

Original Research

Structure of Microbial Communities of *Castanopsis hystrix* Plantations at Different Stand-Ages

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Received: 7 May 2025

Accepted: 31 August 2025

Abstract

Soil microorganisms play an important role in nutrient cycling in forest ecosystems, so it is important to investigate the changes in soil microorganisms with forest age. We collected soil at different soil depths (0-10 cm, 10-20 cm, and 20-30 cm) to investigate the microbial phospholipid fatty acids (PLFAs) and the effects of soil properties and plant diversity on soil microbial PLFAs. The results showed that: (1) with the increase of forest age, the total PLFAs, fungi, and bacteria content of the 0-10 cm soil layer showed a decreasing, increasing, and then decreasing trend. (2) Soil fungi and bacteria showed significant correlations with soil organic carbon, pH, available phosphorus, nitrate nitrogen, available nitrogen, total nitrogen, β -glucosidase activity, acid phosphomonoesterase activity, phenol oxidase activity, peroxidase activity, and microbial biomass phosphorus. (3) The total PLFAs, fungi, and bacteria contents in the 0-10 cm soil layer were higher than those in the 10-20 cm soil layer and the 20-30 cm soil layer. It should also be noted that the microbial PLFAs declined as the stand age increased to 10 years, and fertilizers should be reasonably applied to improve soil fertility in future *C. hystrix* plantation forest management.

Keywords: *Castanopsis hystrix*, forest age, microbial community structure, phospholipid fatty acids, plantation forest

Introduction

China has contributed to the global greening process through intensive afforestation projects and now has the largest planted forest area in the world. Most of the

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planted forests are in the young and middle-aged stages. Due to the forest age factor, planted forests may still have huge potential for carbon (C) sequestration in the future, and scientific management policies for planted forests are of great importance in realizing C neutrality in China [1].

Soil microorganisms play a key regulatory role in plant nutrient acquisition, nitrogen (N) and C cycling, and soil formation [2], and directly or indirectly affect the above-ground vegetation species growth dynamics and soil nutrient cycling turnover, thereby altering the species diversity of terrestrial ecosystems, soil nutrient maintenance, and ecosystem functioning [3]. Weak changes in soil microorganisms may lead to significant changes in aboveground-belowground systems' nutrient transformations [4]. Soil microbial phospholipid fatty acids (PLFAs), as a sensitive ecological indicator in terrestrial ecosystems [4-6], can reflect the soil microorganisms' C and N decomposition and mineralization rates, which are affected by soil nutrients and below-ground root residues C and N [5-7].

Many studies have shown that the soil microbial PLFAs content responds differently to vegetation types, mainly originating from the differences in altitudinal gradient, litter biomass, successional stage, and the mutual synergistic effect among soil microorganisms [6, 8]. Previous studies focused on the impact of forest age on carbon storage capacity and microbial community characteristics [9-14]. The soil microbial biomass carbon (MBC), bulk density (BD), total porosity, and total potassium were key factors that affected the bacterial communities [14]. Soil C and N concentrations, as well as PLFAs abundances, increased in older plantations compared to cropland [15]. Few studies focus on the microbial community characteristics of *Castanopsis hystrix* (*C. hystrix*) plantation forests in southern China.

C. hystrix is a valuable timber species in the southern subtropical zonal forests, with a high growth rate in the tropical, subtropical region, with high economic and ecological value, thus planted on a large scale in forestry production practices, and is the main type of ecological public welfare forests [12]. *C. hystrix* is a high-quality timber for furniture making, shipbuilding, craft carving, and building decoration. Its seeds can be used for fodder and wine-making, and the barks and shells can be used to extract tannin. The *C. hystrix* has a large amount of litter, making it a preferred tree species for soil improvement and water conservation [16].

Our earlier studies have found that, with the increase of stand age, *C. hystrix* forest productivity decreases, soil C stock and N limitation increase, while P limitation is alleviated [9, 12]. Six age-sequenced *C. hystrix* forests (6-, 10-, 15-, 25-, 30-, and 34-year-old) operated in the same way at Guangzhou Longyandong Forest Park in Guangdong Province were selected to investigate the trends of microbial characteristics of different forest ages and soil depths (0-10 cm, 10-20 cm, and 20-30 cm). This study aimed to explore (1) the trends of soil microbial communities in *C. hystrix* plantation forests

with forest age and (2) which factors regulate soil microbial communities.

Materials and Methods

Study Area

The study area is located in Guangzhou Longyandong Forest Park, Guangdong Province (23°10'-23°18' N, 113°21'-113°27' E); the soil type is reddish loam, the climate is subtropical monsoon, and the average annual temperature is 21.7°C. The average annual precipitation is 1,694 mm, the existing woodland area is 1,622 hm², the area of ecological public welfare forests accounts for about 932 hm², and 63% of the elevation is between 100-538 m.

