




Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species

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Citation: Kolstad, A. L., G. Austrheim, E. J. Solberg, L. De Vriendt, and J. D. M. Speed. 2018. Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species. *Ecosphere* 9(10):e02458. 10.1002/ecs2.2458

Abstract. Large herbivores can shape young forest stands and determine the successional trajectory of forested ecosystems by selectively browsing palatable species at the sapling stage. Moose (*Alces alces*) is the dominant vertebrate herbivore in Fennoscandian boreal forests, and high population densities have raised concerns about potential negative effects on ecosystem functioning and properties including biological diversity and timber production. We used 31 herbivore exclosures in Norway to investigate how forests developed after clear-cutting with or without moose present. We tested how tree demography, abundances of understory plant functional groups, community composition, and plant diversity (including bryophytes) across multiple scales varied with moose exclusion. After seven years, the exclosures were dominated by deciduous trees, including many large rowan (*Sorbus aucuparia*) individuals, a functionally important keystone species. In contrast, the open plots subject to moose impacts (browsing, trampling, defecation) were dominated by economically important coniferous trees and there was next to no rowan recruitment to taller height classes. The biomass of large herbs and ferns was much greater inside exclosures. This study emphasizes the large immediate effect of moose on early successional boreal forest stands. Landscape-level alterations caused by reduced deciduous dominance, and a reduction in large flowering herbs is likely to lead to cascading effects on ecosystem functioning. The management of boreal production forests needs to account for the combined effects of silvicultural practices and ungulate herbivory to ensure ecosystem functioning, but this management goal may be jeopardized in our study regions due to drastically reduced abundance of keystone species.

Key words: *Alces alces*; bryophytes; Cervidae; diversity; Fennoscandia; forestry; Norway; silviculture; *Sorbus aucuparia*; succession.

Received 1 July 2018; revised 31 August 2018; accepted 5 September 2018. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Cervids (deer) are key drivers of ecosystem dynamics across boreal and temperate forest biomes, where their continuous feeding, trampling, and defecation are important determinants of

vegetation dynamics and ecosystem functioning (Hobbs 1996, Fuller and Gill 2001, Wardle et al. 2001, Edenius et al. 2002, Kuijper et al. 2010, Côté et al. 2014, Schulze et al. 2014). In recent decades, wild cervid populations have increased in many forest regions (Lavsund et al. 2003, Prins and

Gordon 2008, Apollonio et al. 2010), making it pressing that we understand their role in forest succession and vegetation dynamics to ensure sustainable management of boreal forests.

In boreal forests, selective browsing on palatable tree species by cervids shapes successional trajectories and ultimately forest canopy composition, favoring the less palatable tree species (McInnes et al. 1992, Hidding et al. 2013). Following disturbance, boreal forests usually become dominated by fast-growing deciduous trees which over the course of a few decades become outcompeted by slow-growing conifers. Browsing and commercial thinning are similar processes in that they, during stand development, remove competition around those species that are not eaten or cut. Conflicts and synergies between herbivory and the forestry sector are therefore common and depend on whether the browsed tree species are economically important for timber or pulp production, in which case herbivores diminish forest revenue (Glöde et al. 2004, Wam et al. 2016a). Conversely, browsing may favor forestry interests by reducing competition from deciduous species on the commercial tree species (Heikkilä et al. 2003).

Moose (*Alces alces*) is the largest of the cervids and the dominant vertebrate herbivore in Fennoscandian boreal forests. Their populations have increased rapidly since the 1960s following better control over the hunting pressure, and few limiting factors such as predation. A widespread use of clear-cutting as a forestry method and reduced competition from domestic grazers such as sheep, cows, and horses also improved the conditions for population growth (Lavsund et al. 2003, Austrheim et al. 2011).

Moose in Fennoscandia have been shown to negatively impact preferred food species, especially the subdominant deciduous species rowan (*Sorbus aucuparia*), goat willow (*Salix caprea*), and aspen (*Populus tremula*; Myking et al. 2011, 2013). These could be called keystone species due to their disproportionately large importance to the habitat value for other organisms, including lichens, fungi, insects, and birds (e.g., Bendiksen et al. 2008). Moose also browse common and often dominant species like the two birches *Betula pubescens* and *B. pendula* (hereafter just birch) and the coniferous Scots pine (*Pinus sylvestris*, hereafter just pine; Månsson et al. 2007,

Speed et al. 2013a, Herfindal et al. 2015). Norway spruce (*Picea abies*, hereafter just spruce) is the most economically important timber species in this region, particularly on rich and well-drained soils, while pine is gradually more important in poorer and/or drier areas. Spruce is rarely eaten by moose (Månsson et al. 2007). Instead, moose typically feed in recent forest clear-cut sites where increased light and a flush of nutrients from decomposing cutting residues facilitate the rapid growth of preferred deciduous species with a high food value (Bjørneraas et al. 2011, Wam et al. 2016b). Browsing effects are therefore concentrated and generally stronger in young forest and on recent clear-cuts (Tremblay et al. 2007, Dufresne et al. 2009, Wam et al. 2010).

By removing deciduous biomass, moose make young forest stands more open, reduce the shade, and increase summer soil temperatures (Kielland and Bryant 1998, Kolstad et al. 2018). In general, cervids in boreal ecosystems affect multiple physical and chemical soil properties relevant for tree seedling growth (Dufresne et al. 2009, Kardol et al. 2014). For example, the selective removal of easily decomposable and nutrient rich litter from deciduous trees is assumed to decrease nutrient mineralization (Pastor and Naiman 1992) and hence forest productivity. However, Kolstad et al. (2018) failed to find this effect on recently clear-cut forests (short term study) and stressed that soils may take a long time to respond to aboveground changes.

The effect of wild cervids on understory plant diversity remains an unresolved issue, with studies finding effects that are positive (Chollet et al. 2013, Boulanger et al. 2017), neutral (Speed et al. 2014), negative (Rooney and Waller 2003, Beguin et al. 2011), and non-linear (Hegland et al. 2013). A recent systematic review by Bernes et al. (2018) also highlights the unique responses within different functional groups of plants. Such community responses are always confounded by different plant species having unique responses to herbivory with some species being favored by herbivores and others not (Tremblay et al. 2006, Hegland and Rydgren 2016). Large herbivores can also influence spatial beta-diversity and, in northern ecosystems, cervids can increase floristic homogenization (Lilleeng et al. 2016, Boulanger et al. 2017). In any case, the mechanisms

behind such diversity effects may be direct through cervid-mediated seed dispersal (Albert et al. 2015) or grazing on nutrient rich herbs, or indirect through altered growing conditions such as micro-climate, light regimes, or soil properties. Bryophytes are not eaten by cervids, but have been shown to be positively affected by cervid presence (Chollet et al. 2013) and ungulate densities in general (Bernes et al. 2018), assumedly due to reduced competition from vascular understory plants or from altered light and moisture conditions associated with a browsing related change in canopy composition.

Browsing during early successional stages has been shown to have long-lasting legacy effects on tree species composition (Hidding et al. 2013) and understory vegetation (Nuttall et al. 2014). However, the major determinant of successional trajectories in Fennoscandian boreal forests is silviculture, with cyclic management consisting of harvesting and subsequent planting of timber species (mostly spruce and pine), and removal (commercial thinning/cleansing/cleaning) of unwanted deciduous species. Most of the productive forested area in Fennoscandia is managed as production forests, and only a few percent are protected as reserves. It is therefore critical that ecosystem functioning and biodiversity are also maintained in production forests to ensure the integrity and resilience of these systems. However, we know little about the combined and often additive effects of multiple disturbance factors, such as forestry and herbivory, and this limits the effective implementation of sound ecosystem management where the goal is multiple-use forests.

