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Variable soil carbon stocks across fine spatial scales in a natural boreal forest landscape

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Abstract

Boreal forests, and especially boreal forest soils, are of considerable importance in global carbon dynamics and climate regulation. There are several studies that have modelled and quantified boreal soil carbon stocks, but we still lack knowledge about how much the size of these stocks varies across fine spatial scales, and the factors controlling this variation. Identifying these factors are crucial to understand and predict how global change might affect the forest's role as a carbon source or sink. Here, I quantify carbon stocks, investigate their spatial variability, and make an attempt to identify the factors that control soil carbon content in a natural boreal forest landscape located in the Trillemarka – Rollagsfjell nature reserve, SE Norway. My study is based on the analysis of 189 organic top soil profiles that were collected by a regular grid approach within a 0.1 km² forest area. Dominant forest ground vegetation, topography, tree basal area, nitrogen percent, and fire history (years since last fire and fire frequency) were tested as explanatory variables for soil carbon content, soil depth and soil nitrogen content. I also investigated drivers of carbon- and nitrogen concentrations, C:N-ratios, and soil bulk densities.

My results showed large variations in soil carbon contents, ranging from 1.4 to 96.5 kg m⁻². Similarly, I found large variations in soil depths and soil nitrogen contents. *Sphagnum*-dominated plots had the highest carbon content, and lichen-dominated plots the lowest. Generally, dominant bottom vegetation was important for explaining the fine-scale variation in carbon content. There was a negative relationship between soil carbon content and C:N-ratio, while the relationship was positive between carbon content and nitrogen concentration. Tree species composition and basal area also explained some variation in carbon content, but contrary with our expectations, spruce and pine basal area had a negative relationship with carbon content, while deciduous basal area had a positive relationship with carbon content. This implies that dominant ground vegetation and the associated soil properties might be of higher importance. I found no impact of fire history on soil carbon content.

My thesis highlights the importance of considering spatial scales when investigating carbon stocks. In addition, I emphasize that including several explanatory variables is necessary to obtain reliable estimates and sufficient understanding of boreal soil carbon dynamics.

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1. Introduction

Boreal forests contain approximately one third of the global carbon stored in forests worldwide, which roughly corresponds to the amount stored in tropical forests (Pan et al., 2011). However, and in contrast to tropical forests, the majority of carbon stored in boreal forests is located in the soil. In fact, as much as 60-84% of the boreal forest carbon is stored in the soil (Pan et al., 2011, Malhi et al., 1999), which implies that boreal forest soil organic carbon stocks per unit area are more than twice as large as those in tropical and temperate forests (Lal, 2005). This, combined with the large area of boreal forests, implies that forest soils in the boreal region are of fundamental importance for the global carbon balance.

At a global scale, the amount of carbon stored in organic soil is dependent on temperature and precipitation. Generally, carbon pools increase with precipitation and decrease with temperature, due to differences in productivity and respiration. High latitude areas (e.g., boreal forests) are therefore especially important, as low temperature and wet/anaerobic soil conditions inhibit litter decomposition (Lal, 2005). At a regional scale, elevation is often used as an indicator of soil carbon stocks instead (Wiesmeier et al., 2019). Soil moisture also plays an important role in the accumulation of organic matter in soils, as it controls ecosystem productivity and thus input of organic matter and carbon, but also carbon losses through heterotrophic respiration (Wiesmeier et al., 2019; De Nicola et al., 2014).

Although there are several estimates of soil organic carbon stocks in boreal areas (see e.g., Baritz et al., 2010, and references therein), there are still large uncertainties on the general mechanics controlling the spatial distribution in soil carbon stocks (Zhou et al., 2019). Across the boreal forest, there is, for example, large variability in productivity and decomposition rates, which could be explained by variability in biological, chemical, physical, and environmental factors. Such factors include vegetation type and tree species composition (Liski and Westman, 1995; Schulp et al., 2008), soil properties (Calleesen et al., 2003), climatic conditions (Kirschbaum, 2000; Liski and Westman, 1997), stand age (Kolari et al., 2004), topography (Seibert et al., 2007) and management regimes (Schulp et al., 2008). Taken together, this indicates that there should be a correspondingly large variability in the size of the soil organic carbon pool, also across fine spatial scales (see e.g., Kristensen et al. 2015).

Vegetation controls soil carbon stock levels through differences in productivity and biomass production. In addition, vegetation also controls carbon stocks through differences in litter quality, which is considered a more important controlling agent than biomass production (Marty

et al., 2015). Certain plant species (e.g., crowberry, *Empetrum nigrum*) can also inhibit seed germination, seedling survival, and root elongation in other species through allelopathy (Zackrisson & Nilsson, 1992; Gonzáles et al., 2015), and therefore affect productivity. Numerous studies have shown larger carbon pools in the forest floor under conifers than under deciduous tree species, both due to their high litter production and their recalcitrant litter (Wiesmeier et al., 2019; Strand et al., 2016; Marty et al., 2015., Hansson et al., 2013). In addition, there are feedback effects, so systems with lower productivity support resource conservative plants, that also have lower litter quality, and systems with higher productivity favor resource acquisitive plants with higher litter quality.

Management- and disturbance regime also influence the soil carbon stock. Generally, disturbances (e.g., forest fires, clearcuttings) have a negative effect on the amount of carbon stored in the organic soil layer through removal of live biomass, increased decomposition, and strict limitation of carbon sequestration immediately after a disturbance (Thom & Seidl, 2016). However, there are examples of studies showing a positive effect of disturbance (both fire and clearcutting) on carbon accumulation (Chen & Shrestha, 2012). A positive effect could for example be explained by enhanced growth (Blanck et al., 2013), and thus increased carbon sequestration, in the decades following a disturbance. In a boreal forest in Ontario, Canada, soil carbon stocks peaked between 29 and 140 years after a disturbance, and then declined to a lower level the following decades (Chen & Shrestha, 2012). This suggests that both the direct disturbance-related losses of carbon, and the effect of enhanced growth after a disturbance, must be considered when assessing disturbance effects on soil carbon.

Forest fires are a natural disturbance and have been of large importance in the boreal forest, although some boreal forest types are less prone to fire than others (see e.g., Ohlson et al., 2009 and references therein). Fires can also be of anthropogenic origin, and such fires have been important in our study area (Rolstad et al., 2017). Fires release large amounts of CO₂ to the atmosphere, but also converts a small proportion of biomass to charcoal – approximately 1-3% (Preston & Schmidt, 2006), which is an important part of the slow cycling fraction of the soil carbon pool. In addition, charcoal has an important ecological function through its adsorptive abilities and could play an important role in soil rejuvenation (Zackrisson et al. 1996).

The aim of this study was to assess the spatial variation in boreal forest soil organic carbon content at a fine spatial scale, and to investigate the drivers of this variation. I selected two sites with varying fire history in a nature reserve in the south-eastern part of Norway. Using organic

soil samples, I investigated carbon- and nitrogen stocks and tried to determine the drivers of soil carbon content. Carbon content in the organic soil is highly correlated with organic soil depth and bulk density (Conforti et al. 2016). I therefore investigate both carbon content, bulk density, and soil depth. In addition, I investigate nitrogen content and carbon to nitrogen-ratio (C:N-ratio) in the organic soil layer.

I hypothesize that there is high variability in soil carbon content on a fine spatial scale. Specifically, I predict: (1) More recently burned and more frequently burned areas have a lower carbon content than areas burned a long time ago or less often. I expect soil depth to be shallower in areas with frequent disturbance. (2) Areas dominated by peat mosses and other vegetation favored by wet conditions contain more carbon, and deeper soil, than dry, lichen dominated plots, as anaerobic condition limit decomposition. Differences in litter quality could also affect carbon concentrations and C:N-ratio. (3) Spruce and pine has a positive relationship with soil depth and carbon content, and a negative relationship with nitrogen content, due to recalcitrant litter and high litter inputs. Deciduous tree species have a negative relationship with soil depth and carbon content, and a positive relationship with nitrogen content. (4) Convex curvatures have higher water and nutrient discharge than flat and concave curvatures, which favor water and nutrient accumulation, leading to higher carbon content in flat and concave plots.

Assessing the variation in carbon storage in soil is important in a global change perspective, and there is still lack of agreement on the main mechanisms controlling soil carbon content in boreal forests. Identifying the most important factors controlling the variation in carbon in boreal forest soils will be important to understand and predict how global change might affect the forest's role as a carbon source or sink.

2. Materials and methods

2.1 Study area

The study area is located in Trillemarka – Rollagsfjell nature reserve (60°05'N, 9°13'E, elevational range: 400-550 m a.s.l.), situated in SE Norway, Viken county, spanning between the municipalities of Rollag, Nore og Uvdal, and Sigdal (fig. 1). The reserve was established in 2002, enlarged in 2008, and covers a total area of 156 km² (Anon. 2008). It is one of the few remaining large, forested areas within the boreal zone of southwestern Fennoscandia that is relatively undisturbed by modern forestry and technical developments (Hofton 2003, Rolstad et al., 2017).

The climate in Trillemarka – Rollagsfjell is intermediate continental to oceanic, and the vegetation is representative of the mid-northern boreal zone (Moen, 1999). Monthly average temperatures range from -7°C in January to 17°C in July, and mean annual precipitation is approximately 800 mm (all weather data retrieved from seklima.met.no). Snow usually covers the ground from October to May, with high spatial variability due to the topography and range in elevation (Storaunet et al., 2013).

The landscape is varied, with north-south extending ridges of Precambrian rocks consisting of granite and gneiss. Thickness of morainic deposits varies greatly and impacts vegetation productivity. Scots pine (*Pinus sylvestris*) dominate the areas with low productivity (i.e., areas with thin morainic deposits), while Norway spruce (*Picea abies*) are more prevalent in more productive slopes (i.e., areas with thicker morainic deposits). Deciduous tree species, like downy birch (*Betula pubescens*), grey alder (*Alnus incana*), European aspen (*Populus tremula*), and rowan (*Sorbus aucuparia*) occur sparsely. In areas with low productivity, the field layer is dominated by the common heather (*Calluna vulgaris*) – bog bilberry (*Vaccinium uliginosum*) type, with patches of lingonberry (*Vaccinium vitis-idaea*) and crowberry (*Empetrum nigrum*), while bilberry (*Vaccinium myrtillus*) dominates the field layer in more productive areas (Castagneri et al., 2013). Nomenclature for plants follow Lid and Lid (2005) and Hallingbäck (2016).

Trillemarka is only little influenced by modern technical developments and large-scale forestry. However, there are signs that the area has been influenced by humans for centuries, and local historical records confirm this (Trønnes, 2012). Historic anthropogenic influences include summer dairy farming, grazing by domestic animals, slash-and-burn cultivation, and selective logging. Rolstad et al. (2017) have documented changes in fire regimes, including changes in

seasonality of fires and fire frequencies, which both indicate human activity. Both the arrival of local water-powered sawmills and the silver mines in Kongsberg increased the demand for timber and led to escalated logging in the area (Trønnnes, 2012). While there are many remaining traces of human activity, the reserve consists of old natural forests with high species diversity and rare nature types. Much value is attributed to its large size and hot spots for biodiversity (Bendiksen, 2004).

I selected sites for soil sampling located within an area with known fire history. Here, Rolstad et al. (2017) collected 745 fire scars in 378 remnants of Scots pine, where they determined fire sizes, numbers, burn rates and fire frequencies over the past 700 years. Their study area covers 38.6 km² of the southern section of Trillemarka. To assess if soil organic carbon content varied with local fire history, I selected two sites in proximity to each other (from here on: S1 and S2), that included areas with high and low fire frequencies (fire numbers ranging from 3 to 10), and with varying time passed since last fire (ranging from 195 to 368 years since most recent recorded fire). Both S1 and S2 were located near Heimseteråsen (fig.1).

The sites cover a heterogeneous area with patches of productive spruce-dominated hills, less productive pine-dominated plateaus, and small patches of mire and deciduous tree species. In total, my sites covered an area of approximately 0.1 km². The sites were divided into 94 (S1) and 101 (S2) quadrats, using a 24 m × 24 m grid in QGIS, avoiding quadrats that were clearly located in lakes, streams, and mires. Plots were then placed in the center of each quadrat, where soil collection would take place. The two sites were divided into transects going from west to east.

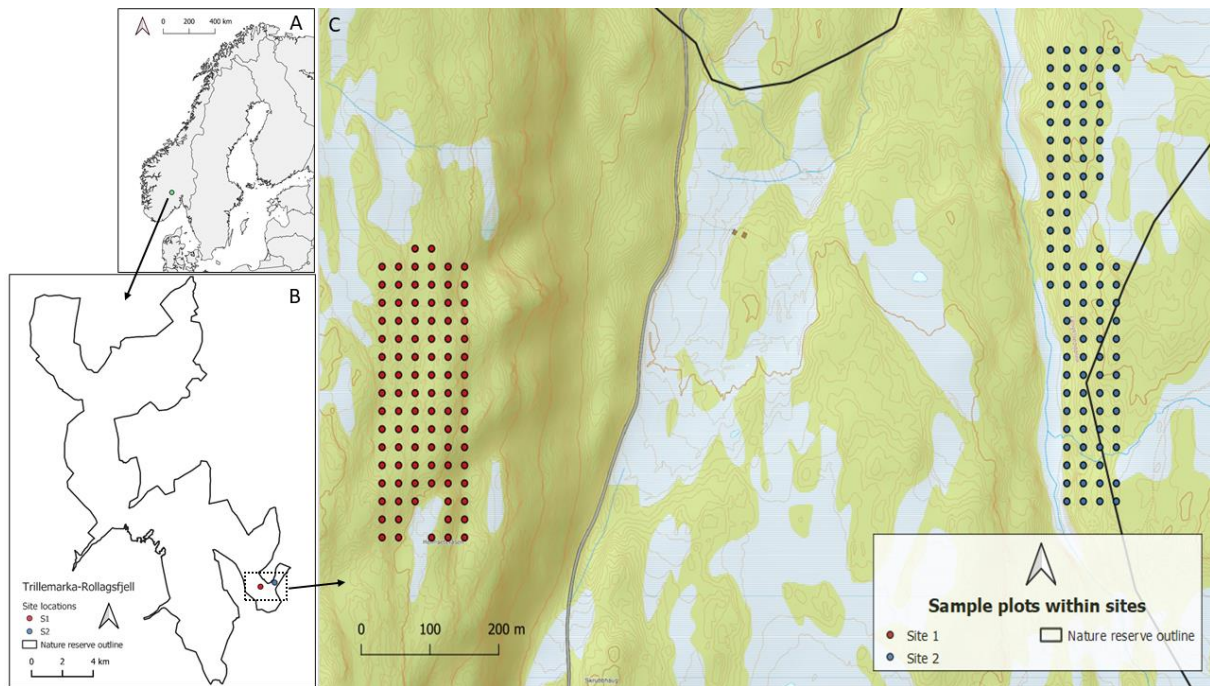


Figure 1: A) Location. Map made in QGIS with Natural Earth (naturalearthdata.com). B): Nature reserve outline. Red and blue dots represent study sites. Map made in QGIS with data from Miljødirektoratet. C): Sample plots in Site 1 and Site 2. Map made in QGIS with data from Kartverket.

