The Role of Moose as a Disturbance Factor in Managed Boreal Forests

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We review the interactions between moose (*Alces alces*) and native tree species in Fennoscandia. The Fennoscandian boreal forests have been intensively managed for wood production over decades. Moose population density is also relatively high in these northern forests. Forest management affects habitat characteristics and food resources from regeneration to final harvest, with the most significant effects occurring early in the stand development. The plant-animal interactions found in such a situation may be different from what has been observed in natural boreal forests with low densities of moose (e.g. in North America). The strong focus on Scots pine (*Pinus sylvestris*) in forest regeneration in conjunction with a homogenisation of the landscape structure by clear-cutting has favoured moose. Forest development is controlled by man from regeneration to final harvest, and in relation to human-induced disturbances the disturbance by moose is relatively small, but occurs on different spatial levels. At the landscape level, the most prominent effects of moose seem to be suppression and/or redistribution of preferred browse species. At the forest stand level moose primarily induce spatial heterogeneity by browsing patchily and exploiting existing gaps. At the tree level, moose damage trees and lower timber quality, but also create substrate types (e.g. dead and dying wood) valuable for many organisms. Co-management of moose and forest requires good monitoring programmes for both plants and animals, as well as extensive ecological knowledge on the relations between moose and their food plants on different spatial levels.

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1 Introduction

In Fennoscandia, a growing interest in the role of large ungulates as disturbance factors has paralleled the recent increase in population density of moose (*Alces alces*) (Fig. 1). Other reasons for the growing interest are the advent of biodiversity issues in forestry (Edenius et al. 1996), and changes in the perception of the structure and functioning of forest ecosystems, with a shift from the Clementian deterministic climax paradigm to emphasis on stochastic processes and

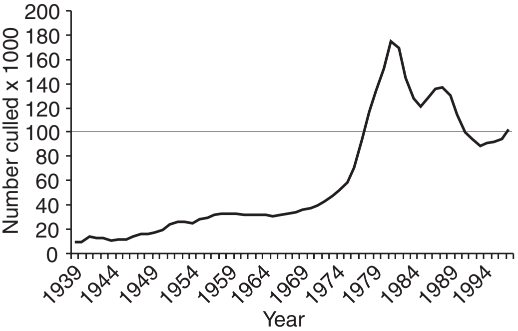

Fig. 1. Development of the Swedish moose population illustrated as yearly harvest (Official hunting statistics, Swedish Environmental Protection Agency, Stockholm).

Table 1. Moose densities in Fennoscandia and Canada around 1980 (Gill 1990).

Country	No. moose km^{-2} forestland
Finland [1]	0.46
Norway [1]	1.21
Sweden [1]	1.38
Canada [2]	0.24

[1] Winter
[2] Summer

non-equilibrium states (Spies and Turner 1999). One striking feature is that large ungulates such as the moose can alter the structural complexity of forest ecosystems and affect successional development by arresting or retarding height development of woody plants (McInnes et al. 1992, Davidson 1993, Jefferies et al. 1994). A great part of the present knowledge on the impact and role of large ungulate herbivores in boreal forests emanate from North America (e.g. Pastor et al. 1988, Pastor and Naiman 1992, Kielland et al. 1997) where moose have been studied mainly in natural boreal forests. The Fennoscandian forests are today quite far from being in the natural forest stage because the forests have been managed for wood production over decades. Due to this, the boreal forests in Finland, Norway and Sweden are significantly different from natural forests in many structural characteristics. Further, the population density of moose in Fennoscandia is also higher than in North America (Table 1), which further stresses the differences in moose-forest interactions between the continents.

Selectivity of herbivores is a key factor for understanding and predicting herbivore impacts in forest ecosystems. At the landscape level, variation in selectivity reflects variation in population density, whereas selectivity at the stand level also reflects adjustments of foraging behaviour of individuals. At the patch and plant level variation in palatability among plants and plant tissue is an underlying reason for selectivity. The selectivity concept thus encapsulates ecological processes operating at different spatial scales, and can be used for deriving qualitative and quantitative predictions of large ungulate impacts. For example, habitat selection at the landscape scale will be less pronounced when there are small differences in quality between stand types, or at high animal population densities. Similarly, food plant selection will be less pronounced during winter when the overall quality of food is low.

