

Tree biomass does not correlate with soil carbon stocks in forest-tundra ecotones along a 1100 km latitudinal gradient in Norway

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Abstract

Due to climate warming, forests are expanding to higher elevations and latitudes at the expense of tundra vegetation. While the subsequent increase in aboveground biomass is well-documented, there is much speculation regarding the effects on soil organic carbon (SOC) stocks. To provide insight into the consequences of tree encroachment into treeless tundra, we sampled SOC stocks across 36 forest-tundra ecotones along a 1100 km latitudinal gradient in Norway. Our results show that SOC stocks vary greatly within, as well as among treeline ecotones, and that tree biomass and tree species are not correlated with this variability. Instead, SOC stocks increase with temperature, and vary with slope steepness, slope aspect, and soil parent material. Applying a ‘space-for-time substitution’ perspective, our findings suggest that tree encroachment into tundra is unlikely to have immediate consequences for SOC stocks.

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Keywords: soil carbon, treeline, boreal forest, tundra, alpine, Norway

Introduction

One of the most striking ecotones is the treeline, which denotes the transition from forests to alpine or arctic tundra in temperate and boreal regions¹. Elevational and latitudinal treeline shifts are well-studied and ecologically highly important examples of climate change-driven shifts in species distributions²⁻⁴, which have the potential to proceed rapidly. In the Swedish Scandes, for instance, mountain birch (*Betula pubescens* ssp. *czerepanovii*), Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*) forests have shown elevational range expansions up to 200 meters over the last century⁵. In Alaska, white spruce (*Picea glauca*) populations have been invading Arctic tundra at a speed >4 km per decade⁶.

Trees substantially modify abiotic soil conditions, and have a major impact on the composition and productivity of co-occurring biotic communities. As such, tree encroachment into tundra is likely to have profound implications for numerous ecosystem processes⁴. At present, there is great concern regarding the consequences for the global carbon (C) cycle. Despite having a relatively low plant productivity, and thus, small aboveground C stocks, tundra communities are important in terms of C storage due to their soil organic carbon (SOC)⁷⁻¹⁰. As a result of tree colonization, a portion of this SOC could get released into the atmosphere as CO₂ or CH₄, thereby providing a positive feedback to climate change^{3,4}. It remains, however, unclear to what extent a shift from tundra to forest impacts SOC stocks.

Given the complex interactions between the numerous biotic and abiotic drivers of SOC dynamics¹¹, it is plausible that study sites exhibit varying responses to treeline shifts. Overall, three main scenarios may occur^{3,7}: (1) the increase in aboveground biomass can result in larger SOC stocks due to increased litter deposition; (2) forest expansion can cause a reduction in SOC stocks due to increased decomposition rates, and; (3) changes in litter input and decomposition rates can balance each other out. In some study sites, field studies found that the replacement of heath tundra with deciduous shrubs and trees accelerates decomposition by increasing the abundance of ectomycorrhizal and saprotrophic fungi¹²⁻¹⁴. Moreover, shrubs and trees seem to stimulate winter decomposition through increased snow accumulation and insulation of the soil¹⁵. During the growing season, however, an increased vegetation cover may slow down decomposition by providing shade and cooling the soil¹⁶. Moreover, forest

expansion could affect SOC turnover differently depending on the type of tundra vegetation that is being replaced^{7,17}, and the tree species that is invading the tundra. Tree species affect soil properties in numerous ways, for instance due to differences regarding litter quantity, litter quality, root activity, and light transmittance through the tree crown^{18,19}. Additionally, the effects of forest expansion on SOC may in some localities be limited due to a relatively greater importance of physicochemical constraints on decomposer activity (e.g. anoxia in waterlogged soils)¹². Unsurprisingly, the literature reports diverging results. Across some treeline ecotones, forest soils seem to store less SOC compared to adjacent tundra soils^{12,13,17,20–23}, while other treeline ecotones store similar amounts of SOC above- and below the treeline^{23,24}.

