THE IMPACT OF MOOSE BROWSING ON TREE SPECIES COMPOSITION IN FINLAND

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ABSTRACT: The attitude usually adopted in Finnish forestry regarding the moose (*Alces alces*) has traditionally been that it influences Scots pine in young mixed stands and therefore intensive treatments have been recommended to favor monocultures. The need to maintain diversity across the landscape is, however, changing attitudes. We tested the hypothesis that selective browsing can influence the composition of tree species in young stands, both in managed and natural forests. Moose browsing effect on sapling heights was compared in exclosures and adjacent open areas in the south- and mid-boreal forest zones of Central and North Finland at the end of the 1990s. Moose appeared to impact young trees by reducing height growth, thereby reducing the possibility of selected broadleaved species to reach maturity. The number of aspen trees can obviously be expected to greatly decrease as a result of regenerating suckers being browsed by moose. Rowan considerably declined under browsing pressure. On the other hand, the results also suggest that moose browsing may be beneficial by releasing conifers from competition among tree species in managed forests. In this sense, the relationship between browsed birches and the condition of conifers is crucial. Browsing obviously reduces tree species diversity in areas of high moose density. However, some trees sheltered by neighboring ones are not browsed, and more information is needed about optimal treatment of young stands. In Finland's relatively small nature conservation areas, repeated browsing can quickly retard the height of slowly-regenerating broadleaf species. This browsing impact may lead to ecosystem changes without significantly impacting moose populations, the management of which by hunting is restricted in the set-aside natural forests and conservation areas.

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The ecology of moose (*Alces alces*) in the boreal forests of Finland is related to forest management. The moose population in the country was recently estimated to have reached its all time record level, which was 113,000-125,000 individuals in winter 2002 (Ruusila et al. 2002). The current situation is similar to that in the late 1970s, when demands to reduce moose damage in forests and vehicle collisions resulted in a high degree of culling. Since the adoption of intensive forest regeneration in the 1960s, the role of moose in relation to the characteristics of young stands has received research interest; specifically, how to mitigate the impact of moose browsing on young forest stands.

Since the late 1950s there has been discussion of the impact of moose browsing on forest succession; that is, how to minimize the impact of browsing on non-commercially treated young stands. Especially young Scots pine (*Pinus sylvestris*) stands, which are often intensively cleaned, both mechanically and chemically in order to improve the condition of commercial stands.

The removal of broadleaf trees 5-10 years after regeneration has been commonly practiced.

Until the late 1980s it was argued that the presence of broadleaf trees in forest stands, aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), and willows (*Salix* spp.), is undesirable because they attract moose and augment browsing activity, thereby impacting growth of commercial species (Yli-Vakkuri 1956, Löyttyniemi and Lääperi 1988). The argument that the harmful impact of moose is likely related to the presence of broadleaf trees justified total removal of tree species favoured by moose. For instance, a total removal of these species has been recommended as a means to reduce the expected moose damage as moose move to their winter ranges (Lääperi 1995).

Also, it was found that a relatively high broadleaf density could expose young pine to browsing risk (Heikkilä and Härkönen 1993). Removing the most suitable moose forage means a considerable reduction in forage availability without it having a damage-reducing effect (Härkönen 1998). The extreme opinions regarding the overall harmfulness of broadleaf trees provided the grounds for their large-scale total removal, and this policy is upheld by some people even today. After the termination of chemical treatment, a lot of mechanical work is now needed to keep stands clean manually. However, favouring of pine monocultures has been considered to be beneficial both from the viewpoint of growing pine as well as that of minimizing moose damage (Kärkkäinen 1998). On the other hand, managing for an admixture of birch has been found to provide opportunities for alternatives in maintaining profitable forestry (Mielikäinen 1980). Nevertheless, total cleaning of deciduous mixtures is still relatively common in practice, although other methods are also being developed.

New ecological and economical aspects are widely discussed to promote both forest yield and maintain the multiple goals of social interest groups. Demands for diversity, forest protection, and the use of forests for recreation, call for new knowledge regarding both moose and forest management. Recent demands for conserving biological diversity, as well as concerns over the status of nature conservation areas, raises new moose-related management issues. From the silvicultural viewpoint, there is the opinion that moose browsing only increases costs without any appreciable benefits. As for conserving biodiversity, the question is whether or not moose population densities can be kept high and not retard the maturation of certain species, which might then lead to long-term "unnatural" ecosystem changes in forest stands. In Finland, the forest areas are mainly managed and nature conservation areas are relatively small. However, they are subjected to continuous browsing by moose populations, the density of which often is high in relation to food availability. Therefore, it is important to define the ecological role of moose as a component of conserved natural ecosystems.

