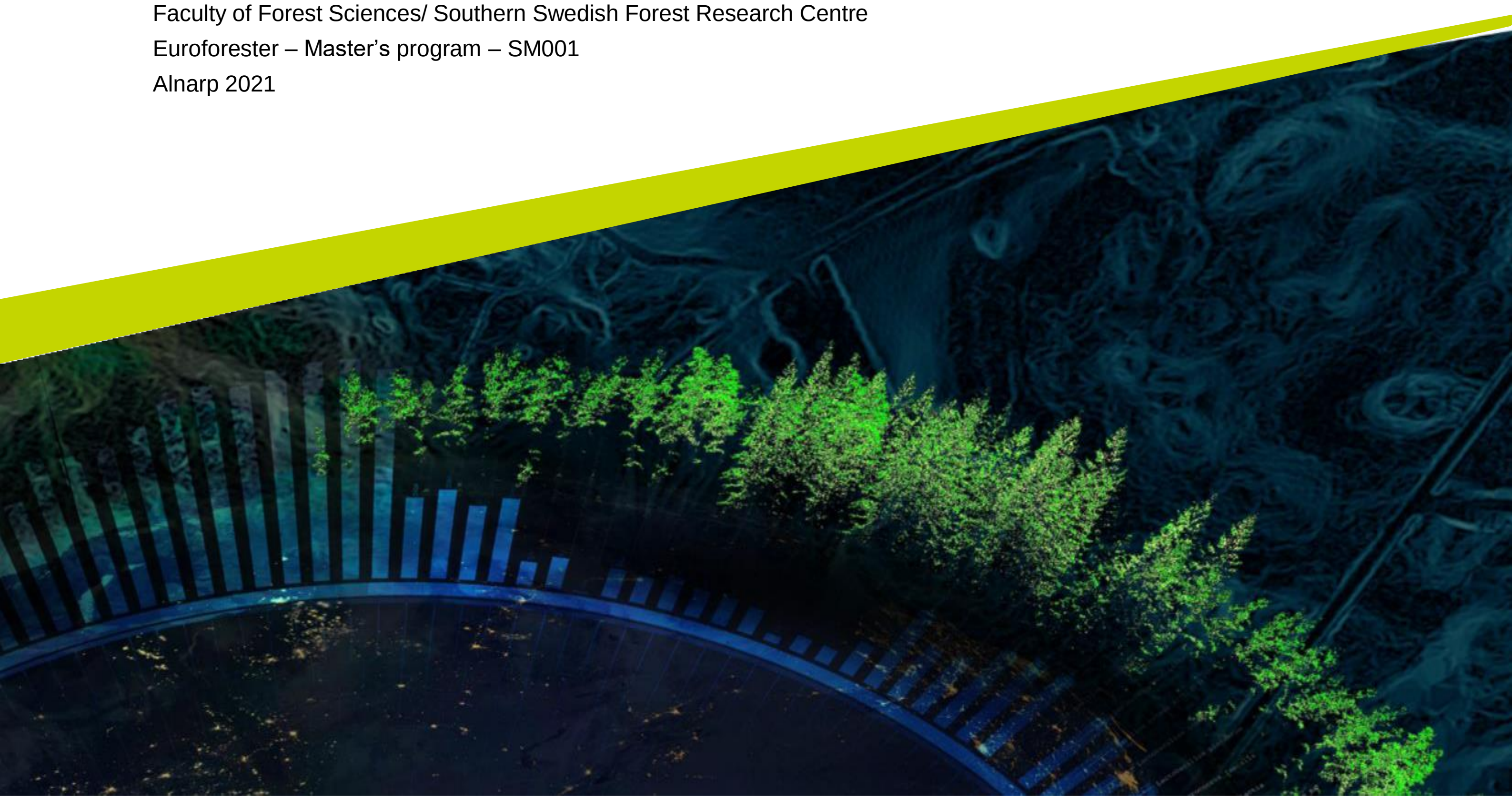
Management and Site Conditions Drive Carbon Dynamics of Forest Understory Vegetation

Emily Delin

Degree project • (30 hp)
Swedish University of Agricultural Sciences, SLU
Faculty of Forest Sciences/ Southern Swedish Forest Research Centre
Euroforester – Master's program – SM001
Alnarp 2021



Management and Site Conditions Drive Carbon Dynamics of Forest Understory Vegetation

Emily Delin

Supervisor:	Per-Ola Hedwall, Swedish University of Agricultural Sciences, Southern Sweden Forest Research Centre
Examiner:	Jörg Brunet, Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre

Credits:	30 hp
Level:	Second cycle, A2E
Course title:	Master’s Thesis in Forest Science
Course code:	EX0984
Programme/education:	Euroforester – Master’s program – SM001
Course coordinating dept:	Southern Swedish Forest Research Centre

Place of publication:	Alnarp, Sweden
Year of publication:	2021

Keywords: carbon sequestration, forest floor vegetation, ground vegetation, mixed model, Sweden

Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Southern Swedish Forest Research Centre

Publishing and archiving

Approved students' theses at SLU are published electronically. As a student, you have the copyright to your own work and need to approve the electronic publishing. If you check the box for **YES**, the full text (pdf file) and metadata will be visible and searchable online. If you check the box for **NO**, only the metadata and the abstract will be visible and searchable online. Nevertheless, when the document is uploaded it will still be archived as a digital file.

If you are more than one author you all need to agree on a decision. Read about SLU's publishing agreement here: https://www.slu.se/en/subweb/library/publish-and-analyse/register-and-publish/agreement-for-publishing/.

☒ YES, I/we hereby give permission to publish the present thesis in accordance with the SLU agreement regarding the transfer of the right to publish a work.

☐ NO, I/we do not give permission to publish the present work. The work will still be archived and its metadata and abstract will be visible and searchable.

Abstract

The forest understory vegetation is largely disregarded in studies of carbon sequestration despite notable contribution to storage and cycling in the ecosystem. In addition to already lacking knowledge on this pool independently, further uncertainty and change is introduced by forest management and the changing climate. Using data from the Swedish NFI and Generalized Linear Mixed Models, we modelled the dynamics of this terrestrial carbon pool under conditions created by management and site characteristics. In order to do so, understory vegetation was categorized into the species groups graminoids, forbs, dwarf shrubs, bryophytes, and lichens. This was done due to differences in carbon storage and turnover of the groups as well as available biometric functions.

Total understory carbon decreased with increasing stand basal area, percent of spruce, and temperature and increased with stand age, CN ratio, and precipitation. Graminoids were negatively influenced by stand basal area, percent of spruce, stand age, and CN ratio and positively influenced by temperature. Bryophytes were positively influenced by stand basal area and percent of spruce and were negatively influenced by stand age and precipitation. Lichens were negatively influenced by stand age, percent of spruce, and precipitation and were positively influenced by CN ratio and temperature. Dwarf shrubs were positively influenced by stand age, CN ratio, temperature, and precipitation and were negatively impacted by higher percent of spruce. Forbs were negatively influenced by stand age, CN ratio, and temperature and were positively impacted by basal area. Based on climate projections towards higher average temperature and increased drought events, as well as popular management techniques, this indicates future higher turnover of carbon within this pool. These dynamics should be further studied alongside the overstory pool in order to ensure balance between all ecosystem services provided.

Keywords: carbon sequestration, forest floor vegetation, ground vegetation, mixed model, Sweden

Table of contents

List of tables

List of figures

Abbreviations

NFI	National Forest Inventory
DOC	Dissolved Organic Carbon
CN	Carbon:Nitrogen
SLU	Swedish University of Agricultural Sciences
GPP	Gross Primary Production
NPP	Net Primary Production

1. Introduction

In recent decades, multinational agreements regarding the responsibility to reduce greenhouse gas emissions have become a focal point in policy and science (Nordhaus 1993; Enkvist *et al.* 2007; West *et al.* 2013; UNFCCC 2015; Ritchie & Roser 2020). Intergovernmental cooperation, represented by such agreements as the Kyoto Protocol and Paris Agreement, showcases a widespread understanding and acceptance of the need to decrease greenhouse gases such as carbon dioxide (CO_2) through emission reduction and sink increase (UNFCCC 1998; UNFCCC 2015).

Such sinks are present naturally all over the globe (Grace 2004). Carbon is constantly transferred between the atmosphere and biosphere in a process known as the carbon cycle, and some of this transferred carbon is sequestered and remains in the biosphere for extended periods of time (Post *et al.* 1990). This occurs on a long-term (geologic) scale starting at hundreds of thousands of years, and a short-term scale spanning days to centuries (NOAA n.d.). When plants photosynthesize, they take up carbon from the atmosphere, about half of which is stored in vegetation and roots/soil and the other half respired (Prentice *et al.* 2001; Lorenz & Lal 2010; Ramachandran Nair *et al.* 2010). In this way, they contribute to the global carbon cycle on the short-term scale (Chapin *et al.* 2006).

Of all vegetated land on Earth, forests cover 30-40% (Waring & Running 2007), and about 31% of all land, occurring in tropical, boreal, temperate, and subtropical biomes (FAO 2020). The amount and variety of land they cover makes them valuable in climate change mitigation through carbon sequestration (Binkley *et al.* 1997; Malhi *et al.* 2002). Forests accumulate carbon in multiple pools including living biomass (both above and below ground), deadwood, detritus, and soil (Schlesinger 1977; Dixon *et al.* 1994; Clemmensen *et al.* 2013; Ķēniņa *et al.* 2018).

Generally, most carbon stored in a forest is in the overstory (tree layer), which can store upwards of 200 times more than the understory (Moore *et al.* 2007; Burton *et al.* 2013). However, the understory vegetation is a carbon pool relevant over both spatial and temporal scales, and lack of recognition results in underestimation of the carbon storage potential of these ecosystems (Dirnbock *et al.* 2020). This is increasingly true in the boreal region, as the relative contribution of the understory may increase with latitude. For the purpose of this paper, overstory vegetation refers to species of trees and tall shrubs whereas understory refers to all other vascular vegetation, mosses, and lichens.

The understory not only contributes to the carbon storage of the forest, but also plays an active role in carbon turnover and cycling on varying levels. Despite the largest proportion of litter dry weight originating from the tree canopy, the understory litter can contribute greater amounts of dissolved organic carbon (DOC) (Hensgens *et al.* 2020). Woody vegetation such as dwarf shrubs generally have the slowest turnover rates due to reallocation abilities to stems before leaf senescence. Graminoids (Poaceae, Cyperaceae, and Juncaceae families) and forbs may be able to allocate nutrients to below-ground biomass before senescence, but have faster turnover rates than dwarf shrubs (Jonasson 1983). Bryophytes have been found to have an intermediate turnover rate, but highly biodegradable DOC (Wickland *et al.* 2007). There is also variation between species groups in lability of DOC in the litter that can be transferred to the below-ground carbon pool through decomposition. Hensgens *et al.* (2020) found that the majority of water extractable DOC in a forest system was contributed by dwarf shrubs, followed by bryophytes and graminoids.

Understory abundance and composition, and therefore qualities of carbon storage and cycling, can vary greatly under different site conditions. Changes in understory species' abundances due to such variations can alter the overall carbon balance of the forest ecosystem (Grau-Andrés *et al.* 2020). A more open canopy benefits the understory by increasing light availability and throughfall from precipitation to decrease competition for resources (Anderson *et al.* 1969; Thysell & Carey 2000). Total understory cover and almost all species groups generally increase with increasing light availability (Weisberg *et al.* 2003; Wagner *et al.* 2011), apart from bryophytes (Thysell & Carey 2000). Reindeer lichens (*Cladonia* subgenus *Cladina*) respond positively to increased light availability until an upper threshold (Sulyma & Coxson 2001; Čabrajič *et al.* 2010; McMullin *et al.* 2011; McMullin & Rapai 2020). For mosses and lichens, too open of a canopy can cause desiccation and therefore decrease cover (Čabrajič *et al.* 2010). Dwarf shrubs and graminoids have a higher demand for light, resulting in dominance in open canopies, whereas in thicker canopies forbaceous species have been found to dominate (Shields & Webster 2007). Vascular plants present in the understory vegetation respond negatively to increased stand density and the decrease in response to increasing stand density is stronger in spruce (*Picea*) than birch (*Betula*) dominated forests (Hedwall *et al.* 2019).

The proportion of certain tree species present in a stand can also influence the level of canopy closure and interference of light and precipitation. Precipitation throughfall is less in coniferous stands than broadleaves generally, and soils tend to be drier (Nihlgård 1970; Barbier *et al.* 2008). Whereas the environment created by a larger proportion of spruce supports the cover of bryophytes, total field layer and other species groups are less tolerant of the microclimate created (Saetre *et al.* 1997; Ewald 2000; Augusto *et al.* 2003). Bryophytes do not have root systems and are therefore more affected by above-ground processes that change with canopy cover such as throughfall and light availability (Weibull 2001; Tinya *et al.* 2009). Spruce also has a relatively shallow root system (Gale & Grigal 1987), potentially creating more competition with understory plants and hindering their development (Barbier *et al.* 2008).

Forest composition and structure changes with time over successional stages (Hedwall *et al.* 2013). In managed forests, following harvest, the site experiences an increase in incident light and precipitation, often allowing graminoids and forbs to dominate. Following this, small shrubs may dominate before seedlings overtake them (Balandier *et al.* 2009; Hedwall *et al.* 2013). Lichen cover in a stand can increase with age (Palmqvist & Sundberg 2000; McMullin *et al.* 2011) until about 150 years at which time mosses may become dominant if already present (Sulyma & Coxson 2001). The total biomass present in the understory can continue to increase for at least a century before experiencing declines (Kumar *et al.* 2018).

These relationships to management variables do not take into account the uncertainty introduced by changes in site conditions. The changing climate may result in novel conditions and increased disturbance frequency and severity (Seidl *et al.* 2014), which may be natural drivers of understory processes (Seidl *et al.* 2017; Dirnbock *et al.* 2020). In boreal biomes, annual temperature is predicted to increase in the future (Lind & Kjellström 2008), along with increased frequency of severe weather events such as droughts (Belusic *et al.* 2019). Due to the uncertainty regarding forest growth response to climate change and disturbance (Albrich *et al.* 2018), it is important to understand how the understory and contributing species groups may respond.

Generally, mosses and lichens dominate understory vegetation where summer temperatures are low and graminoids and forbs dominate where temperatures are higher (Walker *et al.* 2006). In boreal regions of Sweden, increased temperatures have contributed to a decrease in dwarf shrub cover (Hedwall *et al.* 2021). In some high-latitude areas, warming has resulted in an increase of graminoids due to wetter conditions caused by thawing of permafrost (Christensen *et al.* 2004), and increased precipitation can amplify this situation (Douglas *et al.* 2020). Increases in temperature may also increase rates of nitrogen mineralization in forest ecosystems (Verburg *et al.* 1999).

Nutrient availability can vary greatly between sites and promote differences in understory abundance and composition (Hutchinson *et al.* 1999; Adkison & Gleeson 2004). If increased fertility leads to an increase in litter from the overstory this can lead to a decrease in bryophytes or lichens as they are covered and cannot survive (Natalia *et al.* 2008; Wagner *et al.* 2011). Dwarf shrubs have deeper roots (Schenk & Jackson 2002) and therefore can access nutrients that are otherwise inaccessible for other species groups. They are also able to retain nutrients through resource allocation to perennial parts before leaf senescence (Jonasson 1983). Compared to forbs, graminoids have faster root growth meaning they can spread root systems into new areas when stressed for nutrients (Balandier *et al.* 2009).

Prolonged decreases in precipitation are expected to decrease overall understory biomass, with the effect increasing in severity over time (Gimbel *et al.* 2015). Decreased precipitation reduces transpiration and leaf area index (LAI) of graminoids, forbs, and dwarf shrubs, with graminoids reacting the quickest and dwarf shrubs the slowest. Shrubs are also less resilient to decreases in precipitation compared to other species groups (Felsmann *et al.* 2017). Lichens and bryophytes generally benefit from increased precipitation, as they rely on throughfall and humidity for productivity and growth (Čabrajič *et al.* 2010; Virtanen *et al.* 2017; McMullin & Rapai 2020).