In this study, we experimentally excluded moose for eight years from 31 recent boreal forest clear-cut sites in Norway to investigate the effect of moose on secondary forest succession. We predict that excluding moose would favor all tree species except spruce and increase the dominance from deciduous trees. We also expect a change in the development of understory plant community composition in the direction of more browsing-sensitive herbs and less browsing-tolerant grasses inside exclosures. Finally, based on a recent systematic review (Bernes et al. 2018), we expect a negative effect of herbivore exclusion on bryophyte diversity and a weaker negative effect on overall understory plant diversity.

METHODS

Study design

The experiment used 31 study sites in two boreal forest regions in central and southern Norway (Fig. 1a). The surrounding mature forests are dominated by spruce, pine, or a mix of the two. The sites are situated along a strong gradient of forest productivity, and typically, more productive sites have higher abundance of deciduous trees like rowan, birch, and goat willow. All sites were clear-cut between 2002 and 2007 and all but ten sites were replanted with either pine, spruce, or both. No other silvicultural management has been undertaken ever since, except at three sites in the Trøndelag region where trees inside the open plots were inadvertently thinned by forest owners in 2015, that is, between treatment years seven and eight (sites nr 9, 10, and 13 in Fig. 1). At each site, two homogeneous quadrats of 20 × 20 m (hereafter referred to as plots) were marked and randomly assigned to either the exclusion treatment or open (browsed) plots (Fig. 1b). Fences 2.5-m tall were built around the exclusion plots in 2008–2009 to exclude large herbivores from entering. The exclosure and open plots were a minimum of 20 m apart to remove potential edge effects due to the fence. Sampling of field layer vegetation started the same summer as the experiment started (year zero) and measurements of tree densities began in year 1 after exclusion (see *Tree heights and densities* and *Understory vegetation*).

Moose is the dominant vertebrate herbivore in both study regions (median and range of metabolic biomass at municipality level; kg/km²: 90.2; 42.5–111.5), followed by domestic sheep *Ovis aries* (30.1; 3.0–93.4) and cattle *Bos taurus* (9.57; 1.9–54.3), roe deer *Capreolus capreolus* (8.2; 0–36.2), and red deer *Cervus elaphus* (7.3; 0–44.1; Austrheim et al. 2011). Rodents and hare (*Lepus timidus*) are also numerous, and unlike the species listed above, these could freely enter the exclosures. See Speed et al. (2013a) for more details about the study locations.

Tree heights and densities

Species identities and vertical heights were recorded for all individual trees inside four 2 m radius circles (hereafter referred to as subplots) per plot (Fig. 1c). Multi-stemmed individuals were counted as one individual if they branched

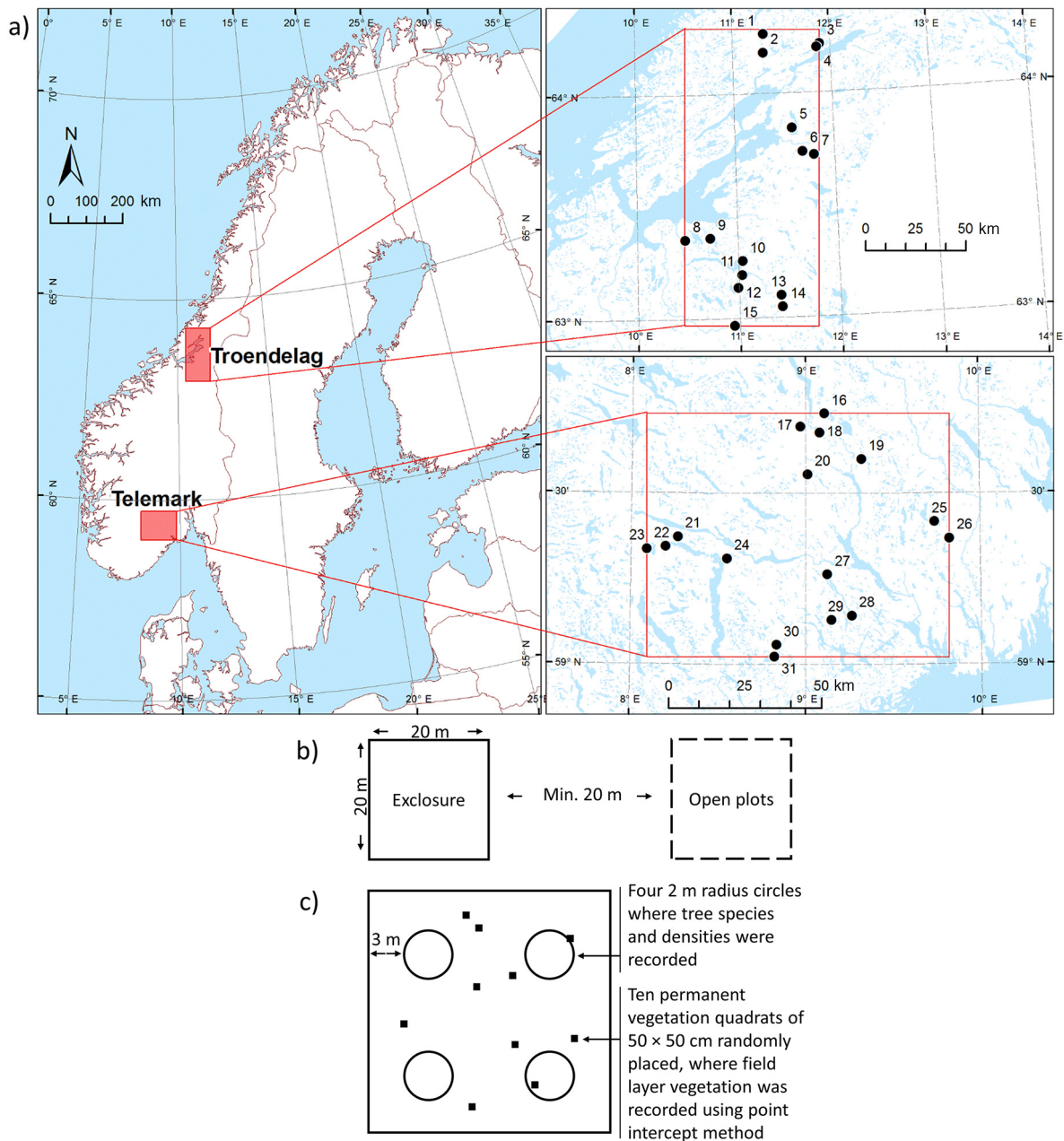


Fig. 1. Hierarchical sampling design with (a) 31 field sites in two regions of Norway, each consisting of (b) two paired plots and (c) subplots within which trees and understory vegetation were recorded. Numbers in the map refer to sites as in Speed et al. (2013a).

above ground. Tree height was recorded in 50-cm categories with all trees above 3 m grouped as category 7. For species-level analyses, we excluded sites where the analyzed species was absent or very rare (<5 occurrences). Sample size (number of paired pots) was then: spruce and

birch = 31; pine = 26; rowan = 30. We also calculated the percent of canopy trees that were from deciduous species and defined the canopy as all trees within one height category smaller than the tallest tree inside each circle each year. In order to investigate the effect of the fencing treatment

on tree recruitment, we set a threshold of 2 m above which trees are considered recruited to the tree layer. This height is somewhat arbitrary, but simply serves to separate small seedlings from larger saplings. Rather than excluding the three thinned sites (see *Study design*), we chose to use only the first seven years of data and keep all the sites in the analyses.

