Carbon, nitrogen, and phosphorus stoichiometry of organic matter in Swedish forest soils and its relationship with climate, tree species, and soil texture

Marie Spohn[1], Johan Stendahl[1]

[1]Department of Soil and Environment, Swedish University of Agricultural Sciences (SLU), Lennart Hjelms väg 9, P.O. Box 7014, 75007 Uppsala, Sweden

Correspondence to: Marie Spohn (marie.spohn@slu.se)

Abstract. While the carbon (C) content of temperate and boreal forest soils is relatively well studied, much less is known about the ratios of C, nitrogen (N), and phosphorus (P) of the soil organic matter, and the abiotic and biotic factors that shape them. Therefore, the aim of this study was to explore carbon, nitrogen, and organic phosphorus (OP) contents and element ratios in temperate and boreal forest soils and their relationships with climate, dominant tree species, and soil texture. For this purpose, we studied 309 forest soils ~~with a stand age >60 years~~ located all over Sweden between 56°N and 68°N. The soils are a representative subsample of Swedish forest soils with a stand age >60 years that were sampled for the Swedish Forest Soil Inventory. We found that the N stock of the organic layer increased by a factor of 7.5 from -2°C to 7.5°C mean annual temperature (MAT), ~~it increased~~ almost twice as much as the increase of the organic layer stock along the MAT gradient. The increase in the N stock went along with an increase in the N:P ratio of the organic layer by a factor of 2.1 from -2°C to 7.5°C MAT (R^2=0.36, p<0.001). Forests dominated by pine had higher C:N ratios in the ~~litter~~ organic layer and mineral soil down to a depth of 65 cm than forests dominated by other tree species. Further, also the C:P ratio was increased in the pine-dominated forests compared to forests dominated by other tree species in the organic layer, but the C:OP ratio in the mineral soil was not elevated in pine forests. C, N and OP contents in the mineral soil were higher in fine-textured soils than in coarse-textured soils by a factor of 2.3, 3.5, and 4.6, respectively. Thus, the effect of texture was stronger on OP than on N and C, likely because OP adsorbs very rigidly to mineral surfaces. Further, we found~~,~~ that the P and K concentrations of the organic layer were inversely related with the organic layer stock. ~~The C and N concentrations of the mineral soil were best predicted by the combination of MAT, texture, and tree species, whereas the OP concentration was best predicted by the combination of MAT, texture and the P concentration of the parent material in the mineral soil. In the organic layer, the P concentration was best predicted by the organic layer stock.~~ Taken together, the results show that the N:P ratio of the organic layer was most strongly related to MAT. Further, the C:N ratio was most strongly related to dominant tree species, even in the mineral subsoil. In contrast, the C:P ratio was only affected by dominant tree species in the organic layer, but the C:OP ratio in the mineral soil was hardly affected by tree species due to the strong effect of soil texture on the OP concentration.

1. Introduction

35 Temperate and boreal forests store large amounts of soil organic matter (SOM) (Bradshaw and Warkentin, 2015; Tau-Strand et al., 2016; Hounkpatin et al., 2021). While most studies on SOM in temperate and boreal forests concentrated exclusively on carbon (C), and some studies also included nitrogen (N) and investigated the C:N ratio (Callesen et al., 2007; Cools et al., 2014; Tau-Strand et al., 2016), very few studies explored the phosphorus (P) content, and the C:P and N:P ratios of SOM in forests (for an exception see Tipping et al., 2016), particularly in North European forests. Thus, we lack knowledge about the

40 C:N:P stoichiometry of the organic matter of temperate and boreal forest soils and the factors that control it.

The N stock of well-drained temperate and boreal forest soils in Northern Europe increases with increasing mean annual temperature (MAT) (Callesen et al., 2007). Yet, it is unknown whether organic P (OP) increases in the same way as N along the MAT gradient in Northern Europe or if the N:P ratio of SOM changes with MAT in North European forest soils. If P availability is high enough to balance the elevated N availability at sites with high N availability and high MAT, the N:P ratio

45 of SOM in North European forests will likely not change with MAT. However, several studies question whether P availability is sufficient to balance the high rates at which N is incorporated into plant biomass in N-rich European forests (Flückiger and Braun, 1998; Braun et al., 2010; Talkner et al., 2015; Jonard et al., 2015; Heuck et al., 2018), which will lead to an increased N:P ratio. In particular, it has been suggested based on modeling exercises that high N availability in South Sweden might lead to P limitations in trees ~~and elevated foliage N:P ratios~~(indicated by molar needle N:P ratio >12) in South Swedish forests

50 (Akselsson et al., 2008; Yu et al., 2018), which likely translates into high N:P ratios of plant litter and potentially of SOM (Zechmeister-Boltenstern et al., 2015). Yet, on the other hand, it has to be considered that most soils in ~~Northern Europe~~Scandinavia are only between 9,000 and 14,000 years old. Thus, comparatively little P leaching and P occlusion has likely occurred during the short duration of pedogenesis, resulting probably in a relatively high P availability in soils of all climate regimes, which should be able to balance the high N availability at sites with high MAT. Taken together, it is currently

55 still an open question if and how the N:P ratio of SOM in Swedish forest~~s~~ soils changes with organic matter N stock and MAT. Several studies showed that the C:N ratios of the organic layer and the mineral topsoil of forests in North Europe are affect by the dominant tree species (Vesterdal and Raulund-Rasmussen, 1998; Vesterdal et al., 2008; Hansson et al. 2011; Cools et al. 2014). In particular, it has been reported that the organic layers of pine forests have a higher C:N ratio than spruce and deciduous forests (Vesterdal and Raulund-Rasmussen, 1998; Vesterdal et al., 2008; Hansson et al. 2011; Cools et al. 2014).

60 However, little is known about the C:N ratio in the mineral soil below the uppermost 10 cm. Furthermore, very little is known about the relationship between dominant tree species and the C:OP and N:OP ratio of the organic layer and the mineral soil in forests in North Europe (for exceptions see Vesterdal and Raulund-Rasmussen, 1998; Hansson et al., 2011). Since N and P contents in leaf litter are strongly associated (McGroddy et al., 2004), it can by hypothesized that C:N and C:P ratios show similar differences between forests dominated by different tree species.

65   Besides climate and tree species, the SOM stoichiometry is likely also affected by soil texture. Recent research showed that OP is more strongly enriched in the clay-size fraction than organic C because OP compounds adsorb rigidly to mineral surfaces in soils (Spohn, 2020a). This suggests that OP has also higher concentrations in fine-textured than in coarse-textured soils because the adsorption of organic compounds protects them against microbial decomposition, and thus should lead to a preferential enrichment of the compounds that adsorb particularly strongly, in soils that provide many sorption sites. Further,

70   it seems likely that besides OP, N is also enriched in fine-textured soils because a large part of N is present in SOM in the form of charged nitrate or ammonium groups that can adsorb to charged surfaces (Knicker et al., 1993; Jones and Hodges, 1999; Kopittke et al., 2018; Miltner et al., 2009). However, previous studies on the effect of texture on the soil N concentration and the C:N ratios in North European forest soils arrived at contradicting conclusions (Vejre et al., 2003; Callesen et al., 2007). The aim of this study was to explore the C, N, and OP contents and element ratios in temperate and boreal forest soils in

75   Sweden and their relationships with climate, dominant tree species, and soil texture. We hypothesized, first, that while the N stock of the organic layer increases with increasing MAT, the N:P ratio of the organic layer does not change with MAT. We hypothesized second, that the C:OP ratio of the organic layer and mineral soil shows similar differences between forests with different tree species as the C:N ratio. Third, we hypothesized that organic matter is N- and P-richer in fine-textured than in coarse-textured mineral soils. In order to test these hypotheses, we studied 309 forest soils with a forest stand age >60 years

80   located all over Sweden between 56°N and 68°N. The soils are a representative subsample of Swedish forest soils with a stand age >60 years that were sampled for the Swedish Forest Soil Inventory. We selected sites with a stand age >60 years in order to minimize the effect of forest management on the results.

2. Material and Methods

85   ### 2.1 Data collection, sampling, and sample preparation

Data and soil samples were collected for the Swedish Forest Soil Inventory (SFSI), which is conducted together with the National Forest Inventory (Riksskogstaxeringen) since 1923. The SFSI 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. The inventory visits about 20,000 permanent plots over a 10-year period, sampling every year about 2,000 plots distributed all

90   over Sweden. 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 8 circular plots (4 in the southwestern region; Ranneby et al., 1987). At each of these circular plots the dominant tree species is classified according to the following classes based on basal area: Deciduous (birch, aspen, beech, and oak), Mixed (mainly mixed coniferous forests), Pine (*Pinus sylvestris* + *Pinus*

95   *contorta*), and Spruce (*Picea abies*). The diameter at breast height is determined for all trees, and from the differences over 10 years, the stem growth rate of the trees at plot level is calculated. A loss of one or more tree(s) can therefore result in a decline

in standing volume between inventories, and thus a negative stem growth rate. In addition, the stand age is determined from the stand history assessed by the repetitive inventory together with ~~tree drillings~~wood coring in the 1980s.

100 Soil sampling is carried out on a subset of the circular plots, i.e. organic layer sampling on c. 10,000 plots and mineral soil sampling on c. 4,500 plots. The organic layer is sampled volumetrically using a 10 cm diameter corer in a 3.14 m^2 subplot within each circular plot throughout the entire depth of the organic layer (up to 30 cm depth), excluding the litter layer. To gain a sample of about 1.5 liter, 1-9 volumetric samples are combined. In addition, a small soil profile is prepared in the subplot. The soil order is determined according to WRB (FAO, 2013), and mineral soil is collected at fixed depth intervals: 0–
105 10 cm, 10–20 cm, and 55–65 cm. The texture of the mineral soil samples is determined in the field according to the following classes; clay ~~(8)~~, fine silt ~~(7)~~, coarse silt ~~(6)~~, fine sand ~~(5)~~, sand ~~(4)~~, and coarse sand ~~(3)~~. 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. The samples are weighed and the stock of the organic layer is calculated based on the weight of the fraction <2 mm of the organic layer. The organic layer stock is the mass of the organic layer on an area basis (t ha^{-1}). Chemical analyses
110 are carried out on the fine soil fraction (<2 mm).

