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Determinants of winter browsing intensity on young Scots pine (Pinus sylvestris) by moose (Alces alces) across a bio-geographical gradient in Sweden

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Avgörande faktorer för intensiteten av vinterbete utav älg (Alces alces) på ung tall (Pinus sylvestris) längs en bio-geografisk gradient i Sverige

Lenka Vyšínová

Keywords: Moose, Alces alces, browsing, Scots pine, Pinus sylvestris, spatial scale, determinants, forage cover, tree species composition, winter

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Abstract

Intensive moose *(Alces alces)* browsing pressure has a large impact on ecosystems as well as economics of forestry companies. Moose winter browsing pressure on young Scots pine *(Pinus sylvestris)* is affected by a range of factors and I modelled effects of such factors across a bio-geographical gradient in Sweden. The tested factors were: density of moose, roe deer (*Capreolus capreolus*), red deer *(Cervus elaphus),* and fallow deer *(Dama dama),* forage availability, height of surveyed tree, thinning, pre-commercial thinning, clear-cutting, dominating forest, tree density, habitat productivity, number of days with snow cover, distance to road, and distance to settlements. The analyses were carried out at three spatial scales – plot, tract, and landscape scale. The data was extracted from a field survey and a digitalized forest stand database of a forestry company.

At the plot scale, in the minimal adequate model, explaining browsing pressure on pine, the factors study area, moose density, dominating forest type and height of surveyed pines were significant. At the tract scale, the factors study area, moose density and dominating forest were significant. At the landscape scale, the proportion of pine in the forest was negatively related to browsing. Nosignificant relationships between browsing pressure and the other factors were found. These finding suggest that dominating type of the forest is the most general factor affecting browsing pressure at all spatial scales. The browsing pressure was nearly significantly higher in the mixed coniferous forest than in the other types of the forest at the tract spatial scale. The moose density is significant at smaller scales, in contrast to the largest scale. This result supports the idea that the browsing pressure at larger scales is affected by other factors than moose density.

I. INTRODUCTION

1.1. Moose in Sweden

Moose *(Alces alces)* is an important element of Scandinavia, from biological, ecological, economical and cultural points of view.
In Sweden, there does not exist any exact estimation of the moose population on the national level. The numbers can be estimated from the moose hunting data where approximately 30% of the whole winter population is harvested every year (Danell 2002). During the hunting season 2008-2009, the moose harvest count was 83 554 individuals, indicating that the moose population contains around 270 000 individuals. The trend of the population development has been decreasing since the 1980s, when the moose harvest count was 174 000 individuals, with an estimated population of 522 000 individuals (Viltdata 2008). Trends in moose density are mainly affected by forestry management, predators, and hunting pressure (Ball 1999). However, in Sweden the main cause of moose mortality is hunting (Ball et al. 1999).
Although the number of moose is decreasing, relatively high moose population is the center of discussion among various stakeholders.

Forestry companies and landowners often consider the moose populations too dense, since it is indisputably the main source of browsing pressure on young Scots pine *(Pinus sylvestris).* Their opinion toward the moose population is summarized by the Swedish Forest Agency: "Dense game populations lead to severe damage, especially in pine and hardwood plantations and young forests. The browsing damages caused by local moose populations are intensive at some places, and in excess of what can be accepted by forestry" (Skogsstyrelsen 2003). Due to the moose browsing pressure which occur mainly in winter on economically valuable trees, such as Scots pine, the income from forestry is lowered and costs for landowners increased (Storaas et al. 2001, Ball and Dahlgren 2002, Gundersen et al. 2004). High proportion of pine in moose diet is on the one hand due to the lack of other food components, such as bilberry *(Vaccinium myrtillus)* and lingonberry *(Vaccinium vitis-idaea)* shrub in winter (Cederlund et al. 1980, Månsson 2009), and on the other hand due to the highest availability of Scots pine among other tree species in winter (Shipley et al. 1998).

High moose densities do not cause only economical cost for forestry, but also economical benefit in form of "hunting industry" (Gundersen et al. 2004). Unfortunately, these benefits and costs come to different groups of people, mainly in areas where moose home range covers large areas. Thus, while some landowners benefit from hunting during autumn, other landowners, owning land within the moose winter range, undergo large forest damages (Storaas et al. 2001). The opinion and principles of **Swedish hunters** are summarized by the following: "Game is a renewable natural resource that shall be cared for and utilized in a wise and long-term manner. The balance between the game populations and the conditions offered by the land is an important principle. Consideration shall be taken not only to the interests of the hunters and hunting but also to the interest of forestry and agriculture together with other sectors of society. Wide cooperation between hunters and foremost landowners is essential" (Swedish Hunter's Association 2003).

In this paper I will mainly address the browsing pressure on the economically important Scots pine. However, it is also relevant to note the impact of browsing pressure on **ecosystems**. Moose have a large and long-lasting impact on ecosystems and influence richness of tree levels in boreal forest (Persson et al. 2005, Suominen et al. 2008). Under very high moose densities (2-4 individuals km^{-2}), impact on preferred tree species is dramatic (Andrén and Angelstam 1993). Few individuals of such a species have a chance to grow into natural tree form and competition between deciduous and coniferous trees is reduced in favour of coniferous trees. Plants also alter geometry of their canopies due to past browsing (Jager et al. 2009) and species depending on adult deciduous trees, such as some birds and mammals, may be negatively affected (Andrén and Angelstam 1993, Abaturov and Smirnov 2002, Herder et al. 2006). Also the abundance of some plants and insect decreases with increasing moose density. This is caused directly and indirectly by urination, defecation, feeding and trampling due to the alteration of soil and plants (Persson et al. 2005) and a decrease in underground respiration rates (Persson et al. 2009). The investigation of Snyder and Janke (1976) gave an overview of what has happened with ecosystem after 60 years of moose browsing. They compared closed ecosystems (islands), where moose was introduced, with ecosystems without moose. Generally, moose browsing results in forests that are more open, more even aged, and richer in low ground cover. Despite these facts, “most of woody plants eaten by moose should sustain browsing pressure at moose densities common in most areas in Sweden“(Persson et al. 2005).

1.2 Spatial scale

The impact of moose on ecosystems and landscape has been reflected in many studies. However, quite often it is not clearly defined at which scale the study has been carried out and this causes considerable differences in the results. Browsing pattern is scale-dependent (Cassing et al. 2006, Månsson 2007, Angelstam et al. 2000, Bergström et al. 1995, Ball et al. 2000, Edenius 1993), various factors affect foraging differently at different scales (Senft 1987). This can cause problems when generalizing results; i.e. results valid at one spatial scale may not be applicable at another. Formerly most studies of moose browsing patterns have considered plant scales but lately the stand and landscape scales have also been the subject of studies (Månsson et al. 2007, Månsson 2009). Moose density, forage availability, weather conditions and landscape patterns are suggested to affect foraging patterns at all spatial scales (Cassing et al. 2006). The need for more spatial scale study is closely reflected by Lundberg et al. (1990) who found that the tree selection should be considered as a patch use problem rather than particulate food item.

1.3. Factors affecting moose browsing pressure

In my study, I will focus mainly on moose winter browsing pressure. The browsing pressure is among others things affected by moose browsing ecology during winter which can be described as following:

- Moose often concentrate near young forest stands (Gundersen et al. 2004).
- Volume of biomass is a more important factor in diet selection than nutrient content (Edenius 1993, Senft et al. 1987, Lundberg et al. 1990).
- Preferred high energetic shrub such as bilberry and lingonberry is covered by snow (Cairns 1980, Cederlund et al. 1980, Månsson 2009).
- Scots pine forms the main volume of diet and consists mainly of branch and leader browsing (Cederlund et al. 1980).
- In central Sweden, the diet composition was 60% pine, 30% birch (*Betula pendula*), and 10% other deciduous trees (Cederlund et al. 1980).
- Moose population north of 60ºN is partially or fully migratory, whereas southern populations are mostly non-migratory (Sweanor and Sandegren 1988, Ball et al. 2001, Ball and Dahlgren 2002).
- Average winter home range of moose varies from 2.2 to 14km^2 (Cassing et al. 2006).
- Average distance between seasonal ranges of migrant moose in northern Sweden is 22km (Ball et al. 2001).
- Estimated daily food requirement of fresh mass is 10kg (Persson et al. 2000).
- Branches and leaves between 0.5 and 3m are generally considered accessible for moose, snow cover taken into consideration (Hörnberg 2001a, Gundersen et al. 2004).
- Most pressure on trees occurs in the winter (Ball and Dahlgren 2002).

The differences in climate, forage cover, habitat patterns, moose density and period of growth have been suggested as the most important factors affecting moose browsing pressure (Hörnberg 2001b).
Relation between **moose density** and browsing pressure has been show to be important at all spatial scales, it is most obvious at the small scale level (Bergström et al. 1995) and with increasing scale the importance decreases (Månsson 2007). Under high moose density, young forest stands are heavily browsed (Andrén and Angelstam 1993, Angelstam et al. 2000). The isodar theory of habitat selection

says that the ratio between moose overall density and habitat density changes as the species populations size change. With decreasing overall population, the less preferred habitats are left and more preferred habitats are still browsed with the same pressure (Morris 1987). Thus, regulation of moose population does not necessarily lead to a decrease of browsing pressure on preferred forest stands. Nevertheless, Månsson (2009) found a proportional relationship between overall density and habitat density.

Tree species composition has been suggested to affect browsing on Scots pine (Angelstam et al. 2000). The importance of tree species composition is related with selectivity of moose for different tree species, which has been examined in several studies (Bergström et al. 1995, Shipley et al. 1998, Hörnberg 2001a, Månsson 2007). Although the results are not uniform, generally, rowan *(Sorbus aucuparia)*, aspen *(Populus tremula)* and willow (*Salix spp*.) are preferred over coniferous trees, and Norway spruce (*Picea abies*), lodgepole pine (*Pinus contorta*) and downy birch *(Betula pubescens)* are the least selected. Silver birch is preferred as much as pine. Although Scots pine is not on the top of moose preferences, it constitutes bulk of consumed forage wintertime. For example, in a study in northern Sweden, Shipley et al. (1998) found hat the winter moose diet consisted of 75% Scots pine and willow, with the remaining proportion equally divided among other available deciduous trees and common juniper (Juniperus communis).

