Norwegian University
of Life Sciences

Master's Thesis 2023 30 ECTS
Faculty of Environmental Sciences and Natural Resource Management

Trees as determinants of soil carbon stock sizes across geographically different treeline ecotones in Norway

Hanne Torsdatter Petlund
Master of Management of Natural Resources

Preface

This thesis concludes my master's degree in management of natural resources at the Faculty of Environmental Sciences and Natural Resource Management, and my time as a student at the Norwegian University of Life Sciences (NMBU). Writing a master's thesis has provided me with valuable experience on how to conduct a project from start to finish. However, I could never have accomplished this without the help and guidance of others.

I sincerely thank my main supervisor Ole Martin Bollandsås for valuable guidance and feedback throughout the process, and for providing feedback on my drafts. I would also like to thank my co-supervisor Claire Devos for guiding us through the fieldwork and lab work, for helping me with the statistical analyses, and for providing feedback throughout the process and on my drafts. I am further grateful to my other co-supervisor Mikael Ohlson for providing valuable feedback on my drafts. Thank you all for spending time on my thesis and answering all my questions.

Thank you to the Forest Potential research group for financial support during the fieldwork and for providing the necessary equipment, and thanks to the other students in my master's group. I also wish to thank my fellow master's student Olav With Aasgård for a good collaboration in the field and in the lab, and for giving master's thesis advice. Thanks to my fiancé Tord for commenting on my map and figures, and for emotional support. Finally, I am grateful to my family for giving me loads of love, and to my friends and flatmates for making sure I had some breaks during the thesis.

Ås, May 2023

Hanne T. Petlund

Hanne Torsdatter Petlund

Norwegian
University of
Life Sciences

Abstract

Treelines in boreal regions migrate uphill as a consequence of global warming. The transition from previous open tundra to forest will likely influence alpine soil carbon stores, and there is considerable concern that increased carbon effluxes from the soil to the atmosphere will induce positive feedback on global warming. Thus, in order to predict what future climate change could mean for soil carbon stores in the forest-tundra ecotone, knowledge about the current carbon stores along the forest-tundra gradient is key. My objective was therefore to look at trees as determinants of soil carbon stock sizes across geographically different treelines. Specifically, I investigated whether there is a difference between carbon stocks in forest and tundra soils in treeline ecotones, and modeled the relationship between soil carbon stocks and tree biomass in treelines at different spatial scales.

To achieve this, carbon stocks were calculated for surface soil samples, together constituting soil sample lines, collected in forest and tundra at 34 treelines along an extensive north-south gradient in Norway. Remote sensing data acquired by drone were supplemented by field collected tree data, and used to estimate tree biomass around soil sample lines. Statistical tests were performed, and mixed models incorporating soil carbon stocks and tree biomass as variables were developed for buffer zones of different sizes.

The results showed that soil carbon stocks in forest and tundra were not significantly different. Moreover, there was not a clear relationship, positive or negative, between soil carbon stocks and tree biomass for any of the buffer zones. Tree biomass therefore seemed to be a weak determinant of soil carbon stock sizes irrespective of spatial scale. However, what study site soil sample lines originated from was important.

A possible explanation for these findings is that increased litter inputs in forest soils are counterbalanced by increased microbial decomposition. In addition, potential implications of study design are discussed, as well as potential sources of error. Complex local interactions between various abiotic and biotic factors may explain the importance of study site in determining soil carbon stock sizes. This site-specificity makes it difficult to predict what consequences future changes in the treeline will have for the soil carbon stocks, but in general my results indicate that a transition from tundra to forest will not cause a net increase in soil carbon losses. More information is needed to get a deeper understanding of carbon dynamics at Norwegian forest-tundra ecotones, and to develop management strategies that maximize carbon storage at treelines and mitigate global warming.

Sammendrag

Den boreale tregrensa forflytter seg oppover som følge av global oppvarming. Overgangen fra tidligere åpen tundra til skog vil trolig påvirke de alpine jordkarbonlagrene, og det fryktes at økt karbonutslipp fra jord til atmosfære vil forverre den globale oppvarmingen. For å kunne forutse virkningen fremtidige klimaendringer vil ha på jordkarbonlagrene i økotonen mellom skog og tundra, er kunnskap om de nåværende karbonlagrene langs denne gradienten avgjørende. Det overordnede målet for denne studien var derfor å se nærmere på hvilken rolle trær spiller for størrelsen på jordkarbonlagre i geografisk adskilte tregrenser. Mer konkret undersøkte jeg om det er en forskjell mellom jordkarbonlagre i skog og tundra i tregrensa, og modellerte forholdet mellom jordkarbonlagre og trebiomasse i tregrenser på ulik romlig skala.

Dette ble gjort ved at karboninnhold ble beregnet for jordprøver fra øvre jordlag, som til sammen utgjorde jordprøvelinjer, samlet i skog og tundra ved 34 tregrenser langs en betydelig nord-sør gradient i Norge. Fjernmålingsdata fra drone i tillegg til tre-data samlet i felt, ble brukt til å estimere trebiomasse rundt jordprøvelinjene. Statistiske tester ble utført, og blandede modeller der jordkarboninnhold og trebiomasse inngikk som variabler ble utformet for buffersoner av ulik størrelse.

Resultatene viste at lagrene av jordkarbon i skog og tundra ikke var signifikant forskjellige. Videre var det ikke et klart forhold, positivt eller negativt, mellom jordkarboninnhold og trebiomasse for noen av buffersonene. Trebiomasse virket derfor å ha liten betydning for mengden jordkarbon uavhengig av romlig skala. Derimot var hvilket studieområde jordprøvelinjene kom fra av viktighet.

Funnene kan muligens forklares med at økt strøfall i skog er i mer eller mindre likevekt med økt mikrobiell nedbrytning i jorda. I tillegg diskuteres potensielle effekter av studiedesign, samt mulige feilkilder. Komplekse lokale samspill mellom ulike abiotiske og biotiske faktorer kan forklare viktigheten av studieområde for mengden jordkarbon. Denne stedegenheten gjør det vanskelig å forutse hvilke konsekvenser fremtidige endringer i tregrensa vil ha for jordkarbonlagrene, men generelt tyder resultatene mine på at en overgang fra tundra til skog ikke vil medføre økt tap av jordkarbon. Mer kunnskap trengs for å få en dypere forståelse av karbondynamikken i norske tregrense-økotoner, og på den måten kunne utforme forvaltningsstrategier som maksimerer karbonlagring i tregrensa og motvirker global oppvarming.

Table of contents

Introduction

For a long time, the boreal zone's carbon storage was vastly underestimated (Tarnocai et al., 2009). However, recent studies state that these regions hold more than 30 % of the total terrestrial organic carbon pool (Pan et al., 2011; Bradshaw & Warkentin, 2015). Although the boreal zone is made up of extensive forests, most of its carbon is not bound in trees and other vegetation, but can rather be found below-ground as soil organic carbon (Apps et al., 1993; Pan et al., 2011; Bradshaw & Warkentin, 2015). In fact, the boreal soil carbon pool is believed to be as much as eighteen times larger than the above-ground carbon pool (Tarnocai et al., 2009; DeLuca & Boisvenue, 2012), and by far exceeds soil carbon pools in temperate and tropical forests (Malhi et al., 1999; Pan et al., 2011).

Whether an ecosystem is a net carbon sink or source depends on the balance between organic matter input, mainly from primary production, and organic matter decomposition by the soil microbial community (Post et al., 1982). The huge quantity of soil carbon in boreal regions is mainly explained by low temperatures inhibiting microbial activity (Post et al., 1982; DeLuca & Boisvenue, 2012), as well as boreal vegetation typically being recalcitrant against biological decomposition due to low nutrient quality (Wardle et al., 2003; Nilsson et al., 2008). Wet and anoxic soil conditions further promote carbon accumulation (DeLuca & Boisvenue, 2012). Therefore, the most carbon rich soils are those found in peatlands (Rapalee et al., 1998) and permafrost-affected mineral soils (Tarnocai et al., 2009). However, because other soil types are widespread, they also constitute a significant carbon store (DeLuca & Boisvenue, 2012).

Soil carbon stores in the boreal forest-tundra heath ecotone (hereafter, forest-tundra ecotone) is a highly relevant topic of discussion. This ecotone is also known as the alpine treeline, and can be defined as the transition zone between mountain forest and treeless tundra at high elevation (Harper et al., 2011). Treeline structure varies considerably among sites, and the forest-tundra ecotone can be gradual spanning over several kilometers but typically span just a few dozen meters (e.g., Sjögersten & Wookey, 2009; Tiwari & Jha, 2018; Hansson et al., 2021). Such abrupt shifts between two distinct habitats can have significant impacts on a variety of ecosystem processes, including litter production, snow cover, and soil development, over relatively short distances (Hagedorn et al., 2014).

Temperature is thought to be the main driver of treeline altitudinal position (Körner & Paulsen, 2004; Harsch et al., 2009), although moisture availability is another strong determinant (Tingstad et al., 2015; Tiwari & Jha, 2018). As trees in the treeline are growing at their thermal limit, they are expected to respond quickly to climate change (Kullman, 1998; Grace et al., 2002). In fact, several studies have documented a treeline advance into previously treeless alpine areas as a consequence of elevated global temperatures. Harsch et al. (2009) found in their global meta-analysis that about half of the sites had experienced treeline advance since 1900. Warmer winter temperatures were considered the most important factor. In a later review, Hansson et al. (2021) revealed that 66 % of the studied treelines had increased in elevation or latitude. For instance in Scandinavia, Kullman (2002) found that several tree species have moved to higher elevations in the southern Scandes mountains since the 1950s. Treeline densification is, however, an equally common response to elevated temperatures as treeline migration (Wang et al., 2016; Camarero et al., 2017). According to Liang et al. (2011), warming over the past two centuries did not cause an upward shift in the location of treelines comprised of Smith fir trees (*Abies georgei* var. *smithii*) in the Tibetan Plateau. Instead, the trees exhibited an increased population density.

Treeline response to climate change may even differ within the same study site. For instance, Dial et al. (2007) reported treeline migration on northerly aspects but increased stand density in south-facing aspects at their study sites, as a response to recent warming. Furthermore, treeline stagnation or even retraction have also been reported (e.g., Wilmking et al., 2004; Harsch et al., 2009; Van Bogaert et al., 2011), potentially due to drought stress associated with increased temperatures (Wilmking et al., 2004; Wilmking & Juday, 2005; Lu et al., 2021). This demonstrates that treeline responses across and within sites are highly variable, and also depend on geography and topography, as well as species traits and biology. In addition, biotic interactions, including facilitation and competition among trees (Tingstad et al., 2015; Wang et al., 2016; Camarero et al., 2017), grazing by domestic and wild herbivores (Speed et al., 2010; Mienna et al., 2020), and human activities at the treeline (Olofsson et al., 2009; Speed et al., 2010; Mienna et al., 2020) further contribute to shaping treeline position and structure.

The transition from open tundra to forest may have substantial consequences by reducing the albedo of an area. As trees typically have a darker color than lichen-covered tundra heath, forest absorbs more heat resulting in warmer local conditions (Chapin et al., 2005; de Wit et al., 2014). Although shade from a denser tree canopy could potentially lead to cooler soil conditions during summer (Sistla et al., 2013), winter soil temperatures generally increase (de Wit et al., 2014; Loranty et al., 2014). The lower albedo could therefore cause positive feedback in which warmer conditions created by the trees, may further contribute to the establishment of more trees (Chapin et al., 2005). This may again have consequences for the soil carbon dynamics (de Wit et al., 2014).

Sjögersten & Wookey (2009) found that the organic horizon was shallower and soil respiration higher in forest compared to tundra soils, resulting in greater carbon stores in the tundra. Similarly, Parker et al. (2015) found that soil carbon stores in low-productivity tundra heath exceeded that of adjacent soils covered by deciduous shrubs and trees. The findings were attributed to increased carbon turnover rates caused by ectomycorrhizal symbionts in the tree and shrub covered areas. Later studies have corroborated these findings, concluding that roots may have a destabilizing effect on soil organic carbon (Dijkstra et al., 2021). In contrast, Devos et al. (2022) more often found that forest soils are richer in carbon than adjacent tundra soils. Despite these conflicting results, there is considerable concern that treeline expansion and densification as a consequence of global warming, may result in a net loss of soil carbon to the atmosphere (Parker et al., 2015; Hansson et al., 2021; Devos et al., 2022). Thus, to predict how soil carbon stores at the treeline may respond to future climate change, it is essential to gain knowledge about the current carbon stores along the forest-tundra gradient.

The overall objective of my master’s thesis is therefore to investigate trees as determinants of soil carbon stock sizes across geographically different treeline ecotones. Specifically, I aim to explore the following research questions: **I) Is there a difference between carbon stocks in forest and tundra soils in treeline ecotones?** The conflicting findings in the literature make it difficult to predict the outcome, however, as most studies have found tundra to have the highest soil carbon stores, this is what I hypothesize. **II) What is the relationship between soil carbon stocks and tree biomass in treeline ecotones across different spatial scales?** My expectations here depend on the outcome of the first research question. If soil carbon stocks are larger in tundra, I expect a negative relationship between soil carbons stocks and tree biomass. However, if soil carbon stocks are larger in forest, I expect to see a positive relationship between the two variables. I want to assess the effect of tree biomass on soil carbon stocks at different spatial scales, as I am not sure at what spatial scale one would expect to see a relationship between them.