The aim of this study is to further understand how site conditions and management influence the total carbon stored in forest understory vegetation and the proportion contributed by each species group. This study analyzed variables that can be controlled through management (tree basal area as an indicator of forest density, forest age, and percentage of spruce) and site conditions that are largely uncontrollable by management and likely to be influenced by climate change (total annual precipitation, annual average temperature, and carbon:nitrogen (CN) ratio).

Using Generalized Linear Mixed Models, the strength and nature of these relationships are modelled based on Swedish National Forest Inventory data. The research questions aimed to answer in this project were: (i) how do both direct and indirect anthropogenic variables impact understory carbon, and (ii) how might understory carbon dynamics change with each explanatory variable? It is hypothesized that the response variables will have nonlinear relationships with the management-oriented and soil variables (Hedwall *et al.* 2013) and linear with climate variables.

2. Methods

2.1. Study Region

The country of Sweden is located in the Fennoscandia region of Northern Europe, ranging from 55°N to 69°N. From 1990 to 2019, the average annual temperature was 6 °C and annual precipitation was 693 mm (SMHI 2021). Over the expansive latitudinal gradient of the country, multiple vegetation zones are present including nemoral, boreo-nemoral, boreal, and alpine (Rydin *et al.* 1999; KSLA 2015). The bedrock of the country is made up of mostly crystalline rocks formed in the Precambrian, as well as a sedimentary layer and the Caledonian orogeny made up of rock more than 420 million years old (SGU 2020b). Glacial activity has carved and scarred this bedrock, leaving behind till which is the soil type that covers the most area in the country (Rydin *et al.* 1999; SGU 2020a).

Of Sweden’s total 40.8 million hectares, productive and unproductive forests (differentiated by a threshold of 1 $m^3ha^{-1}year^{-1}$ of growth) cover 57% and 12% of the area, respectively. Primary forests are rare in the landscape, making up about 9% of the total forest area (FAO 2015). The coniferous species Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) make up the majority of the standing volume, with a combined 78%. The remaining living standing volume is made up of birch (*Betula*) (12%), other deciduous species (6%), and lodgepole pine (*Pinus contorta*) (1%). The rest of the standing volume is dead trees (3%), which are commonly left by land owners due to their benefits for biodiversity and requirement to qualify for certification (FSC 2013; KSLA 2015).

Forest ownership in the country is primarily private with 50% by individual owners, 25% by private companies, and the remaining 25% by the state and others (KSLA 2015; Sténs & Mårald 2020). Management techniques have typically focused on optimizing yield and production, resulting in intensive practices that create even-aged stands being most widely used (KSLA 2015). Modern practices are becoming more inclusive and interdisciplinary due to increased knowledge and shifts in priority (FAO 2018). Forests are more clearly being recognized for their potential as carbon sinks and renewable energy substitution for fossil fuels (Lundmark *et al.* 2014; KSLA 2015; IUCN 2021). Just as forest policy and management goals have changed over time, so have the methods of monitoring forests and the information collected during inventories (Fridman *et al.* 2014).

2.2. The Swedish National Forest Inventory

The Swedish National Forest Inventory (NFI) was created in 1923 over concern for sustainable use of forest resources (Fridman *et al.* 2014). The goal of the NFI is to track changes and conditions of the forests as well as provide data for forecasts of future development. It is made up of the National Forest Assessment as well as the Land Inventory (SLU 2020). Since its implementation, the methods and data collected have changed to be relevant for the modern day.

Currently, square-shaped clusters of temporary and permanent plots cover the five regions of the country (Figure 1), and the permanent ones are revisited every five years. One-fifth of the total number of plots are visited every year over the entire country in order to provide updated information for the entire area. The total area of each individual plot varies depending on the measured variable and may be divided by changes in type of land use or forest stand.

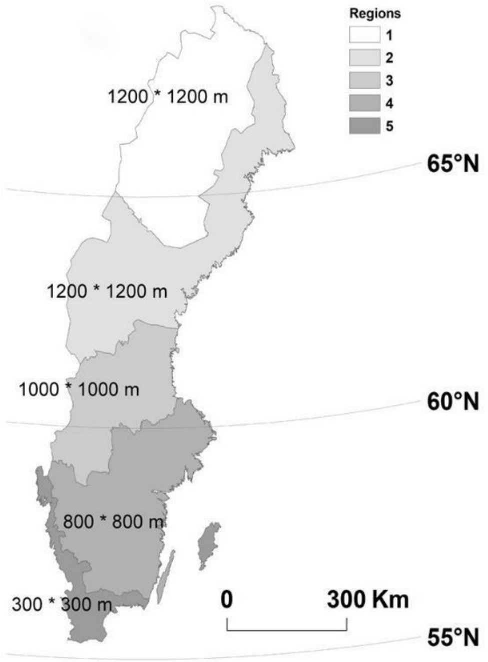


Figure 1: Regional division of the Swedish NFI. The numbers represent the size of clusters used in the NFI.

Productive forest land, for the purpose of the NFI, is defined as land that is suitable for timber production (production capacity at least $1 m^3/ha/year$) and not used extensively for anything else. This also includes abandoned agricultural land (unused for at least three years) or other unused land determined as suitable for forestry use. Tree layer data on these plots is collected over an area with a 10-meter radius.

The understory vegetation survey is done every ten years in a radius of 5.64 meters on half of the permanent plots on which overstory data is collected. The total area of the plot may be less than the intended 100 m^2 however, as areas of disturbed soil are disregarded. Area coverage (in m^2) of 71 species is recorded subjectively and independently (SLU 2020).

2.3. Data

2.3.1. Data Acquisition

The necessary data were obtained directly from an environmental assessment specialist at the department of forest resource management in the division of forest research data at the Swedish University of Agricultural Sciences (SLU). The data were imported to R version 3.6.1 (R Core Team 2019) for analysis.

2.3.2. Data Preparation

The recorded understory species were conglomerated into the species groups “bryophytes”, “forbs”, “dwarf shrubs”, “graminoids”, and “lichens”. In some cases, a species group was found to have a total coverage area higher than the total plot area. This is likely due to the subjective and visual method used to estimate area coverage over such a large plot size, in which individual species may overlap or occur very close together, essentially occupying the same space. In these cases, the coverage area was set equal to the total plot area. The species groups were chosen based on available allometric functions from Lehtonen *et al.* (2016). These functions were chosen as they were created in a Finnish context, being the most geographically similar to Sweden of those available. The functions derive biomass from percentage cover, so the area coverage of each category was converted to coverage percent based on the total plot area. For one category, dwarf shrubs, there were two functions created by Lehtonen *et al.* (2016): one for northern Finland and one for Southern Finland. The outputs from both models were quite similar, so only the southern one was used in the end. This was chosen because the latitudinal southern boundary was 63.3185° N and Sweden’s geographical center is located at 62.3875°N. This means the majority of Sweden falls below this and the southern model is, therefore, assumed more appropriate.

The carbon content for each species group was then calculated by multiplying the biomass results with known carbon proportions for each. These values were 0.5 for dwarf shrubs, 0.47 for graminoids and forbs, and 0.35 for lichens and bryophytes (IPCC 2006; Peichl & Arain 2006; Smith *et al.* 2015; Adamovics *et al.* 2018). All categories were then added together to obtain an overall understory carbon content for each plot.

The data was restricted to a ten-year period due to the time interval between inventories, so that each subplot would be present only once. Of the original 20,125 plots visited in the ten-year period between 2007 and 2016, 15,700 of these were classified as productive forest land, and about half of these (7,816) had understory vegetation coverage data. When further restricted to include only those plots with soil data, the number of qualifying plots was reduced to 3,650. Overall, a further 287 plots were removed due to missing meteorological data (3), outliers in CN ratio, age, and basal area (73), and outliers in forb and lichen carbon proportion that skewed the data (211). This resulted in the final data set consisting of 3,363 plots.

The explanatory variables were tested for intercorrelation with a Pearson correlation test. This helped to prevent collinearity between variables. No variables exceeded a correlation coefficient of 0.49 and were therefore considered appropriate to include in the model together. Morans.I tests were also run for each model to ensure adequate accounting for spatial autocorrelation within the data. P-values of 1 indicated insignificance of any relations (Table 7).

2.3.3. Model

Generalized Linear Mixed Models (GLMMs) were implemented using the gamlss package (v5.3-4) and function in R (Rigby & Stasinopoulos 2005). This allows for the implementation of a random effect to account for the spatial design of the NFI, present in this study as plots nested in regions. A two-dimensional smoother of plot coordinates was also implemented to remove spatial autocorrelation in the residuals using the gam function in the mgcv package (v1.8-28) (Wood 2017) called within the gamlss function.

Due to hypothesized non-linear relationships between the response variables and some explanatory variables, the squared values for total basal area, CN ratio, percent of spruce, and stand age were used in the models. The variables used in the continuous (Formula 1) and binomial (Formula 2) portions of the model are listed below, where y indicates the response variable of total understory carbon or proportion of a species group.

$$\begin{aligned} y = {} & Basal\ area + Basal\ Area^2 + Percent\ of\ Spruce + \\ & Percent\ of\ Spruce^2 + Stand\ Age + Stand\ Age^2 + CN\ Ratio + \\ & CN\ Ratio^2 + Average\ Annual\ Temperature + \\ & Total\ Annual\ Precipitation \end{aligned} \tag{1}$$

$$\begin{aligned} y = {} & Total\ Basal\ Area + Percent\ of\ Spruce + Stand\ Age + \\ & CN\ Ratio + Average\ Annual\ Temperature + \\ & Total\ Annual\ Precipitation \end{aligned} \tag{2}$$

These explanatory variables were all standardized as z-scores before use in the model. Response variables of species groups were divided by total understory carbon to obtain proportion values.

Due to the proportional qualities and zero inflation of the species group carbon data, an inflated beta distribution with the default logit mu and sigma and log nu and tau link functions was used in the case of the response variables. The standardized values of understory carbon contained no zeros and were normally distributed, allowing the use of a Gaussian distribution when total understory carbon was the response variable. The total understory carbon values were then standardized to z-scores before use in the Gaussian distribution model, and the output values were later unstandardized for evaluation and interpretation.

.

3. Results

3.1. Biomass and Carbon Content

Dwarf shrubs and bryophytes made up the majority of the total biomass and carbon content (Figure 2). Bryophytes were the highest in biomass (46%), but dwarf shrubs were highest in carbon (45%) due to the differences in carbon content per unit biomass between the species groups.

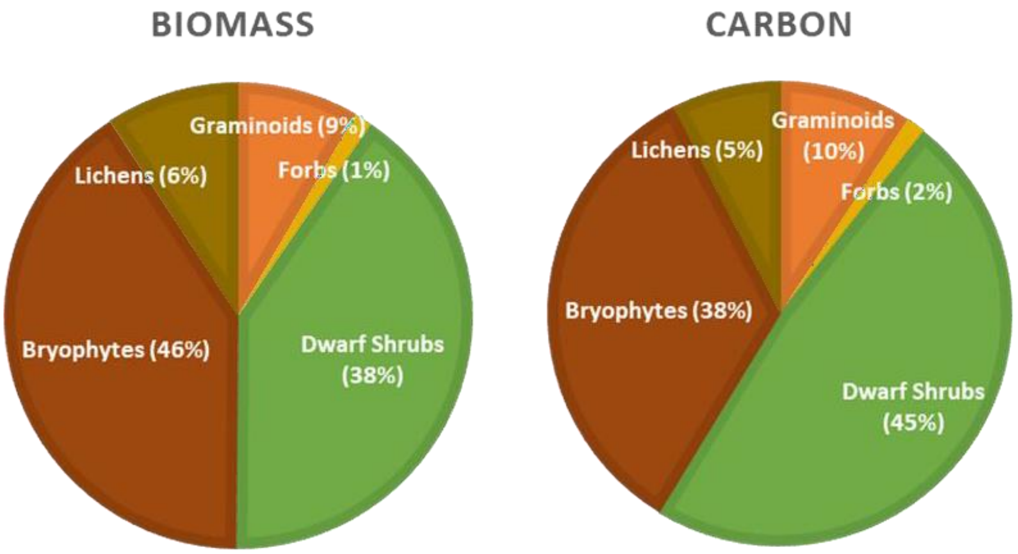


Figure 2: Proportions of biomass and carbon of each understory species group in relation to the total for all studied plots.

3.2. Model Outputs

3.2.1. Total Understory Carbon

All explanatory variables presented a significant relationship with total understory carbon as shown by the linear (β_1) and quadratic (β_2) coefficients in conjunction with the relationship p-values (P) (Table 1). Total basal area (β_1=-0.16 P<.001, β_2=-0.13 P<.001) and yearly temperature (β_1=-0.18 P<.001) displayed negative relationships (Figure 3a&e). Age (β_1=0.44 P<.001, β_2=-0.21 P<.001), CN ratio (β_1=1.03 P<.001, β_2=-0.70 P<.001), and total annual precipitation (β_1=0.06 P<.001) positively impacted the amount of carbon in the understory (Figure 3c,d&f). Age and CN ratio are characterized by an increase that levels off at high values. Percent of spruce in the stand had a negative influence on total understory carbon, with a levelling off at the lowest values of spruce (β_1=0.02 P=.632, β_2=-0.16 P<.001) (Figure 3b).

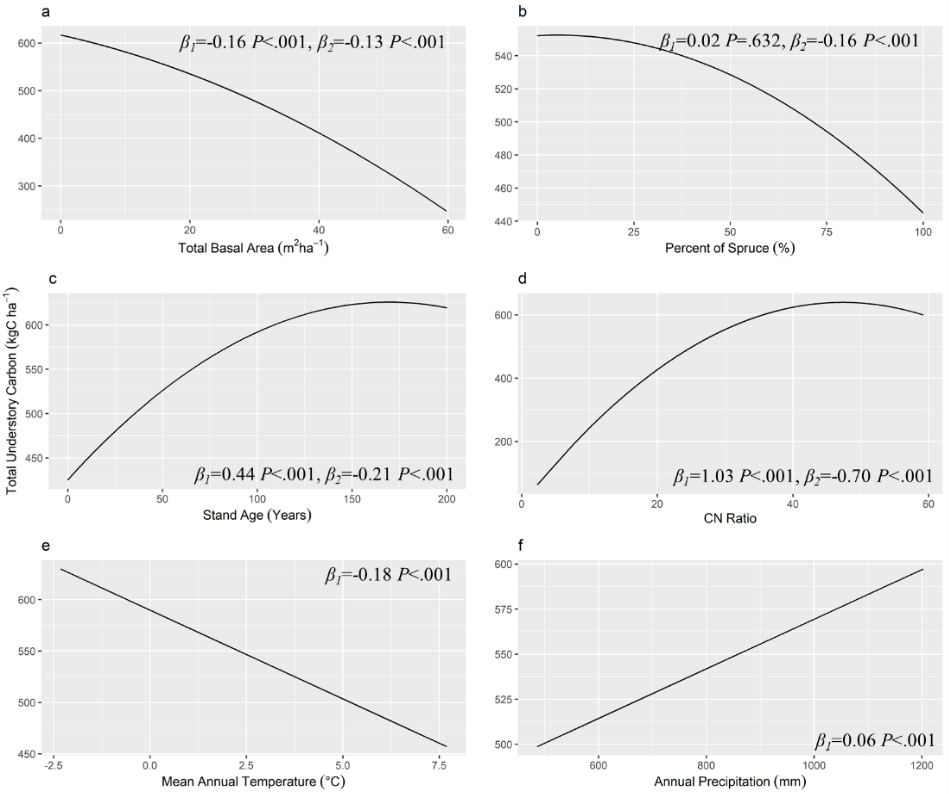


Figure 3: Understory carbon content progression along values of a) total basal area, b) percent of spruce in stand, c) stand age, d) CN ratio, e) average annual temperature, and f) annual precipitation. In each panel, all other variables are kept constant except the one represented on the x-axis. OBSERVE: Y-axis scales differ between panels based on possible carbon contents with each variable. Residual plots (Figures 10-15) can be found in the Appendix.

