



Regional-scale alteration of clear-cut forest regeneration caused by moose browsing

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ARTICLE INFO

Article history:

Received 12 June 2012

Received in revised form 26 October 2012

Accepted 30 October 2012

Keywords:

Alces alces

Cervid

Boreal forest

Herbivory

Succession

Norway

ABSTRACT

Forests are often managed for the timber resources they contain, but they also provide habitat for large and commonly increasing populations of cervids. Interactions between forest management and cervid browsing are thus of importance, but are rarely investigated except within isolated enclosure studies. In this study we use a regional network of enclosures in the forests of mid and south Norway, where large and recently peaked populations of moose *Alces alces* are present, to assess the impact of moose browsing on forests regenerating after clear-cutting. We found marked influences of moose browsing on tree (individual and population) regeneration following clear-cutting. For the highly selected birch and rowan, which dominate in early successional stages from clear-cuts, height growth of 1 m tall individuals was prevented when around 45% of shoots were browsed. By developing a regional-level relationship between moose density and browsing intensity, this was linked to a density of 3.0 moose km⁻². Pine growth was prevented when 30% of shoots were browsed whilst spruce maintained growth when over 60% of shoots were browsed. Although coniferous species were less likely to be browsed, moose browsing caused apparent slowing of succession from coniferous to deciduous trees in the regenerating forests. The increase in height growth and decrease in density of the deciduous species in the exclusion treatment suggests that intra- and inter-specific competition from unbrowsed stems may cause self-thinning and drive a reduction in the density of deciduous species, and hence a shift in community composition towards a more coniferous state in the absence of moose. By taking a regional approach, this study has been able to link the growth response of trees to moose density, and highlights the key role of cervids in influencing regeneration of managed forests.

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1. Introduction

Boreal forests constitute 34% of the world forests (FAO, 2011) and sustain high demand for timber and non-timber resources. Boreal forests are substantial sinks for carbon and play a role in global climate regulation (Foley et al., 1994). Distinct fauna and flora communities are associated with these ecosystems, including a high richness of species associated with dead wood (Siitonen, 2001). The large cervids of boreal forests (notably moose *Alces alces*) are actively harvested for food and recreational purposes and there are feedbacks between moose populations and boreal forest structure and post-harvest regeneration (McInnes et al., 1992; Edenius et al., 2002; Tremblay et al., 2007). Both natural disturbances (such as fire and wild herbivore populations) and anthropogenic disturbances (including as logging and tree planting) influence boreal forests. The array of disturbance processes

affecting boreal forests and the range of resources exploited or valued within them, makes management of boreal forests a challenge (Niemelä, 1999; Simberloff, 2001).

Across the forests of the northern hemisphere, cervid populations are increasing (Fuller and Gill, 2001; Rooney, 2001; Apollonio et al., 2010). High densities or abundances of cervids can have strong ecological impacts on plant communities and productivity, ecosystem state and wider biodiversity (Côté et al., 2004; Mysterud, 2006; Tanentzap et al., 2009; Newson et al., 2012). The influence of wild cervids can be particularly profound within developing forests (Tremblay et al., 2007; Dufresne et al., 2009). Selective browsing by herbivores can reduce height growth of establishing trees, keeping them at lower heights which allows further browsing (preventing the tree reaching a size refuge) and thus further limiting growth (Speed et al., 2011) and providing apparent competitive gain for less preferred species (Tremblay et al., 2007).

Norway is a country with a large extent of forests, with 28% of Norwegian land (excluding the northernmost county of Finnmark)

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being classified as productive forest, with the vast majority of this (97%) used in forestry production (Larsson and Hysten, 2007). Norway spruce (*Picea abies*) is the dominant species at the most productive sites in many forests, with Scots pine (*Pinus sylvestris*), and certain deciduous species including rowan (*Sorbus aucuparia*) and downy birch (*Betula pubescens*) also commonly occurring. Forest management typically involves clear cutting and replanting (most commonly of spruce, although natural regeneration is lately being used more (Hanssen, 2003)) and 25% of forestry land is in an early successional state (recently clear cut, or planted following clear cut (Larsson and Hysten, 2007)). Large and increasing populations of red deer *Cervus elaphus*, moose *A. alces* and roe deer *Capreolus capreolus* are found in the forests of Norway, a trend concurrent with a decrease in livestock (Austrheim et al., 2011). However, there is large spatial variability in the change in livestock and wild herbivores (Austrheim et al., 2011). This spatial variability, combined with the herbivore-sensitivity of regenerating forests, highlights the necessity for regional-level data on herbivore impacts on forest regeneration in order to facilitate management of ecological and economic resources within forests. In this study we test the hypotheses that the moose-dominated cervid community (1) prevents recruitment and growth of preferred species in regenerating forests and (2) leads to the conversion of the tree community toward browsing resistant species. By using a region-scale cervid-exclosure design in clear cut forests of mid and southern Norway, we assess the moose density at which the growth of trees in regenerating forests is prevented.

2. Methods

2.1. Study design

Two study regions were used to investigate the influence of moose on regeneration of clear-cut forests: Trøndelag in mid-Norway and Telemark in southern-Norway. These regions both have established populations of moose, which appear to have peaked within the last 10–15 years (Rolandsen et al., 2011). Populations of roe deer are also present in both regions, whilst red deer are absent or infrequent. Within each region 15 or 16 sites were selected in clear-cut forests with homogenous vegetation (Fig. 1), stratified by forest productivity and municipality to ensure a wide distribution in each region but within the sub-oceanic climatic zone. Both productive spruce forests and less productive pine forests were included in each region (Table 1). Following the clear-cuts, spruce or pine were planted in most sites without other preparation (Table 1) with a density varying from 1600 to 2000 trees per ha at low and high productivity respectively. Scarification or cutting of non-commercial (deciduous) trees has not been practised in any site after the clear-cuts. In each site two 20 × 20 m plots were established and randomly allocated to exclosure or unexclosed treatments. Exclosures were erected using 208 cm tall woven-wire fences, supported by 3 m stakes sunk into the ground. An additional wire was stretched between stakes, making the fences about 2.5 m tall. There was a minimum distance of 20 m between each plot to minimise edge effects. Exclosures were