Forage availability and its changes can strongly influence winter habitat-space use (Hansen 2009) and herbivores generally prefer habitats with high forage availability within the landscapes (Bergström and Hjeljord 1987). The plant biomass explains a significant amount of the variation in consumption by moose on Scots pine (Edenius 1993). There is generally a relation between forage availability and browsing pressure. At smaller spatial scales, plots with high forage availability are underused compared to plots with low forage availability, i.e. the total consumption increases slower than forage availability, thus the proportion of browsed shoots increases as abundance of browse species declines (Shipley et al. 1998, Månsson 2007). At larger scales the consumption of forage increases proportionally with increasing forage availability (Senft et al. 1987, Ball and Dahlgren 2002). Bergström et al. (1995) even claim that the browsing pressure on Scots pine is more influenced by abundance of pine than by moose density at large spatial scales and in areas with low amounts of pine. In contrast, Weixelman et al. (1998) suggests that percent used of a browse species is not significantly related to its availability.

Snow conditions affect browsing pressure on young pine forest in winter. The number of days when land is covered with snow and, partially, the snow depth affect forage availability. This is mainly due to a lack of high energetic forage such as bilberry and heather *(Calluna vulgaris)* growing in old forest and mire, which are covered by snow during winter (Cederlund at al. 1980, Nordengren et al. 2003, Månsson 2009). Snow density, hardness and profile laminations, air temperature, snow depth, and latitude affect snow metamorphisms, which in turn affects the movement of moose over the landscape, habitat selection and may incite migration (Ball et al. 2001, Ball and Lundmark 2008). This may influence browsing pattern indirectly.

Distance to roads influence the use of young pine stands by moose. Proximity to a highway is related to increase of browsing. Animals tend to avoid roads and its presence causes accumulation of moose around roads and consequently increased browsing on pine, mainly within 3 km of the road. Pines further from the road have decreasing probability to be browsed (Ball and Dahlgren 2002).

Human activities can strongly affect moose behavior (Ball et al. 1999). Moose tends to avoid densely populated areas (Schönfeld 2009). To the contrary, it has been shown that proximity of **human settlements** and infrastructure operates for mammals like a cover shield against carnivores, which would make those areas more attractive for moose (Berger 2007).

Forestry management actions have been reported to affect moose behaviour, and browsing pressure. The effect of **pre-commercial thinning** has been discussed in several studies (Heikkilä and Härkönen 1996, Ball and Dahlgren 2002, Cole et al. 2010) and the effect of **thinning** has been investigated by Månsson et al. (2010). They suggest that forestry actions influence mainly forage availability and habitat selection. Also **clear-cutting** has been reported as having negative relationship to moose densities. At the level of habitat range, moose prefer to select areas with less clear-cut, mire and field (Ball et al. 2001).

Habitat productivity has been shown to affect twig biomass consumption (Danell et al. 1991, Ball and Dahlgren 2002). The most productive habitats underwent larger browsing pressure.

Impact of tree density has been tested by Andrén and Angelstam (1993) who suggested that variation in browsing pressure on pine is mainly caused by differences between forest stands, i. e. by density

of young Scots pine in the stands, where the proportion of browsing decreases with increasing density.
Occurrence of **other large herbivores**, such as roe deer (*Capreolus capreolus*), red deer *(Cervus elaphus),* and fallow deer *(Dama dama)* has significant effect on the vegetative structure and composition of the forest (Bergquist et al. 1999, Sage et al. 2004, Götmark, F. 2005).

Because moose browsing pressure on Scots pine causes large economic loss for the forestry industry, it is important to investigate the effect of individual factors on moose browsing behaviour with intent to suggest steps for how to decrease the browsing pressure, eventually concentrate or relocate it to another place.
Although many studies have been carried out with intention to describe moose browsing behaviour, all assumed factors have not been investigated in one model. This can give a general overview of which factors are most important when investigating interactions between moose and what it is browsing.

1.4. Aim

The aim of this study is to describe and analyze the relationships between winter browsing pressure on young Scots pine and potential explanatory factors, such as moose density, forage availability, tree species composition, age of the forest, distances to road and settlements, forestry actions and snow conditions with regard to the bio-geographical gradient in Sweden and three different spatial scales. The following particular questions were asked:

- How do forestry actions and tree species composition change across the bio-geographical gradient and how do they influence the browsing pressure on young Scots pine?

- Which factors are significantly associated with the level of browsing pressure at different spatial scales?

To answer these questions I analyzed data from the forestry stand database of the forestry company Sveaskog and the inventory studies carried out by researchers at the Forestry Faculty at SLU in cooperation with Skogforsk.

II. METHODS

2.1. Study areas

The data was collected within the project "Viltbete och Foderproduction" carried out as a cooperation between SLU, Sveaskog and Skogforsk. I analyzed the data collected in the spring of 2009, i.e. reflecting the browsing and habitat use situation for the winter 2008-2009.. Five study areas were inventoried: Misterhult, Malingsbo, Furudal, Sorsele and Råneå (see Fig. 1). These areas were chosen to represent different bio-geographical gradient in Sweden. ***Misterhult*** is situated in the hemiboreal vegetation zone. The elevation varies between 0 – 80m. It is a densely populated area with a dense transportation network and settlements, characterized by coastal climate. Red deer, roe deer, fallow deer, and wild boar (*Sus scrofa*) occur here. ***Malingsbo*** is situated on the edge of the south boreal and middle boreal vegetation zone. The elevation varies between 160 – 340 m. A wolf *(Canis lupus)* territory is present in this area. ***Furudal*** is situated on the edge of the middle boreal and north-boreal vegetation zones. The elevation varies between 150 – 500m. It is characterized by a large population of bear (*Ursus arctos*). ***Sorsele*** is situated in the north boreal vegetation zone. The elevation varies between 300 – 650m. It is an inland area characterized by low temperatures and deep snow cover. During the winter, the migrating moose population move to Sorsele surroundings from the mountain range. Like in Furudal, it is affected by a bear population. ***Råneå*** is the northernmost area, situated on the edge between the middle boreal and north boreal vegetation zone. The elevation varies between 20 and 280m. The climate is more moderate than in Sorsele because of the sea influence. Also here the bear population occurs to a large extent. For more detailed information about the study areas see Appendix I.

2.2. Experimental design

In every study area two sub-areas were set up, which are considered together in the present study. There were ca ***70 survey tracts defined within each study area***, placed at intervals of 1000 m, except Misterhult (500 m) and Furudal (the tracts were adjacent). The tracts were 1000 x1000 m, except Misterhult (500 x 500 m). Each tract consists of ***16 plots*** located along sides with intervals of 200 m (100m in Misterhult) (see Fig. 1). Each plot was a circle of 100 m^2 with a radius of 5.64m. Some tracts could not be inventoried, as well as some plots within the tracts, due to landscape obstacles (e.g. lake).

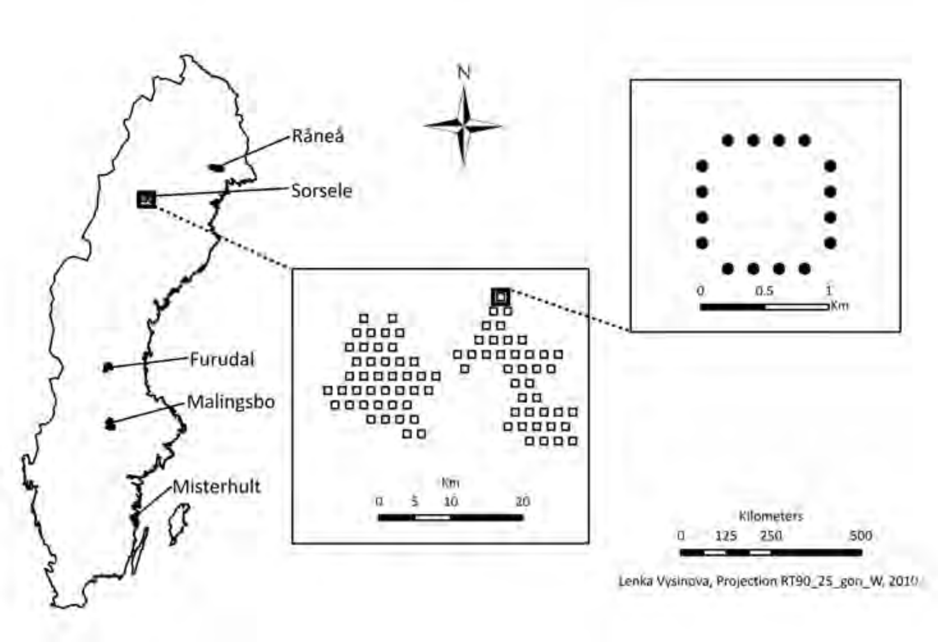


Figure 1. Location of the study areas in Sweden, design of the tracts in the study area Sorsele and position of plots within one of the tracts.

2.3. *Spatial analysis and data sources*

I used software ArcGIS 9.3. (Mitchell 1999, Scally 2006, Gorr 2007) to combine and analyze the data from 3 different datasets – ***forest stand database*** and forest management database (Sveaskog), ***inventory of browsing pressure and moose pellets*** (project "Viltbete och Foderproduktion", unpubl.) and ***inventory of forage cover*** and others (project "Balanserad Älgstam", Bergström et al. 1995). The main part of the analysis was based on the forest stand database of Sveaskog (Swedish state forestry company). This comprehensive database contains detailed information about forest type, tree species composition, tree density, habitat productivity, extent of forest stands and more. In addition, I also analyzed the data from the forest management database, which included information about thinning, pre-commercial thinning and clear-cutting.

2.4. *Factors included in modelling*

2.4.1. Response variable

Browsing pressure

In this study, the browsing pressure was expressed as a percentage of browsed shoots. Within each plot, the browsing on the one young pine closest to the center and with the maximal distance of 5.64 m from the plot center was measured. Only pines within the height 0.3 – 3 m were taken into account. The number of shoots from the previous season was counted, as well as the number of such shoots which were browsed. Note hence, that in this paper the commonly used expression ***"browsing pressure" means percentage of previous year's shoots browsed on one young Scots pine between 0.3 and 3 m in height per plot.***

2.4.2. Explanatory variables

The explanatory variables were chosen in respect to the previous studies, hence for background see above in the Introduction. Although some of the variables are strongly correlated, e.g. forage availability and forest site index, I tested all accessible factors in a one-factor model because some of them can express the browsing pressure better than others. However, I did not include highly correlated variables to the maximal model at the same time (see below in Statistics and Modelling).

