

# Soil carbon and nitrogen contents in forest soils are related to soil texture in interaction with pH and metal cations

Marie Spohn<sup>\*</sup>, Johan Stendahl

Department of Soil and Environment, Swedish University of Agricultural Sciences (SLU), Lennart Hjelm's väg 9, P.O. Box 7014, 75007 Uppsala, Sweden

## ARTICLE INFO

Handling Editor: C. Rumpel

### Keywords:

Soil organic carbon  
Soil nitrogen  
C:N ratio  
Mineral-associated organic matter  
Soil pH  
Charge density  
Aluminum  
Calcium

## ABSTRACT

The aim of this study was to better understand how soil carbon (C) and nitrogen (N) contents and the C:N ratio are related to soil texture, pH, and exchangeable aluminum and calcium in forest soils.

For this purpose, we studied 1992 temperate and boreal forest soils located all over Sweden. We measured organic C and N as well exchangeable aluminum, calcium, and pH in the organic layer and three depth increments in the mineral soil (down to 65 cm), and analyzed the relationship between element contents, soil texture, and soil pH as well as their interactions.

Soil C concentration and the C:N ratio were negatively related to soil pH. The C concentration was on average 2.6 times higher in very acidic soils ( $\text{pH} \leq 4.0$ ) than in soils with  $\text{pH} > 5.0$ , in the uppermost 10 cm of the mineral soil. In contrast, N varied much less with pH, particularly in the organic layer, but was related to soil texture. The N concentration was 2.3 times higher in clayey and fine silty soils than in sandy soils, while the C concentration was only 1.85 times higher in clayey and fine silty soils than in sandy soils (in the uppermost 10 cm). Differences in C and N concentrations between clayey and fine silty soils compared to sandy soils were largest in the class of soils with  $\text{pH} > 5.0$  and smallest in the class of soils with  $\text{pH} \leq 4.0$ . Furthermore, C and N concentrations were both positively correlated with the concentration of exchangeable aluminum in the mineral soil, and these correlations were stronger in coarse-textured than in fine-textured soils. In addition, the C concentration was positively correlated with the concentration of exchangeable calcium in the organic layer.

In conclusion, our results show that C concentration varied much more strongly with pH than N concentration, likely due to effects of pH on microbial respiration. The N concentration was more strongly related to soil texture than the C concentration, which is very likely due to the high charge density of organic N, which gives organic N a high affinity to adsorb to mineral surfaces. Furthermore, exchangeable aluminum seems to play an important role in the sorptive stabilization of organic matter in the mineral soil.

## 1. Introduction

Soils form a major carbon (C) pool in the Earth system, and nitrogen (N) limits primary production in many ecosystems. Therefore, a solid understanding of soil C and N storage is important. Yet, it is still not very well understood how soil texture, pH and multivalent cations affect organic C and N storage (Knicker, 2011; Schmidt et al., 2011; Wiesmeier et al., 2019).

Soil organic matter storage depends on soil texture since the adsorption of soil organic compounds to minerals slows down their decomposition (Sollins et al., 1996; Kleber et al., 2007; von Lützwitz et al., 2006). The capacity of soils to adsorb organic compounds is largely determined by their contents of fine mineral particles with high

surface area and high surface charge density, such as phyllosilicates (clay minerals), as well as Fe and Al oxides and hydroxides (Oades, 1988; Mayer, 1994; Hassink, 1997). In fine-textured soils, a large number of organic compounds is adsorb to minerals, which protects them against decomposition (Kaiser and Guggenberger, 2003; von Lützwitz et al., 2006; Zinn et al., 2007; Kögel-Knabner et al., 2008; Kleber et al., 2015). Sorption protects organic compounds against decomposition by steric hindrance since it physically prevents enzymes from binding to the compounds and catalyzing their decomposition. Further, sorption impedes that organic compounds are taken up and are metabolized by microorganisms (von Lützwitz et al., 2006; Kögel-Knabner et al., 2008; Kleber et al., 2015). It can be hypothesized that soil texture is more important for organic matter stabilization in the subsoil than in the

<sup>\*</sup> Corresponding author.

E-mail address: [marie.spohn@slu.se](mailto:marie.spohn@slu.se) (M. Spohn).

<https://doi.org/10.1016/j.geoderma.2023.116746>

Received 2 August 2023; Received in revised form 8 November 2023; Accepted 5 December 2023

Available online 13 December 2023

0016-7061/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

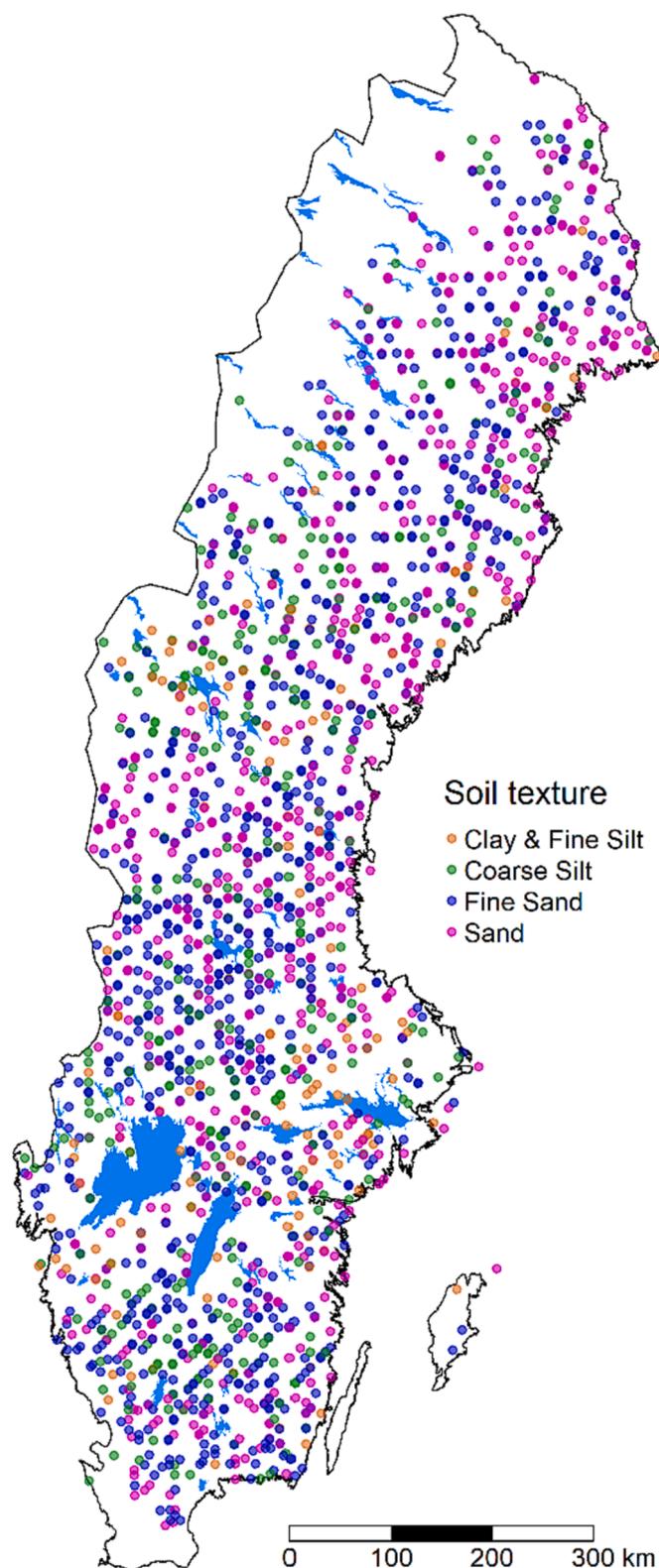


Fig. 1. Map of Sweden showing the location of the 1992 soils and their texture at a depth of 0–20 cm. Please notice that the dots have transparent colors and that new colors emerge from overlying dots. A few dots that appear not to be located on land are in fact located on islands (which are not depicted in the map).

Table 1

Concentration of carbon and nitrogen together with the molar carbon-to-nitrogen (C:N) ratio and pH measured in water as well as the exchangeable aluminum (ex. Al) and calcium (ex. Ca) concentrations. Shown is the arithmetic mean  $\pm$  standard deviation.