The investigation was carried out using a “space-for-time” approach along an extensive north-south gradient in Norway, assuming that current soil carbon stocks along the forest-tundra gradient are representative of future soil carbon stocks with a shift from tundra to forest. This may enable me to predict what future increases in tree biomass as a consequence of global warming could mean for treeline soils as a potential carbon sink or source.

To conduct my research, I collected soil samples consisting of surface soils (O and A horizons), together constituting soil sample lines, at multiple treelines, in order to calculate average soil carbon stocks. Tree data were recorded in the field to supplement remote sensing data, to estimate tree biomass around soil sample lines for buffer zones of different sizes, representing different spatial scales.

I wanted to apply data acquired from remote sensing, as such methods have the potential to become highly useful nature management tools for assessment of multiple treelines, on a larger scale than is practical through field measurements alone. Data obtained through airborne laser scanning have been shown to be a reliable and cost-efficient way to collect tree data in the forest-tundra ecotone (e.g., Næsset & Nelson, 2007; Thieme et al., 2011; Mienna et al., 2022), and can be employed to monitor the position and structure of treelines over time, even in remote areas (Holtmeier & Broll, 2005; Thieme et al., 2011; Mukhopadhyay et al., unpublished).

Materials and methods

Study sites

Initially, 36 study sites were collected in the field but two were omitted due to missing data, and so the final study included 34 study sites. These are distributed along a 1000 km north-south gradient in the Scandes mountains of Norway, spanning 60 to 69 °N from Tinn in south to Senja in north (Fig. 1 A, see elaboration in Appendix A). The study sites were established in 2008, and tree observations from these sites have been used as field reference data for the construction of models for detection of small single trees in the forest-tundra ecotone using airborne laser scanning (Thieme et al., 2011). Important criteria when selecting study sites were distribution evenness along the north-south gradient, accessibility from roads, and proximity to Norway's National Forest Inventory study plots for potential comparison.

Whereas the study sites in southern Norway have a more continental climate, the climatic conditions in central and northern Norway sites are more oceanic. Furthermore, forest-tundra ecotones varied from being abrupt to more gradual and continuous to patchy (Fig. 1 B), and were characterized by different slopes and aspects. The sites ranged in elevation from 309 to 1193 m.a.s.l. depending on latitude, and mean annual air temperature for the sites based on records from 1970-2020 ranged from -1.2 to 3.5 °C (Appendix A). Three tree species dominated the focal treeline ecotones: the deciduous species mountain birch (*Betula pubescens* ssp. *czerepanovii*), and the conifers Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The sites ranged from nutrient poor dominated by lichens and dwarf shrubs to more productive dominated by graminoids and forbs. Common species were in most of the sites dwarf birch (*Betula nana*), crowberries (*Empetrum nigrum*), *Cladonia* lichens, *Vaccinium* spp., common heather (*Calluna vulgaris*), and the bryophytes *Pleurozium schreberi* and *Hylocomium splendens* (Mienna et al., 2022). In addition, willows (*Salix* spp.), *Flavocetraria* lichens, and the grass *Avenella flexuosa* appeared frequently.

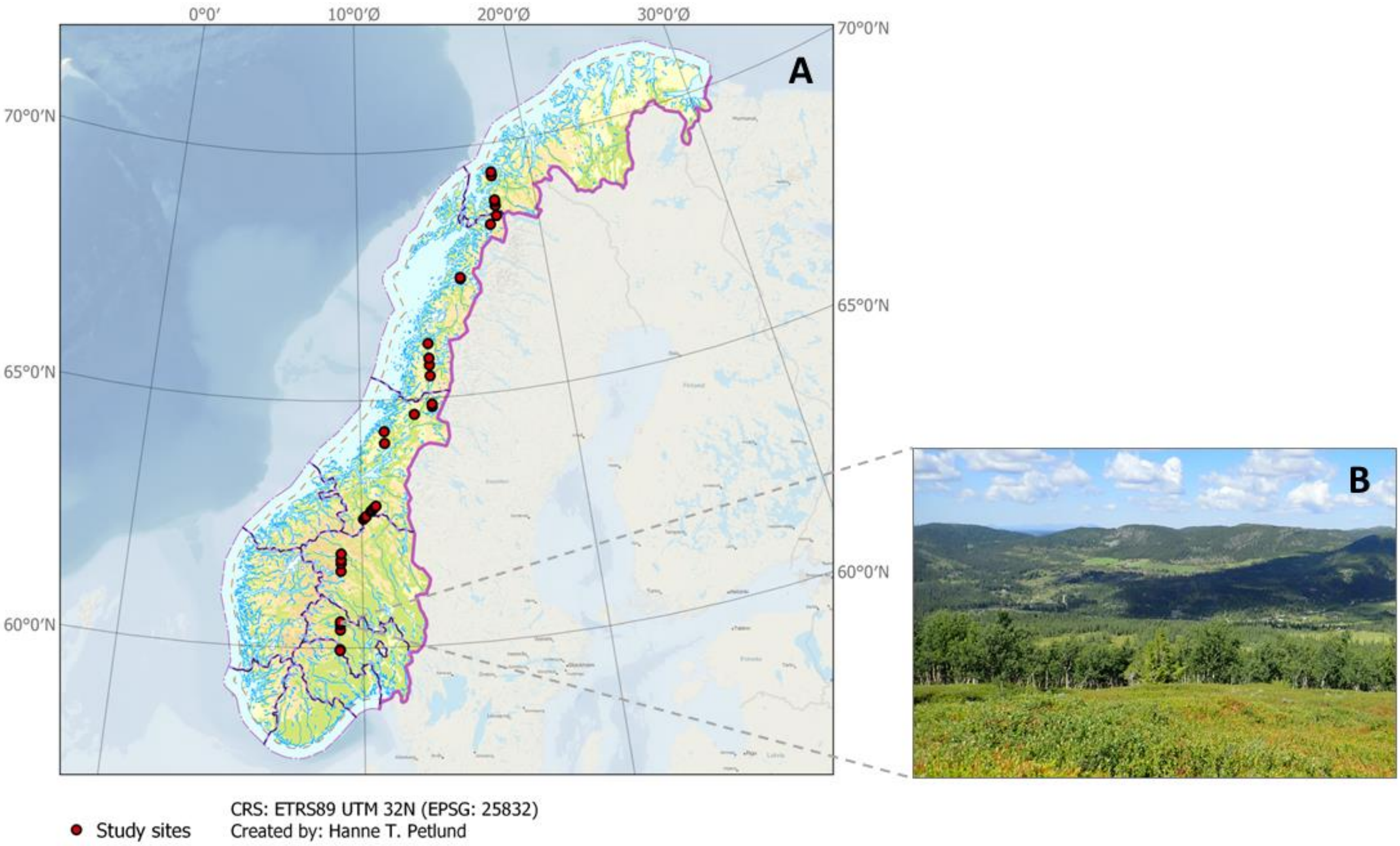


Figure 1. A. Map showing the distribution of study sites included in my study along an extensive north-south gradient in Norway. The map was created using QGIS v. 3.22.16 LTR (QGIS Development Team, 2023). **B.** Picture illustrating what one of the treelines we studied looked like. This particular treeline is from Syningen in Nes municipality (Appendix A), and has a quite abrupt transition between forest and tundra. *Photograph credits: Claire Devos*.

Data collection

Data collection was carried out in August and September 2020 (15 study sites from 65 to 69 °N), and in July and August 2021 (the remaining 19 study sites from 60 to 65 °N). The fieldwork included collection of surface soil samples (O and A horizons), as well as the acquisition of tree data. I focus on the surface soil layers as these are assumed to have a high content of organic matter, and are typically affected more by climatic conditions than deeper layers of mineral soil (Jobbágy & Jackson, 2000; Devos et al., 2022). The O and A horizons were bulked, as they were typically difficult to separate due to lack of a clear border between them.

The basis of our inquiry was a rectangular study area spanning the forest-tundra ecotone (Fig. 2 A). The rectangle was identified for each study site by using a handheld GPS with preloaded coordinates. As the rectangles themselves are used for another scientific purpose, specifically monitoring the development of trees in the treeline over time, it was essential that our data collection did not disturb the natural development of the trees found within the rectangle. Therefore, we only collected data outside the rectangle borders.

At each site, we first identified two trees: a small tree (1-2 m tall) and a big tree (> 2 m tall). The two selected trees were either mountain birch, Norway spruce, or Scots pine, depending on what tree species dominated in that specific treeline ecotone. Specifically, the two trees were selected using the following approach: we walked downhill from the lower elevational border of the rectangular study area, and chose the first small tree and big tree we encountered. The trees were required to be at least 10 m apart, to ensure they were not interacting. Tree height (cm) was measured using a folding ruler or a vertex hypsometer, and tree trunk circumference (cm) was measured with a measuring tape at breast height. In addition, a point (tundra point) was identified near the upper part of the study area with presumable lower tree density. Specifically, the tundra point was situated at the western border of the study area, 10 m downhill from the upper elevational border.

The small tree, big tree, and tundra point constituted center points for the subsequent collection of soil samples, together making up forest and tundra soil sample lines (Fig. 2 A). Soil samples were collected at predefined distances 0.5 m, 1.2 m, 1.6 m, 2.4 m, and 4.0 m uphill and downhill from the respective center points (Fig. 2 B). If there were trees within the interaction zone of a soil sample line, i.e., if the distance to the soil sample line was less than the tree height, the species identity, height (cm), and trunk circumference (cm) at breast height were recorded. Of the total 328 trees recorded in the field, mountain birch was by far the most numerous and widespread (273 individuals compared to 42 and 13 individuals for Norway spruce and Scots pine, respectively), and was the only tree species recorded in northern Norway (Appendix A). The field recorded trees were later used as reference for developing height models to estimate tree biomass around soil sample lines based on LiDAR data.

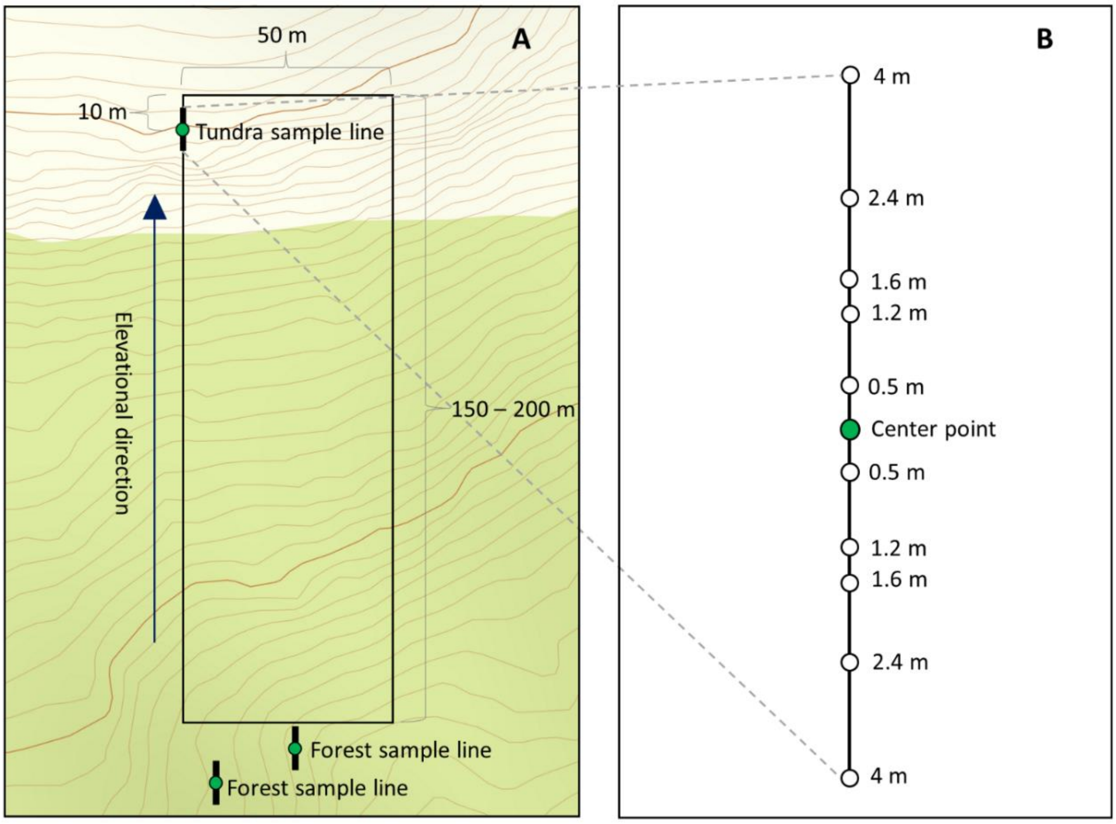


Figure 2. A. Schematic illustration of a rectangular study area used as a basis for our data collection. The center point of the tundra sample line is situated on the western border of the rectangle, 10 m downhill from the upper elevational border. The center points of the forest sample lines (a small tree and a big tree, respectively) are found downhill of the rectangular study area, as close as possible to the lower elevational border. They were required to be separated by at least 10 m. **B.** Distances from the center point at which soil samples were collected, together constituting a soil sample line (tundra sample line or forest sample line).