Understory vegetation

Ten 50 × 50 cm fixed-position vegetation quadrats (hereafter referred to as *subplots*) were randomly distributed inside each plot (Fig. 1c) at the start of the experiment, only avoiding large stones and tree stumps and placed a minimum of 1 m from the plot edge. Point intercept analysis (e.g., Jonasson 1988) was conducted every other year in mid-summer using 16 systematically placed pins per quadrat, and in the last year (2016), the depth (height from the soil) and species identities of bryophytes were also recorded for the Trøndelag region. An experienced botanist confirmed correct identification of bryophytes for a representative collection of species as well as for some that were not identified in the field. This consultation led us to treat certain species groups or species-pairs as one taxa (Appendix S1: Table S2). Some characteristic liverworts (*Marchantiophyta*) were identified to species, and all others were grouped as one single taxa. A list of the most common species and their relative frequencies is given in Table S2 in Appendix S1.

Locally calibrated biomass equation models were used to convert measured intercept frequencies into estimates of biomass. Six models were constructed for morphologically dissimilar plant groups: broad and narrow leaved dwarf shrubs; broad and narrow leaved graminoids; and large and small herbaceous plants. For ferns, we used either the models for large or small herbs depending on the species size. The biomass models were parameterized using destructively harvested vegetation biomass from forty 50 × 50 cm vegetation quadrats and fitted using generalized linear models with a gamma distribution and an identity link. Regression coefficients were obtained with Bayesian estimation through Markov chain Monte Carlo (MCMC) techniques by running JAGS (v. 4.3.0) through R (Su and Yajima 2015, R Core Team 2017). See *Extended methods* in Appendix S1 for more information.

Species richness and Shannon entropy for each subplot (alpha diversity) were calculated for vascular plants and bryophytes separately. Shannon entropy is an index of diversity that takes into account the species richness and the evenness of their abundances (Morris et al. 2014). We also calculated the mean Jaccard dissimilarity for each plot as a measure of beta-diversity between subplots that, due to using only presence-absence of species, is a metric that is very sensitive to turnover of rare species, but less suitable for detecting difference in dominance (Barwell et al. 2015).

Site productivity

To quantify site productivity, which is an important covariate and possible moderating factor for the effects of moose on forests, we used previously published allometric models (see Supporting Information in Kolstad et al. 2018) for estimating standing tree biomass for all plots and all years of the experiment. We then calculated the mean annual biomass increment for each plot. To characterize each site in terms of maximum biomass production potential, we used the value from the plot with the highest annual biomass increment and this became the productivity index for that site. The values were standardized (divided by max value). The two regions had very similar distribution of site productivities. As the sampling design grouped all trees above 3 m in the same height category, the estimated biomass was likely an underestimate and potentially plateauing after some years when trees grew bigger. However, we did not observe this flattening-out of biomass over time and believe our productivity index to have ranked the sites appropriately.

Statistical analyses

All data processing and analyses were done in the R environment (version 3.4.3; R Core Team 2017) and RStudio (version 1.1.423) using packages lmerTest (Kuznetsova et al. 2017), vegan (Oksanen et al. 2018), R2jags (Su and Yajima 2015), and ggplot2 (Wickham 2009).

We used linear mixed effects models to test the effect of the enclosure treatment, site productivity, and their interaction, on vegetation biomass, tree recruitment, species richness, Jaccard dissimilarity, depth of bryophytes, and the proportion of canopy trees that are deciduous. Time was not included in the models to avoid three-way

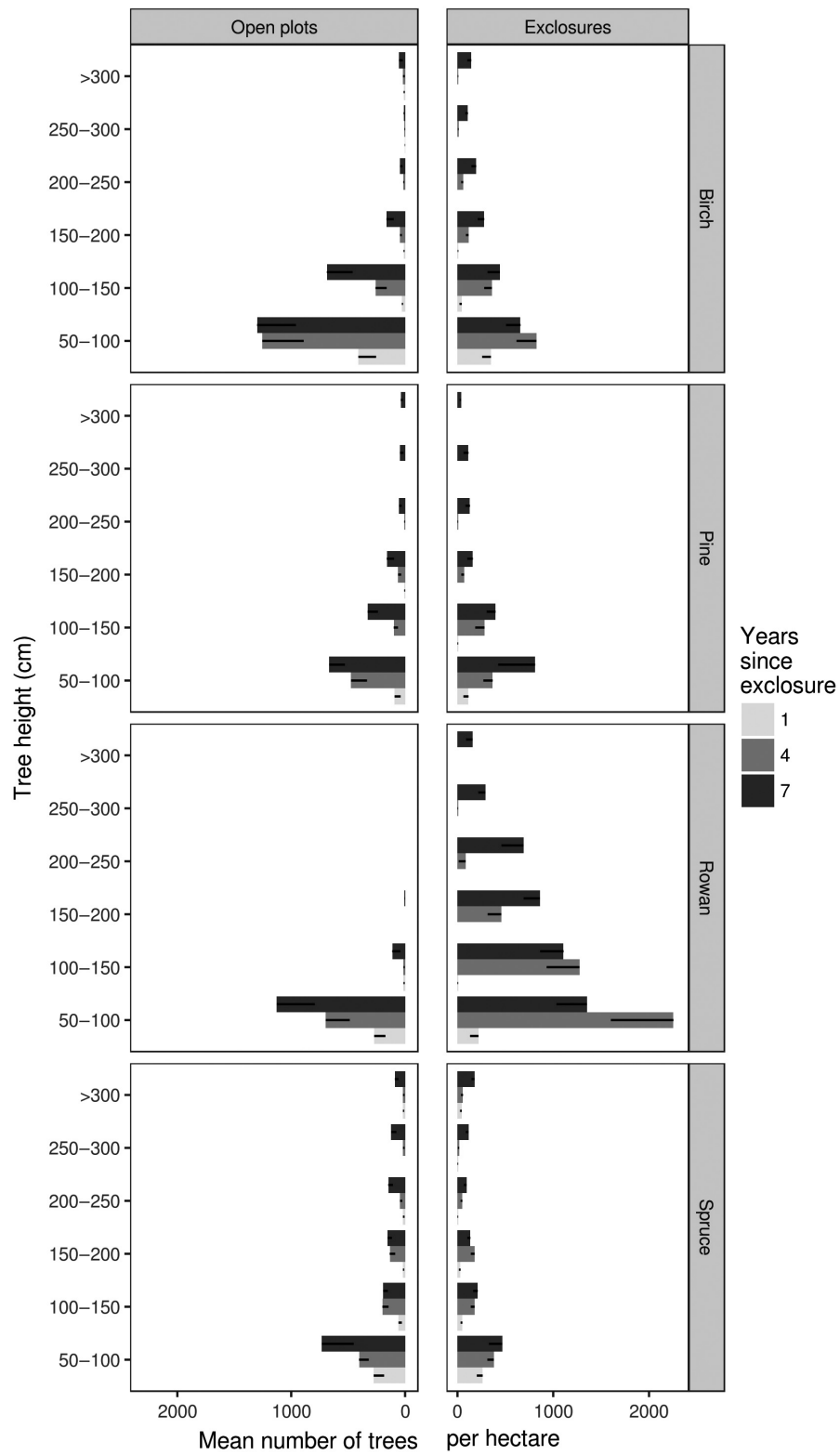


Fig. 2. Mean number of trees per height class of four boreal forest trees species at three time points (1, 4, and

(Fig. 2. *Continued*)

7 yr) after the start of the experiment where large herbivores were either excluded or not (open plots). Error bars are 1 SE, and only the negative range is shown in order to increase figure legibility. The sites were clear-cut a few years prior to the start of the experiment. The first height class is omitted for clarity as the densities were orders of magnitude greater than the other classes (see Appendix S1: Figs. S2 and S3). The bars represent the mean. Abbreviations are birch, *Betula pubescens* and *B. pendula*; pine, *Pinus sylvestris*; rowan, *Sorbus aucuparia*; spruce, *Picea abies*.

interactions that are made increasingly complicated by the non-linear temporal trends in many of the time series. Therefore, only data from the final year were included in the models. To avoid testing an unnecessary amount of correlated variables, we did not formally test the effect of herbivore exclusion on Shannon entropy. To account for the hierarchical sampling design, we fitted random intercepts for site and region (where appropriate) and the variation explained by these are reported as intraclass correlation coefficients (ICC). Models were validated visually to ensure normality and homogeneity of variance for the residuals, and response variables were log-transformed if assumptions were not met. Biomass of functional groups was analyzed as means per plot to reduce zero inflation.

