The Effects of Moose (*Alces alces*) Browsing on Boreal Tree Species in Norway and Quebec

Toril Nes

MSc in Biology
Submission date: May 2015
Supervisor: Gunnar Austrheim, IBI
Co-supervisor: James Speed, IBI

Norwegian University of Science and Technology
Department of Biology

Content

Abstract

The circumpolar boreal forest is important for recreational purposes, timber harvesting, game meat and as a CO_2-storage. Biodiversity is important for maintaining these ecosystem services. Many boreal forests are experiencing an increase in the cervid populations. Densities of moose *Alces alces* not seen before in modern history have been reported several places. Knowledge about the interactions between this selective browser and the regenerating forest is therefore of importance for both the forest management in order to preserve biodiversity as well as for the forest industry. The aim of this paper is to study the impacts of moose browsing on tree height and density for early and late successional species in different boreal ecosystems. An experimental design with 51 exclosures and browsed controls in recent clear-cuts in Norway and Quebec (Canada) have been used to document the effects of browsing on a large regional scale.

The deciduous species in both Canada (rowan *Sorbus americana*, birch *Betula papyrifera*) and Norway (rowan *Sorbus aucuparia*, birch *Betula pubescens*) showed an effect of the browsing treatment with a decreased height growth outside exclosures compared to inside exclosures. Balsam fir (*Abies balsamea*) was also affected by the treatment with a reduced height growth outside the exclosures. Spruce did not show an effect of the treatment in neither Norway (*Picea abies*) nor Quebec (*Picea glauca*). The effect of the treatment on the pine (*Pinus sylvestris*) in Norway was not statistically significant.

This study has shown that although the ecosystem is not the same, species in the same successional stage show similar response to browsing. Since the boreal ecosystems around the world have different successional trajectories depending on their biological legacy and productivity, this knowledge is of importance when managing the forest and the cervid population.

Sammendrag

Den boreale skogen er viktig for både friluftsliv, tømmerdrift, jakt og CO_2-lagring. Det biologiske mangfoldet i disse skogene er med på å understøtte disse økosystemtjenestene. Hjortebestandene i boreale skoger øker, og mange steder opplever nå tettheter av elg som ikke tidligere er observert i nyere historie. Kunnskap om interaksjonene mellom elgen som selektiv beiter og skog i regenerasjonsstadiet er derfor viktig for skogforvaltningen med tanke på å bevare biodiversiteten, samt for skogsindustrien. Denne studien ser nærmere på hvordan elgbeiting påvirker høydeveksten og tettheten av tidlige og sene suksesjonsarter i boreale økosystem. Et eksperimentelt design med 51 inngjerdinger og beitede kontroller i nylig hogde hogstfelt i Norge og Quebec har blitt brukt for å dokumentere effekten av elgbeiting på en stor regional skala.

De tidlige suksesjonsartene både i Quebec (Canada) (rogn *Sorbus americana* og bjørk *Betula papyrifera*) og Norge (rogn *Sorbus aucuparia* og bjørk *Betula* pubescens) viste tegn til påvirkning av elgbeiting i form av redusert høydevekst i de åpne kontrollene sammenliknet med innenfor inngjerdingene. Balsamedelgran (*Abies balsamea*) ble også påvirket av beitingen i form av redusert høydevekst i de åpne kontrollene. Gran viste ingen tegn til påvirkning fra beitingen verken i Norge (*Picea abies*) eller Quebec (*Picea glauca*). Påvirkningen fra beitebehandlingen hadde ingen statistisk signifikant effekt på furu (*Pinus sylvestris*) i Norge.

Denne studien har vist at selv om økosystemet ikke er det samme, ser man samme effekt av elgbeiting på tidlige og sene suksesjonsarter. Siden forskjellige boreale økosystem følger ulike suksesjonsveier, grunnet deres ulike biologiske bakgrunn og produktivitet, er dette viktig kunnskap når man skal forvalte skogen og bestanden av hjortedyr.

Introduction

The boreal forest is found in a circumpolar belt between 50 and 70 degrees north. The climatic zone is cool temperate with cold winters, where snow covers most of the vegetation, and relatively short summers (Moen, 1998). The species in the boreal forest are adapted to this harsh climate. Conifers in the genera *Abies, Picea* and *Pinus* are evergreen trees dominating the forest stands. Deciduous species in the genera *Betula, Populus, Alnus* and *Sorbus* are also present in some areas. The community succession is driven by different disturbance regimes varying between the different regions of the boreal forest (Vitt & Bhatti, 2012). The boreal forest is recognized by a landscape with peatlands and lakes fragmenting the forest and allowing for a high diversity in habitats. We know that habitat diversity is important for biodiversity. About 60 percent of the known mainland species in Norway are related to forests (Gjerde et al., 2010). The anthropogenic disturbances in forests, like clear-cuts and land-use changes, we see in the boreal forest today is considered to be the reason why more than 50 percent of the species on the national red list in Norway are found in forests (Gjerde et al., 2010).

A natural forest, meaning a forest with its original forest cover not influenced by human activities (Parviainen, 1999), is rarely found as large monocultures when it comes to age and species compositions. Natural forest disturbance regimes, like fires, insect outbreaks and wind throw, cause forest gaps that allow succession to start over and new species to come in. This landscape heterogeneity creates habitat diversity, something that is associated with high biodiversity. Several species are for example dependent on dead wood or deciduous tree species during some part of their life cycle (Berg et al., 1994; Sverdrup-Thygeson et al., 2014).

Some species are specialized in taking advantage of disturbances by fast growth in the forest gaps where light is abundant (Grime, 1974; Smith & Smith, 2006). In the boreal forest, these species are often deciduous species with a rapid growth and a low tolerance to shade. The early successional species are eventually not able to recruit in the shade under their own canopy and will be outcompeted and overgrown by the late successional coniferous species (Connell & Slatyer, 1977). In the boreal forest, conifers in the genera fir (*Abies*), spruce (*Picea*), pine (*Pinus*) and larch (*Larix*) usually dominate the late successional stage. They are all shade tolerant species with a slower growth than the early successional species. Their stress tolerant traits enable them to grow even if the conditions are not optimal

(Grime, 1977). They will eventually dominate the canopy cover, until a new disturbance comes along and the whole process starts over.

There has been an increase in the cervid populations in many boreal forests in recent years (Austrheim et al., 2011; Rooney, 2001). These large herbivores are selective browsers on the trees in the forest (Mansson et al., 2007). Recent studies suggest that large herbivores play an important role in deciding the forest composition after a disturbance (Hidding et al., 2013; Speed et al., 2013*a*), but successional trajectories are expected to depend on factors like the forestry, climate, herbivore densities and productivity of the area.

Plants and herbivores have coexisted for thousands of years, and most plants have evolved some sort of protection against the browsing or grazing of herbivores. This protection can be in the form of avoidance, either escape or physical or chemical defence, or tolerance to herbivory (Skarpe & Hester, 2008). The avoidance strategy is often seen in the late successional species. Due to their nutrient content or chemical compounds, they are rarely preferred by the moose. The early successional species often show a tolerance to browsing by being able to sustain growth even when heavily browsed (Speed et al., 2013*a*). Thus, there seems to be a correlation between the successional stage a species occupies and its strategy towards herbivory. Therefore, the high moose densities are likely to affect the successional trajectory of the boreal forest.

Climate affects plant growth and development, and is important for how the species are able to tolerate browsing (Augustine & McNaughton, 1998). In the boreal forest, the snow cover protects the young trees from browsing during the winter. The critical phase is when they have grown tall enough to protrude from the snow cover, but not yet tall enough to grow out of reach of the browser and out of the browsing zone. Snow cover can therefore be important for the height growth of preferred species.

Another factor determining the trees ability to withstand browsing is the forest productivity. Several studies have shown that in order to be able to maintain tolerance traits, the ecosystem must be productive and high in nutrients (Edenius & Ericsson, 2015; Skarpe & Hester, 2008).

The boreal forest in Fennoscandia has been harvested for timber for centuries. Forest management is considered one of the most important disturbance factors in today's boreal forests (Edenius et al., 2002; Gjerde, 2010). However, modern forestry differs from earlier forest harvesting in its magnitude (Ostlund et al., 1997).

Around the 1950s, new technologies and machines made it possible to clear-cut larger areas. The large-scale commercial harvesting in Canada started in the 19th century (Drushka, 2003). Before this, the impacts of the Aboriginal people and the early European settlers on the Canadian forests had been relatively small. Logging roads constructed in the middle of the 20th century made it possible to access forest areas earlier inaccessible to large-scale harvesting (Gauthier et al., 2009).

