Master's thesis

NTNU
Norwegian University of Science and Technology
NTNU University Museum
Department of Natural History

Ingrid Bekken Snøan

Use of LiDAR Data in Assessing Effects of Moose Browsing on Boreal Forests

Master's thesis in Natural Science with Teacher Education
Supervisor: James D. M. Speed
Co-supervisors: Anders L. Kolstad & Gunnar Austrheim
June 2019

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Kunnskap for ei betre verd

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Abstract

Cervid populations in many parts of northern Europe are increasing; this can have severe impacts on the ecosystems they inhabit. Moose (*Alces alces*) is the dominant herbivore in Fennoscandian boreal forests, and through trampling, defecation and selective browsing it has the potential to alter forest structure and species composition. Forest structure can be difficult and time consuming to measure with traditional field methods. Light Detecting and Ranging (LiDAR) systems use laser to map terrain and surface in three dimensions, providing a new perspective on forest stand structure. The objectives of this study were to use airborne LiDAR data to examine the effects of moose browsing on canopy height and variation in canopy height in regenerating boreal forest, in relation to site productivity. We also wanted to test whether canopy height estimates from LiDAR data and field data correlate to see if this is a reliable method for assessing moose impacts on forest structural traits. We used a network of 37 paired exclosures and open plots across central and southern Norway.

Moose browsing can reduce canopy height growth, leading to lower canopy height in forests with high moose densities. The effects of moose on canopy height growth was more pronounced at the more productive sites in the study, suggesting that productivity is a factor affecting the impacts of moose on regenerating boreal forest. Relative variation in canopy height did not differ significantly between the exclosures and the open plots. However, the non-relative variation measure was significantly greater in the exclosures, compared to the open plots. This indicated greater surface roughness in the exclosures. There was a strong correlation between LiDAR and field derived estimates of canopy height. These results demonstrate that moose have potential to affect canopy height and other forest structural characteristics, and that the effects of moose on boreal forest under secondary succession can be assessed by LiDAR systems. LiDAR systems can provide reliable and important information for managing forest browsed by moose.

Keywords: *Alces alces*; airborne laser scanning; exclosure; Fennoscandia; Norway; forest structure; canopy height; variation in canopy height; forestry.

Sammendrag

Hjorteviltbestander i store deler av Nord-Europa vokser; dette kan ha stor påvirkning på økosystemene de lever i. Elg (*Alces alces*) er den dominerende herbivoren i boreal skog i Fennoskandinavia, og gjennom tråkk, avføring og selektiv beiting har elg potensiale til å endre skogens struktur og artssammensetning. Det kan være utfordrende å måle strukturelle karaktertrekk i skogen med tradisjonelle metoder. Light Detecting and Ranging (LiDAR) systemer benytter laser til å kartlegge terreng og overflate i tre dimensjoner, og kan gi et helt nytt perspektiv på skogens tre-dimensjonale strukturer. Målet med dette prosjektet var å benytte LiDAR-data til å undersøke effektene av elgbeiting på trekronehøyde og variasjon i trekronehøyde i regenererende boreal skog, i forhold til produktivitet på stedet. Vi ville også undersøke hvorvidt LiDAR-data og data samlet i felt korrelerte, for å finne ut om LiDAR er en pålitelig metode for å utforske effektene elg har på strukturelle karaktertrekk i skogen. Vi brukte et nettverk av 37 studielokasjoner, på hver lokasjon var det et inngjerdet område hvor elgen ikke hadde tilgang og et åpent kontroll område. Lokasjonene var spredt rundt i Sør- og Midt-Norge.

Elgens beiting kan redusere vekst i trekronehøyde, noe som kan føre til generelt lavere trekronehøyde i skogområder med høy elgtetthet. Påvirkningen av elgbeiting på vekst i trekronehøyde var sterkere i de mer produktive områdene, det kan tyde på at produktivitet er en faktor som påvirker elgens effekt på boreal skog under sekundær suksesjon. Relativ variasjon i trekronehøyde var ikke signifikant forskjellig mellom de to behandlingene. Imidlertid var det ikke-standardiserte variasjonsmålet signifikant større i de inngjerdete områdene, sammenlignet med de åpne områdene. Det indikerer at områder uten elg har en større overlateruhet. Det var sterk korrelasjon mellom LiDAR- og felt-estimert trekronehøyde. Disse resultatene viser at elg har potensiale til å påvirke trekronehøyde og andre strukturelle karaktertrekk i boreal skog under sekundær suksesjon, og at disse endringene kan detekteres med LiDAR data. LiDAR systemer kan bidra med pålitelig og viktig informasjon til forvaltning av skog og hjortevilt.

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MAD	Median absolute deviation
RMAD	Relative median absolute deviation

1. Introduction

1.1 Background

The boreal forest is located at high northern latitudes and has a circumpolar distribution (Brandt, 2009). It is a large biome, covering about 30% of the world's forested area (Gauthier et al., 2015). The climate in the boreal forest is characterized by cold winters, long periods with snow cover, and a short growing season (Moen, 1999). The boreal forest has a relatively low diversity of tree species (Gauthier et al., 2015), the dominant species are typically evergreen coniferous trees belonging to genera such as *Picea, Pinus,* and *Abies.* In addition, robust deciduous trees from the genera *Alnus, Betula, Populus, Salix, and Sorbus* can be found in this biome (Moen, 1999; Brandt, 2009).

Disturbance is an important part of the dynamics in the boreal forest (Brandt et al., 2013), and can be defined in multiple ways. Here it is defined as "any discrete event that changes the vegetation and makes new growing space available" (Edenius et al., 2002). Disturbance in boreal forests can be on small or large scales, biotic or abiotic. Disturbance can contribute to rejuvenation of forest areas, and has the potential to alter species composition, habitat diversity and forest structure (Grime, 2001; Begon et al., 2005). Understanding these disturbance patterns and their impacts on boreal forest is essential for proper management of this ecosystem.

Some of the main disturbance agents in boreal forests are fire (Niklasson and Drakenberg, 2001; Groven and Niklasson, 2005), insects (Hadley and Veblen, 1993), and pathogens (Ayres and Lombardero, 2000; Hansen and Goheen, 2000). Vertebrate herbivores are also potential disturbance agents in boreal forests. For example, moose (*Alces alces*) typically exploit open patches and may create openings in an otherwise closed forest (Persson et al., 2000; Edenius et al., 2002). Forestry is another major disturbance factor, for instance, through clear-cutting, which is common practice in managed forests (Edenius et al., 2002). Today, two-thirds of the boreal forest is managed for wood production (Gauthier et al., 2015).

After a disturbance event, succession takes place. According to Connell and Slatyer (1977), succession can be defined as the changes one can observe in an ecological community after a disturbance that has opened up a relatively large area. Succession typically involves changes in species composition (Rydgren et al., 2004) and diversity (Kumar et al., 2018), biomass, productivity, and ecological function. Early successional species are typically fast-growing species with efficient dispersal. In contrast, late successional species often have lower growth rates and stronger competitive abilities, and they are typically more tolerant (Connell and Slatyer, 1977; Davidson, 1993). Several studies have shown that large herbivores can influence succession in boreal forest (Davison, 1993; Hidding et al., 2013; Speed et al., 2013; Kolstad et al., 2018a).

Cervids have a long history in Norway (Rosvold et al., 2013). However, during the last century, cervid densities and distributions have increased significantly; wild herbivore biomass in Norway increased from 6 kg km^2 in 1949 to 47 kg km^2 in 2009 (Speed et al., 2019). Increase in moose biomass is one of the main factors causing this pattern (Speed et al., 2019). There are several factors that may contribute to the observed increase in moose populations, for example sex- and age-specific harvesting, changes in the forestry (higher frequency of clear-cuts), reduction in number of livestock grazing on unimproved land and reduced populations of predators (e.g. wolves and bears) (Austrheim et al., 2008; Apollonio, Andersen, & Putman, 2010; Austrheim et al., 2011).

