


Net Climate Effects of Moose Browsing in Early Successional Boreal Forests by Integrating Carbon and Albedo Dynamics

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Key Points:

- Field data are used to study the effects of moose on forest albedo and carbon dynamics
- Moose browsing contributes to warming by limiting carbon sequestration, but exerts a cooling effect by increasing surface albedo
- The two effects have the same order of magnitude, but vary regionally, and forest management practices should consider these effects

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Moose (*Alces alces*) is a large herbivore that can mediate boreal forest regeneration after timber harvest through selective browsing of tree species. Despite increasing evidence of moose browsing influence on tree growth in early successional forests, climate effects due to changes in carbon sequestration rates and biophysical factors such as albedo remain largely unexplored. We used 11 years of data from 44 pair-sites of herbivore exclosures within clear-cut forests in Norway to investigate how moose browsing alters aboveground tree biomass and albedo. We find a higher total aboveground tree biomass (mainly deciduous species) in unbrowsed than browsed forest plots, as moose browsing limited the growth of tree biomass. The effect of moose exclosure on relative tree abundances differed between sites, suggesting that moose browsing has stronger effects on forest structure than composition. At the same time, moose increased forest albedo relative to un-browsed forests, driving biophysical cooling. When averaged at regional levels, climate effects due to changes in biomass and albedo are of similar magnitude, but contributions can diverge in specific locations. In a region with intensive forestry operations and high moose density, CO₂ emissions from moose browsing in post-harvested sites can be equal to about 40% of the annual emissions of fossil fuels from that region. Cooling effects from increased albedo can offset about two thirds of this impact. Given its influence on tree growth rates and climate impacts, management of moose browsing density should be integrated into forest management plans to optimize climate change mitigation and forest productivity.

Plain Language Summary Moose play a key role in shaping landscape structure and forest composition. For example, moose influence vegetation and soils via foraging, trampling, and nutrient cycling, thereby affecting tree growth rate, community composition, and ecosystem carbon budget. It is estimated that moose alone can browse 10% of the annual harvest volume in Norway. Moose also alter land cover properties such as surface albedo (i.e., the fraction of reflected solar energy radiation), with direct implications for the climate. A better knowledge of the interactions of the climate-forest-moose nexus can help the identification of integrated management of forest resources and wild herbivores that maximize climate change mitigation benefits and ecosystem services, including timber value. Our study analyzed 11 years of empirical field measurements from 44 post-harvest sites in Norway to study climate impacts from both carbon sequestration and albedo dynamics induced by moose browsing. We found that moose browsing cools the climate by increasing surface albedo and warms the climate by limiting forest carbon sequestration. The two effects tend to compensate for each other, but there are large regional variations. Given the potential effects on both tree growth and the climate, moose browsing should be more actively integrated into forest management plans.

1. Introduction

The boreal forest is among the largest biomes on Earth and provides a variety of ecosystem services, including timber, habitat provision, and climate regulation (DeLuca et al., 2008; Gauthier et al., 2015; Nilsson et al., 2001; Pan et al., 2011). Timber production is an economically important activity in boreal forests, particularly within Scandinavian countries such as Norway. Roughly 70% of Norwegian forests are managed for the production of timber, and mechanized harvesting methods such as clear-cutting are commonly used (Rognstad et al., 2016). These disturbances alter the forest land cover and its structural diversity (Yang & Man, 2018; Zhou et al., 2021). In early successional stages following harvest, pine (*Pinus sylvestris*) and spruce (*Picea abies*) are typically planted but patches of harvested boreal forest may become dominated by deciduous trees and woody shrubs (Carleton & Maclellan, 1994; Edenius et al., 2002). As successional forest grows, forest managers may thin

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these deciduous species to facilitate the growth of more economically valuable coniferous trees (Wiensczyk et al., 2011). After several decades of post-harvest growth, managed forest stands in Norway typically become completely dominated by coniferous species (Carleton & Maclellan, 1994; Trollstøl et al., 2020).

Boreal forest management practices can affect the climate system through different pathways: by altering biogeochemical (e.g., carbon cycling) and biophysical processes (e.g., albedo, evapotranspiration, and surface roughness; Kellomäki et al., 2021; Luysaert et al., 2014). After a harvest disturbance, the net primary production increases as early successional species begin to sequester atmospheric carbon into living biomass (Harmon et al., 2011). At the same time, timber harvest changes biophysical processes that can influence Earth's radiation budget and climate. Among the biophysical processes, both empirical and modeling approaches show that albedo, a property of the land surface corresponding to the proportion of incoming solar radiation that is reflected by the surface (A. K. Betts & Ball, 1997), typically has a dominant effect in boreal forests (Davin & de Noblet-Ducoudre, 2010; Li et al., 2015; Perugini et al., 2017). Albedo is influenced by vegetation characteristics, such as forest volume (Hu et al., 2018), canopy cover (Lukes et al., 2013), and tree species composition (Cherubini et al., 2017; Kuusinen et al., 2016), and by climatic factors, such as temperature and snow (Essery, 2013; Thackeray et al., 2015; Wang et al., 2016). Dense forests with high standing volume and complete canopy closure are generally darker (i.e., have lower albedo) than forests with low volume and sparse canopy, as dense forests mask vegetation on the forest floor that typically has higher reflectivity than the tree canopy. Additionally, forest stands of deciduous tree species tend to have higher albedo than coniferous stands (Zhao & Jackson, 2014), as deciduous, broad-leaved foliage is typically more reflective than coniferous foliage (Hovi et al., 2017; Lukeš et al., 2013). The differences in albedo between forests with differing volumes and species composition is amplified when snow is present. Snow on the forest floor is highly reflective but can be masked by the forest canopy. Forests with low volume and sparse canopy mask less snow and, as a result, have higher surface albedo than dense forests with high canopy closure (Hu et al., 2018; Lukeš et al., 2014). Additionally, deciduous trees lose foliage in winter months, which likely reduces the canopy coverage and masking effects. Timber harvest within boreal forests can thus temporarily increase albedo and cause a biophysical cooling effect on global climate (Kellomäki et al., 2021; Mykleby et al., 2017; Perugini et al., 2017). Harvest opens up the dense, dark forest canopy and exposes the forest floor, which typically has a higher albedo and absorbs less solar radiation to be dissipated as energy at the surface (Anderson et al., 2011). As successional forest grows and the canopy begins to close, however, the cooling albedo effect of timber harvest gradually declines.

A growing body of literature has focused on the potential climate impacts of both biogeochemical and biophysical changes associated with forest dynamics (Alkama & Cescatti, 2016; Anderson et al., 2011). Several studies highlighted the need to account for the impacts of surface albedo alongside those of carbon to avoid suboptimal or even counterproductive mitigation results (R. A. Betts, 2000; Mahmood et al., 2014; Perugini et al., 2017; Zhao & Jackson, 2014). In contrast, less attention has been given to potential climate effects of other types of disturbances within successional forests, such as those of large herbivores. Browsing by large herbivores can critically shape landscape and vegetation structure in the boreal forest biome, and increasing scientific evidence highlights the importance of considering their effects (Vuorinen et al., 2020), as they can increase or decrease rates of biogeochemical processes by 40% on average (but ranging from 15% to 250%; Schmitz et al., 2018). In North American boreal forests, Schmitz et al. (2014) estimated that the annual amount of carbon kept in the atmosphere by moose (*Alces alces*) may equal 42%–95% of Canada's annual fossil fuel emissions. Similar to timber harvest, moose browsing also affects biophysical processes at the land surface (Cahoon et al., 2012; Cohen et al., 2013). Similar dynamics are also seen in other ecosystems, for example, reindeer (*Rangifer tarandus*) herbivory has been shown to increase surface albedo in arctic shrub systems by reducing shrub height and abundance (Cohen et al., 2013; Te Beest et al., 2016).

Large herbivores are widespread in Norwegian forests (mainly moose, but also roe deer *Capreolus capreolus* and red deer *Cervus elaphus*) and have large impacts on boreal ecosystems (moose alone can browse 10% of the annual harvest volume; Austrheim & Kolstad, 2019; Speed et al., 2019). They influence vegetation and soils via foraging, trampling, and nutrient cycling, thereby affecting growth rate, plant resource-use strategies, community composition, and ecosystem carbon budget (Kolstad et al., 2019; Schmitz et al., 2018). Moose browse nutrient-rich leaves and thin branches of mainly deciduous trees, which are easily accessible in post-harvest sites (Månsson et al., 2007; McInnes et al., 1992). In contrast, moose tend to avoid less palatable coniferous species such as Norway spruce (Hörnberg, 2001). Moose occasionally browse on pine, particularly when preferred deciduous forage is unavailable during winter months (Shipley et al., 1998). In successional forests, moose can arrest

the vertical growth of deciduous tree species and release surrounding coniferous species from competition for light, potentially driving these forests to become dominated by unpalatable coniferous species over time (Kolstad, Austrheim, Solberg, de Vriendt, & Speed, 2018; McInnes et al., 1992). The net effects on forest dynamics are complex and highly linked to local climatic conditions. Foraging can limit the vegetation growth of certain species and keep more open landscapes (higher albedo) than areas at lower browsing intensity, but higher availability of nutrients in the top-soil layers can facilitate earlier germination and tree growth (Cromsigt et al., 2018; Schmitz et al., 2018), but no significant effects on soil carbon changes are found in early successional Norwegian forests (Kolstad et al., 2018).