The soil samples were collected with a cylindrical metal soil corer (Ø = 6.35 cm, Fig. 3 A). If a soil sample could not be obtained, for instance due to lack of soil cover because of a big rock, the sample could be collected within 1 m in both directions perpendicular to the original soil sampling point. If this was not possible, the sample was omitted altogether. Thus, for each study site a maximum of 10 samples for each soil sample line, i.e., a total of 30 soil samples, were collected. Roots were considered part of the soil samples, and if it was possible to separate the surface soils (O and A horizons) from deeper mineral soil layers in the field, the deeper mineral soil was removed from the sample and placed back into its respective sampling hole. All collected soil samples were given a unique sample ID and stored in separate plastic bags awaiting further treatment (Fig. 3 B), and the depth of each sampling hole was measured using a folding ruler (Fig. 3 C). Coordinates for center points (small tree, big tree, and tundra point), soil sampling points, and nearby field recorded trees, were obtained with a Topcon HiPer SR real-time kinematic (RTK) GNSS receiver with centimeter accuracy (Fig. 3 D).

Figure 3. The fieldwork summarized. **A**. Collection of a soil sample using the metal soil corer. **B.** Soil samples placed in plastic bags labeled with correct sample ID lying on top of their respective sampling holes. The measuring sticks used to locate the soil sampling points are visible in the picture. **C.** Sampling hole depths are measured using a folding ruler. **D.** Coordinates of center points, soil sampling points, and nearby field recorded trees are retrieved using an RTK GNSS receiver. *Photograph credits: A. Claire Devos, B. Olav W. Aasgård, C. Claire Devos, D. Hanne T. Petlund.*

Furthermore, LiDAR data were collected by drone (DJI Matrice 300 RTK with the sensor DJI Zenmuse L1) at all study sites during the summer of 2022, and the resulting laser point density was > 300 points/m^2. All data points were classified as either “ground” or “vegetation”. Thereafter, a triangulated irregular network (TIN) model (Floriani & Magillo, 2009) was created based on the points classified as ground, to represent the terrain surface. This way, the remaining points (points classified as vegetation) could be assigned a height value relative to the TIN model, and tree biomass around the positioned soil sample line center points could be estimated at a later stage.

Processing of soil samples

Soil samples were frozen at approximately -20 °C awaiting further treatment. Before processing, they were taken out of the freezer and thawed at least one day in advance. Any visible mineral soil from beneath the A horizon was removed from the samples and discarded. Similarly, living vegetation (photosynthetically active biomass) was removed from the samples. The remaining trimmed samples were measured and weighted using a ruler and a milligram scale, respectively. The samples were then placed into separate paper bags with correct soil sample ID. Samples were thereafter dried in drying cabinets at approximately 40 °C for several days (Fig. 4 A), until all samples were dried to constant mass. If there were still deeper mineral soil or living vegetation left on the dried samples (Fig. 4 B), these were cut off. The remaining surface soil samples were measured and weighted a final time, before being placed back into their respective paper bags.

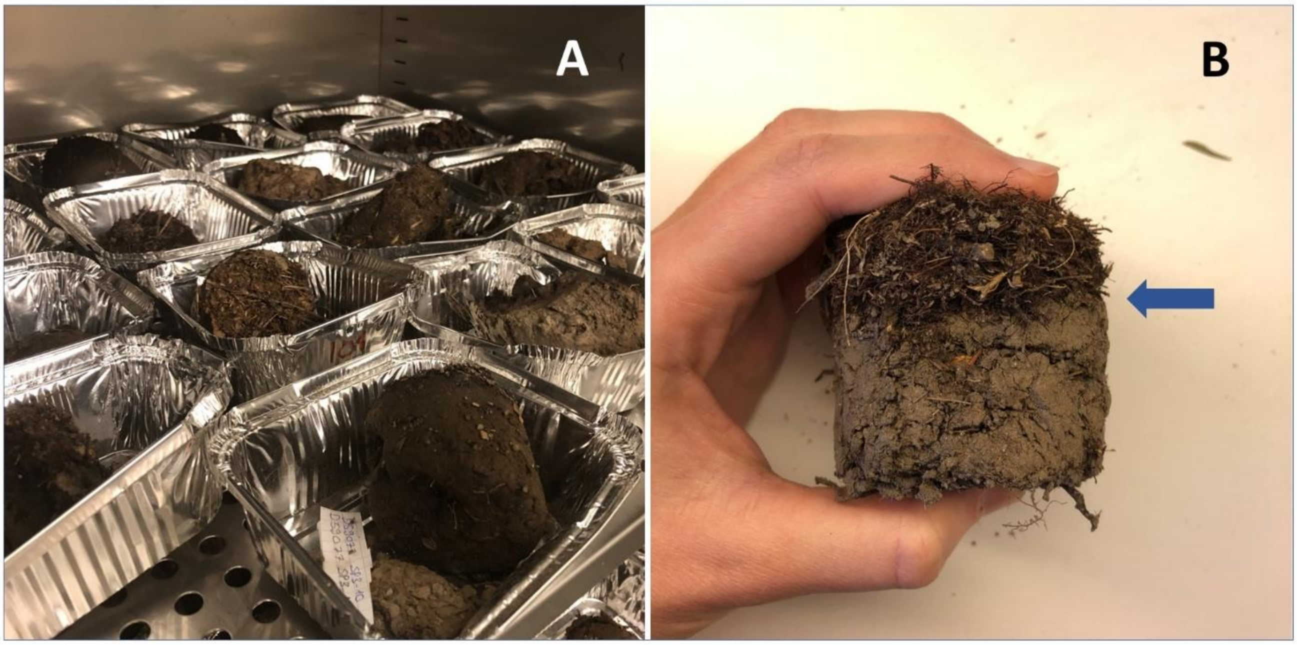


Figure 4. A. Soil samples placed in a drying cabinet to be dried at approximately 40 °C before further processing. **B.** Example of a dried soil sample. The transition between surface soils with high organic matter content (O and A horizons) and mineral soils from beneath the A horizon (marked with arrow), becomes more evident after drying. The deeper mineral soil layers can then be cut off and discarded, and the remaining surface soil sample measured and weighted a final time. Living vegetation was in this case successfully removed prior to the drying. *Photograph credits: Claire Devos.*

Next, the samples were milled to a homogenous powder using a soil grinder (Brabender Rotary mill, Duisburg, Germany). The pulverized soil samples were returned to their respective paper bags, and the soil grinder cleaned between every sample to avoid sample mixing. For each pulverized soil sample, 10 mg ± 2 mg powder were transferred to a small aluminum tray (4 x 4 x 11 mm), that was folded into a package with the soil powder sealed within. Each package was stored in a separate Eppendorf tube marked with correct soil sample ID. Later, the soil packages were analyzed using an element analyzer (Elementar vario MICRO cube, Hanau, Germany), providing the carbon concentration (%) in each sample. The carbon concentrations, together with bulk densities and soil depths obtained by field measurements and in the lab, were used to calculate the carbon stock (kg/m^2) for all soil samples according to the following formula:

Soil organic carbon stock (kg/m^2) =
Bulk density (kg/m^3) x Soil depth (m) x Soil organic carbon concentration (%) x 0.01

Data analyses and statistics

All soil sample data and field recorded tree data were organized into two separate Excel files. Using the R package "readxl" (Wickham & Bryan, 2023), the files were exported to RStudio (RStudio Team, 2015), and R v. 4.2.3 (R Core Team, 2023) was applied for data processing and analyses.

Average soil carbon stocks

Initially, 108 sample lines made up of a total of 1008 soil samples were collected in the field. However, after omitting samples with missing data (lacking coordinates) using the R package "tidyr" (Wickham et al., 2023A), the final dataset comprised a total of 92 sample lines made up of 863 soil samples. Average soil carbon stock (kg/m^2) was calculated for each soil sample line as the carbon stock mean of all individual soil samples making up the sample line, and these mean values were used in all subsequent data analyses. The main reason why I calculated mean values for soil sample lines was to simplify my study by ignoring the difference in micro-terrain properties surrounding the individual soil sampling points.

Data sorting and exploration were conducted, followed by basic plotting of the data by applying the R package “ggplot2” (Wickham, 2016). Calculation of summary statistics for forest and tundra soil carbon stocks was carried out using the R package “dplyr” (Wickham et al., 2023B). A Shapiro-Wilk test (Shapiro & Wilk, 1965) revealed that the average soil carbon stock data were not normally distributed (p-value = 1.395e-08), and were highly right-skewed (i.e., the majority of soil carbon stocks were small). Therefore, rather than using a standard t-test, it was necessary to apply a nonparametric Mann-Whitney U test (Mann & Whitney, 1947) to compare average soil carbon stocks in forest and tundra.

Estimation of tree biomass

To assess the influence of tree biomass on soil carbon stocks, above-ground tree biomass surrounding the soil sample lines was estimated using LiDAR data at different spatial scales, specifically buffer zones with radius 4 m – 10 m. That way, average soil carbon stocks for the field collected soil sample lines could be modeled as a function of the estimated tree biomass. A model for the relationship between tree height and height metrics (height percentiles) from LiDAR data, was first constructed. The LiDAR metrics were calculated from the LiDAR points found inside the tree polygons, as defined by field measured position and their corresponding tree height, and used as potential explanatory variables in the tree height model. Then, a tree segmentation from the LiDAR point data was carried out for the entire study site, and the tree height model was applied to each segment. With the height predicted from the model, tree biomass for each tree segment was estimated using the biomass model of Kolstad et al. (2018). As the goal was not to detect tree species, all trees were assumed to be mountain birch. Finally, total tree biomass for each of the seven buffer zones (radius 4 m – 10 m), was calculated around each soil sample line as the sum of biomass values of the separate tree segments inside each buffer zone. This resulted in circles of different sizes with various amounts of estimated tree biomass (Fig. 5).

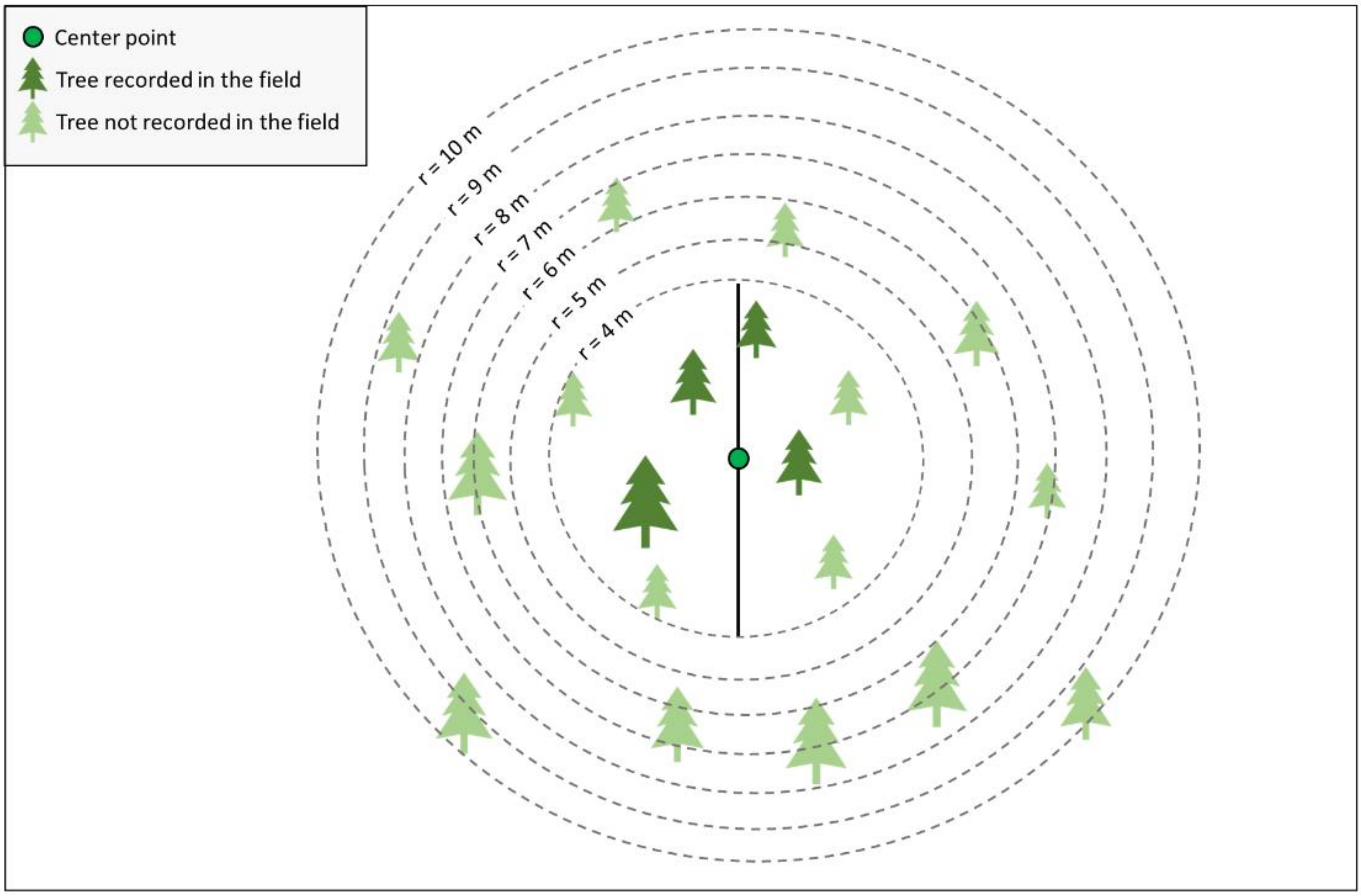


Figure 5. Schematic illustration of buffer zones of different sizes (radius 4 m – 10 m) surrounding the center point (small tree, big tree, or tundra point) of a soil sample line. The buffer zones contain tree biomass of different magnitudes, estimated based on LiDAR point cloud data obtained by drone and reference data from trees recorded in the field.

