

Cool as a moose: How can browsing counteract climate warming effects across boreal forest ecosystems?

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Abstract. Herbivory has potential to modify vegetation responses to climatic changes. However, climate and herbivory also affect each other, and rarely work in isolation from other ecological factors, such as plant–plant competition. Thus, it is challenging to predict the extent to which herbivory can counteract, amplify, or interact with climate impacts on ecosystems. Here, we investigate how moose modify climatic responses of boreal trees by using experimental enclosures on two continents and modeling complex causal pathways including several climatic factors, multiple tree species, competition, tree height, time, food availability, and herbivore presence, density, and browsing intensity. We show that moose can counteract, that is, “cool down” positive temperature responses of trees, but that this effect varies between species depending on moose foraging preferences. Growth of preferred deciduous trees was strongly affected by moose, whereas growth of less preferred conifers was mostly driven by climate and tree height. In addition, moose changed temperature responses of rowan in Norway and balsam fir in Canada, by making fir more responsive to temperature but decreasing the strength of the temperature response of rowan. Snow protected trees from browsing, and therefore moose “cooling power” might increase should a warming climate result in decreased snow cover. Furthermore, we found evidence of indirect effects of moose via plant–plant competition: By constraining growth of competing trees, moose can contribute positively to the growth of other trees. Our study shows that in boreal forests, herbivory cooling power is highly context dependent, and in order to understand its potential to prevent changes induced by warming climate, species differences, snow, competition, and climate effects on browsing need to be considered.

Key words: birch; boreal forest; browsing; climate changes; fir; moose; pine; rowan; spruce; structural equation modeling

INTRODUCTION

As herbivores control multiple ecosystem properties that affect climate, including albedo, carbon cycling, and forest fire prevalence, it has been suggested that herbivory management can play a crucial role in mitigating global warming (Schmitz et al. 2014, Crooms et al. 2018, Schmitz et al. 2018). Large vertebrate herbivores can also act as a buffer of the impacts of climate change by counteracting potential vegetation changes induced by warming climate, also referred to as a “cooling” effect (Fisichelli et al. 2012). Empirical studies have shown

support on the cooling effect in arctic and alpine contexts (Olofsson et al. 2009, Speed et al. 2011, 2012, Bräthen et al. 2017, Vuorinen et al. 2017), but its applicability in other regions is poorly understood. As plant species vary in their herbivory resistance and responses, it is also not clear how cooling works at the plant community level and how it shapes plant–plant competition. To complicate the story even further, climatic changes might affect herbivory pressure by changing forage amount and composition, herbivore population dynamics, or browsing intensity (Niemelä et al. 2001, Turunen et al. 2009, Rempel 2011).

As climate plays a major role for tree growth, its changes are expected to have pronounced effects on boreal forests (Ruckstuhl et al. 2007, Soja et al. 2007, Brecka et al. 2018). Some studies predict increased

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biomass production (Boisvenue and Running 2006, D'orangeville et al. 2016), whereas others highlight the increasing frequency of stress events (Brecka et al. 2018), such as drought (Peng et al. 2011), loss of protective snow layer (Blume-Werry et al. 2016), and forest fires (Soja et al. 2007, de Groot et al. 2013), making overall effects challenging to model. In addition, plant growth is rarely only driven by abiotic factors: herbivory shapes boreal forests by affecting the growth rate, successional pathways, plant competition, and community composition (Hidding et al. 2013, Bernes et al. 2018, Kolstad et al. 2018a, b, Vuorinen et al. 2020). Boreal forest ecosystems are networks of biotic and abiotic factors that cannot be regarded in isolation (Fig. 1), and it is increasingly important to understand these networks for providing predictions on future forestry and forest carbon storage potential under a warmer climate (Soja et al. 2007, Brecka et al. 2018).

Here, we use replicated enclosure experiments to investigate the cooling potential of moose on boreal tree growth at early successional stages on two continents, while considering the ecological pathways regulating this potential. Early succession determines the composition of mature forests (Birch et al. 2019), and it is the phase where ungulate herbivory has most potential to affect climate responses as trees are at reachable heights

(Kolstad et al. 2018a). Thus, it is a key stage for understanding additive, counteracting and interactive effects of climate and herbivory on boreal forest tree growth, composition, and structure. To capture the complexity of the system, we modeled networks including several climate variables, multiple tree species, time effects, tree height, and plant–plant competition, as well as herbivore presence, density, and browsing intensity. We hypothesize that moose cooling power (1) exists for preferred species but not for less preferred species, (2) is, at least partly, realized indirectly via moose effect on tree height (moose keep tree height low and the low height keeps growth rates low), and (3) is weakened or counteracted by decreased plant–plant competition. In addition, we hypothesize that (4) increased snow precipitation decreases browsing pressure, whereas (5) temperature increases it for preferred species (that respond strongly to temperature) but decreases it for less preferred species.

METHODS

Study sites were located in Trøndelag, Vestfold & Telemark, Viken, and Innlandet counties in Norway (59–64° N, 8–12° E), and in Matane, Chic-Chocs, and ZEC Casault wildlife areas in Québec, Canada (48–49° N, 67–66° W; Appendix S1: Fig. S1). The main ungulate

