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Low intensities of red deer browsing constrain rowan growth in mature boreal forests of western Norway[1]

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Abstract: Browsing by cervids plays a key role in structuring forest ecosystems and dynamics. Many boreal forest systems are managed for timber resources, and at the same time the wild cervid populations are also harvested. Thus, the determination of sustainable densities of cervids for the purpose of forest and game management is challenging. In this study we report on a red deer (*Cervus elaphus*) exclosure experiment in the mature forests of Western Norway. Ten pairs of exclosures and browsed plots were initiated in 2008. The rate of browsing and height growth of marked individuals was recorded annually, and the total densities of all tree species assessed over the following 4 y. We found that height growth of rowan (*Sorbus aucuparia*) saplings (1 m tall), the most numerous tree species at the site, was prevented when 20% of the shoots were browsed. Outside of the exclosures, net height growth of rowan saplings tended to be positive when trees were below 40 cm in height, but growth was constrained in rowan saplings over this height. The density of rowan also increased in both treatments, showing that recruitment was occurring, but the increase was greater where browsed than in the exclosure. The increase in density of rowan, combined with the curtailment of height growth in the presence of red deer, serves to create a carpet of short stature rowan saplings. This has parallels with the browsing lawn concept, but it seems to occur in interaction with snow depth; individuals protruding above the snow layer are likely to be browsed during the winter, whilst smaller individuals are protected during this season, when browsing is at its peak.
Keywords: browsing lawns, Cervidae, *Cervus elaphus*, herbivory, snow depth, sustainable management.

Résumé : Le broutement par les cervidés joue un rôle clé dans la composition, la structure et la dynamique des écosystèmes forestiers. De nombreux systèmes forestiers boréaux sont gérés à la fois pour la production de ressources ligneuses et la chasse sportive des cervidés. Un enjeu majeur réside dans la détermination d'une densité de cervidés permettant une exploitation durable de ces ressources. Dans cette étude, nous rapportons une expérience d'exclusion du cerf élaphe (*Cervus elaphus*) dans les forêts matures de l'ouest de la Norvège basée sur 10 paires d'exclos et de parcelles accessibles au broutement établies en 2008. Nous avons mesuré annuellement durant 4 ans le taux de broutement et de croissance verticale de semis et de gaulis marqués et estimé les densités totales de toutes les espèces d'arbres. Hors des exclos, la croissance des gaules (1 m de haut) de sorbier des oiseleurs (*Sorbus aucuparia*), l'espèce ligneuse la plus abondante sur le site, était compromise lorsque 20 % des pousses étaient broutées. Nous avons observé une tendance positive dans la croissance des gaules de moins de 40 cm alors qu'elle était compromise au-delà de ce seuil. La densité de sorbiers a également augmenté à l'intérieur et à l'extérieur des exclos révélant un recrutement positif, toutefois l'augmentation de la densité était plus marquée dans les parcelles soumises au broutement. L'augmentation de la densité de sorbiers, combinée à la réduction de la croissance en hauteur, en présence du cerf élaphe génère une strate dense de sorbiers de petite stature. Cette situation présente des similitudes avec le concept de haie de pâturage (browsing lawn), mais pourrait être liée à l'épaisseur de neige au sol. En effet, les arbustes qui dépassent la couche nivale sont plus susceptibles d'être broutés que les plus petits qui sont protégés en hiver lorsque la consommation d'espèces ligneuses est maximale.
Mots-clés : cervidés, *Cervus elaphus*, épaisseur de neige, exploitation durable, haie de pâturage, herbivorie.

Nomenclature: Lid & Lid, 2005.

Introduction

Browsing is a key structuring process in forest ecosystems (Pastor *et al.*, 1988; Pastor & Naiman, 1992; Rooney & Waller, 2003; Nuttle *et al.*, 2013). Even low densities of ungulate herbivores or low intensities of browsing can reduce tree growth (Speed *et al.*, 2011), and growth reductions of dwarf shrubs caused by browsing can limit population growth rates (Hegland, Jongejans & Rydgren, 2010). In many areas, there is increasing concern

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about the impact of browsing on ecosystem functioning (Côté *et al.*, 2004; Mysterud, 2006). However, it remains unclear what level of browsing, and hence browser density, can be sustained by any one ecosystem without change in ecosystem state or successional trajectory (but see Hidding, Tremblay & Côté, 2013). In heather moorlands, the sustainable utilization level of the dwarf shrub (*Calluna vulgaris*), *i.e.*, the level at which its relative abundance did not decrease, was estimated to be 31.6% of the current-year's shoots being browsed (Pakeman & Nolan, 2009). There is much less information available to estimate sustainable browsing levels in forest ecosystems. However, a density of 3 moose·km^{-2} (*Alces alces*) was estimated to prevent height growth (*i.e.*, height growth was ≤0 cm·y^{-1}) of rowan (*Sorbus aucuparia*) and birch (*Betula pubescens*) saplings following clearcutting in boreal forests (Speed *et al.*, 2013), while local white-tailed deer (*Odocoileus virginianus*) densities over 15·km^{-2} curtailed growth of balsam fir (*Abies balsamea*) (Tremblay, Huot & Potvin, 2007; Hidding, Tremblay & Côté, 2012). However, the influence of reduced growth rates on forest dynamics, and hence whether these densities are sustainable both from forest and animal production perspectives, is unclear in the absence of longer-term studies. Moreover, relationships between cervid densities and tree regeneration may be nonlinear, which further complicates assessment (Tremblay, Huot & Potvin, 2007).