Overall, potential climate impacts of moose may be of particular concern to manage forest stands for both timber value and climate mitigation. However, despite the concern that moose may influence carbon cycling within boreal forests at a landscape scale and consequently affect timber supply potential and global climate (Leroux et al., 2020; Schmitz et al., 2014), its effects on tree growth rates, species composition, and albedo are not yet understood. To the best of our knowledge, no study has integrated empirical data to compare climate impacts from both carbon sequestration and albedo dynamics of moose browsing in successional boreal forest. This new knowledge can support the design of integrated management of forest resources and wild herbivores, for example, by identifying suitable browsing regimes in post-harvest forests to maximize climate change mitigation while securing intended tree growth rates.

In this work, 11 yr of empirical field data on post-harvest aboveground tree biomass and surface albedo dynamics are integrated with statistical regression models to address knowledge gaps regarding the net climate change effects of moose browsing in clear-cut boreal forests. Figure S1 in Supporting Information S1 shows a simplified scheme of the investigation method, while the data sets are summarized in Table S1 in Supporting Information S1. We used paired herbivore enclosure experiments (un-browsed) coupled with browsed open plots at 44 sites located within productive boreal forests in Norway to test the hypotheses that moose browsing (a) reduces aboveground tree biomass and (b) increases surface albedo after timber harvest. Additionally, we calculated relative abundances of deciduous and coniferous trees at our study sites to explore the effects of moose on tree community composition. We then integrated potential carbon and albedo effects using carbon equivalents to quantify the net climate impact of moose browsing in successional boreal forests for each individual plot and at a regional (county) scale. Finally, using data on average forest harvest area per county, we compare the moose browsing impact in terms of CO₂ emissions from biomass reduction with the emissions from fossil fuels in the different regions, so to benchmark the importance of the moose-induced disturbance relative to the regional carbon balance.

2. Methods

2.1. Study Design

To assess the effects of moose herbivory on tree biomass, albedo, and climate dynamics in successional boreal forests, we utilized 44 paired sites in three regions of Norway: Vestfold and Telemark, Innlandet and Viken, and Trøndelag (Figure 1a; county names and borders have changed multiple times since the establishment of our sites, hence the regions are indicated with multiple county names). Study sites were established in forest areas dominated by either Scots pine or Norway spruce trees prior to harvest that had been clear-cut a median of 3 yr prior to establishment. In addition to spruce and pine, forests in the study regions are characterized by a variety of deciduous tree species, including rowan (*Sorbus aucuparia*), downy birch (*Betula pubescens*), aspen (*Populus tremula*), and gray alder (*Alnus incana*).

Post-harvest planting of trees occurred at many of the sites after clear-cutting. Most sites in Trøndelag and Innlandet and Viken were planted with spruce. In Vestfold and Telemark, half of the sites were planted with spruce while the other half were dependent on the natural recruitment of pine. Besides planting, no forest thinning or additional silvicultural interventions occurred. Further details regarding forest type and postharvest treatment at each site can be found in Table S2 in Supporting Information S1, which also shows the clear-cut year, the starting year of enclosure treatments, the site productivity, and the densities of browsing wild herbivores. The climatic conditions of the sites are shown in Table S3 in Supporting Information S1. Several species of large herbivores are found within the study regions. Moose are the dominant forest browser at moderate-to-high densities across all regions (Figure 1b; Austrheim et al., 2011; Speed et al., 2019). Roe deer and red deer are also present, but at lower densities than moose.

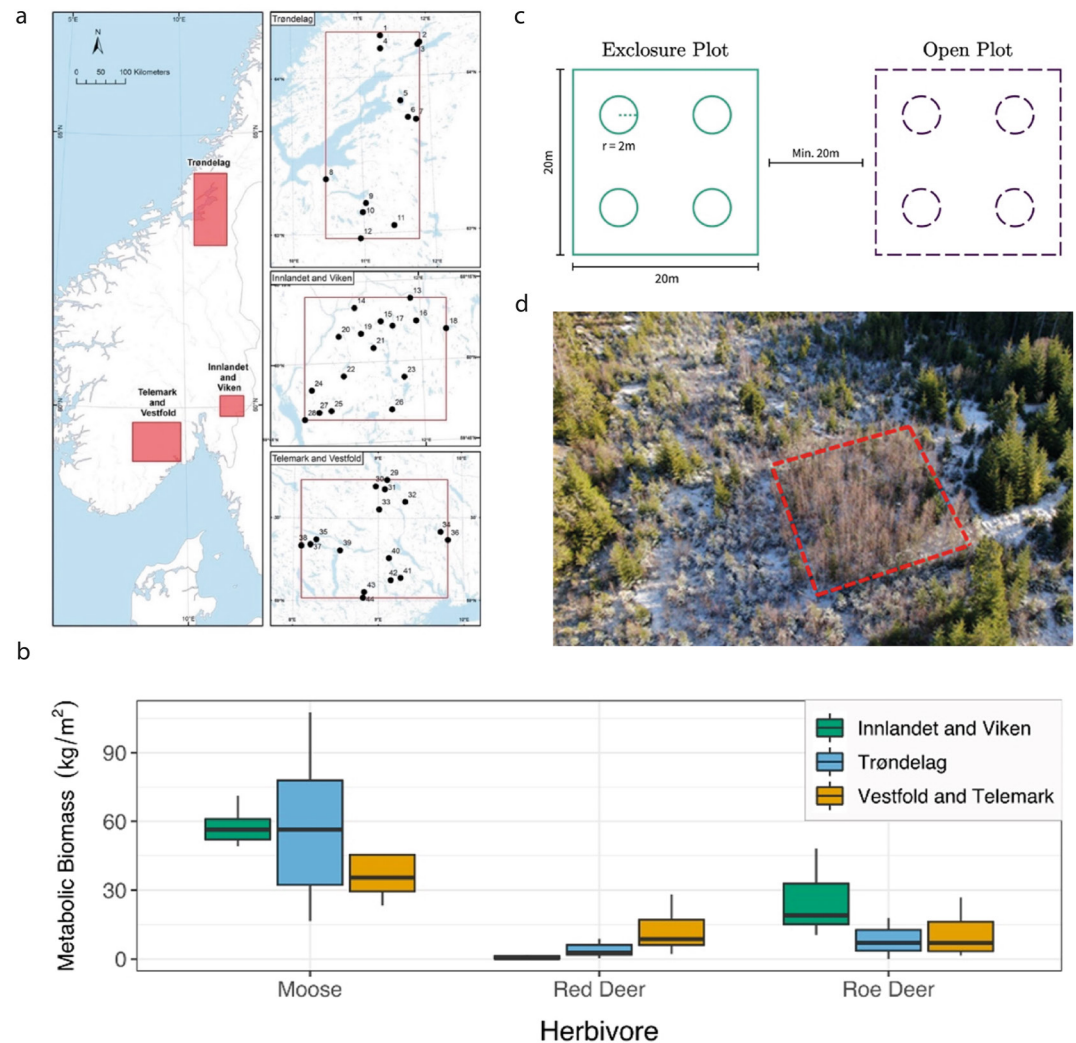


Figure 1. Location of the paired sites in the Norwegian boreal forest and corresponding density of large herbivores. (a) Map of 44 study sites located in three regions: Trøndelag, Vestfold and Telemark, and Innlandet and Viken. Site numbers correspond to those listed in Table S2 in Supporting Information S1, where specific details of animal browsing pressure are given for each site. (b) Densities of moose, red deer, and roe deer in each study region, represented by metabolic biomass per square kilometer (kg km^{-2}) in 2015. Boxes represent interquartile ranges and black lines show median values. Tails indicate minimum and maximum values. (c) An illustration of sampling method with the two plots of identical dimensions (20×20 m) placed at least 20 m apart. The enclosure plot (green) was fenced to a height of 2.5 m and made inaccessible to large herbivores. In contrast, the open plot (purple) was not fenced, allowing moose to browse freely within the plot. Vegetation was sampled annually within circular subplots. (d) An aerial photo of a moose enclosure (red box) at one of the study sites, showing differences in tree density, height, and composition with the surrounding open areas (photo credits: Sten Ivar Tønseth).

Each of the 44 sites used in this study consisted of two square plots (20×20 m) established at a distance of at least 20 m from one another. Each plot at a site was randomly designated as either an enclosure or an open plot. The enclosure was subsequently fenced to a height of roughly 2.5 m, which kept large forest herbivores from entering the plot and eliminated browsing impacts from moose and other cervids, but not medium or small herbivores (i.e., hare *Lepus timidus* and rodents). The open plot remained accessible to large herbivores and subject to moose browsing throughout the study period. Since the moose was the dominant herbivore at all sites (Figure 1b, Table S2 in Supporting Information S1), the study design is referred to as a moose enclosure study henceforth.

Four circular subplots with a radius of 2 m were established within each plot (Figure 1c) to annually monitor tree growth within these subplots after enclosure. The center of each subplot was placed 5 m from the inner edges of the larger plot to reduce potential edge effects from enclosure fencing. Sampling at each site was typically

performed during spring months after snow had melted at each site. Speed, Austrheim, Hester, Solberg, and Tremblay (2013) and Speed et al. (2013) provide more details regarding design of study sites. Figure 1d is an aerial view of the study site design, from which it is possible to visually appreciate the difference in vegetation composition and surface reflectivity between treatments.

