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Plant, mycorrhizal and saprotrophic fungal contributions to soil organic matter fractions differ between tree-mycorrhizal types

Veronica Vasilica [a], Claudia Guidi [b], Khatab Abdalla [a,*], Valentin B. Kurbel [a], Andreas J. Wild [a], Eva Lehndorff [c], Richard P. Phillips [d], Johanna Pausch [a]

[a] *Agroecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, 95447, Germany*
[b] *Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmersdorf, CH-8903, Switzerland*
[c] *Soil Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, 95447, Germany*
[d] *Department of Biology, Indiana University Bloomington, IN, 47405, USA*

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ABSTRACT

Determining the biotic factors most responsible for the formation and stability of soil organic matter (SOM) is critical for understanding soil carbon storage in the wake of shifts in forest composition. We investigated the relative contributions of plant and microbial residues to SOM fractions in temperate forest stands dominated by arbuscular or ectomycorrhizal trees, and exposed to simulated N deposition. Using a Bayesian mixing model informed by stable isotope data, we partitioned contributions of plants, saprotrophic fungi and mycorrhizal fungi to particulate and mineral-associated organic matter fractions under contrasting tree-mycorrhizal dominance. Additionally, we explored bacterial and fungal contributions to both fractions using amino sugar biomarkers extracted from the same soils. Overall, ectomycorrhizal-dominated stands differed from arbuscular mycorrhizal-dominated stands in their particulate and mineral-associated organic matter distributions and sources. Carbon and nitrogen isotope analysis revealed that particulate organic matter was dominated by plant residues in both ectomycorrhizal (76%) and arbuscular mycorrhizal stands (59%), with greater plant contributions occurring in topsoil (0-15 cm) relative to subsoil (15-30 cm). In contrast, mineral-associated organic matter was dominated by fungal residues, with mycorrhizal residues contributing most in ectomycorrhizal stands (58%) and saprotrophic residues in arbuscular mycorrhizal stands (55%). Amino sugar analyses showed that contributions of fungi exceeded those of bacteria by several-fold in both SOM fractions. Under nitrogen deposition, microbial contributions slightly increased in arbuscular mycorrhizal stands, suggesting enhanced SOM turnover, whereas plant inputs increased in the particulate fraction in ectomycorrhizal stands. Collectively, our results highlight the key influence of tree-mycorrhizal dominance on the distribution and composition of SOM fractions, with consequences for soil carbon storage in temperate forests.

1. Introduction

Soil organic matter (SOM) constitutes the largest terrestrial reservoir of both carbon (C) and nitrogen (N) globally (Schlesinger, 1997; Ciais et al., 2014), yet the biological factors that control its formation and persistence remain poorly resolved.

A central uncertainty is the relative contribution of plant-vs. microbially-derived inputs to distinct SOM fractions — particulate organic matter (POM) and mineral-associated organic matter (MAOM) — which differ in their chemical properties, mean residence time, and responses to environmental change (Lavallee et al., 2020). While plant litter has long been viewed as the primary precursor to POM, a growing body of work suggests that microbial residues may contribute disproportionately to the formation and stabilization of MAOM (Christensen, 2001; Von Lützow et al., 2008). However, how these contributions vary across ecosystems, and the biotic controls that regulate them, remain unclear.

Temperate forests are ideal ecosystems to investigate this gap, as most forests are comprised of tree species that associate with arbuscular mycorrhizal (AM) or ectomycorrhizal (ECM) fungi, which differ in their C allocation, nutrient uptake and effects on soil processes (Phillips et al., 2013; Frey, 2019). These differences are hypothesized to promote distinct pathways of SOM formation and turnover in stands dominated

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* Corresponding author. Universitaetsstraße 30, Bayreuth, 95447, Germany.
E-mail address: Khatab.Abdalla@uni-bayreuth.de (K. Abdalla).

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by AM vs. ECM trees (Craig et al., 2018; Ma et al., 2025; Zhang et al., 2025). Indeed, there is emerging evidence that, along a gradient of AM to ECM tree dominance, POM increases and MAOM decreases (Craig et al., 2018; Cotrufo et al., 2019; Lang et al., 2023). While these patterns suggest different pathways of SOM formation in AM vs. ECM stands, the sources of organic matter contributing to these pools remain unresolved.

Differences in SOM fractions between AM and ECM soils have been ascribed to variation in plant and microbial factors. Leaf and root litter of AM trees tends to decompose more quickly than ECM tissues (Keller and Phillips, 2019; Keller et al., 2021; Huang et al., 2022), which can increase MAOM formation. Differences in inputs also select for distinct microbial communities (Eagar et al., 2022; Singavarapu et al., 2022) which, in turn, become precursors for MAOM formation. Yet, despite extensive study of tree-mycorrhizal types, we still lack direct, quantitative evidence of how plant vs. microbial residues contribute to POM and MAOM within these stands. For instance, tree-mycorrhizal differences in POM and MAOM could arise from mycorrhizal fungi or from saprotrophic fungi and bacteria. Mycorrhizal fungi play a large role in SOM inputs and formation (Hawkins et al., 2023), and differences between AM and ECM fungi (Frey, 2019) may drive variation in POM and MAOM pools in AM- and ECM-dominated stands. Likewise, variation in saprotrophs, which can be more abundant and diverse in AM- relative to ECM-dominated stands (Eagar et al., 2023), can influence SOM fractions via differences in extracellular enzyme activities (Zheng et al., 2023) or physical enmeshment of particles (Frey, 2019).

The factors underlying AM-ECM differences in SOM may also depend on soil depth. While many studies have been carried out in upper soil horizons (Barceló et al., 2022; Seidel et al., 2024), those that have sampled deeper report stronger differences between tree-mycorrhizal types (Craig et al., 2018; Lang et al., 2023). This suggests that roots and their associated microbes (as opposed to leaf litter) may be driving differences in SOM stocks between AM and ECM temperate forests — a conclusion further supported by Keller et al. (2021), who found that roots form MAOM rapidly, particularly in AM soils. Moreover, a strong vertical stratification of fungal guilds in the soil profile was reported (Dickie et al., 2002; Rosling et al., 2003), with saprotrophic fungi dominating the recently-shed leaf litter and mycorrhizal fungi the underlying soil horizons (McGuire et al., 2013; Carteron et al., 2020; Khokon et al., 2021). However, despite evidence for depth-dependent shifts in root inputs and fungal guilds, how these factors interact to determine the sources of organic matter in AM vs. ECM stands remains unclear.

Soil organic matter turnover is further influenced by anthropogenic increases in N deposition (Galloway et al., 2003; Meng et al., 2022; Yeung et al., 2025). Globally, declines in soil microbial biomass have been reported under N enrichment (Treseder, 2008; Liu and Greaver, 2010; Guo et al., 2023; Li et al., 2024). Moreover, N deposition alters SOM dynamics and exerts distinct effects on individual SOM fractions (Zak et al., 2017; Chen et al., 2021; Feng et al., 2025). For temperate forests dominated by trees with AM or ECM associations, different responses to N deposition were reported (Midgley and Phillips, 2016). Increased N availability stimulates SOM cycling and nitrate mobilization in AM stands but leads to ammonium accumulation in ECM stands (Midgley and Phillips, 2016).

