esa

ECOSPHERE

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

Anders Lorentzen Kolstad,[1,†] Gunnar Austrheim,[1] Bente J. Graae,[2] Erling J. Solberg,[3] G. Richard Strimbeck,[2] and James D. M. Speed[1]

[1]*Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway*
[2]*Department of Biology, Norwegian University of Science and Technology, NO-7034 Trondheim, Norway*
[3]*Norwegian Institute for Nature Research (NINA), NO-7485 Trondheim, Norway*

Citation: Kolstad, A. L., G. Austrheim, B. J. Graae, E. J. Solberg, G. R. Strimbeck, and J. D. M. Speed. 2019. Moose effects on soil temperatures, tree canopies, and understory vegetation: a path analysis. Ecosphere 10(12):e02966. 10.1002/ecs2.2966

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 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 d. 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 toward 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.

Key words: *Alces alces; Avenella flexuosa;* diversity; European elk; microclimate; moose; path analysis; vegetation.

Received 28 August 2019; accepted 23 October 2019. Corresponding Editor: Troy W. Ocheltree.
Copyright: © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
† **E-mail:** anders.kolstad@ntnu.no

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 compacting or mixing the soil, these animals can indirectly affect ecosystem properties such as the microclimate, litter quality and quantity, decomposition, and nutrient mineralization (McInnes et al. 1992, Kielland et al. 1997, Kielland and Bryant 1998, Ritchie et al. 1998, Kolstad et al. 2018*a*). 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 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 do not 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 generalizable mechanism (Bernes 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 (Olff and Ritchie 1998), or they can facilitating the establishment of new species, for example, by dispersing seeds or creating favorable germination sites through soil disturbance from trampling (Albert 2015, Boulanger 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 favoring 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 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 yr) 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 mineralization (Bai et al. 2013), carbon storage (Kane and Vogel 2009), and 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 interspecific 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 yr 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 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. 2018*b*) 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 exclosure experiments from early-successional boreal forests in Alaska (Kielland and Bryant 1998) and in central Norway (Kolstad et al. 2018*a*), 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 plant community and canopy cover data inside and outside moose exclosures in central Norway. We used exploratory path analysis to model moose impacts on plant communities as mediated by altered forest structure 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. (2018*a*). 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 and 2.0 moose/km^2 (Solberg et al. 2012; E. J. Solberg, *unpublished 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 (A. Kolstad, J. D. M. Speed, and G. Austrheim, *unpublished data*). Most sites were replanted after logging (Table 1). No soil preparation, fertilization, 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.

Soil temperature

Soil temperature loggers (HOBO Pendant UA-001-64; Onset Computer, Bourne, Massachusetts, 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. 2018*a*). 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 toward three randomly chosen corners (as in Kolstad et al. 2018*a*). 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 (Appendix S1: Fig. S1).

Plant abundances and forest structural properties

Vegetation analysis was done in June–July 2016 using the point intercept method (Jonasson 1988) with ten 50 × 50 cm quadrats per plot and 16 pins per quadrat. The data include plant species identity, intercept frequencies per taxon, 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 analyzed as species pairs or groups, notably all (small) liverworts where treated as one taxon except for a few characteristic (large) species. The correct identification of bryophyte species was confirmed by an experienced bryologist (K. Hassel, *personal communication*) for a representative subset of the observations. The full

