THE INFLUENCE OF MOOSE ON TREE SPECIES COMPOSITION IN LIESJÄRVI NATIONAL PARK IN SOUTHERN FINLAND

Risto Heikkilä[1] and Marita Tuominen[2]

[1]Finnish Forest Research Institute, Vantaa Research Unit, P.O. Box 18, FI-01301 Vantaa, Finland
[2]University of Helsinki, Faculty of Forest Ecology, P.O. Box 27, FI-00014 Helsinki, Finland

ABSTRACT: Intensive forest management has promoted a rapid increase in Finland's moose (*Alces alces*) population since the 1970s. The main objective of this study was to determine the role of moose browsing in modifying natural processes of protected forests that are influenced by high moose populations in adjacent managed forests. This study occurred in Liesjärvi National Park located in the mid-boreal vegetation region of Finland. Forest stands were sampled with line-plot sampling (50 m² plots at 100 m distances) in the older (OA; 1956) and newer (NA; 2005) parts of the Park. We found that long-term selective browsing in OA retarded the development of young stands in favor of Norway spruce (*Picea abies*) and low-growing broadleaf species. Browsing in recent years was relatively intensive in NA where young regeneration areas still existed from previous forest management. The most intensive browsing occurred on 18.6 % of trees in NA and 3.1 % in OA; young palatable tree species were taller in NA than OA. Also, in OA the density of preferred aspen (*Populus tremula*) and rowan (*Sorbus aucuparia*) trees was relatively low in the height class that produces the dominant tree canopy. Despite short-term intensive browsing, NA appeared better able to recover to a natural forest state. Fecal pellet groups associated with young Scots pine (*Pinus sylvestris*) and browsing of birch (*Betula* spp.) and aspen indicated the importance and role of forage quantity and quality on winter range of moose. The amount of consumed new twig biomass was 20-fold greater in NA compared to OA, indicating a difference in the size of the moose population and presumably habitat quality between the areas. The effect of browsing on different tree species was measured at the stand level in OA in an area restored with prescribed burning 11 years previous. Comparative measurements in two exclosures and adjacent open areas indicated that regeneration in the burned area was browsed intensively and growth of young trees was retarded, except spruce. The major impacts of browsing on aspen and rowan identify the need for new approaches to maintain forest diversity. A crucial issue will be the contradiction between preferred and sustained high moose harvests and the desire for natural forest diversity in conservation areas.

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Moose (*Alces alces*) herbivory plays an essential role in the dynamics of natural forests (Risenhoover and Maass 1987, Pastor and Naiman 1992, Persson et al. 2000). In intensively managed boreal forests of Finland, natural or unmanaged ecosystems are maintained in relatively small conservation areas where natural processes are the sole disturbance factor. Even during a long unmanaged history, the characteristics of conserved forests are probably affected to some degree by outside influences. For example, forest management over large areas has favored moose populations by creating abundant regeneration similarly as natural disturbance processes such as fire (Linder et al. 1997, Lavsund et al. 2003). Continuous forest management more effectively maintains moose populations than the sporadic occurrence of forest fires occurring irregularly in natural forests. Consequently, the moose density in natural forests adjacent to managed forests is often higher than expected relative to normal regeneration rate and turnover of a natural forest.

The impacts on vegetation by moose, expressed through selective browsing (Bergström and Hjeljord 1987), have become acute in the case of certain tree species like balsam fir (*Abies balsamea*) and aspen (*Populus* spp.) in North America (Brandner et al. 1990, Kay 1997) and Fennoscandia (Kouki et al. 2004). Attention has been paid to the question of population overabundance and generally to the role of moose as a disturbance factor in managed forests (Gill 1992, Edenius et. al 2002). In the long term, high-density moose populations can damage forest habitats in the absence of predation or human control (McLaren et al. 2004).

Heikkilä et al. (2003) suggested that browsing can cause considerable change in the early successional habitats of managed and natural forests in Finland. Nature conservation preserves are often located in close proximity to managed forests that are occupied by moose. Depending on when preserves are established, they may reflect characteristics of previous forest management and fluctuations in the moose population.

Restoration of managed forests for conservation purposes often requires treatment strategies that allow natural processes (e.g., burning). Such work has occurred in both older and more recently conserved areas in Finland. The effects of the traditional, annual concentration of moose on their winter range (Lavsund 1987, Andersen 1991) may be important in this respect, because young conserved areas may still retain the characteristics of managed forests preferred by moose. Further, intensive browsing may occur in older conserved areas from moose seeking sanctuary from nearby hunted areas. It has been suggested that some hunting activity should be permitted in conserved forest areas in Finland (Ympäristöministeriö 2006).

