John Salisbury

Effects of moose browsing on carbon and albedo dynamics in successional boreal forests

Master's thesis in Biology
Supervisor: Gunnar Austrheim
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Abstract

Moose (*Alces alces*) are large herbivores present in boreal forests that can strongly mediate forest regeneration after clear-cut timber harvest through selective browsing of boreal tree species. Although there has been recent concern that moose browsing may influence global climate by altering carbon sequestration in regenerating forests, relatively little attention has been given to its potential climate impacts due to changes in biophysical factors such as surface albedo. Additionally, the relative importance of moose-driven changes to forest carbon and albedo to global climate is currently unknown. In this study, we used long-term data from 44 herbivore exclosures established within clear-cut forests across central and southern Norway to address these knowledge gaps and investigate the effects of moose browsing on aboveground tree biomass and surface albedo in successional boreal forests. We then translated moose-driven changes in biomass and albedo into carbon equivalents, which allowed us to quantify the net climate impact of moose in successional forests. Our results showed that, on a regional scale, moose browsing limits the growth of tree biomass in the years after clear-cutting and exerts a biogeochemical warming effect on climate. In contrast, moose simultaneously increase forest albedo relative to areas of unbrowsed forest and drive an opposing biophysical cooling effect. Climate effects due to changes in biomass and albedo are of similar magnitude and nearly cancel each other out to produce minimal net climate change across study regions. These results indicate that moose can affect albedo in regenerating boreal forests and that the climate impacts of changes to albedo may be of similar importance as those caused by changes in tree biomass and forest carbon. For this reason, we propose that forest managers integrate both biogeochemical and biophysical climate impacts of moose into forest mitigation plans.

Table of Contents

List of Figures

List of Tables

List of Abbreviations and Symbols

NEP	Net ecosystem productivity
NPP	Net primary production
R_H	Heterotrophic respiration
RF	Radiative forcing
TOA	Top of the atmosphere
ΔC	Difference in carbon
$\Delta \alpha$	Difference in albedo
α_c	Composite subplot albedo
α_s	Subplot albedo of forest type s
p_s	Relative subplot abundance of forest type s

1 Introduction

Boreal forests are among the largest biomes on Earth, providing a variety of ecosystem services to human societies, including timber production, habitat provision, and climate regulation [1–4]. Timber production in boreal forests is an economically important activity in both North America and Fennoscandia [5–7]. Mechanized timber harvesting methods such as clear-cutting are commonly used in these forests [8,9] and cause pronounced disturbances to forest land cover and structural diversity [10]. In early successional stages following harvest, patches of harvested boreal forest may become dominated by deciduous trees and woody shrubs present across the entire biome [11,12]. As successional forest grows, forest managers may thin these deciduous species to facilitate the growth of economically valuable coniferous softwood trees [13], mainly pine (*Pinus spp.*) and spruce (*Picea spp*.) in Fennoscandia [7] and also fir (*Abies spp.*) in North America [14]. After several decades of growth post-harvest, managed forest stands may become completely dominated by coniferous species.

Boreal forest management practices and harvest methods such as clear-cutting can affect the global climate system by altering biogeochemical (e.g., carbon cycling and biogenic volatile organic compounds) and biophysical processes (e.g., albedo, evapotranspiration, and surface roughness) [15–18]. In terms of biogeochemical processes, timber harvest can influence the global radiation budget and climate by affecting carbon cycling between forests and the atmosphere [19–21]. After a harvest disturbance, heterotrophic respiration (R_H) and decomposition of woody residues left over after clear-cutting drive a flux of carbon from the forest surface into the atmosphere [22,23]. In contrast, net primary production (NPP) in disturbed forests increases as early successional species begin to sequester atmospheric carbon into living biomass, driving an opposing flux of carbon from the atmosphere into the biosphere [22]. Carbon flux due to R_H and woody residue decomposition is initially greater in magnitude than that due to NPP, which results in negative net ecosystem productivity (NEP), a net flux of carbon from the forest to the atmosphere, and an associated warming effect on global climate [22,24]. Several years after a harvest disturbance, NPP increases and R_H decreases to a point where NEP becomes positive, causing the forest to shift from a carbon source to a carbon sink [22–24].

Timber harvest in boreal forests also changes biophysical processes that can influence Earth's radiation budget and climate [25–27]. Among the biophysical processes, both empirical and modeling approaches show that albedo typically has a dominant effect in boreal forests [28–31]. Albedo is a property of the land surface corresponding to the proportion of incoming solar radiation that is reflected by the surface [32]. Changes to albedo can modify the absorption of solar radiation by the land surface and alter the global radiation budget. The more reflective or brighter a surface is, the higher its albedo and the greater its potential for radiative cooling [32].

In boreal forests, albedo is influenced by characteristics of forest vegetation, such as forest volume [33], canopy cover [34], and tree species composition [35,36], and by climatic factors, such as temperature and snow [32,35,37]. In warmer months when snow is absent, forest structure and tree species composition appear to be the dominant factors that determine boreal forest albedo [32,35]. Dense forests with high standing volume and complete canopy closure generally have lower albedo than forests with low volume and

sparse canopy, as dense forests mask vegetation on the forest floor that typically has higher albedo than trees in the forest canopy [33,34]. Additionally, forest stands of deciduous tree species tend to have higher albedo than coniferous stands [35], as deciduous, broad-leaved foliage is typically more reflective than coniferous foliage [38,39]. The magnitudes of differences in albedo between forests with differing volumes and species composition in months without snow have been shown to be relatively small compared to those in months when snow is present [33,35].

In colder months, interactions between snow, forest structure, and species composition can drive large differences in albedo between forest types [35,37]. Snow that forms on the forest floor is highly reflective, but can be masked by the forest canopy to some degree. 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 [33,37]. Additionally, deciduous trees lose foliage in winter months, which likely reduces both canopy coverage and masking effects on snow. In contrast, coniferous tree species retain foliage throughout the year and may have a stronger masking effect than deciduous species. Accordingly, deciduous boreal forest stands typically have higher winter albedo than coniferous stands [35,37].

Deforestation associated with timber harvest within boreal forests can substantially increase albedo and cause a biophysical cooling effect on global climate [27,30,40]. Harvest opens up dense, dark forest canopy and exposes the forest floor below, which typically has a higher albedo and absorbs less solar radiation [41]. Changes in albedo and associated cooling after deforestation can be especially pronounced in winter and spring months due to formation of reflective snowpack in harvested areas of forest [42]. As successional forest grows and the canopy begins to close, however, the cooling albedo effect of timber harvest gradually declines [19].

A growing body of literature has focused on the potential global climate impacts of both biogeochemical and biophysical changes in forests driven by timber harvest [41,43]. Several studies have highlighted a clear need to account for the harvest impacts of surface albedo alongside those of carbon to avoid suboptimal or even counterproductive mitigation results [30,44,45]. In contrast, less attention has been given to potential climate effects of other types of disturbances within forests, including those of large herbivores. Recent studies suggest that, similar to timber harvest, large herbivores can influence global climate by affecting biogeochemical and biophysical processes at the land surface in ecosystems at high latitudes [46,47]. For example, grazing by reindeer (*Rangifer tarandus*) has been shown to increase surface albedo in arctic shrub systems by reducing shrub height and abundance, allowing for stronger snowpack and higher albedo throughout the year [47,48]. Additionally, there is concern that moose (*Alces alces*) may influence carbon cycling within boreal forests at a landscape scale and consequently affect global climate [49].

Potential climate impacts of moose may be of particular concern to boreal forest managers who seek to manage forest stands for both timber value and climate mitigation, as these herbivores can drive substantial changes in forest carbon and tree species composition in the years after timber harvest [50–55]. Moose are found in both North American and Fennoscandian boreal forests [56–58], especially within areas of forest that have recently been clear-cut [59], where they browse on the apical stems and foliage of deciduous trees and shrubs that typically appear in successional forests [54,60]. In contrast, moose tend to avoid less palatable coniferous species such as Norway spruce (*Picea abies*) [61]. Moose

occasionally browse on Scots pine (*Pinus sylvestris*), particularly when preferred deciduous forage is unavailable during winter months [62]. 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 [52,54].

By driving changes in forest vegetation in the early years after timber harvest, it is possible that moose mediate the effects of timber harvest on biogeochemical and biophysical processes that influence global climate. For example, after a forest disturbance, moose may limit forest carbon sequestration through direct consumption of tree biomass and reduce both post-harvest NPP and NEP, potentially exerting a warming effect on global climate [63]. In North American boreal forests, Schmitz et al. [63] estimated that the annual amount of carbon kept in the atmosphere by moose is substantial and may equal roughly 42–95% of Canada's annual fossil fuel emissions. Moose may also drive changes to forest albedo that occur in the years immediately after timber harvest. Because they limit the vertical growth of deciduous trees that often appear soon after forest disturbance [54], moose may reduce total forest volume and increase albedo, particularly in the early stages of forest succession before unbrowsed coniferous species begin to dominate.

Despite increasing scientific evidence highlighting the need to consider both forest and herbivore management in climate change mitigation strategies [64,65], to our knowledge, the effects of moose on albedo dynamics in boreal forests have not yet been studied and integrated into post-harvest management practices. In addition, the net climate impact of moose herbivory in early successional forests is currently unknown. There are two major counteracting effects at play: on one hand, moose browsing may accelerate ecosystem respiration after harvest and keep more carbon in the atmosphere, thus exerting a warming effect on climate; on the other hand, moose may limit vertical tree growth of deciduous trees and may reduce the snow masking effects of these trees, potentially driving climate cooling effects by increasing surface albedo. To the best of our knowledge, no study has integrated both carbon and albedo effects to quantify the overall climate influence of moose. This integration should consider the local climate context as well as diversity in both tree composition and structure, and is potentially relevant for forest managers who aim to manage boreal forest stands for the purpose of climate mitigation and timber production.

This study integrates 11 years of empirical field data on post-harvest forest dynamics with statistical regression models to address knowledge gaps regarding the effects of moose browsing on aboveground tree biomass, albedo, and climate dynamics in clear-cut boreal forests. We used a paired herbivore exclosure, open plot study design at 44 sites located within productive boreal forests in the Trøndelag, Innlandet and Viken, and Vestfold and Telemark counties of Norway to test the hypotheses that (1) moose browsing reduces aboveground tree biomass and (2) increases surface albedo after clear-cut 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 individual and county-aggregated estimates.

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 study sites in the Vestfold and Telemark, Innlandet and Viken, and Trøndelag counties of Norway (Figure 1A). Study sites were established in areas of forest that had been clear-cut a median of three years prior to establishment. Forests in the study regions are characterized by a variety of coniferous and deciduous tree species, including Scots pine, Norway spruce, rowan (*Sorbus aucuparia*), downy birch (*Betula pubescens*), aspen (*Populus tremula*), and grey alder (*Alnus incana*). Other woody plant species are present, including willow (*Salix caprea*), silver birch (*Betula pendula*), and common juniper (*Juniperus communis*). A majority of study sites were established in areas of forest dominated by either pine or spruce trees prior to harvest.

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 at study sites. Further details regarding forest type and post-harvest treatment at each site can be found in Table B1. Several species of large herbivores are found within the study regions. Moose are important forest browsers found at moderate-to-high densities in both Innlandet and Viken and Trøndelag, but at lower densities in Vestfold and Telemark (Figure 1B) [57,66]. Roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) may also be present, but at lower densities than moose.

Each of the 44 sites used in this study consisted of two square plots (20 m x 20 m) established at a distance of 20 m from one another (Figure 2A). Each plot at a site was randomly designated as either a moose exclosure or an open plot. The moose exclosure 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. The other plot open remained accessible to large herbivores and thus, was subject to moose browsing throughout the study period. Figure 2B provides 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. Four circular subplots with a radius of 2 m were established within each plot (Figure 2A). The center of each subplot was placed 5 m from the inner edges of the larger plot to reduce potential edge effects from exclosure fencing. Vegetation was sampled within these subplots annually after initial exclosure. Sampling at each site was typically performed during spring months after snow had melted at each site. Speed et al. [57] provides more details regarding design of study sites.