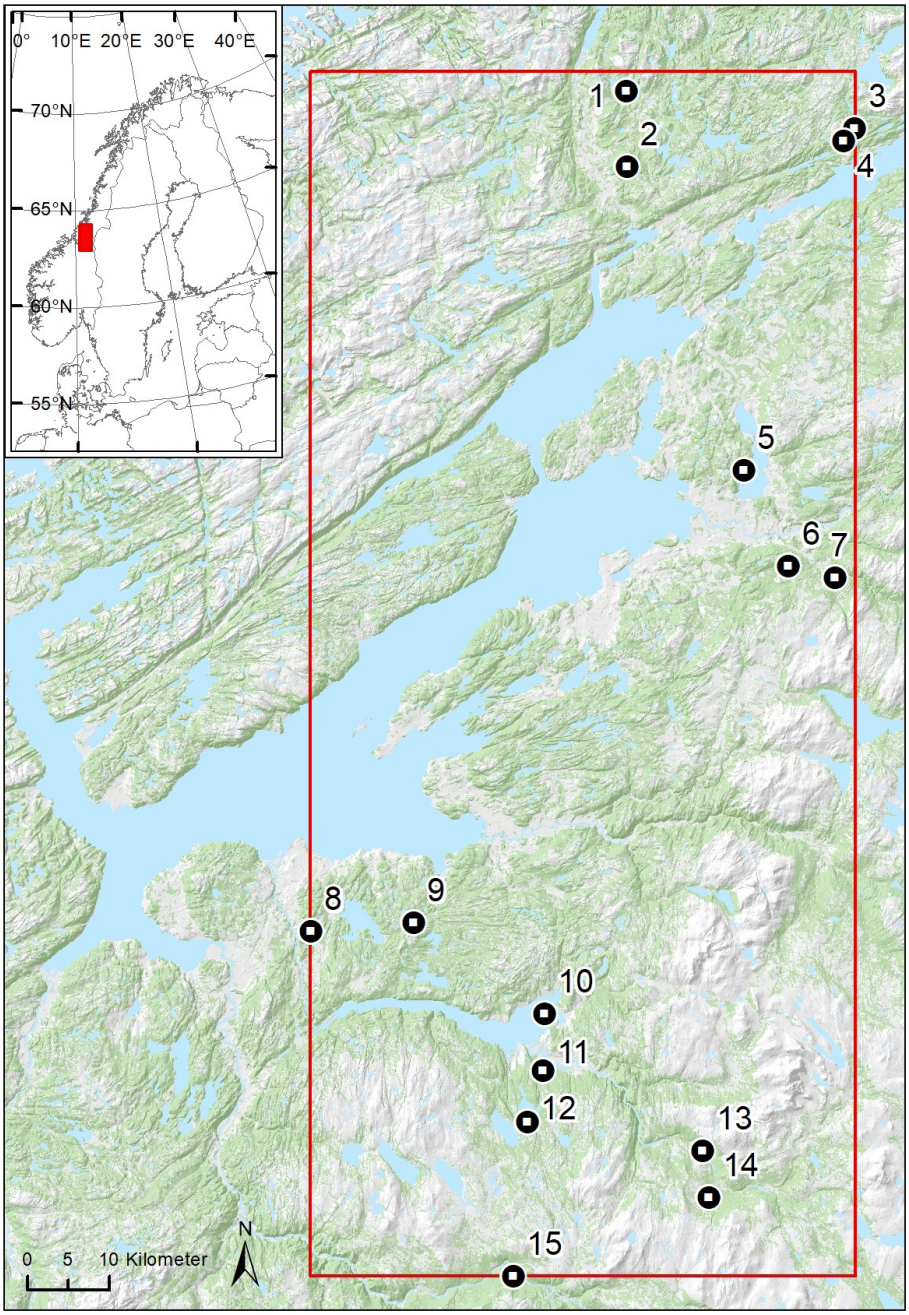


Fig. 1. Map of field sites in Trøndelag County, central Norway. Numbers refer to site numbers in Table 1.

species list is given in Appendix S1: Table S1. Vascular and bryophyte species densities (analogous to *species richness*) and mean bryophyte depth were calculated for each 0.25-m^2 quadrat. Locally calibrated biomass equation models were used to convert measured intercept frequencies into estimates of biomass (dry weight) as in Kolstad et al. (2018*b*).

A canopy cover index (Tichý 2015) was estimated for each vegetation sampling quadrat in the summer of 2016 (see Kolstad et al. 2018*a*) using multiple hemispherical pictures taken at

Table 1. Characteristics of the 15 field sites in Trøndelag, central Norway.

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

Notes: Site numbers correspond with the labels in Fig. 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. 2018*a*). 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. Abbreviation t indicates that the open plots were thinned; a.s.l. is above sea level.

Table 2. Characteristics of the two soil temperature datasets.

		Soil temperature loggers						
Dataset	Data types	Dates	No. days	No. sites	No. loggers	No. faulty loggers	Freq.	Key output analyses
Full year	Soil temp. only	5 May 2016–27 April 2017	344	15†	90	8‡	6–12 h	Seasonal variation
Summer	Soil temp. and vegetation	9 June 2017–6 August 2017	59	5	100	2§	1 h	Path analysis and diurnal variation

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

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 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 as a 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 (Appendix S1: 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 Appendix S1: 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*b*). We also included the first axis from a Bray-Curtis-based nonmetric multidimensional scaling (vegan package, metaMDS function; Oksanen 2018) to represent a gradient in the vascular plant communities that was strongly and positively associated with shrub biomass, that is, shrubbiness (NMDS1; Appendix S1: 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 (Appendix S1: 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 were 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 nonlinear relationships using bivariate scatterplots (Appendix S1: 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 nonsignificant 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 Appendix S1: Fig. S4). After removing nonsignificant 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 Fisher's 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 (<0.5) 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 (Fig. 2; Appendix S1: Fig. S5). Temporal variation in soil temperatures was large in summer and declined abruptly with the onset of constant snow cover in late November (Appendix S1: Fig. S5).