We fitted four candidate models for each response variable using maximum likelihood estimation: a multiplicative model (including the interaction between enclosure treatment and site productivity), an additive model (i.e., excluding the interaction term), and two models with a single independent variable (IV). The best model was chosen using a combination of the corrected Akaike information criterion (AICc) and log-likelihood ratio tests, and this final model was refitted using restricted maximum likelihood before extracting relevant test statistics. For the single IV models and the multiplicative model, we report the *t*-statistic and associated *P*-values from the summary function in R. For additive models, we present the main effects of each covariate as the results of log-likelihood ratio tests with chi-square statistics and associated *P*-values.

Due to high zero inflation and large differences in the variances between the two treatment levels, the non-parametric Kruskal–Wallis rank sum test was used when testing whether the number of trees above 2 m differed between the two treatments. This approach did not allow the inclusion of a second covariate (e.g., site productivity).

Temporal trends in the species composition of vascular field layer plants were explored with principal response curves (PRC) using the *prc* function in *vegan*. PRC is a special case of conditional redundancy analysis (RDA) where the effect of a conditional variable (typically time) is partialled out, leaving only variation due to the treatment effect and the interaction between the treatment effect and the conditioning variable. First, we wanted to understand how community dissimilarities between the two treatment levels evolved over time and so used the time series for the open plots as a dynamic baseline (van den Brink et al. 2009) with time as the conditioning variable. We removed singletons from the dataset and combined rare grasses into one group called other grasses (all except *Deschampsia caespitosa*, *Avenella flexuosa*, *Agrostis cappilaris*, *Anthoxanthum odoratum*, *Calamagrostis phragmitoides*, and *Molinia caerulea*). The species community data were Hellinger transformed to reduce false similarities due to double zeros and reduce biases due to differences in total biomass (Legendre and Gallagher 2001). Data were aggregated to plot level by taking the means of the 10 subplots. Differences between sites were then quantified using an RDA analysis conditioned on site, and the residuals from this model were used in the subsequent PRC. The relative variation explained by each axis in the ordination was found by dividing the eigenvalues of each axis by the sum of the eigenvalues. The significance of the first axis was found using permutation test with 10,000 iterations with non-random shuffling to account for the time series nature of the data. We also made use of a PRC technique with a static reference point defined by the species composition in the first year of sampling and was then able to visualize the successional trends in the community composition for the two treatments separately. The conditioning variable in this case was not time,

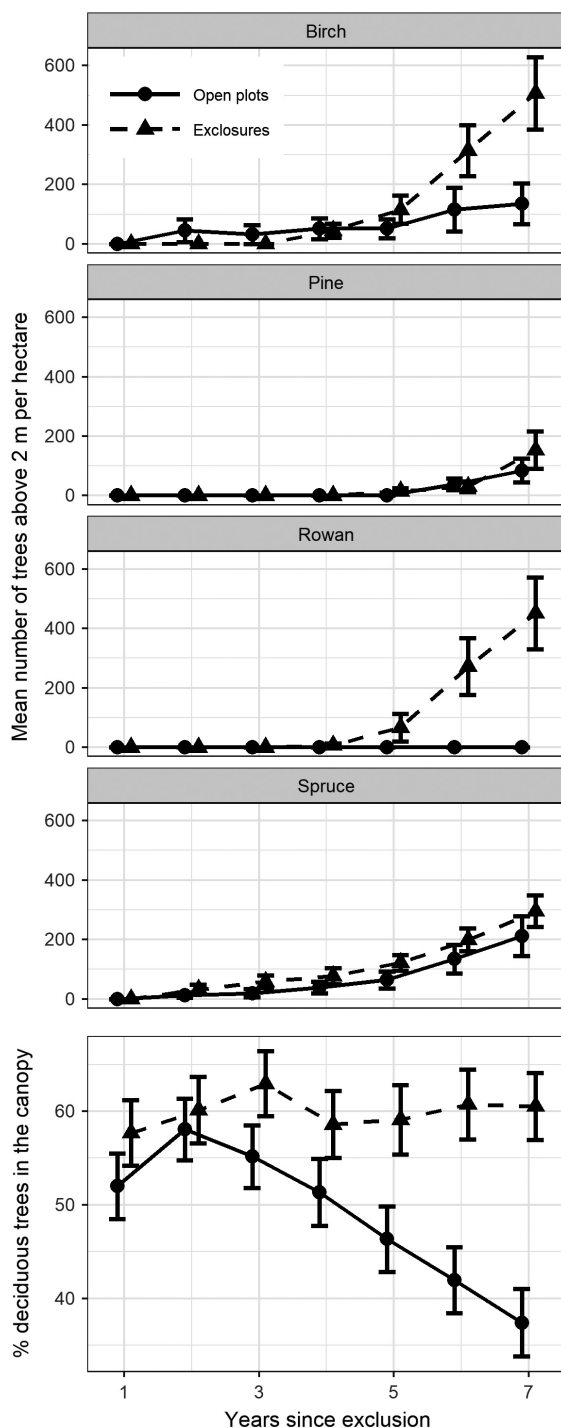


Fig. 3. The recruitment of boreal forest tree species above 2 m tall and the canopy composition in 31 recently clear-cut boreal forests where large herbivores were either excluded or not (means \pm SE). Plots were clear-cut few years before the experiment started.

but a binary indicator where year zero gets the value 0 and all other years get the value 1 (see van den Brink et al. 2009).

RESULTS

Tree species composition and growth

In total, we found eight tree species in the study sites: birch (two species), pine, rowan, spruce, goat willow, aspen, and juniper *Juniperus communis*. The last three species were too sporadically occurring to allow species-level analysis.

Excluding moose had drastic effects on the growth and overall demography of the deciduous trees rowan and birch, but not on the coniferous species pine and spruce (Figs. 2 and 3). During the experiment, the proportion of canopy trees that are deciduous dropped markedly in the open plots and after 7 yr was significantly lower (exclosures = $37.40\% \pm 3.60$ SE; open plots = $60.54\% \pm 3.58$ SE) than in exclosures (Table 1, Fig. 3). Inside exclosures, high initial densities of small deciduous seedlings (Appendix S1: Figs. S2 and S3) evolved into a more even size distribution with several large- and medium-sized trees (Fig. 2). Open plots had less large deciduous trees, and the densities of small individuals were higher.

A total of 1015 rowan were recorded in the open plots in year 1 of the experiment, and the tallest individual across all open plots after 7 yr was a single tree in the 4th height category (150–200 cm). Most individuals (75.9%) were still below 50 cm in year 7. Inside exclosures there were 1136 rowan recorded in year 1. By year 7, 302 individuals (33.9%) were taller than 150 cm with 24.4% below 50 cm. Seven years into the experiment, the number of birch and rowan above 2 m in height was considerably larger inside exclosures (Fig. 3, Table 1). A visual inspection suggests a higher treatment effect on productive than on less productive sites

(Fig. 3. Continued)

Values of tree recruitment are standardized against year one to remove any confounding differences due to remnant trees. Abbreviations are birch, *Betula pubescens* and *B. pendula*; pine, *Pinus sylvestris*; rowan, *Sorbus aucuparia*; spruce, *Picea abies*.

Table 1. Mixed effects models looking at the effects of herbivore exclusion, site productivity, and their interaction on multiple vegetation characteristics.