Around the 1950s, the moose population in Norway started to increase. The metabolic biomass of cervids in Norway increased by 276 percent between 1949 and 1999, moose constituting a large proportion of this increase (Austrheim et al., 2011). Although the population is thought to have reached its peak (Milner et al, 2013; Rolandsen et al., 2011), moose densities seen over the last $30 - 40$ years are unlike anything experienced before in modern history. The increase in the moose population started later in Quebec, but also here have they experienced a growth in the moose population. Data from an aerial inventory indicates that the number of observed moose in Matane (Quebec) increased by 235 percent from 1995 to 2007 (derived from St-Louis & Bastille-Rousseau, 2011).

Both forest clear-cutting and herbivore browsing can be seen as disturbances in the forest. Browsing by moose differ from forestry when it comes to specificity and frequency. As mentioned earlier, moose is a selective browser with more impact on the early successional species. The specificity of the browsing disturbance is therefore high compared to that of forestry. Also, a clear-cut resembles a natural disturbance, like an insect outbreak or a wind-throw, when it comes to frequency and return interval by being punctual. Moose browsing, on the other hand, is a chronical disturbance. So although moose disturbance might seem relatively small compared to disturbances caused by forestry (Edenius et al., 2002), the synergetic effect of the combination of moose browsing and forestry can alter the regeneration of the forest (Hidding et al., 2013; Speed et al., 2013*a*).

This study examines the effects of moose browsing on regenerating boreal trees. Exclosures are used to look at how the height growth of two early and two late successional tree species are affected by moose browsing in an early stage of succession following a clear-cut. In order to examine general vs regional responses, data from exclosure studies in two different boreal ecosystems, Norway and Quebec, are compared.

Study questions

Table 1: Study questions and hypothesis for the early successional species.

	The preferred species	
Region	Quebec	Norway
Species	Rowan (*Sorbus americana*) Birch (*Betula papyrifera*)	Rowan (*Sorbus aucuparia*) Birch (*Betula pubescens*)
Study question 1	*How does browsing affect the height growth and density of the early successional species?*	
Hypothesis H$_1$	Browsing will lead to a reduced height growth but an increased density.	
Study question 2	*Will the differences in climate and productivity between Quebec and Norway have an effect on the response of the species?*	
Hypothesis H$_2$	There will be a stronger response of the browsing on the height growth in Norway compared to Quebec. The ecosystem in Quebec will be able to sustain a higher increase in the stem density than Norway.	

We hypothesis that since the early successional species are preferred by the moose, we will see an effect of the browsing treatment on the height growth of both species in both countries. We expect the trees inside the exclosures to grow taller than the trees in the open plots. An earlier study from Norway by Speed et al., (2013*a*), using data from the same exclosure network used here, showed that height growth of 1 meter tall birch and rowan stopped when approximately 45 % of the shoots were browsed. By looking at local moose densities, they were able to link this browsing pressure to a moose density of about 3 moose/km². The study sites in Quebec have moose densities ranging from 0.8 to 3.3 moose/km², and we therefore expect moose browsing to limit height growth for the early successional species assuming a similar browsing pressure for the preferred species in Quebec as well.

We expect the total stem density to be higher in the open plots. Earlier studies of moose browsing on birch have shown that the shoot density increases with browsing (Bergstrom & Danell, 1987). Rowan has the ability to reproduce vegetatively through root suckers and stump sprouts (Hamberg et al., 2011;

Zerbe, 2001), a growth form that would be expected if heavy browsing prevents it from reaching maturity.

The ecosystem in Norway is less productive than the ecosystem in Quebec, and we therefore expect to see a stronger effect of the browsing treatment on the height growth of the early successional species in Norway. The higher productivity in Quebec is also the reason we expect the density to be higher in Quebec than in Norway. There are more palatable species in Quebec, so the browsing pressure on the preferred species in our study, birch and rowan, is likely to be smaller.

Table 2: Study questions and hypothesis for the intermediately preferred, late successional species.

	The intermediately preferred species	
Region	Quebec	Norway
Species	Balsam fir (*Abies balsamea*)	Pine (*Pinus sylvestris*)
Study question 3	*How are the intermediately preferred species affected by moose browsing?*	
Hypothesis H_3	Browsing will lead to a reduced height growth and a reduction in density.	
Study question 4	*Although not in the same genus, are the responses to browsing in these two intermediately preferred species comparable?*	
Hypothesis H_4	Yes, they are comparable due to similar preference by the moose and the similar growth pattern and browsing tolerance.	

Since both pine and balsam fir are intermediately preferred by the moose, we expect to see some effect of the browsing treatment on the height growth of both species. The height growth has been reported to be prevented when only 30 percent of the shoots are being browsed (compared to 45 percent for rowan and birch) (Speed et al., 2013*a*). But since the coniferous species are less likely to be browsed than the deciduous species we expect the impact of the browsing to be less compared to the early successional deciduous species. When moose densities are high, these species will probably also experience browsing (Hornberg, 2001).

Table 3: Study questions and hypothesis for the unpreferred, late successional species.

	The least preferred species	
Region	Quebec	Norway
Species	Spruce (*Picea glauca*)	Spruce (*Picea abies*)
Study question 5	*How does moose browsing affect the height growth of the spruce?*	
Hypothesis H$_5$	Browsing will not have a strong effect on the height growth of spruce, but we expect to see an increase in height growth outside the exclosures.	
Study question 6	*Are the responses to browsing the same for two different spruce species in two different regions (Norway and Quebec)?*	
Hypothesis H$_6$	Yes, they are comparable due to similar growth pattern, preference by the moose and browsing avoidance strategy.	

We do not expect to see a negative effect on the height growth of spruce in the open plots in this study. The likelihood of moose browsing on spruce is relatively small, as is the browsing intensity. Earlier research has also shown that spruce is able to maintain height growth even when 60 percent of the shoots are being browsed (Speed et al. 2013*a*). Since we expect the height growth of the early successional species to be limited in the open plots, we expect a positive effect of the reduced competition on the height growth of the spruce in the open plots. In an exclosure study on Anticosti Island in Quebec, they found that spruce grew taller in plots that had experienced browsing in the first seven years following a clear-cut, so-called delayed exclosures, compared to both open plots and plots exclosed immediately after the clear-cut (Hidding et al., 2013). The delayed design is similar to what we have for the exclosures in Norway. If we assume the same response, we will see an increased height growth in the exclosed plots compared to the open plots in Norway. This would be the opposite of what we have hypothesised (H$_5$).

Since many of the sites in Norway are planted with spruce, we do not expect the treatment to have an effect on the density of the spruce.
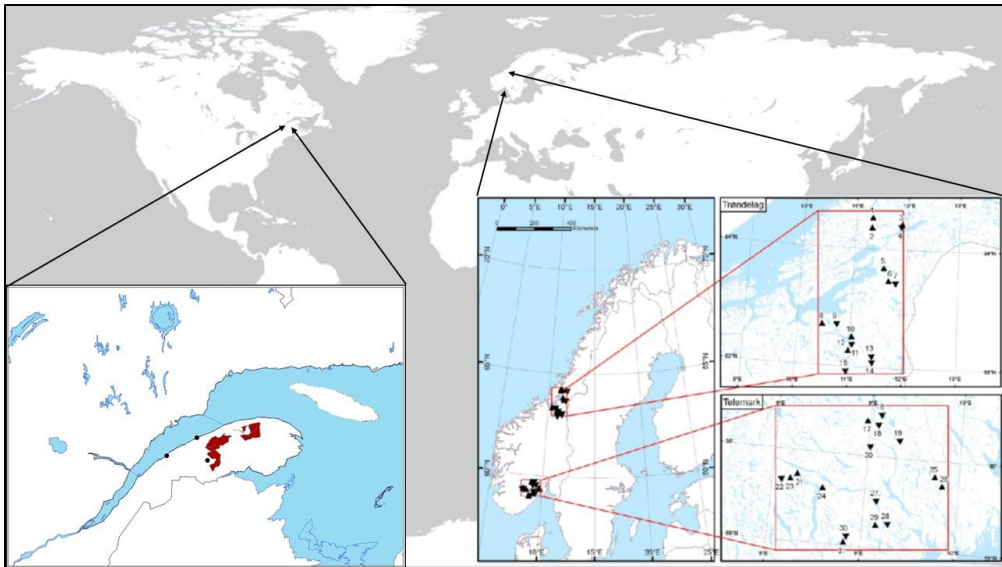
Method

The study area

Figure 1: Map shown the study area. In Norway, there are 31 sites (16 in Telemark and 15 in Trøndelag). In Quebec, there are 20 study sites (10 in Matane, 5 in Chic-Choc and 5 in Causault. These areas are marked with red on the map to the left). (Maps extracted from Speed et al. (2013a) and Sébastien Lavoie (unpublished)).

Site description

This is a comparative study between boreal forest in Quebec and Norway, separated by the Atlantic Ocean.

Due to the population pattern in Norway, with a widespread settlement, most parts of the boreal forest in Norway have been influenced by human activities in some way or another throughout recent history. The forest has been burned, used for timber harvesting and livestock grazing for generations (Gjerde, 2010). Today 97 percent of the productive forest is used for forest production (Larsson & Hylen, 2007).