Currently, only few studies have sampled SOC stocks across the forest-tundra ecotone, and their measurements apply to a small number of study sites^{17,23}. To make meaningful generalizations about the implications of treeline shifts, it is crucial to consider data from a wide diversity and geographic range of study sites. We therefore quantified SOC stocks in 36 forest-tundra ecotones spread along a 1100 km long latitudinal gradient in the Norwegian mountain range. The study sites represent a broad range of regional climates, topography, and vegetation communities, and include three different tundra-invading tree species, i.e., mountain birch (*Betula pubescens* ssp. *czerepanovii*), Norway spruce (*Picea abies*), and Scots pine (*Pinus sylvestris*). Our main goal is to disentangle the role of trees (i.e., variability in tree biomass and tree species) from abiotic factors as drivers of SOC stocks in the present-day treeline ecotone. By focusing on SOC stocks in soil surface horizons (i.e., O and A horizon) right above and below the tree species line (i.e. the upper limit to which trees are capable of growing), our study provides insight into the short-term consequences of tree encroachment.

Methods

Study sites

This study was carried out in 36 study sites (~ 50 m × 200 m) located along a 1100 km long latitudinal gradient stretching from southern (60°N) to northern (69°N) Norway (Fig. 3, Supplementary Table S1). The gradient was first described by *Thieme et al.*²⁵, and originally established to study the capability of airborne laser scanning to detect small, individual trees in the forest-tundra ecotone. The study sites were selected for their proximity to sample plots used in Norway's National Forest Inventory (NFI). Note that the definition of *forest-tundra ecotone* varies throughout the literature. Our study sites consist of transition zones from sparse forests (< 20% canopy cover) right below the tree species line (i.e., the upper limit to which trees are capable of growing), hereafter referred to as 'forest', to treeless tundra above the tree species line, hereafter referred to as 'tundra'. During a field campaign in 2020 (August-September), we sampled 16 study sites along the gradient. The remaining 20 sites were sampled in 2021 (July-August). Due to the wide gradients in latitude and continentality, the study sites vary considerably in terms of climate, topography, and vegetation. The sites range from 1200 m above sea level in southern Norway to 300 m above sea level in northern Norway. The dominating tree species are mountain birch (*Betula pubescens* ssp *czerepanovii*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Common understory vegetation includes shrubs (e.g., *Betula nana*, *Vaccinium* spp., *Empetrum nigrum*, *Calluna vulgaris*), mosses (e.g. *Hylocomium splendens*, *Pleurozium schreberi*, *Sphagnum* spp.), lichens (e.g. *Cladonia* spp., and *Flavocetraria* spp.) and grasses (e.g. *Avenella flexuosa*, *Nardus stricta*). More information on vegetation communities at our study sites can be found in *Mienna et al.*²⁶.

Soil sampling and quantification of SOC stocks

In all study sites, we set up three soil sample transects (Fig. 1), each consisting of 10 soil sample points located 0.5, 1.2, 1.6, 2.4 and 4 m northward and southward from a center point. In the tundra, we set up one soil sample transect, and centered this transect around a point on the western border of the rectangle, 10 m in downhill direction from the upper border. To encompass variation in forest structure, we established two soil sample transects in the forest, and centered these transects around trees of different sizes (one short tree: 1-2 m, one tall tree: > 2 m). The center point trees were located outside the rectangle, as close as possible to the downhill border. The distance between the two center point trees was at least 10 m. At each sample point, we collected a soil core of the entire surface soil (i.e., O and A horizons) using a cylindrical soil sampler ($\varnothing = 6.35$ cm). The samples were stored at -20°C until analysis.

In the laboratory, the soil samples were defrosted. Plant litter, such as leaves and twigs, was removed. The soil samples were dried to constant mass at 40°C in drying cabinets. Bulk densities were determined based on the dry matter mass and sample volume. As there was typically no clear border between the O- and A horizon, we did not attempt to separate the soil horizons. Instead, the dried samples were milled and homogenized to ensure thorough mixing. Afterwards, SOC concentrations were determined by dry combustion using a vario MICRO cube element analyser (Elementar, Hanau, Germany). Finally, volume-based SOC stocks were calculated as follows:

$$\text{SOC stock (kg m}^{-2}\text{)} = \text{bulk density (kg m}^{-3}\text{)} \times \text{soil depth (m)} \times \text{SOC concentration (\%)} \times 0.01$$