(A)
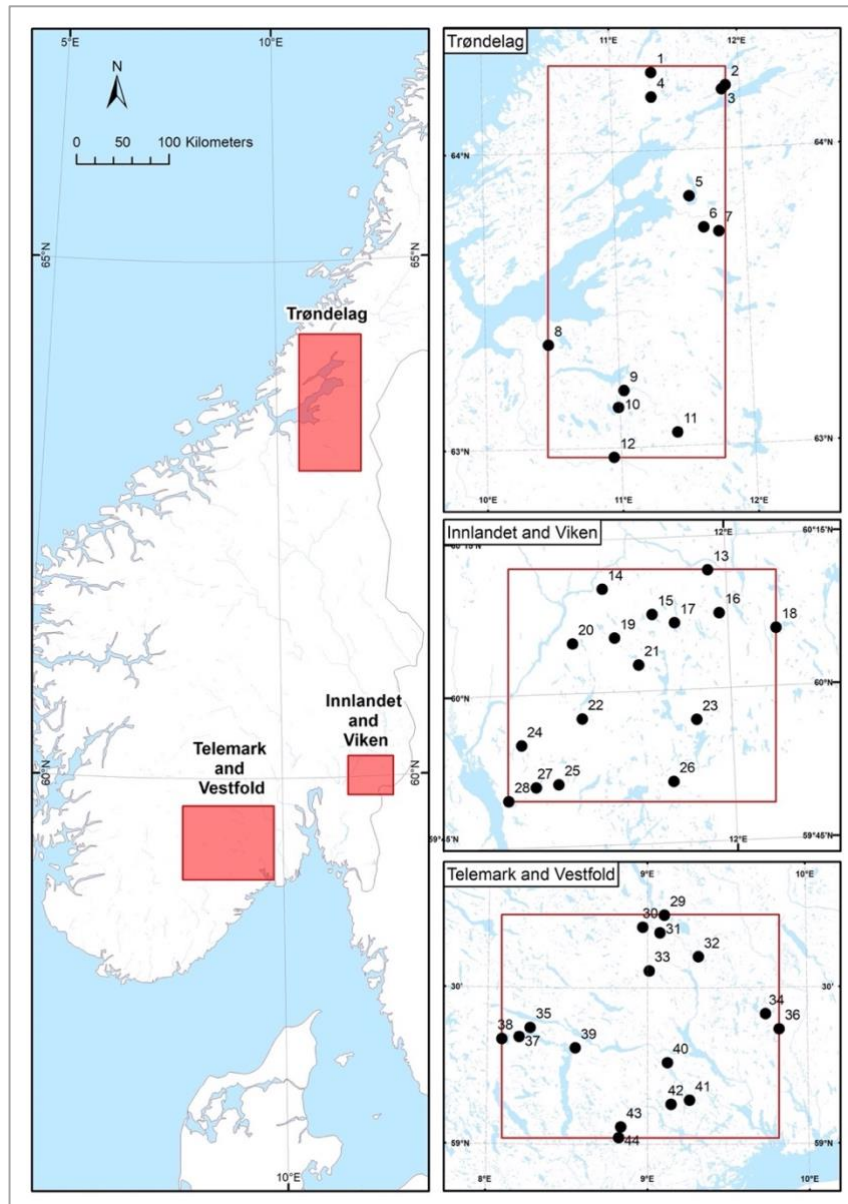
(B)
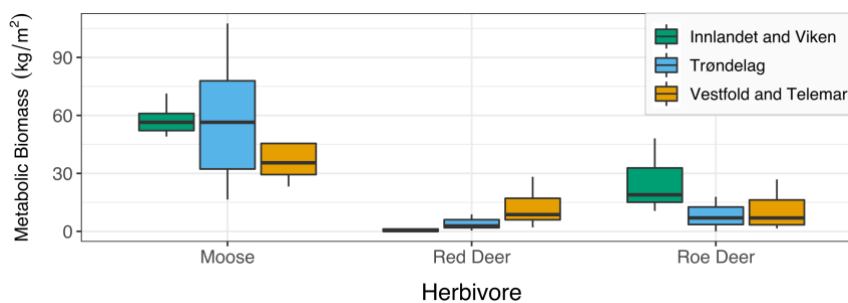
Figure 1. (A) Map of 44 study sites located in Trøndelag, Vestfold and Telemark, and Innlandet and Viken counties of Norway. Site numbers correspond to those listed in Table B1. (B) Densities of moose, red deer, and roe deer in each study region. Herbivore densities are from 2015 and are represented by metabolic biomass per square kilometer (kg km⁻²). Boxes represent interquartile ranges and black lines show median values. Tails indicate minimum and maximum values.

(A)
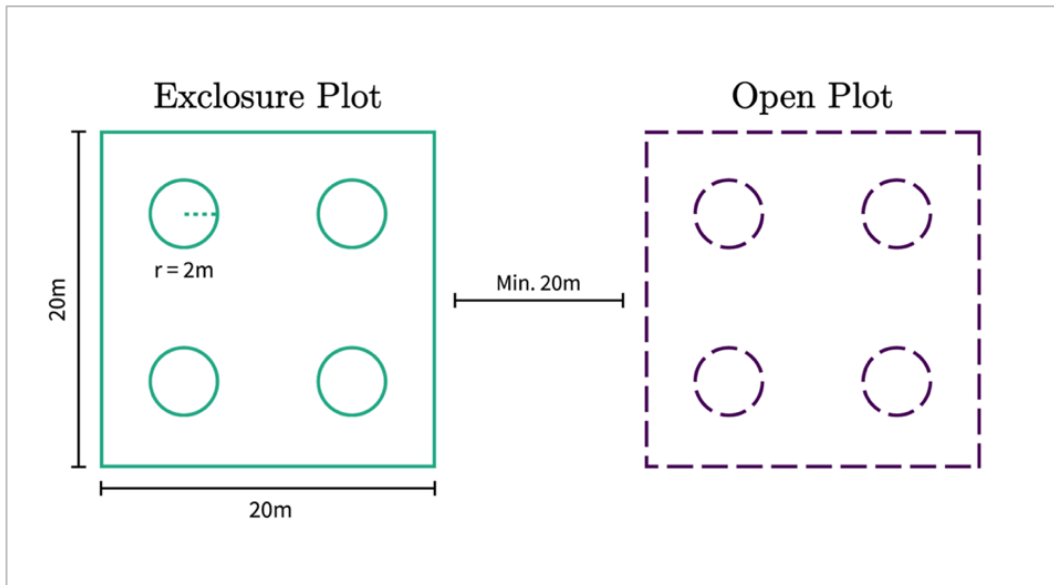
(B)

Figure 2. (A) An illustration of the experimental design used at each study site. Two plots of identical dimensions (20 x 20 m) were placed at least 20 m apart. The exclosure plot (green) was fenced to a height of 2.5 m and thus, inaccessible to large herbivores and the browsing effects of moose throughout the study period. In contrast, the open plot (purple) was not fenced, which allowed moose to browse freely within the plot. Vegetation was sampled annually within circular subplots. (B) An aerial photo of a moose exclosure at one of the study sites.

2.2   Tree Biomass & Abundance

To investigate the effects of moose exclosure on post-harvest tree biomass, we used allometric biomass models to estimate aboveground tree biomass at each study site in the years after exclosure. We relied upon a long-term dataset of individual tree observations recorded at each study site. This dataset included observations of tree density, species, and height class in 50 cm increments recorded annually within circular subplots at each site. The dataset 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 during initial harvest. We then used allometric biomass models to estimate aboveground tree biomass (g) for each tree in the long-term dataset. Although allometric biomass models exist for common boreal tree species in Norway [67–69], 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 dataset 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. [70] produced biomass models for birch, rowan, pine, and spruce trees using tree samples from study sites within Trøndelag (Table B3), combining these models with a back-fitting procedure to produce height-only biomass models for trees in moose exclosures (Table B4). We utilized a similar back-fitting procedure to produce height-only biomass models for trees in open plots (Figure C1; Table B5). Further details about the back-fitting process and the biomass models we used can be found in Appendix A. Using these height-only biomass models for exclosures and open plots, we then estimated aboveground tree biomass for individual birch, rowan, pine, and spruce trees in our long-term dataset. We found relatively few observations of other woody plant species in the dataset, including willow and common juniper. 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 exclosure 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. [70] at our study sites. 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 B1). Instead of excluding these sites from subsequent analyses, we chose to include them, as we assumed that the high productivity values were correct based upon prior site knowledge.

2.4   Herbivore Densities

To assess densities of moose, red deer, and roe deer in each of the study regions, we used spatiotemporal large herbivore density data available across Norway [57,66]. Herbivore densities are represented by average metabolic biomass per square kilometer (kg km^{-2})

and were provided at the municipality level in 10-year increments from 1949–2009, as well as in 2015. Because our long-term tree dataset spanned 2008–2019, we chose to use herbivore densities from 2015 (Table B1; Figure 1B), which represented a temporally intermediate value that could provide reasonable estimates of herbivore densities during our study period.

2.5 Albedo Estimates

2.5.1 Non-Linear Albedo Model

We utilized a non-linear model [33] to assess the effects of moose exclosure on post-harvest albedo dynamics at each study site. The model includes functional forms for temperature and snow as well as an interaction between forest volume and snow to produce monthly estimates of albedo for any given year. The model predicts albedo dynamics using vegetation structure information and climatic conditions as explicit variables. It is produced by decomposing mixed signals via simultaneous un-mixing and non-linear regression of multi-year retrievals of surface albedo (MODIS MCD43A3 data product), high resolution (16 m) datasets of forest composition and structure parameters, and climate records. It has been statistically validated against MODIS albedo observations in Scandinavian boreal forest. The model varies for spruce, pine, and deciduous forest, allowing us to estimate separate values of albedo for each tree type.

2.5.2 Biomass-to-Volume Conversion

To produce albedo estimates using the model described above, we first utilized average wood densities [71] specific to the tree species in our dataset to convert estimates of individual tree biomass into estimates of tree volume. Appendix A 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 (m^3 ha^{-1}) for each of the three forest types. We repeated this process at all study sites and across all years of available tree data to produce a longitudinal dataset of forest volume at the subplot resolution. Figure C2 shows average forest volume within each study region in the years after initial exclosure.

2.5.3 Climate Averages

We calculated the monthly averages of snow water equivalent (mm) and temperature (K) 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 2007–2019. We obtained our data from SeNorge, which provides spatially interpolated estimates of snow water equivalent and temperature at a resolution of 1 km^2 across Norway [72]. Figure C3 shows monthly averages of snow water equivalent and temperature within each study region. Table B2 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 [73].

2.5.4 Albedo Estimates

We then combined subplot estimates of forest volume and site-specific climate averages with the albedo model to produce monthly subplot-level albedo estimates for each forest type (spruce, pine, and deciduous). We repeated this process for each year of tree observations to produce a longitudinal dataset with monthly albedo estimates for each forest type. In addition to albedo estimates specific to each type of forest, we used a weighted average (Equation 1) of subplot albedo for each forest type (α_s) and relative abundance of each forest type (p_s) to calculate composite estimates of albedo (α_c) for each subplot.

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

We also sought to directly compare albedo between moose exclosures and corresponding open plots at each study site. Thus, we decided to average subplot estimates of albedo within each plot to produce plot-level estimates. 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.

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. 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 [74]. Appendix A 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-effects 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 Figure C4, Figure C5, and Figure C6, 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-effects structure as study site within region and crossed with month. This random-effects 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 SeNorge that was used to produce albedo estimates. We chose to include this variable instead of snow water equivalent to address issues with non-linearity between albedo and snow water equivalent in our initial model. We employed a natural log transformation of the response variable to address heteroscedasticity and non-normality 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 C7.

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 (CO_2) equivalents. Using CO_2-equivalents 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 CO_2-equivalents for tree biomass and albedo separately, which ultimately allowed us to examine individual contributions of these factors to net change in CO_2-equivalents and climate. To translate changes in tree biomass due to moose exclosure into CO_2-equivalents, we first calculated the total amount of tree biomass within each exclosure and corresponding open plot. We then converted biomass to a measure of aboveground carbon (ton C ha^{-1}) and subtracted carbon in open plots from carbon in exclosures to produce annual estimates of difference in carbon (ΔC) at each study site for all years in the study period. Estimates of ΔC were then directly converted into CO_2-equivalents.

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 [75]. Shortwave RFs at TOA due to changes in albedo can be approximated by using radiative kernels. This approach was initially developed by the climate modelling community to address internal feedbacks within general circulation models (GCMs) but has been widely adopted by the land surface science community as a tool to estimate variations in RF due to albedo changes [76–78]. Radiative kernels are used to deconstruct the various contributions of feedbacks and forcing to the total change in TOA radiative fluxes in climate. Out of the radiative kernel datasets currently available [79–82], we used a set of kernels validated and made publicly available by Pendergrass et al. [80]. 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 as well as the surface [83].

To compute RF for each of 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 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 kg CO_2-eq m^{-2} is estimated by dividing the annual mean RF for each plot (in W/m^2/m^2) by the radiative efficiency of CO_2 (1.75 *10-15 W yr/kg m^2) [84]. 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.

