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Shifts in genes encoding enzymes that degrade plant- and microbial-derived carbon affect soil organic carbon pools in different subtropical forests of China

Bing Xue[a], Guoping Tang[a,*], Zhongkai Ren[a], Yuqi Li[a], Linwei Zeng[a], Nan Jiang [a], Houbing Chen[a], Xiaobin Li[a], Jingzhi Du[a]

[a] Carbon-Water Observation and Research Station in Karst Regions of Northern Guangdong, School of Geography and Planning, Sun Yat-sen University, Guangzhou 510006, China

[*] Correspondence: Guoping Tang (tanggp3@mail.sysu.edu.cn)

Abstract

Microbial transformation of plant- and microbial-derived carbon plays a central role in soil organic carbon (SOC) formation and stabilization, yet how microbial carbon-degrading potential links forest type to SOC accumulation and persistence remains poorly understood. Here, we investigated three representative subtropical forest types—broadleaf, coniferous, and bamboo forests—and integrated litter quality, soil physicochemical properties, SOC fractions, and metagenomic data. Using the CAZyme database, we quantified genes encoding enzymes involved in the degradation of plant- and microbial-derived carbon and evaluated their relationships with environmental factors and SOC fractions. Forest type significantly altered both the abundance and diversity of genes encoding carbon-degrading enzymes, with a clear decoupling between these two metrics. Litter quality and soil environmental conditions jointly regulated these functional genes and directly influenced SOC, mineral-associated organic carbon (MAOC), dissolved organic carbon (DOC), and microbial biomass carbon (MBC), but not particulate organic carbon (POC). Instead, POC was significantly associated with the abundance of genes encoding enzymes involved in the degradation of plant- and microbial-derived carbon. SOC and MAOC were more strongly linked to genes encoding enzymes that degrade fungal-derived carbon, whereas MBC was more closely associated with genes encoding enzymes involved in bacterial peptidoglycan degradation. Broadleaf forests showed significantly higher SOC and MAOC contents and greater carbon stability than coniferous and bamboo forests. These findings indicate that microbial carbon-degrading potential represents an important functional pathway linking forest type to SOC accumulation and stabilization, highlighting the role of microbial functional traits in regulating soil carbon persistence in subtropical forest ecosystems.

Keywords

Forest ecosystems; Soil organic carbon; Metagenomics; CAZyme; Plant-derived carbon; Microbial-derived carbon

1. Introduction

Soil is the largest active carbon pool in terrestrial ecosystems, with its carbon stock approximately four times that of the vegetation pool and three times that of the atmospheric pool (Eglinton et al., 2021; Chen et al., 2025). Compared with the relatively rapid turnover of vegetation carbon, soil organic carbon (SOC) can persist from decades to millennia, playing a critical role in regulating atmospheric CO_2 concentrations and mitigating climate warming (Basile-Doelsch et al., 2020; Varney et al., 2024). The formation and stability of SOC are controlled by a series of soil biogeochemical processes, among which microbial decomposition, transformation, and assimilation of organic matter are particularly important (Wang et al., 2024; Cong et al., 2025; Pastore et al., 2025; Meng et al., 2026). Globally, soil microorganisms release large amounts of carbon to the atmosphere through organic matter decomposition,

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far exceeding annual anthropogenic carbon emissions (Crowther et al., 2015). Therefore, understanding how microbial processes regulate SOC accumulation and stabilization is essential for predicting whether terrestrial ecosystems function as carbon sinks or sources under environmental change.

SOC accumulation is ultimately sustained by plant-derived carbon inputs, including aboveground litter, root residues, and root exudates (Cotrufo et al., 2015; Feng et al., 2022; Sokol et al., 2019). After entering the soil, plant-derived organic materials can follow different transformation pathways and contribute to distinct SOC fractions. Part of this material may be retained as particulate organic carbon (POC), which is generally enriched in partially decomposed plant residues and is protected mainly through physical occlusion within soil aggregates. Because of its relatively weak chemical association with mineral surfaces, POC is often more vulnerable to microbial decomposition and has a shorter mean residence time (Duan et al., 2023; Wang et al., 2025). In contrast, mineral-associated organic carbon (MAOC) is commonly enriched in microbially transformed organic compounds and microbial necromass that are stabilized through association with soil minerals, resulting in a longer mean residence time (Sokol and Bradford, 2019; Duan et al., 2023). In addition to organic matter inputs, soil physicochemical properties, such as pH, nutrient availability, texture, moisture, and mineral surfaces, can strongly regulate the formation and preservation of POC and MAOC (Buks et al., 2025). For example, low soil pH can suppress microbial decomposition and thereby promote the persistence of organic matter in acidic soils (Rousk et al., 2009). Overall, SOC accumulation and stabilization depend on the balance between plant carbon inputs, microbial transformation, and physicochemical protection. However, how microbial functional processes interact with soil physicochemical conditions to regulate SOC fractions across forest types remains insufficiently understood.

Microbial carbohydrate-active enzymes (CAZymes) are key biochemical mediators of organic matter decomposition because they catalyze the degradation of complex plant- and microbial-derived carbon compounds (López-Mondéjar et al., 2020; Meng et al., 2026). Different CAZyme families show distinct substrate preferences and catalytic functions, allowing microorganisms to use diverse carbon substrates, including cellulose, hemicellulose, lignin-associated compounds, chitin, glucans, and peptidoglycan (Gómez-Silva et al., 2019; Chen et al., 2023). These functional differences may influence the fate of organic carbon by regulating the balance between carbon mineralization, microbial assimilation, and the production of microbial residues that contribute to SOC stabilization (Huang et al., 2024). On the one hand, increased CAZyme-mediated degradation can accelerate the decomposition of plant residues, potentially enhancing POC mineralization and carbon release (Xue et al., 2024; Zhou et al., 2025). On the other hand, efficient enzymatic degradation may also promote microbial carbon assimilation and necromass production, thereby contributing to MAOC formation and stabilization (Zhang et al., 2026). Because forest types differ in litter quality, root inputs, nutrient availability, and soil physicochemical environments, they may create distinct substrate gradients and microbial habitats that shape microbial communities and CAZyme functional profiles (Zhong et al., 2020; Zhu et al., 2024; Qu et al., 2025). However, how forest-type-induced changes in CAZyme functional potential affect the turnover and stability of SOC fractions remains unclear.

Tropical and subtropical forests store approximately one-third of global forest SOC and account for a large proportion of the global forest carbon sink (Pan et al., 2011; Xue et al., 2026). In subtropical China, broadleaf, coniferous, and bamboo forests are among the dominant forest types (Zeng et al., 2021). The convergence of the Pacific and Indian Ocean monsoons provides this region with abundant hydrothermal resources, supporting high plant productivity and active microbial metabolism (Yan et al., 2007; Yu et al., 2019). These conditions make subtropical forests an important natural system for

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examining how forest type regulates microbial carbon transformation and SOC stabilization. However, the microbial functional pathways linking forest type, carbon-degrading potential, and SOC fraction dynamics remain poorly resolved, limiting our understanding of SOC formation and persistence in subtropical forest ecosystems.