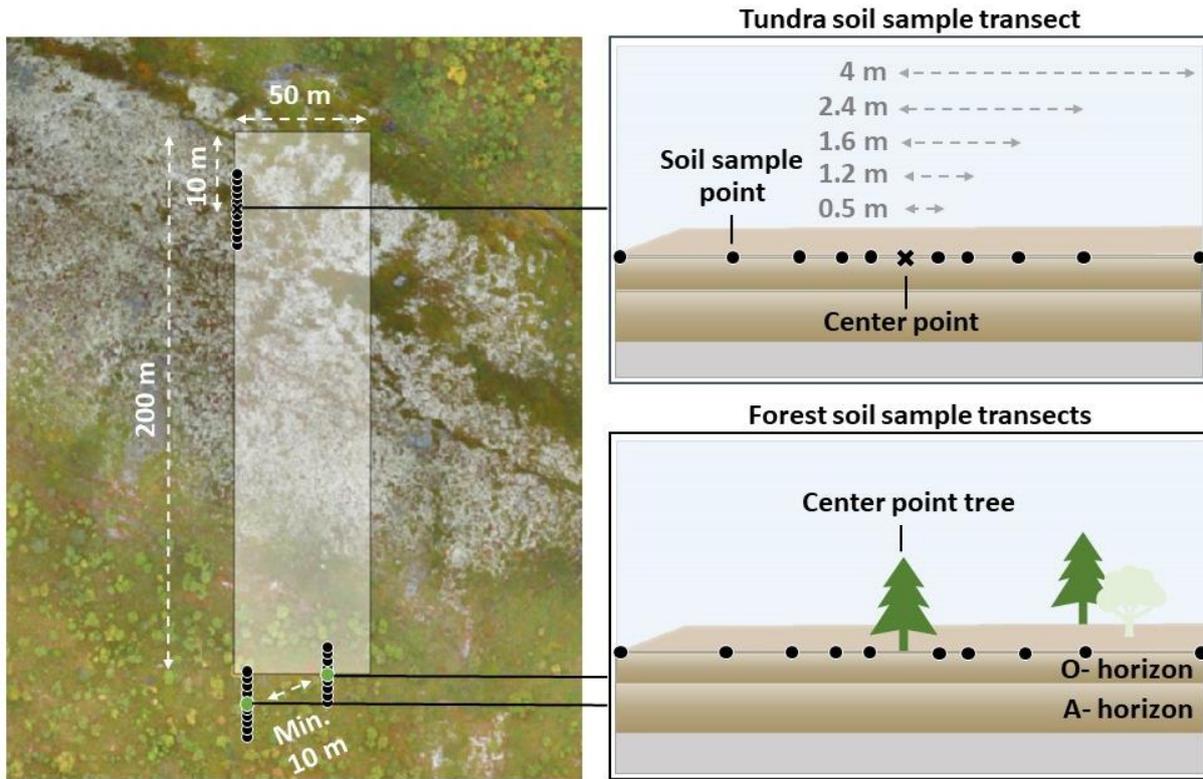


Figure 1. Soil sample design. In all 36 study sites, we established one soil sample transect in the tundra above the tree species line, and two soil sample transects in the forest below the tree species line. Each soil sample transect consisted of 10 soil sample points (marked with black dots). The tundra soil transect was centered around a treeless center point (marked with a black cross), while the forest soil sample transects were centered around a tree (marked with green dots or tree symbols). Soil core samples included the entire surface soil (i.e., O-and A horizons).

Climate, topography and soil parent material

Soil sample point coordinates were obtained using a HiPer SR receiver in real-time kinetic mode, receiving differential corrections of the Global Navigation Satellite System and the Global Positioning System. Climatic variables were constructed on the study site-level based on daily weather predictions interpolated from Norway's official weather stations by the Norwegian Meteorological Institute²⁷. We calculated summer temperature, summer precipitation, and summer solar radiation as the mean of daily observations from June 1st to September 30th between 1970 and 2020. For each soil sample point, topographic attributes (slope aspect and slope steepness) were derived from digital elevation models (DEMs) with a resolution of 1 m provided by the Norwegian Mapping Authority (www.norgeskart.no). The aspect values were cosine transformed to obtain a variable that represents south-north orientation. To avoid 0 values, we added the value of 2 to each observation, thus obtaining values ranging between 1 (south) and 3 (north). For each soil sample point, we also obtained information on soil parent material based on a map by the Geological Survey of Norway. The map is publicly accessible through Norway's national map data portal (www.geonorge.no).