3.2.2. Species Groups

Total Basal Area

Of all the species groups, total basal area had the strongest influence on graminoids ($\beta_1=-0.38$ $P<.001$, $\beta_2=0.24$ $P<.001$). The proportion of understory carbon present in graminoids reached the lowest value around 35 m^2 ha^{-1} before slightly increasing again. Bryophytes had a linear relationship similar in strength to that of graminoids, however the general trend was opposite ($\beta_1=0.36$ $P<.001$, $\beta_2=-0.16$ $P<.001$). Lichens ($\beta_1=-0.19$ $P<.001$, $\beta_2=0.09$ $P=.012$) displayed a weaker but similar progression with increasing basal area as graminoids (Figure 4). Forbs were barely significantly affected, and the nonlinear response was insignificant ($\beta_1=0.08$ $P=.038$, $\beta_2=0.02$ $P=.479$). Neither the linear nor nonlinear relationships were significant with dwarf shrubs ($\beta_1=-0.05$ $P=.330$, $\beta_2=-0.06$ $P=.176$) (Table 2).

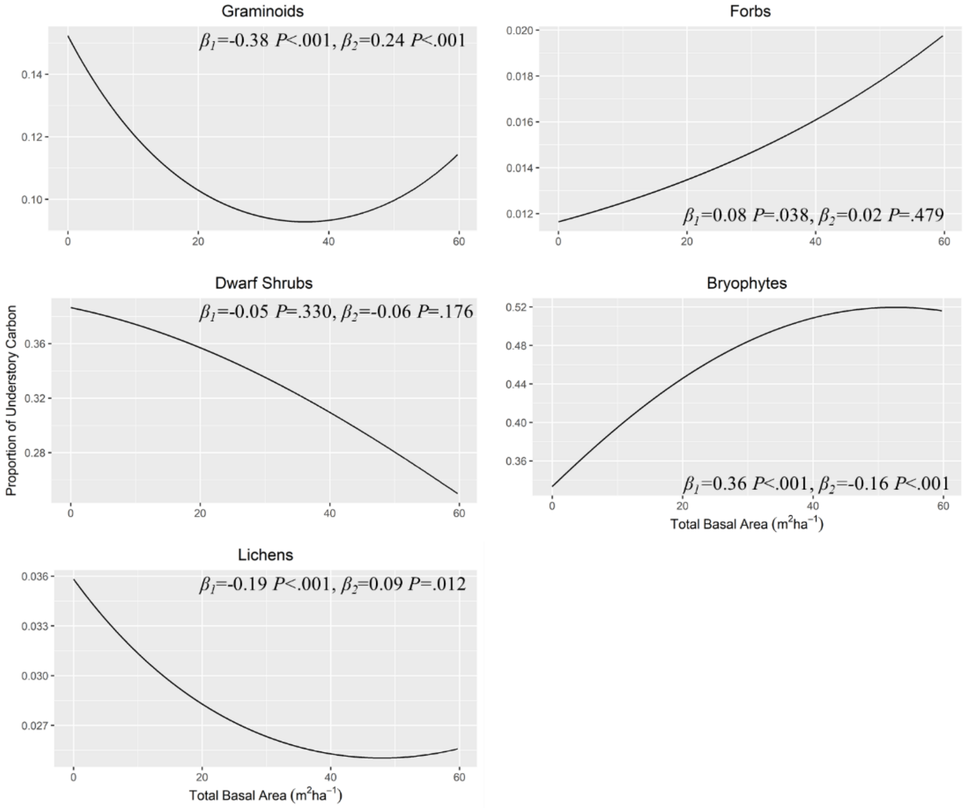


Figure 4: The effect of total basal area on the proportion of understory carbon in each species group. OBSERVE: Y-axis scales differ between panels based on possible carbon contents with each variable. Residual plots (Figures 10-15) can be found in the Appendix.

Percent of Spruce

Percent of spruce in the stand was found to have a significant relationship on some level with all species groups. Lichens (β_1=-0.16 P<.001, β_2=0.03 P=.396) and bryophytes (β_1=0.16 P<.001, β_2=0.16 P<.001) displayed slopes of equal strength in opposite directions at 0% spruce in the stand, but only the upward curve to the trend in bryophytes was significant. The sharpest curve in progression with increasing spruce in the stand was in dwarf shrubs (β_1=0.15 P=.003, β_2=-0.41 P<.001), resulting in the proportion of carbon decreasing at around 25% of the stand comprised of spruce. Graminoids (β_1=-0.40 P<.001, β_2=0.25 P<.001) displayed a significant and upward curve after 75% (Figure 5). Neither coefficient for forbs were significant (β_1=-0.07 P=.086, β_2=0.04 P=.329) (Table 3).

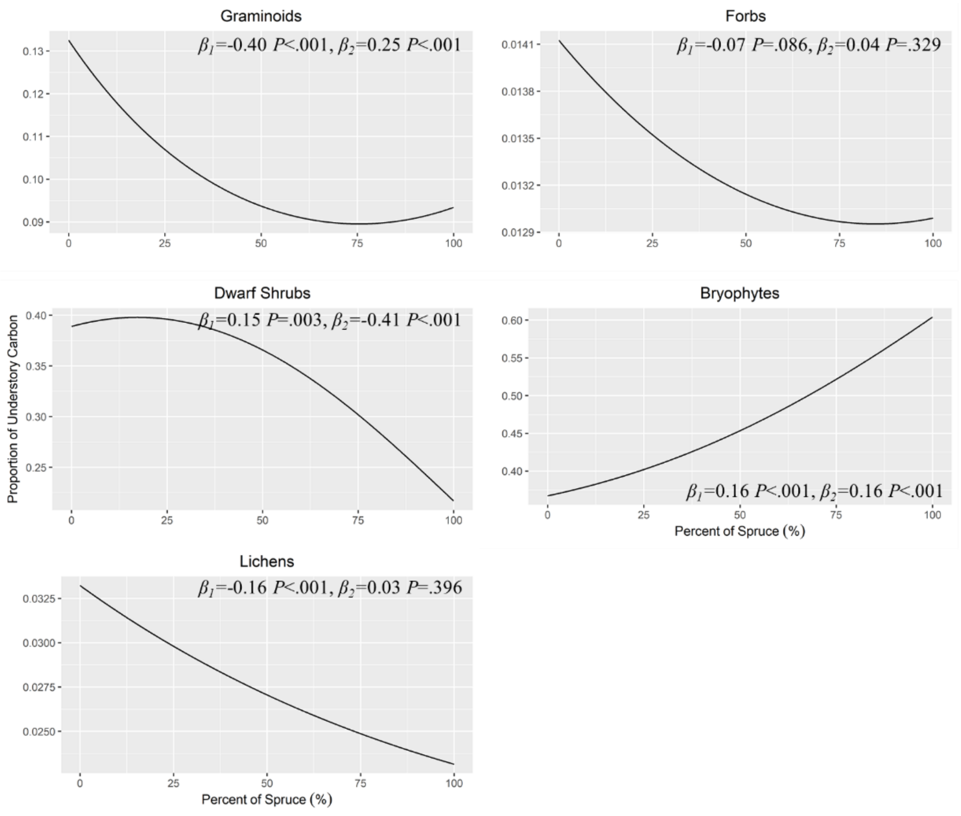


Figure 5: The effect of percent of spruce in the stand on the proportion of understory carbon in each species group. OBSERVE: Y-axis scales differ between panels based on possible carbon contents with each variable. Residual plots (Figures 10-15) can be found in the Appendix.

Stand Age

Stand age showed generally the weakest relationship with all the species groups (Table 4). The strongest relationship was with graminoids ($\beta_1=-0.59$ $P<.001$, $\beta_2=0.44$ $P<.001$). As can be seen in Figure 6, this trend was characterized by an upwards parabolic shape with the direction of the relationship changing at about 100 years. The other significant linear trends were with dwarf shrubs ($\beta_1=0.28$ $P<.001$, $\beta_2=-0.1$ $P=.061$) and forbs ($\beta_1=-0.18$ $P<.001$, $\beta_2=0.09$ $P=.047$). The nonlinear characteristics of the relationship with forbs was only border-line significant. Bryophytes had an insignificant slope at a stand age of 0 years, followed by a negative response with increasing age ($\beta_1=0.04$ $P=.447$, $\beta_2=-0.14$ $P=.003$). Proportion of understory carbon in lichens ($\beta_1=-0.05$ $P=.281$, $\beta_2=0.04$ $P=.303$) was not significantly related to stand age.

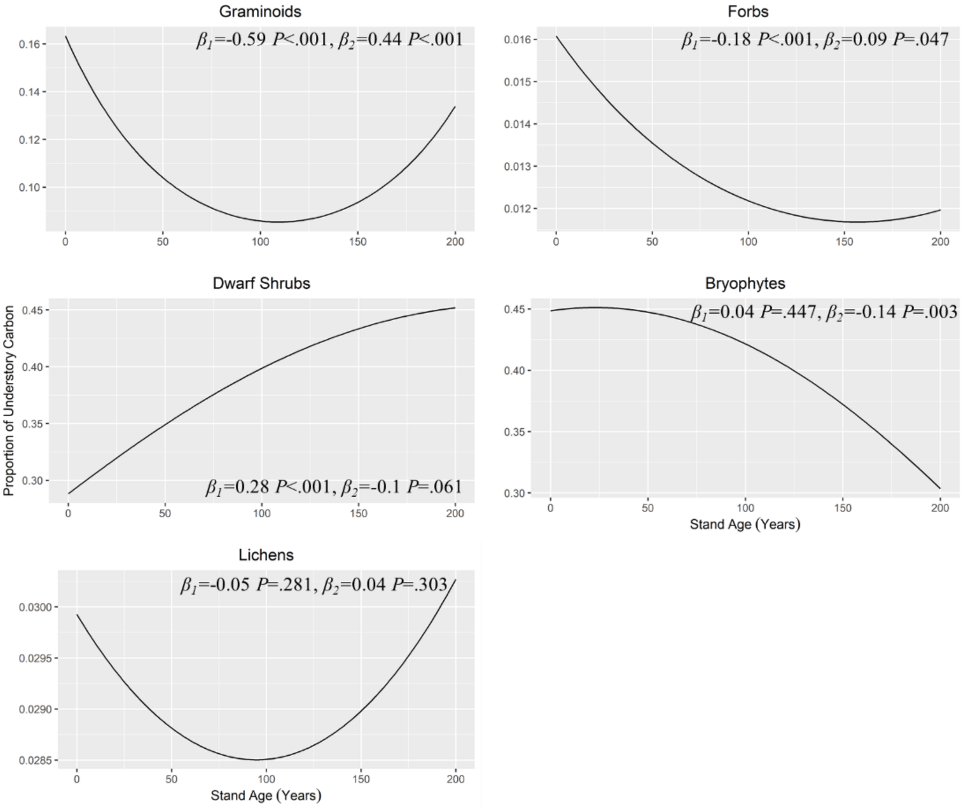


Figure 6: The effect of stand age on the proportion of understory carbon in each species group. OSERVE: Y- axis scales differ between panels based on possible carbon contents with each variable. Residual plots (Figures 10-15) can be found in the Appendix.

CN Ratio

CN ratio generally showed the strongest relationships with proportions of total carbon out of all explanatory variables (Table 5). The strongest relationship was with forbs ($\beta_1=-2.03$ $P<.001$, $\beta_2=1.26$ $P<.001$), which had a similar trend as graminoids ($\beta_1=-1.57$ $P<.001$, $\beta_2=0.92$ $P<.001$), with an L-shaped relationship (Figure 7). By a CN value of 40 both species groups contributed little to none of the total understory carbon. The only other coefficients greater than one occurred with dwarf shrubs ($\beta_1=1.62$ $P<.001$, $\beta_2=-1.22$ $P<.001$), which displayed a downward curve around 45 in an otherwise positive trend. Lichens ($\beta_1=-0.25$ $P<.001$, $\beta_2=0.38$ $P<.001$) displayed the weakest relationships with CN ratio for both levels of the variable, with an increase at CN value of about 25. Bryophytes ($\beta_1=0.10$ $P=.123$, $\beta_2=-0.09$ $P=.165$) were not significantly related on either level.

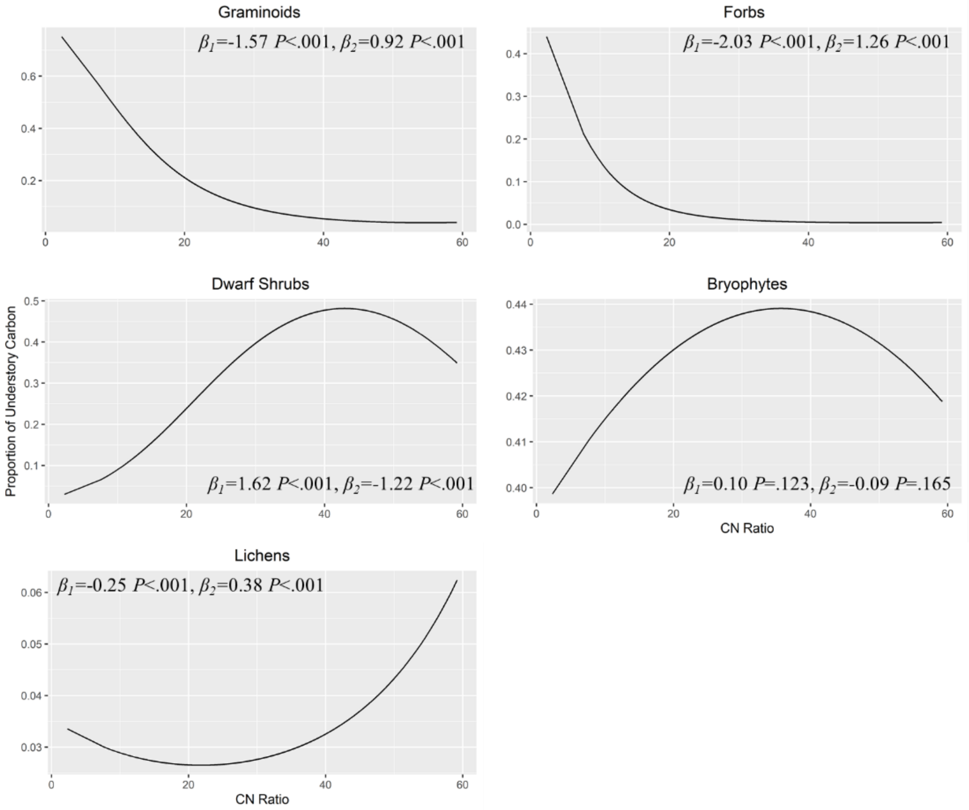


Figure 7: The effect of CN ratio on the proportion of understory carbon in each species group. OBSERVE: Y-axis scales differ between panels based on possible carbon contents with each variable. Residual plots (Figures 10-15) can be found in the Appendix.

Average Yearly Temperature

Temperature had a positive influence on graminoids ($\beta_1=0.09$ $P<.001$) and forbs ($\beta_1=0.19$ $P<.001$). Lichens ($\beta_1=-0.04$ $P=.001$) and dwarf shrubs ($\beta_1=-0.11$ $P<.001$) were negatively impacted by increasing temperature, with a stronger negative influence on dwarf shrubs (Figure 8). The relationship with bryophytes ($\beta_1=0.02$ $P=.126$) was insignificant (Table 6).