Herbivore exclusion lowered soil temperatures in summer (Figs. 2, 3; Appendix S1: Figs. S5 and S6), which has been shown in a previous study to be statistically significant (Kolstad et al. 2018*a*). In 2017, summer soil temperatures were on average 0.62°C (±0.28 standard error [SE]) higher in open plots compared to exclosures (Appendix S1: Fig. S6), and this cooling effect inside exclosures was stronger in late evening when soil temperatures were the highest (Appendix S1: 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, $\chi_1 = 3.642$, $P = 0.056$). Over the full year (344 d), the 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 $\chi_1 = 0.01$, $P = 0.924$; Fig. 3; Appendix S1: Fig. S9). The diurnal variation in summer soil temperatures was greater outside compared to inside exclosures (Appendix S1: 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 lines in Fig. 2). The three thinned sites (also highly productive) were even more extreme in this respect as exclosures

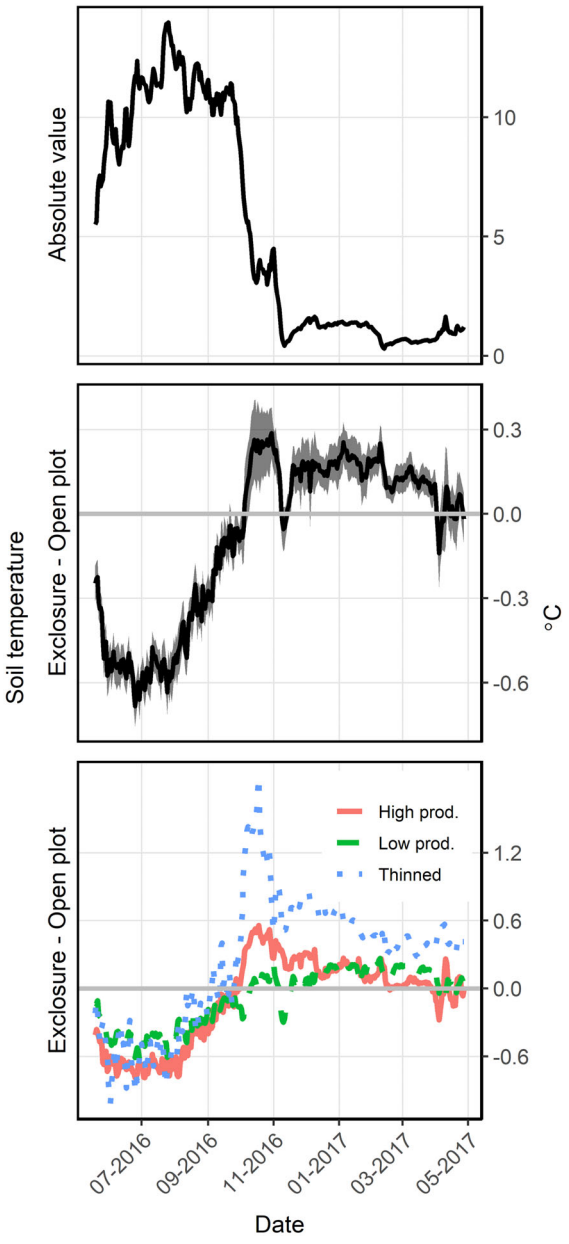


Fig. 2. Time series of mean daily soil temperatures from large herbivore exclosures and adjacent open plots. The top figure shows the mean (daily) soil temperatures ($n = 12$ un-thinned sites, irrespective of treatment). The bottom figure shows the shift in plot mean soil temperature (exclosure minus open plots) with ± 1.96 × 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: $n = 3$]).