Natural abundances of stable isotopes (e.g., ^{13}C and ^{15}N), combined with mixing models, provide a powerful approach to partition sources contributing to SOM (Park et al., 2023). Unlike isotopic labeling, this method captures longer-term ecosystem dynamics, by integrating continuous inputs to SOM. Because microbial biomass is enriched in ^{13}C and ^{15}N compared to plant litter (Hobbie et al., 1999; Klink et al., 2020), isotopic signatures can be used to distinguish microbial and plant contributions to SOM fractions (Klink et al., 2022; Guidi et al., 2023). However, the application of this approach to jointly assess plant and microbial contributions to distinct SOM fractions across soil depths and mycorrhizal associations remains limited.

Despite well-established mechanistic links between mycorrhizal types and SOM turnover, the sources contributing to MAOM and POM in AM and ECM forest stands, particularly at increasing soil depth and under N addition, remain poorly resolved. Quantifying the contributions of plant residues and soil microbial residues to SOM fractions will, therefore, further advance our understanding of SOM formation and decomposition. Here, we investigated the sources (fungi from distinct guilds vs. plants) of distinct SOM fractions in a temperate broadleaf forest of the Midwestern US by combining isotope (δ^{13}C, δ^{15}N) and amino sugar analyses. We focused on forest stands dominated by AM vs. ECM trees and on two soil depths (0-15 cm, 15-30 cm), aiming to quantify the main contributors to SOM fractions across soil layers in stands with different mycorrhizal associations. In addition, we included AM and ECM stands where inorganic N fertilizer was added for 11 consecutive growing seasons to simulate anthropogenic N deposition.

We hypothesized that: (i) Sources of POM and MAOM differ between AM and ECM stands: higher saprotrophic activity and accelerated turnover in AM stands reduces the contribution of plant residues to POM and results in greater saprotrophic vs. mycorrhizal fungal contribution to MAOM compared with ECM stands. (ii) The relative contribution of plant residues decreases with soil depth in both POM and MAOM fractions, whereas mycorrhizal fungal residues increase relative to saprotrophic residues because of the depth-related stratification of fungal guilds. (iii) Inorganic N addition leads to stronger shifts in sources contributing to POM and MAOM in ECM stands with otherwise organic nutrient economies compared to AM stands.

2. Materials and methods

2.1. Study area and sample collection

The site is in a ca. 80-year-old deciduous forest in the center-south of Indiana, USA (Phillips et al., 2013). The site is part of Indiana University's Moores Creek Research and Teaching Preserve, located in a region characterized by a humid continental climate, with an elevation ranging from 165 to 230 m. The mean annual temperature of the area is 11.6 °C and the mean precipitation is approx. 1200 mm per year. The soils, developed from sandstone, siltstone, and shale parent materials, are nutrient-poor (Midgley and Phillips, 2016). According to the USDA Soil Taxonomy (Soil Survey Staff, 2022), they are classified as Typic Dystrudepts, corresponding to Dystric Leptic Cambisols (Siltic, Ochric) in the World Reference Base for Soil Resources (IUSS Working Group WRB, 2022, updated 2024). These soils are characterized by a silt-loam texture and are of shallow nature, underlain by a hard claypan and bedrock between 30 and 60 cm depth (Midgley and Phillips, 2019). The steep topography, dominated by ridges and ravines, further contributes to nutrient scarcity at the site (Midgley and Phillips, 2016).

Tree species include both AM- and ECM-associated taxa. Plots (20 × 20 m) were established to capture the end members of this gradient where AM- or ECM-associated trees constitute >85% of the basal area of each plot (Midgley and Phillips, 2016). Sugar maple (*Acer saccharum* Marshall), tulip poplar (*Liriodendron tulipifera* L.) and sassafras (*Sassafras albidum* (Nutt.) Nees) are dominant in the AM stands, whereas ECM stands contain a mixture of white oak (*Quercus alba* L.), American beech (*Fagus grandifolia* Ehrh.), red oak (*Quercus rubra* L.), pignut hickory (*Carya glabra* (Mill.) Sweet) and black oak (*Quercus velutina* Lindl.) (Phillips et al., 2013; Rosling et al., 2016). The proximity of the plots to one another minimizes topographic and climatic variability across the site. Half of the plots have been regularly fertilized with a mixture of $(NH_4)_2SO_4$ and $NaNO_3$ granular fertilizers (hereafter referred to as AM+N and ECM+N), and the other half were located on adjacent unfertilized plots (AM-N and ECM-N). Starting in May 2011, fertilizers were applied monthly from May to October, for a total of ca. 50 kg N ha^{-1} y^{-1}.

In this study, 3 replicates per tree species were selected across the established plots per mycorrhizal type and N treatment (*L. tulipifera* and *A. saccharum* on AM plots, *Q. alba* and *F. grandifolia* on ECM plots). In total, 2 mycorrhizal types x 2 N treatments x 2 tree species x 3 tree replicates = 24 focal trees represent the experimental units (coordinates of the focal trees provided in Table S1). Samples of soil, fungal sporocarps, litter and living tree roots were collected in June 2022.

Soil, fungal sporocarps and leaf litter samples were taken within a 2 m radius around each focal tree. Sporocarps of ECM and saprotrophic fungi were collected from the soil surface or from wood, identified and cleaned of debris. Soil cores (5 cm diameter) were taken from the mineral soil at 0-15 cm and at 15-30 cm depth (hereafter referred to as topsoil [t] and subsoil [s]). Soil samples were sieved (<2 mm) to remove roots and debris and air-dried. Additionally, samples of fresh tree roots were excavated tracing back each root to its trunk to ensure that roots from each tree species were collected. Roots were subsequently rinsed. All plant and fungal materials were dried at 60 °C.

2.2. *Density-based fractionation of SOM*

Air-dried soil subsamples (5 g) were fractionated by density to separate the SOM into POM and MAOM fractions. Each subsample was suspended in an inert and highly dense sodium polytungstate (SPT) ($\rho = 1.865$ g cm^{-3} at 21.5 °C) solution (SPT-0; TC-Tungsten Compounds GmbH, Grub am Forst, Germany). To disperse soil aggregates, the suspension was ultrasonicated with an ultrasonic homogenizer (ultrasonic generator Sonoplus HD 4100, ultrasonic converter UW 100 and sonotrode TS 106, Bandelin, Berlin, Germany). The homogenizer was previously calibrated on the soil samples under study to achieve an overall energy input of 450 J cm^{-3} per sample, according to Just et al. (2021).