3 Results

3.1 Tree Biomass

We found that total aboveground tree biomass grew significantly more over time in moose exclosures than in open plots ($p = 0.031$). On average, biomass in open plots increased by 18.4% for each year of growth since exclosure ($p < 0.001$; 95% CI: 15.5–21.4%), while biomass in moose exclosures increased by 21.9% ($p < 0.001$; 95% CI: 18.9–24.9%) (Table B6). Additionally, total tree biomass had a positive relationship with site productivity in exclosures (Table B6), where on average, total biomass increased by 15.3% for a 10% increase in productivity ($p = 0.005$, 95% CI: 4.7–26.9%). Figure 3 shows average values of total tree biomass across time and within each region. Few sites in Innlandet and Viken had tree data beyond seven years since exclosure.
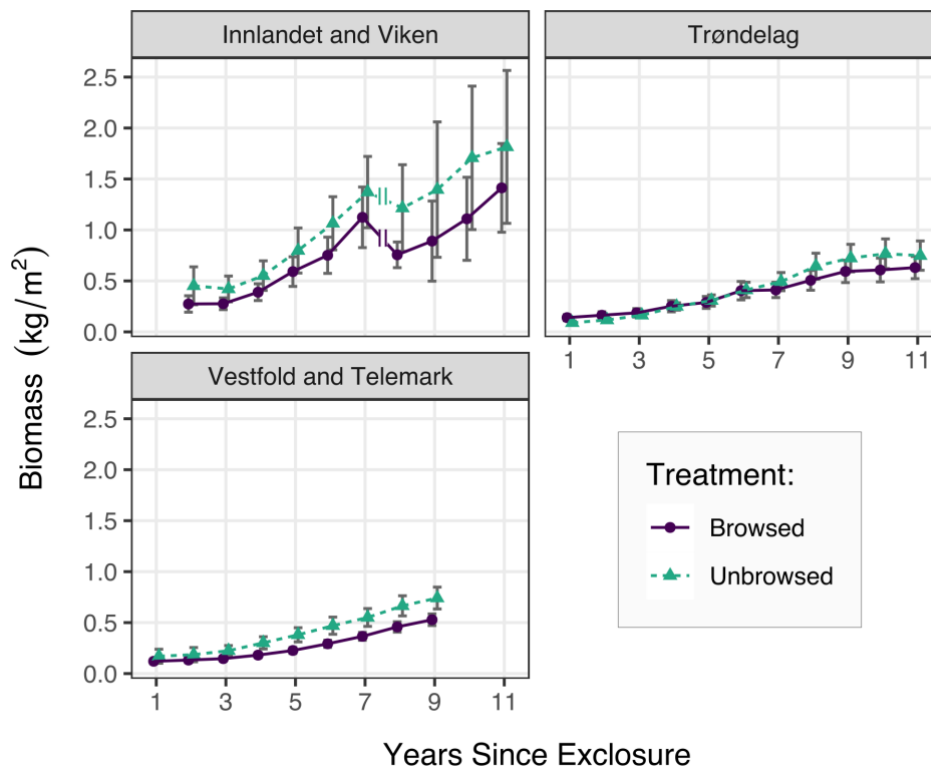
Figure 3. Total aboveground tree biomass (kg m^{-3}) within open plots and moose exclosures in the years after initial exclosure, averaged within each study region. Error bars represent standard error. Few study sites in Innlandet and Viken had data past seven years since exclosure.

We also found that deciduous tree biomass grew significantly more over time in moose exclosures compared to open plots ($p < 0.001$). Deciduous biomass in open plots increased by an average of 12.7% for each year of growth since exclosure ($p < 0.001$; 95% CI: 8.70–16.8%), while deciduous biomass in exclosures increased by an average of 26.0%

($p < 0.001$; 95% CI: 21.5–30.6%) (Table B7). Similar to total tree biomass, we saw a positive relationship between deciduous biomass and site productivity, where biomass increased by an average of 17.5% 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 exclosures and open plots ($p = 0.101$). On average, coniferous biomass in open plots increased by 21.0% for each year since exclosure ($p < 0.001$; 95% CI: 17.8–24.3%), while coniferous biomass in exclosures increased by 18.2% ($p < 0.001$; 95% CI: 15.1–21.4%) (Table B8). Detailed model output for total biomass, deciduous biomass, and coniferous biomass can be found in Table B6, Table B7, and Table B8, respectively.

3.2 Tree Community Composition

We did not find clear differences in the relative abundance of deciduous, pine, and spruce trees in moose exclosures compared to open plots (Figure 4). On a regional scale, deciduous trees were more abundant than spruce or pine trees throughout most of the study period, both within exclosures and open plots. However, the treatment effect of moose exclosure on relative tree abundances appeared to differ between study regions. In Trøndelag, deciduous trees were more abundant in open plots than in exclosures, while the opposite was true in Vestfold and Telemark. 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.

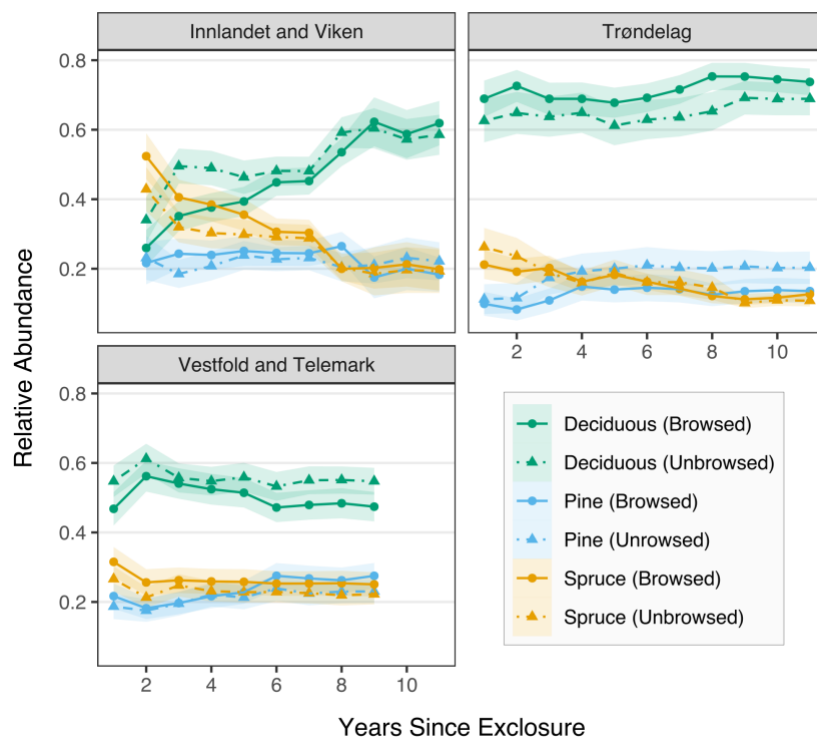**Figure 4. Relative abundance of deciduous, pine, and spruce trees within open plots and moose exclosures in the years after initial exclosure, averaged by study region. Shading represents standard error.**

3.3 Albedo

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 ($p < 0.001$). 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 by an average of 0.85% ($p < 0.001$; 95% CI: 0.76–0.93%) (Table B9). Figure 5 shows the average difference in monthly albedo between moose exclosures and corresponding open plots in each of the three study regions. 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 appeared to be largest during winter months when snow was present in study regions, especially eight-to-ten years after initial exclosure and in the Trøndelag and Innlandet and Viken counties. Despite the apparent effects of snow on albedo seen in Figure 5, 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 13.3% 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%) (Table B9). Detailed model output for albedo can be found in Table B9.
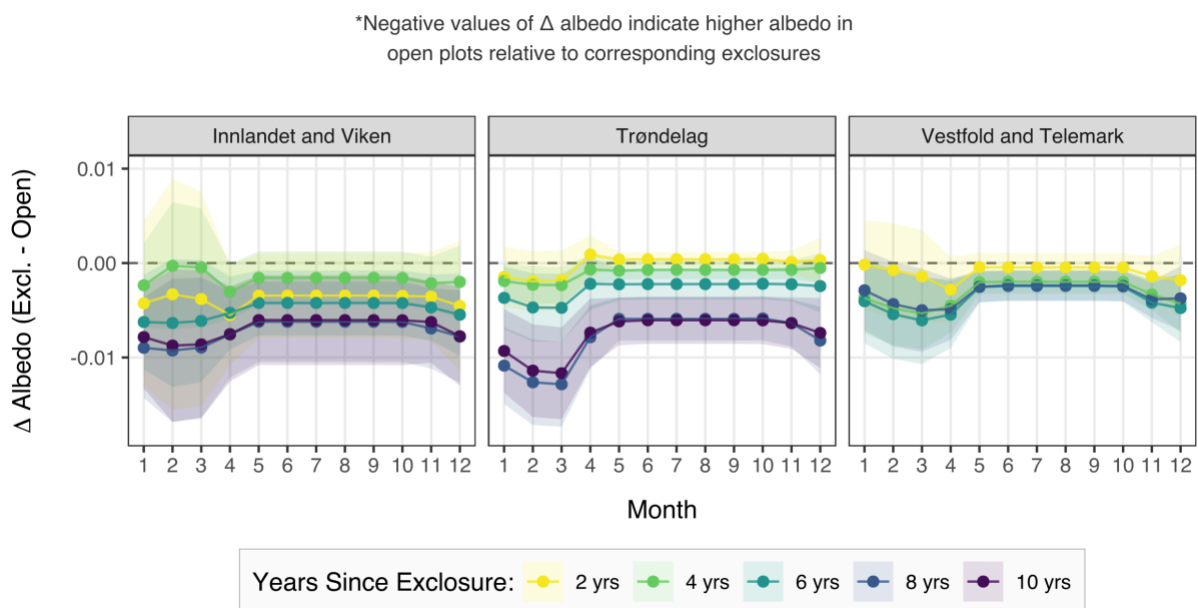
Figure 5. **Mean difference in albedo between moose exclosures and open plots, where difference equals exclosure albedo minus open plot albedo. Differences are averaged within each study region. Line colors correspond to number of years since exclosure, while shading indicates standard error. Horizontal dashed line indicates no difference in albedo. Negative values indicate higher albedo in open plots relative to exclosures. Differences in albedo specific to each forest type (deciduous, pine, and spruce) can be found in Figure C8.**

3.4 Carbon Equivalents

On a regional scale, moose exclosure seemed to minimally impact net annual CO_2-equivalents in early successional forests, with cooling contributions from increased carbon sequestration and warming contributions from decreased albedo of similar magnitudes in opposing directions (Figure 6). In the years after study site establishment, moose exclosure led to higher growth of tree biomass, more carbon sequestration, and a cooling effect on global climate equivalent to less carbon dioxide in the atmosphere. This cooling carbon effect increased in magnitude as differences in tree biomass and carbon sequestration between exclosures and open plots grew over time. In contrast, moose exclosure led to lower albedo and 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 grew in magnitude over time. The cooling effect of carbon sequestration and warming effect of decreased albedo within moose exclosures relative to open plots were of similar magnitude but in opposing directions. Thus, these effects nearly canceled each other out when averaged across study regions, and produce minimal net change in annual CO_2-equivalents and climate, varying only slightly between regions.
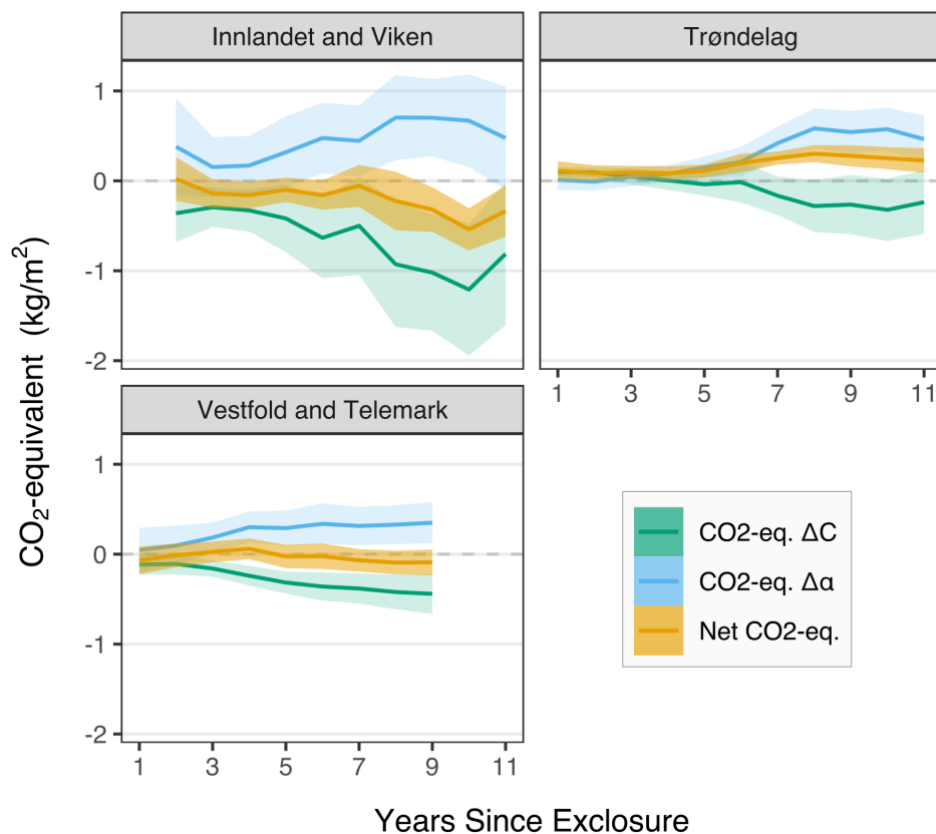
Figure 6. Effect of moose exclosure on annual CO_2-equivalents (kg CO_2-eq. m^{-2}) at 44 study sites in Norway, averaged by region. Positive values indicate that exclosure has a warming climate effect equivalent to more CO_2 in the atmosphere. Negative values indicate that exclosure has a cooling effect equivalent to less CO_2 in the atmosphere. Green lines represent climate changes due to differences in aboveground carbon between exclosures and open plots. Blue lines represent climate changes due to differences in albedo. Orange lines indicate the net climate impact of moose exclosure. Shading represents standard error.

