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Forest Quality Gradients Regulate Soil Microbial Carbon Use Efficiency in Subtropical Coniferous Ecosystems

Feng Wu [1,†], Rui Chen [1,†], Yujing Yang [2], Tao Yang [1,*], Zhitao Huo [1,*], Xin Li [1], Wubiao Huang [1] and Shuangshi Zhou [1]

[1] Changsha General Survey of Natural Resources Center, China Geological Survey, Changsha 410600, China
[2] Hubei Key Laboratory of Regional Development and Environmental Response, Faculty of Resources and Environmental Sciences, Hubei University, Wuhan 430062, China
* Correspondence: yangtao02@mail.cgs.gov.cn (T.Y.); jcyhuozhitao@mail.cgs.gov.cn (Z.H.)
† These authors contributed equally to this work.

Abstract

Soil microbial carbon use efficiency (CUE) is a pivotal determinant of soil carbon sequestration, yet how forest quality gradients regulate CUE through the interplay of mineral-microbial interactions in subtropical conifer ecosystems remains poorly understood. To address this, we examined the CUE response and its drivers across a forest quality gradient (high-quality to poor-quality stands) in subtropical coniferous forests in China. Soil mineral composition (including soil texture and the contents of Fe_2O_3, CaO, and MgO), physicochemical properties, microbial community diversity, and CUE were quantified. The results showed that CUE decreased by 2.7%, from 0.533 in high-quality stands to 0.519 in low-quality stands. Concurrently, soil organic carbon (SOC), nutrient availability, and microbial diversity exhibited consistent declining trends along the forest quality gradient. The CUE showed a significant positive correlation with SOC ($r > 0.90$, $p < 0.001$). Structural equation modeling and random forest revealed that microbial diversity was the most dominant correlated factor of CUE (the total effects on CUE = 0.932), followed by SOC. However, soil minerals indirectly influenced CUE via SOC. These findings highlight microbial diversity as the dominant observed correlate of CUE across forest quality gradients. This study not only deepens the understanding of the microbial mechanisms underlying soil carbon dynamics in subtropical forests but also provides key scientific basis for ecological restoration of poor-quality forests and nature-based climate solutions.

Keywords: forest quality; soil carbon; coniferous forests; forest restoration; carbon sequestration

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1. Introduction

Forest ecosystems are a crucial component of the global terrestrial carbon reservoir, exerting significant influence on regional and global carbon cycles [1]. These ecosystems act as major carbon sinks, with their capacity for carbon sequestration being highly sensitive to environmental changes and anthropogenic disturbances. Central to the material cycles and energy flows within these ecosystems, soil microorganisms play an indispensable role in regulating the carbon balance. Key microbial groups, including bacteria and fungi, drive critical processes such as organic matter decomposition, nutrient mineralization, and carbon fixation [2–4], thereby directly controlling the dynamics of soil carbon stocks. A key factor governing this microbial regulation is microbial carbon use efficiency (CUE).

It is an important indicator for assessing how assimilated carbon is partitioned between microbial biomass synthesis and respiratory loss [5]. Consequently, CUE is fundamental for understanding soil carbon dynamics and determining whether soils function as carbon sinks or sources [6]. Variations in CUE directly influence ecosystem carbon sequestration potential and related climate feedback mechanisms [7].

In recent decades, intensified human activities, global climate change and anthropogenic land-use change have precipitated a marked deterioration in forest health [8,9], compromising not only their ecological services but also the stability of soil carbon pools [9]. Persistent declines in carbon storage and biodiversity are key indicators of reduced stand quality [10]. In subtropical mountainous regions, planted coniferous forests face structural and functional degradation risks due to historical over-exploitation, insufficient management practices, and ecological mismanagement [11–13]. This ecological mismanagement includes specific failures such as the establishment of monoculture plantations, lack of necessary thinning operations, and fire suppression policies. These practices disrupt natural ecological processes and lead to unstable forest stands. This manifests as structural simplification, increased vulnerability to pests and diseases, and higher occurrences of dead trees, forming a continuum from high-quality to poor-quality states. Research suggests that changes in forest quality affect soil organic carbon (SOC) accumulation and turnover [14] by altering carbon inputs from litter and root, root exudate composition, and microenvironmental conditions [15], which in turn modulate microbial activity and CUE [16]. Specifically, the balance between carbon and nitrogen transformations is crucial. Microbial CUE governs the fate of assimilated carbon, directing it towards either growth or respiration. This process directly regulates the retention and loss of carbon in the soil. It should be pointed out that CUE itself is not equivalent to humification or mineralization [5,17]. Although CUE is interrelated with these two processes in soil carbon cycling, its core function is to allocate carbon flow in microbial metabolism. In addition, the availability of nitrogen also plays an important role in regulating CUE [5]. It limits the synthesis of microbial biomass and affects the allocation of assimilated carbon between growth and maintenance of respiration. Although it is theoretically believed that high-quality forests support higher microbial CUE due to greater carbon inputs, balanced C–N ratios, and enhanced nutrient availability, this association remains unverified in subtropical coniferous forests.

The Wuyi Mountain, located in the southeast of China, is an important part of the global subtropical forest ecosystem. This region is a key ecological barrier and biodiversity hotspot in China. Compared to other subtropical regions, its vast coniferous forests play an important role in regional climate regulation, biodiversity conservation, and carbon sequestration [18,19]. Nonetheless, stand conditions vary due to historical logging and inadequate management, leading to a cross-sectional gradient from high-quality to poor-quality stands. The predominant red soils in this region are classified as Ferralsols or Alisols according to the World Reference Base for Soil Resources (WRB). These soils are strongly weathered and have mineral compositions rich in Fe, Ca, and Mg oxides, facilitating substantial physicochemical SOC stabilization [20,21]. Current research mostly focuses on the chemical, biochemical, and microbiological properties of soils [22]. Although there are many research papers on different ecosystems or forest types [23] and land-use changes [24,25], there are few systematic studies on how microbial CUE varies along forest quality gradients. Moreover, the minerals rich in the soils in this region can form stable organo-mineral complexes via adsorption and co-precipitation [26,27]. These complexes physically protect organic matter from microbial decomposition, thereby influencing CUE. However, the way in which soil mineral characteristics and nutrient status jointly relate to CUE at different forest quality levels has received insufficient attention.

Therefore, we hypothesized that soil microbial CUE would decrease along the forest quality gradient in subtropical coniferous forests. The aim of this study was to evaluate the association between forest quality gradient (from high-quality to poor-quality stands) and CUE in these forests and identify key abiotic and biotic factors regulating this process. In the context of global climate change, this research is significant because clarifying the microbial mechanisms underlying carbon processes in subtropical forests is crucial for predicting ecosystem responses to warming and developing effective carbon sequestration strategies. For this purpose, we systematically analyzed soil mineralogical properties, physicochemical characteristics, microbial community diversity, and CUE. The novelty of this study lies in its focus on the forest quality gradient of subtropical coniferous forests in China, providing an integrated framework for understanding how aboveground vegetation conditions relate to underground microbial carbon utilization processes. By linking aboveground forest quality to CUE, this work explores both the direct and indirect pathways through which forest quality influences CUE.

2. Materials and Methods

2.1. Study Area Description

The study area is located in the Mount Wuyi region of northern Fujian Province, China (27°38′–28°16′ N, 117°27′–118°12′ E), encompassing a total area of 2813 km^2. This region falls within a mid-subtropical humid monsoon climate zone, marked by distinct seasonal variation and high rainfall. Long-term meteorological data show a mean annual temperature of 19.7 °C and average annual precipitation of 1926.9 mm. Topographically, the area is bordered by mountains to the east, west, and north, while the central and southern sections feature relatively gentle terrain. The landscape generally slopes from the northwest toward the southeast, reaching its highest point at Huanggang Mountain (2158 m a.s.l.). Renowned for its exceptional biodiversity, the Wuyi Mountains maintain a forest cover exceeding 80%.

This study focused on the widely distributed planted coniferous forests in the region. The soils in these forests are classified as Ferralsols and Alisols, derived from granite parent material. The basic physical and chemical properties of these soils are presented in the following Results section. The studied forests are primarily composed of *Pinus massoniana* and *Cunninghamia lanceolata*, with stand ages ranging from 25 to 45 years.

2.2. Experimental Design and Soil Sampling

Soil sampling was conducted from June to August 2024 across the study area. Given that elevation and aspect are major drivers of environmental heterogeneity in mountainous ecosystems, our experimental design was explicitly structured to isolate the effect of forest quality from topographic variability. To address this, all sampling plots (20 m × 20 m) were confined to a narrow elevational band (420 ± 60 m) with similar slope aspects. This band is the zone where these planted subtropical coniferous forests are predominantly concentrated. Furthermore, to eliminate the effects of geological heterogeneity, all plots were established on the same soil parent material (granite). This rigorous site selection minimized the influence of environmental gradients associated with topography and geology, ensuring that the observed variations in soil properties could be attributed primarily to differences in forest quality.