In Norway, the study sites range from 59 degrees north to above 64 degrees north in the counties Telemark in southern Norway and Trøndelag in mid-Norway. There are 31 sites each comprising of one exclosed plot and one open plot. The plots are located in clear-cuts and the exclosures were put up between 1 to 10 years after the clear-cutting. No baseline data was collected. None of the sites have had scarification or cutting of non-commercial trees after a cut. 16 of the sites were located in spruce forests. 14 of these were planted with spruce after the cut, 1 with

spruce *and* pine and 1 site was not planted at all. 15 of the sites were in pine forests. Of these, 1 was replanted with pine, 1 with spruce *and* pine, 4 with spruce and the remaining 9 sites were not planted after the clear-cut (Speed et al., 2013*a*).

Quebec does not share the history of wide-spread settlement and forest utilization that we see in Norway. Therefore, the forest succession in Quebec has historically been driven by a natural disturbance regime dominated by insect out-breaks and wind-throw. Today, however, the forest industry is important for the disturbance regime of the forest by clear-cutting large areas on the Gaspésie peninsula.

The study sites in Quebec are spread out on the Gaspésie peninsula (around 48 degrees north) in three different territories; Matane wildlife reserve, Chic-Choc wildlife reserve and ZEC (zone d'exploitation contrôlée) Casault (see the red area on the map in figure 1). The study areas in Quebec are all in recent clear-cuts located in balsam fir – white birch forests. The exclosures were put up the summer immediately after the cutting. Four of the 20 sites in Quebec are located in plantations where the woody debris after the clear-cutting was removed and spruce planted. The other sites have not had any form of treatment or planting after the clear-cut.

Browsers
There are populations of moose (*A. alces*), roe deer (*Capreolus capreolus*) and some red deer (*Cervus elaphus*) in the study areas in Norway. The most important browser in the study sites in Norway is the moose. The metabolic biomass of moose in the study sites is estimated from observational data provided by moose hunters. This data is considered to be of high quality (Solberg et al., 2006; Ueno et al., 2014). The metabolic biomass of moose in the study sites varies from about 29 kg/km^2 to about 112 kg/ km^2 (Speed et al., 2013*a*)

The most abundant browser in the study areas in Quebec is the moose. There are also hare and some white-tailed deer (*Odocoileus virginianus*) present. The moose densities in Quebec are based on aerial surveys of the area. The accuracy of these measures is considered to be lower than that of hunter-harvest observational data. The estimated moose densities for the different territories is 3.3 moose/km^2 (Matane), 1.1 moose/km^2 (Chic-Choc) and 0.8 moose/km^2 (Casault).

In addition to the ungulate herbivores, there are also free ranging livestock populations in all the areas in Norway during summer time. This is mainly sheep and cows from the nearby farms. These animals are grazers and do not have the

same effect on the regrowth of the forest as the browsing ungulates. Also, the livestock are only present during summer, and we use data on the winter browsing, so their presence is not taken into consideration in this paper. There are no livestock populations in the study areas in Quebec.

Experimental design

The data in this paper comes from ongoing research programs in both Norway and Quebec. The experimental design is relatively similar in the two regions. Both experiments use exclosures to prevent browsing in certain plots and open control plots where browsing can occur to look at the effect of moose browsing on the regeneration of the forest in clear-cuts. To ensure that any differences detected are due to browsing, the plots were marked out in homogenous vegetation, and randomly assigned as open or exclosed (Newton, 2007).

In Norway, each site has one exclosed plot and one open plot randomly selected, but with a minimum of 20 meters separating them in order to minimize edging effects (Speed et al, 2013*a*). The plots are 20 x 20 meters, and the exclosure has a 2.5 meters tall fence to prevent large herbivores from entering the exclosure. Within each plot there are four circles with a radius of 2 meters, these are referred to as subplots. The data used in this paper comes from these subplots where all the trees are counted and divided into height classes. The height class intervals are 50 cm, the first class from 1 to 50 cm, the second starting at 51 cm and up to 100 cm and so on. Only the height classes 1 to 4 (1- 200 cm) are used in this paper.

The experimental design is quite similar in Quebec. There are 20 sites with one exclosed plot and one open control plot in each site. Of these 20, four sites are located in plantations. The plots are 14 x 28.5 meters and the exclosed plot has a 3 meters tall fence to prevent the intrusion of large herbivores. Within each plot there are 12 circular subplots with a radius of 1.13 meters. The tree height data is collected from these subplots and the total area of these subplots is comparable to the area of the subplots in Norway (48 m^2 in Quebec and 50 m^2 in Norway). The exclosures in Quebec were put up immediately after the clear-cut. The first year of sampling was termed year 0 in Quebec, and represents the baseline data for the site. This is because the effect of the treatment (exclosed/open) was not considered to have had an effect yet. The first data sampling in Norway started 1 year after the exclosure was set up, and is termed year 1.

Data collection

The data used in this paper was collected in Telemark and Trøndelag in Norway between 2008 and 2014, and in Quebec between 2010 and 2014. The data was collected in late spring/early summer after the snow had melted, but mainly before the buds had burst. The timing of the data collection made it possible to look at the winter browsing without interference from the summer browsing.

Within each circular subplot all the trees were counted and the height was measured. The trees in Norway were only registered in height classes whereas the trees in Quebec were registered with their individual height.

Data analyses

This paper is based on a quantitative analysis of the height data of rowan, birch, balsam fir, pine and spruce from the SUSTHERB project in Norway and the FORESTQ project in Quebec.

Because not all the exclosures were put up in the same year in Norway and Quebec, the years have been converted to "years following exclosure" to make it easier to compare the regions. The tree heights from Quebec were originally measured on a cm scale for each individual tree, but have been grouped into similar height classes as the height classes measured in Norway for better comparison.

Since this paper aims to look at the effect of browsing on the early successional stages, only height classes 1 to 4 (1 cm to 200 cm) are presented in the graphs. This will also make it easier to read and interpret the graphs.

The data has been analysed in R and the model *cumulative link models* (CLM) using the package *ordinal* (Christensen, R. H. B. (2013)). This model is similar to the linear models, but treats the response variable as ordinal. Since we have divided the height of the trees into classes, this model was considered to be the best model.

Since we were interested in the effect of browsing (treatment) over time, we wanted to test how the interaction of the treatment over time would affect the height growth of the trees. The data was fitted with a cumulative link model. Height class was the response variable, and the interaction between treatment and time was the explanatory variable. This was done for each species in each treatment. A summary of the models is presented in the result section (table 4).

Results

		Quebec n=20				Norway n=31			
		Estimate	Std. Error	Z value	Pr(<|z|)	Estimate	Std. Error	Z value	Pr(<|z|)
Rowan	Treatment	-0.01	0.28	-2.15	0.031	-0.29	0.31	-0.94	0.348
	Time	0.23	0.07	3.26	0.001	0.21	0.07	3.15	0.002
	Treatment:Time	0.78	0.10	7.54	4.55e-14	0.52	0.08	6.11	9.82e-10
Birch	Treatment	-0.57	0.31	-1.84	0.065	-0.31	0.22	-1.43	0.153
	Time	-0.35	0.09	-4.10	4.12e-05	0.25	0.04	6.33	2.43e-10
	Treatment:Time	0.70	0.11	6.40	1.60e-10	0.22	0.05	4.04	5.25e-05
Balsam Fir / Pine	Treatment	-0.23	0.09	-2.57	0.010	-0.19	0.36	-0.53	0.596
	Time	0.03	0.02	1.47	0.143	0.34	0.06	5.42	5.85e-08
	Treatment:Time	0.12	0.03	3.53	4.42e -4	0.08	0.09	0.93	0.351
Spruce	Treatment	-0.34	0.34	-1.01	0.313	0.19	0.23	0.80	0.421
	Time	0.02	0.10	0.21	0.835	0.42	0.04	9.84	<2e-16
	Treatment:Time	0.10	0.13	0.74	0.459	6.7e -3	0.06	0.12	0.906

The early successional species

From table 4 we see that there was a significant interaction between the time and treatment in determining the height distribution of rowan (Quebec: Z=0.78, p<0.05, Norway: Z=0.52, p<0.05) and birch (Quebec: Z=6.4, p <0.05, Norway: Z=4.04, p<0.05). The difference between the two treatments is presented visually in figure 2 (appendix). For the deciduous tree species, height class 1 (1-50 cm) was no longer the dominate class for the relative proportion of trees in the exclosed plots by the end of the study (figure 3, appendix). For all the open plots except birch in Norway, height class 1 was still the dominant class by the end of the study. The total tree density increased throughout the study in all treatments in Quebec, whereas no increase was detected for any of the treatments in Norway (figure 2).