2.2 Data collection

Soil samples were collected in September and October 2020. I outlined each plot using a 50 cm × 50 cm steel frame. I collected soil from the organic horizon, and the upper part of the mineral horizon, by using a cylindrical soil auger with an inner diameter of 5.8 cm. Green vegetation was carefully removed from the top of the sample, but roots were left in the soil. Although roots are part of the vegetation, they are also an important part of carbon dynamics in the organic soil layer. I then divided the soil cylinder into mineral and organic soil (fig. 2).

In each plot, I also recorded dominant vegetation, organic soil depth, topography, slope, and used a relascope (factor 1) to estimate basal tree area for Scots pine, Norway spruce and deciduous tree species. Each plot was also photographed, and dominant bottom-layer vegetation (from here on dominant bottom vegetation) was later retrieved from those images. These were divided into three categories: Peat mosses (*Sphagnum sp.*), feather mosses (mainly *Pleurozium schreberi* and *Hylocomium splendens*), and lichens, according to the most dominating group below the field-layer vegetation (fig. 2). Feather mosses are referred to as Hypnales from here on.

If sampling was unsuccessful due to obstacles in the soil (large stones or roots), or if there was less than 5 cm organic soil over bedrock, I relocated the steel frame (starting one meter north and moving clockwise until a soil sample was successfully obtained). Where sampling was still unsuccessful, I still measured and recorded dominant vegetation, soil depth, topography, slope, and tree basal area.



Figure 2: Left: Example of a sample plot. This plot was determined to be dominated by *Vaccinium vitis-idaea*. Dominant bottom vegetation was determined to be feather mosses. **Right:** Example of soil sample. The transition from organic soil to mineral soil is visible at the bottom of the sample.

2.3 Sample- and data preparation

After returning to the lab, soil samples were stored in closed plastic bags at 4°C. Then, each soil sample was weighed and placed in paper bags. Subsequently, they were dried at 40°C for at least 72 hours, and then weighed again to obtain sample dry weight. The low temperature was used to ensure that the samples would be useful for possible tannin-analysis in the future and is not important for this study. Bulk density (BD g cm^{-3}) was subsequently calculated, by dividing the dry weight (g) with the soil sample's volume (cm^3).

Soil samples, including roots, were homogenized in two steps. First, either a Brabender grinder or a mechanic sieve was used to do the first round of homogenization. Second, a subsample of approximately one tablespoon was ran through another electrical grinder with a relatively fine mesh and put in separate paper bags. 4-6 mg of each subsample was then packed into individual tin containers. Analysis of total carbon and nitrogen (CN-analysis) was then performed by a Vario MICRO Cube analyzer (Elementar, Langensfeld, Hesse, Germany).

To obtain data from the “unsuccessful” sampling plots (8 plots), I estimated bulk density, carbon concentration, and nitrogen concentration. Estimations were attained by calculating mean values for the corresponding dominating vegetation types. In plots where organic soil depth was deeper than the soil auger (11 plots), I used bulk density and soil depth from the sample obtained to estimate total carbon- and nitrogen content.

Six samples had a conspicuously low carbon concentration (< 40%). I suspected that the samples contained mineral soil (clay or sand) due to sampling error when dividing the soil cylinders into mineral and organic soil. They were therefore tested again manually using loss on ignition (LOI). Six random samples with a carbon percentage close to the mean value were also tested and used as a control. Soil was weighed into individual crucibles and dried at 100°C overnight. Soil and crucibles were weighed again, and then placed in the calcinating oven. Samples were then calcinated at 550°C for 3 hours. The six samples had an apparent lower LOI than the control samples, and we chose to exclude them from further analysis.

Carbon and nitrogen content were calculated using the following formula:

$$\text{E-content (kg m}^{-2}\text{)} = (\text{Soil depth (cm)} \times \text{BD (g cm}^{-3}\text{)} \times \text{E-concentration (\%)}) \times 10,$$

where E-content is the volume-based stock of carbon or nitrogen, and E-concentration is obtained from the CN-analysis.

2.4 Statistical analyses

To investigate drivers of the spatial distribution of soil carbon and nitrogen, I used Kruskal-Wallis rank sum tests, analysis of variance (ANOVA), and mixed effect models. I worked with seven responses: carbon concentration, nitrogen concentration, C:N-ratio, bulk density, soil depth, carbon content, and nitrogen content. Explanatory variables included in this analysis were site, dominant bottom vegetation, topography, fire history (years since last fire and fire frequency), and tree basal area (both total, and pine, spruce, and deciduous individually). Dominant vegetation was also analyzed, but excluded from the results, as bottom layer vegetation was a simpler and more efficient explanatory variable.

Individual linear mixed effect models were fitted to determine if the explanatory variables fire history or tree basal area influenced the responses. Transect nested in site was added as random variable. To fulfill the assumptions of linear models, the responses were transformed by their natural logarithm (residual plots, fig. A4–A6).

To avoid response transformation, Kruskal-Wallis rank sum tests were used to determine if the explanatory factors site, topography, or bottom vegetation affected the responses. Significant relationships were tested again using pairwise Wilcoxon tests to compare groups and identify which were different from each other.

Full models were fitted for log-transformed carbon content, nitrogen content, and soil depth. Akaike information criterion (AIC) was used to rank models. The best fit was selected by following these steps: 1: Fitting a full model, including interaction terms. 2: Removing one explanatory factor at a time and checking AIC-values for full and reduced models. 3: Proceed with model corresponding to the lowest AIC-value. 4: Repeat step 2 and 3 until AIC stops declining. 5: Continue with the model that has the second lowest AIC and keep reducing factors until only one is left. 6: Check AIC-values for all fitted models and select the five lowest AICs. Full models included either total tree basal area, or pine, spruce, and deciduous basal area, not both. Estimated marginal means were calculated to assess differences between factors within fitted models.

All statistical analyses were performed in R version 1.4.1103. Models were fitted using the lmer function from the lme4 package (Bates et al., 2015). Full models were analyzed further using emmeans comparisons (Lenth, 2021). Other plots made with ggplot2 (Wickham, 2016).

3. Results

3.1 Distribution of carbon and nitrogen

Mean (\pm SE) carbon concentration for the entire study area was 47.5 (\pm 0.2)% and ranged from 40.3 to 53.2 % (see table 1 for summary). Both mean and variation were similar at the two sites, and there was no significant difference between the two. Mean nitrogen concentration was 1.2 (\pm 0.02) % and ranged from 0.5 to 1.9 %. C:N-ratio ranged from 25.8 to 89.7, with a mean value of 42.2 ± 0.7 . Mean bulk density for our study area was 0.1 ± 0.004 and ranged from 0.03 to 0.5 g cm^{-3} . There were no significant differences between sites for any of these parameters, according to performed Kruskal-Wallis tests (table A2).

Organic soil depth ranged from 2 to >110 cm. Mean soil depth was 22.4 ± 1.6 cm for the entire study area. Carbon content ranged from 1.4 to 96.5 kg m^{-2} and mean content was $9.6 \pm 0.9 \text{ kg m}^{-2}$. Only one plot had a higher carbon content than 60.5 kg m^{-2} (carbon distribution, fig. 3). Soil depth and soil carbon content was highly correlated ($r=0.82$). Nitrogen content ranged from 0.03 to 2.9 kg m^{-2} . Mean nitrogen content for the entire study area was $0.3 \pm 0.03 \text{ kg m}^{-2}$. Site generally explained a very small amount of the variation in soil depth, carbon content, and nitrogen content, and there was no significant difference between sites for either parameter (summary, table 1 and p-values, table A2).

Both soil depth and soil carbon content varied significantly with nitrogen concentration and C:N-ratio (fig. 4). There was a clear positive relationship with nitrogen concentration, which explained 15 % of the variation in soil depth, and 27 % of the variation in carbon content. Accordingly, there was a clear negative relationship with C:N-ratio, which explained 7 % and 18 % of the variation in soil depth and soil carbon content, respectively.

Table 1: C concentration, N concentration, C:N-ratio, bulk density, soil depth, C content, and N content (range, mean \pm SE, and 95 % confidence interval of mean). Total values for the entire study area, and site-specific values are presented.

	n (plots)	Range (min – max)	Mean \pm SE	95 % CI of mean
C %				
Total	189	40.3 – 53.2	47.5 \pm 0.2	47.2 – 47.9
S1	90	40.3 – 53.2	47.3 \pm 0.2	46.9 – 47.8
S2	99	41.4 – 51.0	47.7 \pm 0.2	47.3 – 48.1
N %				
Total	189	0.52 – 1.85	1.18 \pm 0.02	1.14 – 1.22
S1	90	0.52 – 1.83	1.19 \pm 0.03	1.14 – 1.24
S2	99	0.75 – 1.85	1.17 \pm 0.03	1.12 – 1.22
C:N				
Total	189	25.8 – 89.7	42.2 \pm 0.7	40.9 – 43.5
S1	90	26.6 – 89.7	41.6 \pm 1.0	39.6 – 43.7
S2	99	25.8 – 64.4	42.7 \pm 0.9	41.0 – 44.5
BD g cm⁻³				
Total	189	0.03 – 0.5	0.09 \pm 0.004	0.08 – 0.10
S1	90	0.03 – 0.5	0.10 \pm 0.007	0.09 – 0.11
S2	99	0.03 – 0.3	0.09 \pm 0.004	0.08 – 0.09
Soil depth cm				
Total	189	2 – 110	22.4 \pm 1.6	19.1 – 22.4
S1	90	4 – 110	24.4 \pm 2.7	19.1 – 29.7
S2	99	2 – 110	20.5 \pm 2.0	16.5 – 24.4
Total C kg m⁻²				
Total	189	1.4 – 96.5	9.6 \pm 0.9	7.9 – 11.3
S1	90	1.7 – 96.5	11.2 \pm 1.5	8.1 – 14.2
S2	99	1.4 – 52.8	8.2 \pm 0.9	6.5 – 9.9
Total N kg m⁻²				
Total	189	0.03 – 2.9	0.3 \pm 0.03	0.2 – 0.3
S1	90	0.05 – 2.9	0.3 \pm 0.05	0.2 – 0.4
S2	99	0.03 – 1.7	0.2 \pm 0.03	0.2 – 0.3

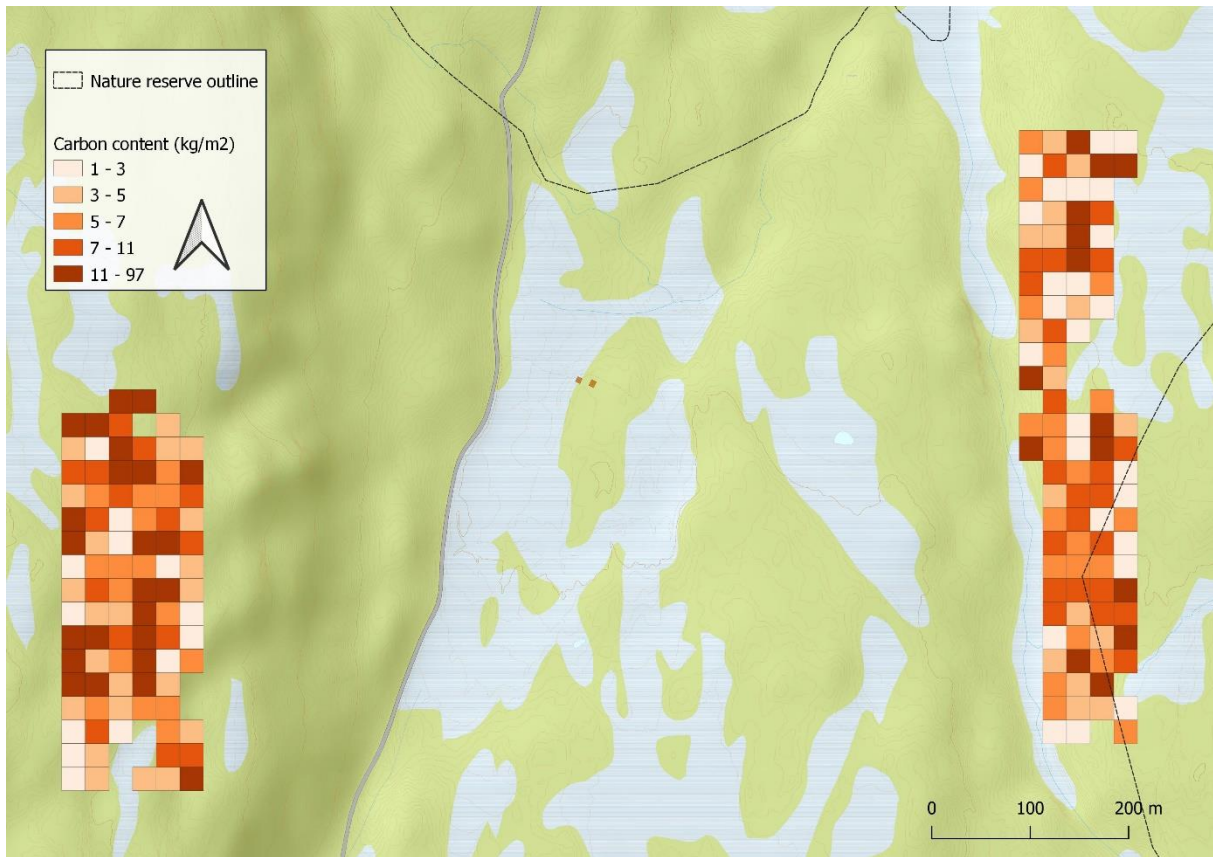


Figure 3. Map showing the spatial distribution of carbon content within S1 and S2. Carbon content divided into quantiles. Map made in QGIS with data from Kartverket.