Moose are selective browsers, which can lead to changes in species composition in the forest they inhabit (McInnes et al., 1992; Gosse et al., 2011). Some species are preferred as forage over others, this may result in a reduced number of seedlings of the more palatable tree species, whereas seedlings of less palatable species can increase in abundance at their expense (Gill, 2006). For example, moose prefer deciduous species to coniferous species, which can increase the deciduous to coniferous biomass ratio (Kolstad et al., 2018b). Moose browsing is often most prevalent on leaves and young shoots of trees and shrub, these are typically the fastest growing and most nutritious parts of a plant. By removing the fastest growing and most nutritious parts of the plant, moose browsing tends to arrest height growth and thereby reduce canopy height (Edenius et al., 2002; Ellis and Leroux, 2017). How much browsing that is tolerated before height growth is halted varies between species (Speed et al., 2013). For rowan (*Sorbus* *aucuparia)* and birch (*Betula pubescens*), height growth of 1 m tall individuals was interrupted when approximately 45% of shoots were browsed. Height growth for Scots pine (*Pinus sylvestris*) individuals stopped when 30% of shoots were browsed, while Norway spruce (*Picea abies*) on the other hand could continue height growth with over 60% of shoots browsed (Speed et al., 2013). Both rowan and birch are considered early successional species in the boreal forest, whereas Scots Pine (*P. sylvestris)* and Norway Spruce (*P. abies)* are regarded as late successional species (Davidson, 1993).

By reducing the height growth of palatable species and changing the species composition in the forest, moose can potentially alter the variation in canopy height as well, but as far as we know, this has not yet been tested. It has been showed that ungulates in African savanna can create so-called "browsing lawns," analogues to grazing lawns (McNaughton, 1984), by changing the plant's resource allocation and structure (Fornara and Toit, 2007). According to Cromsigt and Kuijper (2011), a browsing lawn is a patch of the forest where intense browsing has led to increased availability of resources and increased ratio of palatable plants. It has been found that some tree species in the boreal forest, mostly deciduous trees like birch and rowan, can mitigate the negative effects of browsing by compensatory growth (Hester et al., 2004; Persson et al., 2007). Compensatory growth can potentially lead to formation of browsing lawns, and thereby less variation in canopy height in boreal forest. However, herbivore-plant interactions in general are complex, and many different factors can affect the outcome of the interactions.

A factor that has been found to modify effects of moose on the ecosystem is site productivity (Persson et al., 2007; Suominen et al., 2008). The results of Danell et al. (1991) suggest that moose prefer to browse in productive areas with higher available standing biomass to make foraging more efficient (higher yield per bite). However, severe browsing damage to pines at unproductive sites have been documented, this is typically when moose densities are high (Danell et al., 1991). Site productivity level has also been showed to affect biomass production and compensatory growth potential for tree species with relatively high nutrient requirements, such as birch (Persson et al., 2007). In addition, tree species composition varies with productivity (Larsson and Søgnen, 2003). For example, at unproductive sites, with soil low in nutrients, we often find scattered Scots pines, as they can survive in soil low in nutrients.

Deciduous species in the boreal forest typically require more nutrients, but they also tend to form denser canopies (Larsson and Søgnen, 2003; More and White, 2005).

Variation in canopy height can be used as an estimate of surface roughness. Surface roughness is one of several factors affecting surface albedo (Kung et al., 1964; Kukla and Robinson, 1980), which is a measure of the reflectivity of a surface (Henderson-Sellers and Wilson, 1983). Surface albedo is an important factor when it comes to regulation of climate (Kung et al., 1964; Henderson-Sellers and Wilson, 1983; Mahmood et al., 2014). Because the boreal forest covers a large part of the worlds land area, change in surface roughness in the boreal forest and thereby change in its surface albedo, could potentially affect the global climate (Snyder et al., 2004). Forest structural attributes, such as variation in canopy height, is also an important aspect for wildlife habitat, e.g., for birds (Cardinal et al., 2012) and cervids (Coops et al., 2010; Melin et al., 2013). It has been found that browsing by moose and other cervids can open the understory in the boreal forest and thereby reduce habitat diversity for birds depending on understory vegetation for nesting sites and foraging (Cardinal et al., 2012; Eichorn et al., 2017).

Forest stand characteristics, such as canopy height, are usually recorded either by field measurements or by photogrammetric measurements (Næsset, 1997). These techniques are adequate for many ecological applications but have several limitations. For instance, measuring variation in canopy height is very difficult with traditional field methods and photogrammetry. Light Detection and Ranging (hereafter referred to as LiDAR) is an active remote sensing technology that can map both terrain and vegetation in three dimensions simultaneously. Laser pulses are emitted from the LiDAR system and the time elapsed between the emission of the laser pulse and the return of the reflection of the pulse is used to measure the distance from the sensor to the surface of the target (Dubayah and Drake, 2000; Lefsky et al., 2002). LiDAR systems also include Global Positioning Systems (GPS) for position data, and an Inertial Measurement Unit (IMU) for information on orientation (Wehr and Lohr, 1999). The LiDAR system provides a three-dimensional point cloud, where each point has x, y, and z coordinates. In a forest, the emitted laser pulse will typically intersect several layers of vegetation before it reaches the ground. Therefore, one laser pulse can result in several reflections, or echoes, back to the sensor. The first echo of the laser pulse that reaches the sensor is reflected from the highest surface the laser pulse hits, for instance, the tree canopy in a forest. The last echo is reflected from the lowest surface the laser pulse hits; this is typically the terrain surface (Lefsky et al., 2002; Coops et al., 2012). Classification of points into ground- and surface point enables the production of digital terrain models (DTM) and digital surface models (DSM), also called canopy models when in a forested area (Wehr and Lohr, 1999). Today, increasing amounts of LiDAR data are available for researchers. This makes LiDAR a cost and time efficient tool compared to traditional field methods (Lefsky et al., 2002).

There are many ecological applications of LiDAR data. Several studies have shown that LiDAR systems can provide information on forest three-dimensional structural attributes, such as canopy height, understory foliage density and canopy cover (Falkowski et al. 2009, Coops et al., 2010; Melin et al. 2013; Melin et al., 2015; Eichhorn et al., 2017; Thers et al., 2019). LiDAR data has proven to accurately measure canopy height and other forest structural attributes (Næsset and Økland, 2002; Holmgren and Jonsson, 2004; Kane et al., 2010).

A large body of literature documents the effects of moose on boreal forests, and much research has been undertaken using LiDAR to characterise different forest features. However, few studies have used LiDAR to assess the effects of large herbivores on their ecosystems (e.g., Melin et al., 2015; Eichhorn et al. 2017). The objectives of this study are to use LiDAR data to assess the effects of moose browsing on canopy height and variation in canopy height in boreal forests in Norway in relation to site productivity. This will be done by using a multi-site experimental exclosure network, with paired exclosure and open plots initiated from 2008 across a gradient forest productivity. We will also examine whether LiDAR estimates of canopy height correlate with tree height data collected in the field, to explore whether LiDAR could contribute to forest management with reliable information on forest structural characteristics.

1.2 Objectives

1. Assess how moose exclusion has affected canopy height and variation in canopy height in boreal forest under secondary succession.
2. If the moose exclusion has affected canopy height and variation in canopy height, are these differences related to site productivity?
3. Examine whether the use of LiDAR data will give the same results as field-based methods regarding the effect of moose browsing on boreal forest.

1.3 Hypotheses

$H_{1a:}$ Average canopy height will be higher inside the exclosure than in the open plot.

H_{1b}: Variation in canopy height will be greater inside the exclosure than in the open plot.

H_{2a}: The difference in average canopy height will be greater between treatments at more productive sites.

H_{2b}: The between-treatment difference in canopy height variation will be greatest at unproductive sites.

H_3: LiDAR canopy height data is correlated with field tree height data across treatments and sites.