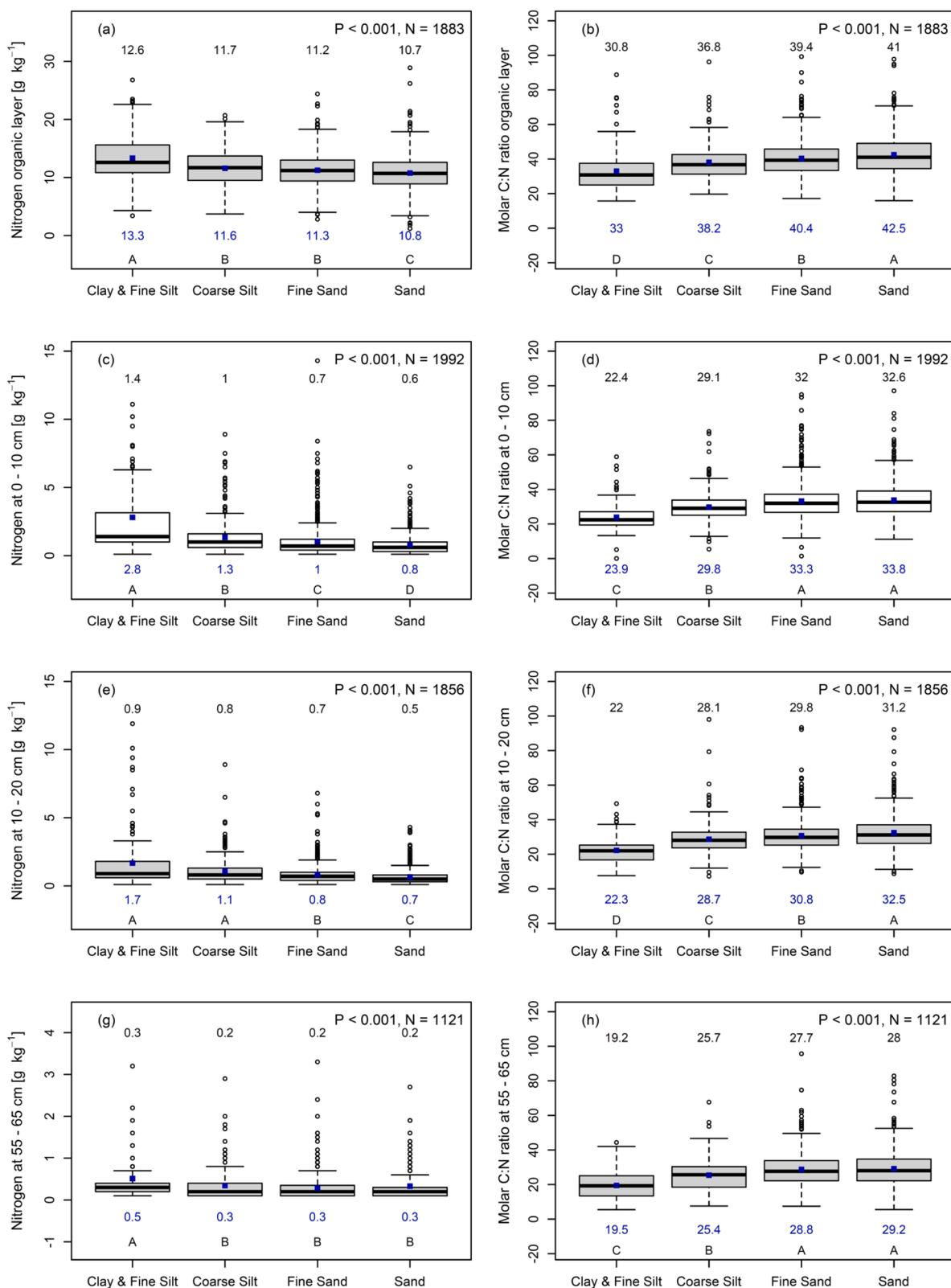
Soil depth	Carbon (g kg <sup>-1</sup> )	Nitrogen (g kg <sup>-1</sup> )	Molar C:N ratio	pH <sub>H2O</sub>	ex. Al (mg kg <sup>-1</sup> )	ex. Ca (mg kg <sup>-1</sup> )
Organic layer	373.9 $\pm$ 90.7	11.2 $\pm$ 3.2	40.2 $\pm$ 11.0	3.8 $\pm$ 0.4	310 $\pm$ 307	2378 $\pm$ 2389
0 – 10 cm	27.15 $\pm$ 25.9	1.1 $\pm$ 2.0	32.2 $\pm$ 10.1	4.4 $\pm$ 0.4	233 $\pm$ 154	148 $\pm$ 446
10 – 20 cm	21.2 $\pm$ 20.4	0.9 $\pm$ 0.9	30.4 $\pm$ 9.3	4.7 $\pm$ 0.4	166 $\pm$ 129	131 $\pm$ 500
55 – 65 cm	7.4 $\pm$ 15.4	0.3 $\pm$ 0.6	27.5 $\pm$ 11.1	5.0 $\pm$ 0.4	66 $\pm$ 70	142 $\pm$ 428

mineral topsoil because in the topsoil, sorption sites might be saturated due to the higher organic matter contents compared to the subsoil (Hassink, 1997; Georgiou et al., 2022).

Soil pH affects the protonation of soil organic matter and minerals, and thus their capacity to engage in sorption processes. Soil organic matter contains different functional groups with variable charge. Carboxyl, hydroxyl, and phenolic moieties are negatively charged when deprotonated, while amino groups are positively charged when protonated. The protonation, and therefore the charge of these functional groups depends on the soil pH. The pK<sub>a</sub> value of carboxyl groups lies in the acidic pH range (pK<sub>a</sub> = 2–6) and varies depending on the functional groups in their vicinity (Blume et al., 2015). The carboxyl group is the most abundant functional group in soil organic matter, and hence the net charge of organic matter is negative. Sorption of soil organic matter also depends on the charge of soil minerals. pH-variable charge is found on the oxides and hydroxides of iron, aluminum, silicon, and manganese, which are positively charged under acidic conditions. Silicates have mostly permanent negative charge and in addition some pH-variable charge at their edges (Blume et al., 2015).

An organic compound can adsorb to a positively charged binding site on a mineral through a negatively charged functional group. Furthermore, organic matter can adsorb to a negatively charged binding site through a positively charged group (i.e., an amino group) or through a negatively charged group and a multivalent metal cation that acts as a metal bridge (von Lützow et al., 2006; Kögel-Knabner et al., 2008; Kleber et al., 2015). In acidic soils, aluminum cations act as bridges between negatively charged clay minerals and negatively charged organic compounds (Kunhi Mouvenchery et al., 2012; Rasmussen et al., 2018; Yu et al., 2021). In addition, also calcium cations may be important in acidic soils for crosslinking organic matter to minerals (von Fromm et al., 2021; Rowley et al., 2023). Sorption of organic compounds to clay minerals and iron and aluminum oxides and hydroxides is strongly pH-dependent. For low molecular weight organic compounds, it has been shown in sorption experiments that a higher proportion of these compounds is adsorbed at low than at high pH to clay minerals as well as iron and aluminum oxides and hydroxides (Gu et al., 1994, 1996; Spark et al., 1997; Filius et al., 2000; Strahm and Harrison, 2008).

Soil N contents might be more strongly related to soil texture than C contents because organic N, which represents most of the soil N in forest soils, has on average a higher charge density than organic C compounds that do not contain N (Sollins et al., 2006; Knicker, 2011) (Fig. S1). Soil N consists mostly of proteinaceous material composed of amino acids (Knicker et al., 1993; Knicker, 2004, 2011). All amino acids have at least one carboxyl group and one amino group. In addition, some amino acids (aspartic acid and glutamic acid) have a second carboxyl group, while others have a second amino group (lysine, arginine, and histidine) (Fig. S1). The amino groups have a pK<sub>a</sub> of approximately 9.0–10.5 and carboxyl groups have a pK<sub>a</sub> of approximately 2.0–2.4 (Nelson and Cox,



**Fig. 2.** Soil nitrogen concentration and the molar carbon-to-nitrogen (C:N) ratio depending on soil texture. The results are shown for the organic layer (a, b) and the mineral soil at a depth of 0–10 cm (c, d), 10–20 cm (e, f), and 55–65 cm (g, h). The number of observations and the P value of the Kruskal-Wallis test are given in the upper right corner of each panel. Different capital letters below the boxes indicate significant differences ( $P < 0.05$ ) tested by Dunn post hoc test separately for the data of each panel. The black numbers depict the medians, blue dots and blue numbers show the arithmetic means. Soil texture indicated for the organic layer (panels a and b) is the texture determined in the uppermost 20 cm of the mineral soil. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 2**

Ratio of clayey and fine silty soils-to-sandy soils for nitrogen and carbon concentrations and the carbon-to-nitrogen (C:N) ratio in the organic layer and different depth increments of the mineral soil (ratios are calculated based on medians shown in Fig. 2 and S2).

Variable	Soil depth	Ratio of clayey and fine silty soils-to-sandy soils
Carbon (g kg <sup>-1</sup> )	Organic layer	0.93
	0 – 10 cm	1.85
	10 – 20 cm	1.44
	55 – 65 cm	0.87
Nitrogen (g kg <sup>-1</sup> )	Organic layer	1.17
	0 – 10 cm	2.33
	10 – 20 cm	1.80
	55 – 65 cm	1.50
Molar C:N ratio	Organic layer	0.75
	0 – 10 cm	0.69
	10 – 20 cm	0.71
	55 – 65 cm	0.69

2004). Thus, in the large majority of soils, the amino group is protonated, and the carboxyl group is deprotonated which allows amino acids to adsorb to charged compounds (Fig. S1). Amino acids have a high affinity to adsorb to soil minerals (Wang and Lee, 1993; Jones and Hodge, 1999; Aufdenkampe et al., 2001; Ding and Henrichs, 2002; Moon et al., 2016; Moon et al., 2019). Accordingly, the C:N ratio of mineral-associated organic matter is lower and less variable than that of particulate organic matter, as recently shown for 186 topsoils from different regions of Europe (Cotrufo et al., 2019).

Sorption of amino acids is pH-dependent and a higher proportion of amino acids is adsorbed at low pH (pH < 4.0) than at higher pH (Strahm and Harrison, 2008). Yet, for proteins, it has been found that the highest number of molecules is adsorbed when the pH is close to the point of zero charge of the protein (Haynes and Norde, 1994; Meissner et al., 2015). This is because the net charge of a given protein equals zero at the point of zero charge, and thus the electrostatic repulsion between adsorbed protein molecules is at its minimum (Meissner et al., 2015). Proteins differ widely in their point of zero charge (Haynes and Norde, 1994), and little is known about pH-dependent sorption of proteins in soil. Yet, Cao et al. (2011) found that sorption of N from extracellular polymeric substances to different clay minerals and iron oxides decreased with increasing pH.

Storage of C and N in soils also depends on factors that modulate microbial activity, and hence decomposition, such as the soil pH. Low soil pH typically leads to a low decomposition rate (Rousk et al., 2009; Malik et al., 2018), and in soils with a pH below 4.5, microbial respiration is strongly reduced compared to less acidic soils (Rousk et al., 2009). Accordingly, liming of forest soils, which increases the pH, typically leads to decreases in C storage in temperate and boreal forests (Persson et al., 2021).