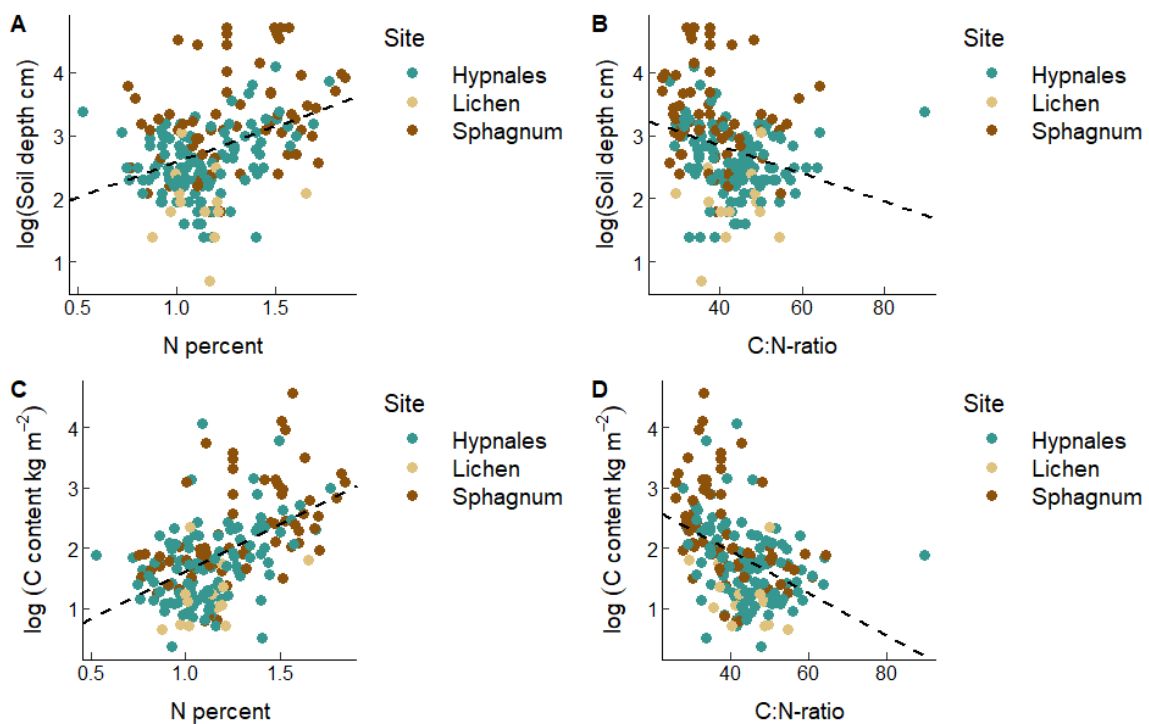


Figure 4: Relationships between **A)** soil depth and nitrogen percent, $\beta=1.1165$, $p=5.99e-08$, **B)** soil depth and C:N-ratio, $\beta=-0.02184$, $p=2e-16$, **C)** soil carbon content and nitrogen percent, $\beta=1.57140$, $p=1.27e-14$, **D)** soil carbon content and C:N-ratio, $\beta=-0.035169$, $p=1.71e-09$.

3.2 Drivers of carbon and nitrogen stocks

3.2.1 Complete models

All the best models included dominant bottom vegetation. The best model for soil depth included dominant bottom vegetation and nitrogen concentration. Topography and spruce basal area are included in several, while fire frequency is included exclusively in the fifth ranking model for soil depth. Fire frequency is still not significant in the model ($p = 0.378$). The best model for total organic soil carbon content included spruce basal area and nitrogen concentration, in addition to bottom vegetation. Two models, including the second best, also included pine basal area. Topography was included in one model. The best model for total nitrogen content included dominant bottom vegetation and deciduous basal area. Spruce basal area was also included in several models, while total tree basal area was included in one. Models for soil depth and carbon content are better at explaining the variation in the response than the models for nitrogen content, according to R^2m -values (marginal R^2) (top 5 models are summarized in Table 2).

Table 2: Top 5 models for log-transformed soil depth, carbon content and nitrogen content. Ranking according to AIC-value. Veg.bottom = Dominant bottom vegetation, N=Nitrogen, Topo=Topography, BA=Basal area, Decid=Deciduous.

Soil depth					
Rank	Model	df	AICc	Δ AICc	R^2m
1	Veg.bottom + N %	6	364	0	0.37
2	Veg.bottom + Topo + N %	8	367	3	0.38
3	Veg.bottom + Spruce BA + N %	7	367	3	0.38
4	Veg.bottom + Spruce BA + Topo + N %	9	370	5	0.40
5	Veg.bottom + Fire frequency + Topo + N %	9	372	8	0.38
Carbon content					
Rank	Model	df	AICc	Δ AICc	R^2m
1	Veg.bottom + Spruce BA + N %	7	374	0	0.40
2	Veg.bottom + Spruce BA + Pine BA + N %	8	375	1	0.42
3	Veg.bottom + N %	6	376	2	0.36
4	Veg.bottom + Spruce BA + Topo + N %	9	379	5	0.40
5	Veg.bottom + Spruce BA + Pine BA + N %	10	381	7	0.42
Nitrogen content					
Rank	Model	df	AICc	Δ AICc	R^2m
1	Veg.bottom + Decid BA	6	468	0	0.22
2	Veg.bottom	5	469	1	0.19
3	Veg.bottom + Spruce BA + Decid BA	7	470	2	0.24
4	Veg.bottom + Total tree BA	6	473	6	0.20
5	Veg.bottom + Spruce BA	6	473	6	0.20

In all five top ranked models for soil depth, all three bottom vegetation types had estimated marginal means different from each other. Sphagnum had the highest estimated marginal mean, while lichen had the lowest (table 3). There was no significant difference for topography where they are included in the models, except for in the fifth ranked model, where concave plots had a lower carbon content than flat plots. Concave and flat plots were close to significantly different in the second and fourth ranked model (comparison-plots, fig. A1).

Table 3: Comparisons of estimated marginal means between dominant bottom vegetation in the #1 ranked model for soil depth. Results are given on the log-scale.

Top ranked model for soil depth					
contrast	estimate	SE	df	t.ratio	p.value
Hypnales - Lichen	0.667	0.1792	183	3.722	0.0008
Hypnales - Sphagnum	-0.622	0.0995	185	-6.248	<.0001
Lichen - Sphagnum	-1.289	0.1875	184	-6.873	<.0001

Similarly, all five top ranked models for carbon content had estimated marginal means that were significantly different between all three vegetation types. *Sphagnum* had the highest estimated marginal mean and lichen had the lowest (table 4). There was no significant difference between topography classes in the model where this was included (comparison-plots, fig. A2).

Table 4: Comparisons of estimated marginal means between dominant bottom vegetation in the #1 ranked model for carbon content. Results are given on the log-scale.

Top ranked model for carbon content					
Contrast	estimate	SE	df	t.ratio	p.value
Hypnales – Lichen	0.617	0.183	183	3.374	0.0026
Hypnales – Sphagnum	-0.334	0.101	184	-3.312	0.0032
Lichen – Sphagnum	-0.951	0.189	184	-5.017	<.0001

In all five top ranked models for nitrogen content, *Sphagnum* had a significantly higher estimated marginal mean than Hypnales and lichen, while Hypnales and lichen were not significantly different from each other (Table 5). Topography was not included in any of the top models (comparison-plots, fig. A3).

Table 5: Comparisons of estimated marginal means between dominant bottom vegetation in the #1 ranked model for nitrogen content. Results are given on the log-scale.

Top ranked model for nitrogen content					
Contrast	Estimate	SE	df	t.ratio	p.value
Hypnales – Lichen	0.425	0.235	184	1.808	0.1696
Hypnales – Sphagnum	-0.701	0.124	182	-5.651	<.0001
Lichen – Sphagnum	-1.126	0.243	183	-4.639	<.0001

3.2.2 Bottom vegetation

Plots dominated by *Sphagnum* had a 1.2 times higher mean nitrogen concentration than Hypnales- and lichen-dominated plots (fig. 5). *Sphagnum* plots also had lower mean C:N-ratio and bulk density than the two others Hypnales plots had a high C:N-ratio, but a relatively low bulk density mean. Differences in nitrogen concentration, C:N-ratio, and bulk density between vegetation types are all significant (table A2). Performed pairwise Wilcox test show that the mean nitrogen concentration and C:N-ratio were significantly different between Hypnales and *Sphagnum*, and that the bulk density was significantly different between lichen and Hypnales. There was no significant difference in mean carbon concentration between the different classes of bottom vegetation (Wilcox comparisons, table A2; p-values, table A3).

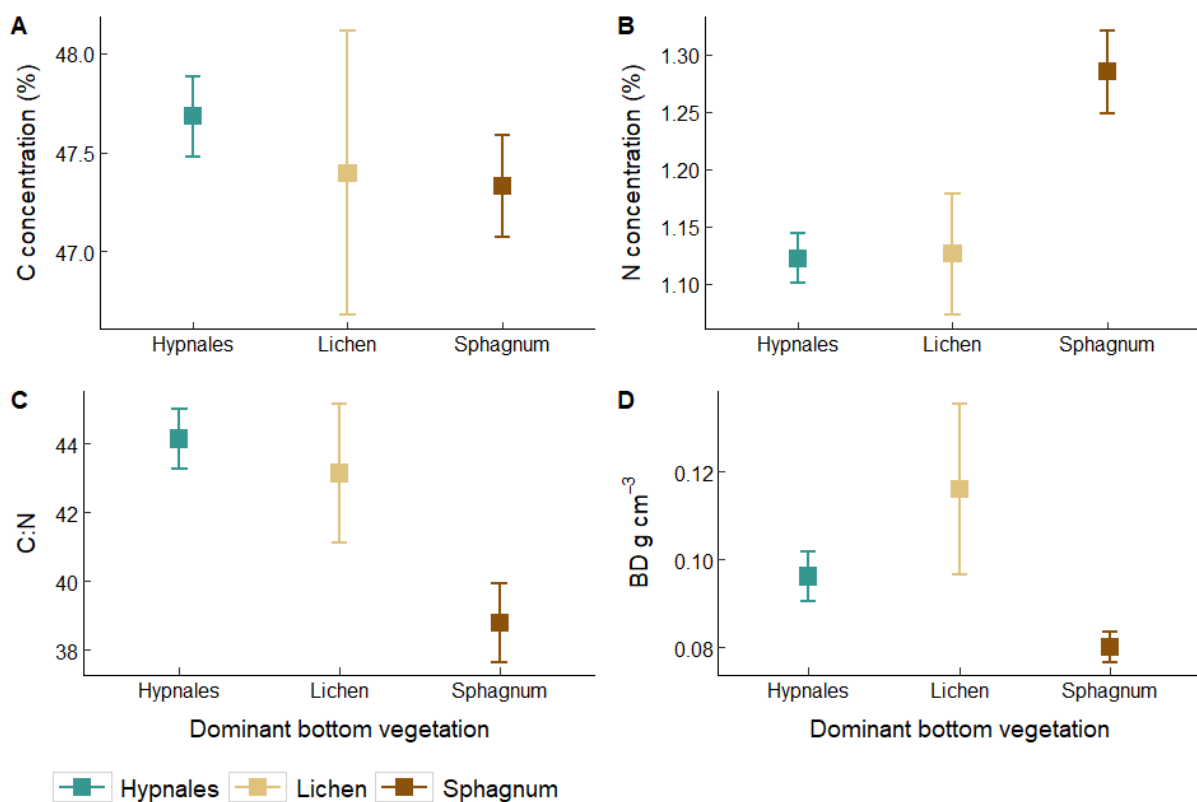


Figure 5: **A)** Mean \pm SE carbon concentration in the different vegetation classes. **B)** Mean \pm SE nitrogen concentration by vegetation type. *Sphagnum* and Hypnales significantly different from each other. **C)** Mean \pm SE C:N-ratio by vegetation type. *Sphagnum* and Hypnales significantly different from each other. **D)** Mean \pm SE bulk density by vegetation type.

Soil depth ranged from 4 to 60 cm in Hypnales-dominated plots, from 2 to 21 cm in lichen-dominated plots, and from 6 to 110 cm in *Sphagnum*-dominated plots. Mean soil depth was highest in *Sphagnum*-plots, 2.5 times higher than in Hypnales-plots, and 4.7 times higher than in lichen-plots (fig. 6A). Kruskal Wallis- and pairwise Wilcox-tests revealed significant

differences between all three vegetation types (table A2 and A3). Dominant bottom vegetation explained 31 % ($R^2m=0.31$) of the variation in soil depth.

Carbon content (kg m^{-2}) varied in a similar way (fig. 6B). Hypnales-dominated plots ranged from 1.4 to 58.2 kg m^{-2} , lichen-dominated plots ranged from 1.9 to 10.5 kg m^{-2} , and *Sphagnum*-dominated plots ranged from 2.2 to 69.5 kg m^{-2} . Like soil depth, mean carbon content was highest in *Sphagnum*-plots, 2 times higher than in Hypnales-plots, and 3.9 times higher than in lichen-plots. There were significant differences between all three vegetation types (table A2 and A3). Dominant bottom vegetation explained 18 % ($R^2m=0.18$) of the variation in carbon content.

Further, nitrogen content also varied in a similar way (fig. 6C). Hypnales-plots ranged from 0.030 to 1.391 kg m^{-2} , lichen-plots from 0.035 to 0.204 kg m^{-2} , and *Sphagnum*-plots from 0.05 to 2.91 kg m^{-2} . Again, mean content was highest in *Sphagnum*-plots, 2.5 times higher than in Hypnales-plots, and 4.8 times higher than in lichen-plots. Differences between all three groups were significant. Bottom vegetation explained 19 % ($R^2m = 0.1867$) of the variation in nitrogen content.