Large herbivores may drive ecosystem productivity in a positive or a negative direction. The degree of selectivity expressed by the herbivores and the balance of the impact of herbivory between the plants in the community, which may differ in growth rate, competitive ability, and herbivore selectivity, are important determinants of the outcome (Augustine & McNaughton, 1998). Observations of increased productivity in heavily grazed African grasslands led to the development of the grazing lawn concept, featuring a positive feedback between intensive grazing and both the abundance and quality of grasses. Central elements of the original grazing lawn concept are increased nutrient cycling and a change in vegetation composition (McNaughton, 1976; McNaughton, 1984). The concept of browsing lawns was developed as a woody-plant equivalent to the grazing lawn, whereby intense browsing leads to increased browse-forage availability and a proportional increase of palatable plant species in a given patch (Fornara & Toit, 2007; Cromsigt & Kuijper, 2011). Currently, a major focus in the forestry-herbivore literature concerns how specific tree and browse species are hindered in the recruitment phase; less attention has been put on understanding the conditions under which palatable species may maintain their densities and indeed facilitate further browsing. In the boreal forest ecosystem, moose browsing has been found to be detrimental to productivity, as it can speed up succession towards the "climax woodland" dominated by spruce trees by removing more palatable forage such as deciduous tree species (Pastor *et al.*, 1988; Pastor & Naiman, 1992). However, the moose is a quite strict browser, and mixed feeders such as red deer (*Cervus elaphus*) might not be expected to have the same effect. Related research on red deer has shown mixed results. For example, the establishment of Scots pine (*Pinus sylvestris*) saplings was found to be positively associated with cervid densities, driven by the creation of suitable sites for germination and a reduction in competition from the field layer vegetation (Scott *et al.*, 2000), while the impact of browsing deer on growth of established pine saplings was found to vary significantly in relation to local conditions, including soil type and aspect (Palmer & Truscott, 2003).

Many forest cervid populations have increased substantially in Europe over recent decades (Milner *et al.*, 2006; Apollonio, Andersen & Putman, 2010; Austrheim, Solberg & Mysterud, 2011). The red deer (*Cervus elaphus*) population in Norway, for example, is currently at an historically high level, with a 70% increase between 1949 and 1999, largely driven by changes in hunting regimes, and also by changes in land-use and a decrease in livestock densities (Austrheim, Solberg & Mysterud, 2011). The population may have reached a level where it is overabundant (defined as when a substantial impact upon vegetation is expected or observed, notably where densities of economically or aesthetically important species are reduced: Côté *et al.*, 2004), with a median of over 60% of shoots browsed for several deciduous tree species, including rowan, aspen (*Populus tremula*), bird cherry (*Prunus padus*), and willows (*Salix* spp.), in western Norway (Mysterud *et al.*, 2010). The boreal forests of Norway are managed for both timber resources and large-game hunting, but they also provide habitats for cervid populations that depend on the forest. Following a decline in livestock densities, there has been a shift to browser-dominance of the large-herbivore community in Norway (Austrheim, Solberg & Mysterud, 2011), with forest regeneration expected to be hindered as a result. Concurrently, forest management is driving increases in the number and volume of trees in Norwegian forests, as well as an increase in forest area (Granhus, Hylen & Nilsen, 2012). This increase in both forest extent and cervid populations means that the dynamics of the boreal forest ecosystem are in a state of flux. Furthermore, while highly selected tree species may be expected to decrease in density relative to less selected species (*e.g.*, Horsley, Stout & DeCalesta, 2003; Nuttle *et al.*, 2013), the highly selected species are sometimes able to tolerate heavier browsing (Speed *et al.*, 2013) and may show high regrowth capacity (Myking *et al.*, 2011; Myking *et al.*, 2013), so the response of forests to increasing browsing pressure is hard to predict. A recent regional-level study has shown that high densities of moose currently have strong impacts upon the forest succession following clearcutting (Speed *et al.*, 2013). In this study, we investigate the impact of red deer browsing on tree recruitment (in terms of growth and density) of different species within mature boreal forests, with a focus on rowan, the most abundant species in the understory. Rowan can be an early pioneer species and can also grow in shaded conditions. It is a species with a short life span, rapid juvenile growth, and a fast regeneration rate in response to disturbance (Myking *et al.*, 2013). We hypothesize that tree growth, particularly of rowan and other highly selected species, is reduced by browsing red deer, with relatively low browsing intensity thresholds preventing growth. Conversely, it is possible that the density of rowan may show a positive response to browsing due to its rapid growth and clonal regeneration.