2. Methods

2.1 Study Region

This study used the SustHerb infrastructure (https://www.ntnu.no/museum/sustherb), which has study sites across five different regions in Norway, with 67 sites in total. Three of these regions, where moose is the dominant cervid, are included in this project: Trøndelag, Telemark and Hedmark-Akershus (Fig. 1). Sites were selected from these regions based on aerial LiDAR data availability, leaving a total of 37 sites (Kartverket, 2018). The sites are located in the middle boreal vegetation zone, characterized by coniferous forest dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), interspersed with mires. Other common species in this vegetation zone are downy birch (*Betula pubescens*), grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and goat willow (*Salix caprea*). The sites are situated in the slightly oceanic section (Moen 1999). All three regions have established populations of moose (*Alces alces)* and roe deer (*Capreolus capreolus*) (Austrheim et al., 2008). Red deer (*Cervus elaphus*) can also be found in Telemark, Trøndelag and at one site in Hedmark and Akershus, but it is less common than moose and roe deer (Table 1; Appollonio et al., 2010; Speed et al., 2013).

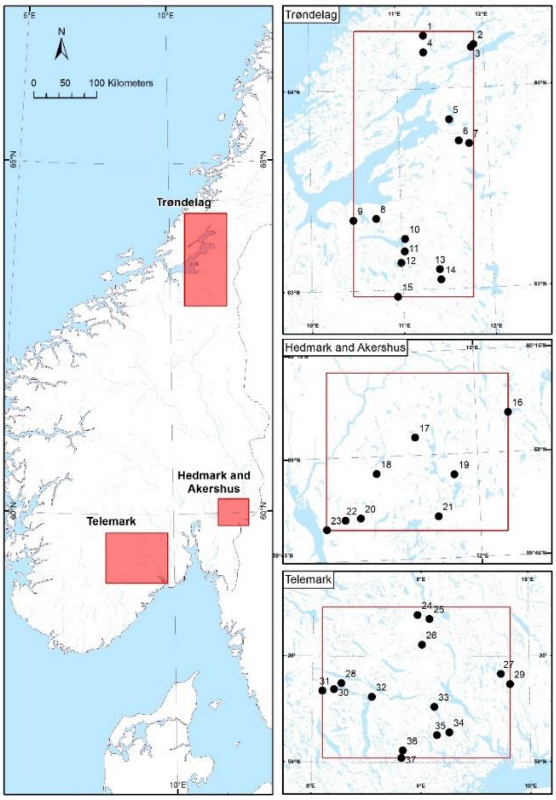

Figure 1: Location of study sites in Norway. Numerical labels correspond to site number in table 1.

Table 1: Information for the 37 sites included in this project. Site numbers correspond to the labels in Fig 1. Cervid densities are expressed as metabolic biomass (kg km^2) in year 2015 (Speed et al., 2019) and the estimates are based on hunter harvest and observation data.

Site no	Region	Clear-cut	Year initiated	LiDAR data	Point density m^{-2}	Productivity index [a]	Moose (kg km^2)	Roe deer (kg km^2)	Red deer (kg km^2)
1	Trøndelag	2006	2008	2010	2	0.223	75.888	7.376	8.758
2	Trøndelag	2005	2008	2011	2	0.116	107.565	17.865	2.431
3	Trøndelag	2004	2008	2011	2	0.087	107.565	17.865	2.431
4	Trøndelag	2004	2008	2010	2	0.077	75.888	7.376	8.759
5	Trøndelag	2006	2008	2015	2	0.110	28.270	6.980	2.827
6	Trøndelag	2003	2008	2015	2	0.241	28.270	6.980	2.827
7	Trøndelag	2005	2008	2015	2	0.012	28.270	6.980	2.827
8	Trøndelag	2002	2008	2016	2	0.160	91.595	20.568	0.842
9	Trøndelag	2002	2008	2017	5	0.196	79.892	31.022	1.335
10	Trøndelag	2004	2008	2015	2	0.271	56.446	4.380	5.438
11	Trøndelag	2003	2008	2015	2	0.116	56.446	4.380	5.438
12	Trøndelag	2002	2008	2015	2	0.124	56.446	4.380	5.438
13	Trøndelag	2005	2008	2015	2	0.214	16.4756	0	0.419
14	Trøndelag	2005	2008	2015	2	0.133	16.4756	0	0.419
15	Trøndelag	2005	2008	2015	2	0.042	36.259	2.712	6.648
16	Hedmark	2008	2010	2016	5	0.336	62.649	13.924	0
17	Hedmark	2009	2011	2016	2	0.250	52.570	32.774	0.364
18	Hedmark	2008	2010	2017	2	1	56.435	18.912	0
19	Hedmark	2008	2010	2016	5	0.090	62.649	13.924	0
20	Hedmark	2008	2010	2018	5	0.234	56.435	18.912	0
21	Hedmark	2008	2010	2017	2	0.295	56.435	18.912	0
22	Hedmark	2008	2010	2018	5	0.114	56.435	18.912	0
23	Hedmark	2009	2011	2016	5	0.140	71.336	32.850	0
24	Telemark	2007	2009	2017	2	0.120	45.750	3.558	7.550
25	Telemark	2002	2009	2017	5	0.142	45.750	3.558	7.550
26	Telemark	2003	2009	2017	2	0.106	45.750	3.558	7.550
27	Telemark	2009	2009	2017	2	0.246	45.549	8.848	2.225
28	Telemark	2000	2009	2017	5	0.091	34.251	2.937	13.402
29	Telemark	2005	2009	2017	2	0.148	45.488	19.916	33.896
30	Telemark	2004	2009	2017	5	0.106	34.251	2.937	13.402
31	Telemark	2007	2009	2017	2	0.058	23.224	1.526	2.079
32	Telemark	2005	2009	2017	5	0.106	34.251	2.937	13.402
33	Telemark	2006	2009	2017	2	0.167	30.188	5.048	28.258
34	Telemark	2006	2009	2017	2	0.080	36.733	26.880	7.238
35	Telemark	2005	2009	2017	2	0.211	27.007	5.032	9.837
36	Telemark	2007	2009	2016	2	0.019	27.007	5.032	9.837
37	Telemark	2007	2009	2016	2	0.205	27.007	5.032	9.837

[a] Productivity index based on mean annual biomass increment (Kolstad et al., 2018b)

2.2 Study Design

To study the effect of moose on regenerating forest, two 20 × 20 m plots were established at each of the 37 sites inside a recently clear-cut, homogenous area (see Table 1 for details). The sites were located in three different regions in middle and southern Norway, 15 sites in Trøndelag, 14 in Telemark and 8 in Hedmark-Akershus (Fig. 1, Table 1). The two plots were randomly allocated to exclosed or unexclosed treatment. At the exclosed plot, a fence was built using 208 cm tall wire mesh fencing attached to wooden poles, and at 250 cm, an additional wire was stretched between the fence poles (Fig. 2). To minimize edge effects, there was a minimum of 20 m between each plot. The exclosures were established in 2008 in Trøndelag, 2009 in Telemark and in 2010-2011 in Hedmark and Akershus (Table1). The fence prevents large herbivores from entering the exclosures, while hares and other small herbivores can enter the plot through the fence.

Four circular subplots with a 2 m radius were established within each plot, towards each corner (Fig. 2). The total number of individual trees of each species were counted inside each subplot. Multi-stemmed trees are considered as one individual if they are branched above ground. In addition, individual data on vertical height and diameter was recorded for all trees within each subplot. Tree heights were registered within 50 cm classes. Fieldwork was conducted annually, so for each site there exist field data from the same year as the LiDAR data.

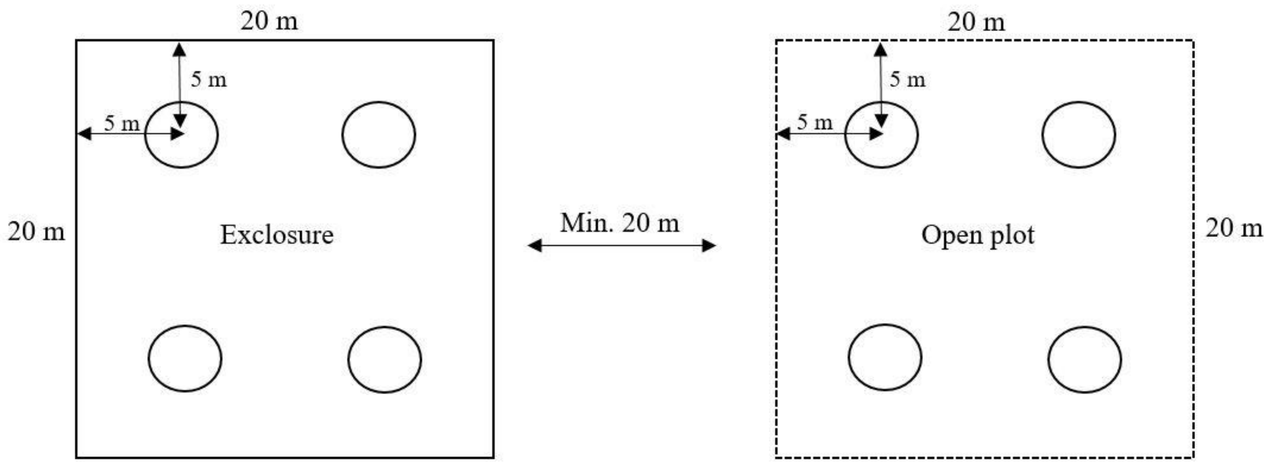

Figure 2: Illustration study design. Two 20 × 20 m plots at each site, circles represent subplots with radius 2 m.

A

B

Figure 3: A: Photograph showing the corner of the exclosed plot at site 9 from April 2019, 11 years after the fence was built (photograph: Ingrid Bekken Snøan). B: Photograph of the exclosed plot at site 7 from April 2016, eight years after the fence was built (photograph: Anders L. Kolstad).

2.3 Productivity index

To quantify site productivity we used a productivity index created by Kolstad et al. (2018b), where productivity is measured as mean annual biomass increment. Allometric models presented in the same paper were used to estimate standing tree biomass for all plots through all the years of the project, from which the mean annual increase in biomass at each site was calculated. The value from the plot with the maximum mean annual biomass production became the productivity index for that site. The productivity index was standardized by dividing by the maximum value.

One site (Site 18 in Hedmark and Akershus) had a much greater annual biomass production than the other sites included in this project, resulting in a very skewed distribution of productivity values. The great difference in productivity between site 18 and the other sites included in the project was assumed to be correct based on site knowledge. However, we had to remove many of the other sites in this region because of lack of suitable LiDAR data. If these sites were included, we would probably have more sites with greater productivity. With one site far more productive than the others, this site became an outlier and was thereby removed from further productivity analysis.

2.4 Collecting and processing LiDAR data

Airborne LiDAR data was downloaded from hoydedata.no, a web site developed by Statens Kartverk. The LiDAR data is part of a project called Nasjonal Detaljert Høydemodell (NDH) (Kartverket, 2019). The LiDAR data was recorded using pulse sensors with full waveform recording; the most commonly used sensor in NDH is Riegl Q1560i. The laser pulse footprint is generally lower than 0.61 m^2, depending on flight height. The data collection platform is either an airplane or a helicopter. We downloaded a 1 × 1 km square with LiDAR data centred on each study site. At sites where there were several different LiDAR projects available, the LiDAR data with the highest point density was downloaded (in all cases this was also the most recent data). Point densities were either 2 or 5 points m^{-2} (Table 1), this is considered sufficient for assessing forest stand inventory according to Gobakken and Næsset (2008).

Plot coordinates were recorded by standard handheld GPS with an accuracy of approximately 6 m. To correct initial inaccuracies in plot coordinates, the coordinates for the exclosures were moved so that they overlaid the corners of the fence in aerial photos (aerial photos from Statens

Kartverk). Since there was no marking of the open plots visible from the aerial photos, the coordinates of the open plots were moved in the precise length and direction as the coordinates of the exclosures (Fig. 4). It is reasonable to assume that the initial error in the plot coordinates would be approximately the same for both treatments at a study site since the coordinates were set at the same time (Rød, 2015). However, whether the errors are systematic or random is not clear, but since the corrected coordinates in the exclosure seem somewhat systematic (Fig. 4), one can argue that it is likely that the errors, in general, have a systematic component.

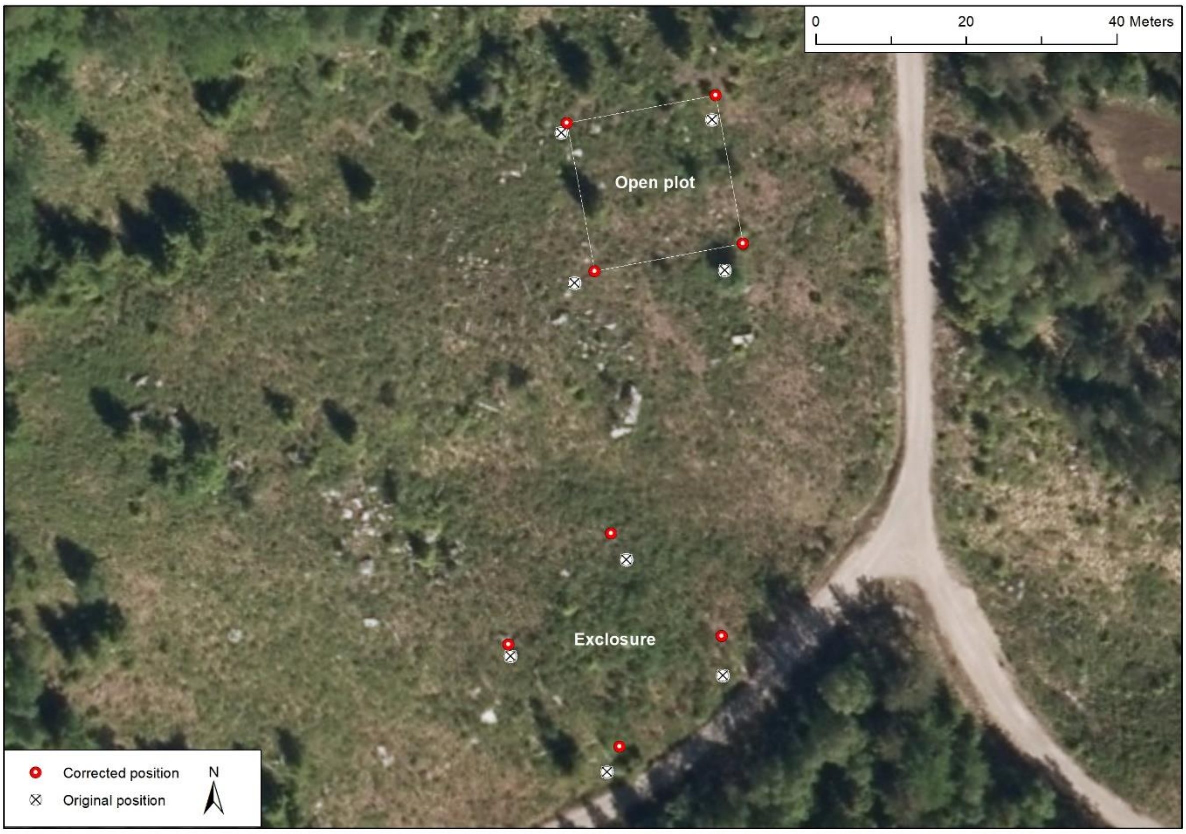

Figure 4: Aerial photo illustrating the correction of the coordinates at site 37. The white circles with crosses represent the original coordinates from GPS, and the red circles represent the coordinates corrected based on the fence seen in the aerial photo.

The downloaded LiDAR data was converted from laz to las format, and imported into R statistical environment (R version 3.5.1; R Core Team 2017) and R studio (Version 1.0.136; R Studio Team 2016). The corrected plot coordinates were used to locate the exclosure and open plot within the original 1 ×1 km square. A buffer of 6 m was added to the plots, making each plot a 32 × 32 m square. The purpose of the buffer was to allow the tree detection function (see below) to detect trees close to the plot, and branches hanging over the fence and into the plot. The function *lasclip* from the “lidR” package (Roussel and Auty, 2018) was employed to clip the 32 × 32 m square from the original las files for each plot across study sites for further analysis. Other packages used in this process were “raster” (Hijmans, 2017) and “rgeos” (Bivand and Rundel, 2018).

Using the “lidR” package (Roussel and Auty, 2018), canopy height models were made for each 32×32 m square by first creating a canopy model and a terrain model for each plot, and then subtracting the terrain model from the canopy model (Dubayah and Drake, 2000). Resolution of canopy height models was set to 1 m. This resolution was selected to be consistent between sites and to attempt to obtain data points for each pixel in the canopy height model. This resolution was lower than the highest possible for the data sets, yet it is still considered a high resolution (Falkowski et al., 2009). Trees larger than 7 m are most likely trees left standing from before the clear-cut and are therefore not interesting when assessing the effect of browsing on regenerating forest. The *tree_detection* function was used to detect all trees taller than 7 m and the *lastrees_dalponte* function was applied for individual tree segmentation. This function adds an ID to each segmented tree. Hulls were made around the trees detected with the *tree_hulls* function, using parameters las file for each plot and treeID. The tree hulls were removed from the canopy height model using the function *lasclip*. The functions *tree_detection, lastrees_dalponte, tree_hulls,* and *lasclip* are all from the “lidR” package (Roussel and Auty, 2018). The buffers around the plots were then removed, and a new canopy height model was made for the 20 × 20 m. The process is illustrated in the flow chart in Fig 5.

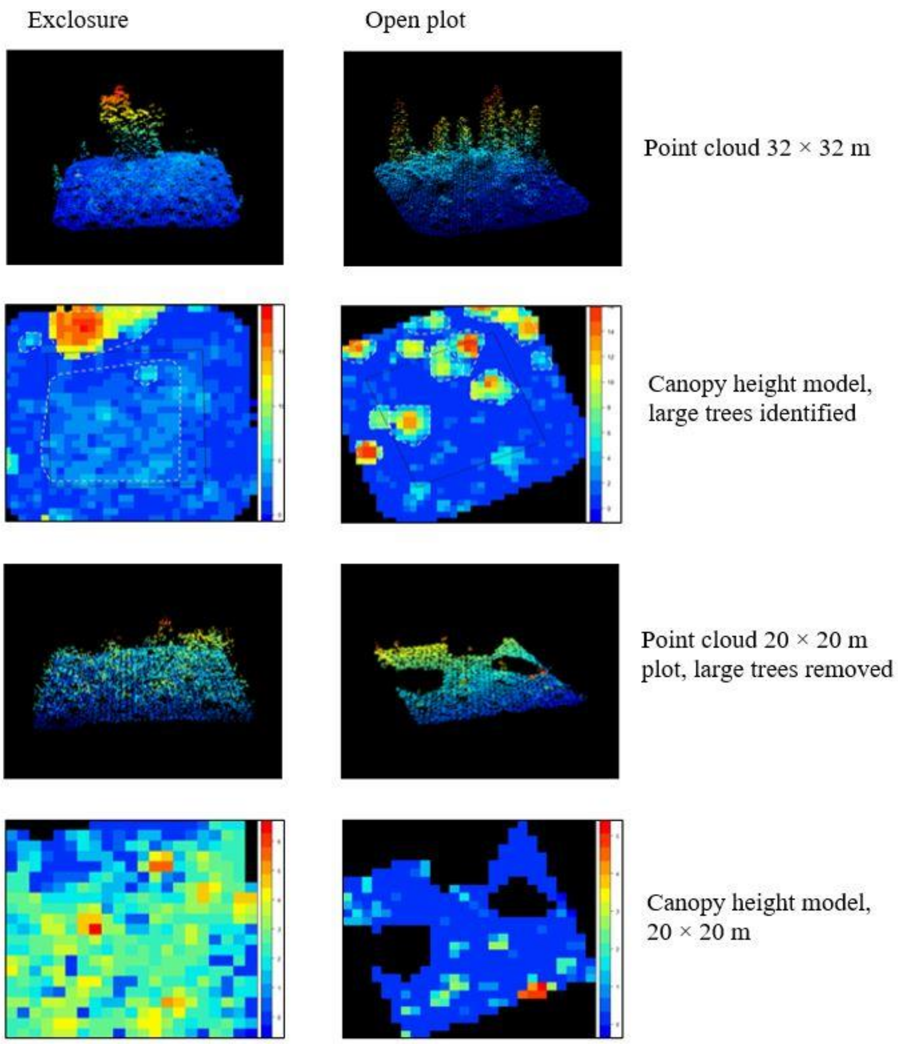

Figure 5: Flow chart (working top to bottom in two parallel examples) showing each step in the process from 32x32 m plot point cloud to canopy height model for the 20x20 m plot.

Canopy height data was extracted from the canopy height models and three estimates were calculated for each plot; median, median absolute deviation (MAD) and the relative median absolute deviation (RMAD, calculated as MAD/median, used as a non-parametric equivalent of the coefficient of variation). Median was used as measure of canopy height instead of mean, due to non-normal distribution of data. To account for the different amount of time between the year the project was initiated and the time of LiDAR data recording at the study sites, the median was divided by the difference between the year of LiDAR data recording and year of project initiation. The resulting median/duration was described as canopy height growth (m year^{-1}) and it was used when plotting the effect of treatment on canopy height to account for different treatment duration. For measuring variability in canopy height, MAD and RMAD were used, instead of the more common standard deviation and coefficient of variation, again because of non-normal data distribution. When calculating RMAD, two sites with median canopy heights of < 0.01 m was excluded to remove an extreme outlier. The relative variation measure was included to account for the possible difference in tree height between the exclosure and the open plot. MAD of canopy height was used as a measure of surface roughness.

2.5 Data analysis

Linear mixed effect models (Kuznetsova, Brockhoff and Christensen, 2017) were used to assess the effect of productivity, treatment (open or exclosed) and duration of treatment on median canopy height, median absolute deviation (MAD) and relative median absolute deviation (RMAD). The appropriate random structure was chosen based on AIC criterion (Akaike, 1974). Used site as random factor to resolve the non-independence between sites at the same location. Adding region as a random intercept did not improve the models (AIC was always smaller in the parsimonious model). Model selection was done for all models by first creating a model with all the factors mentioned above, and with all possible two-way and three-way interactions among these factors. Then, sequentially, insignificant terms were removed from the model. Residuals were visually controlled for normality and homoscedasticity of variance. If model assumptions were violated the response variables were log transformed. The non-parametric Wilcoxon signed rank test was used to assess whether treatment (exclosed or open plot) had a significant effect on median canopy height growth MAD and RMAD. We utilized Pearson's product-moment correlation to examine the association between median canopy height derived from LiDAR data and median canopy height from field data. To determine field median, each tree height was assigned to the median value in the 50 cm interval it belonged to. Then median canopy height was calculated for each subplot. Median canopy height for a plot was assessed by computing the median of the four subplot medians. At each site, we used field data from the same year as the LiDAR data was recorded (Table 1). In addition, Pearson's product-moment correlation was used to check the correlation in between-treatment difference in median from LiDAR and field data. All analysis was performed in R environment (R version 3.5.1; R Core Team 2017) and R studio (Version 1.0.136; R Studio Team 2016).

3. Results

3.1 Effect of moose exclusion on canopy height growth

Moose exclusion had a significant effect on canopy height growth (Fig. 6A, Wilcoxon signed rank test, V = 55, P<0.001) in boreal forest under secondary succession, with a higher median canopy height growth per year within the exclosures (median = 0.096 m, [Q_1 = 0.029, Q_3 = 0.195]) compared to the open plots (median = 0.027 m, [0.015, 0.046]). However, a couple of sites show the opposite pattern, and for some sites, there is little difference in canopy height growth between treatments (Fig. 6A). The difference in canopy height growth between-treatments was greater in the more productive sites (Fig. 6B, Table 2, mixed effects model, P=0.008). At a low productivity level (0.05), the simplified model predicts that between-treatment difference in canopy height growth is 0.010 m, whereas at a high productivity level (0.3), the predicted difference is 0.314 m.

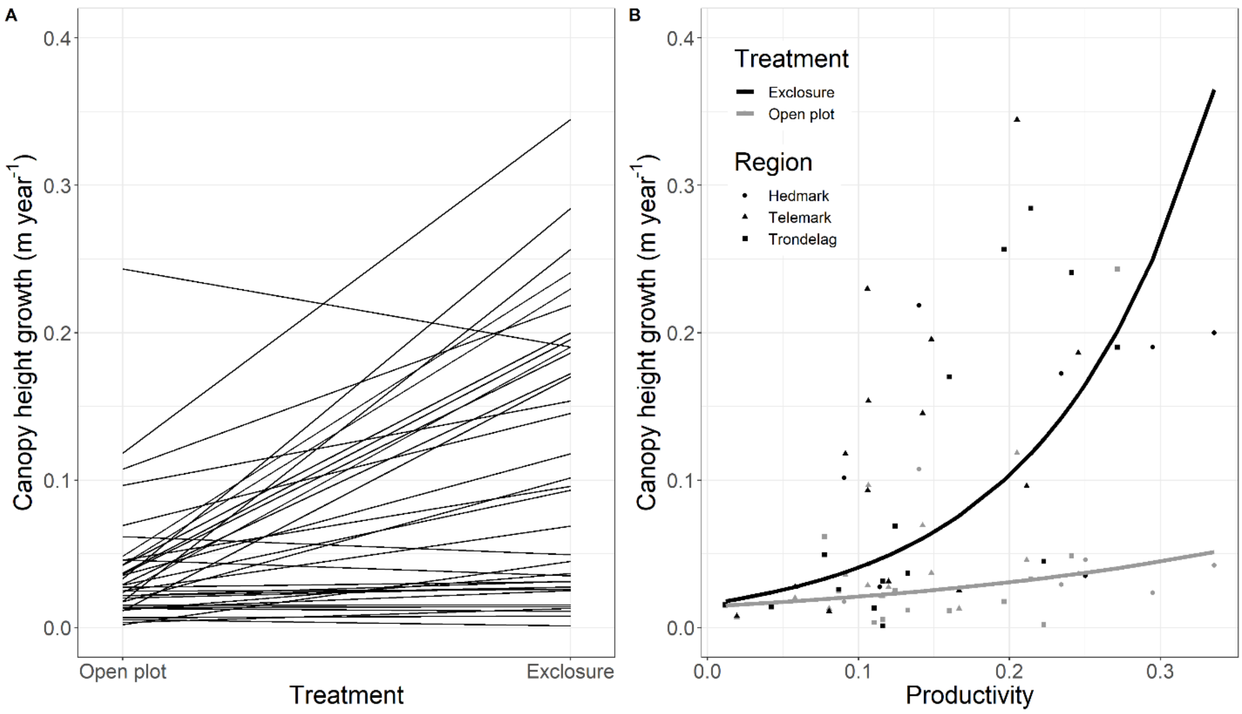

Figure 6: A: Difference in canopy height growth between treatments. Each line represent a paired plot within a site. B: Between-treatment difference in canopy height growth increases with increasing site productivity. The regions are separated by different symbols. Points represent raw data; the lines are based on a simplified model, meant as visual aid.

Table 2: Output from linear mixed effect models that predicted (a) median canopy height (log transformed) as a function of productivity, treatment and duration, (b) MAD in canopy height (log-transformed) as a function of productivity, treatment and duration, and (c) RMAD (log-transformed) as a function of productivity and treatment. Treatment factor reference level is the exclosure.

Fixed effects	Estimate	SE	Df	t-value	p-value
(a) Median canopy height					
Intercept	-4.294	0.689	37	-6.230	<0.001
Productivity	9.386	2.178	49	4.310	<0.001
Treatment Open Plot	-0.105	0.330	34	-0.319	0.751
Duration	0.296	0.086	33	3.452	0.002
Productivity:Treatment Open Plot	-5.530	1.958	34	-2.825	0.008
(b) Median absolute deviation					
Intercept	-3.694	0.571	37	-6.473	<0.001
Productivity	8.411	1.812	50	4.642	<0.001
Treatment Open Plot	-0.322	0.282	34	-1.145	0.260
Duration	0.231	0.071	33	3.257	0.003
Productivity:Treatment Open Plot	-3.814	1.672	34	2.282	0.029
(c) Relative median absolute deviation					
Intercept	0.050	0.122	37	0.405	0.688
Productivity	-0.403	0.706	33	-0.570	0.572
Treatment Open Plot	0.005	0.056	33	-0.092	0.927

3.2 Effect of moose exclusion on variation in canopy height

MAD of canopy height was significantly greater in the exclosures (median = 0.798 [0.128, 1.055]) compared to the open plots (median = 0.182 [0.093, 0.356]; Fig. 7A; Wilcoxon signed rank test, P<0.001), and this effect was more pronounced in productive areas (Fig.7B; Table 2; mixed effects model, P<0.029). At a productivity level of approximately 0.05, the simplified model predicts between-treatment difference in canopy height growth is 0.082 m, whereas at a productivity level of about 0.3, the predicted difference is 1.612 m.

Relative canopy height heterogeneity (RMAD) did not differ significantly between treatments (Fig. 7C, Table 2, Wilcoxon signed rank test, V = 325, P = 0.698). There was no significant relation between treatment variation and site productivity for RMAD (Fig. 7D, Table 2, mixed effects model, P = 0. 927).

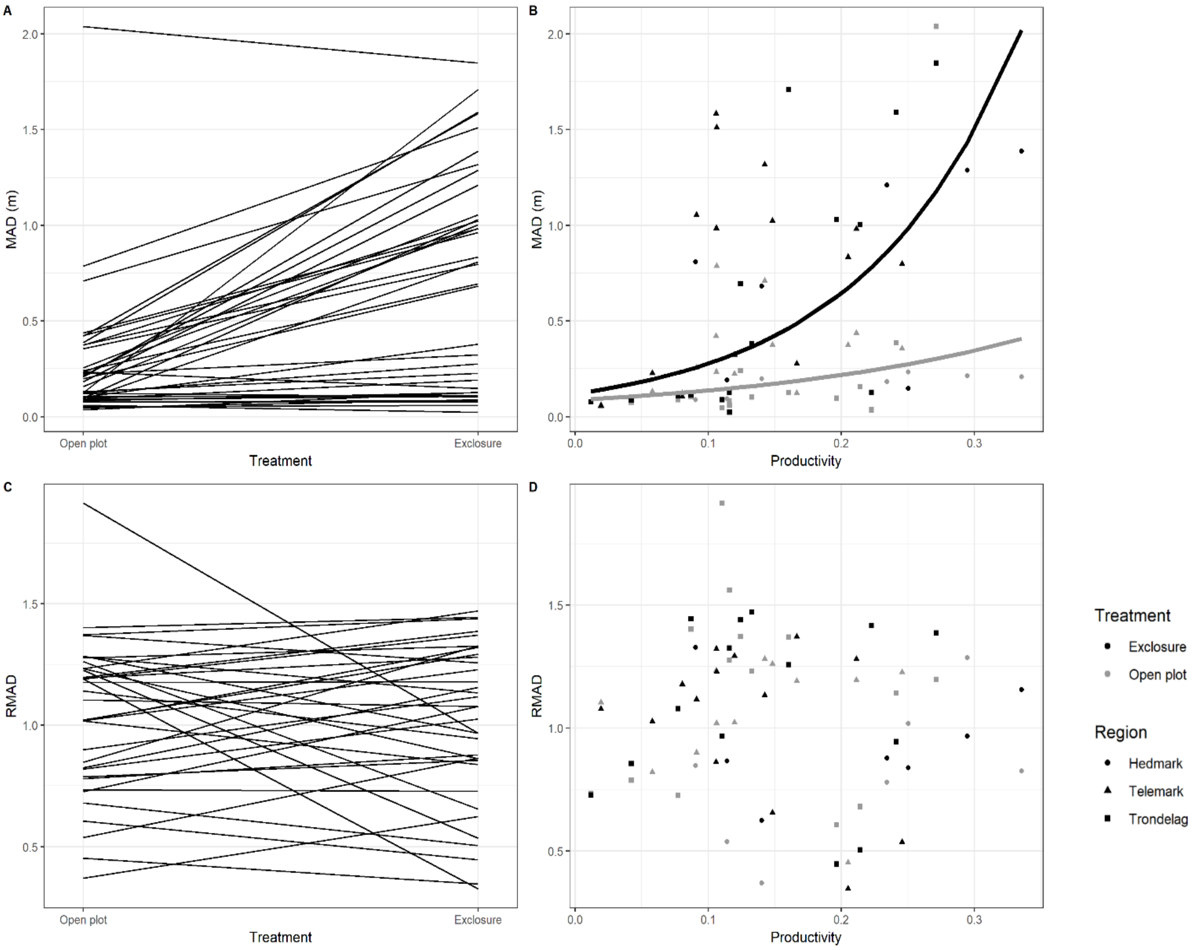

Figure 7: A: MAD across treatments. B: Between-treatment difference in MAD increases with increasing site productivity. C: RMAD across treatments. D: No significant relation between RMAD and productivity. In B and D points represent raw data, the lines are based on simplified models and are meant as visual aid. Coloured by treatment. Symbols represents the different regions.

3.3 Correlation between LiDAR canopy height data and field tree height data

There was a strong correlation between median canopy height calculated from the canopy height models made with LiDAR data, and median canopy height calculated from tree height recorded in the field (Fig 8A; Pearson's product –moment correlation *r* = 0.762). Median canopy height from LiDAR data with a point density of 5 points m^{-2} had a slightly higher correlation with field data (*n* = 20, *r* = 0.838) than LiDAR data with a point density of 2 points m^{-2} (*n* = 54; *r* = 0.765).

Field- and LiDAR between-treatment difference in median canopy height was also correlated (Fig. 8B, *r* =0.644). There was slightly stronger correlation between field data and LiDAR data with a point density of 5 points m^{-2} (*n* = 10; *r* = 0.749) than between field data and LiDAR data with a point density of 2 points m^{-2} (*n* = 27; *r* = 0.607).

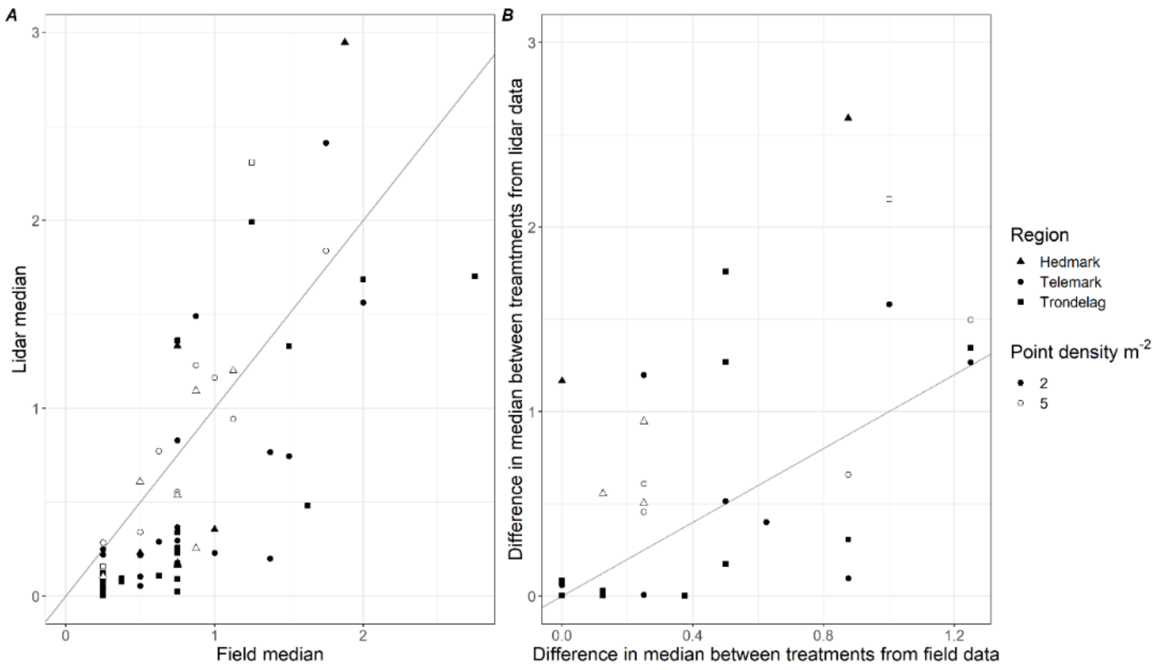

Figure 8: A: Correlation between median canopy heights calculated from field data and LiDAR data. B: Correlation between difference in median between-treatments for field data and LiDAR data. Points coloured by LiDAR point density. The line in both plots is 1:1.

4. Discussion

This study assessed whether LiDAR data could be used to examine the effects of moose on secondary succession in boreal forests, and if this method agreed with results obtained from field-based methods. There were strong correlations between canopy height measures derived from LiDAR data and tree heights measured in the field, which suggests that the effects of moose browsing on boreal forest can be reliably assessed using airborne laser scanners. Canopy height growth was significantly greater in the exclosures, compared to the open plots. Relative variation in canopy height (RMAD) was, contrary to our hypothesis, not significantly different between the exclosure and the open plot. However, MAD of canopy height, which can be used as an estimate of surface roughness, was significantly greater inside the exclosures. These results indicate that intensive moose browsing in regenerating areas of the boreal forest has the potential to affect canopy height and other forest structural attributes. A large body of literature has assessed the effects of moose on the boreal forest, and there is much research using LiDAR systems to measure forest structural traits. However, there are few studies using lidar to assess the effects of large herbivores on ecosystems, and even fewer studies that have used LiDAR in an experimental setting. This study demonstrates that the effects of moose browsing can be assessed using airborne lidar data, even within 20 × 20 m experimental plots.

4.1 LiDAR as a method for assessing the effects of moose forest structural attributes

Using a network of multiple paired exclosures and open plots across three regions in central and southern Norway with annual recordings of tree height, we were able to test the correlation between field data and LiDAR data on canopy height. The strong correlation between LiDAR data and field data indicate that LiDAR can be a useful and reliable method for measuring canopy height and forest structural characteristics. This is in accordance with the findings of Kane et al. (2010) who tested the correlation between field and lidar based measurements describing forest structure. However, airborne LiDAR data is typically applied for studies of patterns a relatively large scale (e.g., Falkowski et al., 2009; Melin et al., 2015; Thers et al., 2019). This study demonstrates that it can also be used on experimental projects at relatively small scale..

Several studies have used LiDAR to assess different forest characteristics; however, few studies have used LiDAR to assess the effects of large herbivores on their ecosystem (e.g., De Stoppelaire et al., 2004; Melin et al., 2015; Asner et al., 2016; Eichhorn et al., 2017). Eichhorn et al. (2017) used terrestrial laser scanning in UK woodlands to investigate the effects of deer on woodland understory foliage. Melin et al. (2015) assessed effect of moose on structural features of regenerating boreal forest. They found that airborne laser scanning could be used to detect moose browsing damage. However, browsing damage in the study area was unusually severe, and with a lower level of damage, it is not certain that it would have been possible to detect the damage (Melin et al., 2015). The strong correlation between LiDAR and field data in this study, and the findings of Melin et al. (2015), indicate that it is possible to assess the effects of moose on regenerating boreal forest using LiDAR data, as long as the moose densities are high enough to have a significant effect on stand characteristics.

4.2 Canopy height growth

As hypothesized (H_{1a}), exclusion of moose for 2-9 years had a significant positive effect on median canopy height growth (hereafter referred to as canopy height growth). This is in line with several studies of similar systems that have shown that moose limit height growth of preferred tree species (Krefting, 1974; Pastor et al., 1988; Gosse et al., 2011; Speed et al., 2013; Ellis and Leroux, 2017). Note that in this study, height growth of the canopy as a whole was measured, and there was no separation of palatable and unpalatable species. Speed et al. (2013) presented short-term data from the same study system as the one examined in this project, and found a strong negative effect of moose browsing on vertical tree height growth. A study from Newfoundland using 15-20-year-old moose exclosures also found evidence that moose browsing interrupts height growth of saplings of preferred species (Ellis and Leroux, 2017). Exclusion studies with a different number of years since exclosure, and studies using different methods to gather data (LiDAR and field methods) find the same negative effect of moose browsing on tree height growth.