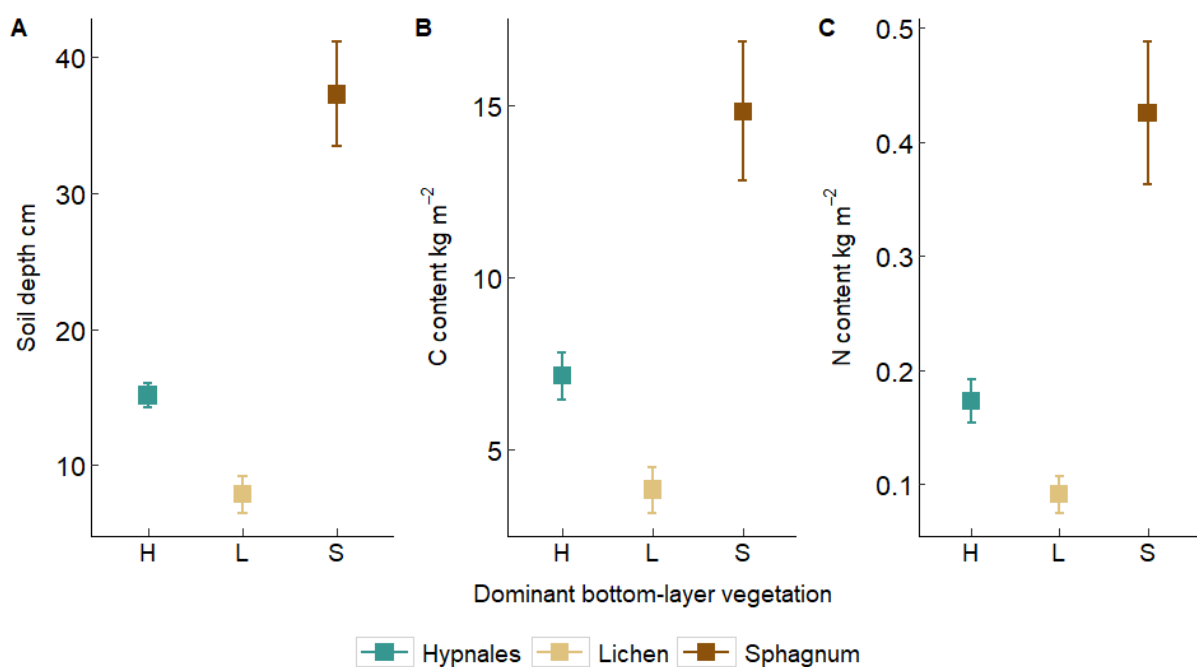


Figure 6. A) Mean \pm SE soil depth in relation to dominant bottom vegetation. B) Mean \pm SE carbon content in relation to dominant bottom vegetation. C) Mean \pm SE nitrogen content in relation to dominant bottom vegetation.

Significant differences between all three groups of bottom vegetation, for all three responses. H: Hypnales, L: Lichen, S: Sphagnum.

3.2.3 Tree basal area

Tree basal area ranged from 3 to 27 m² ha⁻¹, while spruce, pine, and deciduous basal area ranged between 0-15 m² ha⁻¹, 1-21 m² ha⁻¹, and 0-8 m² ha⁻¹, respectively. Mean basal area was 14.3 m² ha⁻¹, and means for spruce, pine, and deciduous basal area were 2.9 m² ha⁻¹, 10.4 m² ha⁻¹, and 0.9 m² ha⁻¹, respectively. Carbon concentration had a positive relationship with pine basal area, and a negative relationship with spruce basal area (fig 7A+B). Nitrogen concentration, on the other hand, had a positive relationship with deciduous basal area (fig. 7C). C:N ratio had a positive relationship with pine basal area, and a negative relationship with deciduous basal area (fig. 7D+E). There was no significant relationship between bulk density and basal area, and total tree basal area did not affect any of the four responses (p-values, table A2).

Soil depth had a significant negative relationship with both total tree basal area and pine basal area, and a positive relationship with deciduous basal area (fig. 8; p-values, table A2). Total tree basal area explained 3 % of the variation in soil depth ($R^2_m=0.033$). Pine and deciduous basal area explained approximately 2 and 3 % of the variation in soil depth, respectively ($R^2_m=0.021$ and $R^2_m=0.026$). Carbon content had a negative relationship with total tree basal area, pine basal area, and spruce basal area, and a positive relationship with deciduous basal area (fig. 9). Total tree basal area explained 4 % ($R^2_m=0.042$) of the variation in carbon content. Pine basal area explained approximately 2 % ($R^2_m=0.022$), spruce explained 3 % ($R^2_m=0.029$) and deciduous explained 3 % ($R^2_m=0.034$). Similarly, nitrogen content had a positive relationship with deciduous basal area, and a negative relationship with total tree basal area and pine basal area (fig. 10). Here, total tree basal area explained 3 % ($R^2_m=0.030$), pine basal area 3 % ($R^2_m=0.028$), and deciduous basal area 5 % ($R^2_m=0.051$).

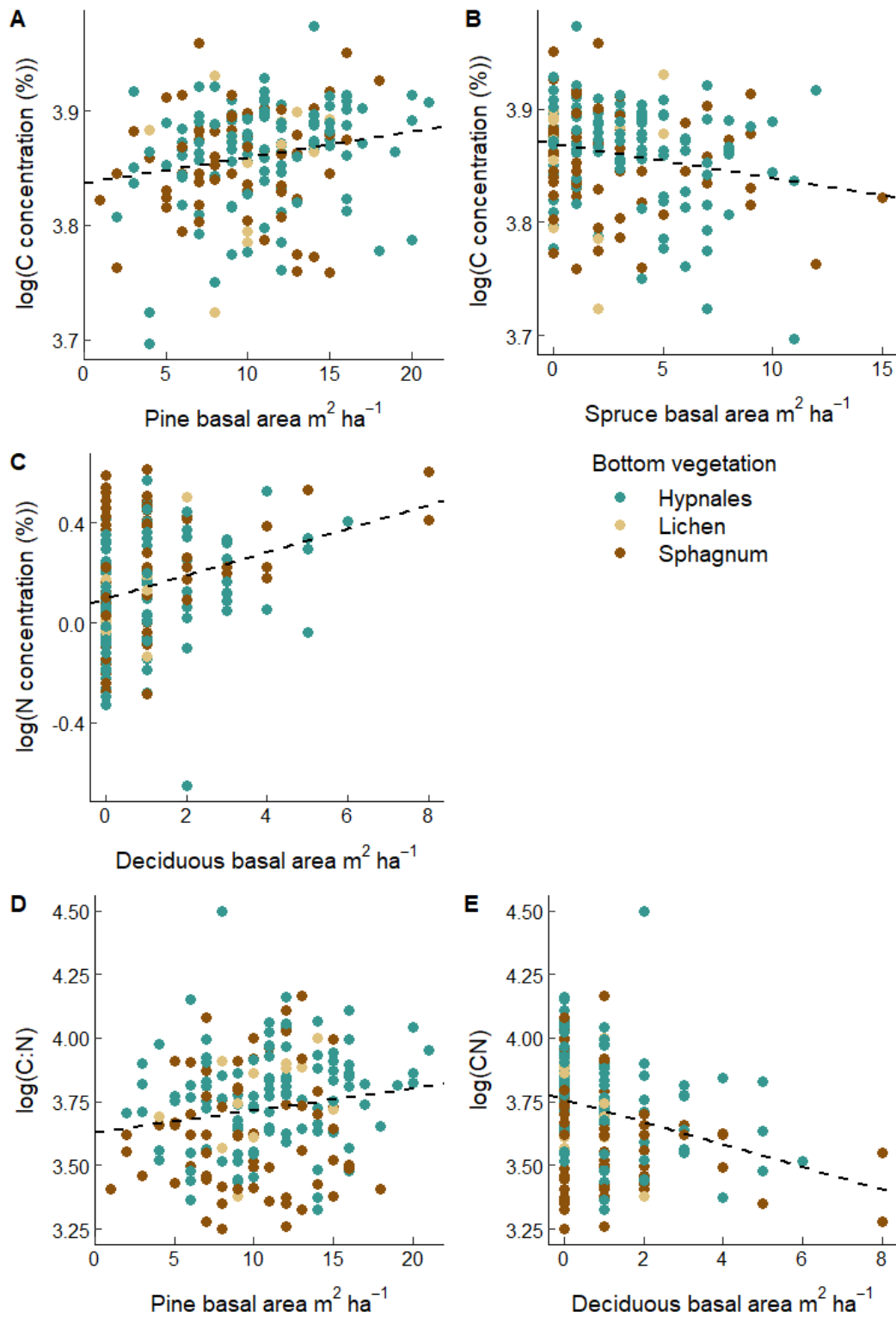


Figure 7: Carbon concentration in relation to **A)** pine basal area ($\text{m}^2 \text{ha}^{-1}$), $\beta = 2.28\text{E-}03$, $p = 0.007$, and **B)** spruce basal area. $\beta = -0.003$, $p = 0.006$. Nitrogen concentration in relation to **C)** deciduous basal area, $\beta = 0.05$, $p = 1.92\text{E-}05$. C:N-ratio in relation to **E)** pine basal area. $\beta = 8.78\text{E-}03$, $p = 0.027$, and **F)** deciduous basal area. $\beta = -0.04$, $p = 3.09\text{E-}05$.

Lines fitted with mixed effect models. All responses are log-transformed.

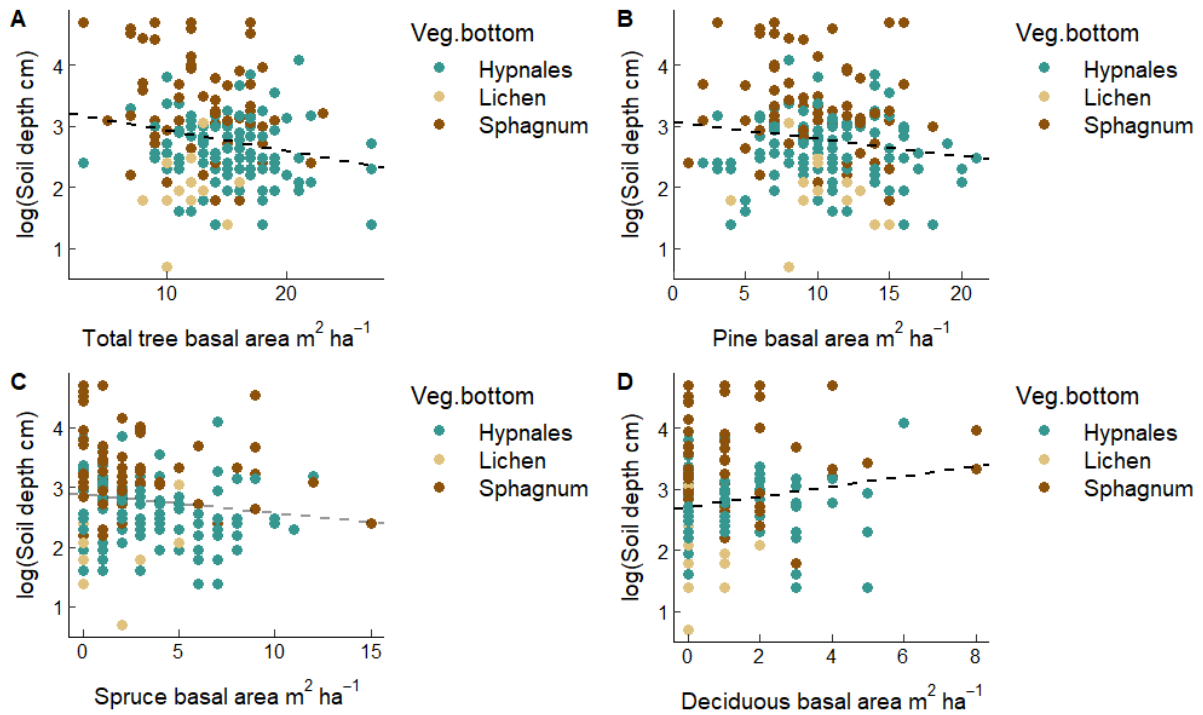


Figure 8: log-transformed soil depth in relation to **A)** total tree basal area. $\beta = -0.03$, $p = 0.013$. **B)** Pine basal area. $\beta = -0.03$, $p = 0.049$. **C)** Spruce basal area. $\beta = -0.03$, $p = 0.081$. **D)** Deciduous basal area. $\beta = 0.08$, $p = 0.026$. Black lines are statistically significant ($p < 0.05$), while grey lines are close to significant ($p < 0.1$). Lines fitted with mixed effect models.