In this study, we collected litter and soil samples from three representative subtropical forest types: broadleaf, coniferous, and bamboo forests. We measured litter quality, soil physicochemical properties, SOC fractions, and SOC stability, expressed as the ratio of MAOC to SOC. We further characterized microbial functional potential using metagenomic sequencing and quantified genes encoding CAZymes involved in the degradation of plant- and microbial-derived carbon. Based on these data, we aimed to: (i) assess how genes encoding CAZymes involved in plant- and microbial-derived carbon degradation respond to different forest types; (ii) identify the linkages among CAZyme genes, litter properties, and soil physicochemical properties; and (iii) determine how these factors are associated with SOC fractions and SOC stability across forest types. We hypothesized that forest type would alter the abundance and diversity of genes encoding CAZymes involved in the degradation of plant- and microbial-derived carbon. We further expected that these shifts in microbial carbon-degrading functional potential would be closely associated with litter quality, soil physicochemical conditions, and SOC fractions, thereby contributing to forest-type differences in SOC accumulation and stability.

2. Materials and methods

2.1. Study area and sample collection

The study area was located in Guangdong Shimentai National Nature Reserve (24°22′29″~24°30′41″N, 113°05′00″~113°30′50″E). The climate of this area is characterized as subtropical monsoon, with an average annual temperature of 20.9 °C, an average frost-free period of 319 days, and average annual precipitation of 1882.8 mm. Rainfall occurs predominantly from April to October. The soil is classified as latosolic red soil according to the Chinese Soil Taxonomy, equivalent to Acrisol in the World Reference Base for Soil Resources (WRB) or Udult in USDA Soil Taxonomy. Details of the studied forests can be found elsewhere (Lu et al., 2024; Chen et al., 2025; Xue et al., 2026).

Six 20 m × 20 m sampling plots were established for each forest type. Within each plot, five soil cores with an inner diameter of 5.0 cm were randomly collected from the topsoil layer (0–20 cm) following an “S”-shaped pattern and then thoroughly homogenized to form one composite soil sample per plot. In total, 18 composite soil samples were obtained, corresponding to three forest types with six independent plot-level replicates per forest type. After being passed through a 2 mm sieve, the soil samples were divided into two subsamples: one was stored immediately at −80 °C for metagenomic sequencing, and the other was stored at 4 °C or air-dried for the determination of soil physical and chemical properties. To assess litter quality and quantity, litter collection traps were deployed in each of the three forest types. Concurrently, litter standing stocks were harvested from the soil surface using 0.25 m^2 quadrats (50 cm × 50 cm) to determine current organic layer accumulation.

2.2. Litter and soil physicochemical properties

Litter accumulation per unit area and gravimetric water content were determined after oven-drying. Total carbon and total nitrogen concentrations in both litter and soil samples were quantified by dry combustion using a CN 802 carbon/nitrogen analyzer (VELP Scientifica, Italy). Litter lignin concentration was measured with a fiber analyzer (ANKOM Technology, USA) following the digestion protocol described by Dorendorf et al. (2015).

Soil physical properties were determined using the undisturbed soil cores collected as described in

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Section 2.1. Soil gravimetric water content was measured by oven-drying at 105 °C for 48 h. Soil bulk density was calculated based on the oven-dried mass and the core volume and total porosity was subsequently estimated from the bulk density assuming a particle density of 2.65 $g \cdot cm^{-3}$. Soil pH (1:2.5) and electrical conductivity (1:5) were measured in aqueous suspensions (Hach meter). Soil ammonium (NH_4^+–N) and nitrate (NO_3^-–N) nitrogen were extracted with 2 $mol \cdot L^{-1}$ potassium chloride solution, and analyzed via a Seal AA3 flow analyzer. Microbial biomass carbon (MBC) and nitrogen (MBN) were determined via the chloroform fumigation-extraction method.

2.3. Soil organic carbon and carbon fractions

SOC and dissolved organic carbon (DOC) were quantified using a total organic carbon analyzer (Vario TOC Select; Elementar, Germany). Soil POC and MAOC fractions were isolated following the method described by Sokol et al. (2019). Briefly, 20 g of air-dried soil was mixed with 60 mL of sodium hexametaphosphate and shaken for 18 h. The resulting slurry was then wet-sieved through a 0.053 mm mesh to separate the POC fraction (> 0.053 mm) from the MAOC fraction (< 0.053 mm). Both collected fractions were dried at 65 °C and subsequently ground to pass through a 0.15 mm sieve for carbon concentration measurement.

2.4. DNA extraction, metagenome sequencing, and functional annotation

The FastDNA® Spin Kit (MP Biomedicals, U.S.) was utilized to extract DNA. Metagenomic sequencing was performed on the Illumina NovaSeq 6000 platform (Illumina, USA). Raw reads were processed using fastp (Chen et al., 2018) to remove adapters and low-quality sequences; specifically, reads were discarded if they had a length < 50 bp, an average quality score < 20, or ontained N bases. Subsequently, the optimized sequences were assembled using MEGAHIT (Li et al., 2015), with only contigs ≥ 300 bp retained for downstream analysis.

Open reading frames (ORFs) were predicted using Prodigal (Wang et al., 2025). A non-redundant gene catalogue was constructed by clustering predicted sequences with CD-HIT (Fu et al., 2012) using a 90% identity and 90% coverage threshold. To determine gene abundance, high-quality reads from each sample were mapped back to the gene catalogue using SOAPaligner (Li et al., 2008) with a 95% identity threshold. Representative sequences from the non-redundant gene catalogue were aligned against the NCBI non-redundant (NR) protein database using DIAMOND (Buchfink et al., 2015) with an e-value threshold of $1e^{-5}$. Information on the metagenome sequencing of samples from each forest plot is shown in Supplementary Table S1.

For carbohydrate metabolism analysis, the CAZy database (http://www.cazy.org/) was used to identify functional genes encoding enzymes involved in the degradation of plant- and microbial-derived carbon. These genes were assigned to six carbohydrate-active enzyme (CAZyme) classes (Huang et al., 2024): glycoside hydrolases (GHs), glycosyltransferases (GTs), polysaccharide lyases (PLs), carbohydrate esterases (CEs), auxiliary activities (AAs), and carbohydrate-binding modules (CBMs). Gene abundances were normalized as TPM values to allow cross-sample comparisons. Detailed information on genes encoding enzymes involved in the decomposition of plant- and microbial-derived components is shown in Supplementary Table S2.

