

## RESEARCH ARTICLE

## Active Remote Sensing for Ecology and Ecosystem Conservation

# Airborne laser scanning reveals uniform responses of forest structure to moose (*Alces alces*) across the boreal forest biome

Tanja K. Petersen<sup>1</sup>  | Anders L. Kolstad<sup>2</sup>  | Jari Kouki<sup>3</sup>  | Shawn J. Leroux<sup>4</sup>  |  
Lynette R. Potvin<sup>5</sup> | Jean-Pierre Tremblay<sup>6</sup>  | Märtha Wallgren<sup>7,8</sup>  |  
Fredrik Widemo<sup>8</sup>  | Joris P. G. M. Cromsigt<sup>8,9</sup>  | Coline Courtois<sup>1</sup> |  
Gunnar Austrheim<sup>1</sup>  | John Gosse<sup>10</sup> | Michael den Herder<sup>11</sup>  | Luise Hermanutz<sup>4</sup>  |  
James D. M. Speed<sup>1</sup> 

<sup>1</sup>Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Norway; <sup>2</sup>Department of Terrestrial Biodiversity, Norwegian Institute for Nature Research, Trondheim, Norway; <sup>3</sup>School of Forest Sciences, University of Eastern Finland, Joensuu, Finland; <sup>4</sup>Department of Biology, Memorial University of Newfoundland, St John's, Newfoundland and Labrador, Canada; <sup>5</sup>National Park Service, Isle Royale National Park, Houghton, Michigan, USA; <sup>6</sup>Département de Biologie, Centre d'étude de la Forêt et Centre d'études Nordiques, Université Laval, Québec, Québec, Canada; <sup>7</sup>Forestry Research Institute of Sweden, Uppsala Science Park, Uppsala, Sweden; <sup>8</sup>Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden; <sup>9</sup>Department of Zoology, Centre for African Conservation Ecology, Nelson Mandela University, Gqeberha, South Africa; <sup>10</sup>Parks Canada Agency, Terra Nova National Park, Glovertown, Newfoundland and Labrador, Canada and <sup>11</sup>European Forest Institute, Joensuu, Finland

## Correspondence

James D. M. Speed

Email: [james.speed@ntnu.no](mailto:james.speed@ntnu.no)

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## Abstract

1. The moose *Alces alces* is the largest herbivore in the boreal forest biome, where it can have dramatic impacts on ecosystem structure and dynamics. Despite the importance of the boreal forest biome in global carbon cycling, the impacts of moose have only been studied in disparate regional enclosure experiments, leading to calls for common analyses across a biome-wide network of moose enclosures.
2. In this study, we use airborne laser scanning (ALS) to analyse forest canopy responses to moose across 100 paired enclosure-control experimental plots distributed across the boreal biome, including sites in the United States (Isle Royale), Canada (Quebec, Newfoundland), Norway, Sweden and Finland.
3. We test the hypotheses that canopy height, vertical complexity and above-ground biomass (AGB) are all reduced by moose and that the impacts vary with moose density, productivity, temperature and pulse disturbances such as logging and insect outbreaks.
4. We find a surprising convergence in forest canopy response to moose. Moose had negative impacts on canopy height, complexity and AGB as expected. The responses of canopy complexity and AGB were consistent across regions and did not vary along environmental gradients. The difference in canopy height between enclosures and open plots was on average 6 cm per year since the start

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of enclosure treatment ( $\pm 2.1$  SD). This rate increased with temperature, but only when moose density was high.

- The difference in AGB between moose enclosures and open plots was  $0.306 \text{ Mg ha}^{-1} \text{ year}^{-1}$  ( $\pm 0.079$ ). In browsed plots, stand AGB was 32% of that in the enclosures, a difference of  $2.09 \text{ Mg ha}^{-1}$ . The uniform response allows scaling of the estimate to a biome-wide impact of moose of the loss of 448 ( $\pm 115$ ) Tg per year, or 224 Tg of carbon.
- Synthesis:** Analysis of ALS data from distributed enclosure experiments identified a largely uniform response of forest canopies to moose across regions, facilitating scaling of moose impacts across the whole biome. This is an important step towards incorporating the effect of the largest boreal herbivore on the carbon cycling of one of the world's largest terrestrial biomes.

#### KEYWORDS

biomass, boreal forest, browsing, carbon, herbivore, LIDAR, moose, plant-herbivore interactions

## 1 | INTRODUCTION

As one of the world's largest terrestrial biomes, the boreal forest covers a vast area of over 15 million  $\text{km}^2$  across both the Palaearctic and Nearctic continental landmasses (Olson et al., 2001). The boreal forest comprises both wilderness areas, and ecosystems under exploitation and management by the forestry, mining, and oil and gas industries (Gauthier et al., 2015; Venter et al., 2016). The boreal forest is a globally important carbon sink and a reservoir for biodiversity (Bradshaw et al., 2009) and provides a large range of ecosystem services (Gamfeldt et al., 2013). However, boreal forest ecosystems are also vulnerable to global environmental change, with impacts from a range of interacting drivers including climate change (Berner & Goetz, 2022), resource exploitation (Pohjanmies et al., 2017), wild-fire (Walker et al., 2019), invertebrate outbreaks (Morin, 1994) and changes in trophic regulation by vertebrates (Frelich et al., 2012; Gosse et al., 2011). How these drivers impact boreal forest dynamics and carbon sink status of boreal forests, however, is rarely measured at a biome extent. Large-scale analyses are needed to predict how the boreal biome will adapt to global environmental change.

Large herbivores exert a major influence on boreal forest dynamics through selective herbivory, trampling and seed dispersal (Leroux et al., 2020; Persson et al., 2000). Ecosystem carbon storage can be impacted by large herbivores (Tanentzap & Coomes, 2012) and, thus, across large scales, trophic interactions can influence global climate (Cromsigt et al., 2018). The moose (Eurasian elk, *Alces alces*) is the largest and most widespread large herbivore distributed across most of the boreal forest biome (Hundertmark, 2016), having been introduced in some regions such as Newfoundland (McLaren et al., 2004). The moose can reach a body mass of over 700 kg and an individual can consume 9000 kg of forage per year (Persson et al., 2000). Moose populations in the boreal biome are influenced by bottom-up forage availability, top-down predation (by the wolf

*Canis lupus*, hunting or parasitism) and abiotic conditions (Vucetich & Peterson, 2004). However, anthropogenic impacts also affect populations of moose across large parts of the boreal biome, as forest practices often increase the abundance of moose-preferred trees, increasing forage availability and hence carrying capacity for moose (Rempel et al., 1997). Moreover, targeted hunting of the moose population can dictate the population size and growth rate, for example, by creating female-biased population demographics (Lavsund et al., 2003). Population densities of moose are, thus, under complex regulation from different drivers, and in many regions currently undergoing changes (Speed et al., 2019; Strong & Leroux, 2014; Vucetich & Peterson, 2004).

Moose impacts on forest ecosystems have clear effects on boreal forest regeneration dynamics after pulse disturbances such as logging, fire and invertebrate outbreaks (De Vriendt et al., 2021; Lord & Kielland, 2015; Speed et al., 2013). Moose browsing impacts on forest canopies can cascade below-ground through impacts on soil temperature (Kolstad et al., 2019). However, impacts on soil nutrient dynamics are generally slower than above-ground responses (Kolstad et al., 2017; Leroux et al., 2021; Pastor et al., 1993). The implication of these changed dynamics is that moose can have large impacts on ecosystem carbon stocks through the secondary successional processes (Leroux et al., 2020). Indeed Schmitz et al. (2014) estimated that the difference between high and low moose densities on net primary production across Canada was comparable (42%–95%) to the nation's annual  $\text{CO}_2$  emissions.

Although moose are widespread across the boreal forest biome, the impacts of moose on forest ecosystems have generally been studied in small-scale, regionally limited enclosure studies. The predominance of disjointed experiments hinders wider synthesis, and this has led to calls for a biome-wide network of enclosure experiments to synthesise the impact of moose on boreal ecosystems (Leroux et al., 2020). Ecological theory predicts that in the absence

of herbivores, vegetation biomass will increase with potential primary productivity, while in the presence of herbivores (and absence of predators), vegetation biomass will not vary with productivity, but herbivore biomass will increase (Oksanen et al., 1981). However, in boreal forests, much of the vegetation biomass is sequestered in fractions (e.g. spruce *Picea* spp.) avoided by, or inaccessible (i.e. wood) to, large herbivores. Thus, the theoretical predictions of the exploitation ecosystem hypothesis can break down (Oksanen & Oksanen, 2000). So, while the removal or reduction of herbivores is suggested as a climate mitigation strategy (Tanentzap & Coomes, 2012), the effect of this strategy across productivity gradients is uncertain, and particularly when all trophic levels are under management. This is important given the impact of climate change and potential increases in productivity in boreal regions. Quantitative analyses across exclosures in multiple regions have suggested that moose browsing could counter the impact of warming on boreal forest tree growth (Vuorinen et al., 2020); however, such analyses are dependent upon comparable study designs and sampling methodologies.