Methods

Study area

A paired design of exclosed/unexclosed plots was initiated in 2008 at 10 sites located in the municipality of Tingvoll in the county of Møre and Romsdal in the mid-west of Norway (62.9°N, 8.2°E, Figure 1). The climate is oceanic, with mild winters and relatively cold summers. Both precipitation (annual mean 1300 mm) and temperature (mean temperature is around –1 °C in January and around 16 °C in July, www.eklima.no) generally decrease with increasing distance from the coast. Snow cover is normally present at the coast from January to March but is highly variable during winter and among years. The maximum snow depth over the winters 2008/2009 to 2012/2013 ranged between 40 and 107 cm (Figure 2).

The study area is situated in the middle boreal zone (Moen, 1999). Natural forests are dominated by deciduous tree species, predominately rowan (*Sorbus aucuparia*), birch (*Betula* spp.), and grey alder (*Alnus incana*), and Scots pine (*Pinus sylvestris*), interspersed with juniper (*Juniperus communis*) and the heathland shrubs bilberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*). Norway spruce (*Picea abies*) occurs in dense plantations, covering up to 25% of the productive forest area up to 300 m asl. The topography is characterized by hills, mountains, and fjords. Agricultural areas are situated on flatter and more fertile ground, often in the bottom of valleys, and consist mainly of pastures and meadows for grass production (Meisingset *et al.*, 2013). The red deer is the most common forest cervid in the region, but there are also minor populations of roe deer (*Capreolus capreolus*) and moose. At the municipality level, the red deer density is estimated to be about 8 deer·km^{-2} of forested area, which is approximately 6 and 25 times higher than the densities of roe deer and moose, respectively (E. L. Meisingset & O. Brekkum, unpubl. data). Sheep, cattle, and other livestock are largely absent from the forested areas within the region.

Experimental manipulation

The 10 study sites were located in mature mixed pine–deciduous forest with a closed canopy cover. At each site two 20- × 20-m plots were laid out, separated by 20–60 m gaps to avoid fence-edge effects and minimize vegetation differences. One of the 2 plots was randomly selected for the exclosure treatment, and the other left as an unmanipulated and unexclosed treatment. Exclosures were