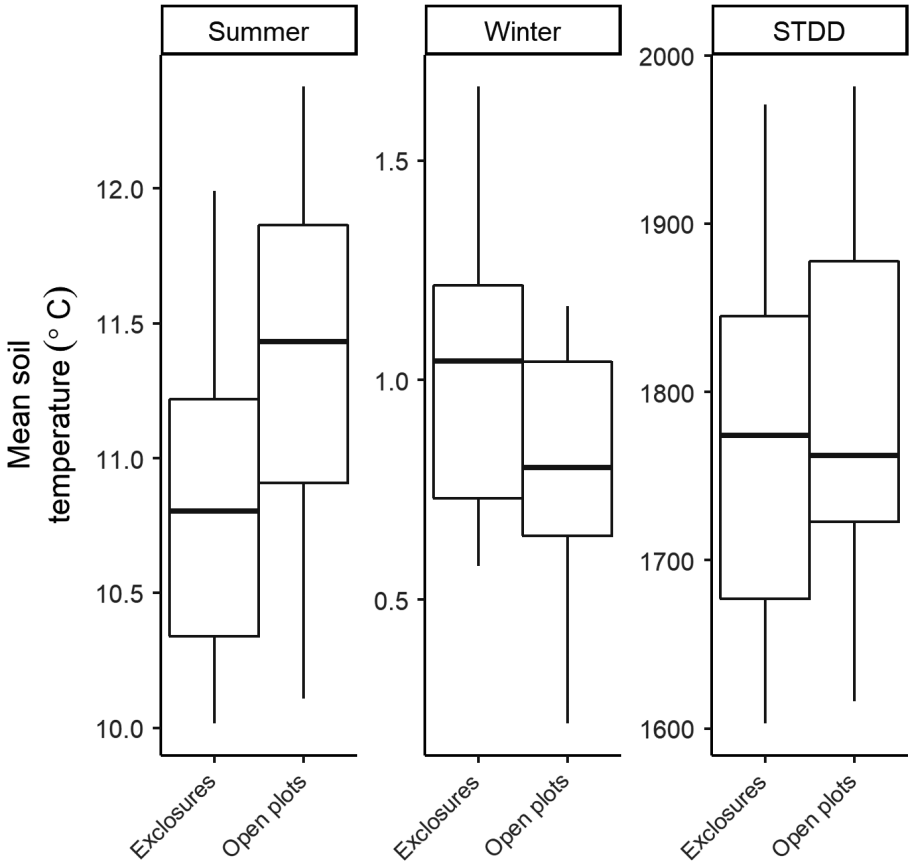


Fig. 3. Mean daily summer (July–August) and winter (January–March) soil temperatures and accumulated soil thawing degree days (STDD) over 344 d inside large herbivore exclosures and adjacent open plots (n = 12 sites).

were ~0.5°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 (Fig. 4; Appendix S1: Fig. 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 (Appendix S1: 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).

Discussion

Besides direct effects of feeding and trampling, large herbivores affect plant communities 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 have both direct and indirect effects on plant composition and species densities, although the direct effects are most prominent. This study builds toward 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. (2018*a*) 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

Table 3. Partial regression coefficients (standardized [std.] and raw), from path analysis exploring the direct and indirect effects of moose exclusion on plant communities.

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	<0.01	89	<0.001	***
NMDS1	Herbivore exclusion	−0.19	−0.22	0.07	92	0.001	**
Avenella flexuosa (g/m^2)	Herbivore exclusion	−0.27	−0.52	0.17	88	0.004	**
Avenella flexuosa (g/m^2)	Soil temperature (°C)	−5.12†	−5.57	1.82	88	0.003	**
Avenella flexuosa (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)	NMDS1	−0.62	−3.02	0.43	92	<0.001	***
Bryophytes (spp/plot)	Bryophyte depth (cm)	1.54†	1.32	0.26	87	<0.001	***
Bryophytes (spp/plot)	(Bryophyte depth)^2	−1.20†	−0.12	0.03	87	<0.001	***
Bryophytes (spp/plot)	Herb biomass (g/m^2)	0.86†	0.05	0.02	87	<0.001	**
Bryophytes (spp/plot)	(Herb biomass)^2	−0.57†	<0.01	<0.01	87	0.030	*
Correlated errors							
Vascular plants	Bryophytes		0.08		98	0.229	
Avenella flexuosa	Bryophyte depth		0.05		98	0.314	
Avenella flexuosa	Herb biomass		−0.23		98	0.011	*
NMDS1	Herb biomass		−0.44		98	<0.001	***
NMDS1	Avenella flexuosa		−0.09		98	0.182	
NMDS1	Bryophyte depth		−0.03		98	0.391	
Bryophyte depth	Herb biomass		−0.03		98	0.369	

Notes: Correlated errors are partial Pearson correlations coefficients. SE, standard error; df, degrees of freedom.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
† Note that standardised estimates will appear unreasonably high for parameters in quadratic models.