Here, we analyse interactions between moose and trees based on this selectivity framework, highlighting factors characterising managed boreal forests. First, we review the typical silvicultural practices and describe how they affect habitat conditions and food resources for large ungulates at the stand level. Second, we address effects of forest management on habitat suitability, carrying capacity, and patterns of plant utilisation at the landscape scale. Third, we highlight impacts by moose in a dynamic perspective by discussing their role as disturbers. Finally, we discuss some emergent issues from monitoring and management perspectives.

The interaction between large ungulates and boreal forests has been the subject of several reviews, and here we build further on these. Bergström and Hjeljord (1987) and Danell et al. (1994) reviewed interactions between moose and trees on different spatial scales, and Suominen and Olofsson (2000) recently reviewed reindeer (*Rangifer tarandus*) – forest vegetation interactions. Persson et al. (2000) reviewed the role of large ungulates as disturbance factors covering the whole boreal forest biome. Sjöberg and Danell (2001) reviewed the relations between moose and an introduced conifer species, the lodgepole pine (*Pinus contorta*). Our focus will be moose and native tree species in managed forests in Fennoscandia.

2 Stand Development in Managed Forests

Typical silvicultural measures used in Fennoscandia after clear-cutting include planting, cleaning and single or multiple thinnings before final cutting at 80–120 years of age (Fries 1995). Hitherto, the silviculture systems adopted in Fennoscandia have been strongly directed towards productive monocultures of conifers of similar size and age (Esseen et al. 1997), with a multitude of different management activities. Most of these have potential to affect the large herbivores. As moose primarily interact with forests during the early stand development, the regeneration and cleaning phases are the most important to moose.

2.1 Selection of Tree Species and Genotypes

In Fennoscandia, there has been a very strong focus on Scots pine (*Pinus sylvestris*) in forest regeneration on almost all site types, not only on xeric and fresh sites to which pine is naturally adapted, but also on more productive or moist sites typically dominated by Norway spruce (*Picea abies*). The focus on Scots pine has resulted in gradual shifts in species compositions and/or species replacements compared to the previous situation when natural forests prevailed.

Intentional changes have also occurred on another level. Tree genotypes showing higher volume production and other positive characteristics for the use of trees for timber and pulp have been favoured. Large herbivores like moose clearly discriminate among pine genotypes (Danell et al. 1990). It has not yet been evaluated which effect the selection of a more narrow set of genotypes may have had on the moose population. However, moose show a preference for more productive fenotypes over less productive fenotypes (Danell et al. 1991b).

2.2 Methods to Cultivate Seedlings

Different techniques have been introduced in order to produce vital seedlings at nurseries aimed for planting on clear-cuts. The herbivores sometimes differentiate among seedlings produced under different growing conditions. For example, containerised seedlings were more heavily browsed by large herbivores than bare-rooted seedlings (Bergström and Bergqvist 1999), indicating higher palatability of cultivated plants. Bergquist and Örlander (1997) found that frequency of browsing on spruce was higher on dark green seedlings (high nitrogen concentration) than on lightly green or yellowish seedlings (low nitrogen concentration).

2.3 Densities of Trees in the Stand

Typical seedling densities in plantation forestry are within the range 1500–2500 plants ha^{-1}, i.e. distances between planted conifer seedlings are about 2–2.5 m. Tree gaps are subsequently filled with self-regenerating pine, pubescent birch (*Betula pubescens*), either from seeds or root stumps. Also pendular birch (*Betula pendula*), willows (*Salix* spp.), aspen (*Populus tremula*) and rowan (*Sorbus aucuparia*) may enter the stand dependent on site conditions. Self-regenerating pine stands are characterised by a much higher density of plants (often 10000 seedlings ha^{-1} or more).

