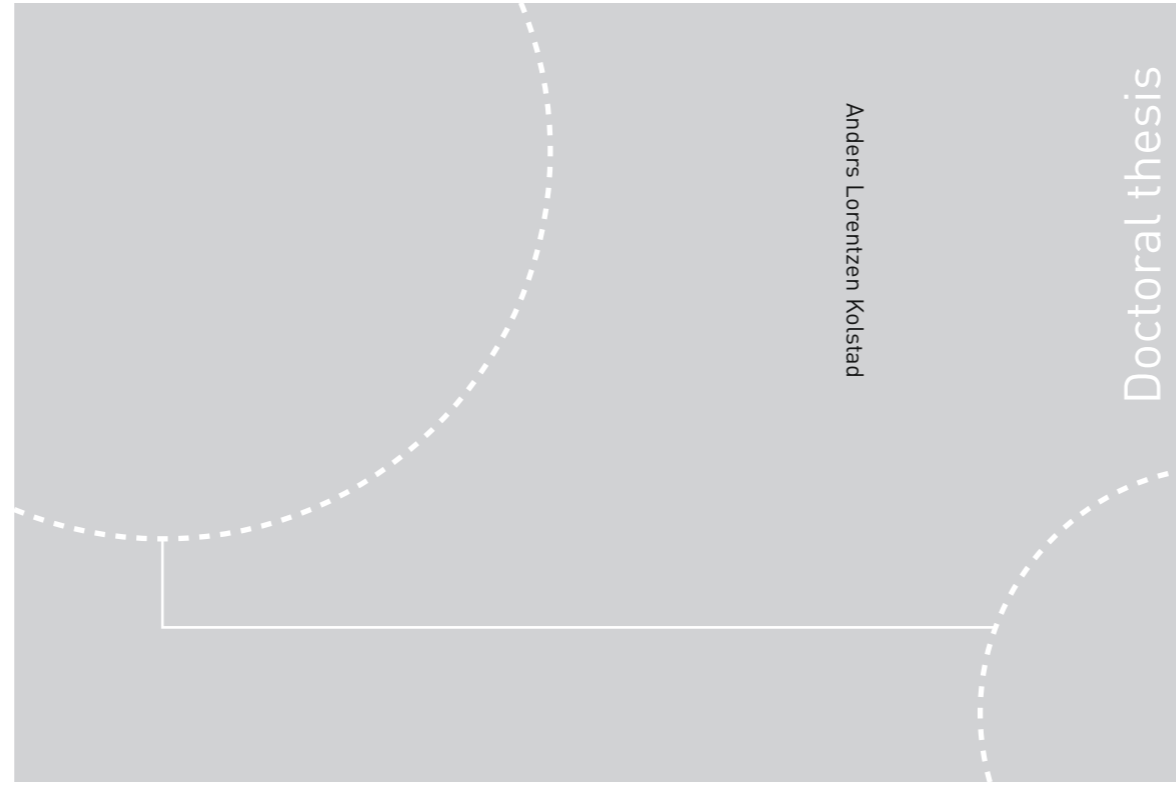


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Anders Lorentzen Kolstad

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 **NTNU**
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Thesis for the Degree of
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Effekten av elgbeite i boreale produksjonsskoger – implikasjoner for økosystemer og samfunn

Thesis for the Degree of Philosophiae Doctor

Trondheim, August 2019

Norwegian University of Science and Technology

Faculty of Natural Sciences

Department of Biology / Department of Natural History

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List of papers

- I. Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species. 2018. *Ecosphere* 9:e02458.
- II. Cervid exclusion alters boreal forest properties with little cascading impacts on soils. 2018. *Ecosystems* 21:1027-1041.
- III. Moose effects on soil properties, tree canopies and understory vegetation – a path analysis.
- IV. Promoting system thinking and collaborative learning in boreal forest management using a web-based knowledge system.

Author contributions.

Paper I: 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. **Paper II:** The study was planned by ALK, GA, EJS, SJW and JDMS. Field work was conducted by ALK, GA, AMAV and JDMS. Laboratory work was conducted by ALK and AMAV. Statistical analyses were conducted by ALK, with significant input from JDMS. ALK wrote the manuscript with input from all co-authors. **Paper III:** Study was planned by ALK, JDMS, GA, GRS, BJG, and EJS. Field work was conducted by ALK, JDMS and GA. Numerical analyses were conducted by ALK. ALK wrote the manuscript with input from all co-authors. **Paper IV:** ALK devised, developed and maintained the web-based knowledge system EcosystemMoose, including all graphics. All authors contributed to the website with one or more science summaries or reviews. ALK wrote a draft of the manuscript and finalized it after receiving comments from all co-authors.

Author abbreviations: ALK, Anders Lorentzen Kolstad; JDSM, James Speed; GA, Gunnar Austrheim, BJG, Bente J. Graae; GRS, G. Richard Strimbeck; EJS, Erling J. Solberg; SJW, Sarah J. Woodin; AMAV, Aurel M. A. Venete; LDV, Laurent De Vriendt, JA, Jørund Aasetre; RB, Ryan Bright; MHM; Melissa H. Mageroy; JOO; Jon Olaf Olausen; HBS, Håkon B. Stokland.

Introduction

The land areas of the world are under increasing pressures to provide us with increasing amounts of food, feed, materials and energy. Humans manage and influence 70% of the ice-free land surface on our planet and about a third of these lands are thought to be in a degraded state (IPCC 2019). Changing the way we manage land is paramount for reducing the adverse effects of climate change (IPCC 2019) and for stopping the loss of biodiversity and ecosystem services (IPBES 2019). The single most common land use globally is pasture land. This does not include wildlife grazing in forested ecosystems, yet in many places, such as Norway, forest-dwelling wild game species are intensively managed to provide meat and hunting opportunities. On Norwegian unenclosed lands, wild herbivores are more abundant than grazing livestock (Speed et al. 2019), and game management is therefore an extensive land use in this country where relatively large areas of nature remains. Current management practices likely cause both conflicts and synergies with the goals for a sustainable development (UN 2015). Important questions for sustainability are then: can we improve the management of our wild game species to the benefit of both the environment and human society, and can game management offer nature-based solutions to combat climate and nature challenges from the local to the global scale?

We can only sustainably manage what we understand, and to manage wild game populations we need to know how they impact on ecosystems as well as on society. Moose (*Alces alces*) is an important species to Norwegians (Brottveit and Agedal 1999) and to Norwegian forest ecosystems where it lives (Persson et al. 2000; Kolstad et al. 2018b). At least up until very recent, the management of this species has been focused on maintaining viable populations for sports hunting. But with a bodyweight of 300-500 kg, an annual food intake of up to 9 tons of leaves, twigs, buds and herbs (Persson et al. 2000), and typical densities well above 1 moose per km² forest, moose has a profound effect on the entire forest ecosystem. This calls for an extended mandate of moose management as a governance tool for biodiversity and multiple-use forests. In addition, because moose hunting is such an important social and physical activity for many Norwegians, moose management also becomes relevant to a discussion about human well-being and for maintaining a continued rural occupation in Norway. The papers presented in this thesis attempts to elucidate some of the more complex interactions between moose, the boreal forest, and society at large, so that we can be better informed when managing our nature.

Although moose has been an integral part of Norwegian and Fennoscandian nature since the last ice age (Grøndahl et al. 2010; Rosvold et al. 2013) they currently exists at densities which are historically high (Lavsund et al. 2003; Speed et al. 2019). Following WWII, the number of moose shot per year increased from around 1000 to reach 39000 at the turn of the century (www.ssb.no/elgjakt). This caused the rise of the modern moose hunting tradition which mainly rely on teams of people, sometimes aided by hunting dogs (Brottveit and Agedal 1999). Moose hunting is a highly valued social activity and around 61000 people partake in the hunt each year.

Moose have both positive and negative values which needs to be balanced in order to maintain an optimum density of animals (Timmermann and Rodgers 2005). Positive values include non-material values such as hunting as mentioned above (see also Boman et al. 2011) as well as the value of the meat itself which in Norway amounts to almost 5000 tons per year (Lindhjem and Magnussen 2012). Moose can also facilitate forestry in spruce (*Picea abies*) dominated areas by eating away its deciduous competition. On the other hand, pine (*Pinus sylvestris*), the second most important timber species in Norway, is eaten by moose and hence

negatively affected (Angelstam et al. 2000; Herfindal et al. 2015). Overbrowsing also cause a reduction in deciduous trees (Edenius et al. 2002; Angelstam et al. 2017; Kolstad et al. 2018b) which is at odds with the goal of maintaining a deciduous component in production forests for the sake of biodiversity (see also Schulze et al. 2014). Moose are also involved in collisions with cars and trains, leading each year to the death of around 1900 animals and a bit less than 10 human injuries on average (Solberg et al. 2009; Niemi et al. 2017).

The above listed effects of moose are amongst the more known and obvious ones. Less understood are the effects of this large herbivore on soil properties and processes, despite these being such vital underpinnings to the functioning of any ecosystem (Adhikari and Hartemink 2016; Kolstad et al. 2016). Studying this is made more challenging due to the presence of the numerous known and unknown indirect effects and feedbacks between the aboveground and belowground processes (Wardle et al. 2004). In addition, soils are notoriously variable in space which makes it hard to detect differences within the time frame of an experimental design. Previous work on the effects of large herbivores on soils has resulted in a general prediction that large herbivores in non-productive ecosystems (such as the boreal forest) negatively affect soil process rates and subsequently also soil fertility (Pastor et al. 1993; Ritchie et al. 1998). More recent studies show promise in terms of elucidating some of the complex interactions between soils, plants and herbivores, although many questions remain unsolved (Stark et al. 2010; Kardol et al. 2014; Andriuzzi and Wall 2017; Kolstad et al. 2018a). As wild cervid populations in many regions of the world have increased to unprecedented levels (Prins and Gordon 2008), it is vital that we learn more about their effect on soils to avoid deteriorating vital ecosystem properties such as soil fertility and carbon storage potentials.

The effect of moose on biodiversity is largely unresolved despite much work on the topic (Bernes et al. 2018). The effect seems to be highly contingent, depending on things like site productivity (e.g. Mathisen et al. 2010), the functional or taxonomic group that is studied (Suominen et al. 2008), and the scale of the study and whether one looks at the alpha or beta facet of diversity (e.g. Lilleeng et al. 2016). More fundamentally, the interpretation of our findings also depend on how much relative weight, emphasis or value we put on rare species (Speed and Austrheim 2017) or keystone species (Kolstad et al. 2018b) contra more simple species counts and widespread generalist species (Boulanger et al. 2017). These are issues that needs to be resolved if wild game management is to account for effects on biodiversity.

The prospect of managing wild game populations for the benefit of ecosystem health and resilience, or climate mediation, necessitates a wider recognition of the diverse and complex interactions in nature as well as between nature and society. We need to know how nature works, as well as how human society responds to and potentially incorporate this knowledge into its social processes (Aasetre 2006; Berbés-Blázquez et al. 2016; Posner et al. 2016). Such a holistic perspective on social-ecological systems, of which the Norwegian production forest is one example, relies on the availability of large amounts of diverse information from fields such as ecology, economics, psychology, environmental history, and more. “Availability” in this context entail a focus on the cognitive processes that enable people to learn from what is physically available to them and this may require synthesising of information as well as the development of stimulating tools and platforms for learning (Partelow et al. 2019). It is naïve to think that much real-world influence arise if researchers undergo closed or isolated processes that result in scientific knowledge being published in specialist journals. Instead, research has shown that inclusive, transparent and iterative social processes that stimulate learning are much more fruitful pathways to social acceptance and incorporation of scientific work because they come across as more credible, legitimate and relevant to society (Cash et al. 2003; Mitchell et al. 2006; Sarkki et al. 2015; Tinch et al. 2018).

Aims

The studies reported in the following four papers examines how moose affects both the ecological and social aspects of boreal production forests. This thesis has three main aims (see also Fig. 1):

1. to quantify the degree that moose browsing constrains tree recruitment and affects understory plant communities in Norwegian boreal production forests (Paper 1).
2. to develop a mechanistic understanding of how direct effects of moose browsing, trampling and defecation affect boreal forest ecosystem properties with potential cascading effects on soil properties (Paper 2) and understory plant communities (Paper 3).
3. to identify and communicate the diverse roles and consequences of moose in Norwegian society in a way that fosters holistic systems thinking and cooperative learning (Paper 4).

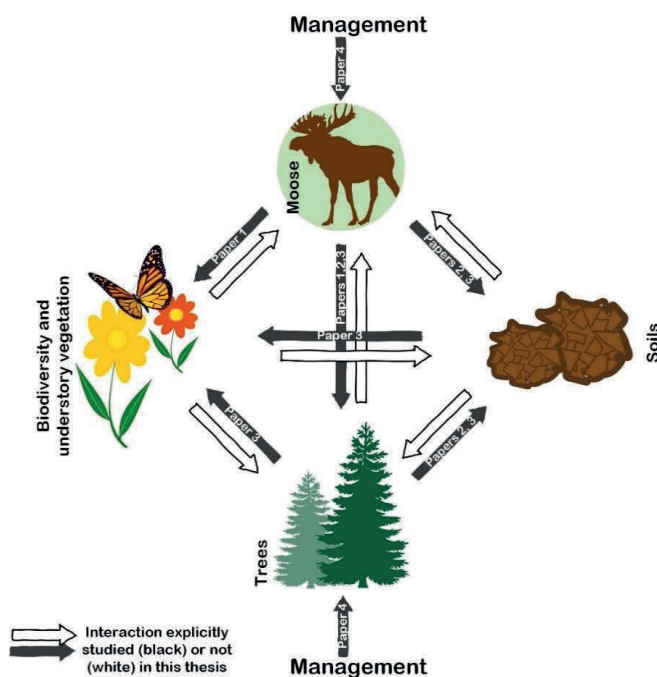


Figure 1. Schematic illustration of the different interactions involving moose and Norwegian boreal forests that have been explicitly studied in this thesis.

General methods

Following is a wider discussion around the main methods used in the four papers presented in this thesis. For more detailed information, see the methods section for each paper.

The field work underlying Papers 1-3 was done as part of the SUSTHERB project (<https://www.ntnu.no/museum/sustherb>) that manages a network of large herbivore exclosures across Norway. This work uses data from a total of 31 forest sites situated in the moose dominated Trøndelag and Telemark regions (Paper 1 – Fig. 1). At each of these sites there is a fence 20 × 20 m wide and 2.5 m tall that excludes large herbivores from entering the plots, including livestock when present. The experimental design relies on comparisons between exclosed plots and adjacent (minimum 20 m) permanent open plots of similar size. Mixed effects models fitted with a random intercept for each site is consistently used for accommodating the spatial autocorrelation arising from this paired design.

Moose is by far the most dominant large herbivore at these sites (Speed et al. 2013), and therefore it makes sense to talk about this experiment as investigating the effects of moose (more precisely the removal of moose) even though other herbivores are also removed. Smaller mammals like hares and rodents, however, are not prevented of entering the plots, and potential interaction between moose removal and the habitat use of hares and rodent remain largely unexplored (but see Gibson 2017).

The vegetation data used in Papers 1-3 are part of a time series of data collected from 2008. The longest time-series reported here is eight years in Paper 1. This is a short time in comparison to the life cycle of a tree, and since these exclosures were erected in recently clear-cut stands, they essentially illustrate the early development of the vegetation following a disturbance (in this case logging). Although understanding ecosystem dynamics in developing stands are important for prediction stand development, findings based on these data cannot be uncritically extrapolated to understand dynamics in mature stands. This is a general challenge to forest ecologists (e.g. <http://ecosystemmoose.com/handeling-different-time-scales/>) and we do not know of any large herbivore exclosure studies that have both the study duration and sample size needed to experimentally explore these aspects. Still, the time series used here is long enough that the successional dynamics are not overly obscured by inter-annual variation, such as weather and sampling effects.

Exclusion studies are very common, but because they essentially provide a comparison between the presence and absence of herbivores, they are not very fitting for analysing things like threshold effects (e.g. how many moose can we accommodate before tree recruitment reach critical levels?) (Hester et al. 2000). To do this would require, or at least benefit strongly from, higher precision data on moose densities than what we have available. Still, because they provide such (unrealistically) extreme levels of comparison, this experimental design is good for detecting smaller or more cryptic changes in vegetation and soils that allows one to develop general mechanistic models of how herbivores affect these systems. The strength of mechanistic models is that they can (in theory) be scaled up.

Paper 4 is a perspectives (opinionated) paper and does not include a methods section. Yet, the paper introduces a web-site (ecosystemmoose.com) which did take some developing. The web-site was built using wordpress (<https://wordpress.org/>). Network figures (e.g. the knowledge map: <http://ecosystemmoose.com/knowledge-map/>) were created using Office Visio which allowed hyperlinks to be added to individual elements in the figure (nodes and arcs). The figures were exported as static html pages, uploaded to the FTP server via Filezilla (an open source FTP client) and embedded on the web-site using the HTML element

<iframe>. A more thorough explanation of the web-site as a tool for collaboration and learning is presented in Paper 4.

Main results and discussion

Moose browsing reduced the biomass of deciduous trees

The most prominent ecological effect of moose is the browsing damages done to trees. In Paper 1 we found that deciduous tree recruitment and growth was severely reduced in the presence of moose. This was especially true for rowan (*Sorbus aucuparia*) for which we found practically zero individuals above 150 cm seven year into the experiment. Concurrently, the exclosures sported a dense deciduous canopy with several rowan stems above 3 m (some up to 5-6 m) and also a 60% greater aboveground tree biomass in general (Gebreyohannis 2017). The consequences of this is not fully understood, especially since the findings do not match those of the national forest inventory where an increase in rowan recruitment is detected over the same period (see also Myking et al. 2013). Our findings nonetheless warrant concern considering the unique ecological role of rowan, it being the only fleshy-fruit bearing tree in these forests.

... and large herbs

A concomitant reduction as for rowan was observed for large herb biomass which was 340% higher in exclosures compared to in the open plots. The most common species in this functional group were *Rubus idaeus* and *Chamerion angustifolium*. Like rowan, these are insect pollinated plants. When large tracts of forests become practically devoid of nectar producing flowers, as we have observed in our study region, this is likely to have negative consequences for insect diversity. Consequently, high moose densities can be at odds with insect conservation (Suominen et al. 2008; Brousseau et al. 2013) which has become a known global problem (Hallmann et al. 2017; Sánchez-Bayo and Wyckhuys 2019). This aspect deserves increased focus in future research and to be acknowledged in current forest and game management.