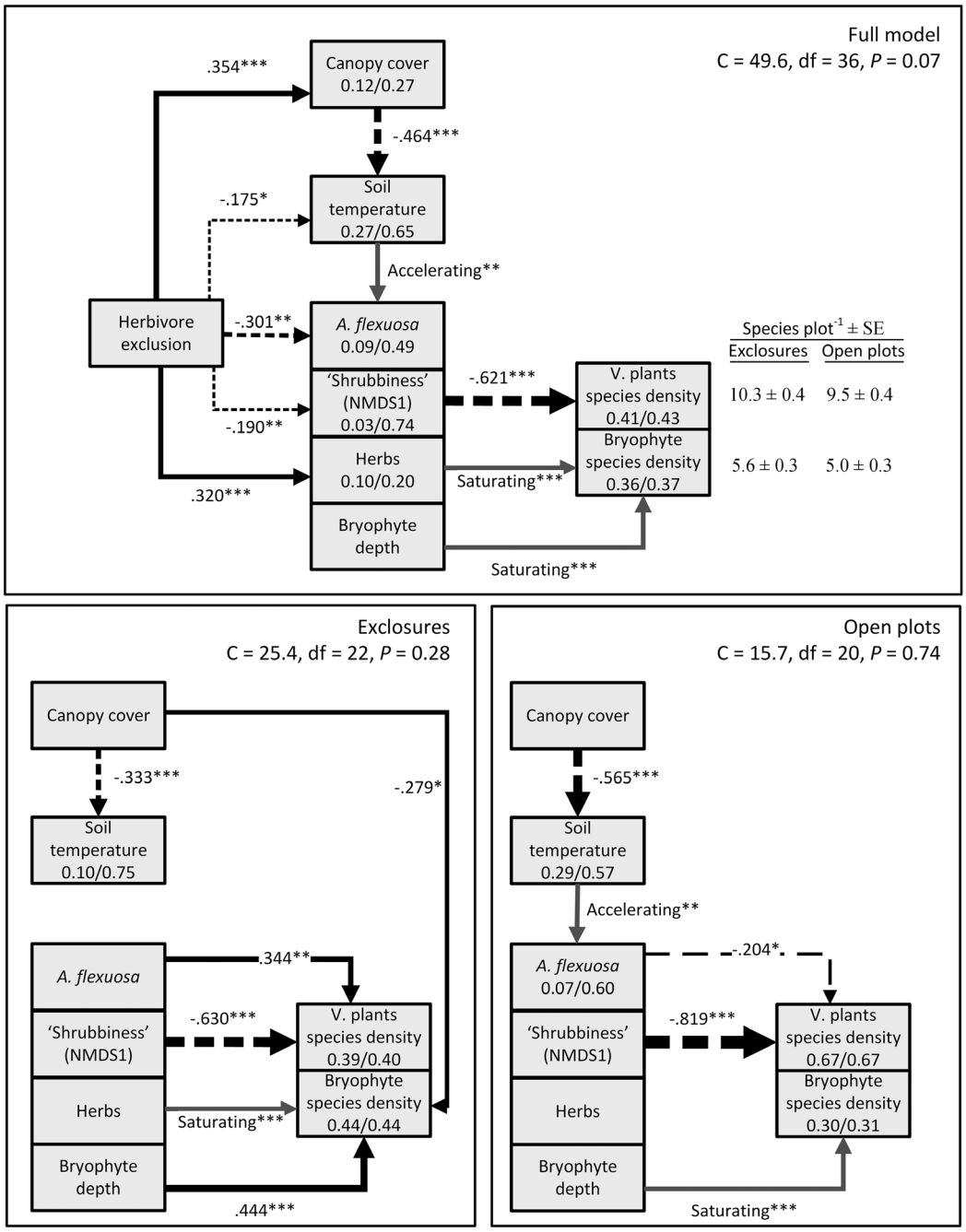


Fig. 4. Results from exploratory piecewise structural equation modeling. The full model (top) includes herbivore exclusion as a categorical exogenous variable, whereas the two sub-models (below) are built using data from only exclosures (left) or open plots (right). Solid and broken lines represent positive and negative relationships, respectively. Numbers on arrows are standardized partial regression coefficients, and the width of the arrows is scaled based on these, except for non-linear relationships (gray lines) which are described according to the shape of the relationship and with a preset arrow width. Asterisks indicate statistical significance (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). Numbers inside nodes are marginal and conditional R^2 values, respectively. Correlated errors were allowed (and no betas estimated) between the nodes that are grouped closely together.

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 in the short term (Ellis and Leroux 2017, Kolstad et al. 2018*a*).

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 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 hump-shaped 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 shrubbiness, leaving no unexplained variation that could be due to other