All study plots were established in planted forests, including both pure stands and mixed stands. In the mixed stands, the proportion of *P. massoniana* to *C. lanceolata* ranged from 3:7 to 7:3. The coniferous forests were classified into three quality classes, which are good (Forest A), medium (Forest B), and poor (Forest C). This classification relied on a multi-dimensional field assessment of canopy density, tree growth, community structure,

and forest health (Table 1). It should be clarified that this classification reflects the current state of stand health and structure, not a historical forest quality sequence (i.e., C areas are not necessarily former A areas). This classification system is based on our actual field survey and represents an artificial stratification of present stand conditions. To ensure spatial independence, plots within each quality class were geographically dispersed (Figure 1).

Table 1. Classification criteria for various forest types. Forest A represents good-quality forest, Forest B represents medium-quality forest, and Forest C represents poor-quality forest. This classification is based on our field survey and empirically categorized.

Variables	Forest A (Good)	Forest B (Medium)	Forest C (Poor)
Canopy density	>70%	40%–70%	<40%
Diameter at breast height (DBH)	>20 cm	10–20 cm	<10 cm
Tree height	>15 m	8–15 m	<8 m
Community structure	Complex vertical layers	Moderate	Simple structure
Incidence of pests/diseases, deadwood ratio	Low (<5% damage)	Moderate (5%–15% damage)	High (>15% damage)

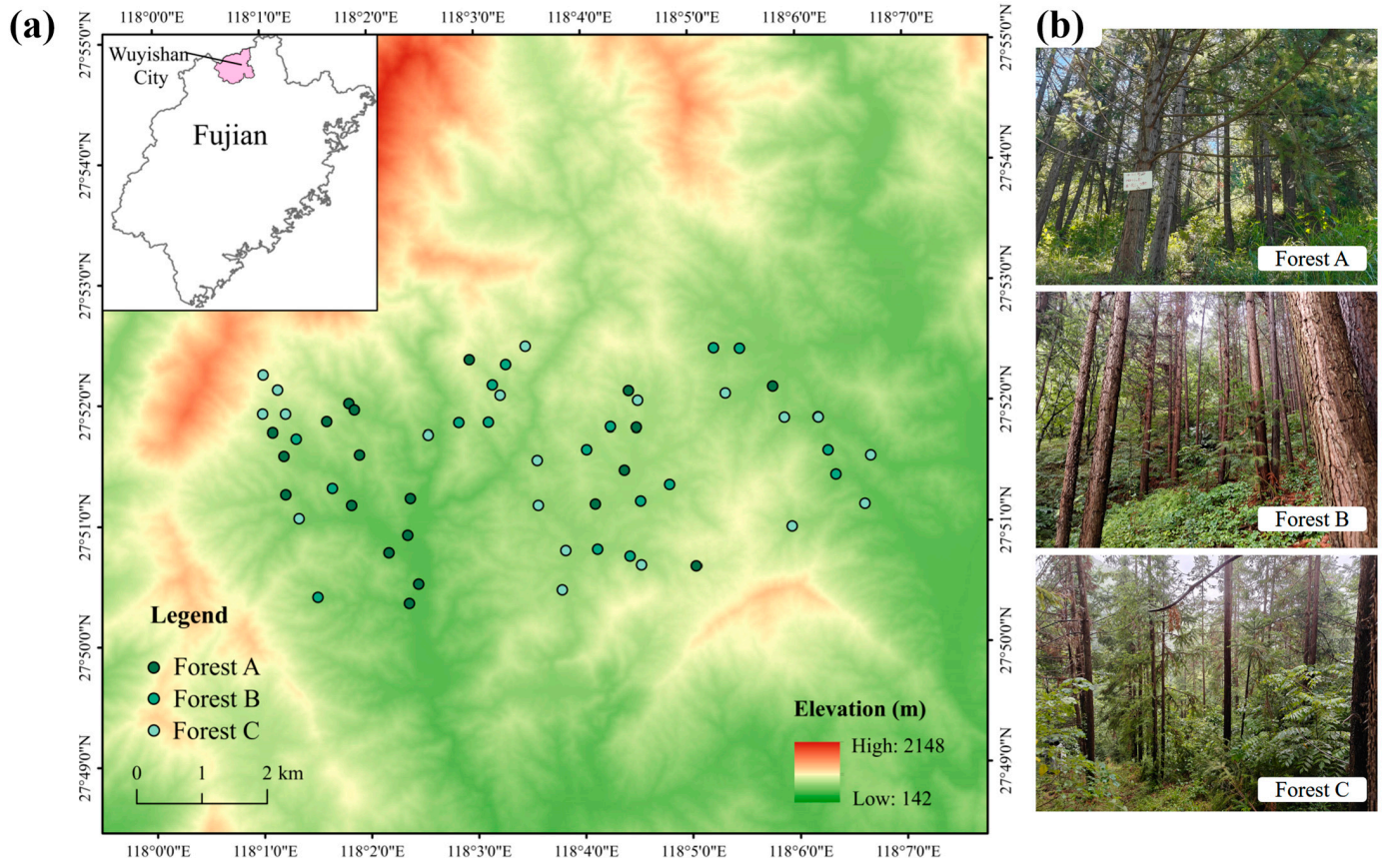

Figure 1. Location of sampling sites (**a**) and photos of different forests (**b**). In figure (**a**), the *X*-axis represents longitude (E), and the *Y*-axis represents latitude (N). Forest A represents good-quality forest, Forest B represents medium-quality forest, and Forest C represents poor-quality forest.

A total of 20, 17, and 20 plots were allocated to Forests A, B, and C, respectively. Within each plot, five soil cores were collected following a standardized five-point sampling scheme and subsequently homogenized to generate a single composite sample per plot for laboratory analysis. Prior to sampling, the organic litter layer (O horizon) was carefully removed. Composite soil samples were then collected from the underlying undisturbed mineral soil (A horizon) at a depth of 0–20 cm.

2.3. Determination of Soil Properties

After air-drying, the soil samples were ground and sieved through a 2 mm mesh for the determination of soil texture and pH and through a 0.149 mm mesh to determine total nutrient contents, according to previous protocols [28]. Briefly, soil texture was analyzed using a laser particle size analyzer (Mastersizer 3000, Malvern Panalytical, UK). Soil pH was measured in a 1:5 (*w*:*v*) soil–water solution using an electrode (MP551, Shanghai, China). The SOC and total nitrogen (TN) contents were determined using an elemental analyzer (Vario EL cube, Elementar, Germany). Total phosphorus (TP) and total potassium (TK) were analyzed by colorimetric and flame photometric determination after H_2SO_4-$HClO_4$ extraction, respectively. Available nitrogen (AN) was determined by the alkaline hydrolysis diffusion method, available phosphorus (AP) by the Olsen method, and available potassium (AK) by ammonium acetate extraction [28].

Microbial CUE was determined via the ^{18}O-H_2O tracing method [29]. Specifically, soils were incubated with ^{18}O-labelled water. Microbial growth was estimated from ^{18}O incorporation into DNA. Respiration was measured as CO_2 production. CUE was calculated as the ratio of growth-derived carbon to total carbon uptake (Figure 2) [29]. Thus, the value of CUE is <1. Additionally, iron oxide (Fe_2O_3), calcium oxide (CaO), and magnesium oxide (MgO), as important soil mineral components, were determined using X-ray fluorescence spectrometry (XRF) [30].

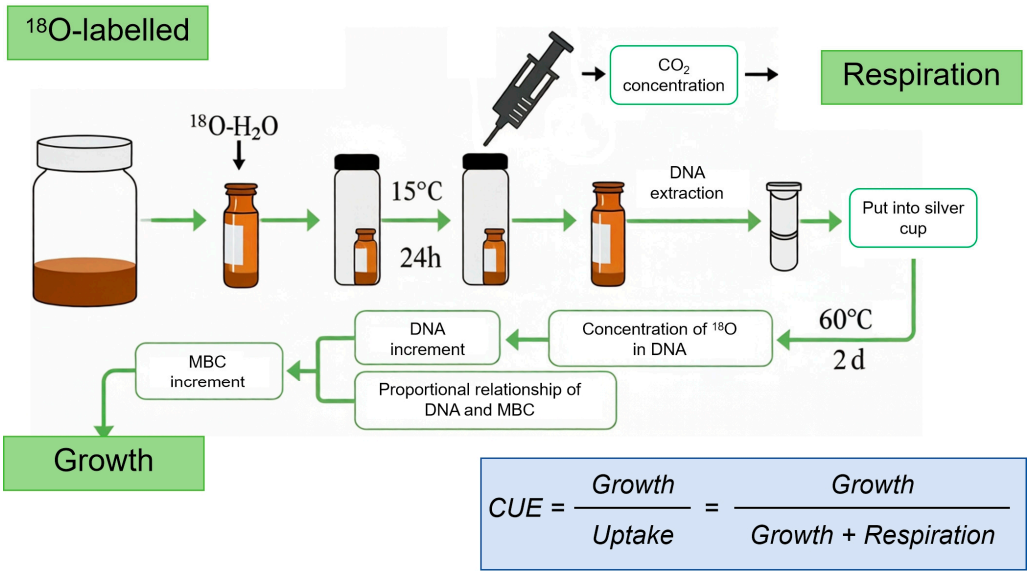

Figure 2. The steps and calculation formula for determining carbon use efficiency (CUE) using the ^{18}O-H_2O method.