We hypothesized that moose browsing can influence the development of young stands for several years after regeneration has started. The aim of this study is to compare the early succession of young stands with and without the impact of browsing. Results of recent investigations in managed and set-aside forests are presented with reference to tree species composition.

STUDY AREAS

The experimental areas were situated in 3 different managed forest areas in Central Finland. The forests represent typical small-scale management, where compartment size is 2-5 ha. The main commercial tree species are Scots pine and Norway spruce (*Picea abies*), but birch species (*Betula pendula* and *B. pubescens*) occur in patches within the conifer stands. All the experimental stands had been managed normally, which means planting 1 year after clearcutting and a light soil preparation. In Kuru (N 61º55', E 23º47') 2 of the stands were planted with pine and 1 stand with spruce in 1990. The stand in Keuruu (N 62º26', E 24º14') was planted with spruce in 1990 and in Viitasaari (N 63º14', E 25º27') 6 stands were planted with pine in 1984. In Viitasaari, the cleaning treatments were done in the same way, with the use of a brush saw to cut stumps to 10-20 cm in height, both within and outside the exclosures in 1988 (cf. Härkönen et al. 1998). In other areas, cleaning was not needed during the study period.

In the nature conservation areas, studies were conducted in 2 nature parks. One exclosure was established in Vesijako, Central Finland (N 61º21', E 25º06') and the other in Pisavaara, Northern Finland (N 66º16', E 25º06'). In these parks natural regeneration of old spruce-dominated forests is slowly proceeding in openings made by disturbance.

The estimated density of moose populations was 0.7-1.0 individuals per km^2, according to information received from the Game Management Districts (Keski-Suomen riistanhoitopiiri, yearly reports).

METHODS

In managed forests, exclosures were built in Viitasaari and Kuru in 1989 (25 x 50 m in size), and Keuruu in 1994 (20 x 30 m in size). In the nature park of Vesijako, the exclosure was built in 1996 (20 x 30 m in size), and in Pisavaara in 1997 (30 x 40 m in size). The exclosures were placed randomly in young stands following the criterion that the stand characteristics should be similar in the exclosures and adjacent open control areas. Comparisons were made between exclosures and adjacent open areas 5-10 m away. Inventories were made by applying a network of 9 plots, each 20 sq. metres in area, situated systematically at similar distances inside and outside the exclosures.

Fieldwork was carried out in 2000 in Kuru, Keuruu, and Vesijako, and in 2001 in Viitasaari and Pisavaara. The heights of trees > 50 cm were measured on all sample plots. Moose browsing was determined by counting all browsed shoots per tree, which made it possible to estimate the browsing pressure for comparisons. The dominant height for each species, indicating the trees most likely to reach maturity in future stands, was calculated from the heights of the 100 tallest trees of each species. Statistical computations were made using 1-way ANOVA in comparisons among groups of trees and *t*-tests for individual species comparisons between exclosures and adjacent open areas (SPSS Advanced Statistics, SPSS Incorporated, Chicago, Illinois, USA).

RESULTS

In the managed forest experimental stands, the mean heights of tree species differed significantly overall between the exclosures and adjacent open areas (F = 143.7, P < 0.001). All species were on average taller within than outside the exclosures, other than juniper (*Juniperus communis*) and grey alder (*Alnus incana*), which were not significantly different, and spruce, which was significantly taller outside than inside the exclosure (Fig. 1).

In managed forests of Viitasaari and Keuruu, moose, on average, had a significant impact only on willows and rowan, the mean heights of which remained at approximately 1 metre (Table 1). In Kuru, Scots pine and broadleaf trees were significantly shorter in the open areas. Norway spruce, on the other hand, was taller outside the

Table 1. Density and height (cm) of tree species in exclosures (E) and open areas (O) of young stands in managed forests. Means are given with their standard errors.