The distance between food items (i.e. trees) affects the foraging behaviour of moose. An experimental study by Vivås and Sæther (1987) showed that moose responded to small-scale variations in the available food supply. At high densities of trees, moose ate less on each tree and selected twigs of better quality but removed more browse biomass per plot than at low tree densities. These results are in accordance with the functional response of large ungulates like the moose, which predicts a decelerating rate of intake with increased food density (Renecker and Schwartz 1998). Many of the predictions from foraging theory have been confirmed in field surveys of forest stands. For example, Lyly and Saksa (1992) showed that the proportion of damaged pine saplings in regenerating clear-cuts in southern Finland decreased from 40 to 20% when stand density increased from 2000 to 11000 plants ha^{-1}. However, in very dense stands and in multi-layered stands susceptibility to browsing may increase. Heikkilä and Härkönen (1993) found that above a threshold value of 5000 stems ha^{-1} of birch, frequency of stem breakage of pine increased dramatically, and stem breakage frequency increased when the birches over-topped the pines with a factor of more than 1.6. One possible explanation to the latter observation could be that the stems become more slender and more easy to break by moose in very dense stands than in sparse stands.

Cleaning abruptly reduces tree density and may take place either early (a few years after regeneration), or just before the stand leaves the browsing sensitive height (around 3 m). In central Finland the total biomass consumed by moose following early cleaning was significantly higher in untreated stands than in cleaned stands (Härkönen et al. 1998). In contrast, no difference was found in consumption following a repeated cleaning five years later. At the stand level, cleaning may temporarily reduce loss due to ungulate browsing, but from a management perspective this effect probably is frequency-dependent, that is to say, it will level off with increasing proportion of cleaned stands.

Different browsing patterns and different levels of damage thus emerge from the distances between trees in a stand. The spatial distribution of food affects the harvesting pattern by the moose. In addition, trees growing in dense stands get different morphological and chemical attributes as compared to trees in sparse stands which, in turn, affects their palatability. For moose both food quantity and quality are important. Further, the density of trees as well as the productivity of the site influences the capacity of the trees to recover after browsing (Danell et al. 1991b, Heikkilä and Mikkonen 1992, Edenius et al. 1993, Hjältén et al. 1993a, Edenius et al. 1994).

2.4 Tree Species Composition in the Stand

It has been common practice to manage forests for single species stands, but in practice additional species occur. The selected species has often been Scots pine and moose have a medium preference for it. An interesting question is then how moose will respond if the second most common species in the stand is highly preferred, such as aspen. Will moose direct browsing to the more preferred species and leave Scots pine, or will the browsing on pine increase instead? What will then be the result if the second species has a lower preference? These questions are of general ecological interest (see e.g. Hjältén et al. (1993b) for discussions on theories), but are also highly relevant for future practices in forestry. In a field experiment Danell et al. (1991a) found that at the stand level total consumption was higher in pine + aspen stands than in pine + alder (*Alnus incana*; low preference) stands. There was also a tendency, albeit not significant, for a higher per capita consumption of pine in the pine + aspen stand type, indicating that species composition was of minor importance in food plant selection. Regulation of species composition may also affect the attractiveness of stands as feeding sites, as demonstrated by Hjeljord et al. (1990) for moose in southeast Norway during summer.

2.5 Fertilisation of Forest Stands

Boreal forests are generally nitrogen limited (Tamm 1991). Consistent with this, the application of nitrogen is a common silvicultural practice in Fennoscandia, and is employed to increase economic yield. So far, mature conifer stands have been the main target for fertilisation, and nitrogen is applied some years prior to the final harvest. The effect of treating mature forests in this way for moose feeding conditions has not yet been evaluated. Some noticeable effects on the field and bottom layers are most likely.

It is probable that nitrogen fertilisation will take place in young forest stands in the future. A large-scale field experiment (Ball et al. 2000) where young pine forests were treated with calcium-ammonium-nitrate (200 kg nitrogen ha^{-1}) showed that moose, as well as many other animal species, selected the fertilized plots.

