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Soil carbon stocks in different vegetation classes across the treeline ecotone in central- and southern Norway

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Preface

This master thesis marks the end of my master´s degree in forest sciences at the Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences (NMBU). It has been interesting to be a part of an entire process of a research project, from fieldwork, processing the field samples, and analyzing the results. Most of all I want to thank my supervisor Ole Martin Bollandsås for his good guidance, text feedback and help with the statistics. I want to thank my co-supervisors Claire Devos for statistical guidance, text feedback, and always having time to give guidance and answer my questions, and Mikael Ohlson for good text feedback. Thanks to Ida Marielle Mienna for supporting me with a classification map of different vegetation classes in the field. I also want to thank my cousin Renate Kristianslund for text feedback on the thesis draft.

Thanks to the research group Forest Potential and UMB research foundation for their financial support during my fieldwork and lab analysis. I also want to thank my fellow student and research partner Hanne Torsdatter Petlund who joined and helped during the fieldwork and lab analysis. In the end a great thanks to my fellow students in the forestry class, flatmates and parents for social support and encouraging words during the writing period.

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Abstract

The expansion of the treeline into the currently treeless alpine tundra may have considerable impacts on carbon storage. Recent studies have shown that the expansion of trees into the alpine tundra could lead to an increase in CO_2 emissions, having positive feedback on global warming. However, few studies have assessed differences in carbon storage between vegetation classes in the forest-tundra ecotone. Here, I have done that by classifying the vegetation according to the Nature Types in Norway (NiN) classification system.

Top organic soil was sampled in five different vegetation classes: forest, lee side, ridge, sub-xeric heath, and xeric heath along a 600-kilometer latitudinal gradient from the south to the middle part of Norway from late July to late August 2021. From the soil samples both carbon stock and carbon concentration were estimated in the lab, and statistical analyses were carried out to see if there were any differences in carbon stock and carbon concentration between the vegetation classes in the alpine tundra and treeline ecotone. To account for spatial dependencies caused by the sampling design (study sites and sample lines), a linear mixed effects model was used. Elevation was also included in the model to account for the possible effect of elevation on soil carbon storage.

All vegetation classes found in the alpine tundra had larger soil carbon stock sizes and higher carbon concentration value than the vegetation class in the treeline ecotone, but not all were significantly different. Elevation had only a very minor influence on carbon concentration, and non-significant effect on carbon stock.

Altogether, the results indicate that carbon stock and carbon concentration in the organic soil layer is larger for the vegetation classes in the alpine tundra than the vegetation class in the treeline. An expansion of the treeline could further lead to higher CO_2 emissions and have positive feedback on global warming. The study illustrates how the expansion of trees into alpine tundra could affect the carbon storage in the top organic soil layer.

Sammendrag

En utvidelse av den nåværende tregrensen til den alpine tundraen kan få ytterligere påvirkninger på karbonlagring. Ny forskning viser at en utvidelse av trær til den alpine tundraen kan føre til høyere CO_2 utslipp, og dermed gi en positiv tilbakemelding på global oppvarming. Da de fleste studier undersøker de mulige påvirkningene en økt tregrense vil få for karbonlagring for alle økosystemer i tundraen, er det ennå få studier som undersøker karbonlagring i de ulike vegetasjonsklassene vi finner i tregrensen og den alpine sonen. Denne studien undersøker eventuelle forskjeller i karbonlager og karbonkonsentrasjon mellom vegetasjonsklasser i tregrensen og den alpine tundraen etter kartleggingsverktøyet Natur i Norge (NiN).

I studiet ble jordprøver fra det øvre organiske laget samlet inn. Totalt fem forskjellige vegetasjonsklasser i tregrenseøkotonen ble undersøkt: skog, leside, rabbe, lavhei, og lynghei langs en 600-kilometer transekt i Midt- og Sør-Norge. Feltarbeidet ble gjennomført fra sen juli til sen august i 2021. Fra jordprøvene ble både karbonlager og karbonkonsentrasjon estimert. Videre statistiske analyser ble gjennomført for å finne eventuelle forskjeller mellom karbonlager- og konsentrasjon for de forskjellige vegetasjonsklassene i tregrenseøkotonen. For å ta hensyn til om variasjon i karbonlager- og konsentrasjon ble forårsaket av prøvetakingsdesignet (studiested og lokasjon for hver prøve), ble en lineær «mixed model» brukt. Høydemeter over havet ble også inkludert for å undersøke mulige endringer i karbonlager- og konsentrasjon ved økt høydemeter.

Alle vegetasjonsklasser i den alpine tundraen hadde et større karbonlager og en høyere verdi for karbonkonsentrasjon sammenlignet med vegetasjonsklassen i tregrensen, men ikke alle hadde en signifikant forskjell. En økning i høydemeter hadde ingen påvirkning for karbonlager, men svak tendens for lavere karbonkonsentrasjon ved økt høydemeter

I alt, indikerer resultatene på at karbonlager og karbonkonsentrasjon er høyere i alle vegetasjonsklasser over tregrensen. En utvidelse av tregrensen inn til den alpine sonen kan derfor føre til et høyere utslipp av CO_2 og dermed gi en positiv tilbakemelding på global oppvarming. Studien illustrerer hvor viktig det er å undersøke hvilke konsekvenser en økt tregrense kan føre til for karbonlagring, og hvordan ulike vegetasjonsklasser har forskjellig karbonlagring i det organiske jordlageret.

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Introduction

The alpine treeline ecotone is expected to expand into the alpine tundra, which will give rise to profound changes in the tundra vegetation. Harsch et al. (2009) carried out a global literature review and found that treelines advanced in 52% of all study sites included in the study during the last century. However, other studies, such as Kullman and Öberg (2009), estimated that 95% of all treelines in Sweden migrated into the treeless alpine zone. The study found that the treeline has risen 70-90 vertical meters in the last century for Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris*), and mountain birch (*Betula pubescens* ssp. *czerepanovii*). Their findings indicated that the main driver was temperature, as they found that treelines trended to decline during two decades of cold periods. Other studies show similar findings, in addition to other factors such as moisture and precipitation. (Beckage et al., 2008; Elmendorf et al., 2012; Grytnes et al., 2014). Danby and Hik (2007) found that a higher annual temperature caused by climate change led to treeline advances higher in the south-facing slope, and that the density increased in the north-facing slope. However, this would be highly site-dependent as Tingstad et al. (2015) found that more seedlings survived and emerged in the alpine zone in contrast with boreal forest in an experimental seedling sowing. Their results indicated that low temperatures do not limit seedling survival but rather that site precipitation is the primary driver of seedling establishment in the alpine zone (Tingstad et al., 2015).

After the publication of Harsch et al. (2009) on treeline migration, a plethora of papers have been published studying local treeline expansion into the alpine tundra and the impact it can have. The reduction of snow cover caused by upward migration of the treeline would exacerbate the net warming feedback, leading to a higher accumulation of energy in the biosphere (de Wit et al., 2014; Wramneby et al., 2010). It would also negatively impact the albedo effect as the reflection from snow cover would be more reduced than previously due to a denser tree cover (de Wit et al., 2014; Kharuk et al., 2009).

Reduced albedo effect could lead to a strengthening of the temperature impacts by causing a higher average temperature in the treeline ecotone and alpine tundra. Additionally, this can increase CO_2 effluxes from forests and tundra soils, as moisture availability would no longer be limited for decomposition processes (Sjogersten & Wookey, 2009). However, the total amount of biomass tends to decrease significantly with the transition from forests to non-forests (Hansson et al., 2021).