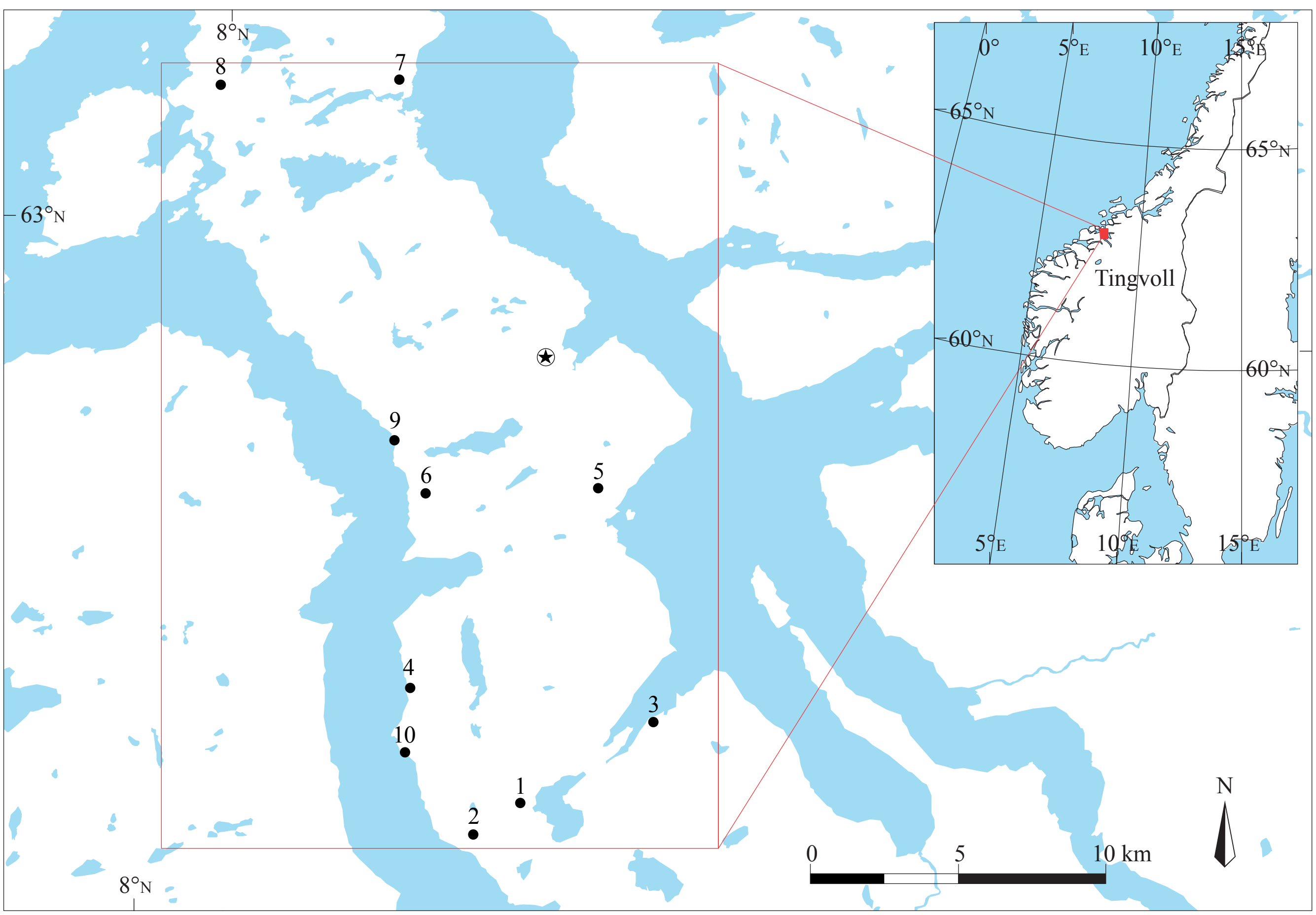

FIGURE 1. Spatial distribution of the 10 study sites of red deer browsing. The inset shows the location of the Tingvoll study region within mid-west Norway. The star symbol shows the location of the weather station where snow depth measurements were taken.

constructed during the autumn of 2008. Woven-wire mesh (2 m tall) was nailed to stakes that had been sunk into the ground. A top wire raised the exclosure height to around 2.5 m tall.

Within each plot, 4 circles of 2 m diameter were systematically located and marked with a central post. Within each of these 4 circles the total number of individuals of each tree species was recorded. Further, up to 4 individuals of each species were marked (or identified on the basis of their position within the circle, *i.e.*, distance and angle from the centre post). The 4 individuals were sampled from four 90° sectors of the circle where possible, selecting the first encountered individual on a systematic clockwise search. Selected trees ranged from 1 to 300 cm in 2009. The functional height (measured vertically) and the number of browsed and unbrowsed shoots on each marked individual were recorded. Tree densities, growth, and browsing intensity were assessed annually from spring 2009 to 2012. New individuals were added in later years when found in circles with fewer than 4 individuals of that species already marked.

STATISTICAL ANALYSES

Analyses were carried out at 2 hierarchical levels: individual (browsing and growth, focusing mostly on rowan, the most frequent species) and species (change in density between 2009 and 2012). Browsing data from 2009 were not included in analyses to avoid including browsing that occurred prior to the experiment initiation. Analyses of browsing incidence used binomial mixed models with a response variable of browsing presence at the individual tree level. Browsing intensity was also modelled with a binomial mixed effects model, with the number of shoots browsed in the preceding winter along with the total number of shoots as the response variable. Random intercepts were fitted for site and tree individual to account for non-spatial independence and the repeated measures of the design. Change in tree height was analyzed utilizing a Gaussian mixed modelling approach, after first visually checking homogeneity and homoscedasticity of the variables, again fitting random intercepts for each site and tree to account for specific differences in growth. Changes in tree density were analyzed with Gaussian mixed effect models, with site as a random factor to allow for initial differences in forest structure. Model selection was carried out using likelihood ratio tests of individual and interactive terms. Browsing treatment, tree species, and the interactive term were tested as predictors of browsing intensity and change in tree density, whilst initial tree height and browsing intensity along with the interaction were tested as predictors of rowan height growth. Statistical analyses were carried out within the R environment (R Development Core Team, 2012), using the lme4 package (Bates, Maechler & Bolker, 2011) for mixed modelling.

Results

The understory at the forest sites was initially (2009) dominated by rowan. The majority of the abundant rowan (72.8%) were of short height (<50 cm, Figure 3). Other deciduous species, including downy birch (*Betula pubescens*), hazel (*Corylus avellana*), and bird cherry, were also abundant, along with the conifers juniper and Scots pine (Figure 3).

Browsing was recorded on 34% of trees outside of the exclosures, whilst inside the exclosures (where red deer were unable to go) 2.5% of trees had browsing