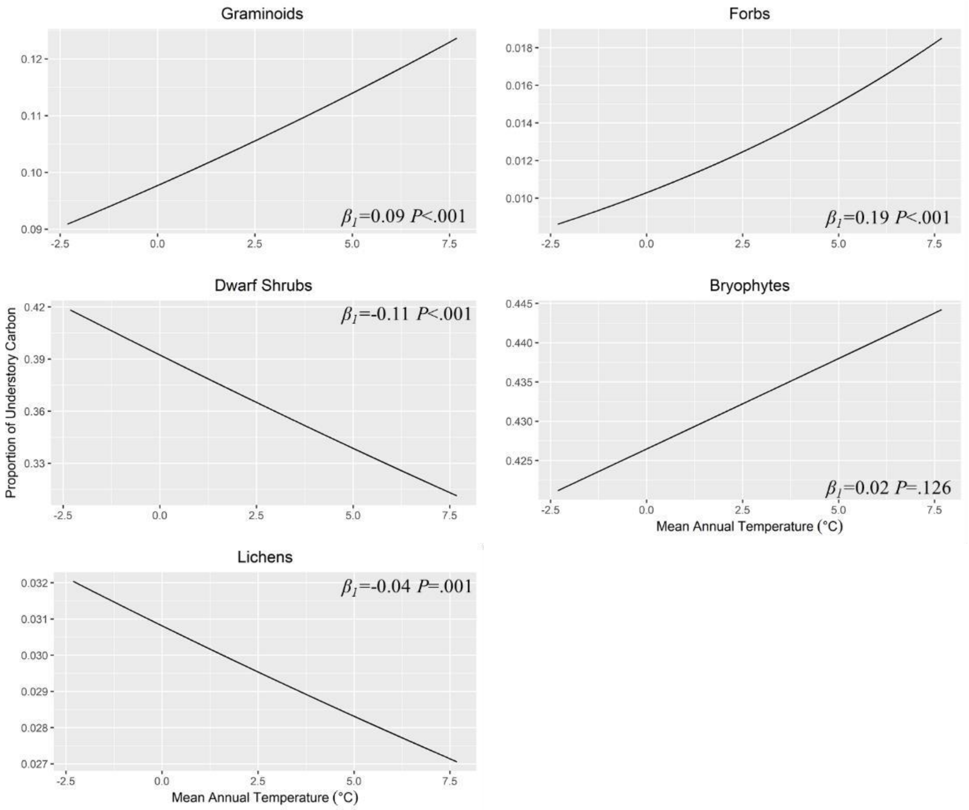


Figure 8: The effect of mean annual temperature on the proportion of understory carbon in each species group. OBSERVE: Y-axis scales differ between panels based on possible carbon contents with each variable. Residual plots (Figures 10-15) can be found in the Appendix.

Total Annual Precipitation

Relationships with precipitation were found to only be significant with dwarf shrubs (β_1=0.06 P<.001), bryophytes (β_1=-0.06 P<.001), and lichens (β_1=-0.06 P<.001). As is indicated by the coefficients (Table 6), precipitation had an equallystrong influence on all of these response variables. The direction of the relationshipdiffered between them with a decrease in the understory carbon proportion presentin the lichen and bryophytes species groups (Figure 9). Neither graminoids (β_1=- 0.00(2) P=0.989) nor forbs (β_1=-0.01 P=.379) were significantly related to precipitation.

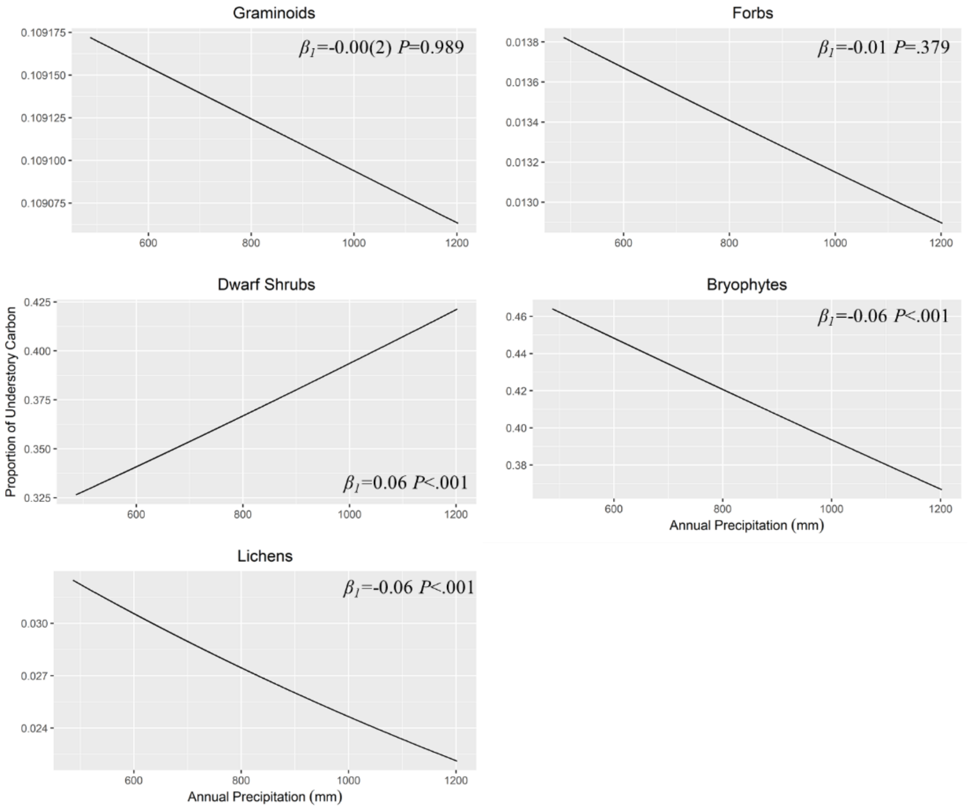


Figure 9: The effect of annual precipitation on the proportion of understory carbon in each species group. OBSERVE: Y-axis scales differ between panels based on possible carbon contents with each variable. Residual plots (Figures 10-15) can be found in the Appendix.

4. Discussion

This study demonstrated that both forest management and site conditions have significant relationships with understory carbon content and composition. To our knowledge, no previous studies have modelled understory carbon dynamics the way it has been done here. A study by Muukkonen and Mäkipää (2006) used similar methods to model understory above-ground biomass, but only included linear responses in their models and did not directly study the carbon content of the understory or contribution of species groups. As the carbon contents modelled here are derived from equations based on cover and biomass, studies of these measurements will also be compared as a proxy for carbon.

4.1. Management

The GLMMs give a more in-depth understanding as to why dwarf shrubs and bryophytes dominate both in cover and in contribution to the understory carbon pool. As indicated by the results here, current management regimes create conditions under which these species groups generally benefit more than others.

A less dense forest with a more open canopy is conducive to overall understory development and carbon storage (Alaback & Herman 1988; Hedwall & Brunet 2016). Forest density (estimated in our study using the basal area variable) had a negative influence on the proportion of understory carbon contributed by most species groups, as well as the total understory. The insignificance of the relationship between stand density and dwarf shrubs was unexpected as canopy structure and shading has previously been shown to have an impact on their cover (Alaback & Herman 1988; Moola & Mallik 1998). However, it agrees with Ali *et al.* (2019) who found that dwarf shrubs did not significantly differ between stands of differing density. The lack of relationship found here could be due to a delayed response to stand density. Moola and Mallik (1998) found that dwarf shrubs were able to persist for longer periods of time in shaded environments. As it is unknown for how long a stand had been at the measured total basal area when the data was collected, it is possible that the dwarf shrub cover had simply not yet responded to the density the stand was currently at. Forbs also responded unexpectedly to basal area, with a linear positive response to increasing stand density. However, it is in line with findings by Wilson and Puettmann (2007) which showed that forbs responded negatively if at all to thinnings, implying a preference for a consistently more closed canopy. Wilson and Puettmann (2007) as well as Ali *et al.* (2019) report a lower sensitivity of forbs to stand density but considering the significance levels of the relationships found here, our results are at odds. McKenzie *et al.* (2000) also found a very weak relation between forbs and canopy characteristics, which agrees with the only borderline significant relationship found in our study. This barely significant relationship could also be explained by species turnover along the light-availability gradient. Individual species in the group have a wide range of light requirements and species turnover may therefore occur within the group while still remaining present overall.

Lichens responded unexpectedly, as they only decreased with increasing forest density. As high levels of light can cause desiccation (Čabrajič *et al.* 2010), it would be expected for them to begin at a low value as bryophytes did, and then peak at an intermediate basal area. Helle *et al.* (1990) reported an initial decrease in lichen cover following clearcutting as would be expected, but an overall lack of response to changes in stand density and canopy cover otherwise. They did, however, find positive correlations between litter and logging residue variables, showing the importance of potentially including variables such as these in similar studies in the future.

Bryophytes were the only other species group to respond positively to increasing density, but that relationship was expected (Weibull 2001; Tinya *et al.* 2009). It is, however, at odds with a study by Saetre *et al.* (1997), who did not find a significant relationship between basal area and bryophyte cover. According to their results, the composition of the overstory was more influential on bryophyte cover, however in our study the relationship between stand density was stronger than that with percent of spruce which represents canopy composition more closely.

A higher percent of spruce in a stand has a negative influence on most species groups and the total understory (Rowe 1956; Saetre *et al.* 1997; Ewald 2000; Augusto *et al.* 2003). Bäcklund *et al.* (2016) found a general lower cover of all species groups except bryophytes when comparing pine and spruce stands in northern Sweden. This negative influence of spruce content on understory presence may not come only from decreased light availability due to the thick canopy, but also from factors such as below-ground competition for resources and accumulation of litter (Saetre *et al.* 1997; Petersson *et al.* 2019). Graminoids had the most severe negative influence from spruce. Graminoids have relatively shallow root systems (Schenk & Jackson 2002), which may mean they compete more directly with shallow spruce root systems and explain the more severe response. Thomas *et al.*

(1999) also reported a more dramatic positive response from graminoids to openings in the canopy compared to other species groups. The negative response of proportion of understory carbon in graminoids found here could be due to this higher sensitivity of graminoids to light availability.

The general negative influence of dense plantation management style may be somewhat offset by the benefits from decreased canopy cover through thinning. Total understory cover as well as the majority of species groups respond positively to openings in the canopy (Alaback & Herman 1988; Thomas *et al.* 1999; Thysell & Carey 2000). A management technique that allows for openings in the canopy is continuous cover, selective harvest. This technique allows not only for openings in the canopy (Lähde *et al.* 2002; Saiful & Latiff 2019), but also more variation in age within a stand (Lundmark *et al.* 2014).

Total understory carbon content increased with the age of the stand. This is at odds with several existing studies (Pregitzer & Euskirchen 2004; Peichl & Arain 2006; Bradford & Kastendick 2010; Uri *et al.* 2012). Kumar *et al.* (2018), however, report that total understory biomass can increase for at least a century. More specifically, they found increases in forbs, bryophytes, and dwarf shrubs over a long period of time. Dwarf shrubs followed this pattern with a linear increase with stand age. Alaback (1982) reported an almost complete disappearance of dwarf shrubs from forest understory after a couple of decades. Results here indicate almost theopposite of this, as dwarf shrubs make up almost half of all understory carbon in the stand at an age of 200 years. Forbaceous carbon decreased initially and then experienced a slight increase at the highest stand ages, similar to results found by Alaback (1982) of reestablishment of forbs in stands after about 140 years. However, the influence of stand age found by Alaback (1982) and others may be influenced by an increase in stand density over time, which has been controlled forin the models created in our study through inclusion of the basal area variable. Theprocesses modelled in this study, therefore, can more likely be attributed to time for establishment and development.

4.2. Site Conditions

The results presented in our study indicate that increasing temperatures decrease total understory carbon whereas increasing precipitation supports understory carbon content. Soil properties represented by CN ratio positively influenced dwarf shrubs and lichens and negatively impacted graminoids and forbs. The proportion of carbon stored in graminoids and forbs increased with increasing temperatures and was uninfluenced by changes in amount of precipitation, whereas lichens and dwarf shrubs decreased with increases in temperature. Dwarf shrubs were positively influenced by increased precipitation while bryophytes and lichens decreased.

According to the relationships modelled here, the shifting climate towards generally higher temperatures and more frequent and prolonged periods of decreased precipitation in boreal regions (Gauthier *et al.* 2015; Ruiz-Pérez & Vico 2020) would decrease total understory carbon in the studied sites. Ciais *et al.* (2005) found higher correlation between forest gross primary production (GPP) anomalies and rainfall rather than temperature increases. However, the relation here between total understory carbon and temperature was stronger than that between total understory carbon and precipitation. It is possible that the negative influence stems from a decrease in soil moisture availability with heightened temperatures (Rustad *et al.* 2001).

Beierkuhnlein *et al.* (2011) reported a higher sensitivity of Swedish graminoid ecotypes to drought but an insignificant impact of warming on biomass production. According to the results here, warming has a weak but significant positive influence on graminoid cover. Both graminoids and forbs had insignificant relations with precipitation in this study, indicating a stronger influence by temperature. This disagrees with existing studies that have found precipitation to have a greater influence on forbaceous vegetation (Fuhlendorf *et al.* 2001; Compagnoni *et al.* 2021). In the Eastern United States, Fridley and Wright (2018) observed a decrease in forbaceous biomass with increasing temperature. However, neither increased precipitation nor cooler temperatures positively influenced graminoids nor forbs in the results presented here. In fact, forbs were positively influenced by increasing temperature. Discrepancies between our study and others could be due to the scope of data used, as temperature and precipitation values in our study are only those within the range that occurs in Sweden. Dwarf shrub response modelled in our study is in agreement with Hedwall *et al.* (2021) who found a negative response of dwarf shrub cover in Sweden with increasing temperatures.

Nitrogen mineralization in boreal soils may increase with higher temperatures (Verburg *et al.* 1999), and fertilization is gaining more interest in the forestry community (Sténs *et al.* 2011). According to the results here, increased N mineralization and fertilization will decrease total understory carbon as well as the proportion of said carbon that is present in dwarf shrubs, bryophytes, and lichens. The decrease of understory carbon with increasing fertility (lower CN ratio) is potentially due to the higher nutrient availability to the overstory, supporting development of the canopy and allowing less light to reach the understory (Thomas *et al.* 1999). However, this is accounted for to some extent with the inclusion of basal area and spruce presence variables in the model, indicating an alternative influence. The results presented here indicate a threshold at which the fertility is low enough that bryophytes and dwarf shrubs begin to suffer as well. This could be a point where resources are low enough that the understory is being outcompeted below ground. The overall decrease in understory carbon is then likely impacted by the species turnover that takes place, with a decrease in species groups with higher carbon contents such as dwarf shrubs towards graminoids and forbs. As these are species groups with longer turnover and decompositions rates than those of graminoids and forbs (Jonasson 1983; Wickland *et al.* 2007; Hensgens *et al.* 2020), this would mean a shorter time of carbon storage in the understory pool.

4.3. Implications for Species and Carbon Turnover

The understory can contribute greatly to forest net primary production (NPP), as this vegetation layer generally has a faster turnover time than that of the overstory (Nilsson & Wardle 2005; Wardle *et al.* 2012). Therefore, with decreasing understory carbon along gradients of stand density, percent of spruce, and temperature the cycling of carbon in the system would slow down. This could influence the soil characteristics of the site, as understory vegetation has been found to influence CN ratio, moisture, and temperature (Gurlevik *et al.* 2004; Pan *et al.* 2018).

Species turnover along the gradients in explanatory variables modelled here impact the carbon turnover time within the aboveground understory carbon pool as well. For example, over a gradient towards more dense, dark forests, as has been the trend in European forestry in recent years (Rautiainen *et al.* 2011), there is a shift towards forbs and bryophytes and away from graminoids and dwarf shrubs found here. Increases in spruce, one of the two dominant forestry species used in Sweden (KSLA 2015), only benefitted the species group bryophytes according to the models in this study, and within the temporal scale of regeneration to harvest (Skogsstyrelsen n.d.), only dwarf shrubs increased. Predicted changes in site conditions will promote only graminoids and forbs according to the models presented here, as all other species groups were either negatively impacted by all variables or more negatively impacted by one or more than the positive effect of the other(s).

A decrease in dwarf shrubs would mean less carbon per unit biomass according to the ratios used in our study. It would also mean shorter longevity of stored carbon, as dwarf shrubs have longer turnover times than most species groups (Jonasson 1983; Hensgens *et al.* 2020). As graminoids and forbs do not contain any woody material that survives year-round, this means carbon will be cycled more quickly through the system. However, some perennial species may maintain biomass throughout the year. In drought scenarios, Beierkuhnlein *et al.* (2011) found more necrotic tissue of graminoids, meaning that these more frequent extreme weather events will cause losses of biomass and increase the rate of carbon cycling as well.

Species turnover within groups will also impact carbon longevity in the system because there are variations in deciduous and evergreen species as well as annual and perennial within the groups categorized here. For example, requirement gradients over light and nutrient availability exist between the dominant dwarf shrub species in Sweden (*Calluna vulgaris*, *Vaccinium vitis-idaea*, and *V. myrtillus*) (Kulmala *et al.* 2018). This means that dwarf shrub cover could remain constant, but the biomass would be stored in deciduous species rather than evergreen under dense forest conditions, and therefore increase the carbon turnover rate.

4.4. Future Studies

The current lack of knowledge regarding the dynamics of the understory carbon pool with management and climate shows potential for future development in this line of research. Moving forward, there are multiple things that could be implemented in order to get a more clear and in-depth understanding to these processes.