To characterize the soil microbial communities associated with different forest quality gradients, genomic DNA was extracted from the soil samples [31]. Soil bacterial and fungal communities were analyzed using 16S rRNA and ITS sequencing, respectively [32]. Bacterial and fungal amplicons were purified, quantified, and sequenced separately on the Illumina MiSeq platform using 2 × 300 bp paired-end reads. Raw sequences were processed with QIIME2, where demultiplexed reads were quality-filtered, denoised, and chimera-checked using DADA2, before being clustered into operational taxonomic units at 97% similarity [33]. Alpha diversity indices, including Shannon (diversity), Chao1 (richness), and Pielou (evenness), were calculated for both bacterial and fungal communities. Beta diversity was assessed using Bray–Curtis dissimilarity and visualized through non-metric multi-dimensional scaling (NMDS) [34].

2.4. Statistical Analysis

Differences in soil properties within forest quality gradient were assessed using one-way analysis of variance (ANOVA). Prior to ANOVA, normality was tested using the Shapiro–Wilk test, and homogeneity of variances was assessed using Hartley's F-test. Duncan's multiple range test was subsequently used to evaluate differences between mean values. To identify the key drivers of microbial CUE, a random forest regression model was implemented. Furthermore, Pearson correlation analysis was conducted to examine the relationship between SOC and CUE.

To elucidate the complex observed associations linking forest quality to CUE, a structural equation model (SEM) was constructed. The final model was evaluated by the chi-square test, Goodness-of-Fit Index (GFI), and Comparative Fit Index (CFI). Models with GFI and CFI values > 0.90 were deemed appropriate [35].

Additionally, the compositional differences in microbial communities across forest types were analyzed. The NMDS based on Bray–Curtis dissimilarity was performed to visualize beta diversity patterns among groups. Permutational multivariate analysis of variance (PERMANOVA) was used to assess significant differences in overall community composition among forest quality groups. All analyses were carried out in R (version 4.5.1), with statistical significance defined as $p < 0.05$.

3. Results

3.1. Soil Mineralogical Properties

Forest quality had no significant effect on soil texture ($p > 0.05$), but significantly influenced the contents of Fe_2O_3, CaO, and MgO ($p = 0.040$, 0.014, and <0.001, respectively; Figure 3). The Fe_2O_3 content in Forest A was significantly higher than in Forest C, while the CaO and MgO contents in Forest A were significantly higher than in both Forest B and C ($p < 0.05$). No significant differences were observed in soil mineralogical properties between Forest B and C ($p > 0.05$).

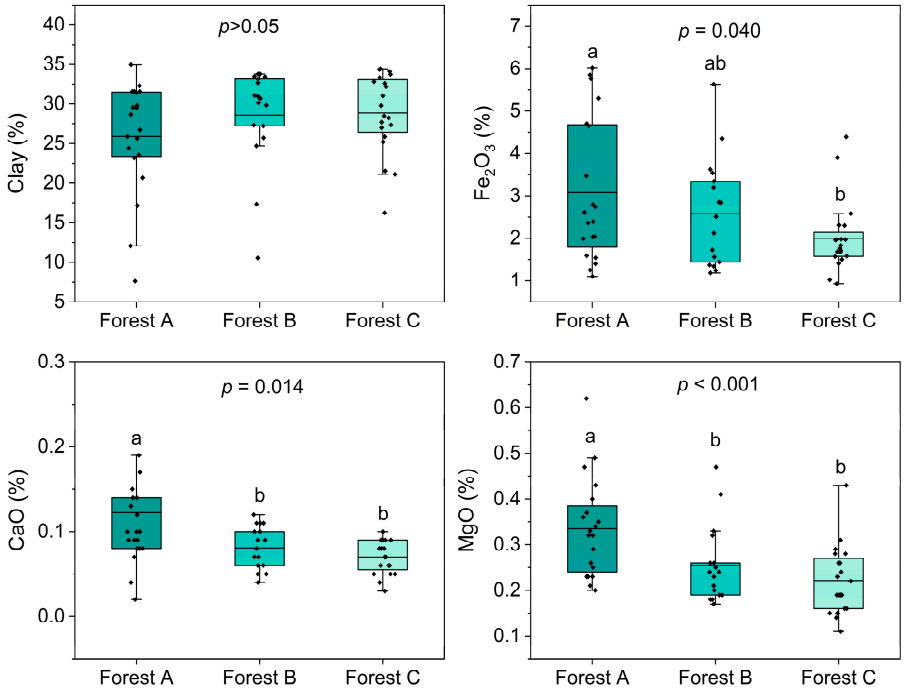

Figure 3. Soil mineralogical properties across forest types. Significant differences ($p < 0.05$) are denoted by different letters. Forest A represents good-quality forest, Forest B represents medium-quality forest, and Forest C represents poor-quality forest.

3.2. Soil Physicochemical Properties and Microbial Diversity

Both SOC and CUE decreased significantly with declining forest quality ($p = 0.005$ and 0.002; Figure 4). However, no significant differences were observed between Forest B and C ($p > 0.05$). The CUE of in Forest A, B and C was 0.533, 0.525, and 0.519, respectively. Thus, the CUE was decreased by 1.5% and 2.7% in Forest B and C as compared to Forest A. Similarly, most soil nutrient contents were significantly affected by forest quality ($p < 0.05$), except for TK content and nutrient stoichiometric ratios (Table 2). Forest quality did not significantly influence soil pH ($p > 0.05$). However, TN ($p < 0.001$), TP ($p < 0.001$), AN ($p < 0.001$), AP ($p = 0.007$), and AK ($p = 0.004$) contents in Forest A were significantly higher than in other forest types.

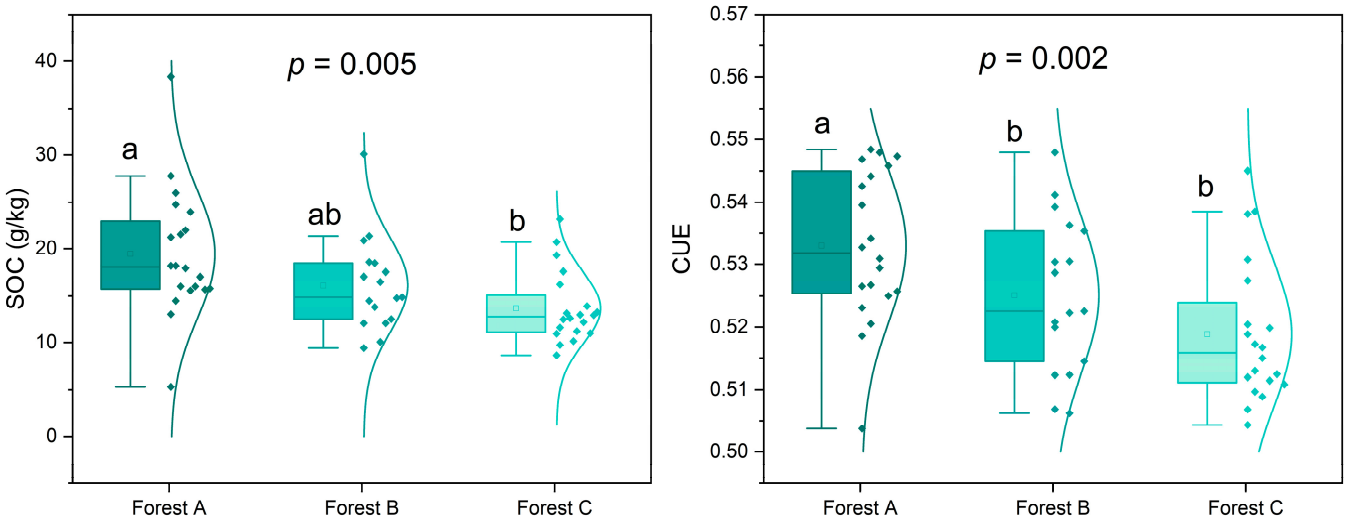

Figure 4. Soil organic carbon (SOC) and carbon use efficiency (CUE) across forest types. Significant differences ($p < 0.05$) are denoted by different letters. Forest A represents good-quality forest, Forest B represents medium-quality forest, and Forest C represents poor-quality forest.