2.5. Statistical analyses

One-way ANOVA followed by the post-hoc Tukey HSD test was carried out using IBM SPSS Statistics 27 (SPSS, Chicago, Illinois, USA) to examine significant differences in litter properties, soil physicochemical properties, microbial biomass, SOC, and carbon fractions among forest types. The diversity, expressed as the Shannon index, of genes encoding enzymes that degrade plant- and microbial-derived carbon was analyzed using the “vegan” package in R (v4.3.2). Principal coordinate analysis

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(PCoA) was used to assess the distribution of CAZyme-encoding gene profiles based on Bray-Curtis distance and hierarchical cluster analysis. Permutational multivariate analysis of variance (PERMANOVA) was used to analyze the significance of dissimilarity among the three forest types. Mantel test analysis was applied to assess the correlations among genes encoding enzymes involved in the degradation of plant- and microbial-derived components, litter properties, and soil physicochemical properties. Variation partitioning analysis, using the "varpart" function in the R package "vegan", was performed to determine the relative importance of environmental variables, including litter properties and soil physicochemical properties, and their contribution to the composition of genes encoding carbon-degrading enzymes. Pearson correlation analysis was performed to explore the relationships between carbon fractions and environmental factors. Random forest analysis was used to assess the impacts of environmental variables and functional genes on SOC and carbon fractions. The percentage increase in the mean squared error was used to rank the relative importance of these predictors. Additionally, linear regression was employed to evaluate the relationships between genes encoding carbon-degrading enzymes and carbon fraction contents.

3. Results

3.1. Litter and soil properties

Litter accumulation in broadleaf and bamboo forests was significantly higher than in coniferous forests (Fig. 1a, $p < 0.05$). Compared with coniferous and bamboo forests, litter in broadleaf forests had the highest water content but lower mass, accompanied by a higher carbon-nitrogen ratio and lignin content (Fig. 1a, $p < 0.05$). Broadleaf soils had the lowest bulk density and highest porosity, indicating a looser soil structure, followed by bamboo soils (Fig. 1b, $p < 0.05$). Regarding soil chemical properties, the carbon-nitrogen ratio in coniferous soils was significantly higher than in broadleaf and bamboo soils, whereas the trends for total nitrogen and NH_4^+–N were opposite (Fig. 1c, $p < 0.05$). No significant differences were observed in NO_3^-–N, microbial biomass nitrogen, or the ratio of microbial biomass carbon to microbial biomass nitrogen among the three forest types (Figs. 1c, 2i–j, $p > 0.05$). Furthermore, electrical conductivity in broadleaf soils was significantly higher than in coniferous and bamboo soils, and all soils were strongly acidic (pH < 4.5, Fig. 1c).

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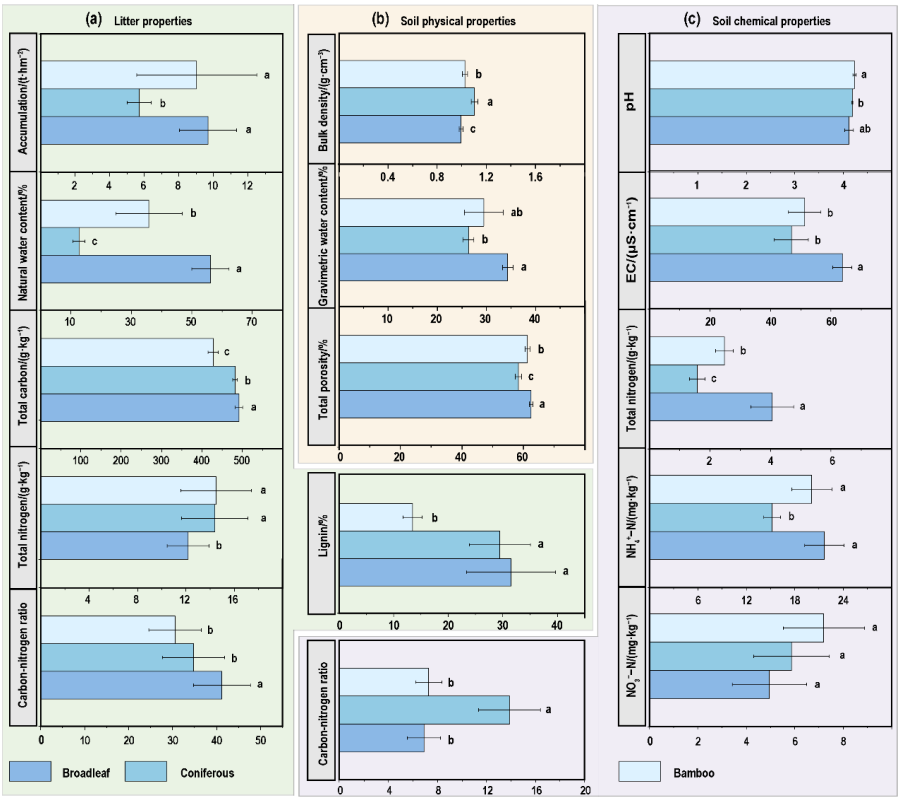

Fig. 1. The litter (a) and soil physicochemical (b-c) properties under different forest types. EC: electrical conductivity; NH_4^+–N and NO_3^-–N represent ammonium nitrogen and nitrate nitrogen respectively. Different lowercase letters indicate significant differences ($p < 0.05$) among forest types. The same letters denote no significant difference.

3.2. Characteristics of soil organic carbon and carbon fractions

The contents of SOC and MAOC in broadleaf forests were 28.67% and 57.27% higher than those in coniferous forests, and 54.35% and 188.63% higher than those in bamboo forests, respectively (Fig. 1a, c, $p < 0.05$). Across all soil types, the relative content of the POC fraction was higher than that of MAOC, while no significant difference in POC content was observed among the three forest types (Fig. 1b, $p > 0.05$). Furthermore, the MAOC:SOC ratio showed a decreasing trend from broadleaf to coniferous to bamboo soils (Fig. 1e, $p < 0.05$), whereas the POC:SOC and POC:MAOC ratios exhibited the opposite trend (Fig. 1d, f, $p < 0.05$). Compared to coniferous and bamboo soils, the contents of DOC and MBC in broadleaf soil were 2.28 and 1.40 times higher, and 1.49 and 1.29 times higher, respectively (Fig. 1g–h, $p < 0.05$).