2.6 Responses by Moose

Moose preferentially select dense pine stands as winter habitat, and pine forms the bulk of the winter diet over much of Fennoscandia (Bergström and Hjeljord 1987, Bergström et al. 1995, Shipley et al. 1998, Ball et al. 2001). High density of edible twigs seems to be one of the main factors underlying the selection for pine sapling stands. Moose aggregate at such sites during

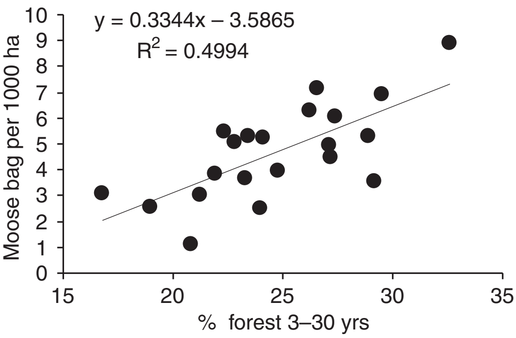

Fig. 2. The relation between number of moose culled and area of young forest in Sweden. Data based on the administrative delineation of counties (Strandgaard 1982).

late winter, frequently leading to high browsing intensity and extensive damage (Lavsund 1987). The activity patterns of moose, as well as home range use, vary with food availability. For example, Sæther and Andersen (1990) compared two moose populations in Norway and found that individual moose were less active, used smaller areas for feeding, and were less selective in diet selection where low quality food (pubescent birch) prevailed. However, responses by moose to habitat change may lag behind environmental changes; Andersen (1991) e.g., argued that altered migratory patterns in order to utilise better quality range may take generations in moose.

The human control of woody plant species composition already at the seedling stage and an array of measures to make the forest stands even-aged, homogenous and rapidly growing have favoured moose by increased habitat suitability and carrying capacity. Thus, the preference of Fennoscandian forestry for pine forests instead of forests dominated by spruce (which has almost no value as food for moose) has favoured the economic return from forestry, but also benefited moose. Further, most silvicultural efforts to achieve stands with vigorously growing trees have also been of positive value for moose, because moose as well as many other herbivores, in general, select such trees (see the 'plant vigour hypothesis'; Price 1991). The management practices of Fennoscandian forestry to a great part explain the high densities of moose in the Fennoscandian countries (Table 1; Fig. 2).

Table 2. Changes in the proportions (%) of different forest types (a) and landscape metrics (b) of a north Swedish coniferous forest landscape (170 km^2 large) during the last 100 yrs (Axelsson and Östlund 2001).

Year	1891	1914	1997
a)			
Even-aged young, 1–50 years	4	3	51
Even-aged, 50–250 years	1	25	44
Multi-aged	95	72	3
b)			
Mean patch size, ha		241	24
SD patch size, ha		1620	48
Mature and old forest share of landscape, %		71	20

3 Changes at the Landscape Level in Managed Forests

The boreal forest landscape in Fennoscandia has undergone dramatic changes in the type and intensity of disturbances during late Holocene (e.g. Lähde et al. 1991, Axelsson and Östlund 2000, Niklasson and Granström 2000). Clear-cutting has transformed the forest landscape into a patchwork of stands of different age classes after World War II (Axelsson 2001, Löfman and Kouki 2001). Characteristic for this managed landscape is a truncated size and age distribution of forest stands compared to when fire disturbance dominated (Table 2). The homogenisation of the landscape has increased habitat suitability and carrying capacity for large ungulates like the moose by increasing the effective habitat area in terms of young forest and edge zones (Table 3). The spatial pattern imprinted on the landscape by active forest management may also indirectly affect the pattern of habitat use by herbivores. For example, contrary to findings in North America (Hamilton et al. 1980), Andrén and Angelstam (1993) found no impact of stand size on patterns of browse utilisation on regenerating clear-cuts in Sweden. They attributed this to differences in moose habitat use at different population densities with higher densities in Sweden. There, subdominant individuals were forced to use inferior (far from cover) habitats. An alternative explanation may be that ungulates rarely encounter very

Table 3. Effects of changing disturbance regime on moose habitat (adapted from Baker 1995).

Cause	Effect on landscape measures	Effect on moose habitat
Smaller mean disturbance size	Shorter distance Smaller size More edges More patches	Increased proximity between forage and cover Landscape becomes more fine-grained Amount of suitable habitat increases A larger fraction of the landscape becomes suitable
Shorter mean disturbance intervals	Lower mean age Less old growth	Higher predictability of food resources (Reduced area of cover)

Table 4. Available browse (kg dry mass ha^{-1}) on regenerating clear-cuts in Fennoscandia. Mean and (SE). Persson et al. (2000) estimated average annual consumption per moose at 2700 kg, and Solbraa (1998) winter consumption at 1524 kg.