	Study Areas											
	Kuru				Keuruu				Viitasaari			
	Trees/ha		Height		Trees/ha		Height		Trees/ha		Height	
Tree Species	E	O	E	O	E	O	E	O	E	O	E	O
Scots Pine	2,664 ± 865	2,849 ± 1,071	235 ± 9	195 ± 8***	259 ± 8	296 ± 9	68 ± 5	84 ± 8	2,256 ± 31	2,303 ± 74	423 ± 11	363 ± 41
Norway Spruce	2,719 ± 1,013	2,257 ± 1,122	113 ± 7	159 ± 8***	1,295 ± 674	1,203 ± 598	139 ± 8	146 ± 8	1,504 ± 104	1,664 ± 88	191 ± 24	135 ± 9
Silver Birch	2,645 ± 918	3,015 ± 976	212 ± 8	148 ± 5***	777 ± 1178	1,017 ± 376	160 ± 17	154 ± 12	818 ± 58	855 ± 65	202 ± 23	199 ± 29
Downy Birch	8,140 ± 1,572	8,658 ± 1,899	169 ± 4	140 ± 2***	648 ± 1,196	1,055 ± 488	152 ± 11	179 ± 15	10,246 ± 226	12,436 ± 637	194 ± 5	178 ± 16
Aspen									921 ± 84	461 ± 35	127 ± 23	109 ± 13
Willows	1,369 ± 1,011	1,313 ± 1,062	120 ± 7	73 ± 3***	556 ± 102	407 ± 175	221 ± 25	79 ± 5***	6,166 ± 318	3,938 ± 226	167 ± 8	127 ± 5**
Rowan	1,443 ± 1,114	962 ± 685	128 ± 7	67 ± 2***	10,256 ± 2,011	9,916 ± 1,879	171 ± 3	108 ± 2***	1,955 ± 88	780 ± 77	174 ± 7	93 ± 4***
Alder									18 ± 11	235 ± 190	140 ± 46	364 ± 0
Juniper									168 ± 95	280 ± 151	88 ± 12	82 ± 13

$^{**}P<0.01$, $^{***}P<0.001$.

exclosure, where broadleaf trees had been kept low in height by browsing. The spruce-dominated young stand in Keuruu had an exceptionally closely-spaced stock of rowan, the average height of which was relatively low outside the exclosures.

Browsing by moose greatly reduced dominant tree heights, especially aspen, willows, and rowan (Fig. 2). These species were transformed to low-growing vegetation, except for willows in Viitasaari and rowan in Keuruu. The relatively tall-growing willow species in Viitasaari was sallow (*Salix caprea*), which had not been severely browsed in some plots where they were protected by other neighbouring trees. The rowans in Keuruu were abundant and because of stem density several individual trees of this species likely were not browsed (t = 2.256, P = 0.054).

The dominant 100 individuals of tree species such as silver birch, aspen, willows, and rowan were, on average, significantly shorter under selective browsing outside than inside the exclosures in managed forests (F = 17.1, P = 0.001) (Fig. 2). Downy birch and dominant conifers were not affected, however.

The dominant heights of Scots pine and Norway spruce were greater outside than within the exclosures in Viitasaari (Fig. 3), which was the oldest experimental stand. There the dominant height of all broadleaf species was significantly affected by browsing.

In both managed and natural forests, moose had only occasionally impacted Norway spruce and grey alder. However, regeneration of the latter species was not abundant but instead formed sparsely-distributed groups.

The two naturally-regenerated young stands were different. The older storm-created opening in Pisavaara was rich in tree species, which were more abundant and taller, compared to the younger and more closed forest in Vesijako (Table 2).

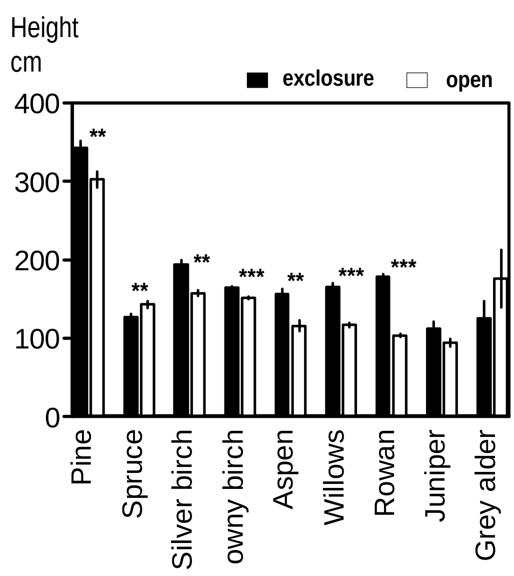

Fig. 1. Mean heights of tree species in exclosures and open areas in experimental young stands of managed forests (Kuru, Keuruu, and Viitasaari). Means are given with their standard errors. Significance: $^{**}P$ < 0.01, $^{***}P$ < 0.001.