Modeling

When plotting average soil carbon stocks as a function of latitude, it was evident that soil sample lines originating closer to each other had more similar carbon stocks compared to more distant sample lines, as one would expect (Fig. 6). To account for this spatial dependence, it was necessary to apply mixed modeling.

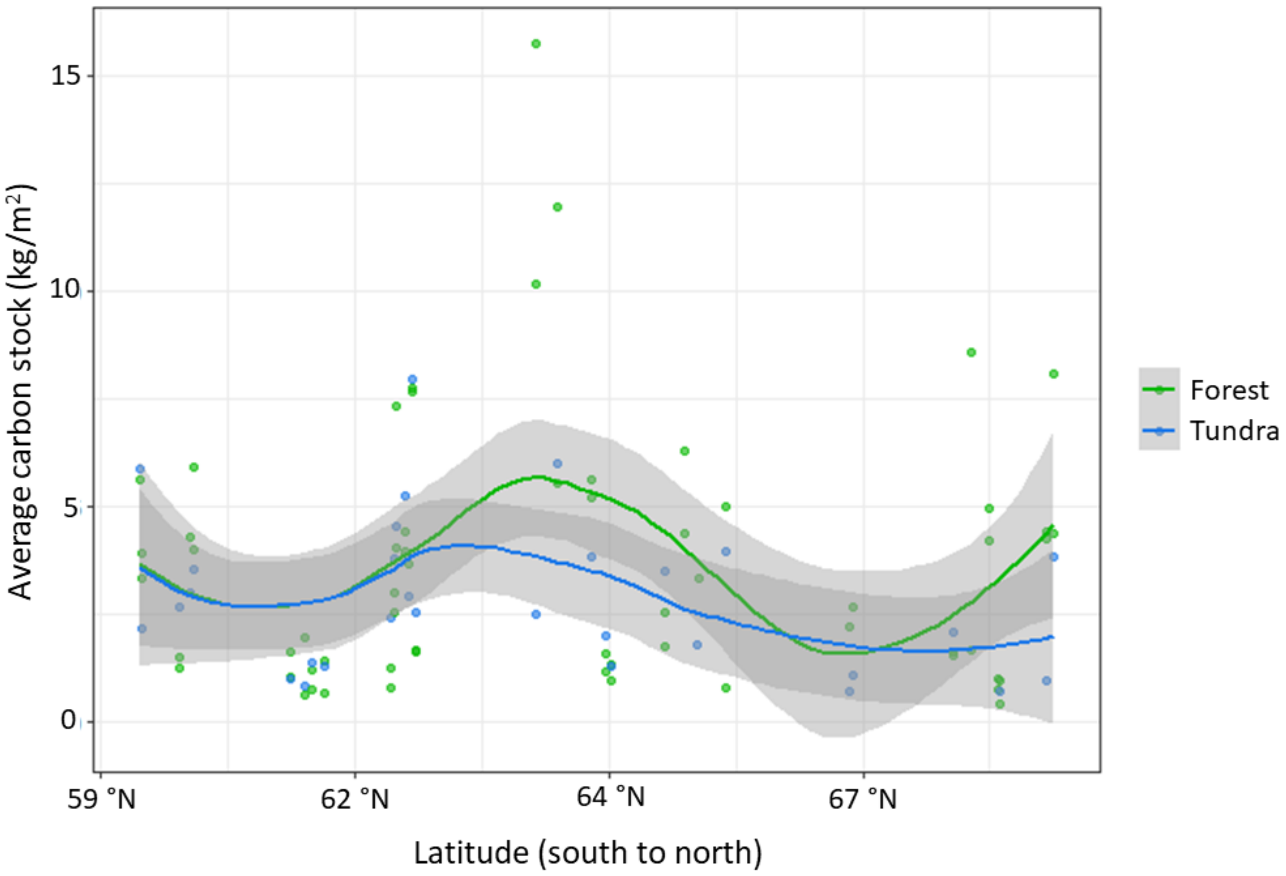


Figure 6. Distribution of average soil carbon stocks for soil sample lines according to area of origin as a function of latitude. The distributions are similar in shape, and this is likely a consequence of soil sample lines collected closer to each other being more similar than more distant sample lines.

I compiled a separate dataset for each buffer zone (radius 4 m – 10 m), comprising average soil carbon stocks and estimated tree biomass within the respective buffer zone for all 92 soil sample lines. I developed linear mixed effects regression models for all seven buffer zones, to see if tree biomass at different spatial scales impact soil carbon stocks differently. In the models, average soil carbon stocks (kg/m^2) for soil sample lines were the response variable (y), whereas estimated tree biomass (kg) within buffer zones was the explanatory variable (x) and fixed effect. In addition, site ID was added as a random effect. Hence, the general form of the models can be summarized as follows:

Average carbon stocks (kg/m^2) for soil sample lines as response variable (y) = *Tree biomass (kg)* in a buffer zone as explanatory variable (x) and fixed effect + *Site ID* as random effect

To perform the linear mixed effects regression modeling in R, I applied the R package “lme4” (Bates et al., 2015). I log-transformed the response variable (average carbon stocks), to make the data more normally distributed and improve linearity between the response variable and the explanatory variable. Then, I extracted the model predictions by applying the R package “ggeffects” (Lüdecke, 2018), and plotted the predictions by using the package “ggplot2”. I acquired *p*-values and R^2 values for the fixed effect (tree biomass) in the different models by applying the R package “jtools” (Long, 2022). I also verified the *p*-values and R^2 values obtained with “jtools” by applying the packages “lmerTest” (Kuznetsova et al., 2017) and “MuMIn” (Barton, 2023), respectively.

Results

Soil carbon stocks in forest compared to tundra

Contrary to my expectations, forest on average seems to comprise somewhat larger soil carbon stocks than tundra, based on visual inspection of preliminary plots (Fig. 7 A and B). Forest also demonstrates more variation in the data, i.e., a greater span in soil carbon stocks.

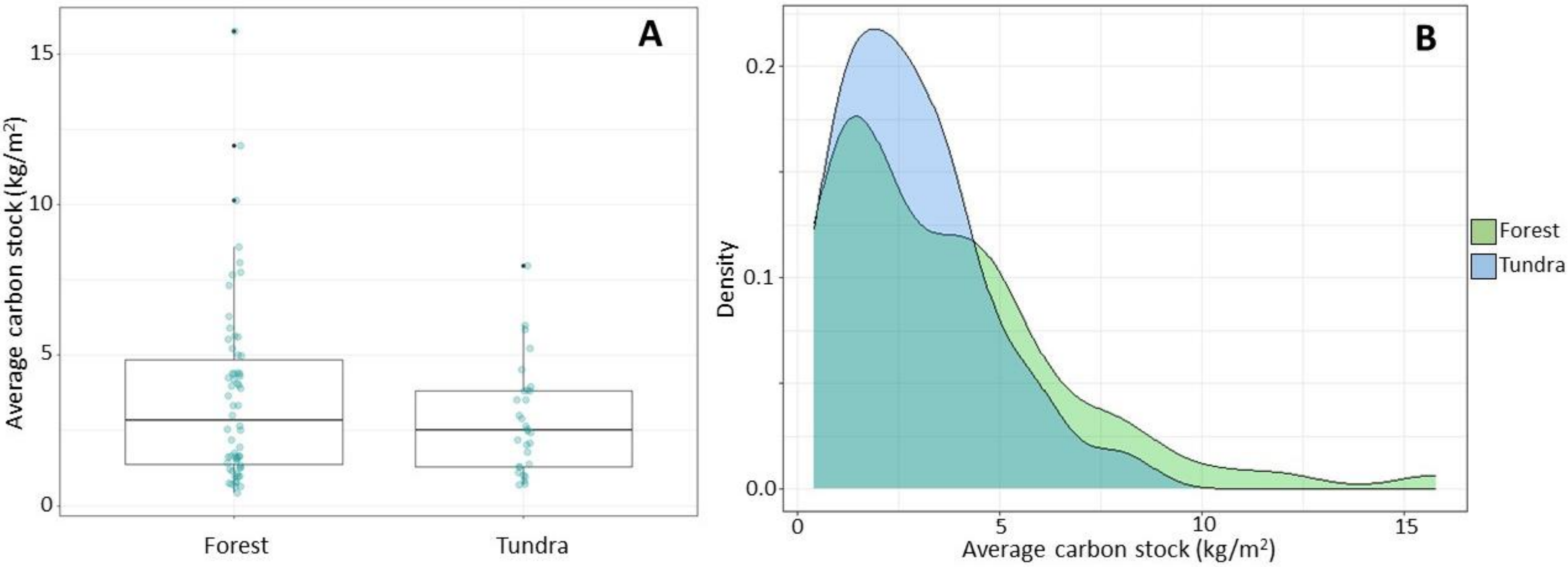
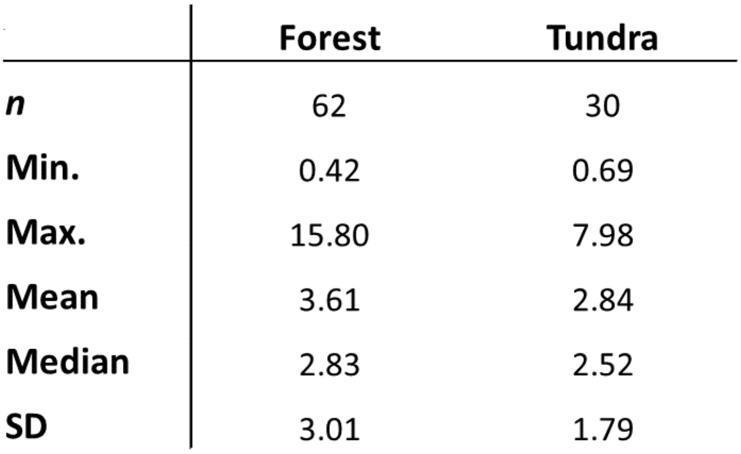


Figure 7. A. Boxplot showing average soil carbon stocks of soil sample lines in forest compared to tundra, and the variation in the data. **B.** Kernel-density plot showing distributions of soil sample lines from forest and tundra with regard to soil carbon stocks.

Similar to the plots in Figure 7, forest also seems to comprise somewhat larger soil carbon stocks than tundra based on summary statistics (Tab. 1). The median soil carbon stock value is higher for forest, and even greater is the difference in the mean values. However, it is not clear whether this difference is statistically significant. Forest again demonstrates more variation in the data. This is evident from the standard deviations and the fact that forest possesses both the lowest and highest soil carbon stock values.

Table 1. Summary table of soil carbon stocks (kg/m^2) in forest and tundra, respectively. The summary statistics include the minimum, maximum, mean, and median soil carbon stock value for both categories, as well as the associated standard deviation. Number of soil sample lines is signified by "*n*".