The homogenized samples were then centrifuged at 4000 rpm (Centrifuge 5810 R, Eppendorf, Hamburg, Germany) – three times for 20 min and a fourth time for 30 min. After each centrifugation, the floating POM was aspirated with a water jet pump and separated from the remaining sedimented MAOM. Each initial 5 g soil sample resulted in two separate POM and MAOM fractions.

To remove residual SPT, the POM samples were placed on a vacuum filter system and repeatedly washed with deionized water until an electrical conductivity lower than 15 µS cm^{-1} was reached. In this step, a hydrophilic polyvinylidene difluoride (PVDF) Durapore membrane filter with a pore size of 0.22 µm was used (Merck Millipore Ltd., Carrigtwohill, Ireland). The MAOM fraction was purified by centrifugation (Rotina 380, Hettich Lab Technology, Tuttlingen Germany) with deionized water and pouring off the supernatant. The procedure was repeated until an electrical conductivity lower than 150 µS cm^{-1} was reached. Both POM and MAOM fractions were then suspended in deionized water and frozen.

A Martin-Christ RVC 2-25 rotary vacuum concentrator and a CT 02-50 solvent-resistant cooling trap (Martin Christ, Osterode am Harz, Germany) were used to remove the residual water from the samples by sublimation. Lastly, the resulting dry MAOM fractions were ground into fine powder with a roll mixer (RM-2, OCS.tec GmbH & CO, Neuching, Germany), whereas for the smaller POM samples, a Retsch MM 301 vibration mill was used (Retsch, Haan, Germany). An agate mortar and pestle were used for the smallest POM samples.

A more detailed description of the density-based SOM fractionation protocol used to separate POM and MAOM is provided by Vasilica et al. (2026).

2.3. *Stable isotope analyses*

The dried fresh roots, litter and fungal sporocarp samples were ground into fine powder with a Retsch MM 400 vibration mill (MM400 Retsch, Haan, Germany). To mill the smallest sporocarp samples, an associated microtube adapter was used in combination with 2 mL round-bottom Eppendorf microtubes (Eppendorf, Hamburg, Germany).

Isotope analyses of ^{13}C and ^{15}N were conducted for tree roots, litter, fungal sporocarps (n ~ 21 spp.), POM and MAOM. For this purpose, the Fisons EA-1108 CHNS–O Element Analyzer was used in combination with the Thermo Fischer Scientific IRMS Advantage V. The two instruments were coupled through an open split (ConFlo IV, Thermo Fisher Scientific). Vienna-Pee Dee Belemnite (R = 0.0111802) and air (R = 0.0036765) were the standards used for C and N, respectively. The reproducibility (standard deviation of repeated measurements of acetanilid) was ±0.1 ‰ for ^{13}C and ±0.3 ‰ for ^{15}N. The precision (based on the IAEA-600 standard, caffeine) was ±0.05 ‰ for ^{13}C and ±0.06 ‰ for ^{15}N.

2.4. *Amino sugar analyses*

Amino sugar analyses were conducted using subsamples of the POM and MAOM fractions. Amino sugars were correlated to microbial residues (Parsons, 1981; Hu et al., 2024) and used to calculate the contribution of bacterial- and fungal-derived C. Analysis of individual amino sugars glucosamine (GlcN) and muramic acid (MurA) was conducted using a modified version of the Appuhn (2004) method. Specifically, glucosamine is often used as an indicator of fungal residues, whereas muramic acid indicates bacterial residues (Joergensen, 2018).

In brief, a 400 mg subsample was hydrolyzed in 6 M HCl for 8 h at 105 °C. Then, 0.5 mL of the resulting supernatant was evaporated at 40 °C under an N_2 stream, washed with 0.5 mL of Milli Q water and evaporated again under the same conditions. The dry sample was then refilled with 1 mL Milli Q water, filtered through a polyamide filter (0.20 µm pore size) and frozen.

The amino sugars were analyzed on an Agilent 1200 Series High-Performance Liquid Chromatography (HPLC) system (Agilent Technologies, Santa Clara, CA, USA) equipped with an EC 125/4 Nucleosil 100-5 C18 column (Macherey-Nagel, Düren, Germany). Thermo Scientific™ Fluoraldehyde™ *o*-Phthaldialdehyde (OPA) Reagent Solution (Thermo Fisher Scientific, Waltham, MA, USA) was used as the amino sugar derivatization reagent.

The HPLC was run with a flow of 1500 mL min^{-1}, a high-pressure limit of 400.0 bar, and a maximum flow gradient of 1000 mL min^{-2}. The following three eluents were used. Eluent A was a 5% tetrahydrofuran (THF) solution. For its preparation, 15.3 g Na-citrate dihydrate and 0.328 g Na-acetate were dissolved in 800 mL Milli Q water, adjusted to a pH of 5.3 with 1 M HCl. 7 mL of methanol and 50 mL THF were then added, and the resulting solution was brought to 1000 mL with the addition of Milli Q water. Eluent B was a 50:50 (v:v) H_2O:MeOH solution. Eluent C was a 1.5% THF solution, obtained with the same method as eluent A, but with only 15 mL THF added in the last phase of the preparation.

The three eluents were mixed in the following initial ratio: 18.6% A, 7.00% B and 74.4% C. The ratio was gradually altered between minutes 25 to 28, to reach a new ratio of 0.00% A, 80.0% B and 20.0% C. The ratio was then gradually brought back to the initial one between minutes 33 to 37.

Fungal and bacterial C were calculated according to Hu et al. (2024) and normalized to the soil C content of the respective fraction (Eqs. (1) and (2)). Here, GlcN and MurA denote the measured concentrations of glucosamine and muramic acid in soil, respectively.

$$\mu\text{g fungal C g}^{-1}\text{ soil C} = ((\text{GlcN-1.16 x MurA}) \text{ x } 10.8)\ /\ \text{soil C} \qquad (\text{Eq. 1})$$

$$\mu\text{g bacterial C g}^{-1}\text{ soil C} = \text{MurA x } 31.3\ /\ \text{soil C} \qquad (\text{Eq. 2})$$

2.5. *Data analysis*

The data were plotted and analyzed using R version 4.2.2 (R Core Team, 2022). Effects of mycorrhizal type, nitrogen addition, and soil depth on isotopic composition (δ^{13}C, δ^{15}N) and C:N ratios of different material fractions (MAOM, POM, litter, and roots) were assessed using one-way analyses of variance (ANOVA). Due to limited sample sizes within factor combinations, full factorial models including interaction terms were not fitted, as such models would have been underpowered. Analyses were conducted using stratified one-way ANOVA models, in which the effect of each focal factor was tested conditionally on fixed levels of the remaining factors (e.g., mycorrhizal type tested within specific nitrogen addition treatment and soil depth). Soil depth effects were evaluated only for MAOM and POM. ANOVA models were fitted using the aov function. Model assumptions were evaluated based on ANOVA residuals using the Shapiro-Wilk test (shapiro.test) for normality and Levene's test (leveneTest in the R car package, Fox et al., 2012) for homogeneity of variances. Assumptions were considered met when test p-values exceeded 0.05. When homogeneity of variance was violated, Welch's ANOVA was applied using the oneway.test function in R. When residual normality was not met, response variables were transformed and models re-fitted; if residual normality could not be achieved, non-parametric Wilcoxon rank-sum tests were used (wilcox.test). In the supplementary data, final p-values from all models are reported after adjustment for multiple testing using the Benjamini–Hochberg false discovery rate (FDR) procedure.