Table 2. Soil pH and nutrients across forest types (mean ± SE). Bold values labeled with different letters denote significant differences ($p < 0.05$). Forest A represents good-quality forest, Forest B represents medium-quality forest, and Forest C represents poor-quality forest.

Soil Properties	Forest A (Good)	Forest B (Medium)	Forest C (Poor)	*p* Value
pH	4.82 ± 0.09	4.84 ± 0.07	4.76 ± 0.06	>0.05
TN (g/kg)	**1.69 ± 0.10 a**	**1.39 ± 0.06 b**	**1.18 ± 0.07 b**	**<0.001**
TP (g/kg)	**0.60 ± 0.04 a**	**0.46 ± 0.04 b**	**0.33 ± 0.03 c**	**<0.001**
TK (g/kg)	17.51 ± 0.92	18.92 ± 1.40	17.07 ± 1.31	>0.05
AN (mg/kg)	**161.98 ± 8.01 a**	**133.18 ± 4.98 b**	**108.23 ± 6.79 c**	**<0.001**
AP (mg/kg)	**55.05 ± 13.38 a**	**25.00 ± 5.77 b**	**16.77 ± 2.87 b**	**0.007**
AK (mg/kg)	**107.72 ± 11.80 a**	**73.62 ± 5.89 b**	**70.58 ± 5.61 b**	**0.004**
C–N	11.32 ± 0.32	11.60 ± 0.61	11.81 ± 0.50	>0.05
C–P	34.96 ± 3.71	42.96 ± 7.31	49.40 ± 7.73	>0.05
N–P	3.02 ± 0.26	3.53 ± 0.44	4.02 ± 0.42	>0.05

Regarding the composition of soil bacterial and fungal communities at the phylum level (Figure A1), the majority of taxa exhibited no significant variation across the forest types ($p > 0.05$). Among the soil bacterial taxa, the relative abundances of actinobacteria ($p = 0.003$) and proteobacteria ($p = 0.028$) decreased with the forest quality, while that of acidobacteria increased from 4.4% in Forest A to 7.5% in Forest C ($p = 0.005$). Meanwhile,

that of ascomycota in the fungal community decreased along the forest quality gradient ($p = 0.002$), from 0.09% in Forest A to 0.01% in Forest C.

In terms of alpha diversity, the Shannon index for both bacterial and fungal communities was significantly influenced by forest quality ($p < 0.05$), whereas the Pielou evenness and Chao1 richness indices showed no significant differences ($p > 0.05$; Figure 5). Specifically, Forest A exhibited the highest Shannon index values, significantly exceeding those of Forest B and C ($p < 0.05$), with no significant difference observed between Forest B and C ($p > 0.05$).

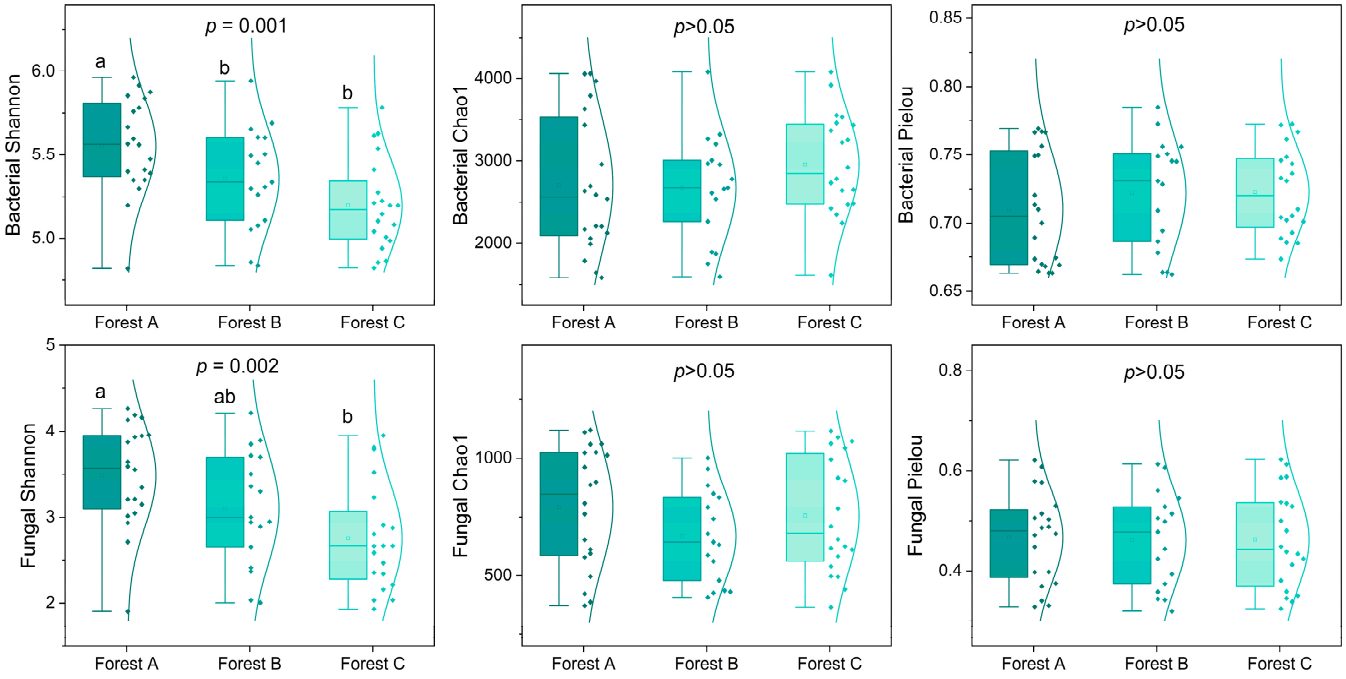

Figure 5. Soil bacterial and fungal diversity across forest types. Significant differences ($p < 0.05$) are denoted by different letters. Forest A represents good-quality forest, Forest B represents medium-quality forest, and Forest C represents poor-quality forest.

Furthermore, the NMDS analysis revealed overlapping distributions of microbial community structures along the NMDS1 and NMDS2 axes among the three forest types (Figure A2). This observation was corroborated by PERMANOVA, which indicated no significant differences in overall community structure across forest types ($F = 1.157$, $p = 0.341$).

3.3. Factors Influencing Soil Microbial Carbon Use Efficiency

Across all forest quality types, SOC and CUE exhibited highly significant positive correlations (Figure 6). The correlation coefficients for Forest A, B, and C were 0.903, 0.948, and 0.993, respectively. Among all measured soil properties, bacterial and fungal Shannon index, SOC, TN, AN, AP, and nutrient stoichiometric ratios were identified as the main factors correlated with CUE (Figure 7).

Within the study area, forest quality significantly influenced microbial diversity by affecting SOC. The SOC, nutrients, and pH together with microbial diversity were associated with CUE (Figure 8a). Except for soil nutrients, these factors had positive associations with CUE. In addition, soil mineralogical properties indirectly related to CUE through SOC. For the total effect of factors, microbial diversity had the greatest association strength with CUE, followed by SOC (Figure 8b).

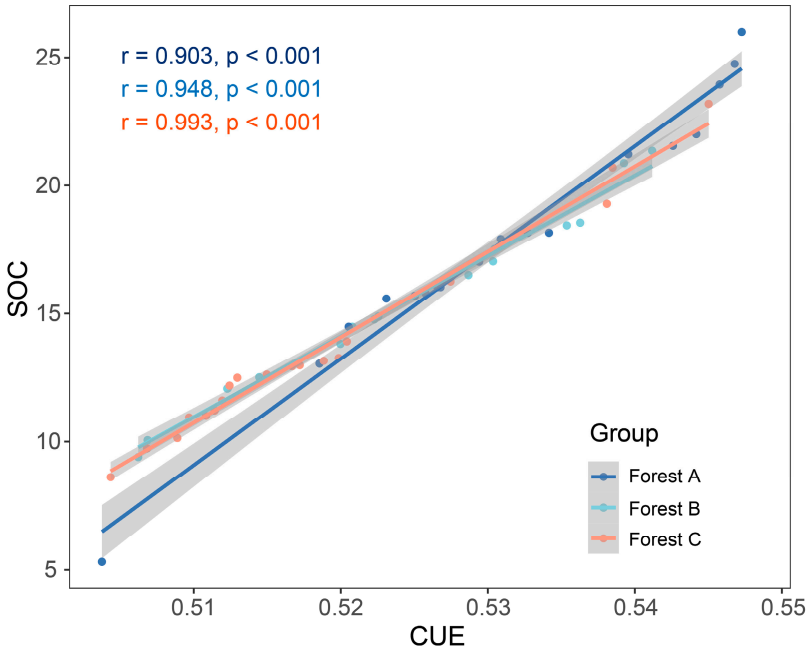

Figure 6. Relationship between soil organic carbon (SOC) and soil microbial carbon use efficiency (CUE). Forest A represents good-quality forest, Forest B represents medium-quality forest, and Forest C represents poor-quality forest. The shaded regions indicate the 95% confidence intervals.