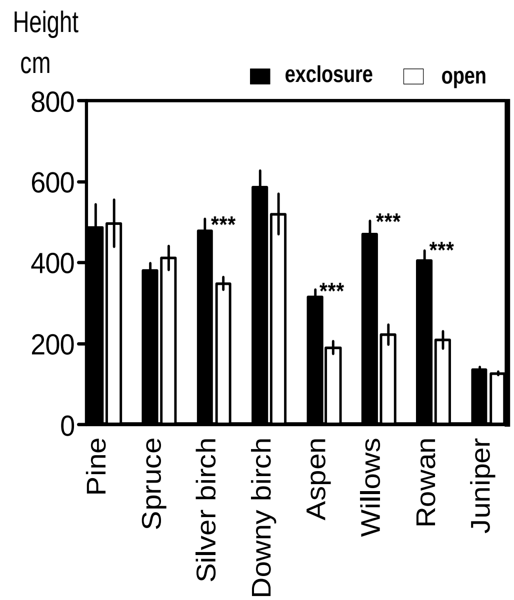

Fig. 2. Dominant heights of tree species in experimental young stands of managed forests (Kuru, Keuruu, and Viitasaari). Means are given with their standard errors. Significance: $^{***}P$ < 0.001.

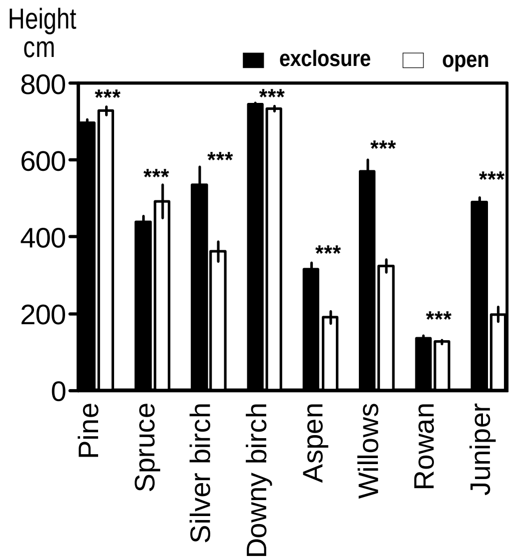

Fig. 3. Dominant heights of tree species in experimental young stands of the Viitasaari managed forest 11 years after fencing. Means are given with their standard errors. Significance: $^{***}P < 0.001$.

The impact of browsing in these two locations was considerable soon after regeneration had started. In the case of Vesijako, the slowly-regenerating aspen and rowan vegetation was soon subject to browsing. In Pisavaara, moose had also browsed intensively on both of the birch species, which was an indication of high browsing pressure. Broadleaf species were losing their dominance in the dense Norway spruce vegetation (Fig. 4). In Vesijako, the average differences were not as clear, despite the retarded growth of aspen. Dominant height there was also low, due to browsing, when compared to dominant height within the exclosure (Fig. 5).

Browsing intensities between the study areas could not be directly compared due to differences in age and tree species. The average number of browsed twigs did not significantly differ among the 3 managed forest areas ($F = 2.6$, $P = 0.11$). The highest values were obtained in Kuru, 5.1 (± 1.3 SE), and Keuruu, 3.1 (± 1.5 SE), while Viitasaari provided the lowest, 1.6 twigs/tree (± 0.4 SE). As the stand in the latter area was several years older, the annual browsing pressure had evidently been relatively low. Comparisons of browsing pressure in natural forests could not be made due to considerable differences in age and tree species composition.

Hares (*Lepus timidus*) and black shoot blight (*Venturia populina*) also caused some damage. The former occurred in some of the plots in Viitasaari, but not frequently. The latter was relatively common among young aspen in the Vesijako natural forest and occurred both within and outside the exclosures.

DISCUSSION

The average tree heights in young stands of managed Finnish forests indicate that both Scots pine and Norway spruce are dominant, in keeping with silvicultural goals. The slight, but still significant, difference in mean heights of trees between exclosures and open areas was to be expected due to the impact of moose browsing. Experimental forests can be regarded as being risky areas, where economically significant damage can occur. However, the estimated local moose population densities indicate that the expected intensity of damage does not usually jeopardize successful regeneration (cf. Heikkilä and Härkönen 1993). The study forests therefore represent relatively large areas where moose populations normally concentrate in winter in above-average densities. In these areas, considerable damage can occur in more restricted, smaller high-risk areas that cannot be exactly predicted because of yearly changes in moose movements.

