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Variability in soil carbon-to-nitrogen ratios explained by environmental conditions in a boreal catchment

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ABSTRACT

Forest soil functions are influenced by interactions among trees, other organisms, and environmental factors such as the soil parent material and climate. Tree productivity and potential for forest C sequestration are currently receiving considerable attention. In boreal forests, plant productivity is commonly limited by the supply of N. Trees and other plants integrate the C and N cycles to form plant organs, which provide organic material for soils and subsequently feed the soil biota. Thus, plant growth has profound impacts on soil and ecosystem biogeochemistry. In this context, the soil C/N ratio is a critical parameter, which can display large variation across forest landscapes. This variation is correlated with forest productivity and other ecosystem functions. The aim of this study was to explore how C/N ratios in boreal forest soils are related to topography, dominant tree species, parent material, and soil texture. This was done by using a spatially-intense dataset of soil C/N ratios which included three sampling depths from 391 forest plots located within a 68 km^2 boreal forest catchment. Hydrological conditions related to topography (i.e., Topographic Wetness Index) demonstrated a significant influence on organic layer C/N ratios (R^2=0.11, p<0.001), which decreased with increaced soil wetness. The topographic control on C/N ratios was strongest in unsorted sediments (R^2=0.15, p<0.001), where topography is the main driver of the variation in soil moisture conditions. The topographic influence on C/N ratios in mineral soil decreased with depth and was found to be non-significant at the 10–20 cm depth. Forests dominated by Scots pine showed higher C/N ratios in the surficial organic layer than forests with other dominant tree species (mainly Norway spruce) or a mixed forests. In contrast, dominant tree species was not found to influence the C/N ratio in mineral soil layers. For mineral soil samples representing sorted sediments, C/N ratios decreased with grain size distribution, while no significant differences in C/N rations were observed in unsorted sediments. The study highlights a large landscape variation in soil C/N ratios within a boreal landscape. It also demonstrates the challenges associated with explaining soil properties, as a sizeable proportion of unexplained variation is caused by the complex interactions between multiple environmental factors linked to the biogeochemistry of forest soils including tree-soil interactions.

1. Introduction

Forests are intimately dependent on the soils on which they grow, while soils are fundamentally shaped by the forest ecosystem they sustain. Complex interplays among trees, other biota, soils, water, and climate shape the biogeochemical processes that control the functioning of forest ecosystems, including forest productivity and carbon sequestration. In boreal forests landscapes, the availability of nitrogen (N) commonly limits forest growth (Tamm, 1991), and thereby influences various other fundamental ecosystem processes. While the soil N pool is large, with estimates ranging from 1200 to 5000 kg N ha^{-1} (Sponseller et al. 2016), the majority of N is bound and sequestered in complex organic compounds; this means that plants and microbes cannot readily take up most of the N present in the soil. Measuring the N pools available to plants is challenging due to their limited sizes and rapid turnover (Högberg et al. 2017). However, the soil carbon-to-nitrogen (C/N) ratio

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is often used as a robust indicator of N availability, and as such used to predict forest productivity and the C sequestration potential (Van Sundert et al. 2018), site quality, nitrogen leaching (Gundersen et al. 1998), and microbial community composition (Högberg et al. 2007).

Understanding the environmental factors regulating C/N ratios in boreal forest soils is vital for accurate descriptions of the biogeochemical dynamics of boreal forest landscapes. Soil properties, including the C/N ratio at a given location in the landscape, cover the integrated effects of several key processes related to plants, climate, topography, and soil texture, all of which vary in importance depending on study design and spatial scale (Liu et al. 2018; Wiesmeier et al. 2019; Amorim et al. 2022). On a global and national scale, climate – commonly represented by mean annual temperature and precipitation – often emerges as the key factor for explaining variation in soil properties (Callesen et al. 2003; Amorim et al. 2022; Spohn & Stendahl, 2022). However, these large-scale dynamics may overshadow the influence of other environmental drivers on small-scale variability. For instance, environmental factors such as climate and deposition can be considered to exert a constant effect on the local scale. In this way, when these factors are controlled for, researchers can specifically examine the impact(s) of a selective set of variables on the local scale (Johnson et al. 2000).

At the landscape level, topography exerts a large influence on the spatial variation of soil properties. This effect is mainly based on how topography influences water flow pathways, which cause variation in soil moisture conditions across the landscape. The importance of water flow paths is especially strong in boreal landscapes dominated by unsorted glacial soils with limited variation in hydrological properties (Larson et al. 2022). Previous research has found that boreal landscapes demonstrate remarkable differences in C/N ratios, vegetation composition, and forest growth within short distances, with rapid decreases in C/N ratios moving from groundwater recharge areas, where the water infiltrates the soil, to discharge areas, where groundwater reaches the soil surface (Giesler et al. 1998, 2002; Högberg et al. 2017).

The correlation between soil C/N ratio and hillslope hydrology can be explained in several ways. First, soluble N will accumulate at lower points in the landscape following downslope transport. Although leaching of N is low in groundwater recharge areas, it is possible for the N which has been lost to accumulate in discharge areas due to high levels of organic matter (Blackburn et al. 2017). Second, the increased residence time of water in the subsurface environment increases base cation concentration downslope (Jutebring Sterte et al. 2021), with a higher pH as a result, which may stimulate decomposition, the release of plant-available N and the process of nitrification (Högberg et al. 2017). Third, the higher soil moisture levels of discharge areas may increase microbial turnover rates, unless saturated anoxic conditions prevail (Clymo, 1984; Wieder & Vitt, 2006). The local soil moisture conditions in discharge areas may also provide favourable habitats for N_2-fixing mosses, which will increase N inputs into the system (Bartels et al. 2018). Developments in the last decades of terrain indices, based on digital elevation models, that model water availability have proven effective for predicting spatial variation in soil properties (Zinko et al. 2006; Seibert et al. 2007; Kuglerová et al. 2014; Li et al. 2017).

Besides climate and topography, factors such as dominant tree species (Vesterdal et al. 2008), parent material, and soil texture have been shown to explain the observed variation in soil chemical properties across the boreal landscape (Callesen et al. 2003; Matus, 2021; Spohn & Stendahl, 2022). For instance, the effects of tree species on C/N ratios have been studied at length, often through either block design in so called garden experiments or by using nation-wide datasets (Vesterdal et al. 2008; Hansson et al. 2011; Cools et al. 2014). Nation-wide studies have reported rather inconclusive correlations between soil C/N ratios and the dominant tree species (Högberg et al. 2021). The strongest relationship between dominant tree species and soil C/N ratios is commonly found in the organic layers, which reflects the importance of direct litter inputs from trees and indicates the presence of an important soil-tree feedback mechanism (Lorenz & Thiele-Bruhn, 2019). Another feed-back mechanism is the tree below-ground C allocation to mycorrhizal fungi and root-associated biota, which increases under conditions of low N supply, i.e. a high soil C/N ratio (Högberg et al. 2017). This feed-back mechanism has been proposed to aggravate the N limitation on plant growth common in boreal forests (Näsholm et al. 2013).