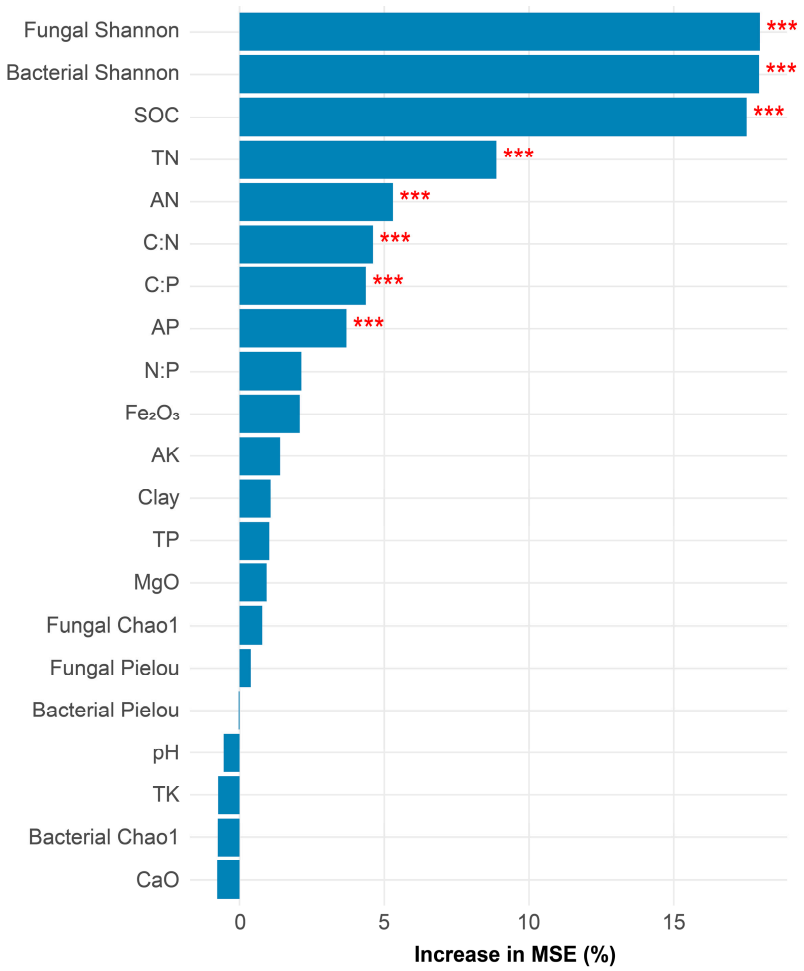

Figure 7. Random forest analysis showing factors influencing soil microbial carbon use efficiency (CUE). MSE (mean squared error) represents the prediction error of the model. ***, $p < 0.001$.

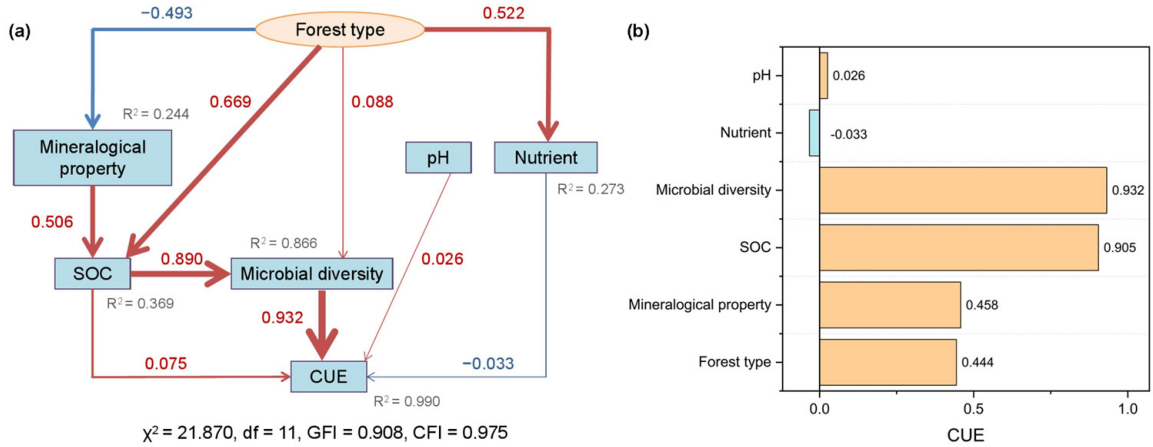

Figure 8. Pathways through which forest quality and soil properties influence soil microbial carbon use efficiency (CUE) (**a**) and the total effects of variables on CUE (**b**). In figure A, red arrows indicate positive effects, while blue arrows denote negative effects. The numbers on the arrows in figure A indicate the standardized path coefficients ($p < 0.05$), and the thickness of arrows indicates the strength of the pathways.

4. Discussion

4.1. Associations Between Forest Quality Gradients on Microbial CUE

This study provides the first systematic evidence of soil microbial CUE patterns across a forest quality gradient in subtropical coniferous plantations. In previous studies, the specific difference in stand conditions within similar forest types has remained underexplored. We observed a significant decline in CUE as forest quality decreased. Microbial CUE represents the balance between anabolism (biosynthesis of biomass) and catabolism [5,6]. A decline in CUE indicates that a smaller proportion of assimilated carbon is allocated to new biomass production. Therefore, the reduced CUE observed in poor-quality forests implies a metabolic shift where carbon retention is diminished, suggesting a lower potential for soil carbon sequestration, rather than an enhancement of the carbon sink.

The decline in CUE was closely correlated with SOC content. High-quality forests maintained higher CUE, likely due to the greater quantity and superior quality of labile carbon substrates derived from abundant vegetation layers and diverse litter inputs [36,37]. In these systems, microorganisms can allocate more assimilated carbon to biomass synthesis rather than respiratory loss, thereby enhancing carbon conversion efficiency. In contrast, poor-quality forests exhibited simplified structures and reduced carbon inputs [9]. Under these resource-limited conditions, microorganisms prioritize energy expenditure for basal metabolic maintenance, which may contribute to a reduction in CUE [5].

Further analyses revealed a remarkably strong positive correlation between CUE and SOC. This underscores the importance of carbon substrate availability in associating with microbial carbon allocation [38,39]. Elevated SOC levels in high-quality forests reflect not only a larger total carbon pool but also an optimized chemical composition, dominated by readily decomposable compounds [40]. This reduces microbial metabolic costs for energy acquisition, thereby potentially facilitating greater carbon allocation toward biomass production.

Notably, contrary to previous studies emphasizing nitrogen and phosphorus as dominant drivers of microbial diversity [41,42], our data showed that soil pH and nutrient levels had no significant correlations with microbial diversity. This discrepancy may stem from the specific context of subtropical coniferous plantations. These factors may include common nutrient limitations or indirect effects of understory microclimate change. However, this inference warrants further testing.

4.2. Association of Microbial Diversity with CUE

Both SEM and random forest analyses identified microbial diversity as the factor with the strongest observed association strength with CUE variation, with its explanatory power significantly surpassing that of other measured environmental variables. Crucially, our analysis reveals that the decline in CUE with reducing forest quality is concurrently accompanied by a reduction in microbial diversity as indicated by Shannon index and a concurrent shift in microbial community composition. Highly diverse microbial communities encompass a greater variety of functional taxa and metabolic pathways, enabling adaptive responses to fluctuating substrates through functional complementarity and redundancy [43]. This functional breadth may optimize the partitioning of carbon resources among growth, reproduction, and maintenance [44,45]. In high-quality forests, complex vegetation structures create heterogeneous soil microhabitats, sustaining community complexity and functional stability [19,46–48]. Conversely, lower forest quality co-occurs with reduced microbial diversity and elimination of critical metabolic pathways, which may contribute to the observed diminishment of CUE.

In our study, while the Shannon diversity index declined significantly with forest quality, neither species richness as indicated by the Chao1 index nor community evenness as indicated by the Pielou index exhibited any significant change. Furthermore, the NMDS confirmed that the overall microbial community structure was not different across forest types. However, the taxonomic analysis revealed significant shifts at the phylum level. The relative abundance of copiotrophic phyla (e.g., Actinobacteria, Proteobacteria, and Ascomycota) decreased with reducing forest quality, whereas oligotrophic Acidobacteria increased. These copiotrophs are typically r-strategists characterized by rapid growth and high efficiency in utilizing labile carbon substrates [49]. Their decline in poor-quality forests suggests a shift in the microbial life history strategy from rapid growth to stress tolerance, potentially contributing to lower CUE. It is crucial to clarify that our primary objective was to link ecosystem function to community-level attributes rather than conducting an exhaustive taxonomic census. Although discussing r/K strategies at the phylum level carries inherent limitations [50,51], our core observed association remains robust as it is based on widely accepted whole-community diversity indices. The SEM model delineates a pathway linking forest quality to microbial diversity and subsequently to CUE, though causal inference is limited by the observational design of this study.