Forest structure

In each study site, we registered characteristics (species, height, stem circumference, and coordinates) of trees in proximity to our soil sample points. Since it was not possible to map all trees due to time constraints, we made the following assumptions: 1) a tree can at most exert influence on SOC dynamics over a distance equal to its height, 2) the influence of a tree is symmetrically distributed around the stem center, and 3) the influence of a tree is independent from that of others (e.g., no competition). Thus, we registered trees if their distance to a soil sample point \leq tree height. Only trees with a height ≥ 50 cm were registered. To measure tree height, we used a surveyor's tape or Vertex III hypsometer. Stem circumference was determined using a surveyor's tape at breast height (1.3 m above the ground) whenever possible. For smaller trees, we measured stem circumference at its widest point. Height and stem circumference measurements were used to estimate the aboveground biomass of each tree according to the species-specific allometric models by *Marklund*²⁸. Finally, to be able to include the registered tree characteristics in regression analyses, we constructed three different continuous *tree biomass* (TB) indices, and one categorical *tree species* variable for each soil sample point. Tree biomass indices account for the distances from a soil sample point to its surrounding trees (i.e., trees within a distance \leq tree height from the soil sample point), and/or the aboveground biomass of these trees. TB_U assumes that the influence of a tree does not decrease with distance, TB_L assumes that the influence of a tree decreases linearly, and TB_E assumes that the influence decreases exponentially (Table 1). The tree species variable indicates by which tree species a soil sample point is surrounded (either “treeless”, “mountain birch”, “Norway spruce”, “Scots pine”, or “mixture of mountain birch and Norway spruce”).

Table 1. Tree biomass (TB) indices assuming that the influence of a trees does not decrease (TB_U), decreases linearly (TB_L), or decreases exponentially (TB_E) with increasing distance. i = tree, j = soil sample point, d_{ij} = distance between tree i and soil sample point j (cm), h_i = tree height (cm), AB_i = aboveground tree biomass (kg).

Name	Formula
TB _U	$TB_U = \sum_{i, d_{ij} < h_i} AB_i$
TB _L	$TB_L = \sum_{i, d_{ij} < h_i} (AB_i * (1 - \frac{d_{ij}}{h_i}))$
TB _E	$TB_E = \sum_{i, d_{ij} < h_i} (AB_i * e^{-\frac{d_{ij}}{h_i}})$

Statistical analyses

All statistical analyses were carried out using R (R Core Team, 2021). First, we applied basic descriptive statistics to report soil depths, bulk densities, SOC concentrations, and SOC stocks. Due to the non-normal distributions of the variables, we used Mann-Whitney *U* tests to examine whether these soil characteristics differed between forest and tundra soils across the entire dataset (forest: $n = 669$, tundra: $n = 335$), as well as within study sites.

Second, we studied how SOC stocks related to biotic and abiotic factors. To do so, we fitted linear mixed-effects models using the R package *lme4*²⁹. Since some soil samples could not be included due to missing coordinates ($n = 85$), this analysis was carried out on a slightly smaller dataset ($n = 919$) than the Mann-Whitney *U* tests. As we wanted to test which tree biomass index explained our data the best, we fitted three initial models. As fixed effects, the three initial models each included one of the tree biomass indices, as well as tree species, summer temperature, summer precipitation, summer solar radiation, slope steepness, south-north slope aspect, and soil parent material. To check for multicollinearity between these variables, we calculated generalized variation inflation factors (GVIF) with the *car* package³⁰. All GVIF values < 2.5 , indicating low multicollinearity. Study site was included as a random effect. The response variable, SOC stock, was log-transformed to normalize the residuals. Variables that did not significantly improve the model fit, as measured by chi-squared tests ($p > 0.05$), were removed one by one, starting with the predictor variable of least significance. After elimination of a predictor variable, the model was re-fit and the process was repeated until all predictor variables remained statistically significant. To eliminate non-significant fixed effect variables, models were fit using maximum likelihood estimation (ML). The three initial models all resulted in the same final, reduced model. The model parameters of the final model were derived using restricted maximum likelihood estimation (REML). To quantify the explained variation in the response variable, we calculated marginal and conditional R^2 values with the *MuMIn* package³¹. Marginal R^2 (R^2_m) values indicate the variation explained by the fixed effects, whereas conditional R^2 (R^2_c) values indicate the variation explained by both the fixed and random effects. To test for differences between soil parent material, we used the *emmeans* package³² and carried out least square mean comparisons with Bonferroni correction.