Given the importance of soil C/N ratios in forest ecosystems, there is a need to better understand the complex interactions between various environmental factors across heterogeneous landscapes. Spatially-intensive observations of soil C/N ratios, although scarce, hold significant value for improving the predictability of forest ecosystem functioning and developing sustainable forest management practices (Sponseller et al. 2016). Therefore, we addressed this knowledge gap by testing the following hypotheses: (1) topography-mediated hydrological pathways are the best predictor of C/N ratios in the organic layer across small landscapes, but this predictability decreases with soil depth; (2) C/N ratios decrease towards discharge areas; (3) and soil texture and parent material drive C/N ratio variation in mineral soil. In order to test these hypotheses, we studied 391 survey plots with samples collected at three depths within a 68 km^2 managed boreal forest catchment in northern Sweden. The main aim of the research was to use spatially-intense observations from a heterogeneous boreal forest landscape to improve knowledge about how the complex interplay of various environmental factors causes noticeable variation in the C/N ratio.

2. Methods

2.1. Site description

The study was conducted within the 68 km^2 Krycklan catchment in northern Sweden (Lat. 64°, 14N, Long. 19°, 46E). The catchment has a gentle topography, with elevations ranging from 127 to 372 m.a.s.l., and is dominated by poorly weathered gneissic bedrock. The region was glaciated and is undergoing isostatic rebound following the last deglaciation. The highest postglacial coastline traverses the catchment at approximately 257 m a.s.l dividing the catchment in two distinctly different areas, one above and one below the highest coastline. Unsorted glacial till dominates the higher elevations of the catchment, while the lower parts are dominated by sorted sediments of sand and silt. The climate is of a cold temperate humid type, with persistent snow cover during the winter season (Laudon et al. 2021a). Mean annual temperature is 2.4°C and mean annual precipitation is 636 mm yr^{-1}. Nitrogen deposition has been low, peaking in the 1990s at 2.5 kg ha^{-1} yr^{-1} dissolved inorganic nitrogen before declining to close to preindustrial levels at ca 1.0 kg ha^{-1} yr^{-1} (Laudon et al. 2021b). Managed forests, cover 87 % of the area, which also includes mires (9 %) and lakes. The forests are shaped by rotation forestry, which has resulted in various forest stands with different age classes and species composition. Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) are the dominating tree species, and cover 63 and 26 % of the forest area, respectively. Understory vegetation is dominated by a field layer of ericaceous shrubs, mainly bilberry (*Vaccinium myrtillus*) and lingonberry (*Vacinium vitis-ideae*), while the ground vegetation layer is dominated by feather mosses (*Hylocomium splendens* and *Pleurozium schreberi)* (Laudon et al. 2021a).

2.2. Survey and soil chemical analysis

Data and soil samples were collected using a systematic 350×350 m survey grid of circular plots with a radius of 10 m (area of 314 m^2) that covered the entire study area (Fig. 1). The survey grid was established using a randomly chosen origin along the Sweref 99 TM projection. The centre of each plot was marked with an aluminium profile, after which highly precise centre positions were obtained using a Trible GeoXTR GPS receiver. The soil survey was conducted during snow-free periods in 2019 and 2020 according to Swedish National Forest Soil Inventory (SFSI) methods. At each sampling site, soil samples were taken from the