Understanding soil N storage is important because N limits primary production in many ecosystems, including forests at high latitudes (De Vries et al., 2006; Högberg et al., 2006; Hyvönen et al., 2008; Sponseller et al., 2016). In boreal and Northern temperate forests, a large part of N is stored in the soil organic layer. Yet, a recent study showed that even in the organic layer, the N concentration is affected by soil texture of the underlying mineral soil (Spohn and Stendahl, 2022). This is likely because plants connect N storage in the mineral soil to the organic layer since they take up N in the mineral soil and provide N to the organic layer through leaf and root litter.

The aim of this study was to better understand how soil carbon (C) and nitrogen (N) contents and the C:N ratio are related to soil texture, pH as well as exchangeable aluminum and calcium in forest soils. For this purpose, we investigated 1992 temperate and boreal forest soils

(Fig. 1) based on data collected for the Swedish Forest Soil Inventory. In a previous study (Spohn and Stendahl, 2022), we showed that the organic layer stock, and hence the soil stocks of C, N, and phosphorus are strongly related to mean annual temperature, based on 309 soil profiles. The present study is based on a substantially larger dataset (1992 soil profiles) and investigates the relationships of soil C and N concentrations with soil texture, pH, and exchangeable aluminum and calcium.

In this study, we tested the following seven hypotheses.

**H1:** C and N concentrations are higher in fine-textured soils than in coarse-textured soils (because fine-textured soils have a higher density of binding places to which organic compounds can adsorb than coarse-textured soils).

**H2:** N is more strongly enriched in fine-textured soils (compared to coarse-textured soils) than organic C in the mineral soil, leading to lower C:N ratios in fine-textured than coarse textured soils (because soil organic N compounds have on average a higher charge density than non-N containing organic compounds).

**H3:** The N concentration in the organic layer is higher in fine-textured soils than in coarse-textured soils (because the higher N concentration in the mineral soil leads to a higher N content in plant biomass and litter that supplies the organic layer with organic matter).

**H4:** Differences in C and N concentrations and the C:N ratio among soils with different texture are larger in the subsoil than in the mineral topsoil (since mineral surfaces in the topsoil but not in the subsoil are saturated with organic matter).

**H5:** The concentrations of exchangeable aluminum and calcium are positively related to C and N concentrations in the mineral soil (because aluminum and calcium cations act as bridges between negatively charged clay minerals and negatively charged organic compounds which slows down the decomposition of organic matter).

**H6:** Soils with a low pH (pH ≤ 4.0) have higher soil organic C contents and C:N ratios than less acidic soils (because the acidity decreases microbial respiration).

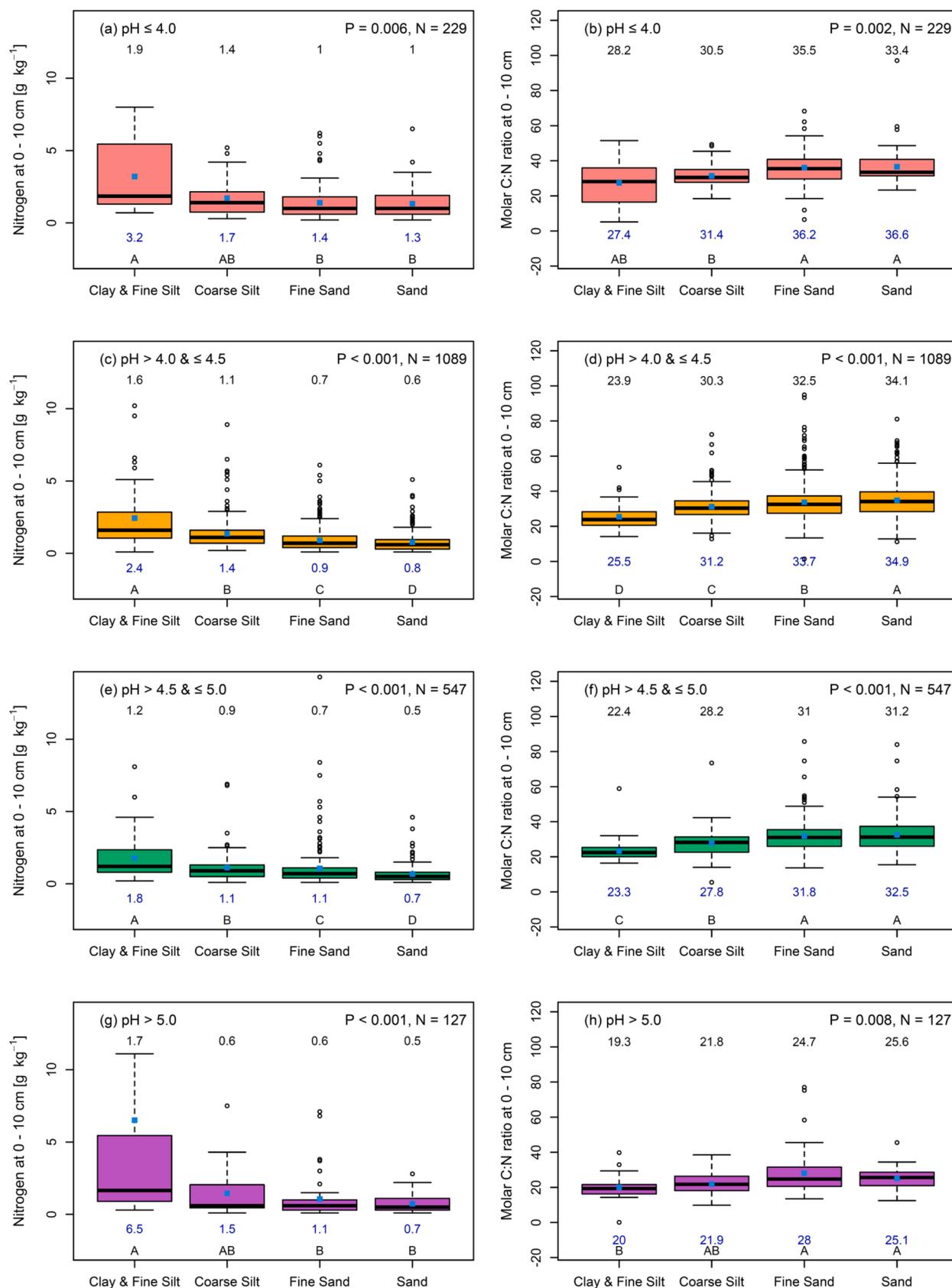
**H7:** Soil C and N concentrations differ more strongly among texture classes in soils with pH ≤ 4 than in soils with higher pH (because a larger proportion of organic compounds is adsorbed to clay minerals and oxides at pH ≤ 4.0 than at higher pH).

## 2. Material and methods

### 2.1. Structure of the inventory and sample collection

Soil samples were collected for the Swedish Forest Soil Inventory. The Swedish Forest Soil Inventory in its current form started in 1983 and monitors the state of the Swedish forests with respect to soil and vegetation. It covers all of Sweden except for arable land and urban areas, and is conducted in collaboration with the Swedish National Forest Inventory. The inventory visits about 20,000 permanent plots distributed all over Sweden over a 10-year period. Circular plots with 10 m radius are located in quadratic clusters on a triangular grid (Ranneby et al., 1987), which is denser towards the south of the country to account for the greater fragmentation of the landscape and a more diverse geology in the south of Sweden. Each quadratic cluster encompasses eight circular plots (or four in the southwestern region). At each of these circular plots, forest characteristics including tree diameter, the dominant tree type and stand age is classified.

Description and sampling of soil profiles is carried out on a subset of the circular plots, in total c. 4,500 plots (visited over a 10-year period). The organic layer is sampled volumetrically in a 3.14 m<sup>2</sup> subplot within each circular plot throughout the entire depth of the organic layer (excluding the litter layer). For this purpose, 1–9 volumetric samples are taken and combined to gain a sample volume of 1.5 L (using a corer with a diameter of 10 cm). In addition, a small soil profile is prepared in the subplot and mineral soil is collected at fixed depth intervals: 0–10 cm, 10–20 cm, and 55–65 cm. The soil group is determined according to the World Reference Base for Soil Resources (IUSS Working Group WRB,



**Fig. 3.** Soil nitrogen concentration and the molar carbon-to-nitrogen (C:N) ratio in the mineral soil at a depth of 0–10 cm depending on soil texture in soils with different pH. The results are shown for soils with pH ≤ 4.0 (a, b) pH > 4.0 and ≤ 4.5 (c, d) pH > 4.5 and ≤ 5.0 (e, f) as well as pH > 5.0 (g, h). The number of observations and the P value of the Kruskal-Wallis test are given in the upper right corner of each panel. Different capital letters below the boxes indicate significant differences (P < 0.05) tested by Dunn post hoc test separately for the data of each panel. The black numbers depict the medians, blue dots and blue numbers show the arithmetic means. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 3**

Ratio clayey and fine silty soils-to-sandy soils for the nitrogen and carbon concentration and the carbon-to-nitrogen (C:N) ratio for soils of four pH classes at a depth of 0–10 cm in the mineral soil (ratios are calculated based on medians shown in Fig. 3 and S3).

Variable	pH class	Ratio of clayey and fine silty soils-to-sandy soils
Carbon (g kg <sup>-1</sup> )	≤ 4.0	1.47
	> 4.0 & ≤ 4.5	2.04
	> 4.5 & ≤ 5.0	1.61
	> 5.0	2.68
Nitrogen (g kg <sup>-1</sup> )	≤ 4.0	1.90
	> 4.0 & ≤ 4.5	2.67
	> 4.5 & ≤ 5.0	2.40
Molar C:N ratio	> 5.0	3.40
	≤ 4.0	0.84
	> 4.0 & ≤ 4.5	0.70
	> 4.5 & ≤ 5.0	0.72
	> 5.0	0.75

2014). The texture of the mineral soil samples is determined in the field for the uppermost 20 cm of the mineral soils, and for the depth increment 55–65 cm according to the following classes: gravel, coarse sand, sand, fine sand, coarse silt, fine silt, and clay, using the so-called finger test (Vos et al., 2016). The texture classes each have a number from 2 for gravel to 8 for clay (which makes it possible to test whether the average texture class for different groups of soils differs). In the laboratory, all soil samples are dried to constant weight at 35 °C. The samples are homogenized and sieved (<2 mm), and living and dead roots > 1 mm diameter are removed from the mineral soil samples. The samples are weighed and the stock of the organic layer is calculated based on the weight of the < 2 mm-fraction of the organic layer. Chemical analyses are carried out on the fine soil fraction (<2 mm).