For the present study, we selected plots that (i) have been sampled between 2013 and 2018, (ii) were ~~vegetated~~ covered by forest with a long-term productivity >1 m^3 yr^{-1} and a stand age >60 years, (iii) had the humus form mor or moder (which excludes peatlands and plots with humus form mull), and (iv) for which data on the concentration of P in the parent material
115 (in a depth of 50 cm) was available (Olsson et al., 1993). We excluded plots with the humus form mull because at these plots, the organic layer is not sampled separately from the mineral soil for the SFSI. The plot selection based on these four criteria resulted in a total number of 309 plots (Fig. 1). Of these, 203 were podzols, 84 were regosols, 12 were arenosols, ~~and each three soils were classified as either~~three were leptosols, ~~-~~ three were gleysols, ~~or~~three were cambisols, ~~while~~and one soil was an umbrisol. Two of the three gleysols were covered by pine forest and the other one by spruce forest. The mean stand age
120 was 113 years. Of the 309 sites, 119 sites had a stand age >120 years, and are thus generally classified as old growth forests (not planted). Further, 25 sites were on formally set-aside land. In the following, the plots are also referred to as forests. Only 10 forests were classified as deciduous with five of them being beech and oak forests.

2.2 Soil chemical analyses and climate data
125 Most soil chemical analyses were conducted for the Swedish Forest Soil Inventory based on the samples taken between 2013 and 2018. The total C and N content was analyzed using an elemental analyzer (TruMac CN, LECO). pH was determined in water (soil: water ratio 1:2.5) using a Pt electrode (Aquatrode plus Pt1000, Methrom). Exchangeable cations (Ca, Mg, Na, K, and Mn) were extracted in 1 M ammonium acetate buffered at pH 7.00 and analyzed by inductively coupled plasma optical emission spectroscopy (ICP-OES; Avivo 200, Perkin Elmer).

130   In addition to the variables determined for the Swedish Forest Soil Inventory, we determined total P and organic P for the present study based on the samples taken between 2013 and 2018. Total P of the organic layer and the mineral soil in a depth of 0-10 cm was extracted in nitric acid and hydrogen peroxide (in a ratio 1:3) in a microwave system (Ethos Easy, Milestone) according to the instructions of the manufacturer, and P was determined using ICP-OES (Avivo 200, Perkin Elmer) after filtration of the extract.

135   Organic P in the mineral soil in a depth of 0-10 cm was determined according to Saunders and Williams (1955) and Williams and Saunders (1956) as specified in Pansu and Gautheyrou (2006). Briefly, each sample was separated in two aliquots, each of 1 g. The first aliquot was directly extracted in 0.5 M H_2SO_4 on a horizontal shaker for 16 h. The other aliquot was ignited at 550°C for 2 h and subsequently extracted in H_2SO_4 in the same way as the non-ignited sample. Inorganic P was measured in the extracts by the molybdenum blue method according to Murphy and Riley (1962) using a continuous flow system

140   (AA500, Seal). Total organic P was calculated as the difference between inorganic P in ignited and non-ignited samples.

Total C in this study is considered organic C since all soils were acidic. Furthermore, total P in the organic layer is considered to be organic P. For the mineral soil, we specify whether we refer to organic or total P, in the following.

Total P in the parent material was determined on samples that were collected from the B/C and C horizon for the SFSI in the 1980s. The samples were ground, sieved (< 2mm), ignited and fused with lithium-metaborate, and subsequently, total P was

145   determined by ICP (Olsson et al., 1993).

Other data used in this study are mean annual temperature (MAT; from 2012), mean annual precipitation (MAP; from 2012) and total N deposition (NDep; from 1998) retrieved from the Swedish Meteorological and Hydrological Institute (https://www.smhi.se/data). We assume that the N deposition flux data of the year 1998 is representative for historic N deposition fluxes in Sweden during the last decades which were highest in the 1990s.

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2.3 Data analysis

For the analysis of soil texture, the texture class clay (8) and fine silt (7) were combined as well as the texture class sand (4), and coarse sand (3). Organic layer element stocks were calculated by multiplying the organic layer stock with the respective element concentration. All element ratios were calculated on a molar basis (mol mol^{-1}). We calculated linear models, power

155   functions, medians and arithmetic means, and conducted (multiple) regression analysis analysesin R (version 4.1.1, R Core Team, 2003). For the multiple regression analysis, the variable N tree was created with the value 1 for pine, 2 for mixed and spruce forests and 3 for deciduous forests. For the regression analyses, all soil chemical variables (element stocks, element concentrations, and element ratios) as well as the organic layer stock and the P concentration the parent material were transformed by calculating their natural logarithm (log-transformation) since they tended to be not normally distributed but

160   were right-skewed. In addition, also the variable atmospheric N deposition was log-transform prior to regression analysis because it was not normally distributed. The variables latitude, MAT, and texture class were not transformed for the regression analysis. All correlations significant regressions referred to in the text are significant at p<0.001 (if not indicated otherwise),

and individual p values for specific ~~correlations~~ regressions are given in the tables ~~and figures~~. . Furthermore, we conducted ANOVA followed by Tukey test after log-transformation of the data, and we considered p=0.05 as the threshold for

165 significance. All data analyses were conducted using R (version 4.1.1, R Core Team, 2021)

3. Results

3.1 Latitude, m~~M~~ean annual temperature, N deposition, and SOM stoichiometry

170 We found correlations between the organic layer stock, C, N and P contents as well as element ratios with latitude, MAT, and N deposition, but hardly with MAP (Table 1).

The log-transformed N stock of the organic layer was positively correlated with MAT (R^2=0.30; Table 1) and with the log-transformed N deposition (R^2=0.30), and negatively with latitude (R^2=0.26; Table 1). In the linear model fitted to the empirical data, the N stock of the organic layer increased by a factor of 7.5 from 192 kg ha^{-1} at -2°C MAT to 1439 kg ha^{-1} at 7.5°C MAT

175 (Fig. 2a).

The log-transformed organic layer stock was positively correlated with MAT (R^2=0.24; Table 1) and with the log-transformed N deposition (R^2=0.23), and negatively with latitude (R^2=0.20; Table 1). In the linear model fitted to the empirical data, the organic layer stock increased by a factor of 3.9 from 30.7 ~~kg~~t ha^{-1} at -2°C MAT to 120.8 ~~kg~~t ha^{-1} at 7.5°C MAT (Fig. 2b).

~~Nitrogen~~ Atmospheric N deposition was below 1.5 kg ha^{-1} year^{-1} in most forests, but in ~~some~~some, it was higher, and in 8

180 forests it was even between 5.5 and 8 kg ha^{-1} year^{-1} (Fig. 2c). The forests with the highest N deposition rate had mostly intermediately high organic layer N stocks, thus the N deposition rate and the N stock of the organic layer were only loosely related (Fig. 2c).

Tree stem growth was positively correlated with MAT (R^2=0.27), and it increased by a factor of 2.5 from 1.87 m^3 ha^{-1} yr^{-1} at -2°C MAT to 4.72 m^3 ha^{-1} yr^{-1} at 7.5°C (Fig. 2d).

185 The log-transformed C:N ratio of the organic layer was negatively correlated with MAT (R^2=0.17; Table 1) and with the log-transformed N deposition (R^2=0.~~17~~21) and positively with latitude (R^2=0.~~08~~16; Table1). In the linear model fitted to the empirical data, the molar C:N ratio of the organic layer decreased from 55.3 at -2°C MAT to 37.8 at 7.5°C MAT (Fig. 2d).

The log-transformed P stock of the organic layer was positively correlated with MAT (R^2=0.~~10~~13, Table 1 ~~Fig. 2e~~) and with the log-transformed N deposition (R^2=0.~~10~~12), and negatively with latitude (R^2=0.~~08~~10; Table 1). In the linear model fitted to

190 the empirical data, the ~~N~~P stock of the organic layer increased by a factor of 2.3 from 28 kg ha^{-1} at -2°C MAT to 65 kg ha^{-1} at 7.5°C MAT (Fig. 2e).

The log-transformed N:P ratio of the organic layer was positively correlated with MAT (R^2=0.36, ~~Fig. 2f~~Table 1), and the log-transformed N deposition (R^2=0.38), and negatively with latitude (R^2=0.36) ~~and the log-transformed N deposition (R^2=0.40)~~. In the linear model fitted to the empirical data, the N:P ratio of the organic layer increased by a factor of 2.1 from 24.0 at -2°C

195 MAT to 49.3 at 7.5°C MAT (Fig. 2f).

The log-transformed C:P ratio of the organic layer was only weakly positively (R^2=0.05~~3~~) correlated with ~~latitude,~~ MAT and the log-transformed N deposition, and negatively with latitude (Table 1). Furthermore, ~~C, N and OP~~ C and N in the mineral soil were only weakly positively correlated with ~~latitude,~~ MAT, and the log-transformed N deposition and negatively with latitude (Table 1).

In most soils, the P concentration of the parent material was below 1.0 g kg^{-1}, but in a small number of forests, it was substantially higher, up to 3.4 g kg^{-1}. The P concentration of the soil parent material and the total P concentration of the upper 10 cm of the mineral soil were only very weakly negatively related with MAT and positively with latitude (Table 1).

3.2 Dominant tree species and SOM stoichiometry

The C:N ratio of the organic layer differed between forests with different dominant tree species (Fig. 3a). The C:N of the organic layer was highest in pine forests, on average 1.8 times higher than in deciduous forests, and 1.3 times higher than in spruce forests (Fig. 3a). A similar relationship between forests dominated by different tree species was observed for the C:N ratio in the mineral soil (Fig. 3b-d). In a depth of 55-65 cm, the C:N ratio of the mineral soil in spruce forests was on average 1.8 times higher than in deciduous forests and 1.2 times higher than in ~~spruce~~ pine forests (Fig. 3d), similar to the organic layer. Some pine forests had very high C:N and C:P ratios due to low N and P contents. It needs to be taken into account that there is some uncertainty regarding the samples with very low N and P concentrations since the determination of N and P contents in very nutrient-poor samples is more strongly affected by sample inhomogeneity than the measurement of nutrient-rich samples.