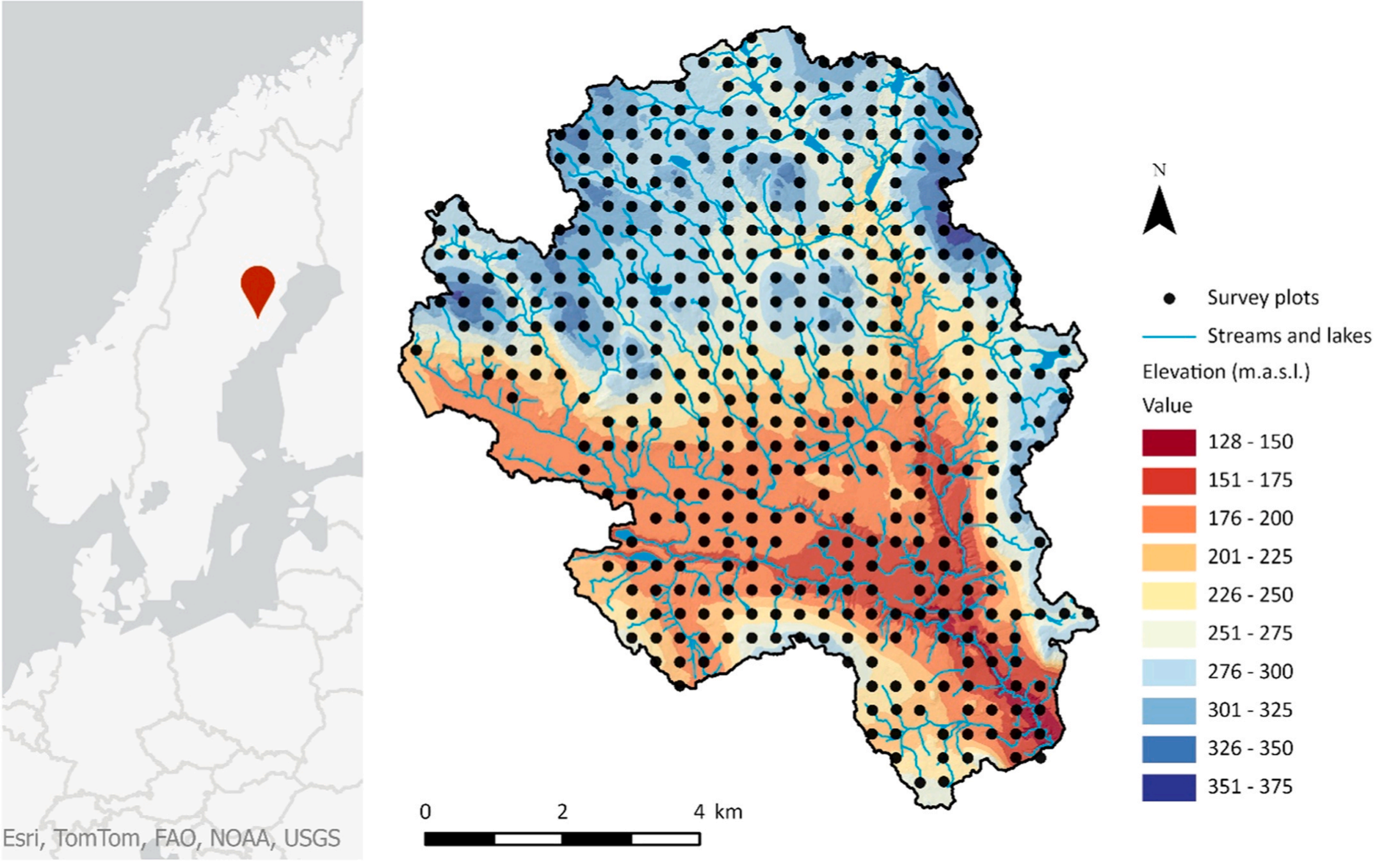

Fig. 1. The plots included in the Krycklan soil inventory.

superficial organic layer and the mineral soil within a 3.14 m^2 subplot that was located close to the plot centre. The organic layer was volumetrically sampled using a 10 cm diameter corer, excluding the litter layer, to a maximum depth of 30 cm; on average the thickness of this layer was 9 cm. Within the 3.14 m^2 subplot, 1–9 sample cores were combined to achieve a total sample volume of approximately 1.5 l. Mineral soil samples were collected from fixed depths (0–10 and 10–20 cm) within the soil profile of the subplot. Soil texture class was determined in the field, and grouped into one of four separate classes within each parent material group of unsorted sediments (Sandy till, Sandy/silty till, Silty/sandy, Coarse & fine silty till) and sorted sediments(Sand, Fine sand, Coarse silt, Clay & fine silt). The soil type was determined according to WRB methods (IUSS Working Group WRB, 2015). As this research concerned forests on mineral soil, we excluded plots defined as Histosols, i.e., an upper organic layer of $\geq$40 cm thickness. Soil sample analysis was conducted on the fine fraction (<2 mm) after the drying and milling of samples. Total carbon and nitrogen content was analysed after dry combustion in an element analyser coupled to a mass spectrometer (Delta IRMS coupled to a Flash EA 2000, Thermo Fischer Scientific, Bremen, Germany). The analyses were performed with 2–50 mg soil material depending on the organic matter content.

2.3. Environmental factors

The environmental covariates included in this study consist of topography, parent material, soil texture, and forest variables. The climate within the study area was considered to be constant across the entire catchment; nevertheless, microclimate variations related to aspect and elevation are included in the topographic environmental factors. A total of four topographic attributes were calculated for each sampling point based on a LiDAR-based Digital Elevation Model (DEM) created from airborne laser scanning data collected in August 2019. The DEM was generated to have a resolution of 0.5×0.5 m from a point cloud with 20 points per m^2; the point cloud was re-sampled to create different resolutions depending on the topographic variable. Elevation (Elev), aspect, and slope were directly derived from a 2 ×2 m DEM. The Topographic Wetness Index (TWI) (Beven & Kirkby, 1979) was used to study spatial effects on hydrological processes; it was calculated based on the local upslope contribution area and slope. TWI is defined as ln (a/tanβ), where *a* is the local upslope contribution area through a certain point per unit contour length and tanβ is the local slope. In this study, TWI was calculated using an aggregated DEM with a resolution of 16×16 m because this was found to be the optimum resolution for predicting soil moisture conditions in a previous study within the same catchment (Larson et al. 2022). High TWI values are usually found in lower areas of the landscape, as large contributing upslope areas cause increased soil moisture conditions (Sørensen et al. 2006). The DEM used to calculate TWI was hydrologically-corrected using the breach and burn method (Lidberg et al. 2017), the flow accumulation area was extracted from the same DEM using the multiple flow direction algorithm (Seibert & McGlynn, 2007). The parent material for each survey plot was classified according to unsorted and sorted sediments. The soil texture of the soil samples was determined during field measurements and grouped into one of four classes for sorted and unsorted sediments: sandy till; sandy-silty till; silty-sandy till; and coarse & silty till; sand; fine sand; coarse silt; clay & fine silt, respectively. Within each 10-m-radius survey plot, the diameter at breast height (DBH, 1.3 m from the ground) and species was recorded for each tree (DBH>4 cm) during fall 2019 and spring 2020. If trees were present on the plot, dominant tree species was defined according to the following classes based on basal area (<65 %): deciduous (mainly *Betula pendula* & *Betula pubescens*); spruce *(Picea abies);* pine *(Pinus sylvestris* & *Pinus contorta)*; and mixed. The mixed category was dominated by coniferous mixed stands. Stand age was determined during the establishment of the survey plots (2014) based on core samples from trees outside of the plot.

2.4. Statistical analyses

The soil chemical properties for the 391 sample plots were compiled as descriptive statistics for each sampled depth. There was some degree of variation in the total number of samples for each depth due to plots being positioned on bedrock, the lack of an organic layer, organic layer depth >50 cm, shallow soil depth, and other conditions that did not allow sampling. We analysed how continuous environmental variables (Elevation, Aspect, Slope, TWI) and forest variables (Stand age, Basal area) were correlated with soil chemical properties (C/N, C%, N%) using Spearman's rank correlation and linear regression analysis. In addition, we conducted a one-way ANOVA, followed by Tukeýs test, to examine the significance of C/N ratio, C% and N% differences among dominant tree species and soil texture classes. Plots with no trees (no basal area) were excluded from the ANOVA. Spatial autocorrelation was evaluated by creating semivariograms (Fig. A.1) and calculating Moran's I (Moran, 1950). The spatial autocorrelation for all of the soil chemical properties was considered low, with Moran's I ranging from 0.02 to 0.16. The threshold for a statistically significant result was set as $p = 0.05$. All of the data analyses were conducted using R Statistical Software (R Core Team, 2021).

3. Results

3.1. Distribution of soil types

The Krycklan catchment was dominated by Podzols (54 %), followed by Regosols (24 %). Arenosols made up 5 % of the sampled soils and were found in the lower parts of the catchment on sorted sediments, while Gleysols (4 %) were found in poorly drained areas and close to streams. Only four (1 %) of the soil profiles were defined as Leptosols, while an additional three plots were grouped as other soils (unclassified, Cambrisol, and Umbrisol). A total of 50 soil profiles were classified as Histosols, which represents 11 % of the area. These were excluded from subsequent analyses, with 391 remaining for analysis.