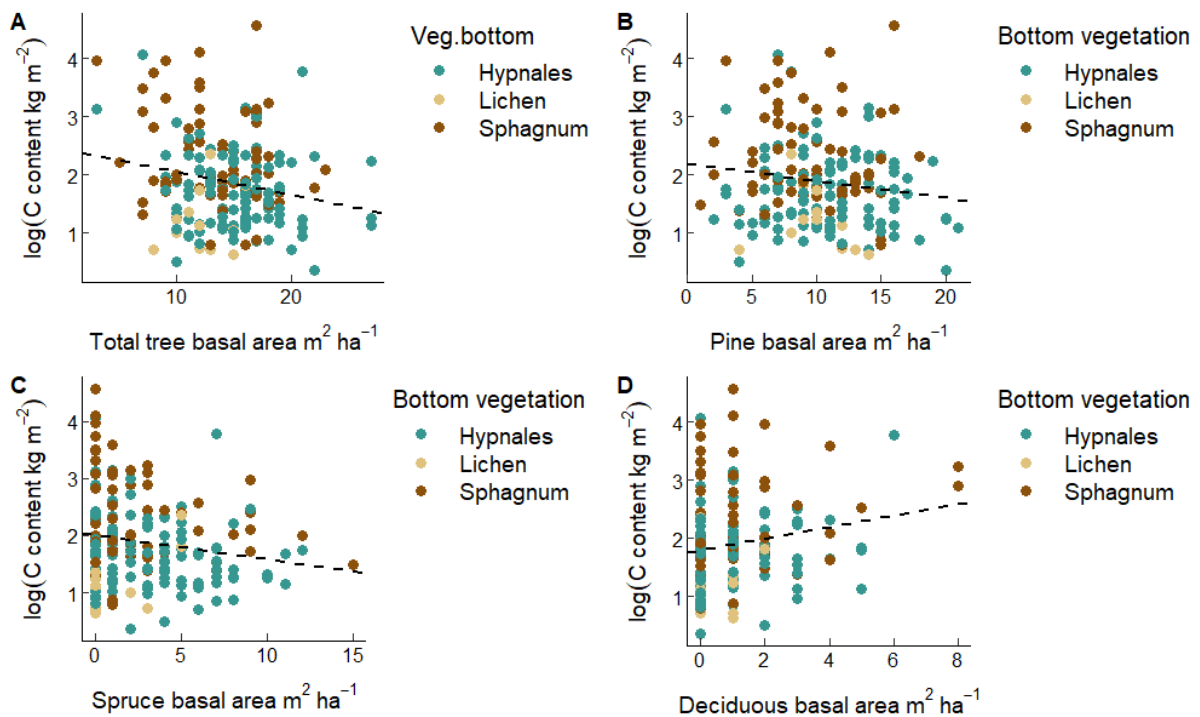


Figure 9: log-transformed carbon content in relation to **A)** total tree basal area. $\beta = -0.03992$, $p = 0.005$, **B)** pine basal area. $\beta = -0.02943$, $p = 0.045$, **C)** spruce basal area. $\beta = -0.04334$, $p = 0.02$, and **D)** deciduous basal area. $\beta = 0.09960$, $p = 0.011$

Black lines are statistically significant ($p < 0.05$), and fitted with mixed effect models.

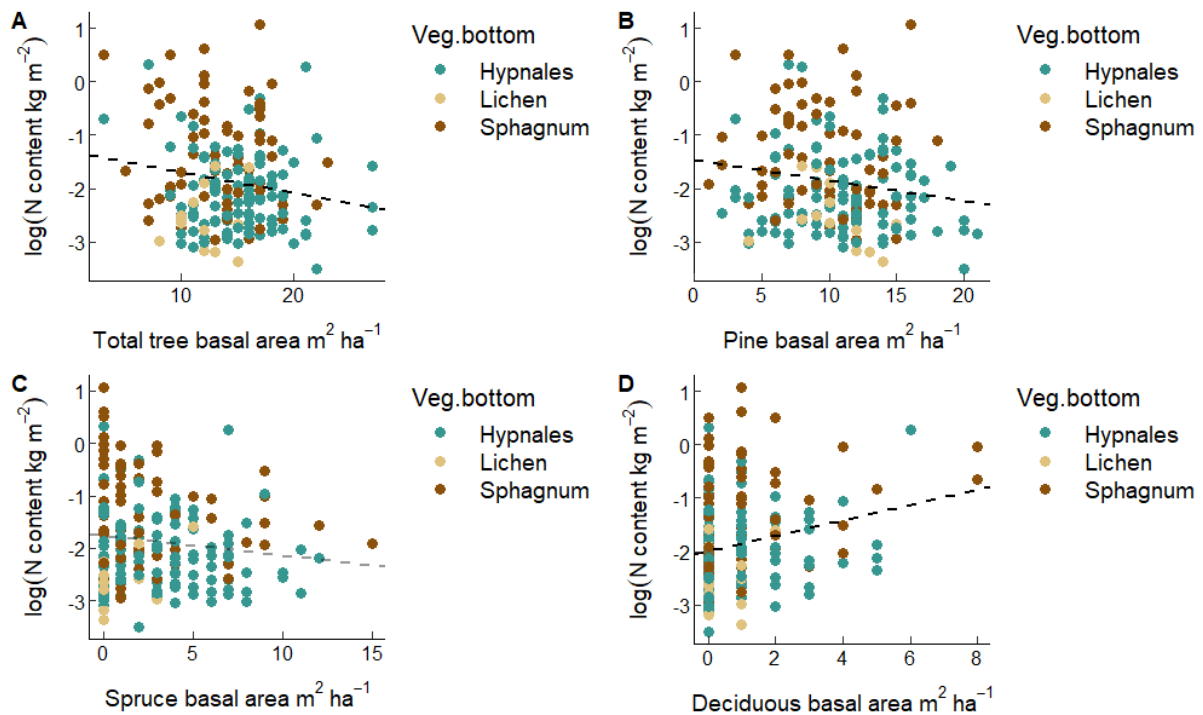


Figure 10: log-transformed nitrogen content in relation to **A)** Total tree basal area, $\beta = -0.0391$, $p = 0.017$, **B)** pine basal area, $\beta = -0.0384$, $p = 0.023$, **C)** spruce basal area $\beta = -0.0375$, $p = 0.081$, and **D)** deciduous basal area $\beta = 0.1416$, $p = 0.002$.

Black lines are statistically significant ($p < 0.05$), while grey lines are close to significant ($p < 0.1$). Lines fitted with mixed effect models.

3.2.4 Fire history

Carbon concentration did have a significant positive relationship with years since last fire (fig. 11A), and years since last fire only explained approximately 3 % of the variation in C-concentration ($R^2 = 0.027$). Bulk density showed a tendency to decrease with increasing time passed since last fire according to a rather low p-value (fig. 11B) ($\beta = -0.0009$, $p = 0.06$). Fire frequency did not affect carbon concentration, nitrogen concentration, C:N-ratio or bulk density, and neither fire frequency nor years since last fire did affect nitrogen concentration or C:N-ratio, soil depth, carbon content, or nitrogen content. See fig. A7 and A8 for all fire history plots.

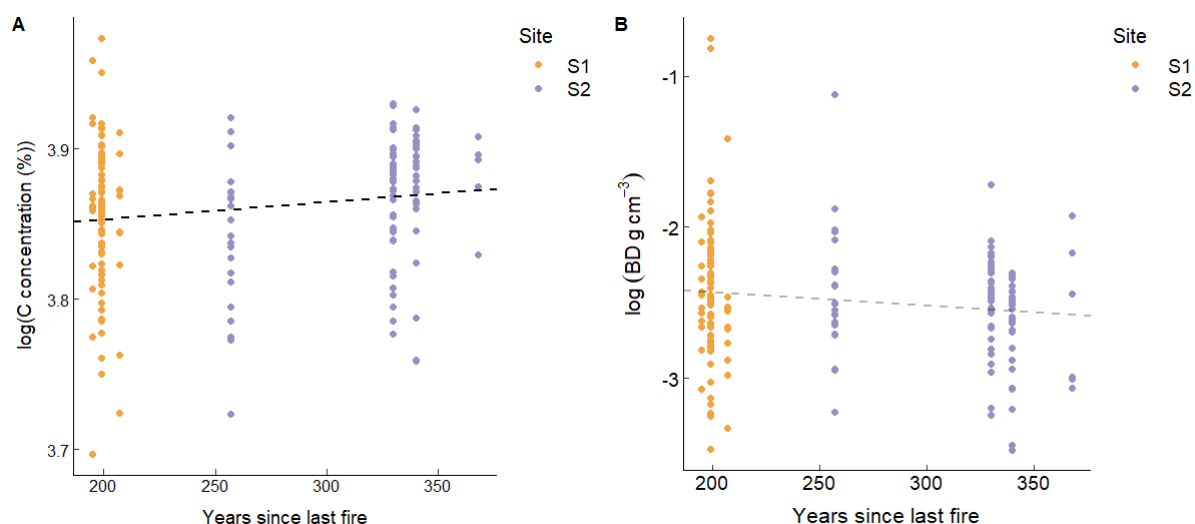


Figure 11: Relationship between years since last fire and **A)** log-transformed carbon concentration. Line fitted from mixed model including random effects (Site:Transect). $\beta=0.005$, $p=0.0436$. **B)** log-transformed bulk density. $\beta = -0.0009$, $p=0.06$.

3.2.5 Topography

Mean carbon concentration was similar in between the convex, concave, and flat plots (convex: 45.9 ± 0.9 , concave: 47.7 ± 0.3 , flat: 47.6 ± 0.2). The variation was largest in convex plots (fig. 12A). Mean nitrogen concentration was lowest in the convex plots (convex: 1.0 ± 0.04 , concave: 1.2 ± 0.03 , flat: 1.1 ± 0.02) (fig. 12B), while mean C:N-ratio was highest in convex plots (fig. 12C) (convex: 44.1 ± 0.9 , concave: 43.1 ± 2.01 , flat: 38.8 ± 1.1). These differences were significant (p-values, table A2), and convex plots were different from the concave and flat plots (table A3). Bulk density was similar between all topography classes (convex: 0.08 ± 0.005 , concave: 0.09 ± 0.005 , flat: 0.09 ± 0.005) (fig. 12D).

Soil depth ranged from 7 to 28 cm in convex plots, from 5 to 93 cm in concave plots, and 2 to 110 cm in flat plots. Mean soil depth for convex plots was 14.1 ± 2.0 cm, 17.2 ± 2.2 cm for concave plots, and 24.6 ± 2.1 cm for flat plots (fig. A10). Carbon content ranged from 2.6 to 8.1 kg m⁻² in convex plots, from 1.4 to 19.7 kg m⁻² in concave plots, and 1.7 – 96.5 kg m⁻² in flat plots. Mean carbon content for convex plots was 4.8 ± 0.6 kg m⁻², 7.2 ± 0.6 kg m⁻² for concave plots, and 13.6 ± 1.2 kg m⁻² for flat plots. Nitrogen content varied similarly and ranged from 0.06 to 0.16 kg m⁻² in convex plots, from 0.03 – 0.6 kg m⁻² in concave plots, and between 0.04 – 2.9 kg m⁻² in flat plots. Mean nitrogen content for convex plots was 1.1 ± 0.01 kg m⁻², 0.2 ± 0.02 kg m⁻² for concave plots, and 0.3 ± 0.04 kg m⁻² for flat plots. None of these differences were significant (table A2).

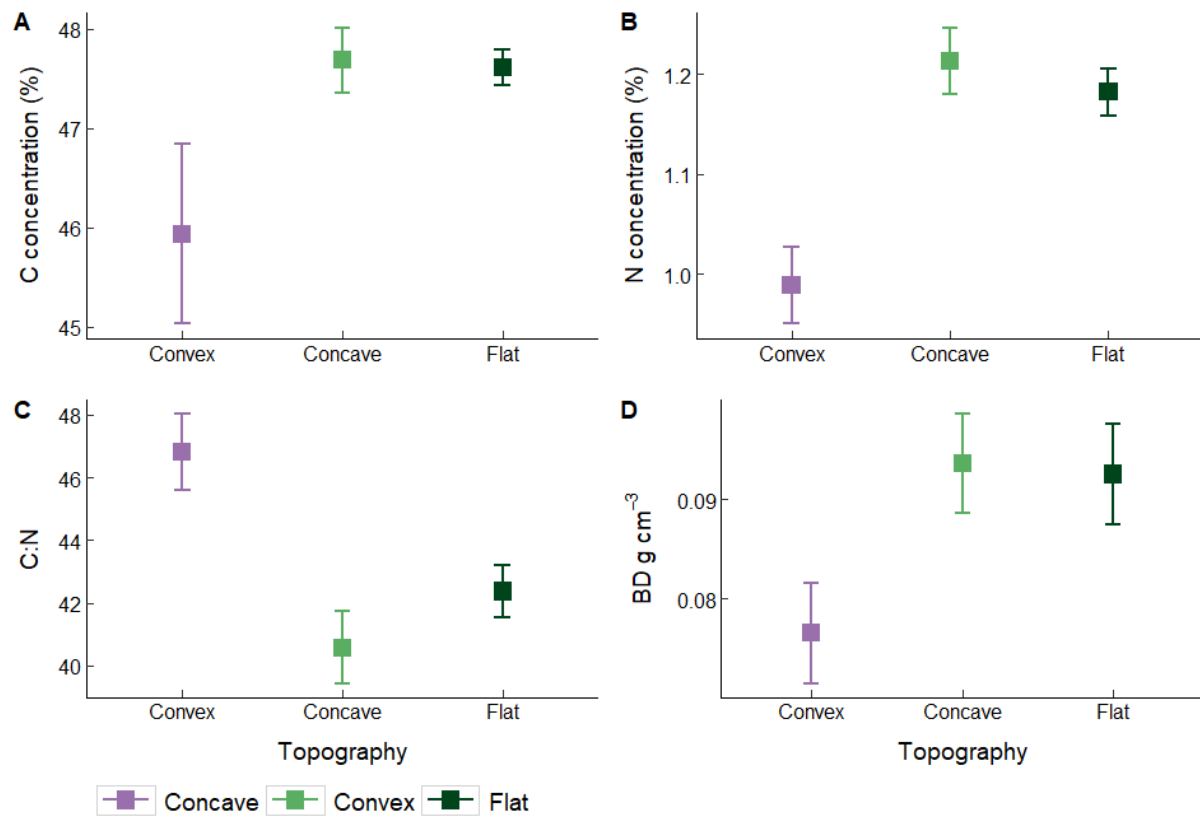


Figure 12: **A)** Mean \pm SE carbon concentration in the different topography classes. **B)** Mean \pm SE nitrogen concentration by topography type. **C)** Mean \pm SE C:N-ratio by topography type. **D)** Mean \pm SE bulk density by topography type.

4. Discussion

My main findings in this study are: 1) Soil carbon content was highly variable across fine spatial scales; 2) Nitrogen concentration is an important factor controlling soil depth and carbon content; 3) There was no clear relationship between fire history and the size of the soil carbon pool.

1) There was large variation in soil carbon content, and soil carbon content was highly correlated with soil depth. Dominant bottom vegetation explained 18 % of the variation in soil carbon content, and all three vegetation classes were significantly different from each other. This is in agreement with our second hypothesis. Plots dominated by peat mosses *Sphagnum* had the highest content of soil carbon and plots dominated by lichen the lowest. However, there was no difference in carbon concentration between the vegetation classes, so the variation was mainly explained by differences in soil depth. Bulk density also explained some of the variation between Hypnales and *Sphagnum*-plots.