The C:P ratio of the organic layer (Fig. 3e) followed a similar pattern as the C:N ratio across forests with different dominant tree species. The C:P ratio of the organic layer in spruce forests was on average 1.3 times higher than in both deciduous and ~~spruce~~ pine forests (Fig. 3e). In contrast, the C:OP ratio in the mineral soil was not elevated in pine forests but ~~rather~~ in deciduous forests (Fig 2f). The N:P ratio was slightly elevated in deciduous forests, but did not substantially differ between mixed, pine and spruce forest (Supplement Fig. S2a). The organic layer stock differed also between forests with different dominant tree species (Supplement Fig. S2b). In deciduous forests, it was on average 2.2 times higher than in pine forests and 1.9 times higher than in spruce forests.

3.3 Texture and SOM stoichiometry

Concentrations of C, N and OP in the uppermost 10 cm of the mineral soil were highest in soils with the texture clay or fine silt (Fig. 4a-c). The concentrations of C, N and OP decreased gradually with increasing particle size ~~from clay and fine silt, to coarse silt, to fine sand, and finally to sand~~ (Fig. 4a-c). C, N and OP ~~contents~~ concentrations were higher in soils with the texture clay or fine silt than in soils with the texture sand or coarse sand by a factor of 2.3, 3.5, and 4.6, respectively (Fig 4~~3~~a-c). Thus, the differences in element concentrations between soils with different texture were largest for OP, and decreased in the order OP>N>C. In contrast to OP, the total P concentration did not differ between soils with the texture class sand, find

sand and coarse sand. Only soils with the texture clay had elevated P concentrations compared to soils of the other three texture
230 classes by a factor of 1.9 (Supplement Fig. S3).

The C:N ratio and the C:OP ratio in the mineral soil (0-10 cm depth) increased gradually with increasing particle size fraction (Fig. 4d and e). The mean C:N ratio and C:OP ratio were 1.5 and 1.4 times higher lower in soils with the texture clay or fine silt than in soils with the texture sand or coarse sand (Fig. 4d and e).

Different soil textures were also associated with differences in the N stock concentration of the organic layer (Fig. 4f). The
235 mean N concentration of the organic layer increased with decreasing particle size, and it was 1.3 times higher in soils with the texture clay or fine silt than in soils with the texture sand or coarse sand (Fig. 4f).

3.4 Organic layer stock and element contents and parent material

The organic layer stock was inversely related with the concentration of exchangeable K in a non-linear way (Fig. 5a), and the
240 variables were correlated when log-transformed (R^2=0.38; Fig. 5b). Further, t The concentration of exchangeable K was positively correlated with the P concentration of the organic layer (R^2=0.66, Supplement Fig. S3). The organic layer stock was also inversely related with its P concentration in a non-linear way (Fig. 5c), and the variables were correlated when log-transformed (R^2=0.27; Fig. 5d). The log-transformed organic layer stock was only weakly negatively correlated with the log-transformed P concentration of the parent material and the P concentration of the uppermost 10 cm of the mineral soil (both
245 R^2=0.03, p<0.01).

The log-transformed concentrations of exchangeable K and P of the organic layer were positively correlated (R^2=0.67, Supplement Fig. S4a). In addition, the log-transformed concentrations of N and Mg in the organic layer were strongly positively correlated (R^2=0.81 64, Supplement Fig. S3 S4b).

In the organic layer, log-transformed C and N (R^2=0.82 87) as well as C and P (R^2=0.75 1) and N and P (R^2=0.78 83) stocks
250 were strongly correlated (Supplement Fig. S4 S5 a, c, e). In the uppermost 10 cm of the mineral soil, log-transformed C and N concentrations were also strongly correlated (R^2=0.82 79, Supplement Fig. S4 S5b)). The data had to be log transformed to allow correlation analysis for Further, the log-transformed C and P (R^2=0.47) and N and P (R^2=0.49) concentrations in the uppermost 10 cm of the mineral soil since the data was not normally distributed were also positively correlated (Supplement Fig. S4 S5d and f).

255 In most soils, the P concentration of the parent material was below 1.0 g kg^{-1}, but in a small number of forests it was substantially higher, up to 3.4 g kg^{-1}. The log-transformed P concentration of the parent material was correlated with the total P concentration of the uppermost 10 cm of the mineral soil (R^2=0.26; correlation not shown), and it was more weakly correlated with the OP concentration of the uppermost 10 cm of the mineral soil (R^2=0.08) as well as with the total P concentration of the organic layer (R^2=0.08).

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3.5 Covariance

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Latitude and MAT were strongly negatively correlated (R^2=0.88). Further, the log-transformed N deposition rate was strongly negatively correlated with latitude (R^2=0.78), and strongly positively with MAT (R^2=0.82). ~~We also analyzed the relationship between latitude, tree species, and soil texture to understand their covariance.~~ Deciduous forests had a lower latitude than all other forests, while mixed, pine, and spruce forests did not differ substantially in latitude (Fig. ~~S5~~S6a). Further, the latitude of forests with different soil texture did not vary substantially (Fig. ~~S5~~S6b). Spruce forests tended to have a higher texture class, i.e., a finer soil texture than all other forests, while there was no substantial difference in texture between deciduous, mixed, and pine forest (Fig. ~~S5~~S6c).

3.6 Multiple regressions

We tested if we could improve the regressions between MAT and several soil properties (Table 1) by including data on texture, ~~dominant tree species,~~ and the P concentration of the parent material (Table 2). The log-transformed C and total P concentrations of the mineral soil (0-10 cm) could be ~~substantially~~ better predicted by the combination of MAT and the log transformed P concentration of the parent material (R^2=0.20, Table 2) than by only MAT (Table 1). The prediction of the OP concentration of the mineral soil (0-10 cm) improved when next to MAT and the log transformed P concentration of the parent material also texture was included (Table 2). Further, also the C:OP and N:OP ratios could be better predicted by the combination of MAT, soil texture, and the P concentration of the parent material (Table 2) than by only MAT (Table 1). For other variables, the improvement of the prediction was smaller, independent of whether the models included interactions between the independent variables or not (compare Tables 1 and 2).

~~The N concentration and the C:N ratio of the mineral soil (0-10 cm) could be substantially better predicted by the combination of MAT, texture, and tree species (R^2=0.22 and 0.13, respectively) than by only MAT and texture (Table 2) or only MAT (Table 1). The OP concentration of the mineral soil was best predicted by the combination of MAT, texture, and the P concentration of the parent material (R^2=0.25, Table 2).~~

4. Discussion

4.1 N stock increases strongly with increasing MAT

Our finding that the N stock of the organic layer, increased more from -2°C to 7.5°C MAT than the organic layer stock (Fig.1a and b) indicates that the formation of the N stock is more sensitive to temperature than the formation of the organic matter stock. The reasons for the strong change in the N stock with MAT could potentially be, first, the higher N deposition towards the south/southwest of Sweden that enriches the organic layer in South/Southwest Sweden with N. Second, it could potentially be that the rate with which N is taken up by trees increases with decreasing MAT, leading to N depletion of the organic layer at sites with low MAT. Third, it might be that N_2 fixation decreases strongly with decreasing MAT.

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Atmospheric N deposition is well known to be an important N input in forest ecosystems in the south of Sweden (Akselsson
et al., 2008, Högberg et al., 2017; Yu et al., 2018). However, our finding that N deposition was only loosely related to the N
stock of the organic layer (Fig. 2c) suggests that N deposition only explains a small part of the increase in the N stock with
increasing MAT (. even if we take into account that the N deposition data is relatively uncertain and might not be fully
representative of the accumulated differences in deposited N).

Concerning the second potential explanation it needs to be considered that the growth rate of trees decreased increased with
MAT (Fig. 2d). Thus, the potential explanation that the organic layer N stock is decreased by a factor of 7.5 due to high tree
N uptake in the forests with the lowest MAT and lowest tree growth rate compared to forests with the highest MAT and growth
rate is rather questionable.

It seems rather most likely that the increase in the organic layer N stock with increasing MAT is related with to an increase in
N_2 fixation with increasing MAT. Rates of N_2 fixation can be as high as 4 kg N ha^{-1}yr^{-1} in boreal ecosystems (DeLuca et al.,
2002; Lagerström et al., 2007; DeLuca et al., 2008; Gundale et al., 2010), which is a larger N input than atmospheric N
deposition in most boreal areas (Gundale et al., 2011) and in the forests studied here. N_2 fixation is known to depend strongly
on temperature in temperate and boreal ecosystems (Sorensen et al., 2011; Gundale et al., 2012; Rousk et al., 2013). Therefore,
it seems likely that fact that the N stock of the organic layer increased more strongly with increasing MAT than the organic
layer stock is related to the temperature-dependence of N_2 fixation. Most studies that explored the temperature-dependence in
high latitudinal ecosystems focused on arctic heath ecosystems (for exceptions see Gundale et al., 2012; Rousk et al., 2013),
and explored the temperature-dependencies of N_2 fixation in short-term incubation experiments, rather than natural gradients
of MAT. Future research should fill this gap and explore the temperature-dependence of N_2 fixation in forest soils along MAT
gradients to investigate to which extent temperature-dependence of N_2 fixation explains the change in N stocks along the MAT
gradient observed here. Mineralization of N is also expected to increase with increasing temperature, and hence should
counteract the accrual of N with increasing temperature. Our finding that the N stock of the organic layer increased with
increasing MAT suggests that MAT has a larger positive effect on N_2 fixation than on net N mineralization. Similarly, the
increase in the organic layer stock with increasing MAT (Fig. 2b) suggests that MAT has a larger positive effect on plant
productivity (Fig. 2d) than on decomposition. Our results are largely in accordance with Callesen et al. (2007) who studied
198 forest soils in North Europe and reported that the N stock of the total soil profiles (organic layer plus uppermost 100 cm
of the mineral soil) was positively correlated with MAT. Furthermore, oOur finding that the C:N ratio tended to decreases with
increasing MAT (Supplement Fig. S1) is in accordance with a recent study on the organic layer C:N ratio in Swedish and
German forests (Högberg et al., 2021).