Moose affected several physical soils properties, but caused few bio-chemical or indirect effects on soils

Less obvious than the effect on tree recruitment, but possibly as important, are the effects of moose on forest soils and the indirect effects that result from altered canopies and vegetation composition in general. Previous work provides strong predictions for a decelerating effect of moose on the nutrient cycling in these relative infertile ecosystems (compared to for example savannahs), caused by a shift towards more recalcitrant litter (Bardgett and Wardle 2003). In Paper 2 we tested this general hypothesis and found that moose exclusion decreased soil compaction and increased the organic soil depth, but that the bio-chemical soil parameters we measured (decomposition, C and N stock, N availability and relative nitrification) remained generally unresponsive to moose exclusion within the timeframe of eight years. This is perhaps not surprising as soils are known to respond relatively slowly to aboveground disturbances (but see Kardol et al. 2014). We did, however, find strong evidence that moose caused decreased canopy cover and increased summer soil temperatures, but we were

surprised that altered soil temperatures did not explain changes in any of the soil processes we measured. If moose do effect important soil properties such as fertility and carbon storage, this is at least not easily observable after only 8 years of experimental moose removal and could indicate that aboveground consequences of high herbivore densities and subsequent overbrowsing are more urgent issues for game managers to address.

Summer soil temperature is reduced inside exclosures due to increased canopy shading, but this has few cascading effects

In Paper 3 we decided to obtain more soil temperature data to verify or debunk the evidence that the induced soil temperature changes really did not have any cascading manifestations (cf. Paper 2), this time looking at properties of the understory vegetation. A main finding in this paper was that the soil cooling inside the exclosures was strictly a summer phenomenon, whereas a warming trend was observed during winter. As many soil processes are accumulative, such as the release of plant available nutrients from litter decomposition, this may explain why we found no clear association between soil temperature and soil processes in Paper 2 where we only looked at data from the summer months. It is also unknown whether the effect size with a 0.6°C shift in soil temperature is enough to induce any large biotic change even though the difference was highly statistically significant.

We found little support for cascading effects from soil temperature to understory plant communities as this was limited to a weak positive (accelerating) association between summer soil temperature and the abundance of a dominant and disturbance-favoured grass species *Avenella flexuosa*. Herbivores that increase the prevalence of dominant plants can cause an indirect reduction in species densities due to increased interspecific competition (Koerner et al. 2018). Although *A. flexuosa* was a prime candidate for documenting such a competitive exclusion effect, we did not find evidence for it within the range of abundances that we observed. This work partly confirms the finding in Paper 2 in that soil temperature changes within the ranges observed following moose exclusion has only minor cascading effects on the ecosystem. Still it is unknown how other unexplored and perhaps more sensitive aspects of the ecosystem, such as the microbiotic communities, responds to changes in temperatures. This is a critical research gap confronting forest ecosystem science today also when considering the advent of climate warming.

The innovative web-based knowledge system EcosystemMoose presents itself as a promising platform or approach for tackling some of the mounting challenges for sustainable and equitable development

Papers 1-3 have added to our understanding of the effects of moose on boreal forest ecosystems, and especially Paper 1 confirms the role of moose as a key ecosystem engineer and major forest disturbance. However, knowing the effect of moose is generally not enough to promote or encourage management action. There are many reasons for this. Moose is for example not only affected by hunting, but also by actions that falls under the jurisdiction of local forest managers who are less likely to read or put much weight on this type of research. Secondly, research published in specialised ecology journals are not readily accessible to most of the targeted knowledge users. Thirdly in this non-exhaustive list, cooperation amongst scientists themselves is made difficult due to the high degree of specialisation in each field.

A novel web-based knowledge system was developed to serve as an interactive and cross-disciplinary learning and collaboration platform, addressing the third aim of this thesis.

The motivation and perceived virtues of this approach is laid out in Paper 4. After been running for less than a year, the web-page has already proved itself as a stimulating platform for discussions as it has brought together 9 different scientists from fields such as plant and animal ecology, economics, human geography, climate science, environmental history and molecular biology.

The main feature of the web-site is the knowledge map (Paper 4 – Fig. 1). This figure integrates ecological, social and political aspects related to forest and moose management in Norway and clearly reveals the high level of interdependence within this system in the shape of reciprocity, feedbacks and cascading effects. Along with several examples explained in Paper 4 this speaks for a more holistic and integrated view on nature and society. This increases the demand on practitioners and decision-makers to obtain and acknowledge a greater breath of information than what is required of them today. It also necessitates that researchers produce more cross-disciplinary science and syntheses and contextualise their findings in relation to the multitude of relevant ecological and social aspects of this management system. Fostering a closer collaboration between science users and science producers, as well as between scientific disciplines, is an obvious way to approach this challenge. Here our knowledge system has proved fruitful in fulfilling the latter point and thus demonstrating the value of EcosystemMoose as a tool social-ecological synthesis making. The knowledge system has also been presented and discussed with several relevant stakeholder groups, including local game managers and the Norwegian environmental agency. E-mails were sent out to 50-ish people or organisations with an interest in forests, resulting for example in that the news of the web-site launch was picked up by a forest owner organisation¹. In addition, the use of blog posts² and tv appearances³ have given EcosystemMoose a broader public attention which is essential for it to become a complete and functioning science-policy platform.

The way forward

The introduction suggested an increased mandate for game- and forest managers to incorporate into their objectives the larger societal goals of combating climate deterioration and preserving biodiversity and ecosystem services. A common goal could be to have a socioeconomic use of forest resources within environmental boundaries (Austrheim and Kolstad 2019). To achieve this in practice relies on taking the information available and adopting it for general use at the appropriate scales. Usually this implies taking information gathered at a small scale, such as an ecological experiment or a series of interviews, and scale it up to become generalisable across some range of space, time or social context. This scaling-up is a major step towards incorporating scientific findings into management decisions and therefore addressing the challenges associated with this process is an obvious challenge now and for the future.

¹ <https://norskog.no/naeringspolitikk/ny-nettside-om-forskning-og-forvaltning-pa-elg-og-skog-i-norge/>

² <https://blogg.forskning.no/viten-om-naturen/nettverksbygging-kan-gi-en-mer-baerekraftig-naturforvaltning/1331568>

³ <https://tv.nrk.no/serie/kunnskapskanalen/2019/MDDP17002818/avspiller>

Scaling-up in space

Paper 1 demonstrated the large effect of moose at current densities in reducing the prevalence of some keystone forest species, notably rowan and large flowering herbs. An unresolved question pertaining to this is how much this matters for the well-functioning of ecosystems at the landscape scale, knowing that these species are common elsewhere beside the clear-cuts where this study was done. A concern could be raised about potentially detrimental effect on insect diversity for example, due to reduced resource connectivity or overall habitat availability. Future studies could include spatial analyses relating species home ranges to the size of clear-cuts or forest elements or studying biodiversity along gradients in the abundance of these keystone species.

Furthermore, a full appreciation of the effects of moose on biodiversity can only be achieved after reflecting on the different facets of diversity: alpha, beta and gamma. Gamma diversity is the diversity (for example the number of species) of the whole area you are studying. Alpha diversity is the same, but for a smaller section of the total area. Beta diversity is the differences in diversity between two measurements of alpha diversity, either recorded at two locations or at two points in time. Moose is predicted to increase floristic homogenisation (lower the beta diversity), and we also found a weak trend in this direction in Paper 1. However, alpha diversity may not change, or could in fact increase as in Boulanger et al. (2017) due to processes like seed dispersal. Ultimately, changes in gamma diversity could ensue, especially when considering the direct or indirect effects of herbivores on rare or endangered species (Speed and Austrheim 2017). Therefore, to generalise (scale up) the effects of moose on biodiversity we need more research on the relative roles of alpha and beta diversity on the aspects of the ecosystems that we study, be they wildlife habitat value or human aesthetical perceptions.

Scaling up the effect of moose in space sometimes requires the integration of some related phenomenon. Carbon storage is interesting to forest ecologist because of its role in climate mitigation (Fig. 2), yet other cooccurring phenomenon, such as surface albedo changes, are perhaps equally important to understand in this regard (Bright et al. 2014). Future work on determining how large herbivores impact the climate (e.g. Schmitz et al. 2018) needs to acknowledge the effect of large herbivores on the entire suite of biophysical climate forcing agents, including all greenhouse gases, albedo, evapotranspiration and aerosols.

Scaling up in time

It is inherently difficult to study organisms with long life spans because so many of the life history aspects are not observable within the time frame available to humans and research projects that rely on funding. The studies presented in this thesis are therefore not unique in studying only a short time frame and then relying on extrapolation or mechanistic models to say something about the overall system behaviour. This is a source for bias and possibly erroneous conclusions. A bias includes a preference or steering towards studies on short term phenomenon. Here are some examples of this.

Due to browsing, moose reduces the aboveground biomass in developing forest stands, indicating a negative role of moose on carbon (C) storage (Fig. 2) and a possible role for wildlife management as a climate mitigation tool (Schmitz et al. 2018). In our study design, eight years of moose exclusion led to an increase in aboveground C storage of 60% compared to open plots (Gebreyohannis 2017), but no change in belowground C stocks (Paper 2). However, most studies on the effect of moose on forest ecosystems have been conducted over similar relatively short time scales, thus leaving it an unanswered question whether the

resulting alternate successional trajectories induced by browsing on young trees (Hidding et al. 2013) could result in a spruce dominated forest type which is relatively conducive to high ecosystem carbon storage, including the soil C pool (Vesterdal et al. 2008). This issue needs urgent attention if game management is to play a positive role in the fight against climate deterioration. Paper 2 illustrates the same point. Here we studied how moose-induced changes in the vegetation could have cascading effects on soils. Although the tree structure and tree species composition were affected by moose after only 8 years, and this most likely affected both the microclimate and the litter quality and quantity, it seems likely that initial change in tree growth and recruitment will augment over time and that the aboveground-belowground links will grow stronger. Therefore, a comparably large part of what we observed in Paper 2 were the direct effects of trampling and defecation, and the indirect effects of altered plant species composition will probably become a more dominant driver of ecosystem dynamics over time.

Studies on the consequences of moose on biodiversity is also dominated by experiments conducted over relatively short time-scales. We found no statistically significant effects of moose exclusion on plant diversity after eight years of experimental moose removal, yet there was a trend towards increased beta diversity over time (Paper 1 – Fig. 6). In addition, Paper 3 identified some potentially important pathways for how moose can influence alpha diversity via increased shrub cover or reduced herb biomass (Paper 3 – Fig. 4). Existing time series like SUSTHERB is therefore becoming increasingly valuable for determining whether these trends or mechanisms will persist as the forest succession proceeds, and if a long latency period for the effects of moose removal is clouding our overall understanding of their effects on biodiversity. Repeating a point from the above paragraph, a longer time perspective may also help elucidate whether changes in tree species composition towards a higher deciduous dominance inside the exclosures will facilitate greater overall biodiversity across species groups.

Scaling-up within society

EcosystemMoose, the web-based knowledge system for Norwegian moose-forests social-ecological systems, is attempting to alleviate some of the barriers to the sustainable and equitable management of nature by fostering a constructive dialogue and cooperation between stakeholders and between disciplines. This is important for many reasons, such as securing the credibility, legitimacy and relevance of the sciences (Cash et al. 2003) and for obtaining different views on the best developmental trajectories for our society. Reaching out to stakeholders as well as researchers in other fields can increase the real-world impact of research initiatives and ultimately lead to more informed and ecologically sound management decisions. For example, in Fig. 2 the management of moose for climate mitigation purposes hinges on some form of effective top-down management, as climate change is of national and not necessarily local interest. However, local support for top-down management decisions could become highly controversial (e.g. Mysterud and Rolandsen 2018). The outcome is likely contingent in how credible and legitimate the local communities perceive the knowledge gathering process leading up to the conclusions. To accommodate these realities, environmental assessments and science that produces management advice needs to think about how to become more transparent and interactive with society. Bridging organisations such as EcosystemMoose, but also many others (e.g.: Tinch et al. 2018; www.conservationevidence.com), will be essential for achieving this aim, and more research should be invested into how to make these initiatives even better.

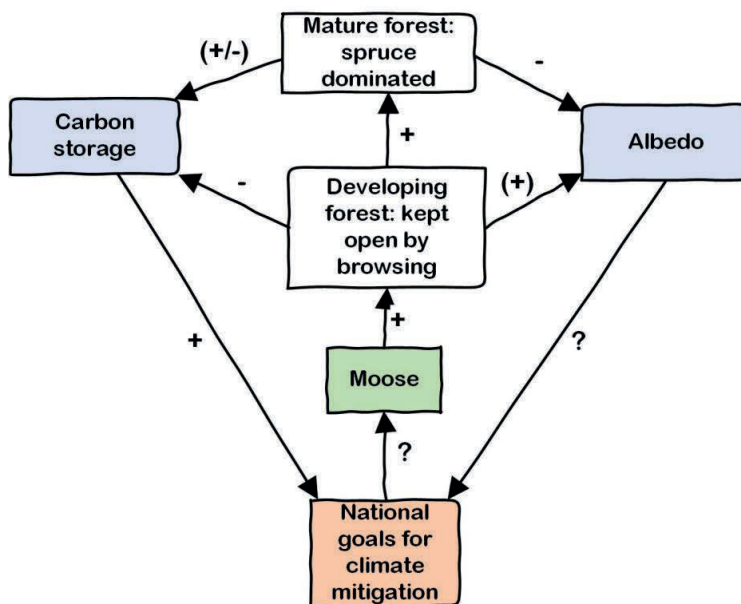


Figure 2. Influence diagram illustrating how understanding the net effect of moose on climate mitigation depends on jointly evaluating multiple climate drivers (e.g. carbon storage and albedo) and on integrating the short and long terms effects on these drivers as they may change over time. The potential use of moose management as a climate mitigation tool finally depends on the effectiveness of incorporating national interests into what is today a local community-based management paradigm. Signs indicate the direction of the response, with parenthesis indicating uncertainty of the direction and question mark indicating uncertainty about the presence (or strength) of the link.

Conclusion

Moose had a strong impact on the recruitment of deciduous trees, especially rowan (*Sorbus aucuparia*). Along with a reduction in large herb biomass, this likely has several largely unexplored ramifications for biodiversity, ecosystem functioning and climate change. Moose was also found to impact directly on several physical soil attributes such as organic soil depth and soil temperature. However, this large herbivore caused few bio-chemical or indirect effects on soils following an 8-year exclusion period. Due to its omnipresence and the accumulative effects from its activities, moose has a greater effect on forested ecosystems than most people appreciate. The diverse roles of moose in the Norwegian boreal forest social-ecological system is one of the main messages fronted by EcosystemMoose.com. This web-based knowledge system has proved a valuable platform for cross-disciplinary collaborations and by facilitating a broad participation-base from both researchers and stakeholders, this web-page is seen as a promising new tool for the future of nature management where the goal of a sustainable and equitable development is approached through dynamic learning environments and holistic systems thinking.

With an increased mechanistic understanding of how moose affect forested ecosystems, and a whole new framework for contextualising these findings within a complex human-nature landscape, this thesis shows the way for an integrated land management where resource management unites with the goals of sustainable development to stop the loss of biodiversity and ecosystem services and ensure the resilience of social-ecological systems.

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Paper 1

Moose browsing on pine. Photo by the author.



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

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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.

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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

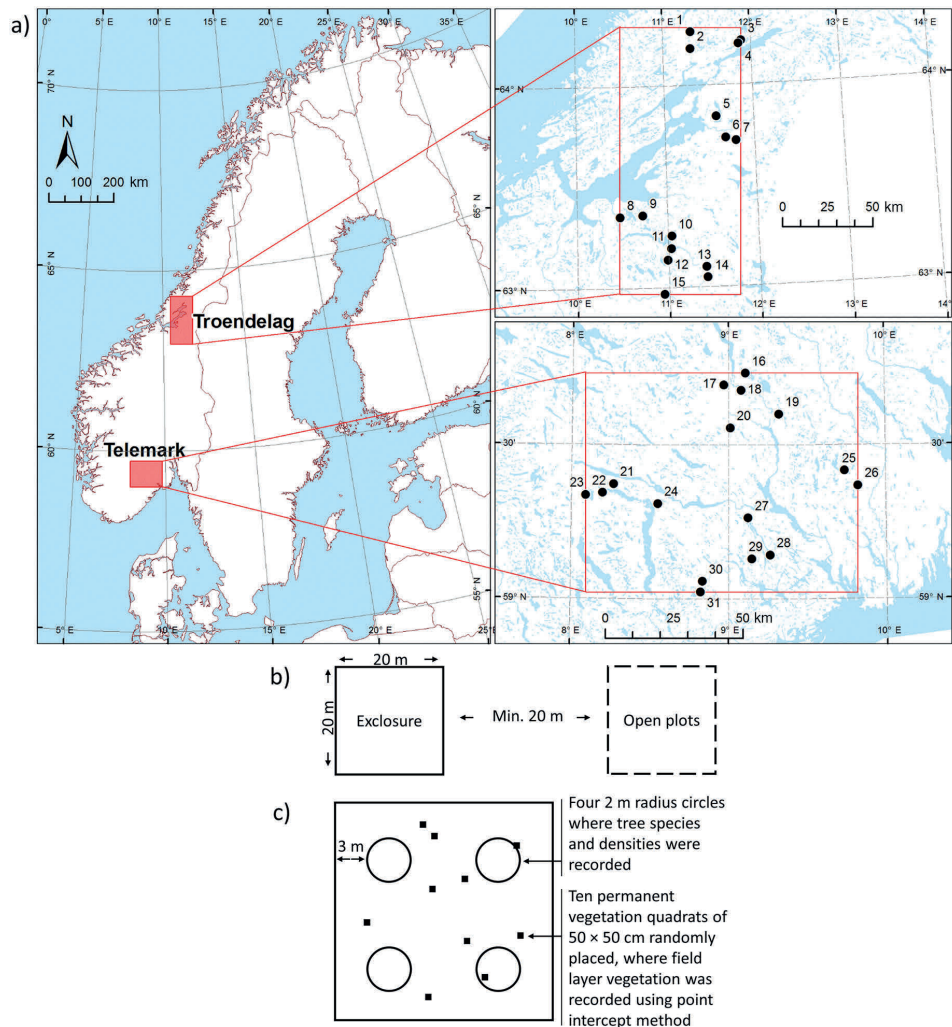


Fig. 1. Hierarchical sampling design with (a) 31 field sites in two regions of Norway, each consisting of (b) two paired plots and (c) subplots within which trees and understory vegetation were recorded. Numbers in the map refer to sites as in Speed et al. (2013a).