3.2. Distribution of soil chemical properties and their correlation with C/N

The number of samples taken at each survey plot depended on the presence of an organic layer and the depth to bedrock or boulders; as such, there were differences in the total number of samples per plot (Table 1). The mean C/N (± SD) ratio in the organic layer was 38.9 ± 8.7, with a range from 18.6 to 86.8. The mean C/N ratio in the mineral layer decreased with depth, from an initial value of 28.8 ± 9.27–25.5 ± 8.28; the range of values remained large at different depths. The organic layer samples showed the highest concentrations of both C and N, with mean values of 38.6 ± 8.75 and 1 ± 0.27, respectively; both of the elements decreased substantially with depth in the mineral soil samples.

3.3. Relationship between C/N and topographic variables

The Spearman's rank correlation calculations showed many significant correlations between topographic variables and soil chemical properties; however, many of these correlations were below the threshold for moderate associations ($r<0.3$) (Table 3). Soil chemical properties in the organic layer samples showed significant correlations with several topographic variables. For example, C/N in the organic layer decreased significantly in relation to TWI ($r=-0.31$), indicating that wetter areas have lower C/N ratios. The linear regression results revealed that TWI explains 11 % of the variation in C/N ratios of the organic layer samples (Fig. 2a). We then separately calculated the linear regressions for the C/N ratio of the organic layer and TWI in the unsorted and sorted sediments. A stronger relationship was found for samples of unsorted sediments, with TWI explaining 15 % of the variation in C/N ratios (Fig. 2b). This negative relationship found in the organic layer also extended to the mineral soil layer, with $r=-0.18$ and $r=-0.16$ at the 10 and 20 cm depths, respectively. In the organic layer, N % was positively related to TWI ($r=0.3$), with the linear regression showing that TWI explains 6 % of the variation of N% (Fig. 3). Slope and aspect had low or non-significant relationships with soil chemical properties (Table 3). Elevation showed significant correlations with almost all of the soil chemical properties in mineral soil (Table 3). However, when the relationships were visualised using scatter plots, the observed correlation was clearly attributed to the distribution of parent material rather than to elevation (Fig. A.2).

3.4. Forest variables

The C/N ratio in the organic layer differed based on the dominant tree species (ANOVA: $f=4.018$, $p=<0.001$). Forests dominated by pine had the highest mean ratio (42 ± 8.9) (Table 4), which was significantly higher than the ratio measured for other plots; plots with dominant tree species other than pine did not show significant between-plot differences (Fig. 3). There were no differences in the mineral soil, which could be related to the dominant tree species (ANOVA: $f=0.17$, $p=1.699$). Although the initial ANOVA indicated that dominant tree species significantly affected the C/N ratio at a depth of 20 cm in mineral soils ($f=3.1$, $p=0.027$), the subsequent Tukey's test revealed that this relationship was insignificant. Analyses of the organic layer samples showed significant difference in N% between spruce and pine forests; this was not the case for C%, which did not significantly differ between spruce and pine forests. Regarding the mineral soil samples, pine forests showed significantly higher C% than spruce forests at both soil depths, and similar patterns were found for N%. Stand age showed positive correlations with all soil chemical properties, with the strongest relationship found for C% ($r=0.3$) (Table 3). However, stand age only showed a significant correlation ($r=0.18$) with C/N ratio in the mineral soil samples, with C/N ratios increasing with stand age in the top 10 cm. Basal area showed weak positive correlations with C% ($r=0.21$) and N% ($r=0.19$) in the organic layer, and with C/N ratio ($r=0.11$) and C% ($r=0.11$) in the top 10 cm of mineral soil samples.

Table 1
Descriptive statistics of soil chemical properties at the sampled depths. M10=mineral soil 0–10 cm; M20=10–20 cm.

Soil property	Sample layer	n	mean	SD	min	max	range	SE
C/N ratio	Organic layer	378	38.90	8.74	18.6	86.8	68.2	0.45
C/N ratio	M10	376	28.84	9.27	10	85	75	0.48
C/N ratio	M20	361	25.50	8.28	6.3	75	68.7	0.44
C%	Organic layer	378	38.64	8.75	6.61	55.07	48.46	0.45
C%	M10	376	2.02	1.71	0.16	15.87	15.71	0.09
C%	M20	361	1.67	1.42	0.15	12.49	12.34	0.07
N%	Organic layer	378	1.02	0.27	0.28	2.15	1.87	0.01
N%	M10	376	0.07	0.06	0.01	0.6	0.59	0.00
N%	M20	361	0.06	0.05	0.01	0.47	0.46	0.00

Table 3

Spearman's rank correlation coefficients for soil chemical properties and the associated topographic and forest factors. Significant results are in boldfaced text, $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$. M10=mineral soil 0–10 cm, and M20=10–20 cm.

Soil property	Sample layer	Elevation	Aspect	Slope	TWI	Stand age	Basal area
C/N ratio	Organic layer	-0.04	**0.14****	-0.06	**-0.31*****	**0.16****	0.02
C/N ratio	M10 (0–10 cm)	**0.26*****	0.06	0	**-0.18*****	**0.18*****	**0.11***
C/N ratio	M20 (10–20 cm)	**0.42*****	0.03	0.01	**-0.16****	0.1	0.02
C%	Organic layer	0.08	0.01	**-0.15****	0.03	**0.3*****	**0.21*****
C%	M10 (0–10 cm)	-0.06	-0.03	0.02	0.05	0.1	**0.11***
C%	M20 (10–20 cm)	**0.5*****	-0.06	0.03	-0.05	0.1	0.04
N%	Organic layer	0.08	**-0.12***	**-0.11***	**0.3*****	**0.14****	**0.19*****
N%	M10 (0–10 cm)	**-0.21*****	-0.07	0.03	**0.16****	0.02	0.06
N%	M20 (10–20 cm)	**0.38*****	**-0.1***	0.02	0.02	0.05	0.01