4.2 Organic layer N:P ratio decreases increases with increasing MAT

Our finding that the organic layer N:P ratio increased with increasing MAT (Fig. 2f) indicates that P is not incorporated into
the organic layer in a constant ratio with N across all temperature regimes. The reason for the change in the N:P ratio with

MAT could be a similar change in the N:P ratio of the plant litter inputs to the soils. This is supported by Akselsson et al. (2015) showing that the N:P ratio of pine and spruce needles was substantially larger in South/Southwest Sweden than in middle and North Sweden. This is further supported by studies about European forests reporting that the foliage N:P ratio

330 decreases increases with increasing N inputs, because trees do not take up enough P to balance the high N availability (Flückiger and Braun, 1998; Braun et al. 2010; Talkner et al. 2015, Jonard et al., 2015). Further, it has was suggested in modelling exercises that high N inputs can lead to P limitation in south Swedish forests (Akselsson et al., 2008; Yu et al., 2018), resulting in increased needle N:P ratios (Yu et al., 2018). Changes in foliage N:P ratio with MAT likely translate into similar changes in the N:P ratio of the organic layer. The reason why P is not incorporated into the plant biomass in a constant

335 ratio with N across all temperature regimes is likely that P availability limits P uptake at sites with high N availability. This is supported by studies showing that despite the young age of Swedish forest soils, a relatively large proportion of the soil P is adsorbed to Fe and Al oxides (Giesler et al., 1998; 2002; Tuyishime et al., 2022). In addition, also latitude-dependent differences in dominant tree species (i.e., more deciduous forests in the South) seem to contribute to the change in the N:P ratio with MAT since the N:P ratio of the organic layer was significantly higher in deciduous forests than in pine and spruce

340 forests (Fig. S2a). In contrast, latitude-dependent differences in dominant tree species (i.e., more deciduous forests in the South) do not seem to contribute to the change in the N:P ratio with MAT since there were no substantial differences in the N:P ratio of the organic layer between forests dominated by different tree species (Fig. S2a).

4.3 Organic matter stoichiometry varies with tree species, even in the subsoil

345 We found that the C:N and C:P ratios of the organic layer were higher in pine forests than in forests dominated by other tree species, and a very similar difference in the C:N ratio between forests dominated by different tree species was still observed in the mineral soil in a depth of 55-65 cm (Fig. 3). The differences in element ratios of the organic layer are likely derived from differences in the C:N and C:P ratio of the leaf/needle plant litter, since particularly the C:N ratios of the organic layer are closely associated with the element ratios of the plant leaf/needle litter in Swedish forest soils (Ladanai et al., 2010).

350 Similarly in the mineral soil, the differences in the C:N ratio between forests dominated by different tree species are likely also due to the difference in the C:N ratio of the leaf and root litter and the litter layer (Cotrufo et al., 2013; Zechmeister-Boltenstern et al., 2015; Spohn and Chodak, 2015). In addition, the relatively low C:N ratio in the mineral soil in spruce forests compared to pine forests might also partially result from the fact that the spruce forests tended to have a slightly finer texture (Supplement Fig. S5 S6c), which is associated with lower C:N ratios (Fig. 4d, see discussion below). This is in accordance with Stendahl et

355 al. (2010) showing that in Swedish forests, spruce tends to grow in more fertile soils than pine. Yet, it has to be considered that we cannot clearly attribute the differences in stoichiometry to differences in vegetation since pine forests might have been established preferably on soils that already had nutrient poor SOM. Further, we cannot exclude that differences in former land use (Goodale and Aber, 2001; Spohn et al., 2016) or the depth of the groundwater table also affect the mineral soil C:N ratio, although at least the former seems unlikely given that the mean stand age of the forests was 113 years. Furthermore, some of

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the pine forests had extremely high C:N and C:P ratios, which might be due to charcoal in the soils which is likely more abundant in pine forests than in other forests due to more frequent fires (Zacckrisson, 1977). Previous studies also reported a very high C:N ratio in the organic layer and the uppermost cm of the mineral soil in pine forests compared to other forests in Europe (Vesterdal and Raulund-Rasmussen, 1998; Vesterdal et al., 2008; Hansson et al. 2011; Cools et al. 2014). However, this is the first study to show that this difference in the C:N ratio between forests dominated by different tree species is also visible in the mineral subsoil, in a depth of 55-65 cm, to our knowledge.

The higher C:P ratio of the organic layer observed for pine forests than for all other forests is very likely also related to differences in the stoichiometry of the plant litter inputs. Our result that the C:P ratio of the organic layer was higher in pine forests than in all other forests is in accordance with similar observations of the difference in the organic layer C:P ratio between pine and spruce forests (Vesterdal and Raulund-Rasmussen, 1998; Ladanai et al., 2010). The reason why we found no substantial differences in the C:OP ratio in the mineral soil between forests dominated by different tree species (Fig. 3f) is that the concentration of OP in the mineral soil was strongly affected by texture (Fig. 4c), more strongly than the N concentration (Fig. 4b), as we will discuss in the following.

4.4. Organic P and N contents are high in fine-textured soils

The concentrations of C, N, and P were higher in fine-textured soils than in coarse-textured soils. The reason for this is very likely the higher charge density of fine-textured than of coarse-textured soils that allows a large number of organic compounds to adsorb to changed charged mineral surfaces, which protects them against microbial decomposition through steric hindrance (Lützow et al., 2006, Kögel-Knabner et al., 2008, Kleber et al., 2015). Our results are in accordance with previous studies showing that the capacity of soils to store OM is largely determined by the proportion of fine mineral particles with high surface area and high charge density, such as for example, phyllosilicates and Fe and Al oxides (Oades, 1988; Mayer, 1994; Christensen, 1996; Hassink, 1997). Sorption of OM to mineral surfaces is one of the most important processes that slows down the decomposition of organic matter in soils (Lützow et al. 2006; Kleber et al. 2007; Kögel-Knabner et al. 2008), and very likely leads to enrichment of OM in the fine-textured forest soils studied here.

Our finding that the enrichment in fine-textured soils (compared to coarse-textured soils) increased in the order C<N<OP, indicates that the capacity to compete for sorption sites is highest for P-containing organic compounds, and higher for N-containing compounds than for N- and P-free compounds. This interpretation is supported by studies demonstrating that phosphorylated organic compounds have a larger capacity to compete for binding sites in soils than non-phosphorylated organic compounds (Afif et al., 1995; Franssson and Jones, 2007; Schneider et al., 2010). Sorption to mineral surfaces makes OP compounds likely more persistent in soil than non-phosphorylated organic compounds (Spohn et al., 2020a, b). The fact that the total P concentration (Fig. S3) differed much less than the OP concentration (Fig. 4c) between the soils of different texture class supports our interpretation that the strong enrichment of OP in the fine-textured soils is mostly caused by rigid adsorption of OP compounds (that protects OP against decomposition) and much less by a higher P concentration or P

availability in these soils. Similarly, a large part of N is present in SOM in the form of charged nitrate or ammonium moieties, for example in peptides that can adsorb to charged surfaces, which decreases their decomposition rate (Knicker et al., 1993; Jones and Hodges, 1999; Miltner et al., 2009; Kopittke et al., 2018). Thus, the high capacity of N- and P-containing organic compounds to adsorb to ~~changed~~ charged surfaces in soils is likely the reason why N, and particularly OP has higher concentrations in the fine-textured soils compared to the coarse-textured soils than C. In addition, regarding the N concentration it could also be that fine-textured soils are commonly formed from nutrient-rich (potassium, phosphorus, magnesium, etc.) minerals which causes high plant productivity and N_2 fixation, resulting in higher N concentrations in fine-textured soils compared to coarse-textured soils (Clarholm and Skyllberg, 2013).

~~The effect of texture was also visible is the organic layer, as the fine-textured soils had higher litter N stocks than the coarse-textured soils (Fig. 4f). The reason for this is most likely that fine-textured soils are commonly formed from nutrient-rich minerals, which causes high plant productivity and N_2-fixation, resulting in high litter layer N concentrations in fine-textured soils compared to coarse-textured soils.~~ This is likely also the reason for the higher N concentration of the organic layer in the fine-textured soils compared to the coarse-textured soils (Fig. 4f).

4.5 P and K contents are negatively related to the organic layer stock

We found that the organic matter stock was negatively related with ~~the~~ its concentration of exchangeable K (Fig. 5a and b). The reason for this negative correlation is likely that K leaches fast from plant litter (Osono and Takeda, 2004; Schlesinger et al., 2021), and thus, thin organic layers that consist largely of relatively young organic matter have a higher K concentration than massive organic layers that mostly consist of old, K-poor organic matter. In addition, it could be that there is a relatively high contribution of fine-woody debris, which is K-poor, to the more massive organic layers. The relationship found here between the K concentration of the organic layer and the organic matter stock (Figs. 4 and b) is in agreement with the relationship reported by Stendahl et al. (2017) between the C stock of the organic layer and both its K and Mn concentration. Furthermore, we ~~also~~ observed a similar relationship between the organic layer stock and its P concentration (Fig. 5c and d)~~,~~ ~~indicating that P follows a similar dynamic as K~~. The reasons for this ~~could be fast leaching of P~~ might be that the decomposition rate of the organic layer is positively related with the organic layer P concentration. This is supported by a study showing that P is the most limiting element for microbial activity during the first phase of decomposition of pine needles in Sweden (Staaf and Berg, 1982). Further, it could be that there is a higher contribution of fine woody debris, which is P-poor (Spohn et al., 2020b) to the organic layer in forests with high organic layer stock.

4.6 Future research questions

Based on the results gained from the analysis of the forest soil inventory, we identified the following questions that should be studied in the future.

First, our finding that the N:P ratio of the organic layer increased strongly with increasing MAT and the atmospheric N deposition rate raises the question if growth of trees in Scandinavia at sites with high atmospheric N deposition is limited by P, and if so, to what extent.

Second, future research should study the temperature-dependence of N_2 fixation in forest soils in Scandinavia along MAT gradients to investigate to which extent temperature-dependence of N_2 fixation explains the change in N stocks along the MAT gradient observed here

Third, the result that the OP concentration in the mineral soil depends strongly on soil texture, which is likely due rigid adsorption of OP compounds on soil minerals calls for future investigations of (a) the role of OP for the sorptive stabilization of SOM and (b) the turnover of the soil OP pool in relation to the soil organic C pool.

Fourth, we speculated that very high C:N ratios in some pine forests might be related to forest fires. Future research should explore the legacy of forest fires on SOM stoichiometry.

Fifth, the negative relationships found between organic layer stock and organic layer P concentration raises the question if and to which extent P limits organic matter decomposition in Scandinavian forests.