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 Trondelag 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

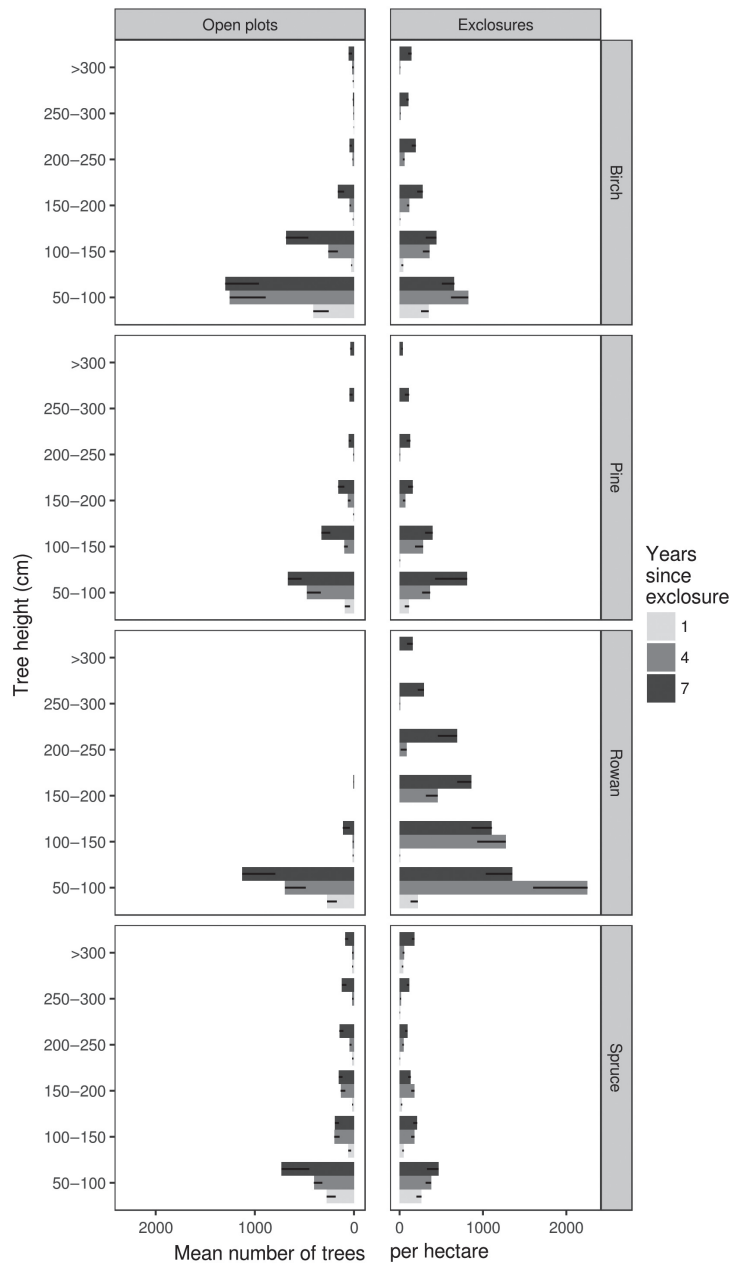


Fig. 2. Mean number of trees per height class of four boreal forest trees species at three time points (1, 4, and

(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 exclosure 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,

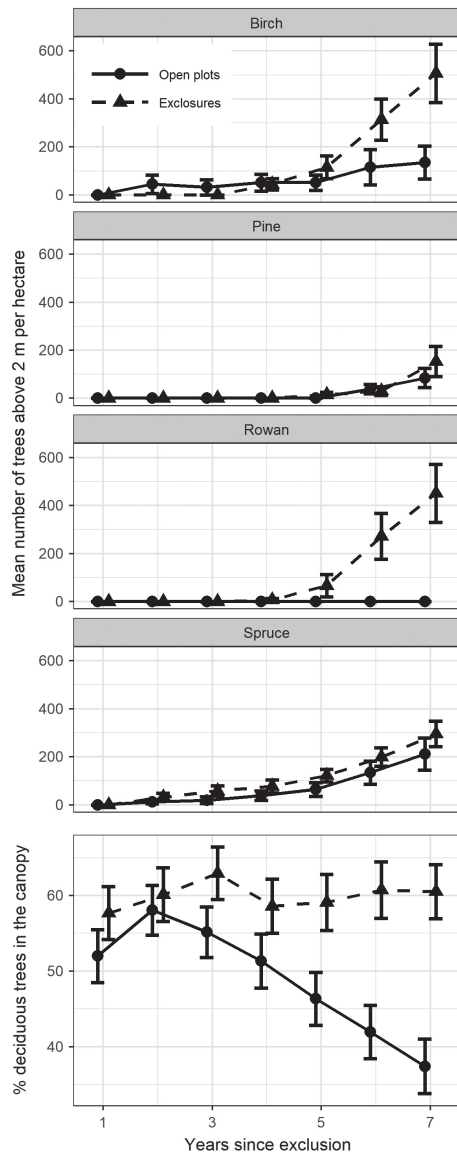


Fig. 3. The recruitment of boreal forest tree species above 2 m tall and the canopy composition in 31 recently clear-cut boreal forests where large herbivores were either excluded or not (means \pm SE). Plots were clear-cut few years before the experiment started.

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 (exlosures = $37.40\% \pm 3.60$ 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 \times Pr: 2.583*	Δ 4.417	Δ 7.128	Δ 9.227	0.286/0.381
Small herbs†	62 plots	AIC: 138.838 E \times 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 \times 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* < 0.05; ***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).

Understorey 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).

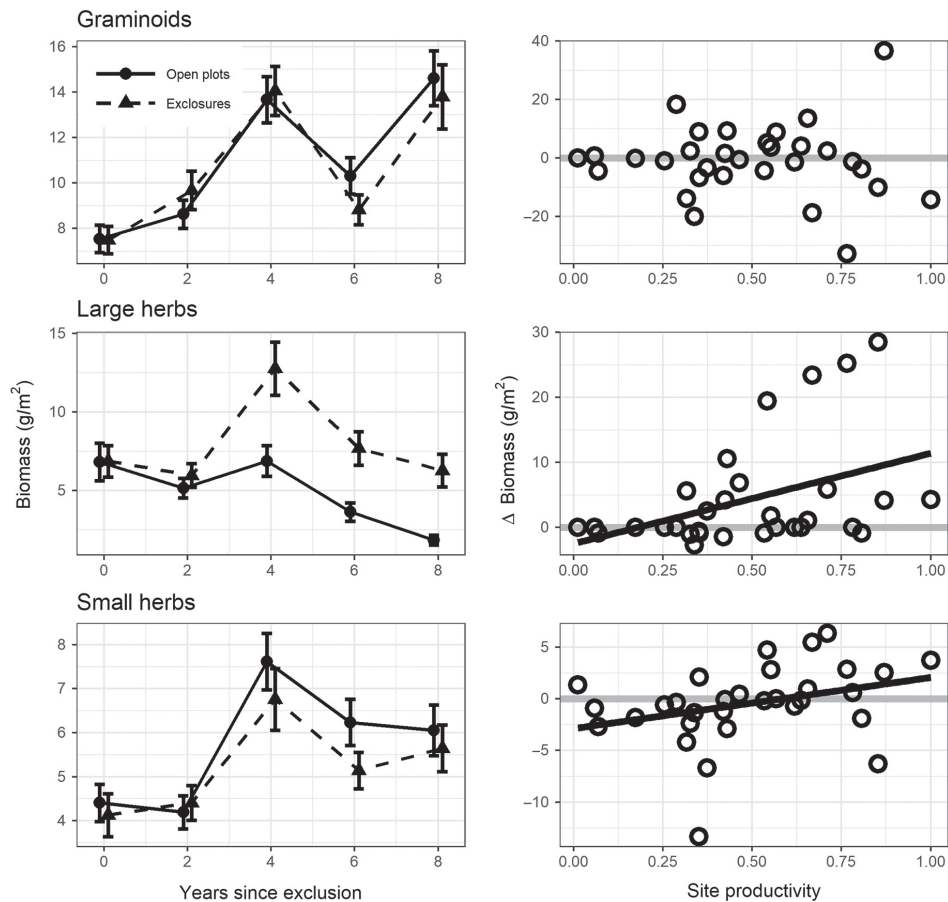
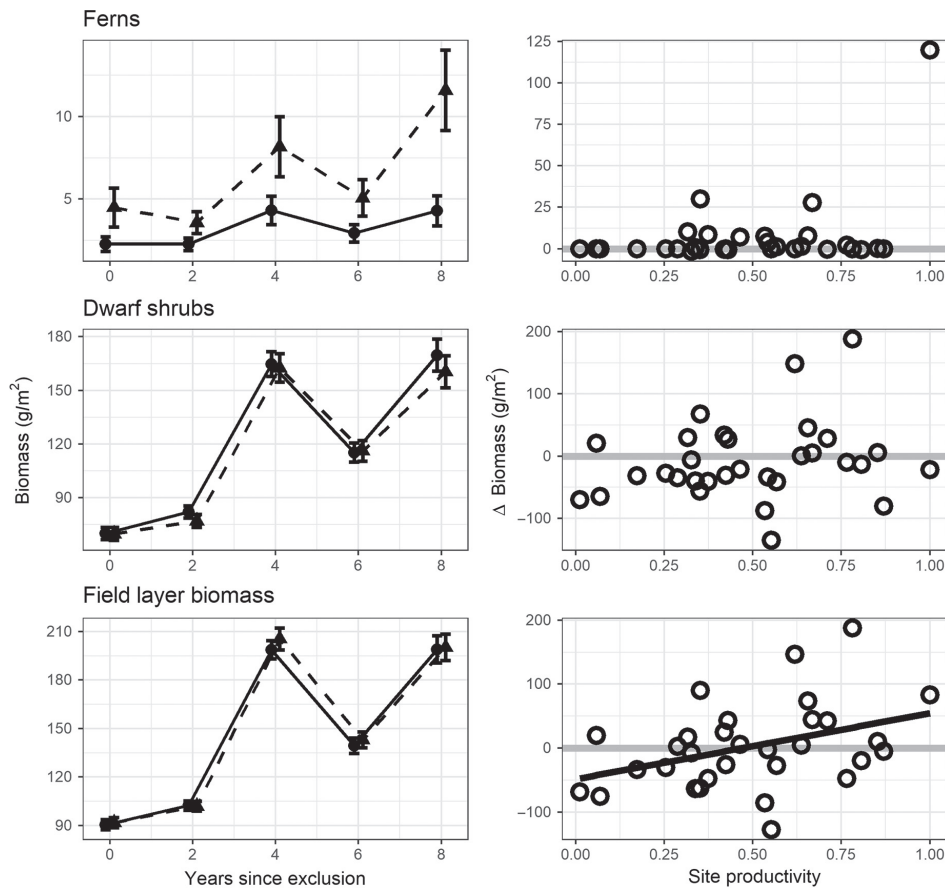


Fig. 4. Mean biomass (\pm SE) of vascular plants (left column) and the relative shift in biomass (exclosure–open plots) in year 8 plotted against site productivity (right column). Functional groups are along individual rows. Note that y-axes have different ranges. Drawn regression lines (lm procedure 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).

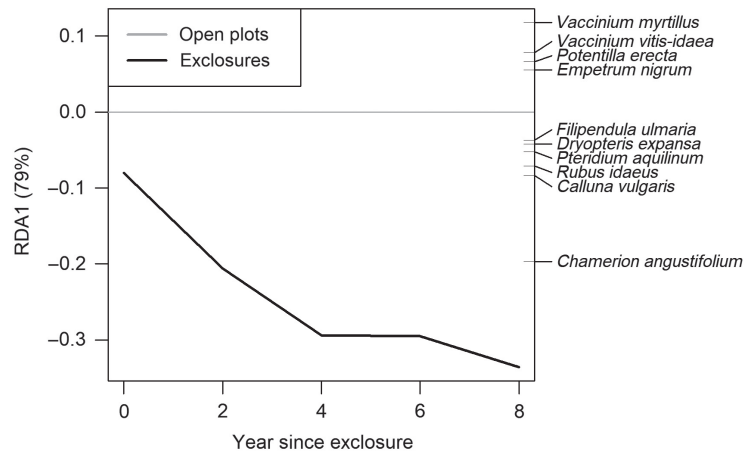


Fig. 5. Principal response curve (first axis) on plant species composition at 31 recently clear-cut locations in boreal forests in Norway. Only species names with loadings higher than 0.1 are shown. The percentage of variation explained by the first ordination axis is given in parentheses, and this was 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).

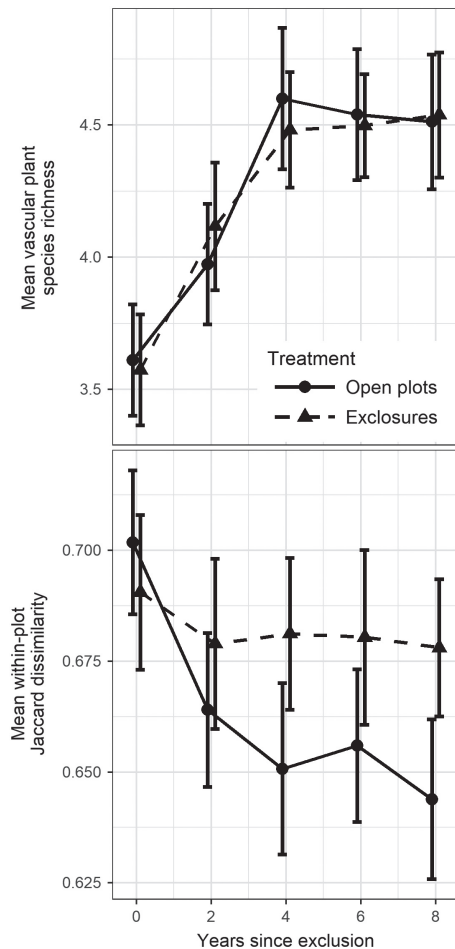


Fig. 6. Mean (\pm SE) species richness and within-plot Jaccard dissimilarity for vascular plants recorded in clear-cut boreal forests in central and southern Norway either enclosure or open to large herbivores. The sample units are the 20 \times 20 m plots ($n = 31$ locations).

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 (± 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 exclosures. 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.

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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>

Appendix S1

Supplementary information for article titled “Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species”

Journal: Ecosphere

Authors: Anders Lorentzen Kolstad, Gunnar Austrheim, Erling J. Solberg, Laurent De Vriendt, James D. M. Speed

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Extended method:

Biomass models for point intercept frequency data on field layer vegetation in boreal forest, central Norway

Here we present six biomass equation models designed to convert measured point intercept values (mean per pin) into estimated biomass in g m^{-2} (Table S1, Figure S1). Forty calibration plots were chosen subjectively using a stratified selection process to ensure adequate sampling across the range of vegetation densities within each growth form. The calibration plots were from seven different sites (number 1, 6, 7, 8, 9, 10 and 14 in Fig. 1) spanning the whole range of forest productivity and therefore covering most of the species found in the region. Most calibration plots were placed in close vicinity to the open plots (control plots), but eight plots were placed inside herbivore exclosures (near the fence to avoid interrupting the experiment) in order to get enough samples of tall herbs and ferns which are scarce outside the exclosures. The models were fitted with generalized linear models using a gamma distribution and an identity link. Parameters were estimated using Markov chain Monte Carlo (MCMC) techniques by running JAGS (v. 4.3.0) through R (Su and Yajima 2015, R Core Team 2016). Due to the simplicity of the models covariates were not scaled or centered. The MCMC procedure used three chains, 200 000 iterations, a burn-in of 4000 and a thinning of 10. Mixing was always good. Model validation as done visually using Person's residuals.

Table S1. Biomass equation models for six growth forms. Calibrated using harvested biomass from forty plots in boreal forest in central Norway.

Growth form	Equation	R ²	Range (avg. frequency)
Tall herbs	$y = 4.0373 + 36.4849x$	0.87	0.16 – 2.94
Small herb	$y = 0.7713 + 15.1209x$	0.77	0.02 – 3.67
Broad leaved grasses	$y = 0.6384 + 23.3885x$	0.84	0.04 – 4.55
Narrow leaved grasses	$y = 0.8747 + 5.9653x$	0.63	0.02 – 4.86
Broad leaves shrubs	$y = 1.2857 + 74.4101x$	0.82	0.04 – 4.31
Narrow leaved shrubs	$y = 7.2471 + 74.1840x$	0.75	0.20 – 5.37

Note: Models are never valid at the intercept (frequency = 0).
 y is biomass in g m^{-2} . x is average intercept frequency.

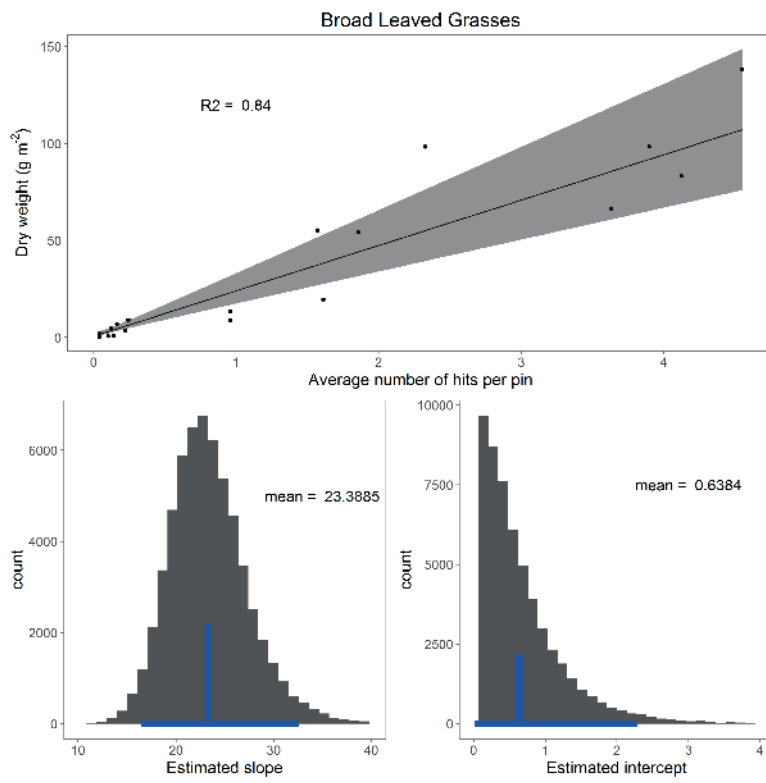


Figure S1 - a.