Moose index - pellet counting

Within each plot with a radius of 5.64 m, the number of moose pellet groups was counted. Only the "true groups" containing more than 20 pellets were included. This method reliably account for an index of game density (Neff 1968). Note, that ***"moose index" further in this paper means either number of pellet groups per plot, or average of pellet groups per tract or per area.*** Only fresh droppings which were estimated to have been produced after the previous growing season were considered. Hence, the moose index represents the actual winter situation.

Dominating forest type

Dominating forest type represents the tree species composition and it was estimated from the forest stand database. The dominating forest was the type of the forest which covered the largest area of the plot or the tract buffer zone. The forest types were classified according to the Riksskogstaxeringen (2006) as following:

- Pine forest - consists of 70% or more of pine
- Spruce forest - consists of 70% or more of spruce
- Mixed deciduous forest - consists of 31-69% of deciduous tree species
- Mixed coniferous forest - consist of 70% or more of different coniferous tree species
- Deciduous forest - consist of 70% or more of deciduous trees or 50% and more of noble deciduous trees such as elm *(Ulmus spp.),* ash (*Fraxinus excelsior*), European beech *(Fagus sylvatica*), English oak *(Quercus robur)* etc.

- No forest - includes other types of land, such as mire, mountains and other types of land (see Riksskogstaxeringen 2006)

At the landscape scale, the factor dominating forest is supplemented by the % representation of pine, spruce, and birch. It was not possible to use the factor dominating forest at that scale, since pine forest dominates all areas.

Forage cover

I estimated the forage cover of all forest stands in Sveaskog's forest stand database on the basis of data obtained during the study Balanserad Älgstam, (Bergström 1995). During this study, 38 study areas (further called "study sites") throughout Sweden have been inventoried. I used the information about forage cover, however other characteristics were measured. The forage cover was estimated so that all forage in the browsing zone was projected to the ground surface and was assessed depending on the proportional cover on the sample plot. Only living branches within the browsing zone (0.25 – 3 m), i. e. above normal snow level and within reach for moose above the ground, were considered in the calculation (Hörnberg 2001b). This measure of forage cover has been shown to explain 60-75% of actual forage availability (Bergström et al. 1995). The tree species taken into account were the following: rowan, sallow/willow, aspen, European beech, English oak, birch (*Betula* spp.), Scots pine and lodgepole pine. I used data from 25 study sites, which are situated within 260 km from the study areas of Misterhult, Malingsbo, Furudal, Sorsele, and Råneå and belong to the same vegetation zone and if possible to the same climate type. I analyzed data from the following study sites: Misterhult, B1, D1, E1, H1, H2; Malingsbo, T1, R1, F1, E2, W3, W1, W4, X3, X2; Furudal, T1, W3, W1, W4, X3, X2, Y1, Y3, Z2, Z3, Z4. I analyzed the same data for the most northern situated study areas Sorsele and Råneå (study sites BD6, BD7, BD3, BD4, BD5, and AC2) (see Fig. 2).

Forage cover is dependent on factors such as longitude and latitude (location), land type, type of forest and forest site productivity index (Bergström et al. 1995). I analyzed the effect of these factors on forage cover (Kruskal-Wallis test, 1-factor model) to find out which factors should be included when estimating forage cover. The factors found to be significant ($P<0.05$) are location, land type, forest type, age group, and site productivity index.

To estimate the forage cover I created 6-digits codes (see Tab. 1, Rikskogstaxeringen, SLU 2003) based on location, land type, forest type and age group. From the database "Balanserad Älgstam" I calculated average value of forage cover for each code (see Tab. 1. and Appendix II.). I did not take into account the productivity index since the number of code levels would increase from the current 260 (see Appendix II) to 6240 (taking into account 24 different levels of site productivity index). There would not have been enough data to calculate statistically reliable average of forage cover for each of those many code levels. Thus, each stand got assigned the value of forage cover which corresponds to its characteristics (Appendix II).

Lenka Vysinova, Projection RT90_25_gon_W; 2010

Figure 2. Location of weather stations and study areas inventoried in the study "Balanserad Älgstam".
The data from these study areas were used to calculate forage cover.

Table 1. Code connecting the data from the database "Balanserad Älgstam 1993" and "Forest stand database". Average forage was dependent on location, land type, forest type and age of forest. These factors were available in both databases.

1st digit - Location		2nd digit - Land type		3rd digit - Forest type		4th -6th digit - Age group	
Code	Comment	Code	Comment	Code	Comment	Code	Comment
M	Misterhult	1	Forest	1	Pine	0	no forest
L	Malingsbo	2	Mires	2	Spruce	5	1 - 5 years old forest
F	Furudal	3	Hills	3	Mixed conifer.	10	6-10 years old forest
S	Sorsele and Råneå	4	Pastures and fields	4	Mixed decid.	15	11-15 years old forest
		5	Water	5	Deciduous	…	…
		6	Other	6	Not forest	200	120 – 200 years old forest

Snow cover

The snow cover data was obtained from the Swedish Meteorological and Hydrological Institute (SMHI). The number of days with snow cover in every study area was estimated as an average of values obtained from nearby weather stations during the winter season 2008-2009 (see Fig. 2). Depth of snow influences mainly the food availability of field layer of dwarf shrub, such as bilberry and lingonberry (Cederlund et al. 1980, Nordengren et al. 2003, Månsson 2009). It is difficult to predict at which snow depth the dwarf shrub is totally covered. Thus, I counted the number of days with a snow cover >10cm, respectively >30 cm. Movement of moose is restricted at depths above 70 – 90 cm (Pole and Stuart-Smith 2005).Thus, I also tested the effect of snow cover >70cm. For the study area Misterhult, data from weather stations Målilla and Oskarshamn were averaged, for Malingsbo, data from Ställdalen, Kloten, Söderbärke, and Norberg were averaged, for Furudal, data from Skattungbyn, Lillhamra, Lobonäs, and Los were averaged, for Sorsele data from Sorsele weather station were used and for Råneå data from Sörbyn, Talljärv, and Orbyn were averaged.

Settlements and roads

I manually digitalized each settlement (each building) situated within the extents of the study areas. I used a topographic raster map of Sweden as a background. From the roads shape file I selected the roads wider than 5 m and with a road number E4-E99 or with a road number 100-499. Consequently I calculated the closest distances of each plot to the settlement or the road.

Forest management

For the forestry actions I considered pre-commercial thinning, thinning, and clear-cutting. The effect of pre-commercial thinning is obvious even after 7 years, when two-thirds of the conifer cover recovers (Cole et al. 2010) and the moose density in thinned areas is higher even after 5 years after the thinning (McLaren 2000). On the base of expected longer-lasting effects of thinning I used the data of the forestry actions performed between 1.1.2000 until 31.12.2008. The factors were calculated as proportion of individual forestry actions on the forest area within the plot, tract, or area buffer.

Tree density, forest site index

Tree density and forest site index were obtained on the base of spatial analysis of forest stand database in ArcGIS 9.3. The levels of forest site index and trees density followed the classification of Riksskogstaxeringen (2006). Tree density means number of trees per hectare. Forest site index indicates how high the tree will be at the certain forest stand in 100 years (50 years for birch and Lodgepole pine). It represents the quality of the forest stand.

Other herbivore species index – pellet counting

Within each plot with a radius of 5.64 m, the number of red deer pellet groups was counted and within each plot of radius 1.78 m, the numbers of roe deer and fallow deer pellet groups were counted. These species occurred to a larger extent only in the study area Misterhult. Note, that "red deer index", "roe deer index" and "fallow deer index" further in this paper means either number of pellet groups per plot, or average of pellet groups per tract, or per area.

2.5. Spatial scale

I studied browsing pressure at three different spatial scales – plot scale, tract scale and landscape scale. I had as my objective to distinguish which factors affect browsing pressure only at a certain scale and which of them are more general.

At the plot scale, the values of browsing pressure, moose index and height of trees were obtained from direct observations on plots during the inventory. I excluded plots where the data was incomplete. I used buffer zone 50 m around the center of each plot to calculate % of forage cover of the buffer zone extent, type of dominating forest, percentage of clear-cutting, thinning, and pre-commercial thinning of the forest area. I removed the buffers which did not totally overlap the forest stand database. The distance to roads and settlements was calculated from the center of the plot.

At the tract scale, I obtained the values of browsing pressure, moose index, height of trees, distances to settlements and roads as an average of values measured on plots situated within the tracts. The tracts where at least 9 of the 16 plots contained inventory data were included in the analysis. I created a buffer zone around each tract, with a width of 500 m (in Misterhult 250m) preventing the buffers from overlapping. The buffer zones which overlaid at least 50% of the forest stand database were included in further analysis. In Furudal, the maximum number of plots was 32 instead 16 due to a different study design. This design increases the power of statistical analyses since the standard error of browsing pressure and moose index decreases. Within each buffer zone I calculated the percent of forage cover and the percent of forestry actions in the forest area.

At the landscape scale, the values of browsing pressure and moose index were calculated as averages of values measured on plots situated within each study area. I used a 1 km buffer zone around the boarder of the study area (i. e. around the outer sides of the outer tracts) to calculate the percentage of forage cover of the whole area, as well as the percentage of forestry actions, tree density and forest site index of the forest area.

2.6. Statistics and modelling

For statistical analyses I used the software R. I used the following model selection procedure:

1. Controlling whether error terms have constant variance (teroscedasticity) and what is the type of errors distribution. The variances were not constant (graphical method) and the errors were not normally distributed (quantile-quantile plot, Shapiro-Wilk test). Thus, I rejected use of parametric testing.

2. Type of response variable. The response variable was a proportion (percentage of browsed shoots) thus strictly bounded (between 0 and 1). In this case, generalized linear model with binomial errors and logit link was the convenient type of model.

3. *Overdispersion*. The model using binomial errors is badly overdispersed (either the errors of distribution are not binomial or I did not include some important factor). To reflect this fact I refit the model by using quasi-binomial errors to specify a more appropriate variance function, where the dispersion parameter is not fixed at one.