4.6 7 Conclusion

We found that the N stock of the organic layer increased more with MAT than the organic layer stock, which is likely due to the temperature-dependence of N_2 fixation. Against our first hypothesis, we observed that the N:P ratio of the organic layer decreased increased substantially with increasing MAT, likely due to an decrease increase in the ratio of N:P availability with increasing MAT. Further, the C:OP ratio showed similar differences between forests dominated by different tree species as the C:N ratio in the organic layer, as hypothesized, but the C:OP ratio in the mineral soil differed little between forests dominated by different tree specieshowever, not in the mineral soil. The reason for this is likely that the OP concentration was very strongly affected by texture in the mineral soil, and the concentration of OP was much higher in fine- than in coarse-textured soils. The difference in element concentrations between fine- and coarse-textured soils decreased in the order OP>N>C, in agreement with the third hypothesis. Taken together, the results show that the N:P ratio of the organic layer was most strongly related to MAT. Further, the C:N ratio was most strongly related to dominant tree species, even in the mineral subsoil. In contrast, the C:P ratio was only affected by dominant tree species in the organic layer, but the C:OP ratio in the mineral soil was hardly affected by tree species due to the strong effect of soil texture on the OP concentration.

Code Availability

The R code will be made publically available once the manuscript is accepted for publication, and is available for editor and reviewers as an asset to this manuscript.

References

Afif, E., Barron, V., & Torrent, J. (1995). Organic matter delays but does not prevent phosphate sorption by Cerrado soils from

475   Brazil. *Soil Science*, *159*(3), 207-211.

Akselsson, C. Karlsson, G.P., Karlsson P.E., & Ahlstrand, J. (2015) Miljöövervakning på Obsytorna 1984–2013, Skogsstyrelsen, p. 142

Akselsson, C., Westling, O., Alveteg, M., Thelin, G., Fransson, A. M., & Hellsten, S. (2008). The influence of N load and harvest intensity on the risk of P limitation in Swedish forest soils. *Science of the Total Environment*, *404*(2-3), 284-289.

480   Bradshaw, C. J., & Warkentin, I. G. (2015). Global estimates of boreal forest carbon stocks and flux. *Global and Planetary Change*, *128*, 24-30.

Braun, S., Thomas, V. F., Quiring, R., & Flückiger, W. (2010). Does nitrogen deposition increase forest production? The role of phosphorus. *Environmental Pollution*, *158*(6), 2043-2052.

Callesen, I., Raulund-Rasmussen, K., Westman, C. J., & Tau-Strand, L. (2007). Nitrogen pools and C: N ratios in well-drained

485   Nordic forest soils related to climate and soil texture. *Boreal Environmental Research 12*, 681-692.

Christensen, B. T. (2001). Physical fractionation of soil and structural and functional complexity in organic matter turnover. *European Journal of Soil Science*, *52*(3), 345-353.

Clarholm, M., & Skyllberg, U. (2013). Translocation of metals by trees and fungi regulates pH, soil organic matter turnover and nitrogen availability in acidic forest soils. *Soil Biology and Biochemistry, 63*, 142-153.

15

490   Cools, N., Vesterdal, L., De Vos, B., Vanguelova, E., & Hansen, K. (2014). Tree species is the major factor explaining C: N ratios in European forest soils. *Forest Ecology and Management*, *311*, 3-16.

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter?. *Global Change Biology*, *19*(4), 988-995.

495   DeLuca, T. H., Zackrisson, O., Gundale, M. J., & Nilsson, M. C. (2008). Ecosystem feedbacks and nitrogen fixation in boreal forests. *Science*, *320*(5880), 1181-1181.

DeLuca, T. H., Zackrisson, O., Nilsson, M. C., & Sellstedt, A. (2002). Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature*, *419*(6910), 917-920.

Feng, W., Plante, A. F., & Six, J. (2013). Improving estimates of maximal organic carbon stabilization by fine soil particles.

500   *Biogeochemistry*, *112*(1), 81-93.

Flückiger, W., & Braun, S. (1998). Nitrogen deposition in Swiss forests and its possible relevance for leaf nutrient status, parasite attacks and soil acidification. *Environmental Pollution*, *102*(1), 69-76.

Fransson, A. M., & Jones, D. L. (2007). Phosphatase activity does not limit the microbial use of low molecular weight organic-P substrates in soil. *Soil Biology and Biochemistry*, *39*(5), 1213-1217.

505   Giesler, R., Högberg, M., & Högberg, P. (1998). Soil chemistry and plants in Fennoscandian boreal forest as exemplified by a local gradient. *Ecology*, *79*(1), 119-137.

Giesler, R., Petersson, T., & Högberg, P. (2002). Phosphorus limitation in boreal forests: effects of aluminum and iron accumulation in the humus layer. *Ecosystems*, *5*(3), 300-314.

Goodale, C. L., & Aber, J. D. (2001). The long-term effects of land-use history on nitrogen cycling in northern hardwood

510   forests. *Ecological Applications*, *11*(1), 253-267.

Gundale, M. J., Deluca, T. H., & Nordin, A. (2011). Bryophytes attenuate anthropogenic nitrogen inputs in boreal forests. *Global Change Biology*, *17*(8), 2743-2753.

Gundale, M. J., Nilsson, M., Bansal, S., & Jäderlund, A. (2012). The interactive effects of temperature and light on biological nitrogen fixation in boreal forests. *New Phytologist*, *194*(2), 453-463.

515   Gundale, M. J., Wardle, D. A., & Nilsson, M. C. (2010). Vascular plant removal effects on biological N fixation vary across a boreal forest island gradient. *Ecology*, *91*(6), 1704-1714.

Hansson, K., Olsson, B. A., Olsson, M., Johansson, U., & Kleja, D. B. (2011). Differences in soil properties in adjacent stands of Scots pine, Norway spruce and silver birch in SW Sweden. *Forest Ecology and Management*, *262*(3), 522-530.

Hassink, J. (1997). The capacity of soils to preserve organic C and N by their association with clay and silt particles. *Plant and*

520   *Soil*, *191*(1), 77-87.

Heuck, C., Smolka, G., Whalen, E. D., Frey, S., Gundersen, P., Moldan, F., ... & Spohn, M. (2018). Effects of long-term nitrogen addition on phosphorus cycling in organic soil horizons of temperate forests. *Biogeochemistry*, *141*(2), 167-181.

Hounkpatin, K. O., Stendahl, J., Lundblad, M., & Karltun, E. (2021). Predicting the spatial distribution of soil organic carbon stock in Swedish forests using a group of covariates and site-specific data. *SOIL*, *7*(2), 377-398.

525 Högberg, P., Näsholm, T., Franklin, O., & Högberg, M. N. (2017). Tamm Review: On the nature of the nitrogen limitation to plant growth in Fennoscandian boreal forests. *Forest Ecology and Management*, *403*, 161-185.

Högberg, P., Wellbrock, N., Högberg, M. N., Mikaelsson, H., & Stendahl, J. (2021). Large differences in plant nitrogen supply in German and Swedish forests–Implications for management. *Forest Ecology and Management*, *482*, 118899.

Jonard, M., Fürst, A., Verstraeten, A., Thimonier, A., Timmermann, V., Potočić, N., ... & Rautio, P. (2015). Tree mineral 530 nutrition is deteriorating in Europe. *Global Change Biology*, *21*(1), 418-430.

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 Biology and Biochemistry*, *31*(9), 1331-1342.

Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R., & Nico, P. S. (2015). Mineral–organic associations: formation, properties, and relevance in soil environments. *Advances in Agronomy*, *130*, 1-140.

535 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.

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-540 mineral associations in temperate soils: Integrating biology, mineralogy, and organic matter chemistry. *Journal of Plant Nutrition and Soil Science*, *171*(1), 61-82.

Kopittke, P. M., Hernandez-Soriano, M. C., Dalal, R. C., Finn, D., Menzies, N. W., Hoeschen, C., & Mueller, C. W. (2018). Nitrogen-rich microbial products provide new organo-mineral associations for the stabilization of soil organic matter. *Global Change Biology*, *24*(4), 1762-1770.

545 Ladanai, S., Ågren, G. I., & Olsson, B. A. (2010). Relationships between tree and soil properties in Picea abies and Pinus sylvestris forests in Sweden. *Ecosystems*, *13*(2), 302-316.

Lützow, M. V., 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. *European Journal of Soil Science*, *57*(4), 426-445.

550 Mayer, L. M., Schick, L. L., Hardy, K. R., Wagai, R., & McCarthy, J. (2004). Organic matter in small mesopores in sediments and soils. *Geochimica et Cosmochimica Acta*, *68*(19), 3863-3872.

McGroddy, M. E., Daufresne, T., & Hedin, L. O. (2004). Scaling of C: N: P stoichiometry in forests worldwide: Implications of terrestrial redfield-type ratios. *Ecology, 85*(9), 2390-2401.

Miltner, A., Kindler, R., Knicker, H., Richnow, H. H., & Kästner, M. (2009). Fate of microbial biomass-derived amino acids 555 in soil and their contribution to soil organic matter. *Organic Geochemistry*, *40*(9), 978-985.

Murphy, J. A. M. E. S., & Riley, J. P. (1962). A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, *27*, 31-36.

Oades, J. M. (1988). The retention of organic matter in soils. *Biogeochemistry*, *5*(1), 35-70.

Olsson, M., Rosén, K., & Melkerud, P. A. (1993). Regional modelling of base cation losses from Swedish forest soils due to whole-tree harvesting. *Applied Geochemistry*, *8*, 189-194.

Osono, T., & Takeda, H. (2004). Potassium, calcium, and magnesium dynamics during litter decomposition in a cool temperate forest. *Journal of Forest Research*, *9*(1), 23-31.

Pansu, M., & Gautheyrou, J. (2006). *Handbook of soil analysis: mineralogical, organic and inorganic methods*. Springer Science & Business Media.

R Core Team, 20032021. 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.

Rousk, K., Jones, D. L., & DeLuca, T. H. (2013). Moss-cyanobacteria associations as biogenic sources of nitrogen in boreal forest ecosystems. *Frontiers in Microbiology*, *4*, 150.

Saunders, W. M. H., & Williams, E. G. (1955). Observations on the determination of total organic phosphorus in soils. *Journal of Soil Science*, *6*(2), 254-267.