Therefore, it is likely that a higher treeline would store a higher amount of above-ground carbon in biomass compared with alpine plant communities and lead to a higher carbon sequestration (Hansson et al., 2021).

As high altitude alpine forests are generally restricted by cold temperatures, treeline intruding into sensitive alpine communities has been observed in Norway (Speed et al., 2015). Therefore, alpine plant communities face a disproportional risk, as range-restricted species have more difficulty finding new suitable habitats (Dirnböck et al., 2011; Hansson et al., 2021). Furthermore, this may force the alpine communities to migrate even higher into the alpine zone, as the competition of the novel species can make survival in their original niches difficult. There is a commonality of evidence that alpine plant communities are negatively affected by treeline migrations upward (Greenwood & Jump, 2014). Alpine species cannot survive in the forest below the treeline, mainly because of competition (Sætersdal & Birks, 1997), and the impacts the forest has on the soil decomposition organisms, pH value, nutrient content, and soil moisture (Greenwood & Jump, 2014; Grytnes et al., 2014).

A change in the treeline would further affect the vegetation communities of small populations, which often occurs in the alpine zone, and suffer from migration due to competition and diseases (Aitken et al., 2008). Wardle et al. (2004) found that aboveground plant communities and belowground microbial communities live in an interdependent relationship, and changes in vegetation communities could further affect carbon sequestration (Friggens et al., 2020; Sjogersten & Wookey, 2009).

There have been relatively few studies on the relationships between soil carbon stock pool sizes and vegetation composition in alpine plant communities, and how the composition influence the decomposition rate of soil organic matter (SOM) (Hartley et al., 2012). Bartlett et al. (2020) linked that from a global perspective, alpine and especially tundra ecosystems are believed to have one of the largest terrestrial soil organic carbon values of all ecosystems' carbon pools, mainly due to the storage capacity of permafrost mires. Moreover, carbon stocks in other alpine communities are also affected by the immigration of species such as Norway spruce, Scots pine, and mountain birch as tundra heaths seem to have a much larger carbon storage in the SOM compared with more productive mountain birch forests (Hartley et al., 2012).

Sjogersten and Wookey (2009) found that decompositions rates are slower in the tundra heath compared with the mountain birch forests, and an advance in mountain birch forests will lead to an initial pulse of CO_2 emission from soil to the atmosphere as decomposer organisms would metabolize the labile carbon stored in the tundra heaths. Other studies indicate that the upward expansion of forests had a small net effect on carbon storage in tundra heaths, but that mineralization rates in forests were much greater and therefore caused a higher carbon turnover rate in the SOM. Furthermore, this led to an accelerated carbon cycling in the forests compared with tundra heaths (Hansson et al., 2021; Kammer et al., 2009).

Sørensen et al. (2018) found that alpine heath and meadow communities undergoing migration of shrubs could decrease the total ecosystems carbon pools and, therefore, also increase the atmospheric CO_2 concentration due to a net CO_2 release from the below-ground carbon pools. Therefore, there is a possibility that treeline expansion into the alpine communities would lead to an adverse change in vegetation classes and carbon storage.

Due to the ongoing climate crises, carbon sequestration and emissions have become an important topic. Therefore, it would be interesting to examine if there is a difference in carbon stocks and concentrations between vegetation classes and which classes store the most carbon in the soil organic layer. Classifying the different carbon stock and concentration in different vegetation classes could help us calculate the carbon storage in the uppermost and not well-defined high altitude plant communities. During the last years, a study has been exploring the usage of aerial imagery to map the vegetation classes in the alpine zone (Mienna et al., 2022). By finding the average expected carbon storage in each vegetation class in the alpine tundra, we could predict the amount of carbon storage and the impact an upward expanding treeline would have on the carbon pools in the tundra with low-cost aerial imagery and fieldwork.

This study investigates the soil carbon stock and carbon concentration in different vegetation classes in the boreal treeline ecotone and alpine tundra. The vegetation classes were defined according to the comprehensive classification system Nature Types in Norway (NiN) (Artsdatabanken, 2015), and the focal ground types in this study were forest, lee side, ridge, sub-xeric heath and xeric heath. Altogether, difference in carbon stock and carbon concentration between vegetation classes along the forest-tundra ecotone gradient in central- and southern Norway can be identified by collecting the top organic soil layer.

The main objective of this study was to study the differences in soil carbon stock and concentration between different vegetation classes in the forest-tundra ecotone. The hypotheses for the study were that 1) the soil carbon stock and concentration is different between vegetation classes and that 2) vegetation classes above the treeline have significantly higher quantity of soil carbon stock and concentration compared to vegetation classes below the tree cover.

Methods and Materials

Study area

The study was conducted at selected study sites along the forest-tundra ecotone in central- and southern Norway (Fig. 1). The study sites were distributed between 59° and 65° north. The climate in the entire study area is continental, with a mean temperature of about 9°C during the summer season (Jun, Jul., Aug., and Sep.) and -6°C during winter (Dec., Jan., Feb., and Mar.), and mean daily rainfall during the growing season is 4 mm (Mienna et al., 2020). The elevation at the sites differed between 1200 meters above sea level and 350 above sea level (Mienna et al., 2022).

In the treeline ecotone, the most prevalent tree species are mountain birch, Scots pine, and Norway spruce with interspersing of low shrubs and bushes, typically dwarf birch (*Betula nana*) and several shrubs in the willow family (Hauglin et al., 2018). At the alpine tundra, vegetation communities varied between and within sites. Shrubs such as *Empetrum nigrum* L., *Calluna vulgaris* (L.) Hull, *Vaccinium spp*, and lichens (e.g., *Cladonia* spp.) dominate at species-poor sites (Fig. 2A), and forbs and graminoids dominate at species-rich sites (Mienna et al., 2020) (Fig. 2B).