In this study we analyzed the effects of moose browsing on a conserved forest area currently being restored in Liesjärvi National Park in southern Finland. It was hypothesized that moose browsing may alter tree species composition and forest diversity. We questioned whether possible changes were unnatural and conflicted with goals to maintain this natural conservation area.

STUDY AREA

The study area was the Liesjärvi National Park established in southern Finland in 1956 (Fig. 1). Part of the original 660 ha area had been under forest management resulting in middle-aged and old closed forest; no inspection was made to classify the structure of the forest afterward. Without disturbance factors, Norway spruce (*Picea abies*) became dominant over less shade tolerant broadleaved species and Scots pine (*Pinus sylvestris*). Shaded undergrowth trees were common with silver birch (*Betula pubescens*) and downy birch (*Betula pubescens*) more dominant

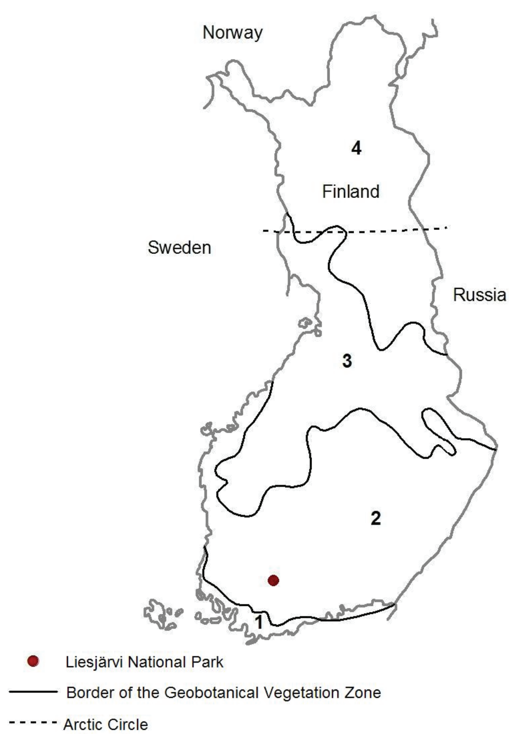

Fig. 1. The location of Liesjärvi National Park in southern Finland. The geobotanical vegetation zones are after Kalliola (1973: 1 = hemiboreal zone, 2 = southern boreal zone, 3 = middle boreal zone, and 4 = northern boreal zone.

than aspen and rowan (*Sorbus aucuparia*). New regeneration occurred mostly as shaded undergrowth in small natural gaps and at forest edges. In 1993 an area of about 3 ha was burned to restore a dry forest site dominated by Scots pine.

In 2005 the Park was enlarged to 2,200 ha by adding a new area where intensive forest management had not occurred for about 20 years. Despite initial restoration measures, the new area (NA) was less natural than the original, older area (OA) relative to forest age structure, although it had denser young stages and an increased proportion of moist sites. The characteristics of a managed forest were still prominent in the forest stands of different age classes.

The average density of moose in the area was 3.1-4.0 moose/1,000 ha (Ruusila et al. 2006). Hunter surveys (information from Game Management Association of Tammela) indicated that the local winter density of moose after hunting was 4.6 moose/1,000 ha (range 4.3-5.1) in 2000-2005.

METHODS

Forest inventory data, browsing intensity, and pellet groups were measured in both the OA and NA portions of the Park in 2005. We established 50 m^2 circular plots on parallel transects with a distance of 100 m between transects and plots. Because sampling in the OA was intended to be relatively intensive, the plot size was reduced to 20 m^2 to measure all trees within a plot; trees >6 m high and fecal pellet groups were measured in the 50 m^2 plots.

The height of all tree species ≤6 m was measured to an accuracy of ±10 cm. The diameter at breast height (1.3 m) was measured on trees >6 m high. To assess forest structure, the abundance of tree species was calculated in 4 height categories: ≤ 2 m, 2.1- 4 m, 4.1-6 m, and >6 m. Five tree condition categories were described: healthy, lightly damaged (no effect on growth), moderately damaged (growth loss obvious), seriously damaged (retarded growth and development), and dead.

Browsing intensity, including shoot and bark damage, was scaled in 4 categories according to a visual estimate of lost biomass: 0-25%, 26-50%, 51-75%, and >75%. The most intensively utilized trees were classified as bushy deformed. Fresh moose browsing points on side shoots were counted to estimate consumed biomass according to the bite diameter and weight calculations for tree species (Heikkilä and Härkönen 1993); new and old main stem breakages were counted. Old and new bites and breakages were distinguished according to the point and color of browsing.