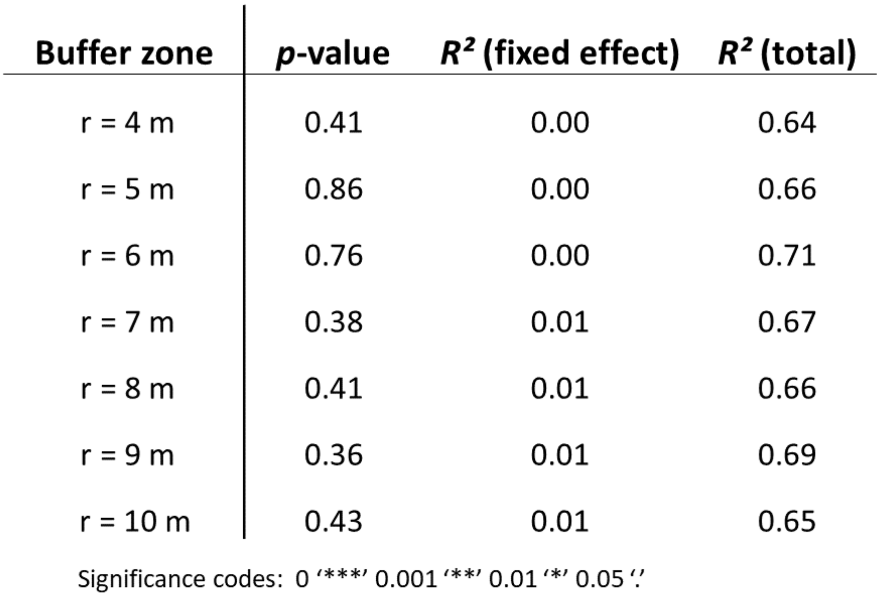
	Forest	Tundra
n	62	30
Min.	0.42	0.69
Max.	15.80	7.98
Mean	3.61	2.84
Median	2.83	2.52
SD	3.01	1.79

However, that soil carbon stocks are larger in forest compared to tundra, as indicated by the preliminary plots and summary statistics, was not corroborated by statistical tests. The Mann-Whitney *U* test showed that soil carbon stocks in forest were not significantly larger than soil carbon stocks in tundra (*p*-value = 0.223). Furthermore, when examining if there was a significant difference between forest and tundra soil carbon stocks at all, the Mann-Whitney *U* test revealed that the difference was not statistically significant (*p*-value = 0.446).

The relationship between soil carbon stocks and tree biomass

Statistical significance and model fit based on the linear mixed effects regression models are shown in Table 2. From the table it is evident that the impact of tree biomass (fixed effect) on soil carbon stocks was not statistically significant for any of the buffer zones. Furthermore, when assessing the model fit for the fixed effect (R^2 (fixed effect)), the R^2 values are almost equal to zero, and so corroborate the very high *p*-values. Phrased differently, tree biomass seems to be a very weak determinant of soil carbon stock size, the results indicating no clear relationship between the two variables, and spatial scale does not seem to be of importance. However, when also considering the random effect site ID (R^2 (total)), the model fit increases considerably for all buffer zones. In other words, what specific study site a sample line originates from seems to be a major determinant of soil carbon stock size.

Table 2. Values representing statistical significance (*p*-values) and model fit (R^2(fixed effect)) for the explanatory variable tree biomass on the response variable average soil carbon stocks, for the different buffer zones (radius 4 m – 10 m). None of the *p*-values are statistically significant. Also model fit when site ID (random effect) is considered in addition to tree biomass (R^2(total)) is shown.



Buffer zone	*p*-value	R^2 (fixed effect)	R^2 (total)
r = 4 m	0.41	0.00	0.64
r = 5 m	0.86	0.00	0.66
r = 6 m	0.76	0.00	0.71
r = 7 m	0.38	0.01	0.67
r = 8 m	0.41	0.01	0.66
r = 9 m	0.36	0.01	0.69
r = 10 m	0.43	0.01	0.65

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’

The lack of a clear relationship, positive or negative, between soil carbon stocks and tree biomass is also exemplified by the plots in Figure 8. The slope of the regression lines for average soil carbon stocks as a function of tree biomass is not significantly different from zero for any of the buffer zones. The removal of extreme outlier biomasses potentially biasing the regression lines also yielded the same result. Same as for Figure 7 and Table 1, forest demonstrates more variation in the data compared to tundra.

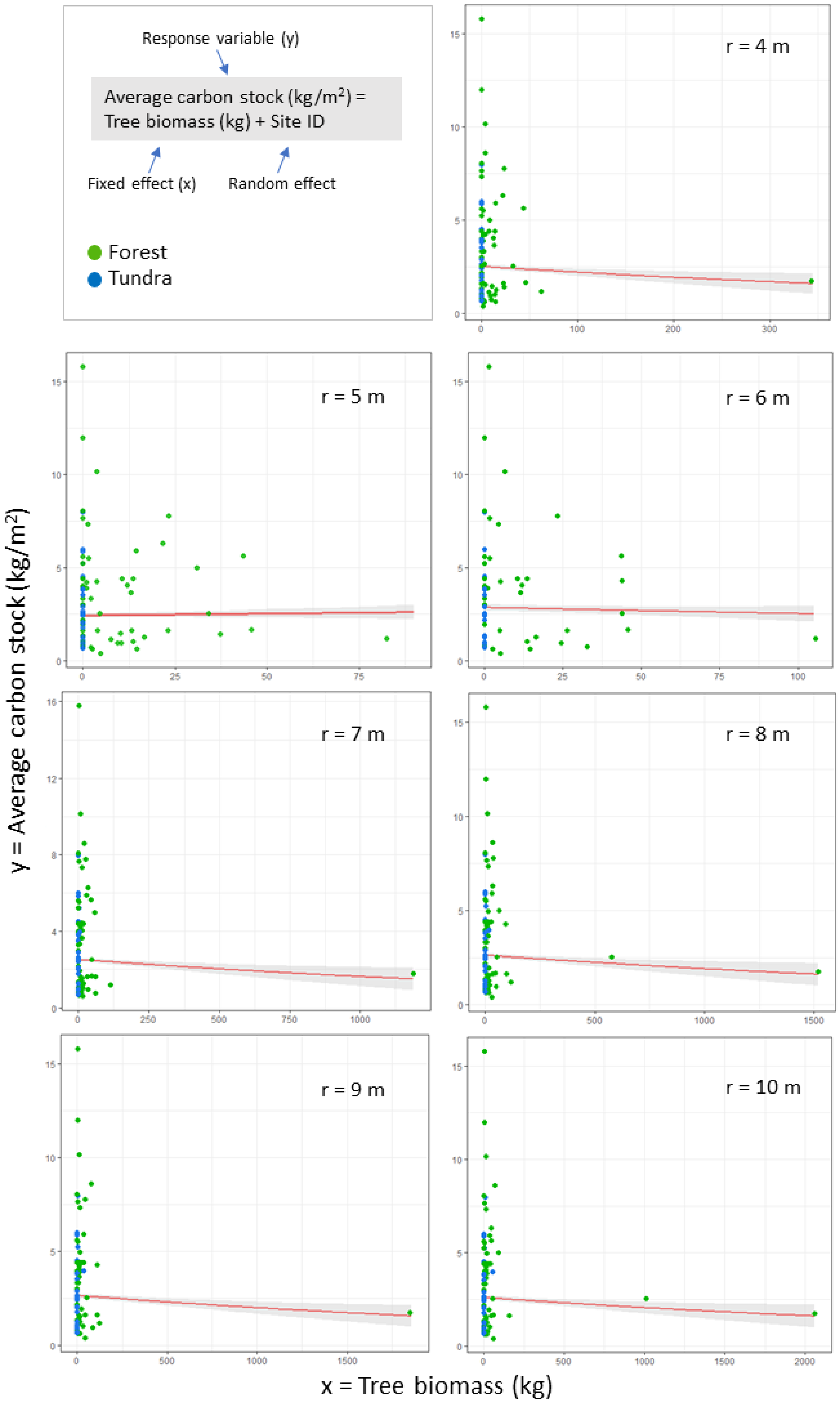


Figure 8. Regression lines with associated 95 % confidence intervals, when plotting the predictions of the linear mixed effects regression models for each buffer zone (radius 4 m – 10 m). The slope of the regression lines for average soil carbon stocks as a function of tree biomass is not significantly different from zero for any of the buffer zones.

Discussion

Possible explanations for my findings

Contrary to most of the existing studies and my expectations (e.g., Sjögersten & Wookey, 2009; Hartley et al., 2012; Parker et al., 2015; Speed et al., 2015), I did not find that tundra soils are richer in carbon than forest soils. The literature is, however, divided, and there are some studies sharing my results. For instance, Kammer et al. (2009) and Sistla et al. (2013) concluded in their studies that forest establishment in tundra, despite altering carbon dynamics and a number of ecosystem processes, did not lead to a significant change in soil carbon stocks. Speed et al. (2014) further found no significant difference in soil carbon content among grazed grasslands and un-grazed woodlands, comparable to tundra and forest, respectively. Similarly, Devos et al. (2022) found that soil carbon stocks in adjacent forest and tundra soils were not significantly different in half of their study sites. Methodological differences should however be born in mind, as Devos et al. (2022) similar to my study, only considered surface soils, whereas the remaining studies also assessed deeper mineral soil layers. It should also be noted that the part of my dataset originating from northern Norway is the same as the data used by Devos et al. (2022) and were collected according to the same field protocol, explaining why we share the same methodologies.

It was interesting to explicitly assess whether tree biomass has an effect on soil carbon stores. However, considering the nonsignificant difference between soil carbon stocks in forest and tundra, the lack of a clear relationship between soil carbon stocks and tree biomass is perhaps not so surprising. Very few studies have sought to find the relationship between soil carbon stocks and tree biomass in the forest-tundra ecotone, and so comparable studies are scarce. However, explanations proposed in the above-mentioned studies, that found no significant difference in forest and tundra soil carbon stores, could be applicable for both my research questions. The general idea that has been proposed is that greater litter inputs, as a result of increased tree biomass and productivity, are roughly balanced by increased decomposition by the soil microbiota. As a consequence, carbon stocks in forest and tundra soils are more or less the same (Kammer et al., 2009). Hence, this carbon gain/carbon loss balance may also explain why different amounts of tree biomass did not significantly alter the soil carbon stocks in my study.

In my case, the small difference in carbon stocks in forest and tundra soils could potentially also be a consequence of the study design. Since the forest sample lines and tundra sample line were relatively close in space, there was not necessarily a very big difference in the amount of tree biomass in what we called “forest” and “tundra” (Appendix B), blurring out the differences between the two categories. On the other hand, the fact that I have pairwise observations, i.e., forest and tundra sample lines collected in the same treeline ecotone, is also a strength. Then, I can more easily isolate the effect of tree biomass on soil carbon stocks, as was my aim, rather than the effect of study site. The effect of study site on soil carbon stocks is further accounted for by the application of mixed modeling. Furthermore, as I found that the amount of tree biomass all in all seemed to be of little importance for soil carbon stock sizes, the explanation proposed above that forest and tundra sample lines had comparable tree biomasses, seems insufficient to explain the nonsignificant difference in forest and tundra soil carbon stocks.

Another more likely explanation could be the age of the forest in my study. If the forested areas sampled are quite young, i.e., comprised of trees that established relatively recently, ecosystem processes and soil development associated with forest habitats may be lagged compared to forest establishment. Considering this, it would potentially have been a greater difference in carbon stocks between forest and tundra soil sample lines if we had sampled farther downhill, where the forest is older and more developed. This notion is supported by previous findings that soil carbon stocks change along with tree age, increasing as trees mature (Steltzer, 2004). Thus, one would potentially observe greater differences between forest and tundra sample lines in the future, along with forest maturation.

The more variation observed in the forest data, both soil carbon stocks (i.e., Tab. 1, Fig. 7, Fig. 8) and tree biomass (i.e., Appendix B), could potentially reflect that trees from the forest vary more in age than trees collected in the tundra (in general thought to be young trees). Assuming that tree biomass and soil carbon stocks increase with tree age, the more variation in tree biomass would explain the greater variation in forest soil carbon stocks. However, as we do not know the age of the trees surrounding the soil sample lines, this is nothing more than speculation and should be explored more closely in order to draw any conclusions. The large tree biomass found around some forest sample lines could for instance be explained by a high number of small and young trees rather than trees that are old and big. As to the greater variation in forest soil carbon stocks, this could potentially be explained by forest having twice as many soil sample lines as tundra (Tab. 1).

Lastly, there are certainly several other factors than tree biomass influencing soil carbon stores, that I have not incorporated in my models. This is supported by the extremely low R^2 values of my fixed effect (tree biomass) in the linear mixed effects regression models (Tab. 2), suggesting that tree biomass alone is a very weak determinant of soil carbon stock sizes. The assertion that soil carbon stocks are influenced by the interaction of a number of abiotic and biotic factors, is pointed out in several studies. Key factors that determine soil carbon quantities at a specific site include local topography, slope, aspect, edaphic conditions, vegetation community, and more (Post et al., 1982; Hansson et al., 2021; Devos et al., 2022). As a consequence, soil carbon stocks are found to be highly site-specific, but also with considerable local variation within sites (e.g., Devos et al., 2022). This site-specificity is evident in my study as the R^2 of my models increase considerably when also taking the random effect site ID into account (Tab. 2), confirming my assumptions that soil sample lines originating from the same study site are more similar to each other than they would randomly. It is also possible that the model fit would have increased even more if I added some environmental variables to the models, for instance elevation, slope, and temperature, that previously have been considered as strong predictors of soil carbon stock sizes (Devos et al., 2022).

Implications of my findings and future perspectives

Despite that soil carbon dynamics are complex and highly site-specific, the findings provided in this study may shed light on what future shifts in treeline position and structure could mean for soil carbon pools in forest-tundra ecotones. As my study includes one of the so far most extensive datasets in this field of research, it could perhaps be generalized and apply to other Norwegian treelines than those included here, or even treelines outside of Norway.

