown), but not between unbrowsed and browsed plots. When site differences were partialled out, vegetation assemblages of unbrowsed and browsed plots could be separated by scores on axes 1 and 4 (Figure 1). Sample scores on partial PCA ordination axis 1 and axis 2 of insect fauna differed between enclosure and references (Figure 1). We conclude that there was a difference in the vegetation and insect fauna of unbrowsed and browsed plots, and that there are similar features in this difference among the sites.

An examination of the species scores on partial vegetation ordination (Figure 1) reveals that *Epilobium angustifolium*, *Solidago canadensis*, *Spiranthes romanzoffiana*, mosses, and *Calamagrostis*, were typically more common in the herb-layer vegetation of browsed plots (Figure 1). Higher abundance of all *Equisetum* species and *Pyrola asarifolia* characterized enclosure vegetation. For the insects, it was mainly the scores on partial PCA axis 2 that differed between treatments (Figure 1). All of the enclosure plots except one received a positive score on this axis, and all except one of the browsed plots received a negative score. Individuals of Acrididae, Tetrigidae, Carabidae, Silphidae, and Corticariidae (Latridiinae) were typically more abundant in browsed plots, whereas Curculionidae, Coccinellidae, Scarabaeidae, and Elateridae received a negative score and were more abundant in the enclosure insect assemblages. There was a significant correlation between the sample scores of partial PCA vegetation axis 4 and insect axis 2 (Pearson correlation, $r = -0.71$, $r^2 = 0.5$, $p = 0.01$), which were the axes that were most clearly linked to browsing.

The total number of insect individuals (of the orders Orthoptera and Coleoptera), individuals of order Coleoptera, coleopteran families Carabidae, and Silphidae differed significantly between browsed and unbrowsed plots (G^2 test, $df = 1$, $p < 0.05$, sequential Bonferroni correction), and all of these taxa were more common in browsed plots (Figure 2). Numbers of individuals of families Tetrigidae and Curculionidae differed significantly in the single taxa test results without Bonferroni correction (Figure 2). Curculionidae was the only one of all these taxa for which the number of individuals was generally higher inside the enclosures. The rest of the coleopteran families were found at only one or two sites and were so uncommon that they were not included in the tests. None of the plant species or combined groups differed significantly between treatments in the single taxa tests (paired t -test: $df = 5$, $t < 1.81$, $p > 0.1$) (Figure 3).

Taxa richness or Shannon-Wiener diversity index of plant species and insect families (richness standardized with rarefaction) did not differ significantly between browsed reference plots and enclosures on the whole-grid scale (Table II). The difference was marginally significant (paired t -test, $df = 6$, $p < 0.051$) only for the mean number of insect families per trap, *i.e.*, "family richness" at trap level.

Mean number of insect individuals per trap decreased when mean of herb-layer vegetation drymass increased (linear regression: slope = -0.15 , $F_{1,10} = 5.64$, $r^2 = 0.36$, $p = 0.039$), but mean of insect and vegetation taxa richness and diversity were not related to vegetation mass. Insect