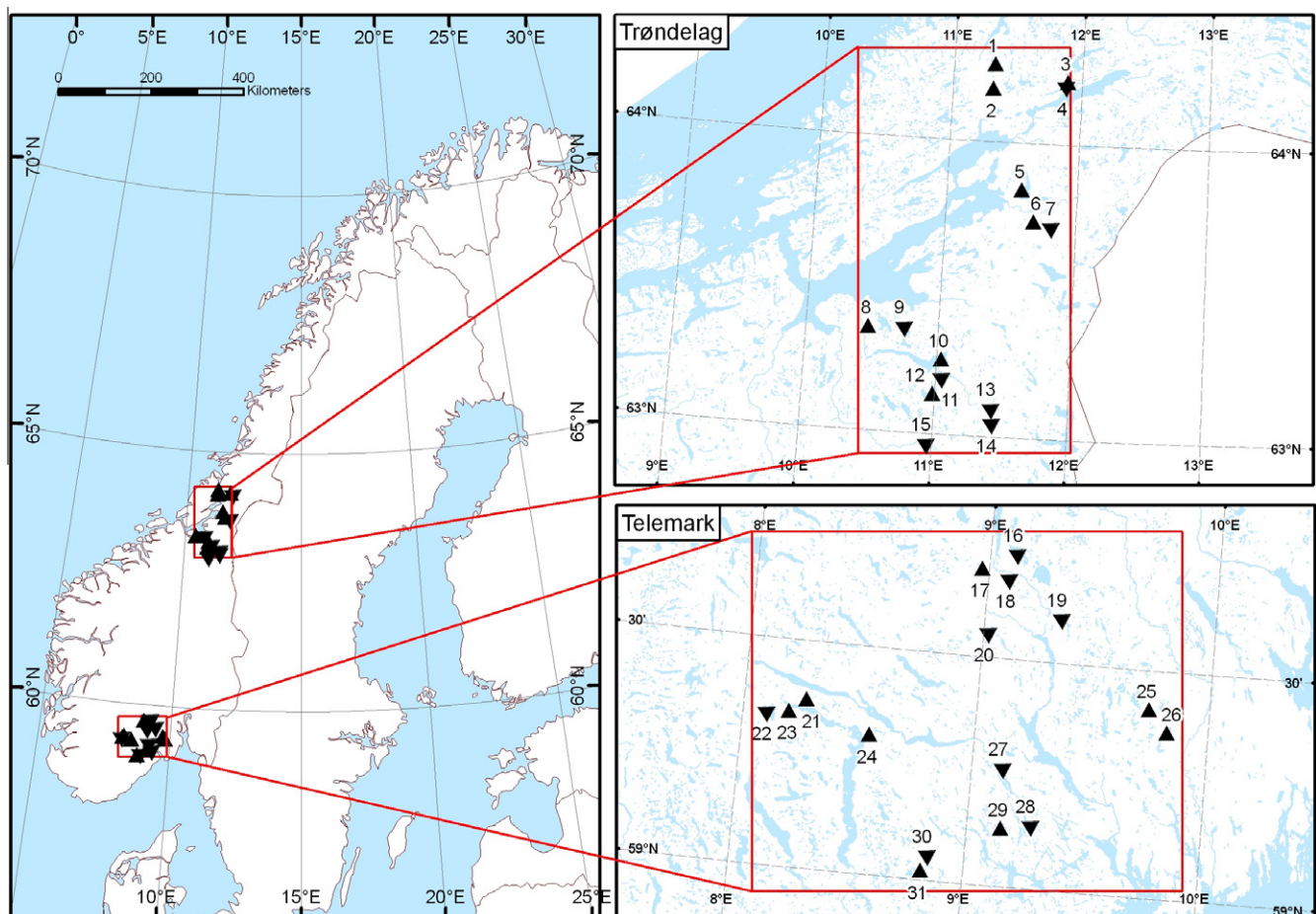


Fig. 1. Location of study sites in Norway. Numerical labels are linked to site names in Table 1. Point-up triangles are less productive spruce forests, and point-down triangles are more productive pine forests.

Table 1

Summary information for the 31 enclosure sites. The site number corresponds to the labels in Fig. 1.

| Site number | Region | Forest type | Clear cut | Species planted after clear cut | Year initiated | Forest productivity ^a | Maximum snow depth ^b (cm) |
|-------------|-----------|-------------|-----------|---------------------------------|----------------|----------------------------------|--------------------------------------|
| 1 | Trøndelag | Spruce | 2004 | Spruce | 2009 | High | 85 |
| 2 | Trøndelag | Spruce | 2006 | Spruce | 2009 | High | 85 |
| 3 | Trøndelag | Spruce | 2005 | Spruce | 2009 | High | 63 |
| 4 | Trøndelag | Pine | 2004 | Spruce | 2009 | Medium | 63 |
| 5 | Trøndelag | Spruce | 2006 | Spruce | 2009 | Medium | 56 |
| 6 | Trøndelag | Spruce | 2003 | Spruce | 2009 | Medium | 56 |
| 7 | Trøndelag | Pine | 2005 | Pine | 2009 | Low | 56 |
| 8 | Trøndelag | Spruce | 2002 | Spruce, pine | 2009 | Medium | 83 |
| 9 | Trøndelag | Pine | 2002 | Spruce, pine | 2009 | Medium | 60 |
| 10 | Trøndelag | Spruce | 2004 | Spruce | 2009 | High | 60 |
| 11 | Trøndelag | Pine | 2002 | None | 2009 | Low | 60 |
| 12 | Trøndelag | Spruce | 2003 | Spruce | 2009 | Medium | 105 |
| 13 | Trøndelag | Pine | 2005 | Spruce | 2009 | Medium | 90 |
| 14 | Trøndelag | Pine | 2005 | Spruce | 2009 | Medium | 105 |
| 15 | Trøndelag | Pine | 2005 | None | 2009 | Low | 85 |
| 16 | Telemark | Pine | 2005 | None | 2010 | Medium | 78 |
| 17 | Telemark | Spruce | 2007 | Spruce | 2010 | Medium | 80 |
| 18 | Telemark | Pine | 2002 | None | 2010 | Low | 78 |
| 19 | Telemark | Pine | 2005 | None | 2010 | Medium | 65 |
| 20 | Telemark | Pine | 2003 | None | 2010 | Medium | 65 |
| 21 | Telemark | Spruce | 2000 | Spruce | 2010 | Medium | 98 |
| 22 | Telemark | Pine | 2007 | Spruce | 2010 | Medium | 98 |
| 23 | Telemark | Spruce | 2004 | Spruce | 2010 | High | 98 |
| 24 | Telemark | Spruce | 2005 | Spruce | 2010 | Medium | 81 |
| 25 | Telemark | Spruce | 2009 | Spruce | 2010 | Medium | 110 |
| 26 | Telemark | Spruce | 2005 | Spruce | 2010 | High | 110 |
| 27 | Telemark | Pine | 2006 | None | 2010 | Low | 89 |
| 28 | Telemark | Pine | 2006 | None | 2010 | Medium | 68 |
| 29 | Telemark | Spruce | 2005 | None | 2010 | Medium | 83 |
| 30 | Telemark | Spruce | 2007 | Spruce | 2010 | Medium | 105 |
| 31 | Telemark | Pine | 2007 | None | 2010 | Medium | 105 |

^a Norwegian Forest and Landscape Institute. Timber productivity per 1000 m² per year. Low: 0.1–0.3 m³ medium 0.3–0.5 m³ high: 0.5–1 m³.^b Data from the nearest weather station with snow observations or automatic measurements for the winter of 2010–2011. Norwegian Meteorological Institute.**Table 2**Density of species by treatment, year and region. Mean m⁻² ± SEM within experimental plots. Number of sites (from 15 in Trøndelag and 16 in Telemark) in which that species was found in that year and treatment is shown in parentheses. Columns are ordered by abundance across regions of species from the most to least abundant.