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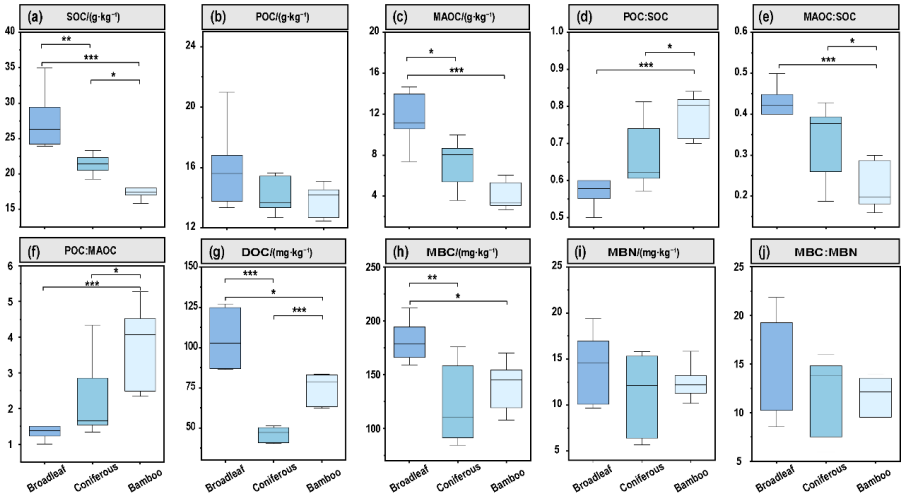

Fig. 2. Contents of soil organic carbon (SOC, a), particulate organic carbon (POC, b), mineral-associated organic carbon (MAOC, c), the ratio of POC to SOC (POC:SOC, d), the ratio of MAOC to SOC (MAOC:SOC, e), the ratio of POC to MAOC (POC: MAOC, f), dissoluble organic carbon (DOC, g), microbial biomass carbon (MBC, h), microbial biomass nitrogen (MBN, i), and the ratio of MBC to MBN (MBC:MBN, j) under different forest types. Asterisks indicate statistical significance: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

3.3. Genes encoding CAZymes that degrade plant- and microbial-derived carbon

A total of 197,466 genes encoding CAZymes were identified from the entire metagenome of all soil samples, accounting for 18.83% of the total genes. Among these, 95.33% (188,240) and 0.06% (123) were assigned to bacteria and fungi, respectively, while 4.61% (9,103) remained unassigned (Fig. S1). The abundances of genes encoding these specific CAZyme classes (PLs, AAs, CBMs, GHs, and GTs) showed significant differences among forest types (Fig. S1).

The composition of genes encoding enzymes for the degradation of plant-, fungi- and bacteria-derived carbon varied significantly across forest types, as revealed by PCoA (Fig. 3a–c, $p < 0.001$). The Shannon index for these gene categories was significantly higher in bamboo forests compared to broadleaf and coniferous forests (Fig. 3d–f, $p < 0.05$), with the exception of genes encoding enzymes for the decomposition of bacteria-derived carbon, which showed no significant difference between bamboo and coniferous forests and had the highest index in broadleaf forests (Fig. 3f).

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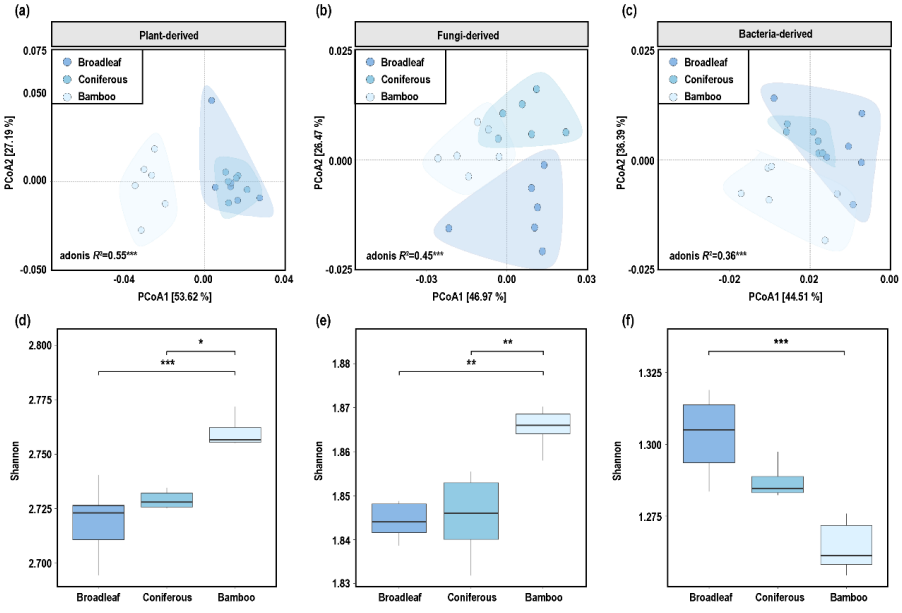

Fig. 3. Principal coordinate analysis (PCoA) of genes encoding CAZymes that degrade plant-derived (a), fungi-derived (b), and bacteria-derived (c) carbon under different forest types based on Bray-Curtis distance. The diversity (Shannon index) of genes encoding CAZymes that degrade plant-derived (d), fungi-derived (e), and bacteria-derived (f) carbon under different forest types. Asterisks indicate statistical significance: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Compared with bamboo soils, the abundance of genes encoding enzymes involved in the decomposition of plant-derived lignin and fungi-derived chitin increased significantly in broadleaf and coniferous forests (Figs. S2, 3). Specifically, the abundance of genes encoding lignin-degrading enzymes increased by 14.63% (broadleaf) and 11.26% (coniferous), while those encoding chitin-degrading enzymes increased by 4.77% and 4.13%, respectively (Fig. 4, $p < 0.05$). In contrast, genes encoding enzymes that degrade plant-derived hemicellulose decreased by 10.18% (broadleaf) and 8.49% (coniferous) (Fig. 4, $p < 0.05$). No significant differences were observed among the three forest types in the abundance of genes encoding enzymes that decompose plant-derived cellulose, fungal-derived glucans, or bacterial-derived peptidoglycan (Fig. 4, $p > 0.05$).

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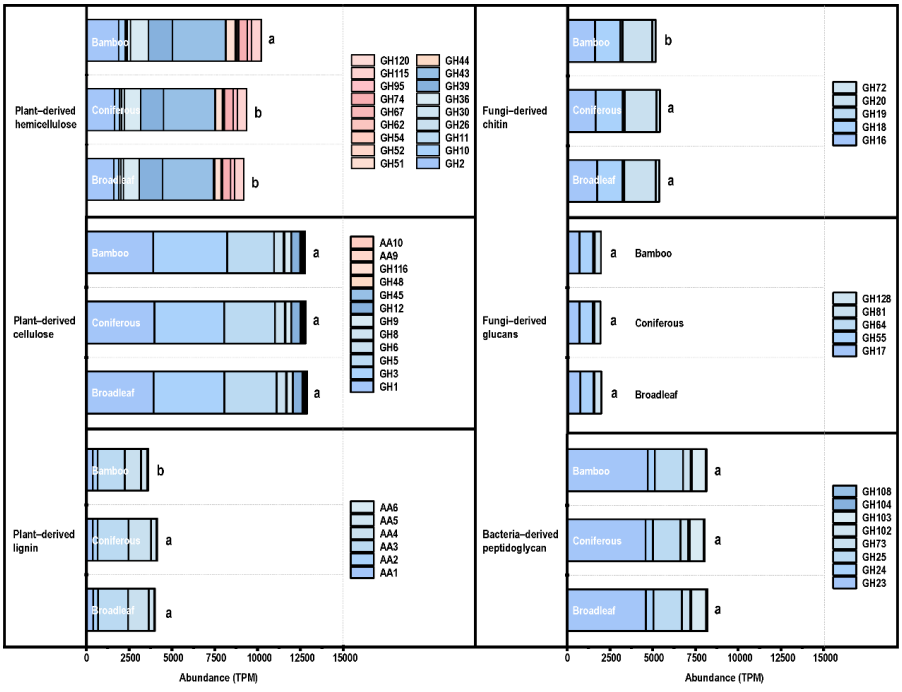

Fig. 4. The abundance (TPM) of genes encoding enzymes that degrade plant-derived (a), fungi-derived (b), and bacteria-derived (c) carbon under different forest types. Different lowercase letters indicate significant differences ($p < 0.05$) among forest types. The same letters denote no significant difference.