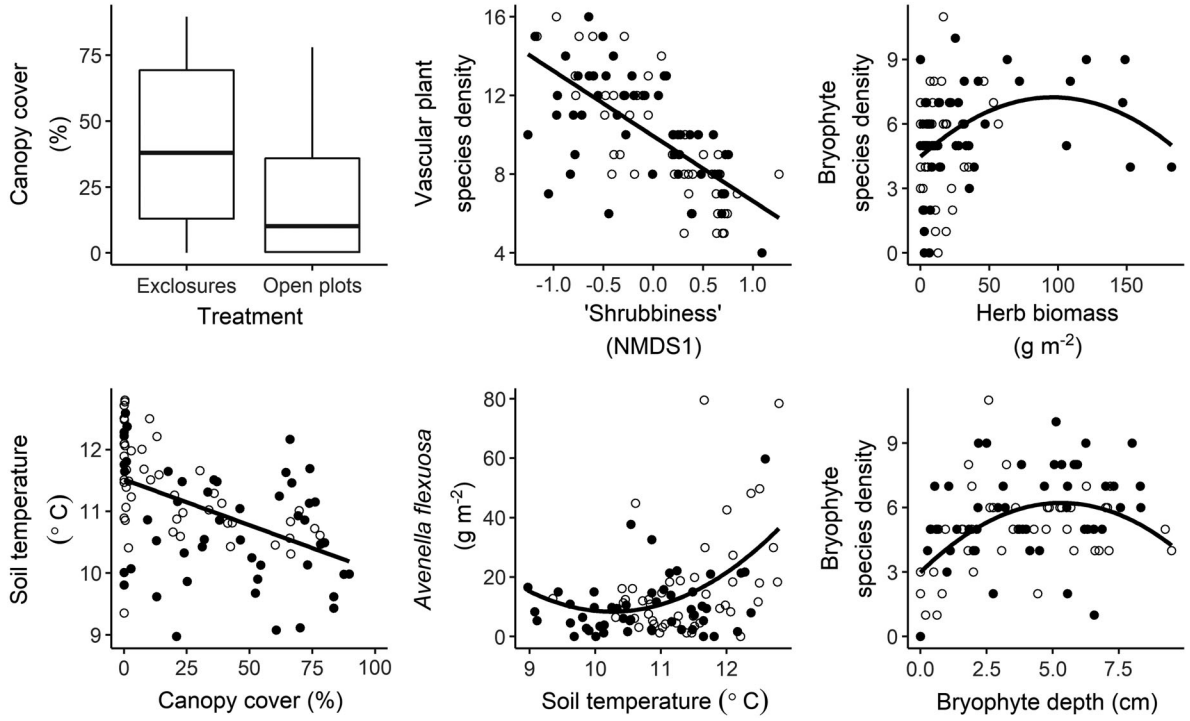


Fig. 5. Bivariate plots for selected relationships included in the path analysis (full model). Regression lines are from models refitted without covariates, using the lm() function in R and data at the subplot level. All relationships are statistically significant ($P < 0.05$) in mixed-effects models. Open circles are open plots; closed circles are herbivore exclosures.

herbivore effects, such as seed dispersal (Albert 2015, Boulanger 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. 2018*b*; see Bernes 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 moose-induced cooling 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 insulation) 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 reduced ground wind speeds and the added heat capacity of the larger biomass in the vegetation (especially in the trees; see Kolstad et al. 2018*b*). 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. 2).

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. (2018*a*) 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. 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. Vernalization, 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 exclosures also had lower diurnal soil temperature fluctuations in summer (Appendix S1: 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 yr 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 exclosures. We also showed that in order to obtain general and predictive theories for how large herbivores affect plant diversity (Olff and Ritchie 1998), path analysis is a valuable tool when multifactorial 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 plant 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?

Acknowledgments

We wish to thank Marc Daverdin for helping with fieldwork, for database management, and for making the map in Fig. 1, and Kristian Hassel from the NTNU University Museum for aiding with bryophyte identification. We also extend our gratitude to the numerous landowners who have let us use their forests for this long-term study. We thank Shawn Leroux and three anonymous reviewers for comments on a previous version of this manuscript. This study was funded by the Research Council of Norway (SUSTHERB 184036), the Norwegian Environmental Agency, and the county council of Trøndelag. The study was planned by ALK, JDMS, GA, RS, BJG, and EJS. Fieldwork was conducted by ALK, JDMS, and GA. Numerical analyses were conducted by ALK. ALK wrote the manuscript with input from all co-authors.

Literature Cited

Albert, A., et al. 2015. Seed dispersal by ungulates as an ecological filter: a trait-based meta-analysis. Oikos 124:1109–1120.

Andriuzzi, W. S., and D. H. Wall. 2017. Responses of belowground communities to large aboveground herbivores: Meta-analysis reveals biome-dependent patterns and critical research gaps. Global Change Biology 23:3857–3869.

Apollonio, M., R. Andersen, and R. Putman. 2010. European ungulates and their management in the 21st century. Cambridge University Press, Cambridge, UK.

Bai, E., S. Li, W. Xu, W. Li, W. Dai, and P. Jiang. 2013. A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. New Phytologist 199:441–451.

Beguin, J., D. Pothier, and S. D. Côté. 2011. Deer browsing and soil disturbance induce cascading effects on plant communities: a multilevel path analysis. Ecological Applications 21:439–451.

Bernes, C., et al. 2018. Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates. A systematic review. Environmental Evidence 7:1–32.

Bjørneraas, K., et al. 2011. Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. Wildlife Biology 17:44–54.