Results

Soil properties across the forest-tundra ecotone

Across the dataset, forests had significantly ($p < 0.001$) thicker surface soils (median: 3.5 cm) than treeless tundra (median: 3.0 cm) (Fig. 2a). SOC concentrations did not differ ($p = 0.15$) between the forest (median: 43.22 %) and the tundra (median: 41.65 %) (Supplementary Fig. S1b). Since forest soils had lower ($p < 0.001$) bulk densities (median: 0.16 g cm^{-3}) than tundra soils (median: 0.18 g cm^{-3}) (Supplementary Fig. S2a), they stored similar ($p = 0.05$) SOC stocks (forest median: 2.02 kg m^{-2} , tundra median: 1.98 kg m^{-2}) (Fig. 2b).

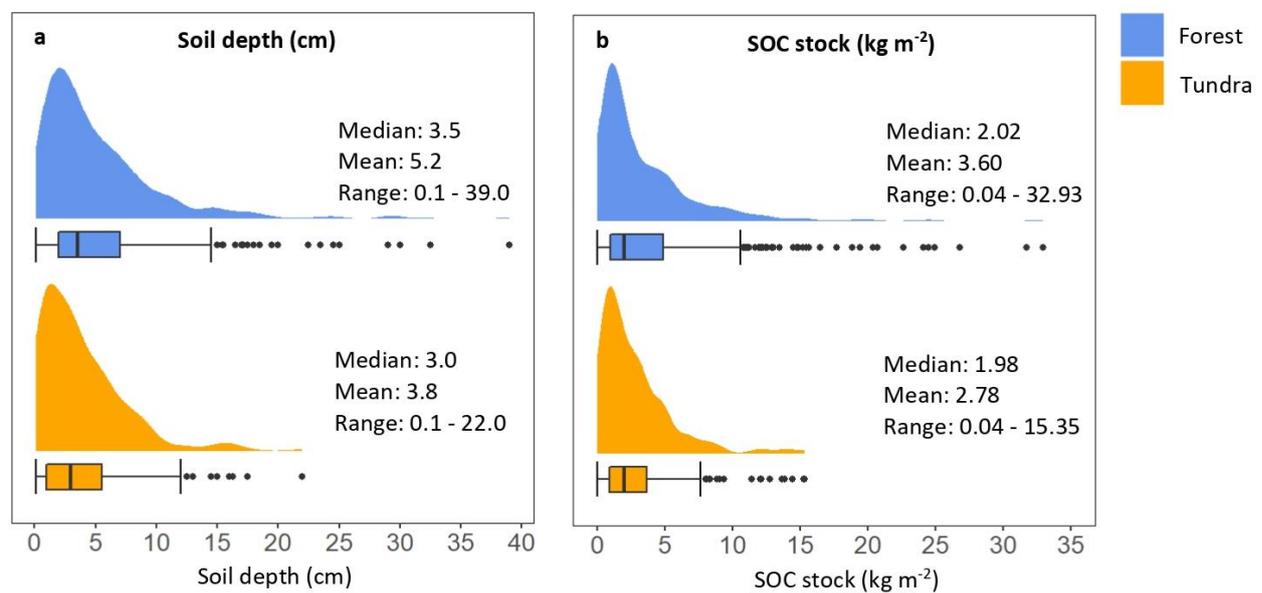


Figure 2. Soil depths (**a**) and soil organic carbon (SOC) stocks (**b**) of surface soils (i.e., O and A horizon) in forests ($n = 669$) and tundra ($n = 335$) across 36 forest-tundra ecotones in Norway.