Remote sensing provides opportunities for standardised analyses across different regions, scales and individual experiments. Remote sensing approaches have been used to detect the impacts of herbivores in different biomes including African savannahs (Asner et al., 2009) and the Arctic tundra (Siewert & Olofsson, 2021). Light detecting and ranging (LIDAR) data have proven particularly useful for research in forest ecosystems due to the wealth of structural information that can be extracted from the emission and reception of laser pulses (Lenoir et al., 2022; Lim et al., 2003; Vauhkonen et al., 2014). Airborne laser scanning (ALS) campaigns are underway across forested areas at large spatial scales providing an invaluable resource for forest ecology. ALS uses aircraft-mounted LIDAR sensors and typically uses time-of-flight of laser pulses to estimate the distance from the sensor to the interception (which may be vegetation or ground) based on the time taken between the pulse emission and reception. Both digital terrain and vegetation models can then be created from ALS data, with the top-level returns representing the upper canopy of the vegetation, and various indices relevant to forest ecology can be estimated from the returned point clouds (Maltamo et al., 2014). ALS can detect moose browsing impacts in boreal forests (Melin et al., 2016) and has been used to investigate the impact of moose on forest structure within experimental exclosures at a regional scale (Kolstad et al., 2021). For analysing experimental exclosures, ALS has the advantage of synthesising responses across whole plots and the entire canopy, in contrast to field data, which are often collected in small subplots or at the stem level.

In this study, we answer the call for unifying a network of moose exclosures across the boreal forest biome, and we use ALS as a platform for a common analysis of moose impacts on forest structure. We test the hypotheses that 1. Canopy height, structural complexity and above-ground biomass (AGB) are all reduced by moose browsing. 2. The impacts of moose are greatest when moose densities and vegetation productivity (or temperature as a proxy) are both high. 3. Moose impacts on forest structure are greatest following large spatial-scale pulse disturbances (such as logging, forest fires and

spruce budworm outbreaks). Our hypothesis 4 is motivated by the exploitation ecosystems hypothesis. This predicts that vegetation biomass will increase with net primary productivity (NPP) in the absence of herbivory but will not vary with productivity in the presence of predator-free herbivores. However, due to the widespread, fundamental role of management in determining moose densities, and the presence of non-palatable tree species (e.g. *Picea* spp.) we predict that above-ground vegetation biomass will increase with productivity in open plots, but at a lower rate than within exclosures. Undertaking a common analysis of forest structure in experiments distributed across the boreal biome, and the identification of environmental modifiers of moose impacts (such as the hypothesised effects of temperature, moose density and scale of disturbance) will allow us to begin to scale up moose impacts to the biome scale.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

This study made use of a network of experimental sites in forests distributed across much of the boreal biome. Sites were selected from existing exclosure studies of ungulate browsing. Only sites meeting the following conditions were included: 1. Ungulate exclosures paired with open plots with a minimum area of each 200 m<sup>2</sup>. 2. Moose was the dominant cervid herbivore in the study area (>50% of cervid metabolic biomass) and 3. ALS data were available to us as of February 2022. In total 106 sites were initially included in the study from Norway (45), Sweden (14), Finland (12), Quebec (20), Newfoundland (10) and Isle Royale, USA (5) (Figure 1, Supporting Information Table S1). Most of the exclosure experiments were established following major forest disturbances (Table S1), including anthropogenic disturbance (logging) and natural disturbances such as spruce budworm outbreaks, and fire (which could be natural or anthropogenic).

For each site, the following metadata were collated (Table S1): coordinates of the corners of the exclosures and corresponding open plots; the age of the forest stand; the year the exclosure was erected; the dimensions and area of the plots; the main disturbance type affecting the plots (if any); the most recent year of disturbance; the area affected by last disturbance; moose density in the focal area. The duration of the exclosure experiment was calculated as the number of years between the erection of the exclosure and the time of laser data capture (see below; Table S1).

### 2.2 | Airborne laser scanning estimates of forest structure

ALS data were retrieved for all sites and sources, and details of the data are shown in Table S1. ALS point densities varied between 0.7 and 5.0 points m<sup>-2</sup> (Table S1). The ALS point clouds were cropped to cover the plots including a 10-m buffer around

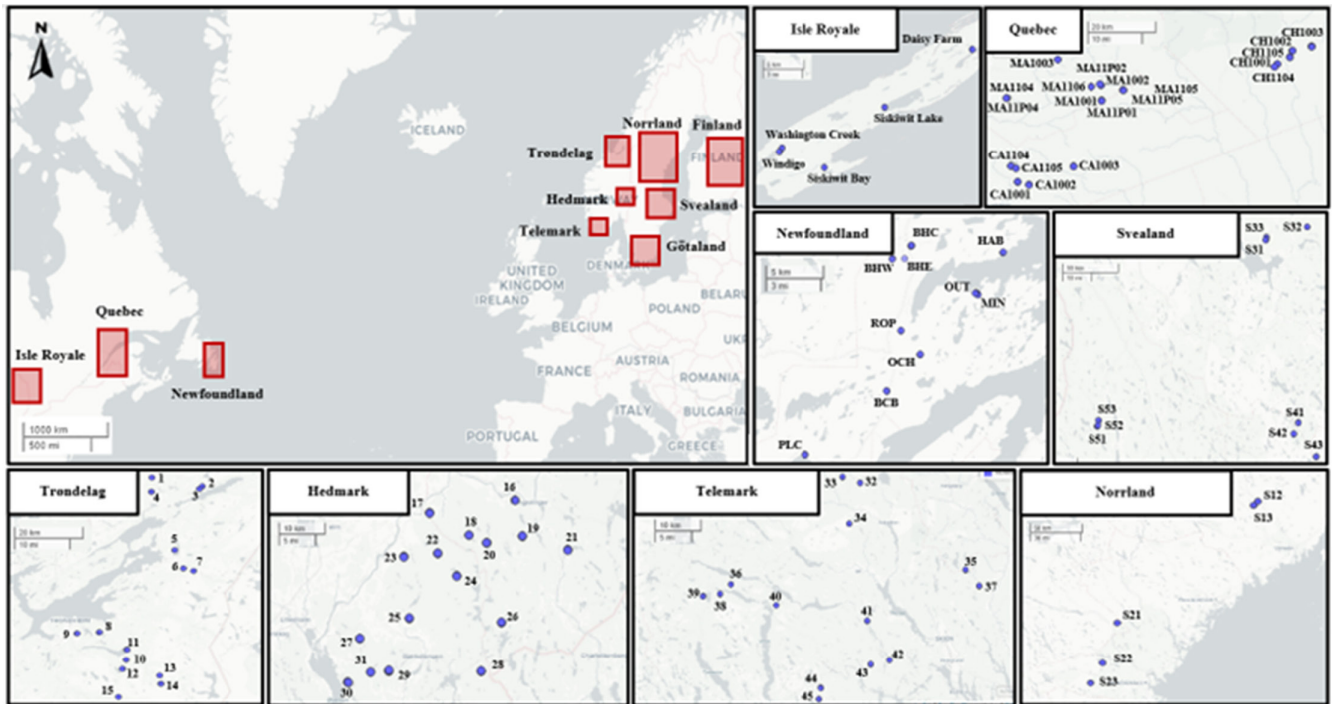


FIGURE 1 Locations of study sites. Note that the exact locations of the sites in Finland are withheld due to conservation concerns.

each plot. In some of the study sites, larger trees were left standing following disturbances. As these were not accessible for moose browsing during the experimental period, these could not be influenced by the experimental treatment (moose browsing presence/absence) and they were therefore removed prior to analyses. Remnant trees were removed only from sites with a stand age of less than 20 years. In stands older than 20 years, all trees were included in the analyses. To select which trees to remove, the height of the ALS points was first normalised to represent height above-ground using the *normalize\_height()* function from the *lidR* package (Roussel et al., 2020, 2022). Second, trees were identified using the *find\_trees()* function, using a moving square window of, respectively, 8 m (Norway, Sweden and Québec) and 6 m (Newfoundland). Forest stands in Isle Royale and Finland were all older than 20 years. Points associated with the identified trees were identified using the *segment\_trees()* function (using the *dalponte2016* algorithm; Dalponte & Coomes, 2016) with growing threshold 1 = 0.35, growing threshold 2 = 0.55, maximum crown diameter = 6 m (Norway, Sweden and Québec) or 5 m (Newfoundland). The difference in maximum crown diameter was necessary due to differences in point densities in the different ALS datasets. The function uses a canopy model (*raster*), which was produced using the *grid\_canopy()* function and the point-to-raster method (*p2r()*, assigning the pixel the maximum point height). The resolution of the canopy model was based on point density of the ALS point clouds using a 2 m resolution when the point density was less than 2 points  $m^{-2}$  and a 1 m resolution if the point density was greater than or equal to two points  $m^{-2}$ . Third, the trees were clipped from the LAS files using the *clip\_roi()*

function, removing trees, respectively, above 10 m (Norway and Newfoundland), 8 m (Québec) and 7 m (Sweden). The thresholds were selected based on visual inspection of canopy height plots and the authors' knowledge of the sites. Canopy models are provided for illustration in Appendix S1 (but note that the response variables were estimated based on point clouds). Lastly, the LAS files were clipped with a 2 m inner buffer. This was done to minimise noise from ecological edge effects and potential imprecision in the coordinates delimiting the plot boundaries. This inner buffer was not necessary for the plots in Newfoundland where the available coordinates were subplots already 5 m inside the plot boundary.