At the plot and tract scale, I based the modelling on selection of a minimal adequate model from a more complex model, using stepwise model simplification. First I tested individually each factor which may be of interest according to the literature review (one-factor model). I selected factors with a P <0.25 for building models with multiple factors (Hosmer and Lemeshow 2000). Consequently I tested correlation (Spearman correlation test) between factors possibly included in the model. I avoided including strongly correlated factors (correlation coefficient >0.7) in the same model. Then

I fitted the maximal model and continued with a model simplification so that I removed the factors and the interaction terms which did not cause a significant increase in deviance by using ANOVA and F test with empirical scale parameter. I continued until I obtained a minimal adequate model with only significant terms. At the landscape scale, I tested each factor only by one-factor modelling since the number of samples, i. e. 5 study areas, did not allow including more factors in the model (Hastie and Pregibon 1992, Crawley 2007, Crawley 2005). There are some disadvantages when using quasi-binomial errors. For instance it is not possible to calculate Akaike´s Information Criterion (AIC), because the log-likelihood value cannot be obtained. Also the coefficient of determination, which expresses how much variation is explained by the model, cannot be calculated for model with quasi-binomial errors.

III. RESULTS

3.1. Descriptive statistics

In total, there were 4465 plots which met the requirements to be included in the analysis (see Methods). Of these there was no pine identified in 2430 of the plots, in 1705 of the plots the pine was not browsed and of the remaining 330 plots only 288 had more than 5 % of the pine shoots browsed.

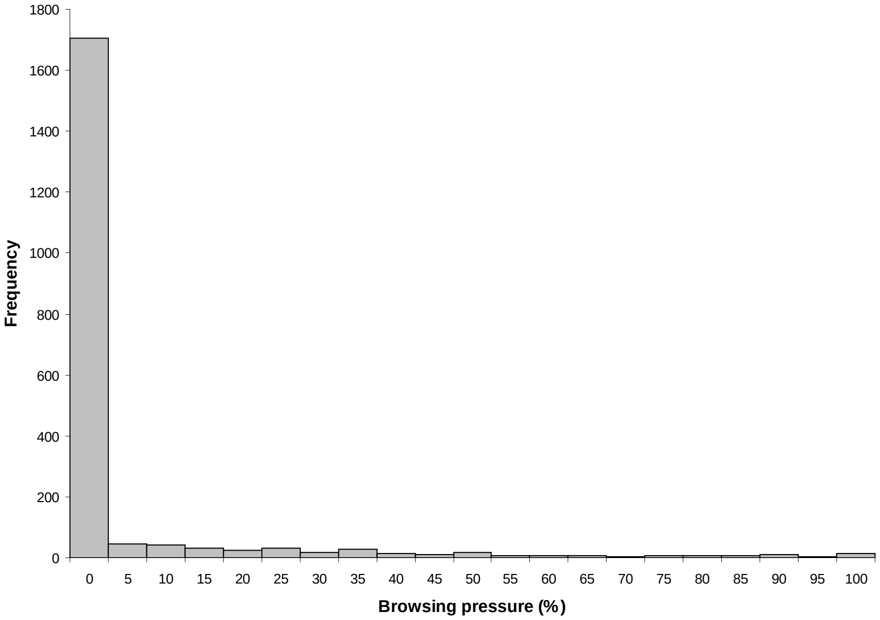


Figure 3. Frequency of browsed shoots. The majority of all pines did not undergo any browsing. The number under each bar represents the upper limit of the interval.

Browsing pressure as well as forage cover differed among the study areas (see Fig 4.). The highest browsing pressure was registered in Misterhult, followed by Sorsele. The lowest browsing pressure was registered in Furudal. The browsing pressure was significantly lower in Furudal compared to the other areas (Tukey test, P<0.05 for every comparison with other study areas).

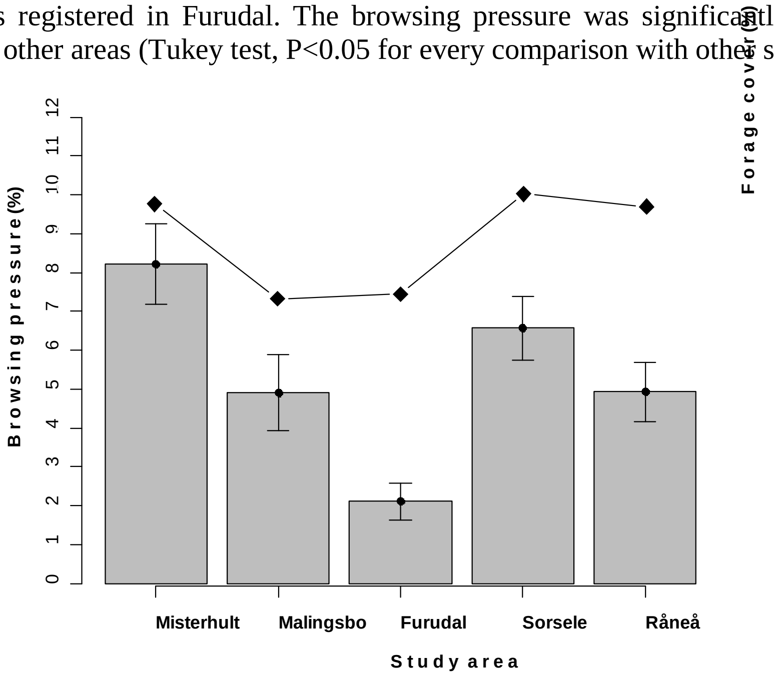


Figure 4. Browsing pressure (mean ± SE) and forage cover in different study areas. High browsing pressure in Misterhult and Sorsele corresponds with high forage cover.

At the landscape scale the positive relationship between moose density and browsing pressure is not obvious (see Fig 5). The browsing pressure varies differently than the moose density.

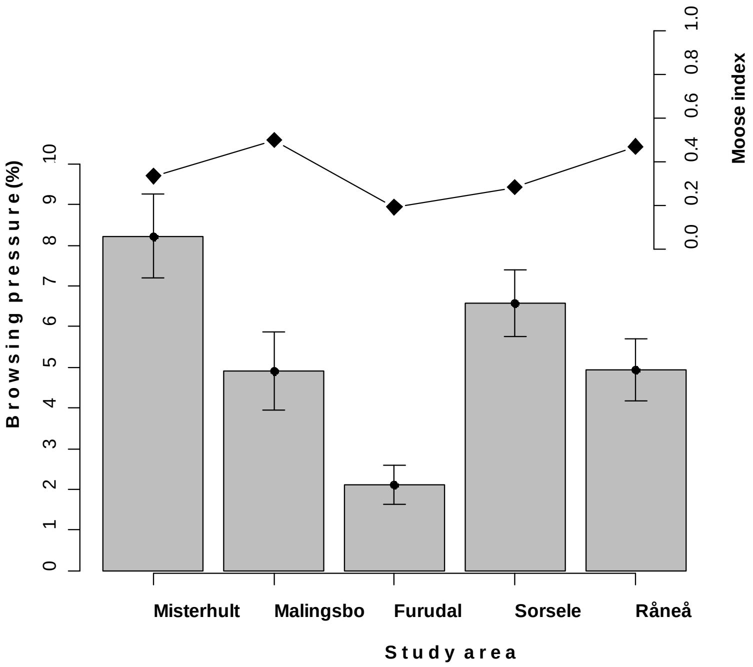


Figure 5. Browsing pressure (mean ± SE). and moose density index in the different study areas at the landscape scale. The increased browsing pressure in Misterhult and Sorsele is not obviously related with higher moose density since the highest moose density occurs in Malingsbo and Råneå.

Focusing on tree species composition, Scots pine dominates in every area. Pine was the most abundant in Furudal and the least in Misterhult. There was no significant difference in pine representation between Sorsele and Malingsbo as well as between Sorsele and Råneå (Tukey test, P>0.05). The other study areas differed significantly. In Råneå and Sorsele there was some lodgepole pine, as well as a larger birch component (see Fig 6.). There was a significant difference in representation of birch among every area, except Malingsbo and Furudal. The study areas differed regarding their recent history of forest management (see Fig.7).

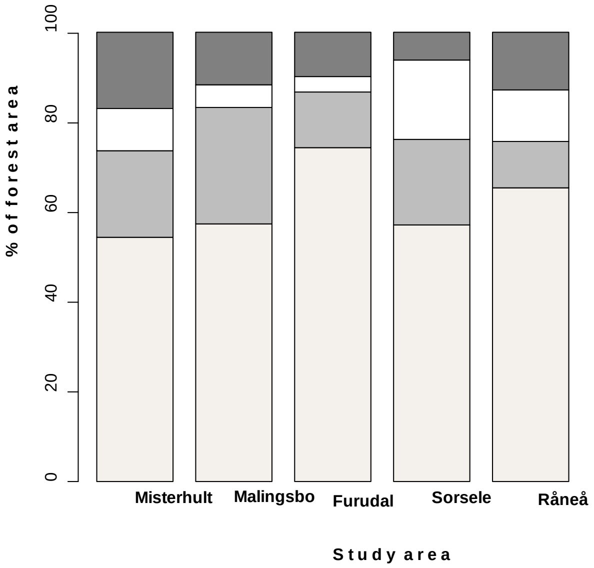


Figure 6. Representation of the tree species. From the bottom – pine, spruce, birch and other species.

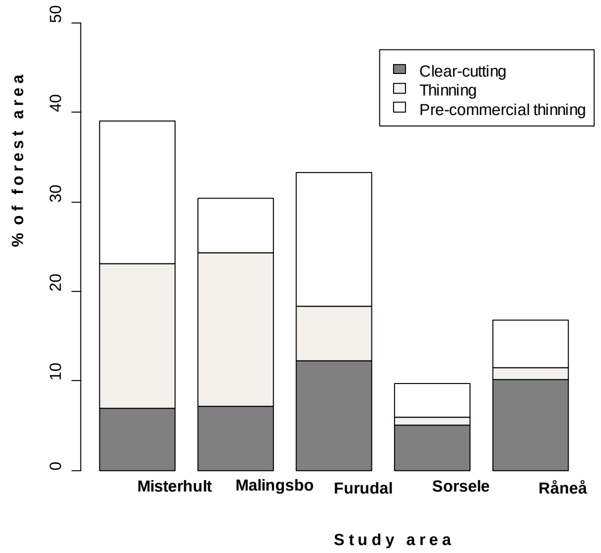


Figure 7. Forestry actions - percentage of forestry actions of the forest land performed from 1.1.2000 to 31.12.2008

For detailed information about characteristics of land, forest and forestry actions in individual study areas, see Appendix I.