New (lying on the forest litter) and old fecal pellet groups (at least 20 pellets) were counted to compare presence and habitat use of moose in the study areas (Neff 1968, Härkönen and Heikkilä 1999). We also used 2 exclosures built in the OA 10 years earlier where a 3 ha area was restored by burning. Data were collected both inside and outside of 9, 20 m^2 sample plots in the 25 m x 25 m exclosures. Height of tree species was measured according to the landscape-level inventory.

Statistical analyses were performed using SAS program version 9.3.1 (SAS Institute, 2005), and comparisons between areas were made with a non-parametric Mann-Whitney U-test. Spearman rank correlation at the sample plot level was used to analyze habitat selection according to fecal pellet groups and characteristics of the forests. Height differences between exclosures and open areas were analyzed with one-way ANOVA (SPSS package).

RESULTS

Norway spruce and downy birch dominated the tree species composition in OA, and spruce, Scots pine, silver birch, and other broadleaf species were abundant in NA. More willow, rowan, and pine occurred in NA (Table 1). The availability of palatable trees (excluding spruce) ≤6 m in height was 447 trees/ha

Table 1. Mean density (± SE) of tree species (trees/ha) in Liesjärvi National Park, southern Finland, 2005. The Park was established in 1956 and consisted of two areas with different histories of forest management and moose population density; the original area was designated OA (old area), and a new area added in 2005 was designated NA (new area).

	OA	NA	U-value	P-value
Pine	904 ± 162	1550 ± 146	6.7290	<0.0001
Spruce	4655 ± 948	2334 ± 230	-1.8487	0.0645
Silver birch	298 ± 70	343 ± 64	3.5385	0.0004
Downy birch	2441 ± 626	1898 ± 238	2.1439	0.0320
Aspen	159 ± 39	217 ± 55	1.3537	0.1758
Willows	255 ± 165	441 ± 106	4.5307	<0.0001
Rowan	928 ± 168	1490 ± 211	4.2995	<0.0001
Juniper	57 ± 52	23 ± 14	1.4411	0.1495
Grey alder	46 ± 23	188 ± 65	3.6821	0.0002
Other spp	23 ± 14			

greater in OA than in NA. The mean height of trees ≤6 m was greater in NA than in OA for all species except grey alder (*Alnus incana*) (Table 2). The number of trees ≤4 m was 9060/ha in OA and 6060/ha in NA; about one third was spruce in both areas. The total tree density in NA was twice that in OA for trees in the 2.1-4 m height category (1633/ha vs. 826/ha); pines and broadleaf trees accounted for 76% of trees in NA and 62% in the more spruce-dominated OA. The proportion of trees ≤2 m was considerably higher in OA than in NA (88% vs. 70%), and their density in OA was twice that in NA.

Moose browsing occurred on 25% of trees in OA, whereas 42% of trees were browsed in NA (Fig. 2). Intensive browsing (>75%) occurred on 18.6% of trees in NA and 3.1% in OA. Browsing was 30% on Scots pine in both areas. Aspen, rowan, and willows were intensively browsed in NA. Bushy deformed trees totaled 224 trees/ha in OA, and included pine, aspen, downy birch, rowan, and willows. In NA only 48 trees/ha were bushy deformed of which >90% were willows and the rest rowans. The mean bite diameter was 2.76

Table 2. The mean (± SE) height (cm) of tree species ≤6 m high in Liesjärvi National Park, southern Finland, 2005. The Park was established in 1956 and consisted of two areas with different histories of forest management and moose population density; the original area was designated OA (old area), and a new area added in 2005 was designated NA (new area).