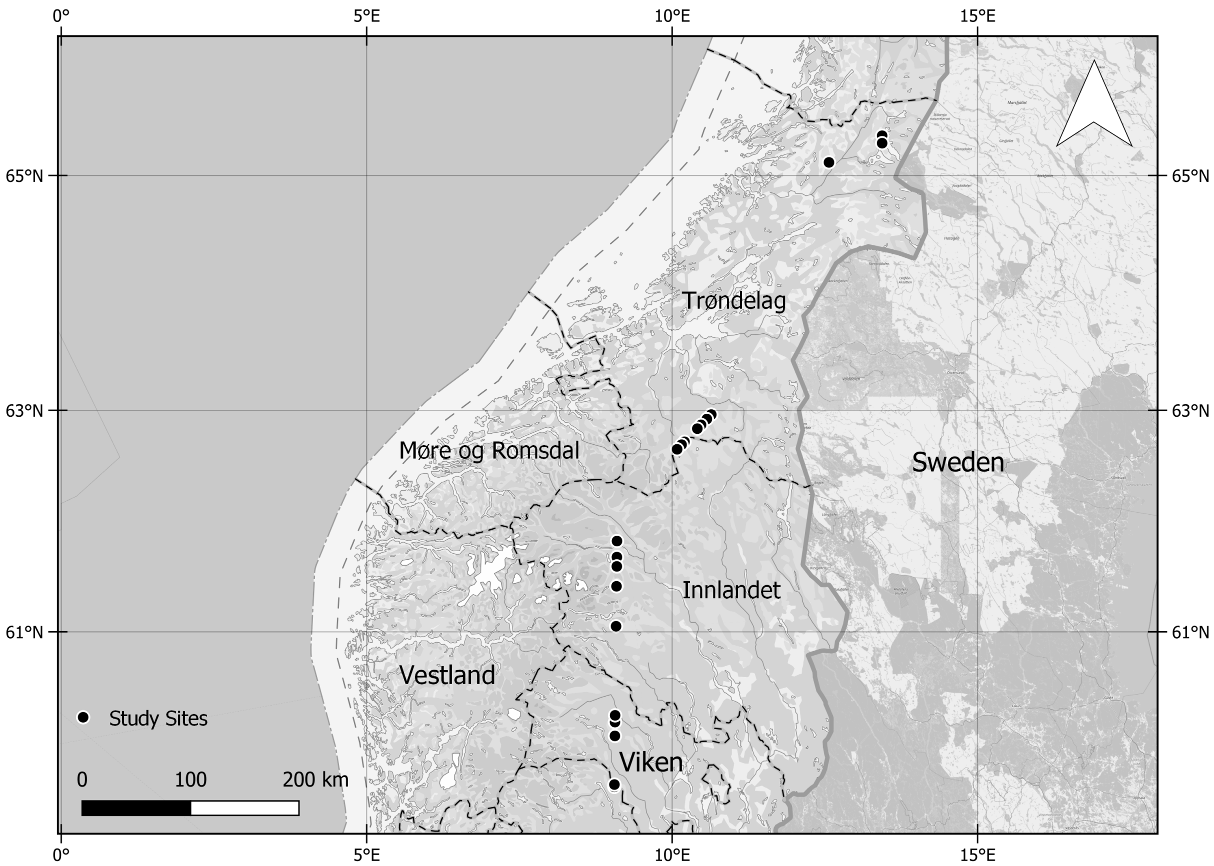

Figure 1: *Location of the 19 study sites (black dots). The map was made using QGIS version 3.16 Hannover (QGIS Development Team, 2021).*

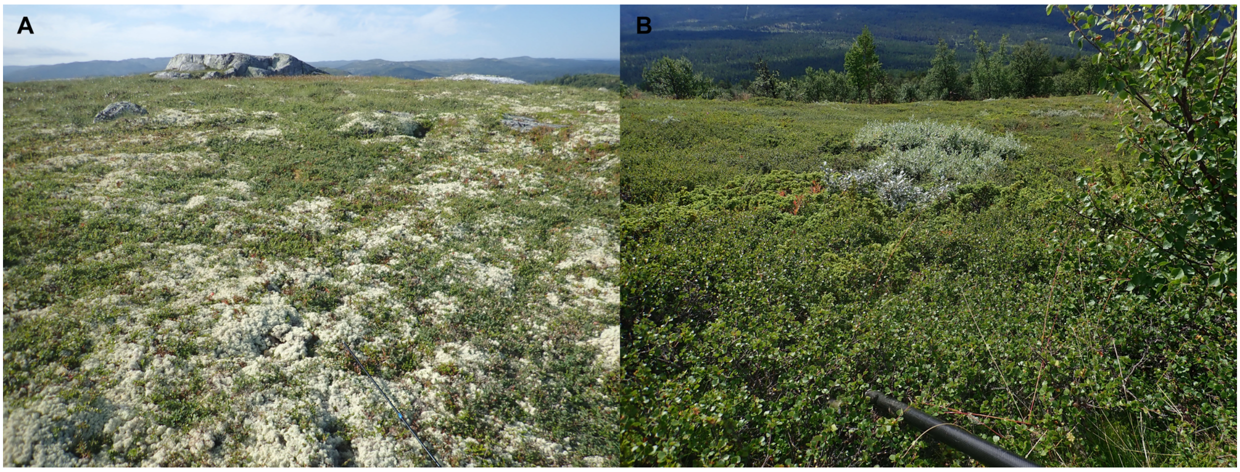

Figure 2: *Picture of typical study sites. To the left (2a) species-poor vegetation classes and to the right (2b) species-rich vegetation classes.*

Data collection

The top organic soil was sampled in vegetation classes in the treeline ecotone and alpine tundra. Altogether, nineteen sites were visited in a transect of 600-kilometer and encompassed three counties (Viken, Innlandet, and Trøndelag) (Fig. 1). Initially, the sites were used to collect field data to determine the expansion of trees using height values from airborne laser scanning (Thieme et al., 2011) and have been revisited in 2018, mapping different vegetation classes with aerial imagery (Mienna et al., 2020).

The sampling was conducted from late July to late August to avoid frost and snow at the sites. A handheld GPS with preloaded coordinates was used for navigation to each site. Each site covered an area of approximately 250 by 50 meters, including both the treeline ecotone and alpine tundra (Fig. 3). Altogether, a base for equipment was established for each site, often in the middle of the study site to get an overall perspective of the study site.

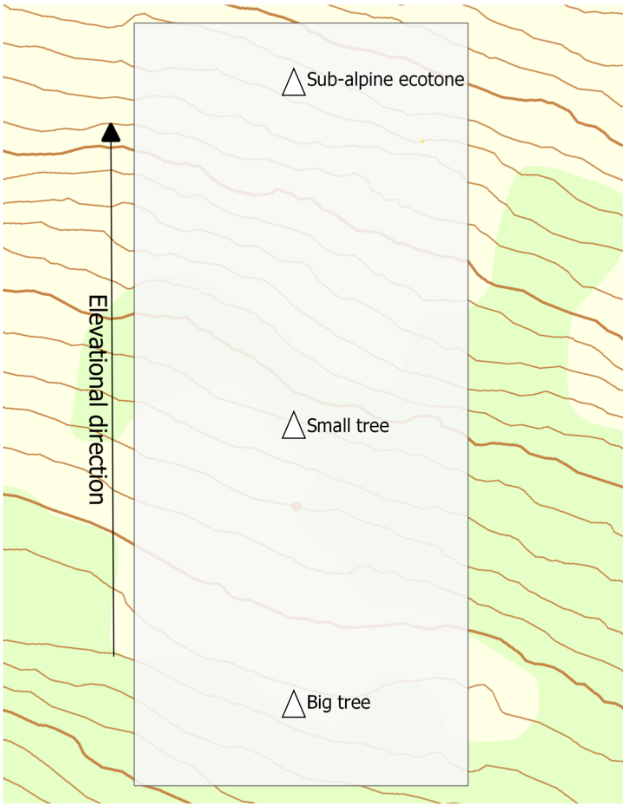

Figure 3: *Sample design for study site, covering the transition from the treeline ecotone into treeless alpine tundra.*

Selection of solid sample points

Four cluster lines were established at each site; two cluster lines in the alpine tundra, one in the transition between the treeline ecotone and alpine tundra, and one in the treeline ecotone, representing different vegetation classes, respectively: forest, lee side, ridge, sub-xeric heath, and xeric heath. Ridge was only represented in two sites, as the other four vegetation classes were prioritized (see Appendix 1 to see which vegetation class was covered at each site). A vegetation map from a previous study (Mienna et al., 2020) developed based on remotely sensed optical data (spectral information) was used as guidance when classifying vegetation class in each cluster lines.