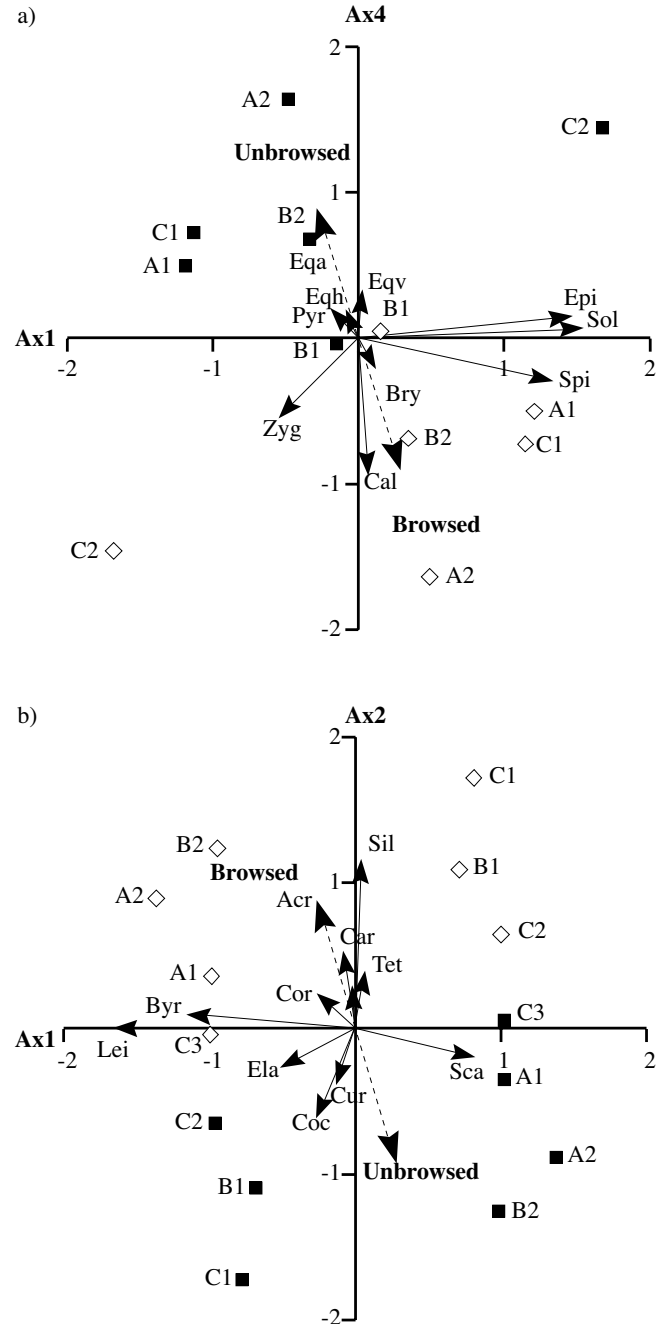


FIGURE 1. Sample and taxa scores on the partial PCA. Site differences partialled out. Sites A1 to C3 are marked with capital letter and number; filled square for unbrowsed plot, and an open rhomb for browsed plot. Taxa scores are marked with vectors (small arrows). Bold arrows with broken line point in the direction of browsed - unbrowsed gradient (mean points of browsed and unbrowsed plots). Scales marked in the axes apply to plot scores, whereas the scale for the taxa is 2:1. a) Axes 1 and 4 of vegetation data. Plant species are: Bry = all moss species combined, Eq1 = *Equisetum arvense*, Eq2 = *E. hyemale*, Eq3 = *E. variegatum*, Cal = *Calamagrostis canadensis*, Epi = *Epilobium angustifolium*, Pyr = *Pyrola asarifolia*, Sol = *Solidago canadensis*, Spi = *Spiranthes romanzoffiana*, Zyg = *Zygadenus elegans*. b) Axes 1 and 2 of insect data. Families are: Acr = Acrididae, Tet = Tetrigidae, Car = Carabidae, Lei = Leiodidae, Sil = Silphidae, Sca = Scarabaeidae, Ela = Elateridae, Byr = Byrrhidae, Coc = Coccinellidae, Cor = Corticariidae, Cur = Curculionidae. Taxa that lie close to origin are not marked (plant species: *Achillea borealis*, *Parnassia palustris*; Beetle families: Staphylinidae, Chrysomelidae).