2.2. Tree Biomass and Abundance

To investigate the effects of moose enclosure on post-harvest tree biomass, we used allometric biomass models to estimate aboveground tree biomass at each study site in the years after enclosure. We relied upon a long-term data set of individual tree observations recorded at each study site (available at Hu et al., 2023, <https://doi.org/10.6084/m9.figshare.21879060.v1>). This data set included observations of tree density, species, and height class in 50 cm increments recorded annually within the circular subplots at each site. The data set also included detailed measurements of diameter-at-ground-level (mm) and height (cm) for trees at Trøndelag sites in 2016. We chose to exclude trees greater than 6 m in height, as these were likely retained at the harvest (Kolstad et al., 2022). We then used allometric biomass models to estimate aboveground tree biomass for each tree in the long-term data set. Although allometric biomass models exist for common boreal tree species in Norway (Braastad, 1966; Brantseg, 1967; Vestfjord, 1967), these models are typically not applicable to trees with small stem diameters. Additionally, they require both diameter-at-ground-level and tree height as model parameters to produce biomass estimates. Because our data set included many small trees with height class as the only associated measurement, we chose to use locally developed biomass models that solely rely upon height as a parameter.

Kolstad et al. (2018) produced biomass models for birch, rowan, pine, and spruce trees using tree samples from study sites within Trøndelag (Table S4 in Supporting Information S1), combining these models with a back-fitting procedure to produce height-only biomass models for trees in moose enclosures (Table S5 in Supporting Information S1). We utilized a similar back-fitting procedure to produce height-only biomass models for trees in open plots (Figure S2 in Supporting Information S1; Table S6 in Supporting Information S1). These models include diameter-at-ground level and height as parameters to produce estimates of biomass and are based upon field samples of trees at study sites. We then generated linear models for birch, rowan, pine, and spruce, where mass values of tree biomass were modeled as a function of tree height (cm). We sequentially removed nonsignificant terms and then chose the model with the highest value of adjusted R^2 as our best-fitting model. Further details about the back-fitting process and the biomass models we used can be found in Text S1 in Supporting Information S1. Using these height-only biomass models for enclosures and open plots, we then estimated aboveground tree biomass for individual birch, rowan, pine, and spruce trees in our long-term data set. We found relatively few observations of willow and common juniper in the data set. We chose to use biomass models corresponding to common tree species with similar morphology—birch for willow and spruce for juniper—to estimate biomass for these species.

To explore the effects of moose enclosure on tree species composition within successional forests, we calculated relative abundances of pine, spruce, and deciduous species (aggregating birch, rowan, and willow) within each subplot at our study sites across all years of available tree data. We then averaged subplot values of relative tree abundance within each of the study regions.

2.3. Site Productivity

To account for site productivity in our statistical analyses, we utilized a productivity index previously developed by Kolstad et al. (2018). The index consists of a standardized value of the maximum annual increase in tree biomass at each study site. Two sites in Innlandet and Viken had productivity values that were substantially higher than the rest (Table S2 in Supporting Information S1). These sites were not excluded from subsequent analyses, as we assumed that the high productivity values were realistic based on prior site knowledge.

2.4. Herbivore Densities

To assess the densities of moose, red deer, and roe deer in each of the study regions, we used spatiotemporal large herbivore density data available across Norway (Austrheim et al., 2011; Speed et al., 2019). Herbivore densities are represented by average metabolic biomass per square kilometer (kg km^{-2}) and were provided at the

municipality level in 10 yr increments from 1949 to 2009, as well as in 2015. There is more than one paired site per municipality, so some sites share the same herbivore pressure (see Table S2 in Supporting Information S1). Because our long-term tree data set spanned 2008–2019, we chose to use herbivore densities from 2015 (Table S2 in Supporting Information S1; Figure 1b), which represented a temporally intermediate value that could provide reasonable estimates of herbivore densities during our study period.

2.5. Albedo Dynamics

2.5.1. Nonlinear Albedo Model and Albedo Estimates

We utilized a nonlinear model to assess the effects of moose exclosure on postharvest albedo dynamics at each study site (Hu et al., 2018). It is produced by decomposing mixed signals via simultaneous un-mixing and nonlinear regression of multi-year satellite retrievals of surface albedo (MODIS MCD43A3 data product; Schaaf & Wang, 2015), high resolution (16 m) data sets of forest composition and structure parameters, and climate records. The model predicts monthly mean albedo values for any given year using tree-specific vegetation structure information and climatic conditions as explicit variables. We selected the best-performing version ($R^2 > 0.8$ against observations) out of many model variants based on various combinations and functional forms for standing volume, temperature, and snow-water equivalent. The model has specific subsets for spruce, pine, and deciduous forest, allowing to estimate separate monthly values of albedo for each tree type (Table S7 in Supporting Information S1). It has been validated against albedo observations across Norwegian boreal forests, showing accuracy in reproducing the seasonal pattern of surface albedo, interactive effects of forest structures and meteorological parameters, as well as the multiyear albedo dynamics with forest volume (Hu et al., 2018). Monthly mean subplot-level albedo estimates are thus produced for each tree type (spruce, pine, and deciduous) by combining subplot estimates of forest volume (calculated as explained in the following subsection) and site-specific climate data. We repeated this process for each year of tree observations to produce a timeseries of monthly albedo estimates for each forest type. In addition to albedo estimates for each species of tree within the subplot, we performed a weighted average to calculate composite estimates of albedo (α_c) for each subplot taking into account the contributions of albedo values (α_s) from each tree species and its relative abundance in the subplot:

$$\alpha_c = \sum(\alpha_s \times p_s) \quad (1)$$

In order to directly compare albedo between moose exclosures and corresponding open plots at each study site, we averaged subplot estimates of albedo within each plot to produce plot-level estimates for both the browsed and un-browsed plots. We then calculated monthly differences in albedo ($\Delta\alpha$) between the moose exclosure and open plot at each study site across all years of the study period. The resulting albedo values for each paired sites are available at Hu et al. (2023), <https://doi.org/10.6084/m9.figshare.21879060.v1>.

2.5.2. Biomass-To-Volume Conversion

To produce albedo estimates using the model described above, we need to convert estimates of individual tree biomass into estimates of tree volume. We used average wood densities (Repola, 2006) specific to the tree species in our data set (Text S2 in Supporting Information S1 details this biomass-to-volume conversion). Within each circular subplot, we then summed individual tree volumes (m^3) to aggregate volumes according to forest type (spruce, pine, and deciduous). We aggregated the individual volumes of spruce and juniper into a cumulative spruce volume and individual pine tree volume into a combined pine volume. We created an aggregate deciduous volume by summing individual birch, rowan, and willow volumes. These summed volumes were then divided by subplot area (ha) to produce estimates of volume per hectare ($\text{m}^3 \text{ha}^{-1}$) for each of the three forest types, which were used to generate albedo estimates (thereafter aggregated at a plot level). We repeated this process at all study sites and across all years of available tree data to produce a data set of forest volume at the subplot resolution. Figure S3 in Supporting Information S1 shows average forest volume within each study region in the years after exclosure.

2.5.3. Climate Averages

We calculated the monthly averages of snow-water equivalent and temperature at each study site for use as parameters in the albedo model. To minimize potential noise in albedo estimates due to interannual and geographical climate variation, we calculated a single set of monthly averages for each study site using historical climate data from 2007 to 2019. We obtained our data from SeNorge, which provides spatially interpolated estimates of

snow-water equivalent and temperature at a resolution of 1 km² across Norway (Lussana et al., 2018). Figure S4 in Supporting Information S1 shows monthly averages of snow-water equivalent and temperature within each study region. Table S3 in Supporting Information S1 provides detailed data on elevation and climate conditions at each study site. Elevation data was manually extracted from Google Earth's digital elevation model based on site coordinates (Rusli et al., 2014).

2.6. Statistical Analysis

2.6.1. Biomass Linear Mixed-Effects Models

All statistical analyses were conducted using *R* Studio (version 4.0.0) and the *lme4* package (Bates, 2010). Linear mixed-effects models were used to model the effects of moose exclosure on aboveground tree biomass. To construct models, we followed a model-building protocol recommended for nested ecological data (Zuur et al., 2009). Text S3 in Supporting Information S1 contains further details on this protocol. We used this process to model the effects of moose exclosure on total aboveground biomass, deciduous biomass, and coniferous biomass over time. Prior to statistical analysis, we aggregated and averaged biomass estimates of individual trees within each plot. For the deciduous biomass model, we summed birch, rowan, and willow biomass within each subplot to produce aggregated deciduous biomass. For the coniferous biomass model, we summed pine, spruce, and juniper biomass to produce an aggregate measure of coniferous biomass.

To account for the nested structure of our experimental design, we specified a random effect structure for each of these models as study site nested within study region. We included region as a random effect instead of fixed effect because we considered region to be an inherent part of the experimental design and were less interested in comparing differences in biomass between regions. In addition to exclosure treatment, we included site productivity and years since exclosure as fixed effects in each model. We employed a natural log transformation of the response variable in all three models to address heteroscedasticity and non-normality of residuals. After selecting our final models, we back-transformed parameter estimates and 95% confidence intervals from model output. Diagnostic residual plots for the total, deciduous, and coniferous biomass models can be found in Figures S5–S7 in Supporting Information S1, respectively.