For the alpine tundra, the cluster line was established at the highest point within the respective study site. By using a surveyors' tape, the samples were extracted 0.5 m, 1.2 m, 1.6 m, 2.4 m, and 4 m parallelly in north and south directions (Fig.4). The middle point of the cluster line was at the start of the surveyors' tape. A cylindrical soil corer with a diameter of 6.35 centimeters was used to extract the soil samples. Altogether, ten samples were extracted from the alpine tundra. The location of the cluster line in the alpine tundra is further called "TP".

For the cluster line in the transition zone, the cluster line had to be established within the first encountered tree of the most abundant tree species with a height lower than 2 meters (small tree <2m, ST). ST was found by walking downhill, starting at the highest point in each site. The cluster line in the treeline ecotone was established by the same procedure, but the tree had to be taller than 2 meters (Big tree >2m, BT), and qualify as a forest after FAO`s definition of forest (UNFCCC, 2001). The cluster lines established in the treeline ecotone and transition zone were required to be located more than 10 meters away from each other. The same procedure for the extraction of soil samples was used for STs and BTs as for TPs, only that the tree stem was the middle-point of the cluster line (Fig. 4). Altogether, ten samples were extracted from each of STs and BTs.

In order to get a respective number of samples from all vegetation classes, five additional samples were collected for the vegetation class not yet represented in the three other cluster lines at each site. For establishment of the cluster line, the vegetation map from Mienna et al. (2020) was used as guide to select potential sampling locations. The samples were taken in the middle of the vegetation class in north pointing direction.

When the vegetation map was missing classification or clearly predicted the vegetation class wrong, the species composition, tree crown cover, moisture ability, and wind-exposure were used, respectively, following the classification of vegetation classes in NiN (see chapter: Comprehensive classification system Nature Types in Norway for a more detailed description of NiN).

When the sample point (SP) was located on bare rock, we moved the SP up to one meter on a perpendicular line to the original sampling point. If the sample still couldn't be extracted, the sample was omitted.

The mineral layer was measured and left behind if samples clearly distinguished between organic and mineral soil in the field. Each sample was packed in plastic 6L bread bags. The depth of the sampling hole was measured at its most profound and shallowest with a folding ruler, and the average height was registered in the field form. The two most abundant plant species were identified within a radius of 30 cm, counting the sample hole (Specie 1 and Specie 2) to classify dominant specie for each SP.

Each SP was given a specific name after where it was extracted, study site – if the SP was taken within ST (SP1), BT (SP2), TP (SP3), or as the five additional samples (SP4) – which elevation direction it was taken in – decreasing elevation starting closest to ST, BT, or TP from 00 - 05, increasing elevation starting closest to the middle 10 - 15 (Fig. 4). Each bag of soil included a label with its specific name.

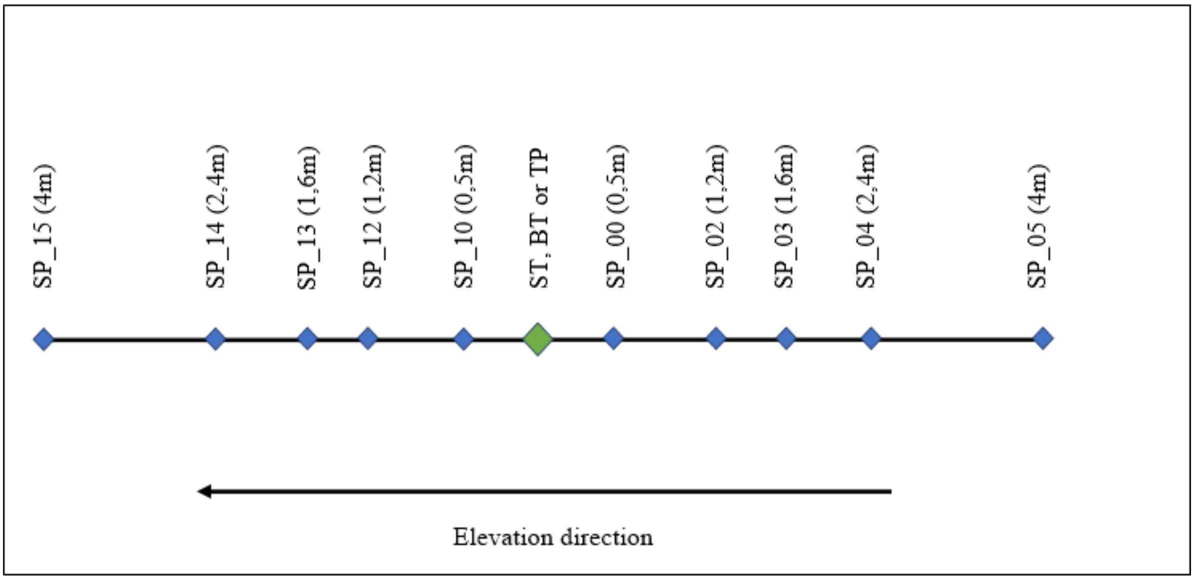

Figure 4: *Sample design for each vegetation class. For the five extra samples, everyone is taken in north going direction and was given the name SP4_00 – SP4_05.*

The position of TP, ST, BT, and the additional five samples was registered using an RTK GNSS receiver and given a position-ID registered in the field form.

Altogether, thirty-five top organic soil samples were extracted at each of the nineteen study sites. Thirteen sites were dominated by mountain birch, three sites were dominated by Norway spruce, and the last three site was dominated by Scots pine.

Comprehensive classification system Nature Types in Norway

For categorizing the vegetation classes, we used the comprehensive classification system NiN, developed by the Norwegian Biodiversity information system (Artsdatabanken, 2015). NiN is the standard instrument describing the nature environment for all nature systems in Norway.

NiN meets the needs of different sectors for a common conceptual framework for mapping nature and handles nature variation on all scales. NiN can be adapted for many different purposes, describing nature environments on a large scale (landscapes) and nature types at a small scale describing an organism's life stages. NiN is supposed to be adaptive to whoever uses it and for different usage. The system covers all of nature in Norway, covering all life from the most profound ocean systems to high altitude mountains.

NiN is divided into three systems: *landscape*, describing large scale areas at a diversity level with few details, *nature system,* describing ecosystems in a delimited area, and *life medium*, describing the living conditions down to each organism to the closest detail.

In this study, the NiN system *nature system* was used to describe the respective vegetation classes studied. Further, NiN divides the *nature system* into two central survey systems, whereas both need to be used to get an overall description of the nature variation in the different ecosystems. These are called type-division (Typeinndeling) and the appellative-system (Beskrivelsessystemet). The type-division is further divided into a tripartite hierocracy. Highest in the hierocracy, we find the main type-group. There are eight main type-groups, and in this study, all vegetation classes examined are to be found under mainland systems (T, Fastmarkssystemer).

Furthermore, there are forty-five under-groups of the mainland system, called *main-groups* (hovedtyper). In three of these groups, we find the vegetation classes chosen in this study; xeric heaths, lee side, and tundra (T3, fjellhei, leside og tundra), mainland-forests (T4, fastmarksskogsmark), and ridge (T14, Rabbe). At last, NiN divides the *main-groups* further into *ground-type classes* (grunntype), which is the closest we come to what NiN categorizes as nature type.

In each *ground-type class*, there is several nature-type groupings depending on lime in the soil and bedrock, but because of limited time and knowledge, we classified each of these under-groups as the same *ground-type class*.