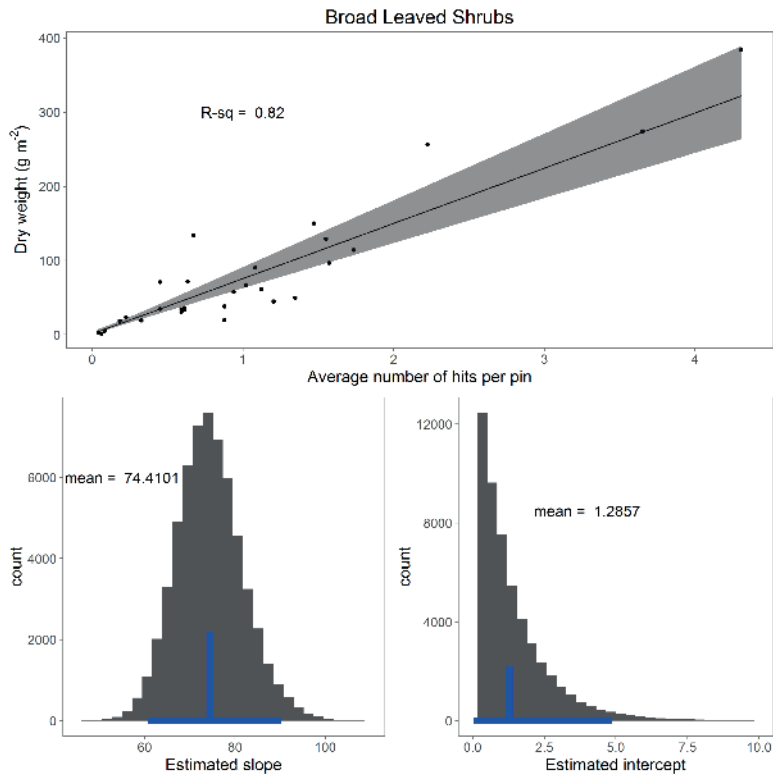


Figure S1 – b.

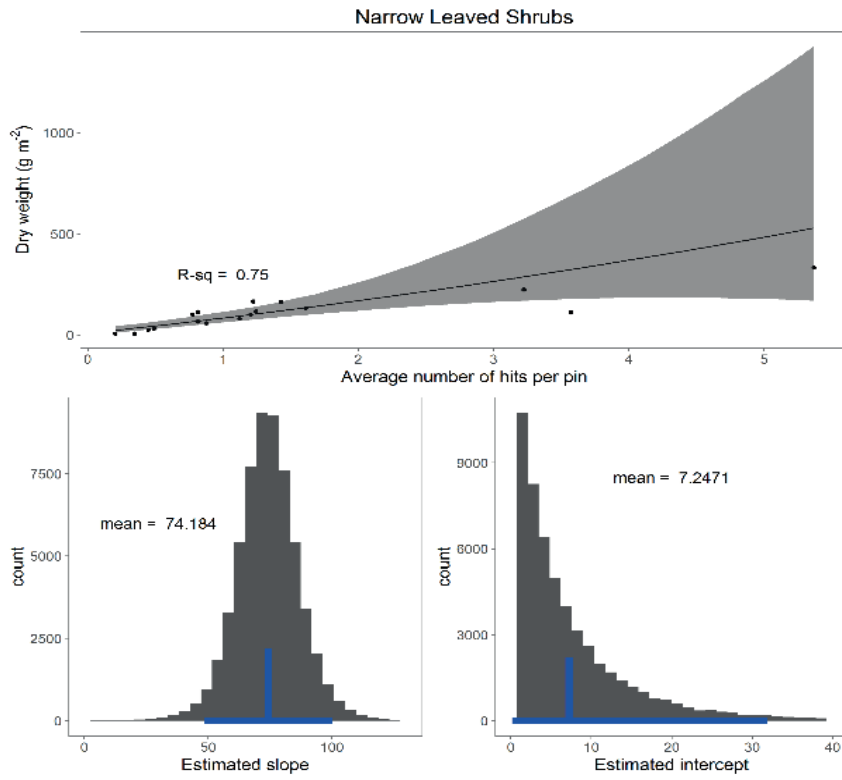


Figure S1 – c.

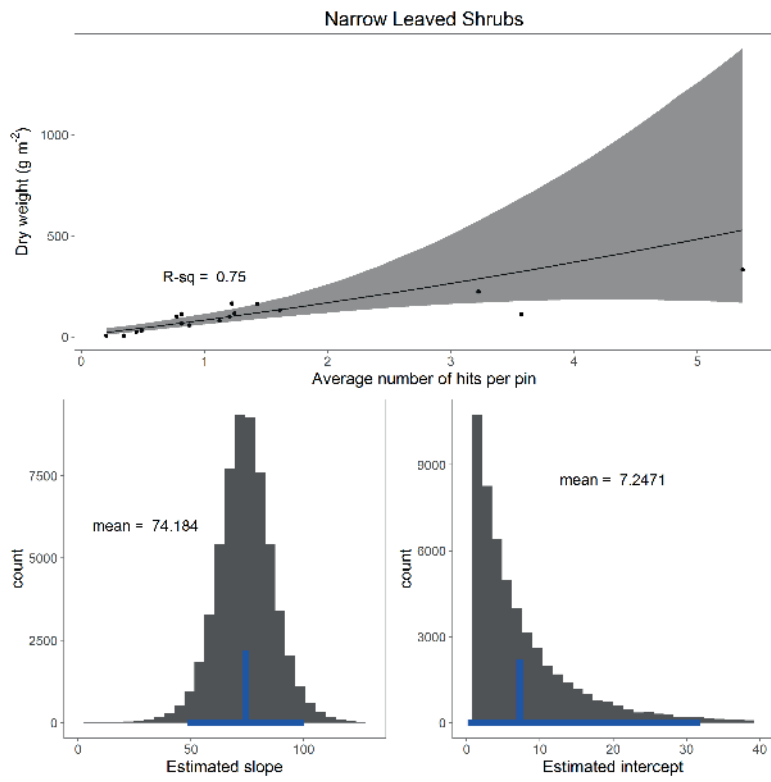


Figure S1 – d.

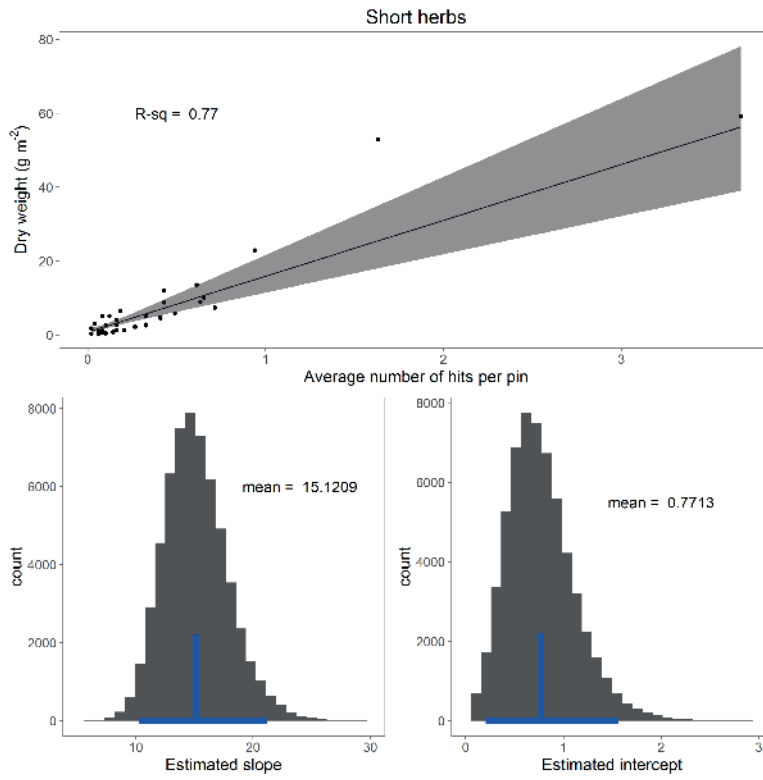


Figure S1 – e.

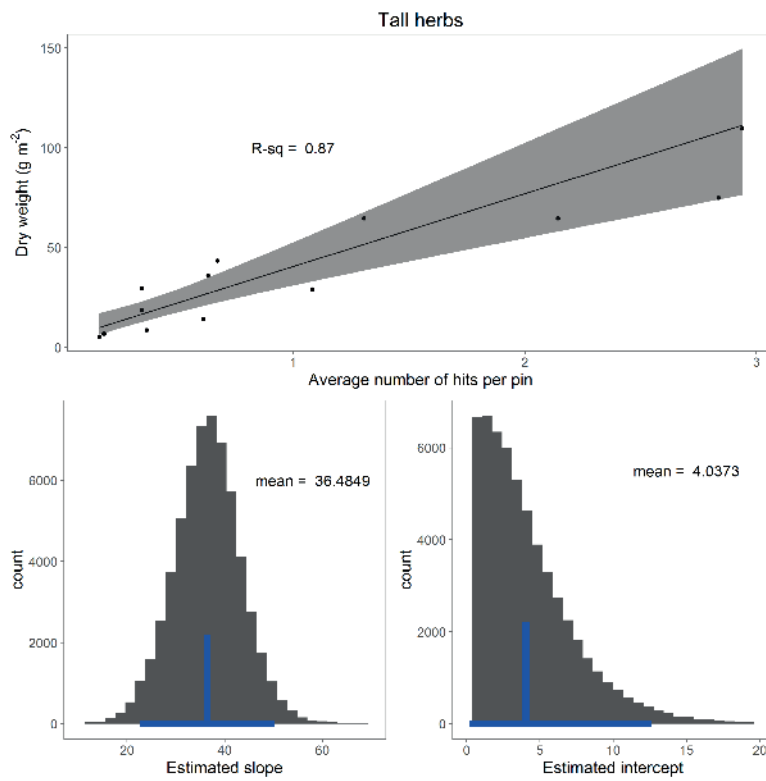


Figure 1 – f.
 Figure S1 a – f. Biomass equation models with histograms showing the posterior distribution for the slope and intercept. Models were calibrated using harvested biomass from forty plots in boreal forest in central Norway. Shaded bands and blue horizontal lines are 95% credible intervals, and vertical blue lines are mean values.

Extended results

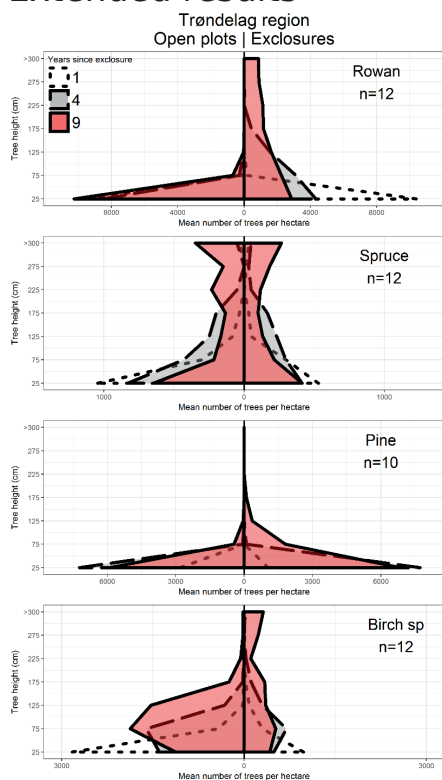


Figure S2. Demography (means per height category) of four boreal forest trees species at three time points (1, 4, and 9 years) after the start of the experiment where large herbivores were either excluded (to the right of the center line) or not (to the left of the center line). The sites were clear-cut a few years prior to the start of the experiment. The median value is used for each 50 cm height category (e.g. 0-50 cm equals 25 cm). There are 12 paired plots in total from the Trøndelag region (tree were removed because the control plots were inadvertently thinned after year 7 since exclusion, see *Methods*). Pairs were excluded when the species was absent or very rare (<5 records across all years).

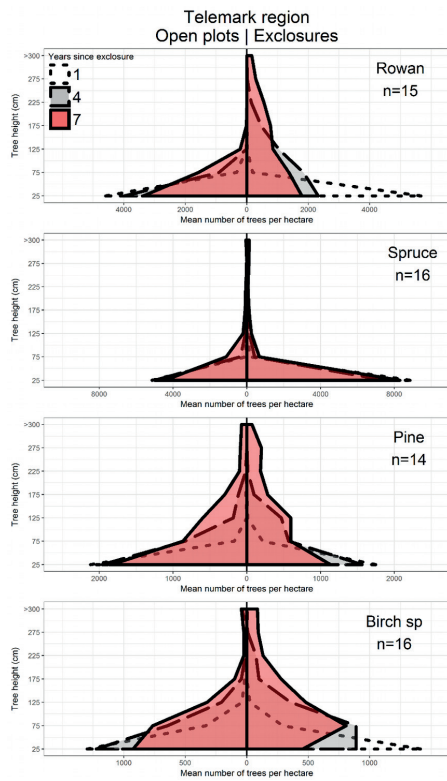


Figure S3. Demography (means per height category) of four boreal forest trees species at three time points (1, 4, and 7 years) after the start of the experiment where large herbivores were either excluded (to the right of the center line) or not (to the left of the center line). The sites were clear-cut a few years prior to the start of the experiment. The median value is used for each 50 cm height category (e.g. 0-50 cm equals 25 cm). There are 16 paired plots in total from the Telemark region, but pairs were excluded if the species was absent or very rare (<5 records across all years).

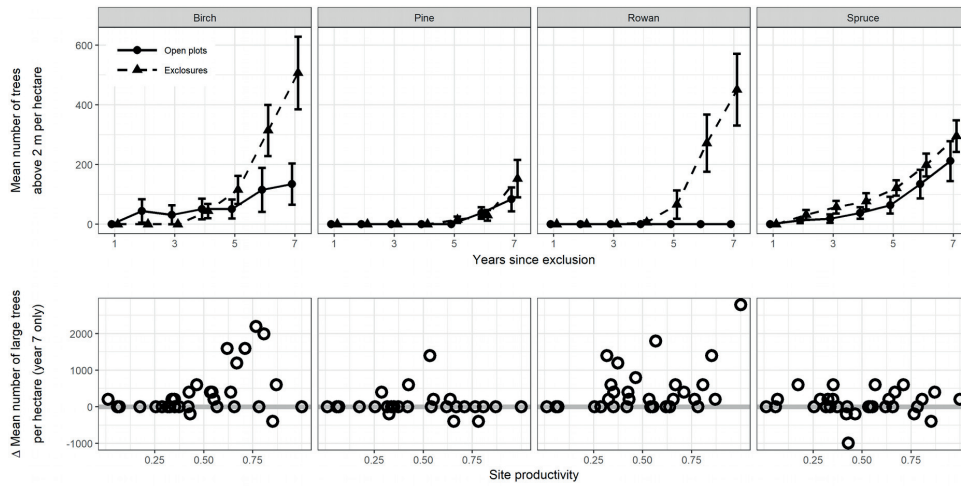


Figure S4. An extended version of Figure 1 showing in the top row the mean (\pm SE) number of large individuals (defined as above 2 m) of four common boreal forest tree species in permanent vegetation plots located either inside large herbivore exclusion or in adjacent open plots. The bottom row shows the relative difference (exclusion minus open plots) in year 7 after exclusion against the site productivity and thus visualizes the interaction between herbivore exclusion and site productivity. Plots were clear-cut few years before the experiment started. Values are standardized against year one to remove any confounding differences due to remnant trees. Sample size (number of paired pots): Spruce and birch = 31; pine = 26; rowan = 30).

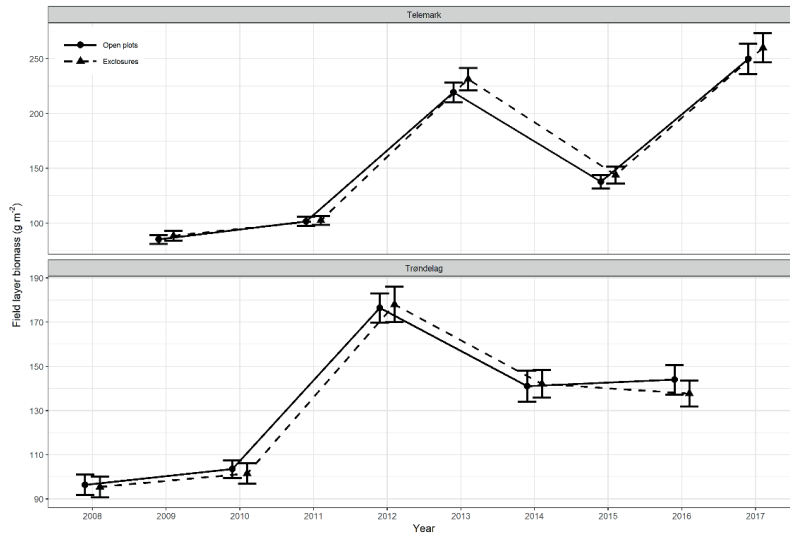


Figure S5. Mean total vascular plant biomass (\pm SE) in the field layer plotted against calendar year for two regions in Norway. Sample plots were either freely available for large herbivores or fenced off (exclosed).

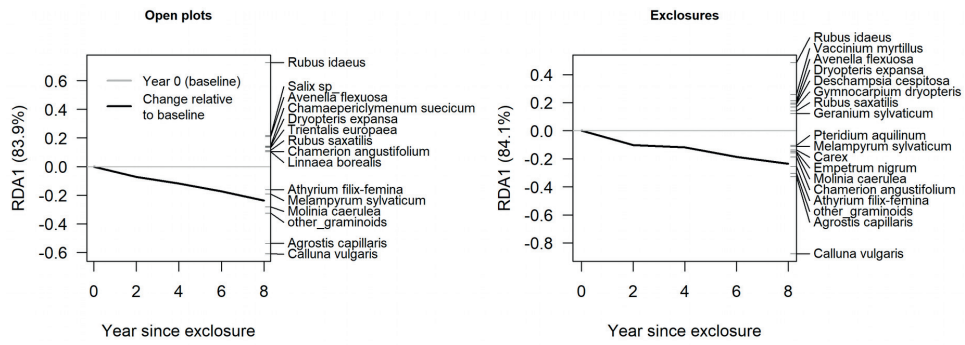


Figure S6. Principal response curve (first axis) on plant species composition at 31 recently clear-cut boreal forests in Norway that were either left open and available to large herbivores (left pane) or exclosed (right pane). Only species names with loadings higher than 0.05 are shown. The percentage of variation explained by the first ordination axis is given in parentheses.

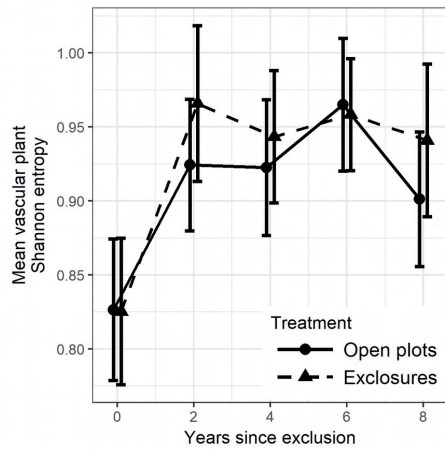


Figure S7. Mean (\pm SE) Shannon entropy for vascular plants recorded clear-cut boreal forests in central Norway either exclosed or open to large herbivores. Sample sizes are taken to be the 20×20 m plots (31 locations).