## 2.2. Selection of plots and basic plot description

For the present study, we selected plots from the inventory that have been sampled between 2013 and 2020 and are classified as sub-alpine forest or productive forest (i.e., productivity > 1 m<sup>3</sup> ha<sup>-1</sup> yr<sup>-1</sup>), which includes all forest types of the inventory, but excludes grasslands. From this dataset, we excluded plots with the humus form mull because at these plots the samples are taken in different depth intervals for the Swedish National Forest Inventory. Furthermore, we excluded soils classified as Histosols, soils that had the texture gravel at a depth of 0–10 cm, and soils that only consisted of an organic layer on solid bedrock (because we aimed at exploring the relationship between soil texture and organic matter). We excluded all profiles for which no data on soil texture and C and N concentrations in 0–10 cm depth in the mineral soil were available, e.g. due to obstacles in the soil. Furthermore, we considered C:N ratios > 100 as outliers, and excluded soils with C:N ratios > 100 from the data analysis (removal of outliers).

The plot selection based on these criteria resulted in a total number of 1992 plots, located between 55.75°N and 68.42°N (Fig. 1). Of these, 1939 plots were classified as productive (lowland) forest (productivity > 1 m<sup>3</sup> ha<sup>-1</sup> yr<sup>-1</sup>) and 53 as sub-alpine forest. The mean stand age was 62 years and the median stand age was 47 years. Of the 1992 plots, 42 % were covered by pine forest, 29 % by spruce forest, 13 % by mixed coniferous forest, 6 % by mixed deciduous-coniferous forest, 5 % by deciduous forest, and 3 % had no tree cover (due to recent logging). Of the 1992 soils, 64 % had the organic layer form mor with dominance of the F subhorizon (mor type 1), 14 % had the organic layer form mor with dominance of the H subhorizon (mor type 2), 12 % had the humus form peaty mor, 5.1 % had no organic layer (likely related to recent clear-cutting), 4 % had the humus form moder, and 2 % had the humus form peat. Furthermore, 56 % of the soils were classified as Podzol, 33 % as Regosol, 5 % as Gleysol, 3 % as Arenosol, 2 % as Leptosol, 1 % as

Cambisol, and 0.6 % as Umbrisol.

At a depth of 0–20 cm, 42 % of the soils had the texture fine sand, 25 % had the texture sand, 18 % had the texture coarse silt, 9 % had the texture coarse sand, 4 % had the texture fine silt, and 3 % had the texture clay. At a depth of 55–65 cm, 35 % of the soils had the texture fine sand, 29 % had the texture sand, 16 % had the texture coarse silt, 10 % had the texture coarse sand, 5 % had the texture fine silt, and 4 % had the texture clay.

## 2.3. Soil chemical analyses

The organic C and total N concentrations were analyzed using an elemental analyzer (TruMac CN, LECO). The pH was determined in water (at a soil:water ratio of 1:2.5) using a Pt electrode (Aquatrode Plus Pt1000, Metrohm). Exchangeable aluminum was extracted in 1 M KCl and exchangeable calcium was extracted in 1 M ammonium acetate buffered at pH 7.00. Both aluminum (Al) and calcium (Ca) were quantified by inductively coupled plasma optical emission spectroscopy (ICP-OES; Avivo 200, Perkin Elmer). The exchangeable aluminum and calcium fractions represent the plant available aluminum and calcium.

## 2.4. Calculations and data analyses

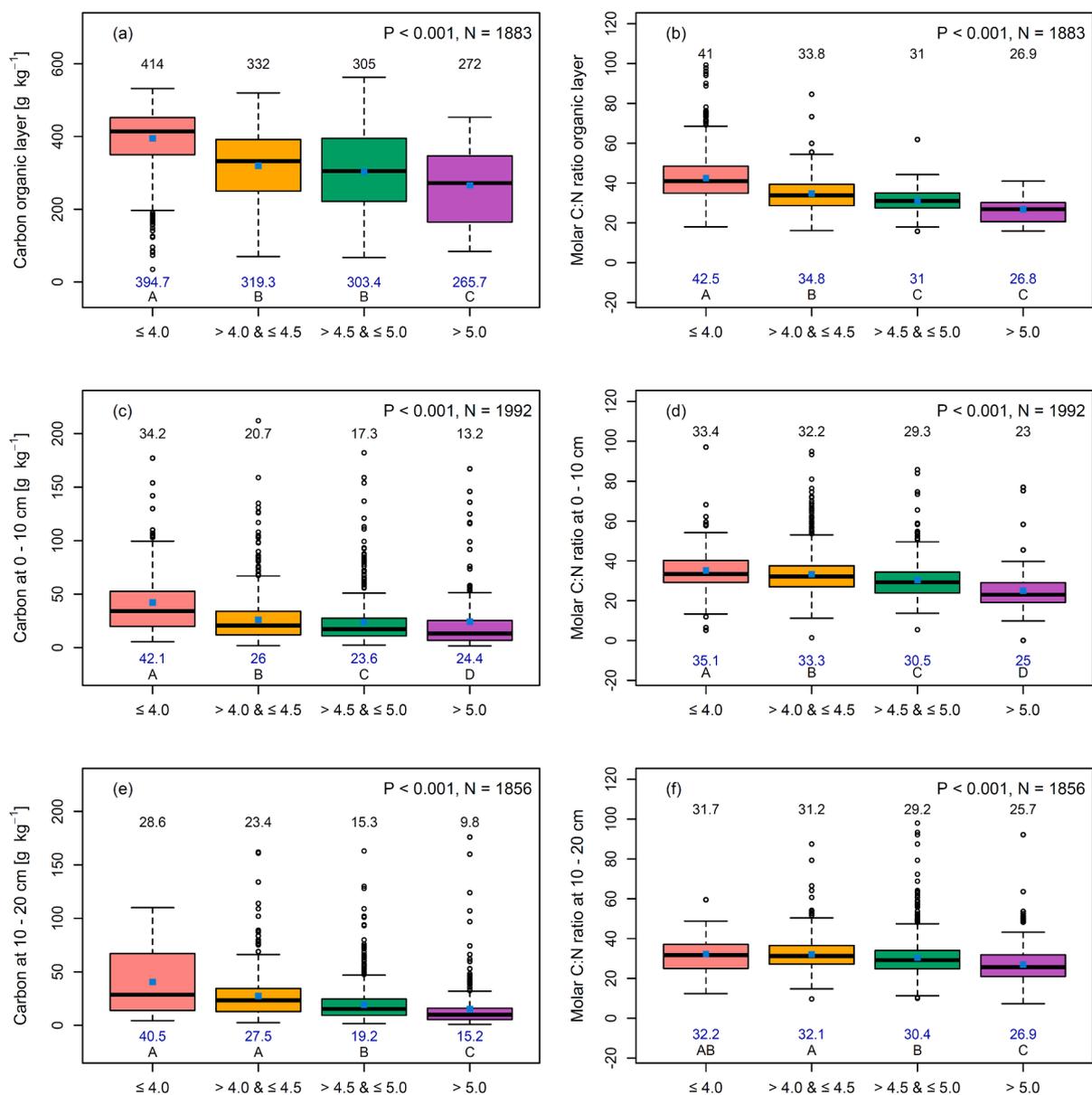
The molar C:N ratio was calculated by dividing the moles of soil organic carbon by the moles of total nitrogen. For the analysis of soil texture, the two texture classes clay and fine silt were combined into one class called clay and fine silt, in order to gain a more equal distribution of the soils across different texture classes. For the same reason also the two texture classes sand and coarse sand were combined. We divided the soils into four pH classes (≤4.0, 4.0–4.5, 4.5–5.0, and > 5.0). Results for these pH classes are presented for all soil depth increments, except for the lowest one (55–65 cm) because in this soil depth increment, only six soils had a pH ≤ 4.0. Furthermore, we calculated mean and median C and N concentrations and C:N ratios of soils in the four texture classes, separately for the four different pH classes. This analysis was exclusively conducted for the soil depth increment 0–10 cm due to the fact we have the highest number of observations for this soil depth increment.

We tested for significant differences in soil chemical properties among different groups of soils by Kruskal-Wallis test followed by Dunn post hoc test (using the R package FSA, version 0.9.4), whereby P < 0.050 was considered to indicate statistically significant differences. This was done separately for the different soil depth increments to compare soils of different texture and pH classes. In addition, we calculated multiple linear regression models with C, N or the C:N ratio as a function of soil texture, pH, exchangeable metal cations and their interactions. This was done separately for the different soil depth increments. For the regression analyses, concentrations of C and N and the C:N ratio were transformed by calculating their natural logarithm since they were not normally distributed. All data analyses were conducted using R (version 4.1.1, R Core Team, 2021).

## 3. Results

Concentrations of C and N declined with increasing soil depth, and varied widely across all soils (Table 1). The molar C:N ratio decreased from a mean of 40.2 in the organic layer to 27.5 at a depth of 55–65 cm (Table 1). The mean pH increased from 3.8 in the organic layer to 5.0 at a depth of 55–65 cm (Table 1). The concentration of exchangeable Al declined with increasing soil depth (Table 1). The concentration of exchangeable Ca was very similar in all depth increments of the mineral soil, and it was on average 16.5-times higher in the organic layer than in the mineral soil (Table 1).