The interaction between treatment over time had a significant effect on the height growth of rowan (*S. americana*) in Quebec. Inside the exclosures, height class 2 (51-100 cm) was the dominant height class by the third year of this study (figure 3). Height class 1 had the highest relative proportion of trees in the open plots, although the proportion of trees in height class 2 was almost the same by year

three. The total density of trees per m² increased from about 0.05 to about 0.25 trees per m² in both the open and the exclosed plots (figure 2).

In the first year of the study, height class 1 was the height class with the highest relative proportion for rowan (*S. aucuparia*) in both treatments in Norway (figure 3). After three years of treatment, height class 1 and 2 were almost identical in relative proportion in the unbrowsed treatment. The total density of trees per m² decreased from a peak of about 0.75 trees per m² in year two to about 0.5 trees per m² in year five. The open plots were dominated by trees in height class 1 all five years of this study. There was a small increase in the proportion of trees in height class 2 throughout the study. A small decline in total density was detectable from a peak of about 0.6 trees per m² in year two, to about 0.5 trees per m² in year five.

Birch (*B. papyrifera*) was present in low numbers in height class 1 and 2 immediately after the cut (year zero) in both treatments in Quebec. The total density of trees increased considerably, from less than 0.1 trees per m² in year one to about 0.4 trees per m² in year two, in the exclosed treatment (figure 2). By the third year, the density had increased to about 0.7 trees per m². In the open treatment, the total density increased from less than 0.1 trees per m² in the first year to about 0.25 trees per m² in year two and 0.4 trees per m² in year three. In year three, there were trees in all four height classes, with height class 3 and 4 having a relative proportion of a little less than 0.2, and height class 1 and 2 having a proportion of a little less than 0.4.

In Norway, trees in height class 1 dominated the height class distribution of birch (*B. pubescens*) the first two years of the study for both treatments (figure 3). In the exclosed plots, height class 2 had the largest relative proportion of trees by the third year of the study. By the fifth year, height class 1, 2 and 3 were almost equally represented in relative proportion in the exclosed treatment. The total density was relatively stable throughout the study for both treatments, with a density of about 0.4 trees per m² for the exclosed treatment and 0.5 trees per m² for the open treatment. Height class 1 was the dominant height class the first four years of the study in the open plots. Height class two increased throughout the study. By year five, the relative proportion of trees was about the same (0.4) in height class 1 and 2 for birch in the open plots. Height class 3 and 4 were present with a proportion of about 0.1 throughout the study in the open plots.

The intermediately preferred species

There was a significant effect of the interaction between the browsing treatment and time for the balsam fir in Quebec (Z=3.53, p<0.05, table 4). This was not the case for the pine in Norway (Z=0.08, p=0.351). Both species showed an increase in total density throughout the study (figure 2).

Balsam fir had the highest total density of all the species at the beginning of the experiment, with about 0.6 trees per m^2 in the exclosed plots and 0.8 trees per m^2 in the open plots. For the exclosed plots, the density increased to about 1.0 trees per m^2 the first year. No increase was detected in the second year with treatment, but the third year, the density increased to 1.5 trees per m^2. The total density was stable from year zero to year two in the open plots, and increased to about 1.3 trees per m^2 in year three. Height class 1 was the most abundant height class throughout the experiment with a proportion of about 0.8 for both treatments (figure 3). This proportion stayed stable for the open plots, but decreased to about 0.6 in the exclosed plots as height class 2 increased from a proportion of about 0.2 to 0.3. All four height classes were present from the beginning, although the relative proportion of trees in height class 3 and 4 was low for all the years in both treatments.

Pine increased steadily from around 0.15 trees per m^2 in year one to about 0.4 trees per m^2 in year four in the exclosed plots in Norway. There was no sign of an increase from year four to five in total density. In the open plots, the total density of trees was relatively stable around 0.2 trees per m^2 the first three years of the study. This increased to about 0.4 trees per m^2 in year four with a small decrease in year five. Height class 1 was the most abundant height class in all years for both treatments. In year one, the proportion of trees in height class 1 was close to 1.0. This proportion dropped to about 0.6 in year four of the exclosed treatment before it increased to about 0.9 in year five. Height class 3 and 4 had a relative proportion of less than 0.2. The proportion of trees in height class 2 increased throughout the study from around 0.1 to 0.3 in the open plots. In the open plots, the proportion of trees in height class 1 dropped to about 0.7 in year five.

The late successional species

There was no effect of the interaction between treatment and time on the spruce in neither Norway nor Quebec (Quebec: Z=0.74, p=0.459, Norway: Z=0.12, p=0.906, table 4).

In Quebec, both the open and the exclosed plots showed a small increase in the total density, from less than 0.05 trees per m^2 in year zero to about 0.15 trees per m^2 in year three (figure 2). The trees were mainly in height class 1 in year zero and year one, but in year two and three both height class 1 and 2 had a proportion of about 0.5 in the exclosed plots. In the open plots, both height class 1 and 2 had proportions of about 0.4 in all the years of the study.

For spruce in Norway, there was a decrease in density, from about 0.5 in year one to about 0.25 trees per m^2 in year five for the exclosed treatment and from about 0.4 at the start of the study to about 0.25 trees per m^2 at the end of the study in the open treatment. Height class 1 was the most abundant height class the first four years of the study for both treatments (about 0.6). Height class 2 had a proportion of about 0.2 the first four years for both treatments. In year five, all four height classes were present with proportions ranging from 0.1 to 0.35 for both treatments.

Discussion

The moose population has increased in boreal ecosystems in both Norway and Quebec in recent time. However, moose is a selective browser, and little is known about how it affects the regrowth of early vs late successional boreal tree species.

A large-scale regional exclosure study was performed across the Atlantic to examine the effects of moose browsing on tree regrowth in recent clear-cut areas. Data was collected from unbrowsed exclosed plots and compared to browsed control plots.

As expected, we documented a reduction in height growth for the early successional deciduous species in the open plots compared to the exclosed plots in both regions. Both balsam fir and pine are intermediately preferred by the moose and we saw some effects of the treatment on both species, although it was not statistically significant for the pine in Norway. There was no detectable difference in the height growth of spruce between the two browsing treatments in any of the regions. These results imply that moose browsing is affecting the tree species at early and late successional stages differently, which might affect the successional trajectories of the ecosystem.

The early successional species

The deciduous trees showed a strong response to the browsing treatment as predicted (H_1, table 1). The trees protected from browsing inside the exclosures were able to grow into height class 4 (151– 200 cm) in both Norway and Quebec within the time frame of the experiment. A study from Ireland, where they looked at unthinned stands of downy birch, showed that the trees had the most rapid growth the first 20 years. Some trees had the capacity to grow more than 1 meter per year within this period (Nieuwenhuis, M., & Barrett, F. 2002).

When exposed to browsing in the open plots, we saw a reduction in the height growth of these early successional species. The main proportion of the deciduous trees in the open plots was in height class 1 and 2. Only a small proportion of the birch in Norway was able to grow into height class 3. These results are concurrent with the estimates of the browsing zone stretching from about 0.5 meters and up to 3 meters. As this study looks at winter browsing, the height of the snow layer is therefore often the lower limit for browsing. A similar browsing study from Sweden showed that a fraction of 0.107 of the rowan below 1 meter were able to transition

into a height class of 100 -200 cm inside exclosures. Outside exclosures, this fraction was only 0.051 within the five year time frame of the study (Edenius, 2015). These heights are equivalent to the transition from height class 2 to 3 in our experiment (from 1 meter to 1.5 meters). Like in Sweden, we see that this seems to be the difficult leap to take for the rowan in the open sites both in Norway and Quebec. We expect this to be because above these heights, the trees will no longer be protected from browsing by the snow during winter. According to data on snow depth from Norway (Daverdin, unpublished data), the maximum snow cover varied between 56 cm and 110 cm the winter of 2010/2011 for the sites. This is concurrent with the height class transition with which they struggle.