2.6.2. Albedo Linear Mixed-Effects Models

We used a similar process to model the effects of moose exclosure on monthly average albedo across study sites. Composite albedo estimates were aggregated within subplots and then averaged in each plot prior to statistical analysis. We specified our random effect structure as study site within region and across the months. This random effect structure produced residual plots that were the most homoscedastic out of any structure assessed and allowed us to account for nested experimental design. We included site productivity and years since exclosure as fixed effects. To account for the effect of snow on albedo, we also included the monthly average proportion of days with snow at each study site as a fixed effect. To produce this variable, we calculated the average monthly proportion of days where the snow-water equivalent at each site exceeded 0 mm, using the same site-specific climate data from Lussana et al. (2018) that was used to produce albedo estimates. We chose to include this variable instead of snow-water equivalent to address issues with nonlinearity between albedo and snow-water equivalent in our initial model. We employed a natural log transformation of the response variable to address heteroscedasticity and nonnormality of residuals. We then back-transformed parameter estimates and 95% confidence intervals from the final model output. Diagnostic residual plots for the albedo model can be found in Figure S8 in Supporting Information S1.

2.7. Carbon Equivalents

To assess the effects of moose exclosure on climate, we translated differences in tree biomass and albedo between exclosures and open plots into carbon dioxide (CO₂) equivalents. The use of a common metric allowed us to directly interpret biogeochemical and biophysical effects of moose as relative changes to carbon dioxide in the Earth's atmosphere. We calculated moose-driven changes in CO₂-equivalents for tree biomass and albedo separately, which ultimately allowed us to examine individual contributions of these factors.

To translate changes in tree biomass due to moose exclosure into CO₂, we first calculated the total amount of tree biomass within each exclosure and the corresponding open plot. We then converted biomass to a measure

of aboveground carbon (ton C ha^{-1}) and subtracted carbon in browsed open plots from carbon in un-browsed exclosures to produce annual estimates of differences in carbon (ΔC) at each study site for all years in the study period. Estimates of ΔC were then directly converted into CO_2 by multiplying by 3.67.

To translate changes in albedo into CO_2 -equivalents, we first assessed the change in radiative forcing (RF) due to albedo changes and then translated RF into CO_2 -equivalents. RF describes the disturbance of the planetary energy balance at the top of Earth's atmosphere (TOA) under the influence of a climate change mechanism (Knutti & Hegerl, 2008). Shortwave RFs at TOA due to changes in albedo can be approximated by using radiative kernels. This approach was initially developed by the climate modeling community to address internal feedbacks within general circulation models, but has been widely adopted by the land surface science community as a tool to estimate variations in RF due to albedo changes (Ghimire et al., 2014; O'Halloran et al., 2012; Vanderhoof et al., 2013). Radiative kernels are used to deconstruct the various contributions of feedbacks and forcing to the total change in TOA radiative fluxes. Out of the radiative kernel data sets currently available (Huang et al., 2017; Pendergrass et al., 2018; Shell et al., 2008; Soden et al., 2008), we used a set of kernels validated and made publicly available by Pendergrass et al. (2018). These kernels were calculated with the large-ensemble version of the Community Atmosphere Model version 5 (CAM5) within the Community Earth System Model version 1.1.2 (CESM1.1.2) at the top of the atmosphere at a horizontal resolution of 1° .

To compute RF for our study sites, we multiplied monthly difference in albedo ($\Delta\alpha$) between exclosures and open plots by the monthly kernel values for the corresponding grid, and then divided by the area of the Earth (510 million km^2) to obtain monthly global RF at the TOA due to albedo changes. RF from surface albedo changes was then translated into CO_2 -equivalents to facilitate the comparison of impacts from surface albedo changes with those from changes in tree biomass and aboveground carbon. The annual impact from albedo changes in $\text{kg CO}_2\text{-eq m}^{-2}$ is estimated by dividing the annual mean RF for each plot (in $\text{W/m}^2/\text{m}^2$) by the radiative efficiency of CO_2 ($1.75 \times 10^{-15} \text{ W yr/kg m}^2$; Stocker, 2014). We then produced estimates of annual net changes in CO_2 -equivalents due to moose exclosure by subtracting carbon equivalents associated with changes in albedo from those associated with changes in carbon.

2.8. Regional Emissions and Forest Harvest Areas

To interpret the contribution of moose browsing in early successional forests within the context of regional carbon budgets, we estimate the annual average forest harvest areas in our study regions to upscale the mean effect and compare it to that from fossil CO_2 emissions from the corresponding regions. Regional emissions of fossil fuels refer to 2020 and are based on national statistics (MiljøDirektoratet, 2020). The approach from Ceccherini et al. (2020) is used to estimate the forest harvested area in the three regions of our exclosure sites in Norway from 2008 to 2018. This is based on the use of the GFC data set (Hansen et al., 2013), to which natural disturbances (e.g., windfalls, wild fires) are subtracted. We refer to Ceccherini et al. (2020) for more detailed information on the method and to Zhou et al. (2021) for its application in the Scandinavian boreal forest.

The carbon loss (denoted as $C_{\Delta\text{C}}$) in each county i due to moose browsing in post-harvested sites can be estimated as follows:

$$C_{\Delta\text{C},i} = \text{HA}_i \times C_{eq\Delta\text{C},i} \quad (2)$$

where HA is the mean of annual forest harvested areas from 2008 to 2018 in each county, $C_{eq\Delta\text{C}}$ is the annual average effect in CO_2 -equivalents from the exclosures in that county. Similarly, we can estimate the carbon-equivalent effect due to changes in albedo

$$C_{\text{albedo},i} = \text{HA}_i \times C_{eq\Delta\alpha,i} \quad (3)$$

where $C_{eq\Delta\alpha}$ is the annual CO_2 equivalent from the effect of changes in albedo.

3. Results

3.1. Tree Biomass

We found that total aboveground tree biomass grew more over time in exclosures where moose browsing is excluded, than in browsed open plots ($p = 0.031$; Figure 2). On average, biomass in open plots increased by 18%

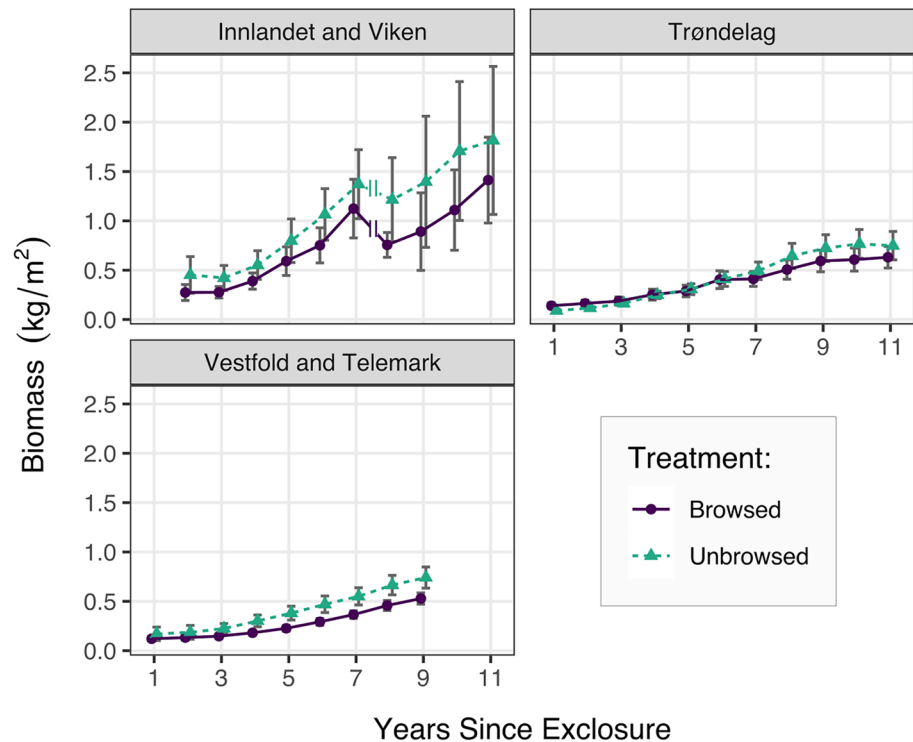


Figure 2. Total aboveground tree biomass (kg m^{-3}) within open plots and moose enclosures in the years after initial enclosure, averaged within each study region. Error bars represent standard error. Few study sites in Innlandet and Viken had data past 7 yr since enclosure (as experimental sites were initiated at different times) so the standard errors are greater after this point and the drop in biomass is attributable to the sub-setting of the larger number of sites.

for each year of growth since enclosure ($p < 0.001$; 95% CI: 15.5%–21.4%), while biomass inside moose enclosures increased by 22% ($p < 0.001$; 95% CI: 18.9%–24.9%; Table S8 in Supporting Information S1). Additionally, total tree biomass had a positive relationship with site productivity in enclosures, where on average, total biomass increased by 15% for a 10% increase in productivity ($p = 0.005$, 95% CI: 4.7%–26.9%). Few sites in Innlandet and Viken had tree data beyond 7 yr since enclosure.

We also found that deciduous tree biomass grew significantly more over time in moose enclosures compared to open plots ($p < 0.001$). Deciduous biomass in open plots increased by an average of 13% for each year of growth since enclosure ($p < 0.001$; 95% CI: 8.70%–16.8%), while deciduous biomass inside enclosures increased by an average of 26% ($p < 0.001$; 95% CI: 21.5%–30.6%; Table S9 in Supporting Information S1). Similar to total tree biomass, there is a positive relationship between deciduous biomass and site productivity, where biomass increased by an average of 17% for a 10% increase in productivity ($p = 0.027$, 95% CI: 2.2%–35.1%). In contrast, we did not observe a significant difference in the growth of coniferous tree biomass over time between moose enclosures and open plots ($p = 0.101$). On average, coniferous biomass in open plots increased by 21% for each year since enclosure ($p < 0.001$; 95% CI: 17.8%–24.3%), while coniferous biomass within enclosures increased by 18% ($p < 0.001$; 95% CI: 15.1%–21.4%; Table S10 in Supporting Information S1). Detailed model output for total biomass, deciduous biomass, and coniferous biomass can be found in Tables S8–S10 in Supporting Information S1, respectively.