Boulanger, V., et al. 2017. Ungulates increase forest plant species richness to the benefit of non-forest specialists. Global Change Biology 24:e485–e495.

Bradford, M. A., B. Berg, D. S. Maynard, W. R. Wieder, and S. A. Wood. 2015. Understanding the dominant controls on litter decomposition. Journal of Ecology 104:229–238.

Brooker, R., and R. van der Wal. 2003. Can soil temperature direct the composition of high arctic plant communities? Journal of Vegetation Science 14:535–542.

Campbell, J. J. L., M. J. M. Mitchell, P. M. P. Groffman, L. M. Christenson, and J. P. Hardy. 2005. Winter in northeastern North America: a critical period for ecological processes. Frontiers in Ecology and the Environment 3:314–322.

Castro, H. F., A. T. Classen, E. E. Austin, R. J. Norby, and C. W. Schadt. 2010. Soil microbial community responses to multiple experimental climate change

drivers. Applied and Environmental Microbiology 76:999–1007.

Chu, C., M. Bartlett, Y. Wang, F. He, J. Weiner, J. Chave, and L. Sack. 2016. Does climate directly influence NPP globally? Global Change Biology 22:12–24.

Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113–147.

Danell, K., R. Bergström, L. Edenius, and G. Ericsson. 2003. Ungulates as drivers of tree population dynamics at module and genet levels. Forest Ecology and Management 181:67–76.

Davidson, E. A., E. Belk, and R. D. Boone. 1998. Soil water content and temperature as independent of confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biology 4:217–227.

Edenius, L., M. Bergman, G. Ericsson, and K. Danell. 2002. The role of moose as a disturbance factor in managed boreal forests. Silva Fennica 36:57–67.

Eichhorn, M. P., J. Ryding, M. J. Smith, R. M. A. Gill, G. M. Siriwardena, and R. J. Fuller. 2017. Effects of deer on woodland structure revealed through terrestrial laser scanning. Journal of Applied Ecology 54:1615–1626.

Ellis, N., and S. Leroux. 2017. Moose directly slow plant regeneration but have limited indirect effects on soil stoichiometry and litter decomposition rates in disturbed maritime boreal forests. Functional Ecology 31:790–801.

Grace, J. B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. Perspectives in Plant Ecology, Evolution and Systematics 2:1–28.

Grace, J. B. 2008. Structural equation modeling for observational studies. Journal of Wildlife Management 72:14–22.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292–1297.

Hidding, B., J.-P. Tremblay, and S. D. Côté. 2013. A large herbivore triggers alternative successional trajectories in the boreal forest. Ecology 94:2852–2860.

Jonasson, S. 1988. Evaluation of the point intercept method for the estimation of plant biomass. Oikos 52:101–106.

Kane, E. S., and J. G. Vogel. 2009. Patterns of total ecosystem carbon storage with changes in soil temperature in boreal black spruce forests. Ecosystems 12:322–335.

Kardol, P., I. A. Dickie, M. G. St. John, S. W. Husheer, K. I. Bonner, P. J. Bellingham, and D. A. Wardle. 2014. Soil-mediated effects of invasive ungulates on native tree seedlings. Journal of Ecology 102:622–631.

Kielland, K., and J. P. Bryant. 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. Oikos 82:377–383.

Kielland, K., J. P. Bryant, and R. W. Ruess. 1997. Moose herbivory and carbon turnover of early successional stands in interior Alaska. Oikos 80:25–30.

Koerner, S. E., et al. 2018. Change in dominance determines herbivore effects on plant biodiversity. Nature Ecology & Evolution 2:1925–1932.

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

Kolstad, A. L., G. Austrheim, E. J. Solberg and J. D. M. Speed. 2018*c*. Data from: Moose effects on soil temperatures, tree canopies and understory vegetation – a path analysis. Figshare. https://doi.org/10.6084/m9.figshare.7375958.v1

Kolstad, A. L., G. Austrheim, E. J. Solberg, A. M. A. Venete, S. J. Woodin, and J. D. M. Speed. 2018*a*. Cervid exclusion alters boreal forest properties with little cascading impacts on soils. Ecosystems 21:1027–1041.

Körner, C. 2006. Significance of temperature in plant life. Pages 44–66 *in* J. I. L. Morrison and M. D. Morecroft, editors. Plant growth and climate change. Blackwell Publishing Ltd, Hoboken, New Jersey, USA.

Kuijper, D. P. J., B. Jedrzejewska, B. Brzeziecki, M. Churski, W. Jedrzejewski, and H. Zybura. 2010. Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieza Primeval Forest, Poland. Journal of Vegetation Science 21:1082–1098.

Kumar, P., H. Y. H. Chen, S. C. Thomas, and C. Shahi. 2018. Linking resource availability and heterogeneity to understorey species diversity through succession in boreal forest of Canada. Journal of Ecology 106:1266–1276.