The sample plots, with trees dominated by *C. hystrix*, had simple stand forest structures. Due to the uniform cessation of anthropogenic disturbance after planting for 5 years in the *C. hystrix* plantation forests, the native species are beginning to appear, such as *Itea chinensis*, *Aporosa dioica*, *Acronychia pedunculata*, *Ardisia quinquegona*, *Evodia lepta*, *Psychotria asiatica*, *Desmos chinensis*, *Blechnum orientale*, *Lophatherum gracile*, *Adiantum flabellulatum*, *Dicranopteris dichotoma*, *Pteris semipinnata*, *Ottochloa nodosa*, and *Lindsaea orbiculata*.

Plot Design

Based on preliminary investigations and multiple treadmills, we finally selected representative *C. hystrix* plantation forests at different restoration stages (6-, 10-, 15-, 25-, 30-, and 34-year-old forest age) as sample plots using a spatial instead of a temporal method (Table 1). Three 20×20 m sample plots were used for each forest age stage. In July-August 2020, to ensure that the selected sample plots had the same or similar stand conditions and forest structural composition, all sample plots were widely distributed spatially. The distance between sample plots of six forest ages was at least 1 km to avoid spatial autocorrelation, and all sample plots were at least 20 m from the forest edge to minimize the forest edge effect [9-12].

Field Sampling and Measurements

Soil samples were collected separately in August 2020 within the *C. hystrix* plantation forest. All soil samples were sieved through a 2 mm sieve, and the mass of each soil sample was about 90 g. The samples were divided into two parts. One sample was stored at -20°C for determining microbial biomass and PLFAs, and the other sample was stored in the refrigerator at 4°C for the determination of soil physical and chemical properties.

Soil microbial community composition was determined by phospholipid fatty acid methods [14, 16-18]. This includes: extraction, separation, purification,

Table 1. Information on the sampling sites.

Site characteristics	Stand Age (years)					
	6	10	15	25	30	34
Location	113.42 E, 23.25 N	113.39 E, 23.23 N	113.42 E, 23.26 N	113.40 E, 23.23 N	113.38 E, 23.26 N	113.40 E, 23.25 N
Altitude (m a.s.l.)	115	120	150	105	175	225
Direction (°)	NW	S	SW	E	N	S
Canopy density (%)	0.7 ± 0.1	0.9 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.9 ± 0.1	0.8 ± 0.1
Tree DBH (cm)	16.7 ± 0.1	12.3 ± 0.9	19.1 ± 4.5	19.0 ± 1.5	13.6 ± 2.6	23.9 ± 2.6
Tree height (m)	6.1 ± 0.1	7.9 ± 0.6	9.8 ± 1.6	11.9 ± 1.0	9.4 ± 1.6	13.1 ± 1.5
Basal area (m ² ha ⁻¹)	18.3 ± 1.1	22.2 ± 6.2	34.1 ± 0.5	35.7 ± 3.3	28.4 ± 0.5	40.1 ± 2.3
Density (tree ha ⁻¹)	750.0 ± 43.3	1391.7 ± 376.1	891.7 ± 316.6	1058.3 ± 158.8	1008.3 ± 232.3	633.3 ± 80.4
Shrub cover (%)	-	21.7 ± 14.9	21.1 ± 7.9	20.8 ± 13.5	30.8 ± 12.5	13.4 ± 5.4
Herb cover (%)	-	6.3 ± 4.9	20.4 ± 10.0	28.9 ± 11.3	24.8 ± 9.0	15.6 ± 5.1
Tree species richness	1.0 ± 0.0	2.7 ± 1.5	5.7 ± 3.8	3.3 ± 0.6	6.0 ± 1.0	3.7 ± 1.2
Shrub species richness	-	5.7 ± 0.6	9.7 ± 1.5	5.7 ± 0.6	6.3 ± 1.5	5.7 ± 1.5
Herb species richness	-	5.0 ± 2.0	5.7 ± 0.6	4.7 ± 1.2	3.0 ± 1.2	4.0 ± 1.7