The abundance of specific genes encoding CAZymes that degrade plant- and microbial-derived carbon components also varied across forest types (Figs. S2–3). Specifically, the relative abundance of genes encoding enzymes that degrade plant-derived hemicellulose and cellulose, such as GH2, GH10, GH11, GH3, and GH9, increased significantly following the shift from broadleaf to bamboo forests ($p < 0.01$, Fig. S3). In contrast, genes encoding lignin-decomposing enzymes, such as AA3 and AA4, showed a significant decreasing trend ($p < 0.01$, Fig. S3). A similar decline was observed for GH16 and GH20, which encode enzymes that degrade fungi-derived chitin ($p < 0.01$, Fig. S3). For genes encoding enzymes that degrade fungi-derived glucans, most showed no significant differences among the three forest types, except for GH128. This gene family exhibited the highest abundance in broadleaf forests, with significantly higher abundance than in coniferous forests ($p < 0.01$, Fig. S3). Among genes encoding enzymes involved in bacteria-derived carbon decomposition, those belonging to the GH23 family were the most abundant and had significantly higher abundance in bamboo forests ($p < 0.05$, Fig. S3).

The genes encoding CAZymes that degrade plant- and microbial-derived carbon were primarily attributed to the bacterial communities, with Proteobacteria, Acidobacteriota, and Actinobacteriota being the dominant phyla (Fig. 5). Specifically, regarding hemicellulose and cellulose degradation, the abundance of Acidobacteriota was significantly higher in bamboo forests compared to broadleaf and coniferous forests ($p < 0.05$, Fig. S4). In contrast, Actinobacteriota exhibited a consistent distribution pattern across all six analyzed carbon sources (comprising plant-, fungi-, and bacteria-derived compounds), with its abundance remaining consistently higher in broadleaf and coniferous forests than

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in bamboo forests (Fig. S4). Distinct habitat preferences were also observed among low-abundance phyla: Desulfobacterota B and Eremiobacterota were significantly enriched in broadleaf and coniferous forests, whereas Verrucomicrobiota and Bacteroidota peaked in bamboo forests ($p < 0.05$, Fig. S4). These results indicate that the functional composition of carbon-degrading microbial communities is significantly reshaped by forest types.

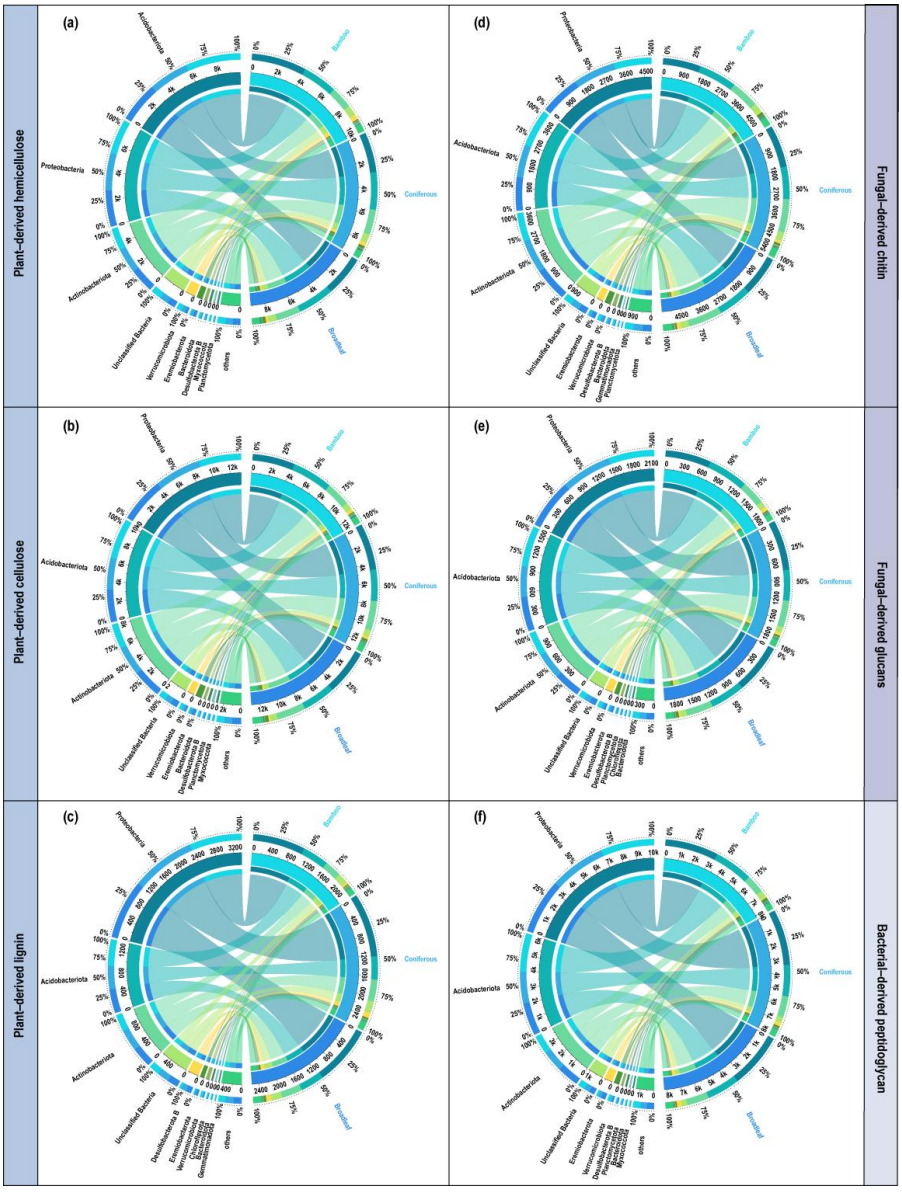

Fig. 5. Contribution of microbial phyla to genes encoding CAZymes that degrade plant-, fungi-, and bacteria-derived components.

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3.4. Relationship between the environmental factors, genes encoding carbon-degrading enzymes, and organic carbon fractions

Mantel tests revealed that the abundance of genes encoding CAZymes that degrade plant- and microbial-derived carbon was significantly correlated with multiple environmental factors (Fig. 6a). Genes encoding enzymes that degrade plant- and bacteria-derived carbon were significantly correlated with litter total carbon and lignin content ($p < 0.01$, Fig. 6a), but showed no association with soil physical or chemical properties ($p > 0.05$, Fig. 6a). In contrast, genes encoding enzymes that degrade fungi-derived carbon were significantly correlated with the natural water content, total carbon, and lignin content of litter, as well as soil gravimetric water content, electrical conductivity, and total nitrogen ($p < 0.05$, Fig. 6a).