Apart from the rowan in Norway, the browsed trees in the open plots showed no sign of reduction in the total density of trees per m^2. Both the deciduous tree species in Quebec increased in abundance the first three years of the study, although they did not seem capable of growing above height class 2. The increase in density was therefore mainly due to an increase in height class 1 and 2 in the open plots. The increase in density can be seen as a tolerance trait to resist herbivory while waiting for a window of opportunity to grow out of the browsing zone. Skarpe and Hester (2008) discuss the different strategies plants can have to minimize the negative effects of herbivory. Tolerance, rather than avoidance, can be an effective strategy in resource-rich environment. Growth and numerous protected meristems are considered one of the tolerance strategies. These traits, in combination with browsing, have been suggested to cause what might be a browsing lawn (Speed et al. 2013*a*). Cromsigt (2011) define a lawn as "*a grazed or browsed patch in which intense foraging leads to increased resource availability and a proportional increase of palatable plant species in the patch*". This is supported by Olofsson et al. (2001) who found that plants with tolerance traits are often preferred by the herbivores. They tend to increase in resource-rich environments and thereby cause a positive feedback loop between the herbivores and the plants due to enhanced nutrient cycling. A recent study from Sweden, where they looked at the effects of browsing on recruitment (the transition from less than 1 meter up to heights of 100-200 cm) of aspen and rowan showed that rowan was able to recruit even with high levels of browsing (Edenius, L., & Ericsson, G. 2015). However, this was not the case for rowan in a study looking at the effects of red deer browsing in western parts of Norway (Speed et al. 2013*b*). Edenius suggests that this might be due to differences in soil productivity. Another study looking at sheep grazing and browsing in the mountains of Norway showed a stronger reduction in net annual growth of birch saplings in the highest altitudes

compared to lower altitudes due to browsing (Speed et al., 2011). The climatic conditions are considered to be more harsh at high altitudes, which might explain why the response to the sheep browsing is highest at high elevations. In our study, the ecosystem in Quebec is more productive than the Norwegian ecosystem, which might explain why we see an increase in the total density of deciduous trees in the open sites in Quebec but not in Norway. Our results therefore support the browsing lawn concept when the ecosystem is productive.

Another explanation for the difference in the density pattern between the two regions might be because the Norwegian experiment is in fact a delayed exclosure experiment. The exclosures were put up 1 to 10 years after the initial clear-cut. The browsing lawn might therefore already have been formed and reached its full potential when it comes to the number of stems the area can sustain in the years from the cut to the exclosures were set up. We see that the total density of stems in the first year in the open plots in Norway is already much higher than the total stem density in the third year in Quebec. Because of the differences between the two experiments, it will be interesting to follow the density of the deciduous trees in the open plots in Quebec. This data can be compared to the Norwegian data when they have been exposed to browsing for an equivalent amount of time to see if the difference in soil productivity can sustain a higher density of deciduous stems in Quebec.

The intermediately preferred late successional species

Balsam fir is a palatable, late successional species. The study sites in Quebec are located in forests known as balsam fir – paper birch forests. As hypothesised (H_3, table 2), our experiment showed an effect of the interaction between treatment and time on the balsam fir. A study from Anticosti Island, where they looked at the effects of different white-tailed deer densities on the survival and growth of balsam fir seedlings and saplings, showed that high densities of deer (15 deer/km^2) had a strong negative effect on the growth of balsam fir into the taller height classes (> 30 cm) (Hidding et al. 2012). In our study, where the highest moose densities is estimated to be between 0.8 and 3.3 moose/km^2, we do not see an increase in the proportion of trees in height class 2 (51 cm to 100 cm) for the balsam fir in the open sites. Height class 2 had a stable proportion of about 0.2 throughout the study (figure 3). Since we see an increase in density in the third year (figure 2) there must be an increase in the total number of trees in class 2 in year three. However, in the exclosed plots, we see a decrease in the proportion of trees in height class 1

and an increase in the proportion of trees in height class 2. Moose tend to utilize forest gaps and already established browsing patches (Bjorneraas et al., 2011; Edenius et al., 2002), so the actual moose density in our study sites established in clear-cuts might be higher than estimated and therefore affect the balsam fir in the open plots.

We expected a decrease in the density of both the balsam fir and the pine in the open plots (H₃, table 2). No such decrease has been detected (figure 2). This is not concurrent with a study from Anticosti Island where the stem density of balsam fir decreased with increasing deer densities (Hidding et al., 2012). The balsam fir in our study showed high densities from the beginning of the study with increasing densities throughout the years. This is probably due to their recruitment strategy with an already established seedling bank under the canopy of the mature trees. One could expect some self-thinning in the exclosed plot, but instead we see an increase in density for both treatments for balsam fir. Silvertown and Charlesworth (2001) present the idea that plant weight is important for the rate of self-thinning. It is possible that the balsam fir has not yet reached sizes that cause self-thinning. Also, one of the characteristics of balsam fir stands is their density. The increase in total density for both pine and balsam fir comes mainly from trees in height class 1. This height class is protected from browsing by the snow cover, which can explain why we do not see a reduction in the density.

Our model analysis showed no effect of the interaction between time and treatment on the height growth of pine. Since pine is one of the economically important tree species in Norway, there have been many studies on the effect of moose browsing on this tree species. Most of these studies show a strong effect of moose browsing on the regenerating pine forest. Saether et al. (1992) found that the proportion of pine in the moose' winter diet was around 43%. They also point to the valley Imsdalen where the pine forest has been replaced by the less preferred spruce due to heavy moose browsing on the pine forest.

One of the reasons why we did not see a significant effect of moose browsing on height growth might be due to the growth rate of the pine. Like most other late successional species, they grow slowly and are still protected from winter browsing under the snow cover. Another explanation for why we do not see an effect of the browsing treatment on pine might be the delay between the clear-cut and the treatment (1 to 10 years). The pine trees might already have suffered from browsing for many years, and this can have affected their ability to grow even when released from the browsing pressure inside the exclosures. Hidding et al

(2013) performed an exclosure study on Anticosti Island where they had some exclosures built right after clear-cut and some exclosures built with a delay of seven years. They found that balsam fir did not recover even when released from browsing pressure in the delayed exclosures. This might be the case for the pine in Norway as well, where the exclosed plots experienced some years of browsing before the treatment was initiated. On Anticosti Island, the difference in tree species composition in the sites exclosed immediately after the clear-cut and the sites exclosed after a delay of seven years was interpreted as a possible alternative successional trajectory (Hidding et al., 2013). Although it is too early to draw any conclusions about the late successional forest composition from our study, the moderate height growth of pine in both the exclosed and the open plots indicate that there are effects of the moose browsing on the early regeneration of the pine, although treatment was not statistically significant in model analysis.

We hypothesised that, although the species do not belong to the same genus, they would be comparable (H_4). This was not the case, as the model analysis showed that only the balsam fir was significantly affected by the interaction between treatment and time. Although both are intermediately preferred late successional species, they have different recruitment strategies and their ecosystems have different productivities. Pine might therefore grow more slowly in Norway than balsam fir in Quebec, and the time frame of this experiment might therefore not detect the responses in pine growth.

The least preferred late successional species
The treatment did not have an effect on the height growth of spruce in neither Norway nor Quebec as predicted (H_5). The same result was found for spruce in an exclosure study on Anticosti island. There, the abundance of spruce saplings was not related to the deer densities of the study (Tremblay et al., 2007). Unlike the deciduous species, we did not expect to see an increase in the height growth of spruce in the exclosed sites compared to the open sites since spruce is not a preferred tree species by the moose (Speed et al. 2013*a*). We did, however, expect there to be a positive effect on the height growth of spruce in the open sites. The reason for this was because moose browse on the more competitive deciduous tree species and therefore reduce the competition from these species in the open plots. We did not see an increase in the height growth of spruce in the open plots. An explanation for this can be the tolerance model proposed by Connell and Slatyer (1977). According to the tolerance model, the growth of some species are independent of earlier successional species.

In Grimes CSR-triangle, spruce is a species with an adaptive strategy screwed more towards stress tolerance than the deciduous species that are better competitors. Spruce is able to maintain growth even when light is limited. After a disturbance, the early successional species have a rapid growth that enable them to compete for the light resources the disturbance often offer in form of a forest gap. Spruce grows more slowly, but is able to tolerate growing in the shade of the early deciduous trees, and will eventually dominate the canopy cover. Even though spruce is adapted to growing in the shade, we did expect to see effects of growing without competition from the deciduous trees in the open sites. One of the reasons why we did not see this effect in our data might be the short time frame of the experiment. In a few years, the deciduous trees protected from browsing inside the exclosure might dominate the canopy to a larger extent, and the difference between the two treatments might be more profound. If we look at life history strategies, spruce is slow growing and can be considered a K-selected species. The deciduous trees have rapid growth more like the r-selected species. The short time frame of this experiment might therefore make it easier to detect responses in the fast growing deciduous species, than in the spruce.

Limitations of the study

This study aims to compare the effects of browsing on a large regional scale. However, the ecosystems vary in types of species, productivity, climate and herbivore density. These are differences we can-not control for even though they limit the basis of comparison. The experimental design however, is something we are in control of. The setup of the exclosures is quite similar in both countries, but the fact that the Norwegian exclosures are all delayed to some extent is likely to affect the effect of the browsing treatment. Still, since the ecosystem in Norway is less productive and therefore the processes are slower, this delay has probably had a smaller effect than if the delayed exclosures had been in Quebec.

Another difference between the two study regions is the historical exploitation of the forest. The forests in Fennoscandia have a long history of forestry. Although much of the forest in Quebec has been harvested for nearly a century, the different baselines in what is considered a natural forest are assumed to be significant (Edenius et al. 2002). The high moose densities also have a longer history in Fennoscandia, which might already have affected the species composition of the forest. One could argue that this makes it even more interesting to compare the two ecosystems, since the trends we see in Norway are likely to occur in Quebec as well, given enough time and a continued forestry in combination with high moose densities.