Soil nutrient status responded markedly to forest quality variation, with TN, TP, AN, and AP all significantly elevated in high-quality forests. This confirms the profound influence of forest condition on soil nutrient pools [52,53]. Nevertheless, modeling analyses indicated that the association of microbial diversity with CUE was more pronounced than that of nutrient factors, and the overall effect of nutrients on CUE was negative. This counterintuitive pattern may reflect a shift in microbial metabolic strategy under nutrient-enriched conditions, which may potentially increase respiratory carbon loss and reduce CUE. Further investigation is warranted to elucidate the mechanistic links between nutrient availability, microbial life-history strategies, and carbon allocation dynamics.

4.3. Indirect Associations of Soil Mineralogical Properties and Implications for Restoration of Poor-Quality Forests

This study also revealed that high-quality forests exhibit elevated contents of Fe_2O_3, CaO, and MgO. This phenomenon may be attributed to the more intact stand structure of high-quality forests. Richer litter returns and more stable soil microenvironments collectively facilitate mineral weathering and the formation of specific soil mineral phases [54,55]. However, our SEM indicates that soil mineral properties are indirectly associated with CUE, predominantly mediated through SOC rather than via direct pathways. In subtropical

soils, characterized by advanced weathering and abundant Fe bearing minerals, reactive mineral surfaces form stable organo-mineral complexes with organic matter [20,56]. This physicochemical protection mechanism substantially suppresses microbial decomposition of SOC, which may contribute to the observed CUE patterns.

These findings carry critical implications for the ecological restoration of poor-quality subtropical coniferous forests. Reduced forest quality diminishes above-ground biomass and biodiversity. The observed decline in protective mineral fractions with decreasing forest quality suggests a weakened capacity of soils to stabilize SOC. The reduction in CUE implies heightened carbon mineralization and CO_2 efflux to the atmosphere. Collectively, these processes underscore the potential adverse impact of low forest quality on soil carbon sequestration potential. This aligns with a previous study linking selective logging to accelerated soil carbon loss [57]. Accordingly, restoration strategies should prioritize holistic improvement of forest quality to concurrently strengthen biotic (e.g., microbial diversity and functional redundancy) and abiotic (e.g., mineral-associated carbon protection) mechanisms governing soil carbon retention. Such integrated approaches can foster a virtuous cycle of carbon accumulation and ecosystem recovery.

We also acknowledge several limitations of this study. First, we cannot establish strict causal relationships between forest quality and CUE, nor can we confirm that lower-quality forests represent a temporal degradation trajectory from high-quality forests. Second, climatic factors like temperature and precipitation influence CUE. Our samples were collected over several summer months within the same growing season. Although this period represents typical conditions in this subtropical climate, subtle variations in temperature and precipitation still occurred. To mitigate these effects, our experimental design emphasized spatial replication across many plots. This strategy helped average out fine-scale temporal heterogeneity. Third, our analysis was confined to 0–20 cm of mineral soil, where microbial activity is typically highest. However, CUE likely decreases with depth due to lower substrate quality and physical constraints. Future research should extend findings to deeper profiles to understand the vertical dimension of carbon cycling. Finally, the patterns observed in this single-year study require further validation over longer timescales.

5. Conclusions

This study elucidates how forest quality relates to CUE across a coniferous forest gradient in the Wuyi Mountains. Forest quality was significantly associated with soil physicochemical properties, nutrient availability, and microbial diversity, with high-quality forests exhibiting higher SOC, nutrients, and microbial Shannon indices. CUE showed strong positive correlations with both forest quality and SOC. SEM identified pathways linking forest quality to CUE through SOC, nutrient availability, pH, and microbial diversity. Crucially, microbial diversity emerged as the factor with the strongest observed association with CUE, exerting a stronger influence than abiotic factors such as SOC and mineralogy. These findings demonstrate that lower forest quality co-occurs with reduced microbial diversity and lower CUE, thereby weakening soil carbon sequestration potential. Given the central role of microbial diversity in associating with soil carbon dynamics, restoring stand structural complexity and fostering microbial diversity should be prioritized in sustainable forest management practices.

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Appendix A

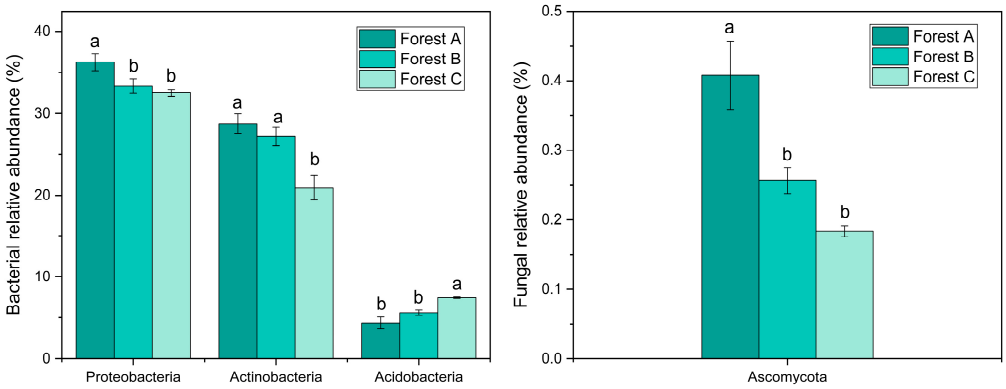

Figure A1. Soil bacterial and fungal taxa with significant differences among forest types ($p < 0.05$). Significant differences ($p < 0.05$) are denoted by different letters. Forest A represents good-quality forest, Forest B represents medium-quality forest, and Forest C represents poor-quality forest.

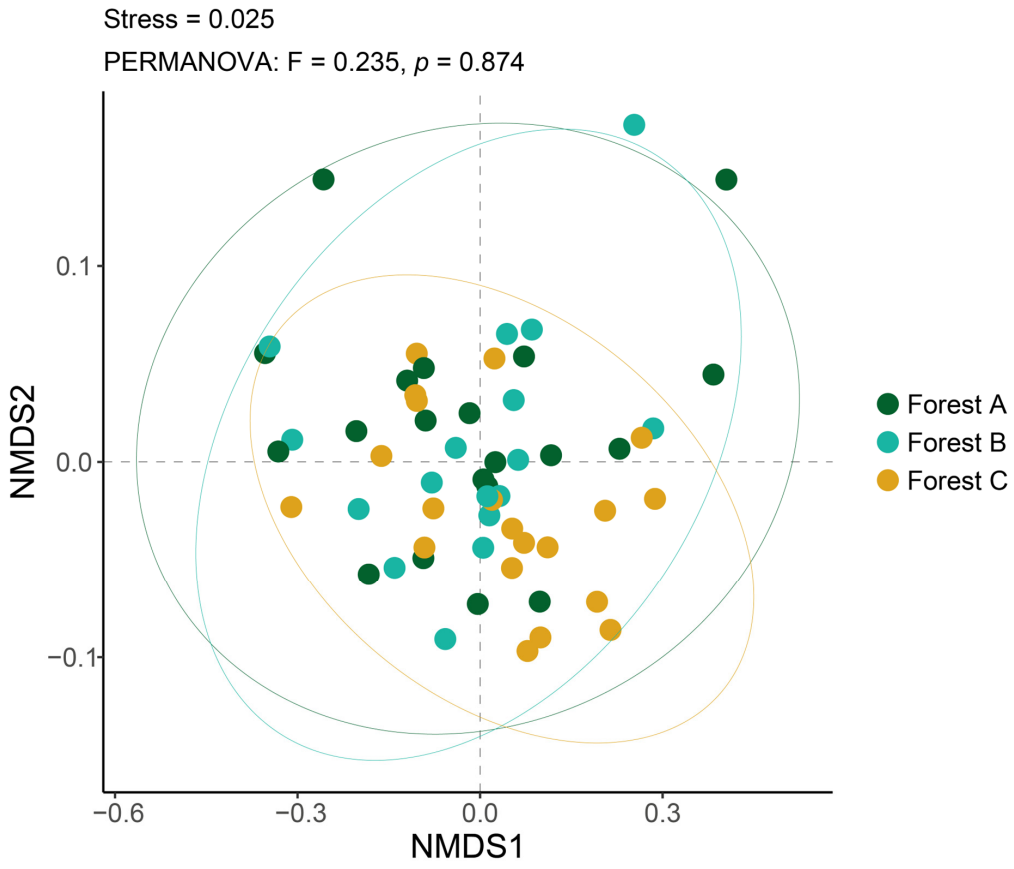

Figure A2. Results of microbial non-metric multi-dimensional scaling (NMDS) based on Bray–Curtis dissimilarity. Forest A represents good-quality forest, Forest B represents medium-quality forest, and Forest C represents poor-quality forest.