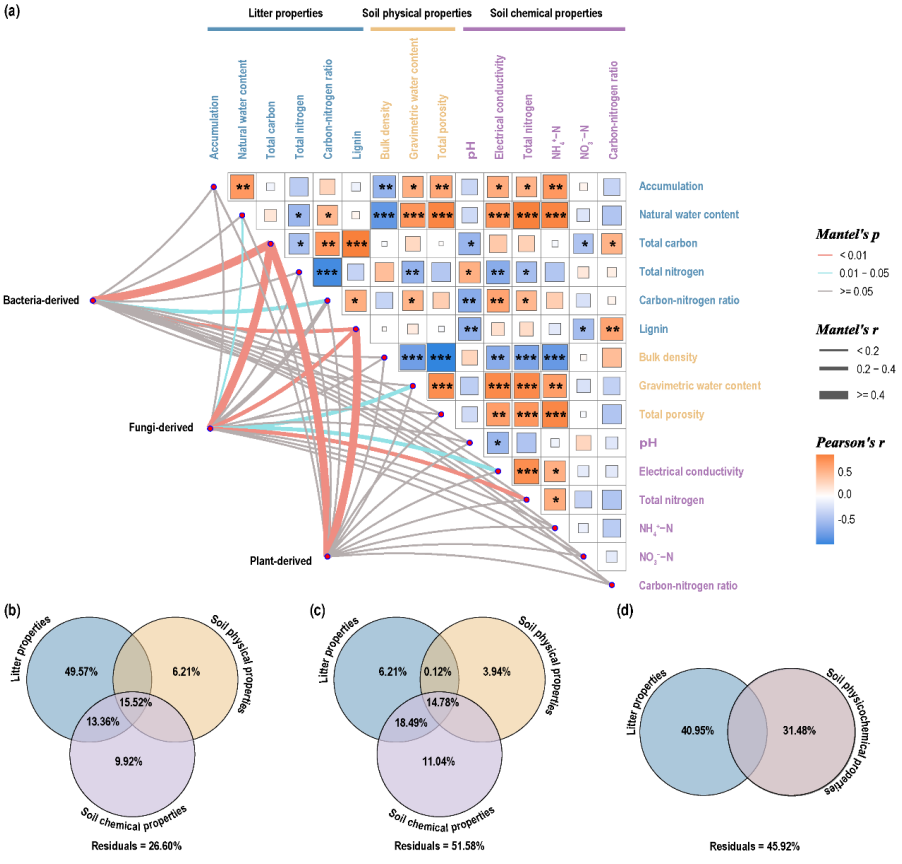

Fig. 6. The relationship between the abundance of genes encoding CAZymes involved in the degradation of plant- (hemicellulose, cellulose, and lignin) and microbial-derived components (peptidoglycan, chitin, and glucans) and microbial metabolic activity, based on Pearson correlation and Mantel test analyses (a). NH_4^+–N and NO_3^-–N represent ammonium nitrogen and nitrate nitrogen, respectively. Asterisks indicate statistical significance: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. The relative contributions of litter traits and soil physicochemical properties to the variation in genes encoding enzymes for plant-derived carbon (b), fungi-derived carbon (c), and bacteria-derived carbon (d) decomposition, based on the variation partitioning analysis (VPA). Soil physical and chemical variables showed strong collinearity in the

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bacteria-derived carbon dataset and were therefore combined into a single soil physicochemical properties group for the final VPA.

The VPA results showed that litter properties (49.57%) explained a substantially larger proportion of the variance in genes encoding enzymes involved in plant-derived carbon decomposition than did soil physical properties (6.21%) or soil chemical properties (9.92%) (Fig. 6b). For genes encoding enzymes involved in fungi-derived carbon decomposition, soil chemical properties accounted for a much greater share of the variance (11.04%) (Fig. 6c). In the case of genes encoding enzymes for bacteria-derived carbon decomposition, litter properties explained a higher proportion of the variance (40.95%) compared to soil physicochemical properties (31.48%) (Fig. 6d). Furthermore, interactive effects among the three types of properties jointly explained 15.52% and 14.78% of the variance in genes encoding enzymes that degrade plant- and fungi-derived carbon, respectively (Fig. 6b, c).

The contents of SOC and carbon fractions increased with increasing litter accumulation, water content, total carbon, lignin and soil water content (Fig. 7a). Additionally, the contents of organic carbon fractions were positively correlated with chemical properties (such as electrical conductivity, NH_4^+–N and total nitrogen) and negatively correlated with pH. Random forest model results showed that SOC and MAOC were closely associated with litter total carbon, lignin content, soil total nitrogen, and electrical conductivity (Fig. 7b). Soil physical properties (bulk density, total porosity, gravimetric water content) were important factors that influenced the DOC and MBC contents. Litter and soil physicochemical variables explained 85.81% of the total variance for DOC, whereas they exhibited limited explanatory power for POC.

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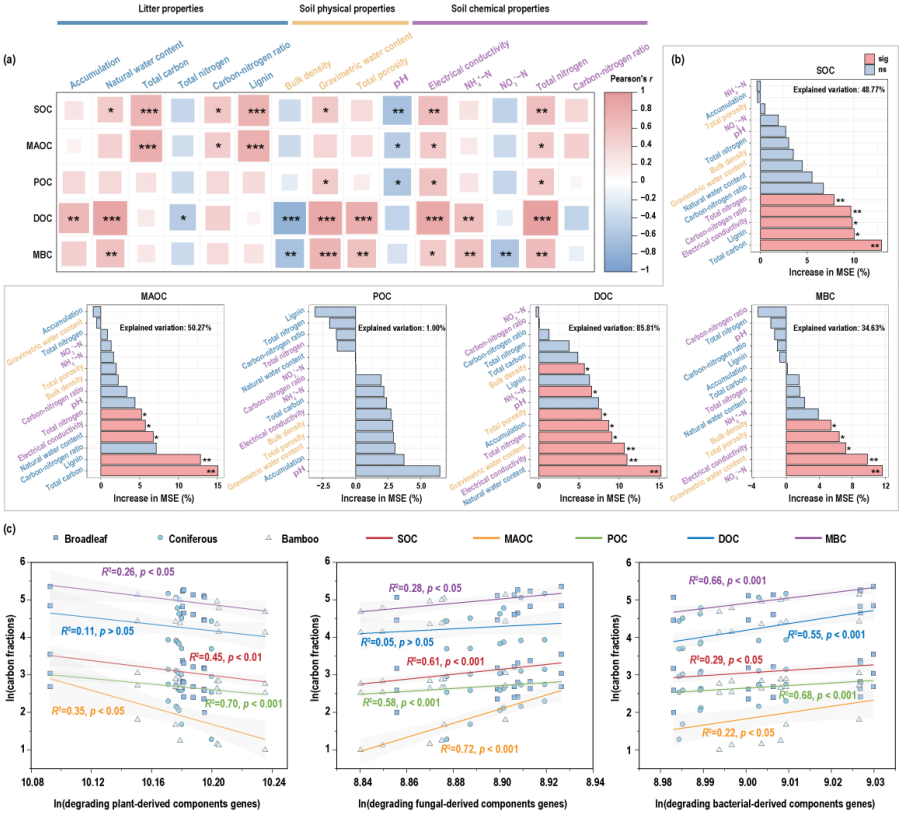