| Region | Year | Treatment | Rowan | Downy birch | Spruce | Scots pine | Juniper | Aspen | Goat willow | Silver birch |
|-----------|------|------------|-----------------------|-----------------------|-----------------------|-----------------------|----------------------|----------------------|----------------------|----------------------|
| Telemark | 2010 | Exclosed | 0.495 ± 0.145 (15) | 0.267 ± 0.12 (14) | 0.884 ± 0.727 (16) | 0.134 ± 0.036 (13) | 0.009 ± 0.009 (1) | 0.167 ± 0.164 (3) | 0.01 ± 0.007 (3) | 0 + 0 (0) |
| Telemark | 2010 | Unexclosed | 0.349 ± 0.139 (11) | 0.256 ± 0.075 (14) | 0.511 ± 0.31 (15) | 0.162 ± 0.044 (11) | 0 + 0 (0) | 0.187 ± 0.187 (1) | 0.06 ± 0.041 (5) | 0 + 0 (0) |
| Telemark | 2011 | Exclosed | 0.361 ± 0.095 (16) | 0.262 ± 0.08 (16) | 0.905 ± 0.73 (16) | 0.159 ± 0.038 (14) | 0.009 ± 0.009 (1) | 0.081 ± 0.078 (3) | 0.009 ± 0.005 (3) | 0 + 0 (0) |
| Telemark | 2011 | Unexclosed | 0.389 ± 0.14 (13) | 0.351 ± 0.109 (15) | 0.541 ± 0.312 (15) | 0.172 ± 0.041 (13) | 0 + 0 (0) | 0.126 ± 0.126 (1) | 0.037 ± 0.02 (6) | 0 + 0 (0) |
| Telemark | 2012 | Exclosed | 0.228 ± 0.061 (16) | 0.183 ± 0.063 (16) | 0.68 ± 0.492 (16) | 0.174 ± 0.048 (14) | 0.002 ± 0.002 (1) | 0.056 ± 0.052 (3) | 0.01 ± 0.007 (3) | 0 + 0 (0) |
| Telemark | 2012 | Unexclosed | 0.374 ± 0.152 (13) | 0.242 ± 0.07 (15) | 0.482 ± 0.271 (15) | 0.172 ± 0.045 (12) | 0 + 0 (0) | 0.053 ± 0.053 (1) | 0.022 ± 0.012 (6) | 0 + 0 (0) |
| Trøndelag | 2009 | Exclosed | 0.699 ± 0.246 (12) | 0.153 ± 0.033 (13) | 0.08 ± 0.012 (15) | 0.081 ± 0.034 (8) | 0.003 ± 0.003 (1) | 0 + 0 (0) | 0.004 ± 0.003 (2) | 0 + 0 (0) |
| Trøndelag | 2009 | Unexclosed | 0.789 ± 0.276 (15) | 0.509 ± 0.202 (13) | 0.129 ± 0.023 (15) | 0.186 ± 0.112 (9) | 0.029 ± 0.026 (3) | 0 + 0 (0) | 0.023 ± 0.011 (5) | 0.007 ± 0.007 (1) |
| Trøndelag | 2010 | Exclosed | 0.623 ± 0.212 (13) | 0.133 ± 0.033 (13) | 0.081 ± 0.012 (15) | 0.129 ± 0.071 (8) | 0.004 ± 0.004 (1) | 0 + 0 (0) | 0.025 ± 0.017 (3) | 0 + 0 (0) |
| Trøndelag | 2010 | Unexclosed | 0.723 ± 0.265 (15) | 0.378 ± 0.108 (14) | 0.101 ± 0.018 (14) | 0.135 ± 0.092 (8) | 0.017 ± 0.012 (3) | 0 + 0 (0) | 0.036 ± 0.015 (5) | 0.013 ± 0.013 (1) |
| Trøndelag | 2011 | Exclosed | 0.378 ± 0.172 (13) | 0.142 ± 0.024 (14) | 0.08 ± 0.013 (15) | 0.296 ± 0.234 (7) | 0.003 ± 0.003 (1) | 0 + 0 (0) | 0.007 ± 0.004 (3) | 0 + 0 (0) |
| Trøndelag | 2011 | Unexclosed | 0.562 ± 0.218 (15) | 0.285 ± 0.078 (14) | 0.099 ± 0.013 (15) | 0.195 ± 0.128 (9) | 0.012 ± 0.009 (3) | 0 + 0 (0) | 0.036 ± 0.016 (4) | 0.008 ± 0.007 (2) |
| Trøndelag | 2012 | Exclosed | 0.332 ± 0.111 (13) | 0.146 ± 0.024 (14) | 0.073 ± 0.014 (15) | 0.523 ± 0.436 (7) | 0.003 ± 0.003 (1) | 0 + 0 (0) | 0.02 ± 0.013 (4) | 0 + 0 (0) |
| Trøndelag | 2012 | Unexclosed | 0.454 ± 0.103 (15) | 0.244 ± 0.076 (14) | 0.121 ± 0.03 (15) | 0.487 ± 0.372 (11) | 0.016 ± 0.016 (1) | 0 + 0 (0) | 0.049 ± 0.019 (7) | 0.012 ± 0.007 (3) |

established in 2009 in Trøndelag and 2010 in Telemark, between 4 and 8 years following the clear cutting.

Within each plot, four circular subplots with a radius of 2 m were established and marked. Within each subplot, the density

Table 3

Herbivore densities expressed as metabolic biomass (kg km^{-2}) for three cervid species and two livestock species and total of the five species. Metabolic biomass was estimated according to the methods in (Austrheim et al., 2011). Cervid metabolic biomass was calculated on the basis of hunter harvest and observation data over the period 2007–2011 whilst livestock metabolic biomass used the official livestock statistics for the year 2009.

| Site number | Region | Moose | Red deer | Roe deer | Sheep | Cattle | Total |
|-------------|-----------|--------|----------|----------|-------|--------|--------|
| 1 | Trøndelag | 102.11 | 7.31 | 7.46 | 34.09 | 21.94 | 172.91 |
| 2 | Trøndelag | 102.11 | 7.31 | 7.46 | 34.09 | 21.94 | 172.91 |
| 3 | Trøndelag | 106.66 | 1.07 | 22.49 | 47.98 | 28.33 | 206.53 |
| 4 | Trøndelag | 106.66 | 1.07 | 22.49 | 47.98 | 28.33 | 206.53 |
| 5 | Trøndelag | 42.5 | 3.51 | 10.59 | 65.87 | 18.80 | 141.27 |
| 6 | Trøndelag | 42.5 | 3.51 | 10.59 | 65.87 | 18.80 | 141.27 |
| 7 | Trøndelag | 42.5 | 3.51 | 10.59 | 65.87 | 18.80 | 141.27 |
| 8 | Trøndelag | 91.93 | 0.17 | 36.39 | 30.07 | 17.07 | 175.63 |
| 9 | Trøndelag | 91.43 | 0 | 19.7 | 81.11 | 54.32 | 246.56 |
| 10 | Trøndelag | 67.86 | 3.77 | 3.31 | 38.06 | 15.73 | 128.73 |
| 11 | Trøndelag | 67.86 | 3.77 | 3.31 | 38.06 | 15.73 | 128.73 |
| 12 | Trøndelag | 67.86 | 3.77 | 3.31 | 38.06 | 15.73 | 128.73 |
| 13 | Trøndelag | 33.79 | 0.57 | 0 | 8.76 | 8.60 | 51.72 |
| 14 | Trøndelag | 33.79 | 0.57 | 0 | 8.76 | 8.60 | 51.72 |
| 15 | Trøndelag | 28.92 | 4.97 | 1.53 | 93.37 | 39.49 | 168.28 |
| 16 | Telemark | 111.5 | 9.77 | 8.19 | 23.99 | 3.20 | 156.65 |
| 17 | Telemark | 111.5 | 9.77 | 8.19 | 23.99 | 3.20 | 156.65 |
| 18 | Telemark | 111.5 | 9.77 | 8.19 | 23.99 | 3.20 | 156.65 |
| 19 | Telemark | 111.5 | 9.77 | 8.19 | 23.99 | 3.20 | 156.65 |
| 20 | Telemark | 111.5 | 9.77 | 8.19 | 23.99 | 3.20 | 156.65 |
| 21 | Telemark | 91.33 | 17.49 | 5.99 | 46.68 | 9.57 | 171.06 |
| 22 | Telemark | 62.12 | 2.91 | 2.76 | 16.37 | 2.61 | 86.77 |
| 23 | Telemark | 91.33 | 17.49 | 5.99 | 46.68 | 9.57 | 171.06 |
| 24 | Telemark | 91.33 | 17.49 | 5.99 | 46.68 | 9.57 | 171.06 |
| 25 | Telemark | 97.03 | 8.61 | 10.06 | 21.23 | 2.14 | 139.07 |
| 26 | Telemark | 90.21 | 38.62 | 26.41 | 12.13 | 17.01 | 184.38 |
| 27 | Telemark | 60.41 | 44.06 | 23.17 | 29.69 | 4.50 | 161.83 |
| 28 | Telemark | 72.16 | 12.39 | 36.24 | 2.98 | 8.42 | 132.19 |
| 29 | Telemark | 62.84 | 17.34 | 9.2 | 11.38 | 1.94 | 102.7 |
| 30 | Telemark | 62.84 | 17.34 | 9.2 | 11.38 | 1.94 | 102.7 |
| 31 | Telemark | 62.84 | 17.34 | 9.2 | 11.38 | 1.94 | 102.7 |