Three response variables were calculated to assess forest canopy structure: Canopy height was represented by the 90th percentile of first echoes rather than the maximum to avoid undue influence of outliers (also referred to as *h90*; Næsset & Gobakken, 2008). Vegetation heterogeneity was represented by the vertical complexity index (VCI) VCI is an estimate of the evenness of point returns on a vertical profile, where a value of 1 indicates a uniform distribution and lower values indicate skewness, and hence low vertical complexity (van Ewijk et al., 2011). AGB was predicted for each plot using equations specific to the location, forest type and stand age of the site. For all Fennoscandian sites, the equation for AGB1999 from (Økseter et al., 2015) was used (accounting for the correction to a typographical error as reported by Kolstad et al. (2021)). For the sites in Canada and the USA, equations from Boudreau et al. (2008) were used, depending on forest type. The equation for boreal coniferous forests was used for all sites in Newfoundland and 14 sites in Québec and

the equation for boreal mixed forests was used for all sites in Isle Royale and six sites in Québec.

## 2.3 | Independent variables

Data-quantifying scale of disturbance, moose densities and productivity were required to test the study hypotheses. The area of stand-impacting disturbances was derived from aerial imagery or historic forest maps for each region. Moose densities were taken from the best available local estimates during the period between the enclosure erection and ALS data acquisition and converted where necessary to individuals  $\text{km}^{-2}$ . Moose densities were taken from annual aerial surveys completed by Michigan Technological University (Hoy et al., 2020) for Isle Royale, for Newfoundland data are from annual aerial surveys completed by Terra Nova National Park. Moose data for Québec data are from aerial surveys (Dorais & Lavergne, 2010; Lamoureux et al., 2012), for Norway from Speed et al. (2019), for Sweden from Widemo et al. (2022) and from Finland from Natural Resources Institute, Finland.

Summer temperature and NPP were both included as measures of site productivity. Bioclimatic variables were downloaded from WorldClim2 (Fick & Hijmans, 2017) through the `RASTER` package (Hijmans, 2016) as a raster with a 30 arc seconds resolution. The coordinates of one corner of each plot were overlaid on the rasters, and the values for mean temperature of the warmest quarter (summer temperature) were extracted using the `extract()` function. As the paired open plots and enclosures potentially fell within different raster cells and, thus, had different values, the mean of the values for a paired site was used in further analyses. NPP estimates were sourced from Copernicus dry matter productivity (Sentinel-3/OLCI, PROBA-V 300m) products taking an average of July value across 2016–2019. The distribution of the predictor variables across the regions is shown in Figure 2, and pairwise correlations are in Figure S1. Forest stand age was correlated with experimental duration ( $r_s = 0.57$ ) but all other absolute pairwise correlation coefficients were below 0.5.

## 2.4 | Statistical analyses

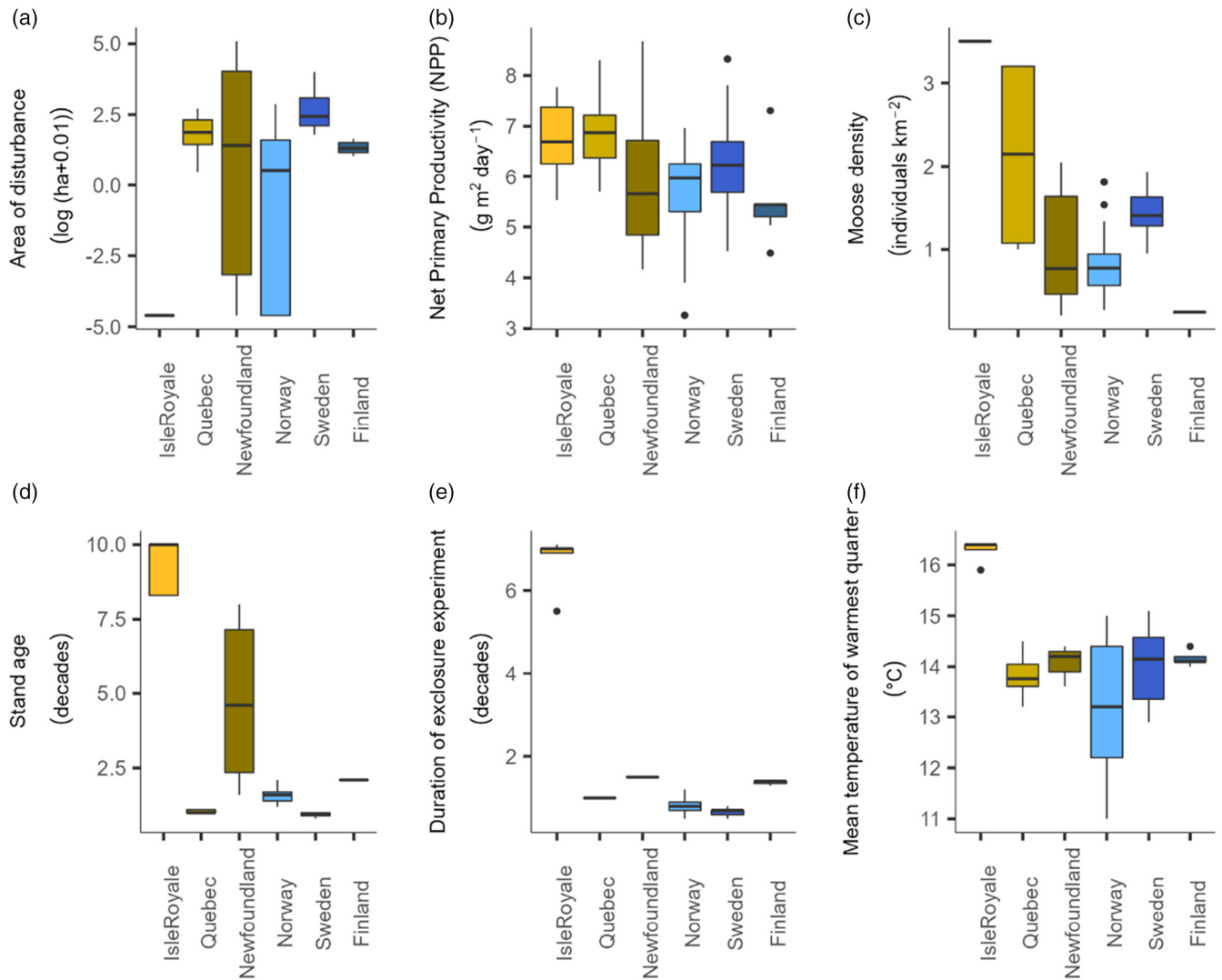
One site in Finland was removed from all analyses as the mean canopy height of the returns within the enclosure was at 0 m. In total, canopy height and AGB were estimated in both enclosures and open plots within 105 of the 106 sites. VCI could not be estimated across at least one of the plots within three Norwegian sites, two Finnish and two Swedish sites, as the 90th percentile of the point cloud were lower than the used height bins (0.5 m). These reflect sites with no actual canopy and a zero value for VCI was imputed. This was deemed appropriate as all canopy returns were in effect in the same height bin (<0.5 m). For modelling how moose impacts varied with environment, only sites with a complete set of response- and predictor variables were used, totalling 100 sites (40 from Norway, 20 from

Québec, 14 from Sweden, 11 from Finland, 10 from Newfoundland and 5 from Isle Royale).