Soil characteristics varied substantially within and among study sites. Among the 36 study sites, eight sites stored significantly higher ($p < 0.05$) SOC stocks in the forest than in the tundra. With the exception of one site, these study sites were situated in the northern half of the latitudinal gradient. Six sites, mostly situated in the southern half of the country, stored significantly less ($p < 0.05$) SOC in the forest than in the tundra (Fig. 3). A detailed overview of soil characteristics at each study site can be found in Supplementary Table S2.

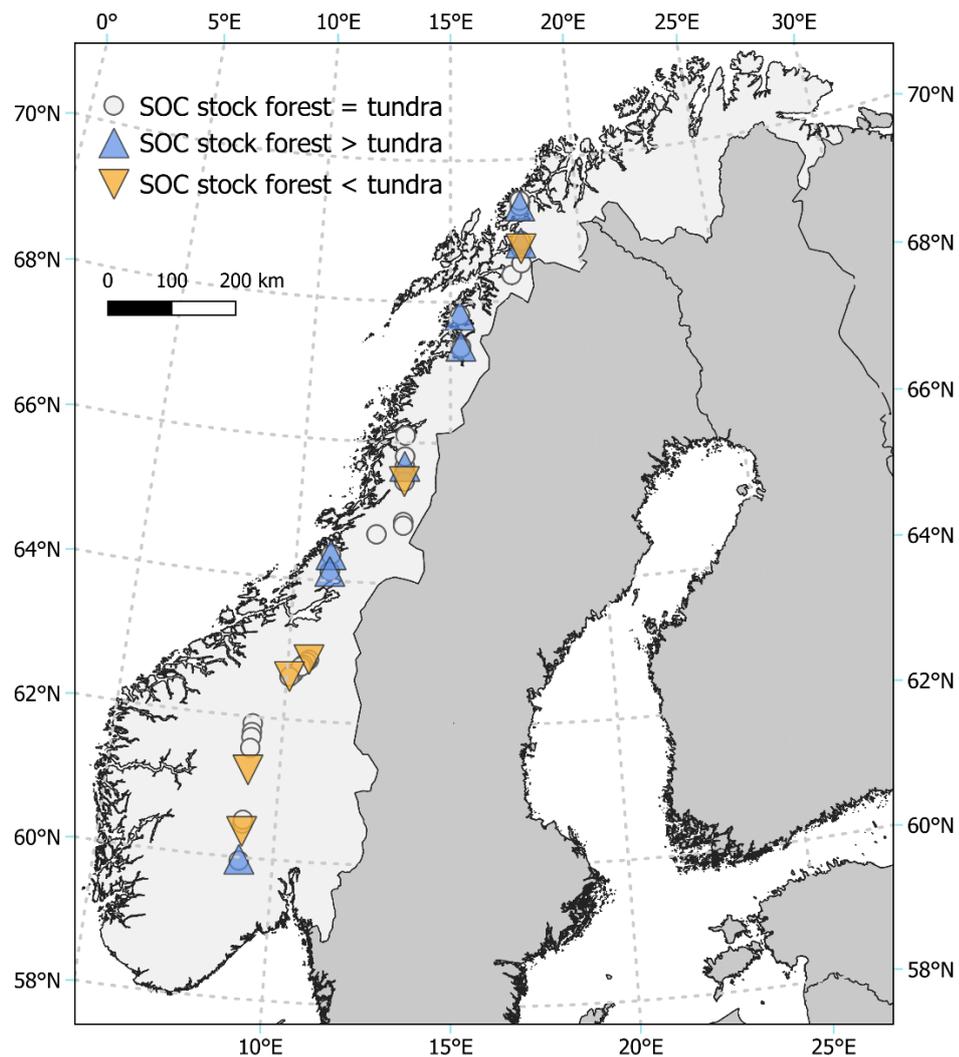


Figure 3. Location of the 36 studied forest-tundra ecotones located along an 1100 km long latitudinal gradient in Norway. Symbols indicate whether SOC stocks differ significantly (Mann-Whitney U tests, $p < 0.05$) between the forest and tundra at each site.