of each tree species was recorded, along with height and extent of browsing of marked individuals. Field recordings were made during early spring, typically during May. Density data was assessed by counting the total number of individual trees of each species present within each subplot (with no limitations of tree size). Individual data was assessed by marking or positioning up to four trees of each species. These individuals were relocated and assessed annually (2009, 2010, 2011 and 2012 in Trøndelag and 2010, 2011 and 2012 in Telemark). The selection of four individuals per species was based on the order of encounter in a systematic clockwise search from due north, until a maximum of four per species was attained, or the whole 2 m radius subplot was searched. Multiple trees of the same species were selected in different quarters of the circular subplot where possible. Height and browsing data were recorded on these individuals. Browsing data was expressed as the number of shoots (>5 cm in length) assessed as recently browsed (in the preceding winter) and unbrowsed. Browsing was not linked to a herbivore species as this could not be done with certainty. Browsing was analysed as both browsing likelihood, using presence absence transformed data, and as browsing intensity, expressed as the proportion of shoots browsed.

A total of 1822 tree individuals were relocated over the period 2009–2012 (Table S1). Some marked individuals were not relocated and thus excluded from further analyses, whilst further individuals were included when relevant (where a new individual was found of a species with less than four marked individuals already selected) and found using the above method. Downy birch, rowan, pine and spruce were the most common species (Table 2), thus individual-based analyses of browsing likelihood, browsing intensity and height growth were restricted to these four species. Juniper (*Juniperus communis*), aspen (*Populus tremula*), goat willow (*Salix caprea*) and silver birch (*Betula pendula*) were also found albeit infrequently.

2.1.1. Herbivore densities

The cervid herbivores in the study areas included the moose, roe deer and very few red deer. In addition, there were free ranging sheep and cattle in some of the municipalities during summer, but at relatively low densities. Also hares and rodents were found in all study areas and were – contrary to the ungulates – free to enter the enclosures. The grazing pressure from ungulates was estimated in terms of the average annual metabolic biomass (kg km^{-2}) of each species at the municipality level. Official livestock statistics from 2009 were used to estimate the metabolic biomass of sheep and cattle, whilst hunter harvest and observation data collected during 2007–2011 were used to estimate the average annual metabolic biomass of cervids using the methods described in Austrheim et al. (2011). This data indicated that moose constitute the dominating part of the browsing pressure in both regions, with roe or red deer being present in some sites but at lower abundances (Table 3). Sheep were abundant in two municipalities, but were typically only present during the summer season and unlikely to forage within the immediate areas of the experimental sites due to their preference for grasslands and heathlands over forests. Hence, mainly moose and to some extent roe and red deer are assumed to have affected the shrub and tree vegetation at these sites, along with hare which were not excluded by the fences.

2.2. Data analysis

2.2.1. Height growth and browsing prevalence

Gaussian mixed effects models were used to analyse the height growth between growing seasons. A random intercept of site nested in region to control for geographic differences in growth between sites and region was fitted as well as a random intercept for tree individual to account for the repeated measures structure.

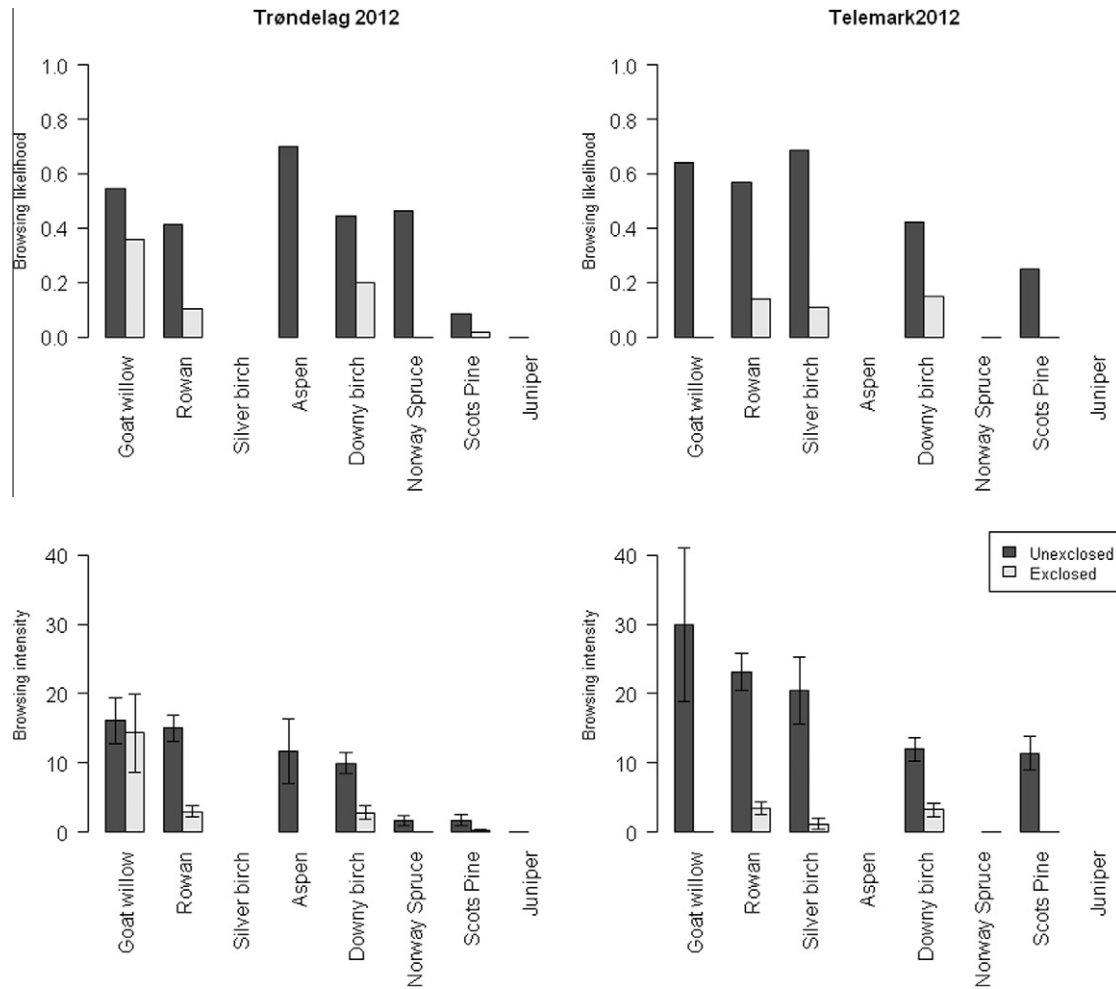


Fig. 2. Top row: the likelihood of browsing for each species outside and within the exclosures in different regions in 2012. Bottom row: the mean and standard error (subplot level) percentage of shoots browsed per species by treatment and region in 2012.