3.2. Tree Community Composition

We did not find clear differences in the relative abundance of deciduous, pine, and spruce trees in moose enclosures compared to open plots (Figure 3). On a regional scale, deciduous trees were more abundant than spruce or pine trees throughout most of the study period, both within enclosures and open plots. However, the effect of moose enclosure on relative tree abundances appeared to differ between study regions. In Trøndelag, deciduous trees were more abundant in open plots than in enclosures, while the opposite was true in Vestfold and Telemark.

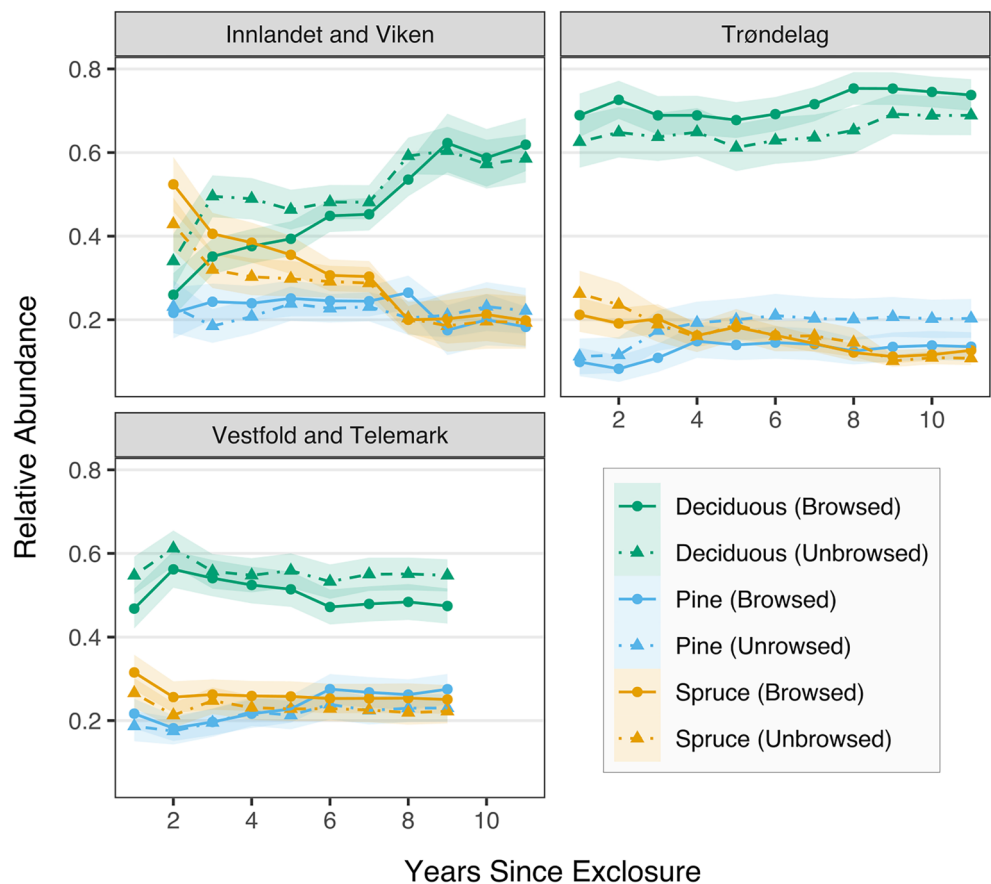


Figure 3. Relative abundance of deciduous, pine, and spruce trees within open plots and moose exclosures in the years after initial closure, averaged by study region. Shading represents standard error.

Similar variability between regions was observed for the coniferous species. For example, pine was generally more abundant in exclosures than open plots in Trøndelag, but not so in Innlandet and Viken or Vestfold and Telemark.

3.3. Albedo Dynamics

After accounting for region, productivity, and snow at each study site, we observed that albedo decreased more in moose exclosures than in open plots for each year of exclosure ($p < 0.001$). Figure 4 shows the average difference in monthly albedo between moose exclosures and corresponding open plots in each of the three study regions. Albedo in open plots decreased by an average of 0.55% for each year of exclosure ($p < 0.001$; 95% CI: 0.46%–0.63%), while albedo in exclosures decreased at a greater rate, by an average of 0.85% ($p < 0.001$; 95% CI: 0.76%–0.93%; Table S11 in Supporting Information S1). As the number of years since exclosure increased, albedo in exclosures decreased relative to albedo in open plots across all study regions. Differences in albedo between open plots and moose exclosures are larger during winter months when snow was present in the study regions, especially 8–10 yr after initial exclosure and in the Trøndelag and Innlandet and Viken regions. So, the albedo difference between exclosures and open plots increased over time owing to the different rates of vegetation growth (and its snow masking effect). Despite the apparent effects of snow on albedo seen in Figure 4, we did not find a statistically significant difference in the relationship between snow and albedo between open plots and exclosures across study regions ($p = 0.118$). On average, for a 10% increase in monthly proportion of days with snow, albedo increased by 13% in both open plots ($p < 0.001$; 95% CI: 13.0%–13.6%) and moose exclosures ($p < 0.001$; 95% CI: 13.1%–13.6%). Detailed model output for albedo can be found in Table S11 in Supporting Information S1. There is a difference in the contribution to albedo changes from individual tree composition types. The major differences are found with deciduous species, which are associated with higher albedo values

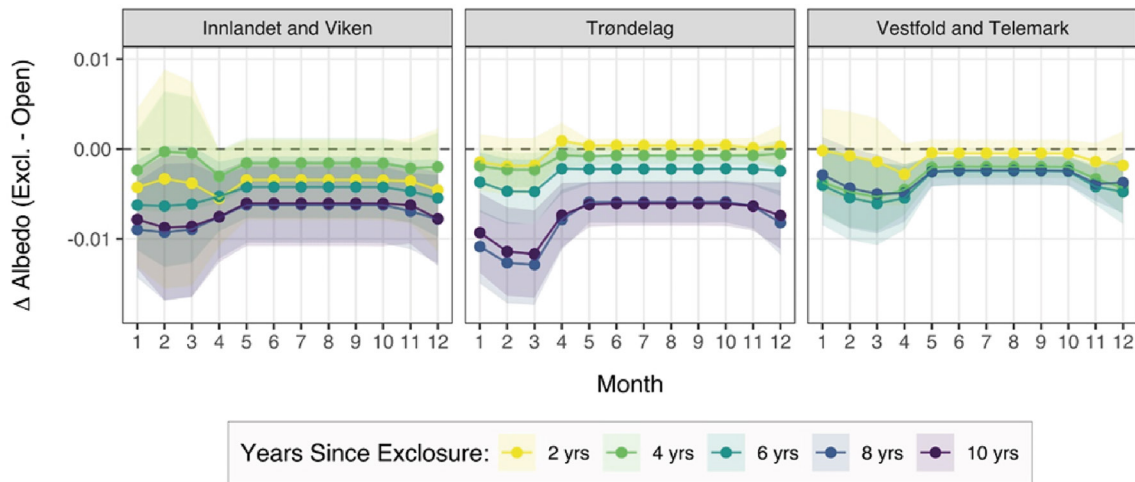


Figure 4. Mean differences in albedo between moose exclosures and open plots, where difference equals exclosure albedo minus open plot albedo (i.e., negative values indicate higher albedo in browsed open plots than un-browsed exclosures). Differences are averaged within each study region. Line colors correspond to number of years since exclosure, while shading indicates standard error. Horizontal dashed line indicates no difference in albedo. Differences in albedo specific to each forest type (deciduous, pine, and spruce) can be found in Figure S9 in Supporting Information S1.

within exclosures than open plots (Figure S9 in Supporting Information S1). This difference increases with the years since exclosure.

3.4. Carbon Equivalents

At a regional scale, moose exclosure had a net annual impact in CO₂-equivalents in early successional forests given by cooling contributions from increased carbon sequestration and warming contributions from decreased albedo, which are generally of similar magnitudes but opposing directions (Figure 5a). Relative to open plots, in the years after study site establishment, avoiding moose browsing within the exclosure led to higher growth of tree biomass, more carbon sequestration, and thus a cooling effect on global climate due to less carbon dioxide in the atmosphere. When averaged across the years, a significant cooling trend associated with higher carbon fluxes within un-browsed plots is reported in all regions except Trøndelag, where the upper end of the standard error falls in the positive domain (Figure 5b). This is primarily connected to the small response that occurs in the Trøndelag sites in the first 5 yr, where carbon sequestration rates in exclosures and open plots are similar (likely because of a relatively slower tree growth due to temperature constraints). Over time, negative carbon effects become more significant, consistently with the findings from the other two regions where the carbon effect increased in magnitude as differences in tree biomass and carbon sequestration between exclosures and open plots increase over time.

In contrast, the exclusion of moose browsing led to closer canopies and lower albedo, causing a warming climate effect equivalent to more carbon dioxide in the atmosphere. Like the cooling effect of carbon, this warming effect due to decreased albedo grows in magnitude over time. All the three study regions consistently show a warming effect from albedo changes when averaged over the time period.