For example, biomass functions specific to Sweden could provide more precise calculations appropriate for the data collected in this region, as applicability of models can vary spatially (GFOI 2016). There is potential for more technologically advanced methods to be used for biomass calculation in the future as well, as demonstrated by Seidel *et al.* (2012) who used terrestrial laser scanning to estimate understory biomass in coppice stands. Both the functions and data collection could be improved upon by inclusion of layer height. Measurements by ICOS Sweden (T Biermann 2021, personal communication, 22 July) found variation in thickness of bryophyte cover within a single stand, and Helle *et al.* (1990) reported an increase in cover of lichens with stand age but a decrease in height. This indicates dynamics in height that are currently being neglected with the methods implemented here due to considering cover in a two-dimensional perspective.

It would also be beneficial to analyze the responses on a finer scale, considering the individual species in each group. Beierkuhnlein *et al.* (2011) looked at resilience to warming and drought between species and ecotypes and found variation on both levels, and Jonasson (1983) found variations in nutrient concentration and allocation between evergreen and deciduous dwarf shrub species. This goes to show that dynamics and responses may not only differ between species groups but also within them. This would consider, for example, the different light and nutrient requirements of species grouped together and, consequently, shifts in composition within species groups along the studied gradients. The same should be considered for carbon allocation in each species, as it may go to either woody or herbaceous components depending on site conditions, and these have differing turnover rates (Moola & Mallik 1998).

As the overstory is the resource most utilized from forests, as well as the larger carbon pool compared to the understory (Moore *et al.* 2007; Burton *et al.* 2013), methods that may improve the carbon sequestration by the understory should not be implemented before the impact on the overstory has also been determined. For example, extending the age of a stand or decreasing density may allow for more carbon in the understory, but it may also lead to a lower number of suitable stems for timber harvest (Ahmad *et al.* 2019). Biodiversity as an ecosystem service should also be considered, as trade-offs between understory and overstory carbon pools and diversity have also been found (Burton *et al.* 2013).

References

Adamovics, A., Platace, R., Gulbe, I. & Ivanovs, S. (2018). The content of carbon and hydrogen in grass biomass and its influence on heating value. *Proceedings 17th International Scientific Conference "Engineering for Rural Development"* May 24-25 2018, Jelgava, Latvia. https://doi.org/10.22616/ERDev2018.17.N014

Adkison, G.P. & Gleeson, S.K. (2004). Forest Understory Vegetation along a Productivity Gradient. *The Journal of the Torrey Botanical Society,* 131(1), 32-44. https://doi.org/10.2307/4126926

Ahmad, B., Wang, Y., Hao, J., Liu, Y., Bohnett, E. & Zhang, K. (2019). Optimizing stand structure for tradeoffs between overstory and understory vegetation biomass in a larch plantation of Liupan Mountains, Northwest China. *Forest Ecology and Management*, 443, 43-50. https://doi.org/10.1016/j.foreco.2019.04.001

Alaback, P.B. (1982). Dynamics of Understory Biomass in Sitka Spruce-Western Hemlock Forests of Southeast Alaska. *Ecology,* 63(6), 1932-1948. https://doi.org/https://doi.org/10.2307/1940131

Alaback, P.B. & Herman, F.R. (1988). Long-term response of understory vegetation to stand density in Picea-Tsuga forests. *Canadian Journal of Forest Research*, 18(12), 1522-1530. https://doi.org/10.1139/x88-233

Albrich, K., Rammer, W., Thom, D. & Seidl, R. (2018). Trade-offs between temporal stability and level of forest ecosystem services provisioning under climate change. *Ecological Applications,* 28(7), 13.

Ali, A., Dai, D., Akhtar, K., Teng, M., Yan, Z., Urbina-Cardona, N., Mullerova, J. & Zhou, Z. (2019). Response of understory vegetation, tree regeneration, and soil quality to manipulated stand density in a Pinus massoniana plantation. *Global Ecology and Conservation*, 20, e00775.

Anderson, R.C., Loucks, O.L. & Swain, A.M. (1969). Herbaceous Response to Canopy Cover, Light Intensity, and Throughfall Precipitation in Coniferous Forests. *Ecology,* 50(2), 255-263. https://doi.org/10.2307/1934853

Augusto, L., Dupouey, J.-L. & Ranger, J. (2003). Effects of tree species on understory vegetation and environmental conditions in temperate forests. *Annals of Forest Science*, 60(8), 823-831. https://doi.org/10.1051/forest:2003077

Bäcklund, S., Jönsson, M., Strengbom, J., Frisch, A. & Thor, G. (2016). A pine is a pine and a spruce is a spruce–the effect of tree species and stand age on epiphytic lichen communities. Plos One, 11(1), e0147004. https://doi.org/10.1371/journal.pone.0147004

Balandier, P., Frochot, H. & Sourisseau, A. (2009). Improvement of direct tree seeding with cover crops in afforestation: Microclimate and resource availability induced by vegetation composition. *Forest Ecology and Management*, 257(8), 1716-1724. https://doi.org/https://doi.org/10.1016/j.foreco.2009.01.032

Barbier, S., Gosselin, F. & Balandier, P. (2008). Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests. *Forest Ecology and Management*, 254(1), 1-15. https://doi.org/https://doi.org/10.1016/j.foreco.2007.09.038

Beierkuhnlein, C., Thiel, D., Jentsch, A., Willner, E. & Kreyling, J. (2011). Ecotypes of European grass species respond differently to warming and extreme drought. *Journal of Ecology*, 99(3), 703-713. https://doi.org/10.1111/j.1365-2745.2011.01809.x

Belusic, D., Berg, P., Bozhinova, D., Bärring, L., Doescher, R., Eronn, A., Kjellström, E., Klehmet, K., Martins, H. & Nilsson, C. (2019). *Climate extremes for Sweden*. https://doi.org/10.17200/Climate_Extremes_Sweden

Binkley, C.S., Apps, M.J., Dixon, R.K., Kauppi, P.E. & Nilsson, L.O. (1997). Sequestering carbon in natural forests. *Critical Reviews in Environmental Science and Technology*, 27(sup001), 23-45. https://doi.org/10.1080/10643389709388508

Bradford, J. & Kastendick, D. (2010). Age-related patterns of forest complexity and carbon storage in pine and aspen–birch ecosystems of northern Minnesota, USA. *Can. J. For. Res.*, 40. https://doi.org/10.1139/X10-002

Burton, J.I., Ares, A., Olson, D.H. & Puettmann, K.J. (2013). Management trade-off between aboveground carbon storage and understory plant species richness in temperate forests. *Ecological Applications*, 23(6), 14. https://doi.org/10.1890/12-1472.1

Čabrajič, A., Moen, J. & Palmqvist, K. (2010). Predicting growth of mat-forming lichens on a landscape scale – comparing models with different complexities. *Ecography*, 33, 949-960. https://doi.org/10.1111/j.1600-0587.2009.06079.x

Chapin, F.S., Woodwell, G.M., Randerson, J.T., Rastetter, E.B., Lovett, G.M., Baldocchi, D.D., Clark, D.A., Harmon, M.E., Schimel, D.S., Valentini, R., Wirth, C., Aber, J.D., Cole, J.J., Goulden, M.L., Harden, J.W., Heimann, M., Howarth, R.W., Matson, P.A., McGuire, A.D., Melillo, J.M., Mooney, H.A., Neff, J.C., Houghton, R.A., Pace, M.L., Ryan, M.G., Running, S.W., Sala, O.E., Schlesinger, W.H. & Schulze, E.D. (2006). Reconciling Carbon-cycle Concepts, Terminology, and Methods. *Ecosystems*, 9(7), 1041-1050. https://doi.org/10.1007/s10021-005-0105-7

Christensen, T.R., Johansson, T., Åkerman, H.J., Mastepanov, M., Malmer, N., Friborg, T., Crill, P. & Svensson, B.H. (2004). Thawing sub-arctic permafrost: Effects on vegetation and methane emissions. *Geophysical research letters*, 31(4). https://doi.org/10.1029/2003GL018680

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C. & Carrara, A. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, 437(7058), 529-533.

Clemmensen, K.E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R.D., Wardle, D.A. & Lindahl, B.D. (2013). Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest. *Science*, 339(6127), 1615. https://doi.org/10.1126/science.1231923

Compagnoni, A., Levin, S., Childs, D.Z., Harpole, S., Paniw, M., Römer, G., Burns, J.H., Che-Castaldo, J., Rüger, N. & Kunstler, G. (2021). Herbaceous perennial plants with short generation time have stronger responses to climate anomalies than those with longer generation time. *Nature communications*, 12(1), 1-8. https://doi.org/10.1038/s41467-021-21977-9

Dirnbock, T., Kraus, D., Grote, R., Klatt, S., Kobler, J., Schindlbacher, A., Seidl, R., Thom, D. & Kiese, R. (2020). Substantial understory contribution to the C sink of a European temperate mountain forest landscape. *Landsc Ecol*, 35(2), 483-499. https://doi.org/10.1007/s10980-019-00960-2

Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexier, M.C. & Wisniewski, J. (1994). Carbon Pools and Flux of Global Forest Ecosystems. *Science*, 263(5144), 185. https://doi.org/10.1126/science.263.5144.185

Douglas, T.A., Turetsky, M.R. & Koven, C.D. (2020). Increased rainfall stimulates permafrost thaw across a variety of Interior Alaskan boreal ecosystems. *NPJ Climate and Atmospheric Science,* 3(1), 1-7. https://doi.org/10.1038/s41612-020-0130-4

Enkvist, P.-A., Naucler, T. & Rosander, J. (2007). A cost curve for greenhouse gas reduction. *The Mckinsey Quarterly* http://rainforestcoalition.org.serv7.temphostspace.com/documents/McKArticleonGHGCostCurves.pdf

Ewald, J. (2000). The Influence of Coniferous Canopies on Understorey Vegetation and Soils in Mountain Forests of the Northern Calcareous Alps. *Applied Vegetation Science*, 3(1), 123-134. https://doi.org/10.2307/1478926

FAO (2015). *Global Forest Resources Assessment 2015 - Country Report - Sweden*. Rome, Italy. http://www.fao.org/3/az346e/az346e.pdf [03.04.2021].

FAO (2018). *Forest Policy - Basic Knowledge* Food and Agriculture Organization of the United Nations http://www.fao.org/sustainable-forest-management/toolbox/modules/forest-policy-and-legislation/basic-knowledge/en/?type=111 [01.04.2021].

FAO (2020). *Global Forest Resources Assessment 2020 - Key Findings*. (978-92-5-132581-0). Rome, Italy:[24/03/2021].

Felsmann, K., Baudis, M., Kayler, Z.E., Puhlmann, H., Ulrich, A. & Gessler, A. (2017). Responses of the structure and function of the understory plant communities to precipitation reduction across forest ecosystems in Germany. *Annals of Forest Science*, 75(1), 3. https://doi.org/10.1007/s13595-017-0681-7

Fridley, J.D. & Wright, J.P. (2018). Temperature accelerates the rate fields become forests. *Proceedings of the National Academy of Sciences,* 115(18), 4702-4706. https://doi.org/10.1073/pnas.1716665115

Fridman, J., Holm, S., Nilsson, M., Nilsson, P., Ringvall, A. & Ståhl, G. (2014). Adapting National Forest Inventories to changing requirements – the case of the Swedish National Forest Inventory at the turn of the 20th century. *Silva Fennica,* 48(3). https://doi.org/10.14214/sf.1095

FSC (2013). The Contribution of FSC Certification to Biodiversity in Swedsih Forests (2). Forest Stewardship Council.

Fuhlendorf, S.D., Briske, D.D. & Smeins, F.E. (2001). Herbaceous vegetation change in variable rangeland environments: the relative contribution of grazing and climatic variability. *Applied Vegetation Science,* 4(2), 177-188. https://www.jstor.org/stable/1478931

Gale, M.R. & Grigal, D.F. (1987). Vertical root distributions of northern tree species in relation to successional status. *Canadian Journal of Forest Research,* 17(8), 829-834. https://doi.org/10.1139/x87-131

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z. & Schepaschenko, D.G. (2015). Boreal forest health and global change. *Science,* 349(6250), 819. https://doi.org/10.1126/science.aaa9092

Gimbel, K.F., Felsmann, K., Baudis, M., Puhlmann, H., Gessler, A., Bruelheide, H., Kayler, Z., Ellerbrock, R.H., Ulrich, A., Welk, E. & Weiler, M. (2015). Drought in forest understory ecosystems – a novel rainfall reduction experiment. *Biogeosciences,* 12(4), 961-975. https://doi.org/10.5194/bg-12-961-2015

Grace, J. (2004). Understanding and managing the global carbon cycle. *Journal of Ecology,* 92(2), 189-202. https://doi.org/https://doi.org/10.1111/j.0022-0477.2004.00874.x

Grau-Andrés, R., Wardle, D., Gundale, M., Foster, C. & Kardol, P. (2020). Effects of plant functional group removal on CO2 fluxes and belowground C stocks across contrasting ecosystems. *Ecology,* 101. https://doi.org/10.1002/ecy.3170

Gurlevik, N., Kelting, D.L. & Allen, H.L. (2004). Nitrogen Mineralization Following Vegetation Control and Fertilization in a 14-Year-Old Loblolly Pine Plantation. *Soil Science Society of America Journal,* 68(1), 272-281. https://doi.org/https://doi.org/10.2136/sssaj2004.2720

Hedwall, P.-O., Brunet, J., Nordin, A. & Bergh, J. (2013). Changes in the abundance of keystone forest floor species in response to changes of forest structure. *Journal of Vegetation Science,* 24(2), 296-306. https://doi.org/https://doi.org/10.1111/j.1654-1103.2012.01457.x

Hedwall, P.-O., Gustafsson, L., Brunet, J., Lindbladh, M., Axelsson, A.-L. & Strengbom, J. (2019). Half a century of multiple anthropogenic stressors has altered northern forest understory plant communities. *Ecological Applications*, 29(4), e01874. https://doi.org/https://doi.org/10.1002/eap.1874

Hedwall, P.-O., Uria-Diez, J., Brunet, J., Gustafsson, L., Axelsson, A.-L. & Strengbom, J. (2021). Interactions between local and global drivers determine long-term trends in boreal forest understorey vegetation. *Global Ecology and Biogeography,* 30(9), 1765-1780. https://doi.org/https://doi.org/10.1111/geb.13324

Hedwall, P.O. & Brunet, J. (2016). Trait variations of ground flora species disentangle the effects of global change and altered land-use in Swedish forests during 20 years. *Glob Chang Biol*, 22(12), 4038-4047. https://doi.org/10.1111/gcb.13329

Helle, T., Aspi, J. & Kilpelä, S.S. (1990). The effects of stand characteristics on reindeer lichens and range use by semi-domesticated reindeer. *Rangifer,* 10(3). https://doi.org/10.7557/2.10.3.839

Hensgens, G., Laudon, H., Peichl, M., Gil, I.A., Zhou, Q. & Berggren, M. (2020). The role of the understory in litter DOC and nutrient leaching in boreal forests. *Biogeochemistry*, 149(1), 87-103. https://doi.org/10.1007/s10533-020-00668-5

Hutchinson, T., Boerner, R., Iverson, L., Sutherland, S. & Sutherland, E. (1999). Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (USA) Quercus forests. *Vegetatio*, 144. https://doi.org/10.1023/A:1009804020976

IPCC (2006). *Guidelines for National Greenhouse Gas Inventories.* Institute for Global Environmental Strategies (IGES).

https://www.ipcc.ch/report/2006-ipcc-guidelines-for-national-greenhouse-gas-inventories/ [30.03.2020]

IUCN (2021). Forests and Climate Change. Gland, Switzerland: IUCN.