Based on my results, treeline expansion and densification will not necessarily lead to a net loss of soil carbon as tundra transitions to forest. A higher number of trees could potentially induce positive feedback where reduced albedo results in locally warmer conditions, favoring the establishment of even more trees (Chapin et al., 2005; de Wit et al., 2014). This is though contingent on further tree establishment not being hampered by competition, herbivory, moisture deficiency, and more (e.g., Tingstad et al., 2015; Mienna et al., 2020; Lu et al., 2021). However, this positive feedback promoting tree establishment will not automatically impact the soil carbon stores, and induce another positive feedback in which increased soil carbon emissions exacerbate global warming, as is a serious concern.

In fact, there is a possibility that the ecosystem carbon stores will increase when the tree biomass, as well as other vegetation biomass, increase. This because soil carbon stores may remain largely unchanged while greater tree and vegetation biomass will constitute a substantial above-ground carbon pool. However, increased above-ground tree biomass and productivity under warmed conditions (Körner, 2000; Kirdyanov et al., 2012) do not always compensate for soil carbon losses (Sjögersten & Wookey, 2009). Furthermore, it may be reasonable to assume that soil carbon stores, at least in deeper soil layers, constitute a more stable and long-term carbon sink than carbon stored in vegetation, with a presumably higher carbon turnover rate. Additionally, even if treeline expansion does not lead to a significant change in soil carbon quantities, there will most likely be changes in soil carbon quality (e.g., Kammer et al., 2009). It is also important to remark that the transition from tundra to forest will certainly have other non-carbon consequences, like a shift in vegetation communities from alpine to more boreal species (Greenwood & Jump, 2014).

There are several things I could have done, and that future studies should consider doing, to improve our understanding of carbon dynamics in the forest-tundra ecotone, and so aid in the development of management strategies to maximize carbon storage in the treeline. Firstly, I did only sample surface soils (O and A horizons). However, to get a more complete picture of the soil carbon stores, all layers down to the bedrock should ideally be sampled. Secondly, an estimation of the above-ground carbon stores, both trees and extant vegetation, should be conducted to enable comparison of total ecosystem carbon stores in forest and tundra. It could further be interesting to investigate if other types of remotely sensed data than LiDAR data obtained by drone, such as spectral data or satellite data, would yield different tree biomass estimates. Finally, an estimation of tree age and its importance for soil carbon sequestration is yet another key factor that would contribute to our understanding of treeline carbon dynamics.

Potential sources of error

Potential sources of error in my study include both sampling errors and measurement errors. For instance, a thunderstorm prevented us from obtaining coordinates at one of the study sites during the fieldwork, so I had to omit that study site from my analyses altogether. Moreover, there are some aspects of the labwork that potentially could have biased the data. Removal of deeper mineral soil from soil samples was conducted by visual inspection, and it was sometimes challenging to separate the O and A horizons from deeper mineral soil layers. Consequently, some samples may, despite tedious effort, have contained traces of deeper mineral soil. Such contamination could have biased the carbon concentrations slightly, and so the carbon stocks, if carbon concentrations in surface and deeper soil layers differed substantially.

Furthermore, there are some uncertainties associated with the LiDAR data used for estimating tree biomass. Previous studies have found a very high detection rate for trees > 1 m tall, however, for trees below this limit the detection success is considerably lower (Næsset & Nelson, 2007; Thieme et al., 2011). For the smaller trees, tree species also seems to be important for detection success (Thieme et al., 2011) as well as the terrain model applied (Næsset & Nelson, 2007). It is therefore reasonable to assume that some small trees were not detected in my study, and hence the tree biomass may have been underestimated. This would perhaps especially be the case for the tree biomass surrounding the tundra sample lines, as these trees in general are expected to be smaller than those found near the forest sample lines. On the other hand, non-tree objects such as rocks and hummocks, could have been interpreted as trees based on the LiDAR data (Næsset & Nelson, 2007; Thieme et al., 2011). This would have the opposite effect by biasing the biomass estimates upward. Irregular crown shapes and stems growing parallel to the ground, typical of trees found in the treeline, represent an extra challenge for estimation of tree biomasses from remote sensing data in forest-tundra ecotones (Mukhopadhyay et al., unpublished). Furthermore, the fact that a biomass model was applied introduces additional uncertainty, especially since the model assumed that all trees were mountain birch. Thus, the tree biomasses should be treated with caution, as they are first and foremost estimates and not true representations of reality. It should however be noted that the point density of our LiDAR data was very high (> 300 points/m^2), and much higher than the point density in many of the previous studies successfully applying LiDAR data for tree detection (e.g., Thieme et al., 2011). This could to some extent make up for the uncertainty associated with this type of data. Also, as the vast majority of trees recorded in this study were in fact mountain birch, this could somewhat justify the use of the simplified biomass model.

Conclusions

Contrary to my expectations, soil carbon stocks initially seemed larger in forest compared to tundra. The observed difference was, however, not statistically significant. When investigating more closely the effect tree biomass has on soil carbon stocks, there was no clear relationship between the two variables, positive or negative, irrespective of spatial scale. I.e., whether the tree biomass was small or large was of little importance for the soil carbon stocks, and this applied to buffer zones of all sizes. What study site soil sample lines originated from however seemed important, probably due to considerable variation in abiotic and biotic conditions among sites. Possible explanations for lack of difference between forest and tundra soil carbon stocks, as well as lack of a clear relationship between soil carbon stocks and tree biomass, include higher litter inputs as a consequence of more tree biomass being counterbalanced by increased soil microorganism decomposition. Small differences in tree biomass around forest and tundra sample lines is another possible explanation for the nonsignificant difference in soil carbon stocks in forest and tundra. However, delayed soil development compared to forest establishment is considered a more likely explanation. In addition, several other factors than tree biomass likely influence soil carbon stock sizes. In the future, studies could sample all soil layers down to the bedrock, estimate above-ground carbon stores, and infer tree age, to better our understanding of carbon dynamics in Norwegian forest-tundra ecotones, and our predictions of how future climate change may change them. Such insights may enable us to develop management strategies to maximize carbon storage at treelines to help mitigate global warming.

References

Apps, M. J., Kurz, W. A., Luxmoore, R. J., Nilsson, L. O., Sedjo, R. A., Schmidt, R., Simpson, L. G. & Vinson, T. S. (1993). Boreal forests and tundra. *Water, Air, and Soil Pollution*, 70: 39-53. DOI: https://doi.org/10.1007/BF01104987

Barton, K. (2023). *MuMIn: Multi-Model Inference* (version 1.47.5). Available from: https://CRAN.R-project.org/package=MuMIn (accessed 10.04 2023).

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4 (v. 1.1.32). *Journal of Statistical Software*, 67 (1): 1–48. DOI: doi:10.18637/jss.v067.i01.

Bradshaw, C. J. & Warkentin, I. G. (2015). Global estimates of boreal forest carbon stocks and flux. *Global and Planetary Change*, 128: 24-30. DOI: https://doi.org/10.1016/j.gloplacha.2015.02.004

Camarero, J. J., Linares, J. C., García-Cervigón, A. I., Batllori, E., Martínez, I. & Gutiérrez, E. (2017). Back to the future: the responses of alpine treelines to climate warming are constrained by the current ecotone structure. *Ecosystems,* 20: 683-700. DOI: https://doi.org/10.1007/s10021-016-0046-3

Deluca, T. H. & Boisvenue, C. (2012). Boreal forest soil carbon: distribution, function and modelling. *Forestry*, 85 (2): 161-184. DOI: https://doi.org/10.1093/forestry/cps003

Devos, C. C., Ohlson, M., Næsset, E. & Bollandsås, O. M. (2022). Soil carbon stocks in forest-tundra ecotones along a 500 km latitudinal gradient in northern Norway. *Scientific Reports*, 12 (1). DOI: https://doi.org/10.1038/s41598-022-17409-3

Devos, C. C., Ohlson, M., Næsset, E., Klanderud, K. & Bollandsås, O. M. (unpublished). Tree expansion into tundra does not impact soil carbon stocks.

de Wit, H. A., Bryn, A., Hofgaard, A., Karstensen, J., Kvalevåg, M. M. & Peters, G. P. (2014). Climate warming feedback from mountain birch forest expansion: reduced albedo dominates carbon uptake. *Global Change Biology*, 20 (7): 2344-2355. DOI: https://doi.org/10.1111/gcb.12483

Dial, R. J., Berg, E. E., Timm, K., McMahon, A. & Geck, J. (2007). Changes in the alpine forest-tundra ecotone commensurate with recent warming in southcentral Alaska: Evidence from orthophotos and field plots. *Journal of Geophysical Research: Biogeosciences*, 112 (4). DOI: https://doi.org/10.1029/2007JG000453

Dijkstra, F. A., Zhu, B. & Cheng, W. (2021). Root effects on soil organic carbon: a double-edged sword. *New Phytologist*, 230 (1): 60-65. DOI: https://doi.org/10.1111/nph.17082

Floriani, L. D. & Magillo, P. (2009). Triangulated Irregular Network. In: Liu, L. & Özsu, M. T. (eds.) *Encyclopedia of Database Systems*. p. 3178–3179. Boston, MA: Springer. DOI: https://doi.org/10.1007/978-0-387-39940-9_437

Grace, J., Berninger, F. & Nagy, L. (2002). Impacts of climate change on the tree line. *Annals of botany*, 90 (4): 537-544. DOI: https://doi.org/10.1093/aob/mcf222

Greenwood, S. & Jump, A. S. (2014). Consequences of treeline shifts for the diversity and function of high altitude ecosystems. *Arctic, Antarctic, and Alpine Research*, 46 (4): 829-840. DOI: https://doi.org/10.1657/1938-4246-46.4.829

Hagedorn, F., Shiyatov, S. G., Mazepa, V. S., Devi, N. M., Grigor'ev, A. A., Bartysh, A. A., Fomin, V. V., Kapralov, D. S., Terent'ev, M., Bugman, H., Rigling, A. & Moiseev, P. A. (2014). Treeline advances along the Urals mountain range–driven by improved winter conditions? *Global change biology*, 20 (11): 3530-3543. DOI: https://doi.org/10.1111/gcb.12613

Hansson, A., Dargusch, P. & Shulmeister, J. (2021). A review of modern treeline migration, the factors controlling it and the implications for carbon storage. *Journal of Mountain Science*, 18 (2): 291-306. DOI: https://doi.org/10.1007/s11629-020-6221-1

Harper, K. A., Danby, R. K., De Fields, D. L., Lewis, K. P., Trant, A. J., Starzomski, B. M., Savidge, R. & Hermanutz, L. (2011). Tree spatial pattern within the forest–tundra ecotone: a comparison of sites across Canada. *Canadian Journal of Forest Research*, 41 (3): 479-489. DOI: https://doi.org/10.1139/X10-221

Harsch, M. A., Hulme, P. E., McGlone, M. S. & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology letters*, 12 (10): 1040-1049. DOI: https://doi.org/10.1111/j.1461-0248.2009.01355.x

Hartley, I. P., Garnett, M. H., Sommerkorn, M., Hopkins, D. W., Fletcher, B. J., Sloan, V. L., Phoenix, G. K. & Wookey, P. A. (2012). A potential loss of carbon associated with greater plant growth in the European Arctic. *Nature Climate Change*, 2 (12): 875-879. DOI: https://doi.org/10.1038/nclimate1575

Holtmeier, F. K. & Broll, G. (2005). Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global ecology and Biogeography*, 14 (5): 395-410. DOI: https://doi.org/10.1111/j.1466-822X.2005.00168.x

Jobbágy, E. G. & Jackson, R. B. (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological applications*, 10 (2): 423-436. DOI: https://doi.org/10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2

Kammer, A., Hagedorn, F., Shevchenko, I., Leifeld, J., Guggenberger, G., Goryacheva, T., Rigling, A. & Moiseev, P. A. (2009). Treeline shifts in the Ural mountains affect soil organic matter dynamics. *Global Change Biology*, 15 (6): 1570-1583. DOI: https://doi.org/10.1111/j.1365- 2486.2009.01856.x

Kirdyanov, A. V., Hagedorn, F., Knorre, A. A., Fedotova, E. V., Vaganov, E. A., Naurzbaev, M. M., Moiseev, P. A. & Rigling, A. (2012). 20th century tree-line advance and vegetation changes along an altitudinal transect in the Putorana Mountains, northern Siberia. *Boreas*, 41 (1): 56-67. DOI: https://doi.org/10.1111/j.1502-3885.2011.00214.x

Kolstad, A. L., Austrheim, G., Solberg, E. J., Venete, A. M., Woodin, S. J. & Speed, J. D. (2018). Cervid exclusion alters boreal forest properties with little cascading impacts on soils. *Ecosystems*, 21: 1027-1041. DOI: https://doi.org/10.1007/s10021-017-0202-4

Körner, C. (2000). Biosphere responses to CO_2 enrichment. *Ecological applications*, 10 (6): 1590-1619. DOI: https://doi.org/10.1890/1051-0761(2000)010[1590:BRTCE]2.0.CO;2

Körner, C. & Paulsen, J. (2004). A world-wide study of high altitude treeline temperatures. *Journal of biogeography*, 31 (5): 713-732. DOI: https://doi.org/10.1111/j.13652699.2003.01043.x

Kullman, L. (1998). Tree-limits and montane forests in the Swedish Scandes: sensitive biomonitors of climate change and variability. *Ambio*: 312-321. DOI: http://www.jstor.org/stable/4314741

Kullman, L. (2002). Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of ecology*, 90 (1): 68-77. DOI: https://doi.org/10.1046/j.00220477.2001.00630.x

Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models (v. 3.1.3). *Journal of Statistical Software*, 82 (13): 1–26. DOI: doi:10.18637/jss.v082.i13.