The N concentrations were significantly higher in fine-textured soils than in coarse textured soils, in all three depth increments of the mineral soil and also in the organic layer (Fig. 2). The ratio of N in the clayey and fine silty soils-to-N in the sandy soils (based on the medians) was largest



**Fig. 4.** Soil carbon concentration and the molar carbon-to-nitrogen (C:N) ratio depending on soil pH. The results are shown for the organic layer (a, b) and the mineral soil at a depth of 0–10 cm (c, d), 10–20 cm (e, f), and 55–65 cm (g, h). The number of observations and the P value of the Kruskal-Wallis test are given in the upper right corner of each panel. Different capital letters below the boxes indicate significant differences ( $P < 0.05$ ) tested by Dunn post hoc test separately for the data of each panel. The black numbers depict the medians, blue dots and blue numbers show the arithmetic means. Soil texture indicated for the organic layer (panels a and b) is the texture determined in the uppermost 20 cm of the mineral soil. The results are not shown for the soil increment 55–65 cm since there were only six soils that had a  $\text{pH} \leq 4.0$  in this depth increment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

at a depth of 0–10 cm (2.33; Table 2). This ratio decreased with increasing soil depth, to 1.50 at a depth of 55–65 cm (Fig. 2, Table 2).

Organic C was less strongly enriched in fine-textured soils (compared to coarse-textured soils) than N in all depth increments (Table 2). Organic C was higher concentrated in the fine-textured than in the coarse textured soils at a depth of 0–10 and 10–20 cm (Fig. S2). The ratio of C concentration in the clayey and fine silty soils-to-C concentrations in the sandy soils (based on medians) was largest at a depth of 0–10 cm (1.85; Table 2). The C:N ratio also varied with soil texture (Fig. 2). The C:N ratio of the clayey and fine silty soils was smaller than the one of the sandy soils, by a factor of 0.69 to 0.75 (Fig. 2; Table 2).

For the depth increment 0–10 cm of the soils, divided into four different pH classes, we found that the difference in N concentration between clayey and fine silty soils compared to sandy soils was largest in

the class of soils with  $\text{pH} > 5.0$ , and smallest in the class of soils with  $\text{pH} \leq 4.0$  (Fig. 3, Table 3). The same was true for the C concentration (Fig. S3, Table 3). In all four pH classes, the ratio clayey and fine silty soils-to-sandy soils was larger for N than for C (Table 3). For instance, in the class  $\text{pH} > 5.0$ , the ratio clayey and fine silty soils-to-sandy soils was 3.40 for N (Fig. S3; Table 3) and 2.68 for C (Fig. 3; Table 3).

Soils with  $\text{pH} \leq 4$  had significantly higher C concentrations than soils with a higher pH, in the organic layer and in the mineral soil at a depth of 0–10 and 10–20 cm (Fig. 4), independently of texture. The largest differences in C concentrations among soils of contrasting pH classes were observed in the uppermost 10 cm of the mineral soil (Table 4). At this soil depth, the C concentration was on average 2.59 times higher in soils with a  $\text{pH} \leq 4$  than in soils with a  $\text{pH} > 5.0$  (Table 4). In contrast, the N concentration in the organic layer did not differ significantly

**Table 4**

Ratio of soils with pH  $\leq$  4.0 to soils with pH  $>$  5.0 (based on medians) for the nitrogen and carbon concentration and the carbon-to-nitrogen (C:N) ratio in the organic layer and different depth increments of the mineral soil (ratios are calculated based on medians shown in Fig. 4 and S4).

Variable	Soil depth	Ratio soils with pH $\leq$ 4.0-to-soils with pH $>$ 5.0
Carbon (g kg <sup>-1</sup> )	Organic layer	1.52
	0 – 10 cm	2.59
	10 – 20 cm	2.01
Nitrogen (g kg <sup>-1</sup> )	Organic layer	0.97
	0 – 10 cm	2.00
	10 – 20 cm	2.50
Molar C:N ratio	Organic layer	1.52
	0 – 10 cm	1.45
	10 – 20 cm	1.23

**Table 5**

Carbon, nitrogen, and the C:N ratio as a function exchangeable aluminum (Al). Shown are the P value as well as the adjusted coefficient of determination (Ad. R<sup>2</sup>) for all significant correlations (P < 0.05).

Function	Soil depth	P value	Ad. R <sup>2</sup>
Ln(Carbon) ~ Al	Organic layer	> 0.05	–
	0 – 10 cm	< 0.001	0.32
	10 – 20 cm	< 0.001	0.34
	55 – 65 cm	< 0.001	0.38
Ln(Nitrogen) ~ Al	Organic layer	< 0.05	0.03
	0 – 10 cm	< 0.001	0.29
	10 – 20 cm	< 0.001	0.32
	55 – 65 cm	< 0.001	0.36
Ln(C:N ratio) ~ Al	Organic layer	< 0.001	0.03
	0 – 10 cm	< 0.01	0.35
	10 – 20 cm	> 0.05	–
	55 – 65 cm	< 0.05	0.01

**Table 6**

Carbon, nitrogen, and the C:N ratio as a function of soil texture, pH, exchangeable aluminum (Al), exchangeable calcium (Ca), and their interactions. Shown are the P value and the adjusted coefficient of determination (Ad. R<sup>2</sup>).

Function	Soil depth	P value	Ad. R <sup>2</sup>
Ln(Carbon) ~ texture $\times$ pH $\times$ Al $\times$ Ca	Organic layer	< 0.001	0.40
	0 – 10 cm	< 0.001	0.46
	10 – 20 cm	< 0.001	0.46
	55 – 65 cm	< 0.001	0.49
Ln(Nitrogen) ~ texture $\times$ pH $\times$ Al $\times$ Ca	Organic layer	< 0.001	0.18
	0 – 10 cm	< 0.001	0.49
	10 – 20 cm	< 0.001	0.47
	55 – 65 cm	< 0.001	0.45
Ln(C:N ratio) ~ texture $\times$ pH $\times$ Al $\times$ Ca	Organic layer	< 0.001	0.38
	0 – 10 cm	< 0.001	0.18
	10 – 20 cm	< 0.001	0.19
	55 – 65 cm	< 0.001	0.18

among soils of the four pH classes (Fig. S4). The C:N ratio was larger in soils with a pH  $\leq$  4 than in soils with a pH  $>$  5.0, by a factor of 1.52 in the organic layer and a factor of 1.45 and 1.23 at 0–10 and 10–20 cm soil depth, respectively (Table 4).

In the organic layer, the median pH was 3.8, 3.7 and 4.0 for spruce, pine, and deciduous forests, respectively. Furthermore, in the uppermost 10 cm of the mineral soils, the median pH was 4.4, 4.4 and 4.6 for spruce, pine and deciduous forests, respectively. Thus, soil pH varied only very little among forests with different tree species. The slightly higher pH values in the deciduous forests have a limited effect on the analysis since deciduous forests represent only 5 % of the forest soils studied here (see section 2.2). Furthermore, the median texture class

(see section 2.1) was 5.0 for spruce, pine, and deciduous forests, showing that there is no co-variation of soil texture and tree species.

Based on multiple linear regression models, we found that C, N and the C:N ratio were significantly related to interactions of soil texture and pH in all soil depth increments (Table S1). The coefficient of determination (R<sup>2</sup>) increased strongly for the mineral soils, if the concentration of exchangeable aluminum was included in the models (Table S2). Aluminum alone was also positively, and relatively strongly correlated with C and N in the mineral soil, but not in the organic layer (Table 5). The C concentration was on average 3.7 times higher in the quartile of soils with the highest aluminum concentration compared to the quartile of soils with the lowest aluminum concentration, in the uppermost 10 cm of the mineral soil. The concentration of exchangeable calcium was only weakly positively correlated with C and N (Table S3). Yet, calcium in combination with texture, and pH was strongly correlated with C and N, particularly in the organic layer (Table S4). Together, texture, pH, and the concentrations of both aluminum and calcium explained almost half of the variability in C and N concentrations in the mineral soil (Table 6).

When calculating models for soils with different texture separately, we found that the coefficients of determination (R<sup>2</sup>) of the linear models of C or N as a function of pH and Al were larger for the coarse-textured soils than for the fine-textured soils (Table 7). The R<sup>2</sup> of the linear models of C as a function of pH and calcium, was substantially larger for the organic layer than for the mineral soil, in the soils of all four texture classes (with one exception) (Table 7). The pH tended to be slightly higher in the clayey and fine silty soils than in all other soils (Fig. S5).

## 4. Discussion

### 4.1. C and N depending on soil texture

In accordance with *hypothesis 1*, we found that C and N concentrations were higher in fine-textured soils than in coarse-textured soils (Fig. 2 and S2). The most likely reason for the higher concentrations in the fine-textured soils is that these contain more binding sites on minerals to which organic compounds can adsorb than coarse-textured soils. Adsorption slows down decomposition of organic compounds, which leads to enrichment of organic matter in soils with a high density of binding sites (Kögel-Knabner et al., 2008; Kleber et al., 2015). In addition, the fine-textured soils contain more nutrients than coarse-textured soils, which tends to cause higher primary production, resulting in high organic matter inputs to the soil. Our results are in accordance with many studies reporting a negative relationship between organic C concentration and the average diameter of mineral particles (Kaiser and Guggenberger, 2003; von Lütow et al., 2006; Zinn et al., 2007; Kögel-Knabner et al., 2008). Our finding is also in accordance with results of our previous study showing enrichment of C and N in fine-textured soils compared to coarse-textured soils in Sweden (Spohn and Stendahl, 2022). The differences between fine- and coarse-textured soils for C and N were slightly higher in the previous study, likely because we considered only forests with a stand age  $>$ 60 years in the former study (the mean stand age was 113 years), which excludes effects of recent clear-cutting and soil preparation on the element contents. In contrast, in the present study, the mean stand age was 62 years, and thus the forests had less time to build up organic matter.