Response variables	No. obs	Multiplicative	Additive	Exclusion only	Productivity only	ICC (region/site)
% deciduous	246 subplots	Δ 0.310	Δ 1.055	AIC: 2497.139 E: 5.110***↑	Δ 23.844	0/0.208
Graminoids†	62 plots	Δ 3.419	Δ 1.624	Δ 6.339	AIC: 161.171 Pr: 2.648*↑	0/0.750
Large herbs†	62 plots	AIC: 166.872 E × Pr: 2.583*	Δ 4.417	Δ 7.128	Δ 9.227	0.286/0.381
Small herbs†	62 plots	AIC: 138.838 E × Pr: 2.817**	Δ 5.500	Δ 5.853	Δ 3.575	0.319/0.514
Ferns†	62 plots	Δ 0.289	Δ 0.520	AIC: 184.352 E: 2.441*↑	Δ 4.138	0/0.819
Dwarf shrubs†	62 plots	Δ 1.998	AIC: 146.608 Excl.: 3.568 Pr: 5.839*↓	Δ 3.839	Δ 1.567	0.428/0.310
Field layer biomass†	609 subplots	AIC: 1121.255 E × Pr: 2.683**	Δ 5.178	Δ 8.278	Δ 3.179	0.273/0.104
Vascular plant SR†	609 subplots	Δ 2.028	Δ 1.833	Δ 0.683	AIC: 349.414 ns	0.209/0.169
Bryophyte SR	290 subplots	Δ 3.541	Δ 1.973	Δ 0.311	AIC: 1242.331 ns	Site: 0.175
Mean Jaccard dissimilarity	62 plots	Δ 2.206	Δ 0.436	AIC: -117.037 E: 1.914 ns	Δ 2.001	0/0.430
Depth of bryophytes	290 subplots	Δ 2.420	Δ 1.771	Δ 4.009	AIC: 1423.466 Pr: -2.057 ns	Site: 0.213
Birch >2 m	62 plots			E: $\chi = 11.52***↑$		
Pine >2 m	62 plots			E: $\chi = 0.52$ ns		
Rowan >2 m	62 plots			E: $\chi = 24.30***↑$		
Spruce >2 m	62 plots			E: $\chi = 3.14$ ns		

Notes: Of the four candidate models, the best model is presented with the AICc score and subsequent models as the change in AICc (Δ) as compared to the best model. Relevant main effects from the best models are presented as *t*-statistics from the summary output, except for additive models where main effects are chi-square statistics from log-likelihood ratio tests, and for the number of large trees which are chi-square values from Kruskal–Wallis rank sum tests. Arrows indicate direction of change. Asterisk refers to *P*-values (**P* < 0.5; ***P* < 0.01; ****P* < 0.001), and significant variables (*P* < 0.05) are in bold. Abbreviations are ICC, intraclass correlation coefficient; Pr, site productivity; E, herbivore exclusion; SR, species richness; ns, not significant.

† log +1 transformed.

(Appendix S1: Fig. S4, bottom row). For pine and spruce, there was no treatment effect on the number of tall individuals (Fig. 3, Table 1).

Understory vegetation

In total, 112 plant taxa were recorded. Of the most frequently encountered species in year 8 of the experiment, 7 out of 10 were bryophytes (most common was *Hylocomium splendens*), and the three most common vascular plants were the dwarf shrub species *Vaccinium myrtillus* and *V. vitis-idaea*, and the dominant grass species *Avenella flexuosa* (Appendix S1: Table S2). Note, however, that bryophytes were only sampled in the Trøndelag region.

After eight years, fern biomass was higher inside exclosures and variation in large and small herbs and total field layer biomass was best explained by an interaction between herbivore

exclusion and site productivity. Hence, these groups seem to be increasingly favored by exclusion at high productive sites (Table 1, Fig. 4). Large ferns had 341% higher biomass inside exclosures than open plots (mean and SE for exclosures and open plots in year 8: exclusion = 6.23 ± 1.0 and open plots = 1.83 ± 0.3 g/m²). Total field layer biomass generally increased with time (Fig. 4), but a large freeze-dry event in the winter of 2013–2014 induced large-scale plant mortality (Meisingset et al. 2015) and a drop in biomass for all functional groups between year 4 and year 6 of the experiment (see also Appendix S1: Fig. S5). Most groups have since then recovered. Productive sites were associated with less dwarf shrubs and more graminoid biomass (Table 1). Depth of bryophytes was neither affected by herbivore exclusion nor site productivity (Table 1).