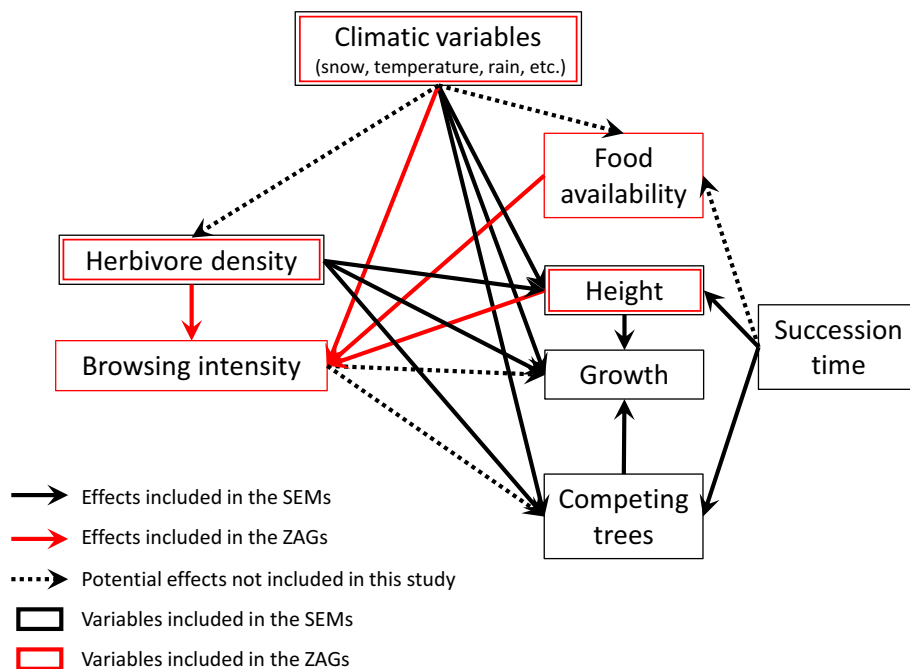


FIG. 1. Schematic illustration of potential effects in the study system, separated by two analysis types applied; structural equation models (SEMs) in black and zero-inflated models (ZAGs) in red. Note that moose density refers to binomial 0 and >0 moose density for SEMs, but to continuous density estimates for ZAGs. Food availability refers to the amount of edible forage available for moose. Browsing intensity refers to the proportion of twigs browsed. Height refers to the height of the target trees. Succession time refers to the number of years since clear-cut. Competing trees refer to interspecific competition, represented by sum of heights of the tree individuals potentially competing with the target trees. Climatic variables, herbivore density, succession time, and food availability are explanatory variables; browsing intensity and growth response variables; and height and competition are serving as both response and explanatory variables.

browser in the study sites in both countries is moose (*Alces alces*, Norway; *Alces americanus*, Canada), but roe deer (*Capreolus capreolus*; Norway), red deer (*Cervus elaphus*; Norway), and white-tailed deer (*Odocoileus virginianus*; Canada) are also present.

Tree growth was followed at 47 clear-cut sites over 11 yr in Norway and at 15 sites over 7 yr in Canada (Appendix S1: Table S1). Study designs were conducted independently of each other and applied somewhat different field methods. Each site consisted of an ungulate exclusion plot, protected by 3- and 2.5-m-tall fences in Canada and Norway, respectively, and an open, browsed plot. Plots were 20 × 20 m in Norway and 14 × 28.5 m in Canada. Each plot included four circular subplots with a radius of 2 m in Norway and 12 circular subplots with a radius of 1.13 m in Canada. (For details on the fence designs, see Appendix S1: Supplementary Methods.) Within these subplots, tree heights were measured late spring each year after the snowmelt. At the same time, browsing intensity on each measured tree was estimated by assessing the proportion of twigs browsed on both continents. In this study, we excluded data from trees >3 m, as these have started to escape moose browsing.

In Norway, up to four individuals of each tree species were randomly selected from each subplot for measurements. These individuals were followed across years and thus individual growth rates could be calculated. In addition, all tree individuals present within subplots were counted in 50-cm height classes for each species. In Canada, all individuals of all species were measured within each subplot, but individuals were not followed across years and thus calculated growth values represent average growth rate across individuals at the subplot level. Here, we studied four species (or species groups) in each country: *Sorbus aucuparia* L., *Betula pubescens* Ehrh., *Pinus sylvestris* L., and *Picea abies* (L.) H. Karst. in Norway, and *Sorbus americana* Marshall, *Betula* spp. (mostly *B. papyrifera* Marshall and some *B. alleghaniensis* Britton), *Abies balsamea* (L.) Mill and *Picea* spp. (mostly *P. glauca* (Moench) Voss and some *P. mariana* (Miller) Britton, Sterns & Poggenburgh) in Canada. These species and species groups (rowans, birches, pine/fir, spruces) correspond to each other functionally across continents, and moose prefer them as forage in descending order as presented above. Tree measurements resulted in 2,109 height-increment observations in Canada and 14,489 in Norway (Appendix S1: Table S1). In addition to the individuals of the target species (and species groups), data allowed for calculating the sum of heights of individuals of all other tree species in each plot to account for potential interspecific plant–plant competition and facilitation.

Daily temperature and precipitation data were obtained from the Norwegian Meteorological Institute's MET database (Lussana et al. 2016, 2018) for Norway, and the climate monitoring program (PSC) of the Ministry of Sustainable Development, Environment and Climate Change (MDDELCC 2018) for Canada. MET

data are based on modified optimal interpolation from weather stations with 1 × 1 km grid cells. PSC data are based on ordinary Kriging interpolation from manned and unmanned weather stations with a 0.1° resolution. Temporally, the data sets cover the whole study period. Based on the temperature and precipitation values, growth period mean temperature (June–September), growth period precipitation and winter snow–water equivalent were calculated for each year. For minimum, maximum, and average values for these variables, see Appendix S1: Table S1.

Moose densities in 2009 and 2015 for each Norwegian municipality were taken from (Speed et al. 2019), and the reports of Ministère des Ressources naturelles et de la Faune provided estimates from aerial surveys for 2010 (Chic-Chocs; Dorais and Lavergne 2010) and 2012 (Matane, ZEC Casault; Lamoureux et al. 2012) in Canada. We estimated the available moose forage amount by ranking all tree species present in subplot into moose forage preference classes, based on the literature (Belovsky 1981, Hörnberg 2001, Månsson et al. 2007) and our own experience from the study sites (Appendix S1: Table S2). Then, by multiplying the number of individuals of each species with given rank number, we obtained a food availability index (FAI) for each subplot (see also Månsson et al. 2007).