A Bayesian mixing model (R package MixSIAR, version 3.1.12; Stock et al., 2018) adapted from Guidi et al. (2023) was used to assess the source contribution to the different SOM fractions. Treatment and depth were set as fixed factors. We did not include fractionation factors in the model, since hypothetical fractionation factors could increase biases. The model was informed with the $\delta^{13}C$ and $\delta^{15}N$ mean and standard deviation of SOM sources (forest-floor litter, tree roots, saprotrophic and mycorrhizal fungi), as well as their C and N content and sample size. Similarly, δ-values and C and N content of the SOM fractions were used for the *mixture* input. Forest-floor litter and tree roots were combined into a single plant source, as their ^{13}C and ^{15}N isotopic signatures did not differ significantly. This improved the discrimination of the remaining sources, as indicated by posterior density plots. Fungal isotopic data from this study were combined with data of sporocarps and AM hyphae from Klink et al. (2022), which were collected in the same study area, and subsequently averaged across treatments. AM and ECM fungal ^{13}C and ^{15}N signatures were combined into a single mycorrhizal source, resulting in a total of three sources for each soil fraction: plant material,

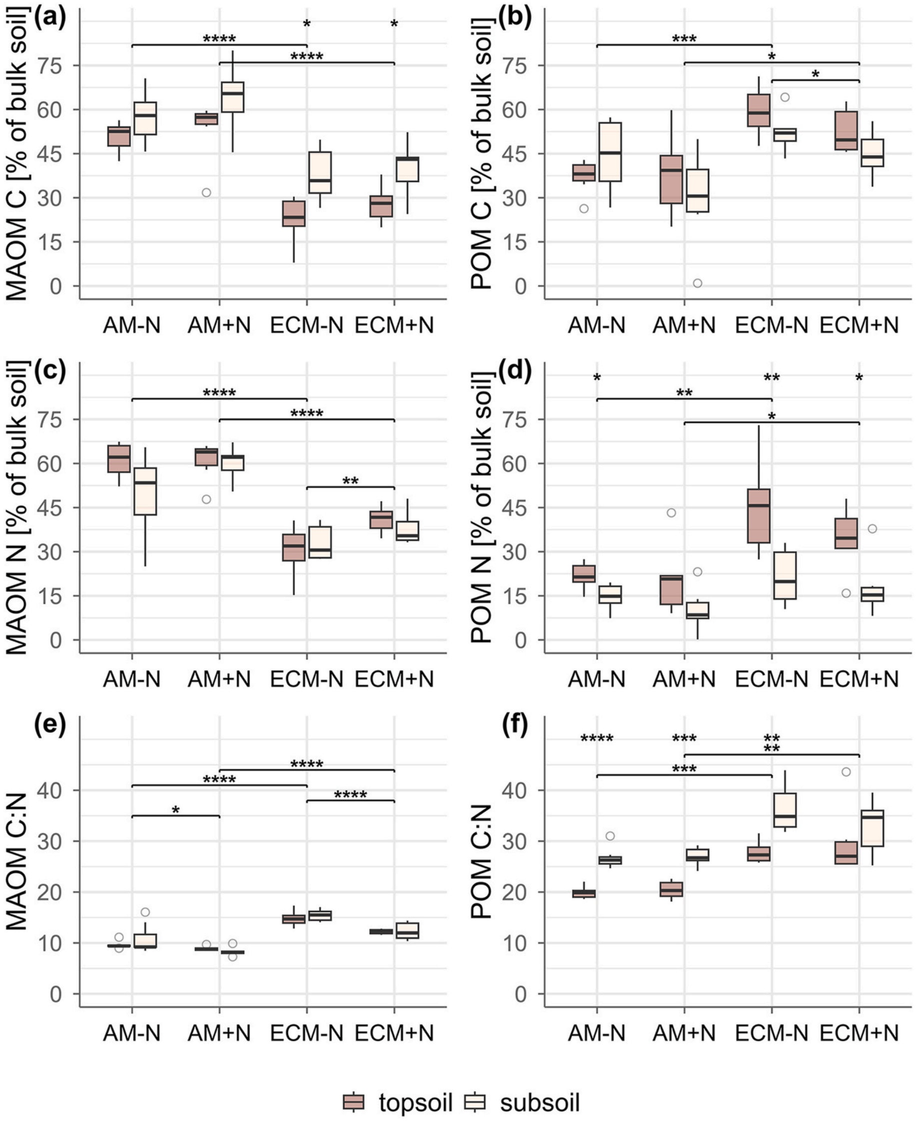

Fig. 1. Amount of carbon (C) in mineral-associated organic matter (MAOM) (a) and in particulate organic matter (POM) (b) as a percentage of total bulk soil C per treatment. Amount of nitrogen (N) in MAOM (c) and POM (d) as a percentage of total bulk soil N per treatment. C:N ratio in MAOM (e) and POM (f) per treatment. AM-N = arbuscular mycorrhizal stands without N addition; AM+N = arbuscular mycorrhizal stands with N addition; ECM-N = ectomycorrhizal stands without N addition; ECM+N = ectomycorrhizal stands with N addition. Brown refers to the top 0-15 cm of soil, whereas beige refers to a depth of 15-30 cm. Error bars represent the standard deviation. T-test p-values are indicated as: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

mycorrhizal fungi and saprotrophic fungi. Model convergence was assessed using the Gelman-Rubin (values < 1.05 considered acceptable) and Geweke diagnostics.

3. Results

3.1. POM and MAOM contribution to SOM

POM-C constituted the largest fraction of total organic carbon (TOC) in the topsoil of ECM stands (ECM-N: 60%; ECM+N: 53%), while MAOM-C represented the largest fraction of TOC in AM stands (AM-N topsoil: 51%; AM-N subsoil: 57%; AM+N topsoil: 53%; AM+N subsoil: 64%) (Fig. 1a and b). Similarly, MAOM-N contributed more to total nitrogen (TN) in AM stands (22% higher on average), whereas the POM-N contribution was higher in ECM compared to AM stands (13% higher on average) (Fig. 1c and d).

The effect of N addition on POM and MAOM contributions to TOC and TN was only significant in the ECM stands (Fig. 1a–d), with the POM contribution to TOC declining by 4% under N fertilization, and the MAOM contribution to TN increasing by 8%.