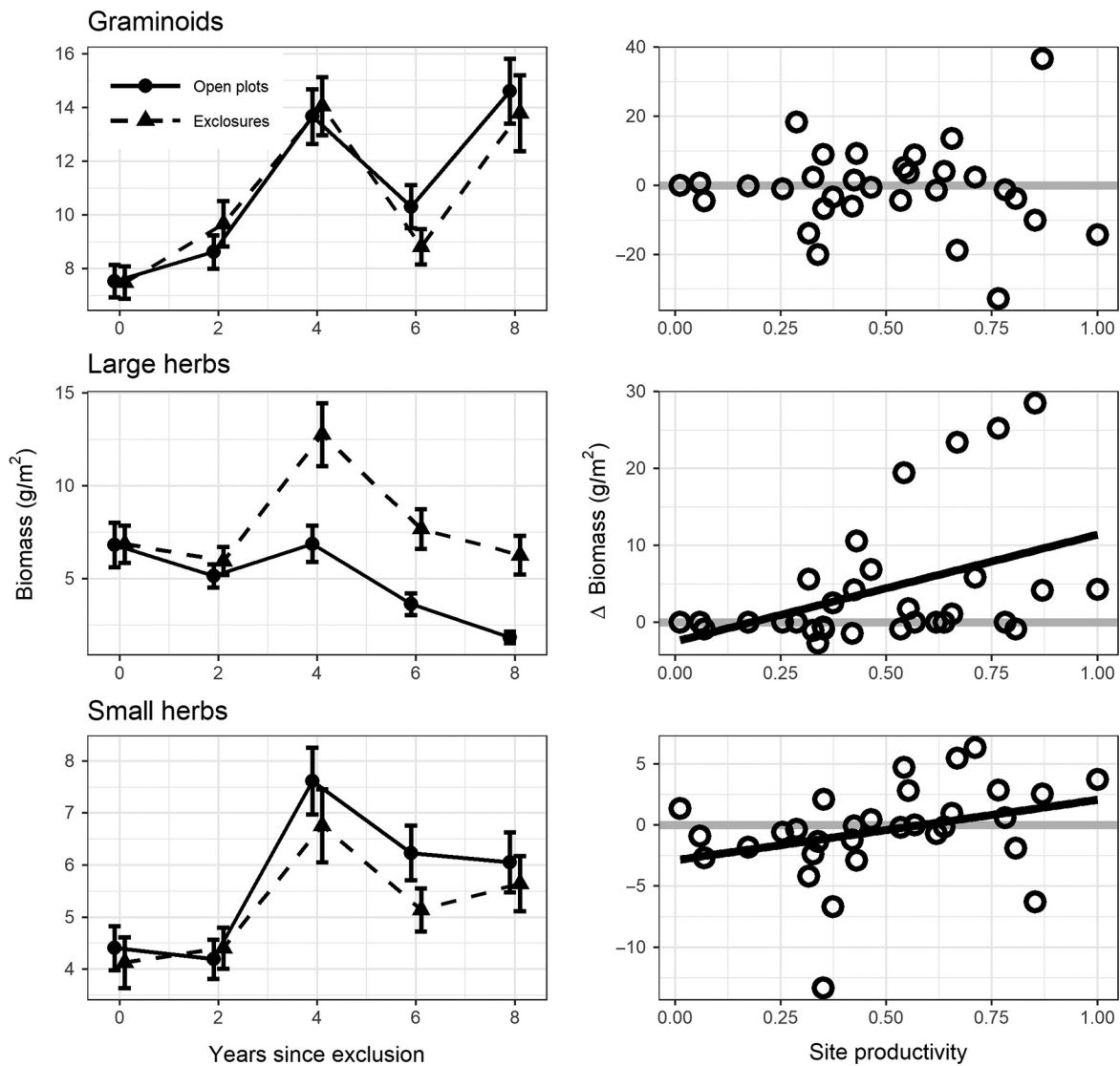
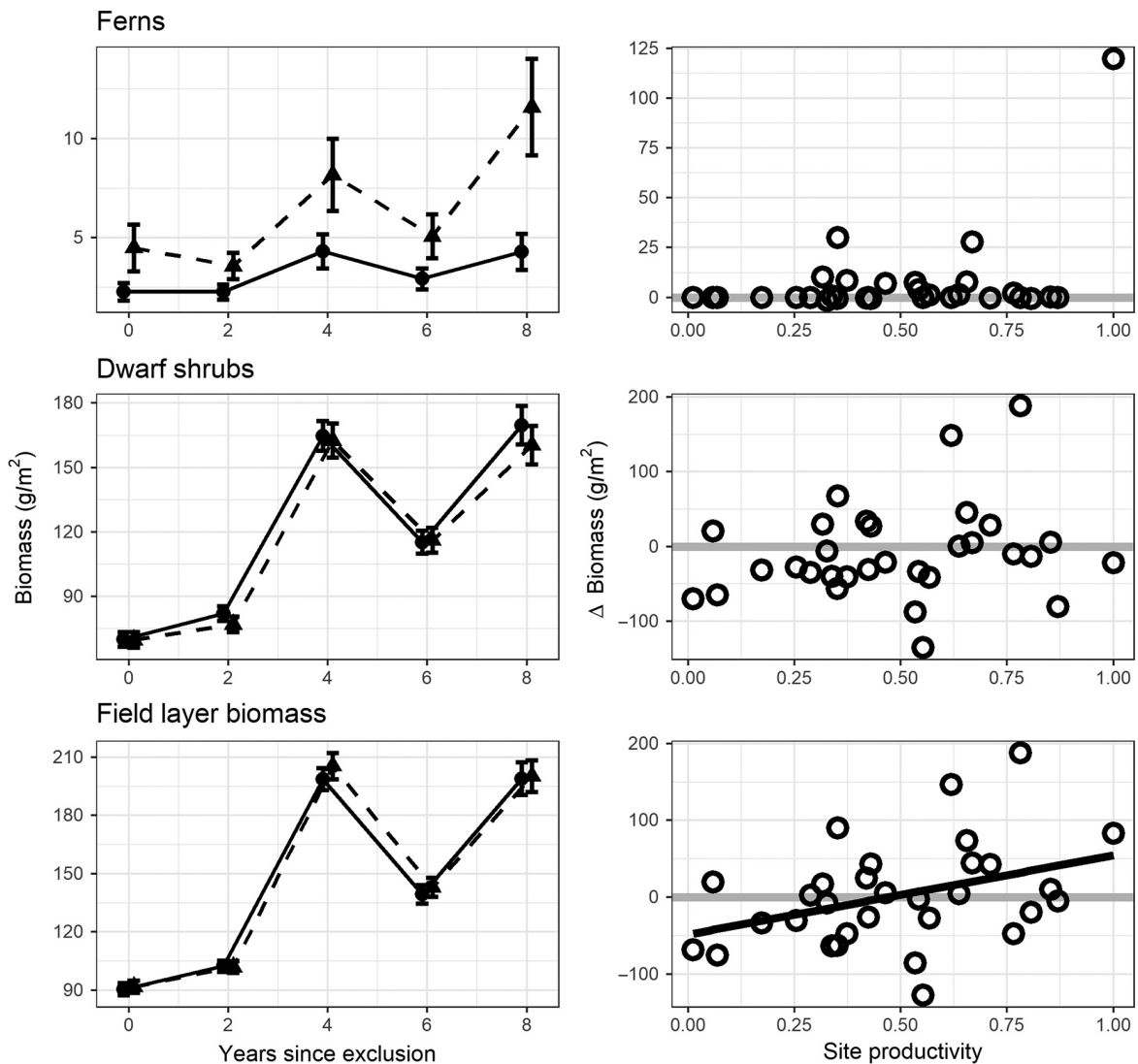


Fig. 4. Mean biomass (\pm SE) of vascular plants (left column) and the relative shift in biomass (exclosure–open plots) in year 8 plotted against site productivity (right column). Functional groups are along individual rows. Note that y-axes have different ranges. Drawn regression lines (lm procedure in R) in the right column indicate significant interaction effect between herbivore exclusion and site productivity. Field layer biomass is the sum of the five functional groups. The sample units are the 20×20 m plots ($n = 31$ locations).

The understory plant communities in the two treatments significantly diverged over time, and the species most associated with this divergence was *Chamerion angustifolium* which generally increased inside exclosures, and *Vaccinium myrtillus* which decreased (Fig. 5). The initial RDA showed that variation between study sites explained 72.2% of the variance in the dataset. In

the subsequent PRC, the temporal effect (conditional effect) explained 6.2% of the remaining variation and herbivore exclusion and its interaction with time (constrained effect) explained 2.2%. The first (PRC) ordination axis explained 79% of that variation and was the only significant axis (permutation test of first axis: $F_{1, 300} = 5.753$, $P < 0.001$).



(Fig. 4. Continued).

The plant communities showed similar succession in both exclosures and open plots, with *Calluna vulgaris*, *Agrostis capillaris* and “other grasses” (see *Methods: Statistical analysis*) increasing, and *Rubus idaeus* and *Avenella flexuosa* decreasing over time (Appendix S1: Fig. S6).

Plant diversity

No measured aspect of plant diversity was affected by herbivore exclusion or site productivity, and this included species richness and Shannon entropy for both vascular plant and bryophytes, as well as Jaccard dissimilarity as a

measure of vascular plant within-plot beta-diversity (Fig. 6, Table 1; Appendix S1: Figs. S7 and S8). Vascular plant diversity increased during the first 2–4 yr of the experiment (Fig. 6; note that forest stands were clear-cut at most 6 yr prior to the start of the experiment). The Jaccard dissimilarity was stable over time inside exclosures and apparently decreased in the open plots (i.e., the species composition in subplots became more homogeneous; Fig. 6), but after 8 yr the difference between treatments was not significant, although the exclusion treatment was included in the best model (Table 1).

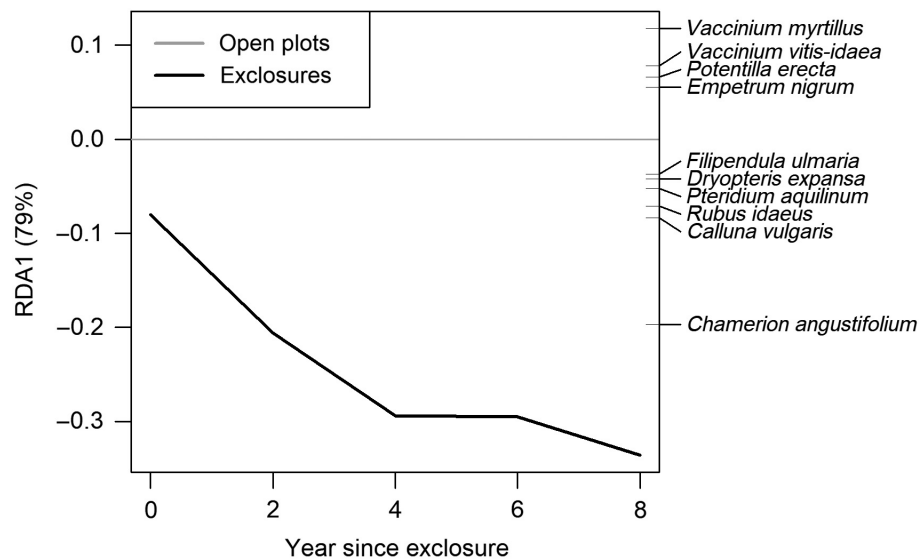


Fig. 5. Principal response curve (first axis) on plant species composition at 31 recently clear-cut locations in boreal forests in Norway. Only species names with loadings higher than 0.1 are shown. The percentage of variation explained by the first ordination axis is given in parentheses, and this was statistically significant (permutation test: $F_{1, 300} = 5.753, P < 0.001$).