In this research, the five most common *ground-type classes* according to NiN represented in each site were chosen: forest (skog), lee side (leside), ridge (rabbe), sub-xeric heath (lavhei), and xeric heath (lynghei) (see Appendix 2. for more detailed categorizing of each NiN class). Classification and description for each *ground-type class* is described more detailed in Mienna et al. (2022).

Processing of soil samples

The samples were stored in a freezer at Ås in Sørhellinga, holding approximately -16 C°, in order to prevent the living green parts with bryophytes from starting decomposition before further treatment.

The samples were taken out of the freezer and stood for thawing overnight until they were "half-frozen." All photosynthetically active biomass was carefully removed with a scalpel. Thickness was measured and registered in an excel sheet.

Afterwards, mineral soil was separated from organic soil if possible. The thickness and weight were measured with a folding ruler and a milligram weight, respectively, and registered in the excel sheet. Weighing was done in an aluminum tube where the weight of each tube was removed before weighing the sample. Thickness and weight were also registered for the organic soil layer.

Next, each sample was dried to a constant weight at 40 C° in a drying cabinet. Labels with IDs were put together with the tubes and the trimmed sample. Every sample was dried over two days. After drying, all mineral soil not already removed was again measured, weighed, registered, and thrown. The mass and length of the dried organic topsoil were then measured, noted, and further stored in paper bags along with the label. Only the organic soil was used in further analysis.

The samples were then grinded into powder with a grinding machine (Rotary mill from Brabender Duisburg). After grinding, the samples were stored in the same paper bags. Each bag was taped at the open parts to avoid losing any powder.

To calculate each sample's carbon stock and concentration, ten milligrams was placed in a small tin weighing boat (4 x 4 x 11 mm) that were folded into tiny packages. A small spoon and a pair of tweezers were used in order to prevent contamination when filling and folding the packages. An XPR micro and ultra-micro balances (Mettler Toledo) weight was used to get the exact weight of the tin boat. The weight of each tin boat was removed before weighing the soil. The weight was automatically registered into a computer, and the sample was put in a microtube (15 ml). Each sample was given a number from 1-to 667, representing its exact location. The number was written down on the computer sheet as well on the microtubes where the tin boats were stored. To determine the carbon concentration, the samples were ran through a microtube elemental analyzer (Elementar analysensysteme GmbH, Hanau, Germany). Further, the carbon concentration was used to find carbon stock in the equation:

$$SOC_{stock}\ (Kg\ m^{-2})\ = Bulk\ densiy\ (g\ cm^{-3})\ \times\ Soil\ depth\ (cm)\ \times\ SOC_{concentration}(\%)\ \times\ 0{,}1\ .$$

Statistical analysis

All statistical analyses were conducted using R-Studio in R version 4.0.4 (R Core Team, 2021). A Shapiro-Wilk test was initially applied to determine if carbon stock and concentration from the samples were normally distributed. The data was not normally distributed; therefore, a Kruskal-Wallis test was used to determine if there are any significantly difference for both carbon stock and concentration between the respective vegetation classes. After confirming differences in carbon stock and concentration between vegetation classes, a Dunn`s test was applied to assess which vegetation classes that differed from each other.

The main aim of the study was to assess the difference in carbon stock and concentration between different vegetation classes, in addition to account for variation due to study sites and sample lines. Therefore, the two different response variables, carbon stock (Model 1) and carbon concentration (Model 2) were fitted using a linear mixed modelling (LMM) approach. Because the data don’t follow a normal distribution, both response variables were log-transformed to get a linear relationship between the dependent and independent variables. The fixed effect was “vegetation class” and “Elevation”, and the random effects were “sample line” and “Site ID”, where sample line was nested within site ID.

The packages ggplot2 (Wickham, 2016), sjPlot, and pbkrtest (Nakagawa et al., 2017) were used to make plots and summary tables for the two linear mixed models.

Model 1 = *Carbon stock* as response variable *Vegetation* class and *Elevation* as fixed effects + *Sample line* and *Site ID* as random effects.

Model 2 = *Carbon concentration* as response variable *Vegetation* class and *Elevation* as fixed effects + *Sample line* and *Site ID* as random effects.

Results

Altogether, 689 soil samples were collected, of which 80 were discarded due to vegetation uncertainty and missing SOM in the samples. In total, 609 samples were used in the statistical analysis. The number of soil samples used per vegetation class varied, with a minimum of twenty (ridge) and a maximum of 280 (forest) (Tab. 1). Forest had the highest number of soil samples (45%), followed by sub-xeric heath (22%), lee side (15%), xeric heath (14%), and ridge (3%). To assess if there is a significant difference between soil carbon stock and concentration in vegetation classes in the treeline ecotone compared to alpine ecotone, the median and means for soil carbon stocks and concentration were calculated (Tab. 1).

Of all vegetation classes, forest had the lowest value of both carbon stock and concentration (Tab. 1, Fig. 5). The quantity of carbon in vegetation class lee side was 94% higher than forest (Tab. 1, *Median*, Fig. 5A). For carbon concentration, the vegetation class with the highest median concentration was 6% higher than the soil samples in the forest (Tab. 1, *Median*, Fig. 5B).

Table 1: *Summary of all the samples used in the study, the number of samples for each vegetation class, the median and mean of soil depth, weight, carbon stock, carbon concentration, and bulk density.*

Vegetation class	Number of samples	Soil depth (cm)	Organic soil mass (g)	Carbon stock (kg/m^2)	Carbon concentration (%)	Bulk density (g/cm^3)
Median						
Forest	279	3.0	15.8	1.8	39.3	0.16
Lee side	90	5.0	27.4	3.5	43.7	0.17
Ridge	20	3.0	17.1	2.4	45.3	0.17
Sub-xeric heath	134	3.0	15.6	2.1	42.1	0.17
Xeric heath	85	3.5	16.5	2.2	44.5	0.15
Mean						
Forest	279	4.2	21.6	2.8	37.8	0.18
Lee side	90	5.6	31.7	4.3	41.2	0.19
Ridge	20	3.0	18.3	2.4	43.5	0.22
Sub-xeric heath	134	3.7	20.9	2.7	39.7	0.20
Xeric heath	85	4.6	23.0	3.3	41.4	0.17