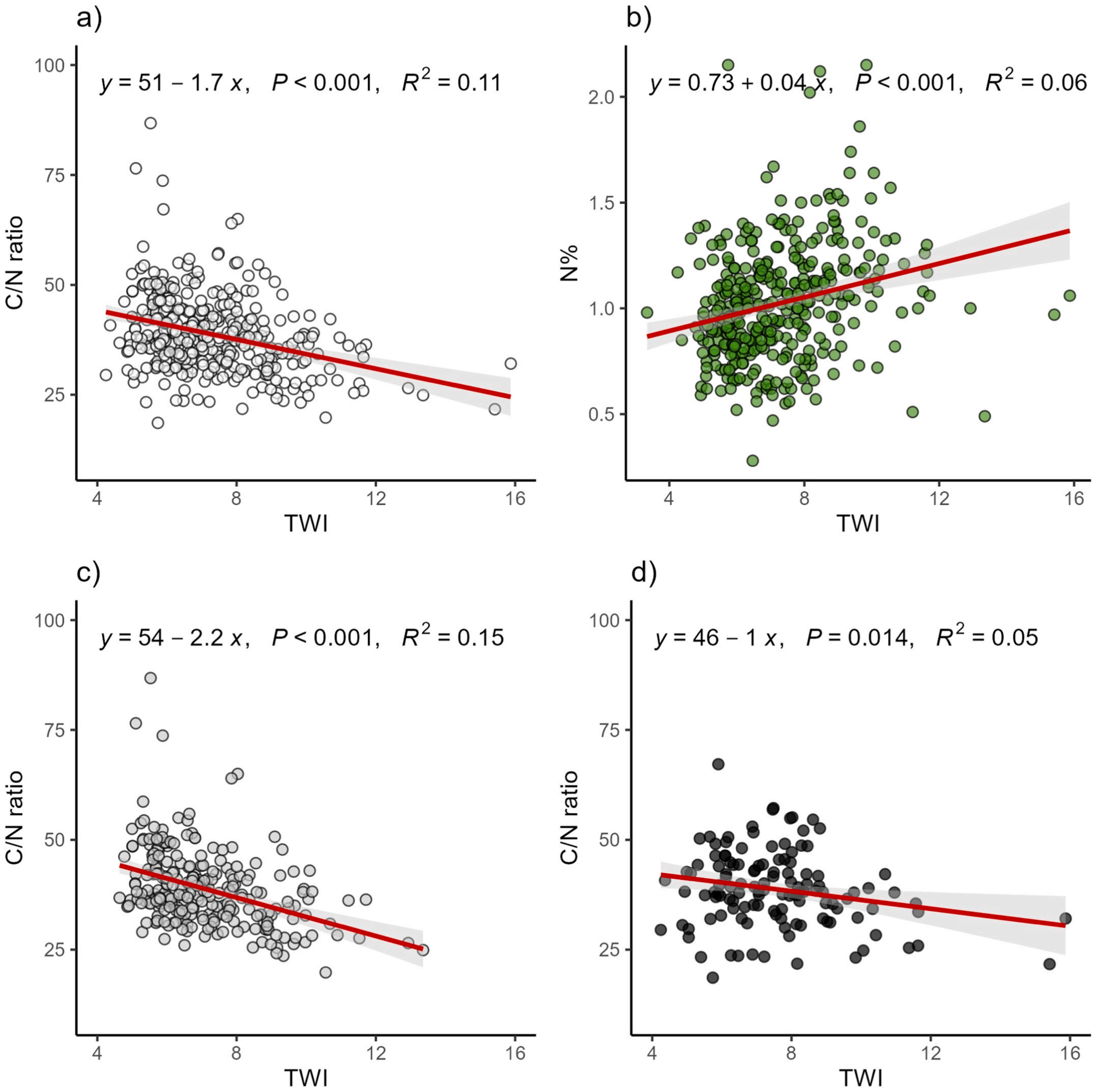

Fig. 2. Linear regression of C/N ratio (a) and N% (b) in relation to TWI in all organic layer samples. The linear regression of C/N ratio in relation to TWI in organic layer samples was also separately derived for unsorted (c) and sorted sediments (d).

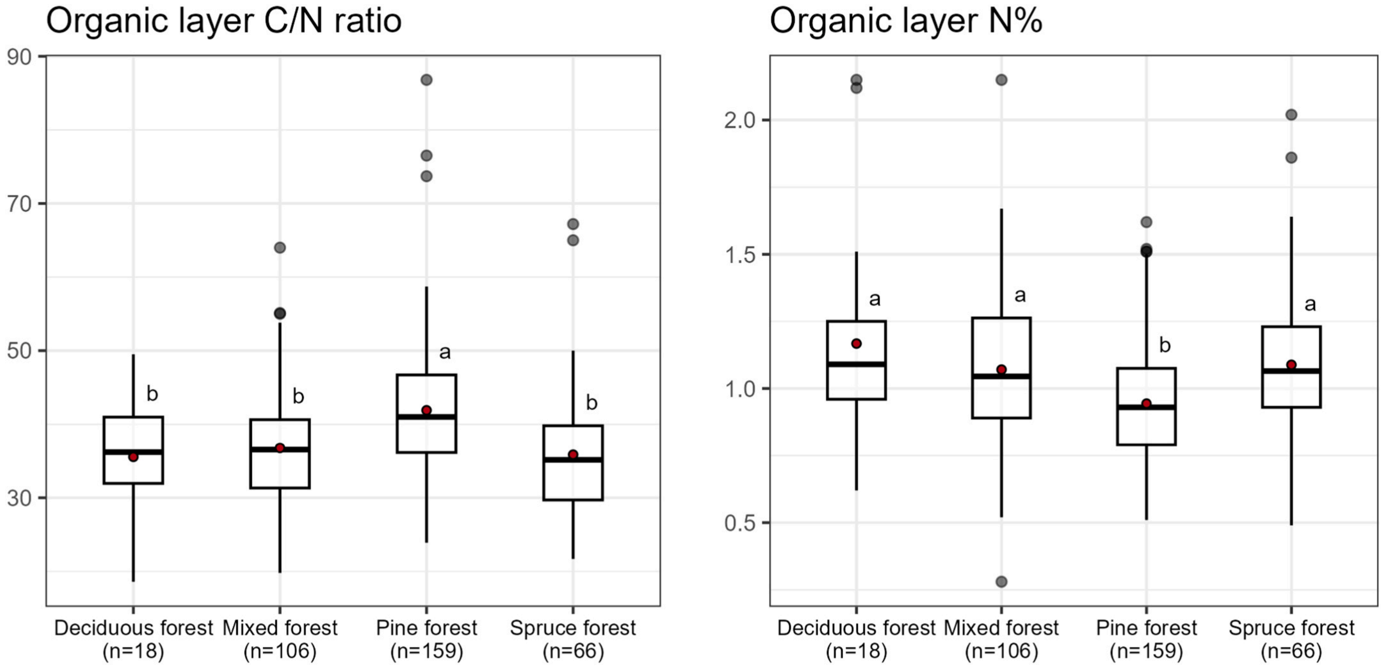

Fig. 3. C/N ratios (left) and N% (right) of the organic layer for different forest types (i.e., dominant tree species). Black lines denote the median, while red circles denote the arithmetic mean. Different letters indicate statistically significant differences (p<0.05) between various soil texture classes.