With increasing soil depth, the differences in POM and MAOM contributions to TOC and TN were also most accentuated in ECM stands (Fig. 1a–d). The share of MAOM-C increased significantly with depth in ECM-N (+15%) and ECM+N (+12%), whereas POM-N decreased by 24% and 17%, respectively.

The C:N ratio was significantly higher in ECM compared to AM stands, and consistently higher in POM compared to MAOM (Fig. 1e and f). POM showed an increase in C:N ratio with depth, although not significant in ECM+N. Under N addition, the C:N ratio of MAOM decreased, whereas no significant effect was observed for POM. The contribution of MAOM and POM mass to the total soil mass as well as mass recovery is given in Supplementary Data 1.

3.2. ^{15}N and ^{13}C natural abundance

Among the analyzed materials, mycorrhizal fungi were the most enriched in ^{15}N (mean $\delta^{15}N = 5.4‰$ in AM stands), whereas forest-floor litter showed the most depleted values for both N (mean $\delta^{15}N$ in ECM-N $= -4.1‰$) and C isotopes (mean $\delta^{13}C$ in AM-N $= -29.5‰$) (Fig. 2; Supplementary Data 2). Among the soil fractions, POM showed lower isotopic values (mean $\delta^{15}N = 1.5‰$; mean $\delta^{13}C = -28.4‰$; averaged across treatments) compared to MAOM, which was generally more enriched in ^{15}N (mean $\delta^{15}N = 3.0‰$) and ^{13}C (mean $\delta^{13}C = -26.0‰$).

Comparing AM and ECM stands, forest-floor litter in AM stands was significantly enriched in ^{15}N (Fig. 2). Similarly, soil fractions in AM stands were enriched in ^{13}C and ^{15}N compared to ECM stands, although this difference was only significant for subsoil POM under N addition (Table S2).

N addition did not affect ^{13}C values in most soil fractions (Fig. 2). However, topsoil MAOM showed a minor enrichment in ^{13}C in AM+N compared to AM-N (+0.3‰). Subsoil POM, in contrast, was enriched in ^{13}C as well as ^{15}N in AM+N, relative to AM-N (+0.5 and + 1.9‰, respectively). In ECM stands, $\delta^{15}N$ values decreased under N addition, particularly in the POM fraction at both depths (−0.7‰ in topsoil POM and −0.9‰ in subsoil POM).

The abundance of heavy isotopes in MAOM increased with depth, with the largest increase observed in AM-N (+1.9‰ in $\delta^{15}N$; +1.2‰ in $\delta^{13}C$). POM $\delta^{13}C$ and $\delta^{15}N$ values in the subsoil did not differ significantly compared to POM topsoil.

3.3. Sources of SOM fractions

POM was predominantly constituted by plant residues in all treatments — with the exception of subsoil POM in AM+N — followed by mycorrhizal and saprotrophic fungal material (Fig. 3). Plant contributions to POM were higher in ECM than in AM stands.

Fungi were the dominant contributors to the MAOM fraction, accounting for >90% of the subsoil MAOM in all treatments. In AM stands, MAOM was primarily composed of saprotrophic fungal residues, whereas in ECM stands it was dominated by mycorrhizal fungi.

N addition had only minor effects on plant vs. fungal source contributions (<10%). Fungal contributions generally increased, except for POM in the ECM stands, where they decreased to 19% in topsoil and 21% in subsoil.

With increasing depth, we observed a greater fungal contribution to the MAOM fraction across stands (AM-N = +19%, AM+N = +12%,

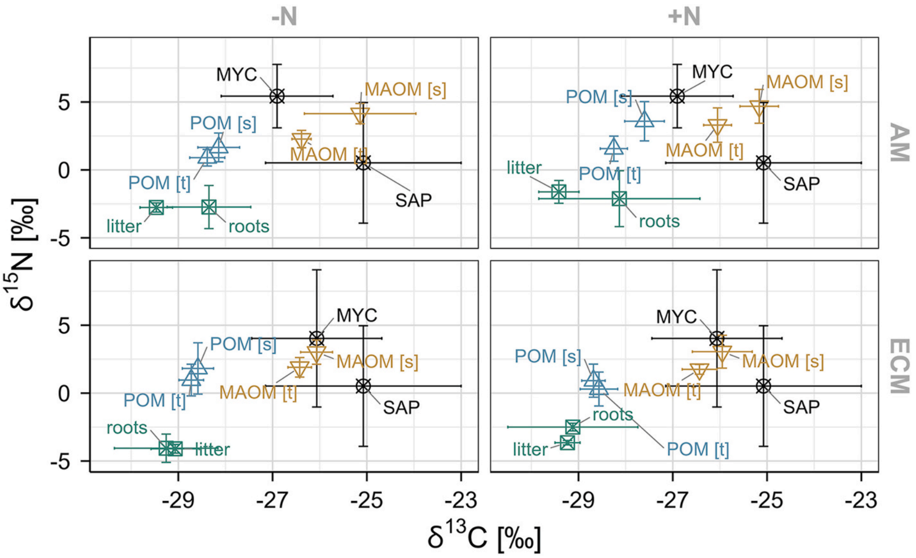

Fig. 2. Comparison of the $\delta^{13}C$ and $\delta^{15}N$ mean values for the four treatments (AM-N = arbuscular mycorrhizal stands without N addition; AM+N = arbuscular mycorrhizal stands with N addition; ECM-N = ectomycorrhizal stands without N addition; ECM+N = ectomycorrhizal stands with N addition). Color scale: green = plant material (litter, roots), light blue = topsoil and subsoil particulate organic matter (POM [t], POM [s]), yellow = topsoil and subsoil mineral associated organic matter (MAOM [t], MAOM [s]), black = fungal material (MYC = ecto- and arbuscular mycorrhizal fungi, SAP = saprotrophic fungi). Values of mycorrhizal and saprotrophic fungi were integrated with fungal data from Klink et al. (2022). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