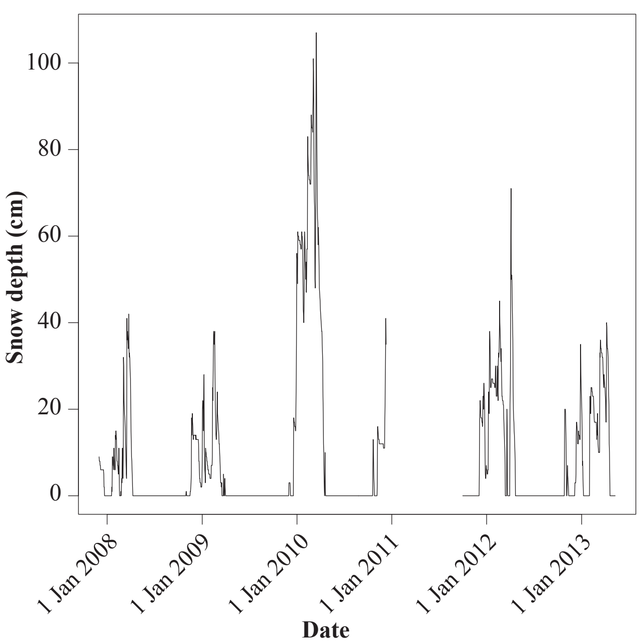

FIGURE 2. Snow depth observations at the Tingvoll Halsafjord II weather station (see map in Figure 1) between winters of 2007–08 and 2012–13. Data are available from the Norwegian Meteorological Institute (www.eklima.no); note the missing data during 2011.

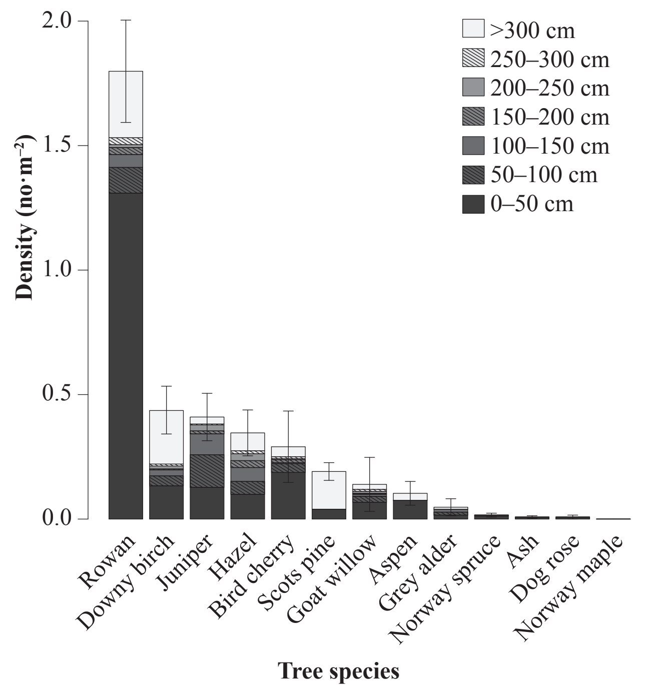

FIGURE 3. Initial density of tree species in 2009 and distribution between height classes. Species are ordered by total abundance. Mean values are shown along with the SE around the mean total density per species.

recorded (current year's browsing averaged between 2010 and 2012). The mean browsing intensity was 2.2% of shoots browsed inside the exclosure and 17.8% outside (current year's browsing averaged between 2010 and 2012). The incidence and intensity of browsing varied between species and browsing treatment, and there was a significant interaction between species and browsing treatment (incidence: binomial mixed effect model likelihood ratio test: $\chi^2 = 27.38$, df = 9, $P = 0.001$; intensity: binomial mixed effect model likelihood ratio test: $\chi^2 = 29.08$, df = 9, $P < 0.001$; note that dog rose [*Rosa canina*] and Norway maple [*Acer platanoides*] were not included in these models due to very low abundance). Aspen, downy birch, goat willow (*Salix caprea*), and rowan were the most intensively browsed species. Scots pine, Norway spruce, grey alder, and Norway maple were not browsed either within or outside the exclosures (Figure 4). The browsing intensities recorded on aspen, downy birch, and goat willow outside the exclosure were significantly different from the browsing intensity on bird cherry (Figure 4). For all browsed species, browsing intensity was greater outside the exclosure than inside the exclosure, with the exception of aspen and ash (*Fraxinus excelsior*). However, these species are rare in the sites, and the high browsing intensity on these species was driven by just a few individual trees being browsed, and this may well have been due to browsing by mountain hare (*Lepus timidus*), which were not excluded by the fences.