The effects of moose exclosure on CO_2-equivalents were more variable at the local level, however. At some of our study sites, trends were opposite of those on the regional scale, where moose exclosure drove warming contributions from carbon and cooling contributions from albedo. To illustrate this, we can look to two sites (Site 5 and Site 8) in Trøndelag, both with similar productivity and established in clear-cut spruce forest, at which moose exclosure had opposite effects on CO_2-equivalents (Figure 7). At Site 5, more tree biomass accumulated in the open plot than in the moose exclosure, while albedo in the open plot simultaneously decreased relative to the albedo of the exclosure. Thus, moose exclosure at this site led to a carbon warming effect, an albedo cooling effect, and a net warming effect equivalent to more CO_2 in the atmosphere that increased in magnitude over time. In contrast, trends in CO_2-equivalents at Site 8 were more similar to regional trends shown in Figure 6. Moose exclosure at this site led to a carbon cooling effect, an albedo warming effect, and minimal net change in CO_2-equivalents over time. Several study sites within all three study regions had CO_2-equivalents trends similar to those of Site 5.
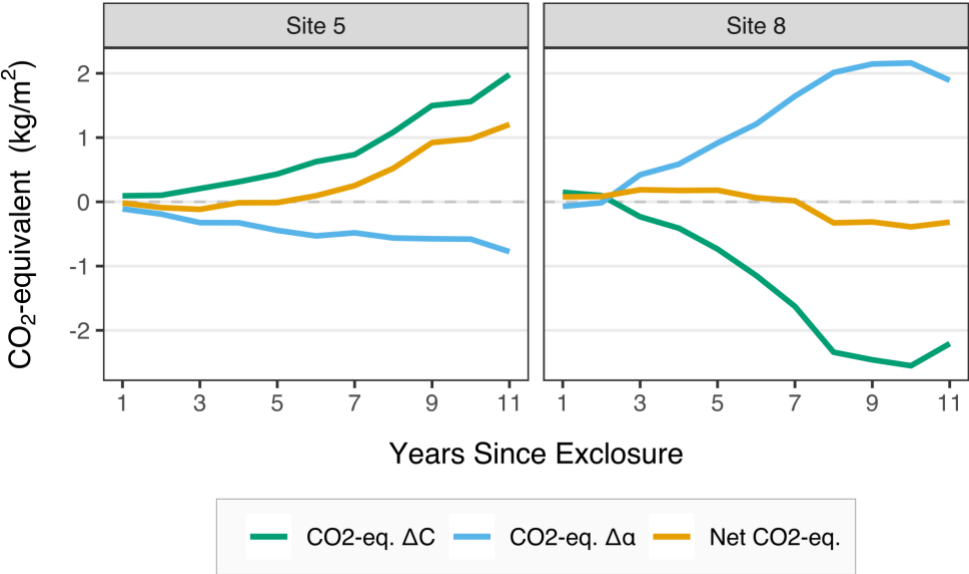
Figure 7. Effect of moose exclosure on annual CO_2-equivalents (kg CO_2-eq. m^{-2}) at two study sites (Sites 5 and 8) in Trøndelag county. Negative values indicate that exclosure has a cooling effect equivalent to less CO_2 in the atmosphere. Green lines represent climate changes due to differences in aboveground carbon between exclosures and open plots. Blue lines represent climate changes due to differences in albedo. Orange lines indicate the net climate impact of moose exclosure.

4 Discussion

Large herbivores such as moose can potentially influence global climate by altering biogeochemical and biophysical processes that occur in boreal forests after timber harvest [63], and may complicate forest management strategies aimed at mitigating climate change. In this study, we used 11 years of vegetation data from clear-cut boreal forests to assess the 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, ultimately causing minimal net climate change on a regional scale. Based on these results, we suggest that moose browsing can drive important changes in biogeochemical and biophysical processes at the land surface that directly oppose each other, particularly in successional boreal forests that have been previously harvested for timber.

4.1 Tree and Biomass Dynamics

On a regional scale, moose browsing appeared to limit the growth of aboveground tree biomass in the years after initial 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. These results are consistent with the predictions of Schmitz et al. [63], who suggested that moose browsing reduces carbon sequestration in North American boreal forests on a landscape scale, as well as with the findings of McInnes et al. [54], who used long-term moose exclosures to show that moose can substantially reduce total tree biomass over time. Moose in our study regions seemed to limit total tree biomass primarily by preventing the accumulation of deciduous tree biomass (Table B7), which suggests that these herbivores preferred to browse on deciduous species at our study sites. Selective browsing by moose and resulting changes in forest communities have been previously documented in both North American and Fennoscandian boreal forests [52,54,85]. For example, Speed et al. [85] 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 et al. [52] observed that moose reduce the number of large deciduous trees in recently clear-cut forests. We also appear to have observed selective browsing, where moose preferentially consumed deciduous species to the point that total forest biomass was reduced.

In contrast, moose did not seem to affect the growth of coniferous biomass, at least on a regional scale. This was surprising since we expected that moose browsing could release unpalatable coniferous species (e.g., spruce and pine) from competition with preferred deciduous species and indirectly facilitate coniferous growth, as has been previously observed in boreal forests [54]. However, we did not find strong evidence of such facilitation, as we observed that coniferous tree biomass grew at similar rates in both exclosures and open plots. These results are in line with those of Kolstad et al. [52], 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-year study period. They suggested that coniferous species such as pine and spruce may grow slowly

enough that substantial differences in biomass between exclosures and open plots would not form in a time span of this length. Our study spanned 11 years and may also have been too short to allow for such differences to form at our study sites.

Although moose browsing had an apparent impact on the growth of tree biomass at a regional scale, we did not find it to have 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. 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 [52,86]; however, few have assessed the effects of moose on relative tree species abundance of both trees in the canopy and saplings, which makes the comparison of our results difficult in this respect. In their study of moose browsing in successional boreal forests, den Herder et al. [87] found that moose increase the mortality of preferred deciduous tree species. We thus expected to see some evidence of increased mortality and decreased relative abundance of deciduous species in open plots compared to exclosures over the course of our study period, yet we did not observe this decline in our study regions 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 [88]. 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 over the course of the study period. 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.

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. 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. As there have been no previous studies on the albedo impacts of moose in boreal forests, we can compare our results with recent investigations into the effects of arctic reindeer grazing on albedo. Cohen et al. [47] examined the effects of reindeer grazing pressure on albedo in arctic regions of Fennoscandia and found that albedo during the regional snowmelt period (80–170 DOY) was higher in regions of tundra with high grazing pressure than in regions with low grazing pressure, with maximum average albedo differences of greater than 0.04 between the two regions. Similar to their study, we found that albedo is higher in areas of 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 exclosures and open plots was just over 0.01 (Figure 5). This difference in albedo, recorded during winter months in Trøndelag, is considerably smaller than that measured by Cohen et al. [47].

The effect of moose on albedo in our study regions appeared to be strongest in months when snow was present (Figure 5), although the magnitude of this interaction between treatment and snow varied across study regions and was not found to be statistically significant. In their study of reindeer grazing, Cohen et al. [47] 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. It is feasible that 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 [35], an important question in our analysis was whether moose-driven changes in albedo were primarily due to changes in forest structure, tree species composition, or both, to some degree. 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 biomass. Examining differences in albedo between exclosures and open plots specific to each forest type (Figure C8), we found that trends in deciduous albedo closely mirror those of plot-level albedo, referred to as composite albedo in Figure C8. 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 forest 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 potential need for boreal forest managers to account for climate impacts of moose impacts to forest carbon cycling [49,63]. However, we found that the climate impacts of moose due to biophysical changes in forest albedo are of similar importance to those of carbon. On 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. To our knowledge, no previous study in the boreal forest biome has compared both biogeochemical and biophysical climate impacts of large herbivores. Nevertheless, we can refer to recent studies that explore the climate impacts of other types of disturbances within boreal forests for perspective. For example, Cherubini et al. [19] 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 years after harvest, they found that post-harvest carbon fluxes associated with increased R_H 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. [89] found that fires in Alaskan boreal forests cause an initial climate warming effect due to combustion of forest biomass and flux of greenhouse gases (CO_2 and CH_4) to the atmosphere, but also have a climate cooling effect due to increased surface albedo, which partially mitigates the warming effect over long timescales. Our results thus seem to fit into a larger, generalized characterization of disturbance 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 (Figure 7), suggesting that moose impacts on forest carbon and albedo are moderated by local factors to some degree. The identities and relative importance of these factors are not entirely clear in our analysis, 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 [32,35]. 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. [88] showed that birch trees in boreal forests with high productivity can regrow more substantially after moose browsing than trees in low productivity forests. These results may suggest that, in areas of successional forest with high productivity, browsed tree species such as birch may be able to 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 in these forests may be more substantial, potentially causing a stronger carbon warming effect on climate. We did not see evidence of this relationship between biomass growth and productivity in our study, however, as 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 (Table B6; Table B7).

Persson et al. [88] also found that the ability of birch trees to compensate for browsing damage is mediated by moose density and associated browsing pressure, where high moose browsing pressure stimulates more birch biomass production after browsing than low browsing pressure. Moose densities were variable across our study regions (Figure 1B; Table B1), and have been found to vary widely throughout North American and Fennoscandian boreal forests in both space and time [56,57,66]. Thus, we see the potential for both biogeochemical and biophysical climate impacts of moose to be influenced by complex interactions of spatially heterogenous factors, such as snow, productivity, and moose density, across the boreal forest landscape. Further research is necessary to clarify the role that these factors have in shaping moose climate impacts at the local level.

In our study, we did not assess the impacts of moose on biophysical factors other than albedo, such as canopy conductance and surface roughness. Nevertheless, moose-driven changes in these factors may have important implications for local climate and should be investigated in future research. For example, differences in canopy conductance between deciduous and coniferous boreal tree species can affect the ratio of sensible to latent heat flux that occurs at the forest surface and consequently influence local temperatures [16,90,91]. Deciduous forests tend to have more latent heat flux relative to sensible heat flux than coniferous forests [90,91], and thus, are thought to cool climate in spring summer

months relative to coniferous forests [41]. Moose in our study regions limited growth of deciduous tree biomass in the years after forest harvest, and therefore, may have driven important changes in the ratio of latent to sensible heat flux at the forest surface, possibly reducing latent heat flux and increasing local temperatures.

Surface roughness is another important biophysical characteristic of the land surface that can affect local climate [42]. In boreal forests, surface roughness can influence the total amount of sensible and latent heat flux that occurs at the forest surface by affecting the efficiency of the exchange of energy between the surface and the atmosphere [42,92]. Lee [92] found that reduced surface roughness in boreal forests may affect local temperatures, particularly in summer months when snow is absent. Snøan [93] also showed that moose can reduce surface roughness in recently clear-cut boreal forests, and thus, it is possible that moose somehow influence local climate through this mechanism. Additional research is needed, however, to clarify the importance of moose for these biophysical factors and integrate local climate impacts with global effects. This synthesis is of particular relevance to forest managers who seek to manage boreal forests for the purpose of both local and global climate mitigation.

4.4   Recommendations

Our results strongly suggest that moose can mediate changes to climate that occur after clear-cut timber harvest in boreal forests. Our results also suggest that the biogeochemical and biophysical climate impacts of moose are of similar importance at a regional scale. Therefore, we recommend that forest managers account for potential moose impacts in future mitigation plans, as moose may cause unexpected changes in forest carbon and albedo that could affect the mitigation potential of post-harvest forest management strategies. Our study was conducted over a relatively short period of forest succession. The long-term climate impacts of moose are largely unknown, however, and we propose that such impacts be studied to help forest managers better account for moose management in climate mitigation plans. Evidence has shown that moose can substantially alter the dynamics of succession within boreal forests [52] and prevent the recruitment of preferred deciduous tree species into the mature forest canopy [54]. Deciduous boreal species have different albedo and differing rates of carbon sequestration over long time periods than coniferous species [35,94]. Thus, by influencing the species of trees that grow into the mature canopy, moose may drive long-term changes in carbon sequestration and albedo that, in turn, affect global climate. Future research should attempt to quantify both the biogeochemical and biophysical consequences of moose browsing across periods of forest succession that are longer than those addressed in this study.

We only used aboveground tree biomass to assess the biogeochemical impacts of moose to climate; however, future studies can integrate moose effects on other sources of forest carbon into their analyses, including those to soil carbon fluxes and understory vegetation biomass. Evidence suggests that moose can affect these sources of carbon in successional boreal forests [95,96], although moose-driven changes to soil carbon may take long periods of time to appear after initial forest disturbance [70]. Accounting for these other sources of carbon so will provide a more comprehensive view of forest carbon fluxes and climate impacts caused by moose. Additionally, our study focused on moose impacts to global climate dynamics, but future studies can also investigate impacts on local climate, particularly by accounting for changes to biophysical factors such leaf area index, canopy conductance, and vegetation surface roughness. A variety of recently developed monitoring techniques can potentially simplify assessments of biophysical changes in the

land surface associated with moose herbivory. For example, surface albedo of vegetated surfaces can be measured efficiently and at a high spatial resolution using albedo sensors mounted on unmanned aerial vehicles (UAVs) [97,98]. This method of data collection may be particularly useful for researchers who seek to measure albedo in plots of forest vegetation that are too small to assess with satellite-based observations of albedo. Light Detection and Ranging (LiDAR), which provides detailed three-dimensional measurements of vegetation structure [99], is another method of spatial data collection that can be used in this context. LiDAR data have been collected for large areas of the global land surface [100] and have been previously used to estimate biophysical vegetation properties, such as leaf area index [101] and canopy roughness [93]. By using novel methods such as these, researchers can potentially integrate biophysical factors that influence local climate into their studies and better compare the effects of moose on global and local climate.