Carbon and albedo effects nearly offset each other out when averaged across study regions and produce minimal net change in annual CO₂-equivalents, varying only slightly between regions. Results are generally net negative (i.e., cooling from excluding moose browsing relative to browsed forest) in Innlandet and Viken, and slightly positive in Trøndelag. The standard error crosses the zero line for Vestfold and Telemark (Figure 5b).

The effects of moose exclosure on CO₂-equivalents were more variable at the local level (Figure 6). At some of our study sites, trends were opposite to those on the regional scale, where avoiding moose browsing in exclosures drove warming contributions from carbon (from lower tree growth rates) and cooling contributions from albedo (from increased surface albedo). To illustrate this, we selected two sites (Site 5 and Site 8) in Trøndelag, both with similar productivity and established in clear-cut spruce forest. In these two cases, moose exclosure had opposite effects on CO₂-equivalents (Figure 6a). Site 5 is one of the cases where more tree biomass accumulated in the

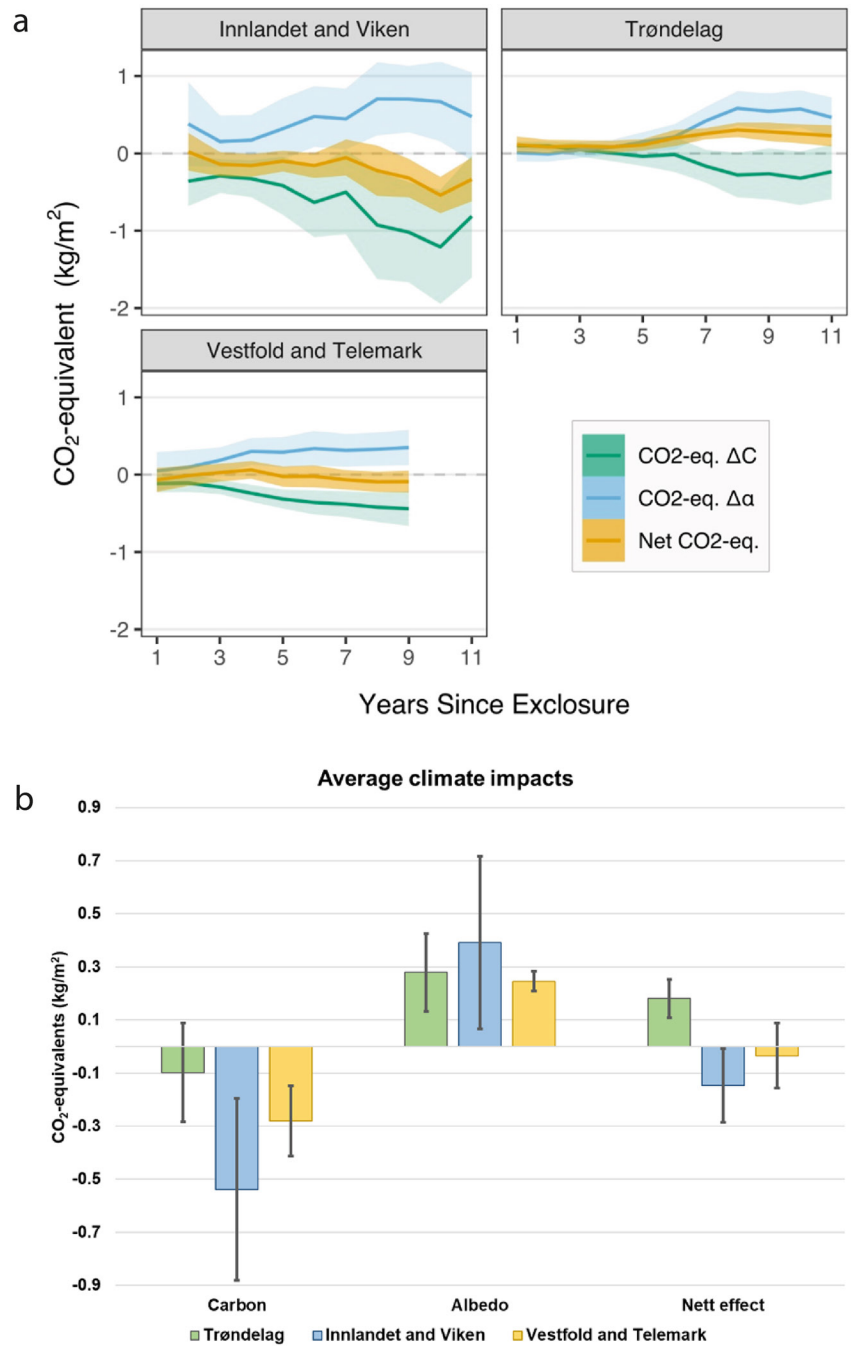


Figure 5. Effect of moose exclusion on annual CO₂-equivalents (kg CO₂-eq. m⁻²) at 44 study sites in Norway, averaged by region (a) and over time (b). Positive values indicate that the un-browsed enclosure has a warming climate effect equivalent to more CO₂ in the atmosphere. Negative values indicate that un-browsed enclosure has a cooling effect equivalent to less CO₂ in the atmosphere. In (a), green lines represent climate changes due to differences in aboveground carbon between enclosures and open plots; blue lines represent climate changes due to differences in albedo; orange lines indicate the net climate impact of moose exclusion; shading represents standard error. In (b), the bar height indicates the regional mean over the study period and the range is the standard error of the regional mean in each region.

browsed open plot than in the moose enclosure, and consequently albedo in the open plot decreased relative to the albedo of the enclosure. Thus, moose enclosure at this site led to a carbon warming effect, an albedo cooling effect, and a net warming effect equivalent to more CO₂ in the atmosphere that increased in magnitude over time. In general, we find that Trøndelag is the region with the highest relative number of sites (40%) where enclosures

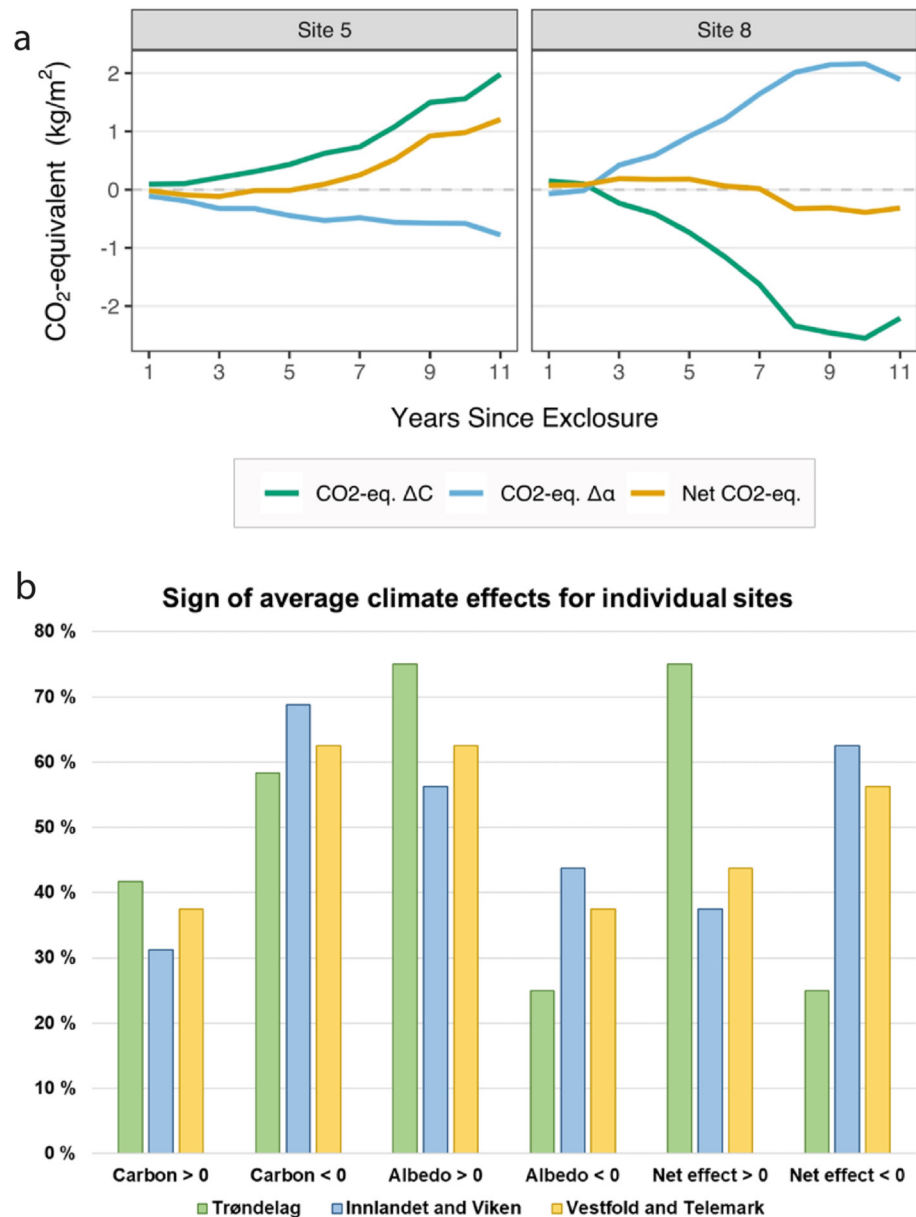


Figure 6. Effect of moose exclusion on annual CO₂-equivalents (kg CO₂-eq. m⁻²) at two study sites (Sites 5 and 8) in Trøndelag county and across all sites. Negative values indicate that exclusion has a cooling effect equivalent to less CO₂ in the atmosphere. In (a), green lines represent climate changes due to differences in aboveground carbon between exclusions and open plots, blue lines represent climate changes due to differences in albedo, and orange lines indicate the net climate impact of moose exclusion. In (b), the percentage indicates the number of sites in each region where the multiyear average of carbon, albedo, and net impacts are positive or negative. Total number of sites: 12 in Trøndelag, 16 in Innlandet and Viken, and 16 in Vestfold and Telemark.