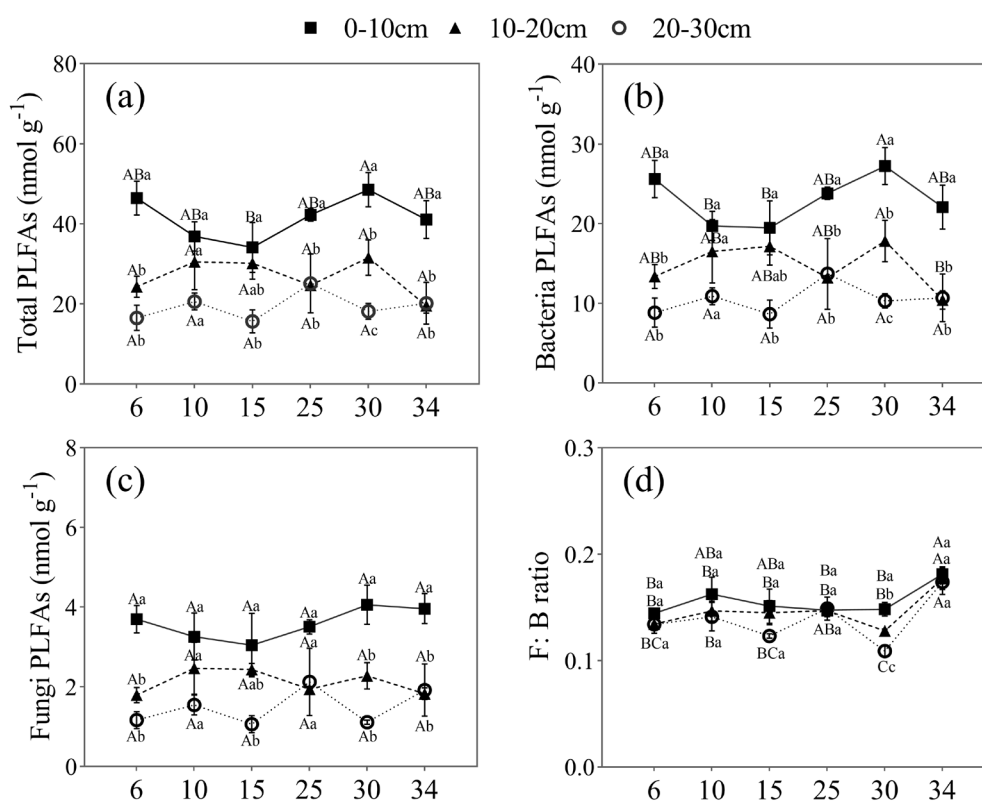


Fig. 1. Characterization of (a) total phospholipid fatty acids (total PLFAs), (b) bacteria PLFAs, (c) fungi PLFAs, and (d) fungi: bacteria ratio (F:B ratio) in *Castanopsis hystrix* plantations of six forest ages (6a, 10a, 15a, 25a, 30a, and 34a). Different capital letters represent significant differences between stand ages on the same soil layer ($p < 0.05$). Different lowercase letters represent significant differences between soil layers (0-10 cm, 10-20 cm, and 20-30 cm) on the same stand age ($p < 0.05$).