To assess the impact of moose browsing on boreal forest canopies, we calculated the difference in the paired sites by subtracting the response variables of canopy structure (canopy height, VCI and AGB) from the open plots from the corresponding enclosure, such that a positive difference indicates a higher value in the enclosure. These differences were then standardised by the duration of the enclosure experiment between the year that the enclosure was erected and the year that the ALS data were acquired to estimate an average annual difference between treatments. We used this duration-standardised difference between the treatments as the response variable to ensure that results remain interpretable in relevant units, for example, canopy height difference in metres per year of moose exposure. We also carried out analyses based on the unstandardised response variables to examine the overall impact of moose across sites at the time that the ALS data were acquired.

To test whether the impacts of moose exclusion on canopy height, vertical complexity and AGB varied with environment, ordinary least square linear models were fitted. For modelling the annual (duration-standardised) responses in canopy height, VCI and AGB, the predictor variables tested were region (country, or Canadian province), the area of last disturbance (ha, log-transformed), and two-way interactions between moose density (individuals  $\text{km}^{-2}$ ) and summer temperature ( $^{\circ}\text{C}$ ) and moose density and NPP ( $\text{kg}/\text{ha day}^{-1}$ ). All these relate to the study hypotheses. In addition, we included a covariate of forest stand age (decades). Region was used as a fixed effect since it is part of the study design. Predictor variables were not scaled (except for expressing stand age in decades) to allow interpretation of coefficients in appropriate units, but summer temperature was mean-centred. The distributions of the predictor variables are shown in Figure 2 and are plotted against the response variables in Figures S3–S5. Stepwise backwards model selection based on likelihood ratio F tests was undertaken. Final models are reported.

Total differences in canopy variables (not standardised by duration) were also modelled as a response of the environment. These models, thus, report the overall difference between open plots and enclosures at the time of ALS data acquisition. Linear models were fitted using region, the area of last disturbance (ha, log-transformed), two-way interactions between each of NPP ( $\text{kg}/\text{ha}/\text{day}$ ) and summer temperature ( $^{\circ}\text{C}$ ) with moose density (individuals/ $\text{km}^2$ ) and an interaction between stand age and duration of the enclosure experiment (both in decades). Stand age and experimental duration were both scaled as decades and the total (unstandardised) AGB difference was log-modulus transformed (retaining the original sign of the difference). Differences in responses between regions were explored within the same models by testing the mean difference in canopy variables as a function of region/original experiment (factorial). Pairwise contrasts were then compared using the `emmeans()` function from the package of the same name (Lenth, 2022). Finally, we tested the fourth hypothesis using the AGB data estimated in both treatments (rather than the treatment difference). We tested for a significant interaction between NPP and enclosure treatment



**FIGURE 2** Distribution of predictor variables across the study sites. (a) log-transformed area of the latest major disturbance of the plots, (b) net primary productivity, (c) moose density, (d) age of the forest stand, (e) duration of the exclusion experiment and (f) mean temperature of the warmest quarter (summer temperature). Regions are ordered by longitude.

in determining AGB across all sites and regions. All analyses and visualisations were carried out in R, version 4.1.2 (R Core Team, 2018). Data are available on FigShare (Petersen et al., 2022).

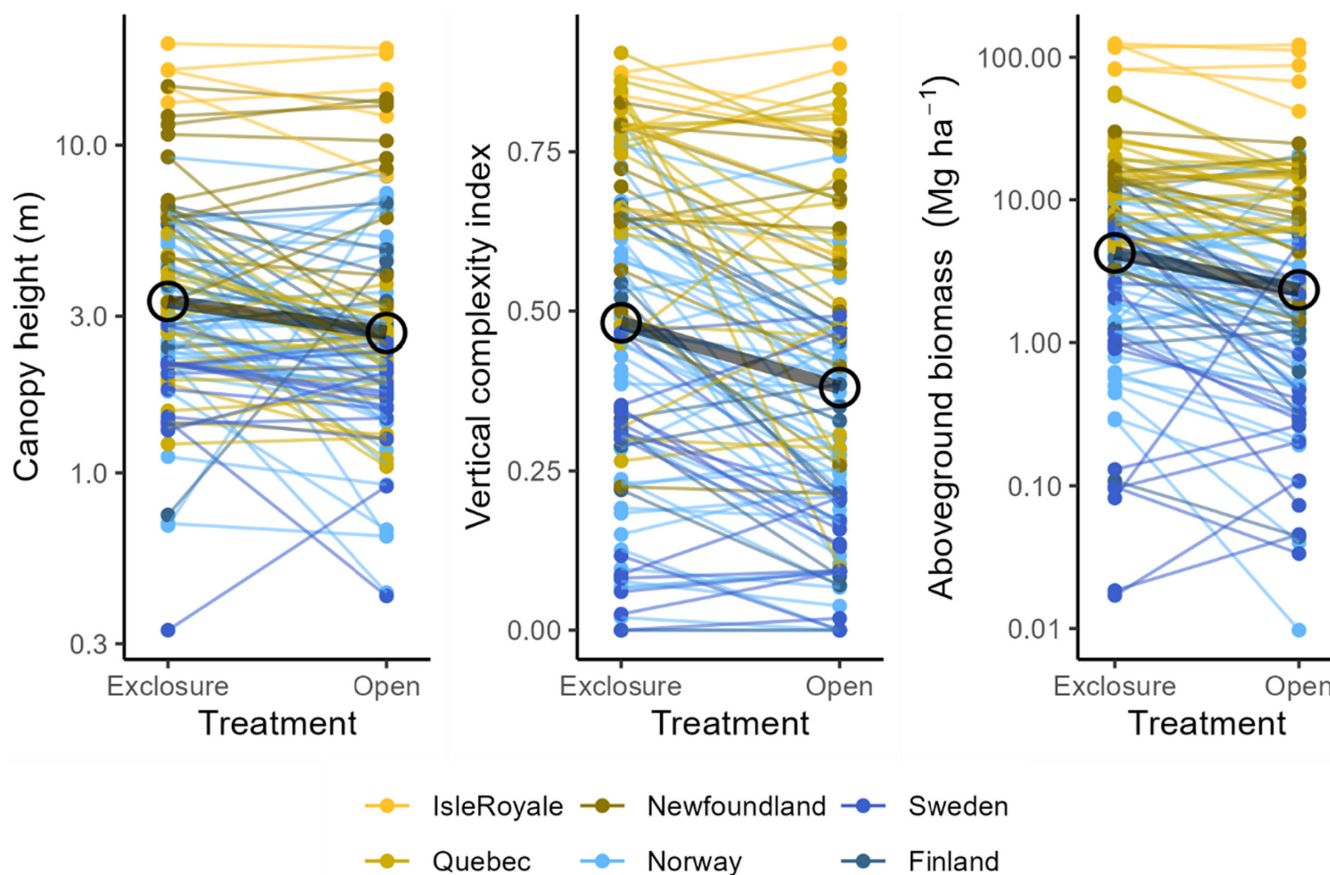
### 3 | RESULTS

Raw response variables across all sites and regions are shown in Figure 3. Canopy height (90th quantile ALS return) varied from 0.3 to 20.4 m. VCI varied between 0 and 0.91 and AGB varied from 0.01 to 124.5 Mgha<sup>-1</sup>. Response variables did not vary with the point density of the LIDAR data (Figure S2).

Across 100 sites in six regions, boreal forest canopy height growth was on average 0.064 m year<sup>-1</sup> ( $\pm$  standard error 0.021) higher in the absence of moose than in the presence of moose (Figure 4a), for each year of moose exclusion. However, the annual difference in canopy height varied with region, temperature, moose density and

the interaction between temperature and moose density (Table S2a, Figure S3). The annual difference between treatments was lower in Isle Royale than in the other regions (Table S2, Figure 4a), although when looking at all pairwise comparisons between regions and correcting for multiple tests (Tukey method), the treatment difference at Isle Royale was only significantly lower than in Norway ( $p = 0.04$ ) and Quebec ( $p = 0.02$ ; Table S3). The treatment difference in canopy height varied with a significant interaction between moose density and summer temperature (Table S2a; this interaction was robust to removing Isle Royale from the dataset). The treatment difference increased with temperature but only where moose densities were high (Figure 5, Table S2).

At the time of ALS data acquisition, canopy height was on average 0.63 m ( $\pm 0.21$ ) higher in the moose exclusions than in the open plots (Figures 3 and 4b). The canopy height difference varied with the duration of the exclusion study, and an interaction between summer temperature and moose density. The canopy height difference was



**FIGURE 3** Raw response variables of canopy height, vertical complexity index and above-ground biomass across enclosure and open plot treatments in all sites in each of the six regions. Paired plots are joined by lines. Overall means are shown with black circles and lines. Note that canopy height and above-ground biomass are plotted on  $\log_{10}$  axes.

lower in longer-term enclosures (by  $0.96\text{ m} \pm 0.39$  for every decade). The interactive effect of temperature and moose density was similar for the annual difference, with the treatment difference increasing with temperature in sites with a high moose density (Figure S6, Table S2b).