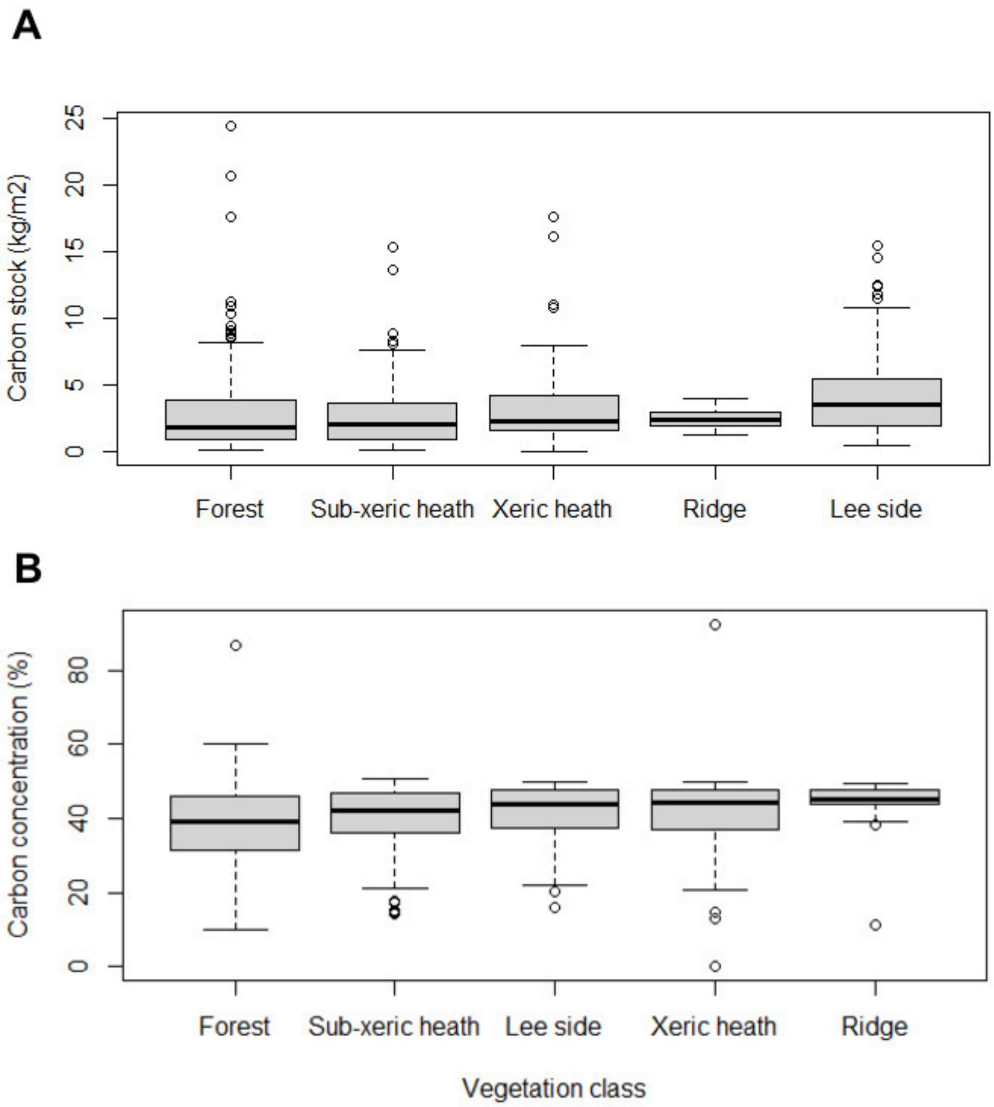

Figure 5: *The median of carbon stock (A) and concentration (B) and their respective outliners in all vegetation classes. The estimates are sorted in descending order, from the highest to the lowest value.*

A Shapiro Wilk test indicated that both predicting variables significantly deviated from a normal distribution (p-value <2.2e-16). The Kruskal test confirmed a significant difference between vegetation classes carbon stock and concentration (P= 0.00001 / P = 0.0003), and a Dunn`s test showed a significant difference in carbon stock between vegetation classes: forest and lee side (P= 4.63e-6), and lee side and sub-xeric heath (P=5.00e-4). For carbon concentration, Dunn`s test revealed a significant difference between forest and lee side (P= 0.04), forest and ridge (P=0.02), and forest and xeric heath (P=0.01).

The variance component of the random effects “Sample line” and “Site ID” was 19% and 35% for model 1 and 5% and 11% for carbon concentration. According to the models, all vegetation classes have a higher carbon stock and concentration value than forest (Tab. 2).

Accordingly, the two models marginal R^2 is close to zero, indicating that the model’s fixed effects do not explain much variation in carbon stock and concentration. The conditional R^2 for carbon stock and concentration indicates that the random effects explain additional variance compared to the fixed effects (Tab. 2).

Elevation did not affect the carbon stocks in different vegetation classes (P= 0.126; Tab. 2). There was a difference in the slope for carbon stock for the vegetation classes lee side (P= 0.01) and xeric heath (P =0.046) compared with forest, but no difference in slope for the vegetation classes ridge and sub-xeric heath. Carbon concentration decreased with elevation (P=0.013; Tab. 2). There was no difference in slope for the different vegetation classes.

Table 2: *LMM summaries and comparison of the two different response variables with the fixed effect vegetation class and elevation. Forest is the reference group that the other vegetation classes are compared with, Df = degrees of freedom of the respective models. σ2 = Population variance, τ00 = random intercept variance, ICC = intraclass correlation.*

	Model 1				Model 2			
Input	**Carbon stock**				**Carbon concentration**			
Predictors	*Estimates*	*CI*	*p*	*Df*	*Estimates*	*CI*	*p*	*Df*
(Intercept)	1.57	0.24 – 2.90	**0.023**	17.74	4.04	3.69 – 4.38	**<0.001**	17.60
Lee side	0.61	0.27 – 0.95	**0.001**	51.14	0.11	-0.02 – 0.23	0.087	58.52
Ridge	0.25	-0.49 – 0.98	0.503	40.00	0.16	-0.09 – 0.40	0.206	39.78
Sub-xeric heath	0.09	-0.23 – 0.41	0.553	40.13	0.07	-0.04 – 0.18	0.230	39.76
Xeric heath	0.39	0.01 – 0.78	**0.046**	46.29	0.03	-0.10 – 0.17	0.626	49.37
Elevation	-0.00	-0.00 – 0.00	0.126	17.36	-0.00	-0.00 – -0.00	**0.013**	17.04
Random Effects								
σ^2	0.55				0.13			
τ_{00}	0.13 Sample line				0.01 Sample line			
	0.29 Site ID				0.02 Site ID			
ICC	0.43				0.15			
N	64 Sample line				64 Sample line			
	19 Site ID				19 Site ID			
Observations	524				536			
Marginal R^2 / Conditional R^2	0.090 / 0.483	0.066 / 0.208						

Discussion

The treeline ecotone is a functional wall separating the different ecosystems between boreal forest and alpine tundra. Treeline ecotones are expected to migrate upwards in elevation with global warming, leading to a change in alpine plant communities. The migration of treelines and its implications for carbon storage have been studied elaborately (Devi et al., 2008; Greenwood & Jump, 2014; Hansson et al., 2021; Harsch et al., 2009; Hartley et al., 2012; Kullman & Öberg, 2009; Sjogersten & Wookey, 2009). However, few research papers have studied how carbon storage differs between different vegetation classes in the treeline ecotone and alpine zone. In this study, differences in soil carbon stock and concentration between five vegetation classes in the treeline ecotone and alpine tundra after the classification system of NiN; forest, sub-xeric heath, xeric heath, ridge, and lee side were estimated. Elevation was also included to study how soil carbon stock and concentration was affected by increasing elevation.

There was a significant difference in carbon stocks between the vegetation classes forest and lee side, and lee side and sub-xeric heath. There was a significant difference between forest and vegetation classes lee side, xeric heath, and sub-xeric heath for carbon concentration. The results acknowledge what other research papers have reported (Hartley et al., 2012; Parker et al., 2015), that the alpine vegetations have a higher amount of carbon storage than the vegetation in the treeline ecotone. The data suggest a higher quantity of carbon stock and concentration in the vegetation classes in alpine communities, as forest had the lowest amount of carbon (Figure 5). There was no significant decrease in carbon stocks with increasing elevation (Table 2). However, there was a significant decrease in carbon concentration with increasing elevation (Table 2).