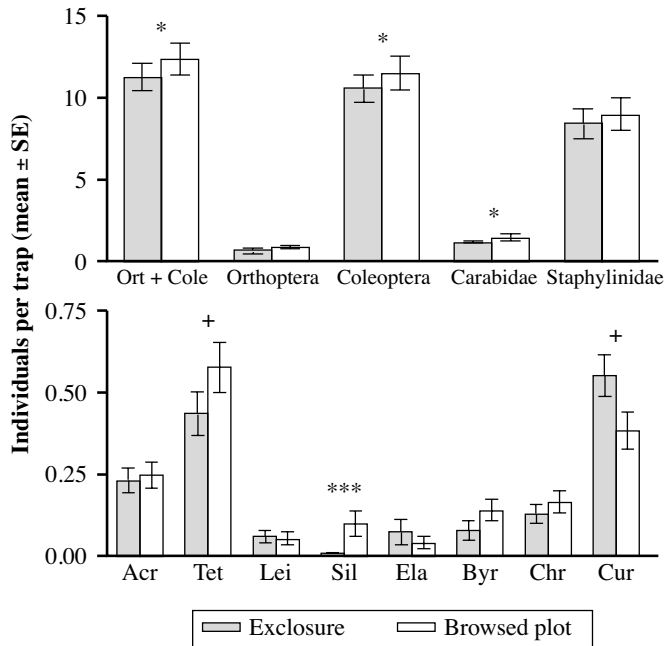


FIGURE 2. Abundances of different taxa caught in pitfall traps, pooled data from seven exclosure/reference (unbrowsed/browsed) pairs. *P*-values of *G*² test of pooled data (df = 1, *** = *p* < 0.005 Bonferroni corrected, * = *p* < 0.05 Bonferroni corrected, + = *p* < 0.05 without but *p* > 0.05 with Bonferroni correction). (Ort + Cole = orders Orthoptera and Coleoptera combined, abbreviations of insect families are as in Figure 1, with additional family Chr = Chrysomelidae).

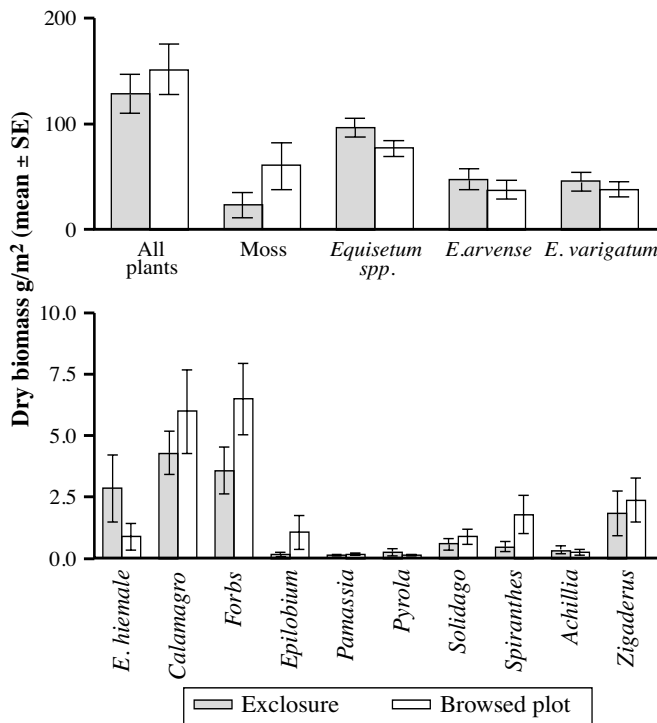


FIGURE 3. Average dry biomasses of field- and bottom-layer vegetation, pooled data from six exclosure/reference (unbrowsed/browsed) pairs. Differences were not statistically significant at 5% significance level (paired *t*-test with plot means). (The plant species are the same as in Figure 1 except *Equisetum* spp. = *Equisetum* species combined, Forbs = all dicotyledonous herbs combined).

TABLE II. Differences in numbers of insect families per trap (“family richness”), plant species richness, and diversity (Shannon-Wiener index *H'*). Paired *t*-test using plot means for numbers of insect families per trap or plant species in a quadrat at trap/quadrat level and number of insect families or plant species in each plot at plot level. For insects at plot level, the expected numbers of families for sample size of 100 individuals calculated with rarefaction were used (for insects df = 6, for plants df = 5)