Schlesinger, W. H. (2021). Some thoughts on the biogeochemical cycling of potassium in terrestrial ecosystems. *Biogeochemistry*, *154*(2), 427-432.

Schneider, M. P. W., Scheel, T., Mikutta, R., Van Hees, P., Kaiser, K., & Kalbitz, K. (2010). Sorptive stabilization of organic matter by amorphous Al hydroxide. *Geochimica et Cosmochimica Acta, 74*(5), 1606-1619.

Sorensen, P. L., & Michelsen, A. (2011). Long-term warming and litter addition affects nitrogen fixation in a subarctic heath. *Global Change Biology*, *17*(1), 528-537.

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. *Global Change Biology*, *26*(8), 4169-4177.

Spohn, M., & Chodak, M. (2015). Microbial respiration per unit biomass increases with carbon-to-nutrient ratios in forest soils. *Soil Biology and Biochemistry*, *81*, 128-133.

Spohn, M., Novák, T. J., Incze, J., & Giani, L. (2016). Dynamics of soil carbon, nitrogen, and phosphorus in calcareous soils after land-use abandonment – A chronosequence study. *Plant and Soil*, *401*(1-2), 185-196.

Staaf, H., & Berg, B. (1982). Accumulation and release of plant nutrients in decomposing Scots pine needle litter. Long-term decomposition in a Scots pine forest II. *Canadian Journal of Botany*, *60*(8), 1561-1568.

Stendahl, J., Berg, B., & Lindahl, B. D. (2017). Manganese availability is negatively associated with carbon storage in northern coniferous forest humus layers. *Scientific Reports*, *7*(1), 1-6.

590 Stendahl, J., Johansson, M. B., Eriksson, E., Nilsson, Å., & Langvall, O. (2010). Soil organic carbon in Swedish spruce and pine forests–differences in stock levels and regional patterns. *Silva Fennica*, *44*(1), 5-21.

Tau-Strand, L., Callesen, I., Dalsgaard, L., & de Wit, H. A. (2016). Carbon and nitrogen stocks in Norwegian forest soils—the importance of soil formation, climate, and vegetation type for organic matter accumulation. *Canadian Journal of Forest Research*, *46*(12), 1459-1473.

595 Talkner, U., Meiwes, K. J., Potočić, N., Seletković, I., Cools, N., De Vos, B., & Rautio, P. (2015). Phosphorus nutrition of beech (*Fagus sylvatica* L.) is decreasing in Europe. *Annals of Forest Science*, *72*(7), 919-928.

Tipping, E., Somerville, C. J., & Luster, J. (2016). The C: N: P: S stoichiometry of soil organic matter. *Biogeochemistry*, *130*(1), 117-131.

Tuyishime, J. M., Adediran, G. A., Olsson, B. A., Spohn, M., Hillier, S., Klysubun, W., & Gustafsson, J. P. (2022). Phosphorus
600 abundance and speciation in acid forest Podzols–Effect of postglacial weathering. *Geoderma*, *406*, 115500.

Vejre, H., Callesen, I., Vesterdal, L., & Raulund-Rasmussen, K. (2003). Carbon and nitrogen in Danish forest soils—contents and distribution determined by soil order. *Soil Science Society of America Journal*, *67*(1), 335-343.

Vesterdal, L., & Raulund-Rasmussen, K. (1998). Forest floor chemistry under seven tree species along a soil fertility gradient. *Canadian Journal of Forest Research*, *28*(11), 1636-1647.

605 Vesterdal, L., Schmidt, I. K., Callesen, I., Nilsson, L. O., & Gundersen, P. (2008). Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *Forest Ecology and Management*, *255*(1), 35-48.

Vincent, A. G., Vestergren, J., Gröbner, G., Persson, P., Schleucher, J., & Giesler, R. (2013). Soil organic phosphorus transformations in a boreal forest chronosequence. *Plant and Soil*, *367*(1), 149-162.

Williams, E. G., & Saunders, W. M. H. (1956). Distribution of phosphorus in profiles and particle-size fractions of some
610 Scottish soils. *Journal of Soil Science*, *7*(1), 90-109.

Yu, L., Zanchi, G., Akselsson, C., Wallander, H., & Belyazid, S. (2018). Modeling the forest phosphorus nutrition in a southwestern Swedish forest site. *Ecological Modelling*, *369*, 88-100.

Zachrisson, O. (1977). Influence of forest fires on the North Swedish boreal forest. *Oikos, 29*, 22-32.

Zechmeister-Boltenstern, S., Keiblinger, K. M., Mooshammer, M., Peñuelas, J., Richter, A., Sardans, J., & Wanek, W. (2015).
615 The application of ecological stoichiometry to plant–microbial–soil organic matter transformations. *Ecological Monographs*, *85*(2), 133-155.

Tables

Table 1: Results of the ~~correlation~~ regression ~~analysis~~ analyses (adjusted R^2, p value) for the organic layer, mineral soil (0-10 cm), and parent material ~~for the total mass of the organic layer as well as organic carbon (C), nitrogen (N) and organic phosphorus (OP) stocks of the organic layer and contents in the mineral soil as dependent variable, and latitude, mean annual temperature (MAT), mean annual precipitation (MAP), and the log transformed N deposition as independent variable~~ in 309 Swedish forest soils (n=309). The signs + and - indicate positive and negative regressions, respectively.

	Latitude (°)	MAT (°C)	MAP (mm)	Log (N deposition) (kg ha⁻¹)
Log (Organic layer stock) (t ha⁻¹)	- 0.20, p<0.001	+ 0.24, p<0.001	+ 0.02, p<0.01	+ 0.23, p<0.001
Log (C stock organic layer) (kg ha⁻¹)	- 0.16, p<0.001	+ 0.18, p<0.001	+ 0.02, p<0.05	+ 0.17, p<0.001
Log (N stock organic layer) (kg ha⁻¹)	- 0.26, p<0.001	+ 0.30, p<0.001	+ 0.04, p<0.001	+ 0.30, p<0.001
Log (P stock organic layer) (kg ha⁻¹)	- 0.10, p<0.001	+ 0.13, p<0.001	+ 0.01, p<0.05	+ 0.12, p<0.001
Log (Molar C:N ratio organic layer)	+ 0.16, p<0.001	- 0.17, p<0.001	- 0.04, p<0.001	- 0.21, p<0.001
Log (Molar C:P ratio organic layer)	- 0.06, p<0.01	+ 0.05, p<0.01	p>0.05	+ 0.05, p<0.01
Log (Molar N:P ratio organic layer)	- 0.36, p<0.001	+ 0.36, p<0.001	+ 0.06, p<0.001	+ 0.38, p<0.001
Log (C concentration mineral soil) (g kg⁻¹)	- 0.17, p<0.001	+ 0.18, p<0.001	p>0.05	+ 0.14, p<0.001
Log (N concentration mineral soil) (g kg⁻¹)	- 0.08, p<0.001	+ 0.10, p<0.001	p>0.05	+ 0.10, p<0.001
Log (OP concentration mineral soil) (g kg⁻¹)	p>0.05	p>0.05	p>0.05	p>0.05
Log (Molar C:N ratio mineral soil)	p>0.05	p>0.05	p>0.05	p>0.05
Log (Molar C:OP ratio mineral soil)	- 0.11, p<0.001	+ 0.12, p<0.001	p>0.05	+ 0.10, p<0.001
Log (Molar N:OP ratio mineral soil)	- 0.15, p<0.001	+ 0.15, p<0.001	p>0.05	+ 0.13, p<0.001
Log (P concentration mineral soil) (mg kg⁻¹)	+ 0.03, p<0.01	- 0.01, p<0.05	- 0.02, p<0.01	- 0.00, p<0.05
Log (P conc. parent material) (mg kg⁻¹)	+ 0.09, p<0.001	- 0.06, p<0.001	- 0.01, p<0.05	- 0.05, p<0.001

Table 2: Results of the multiple regression ~~analysis~~ analyses (adjusted R^2, p value) with (*) and without (+) interactions of the independent variables for the organic layer and mineral soil (0-10 cm) ~~stock as well as organic carbon (C), nitrogen (N) and organic phosphorus (OP) stocks of the organic layer and contents in the mineral soil as dependent variable, and latitude, mean annual temperature (MAT), NTree, and the P content of the parent material (Pparent) as independent variable~~ in 309 Swedish forest soils (n=309). ~~NTree has the value 1 for pine, 2 for mixed forests and spruce forests, and 3 for deciduous forests.~~