can have a warming effect from carbon fluxes (i.e., lower carbon content in trees than in the browsed plots), but the majority of the sites still show a cooling contribution from carbon effects (Figure 6b). At the same time, Trøndelag is also the region with the highest relative presence of sites (75%) where exclusions show positive/warming contributions from albedo (as they have lower albedo values than the corresponding browsed plots). Although a minority, other study sites within all three study regions had carbon trends similar to those of Site 5, and negative (cooling) contributions from albedo. In contrast, trends in CO₂-equivalents at Site 8 were in line with the predominant regional trends shown in Figure 5, and with the trends observed in the majority of the sites in Trøndelag. Moose browsing exclusion at this site led to a carbon cooling effect, an albedo warming effect, and minimal net

Table 1

Data and Statistics on Average Effects of Moose Browsing in Post-Harvested Sites on Carbon and Albedo Dynamics in the Three Study Regions

	Trøndelag	Innland and Viken	Vestfold and Telemark
Mean ΔC (kg CO ₂ /m ²)	-0.098 ± 0.19	-0.538 ± 0.102	-0.283 ± 0.132
Mean $\Delta\alpha$ (kg CO ₂ -eq./m ²)	0.279 ± 0.15	0.392 ± 0.325	0.246 ± 0.038
Mean forest harvested area (Mm ² /yr)	46.0	260	43.4
Fossil-based emissions (ktonne/yr)	888	359	2,970
Total effect, ΔC (ktonne CO ₂ /yr)	4.49 ± 8.57	140 ± 89.4	12.2 ± 5.71
Total effect, ΔC (% yearly fossil emissions)	0.51% ± 0.96%	39.1% ± 24.9%	0.41% ± 0.06%
Total effect, $\Delta\alpha$ (ktonne CO ₂ -eq./yr)	-12.8 ± 6.75	-102 ± 85	-10.8 ± 1.63
Total effect, $\Delta\alpha$ (% yearly fossil emissions)	-1.45% ± 0.76%	-28.4% ± 23.6%	-0.36% ± 0.05%

Note. Data for carbon (ΔC) and albedo ($\Delta\alpha$) are averaged over the assessment period (11 yr). Ranges indicate the standard error of the mean. Note that here the sign is switched relative to the previous results. Positive values for carbon indicate an emission of CO₂ (i.e., a reduction in vegetation carbon stock due to moose browsing).

change in CO₂-equivalents over time. Each individual system is thus different and can have a unique response due to local climatic and environmental factors. There is a potential for identifying context-specific climate mitigation strategies where forest management is integrated with management of herbivore browsing density and pressure.

3.5. CO₂ Emissions From Moose Browsing in a Regional Context

To put the potential climate change effects of moose browsing into context, we upscaled the average factors from each study region to the therein average forest harvest areas and compared the resulting regional CO₂ fluxes from moose browsing with the emissions of fossil CO₂ (Table 1). The mean annual harvested area from 2008 to 2018 in Innlandet and Viken (260 Mm²) is much higher than the other regions (46 Mm² for Trøndelag and 43.4 Mm² for Vestfold and Telemark). When applying to these areas the respective estimated effects on CO₂ from moose averaged at a regional level, moose browsing in Innlandet and Viken is responsible for an annual loss of carbon from vegetation (e.g., an emission) in post-harvested sites of 140 ± 89 ktonne CO₂ per year. This corresponds to 39% ± 25% of the annual emissions from fossil fuels in the county. This impact is only partially (about two thirds) mitigated by a cooling contribution from the increased albedo due to moose browsing. In terms of a regional carbon budget, the effect from wild herbivore browsing is not negligible, especially if the region has high animal density and intensive forestry. In the other counties, the harvested areas and the effect on carbon of animal browsing is smaller, while emissions from fossil fuels are higher, so the impact of animal browsing in post-harvested sites is considerably smaller (0.5% or less). Overall, the impact of animal browsing is larger if one would project the effects to the entire forest areas in Norway, beyond the post-harvested sites.

4. Discussion

In this study, we used 11 yr of tree species data from post-harvest boreal forests to assess the net climate impacts of moose in the years immediately after timber harvest. By calculating carbon-equivalents associated with moose-driven biogeochemical and biophysical changes at the land surface, we observed that moose browsing simultaneously cools climate by increasing surface albedo and warms climate by limiting tree biomass accumulation and forest carbon sequestration. The net climate change effect of moose browsing is overall reduced as the two mechanisms tend to compensate for each other, but it differs between regions and localities. This is the first study to integrate both albedo and carbon dynamics in assessing the climate effect of the largest and most widespread herbivore in the boreal forest, one of the largest biomes in the world. The explanation and interpretation of these outcomes are discussed in the subsections below, while the limitations of the study are detailed in Text S4 in Supporting Information S1.

4.1. Tree and Carbon Dynamics

At a regional scale, moose browsing limits the growth of aboveground tree biomass in the years after clear-cutting, reducing carbon sequestration in regenerating forest stands and causing a warming biogeochemical effect on

climate equivalent to addition of carbon dioxide into the atmosphere. In our study regions, moose primarily prevent the accumulation of deciduous tree biomass (Table S9 in Supporting Information S1), as they prefer to browse on deciduous species. Selective browsing by moose and resulting changes in forest communities have been previously documented in both North American and Fennoscandian boreal forests (Kolstad, Austrheim, Solberg, de Vriendt, & Speed, 2018; McInnes et al., 1992; Speed, Austrheim, Hester, Solberg, & Tremblay, 2013; Speed et al., 2013). For example, Speed, Austrheim, Hester, Solberg, and Tremblay (2013) and Speed et al. (2013) found strong evidence that moose browsing in successional Norwegian forests limits the vertical growth of preferred deciduous tree species (e.g., birch and rowan), while Kolstad, Austrheim, Solberg, de Vriendt, and Speed (2018) observed that moose reduce the number of large deciduous trees in recently clear-cut forests.

In contrast, moose did not seem to affect the accumulation of coniferous biomass, at least at a regional scale. This was to some extent unexpected, since it was observed in a previous study (McInnes et al., 1992) that moose browsing could release unpalatable coniferous species (e.g., spruce and pine) from competition with preferred deciduous species and indirectly facilitate coniferous growth. However, we did not find strong evidence of such facilitation, as coniferous tree biomass grew at similar rates in both exclosures and open plots. This may be due to different responses of spruce and pine to competing trees: height growth of pine, which is browsed by moose at high densities, has been found to be negatively affected by competition from neighboring trees, while spruce, which is largely avoided, was not affected by competition (Vuorinen et al., 2020). Therefore, the two main conifer species have different direct and indirect responses to moose browsing; increasing moose densities increase browsing on pine but reduce tree competition by reducing canopy closure. Our results are also consistent with those of Kolstad, Austrheim, Solberg, de Vriendt, and Speed (2018), who found that moose exclosure in successional boreal forests had little effect on the recruitment of pine and spruce saplings into taller height classes over an 8 yr study period. Coniferous species such as pine and spruce may grow slowly enough that substantial differences in biomass between exclosures and open plots would not occur in the time span of our study.

Although moose browsing had an impact on the growth of tree biomass, we did not find clear effects on tree species composition, as the relative abundance of deciduous, pine, and spruce trees within our study regions were not consistently different between exclosures and open plots when averaged at a regional level. Previous studies have shown that moose can reduce the number of large trees in regenerating boreal forests and drive tree canopies to become dominated by coniferous species (Kolstad, Austrheim, Solberg, de Vriendt, & Speed, 2018), but few studies are available on the effects of moose on relative tree species abundance, which makes the comparison of our results difficult. In their study of moose browsing in successional boreal forests, Den Herder et al. (2009) found that moose increase the mortality of preferred deciduous tree species. In a Canadian exclosure experimental setting, moose browsing was found to alter plant communities, with a lower ground cover of balsam fir, an increased ground cover of raspberry, and a lower abundance of saplings for balsam fir, birches and rowan (De Vriendt et al., 2021). We thus expected to see some evidence of increased mortality and decreased relative abundance of deciduous species in open plots compared to exclosures, yet we did not observe this decline and even found that the relative abundance of deciduous species increased over time within open plots in Innlandet and Viken. Preferred deciduous species, such as birch, have been shown to be highly tolerant of moose browsing and can quickly regrow biomass lost to herbivory, particularly through lateral branching and growth (Persson et al., 2007). It is possible that browsed deciduous trees in our study regions compensated for browsing damage through this mechanism, and as a result, did not decline in abundance. Our results ultimately suggest that moose have a stronger effect on forest structure than on tree species composition in early successional forests, although further research is needed to clarify these mechanisms.

Due to a lack of data, our analysis did not consider potential contributions from changes in soil emissions. However, a previous study that investigated potential changes in soil properties on a selection of the study sites used in our analysis shows that excluding moose decreased soil bulk density and temperature, but it did not affect any measures of soil processes or quality (decomposition, nitrogen availability, C/N ratio, pH, and nutrients; Kolstad et al., 2018). Additional studies can further enlighten potential effects on soil emissions by specifically measuring CO₂ soil fluxes within and outside exclosures, so to register potential differences.