Liang, E., Wang, Y., Eckstein, D. & Luo, T. (2011). Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. *New Phytologist*, 190 (3): 760-769. DOI: https://doi.org/10.1111/j.1469-8137.2010.03623.x

Long, J. A. (2022). *jtools: Analysis and Presentation of Social Scientific Data* (version 2.2.1). Available from: https://cran.r-project.org/package=jtools (accessed 10.04. 2023)

Loranty, M. M., Berner, L. T., Goetz, S. J., Jin, Y. & Randerson, J. T. (2014). Vegetation controls on northern high latitude snow-albedo feedback: observations and CMIP 5 model simulations. *Global change biology*, 20 (2): 594-606. DOI: https://doi.org/10.1111/gcb.12391

Lu, X., Camarero, J. J. & Liang, E. (2021). Threshold responses of juniper tree growth and regeneration to climate warming and drought stress at alpine treeline. *Trees*, 35 (4): 1081-1083. DOI: https://doi.org/10.1007/s00468-021-02135-6

Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models (v. 1.2.0). *Journal of Open Source Software*, 3 (26): 772. DOI: https://doi.org/10.21105/joss.00772

Malhi, Y., Baldocchi, D. D. & Jarvis, P. G. (1999). The carbon balance of tropical, temperate and boreal forests. *Plant, Cell & Environment*, 22 (6): 715-740. DOI: https://doi.org/10.1046/j.1365- 3040.1999.00453.x

Mann, H. B. & Whitney, D. R. (1947). On a test of whether one of two random variables is stochastically larger than the other. *The annals of mathematical statistics*, 18 (1): 50-60. Available from: https://www.jstor.org/stable/2236101

Mienna, I. M., Speed, J. D. M., Klanderud, K., Austrheim, G., Næsset, E. & Bollandsås, O. M. (2020). The relative role of climate and herbivory in driving treeline dynamics along a latitudinal gradient. *Journal of Vegetation Science*, 31 (3): 392-402. DOI: https://doi.org/10.1111/jvs.12865

Mienna, I. M., Klanderud, K., Ørka, H. O., Bryn, A. & Bollandsås, O. M. (2022). Land cover classification of treeline ecotones along a 1100 km latitudinal transect using spectral-and three-dimensional information from UAV-based aerial imagery. *Remote Sensing in Ecology and Conservation*, 8 (4): 536-550. DOI: https://doi.org/10.1002/rse2.260

Mukhopadhyay, R., Næsset, E., Gobakken, T., Mienna, I. M., Bielza, J. C., Austrheim, G., Persson, H. J., Ørka, H. O., Roald, B-E. & Bollandsås, O. M. (unpublished). *Mapping and estimating aboveground biomass in an alpine treeline ecotone under model-based inference.*

Nilsson, M. C., Wardle, D. A. & DeLuca, T. H. (2008). Belowground and aboveground consequences of interactions between live plant species mixtures and dead organic substrate mixtures. *Oikos*, 117 (3): 439-449. DOI: https://doi.org/10.1111/j.2007.00301299.16265.x

Næsset, E. & Nelson, R. (2007). Using airborne laser scanning to monitor tree migration in the boreal–alpine transition zone. *Remote Sensing of Environment*, 110 (3): 357-369. DOI: https://doi.org/10.1016/j.rse.2007.03.004

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T. & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, 15 (11): 2681-2693. DOI: https://doi.org/10.1111/j.1365-2486.2009.01935.x

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R. A., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S. & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333 (6045): 988-993. DOI: https://doi.org/10.1126/science.1201609

Parker, T. C., Subke, J. A. & Wookey, P. A. (2015). Rapid carbon turnover beneath shrub and tree vegetation is associated with low soil carbon stocks at a subarctic treeline. *Global Change Biology*, 21 (5): 2070-2081. DOI: https://doi.org/10.1111/gcb.12793

Post, W. M., Emanuel, W. R., Zinke, P. J. & Stangenberger, A. G. (1982). Soil carbon pools and world life zones. *Nature*, 298: 156-159. DOI: https://doi.org/10.1038/298156a0

QGIS Development Team (2023). *QGIS Geographic Information System* (version 3.22.16 LTR). Open Source Geospatial Foundation Project. Available from: https://download.qgis.org/downloads/ (accessed 01. 02 2023).

R Core Team (2023). *R: A language and environment for statistical computing* (version 4.2.3). R Foundation for Statistical Computing, Vienna, Austria. Available from: https://www.Rproject.org/ (accessed 15.03. 2023).

Rapalee, G., Trumbore, S. E., Davidson, E. A., Harden, J. W. & Veldhuis, H. (1998). Soil carbon stocks and their rates of accumulation and loss in a boreal forest landscape. *Global Biogeochemical Cycles*, 12 (4): 687-701. DOI: https://doi.org/10.1029/98GB02336

RStudio Team. (2015). *RStudio: Integrated Development Environment for R*. Boston, MA. Available from: http://www.rstudio.com/ (accessed 01.02 2023).

Shapiro, S. S. & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, 52 (3-4): 591–611. DOI: https://doi.org/10.1093/biomet/52.3-4.591

Sistla, S. A., Moore, J. C., Simpson, R. T., Gough, L., Shaver, G. R. & Schimel, J. P. (2013). Long-term warming restructures Arctic tundra without changing net soil carbon storage. *Nature*, 497: 615-618. DOI: https://doi.org/10.1038/nature12129

Sjögersten, S. & Wookey, P. A. (2009). The impact of climate change on ecosystem carbon dynamics at the Scandinavian mountain birch forest–tundra heath ecotone. *AMBIO: A Journal of the Human Environment*, 38 (1): 2-10. DOI: https://doi.org/10.1579/0044-7447-38.1.2

Speed, J. D., Austrheim, G., Hester, A. J. & Mysterud, A. (2010). Experimental evidence for herbivore limitation of the treeline. *Ecology*, 91 (11): 3414-3420. DOI: https://doi.org/10.1890/09-2300.1

Speed, J. D., Martinsen, V., Mysterud, A., Mulder, J., Holand, Ø. & Austrheim, G. (2014). Long-term increase in aboveground carbon stocks following exclusion of grazers and forest establishment in an alpine ecosystem. *Ecosystems*, 17: 1138-1150. DOI: https://doi.org/10.1007/s10021014-9784-2

Speed, J. D. M., Martinsen, V., Hester, A. J., Holand, Ø., Mulder, J., Mysterud, A. & Austrheim, G. (2015). Continuous and discontinuous variation in ecosystem carbon stocks with elevation across a treeline ecotone. *Biogeosciences*, 12 (5): 1615-1627. DOI: https://doi.org/10.5194/bg-12-1615-2015

Steltzer, H. (2004). Soil carbon sequestration with forest expansion in an arctic forest tundra landscape. *Canadian Journal of Forest Research*, 34 (7): 1538-1542. DOI: https://doi.org/10.1139/x04-031

Tarnocai, C., Canadell, J. G., Schuur, E. A., Kuhry, P., Mazhitova, G. & Zimov, S. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global biogeochemical cycles*, 23 (2): 1-11. DOI: https://doi.org/10.1029/2008GB003327

Thieme, N., Martin Bollandsås, O., Gobakken, T. & Næsset, E. (2011). Detection of small single trees in the forest–tundra ecotone using height values from airborne laser scanning. *Canadian Journal of Remote Sensing*, 37 (3): 264-274. DOI: https://doi.org/10.5589/m11-041

Tingstad, L., Olsen, S. L., Klanderud, K., Vandvik, V. & Ohlson, M. (2015). Temperature, precipitation and biotic interactions as determinants of tree seedling recruitment across the tree line ecotone. *Oecologia*, 179: 599-608. DOI: https://doi.org/10.1007/s00442-015-3360-0

Tiwari, A. & Jha, P. K. (2018). An overview of treeline response to environmental changes in Nepal Himalaya. *Tropical Ecology*, 59 (2): 273-285. Available from: www.tropecol.com (ISSN 0564-3295).

Van Bogaert, R., Haneca, K., Hoogesteger, J., Jonasson, C., De Dapper, M. & Callaghan, T. V. (2011). A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *Journal of Biogeography*, 38 (5): 907-921. DOI: https://doi.org/10.1111/j.1365-2699.2010.02453.x

Wang, Y., Pederson, N., Ellison, A. M., Buckley, H. L., Case, B. S., Liang, E. & Julio Camarero, J. (2016). Increased stem density and competition may diminish the positive effects of warming at alpine treeline. *Ecology*, 97 (7): 1668-1679. DOI: https://doi.org/10.1890/15-1264.1

Wardle, D. A., Nilsson, M. C., Zackrisson, O. & Gallet, C. (2003). Determinants of litter mixing effects in a Swedish boreal forest. *Soil biology and biochemistry*, 35 (6): 827-835. DOI: https://doi.org/10.1016/S0038-0717(03)00118-4

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis* (version 3.4.1). Springer-Verlag New York. Available from: https://ggplot2.tidyverse.org (accessed 01.02 2023).

Wickham, H. & Bryan, J. (2023). *readxl: Read Excel Files* (version 1.4.2). Available from: https://github.com/tidyverse/readxl (accessed 01.02. 2023).

Wickham, H., Vaughan, D., Girlich, M. (2023A). *tidyr: Tidy Messy Data* (version 1.3.0). Available from: https://github.com/tidyverse/tidyr (accessed 15.03. 2023).

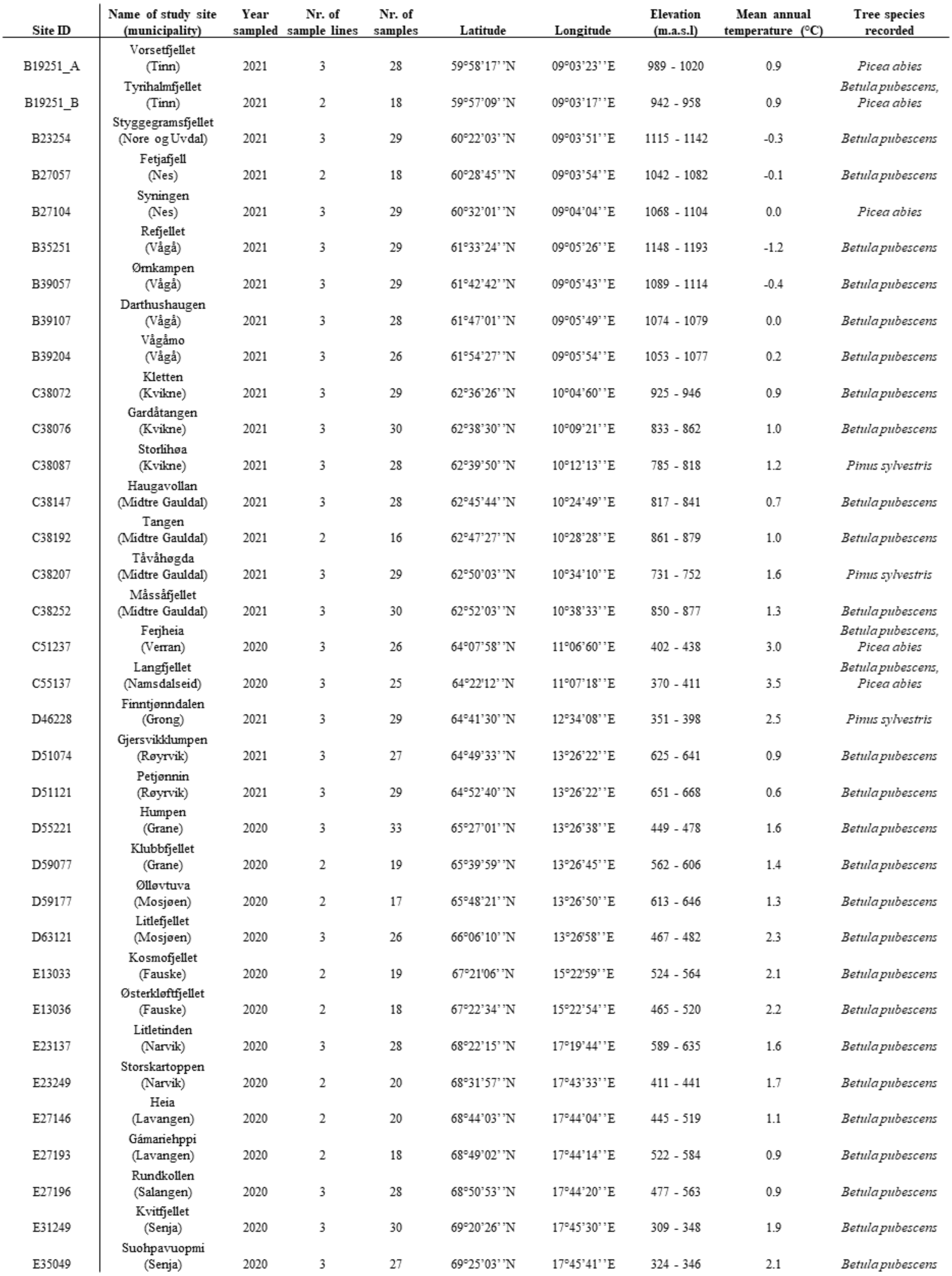
Wickham, H., François, R., Henry, L., Müller, K., Vaughan, D. (2023B). *dplyr: A Grammar of Data Manipulation* (version 1.1.1). Available from: https://github.com/tidyverse/dplyr (accessed 15.03. 2023).