Country	Type of stand	Browse biomass	Note	Reference
Central Finland	Scots pine, 6 yr old	888 (291)	untreated	Härkönen et al. 1998
Central Finland	Scots pine, 6 yr old	644 (174)	cleaned	Härkönen et al. 1998
Central Finland	Scots pine, 11yr old	2268 (239)	cleaned once	Härkönen et al. 1998
Central Finland	Scots pine, 11yr old	2604 (141)	cleaned twice	Härkönen et al. 1998
Southern Norway	Scots pine, height 1.5 m	1000	lowland	Solbraa 1998
Southern Norway	Scots pine, height 2.5 m	5000–6000	lowland	Solbraa 1998

large stands in Fennoscandian managed forest landscape and perceive managed forest landscapes as fine-grained. In such a fine-grained landscape with many and relatively homogenous stands, the intensity in stand use will be more or less the same.

During the last century not only the structure but also the amount of available forest land has increased for moose. Due to drainage of wetlands and conversion of marginal grazing land into productive forests more habitats have been available for moose (Ahlén 1975, Hämet-Ahti 1983). Peatland forests are an important characteristic of moose winter ranges in parts of Fennoscandia (Heikkilä and Härkönen 1993)

For Fennoscandia, there are limited data available to compare browse production in managed and unmanaged forest landscapes. In Norway, average browse availability across different forest types in managed forest was estimated at 20–180 kg ha^{-1}, with a peak at 5000–6000 kg ha^{-1} in dense pine plantations at low altitudes (Solbraa 1998; Table 4). This illustrates the superiority of regenerating clear-cuts as a food source for moose in managed forests.

The results so far available for managed forests in Fennoscandia indicate that the availability of food seems to be a far more important factor for habitat selection and habitat use by moose than landscape structure.

4 Ungulates as “Disturbers” in Managed Forests

Even though herbivory may affect ecological processes at many different temporal scales, these effects will be less apparent in managed forests where regeneration pulses generated by silvicultural measures occur at short intervals relative to natural processes, e.g. tree species replacement by succession. Since large ungulates are an integral part of the forest ecosystem, it is doubtful whether they should be classified as “disturbers” or not, at least when they occur in more or less “natural” densities. However, disturbance can be defined in different ways: In broad terms it can be defined as “any discrete event that changes the vegetation and makes new growing space available”. In this respect large ungulates may clearly be classified as disturbers. However, if we add "disruption" to the definition of disturbance as did Pickett and White (1985), it is questionable whether ungulates qualify as disturbers in managed forest because man initiates forest regeneration and fully controls stand composition and development until final harvest.

Disruptive effects due to ungulates in managed forest are more likely to occur in natural regeneration areas. Engelmark (1993) reports a case study from northernmost Sweden where selective grazing on birch by reindeer induced a shift from spruce to pine in a spruce postfire succession. Birch cover is often a pre-requisite for establishment of spruce in harsh conditions; grazing under such conditions can alter the successional pathway from spruce to pine provided that there is a sufficient amount of pine seeds.

Ungulates may cause considerable economic losses in future timber quality yield, although most woody plants are resilient to this type of herbivory in terms of volume production and mortality, at least on more productive forest sites (Lavsund 1987, Edenius et al. 1993, Danell et al. 1994). Browsing primarily tends to retard stand development by arresting height growth (Hester et al. 2000). Few attempts have been made to model such time lag effects on stand development. In a simulation study, Näslund (1986) calculated a 2–9 year growth loss for birch and aspen exposed to intense moose browsing.

Moose typically display spatially aggregated patterns in resource use as they tend to exploit gaps and may also be creators of such gaps. The most prominent "disturbance" effect of moose on the stand scale may thus be to increase spatial heterogeneity. Westman (1958) and Heikkilä (1990) found the most intense moose browsing in plantations with openings. Such patchily distributed browsing obviously is at odds with economic forest management aiming at reducing spatial heterogeneity so as to maximise timber production.