The treatment difference in vertical complexity of the forest canopy did not vary with any of the hypothesised predictors (Figure S4). Backward model selection arrived at intercept-only models for both annual and total differences in VCI (Tables S2b,e). The intercept for both models significantly differed from zero. Canopy VCI increased at a faster rate in the absence of moose than in the presence of moose with a difference of  $0.012\text{ units year}^{-1}$  ( $\pm 0.002$ , Figure 4b, Table S2,  $t = 6.1$ ,  $p < 0.001$ ). Vertical complexity was on average  $0.104$  ( $\pm 0.016$ ) index units higher in the enclosures than in open plots (Figures 3 and 4e, Table S3,  $p < 0.001$ ).

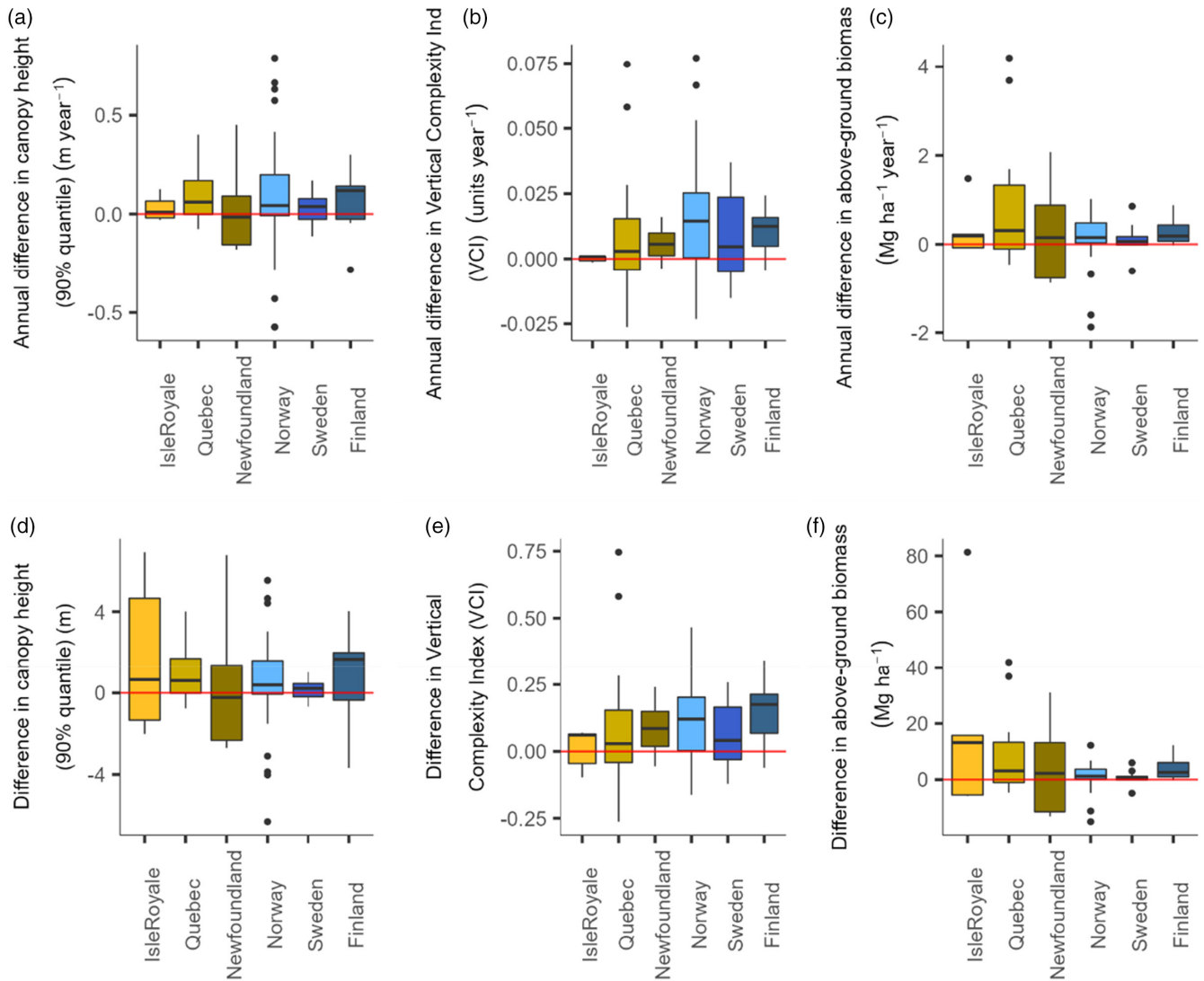
The treatment difference in AGB also did not vary with the predictor variables (Figure S5); all were removed by backward model selection based on likelihood ratio tests. Both intercepts differed from zero in the resultant intercept-only models. The annual difference in AGB increased at a greater rate in the enclosures than outside the enclosures by  $0.31\text{ Mg ha}^{-1}\text{ year}^{-1}$  ( $\pm 0.08$ , Figure 4c, Table S2c,  $t = 3.8$ ,  $p < 0.001$ ). The treatment difference in total AGB was  $2.09\text{ Mg ha}^{-1}$  higher in the enclosures than the open plots (back-transformed, 95%

confidence interval of 1.5 to 2.9,  $t = 4.7$ ,  $p < 0.001$ , Figures 3 and 4f, Table S2f). The difference in AGB between the enclosures and open plots was 32% (median, interquartile range 1.4 to 69%) of the AGB in the enclosures (estimated across sites where the AGB in the enclosures was at least  $2\text{ Mg ha}^{-1}$ , Figure S7).

AGB of the vegetation increased with productivity. However, the rate of increase did not vary between open plots and enclosures (Figure 6, there was no significant interaction between treatment and NPP in determining AGB, linear model  $F_{1,193} = 1.80$ ,  $p = 0.18$ ; Table S4). Moose density also increased with NPP (Figure 6).

## 4 | DISCUSSION

In this study, we unified a network of moose enclosure experiments distributed across the boreal forest biome and used ALS data to identify general patterns and moderators of forest canopy responses to moose. Our findings reveal a remarkable consistency in forest response to moose browsing across regions. AGB and canopy vertical complexity both had uniform responses to moose and did not vary between regions nor with environmental modifier variables. The response of canopy height did vary between regions and with temperature, moose density and study duration; however,



**FIGURE 4** Moose impact on forest canopy properties derived from airborne laser scanning (ALS) data. The top row shows the duration-standardised responses expressed as the difference between paired exclosures and open plots, divided by the duration of the exclosure experiment in years at the time of data acquisition. The bottom row shows the unstandardised responses, showing the canopy state at the time of ALS acquisition. Forest canopy variables shown are (a and d) canopy height (90th percentile), (b and e) vertical complexity index and (c and f) above-ground biomass.

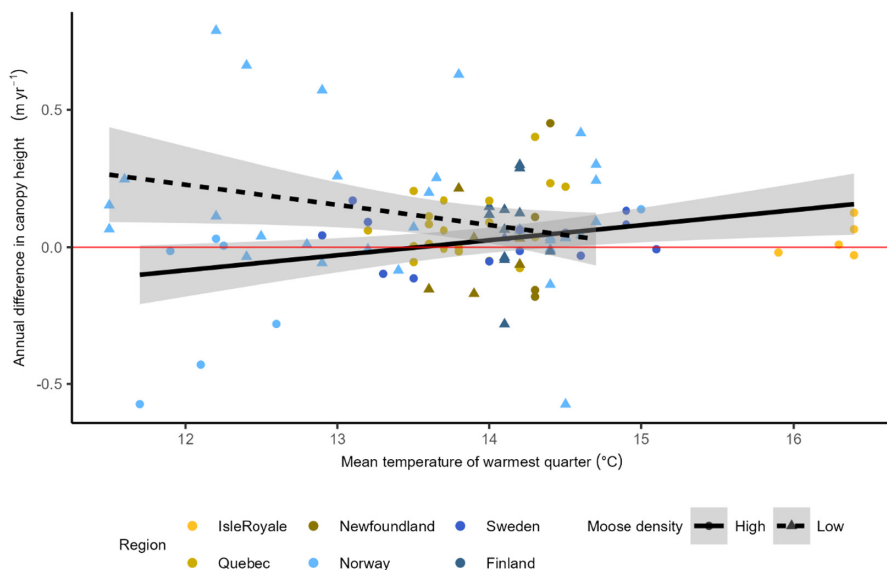
the coefficients of determination were low, and regional differences were largely driven by Isle Royale. These findings imply that moose exert a relatively homogenous influence on boreal forest canopy structure, largely independent of locality and ecological context. While meta-analytical studies (Bernes et al., 2018) and reviews (Leroux et al., 2020) have attempted to integrate ungulate impacts on vegetation across disparate studies, designs and methodologies, we here have used ALS as a common analytical platform enabling us to synthesise moose impacts on boreal forest canopies across the biome.