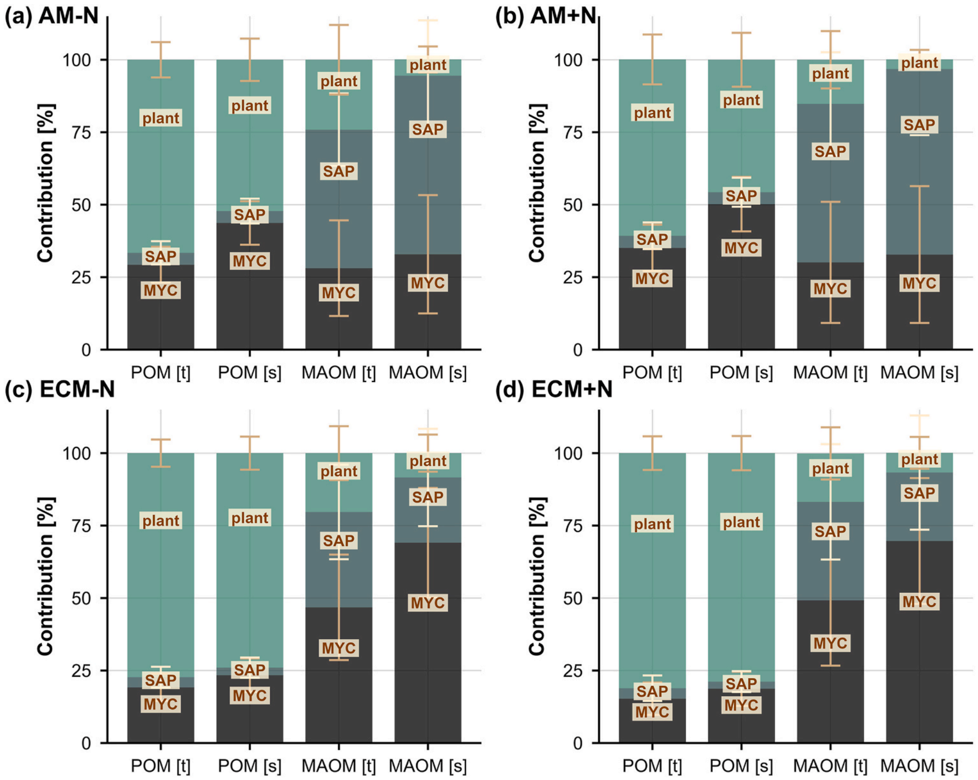

Fig. 3. Source contribution to soil organic matter in mineral-associated organic matter (MAOM) and particulate organic matter (POM) in the four treatments based on Bayesian mixing models: (a) AM-N = arbuscular mycorrhizal stands without N addition, (b) AM+N = arbuscular mycorrhizal stands with N addition, (c) ECM-N = ectomycorrhizal stands without N addition and (d) ECM+N = ectomycorrhizal stands with N addition. [t] and [s] indicate topsoil (0 – 15 cm) and subsoil (15 – 30 cm), respectively. Sources are depicted in different green and grey shades and labelled as follows: MYC = ecto- and arbuscular mycorrhizal fungi, plant = plant root and forest-floor litter, SAP = saprotrophic fungi. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

ECM-N = +12%, ECM+N = +10%), whereas in POM this pattern was only observed in AM stands (AM-N = +14%, AM+N = +15%) (Fig. 3). The higher share of fungi in the MAOM fraction with depth was mainly driven by a greater contribution of mycorrhizal fungi in ECM (+10%) and of saprotrophic fungi (+12%) in AM stands. The percentage contributions of mycorrhizal fungi, saprotrophic fungi and plant material are further reported in Table S5, and Bayesian posterior summary statistics are given in Supplementary Data 4.

3.4. Amino sugars

The amino sugar results showed a higher fungal than bacterial necromass contribution to MAOM-C and POM-C across all treatments (Fig. 4), on average by factors of 4 and 8 for MAOM and POM, respectively (Supplementary Data 3). Without N addition, fungal contributions to soil organic C were significantly higher in AM compared to ECM stands (336 vs. 234 mg g^{-1} in MAOM-C and 193 vs. 109 mg g^{-1} in POM-C, respectively).

Fungal contributions to MAOM-C increased with depth in all treatments except ECM-N, whereas in POM-C, they decreased with depth — most strongly in the absence of N addition. In contrast, N addition increased the fungal contribution to POM-C in all cases except for topsoil in AM stands.

4. Discussion

Our study showed that plant residues were the main source of POM in both AM- and ECM-dominated stands, with higher contribution in ECM vs. AM. In contrast, MAOM was derived primarily from fungi. However, the dominant fungal contributors differed: saprotrophic fungi were the main source of MAOM in AM stands, whereas mycorrhizal fungi dominated in ECM stands. These results support hypothesis (i) that sources of POM and MAOM differ between AM and ECM-dominated forests. In both mycorrhizal stands, plant contributions to POM and MAOM decreased with depth, while the contribution of mycorrhizal fungi increased. Saprotrophic fungal contributions to MAOM increased with depth in AM but decreased in ECM stands. These patterns support hypothesis (ii). N deposition (simulated over 11 years) did not significantly alter sources contributing to POM and MAOM in AM and ECM stands. Thus, our hypothesis (iii) is not supported.

4.1. POM is predominantly plant-derived in both mycorrhizal stands

As expected, plant-derived compounds were the dominant source of POM in both AM and ECM stands (up to 77%). This aligns with the coarse and less decomposed nature of POM, which typically reflects more recent plant inputs such as litter and root detritus. We observed both greater amounts of POM and slightly higher plant contributions to POM in ECM-dominated stands relative to AM-dominated stands (+11% in topsoil, +22% in subsoil). ECM stands are characterized by lower-quality plant litter, with slower decomposition rates. As a result, a greater amount of plant litter accumulates directly in the POM fraction with smaller microbial contribution. In contrast, high quality AM litter decays fast and supports microbial growth, leading to greater accumulation of microbial necromass (e.g., hyphal residues) in POM (Angst et al., 2024; Witzgall et al., 2021). Consistent with this, we observed a higher POM:MAOM ratio in ECM stands, reflecting the accumulation of less-processed plant material as POM rather than mineral-associated forms (cf. Angst et al., 2021; Klink et al., 2022).