4.5 Study Limitations

Our study has several potential limitations inherent to our methods. First, moose are not the only herbivores present at our study sites, so we must be careful when generalizing their impacts on forest dynamics. Both roe and red deer can be found in our study regions. Previous studies have suggested that these species of deer have some degree of diet overlap with moose [102,103]; thus, it is possible that deer browsing is partially responsible for the differences in tree biomass and relative abundance that we observed between open plots and herbivore exclosures. However, moose were present at higher densities than roe or red deer at our study sites (Table B1), especially at several sites in both Trøndelag and Innlandet and Viken, suggesting that they have a larger browsing impact than deer. It is also important to note that large forest herbivores present in our study regions can have important direct and indirect effects on trees other than browsing. For example, Żywiec et al. [104] found that red deer can directly increase tree sapling mortality in boreal forests through physical damage caused by antler rubbing. Additionally, Castro et al. [105] observed that forest herbivores can influence boreal tree regeneration and establishment through trampling. It is possible that the trends we observed in biomass and tree abundance were partially driven by these alternative effects.

Second, small forest herbivores, such as mountain hare (*Lepus timidus*), are also present at study sites, and unlike moose or deer, were able to enter both exclosures and open plots throughout the study period. Prior studies of mountain hare in Finnish boreal forests and snowshoe hare (*Lepus americanus*) in North American forests have found that hare and moose both compete for the same deciduous woody species as a food source [106–108]. We did not account for mountain hare browsing in our analyses, and it is possible that this browsing somehow influenced our results. Further research is necessary to identify potential browsing interactions between moose and hare, as well to clarify the importance of hare browsing to forest regeneration in boreal ecosystems.

Third, the methods we used to estimate post-harvest tree biomass have several important limitations. The allometric height-only biomass models we generated for the main tree species within open plots in our dataset are subject to error that varies between species (Figure C1). For example, multiple R^2 values of allometric models were higher for birch (R^2 = 0.9898) and spruce (R^2 = 0.9059) than for rowan (R^2 = 0.8345) and pine (R^2 = 0.7015). As a result of these differences in model fit, our biomass estimates may have systematic species-specific error. Variation in the accuracy of tree height class estimates between observers is another potential source of error in our study. Several studies have shown that inter-observer variation associated with vegetation sampling can be substantial even

when observers are experienced with sampling methods [109–111]. Our study included estimates from an 11-year time period across three study regions and had multiple observers; thus, it is possible that our measurements of tree height class have some degree of inter-observer variation. Additionally, our dataset included few observations of juniper and willow for which we did not have specific biomass models. By estimating biomass for these species with models for morphologically similar trees, we may have introduced some error into our final biomass estimates. We supposed that this was a better option than excluding juniper and willow from our dataset, since we wanted to account for as much of the deciduous and coniferous woody biomass present at each site as possible. Additionally, observations of juniper and willow were relatively uncommon in our dataset, so it is unlikely that they had a large influence on our final results.

Fourth, the methods we used to estimate post-harvest albedo dynamics have important limitations. When we converted estimates of individual tree biomass into forest volume for use in the non-linear albedo model, we treated each tree as if it had a constant wood density throughout its stem and branches. In reality, wood densities can vary throughout the aboveground portions of boreal trees, and may be higher near the stems than at the tops of trees [71,112]. By using this approach, we may have biased our estimates of forest volume, which possibly influenced our albedo estimates. Development of allometric volume models specific to small trees in boreal forests can eliminate this problem in future analyses and simplify calculations of forest volume in successional forests. Moreover, the climate data we used to model albedo was not recorded directly at our study sites but was spatially interpolated from nearby meteorological stations. The data has occasionally been found to contain erroneous estimates of temperature and precipitation variables, particularly in regions of Norway with few meteorological stations [72]. The climate dataset we utilized may have contained such errors, but we attempted to minimize the possibility of this by using site-specific climate averages from a period of 12 years (i.e., 2007–2019).

Last, we did not account for potential influences from understory vegetation in our estimates of albedo. Several studies have shown that the composition of understory vegetation beneath the forest canopy can influence albedo, particularly in forest stands with low tree densities and sparse canopies [34,36], and that moose browsing may cause changes to this vegetation [95]. Further studies on the impacts of moose on forest albedo can potentially integrate these variables into analyses and improve the accuracy of albedo estimates.

5 Conclusion

This study sought to investigate moose-driven changes to forest carbon and surface albedo in successional boreal forests, as well as to explore the net contributions of these changes to global climate. By translating differences in tree biomass and albedo between exclosed plots and browsed areas of forest into CO_2-equivalents, we found that although moose browsing at a regional scale has minimal net impact on global climate, it drives important biogeochemical and biophysical changes in successional clear-cut forests that have similar magnitude and directly oppose each other. To build a more comprehensive characterization of moose climate impacts in boreal forests, future research in this area 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, such as surface roughness and canopy conductance. Future studies should also explore potential climate impacts of moose over successional periods longer than were examined in this study, since moose strongly mediate the recruitment of boreal tree species into the forest canopy [52,54] and may cause long-term changes in forest carbon sequestration and albedo. Our results ultimately provide evidence that moose can influence processes at the land surface relevant to global climate, and we suggest that both biogeochemical and biophysical effects of moose be integrated into mitigative forest management practices.

6 Acknowledgements

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Appendices

Appendix A: Extended Methods

Biomass Model Back-Fitting Procedure

We utilized a model back-fitting procedure similar to that employed by Kolstad et al. [70] to generate height-only biomass models for trees in open plots at our study sites. First, we isolated our long-term dataset to tree observations recorded within open plots at Trøndelag study sites in 2016. These observations included detailed measurements of diameter-at-ground level and height, which allowed us to estimate biomass for each tree using the detailed biomass models developed by Kolstad et al. [70] (Table B3). 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 the values of tree biomass (g) produced in the previous step were modeled as a function of tree height (cm). In each model, we included cubic, quadratic, and linear terms for height. Next, we performed a backwards elimination process, where we sequentially removed non-significant terms and then chose the model with the highest value of adjusted R^2 as our best-fitting model. Thus, we generated four height-only biomass models for spruce, pine, birch, and rowan trees in open plots at our study sites (Figure C1; Table B5). We generated these models using R Studio (version 4.0.0) and the *lme4* package.

Biomass-to-Volume Conversion

Forest volume (m^3 ha^{-1}) represents a key variable in the non-linear model [33] we used to assess post-harvest albedo dynamics at our study sites. Thus, we decided to convert our estimates of aboveground tree biomass into estimates of forest volume for use in the model. Similar to tree biomass, several allometric volume models exist for common boreal tree species. However, these allometric volume models were not applicable to the small trees in our dataset. Thus, we chose to use an alternative conversion method where we divided the biomass of each tree by an average vertical wood density (kg m^{-3}) specific to the species of that tree to produce an estimate of tree volume (m^3). Average vertical wood densities were obtained from Repola [71], who sampled forest stands in southern Finland to calculate averages of stem wood density for spruce, pine, and birch trees.

We could not find average vertical wood densities for rowan or any of the uncommon woody plant species in our dataset that had been calculated using samples from Fennoscandian forests. Thus, we decided to estimate the volume of all deciduous species, including birch, rowan, and willow, using the average wood density for birch. Additionally, we used

the average wood density for spruce to estimate the volume of both spruce and common juniper. Figure C2 shows the average forest volume within each study region in the years after initial exclosure.

Linear Mixed-Effects Model-Building Procedure

We used a model-building protocol recommended for nested ecological data [74] to generate linear mixed-effects models for total tree biomass, deciduous biomass, coniferous biomass, and monthly average albedo. All models were constructed using R Studio (version 4.0.0) and the *lme4* package. For each model, we first constructed a "beyond optimal" model, fit with restricted maximum likelihoods, that included all covariates of interest and all possible interactions between these covariates. We used a correlation matrix to investigate multi-collinearity between numeric covariates and removed any that were correlated but not of direct interest to our hypotheses. We then compared Akaike information criterion (AIC) values between several models with different random effects but the same combination of fixed effects to identify an optimal random effects structure. In several of our models, AIC values were almost identical for those that included study site nested within region as random effects and those that only included study site. In these cases, we selected study site nested within region as the optimal random effects structure.

We fit the "beyond optimal" model selected in the previous step and several nested models using maximum likelihoods, then compared these models using AIC values. The model with the lowest AIC value was selected as the "best-fitting" model. Throughout this process, diagnostic plots were visually inspected to ensure homoskedasticity and normality of model residuals. If heteroskedasticity of residuals was evident, the response variable was transformed using a natural log transformation. Diagnostic residual plots for each of the models can be found in Figure C4, Figure C5, Figure C6, and Figure C7, respectively. Detailed output from each of the models is available in Table B6, Table B7, Table B8, and Table B9.

Appendix B: Supplemental Tables

Table B1. Supplemental information for each of the 44 sites used in this study. Site numbers correspond to those displayed in Figure 1A. Moose and deer densities are estimated in the year 2015 and are represented by metabolic biomass (kg km^{-2}).

Site	County	Forest Type	Clear-Cut Year	Tree Species Planted	Start Year	Produc-tivity	Herbivore Densities		
							Moose	Roe Deer	Red Deer
1	Trøndelag	Spruce	2006	Spruce	2008	0.22	75.89	7.38	8.76
2	Trøndelag	Spruce	2005	Spruce	2008	0.12	107.57	17.86	2.43
3	Trøndelag	Pine	2004	Spruce	2008	0.09	107.57	17.86	2.43
4	Trøndelag	Spruce	2004	Spruce	2008	0.08	75.89	7.38	8.76
5	Trøndelag	Spruce	2006	Spruce	2008	0.11	28.27	6.98	2.83
6	Trøndelag	Spruce	2003	Spruce	2008	0.24	28.27	6.98	2.83
7	Trøndelag	Pine	2005	Pine	2008	0.01	28.27	6.98	2.83
8	Trøndelag	Spruce	2002	Spruce/Pine	2008	0.20	79.89	31.02	1.34
9	Trøndelag	Pine	2003	None	2008	0.12	56.45	4.38	5.44
10	Trøndelag	Spruce	2002	Spruce	2008	0.12	56.45	4.38	5.44
11	Trøndelag	Pine	2005	Spruce	2008	0.13	16.48	0.00	0.42
12	Trøndelag	Pine	2005	None	2008	0.04	36.26	2.71	6.65
13	Innlandet	Spruce	2008/9	Spruce/Pine	2011	0.51	51.74	10.57	1.63
14	Innlandet	Pine	2004/5	Spruce	2007	0.50	49.09	16.24	0.83
15	Innlandet	Spruce	2004/5	Spruce	2007	0.27	49.09	16.24	0.83
16	Innlandet	Spruce	2008/9	Spruce	2011	0.10	51.74	10.57	1.63
17	Innlandet	Pine	2004/5	Spruce	2007	0.16	49.09	16.24	0.83
18	Innlandet	Pine	2007/8	Spruce	2010	0.34	62.65	13.92	0.00
19	Viken	Pine	2008/9	None	2011	0.98	52.57	32.77	0.36
20	Viken	Spruce	2008/9	None	2011	0.38	52.57	32.77	0.36
21	Viken	Pine	2008/9	None	2011	0.25	52.57	32.77	0.36
22	Viken	Spruce	2007/8	Spruce	2010	1.00	56.43	18.91	0.00
23	Innlandet	Spruce	2007/8	Spruce	2010	0.09	62.65	13.92	0.00
24	Viken	Spruce	2008/9	Spruce	2011	0.17	59.33	48.12	3.44
25	Viken	Spruce	2007/8	Spruce	2010	0.23	56.43	18.91	0.00
26	Viken	Spruce	2007/8	Spruce	2010	0.29	56.43	18.91	0.00
27	Viken	Pine	2007/8	None	2010	0.11	56.43	18.91	0.00
28	Viken	Spruce	2008/9	Spruce	2011	0.14	71.34	32.85	0.00
29	Vestfold &Telemark	Pine	2005	None	2009	0.12	45.75	3.56	7.55
30	Vestfold &Telemark	Spruce	2007	Spruce	2009	0.12	45.75	3.56	7.55
31	Vestfold &Telemark	Pine	2002	None	2009	0.14	45.75	3.56	7.55
32	Vestfold &Telemark	Pine	2005	None	2009	0.15	45.75	3.56	7.55
33	Vestfold &Telemark	Pine	2003	None	2009	0.11	45.75	3.56	7.55
34	Vestfold &Telemark	Spruce	2009	Spruce	2009	0.25	45.55	8.85	2.23
35	Vestfold &Telemark	Spruce	2000	Spruce	2009	0.09	34.25	2.94	13.40
36	Vestfold &Telemark	Spruce	2005	Spruce	2009	0.15	45.49	19.92	33.90
37	Vestfold &Telemark	Spruce	2004	Spruce	2009	0.11	34.25	2.94	13.40
38	Vestfold &Telemark	Pine	2007	Spruce	2009	0.06	23.22	1.53	2.08
39	Vestfold &Telemark	Spruce	2005	Spruce	2009	0.11	34.25	2.94	13.40
40	Vestfold &Telemark	Pine	2006	None	2009	0.17	30.19	15.05	28.26
41	Vestfold &Telemark	Pine	2006	None	2009	0.08	36.73	26.88	7.24
42	Vestfold &Telemark	Spruce	2005	None	2009	0.21	27.01	5.03	9.84
43	Vestfold &Telemark	Spruce	2007	Spruce	2009	0.02	27.01	5.03	9.84
44	Vestfold &Telemark	Pine	2007	None	2009	0.21	27.01	5.03	9.84

Table B2. Elevation (meters above sea level), minimum-to-maximum annual range of temperature (K), and minimum-to-maximum annual range of snow water equivalent (mm) at each of the 44 study sites. Monthly averages of temperature and snow water equivalent were calculated from climate data for the period 2007–2019. Site numbers correspond to those displayed in Figure 1A.