Wilmking, M. & Juday, G. P. (2005). Longitudinal variation of radial growth at Alaska's northern treeline—recent changes and possible scenarios for the 21st century. *Global and Planetary Change*, 47 (2-4): 282-300. DOI: https://doi.org/10.1016/j.gloplacha.2004.10.017

Wilmking, M., Juday, G. P., Barber, V. A. & Zald, H. S. (2004). Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology*, 10 (10): 1724-1736. DOI: https://doi.org/10.1111/j.13652486.2004.00826.x

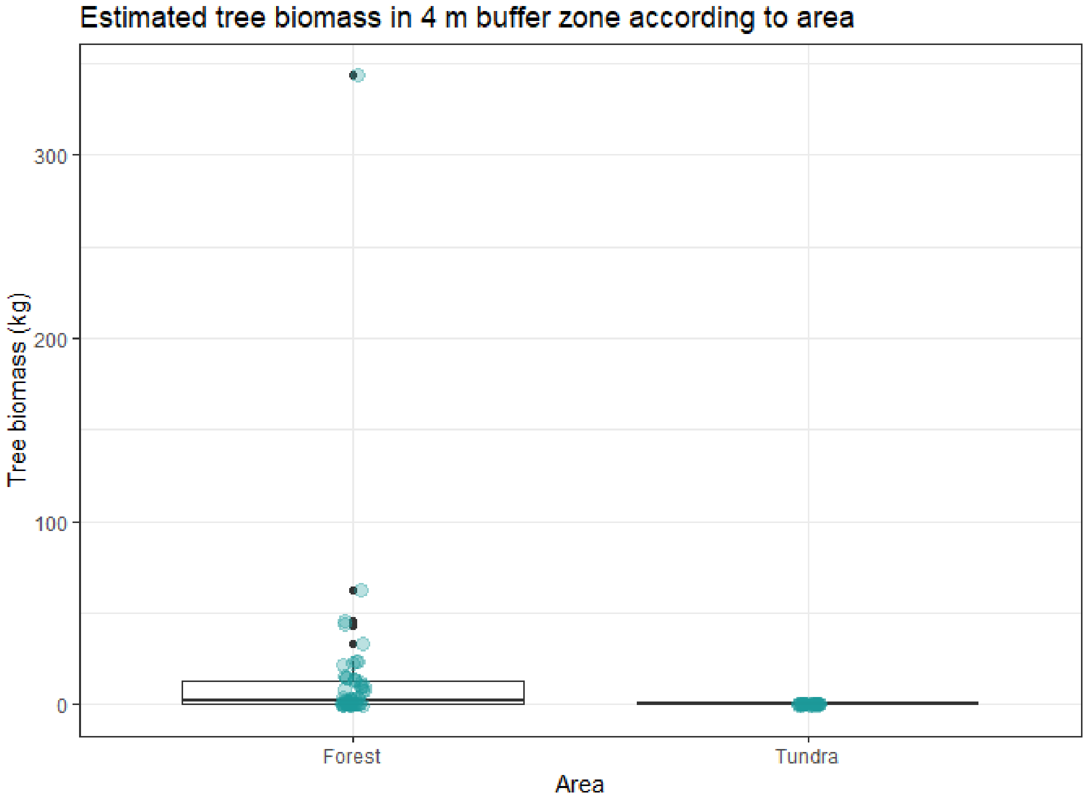
Appendix A – Study sites information

Table A-1. Information summary of the study sites included in my thesis. The information is based on the supplementary material found in Devos et al. (unpublished). Mean annual air temperatures are based on temperature records in the period 1970-2020.



Site ID	Name of study site (municipality)	Year sampled	Nr. of sample lines	Nr. of samples	Latitude	Longitude	Elevation (m.a.s.l)	Mean annual temperature (°C)	Tree species recorded
B19251_A	Vorsetfjellet (Tinn)	2021	3	28	59°58’17’’N	09°03’23’’E	989 - 1020	0.9	*Picea abies*
B19251_B	Tyrihalmfjellet (Tinn)	2021	2	18	59°57’09’’N	09°03’17’’E	942 - 958	0.9	*Betula pubescens, Picea abies*
B23254	Styggegramsfjellet (Nore og Uvdal)	2021	3	29	60°22’03’’N	09°03’51’’E	1115 - 1142	-0.3	*Betula pubescens*
B27057	Fetjafjell (Nes)	2021	2	18	60°28’45’’N	09°03’54’’E	1042 - 1082	-0.1	*Betula pubescens*
B27104	Syningen (Nes)	2021	3	29	60°32’01’’N	09°04’04’’E	1068 - 1104	0.0	*Picea abies*
B35251	Refjellet (Vågå)	2021	3	29	61°33’24’’N	09°05’26’’E	1148 - 1193	-1.2	*Betula pubescens*
B39057	Ørnkampen (Vågå)	2021	3	29	61°42’42’’N	09°05’43’’E	1089 - 1114	-0.4	*Betula pubescens*
B39107	Darthushaugen (Vågå)	2021	3	28	61°47’01’’N	09°05’49’’E	1074 - 1079	0.0	*Betula pubescens*
B39204	Vågåmo (Vågå)	2021	3	26	61°54’27’’N	09°05’54’’E	1053 - 1077	0.2	*Betula pubescens*
C38072	Kletten (Kvikne)	2021	3	29	62°36’26’’N	10°04’60’’E	925 - 946	0.9	*Betula pubescens*
C38076	Gardåtangen (Kvikne)	2021	3	30	62°38’30’’N	10°09’21’’E	833 - 862	1.0	*Betula pubescens*
C38087	Storlihøa (Kvikne)	2021	3	28	62°39’50’’N	10°12’13’’E	785 - 818	1.2	*Pinus sylvestris*
C38147	Haugavollan (Midtre Gauldal)	2021	3	28	62°45’44’’N	10°24’49’’E	817 - 841	0.7	*Betula pubescens*
C38192	Tangen (Midtre Gauldal)	2021	2	16	62°47’27’’N	10°28’28’’E	861 - 879	1.0	*Betula pubescens*
C38207	Tåvåhøgda (Midtre Gauldal)	2021	3	29	62°50’03’’N	10°34’10’’E	731 - 752	1.6	*Pinus sylvestris*
C38252	Måssåfjellet (Midtre Gauldal)	2021	3	30	62°52’03’’N	10°38’33’’E	850 - 877	1.3	*Betula pubescens*
C51237	Ferjheia (Verran)	2020	3	26	64°07’58’’N	11°06’60’’E	402 - 438	3.0	*Betula pubescens, Picea abies*
C55137	Langfjellet (Namsdalseid)	2020	3	25	64°22'12’’N	11°07’18’’E	370 - 411	3.5	*Betula pubescens, Picea abies*
D46228	Finntjønndalen (Grong)	2021	3	29	64°41’30’’N	12°34’08’’E	351 - 398	2.5	*Pinus sylvestris*
D51074	Gjersvikklumpen (Røyrvik)	2021	3	27	64°49’33’’N	13°26’22’’E	625 - 641	0.9	*Betula pubescens*
D51121	Petjønnin (Røyrvik)	2021	3	29	64°52’40’’N	13°26’22’’E	651 - 668	0.6	*Betula pubescens*
D55221	Humpen (Grane)	2020	3	33	65°27’01’’N	13°26’38’’E	449 - 478	1.6	*Betula pubescens*
D59077	Klubbfjellet (Grane)	2020	2	19	65°39’59’’N	13°26’45’’E	562 - 606	1.4	*Betula pubescens*
D59177	Ølløvtuva (Mosjøen)	2020	2	17	65°48’21’’N	13°26’50’’E	613 - 646	1.3	*Betula pubescens*
D63121	Litlefjellet (Mosjøen)	2020	3	26	66°06’10’’N	13°26'58’’E	467 - 482	2.3	*Betula pubescens*
E13033	Kosmofjellet (Fauske)	2020	2	19	67°21'06’’N	15°22'59’’E	524 - 564	2.1	*Betula pubescens*
E13036	Østerkløftfjellet (Fauske)	2020	2	18	67°22’34’’N	15°22’54’’E	465 - 520	2.2	*Betula pubescens*
E23137	Litletinden (Narvik)	2020	3	28	68°22’15’’N	17°19’44’’E	589 - 635	1.6	*Betula pubescens*
E23249	Storskartoppen (Narvik)	2020	2	20	68°31’57’’N	17°43’33’’E	411 - 441	1.7	*Betula pubescens*
E27146	Heia (Lavangen)	2020	2	20	68°44’03’’N	17°44’04’’E	445 - 519	1.1	*Betula pubescens*
E27193	Gámariehppi (Lavangen)	2020	2	18	68°49’02’’N	17°44’14’’E	522 - 584	0.9	*Betula pubescens*
E27196	Rundkollen (Salangen)	2020	3	28	68°50’53’’N	17°44’20’’E	477 - 563	0.9	*Betula pubescens*
E31249	Kvitfjellet (Senja)	2020	3	30	69°20’26’’N	17°45’30’’E	309 - 348	1.9	*Betula pubescens*
E35049	Suohpavuopmi (Senja)	2020	3	27	69°25’03’’N	17°45’41’’E	324 - 346	2.1	*Betula pubescens*

Appendix B – Estimated tree biomass in forest and tundra



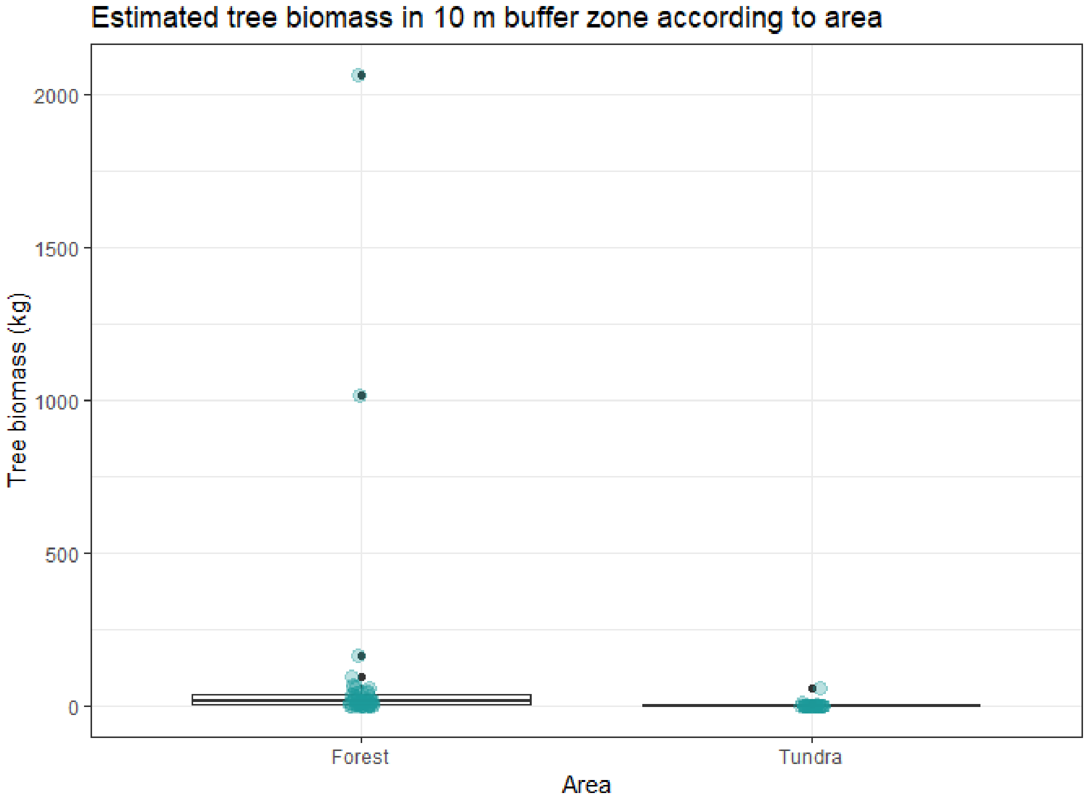


Figure B-1. Boxplots showing average estimated tree biomass, as well as variation in the tree biomass data, in forest compared to tundra for the smallest (radius 4 m) and biggest (radius 10 m) buffer zones.

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway