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Linking moss cover, soil organic matter fractions, and carbon stabilization pathways in temperate forest ecosystems

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Abstract. Moss cover is increasingly recognized as a biotic driver of soil organic carbon (SOC) dynamics in forest ecosystems, yet its influence on C stabilization across functionally distinct soil organic matter (SOM) fractions remains poorly quantified. How moss cover interacts with forest type and parent material to regulate C partitioning into mineral-associated organic matter (MAOM), the most persistent SOC fraction, is largely unknown in temperate forests. To address this gap, we investigated SOC distribution among free particulate organic matter (fPOM), occluded POM (oPOM), and MAOM across moss-covered and no moss soils in two contrasting temperate forest types differing in parent material. A total of 42 topsoil samples (0–2 cm) were collected from a coniferous mixed forest on sandstone and loess parent materials (Baden-Württemberg) and a pine forest on sandy parent material (Brandenburg). Physical density fractionation was applied to resolve SOM fraction distribution, and total nitrogen (TN) and C:N ratios were determined alongside carbon stabilization efficiency (CSE), calculated as mineral-associated organic matter carbon (MAOM-C) / SOC × 100, as an integrative index of stabilization capacity.

Moss-covered soils showed significantly higher SOC and TN concentrations than no moss soils, with the strongest effects observed in the coniferous mixed forest on sandstone parent material and negligible in loess. MAOM-C concentrations significantly increased under moss cover in the coniferous mixed–sandstone environment where CSE nearly doubled compared to no moss soils. Biotic factors, in particular the interaction between moss cover and forest type, were the primary predictors of stable C, while parent material exerted no independent effect. These results demonstrate that moss cover is linked to distinct C stabilization pathways, favoring mineral-associated stabilization in coniferous mixed forests and accumulation of labile C fractions in pine forests, underscoring the importance of incorporating moss cover as a biotic driver in SOC models and temperate forest C accounting frameworks.

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1. Introduction

Temperate forests occupy 25 % of the global forest area and represent a disproportionately important component of the terrestrial carbon (C) cycle (Tyrrell et al., 2012). A significant fraction of this C is stored belowground. Globally, soils hold an estimated 2,157–2,293 Pg C, of which approximately 1,462–1,548 Pg is organic (Batjes, 1996), making soil the single largest actively cycling terrestrial C reservoir. Within these ecosystems, surface vegetation mediates inputs to this reservoir, and bryophytes represent a particularly influential group in this regard (Fenton et al., 2015). Mosses, as the largest division within bryophytes, importantly affect C cycling (Xiao et al., 2023; Slate et al., 2024), supporting 6.43 Pg more C in the soil layer than bare soils (Eldridge et al., 2023). Moreover, mosses significantly reduce soil organic carbon (SOC) displacement and dissolved organic carbon (DOC) in surface runoff (Gall et al., 2024), fostering ecosystem resilience and contributing to terrestrial C sinks and global climate change mitigation (Liu et al., 2024). Similarly, the decomposition rate of moss litter is slower than that of vascular plant litter, leading to higher soil organic matter (SOM) accumulation in moss-covered soils. Mosses also contribute significantly to global C and nitrogen (N) cycles; estimated annual C uptake of approximately 3.6 Pg yr^{-1} (Porada et al., 2014) and N fixation of approximately 45 Tg yr^{-1} (Elbert et al., 2009) linking vegetation to soil biogeochemistry in ways that underpin broader ecosystem function.

Although mosses have been generally confirmed to play a significant role in C cycling (Elbert et al., 2012; Porada et al., 2014), few studies have focused on the influence of moss cover in forest ecosystems, particularly across contrasting forest types such as evergreen coniferous, deciduous broad-leaved, or bamboo forest (Zhang et al., 2026). Furthermore, SOC contents often vary with tree species, yet little is known about how different tree species affect the stability of C in soils (Angst et al., 2019). Some studies confirm an effect of tree species on forest floor C dynamics (Hobbie et al., 2006; Mueller et al., 2015; Cepáková et al., 2016). However, C stability is conferred largely through occluded and mineral-associated SOM fractions, where C can persist within soil aggregates on decadal to centennial timescales (Lützow et al., 2006; Marschner et al., 2008), remains poorly characterized in moss-covered forest soils.

The capacity of forest soils to stabilize and sequester C depends on two interacting factors: the amount and quality of organic matter (OM) fractions and the rate at which OM decomposes. OM fractions span a continuum from labile, rapidly cycling pools, including microbial biomass and DOC, to highly persistent mineral-associated organic C (Lavallee et al., 2020), whose long residence times contribute significantly to the persistence of SOC stocks (Baisden et al., 2002; Bol et al., 2009; Zhou et al., 2024). These heterogeneous compounds (Trumbore, 1997; Amundson, 2001) can be classified into active (labile), intermediate, and passive (persistent) kinetic pools with turnover times ranging from days to several centuries. The relative proportions of these C fractions significantly influence mineralization rates, nutrient availability, and net C exchange between soil, vegetation, and the atmosphere (Fornara et al., 2011; Gan et al., 2020). Mosses, positioned at the soil–atmosphere interface, have the potential to influence SOM dynamics across all three pools. Therefore, effectively predicting SOC sequestration in forest ecosystems requires an understanding of their effects on SOM turnover (Kasimir et al., 2021). At the

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same time, fractionation of both labile and stable SOM pools is essential to understand the origin, composition, and dynamics of SOC fractions that provide insight into the turnover rates and long-term C storage.

Mosses have been shown to significantly influence different forms of SOC fractions, including POM (Zhang et al., 2024a). Despite this, moss cover remains understudied as a biological interface that regulates soil moisture, temperature, and OM inputs, all of which can alter C stabilization pathways (Street et al., 2013; Gall et al., 2024). While most studies quantify bulk SOC, few resolve functional SOM fractions, such as free and occluded POM and MAOM, to examine how moss cover modifies C stabilization across contrasting forest types. To address this research gap, the present study evaluates how moss cover and forest type influence the distribution and stability of SOM fractions, and their contribution to SOC stabilization pathways in temperate forests.

This study investigates the role of moss cover in regulating SOC and TN contents, as well as the distribution of C among physically separated SOM fractions across temperate forest ecosystems. We tested the following hypotheses: H1) moss-covered soils exhibit higher SOC, TN, and C:N ratios than soils without moss cover, with these effects differing between forest types; H2) moss cover and forest type change the relative proportions of SOM fractions, with moss-covered soils showing increased proportions of fPOM, oPOM, and MAOM, particularly in coniferous mixed forests; and H3) SOC stabilization is regulated by both biotic (forest type and moss cover) and abiotic (parent material) factors, primarily expressed through their influence on MAOM contribution to total SOC. By examining these relationships across multiple forest types and parent materials, this research aims to identify the mechanisms through which moss cover shapes C stabilization pathways and the key drivers of SOC persistence in temperate forest soils.

2. Materials and methods

2.1 Study sites

The study was conducted at two different forest sites (Fig. 1): in the Schönbuch Nature Park in southwest Germany, which is located north of Tübingen in Baden-Württemberg (BW), and in the vicinity of the Linde research station in the district of Havelland in Brandenburg (BB) in northeast Germany.

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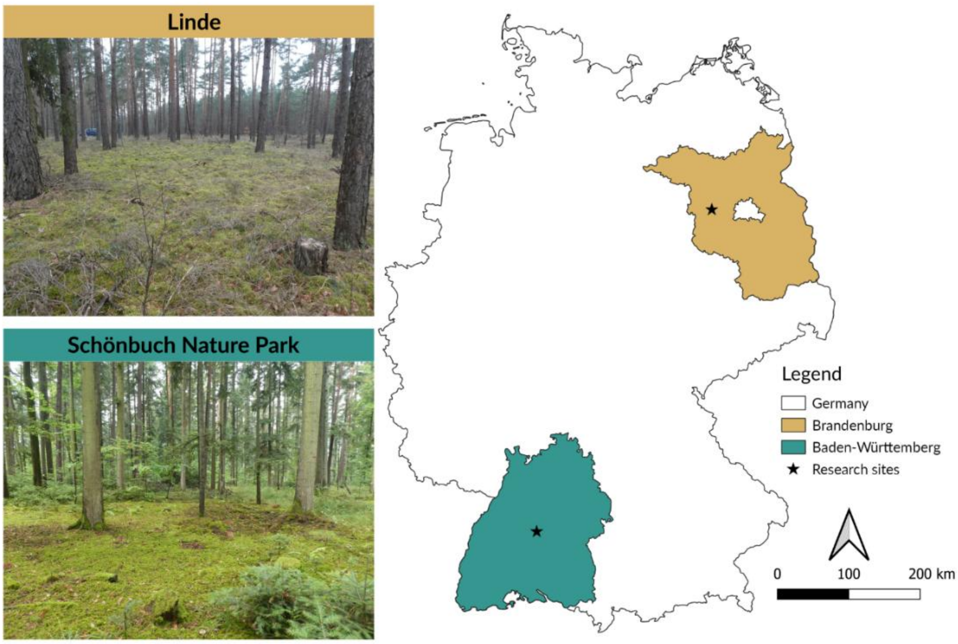

Figure 1: Overview of the research sites in Germany. Linde is in Brandenburg, while the Schönbuch Nature Park is situated in Tübingen, Baden-Württemberg. © BKG (2026) dl-de/by-2-0. Data sources: https://sgx.geodatenzentrum.de/web_public/gdz/datenquellen/datenquellen_vg_nuts.pdf, Modified by the authors (selection of two German states and colour highlighting).

These two research sites differ in terms of soil properties, moss species, forest types, and climatic conditions. The soils at the research site in BW originate either from the geological formation of Angulatensandstein (Lower Jurassic series), hereafter referred to as sandstone, which is overlain by periglacial layers containing loess, or from Lösslehm that mantles the Lower Jurassic plateaus, hereafter referred to as loess (LGRB, 2022). The soil type is a Haplic Vertisol according to the IUSS Working Group WRB (2022), which on average contains around 60 % clay in the upper 10 cm of the soil. The forest stand consists primarily of conifers, with silver fir (*Abies alba*) and Scots pine (*Pinus sylvestris*), being the dominant species, and a few individual deciduous trees, mainly common beech (*Fagus sylvatica*). The forest floor is widely covered with moss, dominated by *Thuidium tamariscinum* (Hedw.) Schimp., with *Rhytidiadelphus loreus* (Hedw.) Warnst. occurring in larger patches.

In contrast, the soil at the research site in BB is derived mainly from fluvial sediments deposited during the Weichselian glaciation, although occasional aeolian sand deposits also occur in the surrounding area (LBGR, 2024). Albic Podzols have developed in BB (IUSS Working Group WRB, 2022), and the upper 10 cm of the soil consists of more than 90 % sand. The forest is a mostly pure Scots pine stand, which is partially mixed with other tree species such as common beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*), and red oak (*Quercus rubra*). The forest floor is largely covered by mosses, as

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is typical of coniferous forests in Germany, with the two dominant species, *Pseudoscleropodium purum* (Hedw.) M. Fleisch. and *Pleurozium schreberi* (Brid.) Mitt. occurring in approximately equal proportions.

The BW and BB sites are situated at elevations of 400 – 580 m and 50 – 60 m above sea level, respectively. The Schönbuch nature park is characterized by a warm, dry, submontane climate, with a mean annual temperature of 8.7 °C and annual precipitation ranging from 740 to 860 mm, whereas the Linde site exhibits slightly higher mean temperature of approximately 9°C but lower annual precipitation (550 – 600 mm), classifying it as among the drier regions of Germany (Reyer et al., 2012; DWD, 2022).

2.2 Experimental design

A total of 42 soil samples were collected from two forest types in Germany. Twenty-eight samples were collected from coniferous mixed forests in BW across two parent materials, sandstone (Angulatensandstein) and loess (Loesslehm), while the remaining 14 samples were collected from pine forests in BB.

At each site, the uppermost mineral soil horizon (0–2 cm depth) directly beneath the organic humus layer was sampled. Two soil cover treatments were compared: soil covered by moss (Moss), and soil without moss cover, consistently covered by leaf litter instead (No moss). For each treatment, seven replicate samples were collected per site, ensuring adequate statistical power for subsequent analyses. Coarse fragments, roots, undecomposed litter and small fauna were manually removed prior to laboratory analysis.

2.3 Laboratory analysis

All soil samples were air-dried and sieved to <2 mm. Density fractionation was conducted using sodium (Na) polytungstate solution, following the procedures outlined by Golchin et al. (1994) and Sohi et al. (2001). Three SOM fractions were isolated as fPOM, oPOM and MAOM. fPOM was separated by floatation after gently shaking the sample in a solution (soil: solution ratio 1:5) with a density of 1.6 g cm^{-3} and centrifugation at 3900 revolutions per minute (rpm) for 30 minutes, followed by vacuum filtration at room temperature. The rationale for using a density threshold of 1.6 gcm^{-3} is based on the lower density of OM, which ranges between 1.0 to 1.4 g cm^{-3}. This allows for an effective separation of OM-rich particulate fractions from mineral-associated soil components. As a result, the organo-mineral complexes have intermediate densities between pure minerals and pure OM (Christensen, 1992). oPOM was separated after ultrasonic dispersion of the settled soil material at 58 J ml^{-1} in Na polytungstate solution (density 1.6 g cm^{-3}, soil) and centrifugation at 4500 rpm for 15 minutes. The remaining soil material, MAOM (density >1.6 g cm^{-3}) was rinsed thrice to remove Na salt residues. The obtained OM fractions were oven dried at 80 °C, finely milled, and analyzed for total C and N. The density solution was recycled according to the method of Six et al. (1999).

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2.4 Calculations and statistical analyses

To evaluate SOC stabilization efficiency under varying moss cover conditions across three forest–soil environments, C stabilization efficiency (CSE) was calculated as the proportion of total SOC stabilized in the MAOM fraction within the uppermost topsoil layer (0–2 cm). Mathematically, CSE is calculated as follows (Sokol et al., 2022):

$$CSE\ (\%) = \frac{MAOM - C}{SOC} \times 100$$

where MAOM- C is the carbon content of the mineral-associated organic matter fraction and SOC is the bulk soil organic carbon content.

Since MAOM is stabilized by organo-mineral linkages that provide resistance to microbial breakdown, it is the most persistent SOC fraction (Kleber et al., 2015). Therefore, in comparison to bulk SOC stocks, CSE was employed as an integrative metric of the soil's ability to stabilize and retain C in mineral-associated forms (Cotrufo et al., 2019; Lavallee et al., 2020). While the individual SOM fractions (fPOM, oPOM, and MAOM) describe the distribution of C across pools with varying levels of stability, CSE assembles this information into one parameter that allows direct comparison of stabilization efficiency across moss-covered and no moss soils within each forest-soil environment.

Statistical analyses were conducted in R 4.4.2 (R Core Team, 2024). The effects of moss cover (moss-covered vs. no moss) and forest type (coniferous mixed vs. pine forest) on soil properties were evaluated using two-way analysis of variance (ANOVA) with Type III sums of squares to account for unbalanced sample sizes (n = 7 and n = 14). Response variables included total SOC, TN, C:N ratio, POM fraction proportions (fPOM, oPOM, and MAOM), and fraction-specific C concentrations. Model assumptions of normality and homogeneity of variance were assessed using the Shapiro–Wilk and Levene's tests, respectively. Significant effects were further examined using estimated marginal means (EMMs) with Tukey-adjusted pairwise comparisons ($p < 0.05$).

Pearson correlation analysis was used to assess relationships among soil variables. To identify the factors controlling mineral-associated organic matter carbon (MAOM-C), multiple linear regression models were fitted with MAOM-C (g kg^{-1}) as the response variable and soil cover (moss-covered vs. no moss), forest type (coniferous mixed forest vs. pine forest), parent material (sandstone, loess, and sand), and the interaction between soil cover and forest type (moss × forest type) as predictor variables. No moss, coniferous mixed forest, and sandstone were used as the reference categories. Because parent materials were nested within forest types (sandstone and loess in coniferous mixed forest; sand in pine forest), a composite forest-soil factor (forest type × parent material) was used where appropriate to avoid coefficient aliasing and improve model stability. Model performance was evaluated using adjusted R^2, and regression coefficients (β) with 95 % confidence intervals were used to estimate the magnitude and direction of predictor effects. Statistical significance was assessed at $p < 0.05$.

Data preparation was performed using *dplyr* and *tidyr* packages (Wickham et al., 2023; Wickham et al., 2024), statistical analyses were conducted using *car* (Fox and Weisberg, 2011) and *emmeans* (Lenth and Piaskowski, 2025), and figures were produced using *ggplot2* (Wickham, 2016) and *ggpubr* (Kassambara, 2025).

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3. Results

3.1 Effects of moss cover and forest type on soil organic carbon, total nitrogen and C:N ratio

The influence of moss cover on SOC varied between forest types, resulting in contrasting numerical patterns between the coniferous mixed forest in Tübingen and the pine forest in Linde in the top 0 to 2 cm soil layer (Fig. 2; Table S1 in the Supplement).

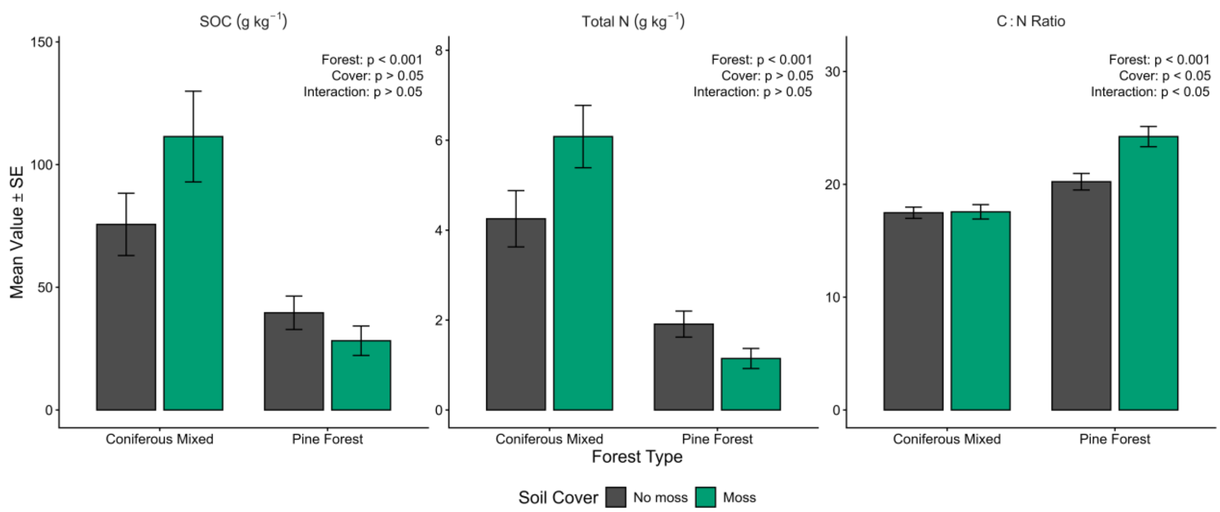

Figure 2: Soil organic carbon (SOC; g kg^{-1}), total nitrogen (TN; g kg^{-1}), and C:N ratio in the 0–2 cm soil layer under moss-covered and no moss soils in coniferous mixed forest (Tübingen) and pine forest (Linde). Bars represent means ± standard error (SE). Results of two-way ANOVA testing the effects of forest type, moss cover, and their interaction are shown within each panel. Forest type significantly affected SOC, TN, and C:N ratio ($p < 0.001$), whereas moss cover and the interaction between forest type and moss cover significantly influenced only the C:N ratio.

Moss-covered soils in coniferous mixed forest contained higher SOC concentrations (111.43 ± 69.19 g kg^{-1}) than no moss soils (75.64 ± 47.51 g kg^{-1}), a pattern which was also shown in SOC stocks (Fig. S3 in the Supplement). A similar trend was observed for TN, which increased from 4.25 ± 2.34 g kg^{-1} in no moss soils to 6.08 ± 2.60 g kg^{-1} in moss-covered soils. The two-way ANOVA showed a strong main effect of forest type on both SOC ($F = 13.26$, $p < 0.001$) and TN ($F = 28.57$, $p < 0.001$), indicating consistently higher concentrations in coniferous mixed forest in contrast to pine forest. In the pine forest, however, lower SOC was measured in moss-covered soils (28.22 ± 15.90 g kg^{-1}) relative to no moss soils (39.61 ± 18.01 g kg^{-1}). Similarly, TN decreased under moss cover (1.15 ± 0.59 g kg^{-1}) compared to the no moss condition (1.91 ± 0.77 g kg^{-1}).
The C:N ratio was influenced by both moss cover and forest type, with a significant interaction between the two factors (moss cover: $p = 0.043$; forest type: $p < 0.001$; interaction: $p = 0.008$). In the coniferous mixed forest, C:N ratios did not differ between moss-covered (17.56 ± 2.39) and no moss soils (17.48 ± 1.87; $p = 0.922$). In the pine forest, however, moss cover resulted in a significantly higher C:N ratio (24.23 ± 1.07) compared to no moss soils (20.23 ± 1.00, $p = 0.001$).

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3.2 Distribution of SOM fractions across moss cover and forest types

The distribution of soil POM fractions differed between forest types and moss cover conditions (Fig. 3; Table 1), highlighting the influence of moss–soil interactions (Table 2). However, the fPOM proportion, in coniferous mixed forests, was quite similar between no moss (9.99 ± 18.09 %) and moss-covered soils (8.80 ± 12.77 %). Likewise, in the pine forest, the fPOM proportions showed very little difference between no moss (15.68 ± 11.85 %) and moss-covered (15.58 ± 12.32 %) soils. No significant effects of forest type, moss cover, or their interaction were observed for fPOM (all $p > 0.20$), indicating that fPOM was unaffected by either factor.

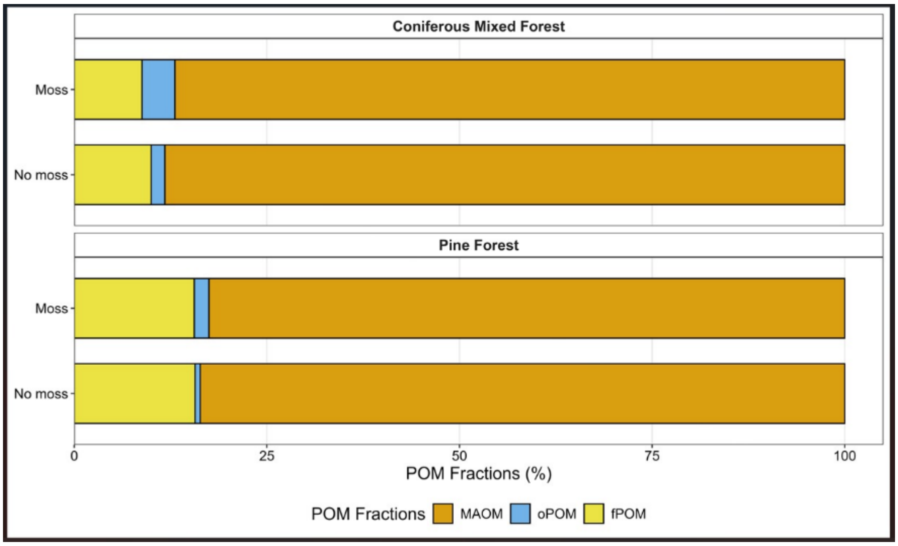

Figure 3: Fractional proportions of free particulate organic matter (fPOM), occluded particulate organic matter (oPOM) and mineral-associated organic matter (MAOM) in moss-covered and no moss soils across two forest types. Values represent the mean percentage contribution of each SOM fraction to total soil organic carbon (SOC).

Table 1: Mean fractional proportions (%) of free particulate organic matter (fPOM), occluded particulate organic matter (oPOM), and mineral-associated organic matter (MAOM) in moss-covered and no moss soils under coniferous mixed and pine forest. Values are presented as mean ± SD.

Forest Type	Cover Type	fPOM (%)	oPOM (%)	MAOM (%)
Coniferous mixed forest	No moss	9.99 ± 18.09	1.78 ± 0.94	88.23 ± 17.95
Coniferous mixed forest	Moss	8.80 ± 12.77	4.27 ± 4.72	86.93 ± 17.40
Pine forest	No moss	15.68 ± 11.85	0.67 ± 0.29	83.65 ± 12.13
Pine forest	Moss	15.58 ± 12.32	1.90 ± 1.18	82.52 ± 13.22

The proportion of oPOM increased from 1.78 ± 0.94 % in no moss soils to 4.27 ± 4.72 % in moss-covered soils in coniferous mixed forests and from 0.67 ± 0.29 % in no moss to 1.90 ± 1.18 % in moss-covered soils in pine forests. Hence, oPOM

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showed a significant effect of moss cover ($p = 0.024$) with higher oPOM under moss-covered soils. However, in the pine forests, oPOM did not differ much between cover types ($p = 0.426$).

MAOM was the dominant fraction and showed comparable values between no moss (88.23 ± 17.95 %) and moss-covered (86.93 ± 17.40 %) top soils in coniferous mixed forests. Similarly, in pine forests, MAOM remained relatively stable across cover types which measured 83.65 ± 12.13 % in no moss and 82.52 ± 13.22 % in moss-covered soils. The moss cover, forest types or their interaction did not influence MAOM fractions (all $p > 0.39$). MAOM remained the dominant SOM fraction across all treatments, representing more than 82 % of total SOM regardless of soil cover or forest type.

3.3 Drivers and pathways of SOC stabilization

3.3.1 Contribution of POM fractions to SOC

SOC within soil physical fractions was primarily driven by the interaction between forest-soil environment group and soil cover ($p < 0.01$ for all fractions) than moss cover as an independent main effect. The complete ANOVA results for C concentrations in the SOM fractions are summarized in Table S1 in the Supplement. In fPOM and oPOM fractions, environmental conditions significantly influenced SOC levels ($p < 0.001$ and $p = 0.014$, respectively), with the highest concentrations observed in the loess coniferous mixed and sandy pine forest systems. The impact of moss was site-specific; while moss cover significantly increased SOC in the fPOM and oPOM pools within the sandstone and sand environments, it had a negligible effect in the loess system (Fig. 4; Table 2). The corresponding C concentrations in the specific SOM fractions are presented in Fig. S1 in the Supplement).

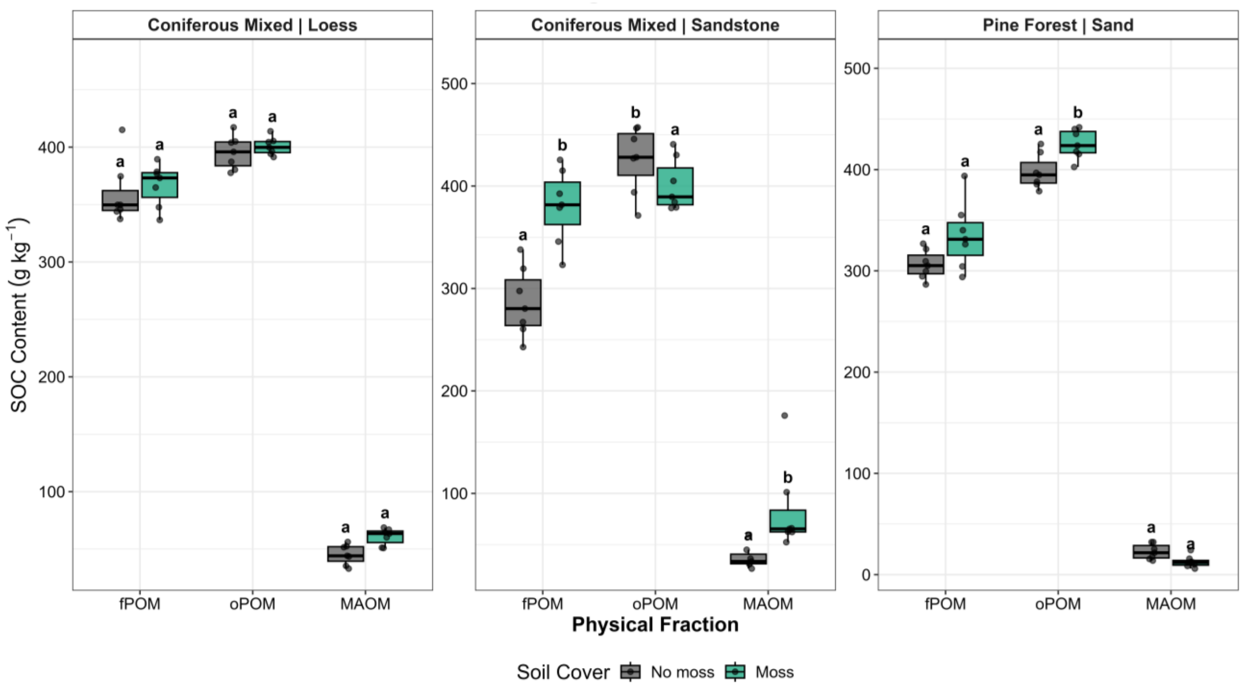

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Figure 4: Contribution of organic matter fractions to soil organic carbon (SOC) content (g kg^{-1}) across three forest-soil environments. Effects of soil cover (moss-covered vs. no moss) are shown for fPOM, oPOM and MAOM fractions. Boxes represent the interquartile range (IQR), horizontal lines indicate the median, whiskers extend to 1.5 × IQR; points represent each individual observation. Different letters indicate significant differences between soil cover types within each forest-soil environment and SOM fraction ($p < 0.05$).

Table 2: Results of two-way ANOVA evaluating the effects of forest-soil environment, moss cover, and their interaction on the relative proportions of free particulate organic matter (fPOM), occluded particulate organic matter (oPOM), and mineral-associated organic matter (MAOM).

Fractions	Source of variation	*df*	*F* value	*p* value
fPOM	Forest-soil environment	2	12.348	**< 0.001**
	Moss cover	1	0.230	0.634
	Forest-soil environment × Moss cover	2	8.812	< 0.001
oPOM	Forest-soil environment	2	4.808	**0.014**
	Moss cover	1	0.251	0.619
	Forest-soil environment × Moss cover	2	5.758	**0.007**
MAOM	Forest-soil environment	2	2.476	0.098
	Moss cover	1	2.301	0.138
	Forest-soil environment × Moss cover	2	7.337	**0.002**

Bold values indicate statistically significant effects ($p < 0.05$).

In contrast, the MAOM fraction representing a more stabilized C pool, showed no significant response to the main effects of environment (p = 0.098) or cover (p = 0.138). However, a highly significant interaction effect (F = 7.34, p = 0.002) was observed in coniferous mixed–sandstone environment. In this context, the presence of moss led to a marked increase in MAOM-associated SOC compared to the no moss control. MAOM-associated SOC increased significantly under moss cover only in the coniferous mixed–sandstone environment. The distributions of N concentrations in the fPOM, oPOM and MAOM fractions are provided in Fig. S2 in the Supplement.

3.3.2 Relationship between labile and stable carbon

The relationship between labile C (fPOM + oPOM) and stable C (MAOM) was significantly influenced by both the forest-soil environment and moss cover. The regression analysis showed moss cover as the primary driver of C stabilization efficiency, particularly in the coniferous mixed–sandstone environment with a strong positive linear relationship (Slope = 0.679, R^2 = 0.677, p = 0.014) (Fig. 5; Table 3). Under moss cover, the sandstone environment showed a positive relationship between labile and stable C pools.

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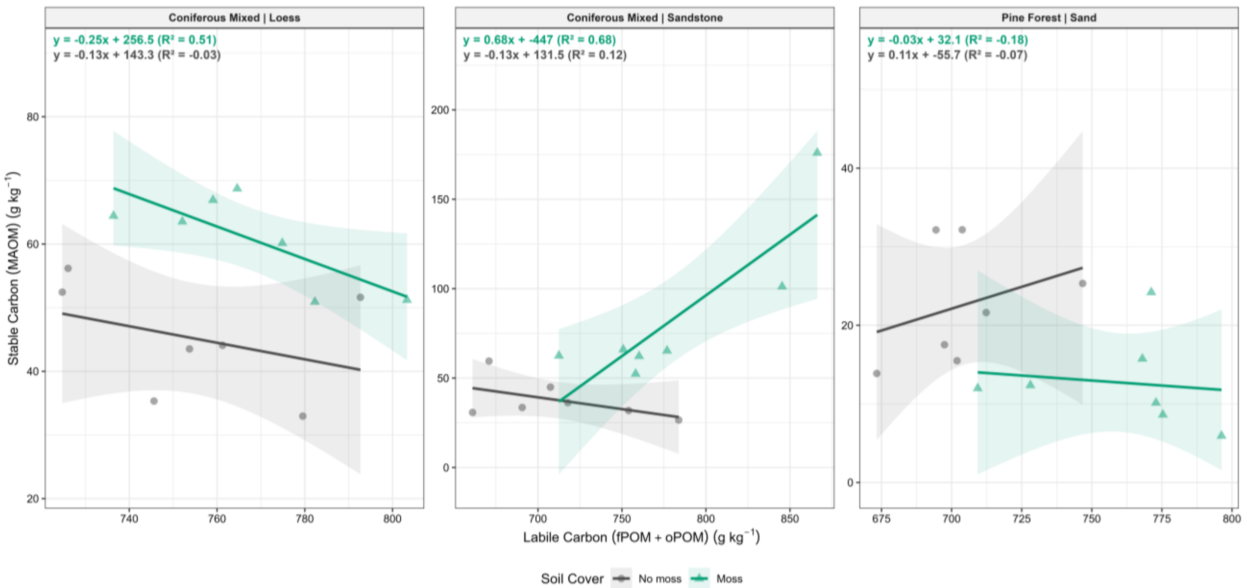

Figure 5: Relationships between labile carbon (fPOM + oPOM; g kg^{-1}) and stable carbon (MAOM; g kg^{-1}) in moss-covered and no moss soils across three forest-soil environments. Lines represent linear regression for each soil cover type and shaded areas indicate 95 % confidence intervals. Regression equations and coefficients of determination (R^2) are shown for moss (green) and no moss (grey) treatments separately.

Table 3: Regression parameters describing the relationship between labile carbon (fPOM + oPOM; g kg^{-1}) and stable carbon (MAOM; g kg^{-1}) under moss and no moss conditions across forest-soil environments.

Forest-soil environment	Cover type	Slope	SE	p value	Adjusted R^2
Coniferous Mixed–Loess	No moss	-0.13	0.143	0.405	-0.03
Coniferous Mixed–Loess	Moss	-0.255	0.094	**0.043**	0.512
Coniferous Mixed–Sandstone	No moss	-0.132	0.097	0.232	0.124
Coniferous Mixed–Sandstone	Moss	0.679	0.185	**0.014**	0.677
Pine Forest–Sand	No moss	0.111	0.143	0.474	-0.071
Pine Forest–Sand	Moss	-0.026	0.087	0.78	-0.18

Bold values indicate statistically significant relationships ($p < 0.05$).

In contrast, the coniferous mixed–loess environment depicted a significant negative correlation under moss cover (Slope = -0.255, $R^2 = 0.512$, $p = 0.043$) which suggests a different C cycling dynamic where higher labile C levels do not correspond to increased stable pool sequestration in silt-rich soils. Likewise, the pine forest–sand environment showed no significant relationship between labile and stable C pools despite the cover types ($p > 0.05$). This shows the lower inherent stabilization efficiencies of sand-based systems. These regression analyses provide a mechanistic explanation for the ANOVA results, indicating that the significant interaction between forest-soil environment and soil cover ($p = 0.002$ for MAOM) reflects site-specific C stabilization pathways that are influenced by moss cover.

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3.3.3 Carbon stabilization efficiency (CSE) across forest type, parent material and moss cover

CSE was significantly influenced by the interaction between forest-soil environment and surface cover ($F = 9.23$, $p < 0.001$), which indicates the impact of moss cover on C stabilization as highly site-specific (Fig. 6; Table 4). Generally, moss cover enhanced the percentage of CSE across study sites ($p = 0.009$), but the effect was statistically significant only in the coniferous mixed–sandstone environment ($p < 0.05$), where the CSE was nearly doubled. In contrast, there were no significant differences in CSE between cover types in the loess or sand environments ($p > 0.05$).

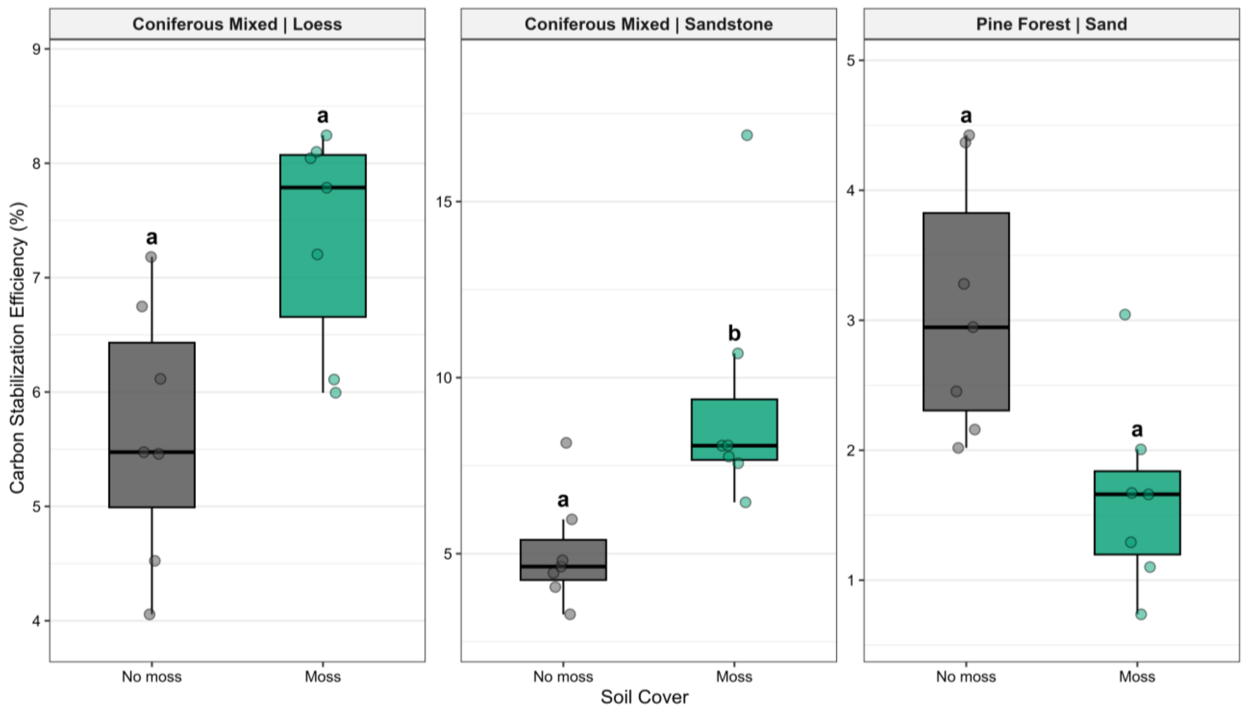

Figure 6: Carbon stabilization efficiency (CSE) (%) of soil organic carbon under moss-covered and no moss conditions across three forest-soil environments. Boxplots represent the percentage stabilization distribution for moss-covered and no moss treatments. The lowercase letters denote statistically significant differences (p < 0.05) between soil cover types within each forest-soil environment.

Table 4: Results of two-way ANOVA evaluating the effects of forest-soil environment, moss cover, and their interaction on stable carbon (MAOM-C)

Term	*df*	Sum Sq	Mean Sq	*F* value	*p* value
Forest-soil environment	2	191.152	95.576	30.355	**< 0.001**
Moss cover	1	24.298	24.298	7.717	**0.009**
Forest-soil environment × Moss cover	2	58.147	29.073	9.234	**0.001**
Residuals	36	113.352	3.149	—	—

Bold values indicate statistically significant effects ($p < 0.05$).

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3.3.4 Predictors of stable carbon (MAOM)

The model explained 54.6 % of the total variation in MAOM content (adjusted $R^2 = 0.55$), with both biotic factors as the significant predictors of stable C, whereas the abiotic factor, parent material showed no statistically significant independent effect (Fig. 7).

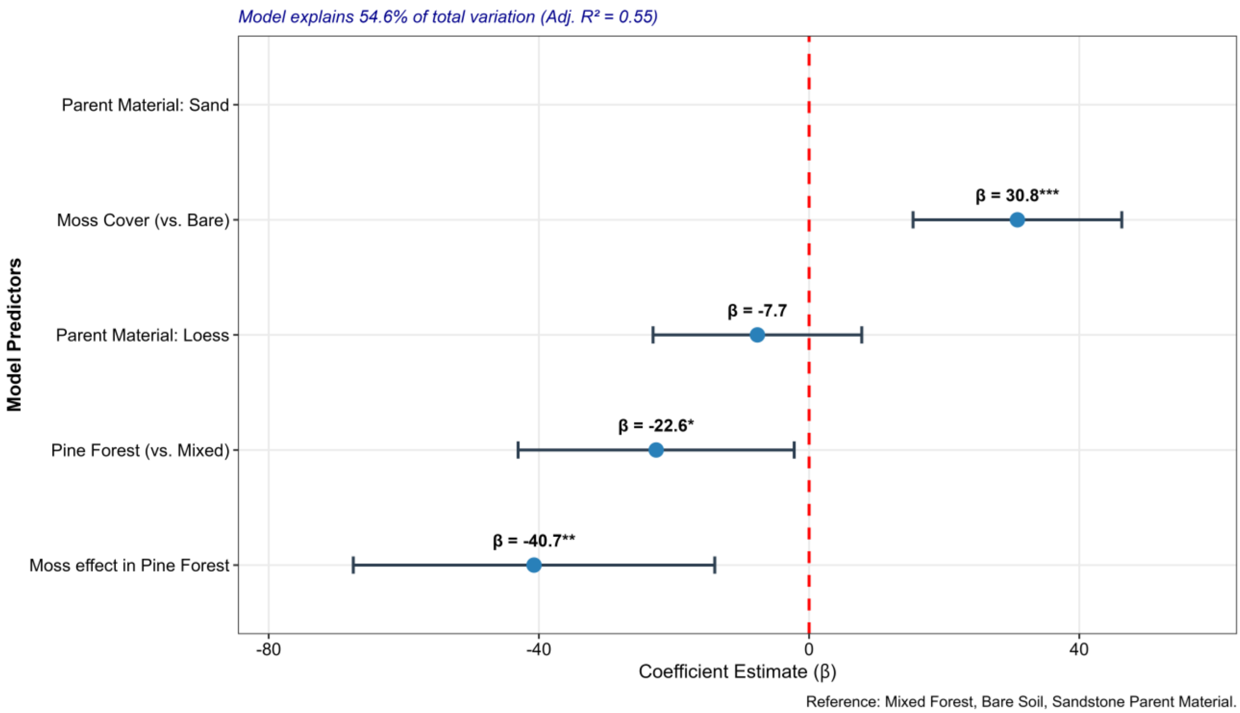

Figure 7: Coefficient estimates (β) from a multiple linear regression model predicting mineral-associated organic matter carbon (MAOM-C; g kg^{-1}). Blue points represent regression coefficients, and horizontal bars indicate 95 % confidence intervals. The red dashed line indicates zero (no effect). The reference category is coniferous mixed forest, no moss (bare soil) conditions, and sandstone parent material. Positive coefficients indicate higher MAOM-C relative to the reference category, whereas negative coefficients indicate lower MAOM-C. Sand parent material occurred exclusively at the pine forest site; therefore, the model could not estimate an independent coefficient for sand parent material. The model explained 54.6 % of the total variation in MAOM content (adjusted $R^2 = 0.55$). Significance levels are denoted as: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Moss cover was the strongest positive predictor of MAOM content ($\beta = 30.84$, $p < 0.001$) which indicated significantly higher MAOM concentrations in moss-covered soils than in no moss soil. Pine forest was associated with significantly lower MAOM content ($\beta = -22.64$, $p < 0.05$) relative to coniferous mixed forest. The interaction between moss cover and pine forest was the strongest and significantly negative predictor ($\beta = -40.72$, $p < 0.01$), indicating the reduced positive effect of moss on MAOM accumulation in pine forests. This interaction highlights that the stabilizing effect of moss on SOC depends on forest type.

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In contrast, parent material had no significant independent effect on MAOM content. The coefficient for loess derived parent material was negative but not statistically significant (β = -7.7, $p > 0.05$), with confidence intervals overlapping zero. Sand parent material occurred exclusively in pine forests; therefore, its independent effect could not be estimated because it was confounded with forest type. These results, under the conditions of this study, suggest that parent material alone did not independently influence stable C formation to a statistically detectable degree.

4. Discussion

4.1 Effects of moss cover and forest type on soil organic carbon, total nitrogen and C:N ratio

Our results support the findings of Zhang et al. (2024a) that moss cover influences SOC, TN, and C:N ratios differently depending on the type of forest. Moss-covered soils exhibited significantly higher SOC (47 %) and TN (43 %) compared to no moss soils in coniferous mixed forests. This aligns with evidence that mosses globally support considerably higher soil C sequestration than no moss soils (Eldridge et al., 2023; Xiao et al., 2023) and in alpine forest soils (Wei et al., 2025), promoting rapid C accumulation on surface layers depending on drainage and forest type (Trumbore and Harden, 1997). Moss cover may further support long-term C sequestration by supplying litter of resistant quality and reducing soil water depletion during dry periods, thereby limiting heterotrophic decomposition (Turetsky et al., 2012; Kasimir et al., 2021). The observed SOC increase under moss cover in coniferous mixed forests likely reflects the ability of mosses to modify microbial activity and alter soil C and N cycling (Slate et al., 2019). Gall et al. (2024) demonstrated that moss cover reduces SOC and TN losses by soil erosion and decreases DOC export in both field and ex-situ experiments, which is consistent with the increased SOC and TN contents under moss-covered soils. In addition, the contribution of resistant moss litter in nutrient-poor soils may further support long-term C retention by promoting C storage over decomposition. The 43 % increase in TN under moss cover in coniferous mixed forests contrasts with the findings from subarctic birch forests (Koranda and Michelsen, 2021), where mosses reduced soil N availability and retarded N cycling. Nevertheless, even where mosses suppress N availability, their net influence on microbial decomposition has been linked to increased SOC stabilization (Koranda and Michelsen, 2021).

In contrast, moss-covered soils in pine forests showed a decline in SOC (29 %) and TN (40 %). Forest types differently influence SOC stability, with mixed forests enhancing topsoil stability through higher productivity and diverse litter inputs (Zhang et al., 2024b; Zhang and Wang, 2026), while coniferous forests have been associated with higher SOC concentrations (Xu et al., 2021). The reversal observed in pine forests is probably a result of the interplay between organic acids derived from moss and the acidic, nutrient-poor pine forest soils, which is further exacerbated by variations in the makeup of microbial communities and mycorrhizal relationships among forest types.

In coniferous mixed forests, C:N ratios were comparable between moss and no moss soils; however, in pine forests, they were significantly higher under moss cover. According to research, mosses lower SOC enrichment ratios more than vascular plants, which may stabilize SOC, especially in disturbed forests (Gall et al., 2024). This predicts slower decomposition and increased N limitation in pine forests under moss cover.

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4.2 Distribution of SOM fractions across moss cover and forest types

The results showed a predominance of MAOM over fPOM and oPOM, consistent with Salonen et al. (2023), who reported that more than 83 % of SOC occurred in the MAOM fraction. Stabilization dominated SOM fraction distribution more strongly than moss cover or forest type. MAOM accounted for more than 82 % of SOM in both coniferous mixed and pine forests, indicating that long-term C storage was primarily achieved through organo-mineral associations rather than POM accumulation (Six et al., 2002; Cotrufo et al., 2019).

Moss cover did not significantly influence fPOM proportions, contrary to the hypothesis. Similar fPOM values between moss-covered and no moss soils indicate that moss-derived inputs were rapidly decomposed or transformed instead of accumulating as free particulate material. fPOM is extremely vulnerable to microbial breakdown and environmental factors since it is a labile and transient SOM pool (Six et al., 2002).

In contrast, oPOM-C was significantly higher under moss cover, particularly in coniferous mixed forests, indicating enhanced physical protection of OM through aggregate occlusion. Moss-mediated regulation of soil moisture and temperature fluctuations likely promotes aggregate formation and stabilization (Lavee et al., 1996; Gornall et al., 2007), while the coniferous mixed forest may respond more strongly than pine forests due to greater litter diversity and structural heterogeneity. MAOM was constant across forest types and cover conditions despite the increase in oPOM. This indicated the control of microbial processing and mineral interactions on mineral-associated C pools other than transient vegetation changes. Current SOM stabilization frameworks emphasize that persistent SOM is formed mainly through the binding of microbial-derived compounds to mineral surfaces (Cotrufo et al., 2013; Liang et al., 2017).

The absence of a pronounced forest-type effect on MAOM proportions suggests that soil mineralogical and pedogenic characteristics exerted a stronger influence on MAOM stability and SOC distribution across forest soils, independent of tree species composition (Kaiser et al., 2012; Gruba et al., 2015).

Overall, the results partially support the second hypothesis, confirming that moss-mediated effects on SOM fraction distribution are forest-type dependent, yet indicate that moss cover induces shifts in C partitioning across fractions without changing the predominance of mineral-associated stabilization in these temperate forest soils.

4.3 Drivers and pathways of SOC stabilization

The findings partially supported our third hypothesis that SOC stabilization is co-regulated by biotic variables (moss cover and forest type) and abiotic factors (parent material), mainly through their impact on MAOM. The significant interaction between forest-soil environment and surface cover across SOM fractions indicates that SOC stabilization pathways are not uniform. Instead, it depended strongly on where and under what conditions moss occurred, reinforcing the idea that stable C formation is shaped by the combined influence of organic inputs, microbial activity, mineral surfaces, and soil structure rather than any single factor (Cotrufo et al., 2013; Park et al., 2018; Rocci et al., 2024).