Fig. 7. Correlations between litter parameters, soil physicochemical properties, and soil organic carbon (SOC) fraction contents (a). The relative importance of independent variables controlling SOC, mineral-associated organic carbon (MAOC), particulate organic carbon (POC), dissolved organic carbon (DOC), and microbial biomass carbon (MBC) was represented by the percentage increase in mean squared error (MSE, %) using random forest models (b). NH_4^+–N and NO_3^-–N represent ammonium nitrogen and nitrate nitrogen, respectively. Asterisks indicate statistical significance: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. The ln-ln correlations between SOC and its fractions and genes encoding enzymes that degrade plant-derived components (hemicellulose, cellulose, and lignin), fungi-derived components (chitin and glucans), and bacteria-derived components (peptidoglycan) (c).

Regression analyses revealed that POC was significantly associated with the abundance of genes encoding enzymes that degrade plant- and microbial-derived components (Fig. 7c). Furthermore, SOC ($R^2 = 0.61$, $p < 0.001$) and MAOC ($R^2 = 0.72$, $p < 0.001$) showed stronger associations with genes encoding enzymes that degrade fungi-derived components, whereas MBC ($R^2 = 0.66$, $p < 0.001$) was more strongly associated with genes encoding enzymes that degrade bacteria-derived peptidoglycan.

4. Discussion

4.1. Effects of forest type on genes encoding CAZymes involved in plant- and microbial-derived carbon degradation

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Forest type markedly altered microbial community structure and genes encoding enzymes involved in carbon degradation (Figs. 3a–c, 5), indicating that changes in dominant vegetation can reshape both microbial taxa and microbial functional potential associated with the decomposition of simple and complex organic compounds (Ren et al., 2021; Huang et al., 2024). This pattern is consistent with previous studies showing that bacteria are major agents responsible for the transformation of plant- and microbial-derived carbon in terrestrial ecosystems (Wilhelm et al., 2019; Chang et al., 2025). The dominant contribution of bacteria may be related to their high metabolic diversity, rapid turnover, and functional plasticity, which allow bacterial communities to respond sensitively to changes in litter input and soil environmental conditions (Morrissey et al., 2017; Huang et al., 2021).

Across all forest types, the Shannon diversity of genes encoding CAZymes followed a consistent gradient: plant-derived carbon > fungi-derived carbon > bacteria-derived carbon (Fig. 3d–f). This pattern likely reflects differences in substrate complexity among carbon sources. Plant-derived polymers, including cellulose, hemicellulose, and lignin-associated compounds, are chemically heterogeneous and require a broad range of enzymes for depolymerization (Bomble et al., 2017; Yan et al., 2018; López-Mondéjar et al., 2020). In contrast, microbial-derived substrates, such as chitin, glucans, and peptidoglycan, may require a narrower but more specialized enzymatic repertoire. These differences suggest that the diversity of CAZyme genes is closely linked to the biochemical heterogeneity of available substrates.

Notably, the abundance and diversity of genes encoding carbon-degrading enzymes were not always coupled. In broadleaf soils, the abundance of genes encoding peptidoglycan-degrading enzymes was comparable to that in bamboo soils, whereas their diversity was significantly higher (Figs. 3f, 4). Similarly, bamboo soils had the lowest abundance of genes encoding chitin-degrading enzymes and showed no significant increase in glucan-degrading gene abundance, but they had significantly higher diversity of genes encoding enzymes involved in fungi-derived carbon degradation (Figs. 3e, 4). These results suggest that microbial communities may maintain or expand carbon-use potential by increasing enzymatic heterogeneity rather than simply increasing the abundance of specific functional genes (Chen et al., 2022; Cong et al., 2025). Therefore, gene abundance alone may be insufficient to fully characterize microbial functional potential in soil carbon cycling. Considering both abundance and diversity provides a more complete view of how forest type influences microbial carbon-degrading strategies.

4.2. Environmental controls on genes encoding carbon-degrading enzymes

Linking microbial functional genes to environmental processes is essential for understanding how microorganisms participate in soil carbon cycling (López-Mondéjar et al., 2020; Chen et al., 2023). At the CAZyme class level, forest type generated distinct functional profiles. GHs and CBMs were highly abundant in bamboo soils, whereas AAs and GTs were enriched in broadleaf and coniferous soils (Fig. S1). These differences suggest that forest types may select for different microbial carbon-use strategies through variation in litter quality, nutrient availability, and soil physicochemical properties (Qi et al., 2025; Yin et al., 2025; Guo et al., 2026; Li et al., 2026). In bamboo soils, the higher abundance of GHs and CBMs may indicate a stronger hydrolytic system that enhances enzyme–substrate binding and promotes the decomposition of relatively labile plant polymers such as hemicellulose (Sidar et al., 2020). In contrast, the enrichment of AAs in broadleaf and coniferous soils suggests greater oxidative potential for degrading more recalcitrant carbon compounds, including lignin-associated substrates (Qu et al., 2025). The higher abundance of GTs in these forests may also reflect stronger microbial anabolic potential, which could be associated with microbial growth and residue production (Fu et al., 2025).

Litter is the primary source of structural carbon input in forest soils, and its chemical composition

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directly determines the quantity and complexity of substrates available for microbial decomposition (Cha et al., 2025; Margida et al., 2020; Li et al., 2026). Our results showed that genes encoding enzymes involved in plant-derived carbon degradation were significantly correlated with litter chemical properties (Fig. 6), supporting the idea that litter quality is a major driver of microbial functional potential for plant carbon decomposition. Genes encoding enzymes involved in fungi-derived carbon degradation were associated with both litter supply and soil environmental conditions, suggesting that the turnover of fungal-derived carbon may be jointly regulated by substrate availability and soil conditions. For genes encoding enzymes involved in bacteria-derived carbon degradation, litter properties explained a greater proportion of the variance than soil physicochemical properties. This may indicate that litter input indirectly affects bacteria-derived carbon turnover by regulating microbial growth, biomass production, and community turnover (Wattenburger et al., 2025).