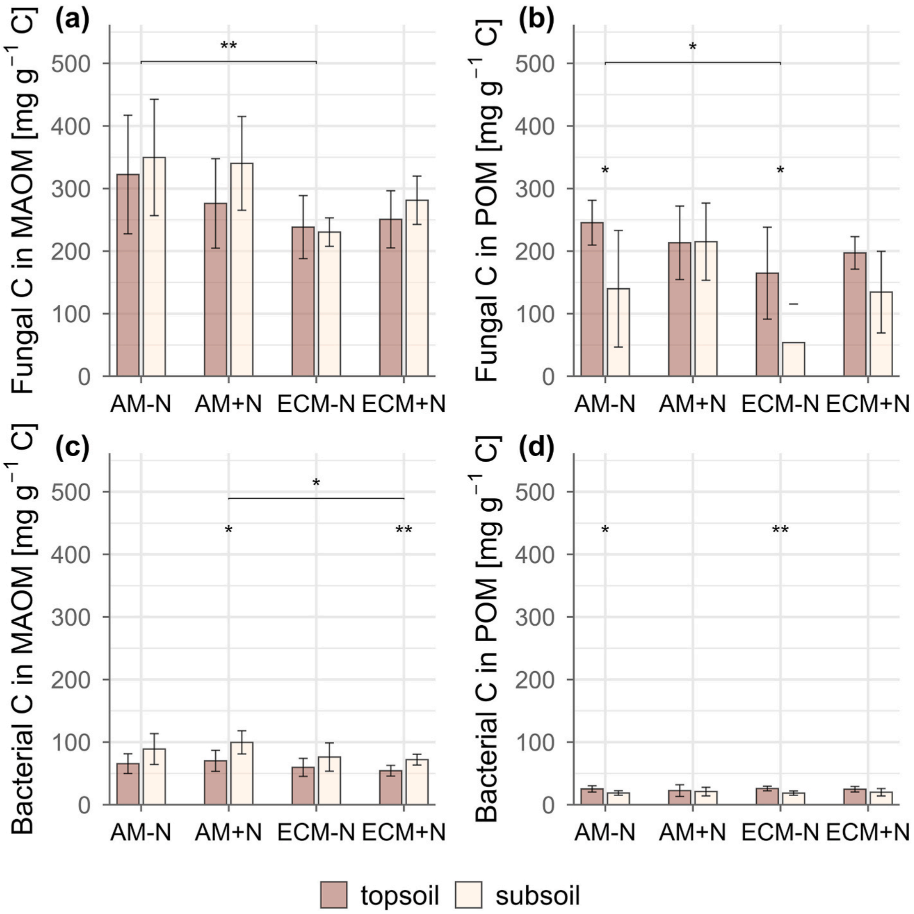

Fig. 4. Amino sugar-based estimates of: (a) fungal carbon (C) contribution to total C in mineral-associated organic matter (MAOM), (b) fungal C contribution to total C in particulate organic matter (POM), (c) bacterial contribution to total C in MAOM, and (d) bacterial contribution to total C in POM per treatment. AM-N = arbuscular mycorrhizal stands without N addition; AM+N = arbuscular mycorrhizal stands with N addition; ECM-N = ectomycorrhizal stands without N addition; ECM+N = ectomycorrhizal stands with N addition. Topsoil (brown) refers to the top 0-15 cm of soil, whereas subsoil (beige) refers to a depth of 15-30 cm. Error bars represent the standard deviation. T-test p-values are indicated as: $p < 0.05$ (*), $p < 0.01$ (**). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.2. Fungi are the main contributors to MAOM in both mycorrhizal stands

Bayesian mixing model results indicate that MAOM is mostly composed of fungal necromass (>75%). This is consistent with amino sugar data and supported by the low C:N ratio of MAOM (12.7), which approximates fungal biomass stoichiometry (Chang et al., 2024). Fungal residues thus contribute more to MAOM than to POM, particularly in AM- compared to ECM-dominated stands.

Although the isotopic mixing models estimated higher fungal contributions to MAOM (>75%) than amino sugar analyses (17-53%), these approaches quantify different pools, making direct comparisons non-trivial. Bayesian mixing models estimate probability distributions for source contributions to SOM (Moore and Semmens, 2008) based on C and N isotopic signatures and concentrations, whereas amino sugar analyses refer exclusively to C, i.e., the contribution of necromass-C to MAOM-C. Assuming a C content of fungal necromass of 42% (similar to the C content of fungal sporocarps, glucosamine and muramic acid), estimates from both methods converge. Across all treatments and the two soil depths, the fungal necromass-C contribution to POM-C estimated by the mixing model and amino sugar data is 8–23% and 5–25%, respectively. For MAOM-C, the contribution is 32–41% based on the mixing model and 23–37% based on amino sugar data.

Discrepancies between approaches may also reflect methodological limitations. Bayesian mixing models may overestimate fungal contributions because bacterial residues were excluded, as reliable δ^{13}C and δ^{15}N values for bacterial biomass are difficult to obtain. However, fungal necromass was far more abundant than bacterial necromass in our study (by a factor of 4 to 8, based on amino sugar data) — consistent with estimates of high fungal-to-bacteria ratios in temperate deciduous forests (He et al., 2020) and reports of the primacy of fungal-derived C inputs to SOM (Fu et al., 2025; Liang et al., 2019). Isotopic differences between fungal tissues (sporocarps vs. mycelium) introduce further uncertainty, although variation among fungal guilds likely exceeds within-organism differences (Zuev et al., 2025). Conversely, amino sugar approaches may underestimate microbial residues due to several limitations. The first source of uncertainty is the limited number of microbial isolates conversion factors are obtained from, which exhibit variations, e.g. between gram-positive and gram-negative bacteria as well as among different fungi (Appuhn and Joergensen, 2006; Joergensen and Wichern, 2018; Hu et al., 2024). Secondly, amino sugar approaches do not comprehensively capture microbial-derived compounds (Angst et al., 2021). Microbial necromass comprises not only cell wall material (captured by amino sugar biomarkers), but also cytoplasmic residues, extracellular enzymes, extracellular polymeric substances, etc. (Joergensen and Wichern, 2018). Lastly, the assumption that specific microbial biomarkers will accumulate in the soil at the same proportions as they appear in microbial biomass may not hold during decomposition and stabilization processes (Whalen et al., 2022).

Collectively, these considerations indicate that fungal residues represent the dominant source of MAOM, with differences between approaches largely arising from the fact that isotopic mixing models estimate total source contributions, whereas amino sugar analyses quantify necromass-C only.

4.3. AM and ECM stands differ in their fungal contributions to MAOM

Fungal residues were the main source of MAOM in both stands, with saprotrophic fungi dominating in AM stands and mycorrhizal fungi in ECM stands, as indicated by the mixing model. Although source partitioning for the MAOM fraction showed relatively large Bayesian confidence intervals (see Supplementary Data 4), likely reflecting partial isotopic overlap between saprotrophic and mycorrhizal fungi, the overall pattern is consistent with reported differences in fungal community composition between AM- and ECM-dominated stands (Beidler et al., 2020; Eagar et al., 2022).

This contrast in fungal dominance aligns with the distinct ecological roles of saprotrophic and mycorrhizal fungi within the nutrient economies of these ecosystems. AM fungi have limited saprotrophic capacity and rely primarily on inorganic nutrient acquisition, whereas many ECM fungi possess saprotrophic genes and can decompose organic matter. Consequently, AM fungi are thought to promote saprotrophic fungi to increase the nutrient availability in soil (Kaiser et al., 2015; Verbruggen et al., 2017), whereas ECM fungi can suppress saprotrophic activity due to competition for resources (Gadgil and Gadgil, 1971; Fernandez and Kennedy, 2016). Although some studies also suggest that AM fungi may have negative effects on microbial activity (e.g. Verbruggen et al., 2016; Bukovská et al., 2018), data from our study site indicate higher activity in AM stands.

The high-quality litter produced by AM-associated trees promotes microbial activity and thereby accelerates organic matter turnover (Phillips et al., 2013). In contrast, ECM stands are characterized by lower-quality litter inputs, which, together with the Gadgil effect, favor ECM fungi over saprotrophs (Keller and Phillips, 2019; Beidler et al., 2020; Eagar et al. 2022; Huang et al., 2022). Additionally, species-specific differences in litter quality among ECM trees can influence SOM dynamics (Edwards et al., 2025), emphasizing the need for studies across a broader range of species from both mycorrhizal associations.

Overall, shifts in fungal community composition — towards a greater abundance of saprotrophs in AM stands and mycorrhizal dominance in ECM stands — explain the higher contribution of necromass from these guilds to MAOM at our study site, independent of soil depth and nitrogen deposition.