Sphagnum-dominated areas are characterized by low decomposition rates, and wet, anoxic, and acidic conditions (see e.g., Rydin et al., 2013). This leads to an imbalance between productivity and decomposition, where productivity exceeds composition, and in turn leads to carbon accumulation (Oke & Hager, 2020). In addition, *Sphagnum*-plots also had a low C:N-ratio. This was expected as the C:N-ratio is one of the main controllers of litter decomposition rates (Zhang et al., 2008), and low C:N-ratio in litter promotes soil carbon accumulation (Zhou et al., 2019). This is also likely to be true for C:N-ratio in soils. In our study, C:N-ratio had a clear negative relationship with both soil carbon content and soil depth.

Tree basal area and tree species composition also affected the spatial distribution and variation in soil carbon content and explained between 2 and 4 % of the variation. However, the basal area effect contradicted my third hypothesis. I found a negative relationship between carbon content and the abundance of coniferous tree species, and a positive relationship between carbon content and abundance of deciduous tree species. This is also inconsistent with several other studies (e.g., Marty et al., 2015; Hansson et al., 2013), where soil carbon content tends to be higher where coniferous tree species dominate, as they typically have more recalcitrant litter. Zajícová & Chuman (2021) found that soil moisture and forest floor cover (including both litter and bottom vegetation) were the most important factors controlling the thickness of the organic soil horizon in managed forests of Norway spruce and European beech (*Fagus sylvatica*), which at least partly corresponds to my findings. The wetter *Sphagnum*-dominated plots had higher

soil carbon content, and generally a higher deciduous basal area than the dry lichen-dominated plots, which generally were more dominated by Scots pine. This implies that, in my study, dominant bottom vegetation, and soil moisture associated with different vegetation types are more important than tree species for explaining the variation in soil carbon content. This also highlights the importance of including several factors when attempting to estimate soil carbon content at fine scales.

Plots with convex topography had lower nitrogen concentration than flat and concave plots. In accordance with this, C:N ratio was higher in convex plots. This is as expected, as convex curvatures have higher water and nutrient discharge (Zajícová & Chuman, 2021), leading to dryer, nutrient poor plots. However, contrary to my fourth hypothesis, I did not find any effect on total soil carbon content or soil depth. It is possible that the topography in the surrounding landscape, and not only that within the 50×50 cm frame, would be better for assessing variation in soil carbon. Another possibility is that I was unable to pick up the variation between topography types due to a large proportion of the plots being flat. Only very few were convex. Increasing sample size might be beneficial to assess variation in soil carbon stocks in relation to topography. Larger sample sizes would also allow for investigation of interaction effects, with e.g., vegetation type.

2) Nitrogen concentration turned out to be important for soil depth and soil carbon content, more important than C:N-ratio. Plots with higher nitrogen concentration also had a higher soil carbon content, and deeper soil. Boreal forests are naturally nitrogen limited (Vitousek & Howarth, 1991; Jarvis & Linder, 2000), so higher nitrogen availability would lead to increased productivity. In addition, nitrogen fertilization experiments and studies of anthropogenic nitrogen deposition have shown a reduction in soil respiration with nitrogen addition (Olsson et al., 2005; Janssens et al., 2010). This could lead to increased accumulation of soil carbon. Nitrogen fertilization of boreal forests have shown to increase soil carbon stocks (Maaroufi et al., 2015), through reductions in autotrophic and heterotrophic respiration. However, nitrogen availability can also affect the chemical defense in needles of Norway spruce. Nybakken et al., (2018) found a decrease in flavonoids and condensed tannins, especially in current year needles. This could lead to less recalcitrant litter, and increased decomposition.

3) I found no impact of fire history on soil carbon content. This contrasts with my first hypothesis. Several studies have found a negative impact on soil carbon from forest fires, and other natural disturbances (reviewed in Thom & Seidl, 2015). However, most of these have studied the effect of more recent fire disturbances than those at my sites. In my study, years

since last fire ranged from 195 to 368 years. It is thus possible that soil organic carbon stocks use < 200 years to regenerate to pre-disturbance levels in my study area. Another possibility is that the time frame could just be too narrow to pick up the effect of time since fire disturbance. For example, Andrieux et al. (2018) found a linear relationship between years since last fire and carbon stocks in the forest humus layer, where sites had burned 2–314 years ago. Further, another study found greater carbon storage in hummus with increasing time since last fire, when looking at almost 4000 years of fire history (Wardle et al., 2003). This implies that including a wider time frame could help assessing the effect of forest fire on soil carbon stocks. A third option is that the spatial scale in my study is too fine to pick up on the variation. Interestingly, there was a significant relationship between years since last fire and carbon concentration. In addition, there was a close to significant relationship between years since last fire and bulk density. More recently burned plots had a lower carbon concentration. However, carbon concentration is easily affected by contamination by mineral sand, silt, or clay. Especially if the organic soil layer is shallow, a very small amount of mineral soil could affect carbon concentration considerably. Therefore, it is important to be careful when drawing conclusions from organic carbon concentrations.

In conclusion, my study shows that soil carbon content is highly variable at a fine spatial scale. This is important to consider when attempting to assess carbon stocks in boreal forest soils. Even though tree species composition and litter type have been shown to influence soil carbon stocks, my study implies that on small scales, several variables need to be considered to accurately estimate soil carbon stocks. I found that dominant bottom vegetation and associated soil moisture, in addition to nitrogen concentration and C:N-ratio, are important variables when explaining the variation. Soil depth and soil carbon content are highly correlated, so measurements of soil depth might be a decent proxy for estimating soil carbon stocks. Fire history had no direct impact in my time frame and spatial scale. However, it is possible that there are important indirect effects of fire history, on for instance vegetation type and tree species composition.

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6. Appendix

6.1 Summaries

Table A1: Summary on the 7 responses in relation to Sites, dominant bottom vegetation, and topography

C %	n (plots)	Range (min – max)	Mean ± SE	95 % CI of mean
Total	189	40.3 – 53.2	47.5 ± 0.2	47.2 – 47.9
Sites				
S1	90	40.3 – 53.2	47.3 ± 0.2	46.9 – 47.8
S2	99	41.4 – 51.0	47.7 ± 0.2	47.3 – 48.1
Bottom vegetation				
Hypnales	110	40.3 – 53.2	47.7 ± 0.2	47.3 – 48.1
Lichen	13	41.4 – 50.9	47.4 ± 0.7	45.8 – 50.0
Sphagnum	66	42.9 – 52.4	47.3 ± 0.3	46.8 – 47.8
Topography				
Convex	10	40.3 – 48.9	45.9 ± 0.9	43.9 – 49.0
Concave	43	42.9 – 50.9	47.7 ± 0.3	47.0 – 48.4
Flat	136	41.4 – 53.2	47.6 ± 0.2	47.3 – 48.0
N %				
Total	189	0.52 – 1.85	1.18 ± 0.02	1.14 – 1.22
Sites				
S1	90	0.52 – 1.83	1.19 ± 0.03	1.14 – 1.24
S2	99	0.75 – 1.85	1.17 ± 0.03	1.12 – 1.22
Bottom vegetation				
Hypnales	110	0.52 – 1.77	1.12 ± 0.02	1.08 – 1.16
Lichen	13	0.87 – 1.65	1.13 ± 0.05	1.01 – 1.25
Sphagnum	66	0.75 – 1.85	1.28 ± 0.04	1.21 – 1.35
Topography				
Convex	10	0.76 – 1.14	0.98 ± 0.04	0.89 – 1.07
Concave	43	0.77 – 1.68	1.18 ± 0.03	1.11 – 1.25
Flat	136	0.52 – 1.85	1.12 ± 0.02	1.07 – 1.17
CN				
Total	189	25.8 – 89.7	42.2 ± 0.7	40.9 – 43.5
Sites				
S1	90	26.6 – 89.7	41.6 ± 1.0	39.6 – 43.7

S2	99	25.8 – 64.4	42.7 ± 0.9	41.0 – 44.5
Bottom vegetation				
Hypnales	110	27.8 – 89.7	44.1 ± 0.9	42.4 – 45.8
Lichen	13	29.3 – 54.5	43.1 ± 2.0	38.8 – 47.5
Sphagnum	66	25.8 – 64.4	38.8 ± 1.1	36.5 – 41.05
Topography				
Convex	10	40.9 – 53.4	46.8 ± 1.2	44.1 – 49.6
Concave	43	28.5 – 58.0	40.6 ± 1.2	38.3 – 42.9
Flat	136	25.8 – 89.7	42.4 ± 0.9	40.7 – 44.1
BD.gcm3	n (plots)	Range (min – max)	Mean ± SE	95 % CI of mean
Total	189	0.03 – 0.47	0.09 ± 0.004	0.08 – 0.10
Sites				
S1	90	0.03 – 0.47	0.10 ± 0.007	0.09 – 0.11
S2	99	0.03 – 0.33	0.09 ± 0.004	0.08 – 0.09
Bottom vegetation				
Hypnales	110	0.03 – 0.47	0.10 ± 0.006	0.09 – 0.11
Lichen	13	0.06 – 0.33	0.12 ± 0.019	0.07 – 0.16
Sphagnum	66	0.03 – 0.17	0.08 ± 0.003	0.07 – 0.09
Topography				
Convex	10	0.06 – 0.12	0.08 ± 0.005	0.07 – 0.09
Concave	43	0.04 – 0.18	0.09 ± 0.005	0.08 – 0.10
Flat	136	0.03 – 0.47	0.09 ± 0.005	0.08 – 0.10
Soil depth cm	n (plots)	Range (min – max)	Mean ± SE	95 % CI of mean
Total	189	2 – 110	22.4 ± 1.6	19.1 – 22.4
Sites				
S1	90	4 – 110	24.4 ± 2.7	19.1 – 29.7
S2	99	2 – 110	20.5 ± 2.0	16.5 – 24.4
Bottom vegetation				
Hypnales	110	4 – 60	15.1 ± 0.9	13.4 – 16.8
Lichen	13	2 – 21	7.9 ± 1.3	45.0 – 10.7
Sphagnum	66	6 – 110	37.3 ± 3.8	29.6 – 44.9
Topography				
Convex	10	7 – 28	14.1 ± 2.0	9.5 – 18.7
Concave	43	5 – 93	17.2 ± 2.2	12.9 – 21.6
Flat	136	2 – 110	24.6 ± 2.1	20.3 – 28.8
Total C kg/m2	n (plots)	Range (min – max)	Mean ± SE	95 % CI of mean
Total	189	1.4 – 96.5	9.6 ± 0.9	7.9 – 11.3
Sites				

S1	90	1.7 – 96.5	11.2 ± 1.5	8.1 – 14.2
S2	99	1.4 – 52.8	8.2 ± 0.9	6.5 – 9.9
Bottom vegetation				
Hypnales	110	1.4 – 58.2	7.1 ± 0.7	5.8 – 8.5
Lichen	13	1.9 – 10.5	3.8 ± 0.7	2.4 – 5.3
Sphagnum	66	2.2 – 69.5	14.8 ± 2.0	10.8 – 18.9
Topography				
Convex	10	2.6 – 8.1	4.8 ± 0.6	3.5 – 6.2
Concave	43	1.4 – 19.7	7.2 ± 0.6	6.0 – 8.4
Flat	136	1.7 – 96.5	13.6 ± 1.2	8.4 – 13.0
Total N kg/m2	n (plots)	Range (min – max)	Mean ± SE	95 % CI of mean
Total	189	0.03 – 2.9	0.3 ± 0.03	0.2 – 0.3
Sites				
S1	90	0.05 – 2.9	0.3 ± 0.05	0.2 – 0.4
S2	99	0.03 – 1.7	0.2 ± 0.03	0.2 – 0.3
Bottom vegetation				
Hypnales	110	0.03 – 1.4	0.2 ± 0.02	0.1 – 0.2
Lichen	13	0.04 – 0.2	0.1 ± 0.02	0.1 – 0.1
Sphagnum	66	0.05 – 2.9	0.4 ± 0.06	0.3 – 0.6
Topography				
Convex	10	0.06 – 0.2	0.1 ± 0.01	0.1 – 0.1
Concave	43	0.03 – 0.6	0.2 ± 0.02	0.1 – 0.2
Flat	136	0.04 – 2.9	0.3 ± 0.04	0.2 – 0.4

Table A2: p-values for the 7 responses and corresponding explanatory variables. Significant values ($p < 0.05$) in **bold**, almost significant values ($p < 0.1$) in *italic*. Values from fitted mixed effect models or Kruskal-Wallis tests. Bottom.veg=Dominant bottom vegetation, BA=basal area, yslf=years since last fire

	C %	N %	CN	BD	Soil depth	C kg/m2	N kg/m2
Site	<i>0.0840</i>	0.2468	0.1858	0.3459	0.3894	0.1381	0.1606
Bottom.veg	0.3098	0.0010	0.0002	0.0418	1.03E-12	3.58E-08	7.24E-08
Topography	0.1392	0.0187	<i>0.0512</i>	0.1248	0.3010	0.2649	0.2469
Total BA	0.4150	0.7530	0.8850	0.4660	0.0126	0.0047	0.0166
Pine BA	0.0071	<i>0.0871</i>	0.0273	0.7980	0.0492	0.0445	0.0233
Spruce BA	0.0061	0.5460	0.2650	0.3520	<i>0.0813</i>	0.0196	<i>0.0809</i>
Deciduous BA	0.2170	0.00002	0.00003	0.5140	0.0264	0.0111	0.0016
yslf	0.0401	0.4880	0.2390	<i>0.0600</i>	0.4670	0.1160	0.1260
Fire frequency	0.1450	0.1640	0.2150	0.9960	0.4020	0.4000	0.3680

Table A3: Showing p-values from pairwise Wilcox comparisons, adjustment method BH. Tests only performed on variables and responses with significant p-value according to Kruskal Wallis test.