In agreement with *hypothesis 2*, we found that N was more strongly enriched in fine-textured soils (compared to coarse-textured soils) than organic C, leading to lower C:N ratios in fine-textured than coarse textured soils (Fig. 2, Fig. S2, and Table 2). The reason for the stronger enrichment of N in the fine-textured soils is likely that organic N has a high charge density, and therefore a high affinity to adsorb to charged mineral surfaces. It was shown in experiments that amino acids bind more strongly than the total dissolved organic matter pool to soil minerals (Aufdenkampe et al., 2001). In addition, it was demonstrated that positively charged amino acids have a particularly high adsorption

**Table 7**

Carbon and nitrogen as a function pH and exchangeable aluminum (Al) or, alternatively, pH and exchangeable calcium (Ca) in soils of the four texture classes (clay and fine silt, coarse silt, fine sand, and sand) at different depths. Shown are the P value and the adjusted coefficient of determination (adjusted R<sup>2</sup>). R<sup>2</sup> > 0.30 are given in bold font.

Function	Soil depth	Clay and fine silt		Coarse silt		Fine sand		Sand	
		P value	Adjusted R <sup>2</sup>	P value	Adjusted R <sup>2</sup>	P value	Adjusted R <sup>2</sup>	P value	Adjusted R <sup>2</sup>
Ln(Carbon) ~ pH × Al	Organic layer	< 0.001	0.14	< 0.001	0.22	< 0.001	0.24	< 0.001	0.23
	0 – 10 cm	< 0.001	0.20	< 0.001	<b>0.30</b>	< 0.001	<b>0.34</b>	< 0.001	<b>0.34</b>
	10 – 20 cm	< 0.001	0.13	< 0.001	<b>0.35</b>	< 0.001	<b>0.41</b>	< 0.001	<b>0.39</b>
	55 – 65 cm	< 0.001	<b>0.39</b>	< 0.001	<b>0.44</b>	< 0.001	<b>0.43</b>	< 0.001	<b>0.46</b>
Ln(Nitrogen) ~ pH × Al	Organic layer	< 0.01	0.07	< 0.001	0.04	< 0.05	0.01	< 0.001	0.02
	0 – 10 cm	< 0.001	0.18	< 0.001	0.26	< 0.001	<b>0.32</b>	< 0.001	<b>0.31</b>
	10 – 20 cm	< 0.001	0.15	< 0.001	<b>0.31</b>	< 0.001	<b>0.38</b>	< 0.001	<b>0.38</b>
	55 – 65 cm	< 0.001	<b>0.32</b>	< 0.001	<b>0.35</b>	< 0.001	<b>0.41</b>	< 0.001	<b>0.44</b>
Ln(Carbon) ~ pH × Ca	Organic layer	< 0.001	<b>0.36</b>	< 0.001	<b>0.41</b>	< 0.001	<b>0.40</b>	< 0.001	<b>0.39</b>
	0 – 10 cm	< 0.001	0.16	< 0.001	0.26	< 0.001	0.16	< 0.001	0.21
	10 – 20 cm	< 0.001	<b>0.37</b>	< 0.001	0.23	< 0.001	0.19	< 0.001	0.20
	55 – 65 cm	< 0.001	0.26	< 0.001	0.13	< 0.001	0.22	< 0.001	0.23
Ln(Nitrogen) ~ pH × Ca	Organic layer	< 0.001	0.10	< 0.001	0.10	< 0.001	0.06	< 0.001	0.10
	0 – 10 cm	< 0.001	0.22	< 0.001	0.23	< 0.001	0.14	< 0.001	0.18
	10 – 20 cm	< 0.001	<b>0.31</b>	< 0.001	0.19	< 0.001	0.17	< 0.001	0.18
	55 – 65 cm	< 0.001	0.14	< 0.001	0.04	< 0.001	0.14	< 0.001	0.21

coefficient (Wang and Lee, 1993; Jones and Hodge, 1999; Aufdenkampe et al., 2001; Ding and Henrichs, 2002; Moon et al., 2016; Moon et al., 2019). Sorption of organic N compounds likely slows down their decomposition in soils because microbes cannot take up adsorbed compounds, and exoenzymes cannot bind to them and catalyze their decomposition. Accordingly, it was shown that sorption of amino acids to minerals restricted their uptake and decomposition (Vieublé Gonod et al., 2006; Hunter et al., 2016). Furthermore, it was found that addition of clays strongly decreased microbial decomposition of proteins (Chevallier et al., 2003), and that amino acids decomposed more slowly than other organic compounds in soil (Miltner et al., 2009), which is likely related to their high affinity to adsorb to charged mineral surfaces. Thus, sorption of organic N compounds very likely results in the strong enrichment of N in fine-textured soils.

Our findings are in line with a study about a soil texture gradient in the Amazon forest reporting a decrease in the C:N ratio with increasing soil clay content (Silver et al., 2000). The findings are also in accordance with results reported in Spohn and Stendahl (2022) about temperate and boreal forests. In this previous study, the difference in the C:N ratio among sandy and clayey soils was larger, mostly due to higher C:N ratios in the sandy soils. The reason for this is most likely that in the previous study, we only considered forests with a stand age >60 years, and these forests had several decades to build up organic matter, and particularly structural tissue of plants with high C:N ratio, in contrast to the forests of the present study which have mean age of 62 years (see section 2.2). Our results are also in accordance with several studies reporting that mineral-associated organic matter is particularly rich in N (e.g. Sollins et al., 2006). These studies were synthesized recently in a meta-analysis which concluded that the C:N ratio of soils is closely related to their particle-size distribution, and tends to be lower in the clay-size than in the sand-size fraction of soils (Amorim et al., 2022).

Our results suggest that N compounds play an important role in organo-mineral interactions. Still, recent studies indicate that organic phosphorus compounds might be even more important for the formation of organo-mineral interactions than organic N since they have a very high affinity to adsorb to mineral surfaces (Spohn, 2020a, Spohn, 2020b; Spohn and Stendahl, 2022).

#### 4.2. C and N depending on soil texture and soil depth

In accordance with hypothesis 3, we found that the N concentration was higher in the organic layer of fine-textured soils than of coarse-textured soils (Fig. 2a and Table 2). This is most likely because of N cycling between soil and plants. The high N concentration in the

mineral, fine-textured soils likely leads to high N contents of plant biomass and litter, which supplies the organic layer with organic matter. This explanation is supported by a recent study about vertical patterns of N isotopes in Swedish forest soils, in which we found indications for strong recycling of N between plants and soils, leading to enrichment of <sup>15</sup>N in the topsoil (Spohn and Stendahl, 2023). In addition, the high N concentration in the organic layer of fine-textured soils could also partly result from high N<sub>2</sub> fixation since fine-textured soils are commonly formed from nutrient-rich minerals, which support higher plant productivity and microbial N<sub>2</sub> fixation (Clarholm and Skjellberg, 2013). We are not aware of any other study, except for Spohn and Stendahl (2022), showing that the N concentration of the litter layer increases with decreasing particle size of the underlying mineral soil.

In disagreement with hypothesis 4, we did not find that differences in C and N concentrations and the C:N ratio among soils with different texture were larger in the subsoil than in the mineral topsoil. On the contrary, we found that differences in C and N concentrations among soils with different texture declined with increasing soil depth (Fig. 2 and Table 2). Given that the C and N concentrations both declined with increasing soil depth, the likelihood for organic matter to be in direct contact with minerals is higher in the subsoil than in the topsoil. Yet, this seems to have no effect on C and N contents in these soils. The reason for this might be related to the fact that the pH in the subsoil is higher than in the topsoil (Table 1), which likely leads to higher adsorption of organic matter to clay minerals in the top- than in the subsoil (Gu et al., 1994, 1996; Spark et al., 1997; Filius et al., 2000; Strahm and Harrison, 2008). However, the reason might also be that the C concentrations are rather low even in the mineral topsoil. Thus, even in the topsoil, the sorption places on mineral surfaces are likely not saturated. This is related to the fact that the soils are mostly Podzols and Regosols in which the organic matter is largely concentrated in the organic layer. Our results are in accordance with Silver et al. (2000) who found no change in the difference in the C:N ratio among sandy and clayey forest soils with increasing soil depth.

#### 4.3. C and N depending on soil texture and cations

In agreement with hypothesis 5, we found that the linear models explained a much higher proportion of the variability in C and N concentrations if they included exchangeable aluminum (Table 6) as compared to the models including only texture and pH (Table S1), particularly for the subsoil. The positive correlations of C and N with the aluminum concentration (Table 6) indicate that aluminum plays an important role in stabilizing organic matter in the mineral soil. This is

likely because the trivalent aluminum cations connect negatively charged organic compounds to negatively charged clay surfaces or to negatively charged organic compounds (Piccolo, 2002; Kunhi Mouvenchery et al., 2012; Yu et al., 2021; von Fromm et al., 2021). Concentrations of C and N in the mineral soil were more strongly correlated with the aluminum concentration (Table 5) than with the combination of texture and soil pH (Table S1). This observation is in accordance with a study demonstrating that multivalent cations are stronger predictors of soil organic C than the clay content in a large dataset on soil profiles from different continents (Rasmussen et al., 2018).

The coefficients of determination ( $R^2$ ) of the models of C and N as a function of pH and aluminum were higher for the coarse-textured than for the fine-textured soils (Table 7), indicating that aluminum is more important for organic matter stabilization in coarse-textured than fine-textured soils. The reason for this might be that aluminum cations do not only connect negatively charged organic compounds to negatively charged minerals, but also contribute to the formation of so-called supramolecules, which consist of organic compounds that are connected through multivalent metal cations (Piccolo, 2001, 2002; Kunhi Mouvenchery et al., 2012). These organo-organ interactions may be relevant for organic matter stabilization in soils with a low clay content because they might prevent microbial uptake and decomposition of organic compounds bound in supramolecules (Piccolo, 2001, 2002; Sutton and Spósito, 2005).