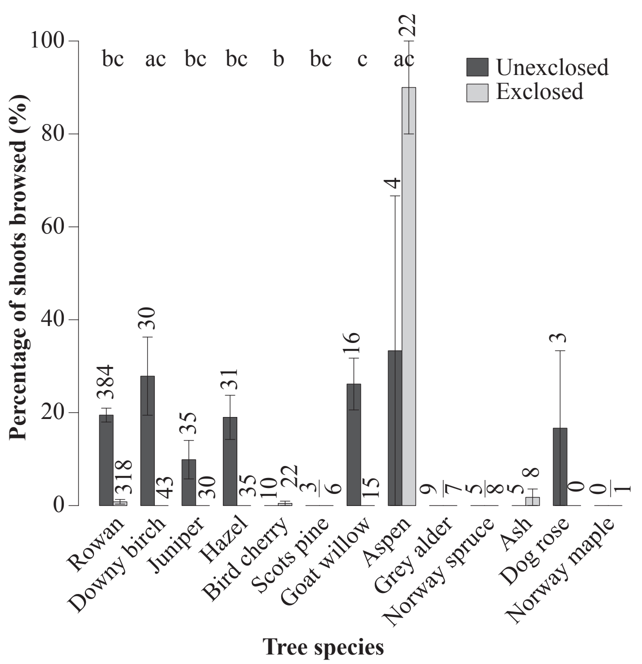

FIGURE 4. Browsing intensity recorded for tree species outside and inside the exclosures. Data are mean and SE averaged across the years 2010 to 2012. Species are ordered according to their initial abundance across sites (as shown in Figure 2). The numbers over the bars represent the number of trees assessed within the combination of species and treatment. Letters above the figure show Tukey pairwise comparisons of browsing intensity between species outside of the exclosures: species sharing a letter do not significantly differ at $P < 0.05$ (the 5 least abundant species were excluded from this analysis).

Using data on rowan growth from both treatments to increase the range of browsing intensities and initial height, rowan height growth was related to the interaction between height in the previous year and current season's browsing intensity (Figure 5; likelihood ratio test $\chi^2 = 6.85$, df = 1, $P < 0.001$). Height growth was prevented when 20% of the shoots of a 1-m-tall sapling were browsed (the SE around the zero growth contour spanned around 10–40%; Figure 5). Rowan was rarely browsed inside exclosures (Figure 4), and the 2 individuals that were browsed were short in height (<30 cm; Figure 5). Rowan growth was faster inside the exclosure than outside the exclosure (Figure 6a), and there was an interaction between initial height and treatment, with the growth of taller rowan trees being more reduced by browsing outside the exclosure (Figure 6a; likelihood ratio test $\chi^2 = 23.43$, df = 1, $P < 0.001$). Outside of the exclosures, rowan individuals that were shorter than 40 cm tended to increase in height, whilst those already taller than 40 cm tended to decrease in height (Figure 6a). However, there was a lot of variation in height growth of shorter individuals. There was a positive change in the number of shoots per rowan individual outside the exclosures (with a mean annual increase of 0.18 ± 0.08 shoots per year; Figure 6b) and a negative change in shoot number within the exclosures (with a mean decrease of 0.08 ± 0.05 shoots per year); this difference between treatments was significant (*t* test: $t = 3.03$, $P = 0.003$).

The most noticeable change in tree density was for rowan, which increased in both treatments (Figure 7). There was a significant interaction between tree species

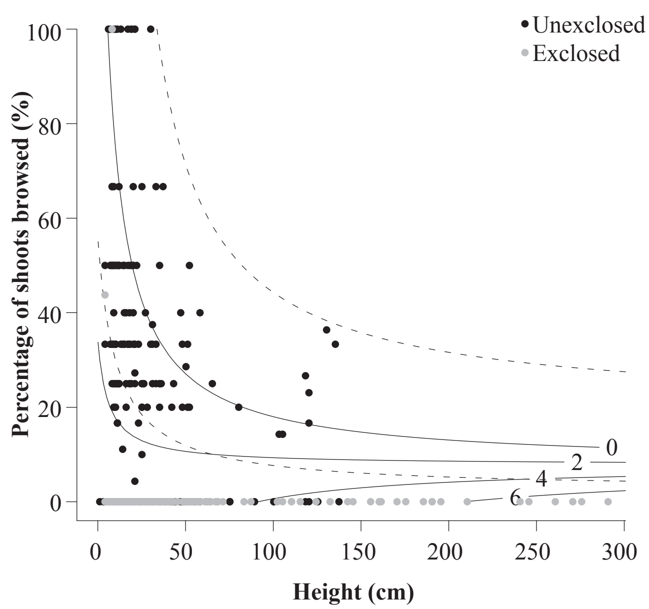

FIGURE 5. Contour plot showing the predicted change in height (shown by contour lines with values shown in cm) of rowan as a function of the tree's height in the previous spring (*x*-axis) and % of shoots browsed since the previous spring (*y*-axis). The predictions are from a Gaussian family mixed effects model including data from all years, with tree as a random effect to account for the repeated measures structure and a random intercept for site. SE of prediction for the zero-growth contour are shown with broken lines.