SOC stocks in relation to biotic and abiotic factors

Linear mixed-effects models showed that variability in SOC stocks could not be explained by tree characteristics. No matter which tree biomass index was included in the initial model, the tree biomass index and tree species variable were always eliminated during the backwards variable selection process (Supplementary Table S3 a-c). Our final, reduced model (R^2_m : 0.18, R^2_c : 0.47) consisted of four fixed effects in addition to the random effects. SOC stocks significantly increased with increasing summer air temperature and north orientation, while they significantly decreased with increasing slope steepness. Covers of peat or moraine material over bedrock stored significantly more SOC than exposed bedrock (Table 2).

Table 2. Final linear mixed-effects model explaining the variability in soil organic carbon (SOC) stocks found in soil samples ($n = 919$) collected across 36 forest-tundra ecotones in Norway. The selection of significant fixed effects (chi-squared tests, $p < 0.05$) was carried out through backwards elimination. To test for differences between soil parent material, we carried out a least square mean comparison with the reference group. The reference group was exposed bedrock.

Random effects	Variance	Std. deviation	
Study site (intercept)	0.37	0.61	
Residual	0.70	0.83	
Fixed effects	Estimate	Std. error	<i>p</i>-value
Intercept	-4.16	1.47	
South-north slope aspect	0.24	0.06	< 0.001
Summer air temperature	0.48	0.17	0.004
Slope steepness	-0.01	0.004	0.04
Soil parent material			< 0.001
Weathered material	0.46	0.65	1
Till with high clay content	0.29	0.29	1
Moraine material, thin cover over bedrock	0.61	0.13	< 0.001
Peat and bog	-0.27	0.65	1
Thin peat cover over bedrock	1.07	0.22	< 0.001

Discussion

Tree biomass and tree species do not control SOC stocks

As many forests are currently advancing into tundra^{2,3}, it is crucial to understand the implications of tree establishment for SOC stocks. The establishment of trees on treeless tundra soils may result in two distinctive patterns. First, there may be differences in SOC stocks along the transition from forest to treeless tundra, and second, SOC stocks may vary locally in relation to variability in tree biomass and tree species. Our results indicate, however, that the surface soils of forests and tundra generally store similar SOC stocks. There are individual study sites that do show a significant increase or decrease in SOC stocks across the treeline, but such variability in SOC stocks cannot be explained by aboveground tree biomass or tree species. Applying a ‘space-for-time substitution’ perspective, our findings suggest that tree encroachment into tundra may not have immediate consequences for SOC stocks. Our findings contrast with those of previous studies in the Scandes mountains, who found an inverse relationship between forest cover and SOC stocks^{12,13,17,20,22}. We propose two explanations that could explain why tree biomass and tree species do not explain SOC stocks in our study sites.

First, trees may have little impact on surrounding SOC stocks if the balance between SOC gains and SOC losses remains unaffected. An increase in plant productivity not only increases the input of organic matter through litter fall and root turnover, but it could also stimulate decomposition rates^{12,22,33}. For instance, recent studies suggest that the soil biota of mountain birch forests are characterized by higher proportions of ectomycorrhizal and saprotrophic fungi than those of nearby heath tundra, which may promote higher SOC turnover rates^{13,14}. Moreover, forest soils tend to accumulate deeper snowpacks, which insulates the soil, and stimulates soil biological activity^{22,24}. Similarly, different tree species may store similar SOC stocks. For instance, a study on adjacent 50-year-old stands of Norway spruce, Scots pine, and silver birch (*Betula pendula*) reported that differences in the SOC stocks of mineral soil layers were small and non-significant despite variation in litter fall and decomposition rates^{18,19}.

Second, we propose that the forests we examined may have been too young to induce substantial changes in SOC stocks. While afforestation of Scottish heather moorland has been shown to impact SOC sequestration on decadal timescales³⁴, these dynamics may occur on a

different temporal scale in the Arctic and subarctic¹⁷. In the Ural mountains, for instance, SOC stocks in the organic layers underneath 50-year-old Siberian spruce (*Picea obovate*) and treeless tundra were found to be similar, while soils underneath 150-year-old spruce stored significantly greater SOC stocks than nearby tundra²⁴. As our forest soil sample transects were situated relatively close (~200 m) to the tundra, we may have sampled relatively young forests in comparison with previous studies. Unfortunately, we were unable to conduct dendrochronological analyses or radiocarbon dating.