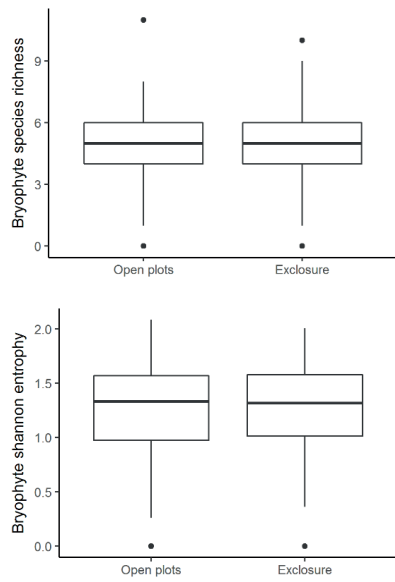


Figure S8. Boxplot showing the diversity of bryophytes at 15 locations in boreal forests in Trøndelag, central Norway. At each location, large herbivore exclosures had been put up 8 year prior to vegetation analysis.

Table S2. Table of plant taxa specifying the functional groups they have been assigned and the relative frequencies (presence/absence in a vegetation quadrat divided by total number of vegetation quadrats) and absolute frequencies (total number of vegetation quadrats with the taxa present). Bryophytes were only recorded for the Trøndelag region. The list includes vegetation surveys in the final year of analysis only and is truncated to included only taxa with more than 2 occurrences. Sp indicates that species within this genus are treated as one taxa due to uncertainty regarding species recognition in the field. Marchantiophyta and Poaceae include all additional liverworts and grasses respectively that are not identified to species.

Taxa	Functional type	Relative frequency	Frequency
<i>Hylocomium splendens</i>	Bryophyte	0.883	264
<i>Vaccinium myrtillus</i>	Dwarf shrub	0.819	502
<i>Avenella flexuosa</i>	Graminoid	0.737	452
<i>Vaccinium vitis-idaea</i>	Dwarf shrub	0.732	449
<i>Pleurozium schreberi</i>	Bryophyte	0.732	219
<i>Dicranum sp</i>	Bryophyte	0.635	190
<i>Ptilium crista-castrensis</i>	Bryophyte	0.605	181
Marchantiophyta	Bryophyte	0.542	162
<i>Rhytidiadelphus squarrosus/R. subpinnatus</i>	Bryophyte	0.355	106
<i>Rhytidiadelphus loreus</i>	Bryophyte	0.341	102
<i>Melampyrum pretense</i>	Small herb	0.299	183
<i>Trientalis europaea</i>	Small herb	0.233	143
<i>Calluna vulgaris</i>	Dwarf shrub	0.196	120
<i>Maianthemum bifolium</i>	Small herb	0.171	105
<i>Polytrichum/Polytrichastrum</i>	Bryophyte	0.147	44
<i>Rubus idaeus</i>	Tall herb	0.127	78
<i>Plagiochila asplenioides</i>	Bryophyte	0.120	36
<i>Gymnocarpium dryopteris</i>	Fern	0.119	73
<i>Chamaepericlymenum suecicum</i>	Small herb	0.108	66
<i>Linnaea borealis</i>	Small herb	0.091	56
<i>Agrostis capillaris</i>	Graminoid	0.090	55
<i>Empetrum nigrum</i>	Dwarf shrub	0.088	54
<i>Luzula pilosa</i>	Graminoid	0.086	53
<i>Melampyrum sylvaticum</i>	Small herb	0.080	49
<i>Chamerion angustifolium</i>	Tall herb	0.075	46
<i>Vaccinium uliginosum</i>	Dwarf shrub	0.070	43
<i>Cirriphyllum piliferum</i>	Bryophyte	0.060	18
<i>Plagiommium undulatum</i>	Bryophyte	0.060	18
<i>Ptilidium ciliare</i>	Bryophyte	0.060	18
<i>Plagiothecium undulatum</i>	Bryophyte	0.043	13
<i>Hylocomiastrum umbratum</i>	Bryophyte	0.040	12
<i>Rhytidiadelphus triquetrus</i>	Bryophyte	0.040	12
<i>Dryopteris expansa</i>	Fern	0.038	23
<i>Pteridium aquilinum</i>	Fern	0.036	22
<i>Anemone nemorosa</i>	Small herb	0.028	17
<i>Rhodobryum roseum</i>	Bryophyte	0.027	8
<i>Potentilla erecta</i>	Small herb	0.026	16
<i>Deschampsia cespitosa</i>	Graminoid	0.024	15
<i>Rubus chamaemorus</i>	Small herb	0.021	13
<i>Blechnum spicant</i>	Tall herb	0.020	12
<i>Equisetum sylvaticum</i>	Small herb	0.020	12
<i>Phegopteris connectilis</i>	Tall herb	0.018	11
<i>Solidago virgaurea</i>	Tall herb	0.018	11
<i>Sciuro-hypnum starkei</i>	Bryophyte	0.017	5
<i>Calamagrostis phragmitoides</i>	Graminoid	0.016	10
<i>Geranium sylvaticum</i>	Tall herb	0.016	10
<i>Molinia caerulea</i>	Graminoid	0.013	8
<i>Oxalis acetosella</i>	Small herb	0.011	7
<i>Sciuro-hypnum reflexum</i>	Bryophyte	0.010	3

<i>Rubus saxatilis</i>	Small herb	0.010	6
<i>Anthoxanthum odoratum</i>	Graminoid	0.008	5
<i>Athyrium filix-femina</i>	Fern	0.008	5
<i>Salix</i> sp	Dwarf shrub	0.008	5
<i>Festuca</i> sp	Graminoid	0.005	3
<i>Filipendula ulmaria</i>	Tall herb	0.005	3
<i>Lycopodium annotinum</i>	Small herb	0.005	3
Poaceae	Graminoid	0.005	3

† = species pair/group (analyzed as one taxa).

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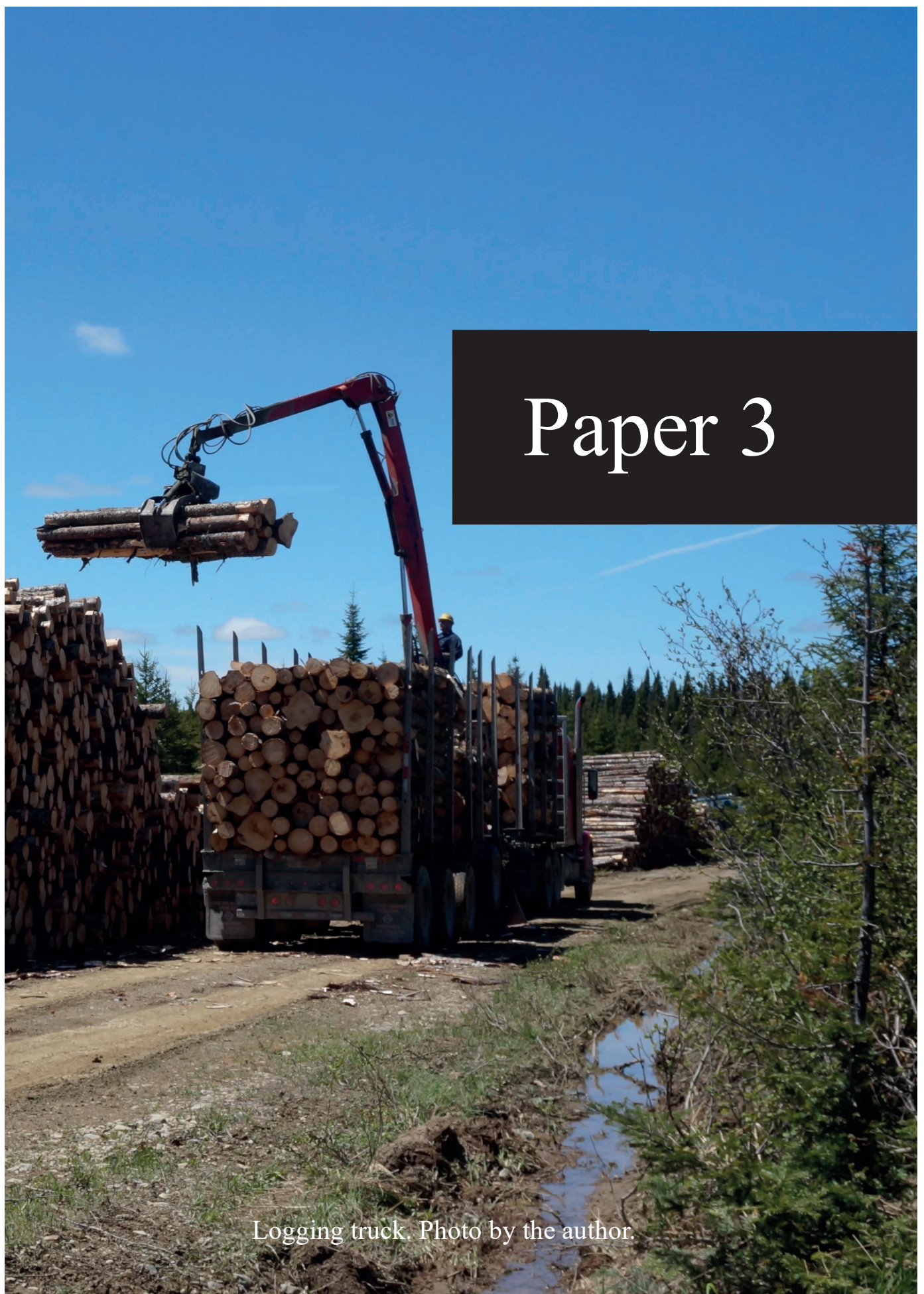


Paper 2

Moose. Photo: Lillian U.Gulliksen

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Paper 3



Logging truck. Photo by the author.

Moose effects on soil temperatures, tree canopies and understory vegetation – a path analysis

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Abstract

Large vertebrate herbivores are ubiquitous and increasingly numerous in boreal forests where they are known to influence ecosystems in many ways. However, separating the direct effects of herbivores from their indirect effects on understory plant communities via forest structural changes and microclimate remains unexplored, limiting the predictability of herbivore impacts. We used an exploratory path analysis approach to investigate potential mechanistic pathways between herbivore removal, forest canopy cover, soil temperature, and understory vegetation dynamics. Moose (*Alces alces*) were excluded from 15 recently clear-cut boreal forest sites in Norway using 20 × 20 m fences with paired open un-fenced plots. Soil temperatures and vegetation data were recorded after eight years (total n = 98). Moose exclusion reduced summer soil temperatures but not winter soil temperatures, leading to no net effect over 344 days. Path analysis showed a strong positive effect of moose exclusion on canopy cover and subsequently reduced summer soil temperatures. There was some support for an increase in the dominant grass species *Avenella flexuosa* with increasing summer soil temperatures, but neither temperature, canopy cover nor *A. flexuosa* had clear links to plant species densities. Moose exclusion directly increased herb biomass and shifted understory species composition towards less shrub-dominated communities, resulting in increased species densities of vascular plants and bryophytes. Our results indicate that in early successional boreal forests, direct effects of large herbivores on plant communities are clearly visible, and indirect effects are detectable but much weaker.

Keywords

Alces alces, *Avenella flexuosa*, diversity, European elk, microclimate, moose, path analysis, piecewiseSEM, vegetation.

Introduction

Large herbivores can be seen as biological disturbance agents that modify and shape the structure of ecosystems from the level of single trees (Danell et al. 2003) to entire forests (Kuijper et al. 2010, Eichhorn et al. 2017). By altering vegetation characteristics such as canopy structure and composition, or by compacting or mixing the soil, these animals can indirectly affect ecosystem properties such as the microclimate, litter quality and quantity, decomposition and nutrient mineralisation (McInnes et al. 1992, Kielland et al. 1997; Kielland and Bryant 1998, Ritchie et al. 1998, Kolstad et al. 2018a). This again influences ground and soil biota (Wardle et al. 2001, Suominen et al. 2008, Andriuzzi and Wall 2017), tree seedling growth and mycorrhizal infection (Kardol et al. 2014), and may be an underlying cause behind observed herbivore-induced changes in biological diversity (Bernes et al. 2018). Over the last few decades many high-latitude ungulate populations have increased in density (Apollonio et al. 2010) and thus their ecological imprint on ecosystems has also increased (Côté et al. 2004). However, we still don't know precisely how this will affect ecosystem

properties that are vital for biodiversity and ecosystem functioning and therefore it is paramount that we learn more about the functional role of large vertebrate herbivores.

A recent systematic review of the effect of large herbivores on multiple aspects of vegetation and diversity highlighted the large number of contingent factors that makes it difficult to reach a synthesis for a generalisable mechanism (Bernes et al. 2018). One reason for this is that, although herbivores can affect communities directly, we know much less about their indirect effect through mechanisms such as biotic and abiotic habitat alterations (but see Beguin et al. 2011). Herbivores can directly reduce plant diversity through selective browsing, causing mortality or reduced fitness (Olf and Ritchie 1998) or they can facilitate the establishment of new species, for example by dispersing seeds or creating favourable germination sites through soil disturbance from trampling (Albert et al. 2015, Boulanger et al. 2017). Herbivores may also affect plant diversity and composition indirectly, for example by altering the forest structure and thereby affecting the resource (e.g. light levels) or substrate availability, or the variation in these. Mathisen et al. (2010) showed that simulated browsing can reduce canopy cover and increase light penetration, thereby favouring a dominant grass species *Avenella* (syn: *Deschampsia flexuosa*). Dominant species and high community level biomass can reduce species density due to competitive exclusion (Grace 1999, Koerner et al. 2018). However, Beguin et al. (2011) found that dominant browsing-tolerant plants were positively associated with herb richness and suggest facilitation, along with associational avoidance/defense, as potential mechanisms to explain this. Long-term effects (>40 years) of deer activities on diversity are less studied than immediate effects, but are probably common, and result from alternate successional pathways and legacy effects from early plant regeneration stages (Hidding et al. 2013, Nuttle et al. 2014).

Temperature is a fundamental property of any ecosystem, and although its effect is easily confounded by variation in soil moisture (Davidson et al. 1998), we know that temperature plays a key role in governing plant productivity (Chu et al. 2016), litter decomposition (Prescott 2010, Bradford et al. 2015), phenology (Richardson et al. 2013, Sanders-DeMott et al. 2018), nutrient mineralisation (Bai et al. 2013), carbon storage (Kane and Vogel 2009), as well as plant (Brooker and van der Wal 2003) and microbial community composition and abundances (Castro et al. 2010). Higher temperature generally increases rates of all metabolic processes through its effects on enzyme activity and reaction rates. If other factors are not limiting, higher temperatures generally imply accelerated nutrient cycling, faster plant growth, and increased primary productivity (at least in the short term, see Körner 2006). Temperature dictates both habitat and community structure through its effect on inter-specific competition and can also drive larger patterns in the distribution of species (Morecroft and Paterson 2006).

Moose (*Alces alces*, including many subspecies) is the largest and most widespread ungulate herbivore in boreal forests in Fennoscandia, Russia, and North America (Telfer 1984). In Fennoscandia, populations have increased substantially during the last 60-70 years and are now at record high densities in many parts of the distributional range (Lavsund et al. 2003, Speed et al. 2019). Moose are browsers and find most of their food in young forests, notably in recent clear cuts with easily accessible and nutrient rich deciduous tree species (Bjørneraas et al. 2011, Wam et al. 2016). In such habitats, moose browsing has a strong impact on the recruitment of preferred tree species (Edenius et al. 2002, Hidding et al. 2013, Kolstad et al. 2018b) and may also indirectly affect the distribution and diversity of field layer plants through several pathways (Beguin et al. 2011). For example, in two moose enclosure experiments from early-successional boreal forests in Alaska (Kielland and Bryant 1998) and

in central Norway (Kolstad et al. 2018a) exclusion caused sites to become more shaded with lower soil summer temperatures, with potential strong impact on plant communities.

In this study we recorded summer and winter soil temperatures and collected data on understory vegetation and forest canopy cover from inside and outside moose exclosures in central Norway. We used exploratory path analysis to model moose impacts on understory vegetation as mediated by altered canopy cover and soil temperatures. We do not attempt to test *a priori* hypotheses concerning the network structure, as there are too many possible configurations, but instead we take an exploratory approach and try to detect possible causal relationships in the data. Based on the strength of these relationships we make a general case for how a large herbivore can simultaneously modify the biotic and abiotic environment, with implications for biodiversity and ecosystem functioning.

Materials and methods

Study design

The study was conducted at 15 sites in Trøndelag county, central Norway (Fig. 1, Table 1) that were clear-cut between 2002 and 2006. The sites cover a range of forest productivities from rich spruce (*Picea abies*) forests to poorer and often drier pine (*Pinus sylvestris*) forests as is represented in a productivity index originally published by Kolstad et al. (2018a). Two similar 20 × 20 m plots minimum 20 m apart were chosen at each homogeneous site and randomly assigned to either the *exclosed* or *open* treatment. Fences 2.5 m tall were erected in 2008 to exclude large herbivores. No deer browsing marks have been observed inside any of the exclosures. Moose (*Alces alces*) is the dominant herbivore with regional densities between 0.5 – 2.0 moose km⁻² (Solberg et al. 2012, Erling J. Solberg, *unpubl. data*). Other large herbivores in the region are roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and low densities of domestic livestock, especially sheep. Smaller herbivores like rodents and mountain hare (*Lepus timidus*) are also present but, unlike larger animals, these could freely enter the exclosures. We have not seen indications that they are more common in either treatment. Most sites were re-planted after logging (Table 1). No soil preparation, fertilisation or thinning has been conducted, except for three open plots (specified in Table 1) that were thinned by forest managers in late 2015. These three sites are excluded from all analyses except from a single figure where they provide a visual comparison only. See Speed et al. (2013) for more information about the sites.

Table 1. Characteristics of the 15 field sites in Trøndelag, central Norway. Site numbers correspond with the labels in Figure 1. Data from five sites were used in the path analysis. The productivity index is based on annual tree biomass increments and more productive sites have a higher index value (see Kolstad et al. 2018a). Herbivore densities are at the scale of municipalities and expressed as metabolic biomass (kg km^{-2}) as in Speed et al. (2013). Total herbivore densities include moose, red and roe deer, sheep, and cattle.

Site	Path analysis	Clear-cut (year)	Species planted	Moose density	Total herbivore density	Elevation (m a.s.l.)	Productivity index
1	yes	2004	Spruce	102.11	172.91	123	1.4
2		2006	Spruce	102.11	172.91	291	0.7
3		2005	Spruce	106.66	206.53	252	0.8
4		2004	Spruce	106.66	206.53	158	0.9
5		2006	Spruce	42.5	141.27	127	0.4
6	yes	2003	Spruce	42.5	141.27	202	1.8
7		2005	Pine	42.5	141.27	229	0.2
8	yes	2002	Spruce, Pine	91.93	175.63	237	1.9
9 t		2002	Spruce, Pine	91.43	246.56	247	1.4
10 t		2004	Spruce	67.86	128.73	184	1.9
11		2002	None	67.86	128.73	311	0.5
12	yes	2003	Spruce	67.86	128.73	379	0.9
13 t		2005	Spruce	33.79	51.72	298	1.3
14	yes	2005	Spruce	33.79	51.72	429	1.0
15		2005	None	28.92	168.82	286	~0.0

t = indicates that the open plots were thinned.

a.s.l. = above sea level.

Soil temperature

Soil temperature loggers (HOBO Pendant® UA-001-64; Onset Computer Corporation, MA, USA) were deployed at all 15 sites for nearly a year from spring 2016 to spring 2017, and then again during peak summer in 2017 for a subset of the five most productive sites as defined by a productivity index (Kolstad et al. 2018a). Both time series were truncated to get a common data range for all sites (Table 2). Loggers were buried 5 cm below the organic layer. In the *full-year* dataset (Table 2) temperature loggers (90 in total) were placed 4 m away from the plot center towards three randomly chosen corners (as in Kolstad et al. 2018a). We calculated mean temperatures for the summer (June-August; period with fully developed canopy) and winter (January-March; period with stable snow cover), as well as total soil thawing degree days (STDD; defined as accumulated daily mean soil temperatures above 0°C) between 19 May 2016 and 27 April 2017. For the *summer* dataset, we placed loggers (98 in total) immediately adjacent to vegetation sampling quadrats ($n=10$ inside each plot; Table 2). Plotting pairwise comparisons of mean soil temperatures against distance confirmed there were no issues with spatial autocorrelation within plots (Fig. S1).

Table 2. Characteristics of the two datasets used in this study.

Dataset	Data types	Dates	Soil temperature loggers				Freq.	Key output analyses
			# days	# sites	# loggers	# faulty loggers		
Full-year	Soil temp. only	5 May 2016 – 27 April 2017	344	15 ^a	90	8 ^b	6-12 h	Seasonal variation
Summer	Soil temp. and vegetation	9 June 2017- 6 August 2017	59	5	100	2 ^c	1 h	Path analysis and diurnal variation

^a Three of which were removed from statistical analyses due to thinning of open plots. ^b Eight loggers recorded only 77, 79, 116, 221, 327, 330, 334 and 335 days, but were still included in the analyses. ^c Two loggers did not record any data.

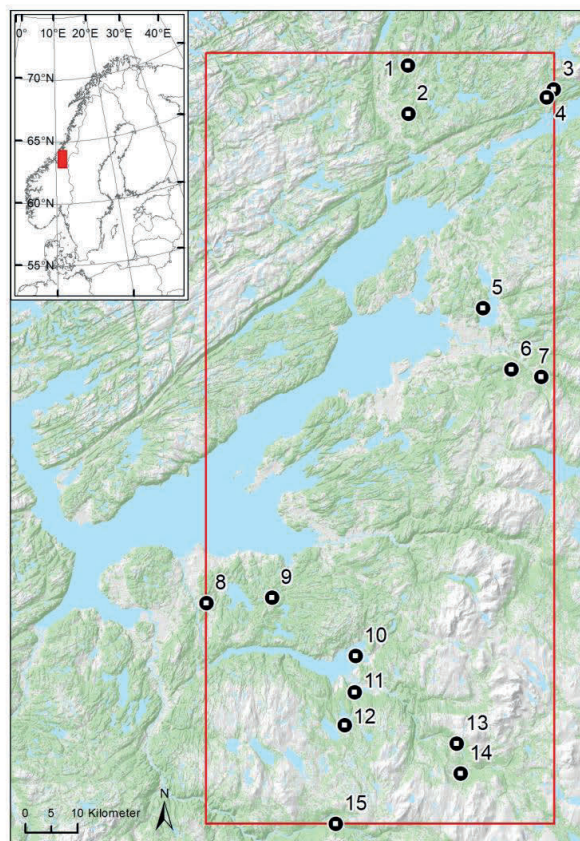


Figure 1. Map of field sites in Trøndelag county, central Norway. Numbers refer to site numbers in Table 1.

Plant abundances and forest structural properties

Vegetation analysis was done in June-July 2016 using the point intercept method (e.g. Jonasson 1988) with ten 50 × 50 cm quadrats per plot and 16 pins per quadrat. The data

include plant species identity, intercept frequencies per taxa and bryophyte depth (distance from the soil to the top of the bryophyte layer) per pin. Tree species were excluded. Some bryophyte taxa were combined and analysed as species pairs or groups, notably all (small) liverworts were treated as one taxon except for a few characteristic (large) species. The correct identification of bryophyte species was confirmed by an experienced bryologist (Kristian Hassel, *personal communication*) for a representative subset of the observations. The full species list is given in Table S1. Vascular and bryophyte species densities (analogous to *species richness*) and mean bryophyte depth were calculated for each 0.25 m² quadrat. Locally calibrated biomass equation models were used to convert measured intercept frequencies into estimates of biomass (dry weight) as in Kolstad et al. (2018b).

A canopy cover index (Tichý 2015) was estimated for each vegetation sampling quadrat in the summer of 2016 (see Kolstad et al. 2018a) using multiple hemispherical pictures taken at 50 cm height, thus capturing small trees and large shrubs, but not field layer vegetation. This index ranges from zero to 100% and represents the fraction of the view that is covered by tree (or shrub) crowns when looking up.

Statistical analyses

We used mixed effects models with random intercept for each experimental site to test the influence of herbivore exclusion, site productivity, and their interaction, on STDD (*glmmTMB* function, gamma distribution; Magnusson et al. 2017), mean winter temperatures and diurnal summer temperature fluctuations (*lme* function; Pinheiro et al. 2017). We report either contrasts or results from log-likelihood ratio test.

In order to investigate the complex multivariate network of interactions between herbivore removal, soil temperature, vegetation characteristics and plant communities, we used the *summer* dataset (Table 2) to perform a path analysis by combining several mixed effects models using the *piecewiseSEM* package (Lefcheck 2016; version 2.0.2) in R (R Core Team 2017; version 3.4.2). In path analyses, a node can serve both as an explanatory variable (exogenous) or response variable (endogenous) and this method therefore allows the testing of indirect or cascading effects, which help close the gap between correlation and causation by having an explicit focus on mechanistic drivers of change in a system (Grace 2008).

We used existing literature and exploratory principal components analyses (Fig. S2) to select the most relevant and interesting understory vegetation variables to investigate further. Based on Mathisen et al. (2010) and the background described in the introduction, we included the abundance of *Avenella flexuosa*, which is a grass species that becomes highly dominant on clear-cut sites in the region and was the most common species in our dataset (found in 95% of all subplots, see Table S1). We included total herb biomass (all non-woody dicots) because herbs, especially the large species, are highly affected by ungulates (Beguin et al. 2011; Kolstad et al. 2018). We also included the first axis from a Bray-Curtis based nonmetric multidimensional scaling (*vegan* package, *metaMDS* function; Oksanen et al. 2018) to represent a gradient in the vascular plant community composition that was strongly and positively associated with shrub biomass, i.e. ‘shrubbiness’ (NMDS1; Fig. S3). Mean depth of the bryophyte layer was included, but not the variation in bryophyte depth as these were positively correlated and the mean value had a longer vector in the ordination (Fig. S2). Two relevant variables (large herb biomass and shrub biomass) were not included due to high zero-inflation. In order to reduce the complexity and facilitate interpretation of the model, and because the causality behind their relationships is somewhat blurry, we constrained the model

to not consider relationships between some nodes (those nodes that are grouped together in Fig. 4). Instead, these relationships are reported as partial Pearson correlations.

We were interested in learning the underlying structure and dependencies in the data, rather than testing *a priori* hypotheses. To that end, we conducted an exploratory path analysis comprised of a combination of forward and backward selection steps. We nevertheless put some restrictions on the final model: “Large herbivores” was never endogenous and the “species density” nodes were never exogenous, even though the causation between altered diversity and altered species composition is ambiguous. There could be no arrows to canopy cover except that from herbivore exclusion: even though understory dynamics can drive tree growth in the long term, it is most likely not an important driver in very young stands. In addition, ‘herbs’, ‘shrubbiness’, and ‘*A. flexuosa*’ could not be predictors of soil temperature, although we acknowledge that understory plants also create shade that can reduce soil temperatures.

We fitted a piecewise structural equation model (*psem*-function; Lefcheck 2016), starting with all arcs (linkages, arrows) except those explained in the above paragraph and with herbivore exclusion only influencing canopy cover and soil temperature. We did a screening for non-linear relationships using bivariate scatterplots (Fig. S4) and subsequently included quadratic terms when they proved statistically significant and when they increased the model fit (R^2). Quadratic terms were therefore added for the relationships between soil temperature and *A. flexuosa* and between herbs and bryophyte depth to bryophyte species density. Sub-models were fitted using linear mixed effects models with the *lme* function (Pinheiro et al. 2017) with random intercepts for each experimental site. *Avenella flexuosa* biomass was log-transformed to normalize model-residuals. One data point with bryophyte depth was excluded as an outlier prior to analysis (4.07 SD units from the mean after it was removed). We then removed non-significant arcs ($p > 0.05$) one at the time, and also removed one marginally significant arc (from canopy cover to *A. flexuosa*, $p = 0.049$) because it did not appear convincing (see Fig. S4). After removing non-significant arcs we added additional arcs that were not originally specified (herbivore exclusion to nodes besides canopy cover or soil temperature) but which were not conditionally independent. This resulted in a parsimonious model, and we evaluated overall model fit by comparing the Fisher C value against a Chi-square distribution (Lefcheck 2016). Conditional and marginal R^2 values were obtained from the *summary* function. Finally, we fitted models for the open-plots and the exclosures separately, starting with the model structure we had just obtained for the full data, which we then evaluated using Fishers’ C values before proceeding with model selection as described above.

Each individual mixed effects model was validated using Pearson’s residuals. Low correlations between slopes and intercept coefficients indicated no problems due to scaling. Soil temperature was centered on the mean to reduce correlation between the linear and quadratic term. Model parameters are presented as both standardized and unstandardized regression coefficients but note that for quadratic relationships standardized estimates are not informative.

Results

Soil temperature

The mean soil temperature was mostly above 10°C in summer, declined sharply at the beginning of autumn in early October, and remained above freezing all winter (Figs 2, S5). Temporal variation in soil temperatures was large in summer and declined abruptly with the onset of constant snow cover in late November (Fig. S5).

Herbivore exclusion lowered soil temperatures in summer (Figs 2, 3, S5, S6), which has been shown in a previous study to be statistically significant (Kolstad et al. 2018a). In 2017, summer soil temperatures were on average 0.62°C (± 0.28 SE) higher in open plots compared to exclosures (Fig. S6), and this cooling effect inside exclosures was stronger in late evening when soil temperatures were the highest (Fig. S7). In contrast, herbivore exclusion had a marginally significant soil warming effect in winter (Fig. 3; likelihood ratio tests against intercept only model: herbivore exclusion, $\chi_1 = 3.750$, $p = 0.053$; site productivity, $\chi_1 = 3.642$, $p = 0.056$). The full-year (344 days) accumulated thawing degree day sum was not significantly different between treatments (likelihood ratio test against intercept-only models: herbivore exclusion $\chi_1 = 2.15$, $p = 0.142$; site productivity $\chi_1 = 0.01$, $p = 0.924$; Figs 3, S9). The diurnal variation in summer soil temperatures was greater outside compared to inside exclosures (Fig. S8; slope for herbivore exclusion = -0.31 (± 0.08); $p < 0.001$).

At the start of autumn, the most productive sites shifted rapidly from a cooling to a warming effect of exclusion, compared to less productive sites (compare red and green line in Fig. 2). The three thinned sites (also highly productive) were even more extreme in this respect as exclosures were $\sim 0.5^\circ\text{C}$ warmer than open plots throughout the winter (blue line in Fig. 2).

Path analysis

The full path model provided a good fit to the data (Fisher's $C = 49.52_{36}$; p -value = 0.066) and included 10 statistically significant ($p < 0.05$) arcs (Table 3, Fig. 4). The same model structure gave poor (Fisher's $C = 43.81_{23}$; p -value = 0.016) and good fits (Fisher's $C = 23.95_{26}$; p -value = 0.579) to the exclosure data and open plot data, respectively, but further model selection improved both these models considerably (Figs 4, S10). Strong support was found for a pathway where herbivore exclusion significantly increased canopy cover, which in turn was related to decreased mean summer soil temperatures (Figs 4, 5). Following this pathway, we found decreased soil temperatures inside exclosures to correspond with reduced biomass of *A. flexuosa*, but this relationship disappeared in the exclusion-only model. Beyond this, canopy cover and mean summer soil temperature were not associated with any other aspects of understory plant communities, including species densities. A link between *A. flexuosa* and vascular plant species density was found in both the exclosure and the open plot models, but with opposite signs (Fig. S10). The depth of the bryophyte layer was not affected by herbivore removal, directly or indirectly, but was itself a strong predictor of bryophyte species density forming a positive or saturating relationship (Table 3; Figs 4, 5). Moose exclusion had a direct path to increased herb biomass and reduced 'shrubbiness', and the cascading effects from

these nodes were sufficient to explain the slightly higher species densities found inside exclosures (Fig. 4).

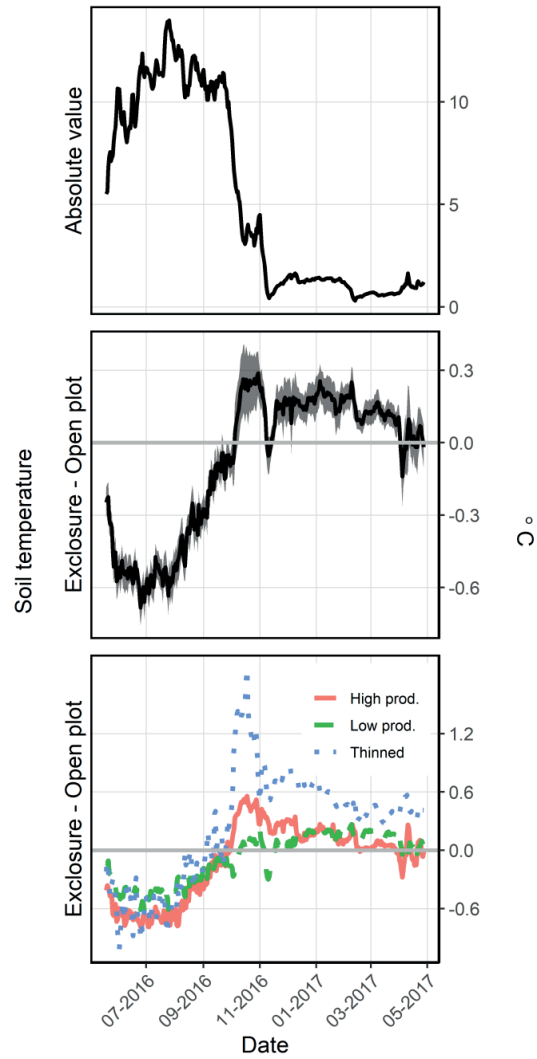


Figure 2. Time series of mean daily soil temperatures from large herbivore exclosures and adjacent open plots. The top pane shows the mean (daily) soil temperatures ($n = 12$ unthinned sites, irrespective of treatment). The middle pane shows the shift in plot mean soil temperature (exclosure minus open plots) with $\pm 1.96 \times$ standard error of the mean as a gray band (thinned sites excluded). The bottom pane shows the same treatment effect conditioned on site productivity (high: $n = 5$; low: $n = 7$, thinned (also high productivity sites: $n = 3$).

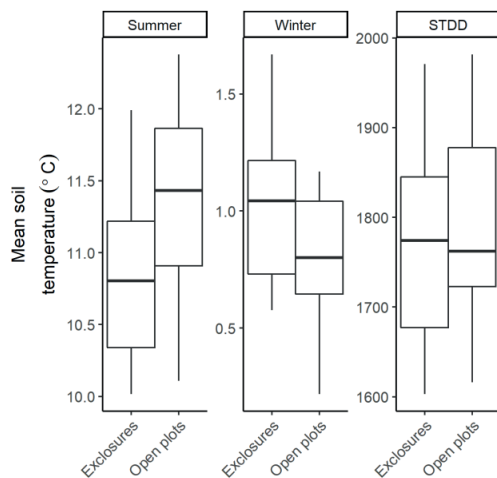


Figure 3. Mean daily summer (July – August) and winter (January – March) soil temperatures and accumulated soil thawing degree days (STDD) over 344 days inside large herbivore exclosures and adjacent open plots (n = 12 sites).

Discussion

Besides direct effects of feeding and trampling, large herbivores affect understory plants via cascading chains of events, or causal pathways, but these complex scenarios are much less explored by ecologists. In this study we have found that moose has both direct and indirect effects on understory plants, including species densities, although the direct effects are most prominent. This study builds towards a more complete and mechanistic understanding of the role of large herbivores, which is essential for predicting community and ecosystem changes following the often eruptive ungulate population developments of the recent decades.

Herbivore removal generated a 21.5% increase in canopy cover, which in turn reduced summer soil temperatures (Fig. 4). Soil temperature was not affected by bryophyte depth (Fig. 5). According to Soudzilovskaia et al. (2013) moss carpets provide effective insulation, but have no effect on long-term mean soil temperatures, making our result not very surprising. Also, the bryophyte depth was not affected directly by herbivore removal as one would expect if bryophytes were sensitive to trampling. Kolstad et al. (2018a) found reduced soil bulk density and increased organic soil depth as an effect of herbivore exclusion within the same experimental design, both indicating that trampling is an important effect of moose at these sites.

Moose exclusion had a cascading effect on reducing the biomass of the very common grass *A. flexuosa* via increased canopy cover and reduced soil temperature in summer (Fig. 5). However, soil temperature only affected *A. flexuosa* in the open plots, thus reducing the generality of this finding. *A. flexuosa* is a species that can grow very dense and seemingly dominate on recent clear-cuts. We found that temperature was a better predictor of *A. flexuosa* than canopy cover (and thus light levels), but there was also a direct pathway from herbivore exclusion to *A. flexuosa* biomass where the actual causation remains elusive. We speculate if unmeasured aspects of interspecific competition are behind this relationship. Altered soil

processes could also underlie this and other relationships from herbivore exclusion to understory vegetation, although some recent studies indicate that soil processes are not very responsive to moose impacts on a short term (Ellis and Leroux 2017, Kolstad et al. 2018a).

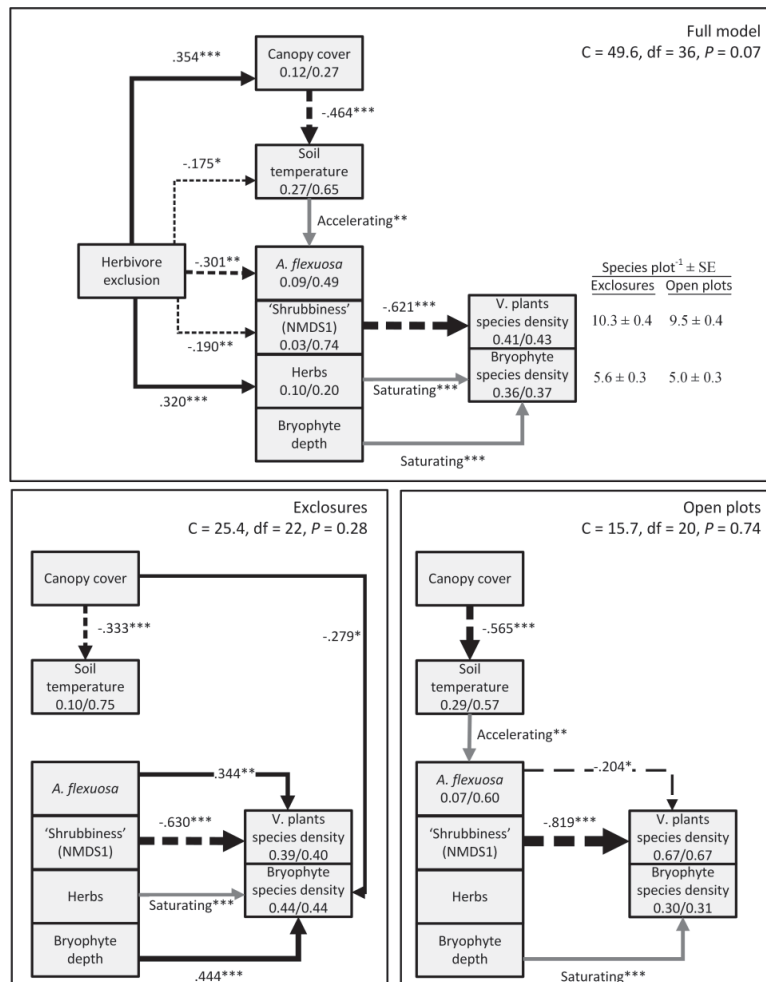


Figure 4. Results from exploratory piecewise structural equation modelling. The full model (top) includes herbivore exclusion as a categorical exogenous variable, whereas the two sub-models (below) are build using data from only exlosures (left) or open plots (right). Solid and broken lines represent positive and negative relationships, respectively. Numbers on arrows are standardised partial regression coefficients and the width of the arrows are scaled based on these, except for non-linear relationships (grey lines) which are described according to the shape of the relationship and with a pre-set arrow width. Asterisks indicate statistical significance (* P < 0.05; ** P < 0.01; *** P < 0.001). Numbers inside nodes are marginal and conditional R² values, respectively. Correlated errors were allowed (and no betas estimated) between the nodes that are group closely together. V = vascular.

Table 3. Partial regression coefficients (standardized (std.) and raw), from path analysis exploring the direct and indirect effects of moose exclusion on plant communities. Correlated errors are partial Pearson correlations coefficients. Asterisks indicate statistical significance (* P < 0.05; ** P < 0.01; *** P < 0.001).

Response	Predictor	Std estimate	Raw estimate	SE	DF	p-value	sig.
Canopy cover (%)	Herbivore exclusion	0.35	20.49	5.11	92	<0.001	***
Soil temperature (°C)	Herbivore exclusion	-0.17	-0.31	0.13	89	0.014	*
Soil temperature (°C)	Canopy cover (%)	-0.46	-0.01	<.01	89	<0.001	***
NMDS1	Herbivore exclusion	-0.19	-0.22	0.07	92	0.001	**
<i>Avenella flexuosa</i> (g m ⁻²)	Herbivore exclusion	-0.27	-0.52	0.17	88	0.004	**
<i>Avenella flexuosa</i> (g m ⁻²)	Soil temperature (°C)	-5.12†	-5.57	1.82	88	0.003	**
<i>Avenella flexuosa</i> (g m ⁻²)	(Soil temperature) ²	5.00†	0.25	0.08	88	0.003	**
Herb biomass (g m ⁻²)	Herbivore exclusion	0.32	22.89	6.59	92	<0.001	***
Vascular plants (spp plot ⁻¹)	NMDS1	-0.62	-3.02	0.43	92	<0.001	***
Bryophytes (spp plot ⁻¹)	Bryophyte depth (cm)	1.54†	1.32	0.26	87	<0.001	***
Bryophytes (spp plot ⁻¹)	(Bryophyte depth) ²	-1.20†	-0.12	0.03	87	<0.001	***
Bryophytes (spp plot ⁻¹)	Herb biomass (g m ⁻²)	0.86†	0.05	0.02	87	<0.001	**
Bryophytes (spp plot ⁻¹)	(Herb biomass) ²	-0.57†	<0.01	<.01	87	0.030	*
<i>Correlated errors</i>							
Vascular plants	Bryophytes		0.08		98	0.229	
<i>Avenella flexuosa</i>	Bryophyte depth		0.05		98	0.314	
<i>Avenella flexuosa</i>	Herb biomass		-0.23		98	0.011	*
NMDS1	Herb biomass		-0.44		98	<0.001	***
NMDS1	<i>Avenella flexuosa</i>		-0.09		98	0.182	
NMDS1	Bryophyte depth		-0.03		98	0.391	
Bryophyte depth	Herb biomass		-0.03		98	0.369	

High abundance of dominant species can reduce plant diversity through competitive exclusion (Hardin 1960, Olff and Ritchie 1998, Grace 1999, Mathisen et al. 2010, Koerner et al. 2018). We found that *A. flexuosa* was associated with low species densities in open plots, but high species densities in exclosures, although effect sizes were only moderate. This nonetheless suggests an interaction between herbivore exclusion and *A. flexuosa* that we do not yet know the nature of.

The depth of the bryophyte layer had a positive or saturating relationship with bryophyte species density (Figs 4, 5), which is the same relationship predicted between biomass and local diversity (see Grace 1999 for a review). This can possibly be explained by shallow moss carpets having fewer individuals and therefore lower diversity, and deep carpets showing a weak effect of competitive exclusion from dominant pleurocarpous species, such as *Hylocomium splendens* and *Pleurozium schreberi* (Rydgren et al. 2004).

Species densities of both vascular plants and bryophytes were only slightly higher inside exclosures, and this probably has few ecological consequences. Nonetheless, these differences could be explained by only considering the indirect effect of moose exclusion via increased herb biomass and reduced 'shrubiness', leaving no unexplained variation that could be due to other herbivore effects, such as seed dispersal (Albert et al. 2015, Boulanger

et al. 2017), soil feedbacks (Kardol et al. 2014), or light levels (Kumar et al. 2018). For example, a negative relationship has been found between boreal forest plant diversity and mean light levels (Kumar et al. 2018), but we speculate that more time is needed for herbivore-induced environmental change to shape new plant assemblages in a system where most species are perennial. In addition, the variation in light levels in space could be more important than mean levels (see Kumar et al. 2018). Note, however, that other mechanisms may be ‘hidden’ as unmeasured correlates to the variables in the model, and that including more variables in the analysis could result in a more nuanced picture. This should remind us that the causality claims in models are restricted by the number and type of measured parameters.

Our analytical approach used only a small number of sites (five) to investigate possible interdependencies between numerous biotic and abiotic variables that may affect local plant communities and diversity. We therefore had a different motivation than testing the effect of herbivores on vegetation and diversity *per se*, which has been done extensively and with more appropriate datasets elsewhere (Speed et al. 2014, Kolstad et al. 2018b, see Bernes et al. 2018 for a systematic review). Results from these studies are idiosyncratic and we believe this is because there is a lack of causal understanding of the underlying processes. Here we explicitly addressed possible indirect ways that herbivores may influence understory vegetation, functionally important groups, keystone species, and local (alpha) diversity of plants. We nonetheless recognize that large herbivores also affect resource heterogeneity, which is known to drive patterns of diversity, especially beta diversity (Kumar et al. 2018), but this was not our target of investigation.

An important aspect of this study was to characterize in detail the changes soil temperature due to moose removal, as temperature was assumed to be an important variable that could underlie indirect or cascading effects of moose on ecosystems. Moose exclusion reduced soil temperatures in summer by about 0.6°C due to increased shading from deciduous trees and possibly other unmeasured parameters such as shading from understory vegetation and differences in evaporative cooling or surface albedo. This effect was reversed in winter when herbivore exclusion led to higher temperatures compared to outside, although not significantly so (Fig. 3). As a result, annual heat sums (STDD) did not differ between treatments. This may be due to differences in snowpack as there could be more snow (and thus higher insolation) inside exclosures due to reduced wind or a snow trapping effect of the vegetation, or because of less moose trampling. We also speculate that the increased temperatures inside the exclosures in winter is an effect of the increased boundary layer thickness and the added heat capacity of the larger biomass in the vegetation (especially in the trees, see Kolstad et al. 2018b). This latter idea is supported by the observation that the three thinned sites, where most of the tree biomass was removed, experienced a rather drastic warming effect of exclosures in late autumn (before the snow) that persisted with diminished effect through winter (blue line in Fig. 3).

Soil processes continue during the dormant season (Campbell et al. 2005), implying that to study long-term soil change such as carbon storage and flux and nutrient cycling one should also consider seasonal variation in soil temperature. This can explain why Kolstad et al. (2018a) failed to find strong links between summer soil temperatures and long-term soil processes within the same study design as in this study. Winter temperatures may have both parallel and contrasting effects on plant communities as compared to summer temperatures.

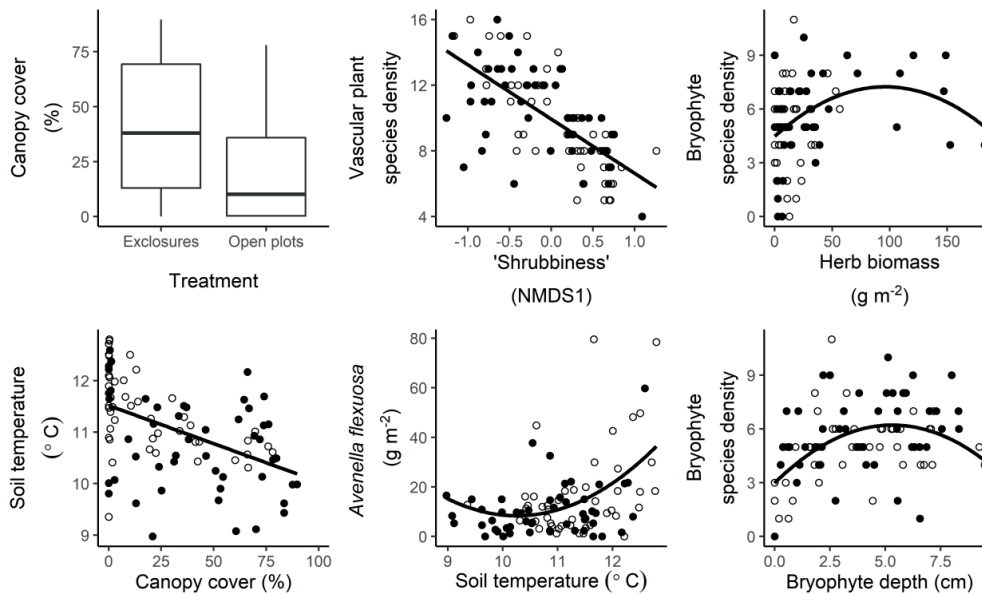


Figure 5. Bivariate plots for selected relationships included in the path analysis (full model). Regression lines are from models refitted without covariates, using the `lm()` function in R and data at the subplot level. All relationships are statistically significant ($p < 0.05$) in mixed effects models. Open circles = open plots. Closed circles = herbivore enclosures.

Besides the aspects of soil processes mentioned above, increased winter soil temperatures can for example increase soil nutrient loss, because there are no active roots to take up new soluble or volatile compounds from decomposition. Vernalisation, timing of leaf flushing, and growing season length may also be affected by winter and spring temperature, with largely unpredictable effects on forest communities. Summer temperatures on the other hand are more directly tied to plant growth via species specific optima and tolerance for physiological processes.

Moose enclosures also had lower diurnal soil temperature fluctuations in summer (Fig. S8) which could be a result of reduced insolation and less heat gain during the day, but also reduced radiative cooling at night due to a higher canopy cover. There are biological implications of reduced diurnal temperature fluctuations as it may for example influence vascular plant regeneration and soil structure (see discussion in Soudzilovskaia et al. 2013). However, it is not known how prevalent these mechanisms are in boreal forests.

In conclusion, we have shown that moose exclusion increased canopy shading, thus reducing summer soil temperatures, but had no effects on annual temperature sums. Summer soil temperature can drive certain aspects of understory plant dynamics, such as the dominance of a common grass species, but the overall cascading effect of altered soil temperatures was small after 8 years of herbivore exclusion. Direct effects on herb biomass and species composition, largely attributable to browsing or trampling, could explain the small increase in species densities inside enclosures. We also showed that in order to obtain general and predictive theories for how large herbivores affect plant diversity (Olf and Ritchie 1998), path analysis is a valuable tool when manipulative experiments are logistically

unfeasible. Many new study questions have emerged from our study, of which we highlight the following: (1) Does the absence of moose have a warming effect during winter and how might this affect important winter soil processes and vegetation dynamics? (2) How prominent is competitive exclusion as a phenomenon in boreal forests? (3) What are the ecosystem/community implications of reduced diurnal temperature fluctuations inside moose exclosures? (4) Will indirect effects of moose via altered forest structure become more important drivers of understory plant communities during the successional progression?

Authors' Contributions

Study was planned by ALK, JDMS, GA, RS, BJG, and EJS. Field work was conducted by ALK, JDMS and GA. Numerical analyses were conducted by ALK. ALK wrote the manuscript with input from all co-authors.

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Data Accessibility

All data used in this manuscript are publicly available at figshare (Kolstad et al. 2018c).

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Supporting Information

for article titled «Moose effects on soil temperature, tree canopies and understory vegetation – a path analysis»

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Contents:

Figure S1 – Pairwise comparison of soil temperature against distance.

Figure S2 – Exploratory PCA plots.

Figure S3 – NMDS on vascular plant species matrix.

Figure S4 – Correlation matrix of covariates

Figure S5 – Soil temperature time series (full year dataset)

Figure S6 – Soil temperature time series (summer dataset)

Figure S7 – Daily soil temperature fluctuations

Figure S8 – Diurnal variation in soil temperature

Figure S9 – Soil thawing degree days

Table S1 – Species list

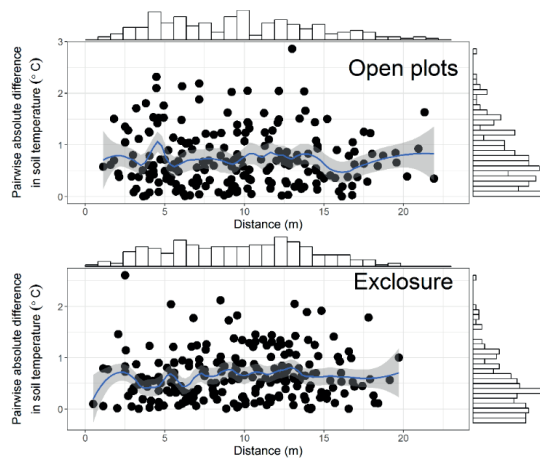


Figure S1. Pairwise within plots comparisons of soil temperature loggers in the summer 2017 dataset. Loess smoothers (span = 0.2) are fitted to the data. Anything but a horizontal line indicates spatial autocorrelation.

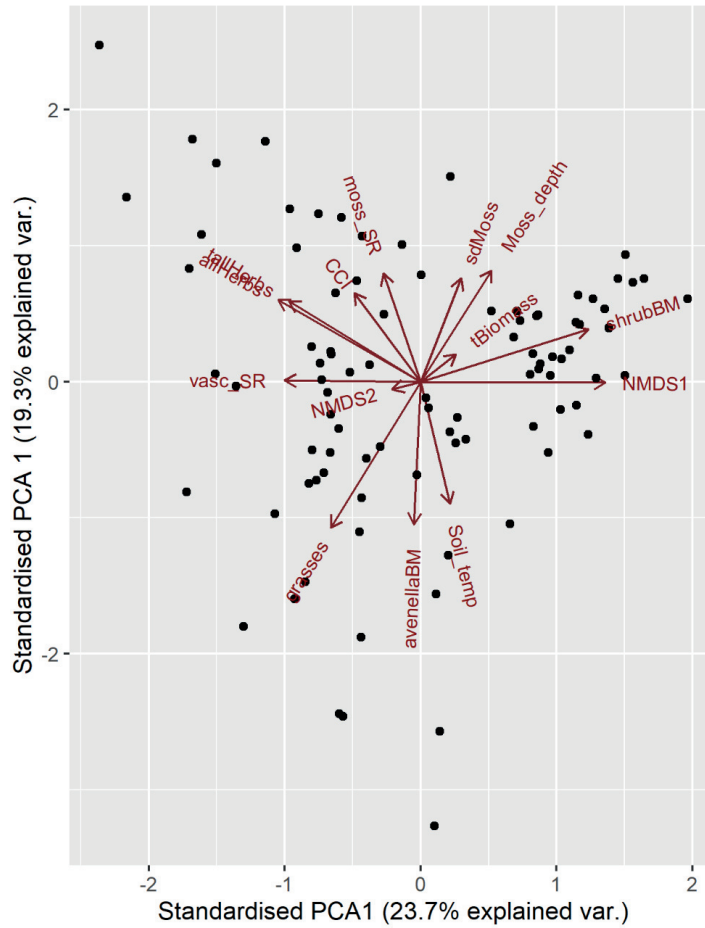


Figure S2. Exploratory ordination (principal component analysis) plot showing relationships between variables, some of which were included in the path analysis. Abbreviations: tBiomass = total understory biomass; CCI = canopy cover; vasc_SC and moss_SR = vascular plant and bryophyte species densities, respectively; sdMoss = standard deviation of moss depth values based on 16 points per plot; avenellaBM = biomass of *Avenella flexuosa*; grasses = total graminoid biomass; tallHerbs = biomass of large herb species; allHerbs = biomass of all non-woody dicots; shrubBM = biomass of dwarf shrub species (*Vaccinium*, *Calluna*, *Empetrum*); NMDs1 and 2 = first and second axis from non-metric multidimensional scaling based on understory plant abundances.

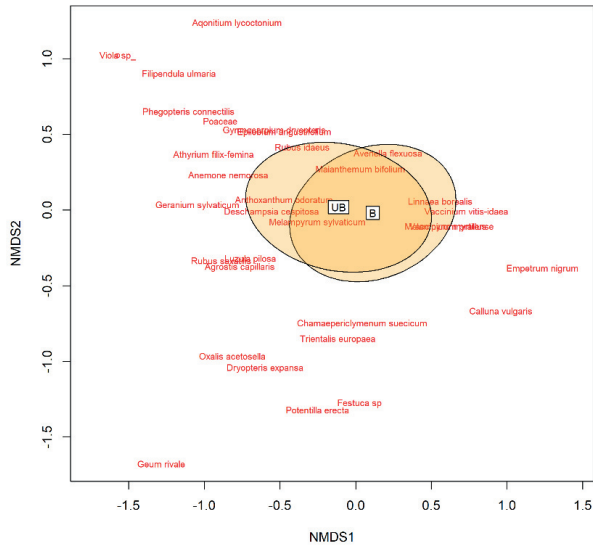


Figure S3. Bray-Curtis based nonmetric multidimensional scaling based on understory plant abundances from vegetation quadrats. Prior to analysis, singletons were removed and Wisconsin double standardisation was performed. Ellipses are centroids for each treatment and show the standard deviation of points (B = Open plots (the centroid most towards the right); UB = Exlosures). The text are the scores for species. Stress = 0.224. The Pearson correlation between axis 1 and the first axis of a similar DCA ordination was 0.94.

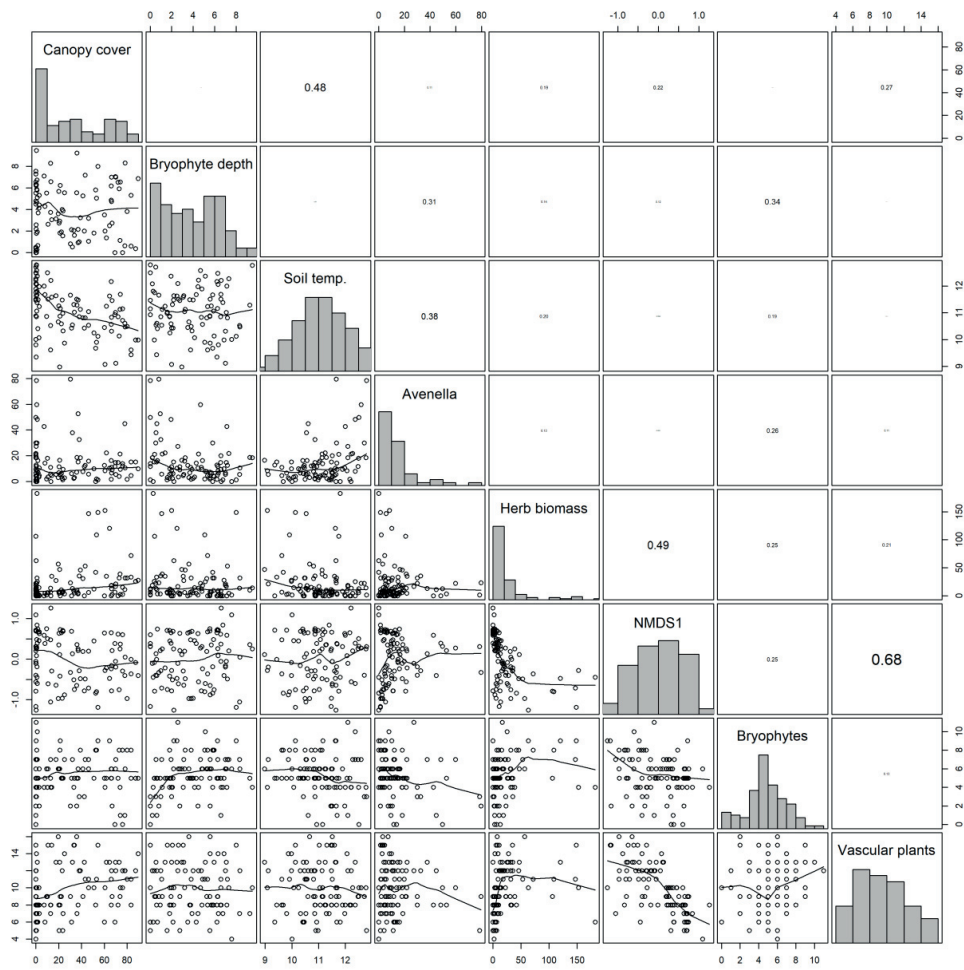


Figure S4. Correlation matrix for variables used in path analysis. Lines are loess smoothers with span equal 0.5. Numbers are Pearson's correlation coefficients.

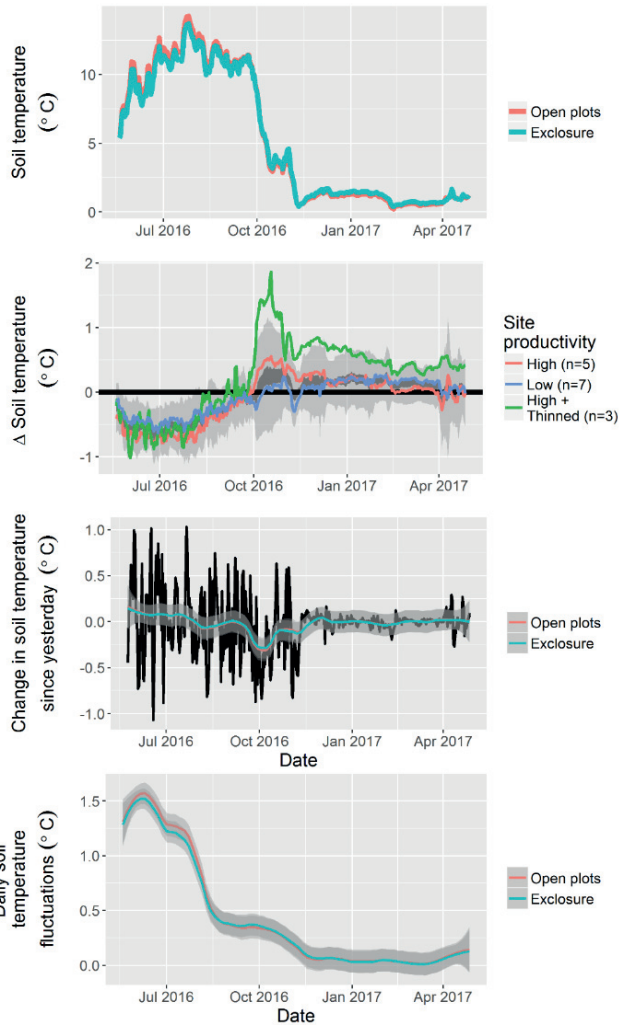


Figure S5. Time series of mean daily soil temperature (5 cm depth) from large herbivore exclosures and adjacent open plots. The top pane shown the mean (daily) soil temperatures. The second pane from the top shows the shift in plot mean soil temperature (exclosure minus open plots) with the standard deviation in light grey and standard error of the mean in dark grey (thinned sites excluded). Means for each forest productivity class are indicated in colour. The third pane shows the difference in mean soil temperature compared to the day before with loess smoothers (span = 0.2) fitted for each treatment category. The bottom pane shows the daily temperature fluctuations (coldest minus warmest recorded temperature) with similar loess smoothers as in the third pane. The two top panes are repeated (modified slightly) from the main results for easy comparison.

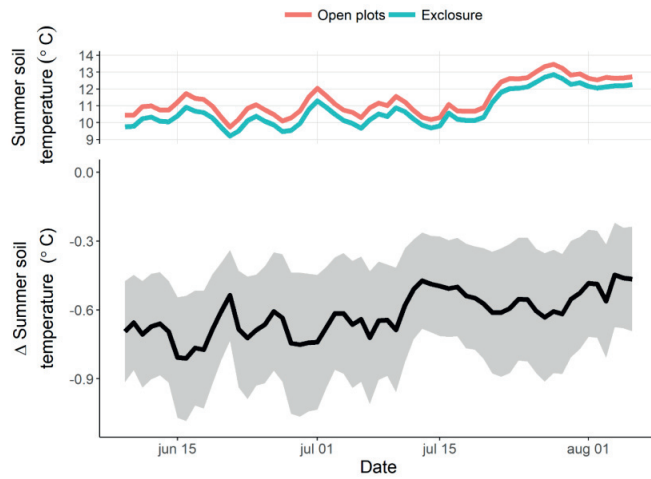


Figure S6. Figure showing summer soil temperatures (top) and treatment effects (exclosures minus open plots; bottom) recorded in 2017 in five productive forest sites in central Norway where large herbivores were either excluded or not.

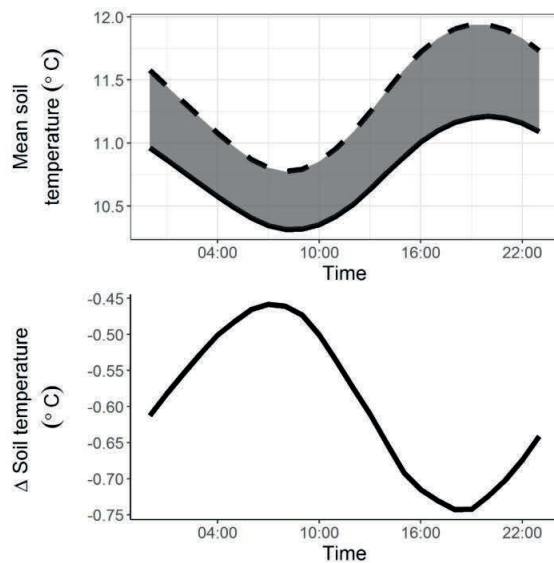


Figure S7. Top: Daily summer soil temperatures for 5 sites ($n=98$) and either open to browsing by moose (dotted line) or from inside large herbivore exclosures (solid line). Bottom: Treatment difference of the same data (open plot minus exclosure).

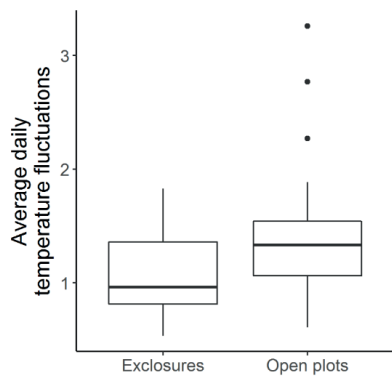


Figure S8. Differences in daily summer soil temperature fluctuations (maximum - minimum) inside large herbivore exclosures and adjacent open plots (n=5 sites).

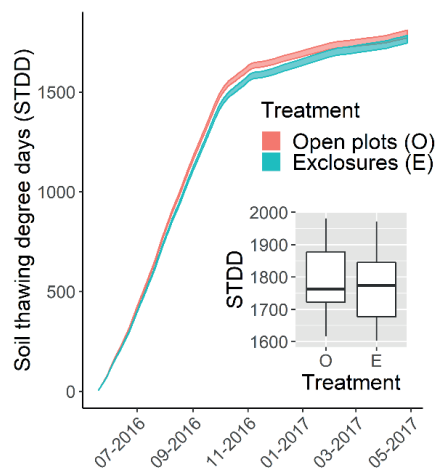


Figure S9. Soil thawing degree days (STDD; defined as accumulated daily mean soil temperature when above 0 °C) for exclosures (herbivores removed) or open plots in 12 boreal forest sites in central Norway. The inserted boxplot shows the accumulated STDD at the end of the experiment when the difference between treatments was not significant.

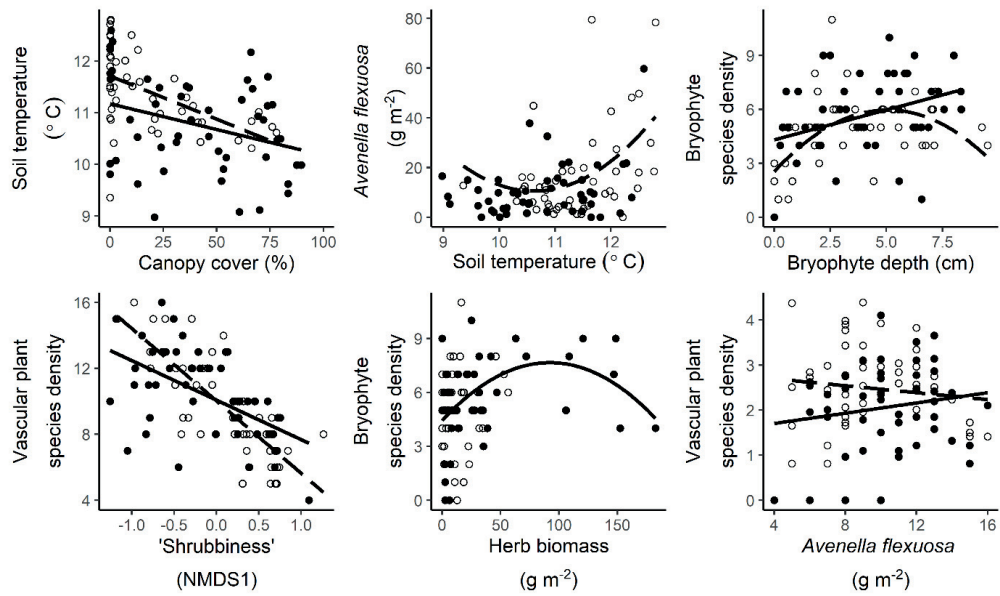


Figure S10. Bivariate plots for selected relationships included in the path analyses. Regression lines (all $p < 0.05$ in mixed effects models) are from models refitted without covariates, using the `lm()` function in R and data at the subplot level. Open circles and dashed lines = open plots. Closed circles and solid lines = herbivore enclosures.

Table S1. Species (taxa) list with relative frequencies (proportion of vegetation quadrats with species present) for five forest sites in Central Norway used in the structural equation model.

Taxa	Relative frequency (overall)	Relative frequency (exclosures)	Relative frequency (open plots)
<i>Avenella flexuosa</i> (NLG)	0.949	0.918	0.98
<i>Hylocomium splendens</i> (M)	0.939	0.959	0.918
<i>Ptilium crista castrensis</i> (M)	0.694	0.653	0.735
<i>Pleurozium schreberi</i> (M)	0.643	0.612	0.673
Marchantiophyta (M)	0.592	0.612	0.571
<i>Vaccinium myrtillus</i> (BLS)	0.592	0.571	0.612
<i>Dicranum</i> sp. (M)	0.571	0.612	0.531
<i>Vaccinium vitis idaea</i> (BLS)	0.561	0.531	0.592
<i>Rhytidiadelphus squarrosus/subpinnatus</i> (M)	0.51	0.531	0.49
<i>Gymnocarpium dryopteris</i> (F/SH)	0.398	0.51	0.286
<i>Rubus idaeus</i> (LH)	0.357	0.429	0.286
<i>Picea abies</i> (T)	0.337	0.306	0.367
<i>Agrostis capillaris</i> (BLG)	0.327	0.367	0.286
<i>Plagiochila asplenioides</i> (M)	0.316	0.388	0.245
<i>Rhytidiadelphus loreus</i> (M)	0.316	0.265	0.367
<i>Trientalis europaea</i> (SH)	0.296	0.286	0.306
<i>Betula pubescens</i> (T)	0.255	0.327	0.184
<i>Sorbus aucuparia</i> (T)	0.255	0.327	0.184
<i>Maianthemum bifolium</i> (SH)	0.224	0.163	0.286
<i>Melampyrum pratense</i> (SH)	0.224	0.163	0.286
<i>Luzula pilosa</i> (BLG)	0.214	0.204	0.224
<i>Cirriphyllum piliferum</i> (M)	0.184	0.224	0.143
<i>Chamerion angustifolium</i> (LH)	0.163	0.327	0
<i>Melampyrum sylvaticum</i> (SH)	0.153	0.143	0.163
<i>Deschampsia cespitosa</i> (BLG)	0.143	0.143	0.143
<i>Anemone nemorosa</i> (SH)	0.133	0.122	0.143
<i>Linnaea borealis</i> (SH)	0.122	0.122	0.122
<i>Hylocomiastrum umbratum</i> (M)	0.112	0.184	0.041
<i>Geranium sylvaticum</i> (LH)	0.092	0.102	0.082
<i>Chamaepericlymenum succicum</i> (SH)	0.082	0.082	0.082

Taxa	Relative frequency (overall)	Relative frequency (exclosures)	Relative frequency (open plots)
Rhytidiadelphus triquetrus (M)	0.071	0.102	0.041
Oxalis acetosella (SH)	0.061	0.061	0.061
Ptilidium ciliare (M)	0.061	0.102	0.02
Polytrichum/Polytrichastrum sp (M)	0.061	0.041	0.082
Rhodobryum roseum (M)	0.061	0.082	0.041
Anthoxanthum odoratum (BLG)	0.051	0.082	0.02
Athyrium filix-femina (F/LH)	0.051	0.061	0.041
Plagiomnium undulatum (M)	0.051	0.082	0.02
Rubus saxatilis (LH)	0.051	0.082	0.02
Sciuro-hypnum starkei (M)	0.041	0.041	0.041
Dryopteris expansa (F/LH)	0.031	0.061	0
Empetrum nigrum (NLS)	0.031	0.02	0.041
Filipendula ulmaria (LH)	0.031	0.041	0.02
Pinus sylvestris (T)	0.031	0.041	0.02
Plagiothecium undulatum (M)	0.031	0.061	0
Poaceae 1 (BLG)	0.031	0.041	0.02
Salix caprea (T)	0.031	0.02	0.041
Aqonitium lycoctonium (LH)	0.02	0.041	0
Festuca sp. (BLG)	0.02	0.02	0.02
Phegopteris connectilis (F/LH)	0.02	0.041	0
Potentilla erecta (SH)	0.02	0	0.041
Alchemilla sp. (SH)	0.01	0.02	0
Blechnum spicant (F/LH)	0.01	0	0.02
Calluna vulgaris (NLS)	0.01	0.02	0
Epilobium sp. (SH)	0.01	0.02	0
Geum rivale (LH)	0.01	0	0.02
Goodyera repens (SH)	0.01	0	0.02
Poaceae 2 (BLG)	0.01	0.02	0
Plagiomnium ellipticum (M)	0.01	0.02	0
Plagiothecium laetum/P. curvifolium (M)	0.01	0.02	0
Ranunculus repens (TH)	0.01	0	0.02
Sciuro-hypnum reflexum (M)	0.01	0.02	0
Taraxacum officinale (LH)	0.01	0	0.02

Taxa	Relative frequency (overall)	Relative frequency (exclosures)	Relative frequency (open plots)
<i>Veronica officinalis</i> (LH)	0.01	0.02	0
<i>Viola</i> sp. (SH)	0.01	0.02	0

Abbreviaton indicate the growth form: BLG = broad-leaved graminoid; NLG = narrow-leaved graminoid; BLS = broad-leaves shrub; NLS = narrow-leaves shrub; LH = large herb; SH = small herb; T = tree; M = moss; F = fern.



Paper 4

The boreal forest, here from a part of Canada where both moose and logging trucks are common sights. Photo by the author.

This article is awaiting publication and is not included in NTNU Open