Table 4

ANOVA results for C/N ratios among forest types (i.e., dominant tree species). O=organic layer, M10=mineral soil 0–10 cm, and M20=10–20 cm. Standard derivation showed within parentheses. Different letters show statistically significant differences (p<0.05), as calculated using a post-hoc Tukey test.

	C/N ratio			C%			N%		
Forest type	**O**	**M10**	**M20**	**O**	**M10**	**M20**	**O**	**M10**	**M20**
Deciduous forest	35.6 (8.2)b	27.9 (9.7)a	21.8 (7.4)a	39.3 (9.1)a	2 (1.3)ab	1.8 (1.8)ab	1.2 (0.4)a	0.07 (0.04)ab	0.07 (0.07)ab
Mixed forest	36.8 (7.6)b	28.3 (9.3)a	24.6 (8.3)a	38.6 (8.8)a	2.2 (2.0)ab	1.7 (1.7)ab	1.1 (0.3)a	0.08 (0.06)ab	0.07 (0.05)b
Pine forest	41.9 (8.9)a	30.2 (9.9)a	27 (8.9)a	38.7 (8.2)a	1.8 (1.1)a	1.4 (1.0)b	0.9 (0.2)b	0.06 (0.04)b	0.05 (0.03)b
Spruce forest	35.9 (9.0)b	27.5a (8.9)	25 (7.5)a	38.0 (9.7)a	2.7 (2.5)b	2.2 (1.9)a	1.1 (0.3)a	0.1 (0.09)a	0.09 (0.07)a
P-value	<0.001	0.17	0.027	0.932	<0.001	0.006	<0.001	<0.001	<0.001
F stat	4.018	1.699	3.1	0.146	4.313	4.264	9.274	7	7.699

3.5. Parent material and soil texture

There were significant differences in C/N ratios among unsorted and sorted sediments as well as soil texture classes, with these differences mainly observed in mineral soil layers (Table 5). In the organic layer, unsorted and sorted sediments did not show noticeable differences in soil chemical properties, while they were rather constant among different soil texture classes. In the organic layer, significant differences in C/N ratios were only observed within sorted sediments, with fine sand showing significantly higher C/N ratios than coarse silt, with mean values of 43.1 and 36.3, respectively (Table 5). Significant differences in C/N ratios among soil texture classes were observed in the sorted sediments, while no significant differences were observed in the unsorted sediments. For the sorted sediments of mineral soil samples collected at a depth of 10 cm, C/N ratios decreased from 28 to 20 in the sand and clay & fine silt samples, respectively (Fig. 4). C/N ratios in the deeper mineral soil layers (20 cm) showed a similar significant decrease from sand to clay & fine silt samples. In samples collected from the top 10 cm

Table 5

The mean values of soil chemical properties for soil texture classes. Standard derivation showed within parentheses. Different letters show statistically significant differences (p<0.05), as calculated using a post-hoc Tukey test, for soil chemical properties among different texture classes. O=organic layer, M10=mineral soil 0–10 cm, and M20=10–20 cm. The dashed line in the table divides unsorted and sorted sediments.

	C/N ratio			C%			N%		
Soil texture	**O**	**M10**	**M20**	**O**	**M10**	**M20**	**O**	**M10**	**M20**
Sandy till	38.7(9.3)ab	32.1(8.5)a	29.3(6.9)a	38.6(10.0)a	1.6(1.1)b	1.5(0.7)abc	1.04(0.34)ab	0.05(0.02)c	0.05(0.02)ab
Sandy/silty till	40.1(10.1)ab	30.8(9.8)a	28.3(6.6)a	39.6(8.4)a	1.8(1.2)b	1.9(1.3)ab	1.02(0.25)ab	0.06(0.03)c	0.07(0.04)a
Silty/sandy till	37.5(7.3)b	30.6(9.6) a	27.5(7.6)a	37.9(8.7)a	2.1(1.9)b	2(1.7)ab	1.03(0.24)ab	0.07(0.07)abc	0.08(0.06)a
Coarse & fine silty till	38.6(6.6)ab	31.3(11.2)ab	29(7.7)a	42.9(8.4)a	3.3(3.3)a	2.5(2.0)a	1.12(0.25)a	0.1(0.10)a	0.08(0.06)a
Sand	40.9(8.1)ab	28.2(7.9)ab	25.7(6.8)ab	39.9(7.4)a	1.5(0.7)b	1.2(0.7)bc	1.03(0.36)ab	0.06(0.03)abc	0.05(0.04)ab
Fine sand	43.1(8.4)a	28.1(5.7)ab	22.3(5.8)b	38.2(7.5)a	1.5(0.9)b	0.8(0.7)c	0.91(0.21)b	0.05(0.03)bc	0.03(0.03)b
Coarse silt	36.3(6.9)b	24.8(4.3)bc	20.9(9.3)b	36.6(9.1)a	2.3(1.8)ab	1.1(1.1)c	1.03(0.30)ab	0.09(0.07)ab	0.05(0.05)ab
Clay & fine silt	37.1(9.4)ab	19.9(5.7)c	15.4(5.2)c	36.5(9.3)a	2(1.3)b	1(1.2)c	1.01(0.31)ab	0.09(0.05)ab	0.06(0.04)ab
P value	0.01	<0.001	<0.001	0.052	<0.001	<0.001	0.19	<0.001	<0.001
F stat	2.657	9.121	19.24	2.022	3.784	7.38	1.442	4.92	4.018