Lavsund, S., T. Nygrén, and E. J. Solberg. 2003. Status of moose populations and challenges to moose management in Fennoscandia. Alces 39:109–130.

Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

Magnusson, A., et al. 2017. glmmTMB: generalized Linear Mixed Models using Template Model Builder. R package version 0.1.3. https://github.com/glmmTMB

Mathisen, K. M., F. Buhtz, K. Danell, R. Bergström, C. Skarpe, O. Suominen, and I. L. Persson. 2010.

Moose density and habitat productivity affects reproduction, growth and species composition in field layer vegetation. Journal of Vegetation Science 21:705–716.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73:2059–2075.

Morecroft, M. D., and J. S. Paterson. 2006. Effects of temperature and precipitation changes on plant communities. Pages 146–161 *in* J. I. L. Morrison and M. D. Morecroft, editors. Plant growth and climate change. Blackwell Publishing Ltd, Hoboken, New Jersey, USA.

Nuttle, T., T. E. Ristau, and A. A. Royo. 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: Forest understoreys reflect past deer density treatments for at least 20 years. Journal of Ecology 102:221–228.

Oksanen, J., et al. 2018. Vegan: community Ecology Package. R package version 2.5-2. https://CRAN.R-project.org/package=vegan

Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution 13:261–265.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2017. nlme: linear and nonlinear mixed effects models. R package version 3.1-131. https://CRAN.R-project.org/package=nlme

Prescott, C. E. 2010. Litter decomposition: What controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry 101:133–149.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. Agricultural and Forest Meteorology 169:156–173.

Ritchie, M. E., D. Tilman, and J. M. H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology 79:165–177.

Rydgren, A. K., R. H. Økland, and G. Hestmark. 2004. Disturbance severity and community resilience in a boreal forest. Ecology 85:1906–1915.

Sanders-DeMott, R., R. McNellis, M. Jabouri, and P. H. Templer. 2018. Snow depth, soil temperature and plant–herbivore interactions mediate plant response to climate change. Journal of Ecology 106:1508–1519.

Solberg, E. J., C. M. Rolandsen, R. Eriksen, and R. Astrup. 2012. Fra Edens hage til vredens druer: Elgens beiteressurser i nord og i sør. Hjorteviltet 2012:22–28 [In Norwegian.].

Soudzilovskaia, N. A., P. M. van Bodegom, and J. H. C. Cornelissen. 2013. Dominant bryophyte control over high-latitude soil temperature fluctuations predicted by heat transfer traits, field moisture regime and laws of thermal insulation. Functional Ecology 27:1442–1454.

Speed, J. D. M., G. Austrheim, A. J. Hester, E. L. Meisingset, A. Mysterud, J.-P. Tremblay, and E. J. Solberg. 2014. General and specific responses of understory vegetation to cervid herbivory across a range of boreal forests. Oikos 123:1270–1280.

Speed, J. D. M., G. Austrheim, A. J. Hester, E. J. Solberg, and J.-P. Tremblay. 2013. Regional-scale alteration of clear-cut forest regeneration caused by moose browsing. Forest Ecology and Management 289:289–299.

Speed, J. D. M., G. Austrheim, A. L. Kolstad, and E. J. Solberg. 2019. Long-term changes in northern large-herbivore communities reveal differential rewilding rates in space and time. PLOS ONE 14: e0217166.

Suominen, O., I. Persson, K. Danell, R. Bergström, and J. Pastor. 2008. Impact of simulated moose densities on abundance and richness of vegetation, herbivorous and predatory arthropods along a productivity gradient. Ecography 31:636–645.

Telfer, E. S. 1984. Circumpolar distribution and habitat requirements of moose (*Alces alces*). Pages 145–182 *in* D. Gill, R. Olson, R. Hastings, and F. Geddes, editors. Northern ecology and resource management: memorial essays honouring Don Gill. University of Alberta Press, Edmonton, Alberta, Canada.

Tichý, L. 2015. Field test of canopy cover estimation by hemispherical photographs taken with a smartphone. Journal of Vegetation Science 27:427–435.

Wam, H. K., T. Histøl, L. Nybakken, E. J. Solberg, and O. Hjeljord. 2016. Transient nutritional peak in browse foliage after forest clearing advocates cohort management of ungulates. Basic and Applied Ecology 17:252–261.

Wardle, D. A., G. M. Barker, G. W. Yeates, K. I. Bonner, and A. Ghani. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecological Monographs 71:587–614.

Data Availability

All data used in this manuscript are publicly available at figshare (Kolstad et al. 2018*c*) https://doi.org/10.6084/m9.figshare.7375958.v1

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2966/full