In the coniferous mixed–sandstone environment, moss cover significantly increased MAOM-associated SOC and reinforced the positive relationship between labile and stable C pools, and almost doubled CSE, providing the strongest evidence for bryophyte-mediated stabilization. These results suggest that mosses facilitate the movement of POM into persistent mineral-associated pools under sandstone environments. Moss cover likely facilitates this process by moderating soil temperature and moisture (Park et al., 2018), minimizing DOC losses (Gall et al., 2024) and providing slowly decaying organic inputs (Kasimir et al., 2021). The positive correlation between labile C and MAOM further suggests efficient microbial processing and mineral stabilization of newly introduced organic inputs, aligning with the microbial efficiency-matrix stabilization (MEMS) framework proposed by Cotrufo et al. (2013). Similar bryophyte-driven improvement of long-term SOC accumulation has been reported in boreal surface mosses (Rapalee et al., 1998) and temperate coniferous forests (Turetsky et al., 2012).

In contrast, the negative relationship between labile and stable C in the loess coniferous mixed environment indicates that increasing particulate C deposition did not result in larger MAOM formation. Loess soils, which include higher silt and clay, may already approach mineral C saturation limits, limiting further organo-mineral stabilization (Kahle et al., 2002; Bucka et al., 2019). However, Feng et al. (2014) concluded that fine-textured soils did not exhibit C saturation likely because organic inputs were insufficient to approach their mineral binding capacity. This contradiction highlights that mineral texture alone is a poor predictor of SOC stabilization potential; site-specific C input rates and existing mineral occupancy together reflect whether fine-particle soils function as active C sinks. Accordingly, moss-derived inputs in the loess system appear to accumulate preferentially in labile and physically protected fractions than in stable mineral-associated pools, which is consistent with the absence of significant moss impacts on MAOM and CSE despite higher particulate SOC fractions. This is in line with Van de Broek et al. (2026), who found that organic inputs had minimal influence on MAOM-C in fine-textured tropical soils, confirming that stabilization in silt- and clay-rich soils is restricted by existing mineral occupancy rather than input quantity.

Similarly, the pine forest–sand environment showed no significant relationship between labile and stable C pools regardless of moss abundance, reflecting the inherent mineralogical limitations of sandy soils, low reactive mineral surface area and weak aggregate stability, which limits MAOM formation and long-term SOC persistence (Amado et al., 2001; Šimanský et al., 2019). Although moss cover increased fPOM and oPOM SOC in sandy parent material, these gains were not accompanied by greater MAOM or CSE, confirming that organic input quantity alone is insufficient for long-term SOC sequestration in the absence of strong mineral protection mechanisms. This is further supported by Wang et al. (2019), who showed that greater mineral surface area does not ensure proportional OM coverage, implying that stabilization capacity in sandy systems is co-limited by both mineral reactivity and organic input availability. Unlike Van de Broek et al. (2026), who found greater organic C stabilization in tropical sandy soils due to low native SOC stocks, our sandy pine system showed no stabilization, indicating that low mineral reactivity, not SOC deficit, is the primary constraint in temperate sandy substrates.

The regression analysis further revealed that biotic controls play a dominant role in stable SOC development. Moss cover was the biggest positive predictor of MAOM accumulation, while pine forest significantly reduced MAOM compared to coniferous mixed forests. The negative moss × pine interaction suggests that the stabilizing impact of mosses is strongly influenced by forest type. In their study, Hobbie et al. (2006); Mueller et al. (2015) and Angst et al. (2019) also reported differences in litter chemistry, root-derived inputs, and microbial activity between tree species which influence microbial processing and organo-mineral interactions. Coniferous mixed forests likely provide more diverse organic inputs and belowground heterogeneity promoting MAOM formation compared to monospecific pine forest systems.

Contrary to our third hypothesis, abiotic factor (parent material) alone did not significantly predict MAOM; however, its strong interaction effects indicate that substrate properties regulate SOC stabilization indirectly by affecting moss-mediated and forest type-driven processes. The reactive minerals stabilize OM via biological, chemical, and physical processes which bind enzymes, adsorb and combine with OM, and influence soil architecture, with Fe and Al oxides especially promoting MAOM formation with N-rich residues increasing microbial carbon use efficiency (CUE) (Wu et al., 2023; Manzoni and Cotrufo, 2024). Minerals thus act consequently as both adsorbents and catalysts, making mineralogical composition a key regulator of C stabilization pathways (Kopittke et al., 2018), and for OM transformation (Kleber et al., 2021), but such effects are only visible when interacting with vegetation and moss cover.

Overall, these findings show that moss cover is a key regulator of SOC stabilization in temperate forests, by enhancing the transfer of labile OM to stable MAOM pools, but its effect depends strongly on forest type and soil conditions. Therefore, moss cover regulates C partitioning within a largely mineral-associated SOC pool rather than fundamentally changing overall SOM fractions composition. This resonates with Van de Broek et al. (2026), who similarly revealed that across contrasting tropical soils that stabilization efficiency varies significantly with soils and sites emphasizing that edaphic environment must be considered when predicting SOC stability.

5. Conclusion

This study demonstrates that moss covers are a significant biotic regulator of SOC dynamics in temperate forests, with moss-covered soils consistently exhibiting higher SOC, TN, and C:N ratios than no moss soils. Biotic factors (moss cover and forest types) were the key drivers of SOC stabilization, while the abiotic factor (parent material) had no independent effect on MAOM formation. Our hypotheses were supported as follows:

1) Moss-covered soils exhibited higher SOC and TN in the coniferous mixed forest, whereas results differed in the pine forest, demonstrating that moss effects depend strongly on forest type.

2) Moss cover and forest type jointly influenced SOM fraction distribution, with higher fPOM and oPOM in sandstone and sandy environments. However, higher MAOM was significant only in the coniferous mixed sandstone environment where moss cover presence nearly doubled CSE, confirming that moss effects on C stabilization depend strongly on soil properties and forest type.

3) SOC stabilization was primarily regulated by biotic factors (moss cover and forest types) with their interaction being the strongest predictor of stable C rather than the abiotic factor (parent material). This confirmed that bryophyte-mediated stabilization is fundamentally shaped by forest composition and edaphic characteristics.

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Based on our results, future research should use isotope tracing to establish C retention durations in moss-associated fractions and investigate the microbial pathways linking moss cover to MAOM formation, particularly CUE and necromass synthesis across forest types. With this in mind, it seems promising to include mosses in future forest disturbance management strategies to improve soil stability and C stabilization, as has already been demonstrated for SOC displacement reduction in disturbed forests and OM retention in post-fire environments (Silva et al., 2019; García-Carmona et al., 2020; Kasimir et al., 2021; Gall et al., 2024).

Data availability

The underlying research data are not publicly available because they form part of an ongoing research project but may be made available by the corresponding author upon reasonable request.

Supplement link

The supplementary material is available through Figshare at: 10.6084/m9.figshare.33052952

Author contributions

MP developed the paper concept, methodology, conducted laboratory analyses, performed data analysis and interpretation, and wrote the original draft of the manuscript. RA contributed to laboratory work, data analysis and interpretation, and manuscript editing. XY contributed to laboratory work and manuscript review. LB and NF assisted with soil sampling and preliminary sample preparation. StS contributed to manuscript review and editing. TS and CG contributed to supervision and manuscript review and editing. All authors contributed to the interpretation of the results, revised the manuscript critically, and approved the final version for publication.

Competing interests

The authors declare that they have no conflict of interest.

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