References

1. Kirschbaum, M.U.F.; Cowie, A.L.; Peñuelas, J.; Smith, P.; Conant, R.T.; Sage, R.F.; Brandão, M.; Cotrufo, M.F.; Luo, Y.; Way, D.A.; et al. Is tree planting an effective strategy for climate change mitigation? *Sci. Total Environ.* **2024**, *909*, 168479. [CrossRef]
2. Raza, T.; Qadir, M.F.; Khan, K.S.; Eash, N.S.; Yousuf, M.; Chatterjee, S.; Manzoor, R.; Rehman, S.U.; Oetting, J.N. Unraveling the potential of microbes in decomposition of organic matter and release of carbon in the ecosystem. *J. Environ. Manag.* **2023**, *344*, 118529. [CrossRef] [PubMed]
3. Wu, H.; Cui, H.; Fu, C.; Li, R.; Qi, F.; Liu, Z.; Yang, G.; Xiao, K.; Qiao, M. Unveiling the crucial role of soil microorganisms in carbon cycling: A review. *Sci. Total Environ.* **2024**, *909*, 168627. [CrossRef] [PubMed]
4. Xu, S.; Song, X.; Zeng, H.; Wang, J. Soil microbial necromass carbon in forests: A global synthesis of patterns and controlling factors. *Soil Ecol. Lett.* **2024**, *6*, 240237. [CrossRef]
5. Hu, J.; Cui, Y.; Manzoni, S.; Zhou, S.; Cornelissen, J.H.C.; Huang, C.; Schimel, J.; Kuzyakov, Y. Microbial carbon use efficiency and growth rates in soil: Global patterns and drivers. *Glob. Change Biol.* **2025**, *31*, e70036. [CrossRef] [PubMed]
6. He, P.; Zhang, Y.; Shen, Q.; Ling, N.; Nan, Z. Microbial carbon use efficiency in different ecosystems: A meta-analysis based on a biogeochemical equilibrium model. *Glob. Change Biol.* **2023**, *29*, 4758–4774. [CrossRef] [PubMed]
7. Shi, J.; Deng, L.; Wu, J.; Huang, Y.; Dong, Y.; Peñuelas, J.; Liao, Y.; Yang, L.; Huang, X.; Zhang, H.; et al. Global change modulates microbial carbon use efficiency: Mechanisms and impacts on soil organic carbon dynamics. *Glob. Change Biol.* **2025**, *31*, e70240. [CrossRef] [PubMed]
8. Stan, K.D.; Sanchez-Azofeifa, A.; Hamann, H.F. Widespread degradation and limited protection of forests in global tropical dry ecosystems. *Biol. Conserv.* **2024**, *289*, 110425. [CrossRef]
9. Babur, E.; Dindaroğlu, T.; Uslu, Ö.S.; Gozukara, G.; Ozlu, E. Long-term effects of land use conversion on soil microbial biomass and stoichiometric indices in eastern mediterranean karst ecosystems (1981–2018). *Land Degrad. Dev.* **2025**, *36*, 5666–5680. [CrossRef]
10. Betts, M.G.; Yang, Z.; Gunn, J.S.; Healey, S.P. Congruent long-term declines in carbon and biodiversity are a signature of forest degradation. *Glob. Change Biol.* **2024**, *30*, e17541. [CrossRef] [PubMed]
11. Jing, M.; Zhu, L.; Cherubini, P.; Yuan, D.; Li, Z.; Wang, X.; Liu, S. Responses of radial growth of Pinus massoniana and Castanopsis eyrei to climate change at different elevations in south China. *Ecol. Indic.* **2022**, *145*, 109602. [CrossRef]
12. Zhang, K.; Gao, D.; Guo, H.; Zeng, J.; Liu, X. Forest structure characteristics on soil carbon and nitrogen storage of Pinus massoniana plantations in southern subtropic region. *Front. For. Glob. Change* **2022**, *5*, 1022221. [CrossRef]
13. Connor, S.E.; Araújo, J.; Boski, T.; Gomes, A.; Gomes, S.D.; Leira, M.; Freitas, M.d.C.; Andrade, C.; Morales-Molino, C.; Franco-Múgica, F.; et al. Drought, fire and grazing precursors to large-scale pine forest decline. *Divers. Distrib.* **2021**, *27*, 1138–1151. [CrossRef]
14. Sun, D.; Qiu, X.; Feng, J.; Ru, J.; Song, J.; Wan, S. Forest types control the contribution of litter and roots to labile and persistent soil organic carbon. *Biogeochemistry* **2024**, *167*, 1609–1617. [CrossRef]
15. Guo, X.; Luo, Z.; Sun, O.J. Long-term litter type treatments alter soil carbon composition but not microbial carbon utilization in a mixed pine-oak forest. *Biogeochemistry* **2021**, *152*, 327–343. [CrossRef]
16. Zeng, J.; Li, X.; Song, R.; Xie, H.; Li, X.; Liu, W.; Liu, H.; Du, Y.; Xu, M.; Ren, C.; et al. Mechanisms of litter input changes on soil organic carbon dynamics: A microbial carbon use efficiency-based perspective. *Sci. Total Environ.* **2024**, *949*, 175092. [CrossRef] [PubMed]
17. Feng, X.; Qin, S.; Zhang, D.; Chen, P.; Hu, J.; Wang, G.; Liu, Y.; Wei, B.; Li, Q.; Yang, Y.; et al. Nitrogen input enhances microbial carbon use efficiency by altering plant–microbe–mineral interactions. *Glob. Change Biol.* **2022**, *28*, 4845–4860. [CrossRef] [PubMed]
18. Wu, Y.; Zheng, J.; Gao, J.; He, X.; Liu, X.; Chen, Y.; Liu, J.; Li, C. Functional diversity explains ecosystem carbon storage in subtropical forests. *Glob. Change Biol.* **2025**, *31*, e70120. [CrossRef] [PubMed]
19. Liu, S.; Plaza, C.; Ochoa-Hueso, R.; Trivedi, C.; Wang, J.; Trivedi, P.; Zhou, G.; Piñeiro, J.; Martins, C.S.C.; Singh, B.K.; et al. Litter and soil biodiversity jointly drive ecosystem functions. *Glob. Change Biol.* **2023**, *29*, 6276–6285. [CrossRef] [PubMed]
20. Xiao, K.-Q.; Zhao, Y.; Liang, C.; Zhao, M.; Moore, O.W.; Otero-Fariña, A.; Zhu, Y.-G.; Johnson, K.; Peacock, C.L. Introducing the soil mineral carbon pump. *Nat. Rev. Earth Environ.* **2023**, *4*, 135–136. [CrossRef]
21. Ren, S.; Wang, C.; Zhou, Z. Global distributions of reactive iron and aluminum influence the spatial variation of soil organic carbon. *Glob. Change Biol.* **2024**, *30*, e17576. [CrossRef] [PubMed]
22. Akbaş, M.; Babur, E.; Tüfekçioğlu, A. Soil physicochemical and biochemical differentiation under dominant broadleaf forest species in the eastern black sea region. *Forests* **2026**, *17*, 458. [CrossRef]
23. Zhang, Q.; Fan, Z.; Wang, Z.; Tian, Q.; Yang, F. Ecosystems and climate determine terrestrial microbial carbon use efficiency. *Catena* **2025**, *258*, 109279. [CrossRef]
24. Li, L.; Huang, X.; Yang, H. Optimizing land use patterns to improve the contribution of land use planning to carbon neutrality target. *Land Use Policy* **2023**, *135*, 106959. [CrossRef]