	OA	NA	U-value	P-value
Pine	109.8 ± 5.0	193.0 ± 5.6	-11.6159	<0.0001
Spruce	91.7 ± 2.8	133.3 ± 3.0	19.6262	<0.0001
Silver birch	188.8 ± 13.2	242.2 ± 8.4	-5.0225	<0.0001
Downy birch	118.1 ± 2.8	213.4 ± 4.1	20.6175	<0.0001
Aspen	76.4 ± 8.0	151.6 ± 7.6	-7.4651	<0.0001
Willows	63.7 ± 2.3	157.6 ± 5.2	-14.2084	<0.0001
Rowan	76.7 ± 3.6	141.2 ± 2.6	-18.0767	<0.0001
Juniper	58.1 ± 2.9	161.6 ± 13.6	4.0430	<0.0001
Grey alder	237.6 ± 35.7	181.3 ± 12.5	0.9246	0.3552
Other spp	65.0 ± 13.0			

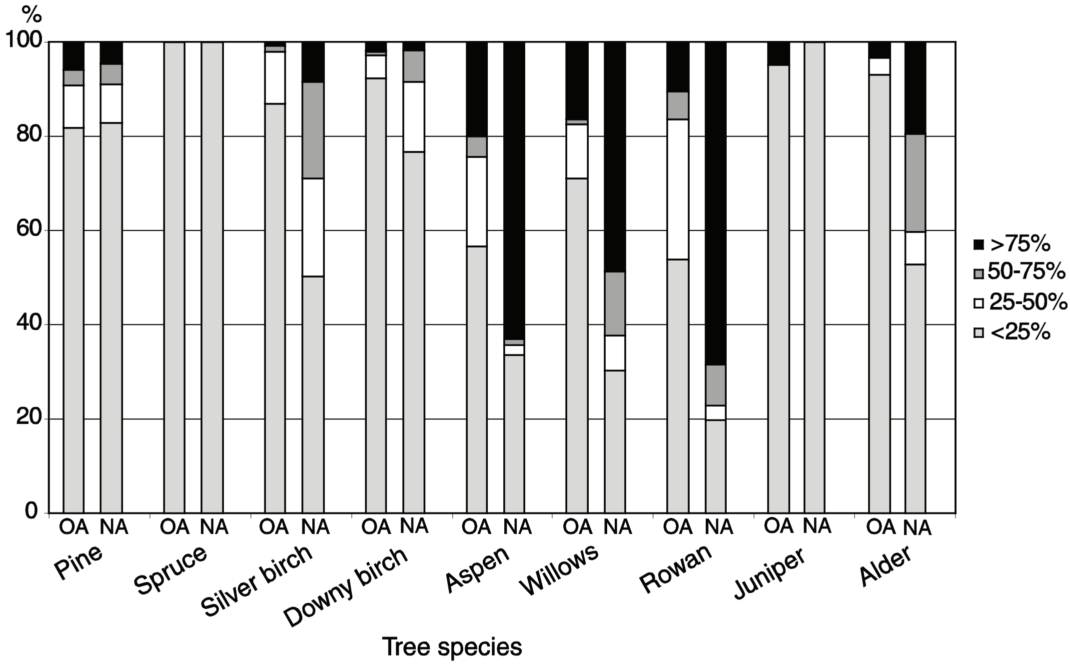

Fig. 2. Proportions of 4 categories of moose browsing intensity on tree species in Liesjärvi National Park in southern Finland. The park was established in 1956; the original area was designated OA (old area), and a new area added in 2005 was designated NA (new area).

mm (± 0.19 SE) in NA and 2.03 mm (± 0.21 SE) in OA. The lowest diameter occurred on downy birch (1.64 mm ± 0.11 SE) and the highest on pine (3.52 mm ± 0.11 SE). Thicker than average bites were taken from rowan and pine in both areas, and from aspen and alder in NA. The estimated consumption of new twig biomass was 2.44 kg/ha in NA and 0.09 kg/ha in OA.

The number of old and new stem breakages was higher in OA than NA (Table 3). The stem damage/tree was consistently higher in OA than NA for all tree species except juniper (*Juniperus communis*). Rowan had the highest number of breakages per tree in both OA (9.3) and NA (0.9). Silver birch, willows, and aspen were also broken more than once in OA.

In general, the ≤6 m high trees in OA were less seriously affected than those in NA. The proportion of dead trees was 16% in NA and 6.5% in OA. Of species preferred by moose, 65% of aspen, rowan, and willows were affected in both OA and NA; dead trees were 7% of the total in OA and 30% in NA. The

Table 3. Damage associated with moose browsing and total number of fecal pellet groups in Liesjärvi National Park, southern Finland, 2005. The Park was established in 1956 and consisted of 2 areas with different histories of forest management and moose population density; the original area was designated OA (old area), and a new area added in 2005 was designated NA (new area).