DISCUSSION

Here, we have shown how excluding moose early in the secondary succession in boreal forests, dramatically increased the growth of deciduous trees, large herbs and ferns, and altered understory plant community composition. As early successional forests are common (e.g., 22% of productive forest area in Norway is in the first and second development classes, typically meaning trees are less than 12 m tall [Statistics Norway 2017]), we interpret the strong immediate effect of moose in our study to represent a landscape-level ecosystem moderation with implications for ecosystem functioning and biodiversity. In addition, as cervid browsing in early successional forests has been shown to have long-lasting effects on tree species composition, we predict that the reduced sapling recruitment of the keystone species rowan will have important and negative ramifications in the future.

Tree species composition and growth

As predicted, fencing off the forest facilitated rapid growth of both rowan and birch, illustrating that moose browsing is a substantially

limiting factor for their growth. Previous studies from the same experimental units have shown that moose annually browse on about 80% of all rowan above 80 cm and of these trees about 15–25% of all available shoots are eaten (Speed et al. 2013a). Furthermore, the growth of a hypothetical one meter tall rowan is estimated to stagnate at browsing pressures exceeding 20% (Speed et al. 2013b, in old, tall forest) or 45% of twigs browsed (Speed et al. 2013a, on recent clear-cuts). Our findings agree with these results as we observed only small increases in the number of rowan taller than one meter in open plots over the duration of the experiment. Seven years into the experiment and across all 31 open forest plots, 76% of rowan individuals were below 50 cm (i.e., below typical snow depth; see Speed et al. 2013b) and we observed only one individual above 150 cm compared to 302 inside exclosures.

This dramatic failure of rowan to recruit into taller height classes is in apparent contrast to the National Forest Inventory of Norway (<https://www.ssb.no/en/lst>) where an increase was observed in the number of rowan above 6 cm diameter at breast height (dbh; meaning typically >4 m tall) since year 1994 (Myking et al. 2013).

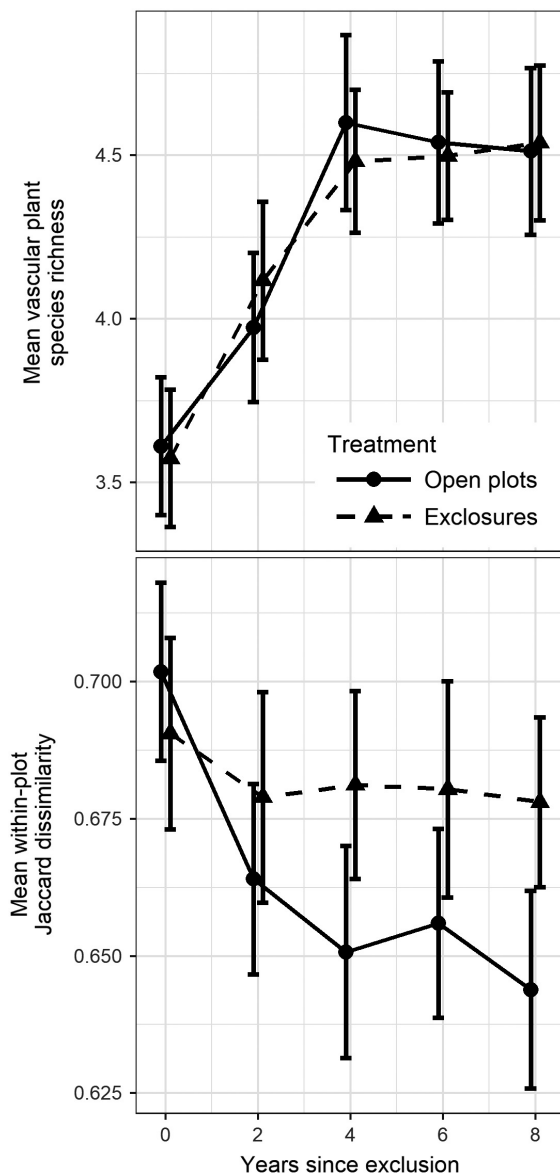


Fig. 6. Mean (\pm SE) species richness and within-plot Jaccard dissimilarity for vascular plants recorded in clear-cut boreal forests in central and southern Norway either enclosure or open to large herbivores. The sample units are the 20 \times 20 m plots ($n = 31$ locations).

Looking at the raw data from a more recent iteration of the same inventory (years 2012–2016), we found the combined number of rowan, goat willow, and aspen with dbh between 2.5 and 4.9 cm (typically 2–5 m tall) in 7–14 yr old productive forest stands to be on average 25 (\pm 13 SE) trees/ha ($n = 111$) in the same two regions as our

experiment. Of these trees, we expect about half to be rowan. The discrepancies can be partly explained by the non-random sampling in our study with plots positioned in flat and easily available areas, whereas the national survey is a grid-based survey which is independent of topography. Even under high moose densities rowan can find escape opportunities in steep and rocky places as well as in areas close to humans where moose are deterred from feeding. In addition, our open plots maintained a high density of very small rowan, indicating that mortality was not very high. As rowan is relatively shade tolerant, it can potentially subsist and mature later as the forest develops and moose browsing decrease (Wam et al. 2010). Together, these uncertainties make it difficult to conclude about the future of rowan in Fennoscandian boreal forests. On the other hand, deer browsing during early forest succession has been shown to have long-lasting legacy effects on both trees (Hidding et al. 2013) and understory plant communities (Nuttle et al. 2014), and moose browsing can have a similar community filtering effect that will determine the state and composition of future forest communities, as appears to have happened already in European temperate forests (Schulze et al. 2014). Alternatively, fluctuating moose densities may create recurring windows of opportunity for successful recruitment of forest trees (e.g., Kuijper et al. 2010). However, as moose management in Norway is aimed at maintaining high and stable game populations, such windows of opportunity may not necessarily appear.

Our experimental plots were not subject to any forest thinning, which is a standard forestry method routinely applied to actively managed forests in Fennoscandia. In many ways, forest thinning mimics moose browsing by selectively removing (non-economic) deciduous trees that compete with the economical important conifer species. The species composition of future boreal forests depends largely on whether thinning induce additive (on top of other factors) or compensatory mortality risk (killing trees that are likely to soon die naturally from other causes) on deciduous tree species. Regardless, in order to reach the set goals for ecosystem functioning, moose and forest management cannot be treated separately. For example, the two most common

forest certification schemes in Fennoscandia (www.pefc.org; www.fsc.org) require that a substantial proportion of standing biomass in late successional stages comes from deciduous trees, preferentially other than birch. This goal is probably best achieved through ecosystem management involving all relevant stakeholders (Van Dyke et al. 2002).

Contrary to our predictions, we did not find any effect of moose exclusion on the demography or recruitment of pine into taller height classes (Figs. 2 and 3). This is surprising since considerable browsing damages were observed in the field and that pine is known to be sensitive to browsing damage (Edenius et al. 1995, Speed et al. 2013a). However, pine grows slowly and takes a relatively long time to establish from seeds and was only planted at three out of 31 sites in our study. Note that the other species in this study were either planted (spruce) or can recruit from existing root systems (birch and rowan). We could therefore expect treatment differences to take longer to reveal themselves for pine compared to deciduous trees.