Abiotic controls on SOC stocks

Temperature is a well-known driver of SOC, as both plant productivity and microbial activity have a high temperature sensitivity^{11,35}. Interestingly, we found SOC stocks to be positively related to summer air temperature, which is inconsistent with commonly reported global trends^{11,36}. At a more regional scale, however, previous studies in Scandinavia did observe a positive correlation^{37–39}. Callesen *et al.*³⁷ proposed that the commonly reported negative relation between SOC and temperature may be due to the inclusion of high frequencies of hydromorphic soils for boreal forests and tundra, where decomposition is hampered by low oxygen levels. When only well-drained soils are included, the trend seems to reverse, presumably due to an increase in net primary production with increasing temperature.

In addition, topographic features can further drive SOC stocks by controlling microclimatic conditions^{11,40}. In our study, we found SOC stocks to be the highest on north-facing, gentle slopes. By determining the angle of incident solar radiation, slope aspect and steepness affect local temperature and moisture conditions. In the northern hemisphere, a combination of south-facing aspects and steep slopes results in dry and warm soil conditions. North-facing aspects are colder and moister, with longer-lasting and deeper snowpacks^{41,42}. Despite shortening the growing season, this snow cover may provide favorable conditions for plant growth by offering protection from winter desiccation and wind abrasion, as well as by providing soil moisture in spring⁴³. Moreover, lower summer soil temperatures may cause soils on north-facing slopes to have lower decomposition rates⁴⁴. Slope steepness also controls water

flow paths, and thereby plays a key role in erosion and sediment redistribution. Steep slopes tend to have more surface runoff, and are therefore bound to lose more organic matter⁴⁰.

Lastly, our results point to soil parent material as a driver of SOC stocks. Due to its glacial history, extensive parts of Norway consist of exposed bedrock, or bedrock covered with a thin layer of deposited sediments⁴⁵. Unsurprisingly, we found that soil sample points located on thin layers of peat or moraine material had larger SOC stocks than soil sample points on exposed bedrock. Exposed bedrock is an inhospitable substrate for most organisms as it has a very low porosity, and as a result, does not provide structural support for roots, or access to water and nutrients. To support vegetation, bedrock first has to develop porosity through biological, chemical, and physical weathering processes⁴⁶. With peat or moraine deposits as parent material, vegetation establishment and soil formation can occur more readily.

SOC stocks along the latitudinal gradient

Although we were able to identify several drivers of SOC stocks, much remains unexplained. For instance, we cannot pinpoint why study sites with larger SOC stocks in the tundra than in the forest are mainly situated in the southern half of Norway, while sites with larger SOC stocks in the forest than in the tundra are mostly found in the northern half of the country. Since our study sites are located along a gradient in both latitude and continentality, we suspect that this pattern reflects complex interactions between climate, plant succession, and soil development. In recently deglaciated areas, time and climate are major determinants of weathering-, and plant succession rates, which are strongly linked to SOC dynamics^{47,48}. Since the timing of glacial retreats varies considerably across the country⁴⁹, it is likely that our latitudinal gradient captures some of that variation. Also, previous studies have shown that elevation and continentality gradients are important drivers of compositional variation in pioneer communities^{50,51}. At present, however, our understanding of the degree to which the ground-, field- and understory vegetation controls SOC stocks in the forest-tundra ecotone is constrained by the low number of studies on above-belowground linkages¹⁷.

Conclusion and outlook

Current measurements of SOC stocks in the forest-tundra ecotone apply to a limited diversity and geographical range of study sites. We therefore sampled 36 study sites with highly variable climates, topography, and vegetation communities. Our measurements indicate that a majority of study sites stores similar SOC stocks in nearby forest and tundra soils. Moreover, SOC stocks are not related to tree species and tree biomass. Since aboveground tree biomass and tree species do not explain SOC stocks in the present-day treeline ecotone, our results suggest that future tree encroachment into currently treeless tundra is unlikely to have short-term consequences for SOC stocks. That being said, we want to emphasize that SOC dynamics may vary considerably with time. By focusing on trees that have recently colonized tundra communities, our study provides insight into a small part of a successional trajectory. To gain a better understanding of SOC responses over both short (years to decennia) and long (centuries to millennia) time scales, we highly recommend future studies to establish soil sample lines extending from moss and lichen dominated tundra into the old-growth forest.

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