4.2. Albedo Dynamics

In the years after clear-cutting, moose browsing kept surface albedo higher in our study regions than it would have been if moose were absent, consequently causing a biophysical cooling effect on climate. This is primarily due to

a lower vegetation structure that reduces snow masking effects of trees, especially during winter and early spring. Our results thus suggest that moose can affect biophysical processes at the land surface and drive measurable changes in the surface albedo of successional boreal forests. Herbivore induced increase in albedo is also shown in arctic ecosystems where Cohen et al. (2013) found that albedo during the regional snowmelt period (80–170 DOY) was higher in regions of high grazing pressure than low grazing pressure, with maximum average albedo differences greater than 0.04 between the two regions. Like their study, we found that albedo is higher in areas of managed forest with greater herbivore pressure (i.e., open plots) than in areas with low herbivore pressure (i.e., exclosures). In contrast, the highest average difference in albedo that we observed between forest exclosures and open plots was just over 0.01 (Figure 4). This difference in albedo, recorded during winter months in Trøndelag, is smaller than that measured by Cohen et al. (2013), and might be due to different radiation exposure and reflectivity between tundra and forests, and to the type of disturbance (grazing of reindeer vs. browsing of moose).

The effect of moose on albedo in our study regions is stronger when snow is present (Figure 4). In their study of reindeer grazing, Cohen et al. (2013) suggested that interactions between snow and vegetation height were primarily responsible for differences in albedo observed between areas of tundra with low and high grazing pressure. They found that sparse, short vegetation in highly grazed areas of tundra enables stronger snowpack formation and higher albedo, while denser vegetation in less intensely grazed areas reduces snowpack formation and albedo. A similar situation occurred in our study regions, where moose browsing reduced tree biomass and allowed for stronger snowpack formation and higher albedo in months when snow was present relative to exclosures.

Since albedo in boreal forests is influenced by both forest structure and species composition (Cherubini et al., 2017; Lukeš et al., 2014, 2016), an important question is whether moose-driven changes in albedo were primarily due to changes in forest structure, tree species composition, or both. We did not observe a strong regional effect of moose browsing on tree species composition throughout the study period, but we did find a strong effect on biomass, which suggests that moose may drive changes to albedo primarily by affecting vegetation structure. Examining differences in albedo between exclosures and open plots specific to each forest type (Figure S9 in Supporting Information S1), we found that trends in deciduous albedo closely mirror those of plot-level albedo, referred to as composite albedo in Figure S9 in Supporting Information S1. This is especially true in Trøndelag and in Vestfold and Telemark, where in the later years of the study period, deciduous biomass in exclosures was substantially higher than in open plots, and thus, deciduous albedo was lower. In contrast, we found that trends in the albedo of pine and spruce forests were variable between study regions and do not closely match those of plot-level albedo. These results suggest that, compared with changes to coniferous biomass, moose-driven changes to deciduous tree biomass are the most important drivers of differences in albedo observed between exclosures and open plots.

4.3. Climate Impacts

Previous studies have highlighted the need for boreal forest managers and policy makers to account for moose impacts on climate driven by its effect on forest carbon cycling (De Vriendt et al., 2021; Leroux et al., 2020; Schmitz et al., 2014). Our study is the first to integrate the biogeochemical and biophysical dimensions of the climate impacts of moose browsing on boreal forests. At a regional scale, we observed that moose have two competing climate effects of similar magnitude in successional boreal forests—one biogeochemical and one biophysical—driven by browsing-mediated changes to regenerating tree biomass and surface albedo. Since no previous analysis in the boreal forest biome has compared both biogeochemical and biophysical climate impacts of large herbivores, we can refer to studies that explored the climate impacts of other types of disturbances within boreal forests for benchmarking. The opposing climate effects from biophysical and biogeochemical mechanisms associated with forest growth or reforestation in boreal ecosystems are consolidated in the scientific literature (Bonan, 2008, 2015; Perugini et al., 2017), with efforts in identifying areas where afforestation can most successfully mitigate climate change by estimating net effects (Mykleby et al., 2017; Windisch et al., 2021). Specifically to empirical studies in managed boreal forests, Cherubini et al. (2018) examined the individual contributions of post-harvest forest carbon fluxes and changes in albedo to climate forcing in clear-cut Swedish pine forests. In the first 15 yr after harvest, they found that post-harvest carbon fluxes associated with increased respiration and decay of woody debris left over from forestry operations cause positive climate forcing and a warming effect, but that this positive forcing was countered by negative forcing and a cooling effect of similar magnitude caused by increased surface albedo. Additionally, Randerson et al. (2006) found that fires in Alaskan boreal forests cause

an initial climate warming effect due to combustion of forest biomass, but also have a climate cooling effect due to increased surface albedo, which partially mitigates the warming effect over long timescales. Our results are thus consistent with a larger, generalized characterization of disturbances within boreal forests at high latitudes, where disturbing factors, such as timber harvest, fire, and herbivory, may cause a biogeochemical warming effect due to the net flux of greenhouse gases into the atmosphere, which is at least partially mitigated by biophysical cooling due to increased surface albedo in the years after the disturbance.

We found that the effects of moose on climate in successional forests are relatively consistent at a regional scale but can vary at the local level, suggesting that moose impacts on forest carbon and albedo are moderated by local factors. The identities and relative importance of these factors are not entirely clear, but it is possible that differences in snowfall, site productivity, and moose densities may be relevant. For example, the albedo cooling effects of moose may be stronger and more apparent in areas of successional forest that receive high amounts of snowfall, since snow can substantially increase albedo in boreal forests. In particular, high amount of snow in the spring contributes to more cooling as the incoming solar radiation is larger than in winter. In comparison, albedo cooling effects may be weaker at sites with low snowfall, where moose-driven warming effects due to reduced carbon sequestration could dominate and possibly cause net climate warming.

Site productivity may be another driver of local variation in moose climate impacts within successional forests. For example, Persson et al. (2007) showed that birch trees in boreal forests with high productivity can regrow more substantially after moose browsing than trees in low-productivity forests. In areas of successional forest with high productivity, browsed tree species such as birch can more effectively compensate for moose browsing damage through continued production of biomass; thus, browsing in these areas could have less of an impact on tree biomass production and resultant carbon sequestration, and therefore, a reduced carbon warming effect on climate, since browsed trees are able to continue sequestering carbon into biomass despite browsing damage. In contrast, browsed trees in low-productivity forests may not be able to compensate with biomass production in response to browsing, and thus, the negative impacts of moose on both tree biomass production and carbon sequestration may be more substantial, potentially causing a stronger carbon warming effect on climate. However, our model results suggest that productivity was not significantly associated with growth of total or deciduous tree biomass in browsed open plots within our study regions (Tables S8 and S9 in Supporting Information S1).

The ability of birch trees to compensate for browsing damage can also be mediated by moose density and associated browsing pressure, as high moose browsing pressure stimulates more birch biomass production after browsing than low browsing pressure (Persson et al., 2007). Moose densities were variable across our study regions (Figure 1b and Table S2 in Supporting Information S1) and have been found to vary widely throughout North American and Fennoscandian boreal forests in both space and time (Austrheim et al., 2011; Jensen et al., 2020; Speed et al., 2019). Furthermore, there are potential feedback mechanisms; tree growth in boreal forests is affected by moose browsing as well as temperature and snow, and in some cases interactions between moose and climate (Vuorinen et al., 2020). Moose impacts on climate, mediated through tree biomass and surface reflectance, are then affected by snow and productivity (which can increase with temperature).

5. Conclusions

This study investigated moose-driven changes to forest carbon and surface albedo in early successional boreal forests, and explored the net contributions of these changes on the climate. By translating differences in tree biomass and albedo between un-browsed and browsed forest plots into CO₂-equivalents, our results strongly suggest that moose can mediate changes to climate that occur after clear-cut timber harvest in boreal forests. Biogeochemical and biophysical climate impacts of moose are of similar importance when averaged at regional scales, but they can significantly differ for specific locations. When compared to the fossil carbon emissions in a county with extensive forest management and high herbivore density, the CO₂ emissions induced by moose browsing can represent about 50% of the regional carbon budget (only partially compensated by the associated increased in surface albedo). Therefore, moose impacts should be an integral part of future management plans of boreal forests, as moose may cause unexpected changes in forest carbon and albedo that affect the mitigation potential of post-harvest forest stands and their timber productivity. However, the observed spatial heterogeneity in the climate effects can raise challenges in identifying optimal management practices in terms of moose browsing pressure and forest harvest at a landscape level. Our analysis has shown the trends in three major managed

forest regions in Norway, and more research is needed to unravel effects in other regions and to better isolate the drivers that shape the climate response.

To build a more comprehensive characterization of moose climate impacts in boreal forests, future studies should attempt to integrate potential climate effects due to moose-driven changes in soil carbon, belowground tree biomass, and additional biophysical factors that influence local climate. Research is also needed to explore potential climate impacts of moose over successional periods longer than those in this study. Our results ultimately provide evidence that moose can influence processes at the land surface relevant to global climate and forest managers, and we suggest that both biogeochemical and biophysical effects of moose be integrated into mitigative forest management practices.

Data Availability Statement

The relevant data of this manuscript are archived by the figshare at: <https://doi.org/10.6084/m9.figshare.21879060.v1>.

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