Several research studies have assessed the difference in carbon storage in the treeline ecotone and alpine tundra with conflicting results. Some found that tundra had higher carbon storage in soil organic litter (Hartley et al., 2012; Sjogersten & Wookey, 2009; Sørensen et al., 2018). Others indicate that an extended treeline into the treeless alpine tundra would increase the above-ground biomass, leading to a slight net loss or even greater carbon storage and sequestration (Epstein et al., 2012; Hansson et al., 2021; Kammer et al., 2009). In this study, the difference between treeline ecotone and alpine tundra soil carbon storage has been assessed, investigating if there could be any difference between five vegetation classes after NiN in both the forest and tundra. However, there are no other studies examining the difference between vegetation classes in the two different zones, and therefore, there are no comparable studies to interpret the results in this study.

Soil carbon stocks in different vegetation classes

As stated above, other studies in the tundra found a higher amount of carbon stock than the treeline ecotone. As forest was reported to have the lowest amount of carbon stock, lee side and ridge were the vegetation classes with the highest reported values.

Carbon stock was highest at the vegetation class lee side and significantly differed from the vegetation class forest. During winter lee side is often covered by a thick layer of snow, providing cover and warmth, further reducing frost damage (Mienna et al., 2022). The snow provides moisture during the growing season, leading to a more favorable habitat for plants such as dwarf shrubs and grasses. As moisture is often the limiting factor (Elmendorf et al., 2012), the growth and photosynthesis are greater in the lee side than in the other vegetation classes and may have favorable conditions to store a higher amount of carbon stock. In this study, lee sides were often found at the border of the treeline ecotone and the start of the alpine tundra. Thereby some samples were taken under some trees classified as "small trees (<2m)". However, the trees growing here did not fall under the classification definition of "forest" after the FAO definition of forest (UNFCCC, 2001), and we can classify lee side as a vegetation class in the alpine tundra zone (Artsdatabanken, 2015).

It was unexpected that the size of the carbon stock in the vegetation class ridge did not differ from that in the forest. Ridge is often found in harsh and windy environments, and species have adapted their lives to a challenging climate and need to endure wind erosion, desiccation, and snow and ice scouring. The vegetation class varies from little top organic layer covered by lichens and mosses to rocky and sandy ground (Artsdatabanken, 2015). As decomposition rates are expected to be low for ridge due to the harsh environment and little moisture availabillity, it was unexpected that the ridge carbon stock size equalled that in the forest. However, the generalizability is limited by a small sample size with only twenty samples collected from two different study sites and are not representative for the whole study area.

As for the vegetation class ridge, it was unexpected that the size of the carbon stock in the vegetation class xeric heath did not differ from forest. Xeric heath is classified under the same main type as lee side and sub-xeric heath, only that it is more exposed to desiccation than lee side. As well as for the vegetation class lee side, xeric heath was found in the border of the treeline ecotone and alpine tundra, but did as lee side, not fulfill the definition of beeing classified as forest. Due to the limiting factor of moisture, lower temperature, and limiting decomposer organisms, it was expected xeric heath should store a higher carbon stock size than forest.

For the vegetation class sub-xeric heath, there was a weak tendency that the vegetation class had a higher value of carbon stock than forest. As mentioned before, sub-xeric heath is classified under the same main type as lee side and xeric heath but is more exposed to wind and desiccation (Artsdatabanken, 2015). Because of the harsh environment, it does not differ as much from the vegetation ridge, except that sub-xeric heath has a bit better snow cover during winter and is not as wind-exposed as ridge, which makes it possible for species such as *Empetrum nigrum* (L.) to get a better establishment along with lichens and mosses.

There may be several reasons for vegetation classes in the alpine tundra to have a higher carbon stock in the top organic layer than vegetation class forest in the treeline ecotone. Some studies have examined the relationship between carbon cycling with net nitrogen mineralization (Kammer et al., 2009) and found that mineralization increases with forest expansion, thereby favoring the microclimate for decomposing organisms, leading to higher emission of CO_2. Others have found that improved thermal energy and moisture would be readily degradable by soil microorganisms (Sjogersten et al., 2003), leading to higher carbon emissions due to favorable climate for novel species such as trees, thereby favoring habitats for decomposer organisms as well. The decomposition rate is generally slower in the alpine tundra compared with the treeline ecotone due to a less favorable climate for decomposer organisms (Sjogersten & Wookey, 2009). For lee side, xeric heath, and sub-xeric heath, one of the most common species is *E. nigrum* (L.) and *Calluna vulgaris* (L.) Hull, where several studies have found that they degrades extremely slowly (Parker et al., 2015; Parker et al., 2018; Van Meeteren et al., 2007) and, over time, stores high values of carbon storage due to the slow decomposition of the dead litter. However, one of the most dominating species in the vegetation class forest in this study were *E. nigrum* L. *Calluna vulgaris* (L.) Hull, indicating the composition of species does not affect the carbon storage, which may explain the unespected non-significant results from ridge, sub-xeric heath, and xerich heath (see Appendix 3 for the most common dominating species in each vegetation class).

Another factor essential to include is that the fungi community changes from forest to alpine tundra, potentially affecting the storage of carbon stock between the treeline ecotone and alpine tundra. Clemmensen et al. (2021) found that the ericoid mycorrhiza in the tundra had a more considerable deposition in the organic matter in the soil compared with the ectomycorrhizal dominating in the forest which restricted organic matter accumulation.

Soil carbon concentration in different vegetation classes

The same results are reported in carbon concentration as reported for carbon stock. Vegetation class forest had the lowest carbon concentration compared with the vegetation classes in the alpine tundra.

Vegetation class ridge had the highest percentage of carbon on average (Table 1, *mean)* for all vegetation classes, and significantly differed from forest. Species growing in the ridge are, as mentioned before, lichens and mosses, which have low decompositions rates. Therefore, they may be better at storing carbon in the soil over a more extended period, and mineralization is not as high compared with vegetation class forest.

Ridge, lee side, and xeric heath had a significantly higher carbon concentration than the forest. Sub-xeric heath had a higher concentration, but was not significantly different from forest. In line with the hypothesis and other research (Hartley et al., 2012; Sjogersten & Wookey, 2009), most of the vegetation classes in the alpine tundra store a higher percentage of carbon than the treeline ecotone.

As previously mentioned, the explanatory factor may be the different compounds of the fungi community, and poorer litter quality may be the reason for higher carbon concentration in the alpine tundra compared to the treeline ecotone (Clemmensen et al., 2021; Kammer et al., 2009; Sjogersten & Wookey, 2009).

Sample line, Site ID, and elevation

The variation in carbon stock and concentration for vegetation classes can be explained with sample line and site ID, as the model predict that the variation increased including these factors. The results indicates that carbon stock and concentration between vegetation classes is site dependent, and as well are dependent on where we are in the forest-tundra ecotone. It may be explained with factors such as temperature, as the study area had a transect of 600 km, temperature decreases the further north we go, and thus, carbon stock and concentration may be affected by temperature changes. However, this study does not include temperature as a factor, and can therefore not prove that temperature changes influence the carbon stocks and concentrations.

When elevation was included, there was no significant decrease in carbon stocks with increasing elevation, implying carbon stocks is not affected by the cold and harsh climate in the high elevational gradient of this study. As photosynthesis tends to be less productive and respiration decreases with lower temperature, plant species in the high elevations has evolved and acclimated to a stressed and colder climate (Ensminger et al., 2006; Öquist & Huner, 2003). Expansion of the treeline could therefore force the alpine species higher up in the elevation and, worst-case scenario, lead to extinction.