The trees in the exclosures in this experiment experienced no browsing from moose. This is an unlikely situation, since management in both Norway and Quebec have deliberately sought to increase the moose populations. Also, moose and other browsing herbivores have a long history in the boreal forest. Therefore, the data from the exclosed plots in this experiment should not be read as an answer book to how the succession should proceed. Instead, it can be useful to look at earlier experiments where they have investigated different densities of browser and their effect on the tree growth (Hidding et al., 2012; Speed et al., 2011; Speed et al., 2013a). Our exclosed plots work as a contrast to the open plots, rather than representatives for the natural or normal succession.

Implications for successional dynamics

This study shows that different species have different abilities to maintain height growth when exposed to browsing. Earlier studies have shown that this might be due to the moose' preference for some species over others, and that these species therefore experience a different browsing pressure than other, less preferred species (Speed et al., 2013a). What is interesting is the correlation between the effects of browsing and the successional stage the species dominate. We have looked at two early successional species, birch and rowan, and two late successional species, spruce and pine/balsam fir in two different boreal ecosystems. The response to the browsing treatment was quite similar across the Atlantic. Both the early successional species were affected by the browsing treatment and showed signs of limited height growth in the open plots. The late successional spruce was unaffected by the treatment in both regions. The correlation between successional stage and effect of browsing will most likely have an effect on the regenerating boreal forest.

Both rowan and birch are early successional species and therefore they need to be good competitors when resources like light and nutrients are abundant (Myking et al., 2013). Their competitive advantage is their ability to colonize forest gaps, occurring naturally or by human induced activities like clear-cuts, by growing rapidly. The rapid growth might also help them escape out of the browsing zone in windows of opportunity (Grime, 1974; Myking et al., 2013; Speed et al., 2011). With the high browsing pressure we see in many boreal forests today, it is questionable whether these species are able to grow tall before the slow growing late successional species have taken over.

An earlier study looking at the browsing likelihood and intensity of rowan, birch, spruce and pine in the SUSTHERB project suggested that the moose preference for early successional deciduous tree species might slow down the succession (Speed et al. 2013*a*). Since the late successional stage in Norway is a spruce dominated forest, and this species do not seem to be dependent on the earlier deciduous stage, but rather follow the tolerance model (Connell & Slatyer, 1977), there is no evidence for the succession being slowed down by moose browsing.

One could argue that since the height growth of the early successional species is being prevented by moose browsing, this might lead to an acceleration of the succession towards the browsing resistant spruce. However, we do not see an increase in the height growth for the spruce in the open sites, implying that the growth of spruce is independent of the browsing treatment. Rather, there is a tendency for the early stage of succession, recognized by dominance of the fast growing deciduous species, being skipped altogether. In the early years of ecology, the trajectory of the succession was considered to be predetermined (Clements, 1916). This view has, to a large extent, been abandoned today. Hidding et al. (2013) discuss the role of herbivores as triggers for alternative successional trajectories (AST) based on an exclosure study on Anticosti Island. They saw a legacy effect on the species composition of the late successional stage even when the browsing was only present for a limited amount of time in the earliest part of the succession following a clear cut. Spruce, or pine in the less productive areas, usually dominates the late successional stages in Norway. Therefore, the effect of moose browsing might not have an effect on the late successional stages in Norway. In Quebec however, the high browsing pressure might have a different effect on the late successional stage of the forest. The forest here is sometimes referred to as balsam fir – paper birch forest, both of whom are species preferred by the moose. Our experiment indicates that these species will struggle to grow out of the browsing zone during the high moose densities we see today. It might therefore be relevant to talk about an AST driven by moose in the ecosystem in Quebec. Edenius (2015) stresses that the ability to recruit (grow from small trees (> 1 m) up to what he calls medium trees (1 – 2 meters)) is dependent on earlier browsing history, soil fertility and land use. Norway has a longer history of both high moose densities and forestry, so the possibility of moose browsing affecting the successional trajectory is stronger in Quebec than in Norway. Jetté et al. (2009) raises concerns that modern forestry might lead to major changes in today's boreal forest in Canada.

Recommendations for future study and practical applications

Forest succession is a slow process. To be able to see the impacts of moose browsing on the regenerating forest and the successional pathways it is necessary to follow the experiment for more years. Both the SUSTHERB project in Norway and the FORESTQ in Quebec are ongoing projects with annual data collection.

To get a better comparison between the two ecosystems, one might set up delayed exclosures in clear-cuts in Quebec, and exclosures in resent clear-cuts in Norway.

Conclusion

This study has shown that different tree species have different responses to browsing. In our study, moose browsing limits the height growth of the early successional species, but does not seem to have an effect on the late successional spruce species. We only have data for the first few years of succession following a clear-cut, but if the trend continues, we might see a forest where a successional stage dominated by deciduous tree species becomes infrequent due to moose browsing in forest gaps. We see some indications for the formations of what might be a browsing lawn in the deciduous species in our study, but it is too early to say this with certainty.

Acknowledgement

References

Augustine, D. J., & McNaughton, S. J. (1998). Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *Journal of Wildlife Management, 62*(4), 1165-1183. doi: 10.2307/3801981

Austrheim, G., Solberg, E. J., & Mysterud, A. (2011). Spatio-temporal variation in large herbivore pressure in Norway during 1949-1999: has decreased grazing by livestock been countered by increased browsing by cervids? *Wildlife Biology, 17*(3), 286-298. doi: 10.2981/10-038

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M., & Weslien, J. (1994). Threatened plant, animal, and fungus species in Swedish forests- distribution and habitat associations. *Conservation Biology, 8*(3), 718-731. doi: 10.1046/j.1523-1739.1994.08030718.x

Bergstrom, R., & Danell, K. (1987). Effects of simulated winter browsing by moose on morphology and biomass of 2 birch species. *Journal of Ecology, 75*(2), 533-544. doi: 10.2307/2260432

Bjorneraas, K., Solberg, E. J., Herfindal, I., Van Moorter, B., Rolandsen, C. M., Tremblay, J.-P., Skarpe, C., Saether, B.-E., Eriksen, R., & Astrup, R. (2011). Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. *Wildlife Biology, 17*(1), 44-54. doi: 10.2981/10-073

Christensen, R.H.B. (2013). Ordinal---Regression Models for Ordinal Data R package version 2013.9-30 http://www.cran.r-project.org/package=ordinal/

Clements, F. E. (1916). *Plant succession: an analysis of the development of vegetation*. Washington, D. C., USA: Carnigie Institution of Washington.

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist, 111*(982), 1119-1144. doi: 10.1086/283241

Cromsigt, J. P. G. M. & Kuijper, D. P. J. (2011). Revisiting the browsing lawn concept: Evolutionary Interactions or pruning herbivores? *Perspectives in Plant Ecology Evolution and Systematics* 13(3): 207-215

Daverdin, M. (2014). Towards sustainable management of moose, red deer and their food resources. Retrieved August 2014, from the SUSTHERB database

Drushka, D. (2003). *Canada's forest: A history.* Montréal, Quebec: McGill-Queen's University Press

Edenius, L., & Ericsson, G. (2015). Effects of ungulate browsing on recruitment of aspen and rowan: a demographic approach. *Scandinavian Journal of*

Forest Research 30(4): 283-288.

Edenius, L., Bergman, M., Ericsson, G., & Danell, K. (2002). The role of moose as a disturbance factor in managed boreal forests. *Silva Fennica, 36*(1), 57-67.