4.4. Fungal-derived MAOM increases with depth

At greater soil depth (15-30 cm), the contribution of mycorrhizal fungi to the MAOM fraction increased by ca. 14% in both mycorrhizal stands. This shift coincided with significant changes in SOM composition at different depths, including an increase in the MAOM-C contribution to TOC and a decrease in the POM-N contribution to TN in the subsoil compared to the topsoil.

The higher contribution of mycorrhizal fungi to SOM in deeper soil layers may be attributed to a smaller influx of forest-floor litter as well as reduced fine root production at greater depth, thus leading to a reduced plant:fungal ratio. Indeed, previous findings reported a decrease in the contribution of forest-floor litter to SOM at depth (Bird et al., 2003) and highlighted how mycelia can channel more C into the soil profile than plant litter and fine root turnover (Godbold et al., 2006). Differences in mineral composition (e.g., high clay content) and greater sorption capacity and reactivity of minerals in deep soil can also explain the greater contribution of MAOM-C to total organic C (Poirier et al., 2020).

Interestingly, the lower saprotrophic fungal contribution to MAOM in the ECM stands was most pronounced at depth. This pattern may be linked to the steep decline in the N content with depth (ca. 44% decrease in subsoil), which likely intensifies competition for N between ECM and saprotrophic fungi (cf. Gadgil and Gadgil, 1971; Fernandez and Kennedy, 2016). This interpretation is further supported by the concomitant increase in the POM C:N ratio, and the decrease in the POM-N contribution to total N with depth. Together, these findings highlight a depth-dependent shift in SOM composition, particularly accentuated within ECM-dominated stands, where the reduced influx of plant-derived inputs and intensified competition for N favor the accumulation of microbially processed organic matter.

4.5. Minor effects of N deposition on AM and ECM stands

Simulated N deposition did not significantly affect the source contribution to SOM fractions in either AM or ECM stands, and responses were not more pronounced in ECM than in AM stands, thus not supporting hypothesis (iii). Nevertheless, consistent patterns emerged. In AM stands, we observed a slight decrease in direct plant contributions to SOM (−6% on average), and a complementary increase in fungal contributions. This pattern coincided with stronger ^{13}C enrichment in most plant tissues and soil materials and ^{15}N enrichment in all soil fractions within the AM stands, although not statistically significant.

These observations suggest that N deposition may stimulate microbial processing of SOM, leading to greater stocks of ^{13}C- and ^{15}N-enriched, microbial-derived SOM (Dijkstra et al., 2006), rather than the direct accumulation of less processed plant litter. Higher inputs of microbial residues would also explain the observed increase in MAOM contributions to bulk topsoil in AM+N and ECM+N, as microbial-derived SOM preferentially accumulates in association with soil minerals (Von Lützow et al., 2008; Sollins et al., 2009). This interpretation is further supported by a significant decrease in the C:N ratio in the subsoil MAOM fraction of the AM+N treatment compared to AM-N.

In ECM stands, plant contributions to the POM fraction increased slightly with N addition (+4% and +5% in upper and deeper soil layers, respectively), with a concomitant decrease in mycorrhizal contributions. These patterns suggest increased plant productivity (and associated litter inputs) under elevated N availability that is not matched by microbial turnover. Indeed, Janssens et al. (2010) suggested that higher levels of available mineral N stimulate leaf photosynthesis and SOM accumulation in N-limited temperate forests. In line with this, we observed a significant ^{15}N enrichment of root biomass in the ECM+N treatment, that confirms a substantial plant uptake of the applied inorganic fertilizer (δ^{15}N ~ 0‰).

The complementary decrease in mycorrhizal contributions in the ECM+N treatment may reflect a shift towards direct N foraging from plants (Carrara et al., 2022), reducing the need for microbial N mining under increased availability of inorganic N (N mining hypothesis; cf. Fontaine et al., 2011). In soils where N availability is high, trees have been observed to shift towards direct root uptake of mineral N and therefore reduce their C investment in mycorrhizal associations (Carrara et al., 2022). This shift likely leads to lower mycorrhizal biomass and reduced decomposition of organic matter, resulting in greater accumulation of less processed plant litter.

Collectively, these patterns suggest faster SOM cycling in AM stands, but increased plant productivity and/or reduced SOM decomposition in ECM stands under N addition.

These contrasting responses are consistent with fundamental differences in nutrient acquisition strategies between AM- and ECM-dominated stands. AM fungi can forage mineral N more efficiently (Phillips et al., 2013) and may therefore benefit more directly from increased mineral N abundance. In contrast, ECM fungi rely primarily on organically bound N accessed through secretion of exoenzymes, and may therefore benefit less from a higher abundance of mineral N. The observed faster SOM cycling in AM stands following N addition is consistent with results from Seyfried et al. (2023), reporting higher rates of net N mineralization in AM stands at our study site. Notably, microbial community composition, expressed as operational taxonomic unit (OTU) richness, was not affected by N addition (Eagar et al., 2022).

Overall, while N deposition effects were modest, our results indicate that AM and ECM systems may differ in their responses to increased N availability, with implications for SOM cycling and stabilization. Other factors, such as shifts in litter quality, root exudation, and soil pH, need further consideration in future studies.

5. Conclusions

Our results provide evidence that mycorrhizal type (AM vs. ECM) shapes the origin and composition of SOM across fractions and soil depths. We observed a higher direct contribution of plant-derived materials, and a concomitantly lower contribution of fungal-derived materials to POM in ECM vs. AM stands. Under both mycorrhizal types, plant inputs are the main contributors to the POM fraction, whereas fungal residues constitute the primary source of MAOM. However, saprotrophic fungi contribute most to MAOM in AM stands, whereas mycorrhizal fungi dominate MAOM formation in ECM stands.

The contribution of mycorrhizal fungi to SOM increases with depth in both AM- and ECM-dominated stands. Furthermore, N deposition (simulated for 11 years) had only minor effects on SOM composition, but results suggest accelerated SOM turnover in AM and increased plant inputs in ECM stands, which should be verified in future studies.

Our results highlight clear differences in SOM composition between AM- and ECM-dominated forest stands and across soil depths, with potential implications for SOM fate and stability. Together, these findings identify mycorrhizal type, alongside depth-related effects, as key controls on SOM dynamics in temperate forest soils.

CRediT authorship contribution statement

Veronica Vasilica: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Claudia Guidi:** Conceptualization, Formal analysis, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Khatab Abdalla:** Project administration, Writing – original draft, Writing – review & editing. **Valentin B. Kurbel:** Visualization, Writing – original draft, Writing – review & editing. **Andreas J. Wild:** Formal analysis, Writing – original draft, Writing – review & editing. **Eva Lehndorff:** Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Richard P. Phillips:** Conceptualization, Resources, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Johanna Pausch:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2026.110202.

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