As we hypothesised, canopy height, complexity and AGB were all higher in the absence of moose across the boreal biome. Canopy height was the only response variable, which varied with environment. We found a significant interaction between moose and temperature (but not NPP) in determining canopy height both on

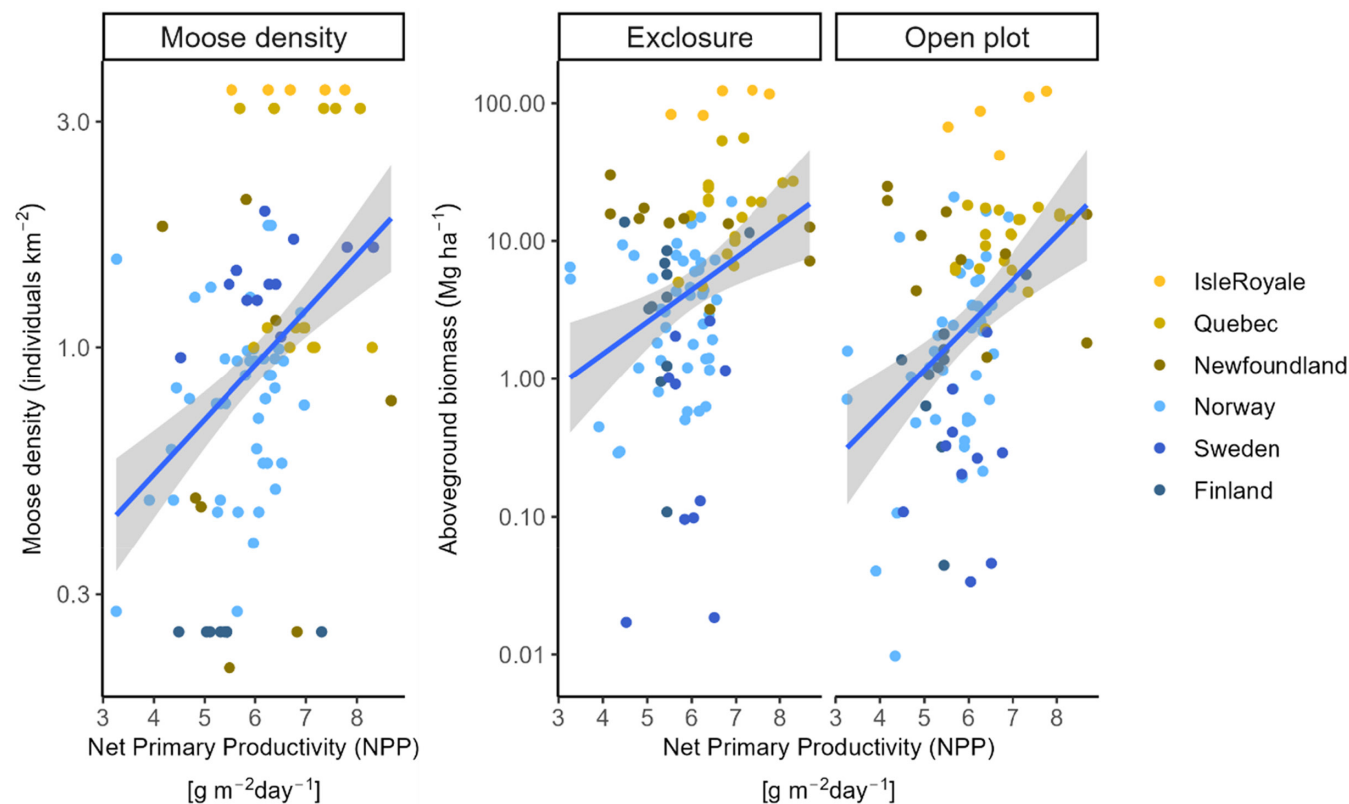
an annual and total, accumulated basis. The interaction was such that the impact of moose increased with temperature where moose density was high but decreased slightly where moose density was low (although low densities of moose were not found in warmer localities, Figure 5). This is in line with our second hypothesis of a greater impact of moose where moose densities were high and temperatures low. However, there are many uncertainties around potential interactions between temperature, moose browsing and tree growth across the boreal forest biome (Vuorinen et al., 2020).

On average canopy height differed between exclosures and open plots by 64 cm, or by 6 cm per year of study. These values are relatively modest compared with field-measured variation in height growth (Kolstad et al., 2018). However, our study measures the whole canopy and, thus, integrates the responses of tree and shrub species with varying utilisation by browsing moose, including





**FIGURE 5** Model predictions based on the linear models of canopy height standardised by duration, visualising the interaction between summer temperature and moose density. Points indicate the observed values with colour indicating region. Prediction lines are shown for high (circle points,  $\geq 1$  moose  $\text{km}^{-2}$ ) and low (triangular points  $< 1$  moose  $\text{km}^{-2}$ ) moose densities. This threshold approximates to the average moose density across the sites (median = 0.94, mean = 1.2 moose  $\text{km}^{-2}$ , Figure 2). 95% confidence intervals of the model predictions are shown by shaded regions. Model coefficients are shown in Table S2.



**FIGURE 6** Moose density and vegetation above-ground biomass in enclosure and open plots plotted along the gradient of net primary productivity across sites. Points are coloured by region. Note that y axes are log scaled in all panels. Regression lines are shown. The slope of the regression did not significantly differ between enclosure and open plots (Table S4).

rarely browsed, unpalatable species such as spruce (*Picea*; McLaren et al., 2009; Speed et al., 2013). Indeed, moose browsing may facilitate the growth and expansion of unpalatable tree species to the canopy (Leroux et al., 2021) and also promote the relative abundance of slow-growing conifers over fast-growing deciduous trees (Pastor et al., 1988). It also does not account for that height growth responses may vary with the size of the trees (Speed et al., 2013),

and our measures also include the growth of individuals out of reach of moose browsing. Isle Royale was the only region that diverged from the other regions with a lower annual response of canopy height to moose exclusion. This is likely because the enclosures there were of far longer duration (with a mean duration of 67 years on Isle Royale, compared to a mean of 10 years elsewhere; Figure 2, Table S1) than the other studies, providing more opportunities for

trees to eventually escape browsing height. This is supported by study duration being a predictor with a negative slope of total canopy height difference between the treatments.

The lack of variation in moose impact with environmental variables, and in particular moose density and productivity was surprising and counter to our hypotheses. Even for canopy height, where a significant interaction was found between moose density and summer temperature, the coefficient of determination was low ( $<0.15$ ). The lack of effect is unlikely to be caused by the low quality of environmental data, since we found no differences between regions (which varied in environment [Figure 2](#)) except for the regional difference in canopy height between Isle Royale and other regions. Covariation of environmental variables may have also masked potential effects. For example, more productive regions and younger forest stands have higher moose densities ( $r = 0.42$  and  $0.45$ , respectively), yet this should then imply a greater impact of moose exclusion in productive regions. Our hypothesis of an interaction between moose density and productivity (as seen to a limited extent for canopy height) assumes that moose densities are set by bottom-up dynamics. In reality, moose densities are set by management (controlled hunting) over most of our study sites (Speed et al., 2019), and partly by predation and parasite outbreaks on Isle Royale, rather than bottom-up dynamics (Vucetich & Peterson, 2004). The occurrence of extreme weather events such as extreme winters or hot summers can also have more dramatic impacts on moose population densities than climatic averages (Holmes et al., 2021; Vucetich & Peterson, 2004).