3.2. Modelling of moose browsing on pine at three spatial scales

The significance of factors included in the minimum adequate generalized linear model explaining browsing pressure on Scots pine changed at different spatial scales (see Tab. 2, 3 and 4). With respect to the whole bio-geographical gradient it was not possible to test the factors “fallow deer”, “roe deer” and “red deer”. I tested these factors separately only for the study area Misterhult, since it was the only study area where these species occur at meaningful densities.
The same problem arose when testing for the significance of the distances to roads, since major roads occur only in Misterhult, Malingsbo and Sorsele. Thus, the testing was carried out only within these three areas.

3.2.1. Plot scale

At the plot spatial scale, the factors study area, height of measured trees, moose index, and dominating forest seem to be important factors for explaining the browsing pressure. There were significant differences in browsing pressure among study areas (see Fig. 4). The relationship between height of browsed trees and browsing pressure was positive, indicating that the browsing pressure increased as the height of the pines increased. Also the moose index has a positive effect on browsing pressure. There was significantly lower browsing pressure on pines which were situated in non-productive stands, i.e. in mires or hilly areas. The browsing pressure in the pine forest differed from the other forest types in the one-factor model but in the minimal-adequate model it was not significant. Also the interaction of the terms “area vs. clear cutting” and “area vs. forage cover” appeared significant. It means that clear-cutting and forage cover had different influence on browsing pressure in different areas. However, these interaction terms were not retained in the minimal adequate model. Thinning, pre-commercial thinning, and distance to settlements did not significantly relate with browsing pressure. The separately tested factors “other large herbivores” in Misterhult did not improve the model either (see Tab. 3). The correlation test (Spearman) showed significant correlation of moose index and clear-cutting (see Appendix III.), thus in the maximal model I did not include both factors at the time. The model including moose index turned out better than the one including clear-cutting.

Table 3. Model for browsing pressure on Scots pine at the plot scale. [1] tested only for study area Misterhult. [2] tested only for study areas Misterhult, Malingsbo and Sorsele. Factors marked in bold are included in the minimal adequate model. Factors marked in italic were tested only by 1-factor model. * Significant factor, ° nearly significant factor. For explanation of the model simplification see Methods.

Tested factors		1-factor model		maximal model		minimal adequate model	
		estimate	P	estimate	P	estimate	P
Study area	**Misterhult**	1.51	0.00*	0.84	0.03*	1.47	0.00*
	Malingsbo	0.95	0.00*	0.32	0.49	0.66	0.03*
	Råneå	0.96	0.00*	0.37	0.41	0.95	0.00*
	Sorsele	1.26	0.00*	0.85	0.04*	1.32	0.00*
Height of measured pines		0.03	0.00*	0.03	0.00*	0.03	0.01*
Moose index		0.36	<2e-16*	0.38	<2e-16*	0.36	< 2e-16*
Dominating forest	**No forest**	-0.82	0.01*	-0.04	0.01*	-0.04	0.02*
	Mixed coniferous	0.09	0.72	0.00	0.81	0.00	0.85
	Mixed deciduous	-0.21	0.54	-0.03	0.15	-0.02	0.19
	Pine	-0.47	0.04*	-0.03	0.05*	-0.02	0.11
	Spruce	-0.30	0.45	-0.03	0.17	-0.02	0.29
Forage cover		0.03	0.97	-5.69	0.19		
Clear-cutting		-0.21	0.23	-0.38	0.66		
Study area : Clear-cutting	Misterhult:Clearcut	1.61	0.09°	1.27	0.18		
	Malingsbo:Clearcut	-0.80	0.61	-1.50	0.36		
	Råneå:Clearcut	-0.06	0.96	-0.08	0.95		
	Sorsele:Clearcut	-0.03	0.98	-0.86	0.52		
Study area: forage cover	Misterhult:Forage	6.68	0.13	5.88	0.17		
	Malingsbo:Forage	2.66	0.62	5.45	0.30		
	Råneå:Forage	9.13	0.06°	6.21	0.19		
	Sorsele:Forage	6.23	0.18	5.71	0.21		
Thinning		0.28	0.42				
Pre-commercial thinning		0.02	0.92				
Distance to settlements		<0.001	1.00				
Fallow deer index[1]		*0.54*	*0.20*				
Roe deer index[1]		*0.07*	*0.76*				
Red deer index[1]		*-0.40*	*0.52*				
Distance to roads[2]		*0.00*	*0.65*				

3.2.2. Tract scale

At the tract spatial scale, the minimal adequate model contained the factors study area, dominating forest, and moose index (see Tab. 3). Dominating forest seems to be an important factor affecting browsing pressure, where the browsing pressure in mixed coniferous forest is notably higher than in the other forest types. The moose index, which expresses average number of pellets groups per plot within the tract, had a positive effect on the browsing pressure at the tract spatial scale ($P< 0.001$). The forage cover had a positive significant effect on the browsing pressure in the one-factor model ($P=0.02$), whereas it was not retained in the minimal-adequate model. Clear-cutting had a nearly significant negative effect on browsing pressure in one-factor model ($P=0.06$), but it was not retained in the minimal-adequate model.

Improvement of the model could be achieved by including fallow deer, roe deer and red deer indices into the model. However, these species occurred at significant densities only in one study area (Misterhult), thus the generalization for the whole geographical gradient was not possible. The significance of these factors was tested separately using only the data from Misterhult. In the 1-factor model, fallow deer index and roe deer index appear significant for browsing pressure. The same problem arose from adding the distance to roads as a factor. I tested this factor separately for the study areas Misterhult, Malingsbo and Sorsele. However, it did not turn out to be significant in the model. All interaction terms between study area and other factors were non-significant (see Tab.4). The Spearman correlation test confirmed that there is no correlation of factors at the tract scale (see Appendix III.)

Table 4. Model for browsing pressure on Scots pine at the tract scale[1] tested only for study area Misterhult. [2] tested only for study areas Misterhult, Malingsbo and Sorsele. Factors in bold are included in the minimal adequate model. Factors in italic were tested only by 1-factor model. * significant factor, ° nearly significant factor. For explanation of the model simplification see Methods.

		1-factor model			maximal model			minimal adequate model		
	Tested factors	estimate	P		estimate	P		estimate	P	
Study area	**Misterhult**	1.44	0.00	*	1.13	0.01	*	1.08	0.01	*
	Malingsbo	0.79	0.09	°	0.32	0.49		0.25	0.58	
	Råneå	0.89	0.08	°	0.62	0.20		0.62	0.19	
	Sorsele	1.15	0.01	*	1.06	0.01	*	1.01	0.02	*
Dominating forest	**No forest**	-0.12	0.20		-0.09	0.19		-0.08	0.24	
	Mixed coniferous	0.72	0.15		0.91	0.06	°	0.83	0.07	°
	Mixed deciduous	0.84	0.12		0.77	0.15		0.74	0.14	
	Pine	-0.17	0.69		-0.18	0.67		-0.09	0.82	
	Spruce	-1.11	0.20		-0.76	0.35		-0.85	0.28	
Moose index		0.96	1.08E+00	*	1.16	2.53E-08	*	1.16	1.58E-08	*
Clear-cutting		-0.55	0.06	°	0.63	0.48				
Forage cover		6.25	0.02	*	1.25	0.68				
Distance to settlements		0.00	0.33							
Pre-commercial thinning		0.29	0.67							
Thinning		0.84	0.91							
Height of measured pines		0.03	0.35							
Fallow deer index[1]		*4.30*	*0.00*	*						
Roe deer index[1]		*1.98*	*0.06*	°	.					
Red deer index[1]		*0.00*	*1.00*							
Distance to roads[2]		*-2.13E-05*	*0.42*							

Note: Dominating forest is a type of forest, which covers the major part of the tract buffer. Game indices are calculated as averages of pellet groups per tract. Clear-cutting, thinning, and pre-commercial thinning are calculated as percent of the forest area within the tract buffer. Forage cover is a percent of tract buffer area covered by forage. Distances to settlements and roads are calculated as average of each plot within the tract buffer to the roads and settlements.

3.2.3. Landscape scale

At the landscape scale it was not possible to test the factor dominating forest since pine forest dominated all areas. Instead, I used the factors pine, spruce and birch which represent the percentage of the forest area covered by given tree species. It was not meaningful to include factor study area since it is a categorical variable with 5 levels. Other factors such as snow cover, and tree density were added to the analysis. I analyzed the effects of the factors only by one-factor model. At this spatial scale, the browsing pressure was affected only by percentage of pine in the forest (P=0.04). The browsing pressure decreased with increasing amount of pine thus, young pines in the areas with smaller extent of pine forests were more heavily browsed than young pines in areas with larger extent of pine forest. The other factors were not significant (see Tab.5). I also tested whether the ratio between forage cover and moose index (i.e. amount of forage per moose unit) was significant in one-factor model. This was not confirmed (P=0.75), thus the interaction between amount of forage and moose density is not significant at the landscape scale. I tested for correlation of factors (see Appendix 3). There was a strong correlation of factors pine and thinning, as well as individual snow-cover factors. The results of correlation are informative at the landscape scale and give us an interesting overview of relation-ships between forestry actions and forest structure.

Table 5. Model of browsing pressure on Scots pine at the landscape scale. At this scale, only the 1-factor model was performed to avoid over-fitting. * significant factor

Tested factors	1-factor model	
	estimate	P
% of pine	-0.0673	0.04*
Clear-cutting	-0.1400	0.16
Forage cover	0.0305	0.27
Moose index	0.9000	0.72
Tree density	-0.0001	0.73
Snow cover >10cm	-0.0047	0.34
Snow cover >30cm	-0.0035	0.41
Snow cover >70cm	-0.0029	0.77
% of birch	0.0464	0.38
% of spruce	0.0295	0.55
Pre-commercial thinning	0.0018	0.97
Thinning	0.0199	0.60

Note: Pine, Birch, Spruce, Clear-cutting, Thinning, and Pre-commercial thinning are calculated as percent of the forest area. Forage cover is counted as percent of the whole study area covered by forage. Snow cover indicates number of days with snow cover exceeding given depth. Moose index is the average of moose pellet groups per plot.

IV. DISCUSSION

It is important to consider the spatial scale of the study and bio-geographical location of the study area when comparing the results of studies addressing moose browsing. Many studies concerning the moose browsing pressure have been conduced, but the results are not uniform. One should be aware of differences that can originate from different spatial approaches. In my study, as expected, it was shown that the browsing on young Scots pine is affected by various factors at different spatial scales. No general conclusions could be made for all spatial scales, but the results showed that some factors are more or less important at all scales. There were also differences between significance of factors in one-factor models and minimal adequate models. For instance, the clear-cutting and forage cover at the tract scale seem to be nearly significant in one-factor model, however, when including moose index, study area and dominating forest into the model, the significance of these two factors disappears. This result suggests that it is important to take into account multiple factors; otherwise the importance of one factor may be overvalued.