However, at some of the sites, there was greater canopy height growth in the open plot than in the exclosure (Fig. 6A). We speculate that this can be because of low browsing intensities at these sites, patchy distribution of nutrients in the soil, variations in microclimate, heavy hare browsing inside exclosure or maybe large stones in the exclosure. Eichhorn et al., (2017) found that at sites in mature, temperate forest with high deer densities, the canopy was on average 5 m taller than at low deer density sites. They suggest that one possible explanation is that deer browsing affects canopy height through the process of compensatory growth. However, there is little evidence of trees overcompensating for herbivory (Skarpe & Hester, 2008). Therefore it is plausible to assume that browsing by cervids will either have no effect or have a negative effect on sapling growth and survival for palatable species.

There was a stronger effect of treatment (exclosure and open plot) on canopy height growth in the more productive sites compared to less productive sites; this is in accordance with hypothesis H_{2a}. In productive areas, the canopy grows faster. In the open plot at a productive site, moose browsing can arrest sapling height growth, while the trees in the exclosure can grow tall undisturbed by moose. At an unproductive site, on the other hand, the canopy will generally grow slower, and the difference in canopy height growth will not be as large despite moose browsing in the control plot. In addition, moose densities might be higher in productive areas, as moose typically prefer to browse in productive areas where the standing crop of available twigs is higher (Danell et al., 1991). The stronger effect of moose exclusion at the more productive sites compared to the less productive sites suggests that productivity is a factor affecting the impacts of moose on regenerating boreal forest, this result is in accordance with the findings of Persson et al., (2007) and Suominen et al. (2008) who simulated moose browsing along productivity gradients.

4.3 Effect of moose exclusion on canopy heterogeneity

It has been suggested that herbivores may create browsing lawns, analogous to grazing lawns (Fornara and Toit, 2007; Cromsigt and Kuijper, 2011). At some of the sites in this project, the vegetation outside the exclosures resemble a browsing lawn: most of the deciduous trees are much branched and have approximately equal height. Therefore, it was hypothesized that there would be greater canopy height variation within the exclosures (H_{1b}). However, results presented herein show that there was no significant difference in relative canopy height variation (RMAD) between the exclosures and the open plots. Cromsigt and Kuijper (2011) argue that because intense browsing in boreal forest often is followed by an increase in the proportion of unpalatable species, the browsing lawn concept does not seem to apply to this ecosystem. The height growth of the palatable species might be halted, but some species of the boreal forest (e.g., Norway spruce) are unpalatable to moose and will therefore continue to grow. Therefore, there will be variation in canopy height in the boreal forest despite high browsing intensity.

We hypothesized (H_{2b}) that between-treatment difference in canopy height variation would be greatest at unproductive sites. Contrary to our expectations, there was no evidence that between-treatment difference in canopy height variation changed in relation to site productivity. As discussed above, the browsing lawn concept does not seem to apply for the boreal forest where there are unpalatable species present, and therefore canopy height variation might have been greater in the open plots than expected, reducing the difference between treatments. In addition, the canopy height variation in the more productive exclosures may be greater than expected, this could be because successional dynamics are quite stochastic and all trees may not have recruited at the same time, or it might be due to differences in individual growth rates.

There is abundant evidence that surface structure affects surface albedo (Kung et al., 1964; Betts, 2000, 2014; Bright et al., 2015; Bright et al., 2017). Cohen et al. (2013) found that reindeer summer grazing in the tundra areas of Fennoscandia reduced the amount of vegetation protruding over the snow, and thereby contributed to increased albedo in winter/early spring. Large parts of the boreal forest are covered by snow in the winter season, and one can speculate that the amount and the structure of vegetation above the snow cover can affect the reflective abilities of the boreal forest in a similar way as in the tundra. It has been showed in multiple studies that moose can affect species composition in boreal forest as well as forest structural attributes, and they can potentially convert the forest to a “spruce savanna” (Krefting, 1974; Pastor 1988). As mentioned above, this study has found a negative effect of moose browsing on canopy height growth as well as MAD of canopy height. MAD of canopy height, can be used as an estimate of surface roughness. This lower canopy height growth and the lower surface roughness could result in less vegetation masking the snow cover in winter, which in turn can increase surface albedo. Furthermore, since the boreal forest is a large biome, changes in the surface albedo could potentially affect regional, if not global, climate (Snyder et al., 2004).

4.4 Correlation between tree height measurements from field and LiDAR data

The results presented herein showed a strong correlation between median canopy height derived from LiDAR data and median canopy height from field data. This is in accordance with hypothesis H_3. Other studies suggest that mean tree height could be estimated with higher accuracy using LiDAR data, compared to earlier methods (Næsset and Økland (2002); Holmgren and Jonsson, 2004). When measuring tree height in the field, tree height was recorded within 50 cm intervals instead of accurate height. To account for this, median between-treatment difference from field and LiDAR data was checked for correlation. Here too, there was a strong correlation between the between-treatment LiDAR data and the between-treatment field data. The strong correlation between LiDAR and field derived canopy height measures suggest that LiDAR data can be used to characterise forest structure in small scale, experimental studies. This is supported by De Stoppelaire et al. (2004) who used LiDAR data in an exclusion study, with exclosures of 15 × 20 m, where they documented the effects on feral horses on sand dune topography.

However, it should be mentioned that the correlation for the between-treatment differences was not as strong as the correlation between median canopy height derived from LiDAR data and median canopy height from field data. This can be due to compounding errors. When assessing the correlation in difference between treatments using field data we combine two interval errors, whereas when assessing correlation between LiDAR and field median canopy height there is only one interval error.

Correlation with field data was consistently higher when using LiDAR data with higher point density (5 points m^{-2}), compared to when using the lowest point density (2 points m^{-2}). When making a canopy model, the function *grid_canopy* uses the LiDAR point cloud, and for each pixel, the function returns the highest point found (Roussel, 2018). Higher point density means a greater chance of hitting the highest point within that pixel. Therefore, it is reasonable to assume that higher point density could affect the correlation between field and lidar estimates of canopy height. However, both LiDAR data with 2 points m^{-2} and LiDAR data with 5 points m^{-2} produced canopy height data that was in accordance with tree height measured on the ground.

4.5 Limitations of the study

One limitation of this study was the technique we used when correcting inaccuracies in plot coordinates. First, correcting the coordinates to overlay the corners of the fence in aerial photographs does not necessarily give the correct coordinates because the aerial photograph itself can have georeferencing errors. Second, coordinates of the open plots were moved in the precise length and direction as the coordinates of the exclosures. Since the GPS coordinates were recorded the same day, it is likely that the error in the plot coordinates would be approximately the same (Rød, 2015). However, it is not certain that the errors were identical, meaning that our open plots may not have correct GPS coordinates. For measuring canopy height growth and variation in canopy height, inaccuracies in coordinates of the open plots would probably not have a large effect on our results, since the open plot is located in a relatively homogenous area. Nonetheless, it would have been better having high precision GPS coordinates, but that was not available at the time.

Another possible limitation is the choice of resolution. In this project, LiDAR data point density was either 2 points m^{-2} or 5 points m^{-2}, whereas the canopy height models had a resolution of 1×1 m. To have the same resolution for all sites and highest possible resolution we could have used 0.5×0.5 m. However, that would lead to fewer data points per pixel and more empty pixels in the canopy height models as the *grid_canopy* function did not fill these empty pixels by interpolation. It is possible to make the function use interpolation to fill the empty pixels. Using a higher resolution with interpolated points would probably improve future studies.

5. Conclusion

Moose densities in Norway are at an all-time high (Speed et al. 2019). This requires an understanding of the effects of this large herbivore on the boreal forest it inhabits. This study is a novel application of LiDAR within a forest browsing experiment. Our results demonstrate that intensive moose browsing in regenerating areas of the boreal forest has the potential to affect both canopy height and other forest structural attributes, and that this effect of moose browsing can be reliably assessed using airborne LiDAR data. This implies that LiDAR may have wider applications in monitoring moose browsing impacts in boreal forests.

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