Jonasson, S. (1983). Nutrient Content and Dynamics in North Swedish Shrub Tundra Areas. *Holarctic Ecology,* 6(3), 295-304. http://www.jstor.org/stable/3682384 [2021/08/08/]

Ķēniņa, L., Elferts, D., Bāders, E. & Jansons, Ā. (2018). Carbon Pools in a Hemiboreal Over-Mature Norway Spruce Stands. *Forests*, 9(7). https://doi.org/10.3390/f9070435

KSLA (2015). *Forests and Forestry in Sweden*: Royal Swedish Academy of Agriculture and Forestry. https://www.skogsstyrelsen.se/globalassets/in-english/forests-and-forestry-in-sweden_2015.pdf [01.04.2021]

Kulmala, L., Dominguez Carrasco, M.d.R. & Heinonsalo, J. (2018). The differences in carbon dynamics between boreal dwarf shrubs and Scots pine seedlings in a microcosm study. *Journal of Plant Ecology*, 11(5), 709-716. https://doi.org/10.1093/jpe/rtx051

Kumar, P., Chen, H.Y.H., Searle, E.B. & Shahi, C. (2018). Dynamics of understorey biomass, production and turnover associated with long-term overstorey succession in boreal forest of Canada. *Forest Ecology and Management*, 427, 152-161. https://doi.org/10.1016/j.foreco.2018.05.066

Lähde, E., Eskelinen, T. & Väänänen, A. (2002). Growth and diversity effects of silvicultural alternatives on an old-growth forest in Finland. *Forestry: An International Journal of Forest Research*, 75(4), 395-400. https://doi.org/10.1093/forestry/75.4.395

Lehtonen, A., Linkosalo, T., Peltoniemi, M., Sievänen, R., Mäkipää, R., Tamminen, P., Salemaa, M., Nieminen, T., Ťupek, B., Heikkinen, J. & Komarov, A. (2016). Forest soil carbon stock estimates in a nationwide inventory: evaluating performance of the ROMULv and Yasso07 models in Finland. *Geoscientific Model Development*, 9(11), 4169-4183. https://doi.org/10.5194/gmd-9-4169-2016

Lind, P. & Kjellström, E. (2008). *Temperature and precipitation changes in Sweden; a wide range of model-based projections for the 21st century*. (RMK No. 113). Norrköping, Sweden: Swedish Meteorological and Hydrological Institute. http://urn.kb.se/resolve?urn=urn:nbn:se:smhi:diva-2636

Lorenz, K. & Lal, R. (2010). *Carbon Sequestration in Forest Ecosystems*. Springer, Dordrecht. https://doi.org/ 10.1007/978-90-481-3266-9

Lundmark, T., Bergh, J., Hofer, P., Lundström, A., Nordin, A., Poudel, B., Sathre, R., Taverna, R. & Werner, F. (2014). Potential Roles of Swedish Forestry in the Context of Climate Change Mitigation. *Forests*, 5(4), 557-578. https://doi.org/10.3390/f5040557

Malhi, Y., Meir, P. & Brown, S. (2002). Forests, carbon and global climate. *Philosophical transactions. Series A, Mathematical, physical, and engineering sciences*, 360, 1567-91. https://doi.org/10.1098/rsta.2002.1020

McKenzie, D., Halpern, C.B. & Nelson, C.R. (2000). Overstory influences on herb and shrub communities in mature forests of western Washington, USA. *Canadian Journal of Forest Research*, 30(10), 1655-1666. https://doi.org/10.1139/x00-091

McMullin, R. & Rapai, S. (2020). A review of reindeer lichen (Cladonia subgenus Cladina) linear growth rates. *Rangifer*, 40, 15-26. https://doi.org/10.7557/2.40.1.4636

McMullin, R., Thompson, I., Lacey, B. & Newmaster, S. (2011). Estimating the biomass of woodland caribou forage lichens in boreal Ontario. *Canadian Journal of Forest Research*, 41, 1961–1969. https://doi.org/10.1139/x11-108

Moola, F.M. & Mallik, A.U. (1998). Morphological plasticity and regeneration strategies of velvet leaf blueberry (Vaccinium myrtilloides Michx.) following canopy disturbance in boreal mixedwood forests. *Forest Ecology and Management*, 111(1), 35-50. https://doi.org/https://doi.org/10.1016/S0378-1127(98)00306-5

Moore, P.T., Van Miegroet, H. & Nicholas, N.S. (2007). Relative role of understory and overstory in carbon and nitrogen cycling in a southern Appalachian spruce–fir forestAES Publication 7863. Utah Agricultural Experiment Station, Utah State University, Logan, Utah. *Canadian Journal of Forest Research*. 37(12), 2689-2700. https://doi.org/10.1139/x07-115

Muukkonen, P. & Mäkipää, R. (2006). Empirical biomass models of understorey vegetation in boreal forests according to stand and site attributes. *Boreal Environment Research*. 11(5), 355-369.

Natalia, S., Lieffers, V.J. & Landhäusser, S.M. (2008). Effects of leaf litter on the growth of boreal feather mosses: Implication for forest floor development. *Journal of Vegetation Science*. 19(2), 253-260. https://doi.org/https://doi.org/10.3170/2008-8-18367

Nihlgård, B. (1970). Precipitation, Its Chemical Composition and Effect on Soil Water in a Beech and a Spruce Forest in South Sweden. *Oikos*. 21(2), 208-217. https://doi.org/10.2307/3543676

Nilsson, M.-C. & Wardle, D.A. (2005). Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment.* 3(8), 421-428. https://doi.org/https://doi.org/10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO;2

NOAA (n.d.). *Basics of the Carbon Cycle and the Greenhouse Effect*. https://gml.noaa.gov/education/carbon_toolkit/ [14/05/2021]

Nordhaus, W.D. (1993). Optimal Greenhouse-Gas Reductions and Tax Policy in the "DICE" Model. *The American Economic Review*. 83(2), 313-317. http://www.jstor.org/stable/2117683

Palmqvist, K. & Sundberg, B. (2000). Light use efficiency of dry matter gain in five macro-lichens: relative impact of microclimate conditions and species-specific traits. *Plant, Cell & Environment.* 23(1), 1-14. https://doi.org/https://doi.org/10.1046/j.1365-3040.2000.00529.x

Pan, P., Zhao, F., Ning, J., Zhang, L., Ouyang, X. & Zang, H. (2018). Impact of understory vegetation on soil carbon and nitrogen dynamic in aerially seeded Pinus massoniana plantations. *Plos One.* 13(1), e0191952. https://doi.org/10.1371/journal.pone.0191952

Peichl, M. & Arain, M.A. (2006). Above- and belowground ecosystem biomass and carbon pools in an age-sequence of temperate pine plantation forests. *Agricultural and Forest Meteorology*. 140(1-4), 51-63. https://doi.org/10.1016/j.agrformet.2006.08.004

Petersson, L., Holmström, E., Lindbladh, M. & Felton, A. (2019). Tree species impact on understory vegetation: Vascular plant communities of Scots pine and Norway spruce managed stands in northern Europe. *Forest Ecology and Management.* 448, 330-345. https://doi.org/https://doi.org/10.1016/j.foreco.2019.06.011

Post, W.M., Peng, T.-H., Emanuel, W.R., King, A., Dale, V. & Deangelis, D. (1990). The Global Carbon Cycle. *American Scientist.* 78, 310-326. https://doi.org/10.1007/978-3-642-84608-3_10

Pregitzer, K.S. & Euskirchen, E.S. (2004). Carbon cycling and storage in world forests: biome patterns related to forest age. *Global change biology*. 10(12), 2052-2077. https://doi.org/10.1111/j.1365-2486.2004.00866.x

Prentice, I.C., Farquhar, G.D., Fasham, M.J.R., Goulden, M.L., Heimann, M., Jaramillo, V.J., Kheshgi, H.S., Le Quere, C., Scholes, R.J., Wallace, D.W.R., Archer, D., Ashmore, M.R., Aumont, O., Baker, D., Battle, M., Bender, M., Bopp, L.P., Bousquet, P., Caldeira, K., Ciais, P., Cox, P.M., Cramer, W., Dentener, F., Enting, I.G., Field, C.B., Friedlingstein, P., Holland, E.A., Houghton, R.A., House, J.I., Ishida, A., Jain, A.K., Janssens, I.A., Joos, F., Kaminski, T., Keeling, C.D., Keeling, R.F., Kicklighter, D.W., Kohfeld, K.E., Knorr, W., Law, R., T., L., Lindsay, K., Maier-Riemer, E., Manning, A.C., Matear, R.J., McGuire, A.D., Melillo, J.M., Meyer, R., Mund, M., Orr, J.C., Piper, S., Plattner, K., Rayner, P.J., Sitch, S., Slater, R., Taguchi, S., Tans, P.P., Tian, H.Q., Weirig, M.F., Whorf, T. & Yool, A. (2001). *Chapter 3: The Carbon Cycle and Carbon Sequestration*. (Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report
of the Intergovernmental Panel on Climate Change). Cambridge, United Kingdom New York, NY, USA: Press, C.U. https://www.ipcc.ch/site/assets/uploads/2018/02/TAR-03.pdf

R Core Team (2019). *R: A language and environment for statistical computing*. [Programvara]. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Ramachandran Nair, P.K., Nair, V.D., Mohan Kumar, B., Showalter, J.M. & Sparks, D.L. (2010). Chapter Five - Carbon Sequestration in Agroforestry Systems. In: Kumar, B.M., Nair, P. K.R. (108). *Carbon Sequestration Potential of Agroforestry Systems*. Academic Press. 237-307. https://www.sciencedirect.com/science/article/pii/S0065211310080053

Rautiainen, A., Wernick, I., Waggoner, P., Ausubel, J. & Kauppi, P. (2011). A National and International Analysis of Changing Forest Density. *Plos One.* 6, e19577. https://doi.org/10.1371/journal.pone.0019577

Rigby, R.A. & Stasinopoulos, D.M. (2005). Generalized additive models for location, scale and shape. *Journal of the Royal Statistical Society: Series C (Applied Statistics).* 54(3), 507-554. https://doi.org/https://doi.org/10.1111/j.1467-9876.2005.00510.x

Ritchie, H. & Roser, M. (2020). CO_2 and Greenhouse Gas Emissions. Published online at OurWorldInData.org.

Rowe, J.S. (1956). Uses of Undergrowth Plant Species in Forestry. *Ecology.* 37(3), 461-473. https://doi.org/10.2307/1930168

Ruiz-Pérez, G. & Vico, G. (2020). Effects of Temperature and Water Availability on Northern European Boreal Forests. *Frontiers in Forests and Global Change*. 3(34). https://doi.org/10.3389/ffgc.2020.00034

Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J. & Gurevitch, J. (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*. 126(4), 543-562.

Rydin, H., Snoejis, P. & Diekmann, M. (1999). *Swedish Plant Geography*. Uppsala, Sweden.http://www.diva-portal.org/smash/get/diva2:565333/FULLTEXT01.pdfBengt

Saetre, P., Saetre, L.S., Brandtberg, P.O., Lundkvist, H. & Bengtsson, J. (1997). Ground vegetation composition and heterogeneity in pure Norway spruce and mixed Norway spruce - birch stands. *Canadian Journal of Forest Research*. 27(12), 2034-2042. https://doi.org/10.1139/x97-177

Saiful, I. & Latiff, A. (2019). Canopy Gap Dynamics And Effects Of Selective Logging

A Study In A Primary Hill Dipterocarp Forest In Malaysia. *Journal of Tropical Forest Science*. 31(2), 175-188. https://www.jstor.org/stable/26626989

Schenk, H.J. & Jackson, R.B. (2002). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*. 90(3), 480-494. https://doi.org/https://doi.org/10.1046/j.1365-2745.2002.00682.x

Schlesinger, W.H. (1977). Carbon balance in terrestrial detritus. *Annual Review of Ecological Systematics*. 8, 51-81. https://doi.org/10.1146/annurev.es.08.110177.000411

Seidel, D., Albert, K., Fehrmann, L. & Ammer, C. (2012). The potential of terrestrial laser scanning for the estimation of understory biomass in coppice-with-standard systems. *Biomass and Bioenergy*. 47, 20-25.

Seidl, R., Schelhaas, M.J., Rammer, W. & Verkerk, P.J. (2014). Increasing forest disturbances in Europe and their impact on carbon storage. *Nat Clim Chang*. 4(9), 806-810. https://doi.org/10.1038/nclimate2318

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A. & Reyer, C.P.O.

(2017). Forest disturbances under climate change. *Nat Clim Chang.* 7, 395-402. https://doi.org/10.1038/nclimate3303

SGU, S.G.U. (2020a). *The Geology of Sweden* https://www.sgu.se/en/geology-of-sweden/#:~:text=The%20overburden%20is%20mainly%20formed,as%20earthquakes%2C%20volcanism%20and%20glaciations.

SGU, S.G.U. (2020b). *The Bedrock of Sweden*. https://www.sgu.se/en/geology-of-sweden/rocks/the-bedrock-of-sweden/

Shields, J.M. & Webster, C.R. (2007). Ground-layer response to group selection with legacy-tree retention in a managed northern hardwood forest. *Canadian Journal of Forest Research.* 37(10), 1797-1807. https://doi.org/10.1139/X07-052

Skogsstyrelsen (n.d.). *The Forestry Act*. https://www.skogsstyrelsen.se/en/laws-and-regulations/skogsvardslagen/

SLU (2020) *Fältinstruktion 2020 - Riksinventeringen av skog* Uppsala, Sweden Umeå, Sweden: SLU.

SMHI (2021). *Sweden's climate*. https://www.smhi.se/kunskapsbanken/klimat/sveriges-klimat/sveriges-klimat-1.6867

Smith, R.J., Benavides, J.C., Jovan, S., Amacher, M. & McCune, B. (2015). A rapid method for landscape assessment of carbon storage and ecosystem function in moss and lichen ground layers. *The Bryologist.* 118(1). https://doi.org/10.1639/0007-2745-118.1.032

Sténs, A. & Mårald, E. (2020). “Forest property rights under attack”: Actors, networks and claims about forest ownership in the Swedish press 2014–2017. *Forest Policy and Economics.* 111. https://doi.org/10.1016/j.forpol.2019.102038

Sténs, A., Örjan, K. & Christer, N. (2011). Intensive Forestry as Progress or Decay? An Analysis of the Debate about Forest Fertilization in Sweden, 1960–2010. *Forests.* 2. https://doi.org/10.3390/f2010112

Sulyma, R. & Coxson, D.S. (2001). Microsite Displacement of Terrestrial Lichens by Feather Moss Mats in Late Seral Pine-Lichen Woodlands of North-Central British Columbia. *The Bryologist.* 104(4), 505-516. http://www.jstor.org/stable/3244583

Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A. & Austin, K.A. (1999). Plant diversity in managed forests: understory responses to thinning and fertilization. *Ecological Applications.* 9(3), 864-879.

Thysell, D. & Carey, A. (2000). Effects of Forest Management on Understory and Overstory Vegetation: A Retrospective Study. *USDA Forest Service - General Technical Report PNW.*

Tinya, F., Márialigeti, S., Németh, B. & Ódor, P. (2009). The effect of light conditions on herbs, bryophytes and seedlings of temperate mixed forests in Orseg, Western Hungary. *Plant Ecol.* 204, 69-81. https://doi.org/10.1007/s11258-008-9566-z

UNFCCC (1998). *KYOTO PROTOCOL TO THE UNITED NATIONS FRAMEWORK CONVENTION ON CLIMATE CHANGE* Kyoto, Japan: United Nations. https://unfccc.int/resource/docs/convkp/kpeng.pdf [24/03/2021].

UNFCCC (2015). *Paris Agreement*. Paris, France: United Nations. https://unfccc.int/sites/default/files/english_paris_agreement.pdf [24/03/2021].

Uri, V., Varik, M., Aosaar, J., Kanal, A., Kukumägi, M. & Lõhmus, K. (2012). Biomass production and carbon sequestration in a fertile silver birch (Betula pendula Roth) forest chronosequence. *Forest Ecology and Management*, 267. 117-126.

Verburg, P., Van Dam, D., Hefting, M. & Tietema, A. (1999). Microbial transformations of C and N in a boreal forest floor as affected by temperature. *Plant and Soil.* 208(2), 187-197.