The average heights of broadleaved tree species consistently declined under browsing pressure. This occurs in young stands due to both silvicultural cleaning and

Table 2. Density and height (cm) of tree species in exclosures (E) and open areas (O) of young stands in natural forests. Means are given with their standard errors.

	Study Areas							
	Vesijako				Pisavaara			
	Trees/ha		Height		Trees/ha		Height	
Tree Species	E	O	E	O	E	O	E	O
Norway Spruce	1,610±405	1,390±380**	37±6	25±3*	3,888±934	10,050±2,554**	127±10	105±5*
Silver Birch					2,112±491	2,943±1,008*	155±11	78±5***
Downy Birch					1,056±315	3,612±1,009	136±16	86±7***
Aspen	3,220±1,435	3,610±1,268	78±5	56±3***	830±250	1,389±654	107±10	79±6**
Willows					611±102	111±111	147±23	60±3**
Rowan	889±302	1,111±331*	69±11	52±4***	7,332±1,245	2,116±448**	87±3	70±3***
Alder					2,442±1,173	721±602	218±24	219±47
Juniper					56±0	112±0	100±0	60±0

$^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

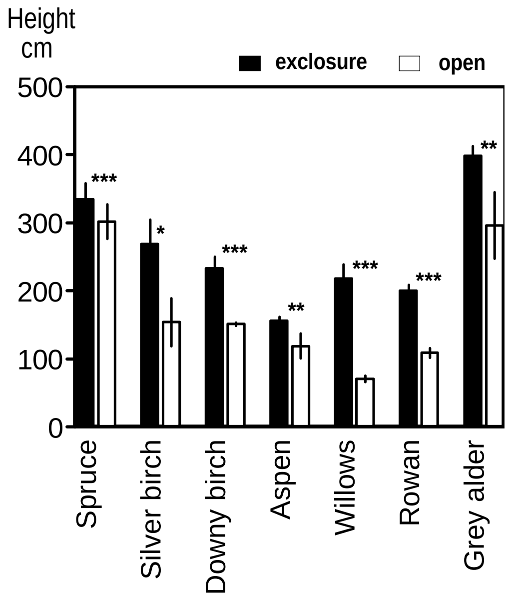

Fig. 4. Dominant heights of tree species in experimental young stand of the Pisavaara nature conservation area. Means are given with their standard errors. Significance: $^{*}P <$ 0.05, $^{**}P < 0.01$, $^{***}P < 0.001$.

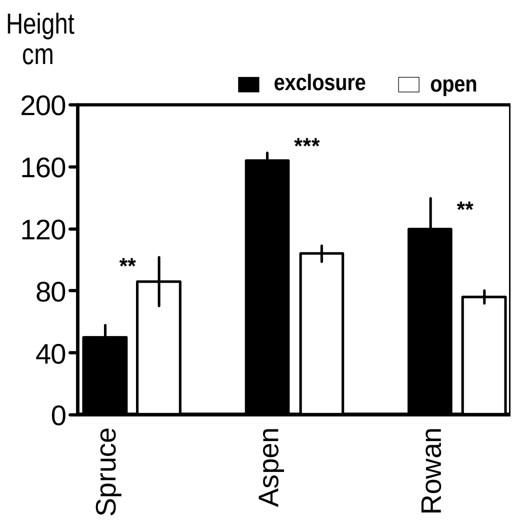

Fig. 5. Dominant heights of tree species in experimental young stand of the Vesijako nature conservation area. Means are given with their standard errors. Significance: $^{**}P <$ 0.01, $^{***}P < 0.001$.

the impact of moose browsing. Cleaning greatly reduced the numbers of stems of both downy birch and aspen in Viitasaari (Härkönen et al. 1998), whereas the relatively wide spacing of rowan was obviously due to browsing. It is a matter of opinion how intensively early non-commercial treatment should be done, although excess broadleaved vegetation has to be removed to release conifer growth. Moose browsing may be beneficial if the density of competing tree species is reduced, since the proportion of dominant pine is economically important in the future stands. The pines were taller in height outside the exclosures in Viitasaari, indicating a release effect likely caused by moose browsing in open areas. Thus the release may have compensated for the effect of moose stem breakages that can reduce pine height (Heikkilä and Löyttyniemi 1992). The per-tree effect of browsing declines with increasing food availability in terms of stand density (Vivås and Saether 1987, Heikkilä and Mikkonen 1992). According to studies by Thompson and Curran (1993) in Newfoundland, moose browsing can be beneficial in thinning young dense stands.