	Mean number of families		<i>t</i>	<i>P</i>
	Exclosure	Reference		
ORTHOPTERA + COLEOPTERA				
FAMILY RICHNESS				
Trap	2.41	2.73	2.43	0.051
Plot	6.55	7.50	1.66	0.150
Diversity (<i>H'</i>), plot	1.56	1.63	0.40	0.702
PLANT SPECIES RICHNESS				
Quadrat	5.83	5.97	1.00	0.360
Plot	9.00	9.17	0.18	0.867
Diversity (<i>H'</i>), plot	1.39	1.51	0.86	0.429

taxa richness and diversity at plot level decreased as number of insect individuals increased (linear regression, richness: slope = -0.19, *F*_{1,12} = 21.2, *r*² = 0.64, *p* < 0.0001; diversity: slope = -0.08, *F*_{1,12} = 39.2, *r*² = 0.77, *p* < 0.0001). Unbrowsed and browsed plots were not segregated by these regression lines, except for the regression of number of insect individuals and insect taxa richness. In browsed plots, insect taxa richness was higher in relation to the number of insects than in unbrowsed plots (means of residuals of unbrowsed and browsed plots: -0.59 and 0.58 respectively, paired *t*-test: *t* = 3.26, df = 6, *p* = 0.017).

Discussion

Our results show that both insect and plant assemblages at ground level differed between browsed and unbrowsed plots. In browsed plots the tree canopy was lower and more open, thus light intensity and temperature at ground level were higher (Kielland & Bryant, 1998). Soil moisture and relative humidity were lower in browsed plots (Kielland & Bryant, 1998). Moose and hare were thus acting as ecosystem engineers that altered the physical properties of the habitat (Jones, Lawton & Shachak, 1994; 1997). The herb-layer vegetation differed between exclosures and references in the study sites such that forbs, grasses, and mosses were more common in browsed plots, and horsetails and wintergreen (*Pyrola asarifolia*) in unbrowsed plots. The amount of leaf litter in our study sites was slightly higher inside the exclosures, but nitrogen input was higher in browsed plots owing to moose fecal input (Kielland & Bryant, 1998).

Two of the herb species that partial PCA pointed out as being typically more common in browsed plots, *Epilobium* and *Solidago*, are preferred summer forage of moose. The positive effect of opening the canopy seems to be more important for these herbs than the direct effect of grazing on them. The significant correlation between the partial vegetation PCA axis and partial fauna PCA axis which differed between treatments could mean that changes in vegetation caused by moose are one reason for the differences in insect assemblage. In contrast, same factors

of the abiotic environment changed by moose can affect both flora and fauna independently.

Browsing increased the number of insect individuals (of studied orders) in general, as well as individuals of most of the taxa for which the number of individuals differed between browsed and unbrowsed plots. The beetle family Curculionidae was the only relatively common group whose numbers tended to be lower in browsed plots. They are specialized herbivores, and the observed differences are probably due to the changes in biomasses and occurrence of one or a few common food plant species.

At plot level, there was an inverse relationship between number of insect individuals and insect taxa richness and diversity. Richness in relation to number of individuals was higher in browsed plots. A similar relationship was found in a comparison of carabid communities in different forest types in Canada: the species diversity was lowest in the habitat where the number of carabid individuals was highest (Niemelä, Spence & Spence, 1992). Moderate mammalian herbivory has been observed to increase plant species richness or diversity of many communities (Helle & Aspi, 1983; Fox, 1985; Olf & Ritchie, 1998). Our results of taxa richness and diversity are not so clear, but there is apparently a trend for higher insect richness in browsed plots. In our case the browsing, trampling, and defecation by moose contribute to microhabitat variation outside the exclosures, which might have enhanced the conditions for ground-dwelling insects.

Our results show that the impact of mammalian herbivores in shaping the early successional forest ecosystems may even affect ground-living insects. The influence on insects varied among different taxa, but there was a trend for both higher taxa richness and relative density in browsed plots. This differs from the results of the study of the effects of moose browsing on the ground-living insects in Swedish pine forests (Suominen, Danell & Bergström, 1999). In that study the successional stage and tree species composition were different from those presented here. The impact on herb-layer vegetation in our study, *i.e.*, more forbs and grasses in browsed plots, resembled observations from other studies (McInnes *et al.*, 1992, Suominen, Danell & Bergström, 1999) and can probably be attributed to the more open canopy of browsed plots. The effects of moose and hare on the insect fauna and herb-layer vegetation are most probably of an indirect nature, resulting from their browsing on trees, and its influence on microclimate, light regime, vegetation composition, litter, and soil.