In my study areas, 70 % of observed trees did not undergo any browsing and only 11% of the young pines underwent a more extensive browsing than 5%. This level corresponds well with the study of Shipley et al. (1998) that reported that 74-83% of the available mass was untouched. Similar result have been reported by SLU (2007) which, during the forest inventory of browsing damages in forest, found 9.6 % of pines damaged. The damages in that study were measured according to the ÄBIN method.

4.1. Tested factors at all scales

The **study areas,** i.e. location of the inventory, influence the browsing pressure at both the plot and the tract scale. This means that there were significant differences in browsing pressure between individual study areas. This finding was similar to that of the SLU report (2007) and Hörnberg (2001b) that showed differences in browsing pressure on trees between different regions in Sweden. Although the differences in browsing pressure among the study areas differed significantly, the differences do not seem to be related with the moose density (see Fig. 5). The differences may be more depend on the forest characteristics and on differences in the moose ecology, such as migratory and non-migratory behaviour (Ball et al. 2001).

As predicted, **moose density**, substituted by moose index, appeared important when modelling browsing pressure at the plot and tract scale. However, the impact at the landscape spatial scale disappeared. This means that there is no significant relationship between the overall moose density (for the whole area) and browsing pressure, whereas the habitat-specific density (plot and tract scale) significantly influence browsing within the specific habitat bordered by the plot or scale buffer. Månsson (2009) and Bergström et al. (1995) observed a similar pattern. The negative effect of high moose densities at smaller spatial scales was observed in many other studies (Andrén and Angelstam 1993, Angelstam et al. 2000, Persson 2003). My result at the landscape spatial scale mostly corresponds with the finding of Hörnberg (2001b) who did not find any correlation between moose density and damage level and reported that “even with low moose densities, large areas can be seriously damaged”.

Dominating forest (at the landscape scale expressed as percentage of individual tree species) was significantly related to browsing pressure at all spatial scales. This makes it one of the most important factors, which can be used for generalization of results over the different spatial scales. At the tract scale, the browsing pressure in the mixed coniferous forest emerged nearly significantly higher (P=0.07) than in the other types of forest, and at the plot scale the browsing pressure was the lowest in the pine forest (at the landscape scale in the forest with higher percentage of pine). This is consistent with a study performed by Heikkilä and Härkönen (1996) that proved that there was a larger extent of browsing on pine in the patches with high density of preferred deciduous trees species. Other studies reported that the moose browsing is affected by tree species composition (Angelstam et al. 2000). Actually, at larger scale levels, vegetation composition becomes more important than moose density (Bergström 1995). My analysis showed that the browsing pressure on pine is negatively associated with the amount of pine in the forest at the landscape scale. This result is in contrast with the findings of Hörnberg (2001a) which showed that the proportion of available pine forage is positively correlated with its consumption. The differences in these results may be caused by different classifying of the "pine forest". I took into account all age groups, whereas the other studies considered only young pine forests. The effect of **birch** and **spruce** amounts did not appear to affect browsing on pine, which is in contrary to finding of Ball and Dahlgren (2002) that found a slight tendency for increased browsing with increased birch density.

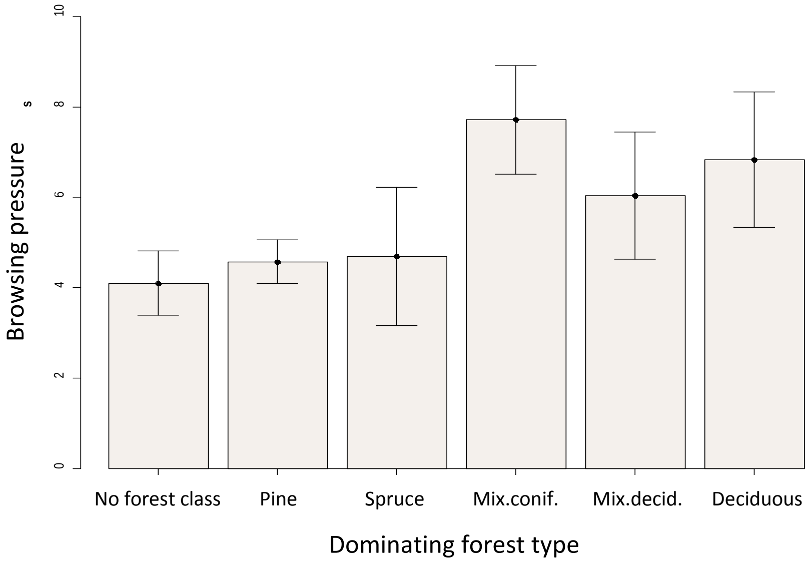


Figure 8. The relationship of forest type and browsing pressure on the plot scale. Mean ± SE.

The analysis indicated that the **forage cover** was not an important factor in determining the browsing pressure as expected, since it was not significant at any spatial scale. Thus, the browsing pressure is affected neither by the forage cover in close surrounding of the plots nor by the forage cover in the whole area. In previous studies there is some disagreement about how forage cover influences pine browsing. Shipley et al. (1998), Ball and Dahlgren (2002) and Månsson (2007) showed that increased forage cover was associated with an increase of the total amount of consumption, however because of the slower rate than 1:1, the proportion of browsing decreased. Bergström and Hjeljord (1987), Edenius (1993) and Hörnberg (2001a) reported that the plant biomass explains a significant amount of the variation in pine consumption and habitat selectivity. My results mostly corresponds to the study carried out by Shipley et al. (1998) that did not find any relationship between the absolute amount of all browse species available and use of particular browse species. Also Weixelman et al. (1998) reported that percent use of a browse species is not significantly related to its availability at all. Similarly, Lundberg et al. (1990) tested browsing on birch and found no relation between browsing and total biomass available. Vivås and Sæther (1987) also reported that there is no tendency for a higher frequency of moose visits to plots with high density of browse.

Previous studies have reported that snow depth and **number of days with snow cover** affects forage availability and consequently moose habitat selection and movement patterns (Ball et al. 2001, Ball and Lundmark 2008, Månsson 2009,). However, at the larger spatial scale, the effect of snow depth on forage availability is very small (Nordengren 2003) and it does not influence foraging activity (Poole and Smith 2005). This is in accordance with the present study: there was no association between the numbers of days with snow cover and browsing pressure at the landscape scale. In my study I focused on the whole study area during one winter. The snow cover at the larger scale is related to the latitude and elevation so that with increasing latitude and elevation the number of days with snow cover increases. Hence there in no doubt that the browsing pressure is not related with these characteristics either. The snow depth may instead have an impact on the browsing pressure at smaller spatial scales within certain habitat or region.

The height of measured pines, which to some extent expresses the actual age of the surveyed pine tree, significantly influences the browsing pressure at the plot scale. At the tract scale where the heights were averaged the association was not confirmed. The smallest trees, around 0.3 m may be hidden in the snow in northern areas during winter, thus protected against browsing. The increasing height of measured trees is associated with increasing browsing pressure. Thus, it seems that the higher trees, but still situated within the moose available range are more likely to be browsed than the smaller one.

Clear-cutting has been reported to affect moose movement over the landscape, since moose prefers to select areas with fewer clear-cuts, mires and fields (Ball et al. 2001). In my results, I confirmed the same tendency. Clear-cutting was nearly significant (P=0.06) at the tract scale and in combination with the study area it was significant also at the plot scale in the one-factor model. The relationship was negative, thus with increasing amount of clear-cuts the browsing pressure decreased. This supports the idea that the moose preferred home range area can be defined as an area where clear-cutting has not been carried out to a large extent.

Winter forage availability is increased by **pre-commercial thinning** for snow-free conditions but is unaffected for conditions when shrub is covered by snow (Cole et al. 2010). Pre-commercial thinning can considerably change the density of young trees and forage availability for moose. The pre-commercial thinning should be postponed until the pines exceed 3.5 m in height to avoid increased proportion of browsing at the less dense pine stands (Ball and Dahlgren 2002, Heikkilä and Härkönen 1996). In my study, I did not find any proof of this hypothesis, since the amount of pre-commercial thinning was not significantly important. However, I tested only long-term impacts of forestry actions; hence it may be interesting to test whether the forestry actions performed in a shorter time before the winter, i.e. one year, will have a stronger effect. Additionally I also tested the significance of **thinning**, which did not appear significant either, although Månsson et al. (2010) suggested that felled trees may increase forage availability and thus act as supplemental forage for moose and consequently affect browsing pattern.

Distance to roads did not appear significant at any spatial scale. Although Ball and Dahlgren (2002) reported that the pines further from the major road have decreasing probability to be browsed, no such trend was found here. There was no significant relationship at plot scale nor at tract scale. Thus, the results suggest that the proximity to roads broader than 5 m and with road number E4-E99 or 100-499 do not significantly affect browsing pressure. This factor could be be improved by including only the main roads such as E4-E99 or by including roads which could be considered major roads according to the observation.

Human activities can strongly affect the moose behaviour (Ball et al. 1999). It has been shown that proximity of **human settlements** and infrastructure operates for mammals like cover shield against carnivores thus more attractive to moose (Berger 2007). On the other hand moose avoid densely populated areas and prefer habitats characterized by forests (Schönfeld 2009). I quantified the human impact by setting the distances to buildings. Distance to settlements did not significantly influence browsing pressure at any spatial scale (it was not calculated for the landscape scale). In this case, settlement corresponds to any kind of house or building, no matter if it is inhabited or not. Thus, I did not find any support for the hypothesis that human buildings in nature have any effect on moose browsing behaviour.

Danell et al. (1991) suggested that the consumption of twig biomass was highest on pines from the most **productive habitats**, although pine mortality and damages in unproductive habitats was greater. Preferences of moose for high productive habitats were confirmed also by Ball and Dahlgren (2002). In my study, the land productivity tested at the landscape spatial scale did not appear significant. It may be interesting to test whether the relationship is different at the smaller spatial scales.

The **tree density** appeared non-significant at the landscape spatial scale. This is in contrast with earlier studies carried out by Shipley and Spalinger (1995) and Heikkilä and Härkönen (1996). Ball and Dahlgren (2002) reported increased amount of cropped shoots per tree with decreasing tree density, although the total amount of browsed shoots increased. Similarly Andrén and Angelstam (1993) reported increasing pressure with decreasing density of young Scots pine and Poole and Smith (2005) found evidence that the moose foraging plots have fewer trees. However these studies were carried out at the stand spatial scale and the density was calculated only in the young Scots pine forests, thus the comparison may not be reliable.