|	MAT + Texture	MAT * Texture	MAT + Log (Pparent)	MAT * Log(Pparent)	MAT + Texture + Log (Pparent)	MAT * Texture * Log (Pparent)
Log (Organic layer stock) (t ha^{-1})	0.24, p<0.001	0.24, p<0.001	0.24, p<0.001	0.24, p<0.001	0.24, p<0.001	0.24, p<0.001
Log (C stock organic layer) (kg ha^{-1})	0.18, p<0.001	0.18, p<0.001	0.19, p<0.001	0.18, p<0.001	0.18, p<0.001	0.18, p<0.001
Log (N stock organic layer) (kg ha^{-1})	0.30, p<0.001	0.30, p<0.001	0.30, p<0.001	0.30, p<0.001	0.30, p<0.001	0.30, p<0.001
Log (P stock organic layer (kg ha^{-1})	0.14, p<0.001	0.14, p<0.001	0.13, p<0.001	0.13, p<0.001	0.14, p<0.001	0.14, p<0.001
Log (Molar C:N ratio organic layer)	0.21, p<0.001	0.21, p<0.001	0.19, p<0.001	0.21, p<0.001	0.21, p<0.001	0.23, p<0.001
Log (Molar C:P ratio organic layer)	0.07, p<0.001	0.08, p<0.001	0.09, p<0.001	0.09, p<0.001	0.08, p<0.001	0.09, p<0.001
Log (Molar N:P ratio organic layer)	0.35, p<0.001	0.35, p<0.001	0.36, p<0.001	0.37, p<0.001	0.36, p<0.001	0.37, p<0.001
Log (C concentration mineral soil) (g kg^{-1})	0.23, p<0.001	0.23, p<0.001	0.22, p<0.001	0.27, p<0.001	0.27, p<0.001	0.26, p<0.001
Log (N concentration mineral soil) (g kg^{-1})	0.26, p<0.001	0.26, p<0.001	0.20, p<0.001	0.20, p<0.001	0.30, p<0.001	0.28, p<0.001
Log (OP concentration mineral soil) (g kg^{-1})	0.11, p<0.001	0.12, p<0.001	0.08, p<0.001	0.08, p<0.001	0.18, p<0.001	0.18, p<0.001
Log (Molar C:N ratio mineral soil)	0.05, p<0.001	0.05, p<0.001	>0.05	>0.05	0.05, p<0.001	0.06, p<0.01
Log (Molar C:OP ratio mineral soil)	0.15, p<0.001	0.16, p<0.001	0.13, p<0.001	0.13, p<0.001	0.16, p<0.001	0.17, p<0.001
Log (Molar N:OP ratio mineral soil)	0.15, p<0.001	0.16, p<0.001	0.17, p<0.001	0.17, p<0.001	0.16, p<0.001	0.18, p<0.001
Log (P concentration mineral soil) (mg kg^{-1})	0.03, p<0.01	0.03, p<0.01	0.20, p<0.01	0.20, p<0.01	0.19, p<0.01	0.20, p<0.01
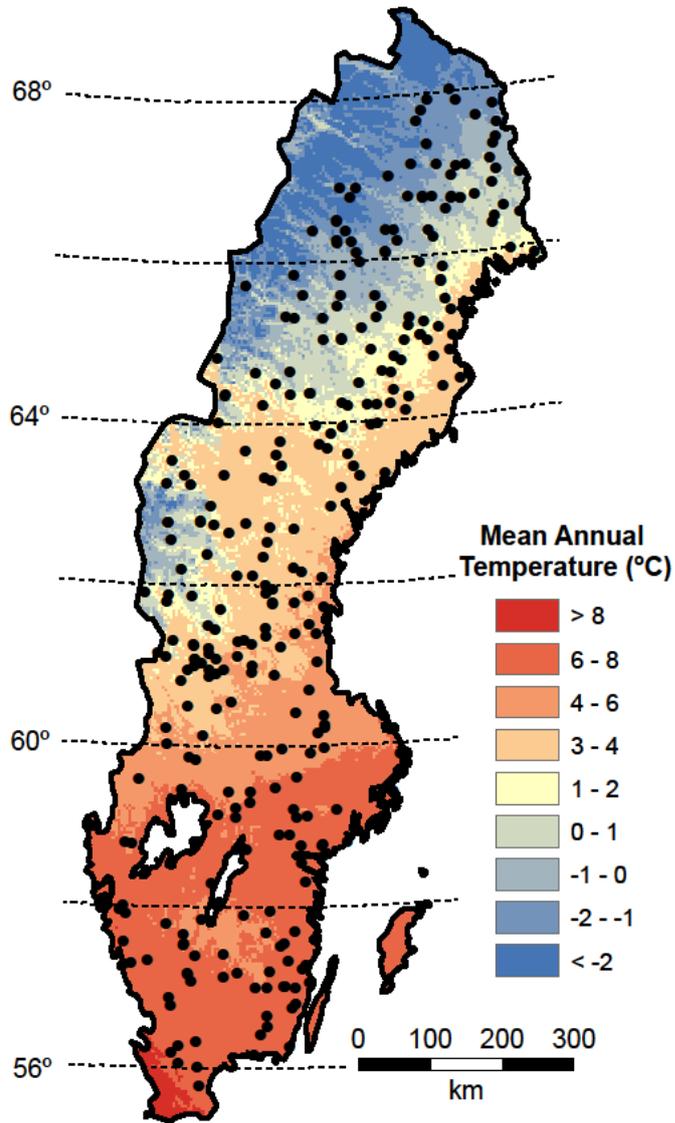
Figures

**Figure 1:** Map depicting mean annual temperature (MATP), latitude, and the plot locations (black dots).
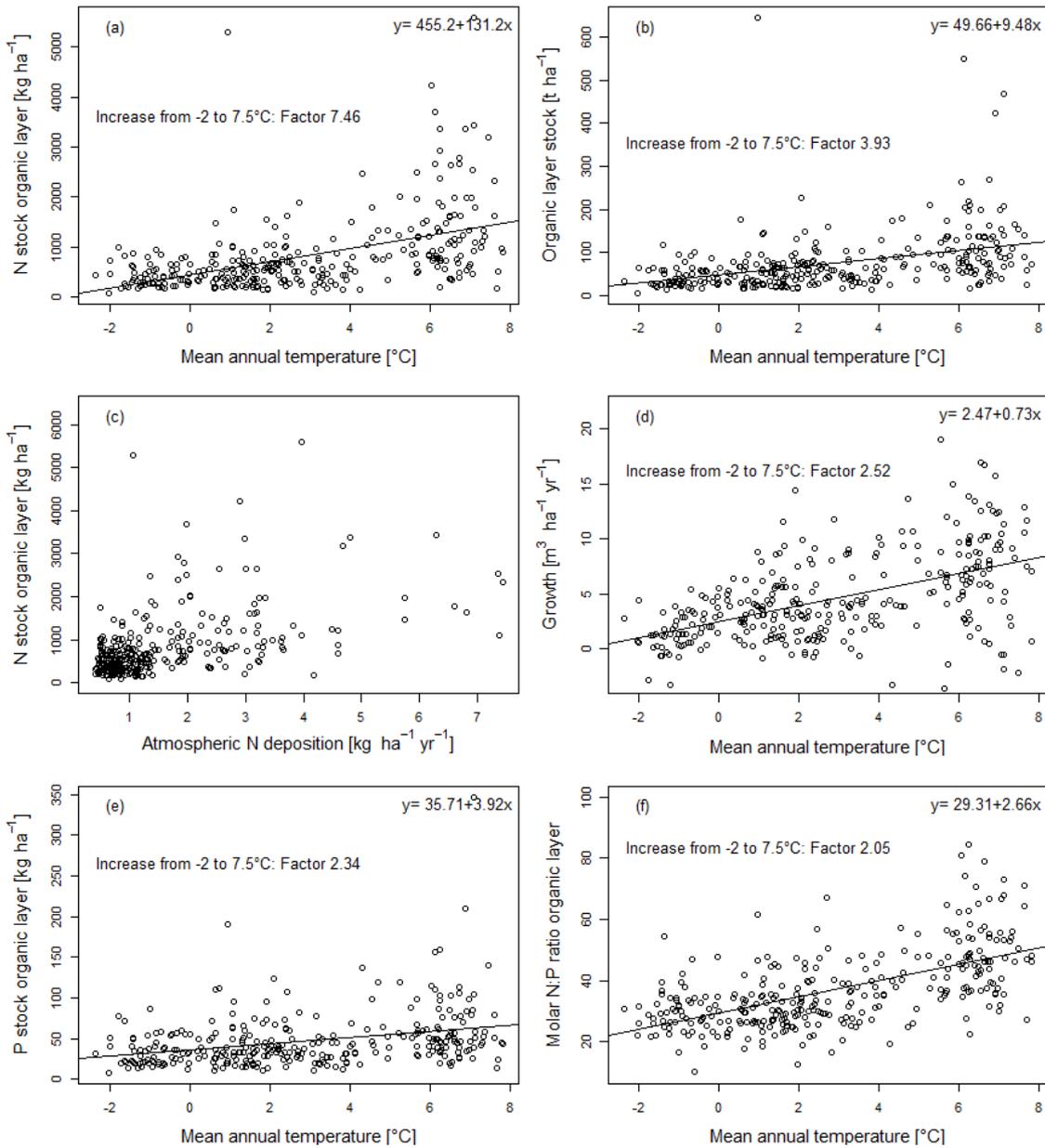
Figure 2: The nitrogen (N) stock of the organic layer (a) and the organic layer stock (b) as a function of mean annual temperature together with the N stock of the organic layer as a function of N deposition (c) as well as tree stem growth (d), the P stock of the organic layer (e), and the molar nitrogen-to-phosphorus (N:P) ratio of the organic layer (f) as a function of mean annual temperature in 309 Swedish forest soils with a stand age >60 years.
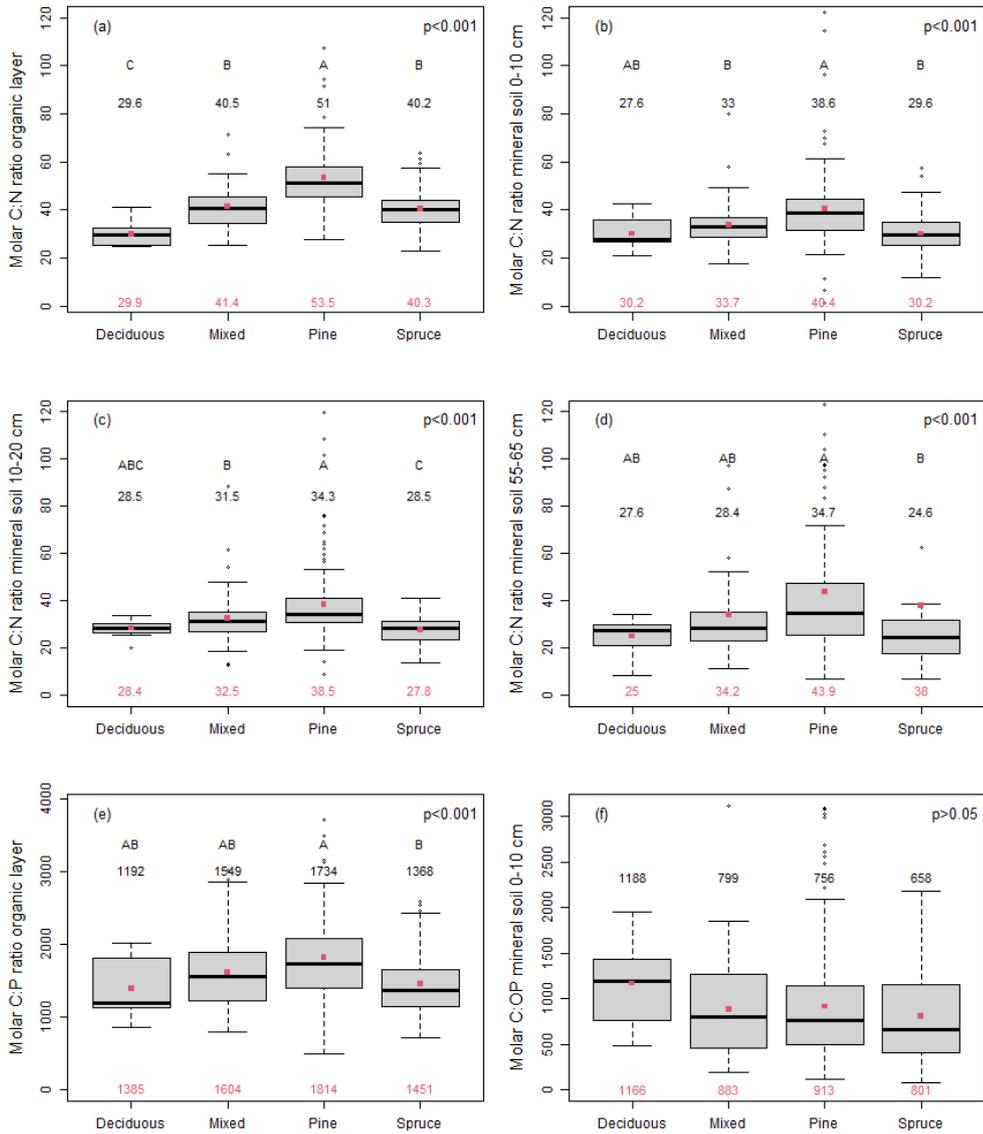
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Figure 3: Molar carbon-to-nitrogen (C:N) ratio of the organic layer (a) and the mineral soil in 0-10 cm depth (b), 10-20 cm depth (c), and 55-65 cm depth (d) as well as the molar carbon-to-phosphorus (C:P) ratio of the organic layer (e) and the molar carbon-to-organic phosphorus (C:OP) ratio in the mineral soil in 0-10 cm (f) depending on the dominant tree species (deciduous n= 10, mixed n=67, pine n=144, and spruce n=88). Please notice that mixed refers to mixed pine and spruce. Black numbers