Height growth was modelled as a function of tree height in the previous spring, browsing intensity since the previous spring and tree species. Data from both the exclosed and unexclosed plots were included to increase the range of browsing intensity. Analysis of browsing likelihood and browsing intensity used all available data in a repeated measures design. Browsing likelihood was modelled using binomial family mixed effects models, and analysis of browsing intensity used Poisson family mixed effects models, offsetting the number of shoots browsed against the total number of shoots. Site and tree were taken as random effects to account for the repeated measures structure.

2.2.2. Tree density

The density of trees of each species was compared between years within each region. Changes in tree density by species were modelled offsetting the number recorded per subplot against the number recorded in the previous year to account for initial density. Forestry activity did not take place during the experimental period, so all changes in vegetation are assumed to be caused by successional processes and herbivore – vegetation dynamics. Site nested within region was taken as a random intercept effect to account for geographic differences in tree populations. Data were analysed within R (R Development Core Team, 2012). The package lme4 (Bates et al., 2012) was used for mixed effects modelling.

3. Results

3.1. Effects of moose exclusion

The browsing treatment (exclosures vs. unexclosed) had a significant influence on the likelihood of a tree being browsed (Fig. 2), as did both tree height and tree species (Table S2). Interactions between height and treatment, height and tree species and treatment and tree species were also retained in the selected model of browsing likelihood (the selected model is presented in Table S2). For the two common deciduous species (rowan and birch) the likelihood of browsing was greater outside the exclosures than inside, although small rowan trees were almost as likely to be browsed within and outside the exclosures (Fig. 3). However the likelihood of rowan being browsed decreased with increasing height inside the exclosures but increased with increasing height outside. New recruits of rowan had approximately a 25% chance of being browsed inside and 35% chance of being browsed outside of the exclosure, whilst 80 cm tall individuals were four times as likely to be browsed outside the exclosure (around 80%) as inside (20%). The model of browsing likelihood was less able to predict browsing on the less abundant coniferous trees (pine and spruce).

Browsing intensity also differed between treatments and species. The intensity of browsing tended to be higher outside of exclosures, particularly for the species less frequently browsed

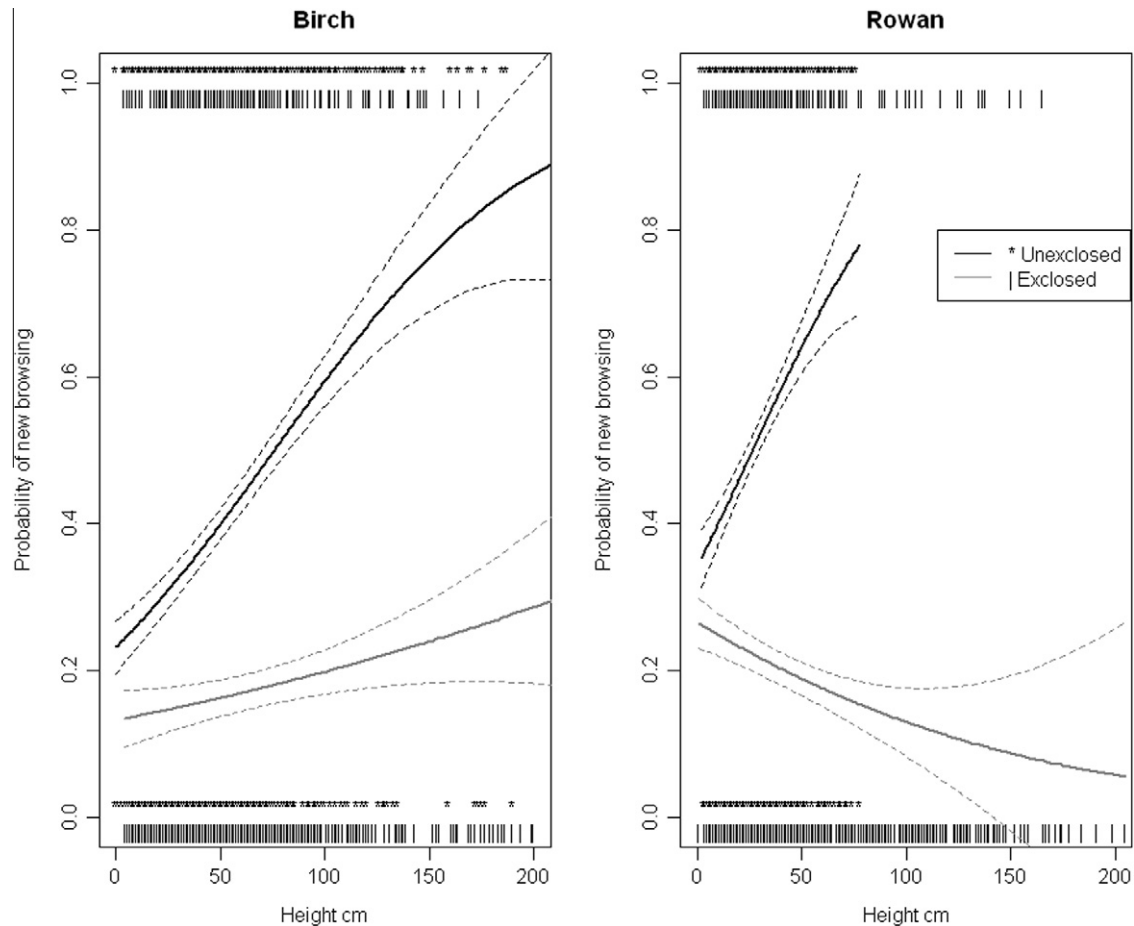


Fig. 3. Likelihood of a birch or rowan tree being browsed as a function of height within (grey) and outside of (black) enclosures. The rug indicates the height and browsing (presence absence) of sampled trees within (line) and outside (star) enclosures.

(Fig. 2). The intensity of browsing (expressed as the number of shoots browsed, offset against the total number of shoots) was modelled only for birch and rowan since there were very few browsed spruce and pine trees. Browsing intensity (the proportion of shoots browsed on trees with at least one shoot browsed) was predicted by browsing treatment and tree height but did not differ between these two deciduous tree species (Table S3). Inside the enclosures, browsing intensity on both birch and rowan was lower and decreased with tree height.

The differences in browsing likelihood and intensity led to differences in height growth of the individual trees (Fig. 4, Table S4). However, this was only for the highly selected rowan (Fig. 4). Tall rowan trees had a higher height growth rate inside the enclosure where protected from moose browsing than outside of the enclosure, although smaller rowan trees had similar growth rates inside and outside the enclosures. For birch, there was a small increase in height growth inside the enclosure, but this was not significant, and for the rarely browsed spruce and pine, height growth did not differ significantly between treatments.