Inclusion of the exchangeable calcium concentration in the models did not increase the proportion of explained variability as much as inclusion of the aluminum concentration (compare Table 6 and S4), indicating that aluminum cations play a more important role than calcium cations for the stabilization of organic matter in acidic mineral forest soils. Yet, in the organic layer, the  $R^2$  of the linear models of C as a function of pH and calcium was comparatively high (Table 7 and S4). This might suggest that calcium cations are relevant for stabilizing organic C in the organic layer, potentially by interconnecting negatively charged organic compounds, and thereby forming supramolecules that are difficult to decompose (Piccolo, 2001, 2002; Kunhi Mouvenchery et al., 2012). One main reason why exchangeable calcium was more strongly related to the C concentration in the organic layer than in the mineral soil is likely that the exchangeable calcium concentration was about 16.5-times higher in the organic layer than in the mineral soil (Table 1).

#### 4.4. C and N depending on soil texture and pH

In accordance with *hypothesis 6*, we found that soils with a very low soil pH ( $\text{pH} \leq 4.0$ ) had higher soil organic C concentrations and C:N ratios than less acidic soils (Fig. 4). Our result that soils of different pH classes differed significantly in C but not in N concentration of the organic layer (Fig. S4) indicates that pH largely affects microbial respiration, and hence the loss of C from the soil. This is in accordance with studies showing that soil pH strongly influences microbial respiration, and leads to very low respiration rates at  $\text{pH} < 4.5$  (Rousk et al., 2009). The C concentration in the mineral topsoil was on average 2.6 times higher in very acidic soils compared to soils with a  $\text{pH} > 5.0$  (Fig. 4 and Table 4). This finding suggests that pH has a major effect on soil C contents in temperate and boreal forest soils. Recent reviews on the main factors controlling soil organic C stocks hardly mentioned pH as an influencing factor of soil C sequestration (Schmidt et al., 2011; Wiesmeier et al., 2019). Yet, the results of our study indicate that pH should be considered as an important determinant of the soil organic C content, particularly in temperate and boreal forest soils.

In contrast to *hypothesis 7*, we did not find that soil C and N concentrations differed more between texture classes at  $\text{pH} \leq 4$  than at higher pH (Fig. 3 and S3, Table 3), as we had hypothesized based on results about sorption of amino acids and other low molecular weight organic compounds (Spark et al., 1997; Strahm and Harrison, 2008). On the contrary, we found that the clayey and fine silty soils contained more

N than the sandy soils by a factor of 3.4 at  $\text{pH} > 5.0$  and by a factor of only 1.9 at  $\text{pH} \leq 4$  (Table 3). These findings seem to be in contradiction with the result of many laboratory studies, concluding that organic compounds have a higher affinity to adsorb to clay minerals and iron and aluminum oxides and hydroxides at  $\text{pH} < 4.0$  than at  $\text{pH} > 5.0$  (Gu et al., 1994, 1996; Spark et al., 1997; Filius et al., 2000; Strahm and Harrison, 2008). The main reason for this apparent contradiction could be that pH also strongly affects decomposition and other biotic processes, which leads to increased organic C and N contents in the mineral soil at low pH, irrespective of soil texture (see above). Thus, the effect of pH on organic matter contents likely reduces the texture-dependent differences in C and N concentrations under very acidic conditions. However, it could also be that proteins in these soils have a point of zero charge at  $\text{pH} > 5.0$ , which causes highest adsorption of these compounds at  $\text{pH} > 5.0$  (Quiquampoix et al., 1993; Haynes and Norde, 1994; Meissner et al., 2015). Future studies should explore experimentally the pH-dependent sorption of proteins to soil minerals.

While we concentrated on analyzing the relationship of soil C and N with soil pH, texture, and the concentrations of metal cations in this study, it should be mentioned that soil C and N contents in temperate and boreal forest soils are also influenced by other factors. Mean annual temperature affects both organic matter inputs to soil and the decomposition rate and hence has a large effect on soil organic matter stocks (Spohn and Stendahl, 2022). Furthermore, topography influences organic matter stocks through its effect on soil moisture (Seibert et al., 2007). In addition, tree species affect the C:N ratio of the soils (Spohn and Stendahl, 2022), and the fungal community in the organic layer influences decomposition, and thus organic carbon stocks (Lindahl et al., 2021).

#### 4.5. Conclusions

Based on an exceptionally large dataset containing data on 1992 soil profiles, we showed that soil C and N concentrations and the C:N ratio are strongly related to texture, pH, and aluminum in temperate and boreal forest soils. Specifically, our results demonstrate that N concentration is more strongly related to soil texture than C concentration, which is very likely due to the high charge density of organic N compounds, which allows organic N to adsorb to mineral surfaces. In contrast, C concentration was more strongly related to pH than N concentration, likely due to effects of pH on microbial respiration. The concentration of exchangeable aluminum was a good predictor of C and N in the mineral soil, suggesting that aluminum cations play an important role in slowing down soil organic matter decomposition by interconnecting charged compounds in soil.

#### Author contributions

MS designed the study, conducted the data analysis, and wrote the manuscript, JS leads the Swedish Forest Soil Inventory and provided comments on the manuscript.

#### 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.

#### Acknowledgements

The authors thank all technical staff who conducted sampling and chemical analyses. Furthermore, we thank Christofer Engberg Hydén for

preparing the map in Fig. 1. The Swedish Forest Soil Inventory is part of the national environmental monitoring program commissioned by the Swedish Environmental Protection Agency.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2023.116746>.