	OA	NA	U-value	P-value
New twig browsing/ha	909.0 ± 48.9	155.0 ± 9.5	2.8777	0.0040
Old stem breakage/ha	5294.0 ± 256.2	2111.0 ± 159.0	-24.5731	<0.0001
New stem breakage/ha	67.0 ± 4.0	50.0 ± 2.0	5.6691	<0.0001
Stem breakage/tree	2.9 ± 0.1	0.4 ± 0.0	12.5000	0.0110
Pellet groups/ha	18.6 ± 6.3	80.3 ± 20.5	4.0442	<0.0001

proportion of live aspen was 75% in OA (126 aspens/ha) and 62% in NA (114 aspens/ha).

Most live trees 4.1-6.0 m tall (313/ha in OA and 260/ha in NA) were spruce and downy birch (79%) in OA, and downy birch and pine (67%) in NA. All aspen (2.1/ha) were dead and willows were absent in OA. In NA 5.9 aspens/ha were live of which 4.4/ha were injured; no dead aspens were found. In OA 16.3 rowans/ha were healthy or injured, whereas 12.0 rowans/ha were injured and 3 rowans/ha were dead in NA. Grey alder was either injured or dead in both OA and NA.

Conifers were the dominant trees >6 m tall in both OA (81%) and NA (70%). Aspen, rowan, and willows accounted for 2% of trees >6 m in OA and 3.5% in NA. In OA 13% of the 48 aspens/ha were dead; 4% of 33 aspens/ha were dead and 22% affected by bark stripping in NA. The maximum stem diameter of aspen was ≤20 cm and that of rowan and willows ≤15 cm. The diameter of the largest conifers was 46-50 cm in OA and 36-40 cm in NA.

The abundance of fecal pellet groups indicated that moose used NA more than OA during the previous winter (80.3 groups/ha ± 20.5 SE vs. 18.6 ± groups/ha ± 6.3 SE, Mann-Whitney U = 4.0442, P <0.0001). In OA the number of fecal pellet groups correlated positively with the number of pines <2.5 m tall (r = 0.21, P = 0.004), the number of stem breakages of silver birch (r = 0.318, P <0.0001) and aspen (r = 0.168, P = 0.023), and the total number of moose-affected pines and downy birches (r = 0.465, p <0.0001). In NA the number of pellet groups correlated positively with the number of pines <2.5 m tall (r = 0.198, P = 0.02). The fresh browsing of pine correlated with pellet groups (r = 0.332, P <0.0001); fresh willow browsing was nearly significant (P = 0.08). The number of pellet groups increased with the number of stem breakages on pine (r = 0.210, P = 0.016) and silver birch (r = 0.216, P = 0.011), and with rowans that were seriously damaged (r = 0.179, P = 0.037) or dead (r = 0.250, P = 0.003).

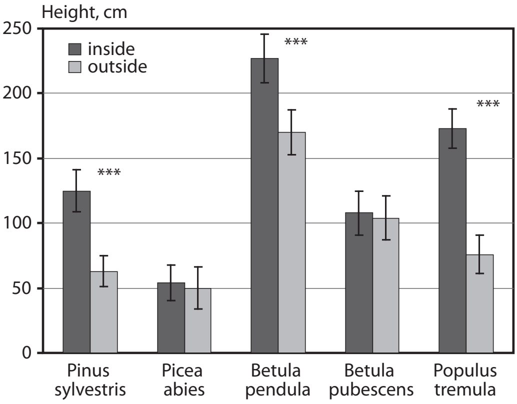

Fig. 3. Height of tree species inside and outside two exclosures in a forest restoration treatment area in OA, 10 years post-burn, Liesjärvi National Park, southern Finland.

Measurements within the exclosures indicated that moose reduced (P <0.05) the growth (height) of pine, silver birch, and aspen during the 11 year period post-burn (Fig. 3). Downy birch was uncommon and spruce was not browsed. Aspen was 1 m higher in the exclosures, and rowan did not occur outside the exclosure. Willows were absent inside the exclosures. Silver birch and pine combined accounted for about 80% of the total sapling density per ha, about 7,500 inside and 10,500 outside the exclosures.

DISCUSSION

Liesjärvi National Park in Finland provides an excellent example of how previous and current forest and moose management can influence natural forest succession in a conservation area. The management history of the original portion of the Park (OA) was different from that added later (NA), both in forest management and moose population density. The forests in OA developed with minimal disturbance in the 1950-1970s when the moose population density was relatively low thereby allowing tree species typical of moose forage to grow. The subsequent rapid increase in moose population density and the forest management history in NA (added in 2005) created the structural differences evident in forests in OA and NA. The long-term impact from browsing that occurred after the 1970s retarded the development of young trees in OA, and created a low-growing community of palatable tree species (Table 2; Risenhoover and Maass 1987, Abaturov and Smirnov 2002).