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Literature cited

- Belovsky, G. E., 1986. Generalist herbivore foraging and its role in competitive interactions. *American Zoologist*, 26: 51-69.
- Bryant, J. P. & F. S. Chapin III, 1986. Browsing-woody plant interactions during boreal forest plant succession. Pages 213-225 in K. Van Cleve, F. S. Chapin III, P. W. Flanagan, L. A. Viereck & C. T. Dyrness (ed.). *Forest Ecosystems in the Alaskan Taiga*. Springer, New York.
- Bryant, J. P., F. D. Provenza, J. Pastor, P. B. Reichard, T. P. Clausen & J. T. du Toit, 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review in Ecology and Systematics*, 22: 431-446.
- Fox, J. F., 1985. Plant diversity in relation to plant production and disturbance by voles in Alaskan tundra communities. *Arctic and Alpine Research*, 17: 199-204.
- Helle, T. & J. Aspi, 1983. Effects of winter grazing by reindeer on vegetation. *Oikos*, 40: 337-343.
- Jones, C. G., J. H. Lawton & M. Shachak, 1994. Organisms as ecosystem engineers. *Oikos*, 69: 373-386.
- Jones, C. G., J. H. Lawton & M. Shachak, 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, 78: 1946-1957.
- Jongman, R. H., C. J. F. ter Braak & O. F. R. van Tongeren, 1995. *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge.
- Kielland, K. & J. P. Bryant, 1998. Moose herbivory in taiga: Effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos*, 82: 377-383.
- Krebs, C. J., 1989. *Ecological Methodology*. Harper & Row, New York.
- McAvinchey, R. J. P., 1991. Winter herbivory by snowshoe hares and moose as a process affecting primary succession on an Alaskan floodplain. M.Sc. Thesis, University of Alaska, Fairbanks, Alaska.
- McInnes, P. F., R. J. Naiman, J. Pastor & Y. Cohen, 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, U.S.A.. *Ecology*, 73: 2059-2075.
- Naiman, R. J., 1988. Animal influences on ecosystem dynamics. *BioScience*, 38: 750-752.
- Niemelä, J., J. R. Spence & D. H. Spence, 1992. Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. *Canadian Entomologist*, 124: 521-540.
- Olf, H. & M. E. Ritchie, 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution*, 13: 261-265.
- Pastor, J. & R. J. Naiman, 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist*, 139: 690-705.
- Pastor, J., B. Dewey, R. J. Naiman, P. McInnes & Y. Cohen, 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology*, 74: 467-480.
- Rossow, L. J., J. P. Bryant & K. Kielland, 1997. Effects of above-ground browsing by mammals on mycorrhizal infection in an early successional taiga ecosystem. *Oecologia*, 110: 94-98.

- SAS Institute, 1990. SAS User's Guide: Statistics, Version 6. SAS Institute Inc., Cary, North Carolina.
- Suominen, O., K. Danell & R. Bergström, 1999. Moose, trees, and ground living invertebrates: Indirect interactions in Swedish pine forests. *Oikos*, 84: 215-226.
- ter Braak, C. J. F., 1988. CANOCO: A FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal component analysis and redundancy analysis. Technical Report LWA-88-02, Ministerie van Landbouw en Visserij Directoraat-Generaal Landbouw en Voedsel-voorziening Directie Landbouwkundig Onderzoek, Wageningen.
- Van Cleve, K., L. A. Viereck & G. M. Marin, 1993. Introduction and overview of a study dealing with the role of salt-affected soils in primary succession on the Tanana River floodplain, interior Alaska. *Canadian Journal of Forest Research*, 23: 879-888.
- Viereck, L. A., C. T. Dyrness & M. J. Foote, 1993. An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. *Canadian Journal of Forest Research*, 23: 889-898.
- Wolf, J. O. & J. C. Zasada, 1979. Moose habitat and forest succession on the Tanana River flood plain and Yukon-Tanana upland. *Proceedings of the North American Moose Conference Workshop*, 15: 213-244.