Gauthier, S., Vaillancourt, M.-A., Kneeshaw, D., Drapeau, P., De Grandpré, L., Claveau, Y., & Paré, D. (2009). Forest Ecosystem Management, -Origins and Foundations *Ecosystem Management in the Boreal Forest* (pp. 13-38). Quebec, Canada: Presses de l'Université du Québec

Gjerde, I., Brandrud. T. E., Ohlson, M., & Ødegaard, F. (2010). Skog –I: Kålås, J. A., Henriksen, S., Skjelseth, S., & Viken, Å. (red.) (2010). *Miljøforhold og påvirkninger for rødlistearter*. Artsdatabanken, Trondheim

Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature, 250*(5461), 26-31. doi: 10.1038/250026a0

Grime, J. P. (1977). Evidence for existence for three primary strategies in plants and its relevance to ecological and evolutionary theory. *American naturalist*. 111(982): 1169-1194

Hamberg, L., Vartiamaki, H., Malmivaara-Lamsa, M., Lofstrom, I., Valkonen, S., & Hantula, J. (2011). Short-term effects of mechanical and biological treatments on *Sorbus aucuparia L.* sprouting in mesic forests in Finland. *Scandinavian Journal of Forest Research, 26*(6), 505-514. doi: 10.1080/02827581.2011.592144

Hidding, B., Tremblay, J.-P., & Cote, S. D. (2012). Survival and growth of balsam fir seedlings and saplings under multiple controlled ungulate densities. *Forest Ecology and Management, 276*, 96-103. doi: 10.1016/j.foreco.2012.03.023

Hidding, B., Tremblay, J.-P., & Cote, S. D. (2013). A large herbivore triggers alternative successional trajectories in the boreal forest. *Ecology, 94*(12), 2852-2860. doi: 10.1890/12-2015.1

Hornberg, S. (2001). The relationship between moose (*Alces alces*) browsing utilisation and the occurrence of different forage species in Sweden. *Forest Ecology and Management, 149*(1-3), 91-102. doi: 10.1016/s0378-1127(00)00547-8

Jetté, J.-P., Vaillancourt, M.-A., Leduc, A., & Gauthier, S. (2009). Ecological Issues Related to Forest Management. In S. Gauthier, M.-A. Vaillancourt, A. Leduc, D. Kneeshaw, H. Morin, P. Drapeau, & Y. Bergeron (Eds.), *Ecosystem Management in the Boreal Forest* (pp. 1-9). Quebec, Canada: Presses de l'Université du Québec

Larsson, J. Y., & Hylen, G. (2007). Statistics of Forest Conditions and Forest Resources in Norway. *Viten fra Skog og landskap 1/07.* Norsk institutt for skog og landskap, Ås, Norway

Mansson, J., Kalen, C., Kjellander, P., Andren, H., & Smith, H. (2007). Quantitative estimates of tree species selectivity by moose (*Alces alces*) in a forest landscape. *Scandinavian Journal of Forest Research, 22*(5), 407-414. doi: 10.1080/02827580701515023

Milner, J. M., van Beest, F. M., & Storaas, T. (2013). Boom and bust of a moose population: a call for integrated forest management. *European Journal of Forest Research* 132(5-6): 959-967

Moen, A. (1998). *Atlas of Norway. Vegetation*. Hønefoss: Norwegian Mapping

Myking, T., Solberg, E. J., Austrheim, G., Speed, J. D. M., Bohler, F., Astrup, R., & Eriksen, R. (2013). Browsing of sallow (*Salix caprea L.*) and rowan (*Sorbus aucuparia L.*) in the context of life history strategies: a literature review. *European Journal of Forest Research, 132*(3), 399-409. doi: 10.1007/s10342-013-0684-3

Newton, A. C. (2007). *Forest Ecology and Concervation - A handbook of Techniques*. New York: Oxford University Press Inc.

Nieuwenhuis, M. & F. Barrett (2002). The growth potential of downy birch (*Betula pubescens* (Elrh)) in Ireland. *Forestry* 75(1): 75-87

Olofsson, J., Kitti, H., Rautiainen, P., Stark, S., & Oksanen, L. (2001). Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography* 24(1): 13-24

Ostlund, L., Zackrisson, O., & Axelsson, A. L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 27*(8), 1198-1206. doi: 10.1139/cjfr-27-8-1198

Parviainen, J. (1999). Strict forest reserves in Europe -efforts to enhance biodiversity and strengthen research related to natural forests in Europe. In J. Parviainen, Little, D., Doyle, M., O`Sullivan, A., & M. Kettunen, & Korhonen, M. (red.) (Eds.), *Research and forest reserves and natural forests in Europeancountries* (Vol. 16, pp. 7-22): EFI Proceedings

Peinetti, H. R., Menezes, R. S. C., & Coughenour, M. B. (2001). Changes induced by elk browsing in the aboveground biomass production and distribution of willow (*Salix monticola Bebb*): their relationships with plant water, carbon, and nitrogen dynamics. *Oecologia, 127*(3), 334-342. doi: 10.1007/s004420000593

Rolandsen, C. M., Solberg, E. J., Herfindal, I., Van Moorter, B., & Saether, B. E. (2011). Large-scale spatiotemporal variation in road mortality of moose: Is it all about population density? *Ecosphere* **2**(10)

Rooney, T. P. (2001). Deer impacts on forest ecosystems: a North American perspective. *Forestry* 74(3): 201-208

Saether, B.-E., Solbraa, K., Sodal, D. P., & Hjeljord, O. (1992). The final report from the project "moose-forest-society". *NINA (Norsk Institutt for Naturforskning) Forskningsrapport, 0*(28), 3-153

Silvertown, J. W., & Charlesworth, D. (2001). Intraspecific interactions *Introduction to Plant Population Biology* (fourth ed.): Blackwell Science Ltd.

Skarpe, C., & Hester, A. (2008). Plant traits, browsing and grazing herbivores, and vegetation dynamics. In I. J. Gordon & H. H. T. Prins (Eds.), *Ecological Studies* (Vol. 195, pp. 217-261)

Smith, T. M., & Smith, R. L. (2006). Community Dynamics. In B. Wilbur (Ed.), *Elements of Ecology* (sixth ed.). San Francisco: Pearson Education

Solberg, E. J., Rolandsen, C. M., Heim, M., Grøtan, V., Garel, M., Sæther, B.-E., Nilsen, E. B., Austrheim, G., & Herfindal, I. (2006). Elgen i Norge sett med jegerøyne - En analyse av jaktmaterialet fra overvåkningsprogrammet for elg og det samlede sett elg-materialet for perioden 1966-2004. In NINA (Ed.), *Rapport* (Vol. 125, pp. 197). Trondheim: NINA

Speed, J. D. M., Austrheim, G., Hester, A. J., & Mysterud, A. (2011). Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. *Forest Ecology and Management, 261*(7), 1344-1352. doi: 10.1016/j.foreco.2011.01.017

Speed, J. D. M., Austrheim, G., Hester, A. J., Solberg, E. J., & Tremblay, J.-P. (2013*a*). Regional-scale alteration of clear-cut forest regeneration caused by moose browsing. *Forest Ecology and Management, 289*, 289-299. doi: 10.1016/j.foreco.2012.10.051

Speed, J. D. M., Meisingset, E. L., Austrheim, G., Hester, A. J., Mysterud, A., Tremblay, J.-P., & Solberg, E. J. (2013*b*). Low intensities of red deer browsing constrain rowan growth in mature boreal forests of western Norway. *Ecoscience* 20(3): 311-318

St-Louis, A., & Bastille-Rousseau, G. (2011). Influence de l'habitat forestier, de la prédation et des modalités de chasse sur l'évolution des densité d'orignaux au Québec. Université Laval, Quebec

Sverdrup-Thygeson, A., Sogaard, G., Rusch, G. M., & Barton, D. N. (2014). Spatial Overlap between Environmental Policy Instruments and Areas of High Conservation Value in Forest. *Plos One, 9*(12). doi: 10.1371/journal.pone.0115001

Tremblay, J.-P., Huot, J., & Potvin, F. (2007). Density-related effects of deer browsing on the regeneration dynamics of boreal forests. *Journal of Applied Ecology, 44*(3), 552-562. doi: 10.1111/j.1365-2664.2007.01290.x

Ueno, M., Solberg, E. J., Iijima, H., Rolandsen, C. M., & Gangsei, L. E. (2014). Performance of hunting statistics as spatiotemporal density indices of moose (*Alces alces*) in Norway. *Ecosphere, 5*(2). doi: 10.1890/es13-00083.1

Vitt, D. H., & Bhatti, J. S. (2012). *Restoration and reclamation of boreal ecosystems. Attaining sustainable development.* Cambridge, UK: Cambridge University Press

Zerbe, S. (2001). On the ecology of *Sorbus aucuparia* (Rosaceae) with special regard to germination, establishment and growth. *Polish Botanical Journal, 46*(2), 229-239

Appendix

Table 5: The result from the hypothesis testing of the effect of variables on the height growth. The effect of variables was tested by comparing Model 2 against a more simple Model 1 using an ANOVA. The likelihood ratio (LR. Stat) and the p-value is presented for each test.