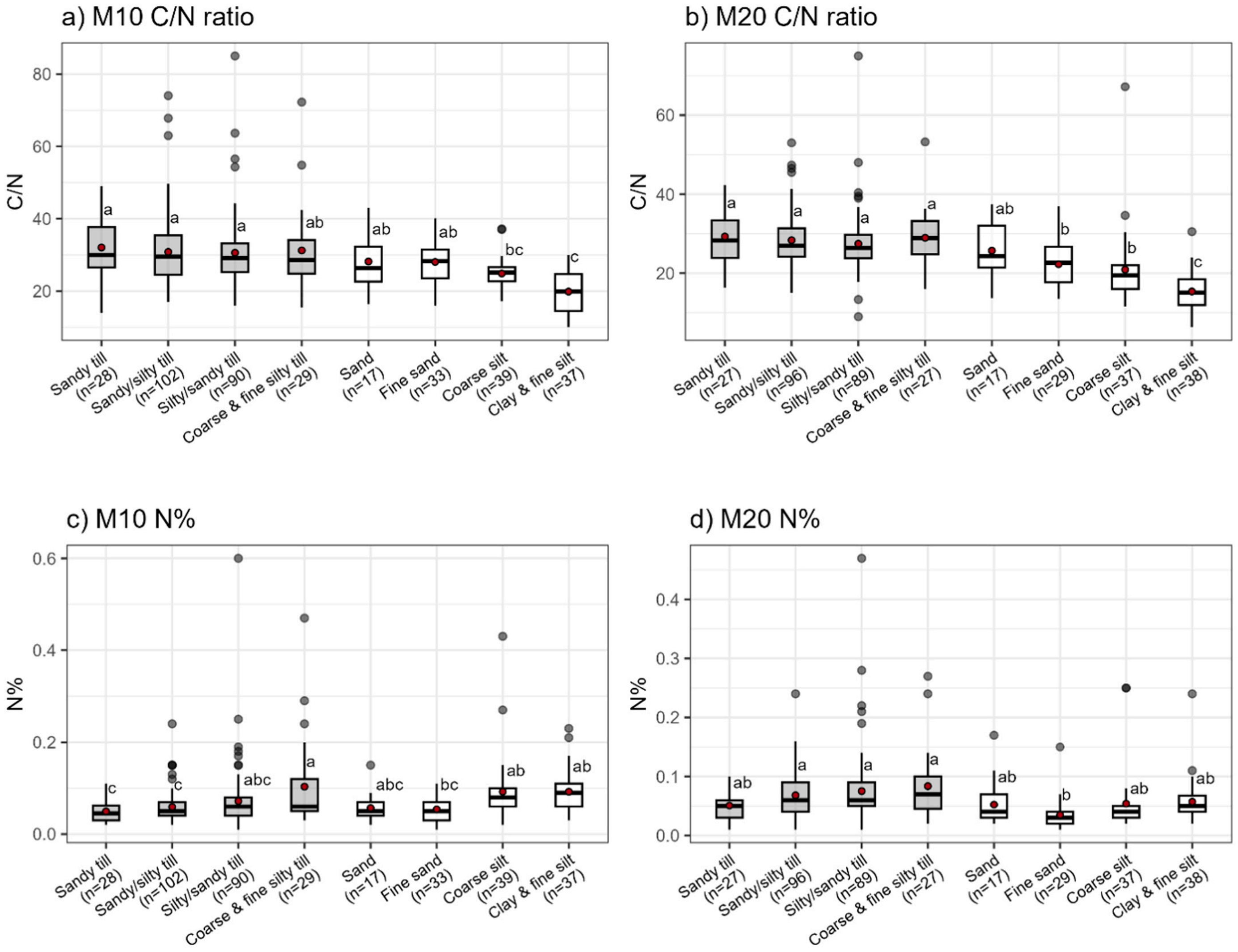

Fig. 4. C/N ratios (a-b) and N% (c-d) in mineral soil samples for different soil texture classes, with the parent material class depicted using grey (Unsorted sediments) and white (Sorted sediments) box plots. Black lines denote the median and red circles depict the arithmetic mean. Different letters indicate statistically significant differences ($p<0.05$) between soil texture classes. M10=mineral soil 0–10 cm, and M20=10–20 cm.

of mineral soil, coarse & fine silty till had C and N concentrations that were twice as high as what was observed in sandy till. A similar trend, albeit statistically insignificant, in C and N concentrations were observed in mineral soil samples collected from a depth of 20 cm. No significant differences in C and N concentrations were observed among soil texture classes in the sorted sediments.

4. Discussion

Understanding how the interplay between trees, other biota, and various environmental factors influences soil C/N ratios at the landscape scale could unravel how boreal forest ecosystems function and inform forest management decisions. Our analyses of samples from an extensive soil and forest survey, provides unique insight into how C/N ratios vary along with environmental factors in a boreal landscape. We provide empirical evidence that support: (1) the importance of topographically-driven hydrological conditions, with C/N ratios decreasing as soil moisture conditions increase; and (2) that soil texture is the most important factor explaining variations in soil chemical properties within mineral soil. Although the relationships among various environmental factors and soil C/N ratios were clearly statistically significant, they nevertheless demonstrated weak correlations, which signify the complex interactions between various factors in boreal forest. In addition, we found differences in soil C/N ratios under different dominant tree species. However, as was the case with other factors, dominant tree species could only explain a small proportion of the variation in C/N ratios.

4.1. Landscape variation of C/N ratio

Our study provides a rare and important insight to the large variation of C/N ratio present within boreal forest landscapes. The variation and range of C/N ratio within the 68 km^2 study area was comparable to studies conducted on national, regional and subcontinental scales for both of organic and mineral soil layer (Callesen et al. 2007; Cotrufo et al. 2019; Högberg et al. 2021; Spohn & Stendahl, 2024). The large variation in C/N ratio found in our study follows are in line with several previous studies on smaller spatial scales from different regions (Johnson et al. 2000; Zinko et al. 2006; Li et al. 2017). The large variation in soil C/N ratios and other soil properties within smaller landscapes demonstrates the importance of site-specific studies on smaller spatial scales to understand how environmental factors influence soil properties.