Virtanen, R., Eskelinen, A. & Harrison, S. (2017). Comparing the responses of bryophytes and short-statured vascular plants to climate shifts and eutrophication. *Functional Ecology*. 31(4), 946-954. https://doi.org/https://doi.org/10.1111/1365-2435.12788

Wagner, S., Fischer, H. & Huth, F. (2011). Canopy effects on vegetation caused by harvesting and regeneration treatments. *European Journal of Forest Research.* 130(1), 17-40. https://doi.org/10.1007/s10342-010-0378-z

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B., Epstein, H.E., Jónsdóttir, I.S., Klein, J.A., Magnússon, B., Molau, U., Oberbauer, S.F., Rewa, S.P., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, Ø., Turner, P.L., Tweedie, C.E., Webber, P.J. & Wookey, P.A. (2006). Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, 103(5). 1342-1346. https://doi.org/10.1073/pnas.0503198103

Wardle, D.A., Jonsson, M., Bansal, S., Bardgett, R.D., Gundale, M.J. & Metcalfe, D.B. (2012). Linking vegetation change, carbon sequestration and biodiversity: insights from island ecosystems in a long-term natural experiment. *Journal of Ecology*, 100(1), 16-30. https://doi.org/https://doi.org/10.1111/j.1365-2745.2011.01907.x

Waring, R. & Running, S. (2007). CHAPTER 9. The Role of Forests in Global Ecology. In. https://doi.org/10.1016/B978-012370605-8.50016-5

Weibull, H. (2001). Influence of tree species on the epilithic bryophyte flora in deciduous forests of Sweden. *Journal of Bryology*, 23(1), 55-66. https://doi.org/10.1179/jbr.2001.23.1.55

Weisberg, P., Hadorn, C. & Bugmann, H. (2003). Predicting Understorey Vegetation Cover from Overstorey Attributes in Two Temperate Mountain Forests. *Forstwissenschaftliches Centralblatt*, 122, 273-286. https://doi.org/10.1007/s10342-003-0004-4

West, J.J., Smith, S.J., Silva, R.A., Naik, V., Zhang, Y., Adelman, Z., Fry, M.M., Anenberg, S., Horowitz, L.W. & Lamarque, J.-F. (2013). Co-benefits of mitigating global greenhouse gas emissions for future air quality and human health. *Nature Climate Change*, 3(10), 885-889. https://doi.org/10.1038/nclimate2009

Wickland, K.P., Neff, J.C. & Aiken, G.R. (2007). Dissolved Organic Carbon in Alaskan Boreal Forest: Sources, Chemical Characteristics, and Biodegradability. *Ecosystems*, 10(8), 1323-1340. https://doi.org/10.1007/s10021-007-9101-4

Wilson, D.S. & Puettmann, K.J. (2007). Density management and biodiversity in young Douglas-fir forests: challenges of managing across scales. *Forest Ecology and Management*, 246(1), 123-134.

Wood, S.N. (2017). *Generalized additive models: an introduction with R*. CRC press.

Acknowledgements

The completion of this study would not have been possible without my supervisor, Per-Ola Hedwall, who provided much-needed support and knowledge throughout this process. I would also like to thank Jonas Dahlgren at the department of forest resource management in the division of forest research data at SLU for providing the NFI data and being available to answer any questions. Much appreciation also to Jörg Brunet for his valuable input on a previous draft of this document.