N %		
Bottom vegetation		
	Hypnales	Lichen
Lichen	0.94425	-
Sphagnum	0.00076	0.10054
Topography		
	Convex	Concave
Concave	0.0048	-
Flat	0.0305	0.2674
CN		
Bottom vegetation		
	Hypnales	Lichen
Lichen	0.91157	-
Sphagnum	0.00012	0.13021
Topography		
	Convex	Concave
Concave	0.017	-
Flat	0.07	0.351
BD		
Bottom vegetation		
	Hypnales	Lichen
Lichen	0.216	-
Sphagnum	0.085	0.085
Soil depth cm		
Bottom vegetation		
	Hypnales	Lichen
Lichen	0.00025	-
Sphagnum	1.00E-09	9.70E-07
C kgm2		
Bottom vegetation		
	Hypnales	Lichen
Lichen	0.0038	-
Sphagnum	6.70E-06	1.80E-05
N kgm2		
Bottom vegetation		
	Hypnales	Lichen
Lichen	0.0206	-
Sphagnum	2.30E-06	0.0001

6.2 Models

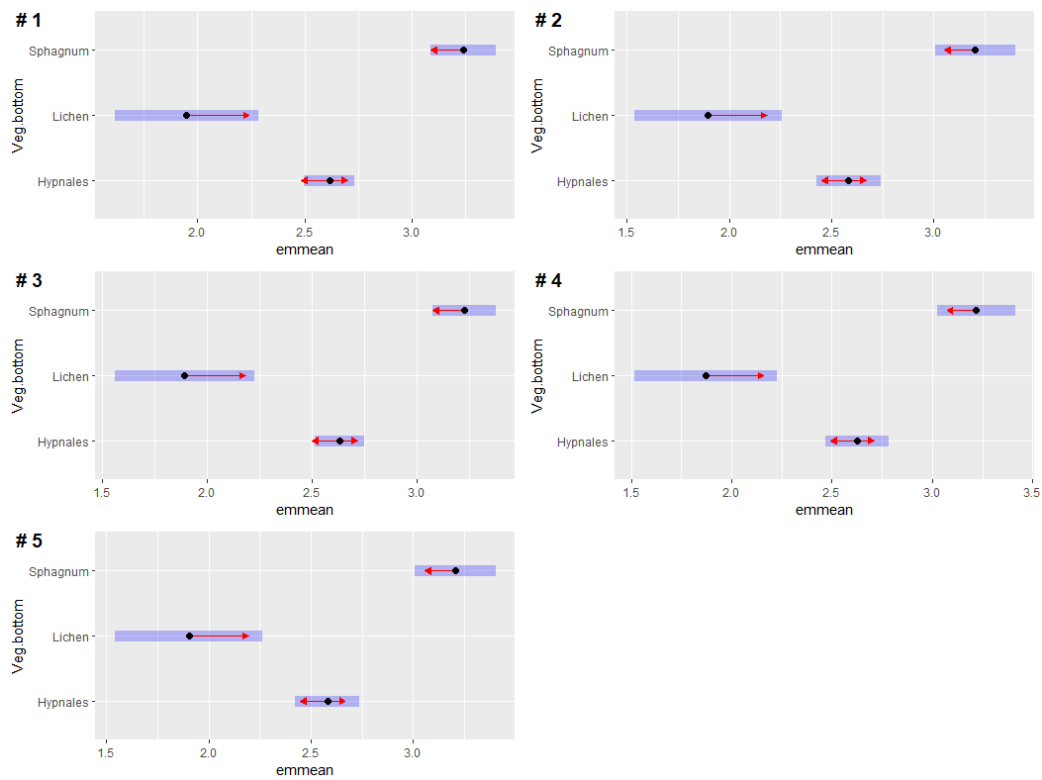


Figure A1: Graphical comparison of estimated marginal means of dominant vegetation as factor in top five models for soil depth. Non-overlapping red arrows indicate significance.

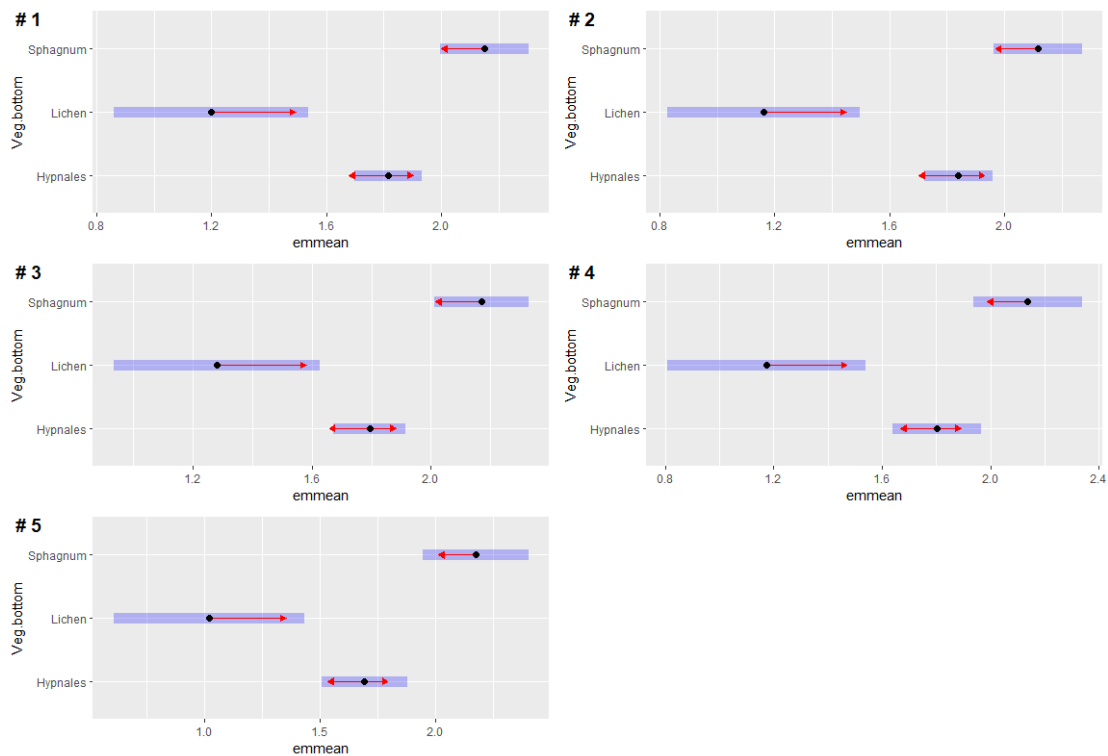


Figure A2: Graphical comparison of estimated marginal means of dominant vegetation as factor in top five models for carbon content. Non-overlapping red arrows indicate significance.

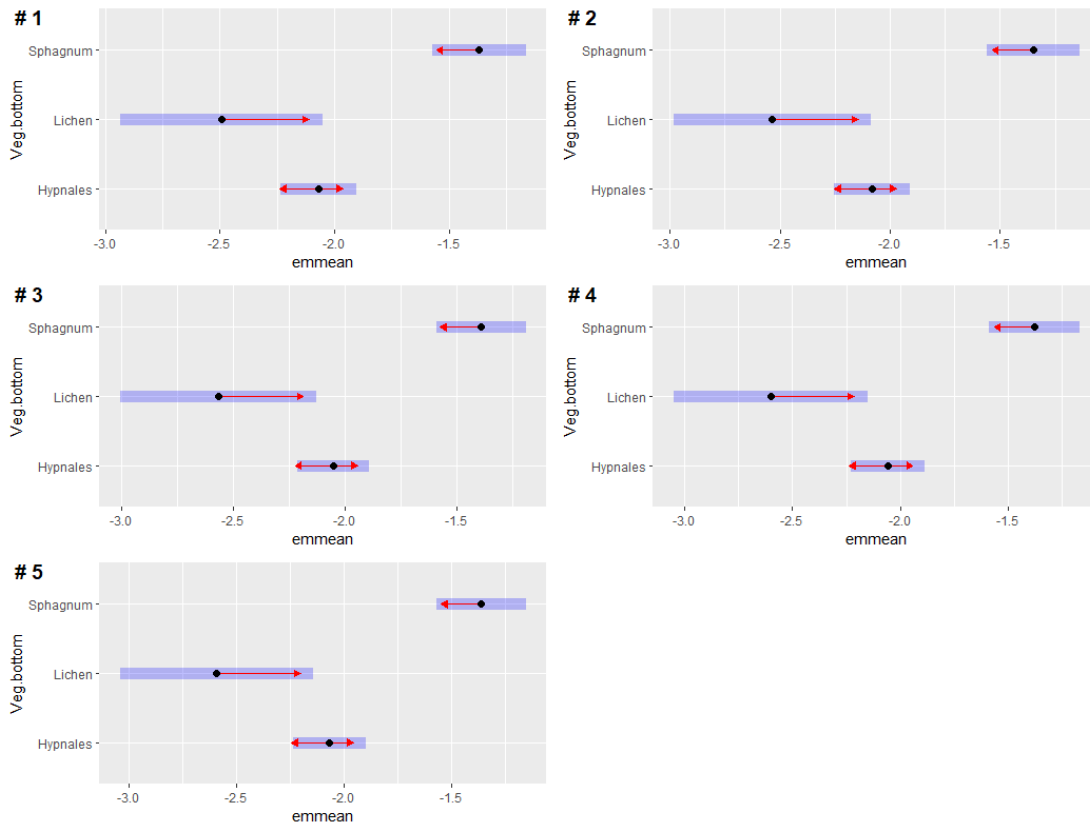


Figure A3: Graphical comparison of estimated marginal means of dominant vegetation as factor in top five models for nitrogen content. Non-overlapping red arrows indicate significance.

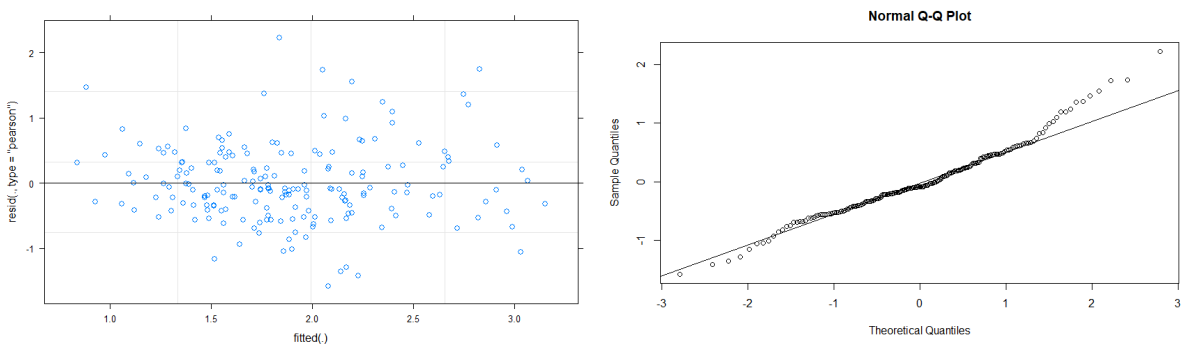


Figure A4: Residual plots for top ranked model for carbon content: $\log(\text{totC_kgm2}) \sim \text{Veg.bottom} + \text{Spruce_no} + \text{N.percent} + (1|\text{Site:Transect})$

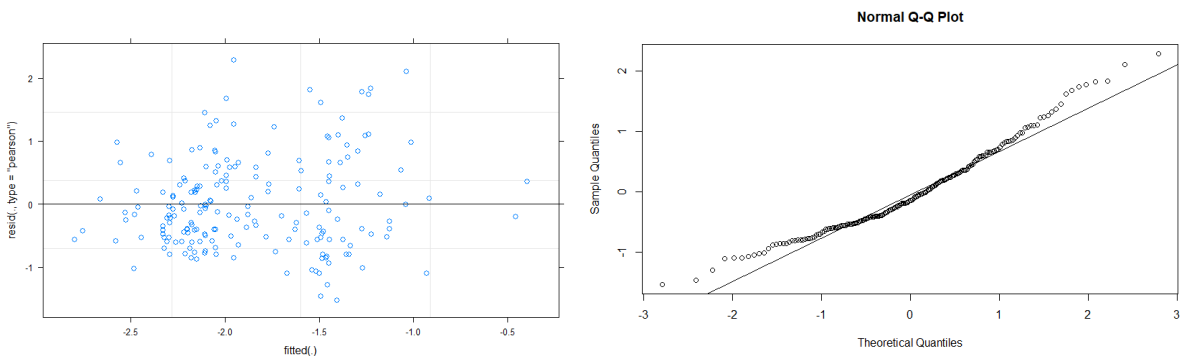


Figure A5: Residual plots for top ranked model for nitrogen content: $\log(\text{totN_kgm2}) \sim \text{Veg.bottom} + \text{Decid_no} + (1|\text{Site:Transect})$

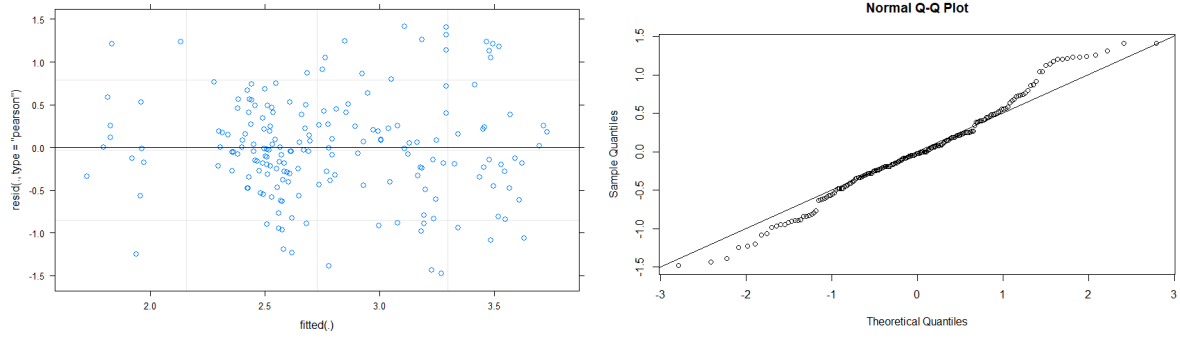


Figure A6: Residual plots for top ranked model for soil depth: $\log(\text{Soil_depth.cm}) \sim \text{Veg.bottom} + \text{N.percent} + (1|\text{Site:Transect})$