Site	County	Elevation (m.a.s.l.)	Temperature range (K)	Snow water equivalent range (mm)
1	Trøndelag	134	17.28	81.71
2	Trøndelag	358	18.62	136.49
3	Trøndelag	213	18.53	137.40
4	Trøndelag	308	17.34	156.22
5	Trøndelag	145	18.21	27.46
6	Trøndelag	194	18.23	37.91
7	Trøndelag	216	18.40	47.46
8	Trøndelag	240	17.42	70.64
9	Trøndelag	311	18.61	92.68
10	Trøndelag	374	18.78	128.83
11	Trøndelag	421	19.75	188.76
12	Trøndelag	283	19.74	139.47
13	Innlandet	255	21.63	81.55
14	Innlandet	191	21.59	47.21
15	Innlandet	274	21.39	66.15
16	Innlandet	377	21.43	93.46
17	Innlandet	356	21.32	82.82
18	Innlandet	222	21.82	50.85
19	Viken	239	21.22	58.50
20	Viken	182	21.29	42.98
21	Viken	244	21.27	51.60
22	Viken	192	21.02	47.05
23	Innlandet	233	21.27	44.31
24	Viken	216	20.80	55.46
25	Viken	247	20.67	60.38
26	Viken	308	20.87	66.55
27	Viken	279	20.58	72.41
28	Viken	171	20.65	63.72
29	Vestfold &Telemark	432	20.57	144.31
30	Vestfold &Telemark	492	20.15	168.78
31	Vestfold &Telemark	462	20.44	142.48
32	Vestfold &Telemark	419	20.44	130.72
33	Vestfold &Telemark	323	20.64	121.99
34	Vestfold &Telemark	456	19.53	214.12
35	Vestfold &Telemark	647	19.16	240.74
36	Vestfold &Telemark	295	19.70	129.36
37	Vestfold &Telemark	551	19.44	165.71
38	Vestfold &Telemark	387	19.51	130.38
39	Vestfold &Telemark	575	19.21	272.62
40	Vestfold &Telemark	173	20.10	89.07
41	Vestfold &Telemark	158	19.51	108.83
42	Vestfold &Telemark	273	19.52	141.20
43	Vestfold &Telemark	351	19.28	145.92
44	Vestfold &Telemark	385	19.19	146.41

Table B3. Aboveground tree biomass models generated by Kolstad et al. [70] from tree samples at study sites. Models produce estimates of aboveground tree biomass (g) and include both diameter-at-ground-level (mm) and height (cm) as variables. Models specific to trees inside and outside exclosures were used to estimate biomass for rowan. Values of multiple R^2 are reported for each model.

Tree Species	Biomass Model Equation	Multiple R^2
Birch	$Y = 0.078843(DGL)^2 + 0.009197(HGT)^2$	0.9458
Pine	$Y = 0.325839(DGL)^2 + 0.0007434(DGL)^3$	0.9856
Spruce	$Y = 0.020293(HGT)^2 + 0.006092(DGL)^3$	0.9671
Rowan (Browsed)	$Y = 0.006664(HGT)^2 + 0.082983(DGL)^2$	0.8123
Rowan (Exclosure)	$Y = 0.0053962(HGT)^2$	0.9841

Table B4. Height-only biomass models generated by Kolstad et al. [70] for trees in exclosures at study sites. Models produce estimates of aboveground tree biomass (g) and include tree height (cm) as the only variable. Values of multiple R^2 are reported for each model.

Tree Species	Biomass Model Equation (Exclosures)	Multiple R^2
Birch	$Y = 0.170274(HGT) + 0.010018(HGT)^2$	0.9937
Pine	$Y = 0.0149667(HGT)^2$	0.8841
Spruce	$Y = 0.038068(HGT)^2$	0.9481
Rowan	$Y = 0.0053962(HGT)^2$	0.9841

Table B5. Height-only biomass models generated in this study for trees in open plots at study sites. Models produce estimates of aboveground tree biomass (g) and include tree height (cm) as the only variable. Values of multiple R^2 are reported for each model.

Tree Species	Biomass Model Equation (Open Plots)	Multiple R^2
Birch	$Y = 0.2072(HGT) + 0.009974(HGT)^2$	0.9898
Pine	$Y = 0.027464(HGT)^2$	0.7015
Spruce	$y = 0.02014(HGT)^2 + 6.086e\text{-}05(HGT)^3$	0.9059
Rowan	$y = 0.2620264(HGT) + 0.005844(HGT)^2$	0.8345

Table B6. Detailed output from a linear mixed model of total aboveground tree biomass in 44 study sites within Norway. Parameter estimates are on a multiplicative scale.

Model Variable	Estimate	95% CI	P-value
Treatment (Exclosure)	0.9463	(0.7926, 1.130)	0.5422
Productivity Index (Browsed)*	1.099	(0.9987, 1.212)	0.0576
Productivity Index (Exclosure)*	1.153	(1.047, 1.269)	**0.0051**
Years Since Exclosure (Browsed)	1.184	(1.155, 1.214)	**< 0.0001**
Years Since Exclosure (Exclosure)	1.219	(1.189, 1.249)	**< 0.0001**

*Estimates and 95% confidence intervals are for a 10% increase in productivity index

Table B7. Detailed output from a linear mixed model of deciduous aboveground tree biomass in 44 study sites within Norway. Parameter estimates are on a multiplicative scale.

Model Variable	Estimate	95% CI	P-value
Treatment (Exclosure)	0.6699	(0.5169, 0.8682)	**0.0026**
Productivity Index (Browsed)*	1.058	(0.9207, 1.213)	0.4339
Productivity Index (Exclosure)*	1.175	(1.022, 1.351)	**0.0265**
Years Since Exclosure (Browsed)	1.127	(1.087, 1.168)	**< 0.0001**
Years Since Exclosure (Exclosure)	1.260	(1.215, 1.306)	**< 0.0001**

*Estimates and 95% confidence intervals are for a 10% increase in productivity index

Table B8. Detailed output from a linear mixed model of coniferous aboveground tree biomass in 44 study sites within Norway. Parameter estimates are on a multiplicative scale.

Model Variable	Estimate	95% CI	P-value
Treatment (Exclosure)	1.201	(1.010, 1.429)	**0.0387**
Productivity Index*	1.050	(0.9314, 1.184)	0.4273
Years Since Exclosure (Browsed)	1.210	(1.178, 1.243)	**< 0.0001**
Years Since Exclosure (Exclosure)	1.182	(1.151, 1.214)	**< 0.0001**

*Estimate and 95% confidence intervals are for a 10% increase in productivity index

Table B9. Detailed output from a linear mixed model of monthly average albedo in 44 study sites within Norway. Parameter estimates are on a multiplicative scale.

Model Variable	Estimate	95% CI	P-value
Treatment (Exclosure)	0.9975	(0.9898, 1.005)	0.5250
Monthly Proportion of Days with Snow (Browsed)*	1.133	(1.130, 1.136)	**< 0.0001**
Monthly Proportion of Days with Snow (Exclosure)*	1.133	(1.131, 1.136)	**< 0.0001**
Years Since Exclosure (Browsed)	0.9945	(0.9937, 0.9954)	**< 0.0001**
Years Since Exclosure (Exclosure)	0.9915	(0.9907, 0.9924)	**< 0.0001**

*Estimates and 95% confidence intervals are for a 10% increase in the monthly proportion of days with snow

Appendix C: Supplemental Figures

(a)

$y = 0.2072X + 0.009974X^2$
$R^2 = 0.9898$

(b)

$y = 0.2620264X + 0.005844X^2$
$R^2 = 0.8345$

(c)

$y = 0.027464X^2$
$R^2 = 0.7015$

(d)