3.2. Limitation of tree growth

There were significant impacts of herbivores on trees within the regenerating clear-cut forests. Individual tree height growth was predicted across tree height, browsing intensity (proportion of shoots browsed) and species (spruce, pine, rowan and birch). As browsing was affected by treatment, treatment was not used as a predictor in this model. Modelled height growth across previous

year's tree height and the percentage of shoots browsed is shown in contour plots in Fig. 5, showing the browsing intensity at which height growth is prevented at different tree heights. For example, 1 m tall pine trees are predicted to stop growing at browsing intensities of greater than 30% of shoots browsed, while spruce trees of the same height can maintain height growth at over 60% shoots browsed. Both birch and rowan trees of 1 m tall were predicted to cease height growth when around 45% or more shoots were browsed (Fig. 5 and Table S5).

To estimate the moose density at which tree growth is prevented, the percentage of rowan and birch shoots browsed was averaged within the browsed treatment for each site, and the site mean compared to the density of moose at the municipality level. The proportion of rowan and birch shoots browsed averaged across sites was positively related to the density of moose at the municipality scale ($n = 31$, $R^2 = 0.13$, $F = 5.67$, $P = 0.024$), although the relationship was not strong (Fig. 6a). Extrapolation of this relationship gives an estimated mean moose metabolic biomass density of 184 kg km^{-2} for a mean browsing intensity of 45% of birch and rowan shoots, which is the browsing intensity estimated to prevent height growth of 1 m tall individuals of these species (Fig. 5, with estimates of 135 and 254 kg km^{-2} for the 95% confidence intervals of 30% and 80% of browsing intensities required to prevent height growth). At the regional level, browsing intensity tended to be higher in more productive forests than less productive forests, although the difference between high and low forests productivity was not significant (Fig. 6b, ANOVA, $n = 31$, $F = 1.46$, $P = 0.24$). However, the height-growth of trees was not related to forest

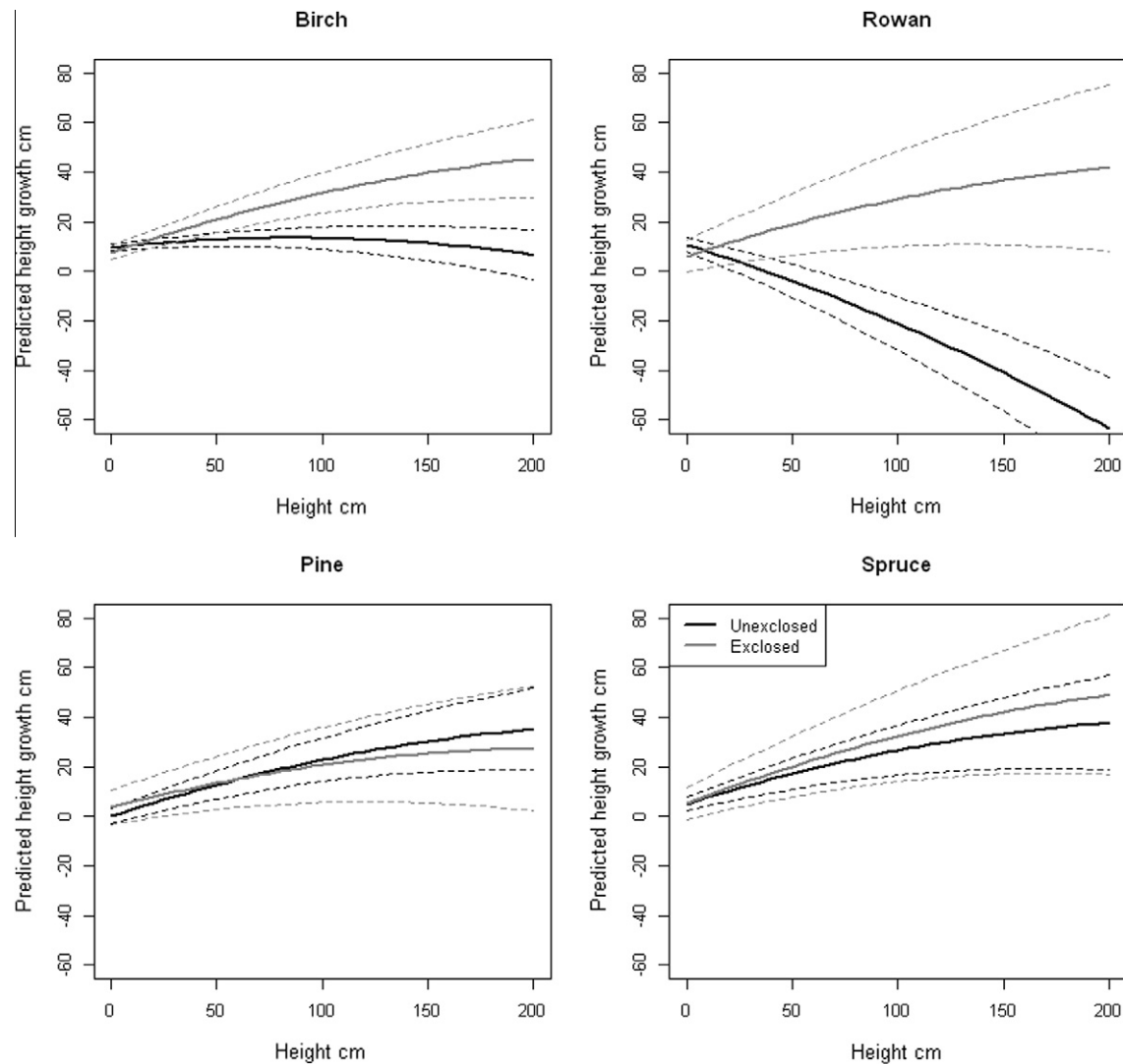


Fig. 4. Predicted height growth of the four dominant tree species inside (grey) and outside (black) of exclosures, plotted against the initial tree height. Standard errors are shown with broken lines.

productivity, moose density nor time since logging at the same scale: therefore, these terms were not retained during model selection (see [Supplementary material](#)).

3.3. Tree density

A total of 6618 individuals of eight tree species were recorded (in 2012). The mean density of species in each treatment is shown in [Table 2](#). Rowan, birch, spruce and pine were the most abundant species across the regions, with aspen being abundant within Telemark. There was a tendency for a shift from deciduous species to coniferous trees over the first few years of the experiment, and this shift in community structure was more evident in the exclosed treatment than the unexclosed treatment ([Fig. 7](#) and [Table S6](#)). For example, rowan decreased over time with a greater decrease within the exclosures than outside (and no decrease at all outside the exclosures in Telemark), whilst Scots pine had a more positive change in abundance inside the exclosures than outside of them.

4. Discussion

Regeneration of clear cut forests is a long-term process, acting over decades. Here short term data are presented, showing that

browsing moose can have a strong impact on the regeneration of clear-cut forests even in the early phases of forest succession. We have also been able to estimate the moose density at which the height-growth of developing trees of dominant species is halted in the forests of central and southern Norway. However, the width of the confidence intervals shows that these estimates should be interpreted with caution.