As complex ecological systems cannot readily be described by simple (univariate) models (Grace et al. 2010), we applied structural equation models (piecewise SEMs), that can combine multiple predictors and response variables into one model network (Lefcheck 2016). Separate models were developed for each country and each target species/species group. The following a priori (linear mixed effects) full submodels were defined: (1) annual tree growth of the target species explained by growth period temperature, precipitation, and snow–water equivalent, ungulate exclusion, tree height of the target species, and competition with other trees, represented by the sum of the heights of the all other tree individuals but the individuals of the target species in each subplot (for full species list, see Appendix S1: Table S2); (2) tree height of the target species in a given year explained by the number of years since clear-cutting (called “succession time” from now on), long-term average growth-period temperature, precipitation and snow–water equivalent across all years, and ungulate exclusion; and (3) competition explained by succession time, long-term average growth period temperature, precipitation, and snow–water equivalent across all years, and ungulate exclusion. These effects are illustrated in Fig. 1 with black arrows.

To account for typical optima in species' responses, each full submodel included potential quadratic terms of temperature, snow and tree height, and interactions between ungulate exclusion and temperature and ungulate exclusion and snow. Predetermined correlations for these models can be seen in Appendix S1: Supplementary Methods, and correlations for all explanatory variables in Appendix S1: Fig. S2. Nonsignificant effects

were dropped, starting from the least significant until only significant variables remained (exploratory SEM approach; see final model structures in Appendix S1: Table S4). Models were run separately for each species and country. Continuous first-order autoregressive correlation structures AR(1) were built in every model to account for temporal autocorrelation, and trees nested within subplots and within sites were accounted for as random factors (three-way nested term in a priori linear mixed-effects models).

For all SEMs, model assumptions were fulfilled (see Appendix S1: Table S3 for model R^2 -values and Fisher's test results for global goodness of fit). To visualize the strength of effects in SEMs (Fig. 2), we used R^2 differences between the full final model and a model without the variable in question, thus quantifying amount of variation explained by each variable (as we detected quadratic effects and interactions, model coefficient estimates could not be used to describe the response strength; Fairchild et al. 2009).

Ideally, all factors presented in Fig. 1 could be analyzed in one SEM. However, as browsing was zero inflated (most trees were not browsed), we cannot use it as a response variable in piecewise SEM. Furthermore, it cannot be used as a simple explanatory variable because it was collinear with climate variables. Instead, we constructed zero-inflation hurdle models with separate gamma and Bernoulli parts (zero-altered gamma, ZAG; Zuur and Leno 2016) to test the effects of temperature, rain, snow, moose density, tree height, and food availability on browsing intensity. These effects are visualized in Fig. 1 as red arrows. In Canada, we only had moose density estimates from one year for each region, with no temporal variation, whereas in Norway we used linear interpolation to estimate moose density in each year.

All analyses were carried out within the R environment (R version 3.5.1, R Core Team, R Foundation for Statistical Computing, Vienna, Austria). For SEMS, we used the piecewiseSEM-package that admits random factors (Lefcheck et al. 2016). As we ran eight SEMs and eight ZAG models, an alpha level of 0.01 was applied.

RESULTS

For four species, growth increased linearly with temperature: a warming of 1°C resulted in a 7.3 cm (± 1.4 SE) increase of annual growth for rowan, 7.5 cm (± 1.6 SE) for birch and 6.4 cm (± 1.4 SE) for spruce in Canada, and 1.1 cm (± 0.3 SE) for birch in Norway (Figs. 2, 3; Tables 1, 2). However, decreasing and quadratic trends were also observed: pine in Norway responded negatively to temperature as a warming of 1°C resulted in a 1.5 cm (± 0.3 SE) decrease of annual growth. Spruce in Norway responded quadratically, with highest growth rates at high and low temperatures. Observed snow responses were positive or quadratic (Appendix S1: Fig. S3; Tables 1, 2): a 100-mm/yr increase in snow–water equivalent resulted in an annual

growth increase of 2.1 cm (± 0.5 SE) and 2.7 cm (± 0.6 SE) for pine and spruce in Norway, respectively, whereas fir in Canada and birch in Norway responded quadratically, expressing highest growth rates at intermediate snow–water equivalent values. Only one significant effect of annual rain on growth was observed (for pine in Norway), but long-term rain in Norway negatively affected the height of three species (Fig. 2, Tables 1, 2).

Herbivore presence lowered the annual growth of rowan and birch in Canada, and birch and pine in Norway by 12.0 cm (± 2.0 SE), 12.5 cm (± 2.1 SE), 7.9 cm (± 0.8 SE), and 3.3 cm (± 0.6 SE), respectively. In addition, we observed interactive effects of herbivore presence and temperature on rowan growth in Norway, and on fir growth in Canada (Figs. 2, 3; Tables 1, 2), and an interactive effect of herbivore presence and snow on rowan growth in Norway (Appendix S1: Fig. S3; Tables 1, 2). There were no herbivore effects on spruce growth in either country.

In Norway, herbivore presence limited the height of rowan, birch, and pine, which reflected on growth as an additional, indirect negative effect (because height had a direct positive effect on growth; Fig. 2). However, in the cases of rowan and fir in Canada and birch and pine in Norway, herbivore presence also lowered the growth of competing trees, resulting in a positive indirect, cascading effect on growth (because competition had a direct negative effect on growth).

Along with moose density, tree height, and food availability, browsing pressure was affected by climatic variables in several cases (Appendix S1: Fig. S4, S5; Appendix S1: Table S5). In general, increasing snow lowered both the likelihood and intensity of browsing (Appendix S1: Fig. S5), whereas increasing temperatures increased browsing on rowans, but for coniferous species, results were mixed (Appendix S1: Fig. S4).

DISCUSSION

By modeling multiple ecological pathways in boreal ecosystems on two continents, we have shown evidence of a cooling effect of moose. However, this effect is highly dependent on other ecosystem factors and the tree species in question. In comparison to climatic factors, herbivore presence explained more variation in growth of preferred forage species than in less preferred species in both continents. Herbivore presence also lowered the growth of preferred species more than that of less preferred species. In addition, indirect herbivore effects, operating via plant–plant competition and tree height, were observed, as were climatic effects mediating browsing. Our results thus show how the ability of browsing to cool the growth of trees in a warmer climate (Fischelli et al. 2012) varies with ecological context.

Fast-growing deciduous species may be more responsive to climatic factors than trees with conservative growth strategies, such as conifers (Way and Oren 2010), and thus climate change might have pronounced effects

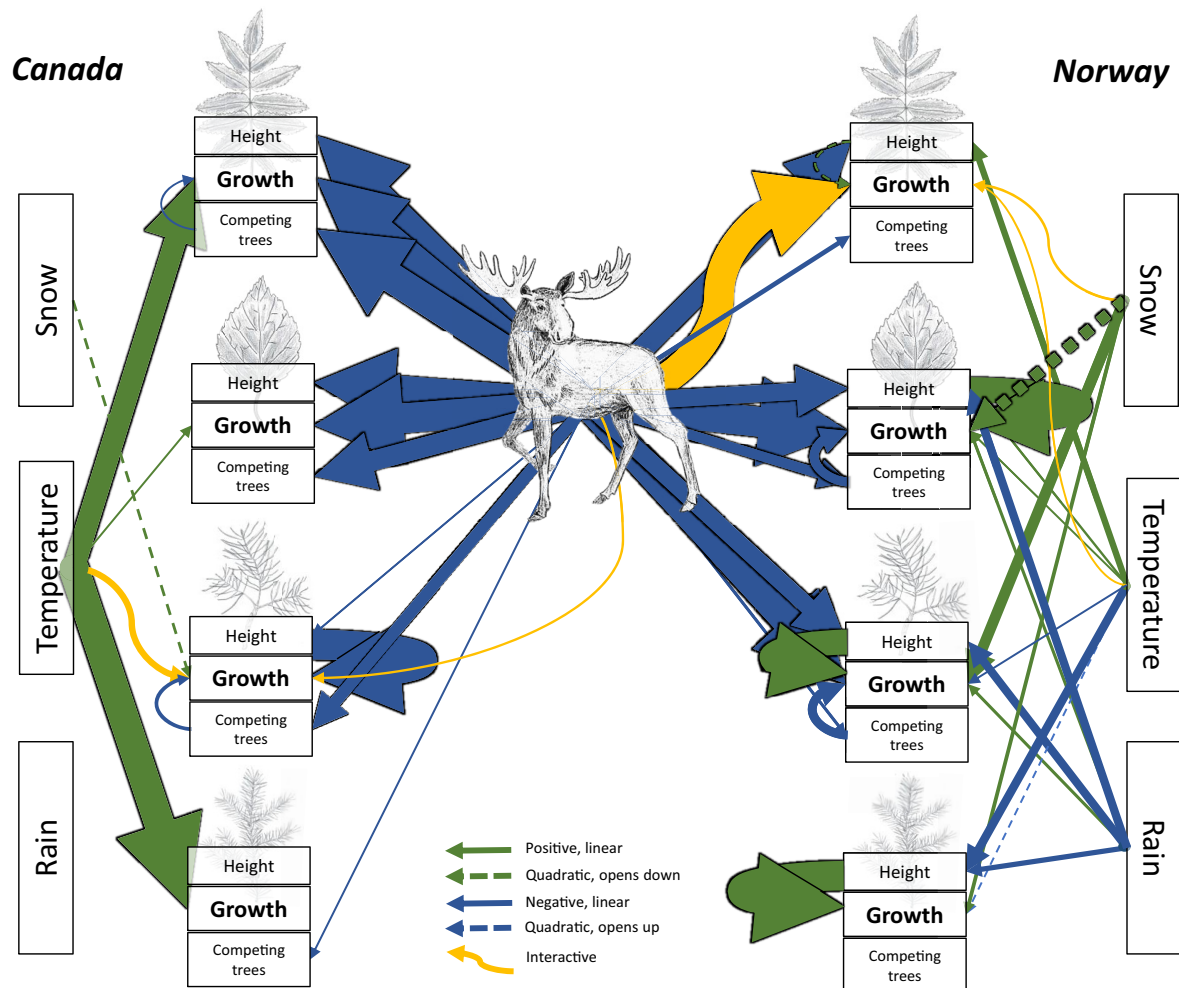


FIG. 2. Visualization of SEMs with significant effects presented as arrows. Arrow size represents R -squared contribution of the variable in question (for interactions, R -square contribution was defined separately for both terms). Sizes were scaled within species by giving the significant explanatory variable that explained least variation a set minimum size and by giving the significant explanatory variable that explained most variation a set maximum size. Thus, individual arrow sizes are comparable within species, but not between species. Species are indicated as background images (from top to bottom: rowan, birch, fir/pine, spruce). Quadratic effects are separated based on response curve ($y = ax^2$) shape: When a is positive, the parabola opens up; when a is negative, the parabola opens down. Competing trees refer to interspecific competition, represented by sum of heights of the tree individuals potentially competing with the target trees.

on boreal forest composition (Ruckstuhl et al. 2007, Fisichelli et al. 2012). In our study, the strongest positive temperature effects were also observed for deciduous species in Canada. However, as we hypothesized (Hypothesis 1), deciduous trees were also the species with higher sensitivity to moose cooling (Fig. 3), likely because of higher browsing intensity and likelihood (Appendix S1: Fig. S5). Taking into account moose forage preferences (Belovsky 1981, Pastor and Naiman 1992, Hörnberg 2001, Månsson et al. 2007), it is possible that herbivory could balance the competitive advances brought to deciduous species by global warming, preventing them from taking over in succession. Benefits from higher temperatures for preferred forage species are likely to be lower if browsing is affected by other

climatic factors: we showed that browsing pressure increased with temperature for rowan, and decreased with snow cover for rowan and birch (see also Norden-gren et al. 2003), whereas trends for coniferous species were weaker or nonexistent (Appendix S1: Figs. S4, S5; note, however, that if climate change results in increased snow cover, exposition effect will not realize). These results give some support to our Hypotheses 4 (on the protective effect of snow) and 5 (on the varying effects of temperature), but show that the effects are species dependent.

We expected that moose would change competitive dynamics by directly decreasing competition between trees (Hypothesis 3). For birch and pine in Norway, and for fir and rowan in Canada, we found that herbivory

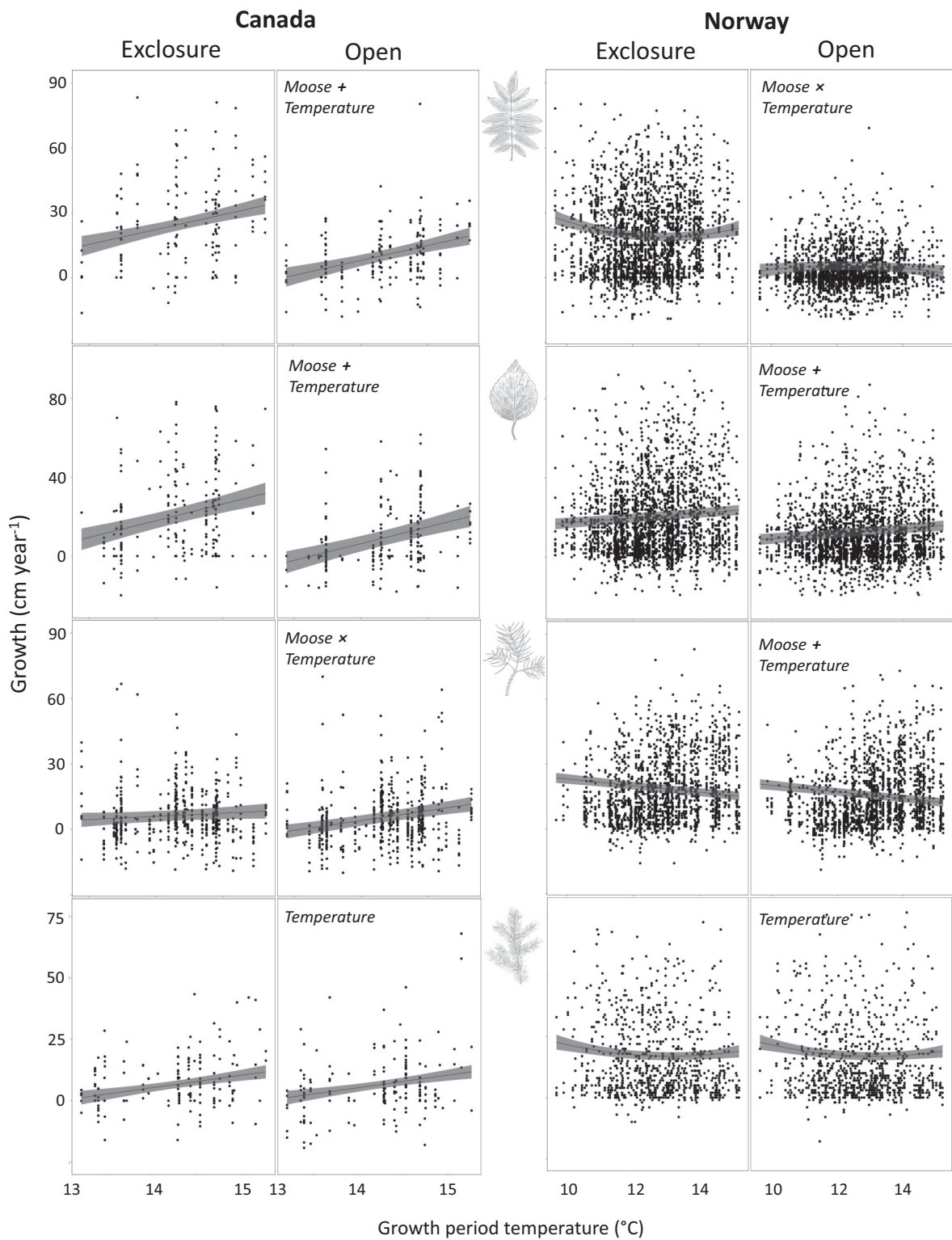


FIG. 3. Tree growth response to temperature at excluded and open sites, presented separately for each species. Species are indicated as background images (from top to bottom: rowan, birch, fir/pine, spruce). Significant herbivore and temperature effects are written on the right panels with italics.

TABLE 1. Model coefficients (estimates [Est.], SEs, dfs, critical values [Crit. val.], *P* values, and standard estimates [Std. est.]) for significant effects that were retained in the SEMs for Canada, presented for each species and species groups.

	Resp	Pred	Est.	SE	df	Crit. val.	<i>P</i>	Std. est.
Rowan	G	Exclosure	−12	2.0	94	−5.9	<0.0001	−0.3
	G	Temperature	7.3	1.4	225	5.2	<0.0001	0.3
	G	Competition	−0.47	0.15	225	3.1	0.0023	0.2
	H	Succession	15.5	1.1	226	14	<0.0001	0.5
	H	Exclosure	−20.3	4.2	94	−4.9	<0.0001	−0.3
	C	Succession	277.2	21.5	226	12.9	<0.0001	0.4
	C	Exclosure	−399.5	87.7	94	−4.6	<0.0001	−0.3
Birch	G	Exclosure	−12.5	2.1	153	−5.9	<0.0001	−0.3
	G	Temperature	7.5	1.6	243	4.7	<0.0001	0.2
	H	Succession	12.5	1.3	245	9.9	<0.0001	0.3
	H	Exclosure	−26.4	4.8	153	−5.5	<0.0001	−0.3
	C	Succession	241.4	19.7	245	12.2	<0.0001	0.3
	C	Exclosure	−422.4	102	153	−4.1	0.0001	−0.3
	C	Exclosure	−62.5	18.8	313	−3.3	0.001	−2.1
Pine/fir	G	Temperature	0.6	1.1	790	0.6	0.569	0
	G	Snow	28.23	8.32	790	3.4	0.0007	1.1
	G	Height	−16.32	1.86	790	−8.8	<0.0001	−0.3
	G	Competition	0.28	0.09	790	3.3	0.001	0.1
	G	Snow ²	−0.04	0.01	790	−3.6	0.0004	−1.2
	G	Exclosure:Temperature	4.3	1.3	790	3.3	0.0011	2
	H	Succession	1.4	0.4	795	3.3	0.0012	0.1
	H	Exclosure	−5.5	2.4	313	−2.3	0.0029	−0.1
	C	Succession	158.1	10.1	795	15.6	<0.0001	0.3
	C	Exclosure	−229.2	44.2	313	−5.2	<0.0001	−0.2
	G	Temperature	6.4	1.4	212	4.7	<0.0001	0.2
	H	Succession	3.8	0.9	214	4.1	0.0001	0.1
	C	Succession	154.4	17.4	214	8.9	<0.0001	0.3
	C	Exclosure	−304.2	90.2	113	−3.4	0.001	−0.2

Notes: Response codes G, H, and C stand for growth, height, and competition. Temperature_av and Rain_av represent averages across years, used to explain tree height and competition instead of annual averages. For full model output, see Appendix S1: Table S5.

presence indeed decreased the height of competing trees, which, in turn, positively affected the growth of individual trees. Interestingly, these indirect positive effects were not strongest for less preferred species, as could be expected (Pastor and Naiman 1992). Moose effects on plant–plant interactions might also explain why temperature response of fir in Canada was stronger in the presence of moose: firs in browsed plots might respond to temperature more strongly than firs in exclosures, where growth is constrained by plant–plant competition and shelter provided by other trees protects firs from extreme cold events. This effect may be amplified by selective moose browsing: during the warm years, moose prefer deciduous species that grow faster in relation to conifers, and avoid fir, whereas in cold years, fir is more preferred as deciduous species suffer more from low temperatures than conifers (this interpretation is also partly supported by ZAGs; Appendix S1: Fig. S4).

Competition effects were found to explain only a small part of variation in growth in comparison to other factors (Fig. 2), although this might be partly caused by our methods: by measuring competition as sum of tree heights, we account for both density and height effects

of competing trees, but not, for example, for the density of branches and leaves that might determine shading effects (Canham et al. 2004, Stadt et al. 2007). We suggest that observed negative temperature trends could be caused by this neglected competition effect: In Norway, the growth of rowan and spruce individuals was lowest at intermediate temperatures and pine growth at high temperatures, which might be caused by increased shading under these conditions.

Tree height was found to be a crucial component mediating moose cooling effect: tall trees have a different growth rate compared to lower trees, browsing pressure is different on them and their height is differently mediated by moose. Our results show that the cooling effect of moose is only apparent when trees are at browsable heights (Appendix S1: Table S6; Kolstad et al. 2018a). However, by acting at the crucial early stage of succession, moose effect can reflect to the climax stage of boreal forests. Even when mediated by herbivory, height itself is an important factor affecting growth. For example, for less preferred species in Norway, height explained a considerable amount of growth variation in comparison to herbivore presence. However, as we

TABLE 2. Model coefficients (estimates [Est.], SEs, dfs, critical values [Crit. val.], *P* values, and standard estimates [Std. est.]) for significant effects that were retained in the SEMs for Norway, presented for each species and species groups.

	Resp	Pred	Est.	SE	df	Crit. Val.	<i>P</i>	Std. Est.
Rowan	G	Exclosure	−195.2	41	185	−4.8	<0.0001	−5.8
	G	Temperature	−21.4	4.7	3,623	−4.6	<0.0001	−1.4
	G	Snow	0.45	0.53	3,623	0.8	0.3967	0.1
	G	Height	3.15	1.7	3,623	2	0.0436	0.1
	G	Height ²	−0.01	0.01	3,623	−2.3	0.0098	−0.1
	G	Temperature ²	0.8	0.2	3,623	4.4	<0.0001	1.4
	G	Exclosure:Temperature	28.4	6.7	3,623	4.3	<0.0001	10.5
	G	Exclosure:Temperature ²	−1.1	0.3	3,623	−4.2	<0.0001	−5.3
	G	Exclosure:Snow	2.84	0.75	3,623	3.8	0.0002	0.1
	H	Succession	10.6	0.2	3,630	42.6	<0.0001	0.4
	H	Exclosure	−46.1	3.6	185	−12.9	<0.0001	−0.4
	H	Temperature_av	14.9	3	42	5	<0.0001	0.2
	C	Succession	310	10.3	3,630	30.2	<0.0001	0.2
	C	Exclosure	−1,033	299	185	−3.4	0.0007	−0.2
Birch	G	Exclosure	−7.9	0.8	253	−9.3	<0.0001	−0.2
	G	Temperature	1.1	0.3	3,943	3.9	0.0001	0.1
	G	Rain	70.78	23.04	3,943	3.1	0.0021	0.1
	G	Snow	8.27	1.14	3,943	7.3	<0.0001	0.3
	G	Height	7.13	0.52	3,943	13.7	<0.0001	0.2
	G	Competition	−0.06	0.01	3,943	−4.9	<0.0001	−0.1
	G	Snow ²	−0.02	0.0	3,943	−4.7	<0.0001	−0.2
	H	Succession	13.3	0.2	3,948	53.6	<0.0001	0.5
	H	Exclosure	−24.1	3.7	253	−6.5	<0.0001	−0.2
	H	Temperature_av	11.7	4.1	44	2.8	0.0067	0.2
	H	Rain_av	−20.8	6	44	−3.5	0.0012	−0.2
	C	Succession	340	10	3,948	33.9	<0.0001	0.2
	C	Exclosure	−933	284	253	−3.3	0.0012	−0.1
Pine/fir	G	Exclosure	−3.3	0.6	180	−5.4	<0.0001	−0.1
	G	Temperature	−1.5	0.3	2,702	−5.7	<0.0001	−0.1
	G	Snow	2.06	0.47	2,702	4.4	<0.0001	0.1
	G	Height	24.92	1.25	2,702	20	<0.0001	0.9
	G	Competition	−0.03	0.01	2,702	−2.9	0.0034	−0.1
	G	Height ²	−0.05	0.01	2,702	−8.1	<0.0001	−0.3
	G	Rain	51.11	19.72	2,702	2.6	0.0096	0.1
	H	Succession	14.2	0.3	2,707	56	<0.0001	0.6
	H	Exclosure	−11.7	4.4	180	−2.7	0.0086	−0.1
	H	Rain_av	−31.2	8.4	40	−3.7	0.0006	−0.4
	C	Succession	303.5	10.7	2,707	28.4	<0.0001	0.2
	C	Exclosure	−822.1	349	180	−2.4	0.0097	−0.1
Spruce	G	Temperature	−11.3	4	1,392	−2.8	0.0048	−0.9
	G	Snow	2.71	0.55	1,392	4.9	<0.0001	0.1
	G	Height	29.5	1.92	1,392	15.4	<0.0001	1.2
	G	Temperature ²	0.4	0.2	1,392	2.7	0.0069	0.9
	G	Height ²	−0.07	0.01	1,392	−9.7	<0.0001	−0.7
	H	Succession	13.1	0.4	1,396	35.8	<0.0001	0.4
	H	Temperature_av	−16.3	5.8	44	−2.8	0.0073	−0.3
	H	Rain_av	−25.4	8.7	44	−2.9	0.0052	−0.3
	C	Succession	298.2	18.7	1,396	15.9	<0.0001	0.2

Notes: Response codes G, H, and C stand for growth, height, and competition. Temperature_av and Rain_av represent averages across years, used to explain tree height and competition instead of annual averages. For full model output, see Appendix S1: Table S5.

expected (Hypothesis 2), indirect negative moose effects via reduced height also play a role. For preferred forage species, it is possible that moose herbivory creates “browsing traps” (Staver and Bond 2014, Faison et al.

2016, Churski et al. 2017, Olofsson and Post 2018), from which trees are unable to escape (Kolstad et al. 2018a) and thus the growth rates are permanently low, as smaller trees grow slower than taller ones.

Qualitatively, the results were fairly similar between the two continents, suggesting broad applicability of our study across the boreal forest biome. However, there are some apparent differences that are likely to be explained rather by differing methods than differences in study systems. The number of growth observations from Canada was lower, and as expected, we observed fewer significant results than in Norway. Furthermore, we observed no positive effects of height on growth in Canada, likely because growth rates and height measures were average values across subplots, as individual trees were not followed between years. Average tree height may not increase average tree growth at the subplot level, or it might even have a negative impact via competition effects, as in the case of fir. An additional constraint in our study is that even though we accounted for several ecosystem properties, some neglected factors, such as soil properties and branching structure, might be crucial in mediating herbivory effect (Augustine and McNaughton 2006).

Herbivory has been suggested to have various mediating effects on climate-driven vegetation changes by inhibiting shrubification and constraining tree growth. Our findings show support for cooling effects of moose on growth of trees in different boreal forest ecosystems. However, these effects are highly context-dependent. If we are to place hope on herbivory as a cooler of climate change impacts, constraints imposed by species differences, snow, and competition, as well as climate effects on browsing, must be acknowledged.

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LITERATURE CITED

- Augustine, D. J., and S. J. McNaughton. 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems* 9:1242–1256.
- Belovsky, G. E. 1981. Food plant selection by a generalist herbivore: the moose. *Ecology* 62:1020–1030.
- Bernes, C., B. Macura, B. G. Jonsson, K. Junninen, J. Müller, J. Sandström, A. Löhmus, and E. Macdonald. 2018. Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates. A systematic review. *Environmental Evidence* 7:13.
- Birch, J. D., J. A. Lutz, E. Hogg, S. W. Simard, R. Pelletier, G. H. LaRoi, and J. Karst. 2019. Decline of an ecotone forest: 50 years of demography in the southern boreal forest. *Ecosphere* 10:e02698.
- Blume-Werry, G., J. Kreyling, H. Laudon, and A. Milbau. 2016. Short-term climate change manipulation effects do not scale up to long-term legacies: effects of an absent snow cover on boreal forest plants. *Journal of Ecology* 104:1638–1648.
- Boisvenue, C., and S. W. Running. 2006. Impacts of climate change on natural forest productivity—evidence since the middle of the 20th century. *Global Change Biology* 12: 862–882.
- Bräthen, K. A., V. T. Ravolainen, A. Stien, T. Tveraa, and R. A. Ims. 2017. Rangifer management controls a climate-sensitive tundra state transition. *Ecological Applications* 27: 2416–2427.
- Brecka, A. F., C. Shahi, and H. Y. Chen. 2018. Climate change impacts on boreal forest timber supply. *Forest Policy and Economics* 92:11–21.
- Canham, C. D., P. T. LePage, and K. D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34:778–787.
- Churski, M., J. W. Bubnicki, B. Jędrzejewska, D. P. Kuijper, and J. P. Cromsigt. 2017. Brown world forests: increased ungulate browsing keeps temperate trees in recruitment bottlenecks in resource hotspots. *New Phytologist* 214:158–168.
- Cromsigt, J. P., M. te Beest, G. I. Kerley, M. Landman, E. le Roux, and F. A. Smith. 2018. Trophic rewilding as a climate change mitigation strategy? *Philosophical Transactions of the Royal Society B* 373:20170440.
- de Groot, W. J., M. D. Flannigan, and A. S. Cantin. 2013. Climate change impacts on future boreal fire regimes. *Forest Ecology and Management* 294:35–44.
- Dorais, M., and D. Lavergne. 2010. Inventaire aérien de l'original dans la réserve faunique des Chic-Chocs à l'hiver 2010. Ministère des Ressources naturelles et de la Faune, Québec, Canada.
- D'orangeville, L., L. Duchesne, D. Houle, D. Kneeshaw, B. Cote, and N. Pederson. 2016. Northeastern North America as a potential refugium for boreal forests in a warming climate. *Science* 352:1452–1455.
- Fairchild, A. J., D. P. MacKinnon, M. P. Taborga, and A. B. Taylor. 2009. R^2 effect-size measures for mediation analysis. *Behavior Research Methods* 41:486–498.
- Faison, E. K., S. DeStefano, D. R. Foster, J. M. Rapp, and J. A. Compton. 2016. Multiple browsers structure tree recruitment in logged temperate forests. *PLoS ONE* 11:e0166783.
- Fischelli, N., L. E. Frelich, and P. B. Reich. 2012. Sapling growth responses to warmer temperatures “cooled” by browse pressure. *Global Change Biology* 18:3455–3463.
- Grace, J. B., T. M. Anderson, H. Olff, and S. M. Scheiner. 2010. On the specification of structural equation models for ecological systems. *Ecological Monographs* 80:67–87.
- 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.
- Hörnberg, S. 2001. The relationship between moose (*Alces alces*) browsing utilisation and the occurrence of different forage species in Sweden. *Forest Ecology and Management* 149:91–102.
- Kolstad, A. L., G. Austrheim, E. J. Solberg, L. De Vriendt, and J. D. Speed. 2018a. 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, A. M. Venete, S. J. Woodin, and J. D. Speed. 2018b. Cervid exclusion alters boreal forest properties with little cascading impacts on soils. *Ecosystems* 21:1027–1041.