Tree species selected by moose, such as aspen, willows, and rowan (Bergström and Hjeljord 1987), were generally of shorter height under browsing, and only in Keuruu was the closely-spaced rowan vegetation still present in the dominant tree layer. Mature trees of these species are likely to be reduced in numbers over large areas due to browsing. This depends also on the intensity of early cleaning as well as on stand treatments applied in first thinning cuttings. The sustainability of young trees varies between species (Saether 1990), the resistance of birches to browsing being relatively high due to numerous twigs. These species react to browsing by producing numerous new shoots which are palatable to moose (Bergström 1984). The response of sparsely-branched rowan easily leads to loss in height development, following which this tree species will most likely fail to reach maturity as it is a weak competitor to other species.

Conserving tree species diversity necessitates space to be created by silvicultural treatments favouring species selected by moose. The survival strategy of aspen is based on dense suckering (Zackrisson 1985), whereas the spreading of abundantly-produced rowan seeds enables this species to reproduce far from mature trees. Both of these species are known to favour relatively fertile sites where Norway spruce is the main timber species. Rowan has been found to regenerate abundantly in pine-dominated young stands, and since it is a weak competitor, can be favoured in early stand treatments. Conflicts may arise between economy and diversity-oriented ecology, if, for example, it is decided to favour fast-growing Scots pine on fertile sites instead of ecologically-suitable Norway spruce. Because moose "take the remains", browsing the reduced number of stems after stand treatments, a threat to aspen survival may arise, reducing this species over large areas in the future as a result of both forestry and browsing (Heikkilä and Härkönen 2001). In Finland, however, the species selected by moose (e.g., aspen, rowan, and sallow) can become threatened by browsing mainly in relatively restricted, highest-density moose winter range areas. This conclusion can be drawn also from the results of national forest inventories conducted since 1950, in which the frequency of these species has been constant since 1995 (Reinikainen et al. 2001). On the other hand, grey alder, not commonly browsed by moose, is ranked lower in numbers per hectare than moose-selected trees (Finnish Forest Research Institute 2001). In addition to moose, the occasional feeding by hares probably indicates low-density populations.

In natural forests of Vesijako and Pisavaara, moose browsing significantly reduced regeneration of broadleaf species. The height differences indicate that it is hard for young broadleaf trees to reach heights above the snow level. Birches were available in Pisavaara, where they also were severely affected and remained low in height under browsing. The conditions in generally small nature conservation areas are exceptional, because the size of moose populations depends mainly on the surrounding forests. The number of moose utilizing broadleaf species in natural forests can be considerable from year to year. The carrying capacity of slowly regenerating nature conservation areas is relatively low. However, the situation is different from Isle Royale (Michigan, USA), for example, where moose are controlled by wolves, and in island conditions do not likely move away as a result of reduced food resources. There the tree species diversity increased as a result of browsing, but the palatable tree species remained low-growing (Risenhoover and Maass 1987). In Finland, on the other hand, the small natural forest areas, utilized by moose populations, are controlled only by hunting outside the conserved forests. Consequently, the continuous consumption by moose in natural forests is not a natural element of the ecosystem because it depends on the decisions made for managing moose under the conditions of commercial forests.

CONCLUSIONS

The broadleaved tree species selected by moose occur in varying densities in young stands. In managed forests, moose often "take the remains" following early silvicultural treatments in stands managed for conifer release. Browsing causes damage to young pines and can also retard the height development of tree species such as aspen and rowan, reducing their competitive advantage and retarding maturation. In Finnish forests, these species are still commonly available, indicating a threat to tree species diversity to be found in restricted high-density moose areas only. On the other hand, the impact of moose browsing can be beneficial in releasing conifers from competition with broadleaf species. More knowledge is still needed for successful modelling of the structure of young stands and optimal stand treatments. Silvicultural goals should also include diversity aspects important to moose in terms of food resources of good quality. The relationships between tree species abundance, consideration for diversity, and impact of moose browsing in managed forests constitute a complicated ecological-economic problem. Regeneration of forest stands in small nature conservation areas can be negatively affected by continuous browsing: this does not result in a corresponding reduction in moose populations because of benefits afforded them by the surrounding managed forests. The fact that hunting is not allowed in conserved forests likely increases the browsing effect. Consequently, ecosystem changes can be expected to occur in natural forests without negatively impacting moose populations, which will continue to challenge integration of moose and forest management objectives.

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