6.3 Fire history

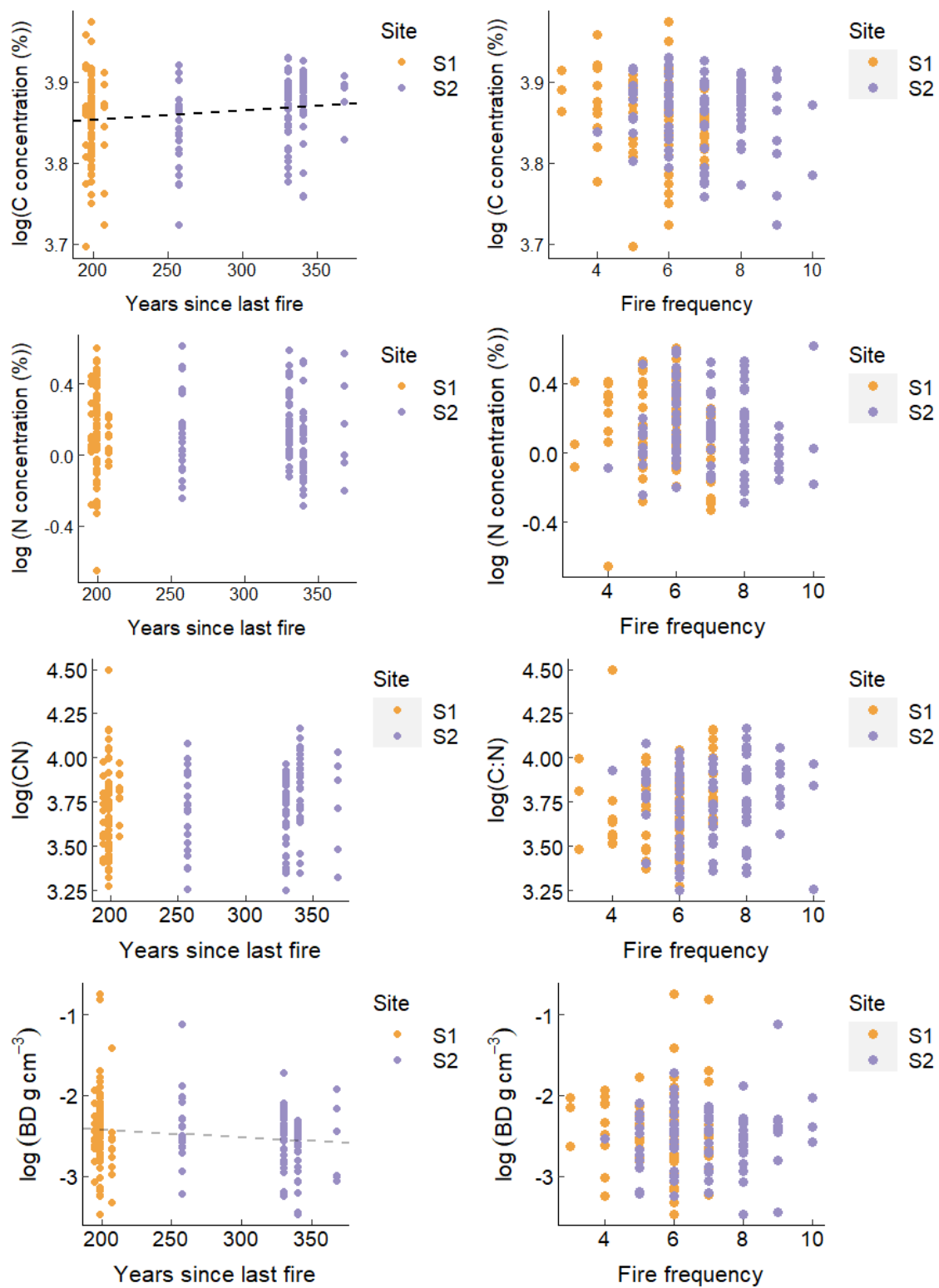


Figure A7: Carbon concentration, nitrogen concentration, C:N-ratio, and bulk density in relation to fire history. Black lines show significant relationship ($p < 0.05$), while grey lines show relationships close to significant ($p < 0.1$).

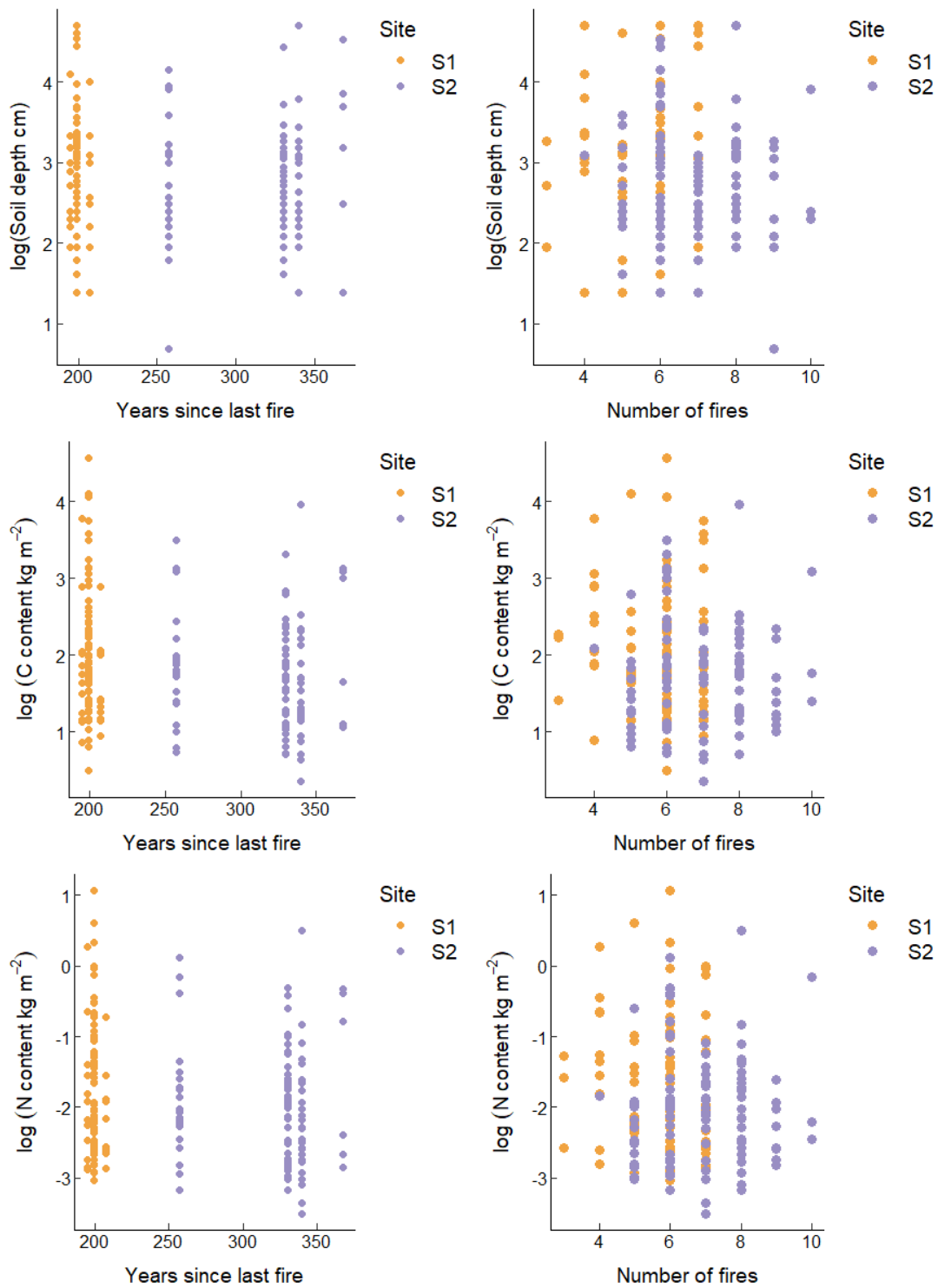


Figure A8: Soil depth, carbon content, and nitrogen content in relation to fire history. No relationships found.

6.4 Tree basal area

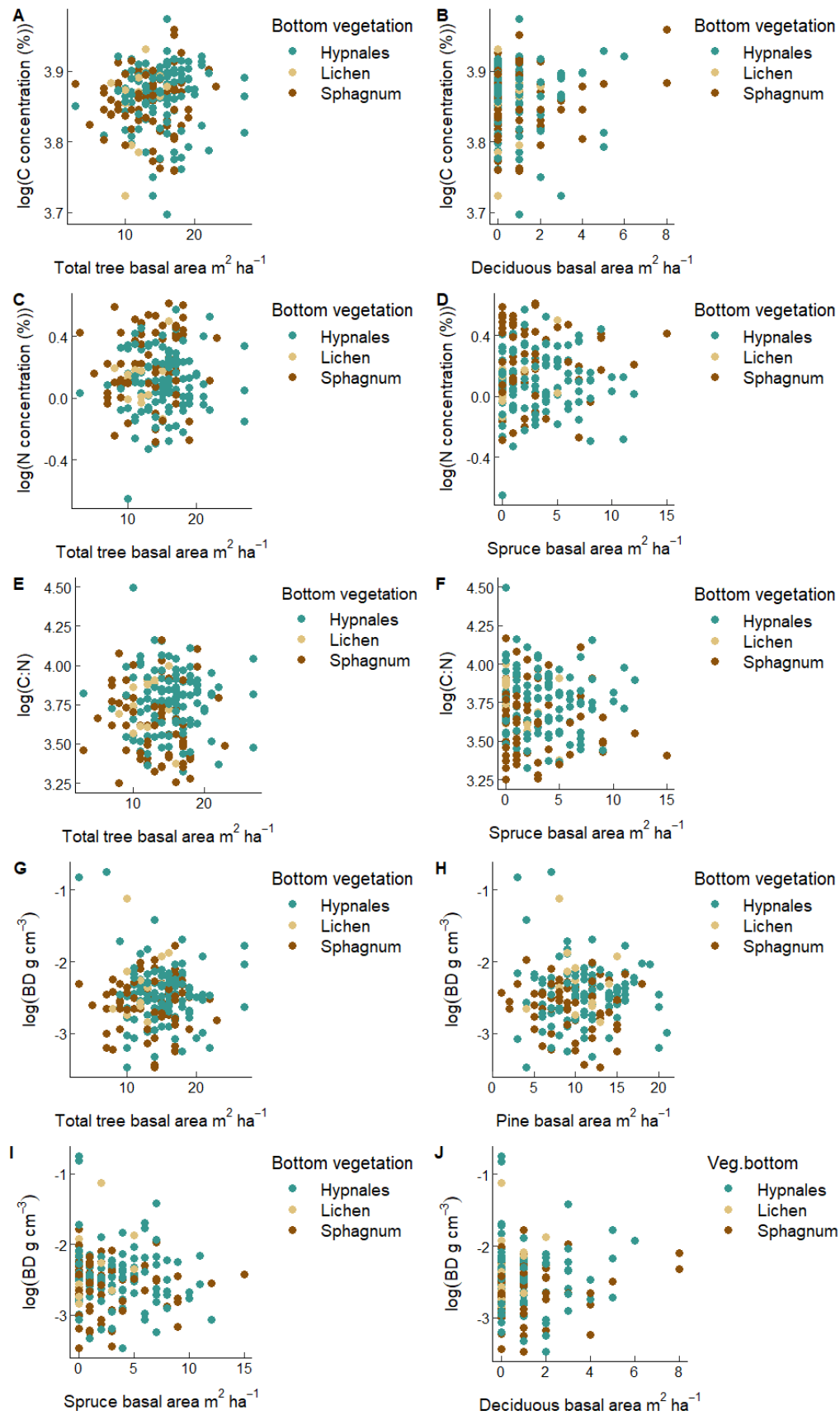


Figure A9: Additional figures for tree basal area in relation to carbon concentration, nitrogen concentration, C:N-ratio, and bulk density.

6.5 Topography

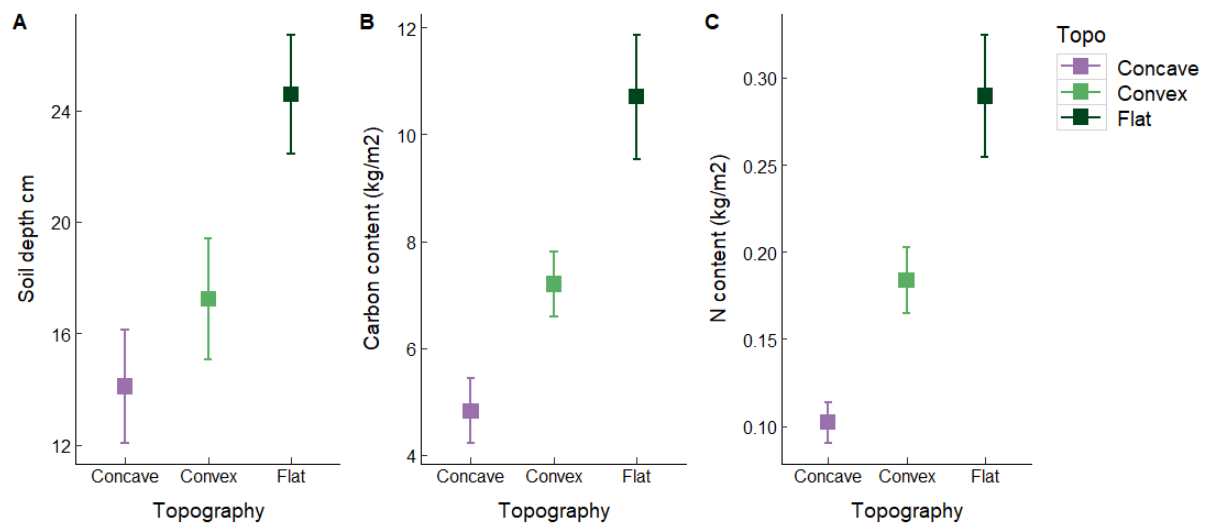


Figure A10: **A)** Mean \pm SE soil depth in relation to topography. **B)** Mean \pm SE carbon content in relation to topography. **C)** Mean \pm SE nitrogen content in relation to topography.



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