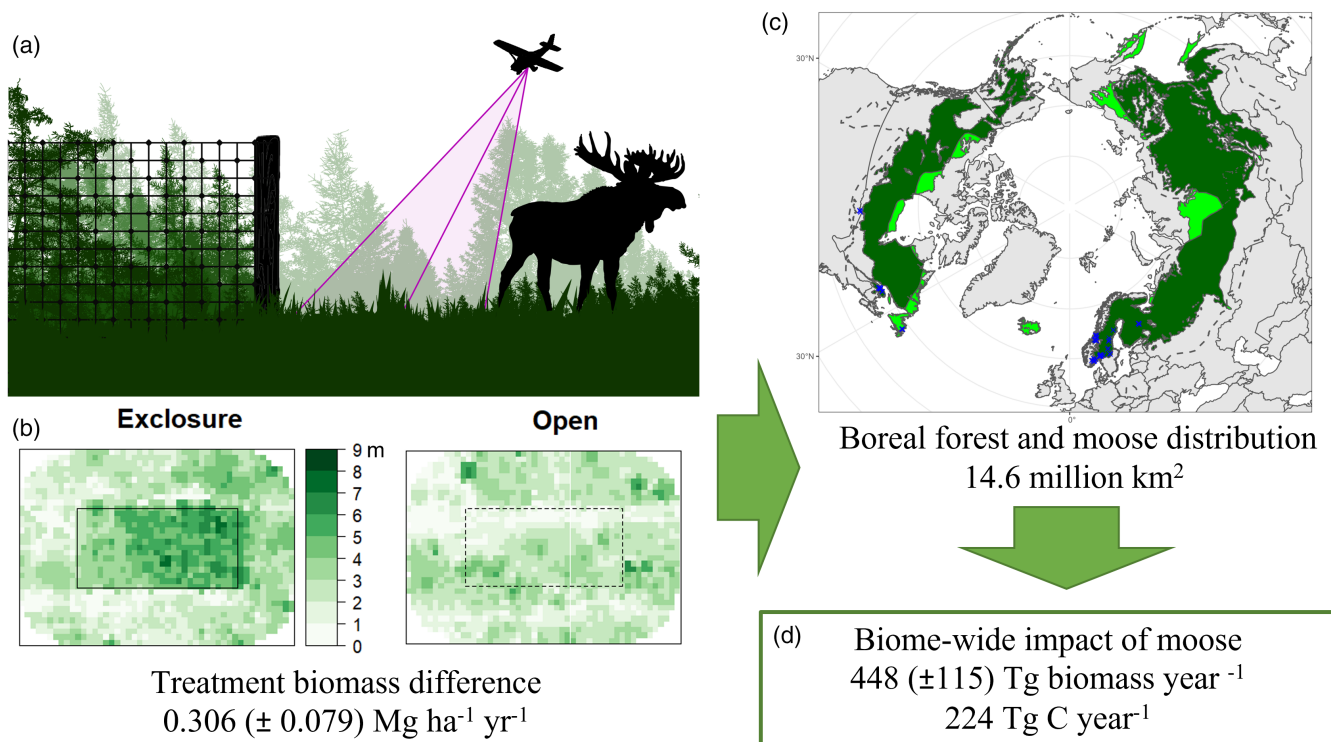
AGB increased with productivity, however, counter to our predictions, this increase was the same between exclosures (where theory predicts vegetation biomass to increase with productivity in the absence of herbivores) and open plots (where theory predicts vegetation biomass should be independent of productivity; Oksanen et al., 1981). The two processes described above can also explain these counter-theoretical results regarding vegetation biomass variation with productivity across open plots and exclosures. The presence of unpalatable species in the canopy (and in many regions, the preference of forestry management for these species leading to planting and stand-tending to facilitate their growth), reduces the ability of moose to regulate plant biomass; some plant species, thus, escape the trophic cascade (Oksanen & Oksanen, 2000). Additionally, the regulation of moose populations through management by humans is in large part independent of either predation or forage availability across most of the biome. Thus, the application of traditional trophic theories, such as the ecosystem exploitation hypothesis, to manage boreal forest ecosystems is not simple.

We hypothesised that the impact of moose on forest canopies would be greater following large-scale pulse disturbances such as logging and spruce budworm outbreaks (see Leroux et al., 2020). However, we did not find any evidence to support this. We had very few study sites in undisturbed forests, but those that we did have showed no difference in response to browsing, although these were also the oldest sites ([Figure S8](#)). A further complication is the varying time between disturbance and moose exclusions which could initiate

alternative successional trajectories (De Vriendt et al., 2021). While we did not find that forest responses to moose varied with disturbance, it remains likely that interactions between disturbance, forest successional dynamics and moose populations do exist (Arsenault et al., 2016; Bjørneraas et al., 2011; Wam et al., 2016). The magnitude of the moose effect on AGB (32%) should also be placed in the context of the impact of forest management practices, where thinning can alter standing biomass by 50% (Jørgensen et al., 2021). The interactive effects of stand thinning and moose browsing on forest successional dynamics remain to be quantified at broad scales.

The uniform response of AGB to moose across the exclosure network allows us to upscale the impact of moose on biomass across the boreal biome. The area of the boreal forest biome with moose is 14.6 million km<sup>2</sup> (estimated as the intersection of the IUCN Red List distribution of *A. alces* (Hundertmark, 2016) and the boreal forest biome from the WWF global biome map (Olson et al., 2001)). The mean annual impact of moose on AGB is 0.306 Mgha<sup>-1</sup> year<sup>-1</sup> ( $\pm 0.079$  [Table S2](#)). Thus, the biome-wide impact of moose on AGB may be 448 ( $\pm 115$ ) Tg per year. Assuming that 50% of the AGB is carbon, this biomass would translate into an annual difference above-ground carbon of 224 Tg C year<sup>-1</sup> across the biome ([Figure 7](#)). This is somewhat conservative as areas such as Newfoundland where the moose is introduced are not included in this estimate. Our estimate of moose impact on above-ground carbon flux of 224 Tg year<sup>-1</sup> is comparable on an area basis to the 66 to 141 Tg C year<sup>-1</sup> as the difference between NPP at high and low moose densities estimated by Schmitz et al. (2018) across only Canada (which spans around 30% of the total area of the moose distribution within the boreal forest biome). This is not surprising as Schmitz et al. (2014) based their calculations on Isle Royale data, and our study shows consistency of moose impact on AGB across the biome. However, our study is the first estimate of how above-ground carbon is affected by moose across the whole biome, This highlights the potential of management of moose populations as an approach to climate mitigation and adaptation (Malhi et al., 2022). For example, Wilmers and Schmitz (2016) estimated that the restoration of grey wolf populations across North America would compensate for a significant proportion of carbon emissions due to population control of moose by predation. However, our analyses suggest that wolf restoration would only affect above-ground carbon storage in forest regions where moose populations are limited by bottom-up processes. Of course, the impact of moose browsing on below-ground carbon cycling, mediated through changes in litter types associated with vegetation change (Kielland et al., 1997; Pastor & Naiman, 1992), is likely to be significant, and also requires scaling across the biome.

While the ALS approach in this study allows for the estimation of AGB (and hence carbon), a large uncertainty in ecosystem carbon net responses to moose lies below-ground (Leroux et al., 2020; Schmitz et al., 2018). Moose can impact soil carbon by modifying tree species compositions (and hence litter types) and trampling (Pastor et al., 1988; Pastor & Naiman, 1992). While the impacts of moose on vegetation are clear and notable, studies have not found evidence that the impacts cascade into soil nutrient stocks or cycling



**FIGURE 7** Scaling of average annual effect of moose on above-ground biomass as the mean difference between enclosures and open plots to the whole biome. (a) Airborne laser scanning (ALS) of sites with paired enclosures and open plots allows quantification of canopy responses to moose (b, example canopy height models (m) visualised is site CA1001 from Quebec [see Table S1]). The treatment difference in above-ground biomass is multiplied by the area of boreal forest with moose (c, dark green) shown as the intersection of the area of boreal forest (light green) with the moose distribution (dashed line; study regions are shown by blue points). This results in the annual estimate of moose impact on above-ground biomass and carbon (d). Drawings in (a) by Kirsten Engeseth.

within one to two decades of moose exclusion (Ellis & Leroux, 2017; Kolstad et al., 2017, 2018). It is clear that a longer-term perspective on soil biogeochemical responses to moose browsing is required to estimate net ecosystem carbon responses to moose (Leroux et al., 2020).

The above estimation assumes that the whole boreal biome responds to moose in the same way as our 100 enclosures distributed across large parts of the biome. However, our study sites are not a random sample of available boreal forest–moose range. There could be inherent biases in where the enclosure experiments (with available ALS data) have been set up. For example, it may be that experiments are more likely to be initiated in localities with regionally high moose densities, or where there are management or stakeholder interests in understanding the impacts of moose on boreal forests. Indeed our studies are primarily from the more productive southern regions of the boreal biome (Figure 7) Furthermore, our study does not include sites from the Eastern Palaearctic or Western Nearctic boreal forests (moose densities are low in the former but high in the latter; Jensen et al., 2020). While we do not expect that the ecology in these regions will greatly differ from the localities studied here, it could be argued that as moose populations (and subspecies) differ in body mass, their impact may vary, or have different dependencies on ecological contexts. A systematic mapping of knowledge of herbivore impacts on boreal forest ecosystems, as undertaken across the

Arctic tundra by Soininen et al. (2021), would illuminate knowledge gaps and better allow scaling-up of herbivore impacts.

LIDAR data have a broad application potential in ecological research (Davies & Asner, 2014; Simonson et al., 2014; Vierling et al., 2008). In our study, we used ALS as a common analytical platform to synthesise the response of forest canopies to moose across multiple enclosure experiments distributed around the boreal forest biome. This allowed us to undertake the same analyses on sites where different field methodologies have been deployed. For all our sites, the ALS data used were available publicly or from land management agencies, and data were available for the vast majority of enclosure sites available to us. This highlights the ease of application, and financial and temporal feasibility of using ALS for such integrative studies. The ALS data available to us were at relatively low point densities ( $\leq 5$  points  $\text{m}^2$ ) in contrast to what can be achieved using bespoke collected data (either from airborne or terrestrial-based LIDAR scanning). However, the available data were clearly at high enough resolution to detect moose impacts on forest canopies, and a previous study has highlighted the similarity between ALS and field data in assessing moose effects on forest canopies (Kolstad et al., 2021; Snøan, 2019). We used externally calibrated models to estimate AGB from ALS metrics. Some concerns have been raised regarding such models as both variable selection and parameter estimates are dependent on properties of field data (de Lera Garrido

et al., 2020). However, by using models specific to region, stand age and forest type, we assume to minimise these concerns, and correlations between treatment differences were high between all methods ( $0.46 \leq r_s \leq 0.86$ , Figure S9).

In this study, we have answered a call for both a distributed network of moose exclosure experiments across the boreal forest biome and the application of remote sensing data to understand moose impacts. By using ALS data, we have synthesised responses to moose, identifying a surprising degree of convergence in forest canopy response to moose browsing across the boreal forest biome. Our study highlights how ALS data can be used to investigate plant–animal interactions across distributed experiments and scale up these findings. While we have performed a basic scaling of our AGB findings across the biome, further challenges exist in scaling exclosure studies to the landscape scale, and predicting across moose densities, as opposed to the binary contrasts of exclosure experiments.

### AUTHOR CONTRIBUTIONS

The study was designed by James Speed with Joris P. G. M. Cromsigt, Anders L. Kolstad, Jari Kouki, Shawn Leroux, Lynette R. Potvin, Jean-Pierre Tremblay, Märtha Wallgren and Fredrik Widemo. Data were contributed by Anders L. Kolstad, Jari Kouki, Shawn J. Leroux, Lynette R. Potvin, Jean-Pierre Tremblay, Märtha Wallgren and Fredrik Widemo while Gunnar Austrheim, John Gosse, Michael den Herder, and Luise Hermanutz also contributed to the exclosure experiments. Data were analysed and visualised by Tanja K. Petersen and James D. M. Speed with support from Anders L. Kolstad, Shawn Leroux and Coline Courtois. Tanja K. Petersen and James D. M. Speed wrote the manuscript with input from all authors.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.14093>.

### DATA AVAILABILITY STATEMENT

Data are available on FigShare <https://doi.org/10.6084/m9.figshare.21564030.v1>. The localities of the Finnish sites (12 out of 106 total sites) are withheld due to conservation concerns, in line with Finnish law; for further information regarding these sites contact co-author Jari Kouki: [jari.kouki@uef.fi](mailto:jari.kouki@uef.fi).

### ORCID

Tanja K. Petersen  <https://orcid.org/0000-0002-7599-712X>  
 Anders L. Kolstad  <https://orcid.org/0000-0002-9623-9491>  
 Jari Kouki  <https://orcid.org/0000-0003-2624-8592>  
 Shawn J. Leroux  <https://orcid.org/0000-0001-9580-0294>  
 Jean-Pierre Tremblay  <https://orcid.org/0000-0003-0978-529X>  
 Märtha Wallgren  <https://orcid.org/0000-0002-3172-4496>  
 Fredrik Widemo  <https://orcid.org/0000-0002-3688-9847>  
 Joris P. G. M. Cromsigt  <https://orcid.org/0000-0002-8632-9469>  
 Gunnar Austrheim  <https://orcid.org/0000-0002-3909-6666>  
 Michael den Herder  <https://orcid.org/0000-0002-6562-3407>  
 Luise Hermanutz  <https://orcid.org/0000-0003-0706-7067>  
 James D. M. Speed  <https://orcid.org/0000-0002-0633-5595>

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Canopy models (raster, m) all experimental sites/paired plots. Circular points indicate the corners of the plots, and thin black lines indicate the fences (of the exclosures). Stand age and main disturbance type are indicated in the plot. Black polygons indicate the

remnant trees (>8 m) clipped from the LAS files. **Table S1.** Compiled (meta-)data on each of the paired study sites. Country and region are coded as N = Norway, F = Finland, S = Sweden, USA = USA, C = Canada, IR = Isle Royale, Q = Québec, NF = Newfoundland. Main disturbance type is coded as LC = logging/cutting, B = budworm outbreak, F = fire, N = no disturbance. The year of the most recent natural disturbance or clearcutting is only shown for sites where this disturbance occurred. Site A23 was omitted from analyses as the mean height of returns in the enclosure plot was 0 m. Positive differences in response variables indicate a higher value in the enclosure than in the open plot.

**Table S2.** Coefficient estimates for selected model for three response variables (canopy height, VCI and aboveground biomass) in terms of annual (a–c) and total (d–f) differences between treatment. Models were selected through backward selection from the full models based on likelihood ratio tests. Estimates and standard errors (SE) shown. Coefficients differing from 0 at  $p < 0.05$  are shown in bold text. Multiple  $R^2$  values are shown for models where independent variables were retained. Summer temperature was centred on the mean. The factor reference level for region was Isle Royale. Pairwise comparisons between all regions are shown in Table S3.

**Table S3.** Pairwise contrasts between all regions in the linear model of annual treatment difference in canopy height (see Table S2). P values are corrected for multiple tests using the Tukey method.

**Table S4.** Analysis of variance for linear model of aboveground biomass within each plot (enclosure and open plot). NPP, treatment, their interaction and region were fitted as fixed effects.

**Figure S1.** Pairwise correlations between environmental variables, as well as LIDAR point densities. The upper triangle shows the Spearman correlation coefficients with the text size proportional to the absolute value. Disturbed area is log transformed. Stand age and duration are in decades. Summer temperature is the mean temperature of the warmest quarter (°C). Moose density is individuals km<sup>-2</sup>, NPP in g m<sup>-2</sup> day<sup>-1</sup> and point density in points m<sup>-2</sup>.

**Figure S2.** Response variables plotted against the point density of the LIDAR data. Points are coloured by region.

**Figure S3.** Univariate pair plots between canopy height difference (total – top row, annual – bottom row) and predictor variables. Positive differences indicate higher values in the enclosure.

**Figure S4.** Univariate pair plots between canopy vertical complexity

index difference (total – top row, annual – bottom row) and predictor variables. Positive differences indicate higher values in the enclosure.

**Figure S5.** Univariate pair plots between aboveground biomass difference (total – top row, annual – bottom row) and predictor variables. Positive differences indicate higher values in the enclosure.

**Figure S6.** Model predictions based on the linear models of canopy height at the time of ALS data acquisition (and not scaled by study duration), visualising the interaction between summer temperature and moose density. Points indicate the observed values (positive values indicate taller canopies in the enclosures) with colour indicating region. Prediction lines are shown for high (circle points,  $\geq 1$  moose km<sup>-2</sup>) and low (triangular points  $< 1$  moose km<sup>-2</sup>) moose densities. This threshold approximates to the average moose density across the sites (median = 0.94, mean = 1.2 moose km<sup>-2</sup>, Figure 2). 95% confidence intervals of the model predictions are shown by shaded regions. Model coefficients are shown in Table S2.

**Figure S7.** Plot of treatment difference in aboveground biomass (positive value indicates higher biomass in the enclosure) against the stand biomass in the enclosure. Points are coloured by region. The no difference ( $x = 0$ ) and 100% difference (1:1) lines are shown.

**Figure S8.** Boxplot of response variables by disturbance type. Most sites were logged/cut (85) with few with other disturbance (7 of which spruce budworm 6, and fire 1) or undisturbed (8, Table S1).

**Figure S9.** Pairwise correlations between treatment differences in aboveground biomass as estimated by three different formulae; that of Økseter et al. (2015) and the boreal-coniferous and boreal-mixed forest estimates of Boudreau et al. (2008). Upper triangles show the Spearman correlation coefficients.

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