Roe deer, red deer and fallow deer have a significant effect on the vegetative structure and composition of forest (Bergquist et al. 1999, Sage et al. 2004, Götmark, F. 2005). Thus, the information about occurrence **of other large herbivores** may improve the model; however it could not be tested at larger geographical scale. Nevertheless, when taking into account only one area, the presence of fallow deer and roe deer at the tract scale seems to significantly influence the amount of browsing pressure. The browsing may not be the only one effect caused by the other large herbivores. Red deer, roe deer and fallow deer are in contrast to moose mixed-feeders, i.e. they prefer to graze during the summer and the tree shoots are taken only during winter, when the other food is limited (Veiberg et al. 2007, The British Deer Society 2010). In Misterhult, the snow cover was nearly inexistent (see Appendix I.), thus other interactions than the resource competition between moose and the other species may be involved. The interference competition which includes adverse social interactions may appear. For instance there has been evidence of fallow deer aggressive behaviour toward other deer species and roe deer differs from the other due to the solitary and territorial behaviour (Latham 1999).

The interaction terms study area vs. forage cover appeared significant in the one factor model at the plot scale. It means that the forage cover has a different impact upon browsing pressure in different study areas. This is pronounced in study area Furudal, where the forage cover had more positive effect to the browsing than in the other areas. The interaction term study area vs. clear-cutting appeared significant at the plot scale. The amount of clear-cutting in Misterhult had positive effect on the browsing pressure contrary to clear-cutting in the other study areas. This may be caused by occurrence of other large herbivore species.

4.2. Biases

4.2.1. Omitted factors

Although I tried to cover as many aspects as possible I did not take into account some factors, such as supplemental feeding, occurrence of predators, local snow conditions and landscape characteristics, which may affect the moose population and consequently browsing pressure. This was mainly due to the lack of data regarding these factors.

Supplemental feeding reduces browsing pressure on young forest stand during winter and re-distributes browsing pressure (Gundersen et al. 2004). Besides supporting the survival of moose in the winter, it is intended as reduction of forest damages, since moose concentrate around the feeding stations. The number of feeding stations, distances between stations, position in landscape, and large-scale landscape patterns influence the frequency of use and browsing pressure in surrounding of the feeding stations. The moose–induced browsing pressure is extensive at short distance (<200m) to feeding station and decreases at distances 1 – 2km (Gundersen et al. 2004). High browsing pressure surrounding the feeding station is caused by need of moose to feed diverse food items in addition to the supply of silage (Doenier et al. 1997).

Predators, such as bear, wolf and wolverine *(Gulo gulo)* modify the size of large herbivores populations. Besides this direct interaction, moose react on occurrence of predators by seeking for cover, thus the “indicating risk of predation plays significant role in the foraging dynamics of moose” (Weixelman et al. 1998). This may also affect browsing pressure on Scots pine. Unfortunately, the data about occurrence of large predators was not available for my study.

Landscape characteristics, such as elevation, slope, hills and valleys affect moose movement over the landscape (Cederlund and Bergström 1996). Also distances between forage patches and patch sizes increase time spent by foraging (Shipley and Spalinger 1995). Such detailed analyses were not possible to carry out in the given time period, although still more modern techniques and spatial analysis tools are available.

Moose migration is the cause of different distribution of browsing pressure between winter and summer habitats, where the forest in the winter habitats undergo large pressure (Storaas et al. 2001), thus the areas which have been left by the migratory moose may undergo less pressure than the winter ranges. There are also slight differences in winter habitats composition of migratory and non-migratory moose (Ball et al. 2001). There are large differences in actual moose density and the overall year density where migration and local concentration of moose occurs and consequently some areas can undergo extensive pressure on pine trees in spite of reported low moose densities (Hörnberg

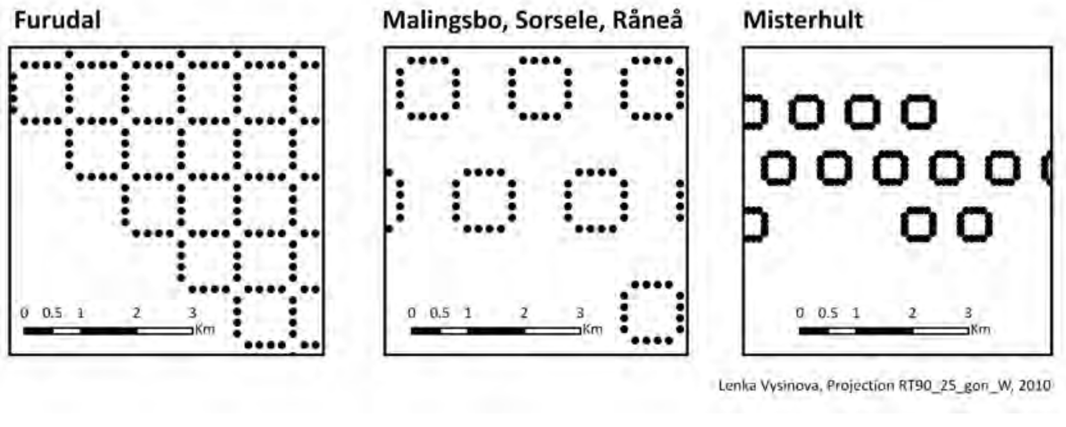
2001b). This may explain the relatively large browsing pressure in the study area Sorsele although the moose population is not so dense there at the landscape spatial scale (see Fig. 5)

Food plant quality and nutrient content has been shown to influences herbivore's decisions making. MacArthur and Pianka (1996) presented the hypothesis that foraging varies with the quality of forage and Ball et al. (2000) revealed that mainly stands with high browse quality are objects of more frequent moose browsing than low quality stands. This may be because moose adjust their foraging strategies to increase probability of survival and reproduction, which is affected by diet digestibility (Moen et al. 1997). In contrast, Weixelman et al. (1998) and Shipley et al. (1998) suggested that the percent use of a browse species is not significantly related to its nutrient content and digestibility. Likewise Edenius (1993) suggested that nutrient factors play an insignificant role in diet selection and Senft et al. (1987) and Lundberg et al. (1990) narrowed this opinion to concern only winter, when moose shift from "nutrient maximization", whereas in spring, summer and autumn they switch to "energy maximization". At the landscape spatial scale this was substituted by the forest site index which influences the nutrient content in plants, however I did not include this variable in the model.

4.2.2. Data collection, study extent, time consideration and statistics

This study was based on spatial analysis of a large forest stand database. The data can be incomplete, obsolete or collected by different persons or by different methods. For example the trees density may change considerably after thinning and pre-commercial thinning. Biases could arise if some parcels within the study area are not included in the database, e.g. water surfaces, non-productive land such as mountains and mires and other land owned by private persons or state. It is evident that forestry companies attempt to own only productive land, thus using of the forest stand database for determination of habitats over a larger extent may cause considerable distortion.

The inventory design was unbalanced which may cause inaccuracies in statistic analysis and lower the reliability of the spatial analyses and statistic results. There were different numbers of tracts in every study area, as well as the distances between tracts differed (adjacent tracts in Furudal, 500 m in Misterhult, 1000 m in other study areas). Also the distances between the plots within the tracts differed (100 m in Misterhult, 200 m in other study areas) (see Fig. 9). For the next studies, where comparison of more study areas is intended I would suggest decreasing the number of inventoried tracts and implementing a balanced design.



Lenka Vysinova, Projection RT90_25_gon_W, 2010

Figure 9. The plot and tract design in individual study areas. For better comparison the same scale was used in all three maps.

In this study I took into consideration all land types and all forest types and included all available factors, which may affect moose browsing behaviour. However, focus on one certain habitat, land type or forest type may bring more understandable results which would be applicable in practice. The intended extent of the study requires a larger time period to extract and test all considered variables at all spatial scales. The reliability of results at the study landscape scale is discussable, since the sample size counted only five observations (five study areas) and thus there was a low power to detect significant effects. Hence, the results at that scale should be considered rather conservative.

V. CONCLUSION

This study was new in terms of connection and analyzing the forest stand database of Sveaskog and two research inventory data sets, from the project “Viltbete och Foderproduktion” and the project “Balanserad Älgstam”. I suggest that examination of browsing pressure in conjunction with forest stand database is a convenient way to obtain the data needed for population ecology research at all spatial scales. Forest stand databases of forest companies contains large number of diverse biological stand data, parameters and characteristics measured over a long time period that can be hardly collected by researches. Nevertheless, I supplemented the forest stand database by the information on forage cover, which has not been included before.

I respected the complex relationships in ecosystems, taking into account not only one or a few variables, but trying to summarize the effects of all accessible variables into one model. This study offers a summary of factors which significantly influence browsing pressure not only at the plot scale (individual trees and their surrounding) but also at the larger scales (groups of forest stands and larger forest landscapes). The most important factor significant at all scales appears to be dominating forest type. The browsing on pine is lower in pine forest than in the deciduous forest and it is always the highest in the mixed coniferous forests. Thus, forest management oriented on clustering of browsing pressure to a one stand with deciduous trees may be successful in protection of pine plantations. Furthermore, perhaps not surprisingly moose density affects the browsing pressure, mainly at smaller scales. In Sweden, the moose population is mainly regulated by hunting, thus the agreement between hunters and foresters is necessary.

There are not many other mammalian herbivore species that fan so many discussions, emotions and negotiation. It is a question whether gained knowledge will be used in applied forestry or ecology or whether it will just stay at the theoretical level, as many other studies. The findings of this and similar studies are important for forestry as well as ecology, since finding patterns of moose browsing may help people either to protect large yield from forestry or biodiversity. Unfortunately, it is probably impossible to achieve both of these objectives at the same time. At the end I would like to cite one statement which I identify with: “There are in principle 3 ways of reducing the browsing pressure on preferred tree species: (1) to reduce moose densities /hunting/; (2) to increase the amount of food /supplemental feeding, change in forestry practices/; and (3) to reduce the availability of food /physical protection, change in forestry practices/” (Angelstam et al. 2000).

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APPENDIX I.

Table 6. Forest characteristics, forest management and tree species distribution in individual study areas.