25. Shi, J.; Deng, L.; Wu, J.; Bai, E.; Chen, J.; Shangguan, Z.; Kuzyakov, Y. Soil organic carbon increases with decreasing microbial carbon use efficiency during vegetation restoration. *Glob. Change Biol.* **2024**, *30*, e17616. [CrossRef] [PubMed]
26. Che, M.; Gong, Y.; Xu, M.; Kang, C.; Lv, C.; He, S.; Zheng, J. Effects of elevation and slope aspect on the distribution of the soil organic carbon associated with Al and Fe mineral phases in alpine shrub–meadow soil. *Sci. Total Environ.* **2021**, *753*, 141933. [CrossRef] [PubMed]
27. Chen, Q.; Zhang, P.; Hu, Z.; Li, S.; Zhang, Y.; Hu, L.; Zhou, L.; Lin, B.; Li, X. Soil organic carbon and geochemical characteristics on different rocks and their significance for carbon cycles. *Front. Environ. Sci.* **2022**, *9*, 784868. [CrossRef]
28. Na, M.; Xiang, M.; Wang, Y.; Lu, H.; Zhou, J.; Tian, C.; Li, L.; Miao, Y.; Sun, H.; Xu, S.; et al. Freeze-thaw perturbation decreases priming of soil organic carbon mineralization induced by straw return in croplands. *Soil Biol. Biochem.* **2026**, *219*, 110180. [CrossRef]
29. Zhang, Q.; Qin, W.; Feng, J.; Li, X.; Zhang, Z.; He, J.-S.; Schimel, J.P.; Zhu, B. Whole-soil-profile warming does not change microbial carbon use efficiency in surface and deep soils. *Proc. Natl. Acad. Sci. USA* **2023**, *120*, e2302190120. [CrossRef] [PubMed]
30. Xu, H.; Zhang, D.; Tang, Y.; Dai, L.; Kong, W.; Li, X. Response of soil oxides in complex terrain region to environment revealed by hyperspectral observations. *Front. Environ. Sci.* **2023**, *11*, 1138177. [CrossRef]
31. Piaszczyk, W.; Lasota, J.; Foremnik, K.; Błońska, E. Tree species determine soil microbial diversity: Variation in fungal and bacterial communities in temperate forests. *Sci. Rep.* **2026**, *16*, 11022. [CrossRef] [PubMed]
32. Yang, Y.; Wang, H.; Liu, S.; Xue, J.; Clinton, P.; Liu, Y.; Chen, L.; Xiong, J.; Wang, J.; Jiang, W.; et al. Mild decade-warming shifts soil organic carbon composition without altering total stock in temperate and subtropical forests. *Ecol. Lett.* **2026**, *29*, e70339. [CrossRef] [PubMed]
33. Mishra, S.; Mishra, P.; Dubey, P.; Naseem, M.; Patel, A.; Asif, M.H.; Srivastava, P.K. Soil bacterial diversity and its functions shift under varying chromium concentration in tannery waste dumpsite. *Environ. Sustain.* **2025**, *8*, 569–588. [CrossRef]
34. Gao, Y.; Zhang, G.; Jiang, S.; Liu, Y.-X. Wekemo Bioincloud: A user-friendly platform for meta-omics data analyses. *iMeta* **2024**, *3*, e175. [CrossRef] [PubMed]
35. Schermelleh-Engel, K.; Moosbrugger, H.; Müller, H. Evaluating the fit of structural equation models: Tests of significance and descriptive goodness-of-fit measures. *Methods Psychol. Res.* **2003**, *8*, 23–74.
36. Bai, X.; Zhai, G.; Yan, Z.; An, S.; Liu, J.; Huo, L.; Dippold, M.A.; Kuzyakov, Y. Effects of microbial groups on soil organic carbon accrual and mineralization during high- and low-quality litter decomposition. *Catena* **2024**, *241*, 108051. [CrossRef]
37. Cheng, H.; Zhou, X.; Dong, R.; Wang, X.; Liu, G.; Li, Q. Natural vegetation regeneration facilitated soil organic carbon sequestration and microbial community stability in the degraded karst ecosystem. *Catena* **2023**, *222*, 106856. [CrossRef]
38. Okano, H.; Hermsen, R.; Hwa, T. Hierarchical and simultaneous utilization of carbon substrates: Mechanistic insights, physiological roles, and ecological consequences. *Curr. Opin. Microbiol.* **2021**, *63*, 172–178. [CrossRef] [PubMed]
39. Yang, L.; Canarini, A.; Zhang, W.; Lang, M.; Chen, Y.; Cui, Z.; Kuzyakov, Y.; Richter, A.; Chen, X.; Zhang, F.; et al. Microbial life-history strategies mediate microbial carbon pump efficacy in response to N management depending on stoichiometry of microbial demand. *Glob. Change Biol.* **2024**, *30*, e17311. [CrossRef] [PubMed]
40. Xu, C.; Lin, T.-C.; Yang, Z.; Liu, X.; Xiong, D.; Chen, S.; Wu, F.; Yang, Y. Forest conversion effects on soil organic carbon are regulated by soil aggregate stability and not by recalcitrance: Evidence from a reforestation experiment. *Catena* **2022**, *219*, 106613. [CrossRef]
41. Ma, X.; Zhou, Z.; Chen, J.; Xu, H.; Ma, S.; Dippold, M.A.; Kuzyakov, Y. Long-term nitrogen and phosphorus fertilization reveals that phosphorus limitation shapes the microbial community composition and functions in tropical montane forest soil. *Sci. Total Environ.* **2023**, *854*, 158709. [CrossRef] [PubMed]
42. Smith, V.H. Effects of resource supplies on the structure and function of microbial communities. *Antonie Van. Leeuwenhoek* **2002**, *81*, 99–106. [CrossRef] [PubMed]
43. Silverstein, M.R.; Bhatnagar, J.M.; Segrè, D. Metabolic complexity drives divergence in microbial communities. *Nat. Ecol. Evol.* **2024**, *8*, 1493–1504. [CrossRef] [PubMed]
44. Blair, E.M.; Dickson, K.L.; O'Malley, M.A. Microbial communities and their enzymes facilitate degradation of recalcitrant polymers in anaerobic digestion. *Curr. Opin. Microbiol.* **2021**, *64*, 100–108. [CrossRef] [PubMed]
45. Ding, S.; Zhong, J.; Du, S.; Liu, X.; Yao, A.; Xu, X.; Wu, D. Exploring the function of key species in different composting stages for effective waste biotransformation. *J. Environ. Manag.* **2025**, *381*, 125234. [CrossRef] [PubMed]
46. Chapman, S.K.; Newman, G.S. Biodiversity at the plant–soil interface: Microbial abundance and community structure respond to litter mixing. *Oecologia* **2010**, *162*, 763–769. [PubMed]
47. Lyu, M.; Homyak, P.M.; Xie, J.; Peñuelas, J.; Ryan, M.G.; Xiong, X.; Sardans, J.; Lin, W.; Wang, M.; Chen, G.; et al. Litter quality controls tradeoffs in soil carbon decomposition and replenishment in a subtropical forest. *J. Ecol.* **2023**, *111*, 2181–2193. [CrossRef]
48. Liu, X.; Lie, Z.; Reich, P.B.; Zhou, G.; Yan, J.; Huang, W.; Wang, Y.; Peñuelas, J.; Tissue, D.T.; Zhao, M.; et al. Long-term warming increased carbon sequestration capacity in a humid subtropical forest. *Glob. Change Biol.* **2024**, *30*, e17072.

49. Shao, P.; Lynch, L.; Xie, H.; Bao, X.; Liang, C. Tradeoffs among microbial life history strategies influence the fate of microbial residues in subtropical forest soils. *Soil Biol. Biochem.* **2021**, *153*, 108112. [CrossRef]
50. Ho, A.; Di Lonardo, D.P.; Bodelier, P.L. Revisiting life strategy concepts in environmental microbial ecology. *FEMS Microbiol. Ecol.* **2017**, *93*, fix006. [CrossRef] [PubMed]
51. Eme, L.; Tamarit, D. Microbial diversity and open questions about the deep tree of life. *Genome Biol. Evol.* **2024**, *16*, evae053. [CrossRef] [PubMed]
52. Du, X.; Li, X.; Wang, J.; Xu, J.; Gao, J. Climate factors dominate the spatial variation of forest soil nutrients: A meta analysis. *Front. For. Glob. Change* **2025**, *7*, 1525250. [CrossRef]
53. Maaroufi, N.I.; De Long, J.R. Global change impacts on forest soils: Linkage between soil biota and carbon-nitrogen-phosphorus stoichiometry. *Front. For. Glob. Change* **2020**, *3*, 16. [CrossRef]
54. Lucas-Borja, M.E.; Hedo de Santiago, J.; Yang, Y.; Shen, Y.; Candel-Pérez, D. Nutrient, metal contents and microbiological properties of litter and soil along a tree age gradient in Mediterranean forest ecosystems. *Sci. Total Environ.* **2019**, *650*, 749–758. [CrossRef] [PubMed]
55. Castellano, M.J.; Mueller, K.E.; Olk, D.C.; Sawyer, J.E.; Six, J. Integrating plant litter quality, soil organic matter stabilization, and the carbon saturation concept. *Glob. Change Biol.* **2015**, *21*, 3200–3209. [CrossRef] [PubMed]
56. Vaughan, D.J.; Lloyd, J.R. Mineral-organic–microbe interfacial chemistry. In *Fundamentals of Geobiology*; John Wiley & Sons, Ltd.: Hoboken, NJ, USA, 2012; pp. 131–149.
57. Qin, Q.; Wagai, R.; Aoyagi, R.; Titin, J.; Kitayama, K. Destructive selective logging in tropical forests causes soil carbon loss through forest degradation and soil redox change. *For. Ecol. Manag.* **2024**, *551*, 121555. [CrossRef]