These results highlight the need to distinguish carbon sources when evaluating microbial functional controls on SOC dynamics. Plant-derived, fungi-derived, and bacteria-derived carbon substrates differ in biochemical composition, decomposability, and stabilization pathways. Therefore, their degradation may respond differently to litter quality and soil physicochemical gradients. Such source-specific responses provide a mechanistic basis for understanding how forest type influences microbial carbon transformation and subsequent SOC stabilization.

4.3. Associations between genes encoding carbon-degrading enzymes and SOC fractions

Genes encoding carbon-degrading enzymes represent an important component of microbial functional potential involved in SOC turnover. In this study, the abundance of genes encoding enzymes involved in plant-derived carbon degradation was consistently higher than that of genes related to microbial-derived carbon degradation across forest types (Fig. 4). This pattern indicates that microbial communities maintained a strong potential to process plant-derived organic matter, which is the major source of soil carbon input in forest ecosystems (Ren et al., 2021; Zhang et al., 2021). However, the relationships between carbon-degrading genes and SOC fractions differed among carbon pools, suggesting that SOC accumulation and stabilization are not controlled by a single microbial pathway but by fraction-specific interactions among substrate input, microbial transformation, and soil physicochemical protection.

MAOC was more closely associated with litter quality, soil nutrients, and genes encoding enzymes involved in fungal-derived carbon degradation. This pattern is consistent with the recognized contribution of microbial residues, particularly fungal-derived compounds, to mineral-associated carbon formation (Liang et al., 2017). Because microbial residues can be stabilized through interactions with soil mineral surfaces, such as ligand exchange and other mineral-associated mechanisms, stronger links between fungal-derived carbon degradation genes and MAOC may reflect a greater potential for microbial residue turnover and subsequent stabilization in mineral-associated forms. The MAOC ratio is commonly used as an indicator of SOC stability (Zhang et al., 2025). In this study, broadleaf forests had the highest MAOC ratio, together with greater diversity of genes encoding enzymes involved in bacteria-derived carbon degradation and higher abundances of AAs and GTs (Figs. 2e, 3f, S1). These results suggest that broadleaf soils may provide more favorable conditions for microbial carbon transformation and mineral-associated carbon accumulation, thereby contributing to greater SOC stability.

In contrast, POC showed weak associations with the measured environmental variables but was significantly related to genes encoding enzymes involved in the degradation of plant- and microbial-derived carbon. Because POC is generally enriched in plant residues, fungal hyphae, and inter-aggregate organic particles, it is more directly exposed to enzymatic decomposition and usually has a faster

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turnover rate than MAOC (Wang et al., 2025). Therefore, the close association between POC and carbon-degrading genes may indicate that microbial functional potential plays a particularly important role in regulating particulate carbon dynamics. The higher POC content observed in broadleaf soils likely reflects greater organic matter input and transient accumulation under conditions where input and decomposition are not fully synchronized. This also suggests that the accumulation of POC does not necessarily indicate long-term carbon stabilization unless it is further transformed or protected within aggregates and mineral-associated pools.

DOC and MBC were more strongly related to soil physical conditions, highlighting the importance of soil structure and moisture in regulating labile carbon turnover and microbial activity (Lee et al., 2023; Philippot et al., 2024). The association between MBC and genes encoding enzymes involved in bacterial peptidoglycan degradation further suggests that bacterial turnover may contribute to microbial biomass carbon dynamics (Huang et al., 2024). Together, these results indicate that different SOC fractions are associated with distinct environmental and microbial controls: MAOC is more closely linked to litter quality, nutrient status, and fungal-derived carbon turnover; POC is more directly associated with microbial carbon-degrading potential; and DOC and MBC are more sensitive to soil physical conditions and microbial activity.

Overall, our findings suggest that microbial carbon-degrading potential is an important functional pathway linking forest type to SOC accumulation and stabilization. Broadleaf forests, characterized by higher SOC and MAOC contents and greater SOC stability, may favor microbial transformation and mineral-associated carbon formation more than coniferous and bamboo forests. In contrast, the lower SOC stability observed in bamboo soils suggests that forest-type shifts may alter the balance between carbon input, microbial degradation, and physicochemical stabilization, which is consistent with previous evidence that bamboo expansion can destabilize soil organic carbon pools (Qian et al., 2026). From a forest soil carbon management perspective, maintaining or restoring broadleaf forest composition may help promote stable SOC storage in subtropical regions, whereas forest-type shifts that enhance rapid decomposition without a proportional increase in MAOC formation may weaken long-term SOC persistence. Because metagenomic sequencing reflects microbial functional potential rather than realized enzyme activity or carbon fluxes, future studies combining metagenomics with enzyme assays, microbial necromass biomarkers, or stable isotope tracing would further clarify the transformation pathways of plant- and microbial-derived carbon into stable SOC pools.

5. Conclusions

This study revealed, at the molecular level, the component-specific regulatory mechanisms of soil carbon pool turnover under different subtropical forest types. Different forest types influence the abundance and diversity of genes encoding enzymes that degrade plant- and microbial-derived carbon by altering litter quality and soil environmental conditions, thereby affecting the accumulation and stabilization of soil carbon fractions. The abundance of genes encoding enzymes that degrade plant-derived carbon is primarily associated with substrate quality, whereas the abundance of genes encoding enzymes that degrade microbial-derived carbon is linked to bacterial community turnover and the mineral stabilization of fungal necromass, consequently influencing the accumulation of SOC, MAOC, and MBC. Bacteria are the main microbial groups harboring genes encoding enzymes involved in both plant- and microbial-derived carbon degradation; however, a certain degree of decoupling between gene abundance and diversity was observed during the degradation process, suggesting that microbial communities in different forest ecosystems may regulate their carbon metabolic potential through distinct

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functional strategies. Notably, shifts in forest types, such as conversion from coniferous to broadleaf forests or expansion of bamboo forests into coniferous forests, may alter the compositional structure of the soil carbon pool, thereby affecting its stability. Overall, this study demonstrates that forest type can influence soil carbon accumulation and stability by regulating microbial functional pathways, providing new evidence for understanding soil carbon sequestration capacity across different forest types. These findings not only improve our understanding of the combined effects of vegetation composition, litter quality, and microbial carbon transformation on soil carbon persistence in subtropical forests of China, but also provide a functional perspective for sustainable management and ecosystem-based climate mitigation strategies in similar forest ecosystems.

Data availability

The metagenomic sequencing data have been deposited in the NCBI Sequence Read Archive under accession number PRJNA1391496.

Author contributions

Guoping Tang: Writing – review & editing, Validation, Supervision, Investigation, Funding acquisition, Data curation. Bing Xue: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation. Zhongkai Ren: Investigation, Formal analysis, Data curation. Yuqi Li: Formal analysis, Data curation. Linwei Zeng: Supervision, Resources, Investigation. Nan Jiang: Investigation, Formal analysis, Data curation. Houbing Chen: Investigation, Formal analysis, Data curation. Xiaobin Li: Supervision, Resources, Investigation. Jingzhi Du: Investigation, Formal analysis, Data curation.

Competing interests

The contact author has declared that none of the authors has any competing interests.

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