Study Area	Area of forest (% of total area)	Age of forest (mean)	Forest site index (mean)	Basal area (m2 per ha)	Nb. Of Trees per ha	% of area cultivated (from 1.1.2000 till 31.12.2008)			Tree species distribution (% of forest)			
						Clear-cutting	Pre-comm. thinning	Thinning	Scots Pine	Norway Spruce	Birch	Lodgepole Pine
Misterhult	76.2	46	23	18.4	1284	6.93	15.89	16.21	54.5	19.3	9.3	0.1
Malingsbo	79.5	39	22	18.3	1801	7.20	6.06	17.12	57.3	26.0	5.1	0.0
Furudal	79.5	55	20	15.6	1320	12.23	14.96	6.14	74.4	12.5	3.4	0.8
Sorsele	74.1	59	16	9.8	1268	5.09	3.80	0.85	57.1	19.1	17.7	3.2
Råneå	71.8	59	18	13.5	2006	10.14	5.32	1.36	65.4	10.5	11.4	3.9

Table 7. Landscape structure, weather characteristics and other characteristics in individual study areas.

Study Area	Area (ha)	% of browsing pressure (mean ± SD)	Moose index		Land-type distribution (% of the whole study area)				Weather conditions		Forage cover (% of area)
			Pine yes[1]	Pine no[2]	Forest	Mire	Hills	Other	Snow cover[3]	Temperature[4]	
Misterhult	8320	8.22 ± 20.7	0.44	0.23	79.5	0.2	14.3	6.0	0	-	9.81
Malingsbo	36388	4.91 ± 16.7	0.74	0.38	76.2	12.6	3.1	7.9	46	-2.7	7.38
Furudal	22680	2.11 ±10.9	0.27	0.11	79.5	0.5	8.4	11.7	109	-4.30	7.50
Sorsele	39764	6.56 ± 16.9	0.37	0.19	71.8	2.3	19.3	6.6	147	-8.58	10.07
Råneå	20981	4.93 ± 14.6	0.47	0.28	74.1	1.9	16.8	7.1	152	-7.72	9.75

[1] Moose index (average of moose pellets per plot) for plots, where at least one pine was found

[2] Moose index (average of moose pellets per plot) for plots, where no pine was found

[3] Number of days with a snow cover >30cm during the winter season 2008-2009

[4] Average temperature during days with a snow cover >10cm during the winter season 2008-2009

APPENDIX II.

Table 8. Mean forage cover for different combinations of study area (1st digit), land type (2nd digit), forest type (3rd digit) and forest age group (4th -6th digit).

CODE	Forage cover (%)	CODE	Forage cover (%)	CODE	Forage cover (%)	CODE	Forage cover (%)	CODE	Forage cover (%)
M11000	7.500	M15020	35.000	L14015	19.813	F13010	17.220	S12005	2.667
M11005	12.362	M15025	24.000	L14020	19.500	F13015	18.252	S12010	7.500
M11010	28.326	M15030	10.000	L14025	15.000	F13020	20.515	S12015	6.500
M11015	33.565	M15050	12.917	L14030	16.400	F13025	14.077	S12020	8.600
M11020	32.082	M15070	8.583	L14050	9.304	F13030	7.125	S12025	12.583
M11025	11.000	M15090	20.000	L14070	2.875	F13050	6.155	S12030	8.111
M11030	10.238	M15120	14.500	L14090	1.417	F13070	2.373	S12050	9.698
M11050	7.021	M15200	2.000	L14120	2.000	F13090	2.357	S12070	6.303
M11070	6.500	M20000	6.179	L14200	2.000	F13120	2.248	S12090	6.400
M11090	7.971	M30000	4.703	L15000	23.000	F13200	2.300	S12120	5.944
M11120	6.410	M40000	0.000	L15005	15.000	F14000	2.000	S12200	3.061
M11200	2.000	M50000	0.000	L15010	35.375	F14005	6.000	S13000	2.050
M12000	0.000	M60000	5.865	L15015	41.875	F14010	20.537	S13005	9.241
M12005	8.116	L11000	1.333	L15020	43.857	F14015	17.833	S13010	19.568
M12010	21.067	L11005	10.130	L15025	15.800	F14020	22.444	S13015	21.500
M12015	11.186	L11010	20.929	L15030	4.000	F14025	18.000	S13020	13.083
M12020	7.167	L11015	25.641	L15050	15.348	F14030	15.818	S13025	24.000
M12025	6.800	L11020	21.600	L15070	15.917	F14050	6.929	S13030	14.444
M12030	2.455	L11025	10.367	L15090	18.500	F14070	3.333	S13050	10.951
M12050	2.500	L11030	4.290	L15120	6.000	F14090	3.750	S13070	8.947
M12070	3.231	L11050	3.232	L15200	2.000	F14120	4.167	S13090	6.829
M12090	3.290	L11070	2.446	L20000	5.306	F14200	10.500	S13120	5.591
M12120	3.571	L11090	2.192	L30000	5.050	F15000	23.000	S13200	4.576
M12200	2.000	L11120	1.500	L40000	0.000	F15005	22.333	S14000	2.000
M13000	1.537	L11200	1.400	L50000	0.000	F15010	25.067	S14005	4.000
M13005	13.583	L12000	2.000	L60000	3.427	F15015	24.563	S14010	22.000
M13010	26.130	L12005	7.517	F11000	0.000	F15020	31.000	S14015	38.100
M13015	24.360	L12010	17.397	F11005	7.333	F15025	17.000	S14020	41.571
M13020	20.667	L12015	14.067	F11010	17.237	F15030	17.000	S14025	42.000
M13025	8.571	L12020	9.276	F11015	21.887	F15050	13.000	S14030	22.900
M13030	13.750	L12025	4.029	F11020	21.423	F15070	5.875	S14050	21.500
M13050	5.543	L12030	3.472	F11025	17.948	F15090	5.500	S14070	13.333
M13070	8.679	L12050	2.333	F11030	6.123	F15120	2.000	S14090	11.375
M13090	5.453	L12070	1.912	F11050	3.575	F15200	2.000	S14120	7.545
M13120	7.800	L12090	2.094	F11070	2.580	F20000	5.655	S14200	7.875
M13200	2.000	L12120	1.000	F11090	1.956	F30000	1.563	S15000	18.500
M14000	2.000	L12200	0.000	F11120	1.923	F40000	0.000	S15005	2.000
M14005	20.500	L13000	2.669	F11200	2.069	F50000	0.000	S15010	36.333
M14010	44.857	L13005	7.000	F12000	4.000	F60000	3.488	S15015	39.800
M14015	53.400	L13010	17.794	F12005	12.176	S11000	3.333	S15020	25.800
M14020	37.750	L13015	20.408	F12010	15.763	S11005	2.612	S15025	25.000
M14025	18.200	L13020	22.267	F12015	13.368	S11010	10.979	S15030	41.778
M14030	23.833	L13025	11.000	F12020	8.720	S11015	17.076	S15050	22.250
M14050	10.375	L13030	11.077	F12025	8.410	S11020	17.308	S15070	13.333
M14070	10.000	L13050	5.068	F12030	5.097	S11025	14.840	S15090	4.000
M14090	10.875	L13070	3.016	F12050	3.076	S11030	16.103	S15120	26.000
M14120	7.667	L13090	1.989	F12070	1.865	S11050	9.202	S15200	42.000
M14200	2.000	L13120	1.854	F12090	2.485	S11070	4.646	S20000	7.349
M15000	3.000	L13200	2.000	F12120	1.929	S11090	3.388	S30000	5.350
M15005	23.444	L14000	2.000	F12200	2.229	S11120	5.305	S40000	0.000
M15010	50.800	L14005	6.000	F13000	2.960	S11200	1.969	S50000	0.000
M15015	57.286	L14010	17.333	F13005	5.220	S12000	2.000	S60000	2.472

APPENDIX III.

Factors correlation

Table 9. Spearman correlation of factors included to the maximal model at the plot spatial scale. There is strong correlation between moose index and clear-cuts.
The factor clear-cut was not included in the minimal adequate model.

	Height of measured trees	Clear-cut	Forage cover	Dominating forest	Moose index	Area
Height of measured trees	x					
Clear-cut	0.11	x				
Forage cover	0.07	0.05	x			
Dominating forest	0.61	-0.19	-0.16	x		
Moose index	0.08	**0.82**	0.21	0.63	x	
Study Area	-0.18	-0.13	0.1	0.003	0.06	x

Table 10. Spearman correlation of factors included to the maximal model at the tract spatial scale. There did not occur any strong correlation.

	Study Area	Forage cover	Dominating forest	Moose index	Clear-cut
Study Area	x				
Forage cover	0.25	x			
Dominating forest	0.07	-0.16	x		
Moose index	0.03	0.06	-0.03	x	
Clear-cut	-0.23	-0.13	-0.02	0.07	x

Table 11. Spearman correlation of factors tested at the landscape spatial scale. Some of the factors are strongly correlated, however I tested only one factor at the time thus the correlation did not influence the model.

	Pine	Clear-cut	Forage cover	Moose index	Trees density	Snow cover >10cm	Snow cover >30cm	Snow cover >70cm	Forest site index	Birch	Spruce	Pre-com. thinning	Thinning
Pine	X												
Clear-cut	**0.9**	x											
Forage cover	-0.3	0.1	x										
Moose index	-0.2	-0.1	0.3	x									
Trees density	0.6	0.7	0.1	0.6	x								
Snow cover >10cm	0.5	0.2	**-0.9**	-0.1	0.3	x							
Snow cover >30cm	0.5	0.2	**-0.9**	-0.1	0.3	**1**	x						
Snow cover >70cm	0.2	-0.15	**-0.97**	-0.4	-0.2	**0.87**	**0.87**	x					
Forest site index	-0.3	0.1	**1**	0.3	0.1	**-0.9**	**-0.9**	**-0.97**	x				
Birch	-0.5	-0.7	-0.6	0.1	-0.3	0.5	0.5	0.66	-0.6	x			
Spruce	-0.6	-0.5	0.60	0.4	-0.3	**-0.8**	**-0.8**	-0.66	0.6	-0.2	x		
Pre-com. thinning	-0.1	0.3	**0.9**	-0.1	0	**-0.8**	**-0.8**	**-0.8**	**0.9**	-0.7	0.3	x	
Thinning	-0.1	0.2	**0.9**	0.5	0.3	**-0.8**	**-0.8**	**-0.9**	**0.9**	-0.7	0.7	0.7	x

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