After 7 yr, the exclosures were dominated by deciduous trees in the canopy (60%), whereas the open plots were dominated by conifers (37% deciduous trees). The forest sites in this study are, like most of the forested area in Fennoscandia, managed for the economic exploitation of conifers. We found no positive effect of the exclosure treatment on spruce growth that would indicate that browsing hastens succession due to the system passing through each successional stage faster. However, we still see that browsing causes acceleration of succession through the process of skipping the early deciduous-dominated stage and hence a more rapid transition to a coniferous state occurs, in accordance with existing theory (Davidson 1993). Over time, this may still favor spruce growth (but not necessarily pine forests; see above paragraph), as it means there will be less competition with deciduous trees, suggesting that keeping high moose densities as a management objective could be beneficial to spruce production in the timber industry.

Forests are important in climate regulation. The effect of moose browsing on ecosystem carbon storage is potentially very large (Schmitz et al. 2014), but much remains unknown regarding combined short- and long-term effects and

especially soil carbon stocks (e.g., Kolstad et al. 2018) and fluxes (e.g., Persson et al. 2009). However, deciduous trees increase the year-round surface albedo of boreal forests in contrast to coniferous species, resulting in a direct global cooling effect that offsets the warming effect due to differences in carbon fluxes between forest types (Bright et al. 2014). Therefore, favoring deciduous trees in boreal forests can be a beneficial climate change mitigation tool. Mixed forests, as compared to monocultures, also provide an insurance against future environmental change due to the increased resilience that comes with a high functional dispersion, and a greater human benefit in terms of ecosystem service delivery (Felton et al. 2016).

Understory vegetation

Browsing can increase field and shrub layer abundance due to the creation and maintenance of canopy openings (McInnes et al. 1992) but may also reduce it if browsing occurs on shrubs (Eichhorn et al. 2017) or herbs directly (as is the case for this study). We found that moose exclosures greatly increased the biomass of large herbs and ferns (Fig. 4). Although ferns are thought to be browsing tolerant and increase with herbivore pressure (Nuttall et al. 2014), we believe some species, like *Dryopteris expansa* and *Athyrium filix-femina*, are trampling intolerant and that this can explain why we see more ferns inside the exclosures. Persson et al. (2000) estimated that an average moose may trample a combined (accumulated) area of 0.9 ha per year, which illustrates that moose impacts are not restricted to browsing effects alone.

Many of the large herb species are highly preferred by moose, and direct browsing is likely the explanation for the higher biomass of this functional group (340% higher) inside exclosures, at least at this early successional stage before environmental differences between treatments become more important in species filtering. The understory species composition showed significant diverging trajectories over time, with the large herb species *Chamerion angustifolium* being the species most uniquely associated with the exclosures (Fig. 5). This increase was observed after only 4 yr for the spruce-dominated sites in the same experiment (Speed et al. 2014) and is also in accordance with Tremblay et al. (2006) who

showed that *C. angustifolium* biomass is very high on recent clear-cuts but declined exponentially with increasing white-tailed deer (*Odocoileus virginianus*) densities. Large flowering herbs, exemplified by species like *C. angustifolium* and *Rubus idaeus*, are keystone species as they are important food species for moose and other mammalian herbivores, as well as insect herbivores and pollinators. Potentially cascading ecosystem effects caused by the removal by moose of these and similar species deserves further attention.

We expected graminoids to become relatively more common in the open plots as these are often grazing tolerant and light demanding and are shown to increase with increasing browsing pressure (Tremblay et al. 2006, Rooney 2009, Mathisen et al. 2010). Contrary to our prediction, we found only weak indications of this in our study (moose exclusion appeared in the second best model with $\Delta AIC < 2$; Table 1). This agrees with the discussion in Speed et al. (2014) that stressed the context dependency of plant community responses to herbivory. Graminoids are similar in many functional aspects and are in general found to have the highest biomass shortly after disturbance (Uotila and Kouki 2005). However, different species showed unique temporal development. For example, in both treatments, *Agrostis capillaris* became more common with time, whereas *Avenella flexuosa* decreased with time (Appendix S1: Fig. S6).

Dwarf shrub biomass was not affected by the exclusion treatment (although it was part of the best model; Table 1). This contrasts with Hegland and Rydgren (2016) who showed an overall decline in dwarf shrub abundance with increasing red deer density. This can be due to differences in feeding strategies between red deer and moose, with moose being less likely to eat shrubs. In our study, the two berry-producing and highly dominant dwarf shrub species, *Vaccinium myrtillus* and *V. vitis-idaea*, became increasingly associated with the open plots with time (Fig. 6) in accordance with a previous analysis by Speed et al. (2014), but in contrast to a recent meta-analysis (Bernes et al. 2018). This highlights the complexity of plant-herbivore interactions and implies that there are both winners and losers under high herbivore pressure and some species are likely better adapted to intermediate browsing intensities (Hegland and Rydgren 2016).

Plant diversity

In partial agreement with our predictions, we found no effect of moose exclusion or site productivity on any aspect of diversity, whether it was species richness or Shannon entropy, vascular plants or bryophytes, alpha diversity or beta-diversity. Previous studies have found remarkably varying results of cervid herbivory effects on vascular plant diversity (see *Introduction*). However, a recent meta-analysis showed that ungulates can have idiosyncratic effects on the diversity within different groups of plants that can balance out to no overall effect on diversity (Bernes et al. 2018). The same meta-analysis also showed that the effect of ungulates on bryophyte diversity has predominantly been reported as positive (Bernes et al. 2018).

Increased diversity is not necessarily seen as beneficial if the cause or side effect of this increase is a homogenization of the flora caused by an increase in generalist species and decrease in specialist species (Boulanger et al. 2017, but see also Fløjgaard et al. 2018). Variation between forest localities gave by far the strongest explanation of understory plant communities explaining 72% of the variation, and only 2% of the remaining variation was explained by the exclusion treatment. We therefore found no evidence for region-wide homogenization, which is unsurprising given the large geographic separation of the sites. We also investigated if moose exclusion had a homogenization effect at the local scale, that is, between subplots. We found that, although the mean Jaccard distance decreased steadily with time in the open plots indicating increased homogenization since disturbance, this difference was not significant between treatments after 8 yr (Fig. 6).

CONCLUSION AND MANAGEMENT RECOMMENDATIONS

We showed that excluding moose from the early successional stage in Fennoscandian boreal forests favored a dominance of deciduous trees, including rowan, which was severely suppressed in open plots subject to browsing. Ferns and large herbs were also much more abundant inside enclosures. Due to high spatial replication and the analysis of non-taxonomic plant groups, we believe our findings are generally transferable to

other early successional boreal forests with moose. The overall implication of this study is that moose browsing may cause large tracks of forests to develop rapidly into a coniferous state after disturbance, something which is observed across the boreal biome. However, future management need to acknowledge that landscape-level alterations caused by the reduced prevalence of deciduous trees and large flowering herbs in early successional stands is likely to have cascading effects on important aspects of ecosystem functioning which appear compromised under current levels of browsing pressures.

ACKNOWLEDGMENTS

We wish to thank Marc Daverdin for helping with fieldwork, database management, and for making the map in Fig. 1, and Kristian Hassel from the NTNU University Museum for aiding with bryophyte identification. We also extend our gratitude to the numerous landowners who have let us use their forests for this long-term study and the two reviewers for their valuable input which helped improve the manuscript. Study was planned by ALK, JDMS, GA, and EJS. Field work was conducted by ALK, JDMS, and GA. Numerical analyses were conducted by ALK and LDV. ALK wrote the manuscript with input from all co-authors.

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DATA AVAILABILITY

All data used in manuscript are publicly available at figshare.com. <https://doi.org/10.6084/m9.figshare.6216386>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2458/full>