$y = 0.02014X^2 + 6.086e\text{-}05X^3$
$R^2 = 0.9059$
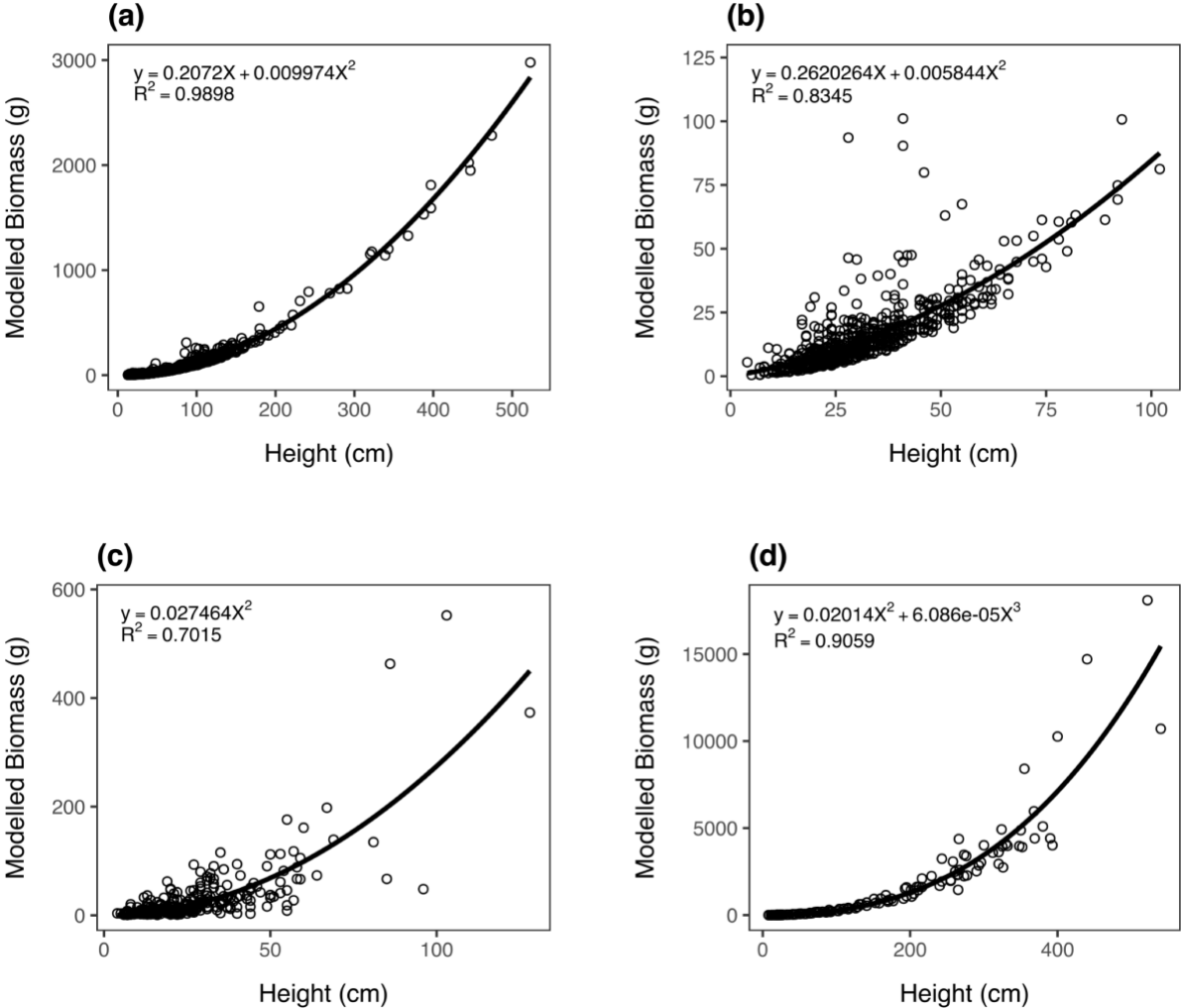
Figure C1. Height plotted against modelled biomass for observations of (a) birch, (b) rowan, (c) pine, and (d) spruce trees. Observations were recorded in 2016 within study sites at Trøndelag and were used to generate height-only allometric biomass models (represented by black lines) for each tree species in open plots at study sites. Equations (where the variable X represents tree height in cm) and multiple R^2 values for each model are provided in the top-left corner of each plot.
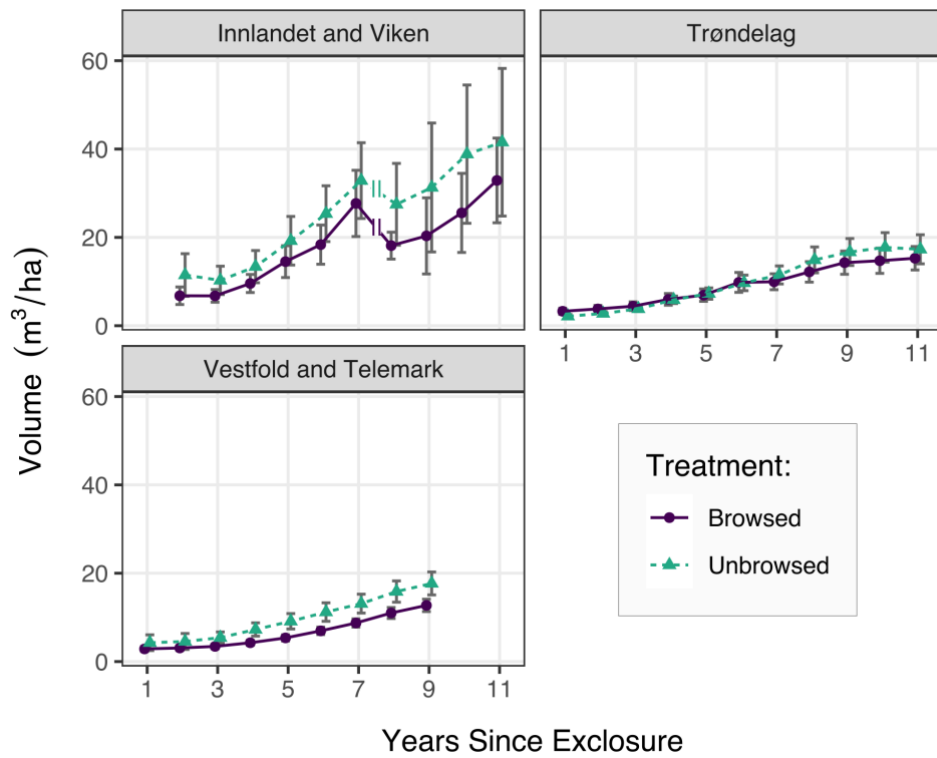
Figure C2. Average forest volume (m³ ha⁻¹) within each of the study regions in the years after exclosure. Error bars represent standard error. Few study sites in Innlandet and Viken had data past seven years since exclosure.
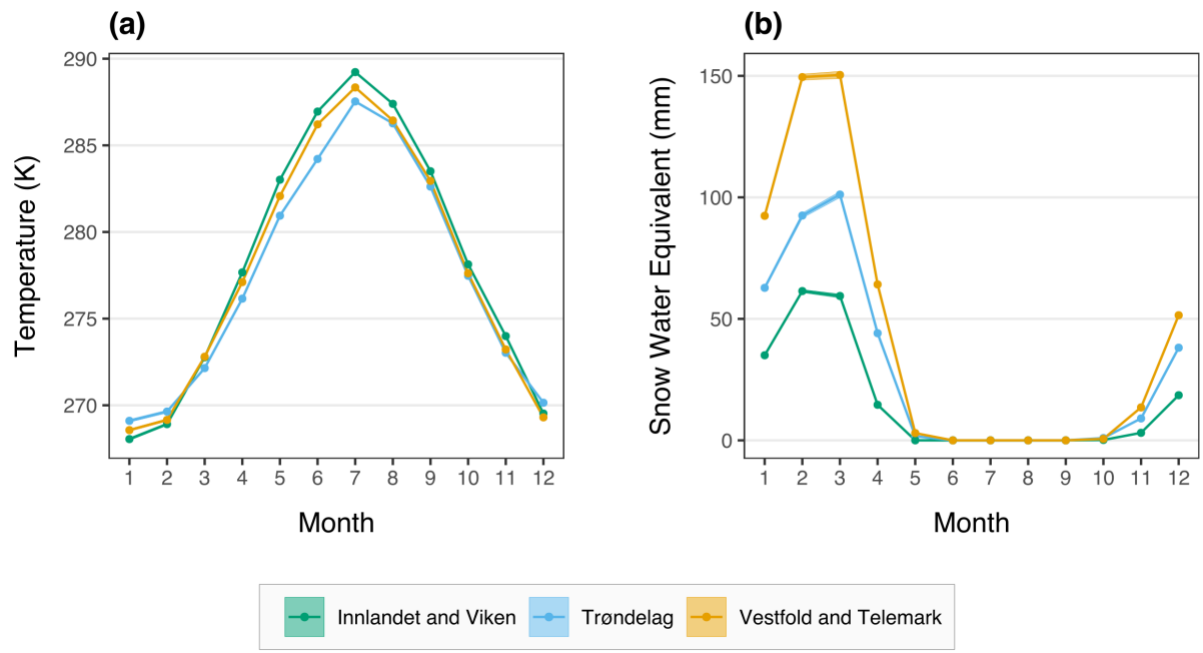
(a)

(b)

Figure C3. (A) Average monthly temperature (K) within each study region. (B) Average monthly snow water equivalent (mm) within each study region. Averages are produced from site-specific climate data in the period 2007–2019. Shading represents standard error.
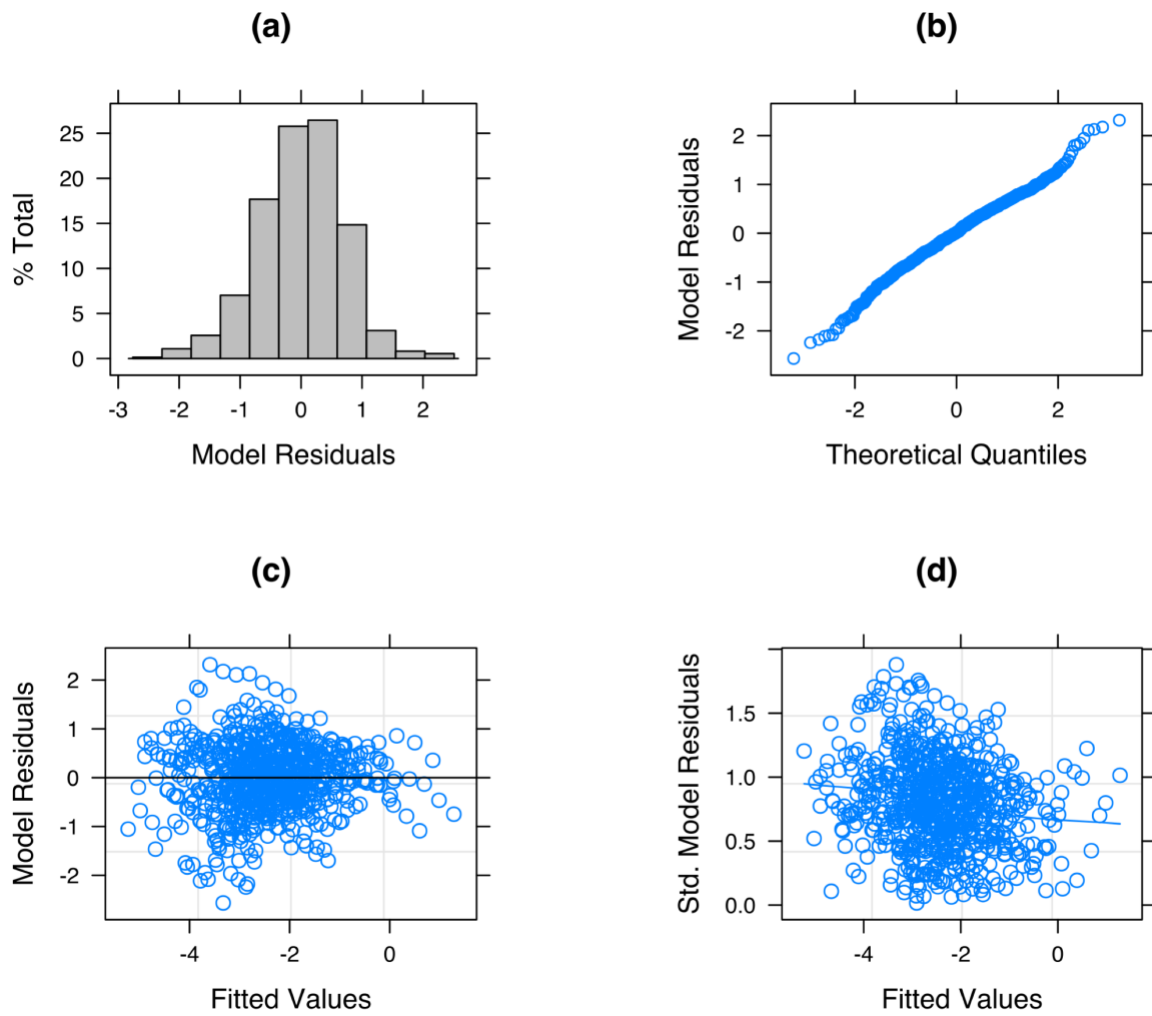
(a)

(b)

(c)