	Tree species	Rowan				Birch			
	Region	Quebec		Norway		Quebec		Norway	
Model 1	**Model 2**	LR. stat	Pr(>Chisq)	LR. stat	Pr(>Chisq)	LR. stat	Pr(>Chisq)	LR. stat	Pr(>Chisq)
Intercept	Time	110.92	2.2e -16	183.06	2.2e -16	3.72	0.054	178.57	2.2e -16
Intercept	Treatment	77.44	2.2e -16	181.89	2.2e -16	167.27	2.2e -16	30.32	3.66e -08
Intercept	Time + Treatment	229.61	2.2e -16	363.74	2.2e -16	170.67	2.2e -16	213.58	2.2e -16
Time + Treatment	Time * Treatment	57.59	3.23e -14	36.54	1.5e -09	40.78	1.71e -10	16.36	5.23e -05

|	Tree species	Balsam fir		Pine		Spruce			
	Region	Quebec		Norway		Quebec		Norway	
Model 1	**Model 2**	LR. stat	Pr(>Chisq)	LR. stat	Pr(>Chisq)	LR. stat	Pr(>Chisq)	LR. stat	Pr(>Chisq)
Intercept	Time	26.98	2.06e -7	77.42	2.2e -16	1.11	0.29	198.75	2.2e -16
Intercept	Treatment	1.08	0.3	1.03	0.31	0.63	0.43	3.73	0.053
Intercept	Time + Treatment	27.69	9.71e -7	78.33	2.2e -16	1.80	0.40	204.06	2.2e -16
Time + Treatment	Time * Treatment	12.46	0.0004	0.87	0.35	0.55	0.46	0.01	0.90
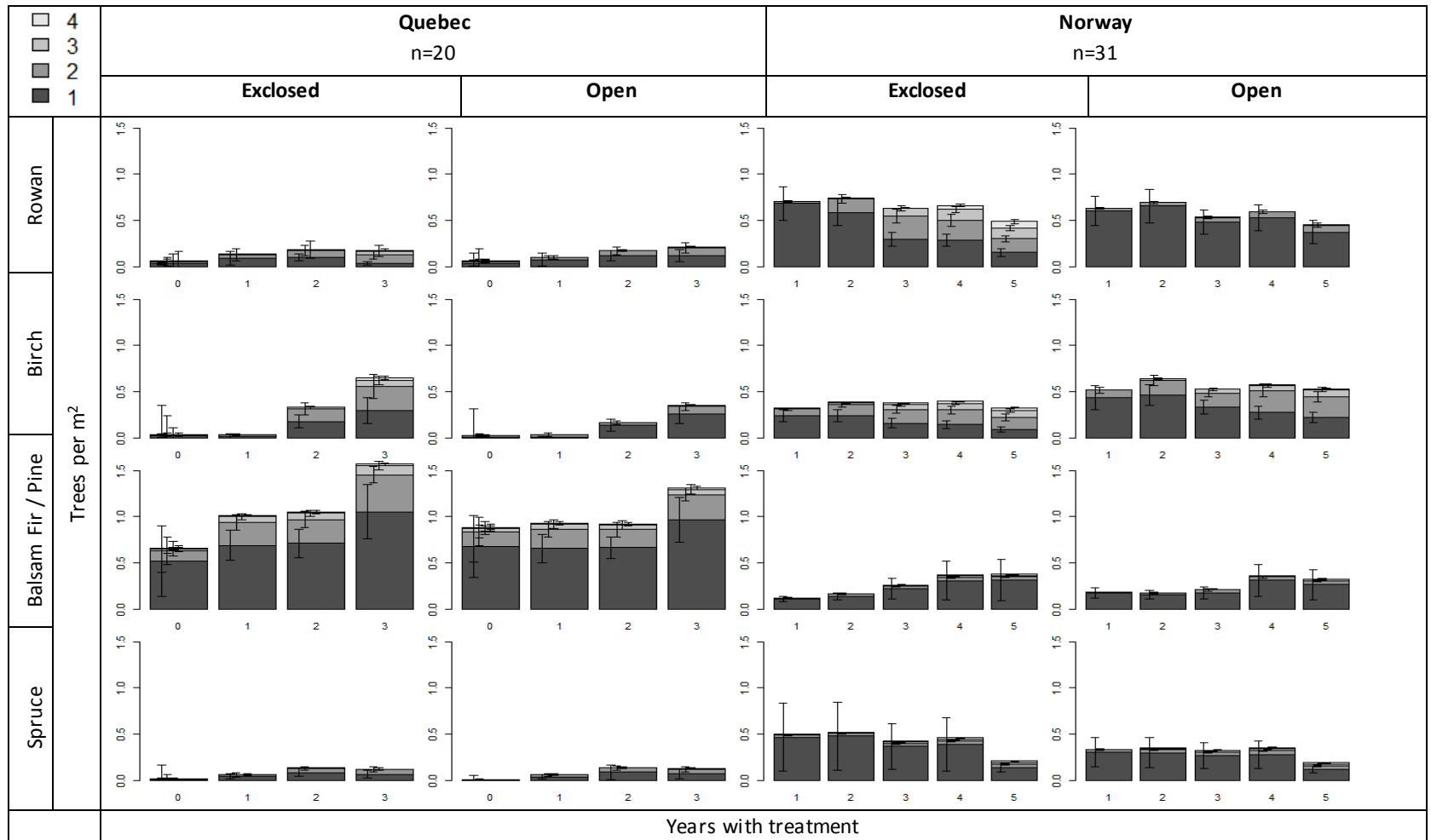
Figure 2: The mean density (trees per m²) of trees in each height class in year 0-3 in Quebec and year 1-5 in Norway, presented with SE. The density is presented for each treatment (exclosed/open) in both regions (Quebec, Norway) and for all tree species. Height class 1-4 are represented with dark grey to light grey colours respectively.
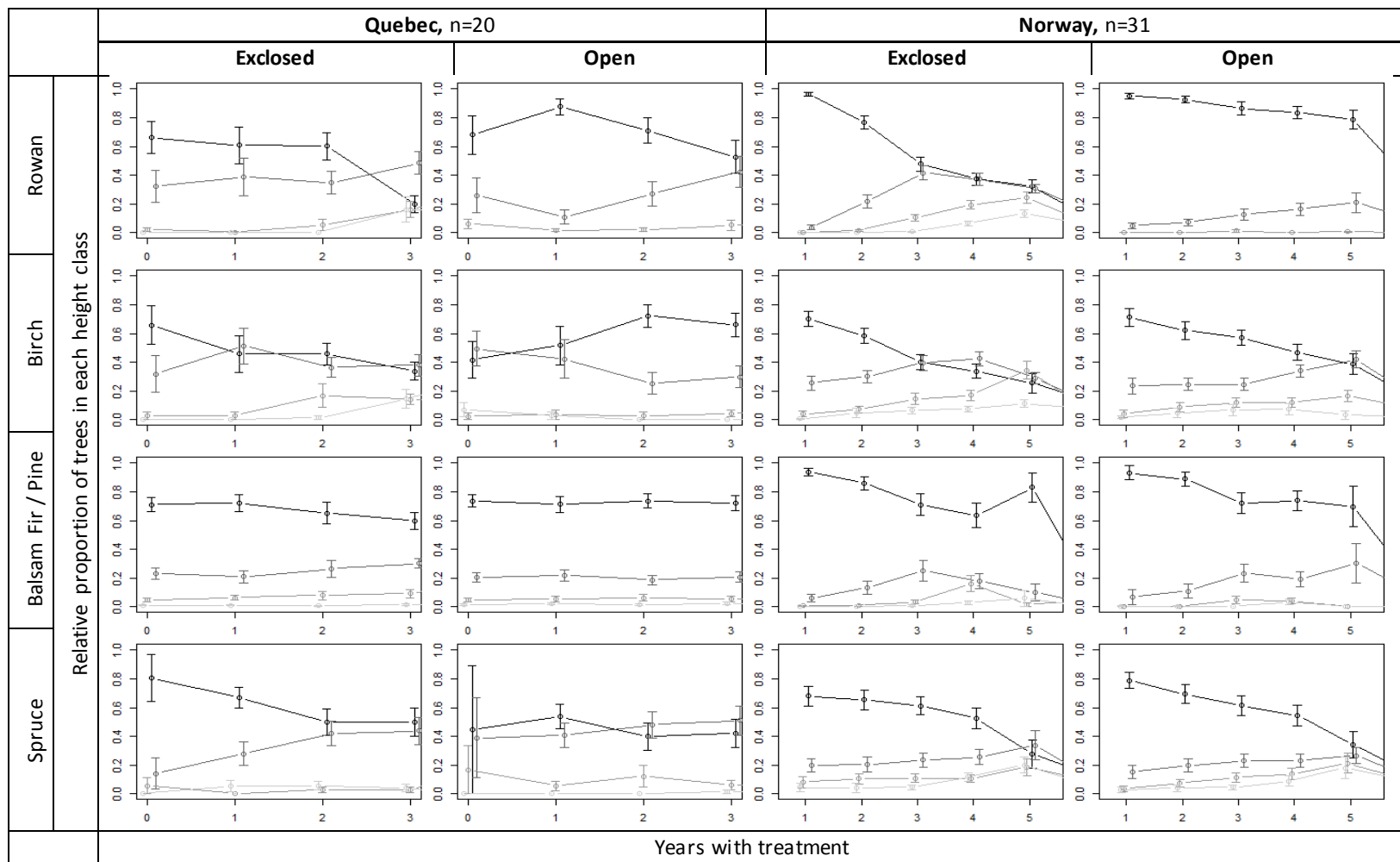
Figure 3: The relative proportion of trees in each height class for each year, presented with SE. Height class 1-4 are presented with dark grey to light grey colours respectively. The graph shows the height class proportion for each species with each treatment (exclosed/open) in each region (Quebec/Norway).