5. Appendix 1

5.1. Model Outputs

5.1.1. Partial Regression Plots

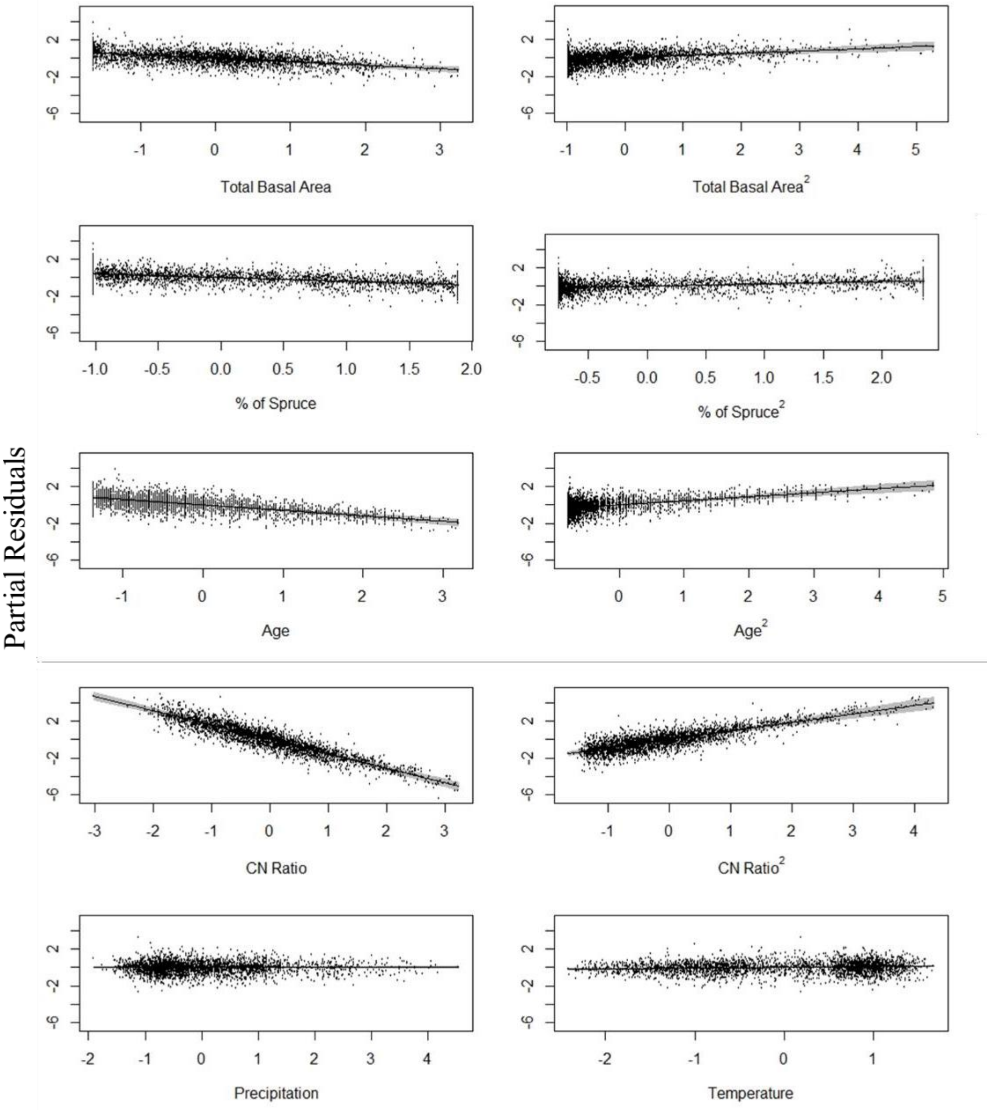


Figure 10: Partial residual plots for graminoid model

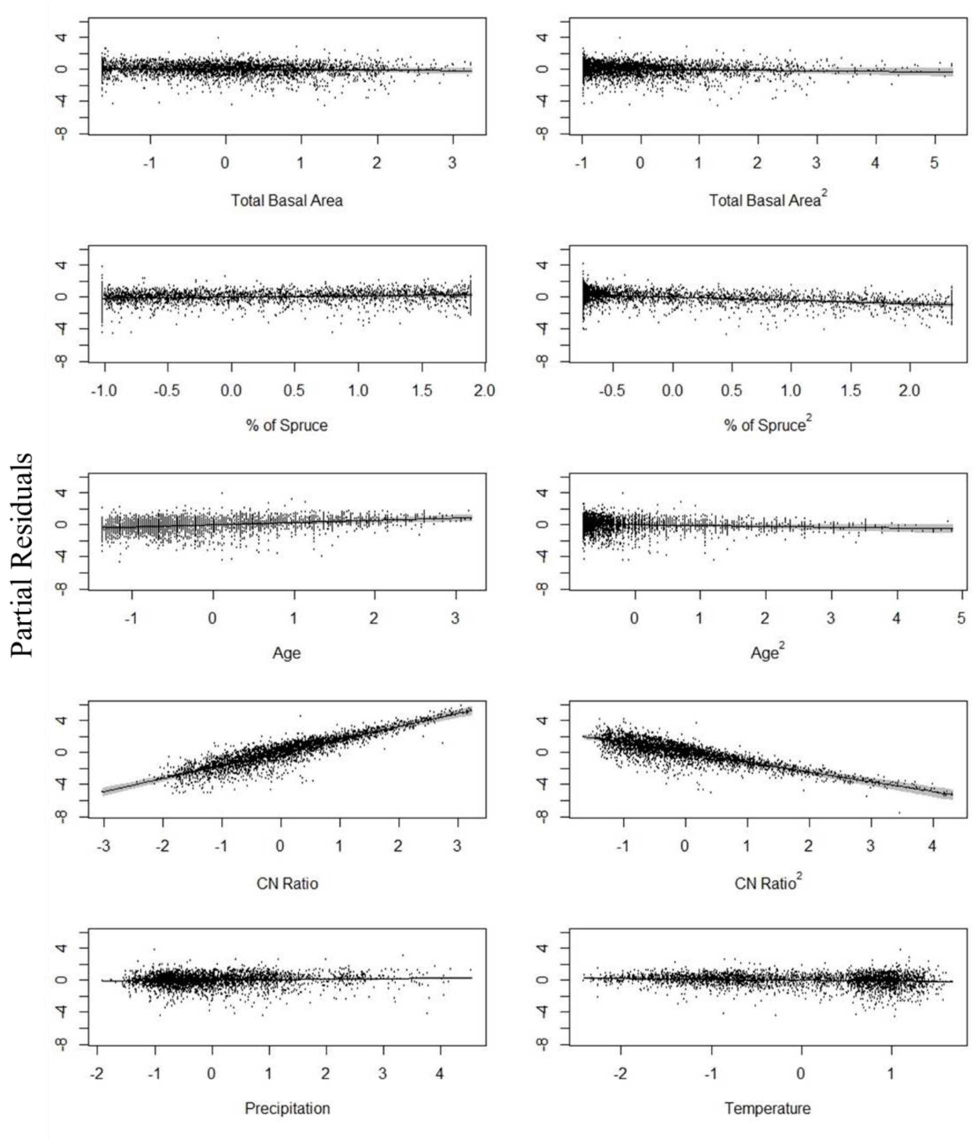


Figure 11: Partial residual plots for dwarf shrub model

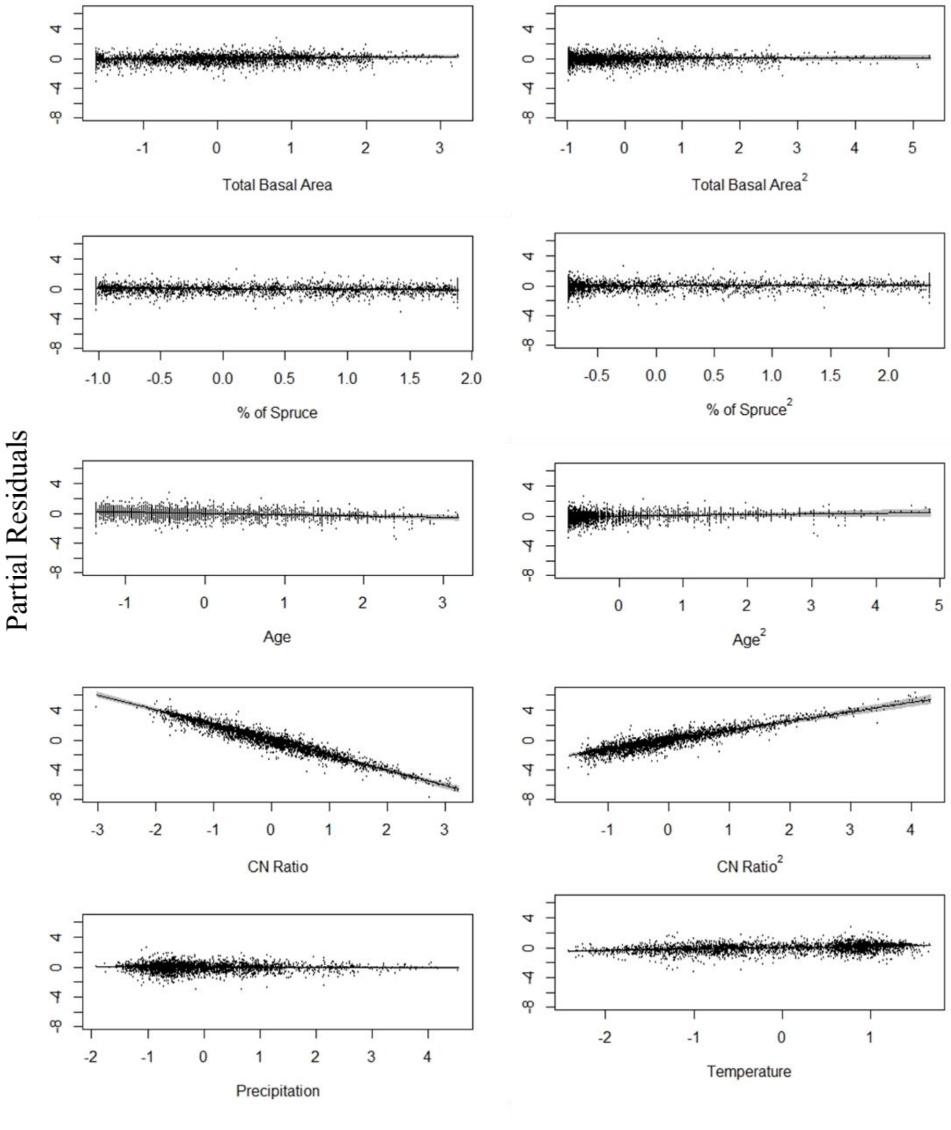


Figure 12: Partial residual plots for forb model

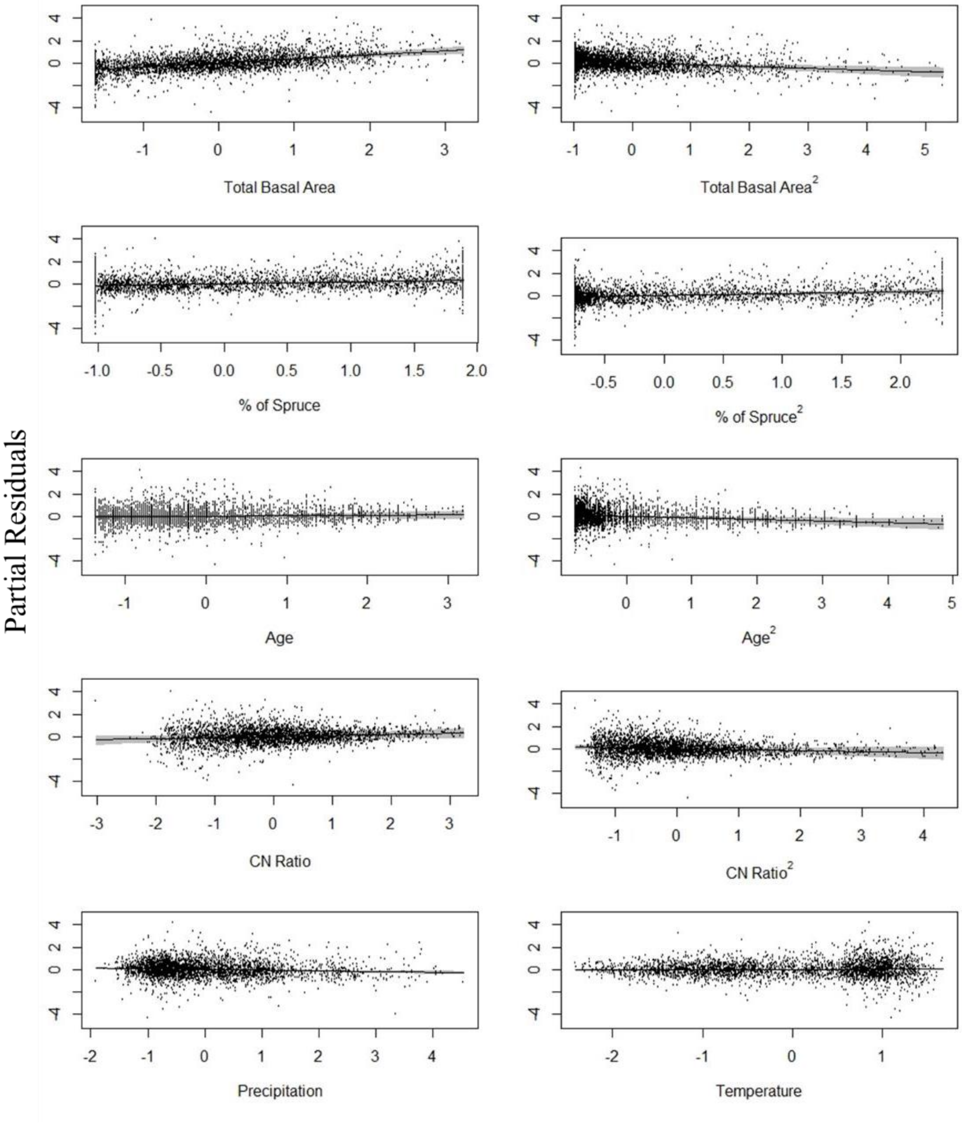


Figure 13: Partial residual plots for bryophyte model

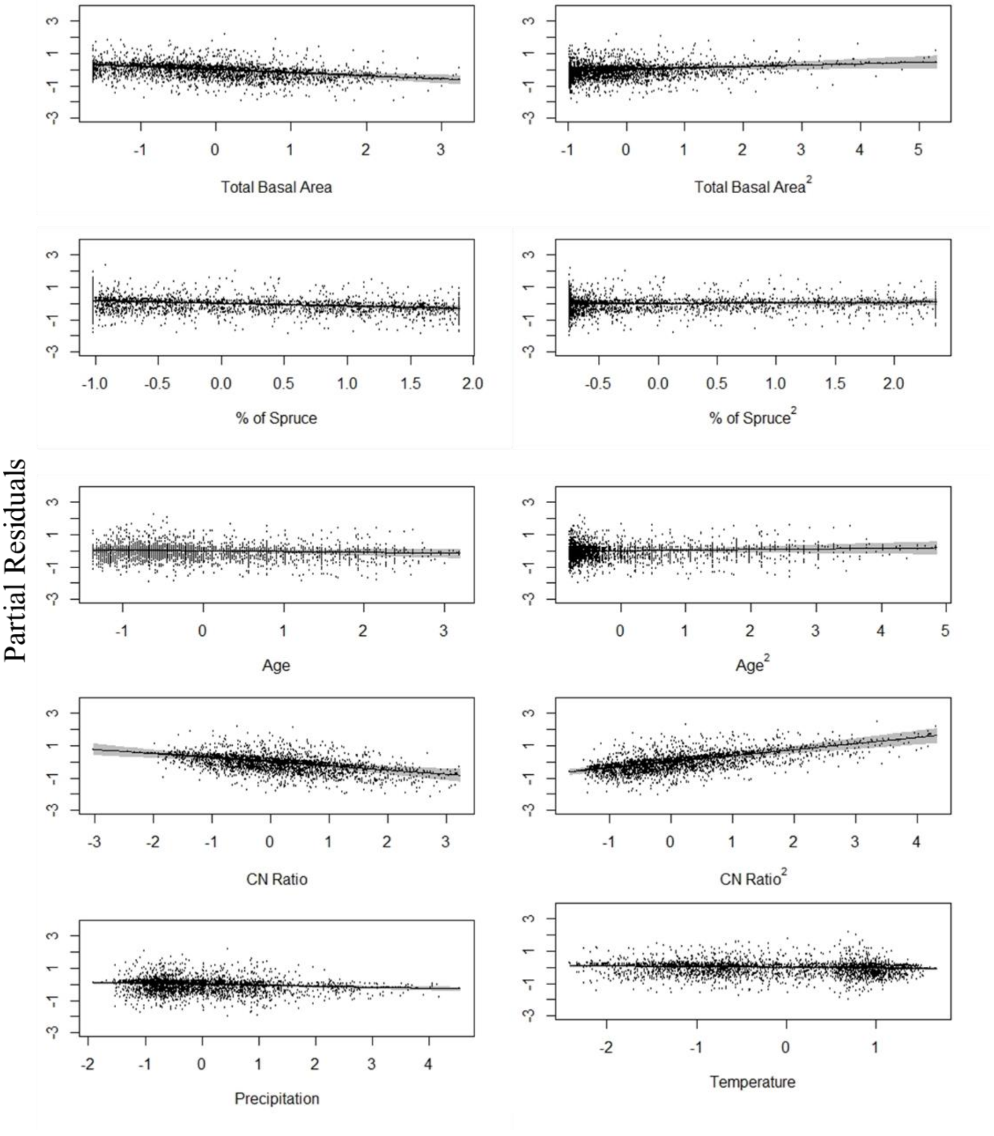


Figure 14: Partial residual plots for lichen model

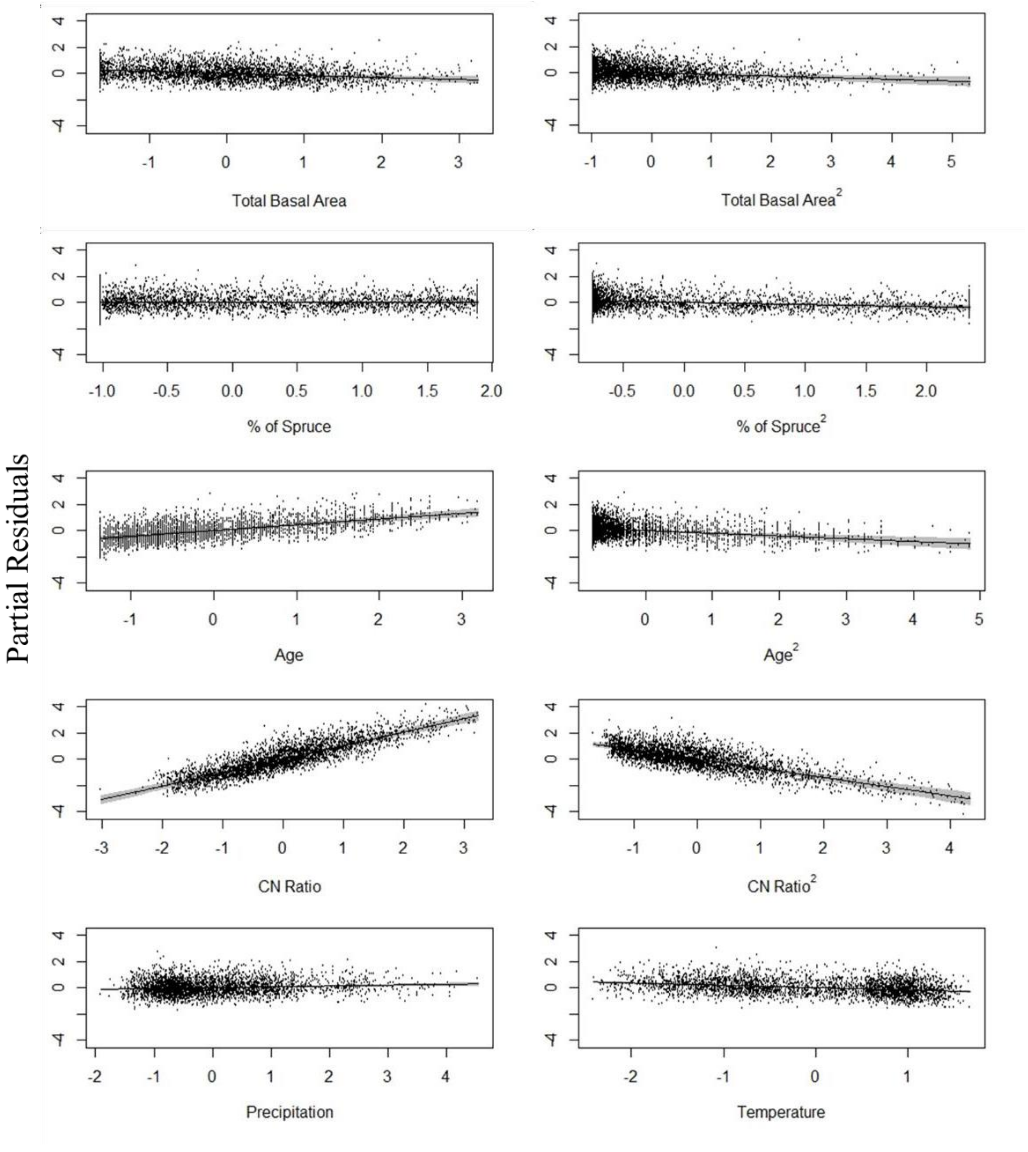


Figure 15: Partial residual plots for total understory carbon model

5.1.2. Model Summaries

Total Understory Carbon

Table 1: Model outputs of coefficients and corresponding statistics for the standardized total understory carbon response variable.

Variable	Estimate	Std. Error	T value	P value
Intercept	0.00	0.01	0.00	1.000
Basal Area	-0.16	0.04	-4.07	<.001
Basal Area ^{2}	-0.13	0.03	-3.81	<.001
% Spruce	0.02	0.04	0.48	0.632
% Spruce ^{2}	-0.16	0.04	-4.35	<.001
Age	0.44	0.04	9.84	<.001
Age ^{2}	-0.21	0.04	-5.19	<.001
CN ratio	1.03	0.05	19.45	<.001
CN ratio ^{2}	-0.70	0.05	-13.30	<.001
Temperature	-0.18	0.01	-14.09	<.001
Precipitation	0.06	0.01	5.85	<.001

Graminoids

Table 2: Binary (Nu) and nonbinary (Mu) model outputs of coefficients and corresponding statistics for the standardized carbon proportion in graminoids response variable.

Variable	Estimate	Std. Error	T value	P value
Mu Coefficients				
Intercept	-2.10	0.02	-131.80	<.001
Basal Area	-0.38	0.05	-8.35	<.001
Basal Area ^{2}	0.24	0.04	6.03	<.001
% Spruce	-0.40	0.05	-8.31	<.001
% Spruce ^{2}	0.25	0.05	5.24	<.001
Age	-0.59	0.06	-10.56	<.001
Age ^{2}	0.44	0.05	8.29	<.001
CN ratio	-1.57	0.07	-23.26	<.001
CN ratio ^{2}	0.92	0.07	12.68	<.001
Temperature	0.09	0.02	5.31	<.001
Precipitation	-0.00	0.01	-0.01	0.99
Nu Coefficients				
Intercept	-3.82	0.15	-26.21	<.001
Basal Area	0.63	0.15	4.06	<.001
% Spruce	-0.77	0.15	-5.23	<.001
Age	1.15	0.14	8.17	<.001
CN ratio	0.79	0.14	5.57	<.001
Temperature	0.72	0.16	4.67	<.001
Precipitation	-0.05	0.15	-0.33	0.75

Dwarf Shrubs

Table 3: Binary (Nu) and nonbinary (Mu) model outputs of coefficients and corresponding statistics for the standardized carbon proportion in dwarf shrubs response variable.

Variable	Estimate	Std. Error	T value	P value
Mu Coefficients				
Intercept	-0.59	0.01	-43.76	<.001
Basal Area	-0.05	0.05	-0.97	0.330
Basal Area ^{2}	-0.06	0.05	-1.35	0.176
% Spruce	0.15	0.05	2.98	0.003
% Spruce ^{2}	-0.41	0.05	-8.11	<.001
Age	0.28	0.06	4.75	<.001
Age ^{2}	-0.10	0.05	-1.88	0.061
CN ratio	1.62	0.08	20.96	<.001
CN ratio ^{2}	-1.22	0.07	-16.47	<.001
Temperature	-0.11	0.02	-6.89	<.001
Precipitation	0.06	0.0	4.25	<.001
Nu Coefficients				
Intercept	-7.19	0.42	-17.129	<.001
Basal Area	0.55	0.22	2.493	0.013
% Spruce	-0.22	0.19	-1.180	0.238
Age	-0.91	0.33	-2.764	0.006
CN ratio	-3.16	0.30	-10.468	<.001
Temperature	1.01	0.29	3.526	<.001
Precipitation	-0.34	0.19	-1.822	0.069

Forbs

Table 4: Binary (Nu) and nonbinary (Mu) model outputs of coefficients and corresponding statistics for the standardized carbon proportion in forbs response variable.

Variable	Estimate	Std. Error	T value	P value
Mu Coefficients				
Intercept	-4.25	0.01	-323.35	<.001
Basal Area	0.08	0.04	2.08	0.038
Basal Area ^{2}	0.02	0.03	0.71	0.479
% Spruce	-0.07	0.04	-1.72	0.086
% Spruce ^{2}	0.04	0.04	0.98	0.329
Age	-0.18	0.05	-3.68	<.001
Age ^{2}	0.09	0.05	1.99	0.047
CN ratio	-2.03	0.06	-34.59	<.001
CN ratio ^{2}	1.26	0.07	19.06	<.001
Temperature	0.19	0.01	14.10	<.001
Precipitation	-0.01	0.01	-0.88	0.379
Nu Coefficients				
Intercept	-2.43	0.09	-28.29	<.001
Basal Area	0.31	0.10	3.15	0.002
% Spruce	-0.25	0.09	-2.86	0.004
Age	0.40	0.09	4.31	<.001
CN ratio	1.11	0.09	11.83	<.001
Temperature	0.42	0.11	3.91	<.001
Precipitation	0.52	0.08	6.15	<.001

Bryophytes

Table 5: Binary (Nu) and nonbinary (Mu) model outputs of coefficients and corresponding statistics for the standardized carbon proportion in bryophytes response variable.

Variable	Estimate	Std. Error	T value	P value
Mu Coefficients				
Intercept	-0.21	0.01	-17.63	<.001
Basal Area	0.36	0.05	7.88	<.001
Basal Area ^{2}	-0.16	0.04	-4.00	<.001
% Spruce	0.16	0.05	3.54	<.001
% Spruce ^{2}	0.16	0.04	3.68	<.001
Age	0.04	0.05	0.76	0.447
Age ^{2}	-0.14	0.05	-2.97	0.003
CN ratio	0.10	0.06	1.54	0.123
CN ratio ^{2}	-0.09	0.06	-1.39	0.165
Temperature	0.02	0.02	1.53	0.126
Precipitation	-0.06	0.01	-4.85	<.001
Nu Coefficients				
Intercept	-69.14	557.99	-0.12	0.901
Basal Area	-17.65	347.19	-0.05	0.959
% Spruce	2.78	365.32	0.01	0.994
Age	1.77	419.90	0.00	0.997
CN ratio	-32.66	311.67	-0.11	0.917
Temperature	-3.98	183.28	-0.02	0.983
Precipitation	-0.37	197.76	-0.00	0.999

Lichens

Table 6: Binary (Nu) and nonbinary (Mu) model outputs of coefficients and corresponding statistics for the standardized carbon proportion in lichens response variable.

Variable	Estimate	Std. Error	T value	P value
Mu Coefficients				
Intercept	-3.46	0.01	-305.37	<.001
Basal Area	-0.19	0.04	-4.85	<.001
Basal Area ^{2}	0.09	0.04	2.53	0.011
% Spruce	-0.16	0.04	-4.21	<.001
% Spruce ^{2}	0.03	0.04	0.85	0.396
Age	-0.05	0.04	-1.08	0.281
Age ^{2}	0.04	0.04	1.03	0.303
CN ratio	-0.26	0.06	-4.58	<.001
CN ratio ^{2}	0.38	0.05	7.43	<.001
Temperature	-0.04	0.01	-3.32	0.001
Precipitation	-0.06	0.01	-5.17	<.001
Nu Coefficients				
Intercept	-1.37	0.06	-24.60	<.001
Basal Area	0.10	0.06	1.67	0.096
% Spruce	-0.03	0.05	-0.57	0.567
Age	0.16	0.07	2.33	0.020
CN ratio	-1.14	0.07	-16.61	<.001
Temperature	0.27	0.07	4.11	<.001
Precipitation	-0.08	0.05	-1.57	0.117

5.2. Morans.I

Table 7: Results of Morans.I tests for each model to ensure absence of spatial autocorrelation.

	Statistic	Expectation	Variance	Std. Deviate	P-value
Total Carbon	-0.14	-0.00	0.00	-6.30	1.000
Graminoids	-0.38	-0.00	0.00	-16.61	1.000
Forbs	-0.54	-0.00	0.00	-23.70	1.000
Dwarf Shrubs	-0.12	-0.00	0.00	-5.48	1.000
Bryophytes	-0.06	-0.00	0.00	-2.64	0.996
Lichens	-0.50	-0.00	0.00	-22.06	1.000