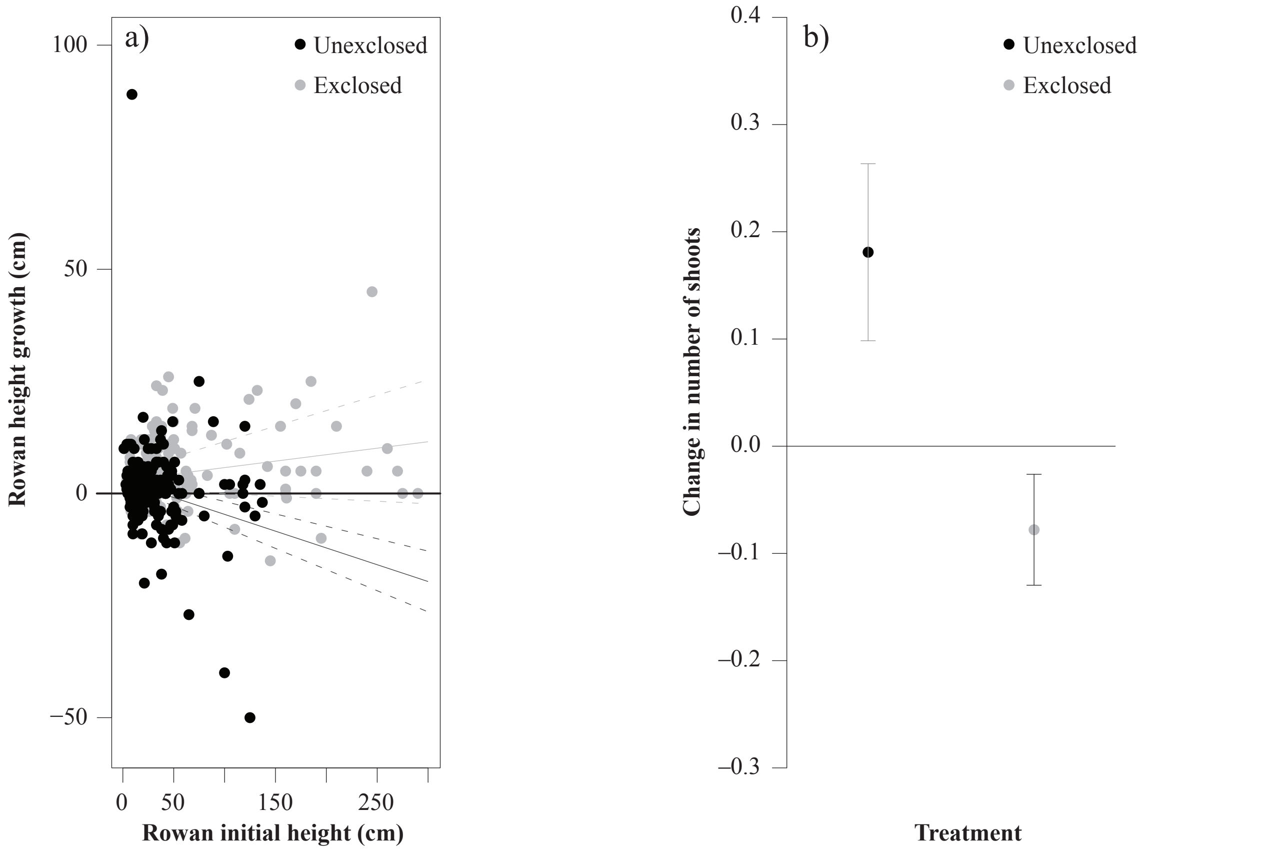

FIGURE 6. Height growth of rowan plotted against the previous year's height in the 2 treatments. Regression lines (mean as solid lines and SE as broken lines) from a Gaussian mixed model with initial rowan height and treatment as fixed effects and with tree individual and site as random intercepts (a). Change in the number of rowan shoots per tree averaged over 4 y across treatments (mean ± SE) (b).

and exclosure treatment in explaining change in tree density (mixed effects model, likelihood ratio test $\chi^2 = 20.47$, df = 11, $P = 0.04$). The increase in rowan density was significantly greater outside the exclosure than inside the exclosure ($\chi^2 = 17.31$, Holm adjusted $P < 0.001$). There were no significant differences between treatments for the other species, but pine and bird cherry tended to increase in density outside the exclosure and decrease inside the exclosure. Conversely, hazel density decreased outside the exclosure but increased inside the exclosure (Figure 7).

Discussion

In this study we have demonstrated a reduction in height growth of the most abundant and selected other tree species caused by browsing red deer in the boreal forests of mid-west Norway. At the same time, the density of trees changed in different trajectories in the presence and absence of red deer. The height growth of rowan individuals of 1 m height or higher was prevented when around 20% of shoots were browsed. The threshold browsing intensity at which rowan growth was halted in the mature forests in our study region was substantially lower than the threshold when browsed by moose (around 45%) in developing clearcut forests (Speed *et al.*, 2013). As rowan is the most abundant understory tree species, this represents a browsing-intensity threshold above which forest dynamics and composition may be substantially altered by cervids.