Analysing moose browse supply from national forest inventory data in Sweden, Hörnberg (1995) recorded a significant reduction in the proportion of preferred species such as aspen and rowan between the periods 1969–72 and 1983–87, coinciding with the increase and peak in the moose population (Fig. 1). Angelstam et al. (2000) found that the cover of aspen, rowan and goat willow (*Salix caprea*) was strongly negatively related to moose density in 1000 km^2 large landscapes with variable tree species composition and moose density across Fennoscandia and Russian Karelia. Although different factors may contribute to the reported large-scale changes in browse species composition over time, these observations indicate that high population densities of large ungulates may have region-wide impacts on the distribution of selected plants.

We conclude that the most prominent effects of large ungulate herbivory at the landscape scale is the suppression and/or redistribution of preferred trees such as aspen and rowan. For example, Ericsson et al. (2001) found that utilization of aspen by moose was related to landscape composition, with more intense browsing occurring in aspens stands located in young forest than in old forest. On the stand level one important result of moose "disturbance" is the increased spatial heterogeneity, or gaps. On the tree level moose browsing creates substrate types (e.g. dead and dying trees) that would be less frequent in forests without moose or with low densities of this large herbivore.

5 Management Implications

Today there is a strong momentum towards multiple use forest management. Measures to achieve this include attaining larger shares of natural regeneration and deciduous trees, and green tree retention (e.g. Forest Stewardship Council, http//:www.fsc-sweden.org; Pan-European Forest Certification, http//:www.pefc.se), in order to incorporate elements of natural forest structures and dynamics in managed forest (see also Larsson and Danell 2001) . These actions will have both direct and indirect consequences for the ungulates. For example, the food resources for moose at the stand scale are likely to be affected immediately; moose will face increased shares of preferred deciduous trees at the stand scale, and accesses to food may increase as a result of improved cover conditions provided by residual tree patches or buffer zones. Effects of multiple forest management on the landscape scale will be less readily apparent, as the imprint on landscape spatial patterns by the previous forestry paradigm will continue to affect ungulate-woody plant interactions for several decades. However, there may be a clear risk that actions to promote biodiversity by adhering to natural disturbance principles, such as favouring of highly preferred browse species, may be at stake when there are high population densities of ungulates.

Are the goals to achieve more elements of the structure and dynamics of natural forests in the managed forest landscape compatible with high population densities of ungulates? Large ungulates are not only a threat to biodiversity by suppressing the abundance and/or re-distributing preferred deciduous trees at the landscape scale. They are also facilitators of biodiversity at the stand level by increasing spatial heterogeneity, and on the tree level they increase the abundance of special substrates (e.g. dead and dying trees) which are important for many species of invertebrates and plants. A pre-requisite to balance the opposing roles of ungulates is to have good tools for monitoring and management of both woody plant and ungulate populations. Robust and compatible monitoring systems are urgently needed. In Sweden, for example, the total standing wood volume has increased steadily since the first National Forest Inventory in the 1920's. However, the design of inventory programmes, inconsistency and changes in methodology over time makes it difficult, and sometimes even impossible to reconstruct the structural development of the Swedish forests and to follow long-term effects of browsing in a consistent way. We therefore lack reliable data from the past for evaluation of the present situation to be used to project the future. In order to rectify this problem, consistent and harmonised monitoring programmes within and among countries need to be developed and implemented.

We also need to integrate the population monitoring of moose with forestry and biodiversity management. This will shorten the time between population survey and management actions. With an integrated approach that allows one to predict population dynamics of large ungulates, forestry and biodiversity management can be pro-active instead of re-active to high moose densities, for example. A pro-active and integrated management system is crucially important in a basically predator-free environment like Fennoscandia, where the population densities of large ungulates are strongly influenced by stochastic environmental variation (Sæther et al. 1996). In such environments density-dependent population regulation mechanisms are relaxed (Sæther 1997), making simple deterministic population growth models less useful. Different indicator systems for setting measurable goals for ungulate numbers have been proposed, such as the browsing intensity in sapling stands (National Board of Forestry, Sweden; http/:www.svo.se/fakta/invent/algbete), and the moose-forage ratio at the landscape scale (Angelstam et al. 2000). It will be important to make such programmes accountable for the dynamic nature of ungulate populations by integrating them with population monitoring of large ungulates (e.g. Ericsson and Wallin 1999, Solberg and Sæther 1999). However, to acknowledge the complexity in ungulate-forest systems means that we have to accept that not all "disturbance" can be foreseen, nor controlled.

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