The recent intensive browsing in NA (>75 % browsing of 18.6 % of trees vs. 3.1% in OA) is reflected in the high proportion of injured and dead trees. In this short time NA experienced more damage than OA (Table 2, Fig. 2). However, the availability of palatable trees in NA was greater than in OA, especially in the 2.1-4.0 m height class that contains relatively abundant moose forage (Parker and Morton 1978, Heikkilä and Härkönen 1998).

In the absence of past disturbances other than browsing, the OA forest developed towards spruce dominance (Table 1). This trend gradually reduced habitat value for moose that prefer highly available deciduous forage (Saether and Andersen 1990, Ball et al. 2000) that is associated with high moose population densities. However, an abundant moose population affects tree species diversity in ways that are difficult to predict (McLaren et al. 2004). Because the local management goal is to maintain moose populations at levels that provide widespread hunting opportunity, understanding browsing impacts by high populations is critical. Our data indicate that browsing pressure within a conservation area needs to be related to management goals in surrounding managed forests to best ascertain the effects on biodiversity within conservation areas.

The high pellet group density in NA indicated that a concentrated winter population of moose may reduce and alter diversity of tree species (Andersen 1991). Generally, the pellet group density increased with browsing intensity which is consistent with earlier findings (Heikkilä and Härkönen 1993). In both OA and NA the number of pellet groups correlated positively with the density of young pine that is palatable winter browse (Lundberg et al. 1990).

The positive correlation between pellet groups and stem breakage on aspen in OA indicated higher and more frequent use by moose than in conserved forests in Koli National Park in eastern Finland where moose used aspen much less (Härkönen et al. 2008). Gap dynamics may keep aspen inaccessible to moose and completely avoid browsing damage (Syrjänen et al. 1994, Cumming et al. 2000, Edenius et al. 2002). Local moose population density may also influence whether aspen escapes browsing damage.

The risk of reduced biodiversity is recognized in managed forests located in high-density moose winter range (Heikkilä and Härkönen 1993). Most concern is for rowan and especially aspen, one of the most threatened tree species (Kouki et al. 2004). Although rowan was relatively abundant in Liesjärvi National Park, only a few individuals grew beyond the browsing height of moose. Because rowan does not resist intensive browsing well, it commonly remains low-growing (Saether 1990). Rowan disperses widely even from a few seed producing trees, whereas aspen reproduces mainly from suckering (Zackrisson 1985). Aspen was much less abundant than rowan in both OA and NA, and only a few were >2 m-≤ 6 m high. No live aspen was found in the 4.1-6.0 m height class in OA indicating a lack of recruitment of dominant trees and risk for future forest diversity.

There are several ways of enhancing the diversity of intensively browsed tree species beyond population management of large ungulates, for example, as in aspen communities of conserved forests in North America (Suzuki et al. 1999, Kaye et al. 2005, Romme et al. 2005). The strategy of aspen to resist ungulate browsing presupposes favorable conditions for regeneration. Small-scale restoration by burning at the stand level was attempted in Liesjärvi National Park to compensate for the lack of natural disturbance. However, no young aspens in the burned area grew beyond moose browsing after 10 years. Rowan, preferred by moose year-round, was also absent due to intensive browsing, and even low-density moose populations can influence tree species composition. Our results suggest that a small-scale restoration needs to be supplemented with protection against moose browsing; partial fencing might ensure aspen regeneration (McLaren et al. 2004, Edenius and Ericsson 2007).

One crucial issue is the conflict between a sustained high harvest desired by hunters and the need for natural high forest diversity. Diversity may vary widely in conserved areas (Kouki et al. 2004); for example, Härkönen et al. (2008) reported that browsed aspens recover well at low moose density. However, moose populations often impact development of conserved forests by retarding primary succession and causing conifer dominance (Davidson 1993). Further, the absence of natural disturbance results in a closed spruce-dominated boreal forest (Linder et al. 1997). High density moose populations require large-scale disturbances to create preferred regeneration habitat to maintain balance between browsing pressure and forage availability. Our data indicate that the continuous selective browsing pressure by moose in Liesjärvi National Park gradually reduced forage diversity and availability. It is clear that potentially threatened species and the composition and availability of all forage trees need to be addressed in management plans because management practices to date have not prevented a critical drop in forest health and diversity in Liesjärvi National Park. A cooperative decision-making process among adjacent landowners and moose managers is needed to help establish and maintain natural development in recently conserved forest areas.

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