- Lamoureux, J., M. Bélanger, and C. Larocque. 2012. Inventaire aérien de l'original dans les réserves fauniques de Matane et Dunière à l'hiver 2012. Page 40. Ministère des Ressources Naturelles et de la Faune, Direction de l'Aménagement de la Faune du Bas-St-Laurent, Rimouski, Québec, Canada.
- Lefcheck, J., J. Byrnes, and J. Grace. 2016. Package 'piecewiseSEM'. R package version 1. <https://CRAN.R-project.org/package=piecewiseSEM>
- Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution* 7:573–579.
- Lussana, C., E. Ole, and U. Francesco. 2016. seNorge v2. 0: an observational gridded dataset of temperature for Norway. Met. no report 14. Norwegian Meteorological Institute, Norway.
- Lussana, C., T. Saloranta, T. Skaugen, J. Magnusson, O. E. Tveito, and J. Andersen. 2018. seNorge2 daily precipitation, an observational gridded dataset over Norway from 1957 to the present day. *Earth System Science Data* 10:235–249.
- Månsson, J., H. Andrén, Å. Pehrson, and R. Bergström. 2007. Moose browsing and forage availability: A scale-dependent relationship? *Canadian Journal of Zoology* 85:372–380.
- Ministry of Sustainable Development, Environment and Climate Change (MDDELCC). 2018. Data from Climate Monitoring Program. MDCC, State of the Environment Monitoring Branch, Quebec City, Quebec, Canada.
- Niemelä, P., F. S. Chapin, K. Danell, and J. P. Bryant. 2001. Herbivory-mediated responses of selected boreal forests to climatic change. *Climatic Change* 48:427–440.
- Nordengren, C., A. Hofgaard, and J. P. Ball. 2003. Availability and quality of herbivore winter browse in relation to tree height and snow depth. *Annales Zoologici Fennici* 40:305–314.
- Olofsson, J., L. Oksanen, T. Callaghan, P. E. Hulme, T. Oksanen, and O. Suominen. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* 15:2681–2693.
- Olofsson, J., and E. Post. 2018. Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philosophical Transactions of the Royal Society B* 373:20170437.
- Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139:690–705.
- Peng, C., Z. Ma, X. Lei, Q. Zhu, H. Chen, W. Wang, S. Liu, W. Li, X. Fang, and X. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change* 1:467–471.
- Rempel, R. S. 2011. Effects of climate change on moose populations: exploring the response horizon through biometric and systems models. *Ecological Modelling* 222:3355–3365.
- Ruckstuhl, K., E. Johnson, and K. Miyanishi. 2007. Introduction. The boreal forest and global change. *Philosophical Transactions of the Royal Society B* 363:2243–2247.
- Schmitz, O. J., P. A. Raymond, J. A. Estes, W. A. Kurz, G. W. Holtgrieve, M. E. Ritchie, D. E. Schindler, A. C. Spivak, R. W. Wilson, and M. A. Bradford. 2014. Animating the carbon cycle. *Ecosystems* 17:344–359.
- Schmitz, O. J., C. C. Wilmers, S. J. Leroux, C. E. Doughty, T. B. Atwood, M. Galetti, A. B. Davies, and S. J. Goetz. 2018. Animals and the zoogeochimistry of the carbon cycle. *Science* 362:eaar3213.
- Soja, A. J., N. M. Tchepakova, N. H. French, M. D. Flannigan, H. H. Shugart, B. J. Stocks, A. I. Sukhinin, E. Parfenova, F. S. Chapin III, and P. W. Stackhouse Jr. 2007. Climate-induced boreal forest change: predictions versus current observations. *Global and Planetary Change* 56:274–296.
- Speed, J. D., G. Austrheim, A. J. Hester, and A. Myrsterud. 2011. Browsing interacts with climate to determine tree-ring increment. *Functional Ecology* 25:1018–1023.
- Speed, J. D., G. Austrheim, A. J. Hester, and A. Myrsterud. 2012. Elevational advance of alpine plant communities is buffered by herbivory. *Journal of Vegetation Science* 23: 617–625.
- Speed, J. D., 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.
- Stadt, K. J., C. Huston, K. D. Coates, Z. Feng, M. R. Dale, and V. J. Lieffers. 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. *Annals of Forest Science* 64:477–490.
- Staver, A. C., and W. J. Bond. 2014. Is there a 'browse trap'? Dynamics of herbivore impacts on trees and grasses in an African savanna. *Journal of Ecology* 102:595–602.
- Turunen, M., P. Soppela, H. Kinnunen, M.-L. Sutinen, and F. Martz. 2009. Does climate change influence the availability and quality of reindeer forage plants? *Polar Biology* 32:813–832.
- Vuorinen, K. E., L. Oksanen, T. Oksanen, A. Pyykönen, J. Olofsson, and R. Virtanen. 2017. Open tundra persist, but arctic features decline—vegetation changes in the warming Fennoscandian tundra. *Global Change Biology* 23:3794–3807.
- Vuorinen, K. E., S. J. Rao, A. J. Hester, and J. D. Speed. 2020. Herbivory and climate as drivers of woody plant growth: Do deer decrease the impacts of warming? *Ecological Applications* 30:e02119.
- Way, D. A., and R. Oren. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology* 30:669–688.
- Zuur, A. F., and E. N. Ieno. 2016. Chapter 7, Beginner's guide to zero-inflated models with R. Highland Statistics Limited, Newburgh, UK.

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