## References

- Amorim, H.C., Hurtarte, L.C., Souza, I.F., Zinn, Y.L., 2022. C: N ratios of bulk soils and particle-size fractions: Global trends and major drivers. *Geoderma* 425, 116026.
- Aufdenkampe, A.K., Hedges, J.I., Richey, J.E., Krusche, A.V., Llerena, C.A., 2001. Sorptive fractionation of dissolved organic nitrogen and amino acids onto fine sediments within the Amazon Basin. *Limnol. Oceanogr.* 46 (8), 1921–1935.
- Blume, H.P., Brümmer, G., Hartge, H., Schwertmann, U., 2015. Scheffer/Schachtschabel Soil Science. Springer.
- Cao, Y., Wei, X., Cai, P., Huang, Q., Rong, X., Liang, W., 2011. Preferential adsorption of extracellular polymeric substances from bacteria on clay minerals and iron oxide. *Colloids Surf. B Biointerfaces* 83 (1), 122–127.
- Chevallier, T., Muchaonyerwa, P., Chenu, C., 2003. Microbial utilisation of two proteins adsorbed to a vertisol clay fraction: toxin from *Bacillus thuringiensis* subsp. *tenebrionis* and bovine serum albumin. *Soil Biol. Biochem.* 35 (9), 1211–1218.
- Clarholm, M., Skjellberg, U., 2013. Translocation of metals by trees and fungi regulates pH, soil organic matter turnover and nitrogen availability in acidic forest soils. *Soil Biol. Biochem.* 63, 142–153.
- Cotrufu, M.F., Ranalli, M.G., Haddji, M.L., Six, J., Lugato, E., 2019. Soil carbon storage informed by particulate and mineral-associated organic matter. *Nat. Geosci.* 12 (12), 989–994.
- De Vries, W.I.M., Reinds, G.J., Gundersen, P.E.R., Sterba, H., 2006. The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. *Glob. Chang. Biol.* 12 (7), 1151–1173.
- Ding, X., Henrichs, S.M., 2002. Adsorption and desorption of proteins and polyamino acids by clay minerals and marine sediments. *Mar. Chem.* 77 (4), 225–237.
- Filius, J.D., Lumsdon, D.G., Meeussen, J.C., Hiemstra, T., Van Riemsdijk, W.H., 2000. Adsorption of fulvic acid on goethite. *Geochim. Cosmochim. Acta* 64 (1), 51–60.
- Georgiou, K., Jackson, R.B., Vinduškova, O., Abramoff, R.Z., Ahlström, A., Feng, W., Torn, M.S., 2022. Global stocks and capacity of mineral-associated soil organic carbon. *Nat. Commun.* 13 (1), 3797.
- Gu, B., Schmitt, J., Chen, Z., Liang, L., McCarthy, J.F., 1994. Adsorption and desorption of natural organic matter on iron oxide: mechanisms and models. *Environ. Sci. Tech.* 28 (1), 38–46.
- Gu, B., Mehlhorn, T.L., Liang, L., McCarthy, J.F., 1996. Competitive adsorption, displacement, and transport of organic matter on iron oxide: I. Competitive Adsorption. *Geochim. Cosmochim. Acta* 60 (11), 1943–1950.
- Hassink, J., 1997. The capacity of soils to preserve organic C and N by their association with clay and silt particles. *Plant and Soil* 191 (1), 77–87.
- Haynes, C.A., Norde, W., 1994. Globular proteins at solid/liquid interfaces. *Colloids Surf. B Biointerfaces* 2 (6), 517–566.
- Högberg, P., Fan, H., Quist, M., Binkley, D.A.N., Tamm, C.O., 2006. Tree growth and soil acidification in response to 30 years of experimental nitrogen loading on boreal forest. *Glob. Chang. Biol.* 12 (3), 489–499.
- Hunter, W.R., Niederdorfer, B., Gernand, A., Veuger, B., Prommer, J., Mooshammer, M., Battin, T.J., 2016. Metabolism of mineral-sorbed organic matter and microbial lifestyles in fluvial ecosystems. *Geophys. Res. Lett.* 43 (4), 1582–1588.
- Hyvönen, R., Persson, T., Andersson, S., Olsson, B., Ågren, G.I., Linder, S., 2008. Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. *Biogeochemistry* 89, 121–137.
- Jones, D.L., Hodge, A., 1999. Biodegradation kinetics and sorption reactions of three differently charged amino acids in soil and their effects on plant organic nitrogen availability. *Soil Biol. Biochem.* 31 (9), 1331–1342.
- Kaiser, K., Guggenberger, G., 2003. Mineral surfaces and soil organic matter. *Eur. J. Soil Sci.* 54 (2), 219–236.
- Kleber, M., Sollins, P., Sutton, R., 2007. A conceptual model of organo-mineral interactions in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces. *Biogeochemistry* 85 (1), 9–24.
- Kleber, M., Eusterhues, K., Keilweid, M., Mikutta, C., Mikutta, R., Nico, P.S., 2015. Mineral-organic associations: formation, properties, and relevance in soil environments. *Adv. Agron.* 130, 1–140.
- Knicker, H., 2004. Stabilization of N-compounds in soil and organic-matter-rich sediments—what is the difference? *Mar. Chem.* 92 (1–4), 167–195.
- Knicker, H., 2011. Soil organic N-An under-rated player for C sequestration in soils? *Soil Biol. Biochem.* 43 (6), 1118–1129.
- Knicker, H., Fründ, R., Lüdemann, H.D., 1993. The chemical nature of nitrogen in native soil organic matter. *Naturwissenschaften* 80 (5), 219–221.
- Kögel-Knabner, I., Guggenberger, G., Kleber, M., Kandeler, E., Kalbitz, K., Scheu, S., Leinweber, P., 2008. Organo-mineral associations in temperate soils: Integrating biology, mineralogy, and organic matter chemistry. *J. Plant Nutr. Soil Sci.* 171 (1), 61–82.
- Kunhi Mouvenchery, Y., Kučerik, J., Diehl, D., Schaumann, G.E., 2012. Cation-mediated cross-linking in natural organic matter: a review. *Rev. Environ. Sci. Bio/technol.* 11, 41–54.
- Lindahl, B.D., Kyaschenko, J., Varenus, K., Clemmensen, K.E., Dahlberg, A., Karlton, E., Stendahl, J., 2021. A group of ectomycorrhizal fungi restricts organic matter accumulation in boreal forest. *Ecol. Lett.* 24 (7), 1341–1351.
- Malik, A.A., Puissant, J., Buckeridge, K.M., Goodall, T., Jehmlich, N., Chowdhury, S., Griffiths, R.I., 2018. Land use driven change in soil pH affects microbial carbon cycling processes. *Nat. Commun.* 9 (1), 3591.
- Mayer, L.M., 1994. Surface area control of organic carbon accumulation in continental shelf sediments. *Geochim. Cosmochim. Acta* 58 (4), 1271–1284.
- Meissner, J., Prause, A., Bharti, B., Findenege, G.H., 2015. Characterization of protein adsorption onto silica nanoparticles: influence of pH and ionic strength. *Colloid Polym. Sci.* 293, 3381–3391.
- Miltner, A., Kindler, R., Knicker, H., Richnow, H.H., Kästner, M., 2009. Fate of microbial biomass-derived amino acids in soil and their contribution to soil organic matter. *Org. Geochem.* 40 (9), 978–985.
- Moon, J., Ma, L., Xia, K., Williams, M.A., 2016. Plant-Microbial and mineral contributions to amino acid and protein organic matter accumulation during 4000 years of pedogenesis. *Soil Biol. Biochem.* 100, 42–50.
- Moon, J., Xia, K., Williams, M.A., 2019. Consistent proteinaceous organic matter partitioning into mineral and organic soil fractions during pedogenesis in diverse ecosystems. *Biogeochemistry* 142, 117–135.
- Nelson, D.L., Cox, M.M., 2004. *Lehninger Principles of Biochemistry*. Springer.
- Oades, J.M., 1988. The retention of organic matter in soils. *Biogeochemistry* 5 (1), 35–70.
- Persson, T., Andersson, S., Bergholm, J., Grönqvist, T., Högbom, L., Vegerfors, B., Wirén, A., 2021. Long-term impact of liming on soil C and N in a fertile spruce forest ecosystem. *Ecosystems* 24, 968–987.
- Piccolo, A., 2001. The supramolecular structure of humic substances. *Soil Sci.* 166 (11), 810–832.
- Piccolo, A., 2002. The supramolecular structure of humic substances: a novel understanding of humus chemistry and implications in soil science. *Adv. Agron.* 75, 57–134.
- Quiquampoix, H., Staunton, S., Baron, M.H., Ratcliffe, R.G., 1993. Interpretation of the pH dependence of protein adsorption on clay mineral surfaces and its relevance to the understanding of extracellular enzyme activity in soil. *Colloids Surf. A Physicochem. Eng. Asp.* 75, 85–93.
- IUSS Working Group WRB: World Reference Base for Soil Resources 2014, update 2015, International soil classification system for naming soils and creating legends for soil maps, World Soil Resources Reports No. 106, FAO, Rome, 2015.
- R Core Team, 2021. *A Language and Environment for Statistical Computing R Foundation for Statistical Computing*. Austria, Vienna.
- Ranneby, B., Cruse, T., Hägglund, B., Jonasson, H., Swärd, J., 1987. Designing a new national forest survey for Sweden. *Studia Forestalia Suecica* 177.
- Rasmussen, C., Heckman, K., Wieder, W.R., Keilweid, M., Lawrence, C.R., Berhe, A.A., Wagai, R., 2018. Beyond clay: towards an improved set of variables for predicting soil organic matter content. *Biogeochemistry* 137, 297–306.
- Rousk, J., Brookes, P.C., Bååth, E., 2009. Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. *Appl. Environ. Microbiol.* 75 (6), 1589–1596.
- Rowley, M.C., Nico, P.S., Bone, S.E., Marcus, M.A., Pegoraro, E.F., Castanha, C., Peña, J., 2023. Association between soil organic carbon and calcium in acidic grassland soils from Point Reyes National Seashore, CA. *Biogeochemistry* 1–21.
- Schmidt, M.W., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478 (7367), 49–56.
- Seibert, J., Stendahl, J., Sørensen, R., 2007. Topographical influences on soil properties in boreal forests. *Geoderma* 141 (1–2), 139–148.
- Silver, W.L., Neff, J., McGroddy, M., Veldkamp, E., Keller, M., Cosme, R., 2000. Effects of soil texture on belowground carbon and nutrient storage in a lowland Amazonian forest ecosystem. *Ecosystems* 3, 193–209.
- Sollins, P., Homann, P., Caldwell, B.A., 1996. Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma* 74 (1–2), 65–105.
- Sollins, P., Swanston, C., Kleber, M., Filley, T., Kramer, M., Crow, S., Bowden, R., 2006. Organic C and N stabilization in a forest soil: evidence from sequential density fractionation. *Soil Biol. Biochem.* 38 (11), 3313–3324.
- Spark, K.M., Wells, J.D., Johnson, B.B., 1997. Characteristics of the sorption of humic acid by soil minerals. *Soil Res.* 35 (1), 103–112.
- Spohn, M., 2020a. Phosphorus and carbon in soil particle size fractions: A synthesis. *Biogeochemistry* 147 (3), 225–242.
- Spohn, M., 2020b. Increasing the organic carbon stocks in mineral soils sequesters large amounts of phosphorus. *Glob. Chang. Biol.* 26 (8), 4169–4177.
- Spohn, M., Stendahl, J., 2022. Carbon, nitrogen, and phosphorus stoichiometry of organic matter in Swedish forest soils and its relationship with climate, tree species, and soil texture. *Biogeosciences* 19 (8), 2171–2186.
- Spohn, M., Stendahl, J., 2023. Spatial patterns of nitrogen isotope ratios in forest soils are related to latitude and soil phosphorus concentration. *Biogeochemistry* 1–14.
- Sponseller, R.A., Gundale, M.J., Fitter, M., Ring, E., Nordin, A., Näsholm, T., Laudon, H., 2016. Nitrogen dynamics in managed boreal forests: Recent advances and future research directions. *Ambio* 45, 175–187.
- Strahm, B.D., Harrison, R.B., 2008. Controls on the sorption, desorption and mineralization of low-molecular-weight organic acids in variable-charge soils. *Soil Sci. Soc. Am. J.* 72 (6), 1653–1664.
- Sutton, R., Sposito, G., 2005. Molecular structure in soil humic substances: the new view. *Environ. Sci. Tech.* 39 (23), 9009–9015.
- Vieublé Gonod, L., Jones, D.L., Chenu, C., 2006. Sorption regulates the fate of the amino acids lysine and leucine in soil aggregates. *Eur. J. Soil Sci.* 57 (3), 320–329.

- von Fromm, S.F., Hoyt, A.M., Acquah, G.E., Aynekulu, E., Berhe, A.A., Haefele, S.M., Doetterl, S., 2021. Continental-scale controls on soil organic carbon across sub-Saharan Africa. *Soil* 7, 305–332.
- von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., Flessa, H., 2006. Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions – a review. *Eur. J. Soil Sci.* 57 (4), 426–445.
- Vos, C., Don, A., Prietz, R., Heidkamp, A., Freibauer, A., 2016. Field-based soil-texture estimates could replace laboratory analysis. *Geoderma* 267, 215–219.
- Wang, X.C., Lee, C., 1993. Adsorption and desorption of aliphatic amines, amino acids and acetate by clay minerals and marine sediments. *Mar. Chem.* 44 (1), 1–23.
- Wiesmeier, M., Urbanski, L., Hobley, E., Lang, B., von Lützow, M., Marin-Spiotta, E., Kögel-Knabner, I., 2019. Soil organic carbon storage as a key function of soils – a review of drivers and indicators at various scales. *Geoderma* 333, 149–162.
- Yu, W., Weintraub, S.R., Hall, S.J., 2021. Climatic and geochemical controls on soil carbon at the continental scale: interactions and thresholds. *Global Biogeochem. Cycles* 35 (3) e2020GB006781.
- Zinn, Y.L., Lal, R., Bigham, J.M., Resck, D.V., 2007. Edaphic controls on soil organic carbon retention in the Brazilian Cerrado: texture and mineralogy. *Soil Sci. Soc. Am. J.* 71 (4), 1204–1214.