However, soil carbon concentration had a significant decrease with increased elevation. The possible contamination of mineral soil in the samples may have affected the results, as mineral soil leads to a lower value of carbon concentration in each sample. Looking at Figure 5B, we can see that there are some values with extreme outliers for all vegetation classes, and that most of the outliners are closest to the minimum value. The distribution of all vegetation classes is also negatively skewed, indicating, as mentioned before, contamination of mineral soil leading to a lower carbon concentration value.

Further, the study did not look at the possible positive effect of increased above-ground carbon storage a higher treeline could result in, and we can therefore not conclude that a treeline expansion to the alpine tundra would decrease or increase the overall carbon storage. However, the results show that more carbon is stored in the organic soil layer for vegetation classes in the alpine tundra compared with the treeline ecotone. As an invasion of shrub species in the alpine heath and meadow communities is reported to decrease the total ecosystems carbon pools in alpine communities (Sørensen et al., 2018), there is reason to believe that the now ongoing expansion of the treeline (Harsch et al., 2009; Kullman & Öberg, 2009) would have to similar results, and additionally, lead to positive global warming feedback (Hansson et al., 2021).

Future studies

This study addressed how soil carbon stock and concentration differed between five abundant vegetation classes in the treeline ecotone and alpine tundra; i.e., forest, xeric heath, sub-xeric heath, ridge, and lee side. All vegetation classes in the alpine tundra had higher carbon stock and concentration in the top organic soil layer than the vegetation class in the treeline ecotone. If the treeline expands into the higher alpine tundra and changes the endemic communities, the potential loss of carbon is conceivable, leading to higher emission of carbon dioxide in the atmosphere and positive feedback on global warming.

All vegetation classes examined in the study are common in other countries in Scandinavia, and there may therefore be a public interest to evaluate a higher quantity of samples in order to estimate carbon stock differences between the treeline ecotone and alpine tundra. Global warming and the possible negative feedback of climate change is a hot debate today. Therefore, studies like this can increase the knowledge of potential carbon storage loss due to climate changes and increase the awareness of the consequences expanding treeline may have on the global warming feedback.

In future studies, it would be interesting to evaluate a more detailed classification of differences in carbon stock and concentration in more vegetation classes than those mentioned in this study. Further, with the increased accuracy of remote sensing, and studies finding mean estimated soil carbon stock and concentration for each vegetation class in the forest-tundra ecotone, there would be possible to estimate approximately loss/gain in soil carbon storage with an expanding treeline all over Norway. There would also be interesting to include factors such as mycorrhiza, to study how different mycorrhiza species would impact the carbon storage in the treeline and alpine ecotone.

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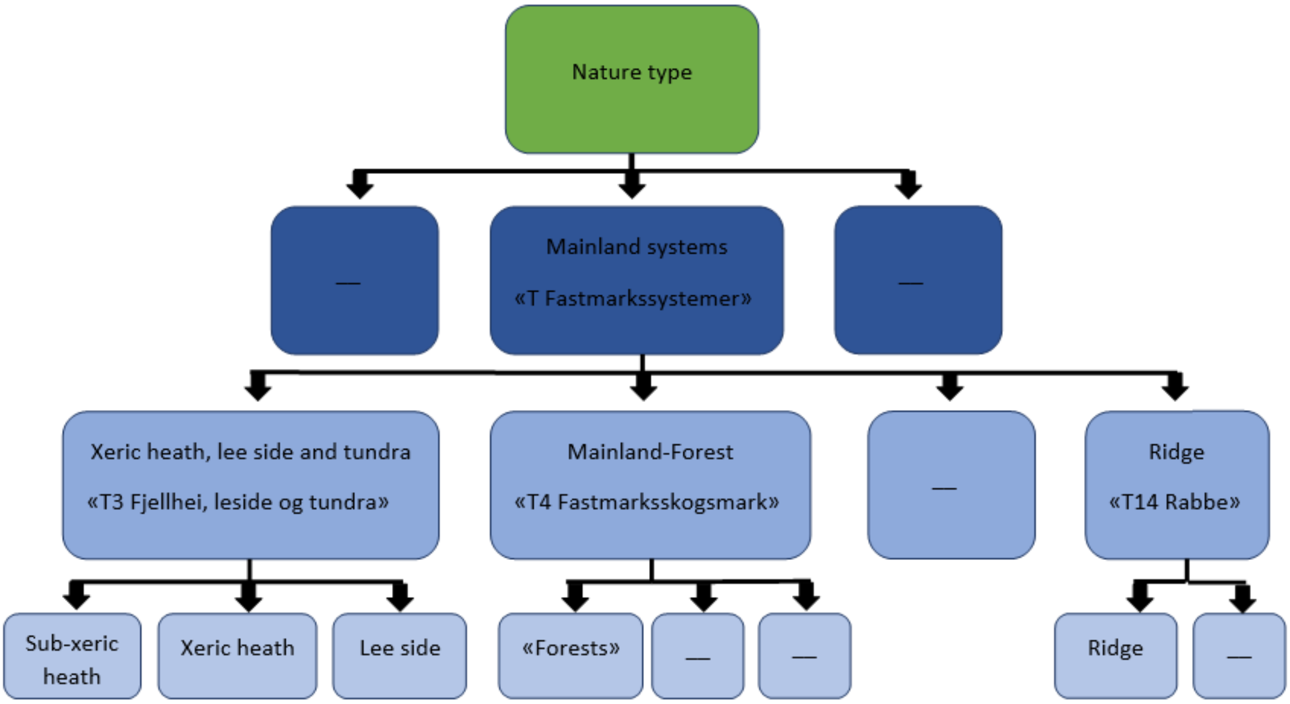
Appendix

Appendix 1: *The number of samples taken from each study site. The sites are ordered in letters starting from south (B) to north (D). B = study sites in Viken and Innlandet. C = study sites in south Trøndelag. D = study sites in North Trøndelag.*

Study sites	Forest	Lee side	Ridge	Sub-xeric heath	Xeric heath
B19251_A	20	-	10	-	5
B19251_B	10	10	-	-	10
B23254	19	-	10	-	-
B27057	10	10	-	10	5
B27104	10	-	-	10	-
B35051	10	5	-	10	10
B35251	10	-	-	-	5
B39057	10	5	-	10	10
B39107	20	5	-	10	-
B39204	30	-	-	-	-
C38072	10	5	-	10	-
C38076	10	5	-	10	10
C38087	10	10	-	-	-
C38147	10	10	-	5	10
C38192	20	5	-	10	-
C38207	20	5	-	10	-
C38252	10	10	-	-	5
D46228	20	-	-	10	-
D51074	10	5	-	9	10
D51121	10	-	-	20	5
Summary	279	90	20	134	85

Appendix 2: *The comprehensive classification system NiN and the following order of classification of the respective vegetation classes used in this researched.*



Appendix 3: *The most dominant species in the different vegetation classes.*

The most dominant species in different vegetation classes

Vegetation class	*Empetrum nigrum*	*Betula nana*	*Calluna vulgaris*	*Vaccinium myrtillus*	*Vaccinium uliginosum*	*Cladonia rangiferina*	*Cladonia stellaris*
Forest	59	55	32	30	17	-	-
Lee side	18	34	12	16	4	-	-
Ridge	5	5	6	-	3	1	-
Sub-xeric heath	36	10	11	1	10	11	39
Xeric heath	34	19	3	2	15	1	1

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