670 give the median, red dots and red numbers depict the arithmetic mean. Different capital letters indicate statistically significant differences (p<0.05) between plots with different dominant tree species, while the p values of the ANOVA is indicated in the right corner.

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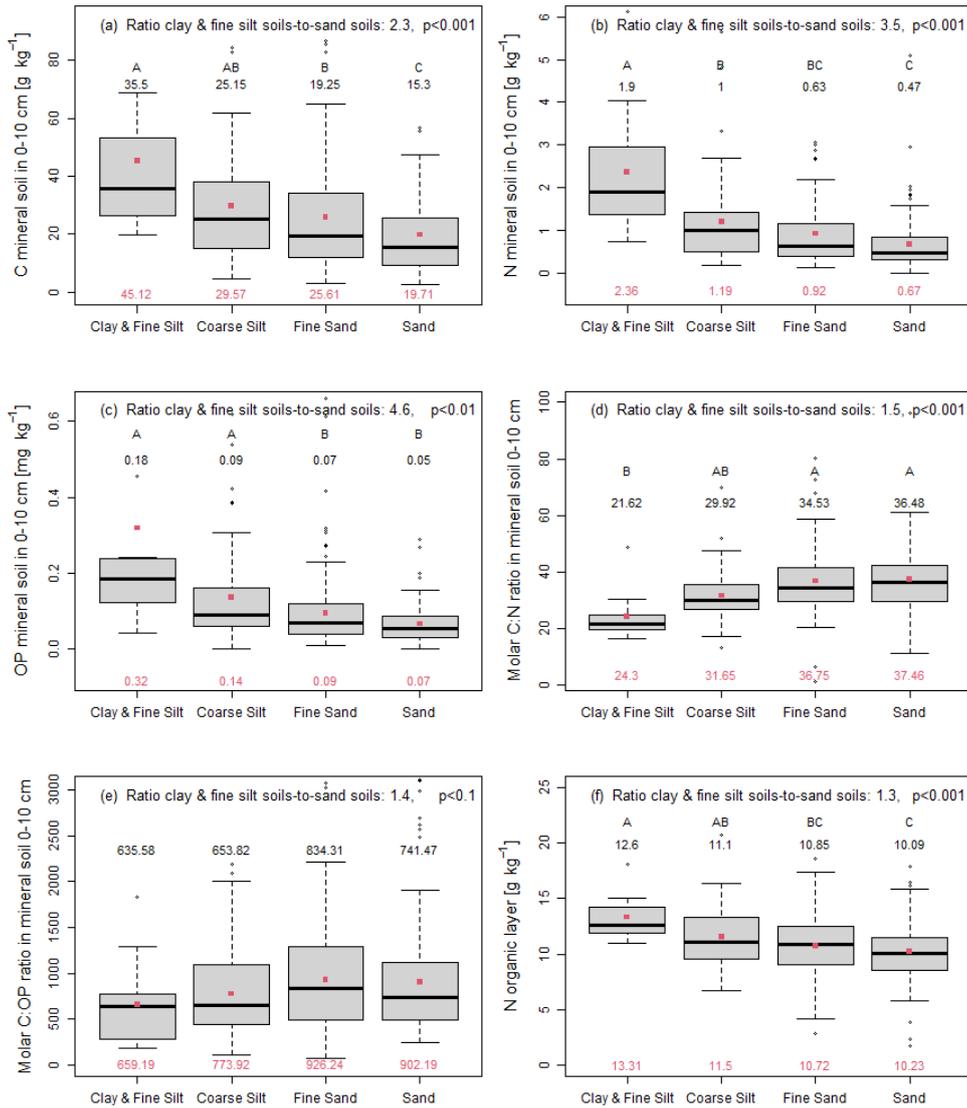
Figure 4: Carbon (a), nitrogen (b) and organic phosphorus (c) concentration, the molar carbon-to-nitrogen (C:N) ratio (d) and molar carbon-to-organic phosphorus (C:OP) ratio (e) in the mineral soil in a depth of 0-10 cm as well as the nitrogen (N) ~~stock~~ concentration of the organic layer (f) depending on the soil texture (clay and fine silt n=11, coarse silt n=52, fine sand n=136, and sand n=110) in 309 Swedish forest soils with a stand age >60 years. The texture class called sand here encompasses sand and coarse sand. Black numbers give the median, red dots and red numbers depict the arithmetic mean. Different capital letters indicate statistically significant differences (p<0.05) between the soils of different texture classes, while the p values of the ANOVA is indicated in the right corner.
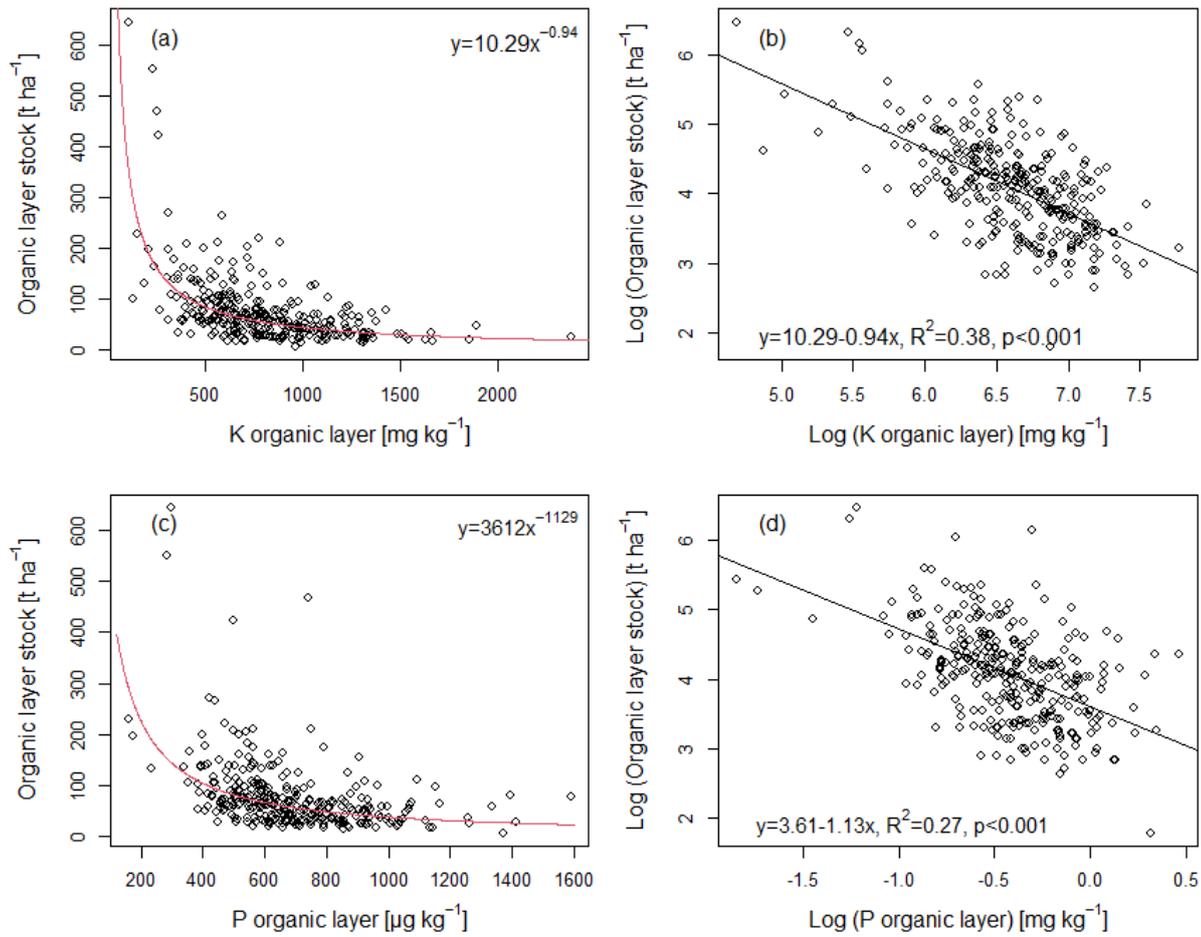
Figure 5: The organic layer stock as a function of the organic layer K concentration shown for the original data with a power function (a) and the log-transformed data with a linear model (b) as well as the organic layer stock as a function of the organic layer P concentration shown for the original data with a power function (c) and the log-transformed data with a linear model (d).