4.2. Topography and its relation to C/N ratio

Due to the gentle topography within the study area, low correlations with aspect and elevation were expected. We did, however, identify a clear negative relationship between C/N ratios and TWI, with the most pronounced effects observed in the organic layer (Fig. 2). Despite large variability, the observed relationship was stronger in comparison to previous findings from both nation-wide and landscape-focused studies of soil-topography relations in the boreal region (Zinko et al. 2006; Seibert et al. 2007). Several factors may contribute to this relationship, with the absence of climatic variation among study plots potentially allowing a clearer focus on environmental drivers that may have been overshadowed by climatic variation at the national scale (Spohn & Stendahl, 2022). Moreover, our study differs from previous studies in that the research process utilised enhanced DEM resolution, high GPS positioning accuracy, and pre-validated terrain indices (Larson et al. 2022). A similar negative relationship for TWI and C/N ratio was shown in an extensive soil survey using 471 of a broad leaf forest hillslope in subtropical China (Li et al. 2017). In contrast, no significant relationship with terrain indices has been found in other smaller landscape studies (Johnson et al. 2000). The variation in importance of topographical relationships with soil properties are expected due to differences in both landscape type, climate conditions as well as scale (Wiesmeier et al. 2019). The stronger relationship between the C/N ratio and TWI observed for organic layer samples from unsorted sediment was expected due to the strong topographic control of soil moisture conditions in these soils. This is in comparison to the areas of the catchment with sorted sediments, dominated by flat areas, where previous studies have demonstrated that these soils are not subjected to strong topographic control of soil moisture conditions (Ågren et al., 2014; Larson et al. 2022). Furthermore, the influence of soil moisture conditions on C/N ratios aligns with previously observed decreases in the C/N ratio along hillslopes towards discharge areas, where large increases in base cations and N availability occur over short distances in the boreal forest (Giesler et al. 1998). Hydrological conditions are evidently important for the variation in C/N ratios within boreal landscapes, but the development of improved terrain indices that better describe these relations remains a challenge.

4.3. Forest type and its relation to C/N ratio

Our analysis of mean C/N ratios among various forest types revealed noteworthy differences in the soil organic layer. Notably, only plots dominated by pine displayed significantly higher C/N ratios than plots dominated by other tree species (Table 4). Previous garden experiments have found that the organic layer of soils under pines show high C/N ratios (Vesterdal et al. 2008; Hansson et al. 2011). In previous surveys covering the whole of Sweden (Högberg et al. 2021; Spohn & Stendahl, 2022) it was proposed that differences between forest types may occur because not all tree species can establish and grow well under strong N-limitation. Hence, the high C/N ratio in plots dominated by pine may reflect the ability of this species to grow under strong N-limitation rather than a tendency to form litter with a high C/N ratio. No significant between-forest type differences in the C/N ratio were observed based on mineral soil layer samples, which supports previous reports that the influence of tree species on the C/N ratio decreases with depth (Vesterdal et al. 2008; Hansson et al. 2011; Getino-Álvarez et al. 2023). However, our results contradict what was reported in a recent nation-wide study, more specifically, significant between-forest type differences in C/N ratios extending to depths of 55–65 cm in the mineral soil (Spohn & Stendahl, 2022). It should be noted that actual tree species-dependent effects are difficult to discern in survey studies due to other factors such as forest management decisions and stand age. Pinpointing causal effects within the complex web of interactions between tree species and soil factors is challenging and benefits from common garden experiments.

4.4. Soil texture and its relation to C/N ratio

Significant differences in C/N ratios among soil texture classes were only observed within the sorted sediments of mineral soil samples; more specifically, a gradual decrease in C/N ratio was observed from coarse to fine-textured soils (Fig. 4a-b). The observed decrease in C/N ratio is most likely related to the increased concentration of nitrogen (Fig. 4c-d). In a recent study, the same trends were observed using the Swedish national forest soil survey of Sweden (Spohn & Stendahl, 2024), which also follows other large scale studies (Callesen et al. 2007; Amorim et al. 2022). The most likely explanation for the lower C/N ratio and higher N concentration in fine textured soils in comparison to coarse textured soils is the difference in the number of binding sites on charged mineral soil surfaces where organic compounds can be absorbed (Spohn & Stendahl, 2024). The absorption of organic compounds leads to enrichment of organic matter in the soil due to slower decomposition (Lützow et al. 2006; Kleber et al. 2015). The lack of differences in the observed C/N ratios for unsorted sediments, which contain a mixture of soil particle sizes, highlights the importance of separating on parent material when studying soil texture effects. It can be postulated that the sorption of organic matter to clay and silt particles is one of the predominant processes explaining the observed differences between soil texture classes and parent material (Matus, 2021).

4.5. Weaknesses and further research

Even though the analysed data revealed several clear trends, there was considerable unexplainable variability. This is expected due to the large degree of variability across small study areas, with the utilised sampling methods also potentially introducing variability. For example, a previous Finnish study reported that the distance to a tree has a significant effect on C/N ratios (Häkkinen et al. 2010). Despite the large number of mineral soil samples, these samples were collected from one single profile within the plot, while the organic layer samples were collected from several cores within a subplot. Increasing the sampling density across the entire plot would most likely increase the strength of observed relationships. However, it is important to note that using the same sampling methods as the national forest soil inventory of Sweden can provide valuable information about the scalability of this approach for future studies. For example, the national inventory found only a few percent of the soils in N. Norrland to be mull soils (with an average C/N of 16, Högberg et al. 2021), which is comparable to a fraction of a percent (1 out of 391) of mull soils found in the Krycklan catchment (C/N of 23). The additional investigation of other terrain indices, along with improvements in modelling techniques, may provide further insight which environmental factors have the largest impact on soil C/N ratios. For example, stratifying soil samples based on terrain indices might improve our knowledge of the distribution of topography-related biogeochemical hotspots such as groundwater discharge areas (Giesler et al. 1998; Zinko et al. 2006; Laudon et al. 2016). The complex interplay between various factors in explaining soil C/N variation has been a central feature of previous studies, even those performed on smaller scales that the present research, with the observed relationships rarely explaining more than 40 % of the variation in C/N ratios (Li et al. 2017). This is expected due to the multiple factors that influence soil chemistry within forest ecosystems, yet research areas such as digital soil mapping seldom attempt to provide a comprehensive picture of various processes. A comprehensive picture may need the inclusion of a perspective on how interactions among trees, soil microorganisms and soil factors vary across the landscape (Högberg et al. 2017).

5. Conclusion

The presented research describes how various environmental factors influence soil chemical properties in a boreal landscape, as well as illustrates the challenges in adequately explaining variation in soil C/N ratios across a landscape. In the organic layer, C/N ratios showed a significant relationship with topography due to its control on hydrological conditions. The C/N ratio in mineral soil was mainly affected by soil texture. Finally, our approach could not explain noticeably more of the variation in soil chemical properties previously reported from national levels, which provides evidence of the complex interplay among organisms and processes across heterogeneous boreal landscapes.

CRediT authorship contribution statement

Johannes Larson: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lenka Kuglerová:** Writing – review & editing, Supervision. **Peter Högberg:** Writing – review & editing. **Hjalmar Laudon:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data Availability

Data will be made available on request.

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Author contributions

JL developed the research idea in collaboration with HL. JL was in charge of, and conducted, the field survey, as well as performed the data compilation and statistical analysis. JL wrote the manuscript in with assistance from the co-authors.

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