The most common species amongst the recruits are birch, rowan along with the commercially planted spruce and pine. Of these four common species, the deciduous birch and rowan were more likely to be browsed than the pine and spruce. Pine was found to be the most susceptible to browsing with height growth of 1 m individuals predicted to be prevented when 30% of shoots were browsed. Birch and rowan were able to maintain height growth at higher browsing intensities of around 45% of shoots (and rowan a little more so than birch), whilst spruce, although rarely browsed, was predicted to maintain height growth even when over 60% of shoots were browsed. The estimates of the sensitivity of growth to browsing were less certain for the coniferous species. However, the estimated high sensitivity of pine in relation to the deciduous species is not unexpected, with similar results reported from other systems ([Millard et al., 2001](#); [Hester et al., 2004](#)). However, it should be noted that lateral and terminal

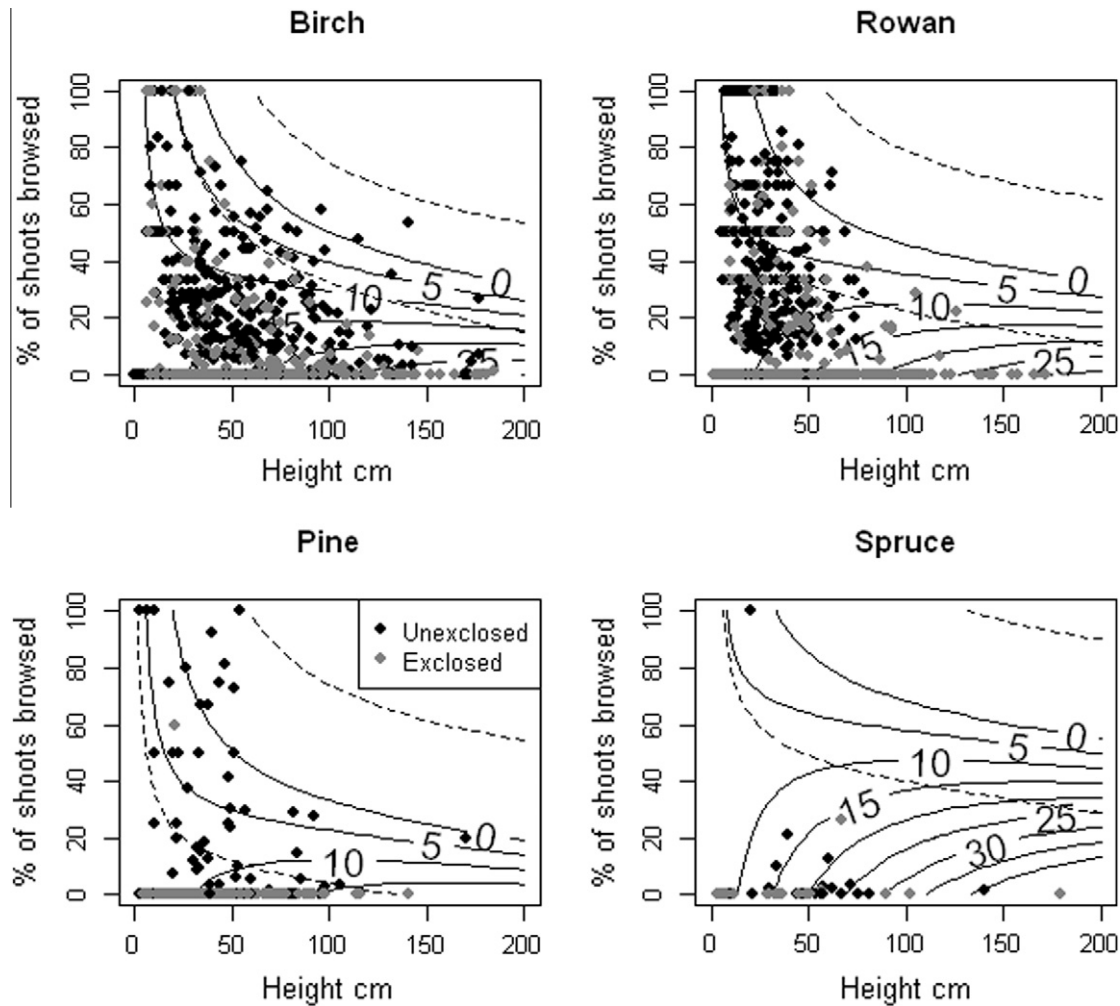


Fig. 5. Contour plot showing the predicted change in height (contour lines; cm) of different tree species as contours, as a function of the tree's height in the previous spring (x) and % of shoots browsed since the previous spring (y). Data from all years is used with tree as a random effect to account for the repeated measures structure. Standard errors of prediction for the zero-growth contour are shown with broken lines. The exclosures were used to increase the range of browsing intensities in the model and observations are shown with points (black for open and grey for exclosed). Browsing within the exclosures is likely to be due to hare.

browsing, which may differentially influence tree growth, were not differentiated in our study. Previous studies have found complex interactions between browsing, snow and shading in determining growth of Norway spruce as well as short term increases in growth following simulated browsing (Cunningham et al., 2006), consistent with the relatively low sensitivity of spruce to browsing found in our study. The higher browsing sensitivity of taller trees than smaller trees observed across species may be a result of the smaller trees having a higher proportion of their shoots unavailable under snow during the winter, or alternatively due to ontogenetic variation in resistance (Boege and Marquis, 2005), for example with a lower shoot to root ratio in smaller plants allowing them to better compensate for the above-ground biomass loss. A third possibility is that the shorter trees are more browsed by smaller herbivores (e.g. hare) which may remove less biomass than larger cervids.

Using the relationship between site-level mean percentage of shoots browsed of birch and rowan, and the density of moose at the municipality level (Fig. 6a), we extrapolated a moose density of ≥ 184 kg metabolic biomass of moose km^{-2} (equivalent to 3.0 moose km^{-2}) to prevent further height growth of these deciduous tree species (at 45% of birch or rowan shoots browsed Fig. 5), and to thus strongly affect the tree community during succession from clear-cutting. However, while being increasingly more

browsed (Fig. 3), birch and rowan are more sensitive to browsing as tree height increases (Fig. 5). Hence, we predict that height growth of the taller individuals may be prevented even at densities below 3.0 moose km^{-2} . Moreover, as herbivore selectivity occurs at a range of scales (Senft et al., 1987) and a range of other factors affect browsing selection, some independent of herbivore density, such as nutritional content or concentrations of secondary metabolites (Duncan and Gordon, 1999), the density of moose at the experimental site may not be representative of the moose density across the municipality. Indeed, there is a lot of variance in the relationship between browsing intensity at the site level and moose density at the municipality level (Fig. 6a), showing that some sites were more heavily utilised by cervids than predicted. This local scale variance is inevitable and must be taken into account when predicting browsing density-related impacts at the regional scale.

The impact of browsing on individual trees led to some apparent differentiation in community composition between exclosed and unexclosed treatments over the short time frame of this study. There was a trend for decreasing rowan dominance across all treatments (with the exception of outside the exclosures in Telemark where there was no change), as this is a highly preferred species, both for cervids and also for hare. In the exclosed treatment, there

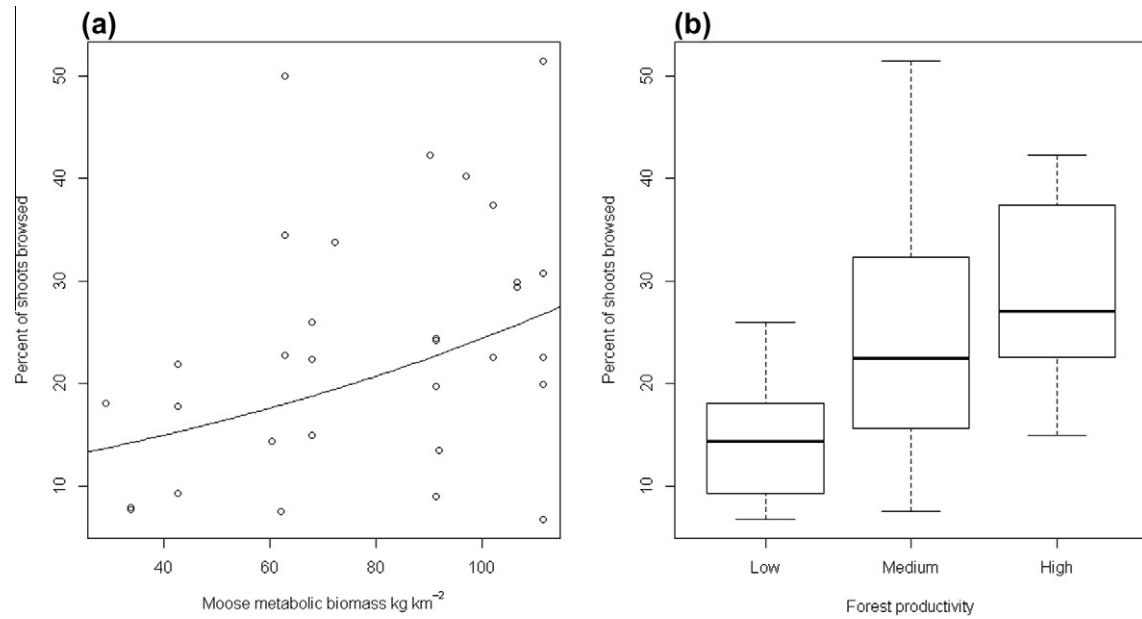


Fig. 6. (a) Relationship between moose density within municipalities and the site-mean percentage of rowan or downy birch shoots browsed in the unexclosed plot during winter and (b) boxplots showing the percentage of rowan or downy birch shoots browsed within forest productivity classes.

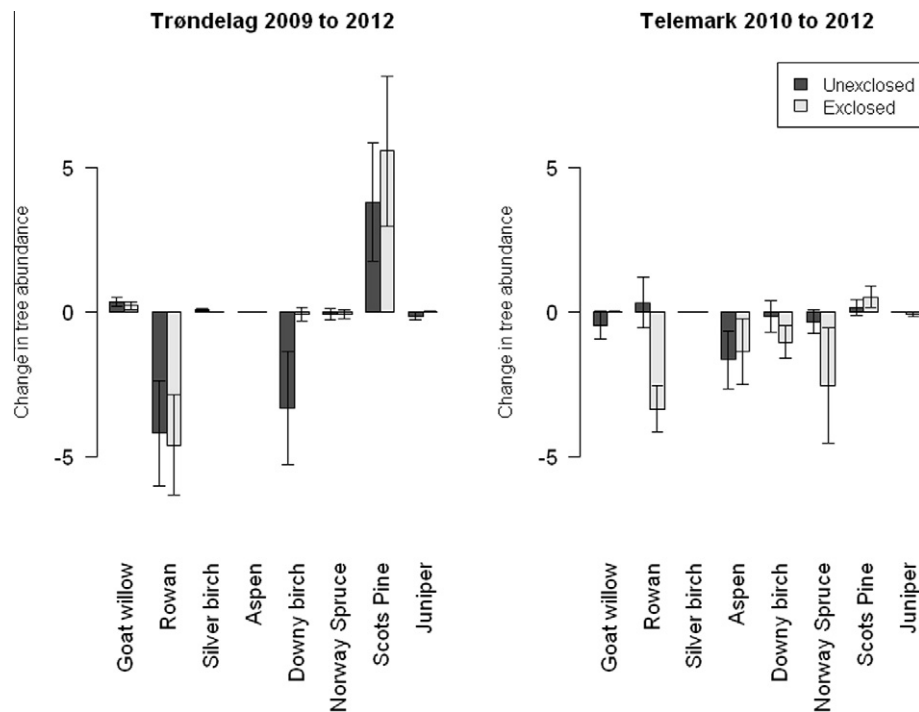


Fig. 7. Change in abundance of trees by species between years in the exclosed and unexclosed treatments expressed as the mean change in number of individuals per subplot. Species are ordered by the mean proportion of shoots browsed per individual across regions, from most to least browsed.

was a more negative change in abundance for deciduous species and the change in coniferous species was more positive as compared to the unexclosed treatment. Thus in the absence of moose there was a suggested shift from deciduous to coniferous community than in the unexclosed treatment, indicating that browsing moose may slow the process of succession from deciduous to conifer domination in clear-cut Norwegian forests in the early stages of succession. However, these patterns are not strong and vary

between regions and species. In Canadian forests, both regeneration (Tremblay et al., 2007) and reductions (McLaren et al., 2009) of coniferous species have been reported following cervid exclusion or reduction, respectively attributed to decreases in mortality of conifer seedlings or competition from deciduous species following depletion of coniferous seedlings. In our study, although an influence of hares cannot be ruled out, the increase in height growth and decrease in density of the dominant deciduous species

in the exclusion treatment (where browsing probability and intensity is reduced) suggests that intra- and inter-specific competition in the form of self-thinning drives the reduction in the population of deciduous species, and hence the community composition shifting towards a more coniferous state. However, it is not certain whether the fewer, taller deciduous trees in the absence of cervids will outcompete the smaller, more numerous coniferous species later in the successional process.

The timing of browsing is an important factor in determining the response of trees (Hester et al., 2004). In boreal environments, tree browse is a very important resource for cervids during winter time. The interaction between plant height and snow depth is an important factor in determining the availability of browse for herbivores during winter (Dussault et al., 2005; Visscher et al., 2006). The experimental exclosures prevented access from cervids, but not smaller herbivores such as hares and rodents, which were not prevented from browsing trees in the exclosure treatment. This is reflected in the height profiles of trees browsed within and outside of the experimental exclosures, with small individuals more likely to be browsed than taller individuals within the exclosures, and the height growth being equal in short rowan trees but greater in the exclosure for larger individuals. Previously studies have found no differences in hare browsing frequency following earlier moose browsing (Danell and Huss-Danell, 1985), so whilst there may not have been differences in hare browsing between treatments, we cannot rule out a substantial influence of hare browsing on forest regeneration both inside and outside of the exclosures, and particularly in the case of the highly selected rowan.

5. Conclusion

This study shows that a forest regenerating following clear felling is rapidly influenced in terms of tree growth and density by browsing moose and other herbivores. The current high densities of moose in Norway (Austrheim et al., 2011) are therefore expected to have strong influences on forest structure, and potentially biodiversity and economic potential of regenerating forests. Succession from clear cut forests is a long-term process and the results presented here document only the start of this process with trees still being of low height and providing a relatively low abundance of forage for moose. Long-term continuation of this experiment will allow browsing pressure and intra-guild competition to be assessed, as well as herbivore impacts on the field layer vegetation as the trees and forests develop. However, forest development often occurs during “windows of opportunity” – periods of low herbivore density (Dobson and Crawley, 1994; Sage et al., 2003; Speed et al., 2010). In the current study, despite high densities of cervids, trees were observed to establish and grow outside of the exclosures, but the frequency and species composition of recruits are different compared to where herbivores have been excluded, supporting the premise that moose is a keystone herbivore in these boreal forest ecosystems.

Acknowledgements

We are grateful to Marc Daverdin, Lars Erik Gangsei, Stein-Narve Kjølsvik, Lars Egil Libjå, Varinia Lietsch and Torstein Myre for assistance with fieldwork and Marc Daverdin for database management. We also thank the large number of landowners who allowed us to establish exclosures on their land. Constructive comments from two anonymous reviewers helped improve this manuscript. Funding was gratefully received from the Research Council of Norway Environment 2015 program (Project 184036) and the Norwegian Directorate for Nature Management.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2012.10.051>.

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