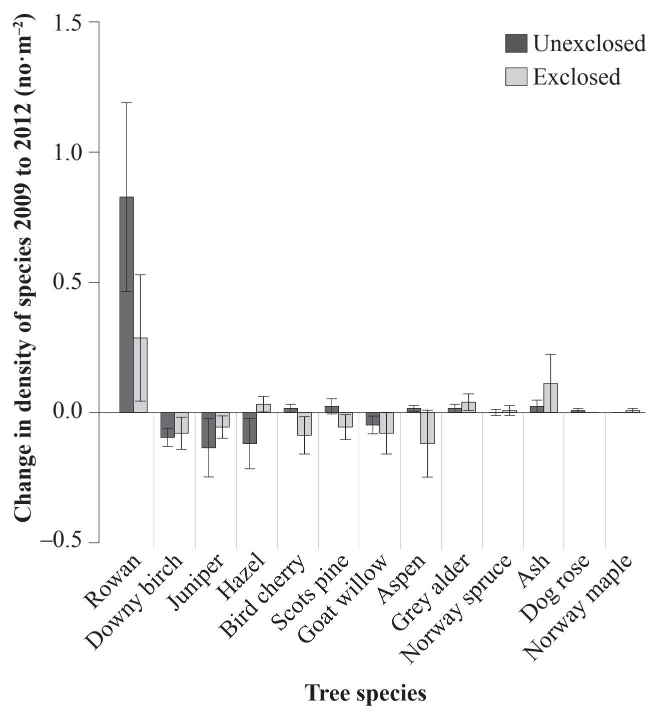

FIGURE 7. Change in density of tree species between 2009 and 2012. Mean change·m^{-2} ± SE. Species are ordered according to their initial abundance in 2009 (as shown in Figure 2).

The impact of cervid browsing on forest ecosystems is particularly severe in the cases where the cervid is a novel or invasive species (Tanentzap *et al.*, 2009; Martin *et al.*, 2010; Gosse *et al.*, 2011). In our case, red deer have been a dominant cervid for several thousand years (Rosvold *et al.*, 2013), but there has been a recent increase in the population density of red deer in Norway (Austrheim, Solberg & Mysterud, 2011), and this has led to clear impacts on the forest structure. The effect of browsing may also be partly explained by the lower browsing tolerance of rowan in mature forests (this study) than in clearcut forests (Speed *et al.*, 2013), linked to a lower compensatory growth potential of rowan in this shaded environment (Myking *et al.*, 2013). Indeed, height growth rates were generally slower in the mature forests in this study than in clearcuts: this is probably also related to the lower-light environment. However, we cannot rule out an influence of other factors.

Browsing lawns are approximately analogous to grazing lawns in that browsing leads to an increase in forage quality and quantity (McNaughton, 1984; Fornara & Toit, 2007; Cromsigt & Kuijper, 2011). Two factors are involved in the formation of a grazing or browsing lawn: 1) an increase in forage availability and/or quality and 2) an increase of preferred grazed/browsed species in the community. In this study we observed an increase in rowan density in both treatments, but a greater increase in the browsed treatment. Concurrently we also observed a decrease in annual height growth of rowan in the browsed treatment, preventing escape to a height refuge, as well as an increase in the number of shoots. This has parallels with the browsing lawn concept (Cromsigt & Kuijper, 2011). Cromsigt and Kuijper (2011) report a browsing lawn in a Polish forest with red deer (amongst other herbivores) browsing hornbeam (*Carpinus betulus*) in a regeneration patch of forest. In their study they found that tree height was maintained at around 80 cm, the approximate browsing height of red deer. In our study we find that the mean height growth of rowan (outside of the exclosures) is negative above approximately 40 cm and positive below that height. However, this difference may be due to interactions between browsing herbivores, trees, and snow depth, as red deer are predominantly browsers during winter (Mysterud, 2000) and smaller tree individuals are protected from browsing whilst buried under snow (Visscher *et al.*, 2006). Indeed, although snow depth has high spatial variability, it should be noted that the maximum snow depth at the nearest weather station was at least 40 cm during 2008 to 2013. Thus, in our boreal forest study system, it may be the interaction between browsing and snow depth that maintains a vegetation state that has similarities to a browsing lawn. Longer-term studies are required to test this assertion, since it is possible that rowan could eventually be overgrown by slower-growing and more browsing-tolerant species.

The greater increase in rowan density outside of the exclosures, where trees may be heavily browsed, may indicate opening up of the dwarf shrub vegetation layer by the activities of red deer acting as a disturbance agent and facilitating higher rates of recruitment and growth of rowan. Alternatively, or additionally, the increase in small rowan may be related to vegetative reproduction from subterranean root and sucker systems (Myking *et al.*, 2013). However, some deciduous species showed a decrease in density both inside and outside the exclosures, with the decline being greater outside than inside, while hazel declined in density outside the exclosures but showed a small increase in density inside. The significant interaction between tree species and exclosure in explaining the change in density shows that browsing had a species-specific impact on tree density, and species responded in different directions. However, the response of rowan, the most abundant species, will have the greatest impact on the forest dynamics. One question remaining is whether the increase in preferred browsing species or a decrease in non-preferred species will be maintained or there will be a decrease over the longer-term in preferred species, as is commonly seen in the case of browser–tree interactions (Skarpe & Hester, 2008). Should the red deer population remain high, a boreal forest browsing lawn of low statured palatable species with a dense canopy could increase the strength of competitive interactions for saplings of less preferred species, hindering any increase of slower growing and less preferred species.

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