(d)
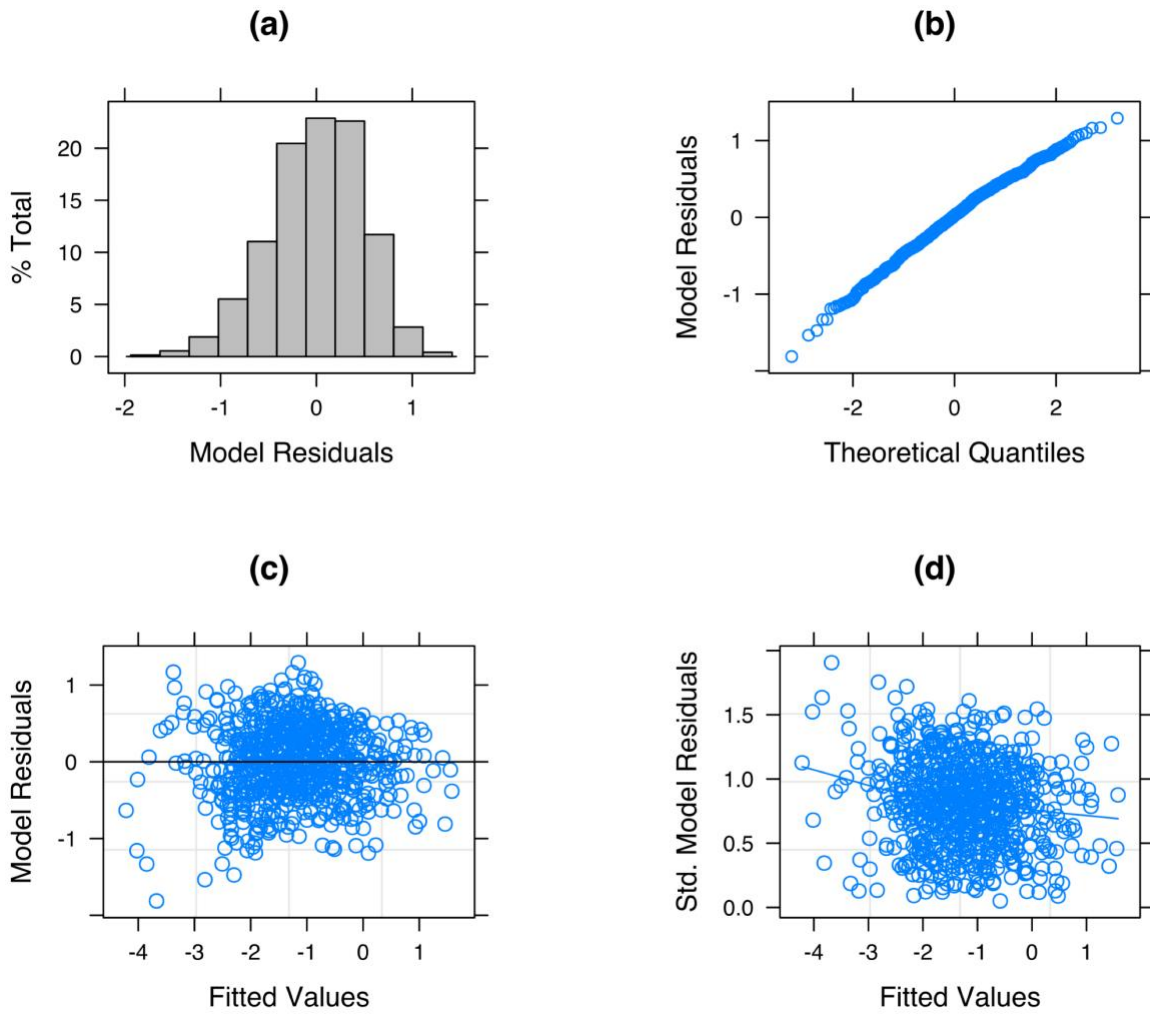
Figure C4. Diagnostic plots of a linear mixed-effects model for total aboveground tree biomass at 44 study sites in Norway. (a) Histogram of model residuals. (b) Model residuals plotted against theoretical quantiles. (c) Model residuals plotted against fitted model values. (d) Standardized model residuals plotted against fitted model values.
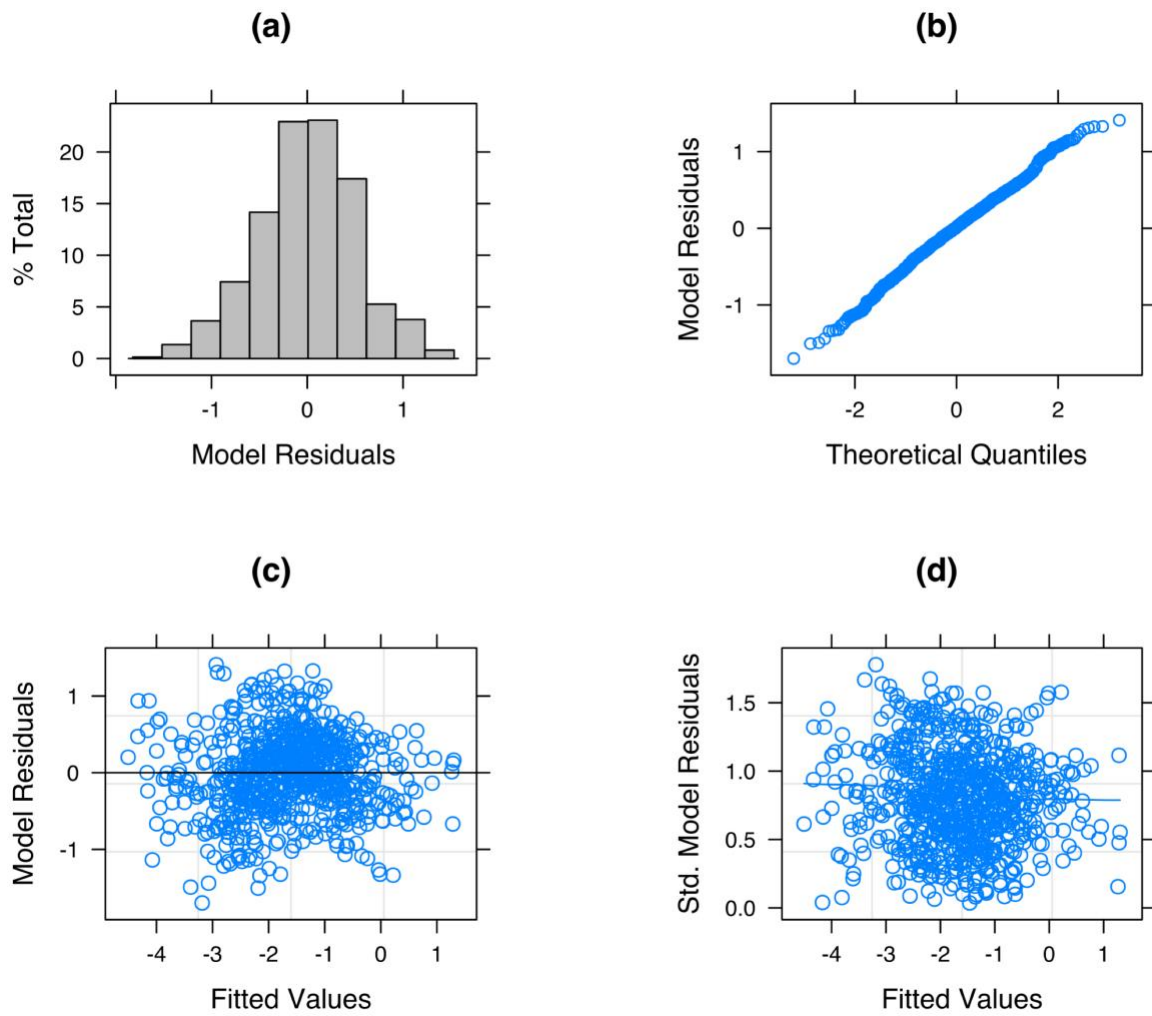
(a) **(b)**

(c) **(d)**

Figure C5. Diagnostic plots of a linear mixed-effects model for deciduous aboveground tree biomass at 44 study sites in Norway. (a) Histogram of model residuals. (b) Model residuals plotted against theoretical quantiles. (c) Model residuals plotted against fitted model values. (d) Standardized model residuals plotted against fitted model values.
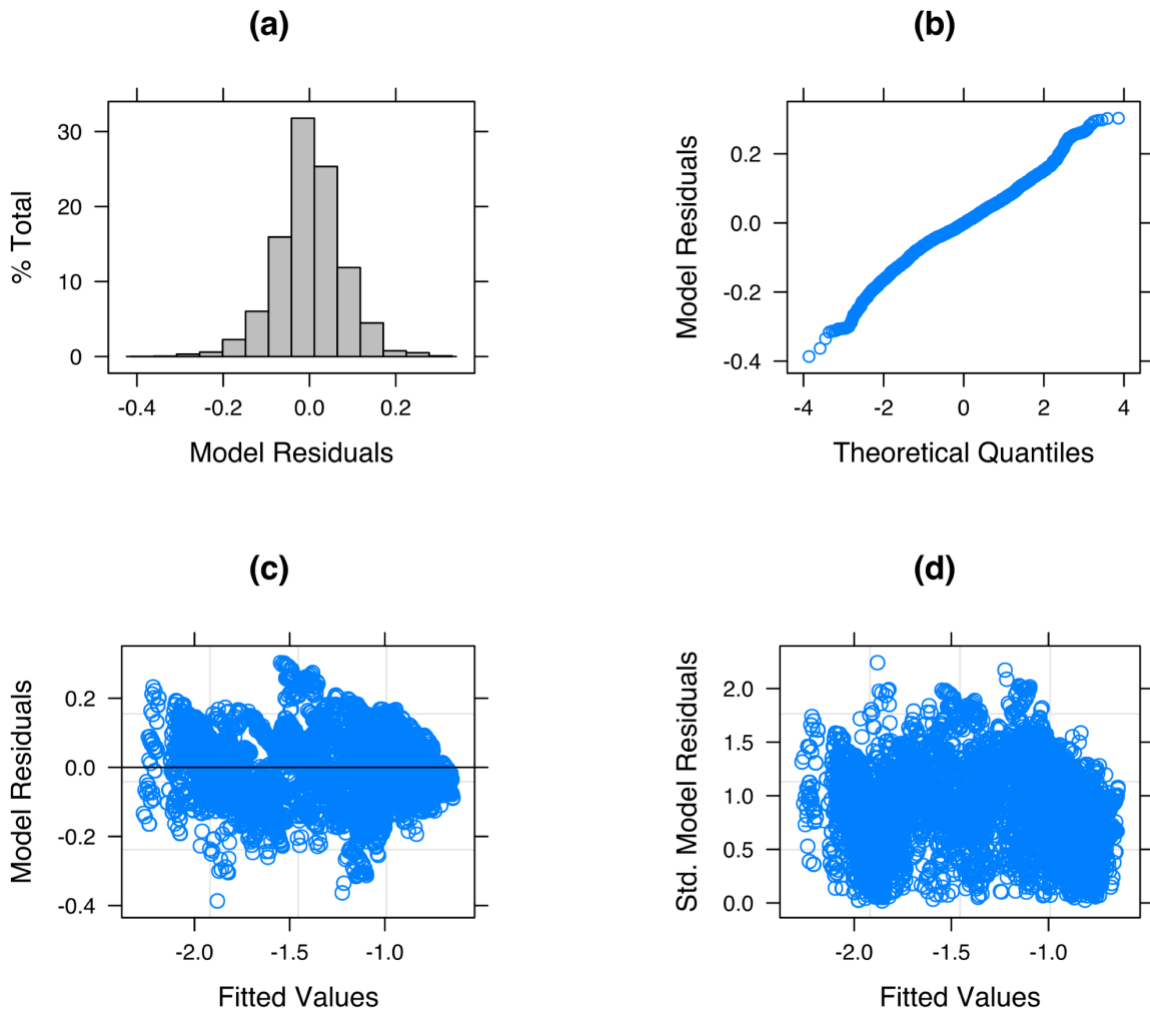
Figure C6. Diagnostic plots of a linear mixed-effects model for coniferous aboveground tree biomass at 44 study sites in Norway. (a) Histogram of model residuals. (b) Model residuals plotted against theoretical quantiles. (c) Model residuals plotted against fitted model values. (d) Standardized model residuals plotted against fitted model values.

Figure C7. Diagnostic plots of a linear mixed-effects model for monthly average albedo at 44 study sites in Norway. (a) Histogram of model residuals. (b) Model residuals plotted against theoretical quantiles. (c) Model residuals plotted against fitted model values. (d) Standardized model residuals plotted against fitted model values.
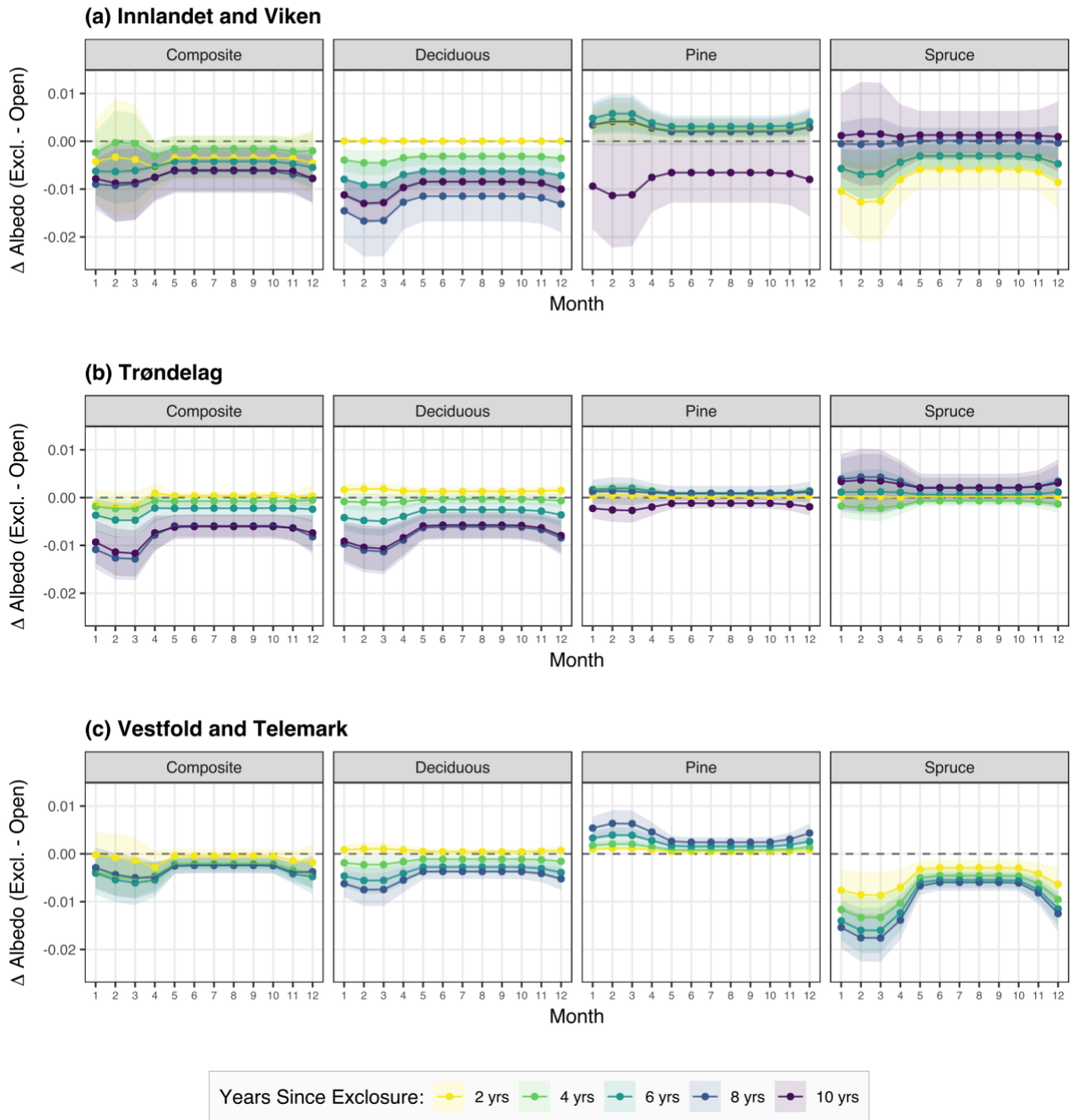
Figure C8. Mean difference in both composite albedo and albedo for each forest type (deciduous, pine, and spruce forest) between moose exclosures and open plots, where difference equals exclosure albedo minus open plot albedo. Differences are averaged within each study region. Line colors correspond to number of years since exclosure, while shading indicates standard error. Horizontal dashed line indicates no difference in albedo. Negative values indicate higher albedo in open plots relative to exclosures.