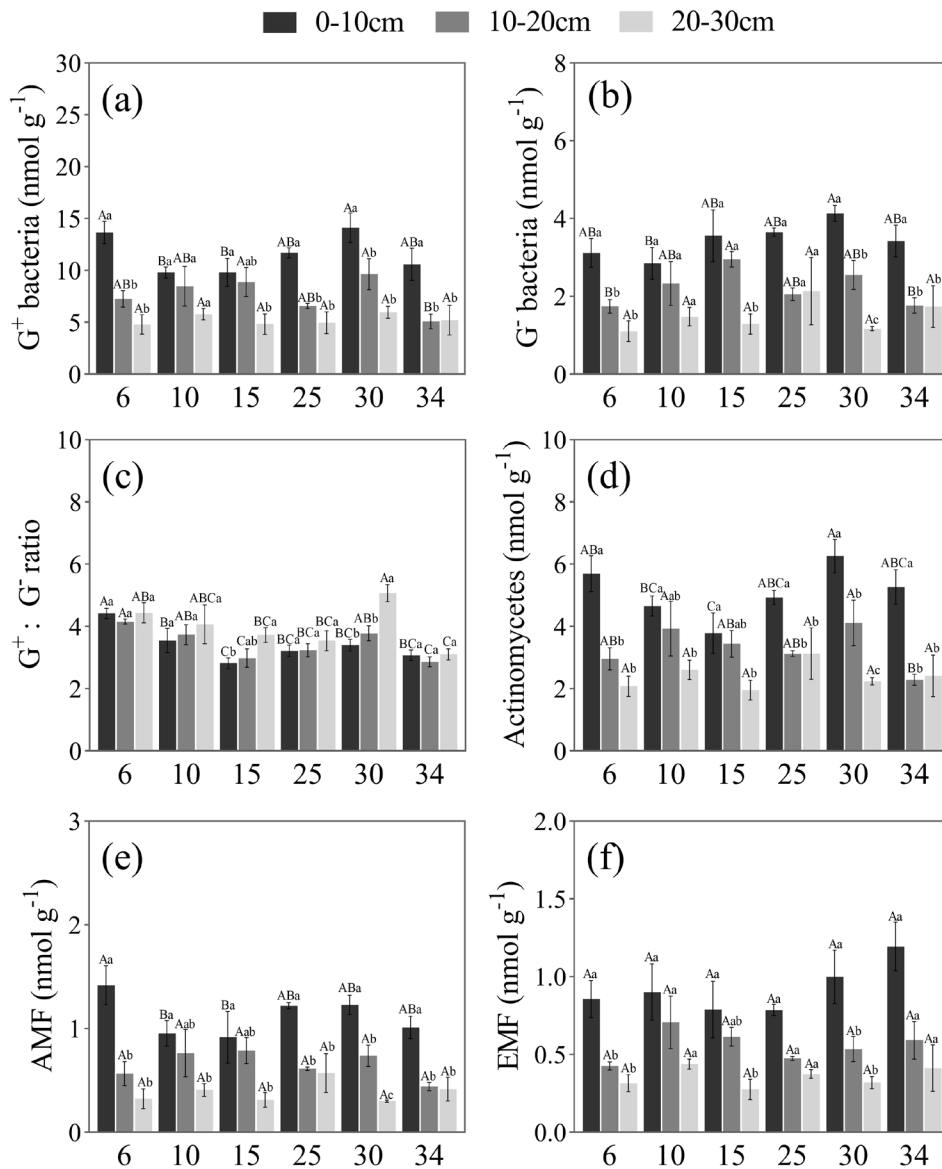


Fig. 2. Characterization of soil (a) Gram-positive bacteria (G^+ bacteria), (b) Gram-negative bacteria (G^- bacteria), (c) $G^+ : G^-$ ratio, (d) actinomycetes, (e) arbuscular mycorrhizal fungi (AMF), and (f) ectomycorrhizal fungi (EMF) in *Castanopsis hystrix* plantations of six forest ages (6a, 10a, 15a, 25a, 30a and 34a). Different capital letters represent significant differences between stand ages on the same soil layer ($p < 0.05$). Different lowercase letters represent significant differences between soil layers (0-10 cm, 10-20 cm, and 20-30 cm) on the same stand age ($p < 0.05$).

and extraction of phospholipids from soil extracts, followed by the addition of methanol for reaction to form fatty acid methyl esters, and determination of the content of various fatty acids by chromatography [16, 17]. According to the method mentioned by Sheng et al. (2025) [16], the soil pH was determined by air-drying with a water-soil ratio of 2.5:1; the soil BD and water content (SWC) was determined by drying and weighing; soil organic carbon (SOC) was measured by oxidation with potassium dichromate and external heating; soil dissolved organic carbon (DOC) was analyzed using a TOC analyzer; total nitrogen (TN) was analyzed by the Kjeldahl method. Total phosphorus (TP), ammonium nitrogen (NH_4^+-N), nitrate nitrogen ($NO_3^- -N$), and available phosphorus (AP) were determined by the

methods according to Li et al. (2024) [11]. Plant diversity (species richness, Simpson dominance, Shannon-Wiener diversity, Pielou dominance, and Margalef richness), microbial biomass C, N, and P (MBC, MBN, and MBP), and enzyme activities (BG, NAG, ACP, CBH, PhOx, and Perox) were determined by the methods according to Sheng et al. (2025) [16].

Statistical Analysis

One-way analysis of variance (ANOVA) was used to test the effect of stand age on soil properties, soil microbial biomass, and microbial PLFAs. Data were processed and analyzed using Excel 2020 and SPSS 22.0 software and graphed using GraphPad Prism 8

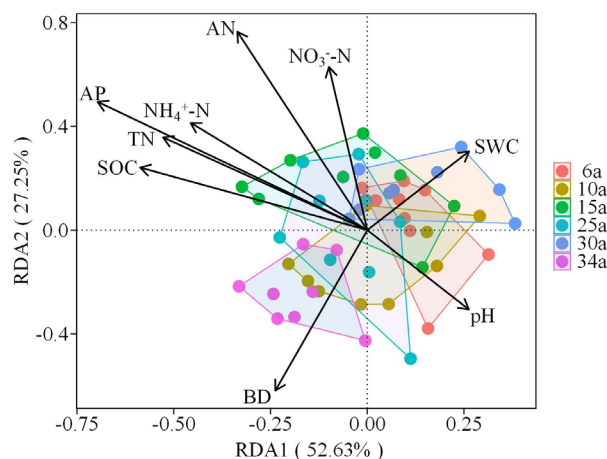


Fig. 3. Redundancy analysis of soil microbial communities and soil properties in *Castanopsis hystrix* forests of six stand ages (6a, 10a, 15a, 25a, 30a, and 34a). The arrows represent soil factors, and the dots of different colors represent samples of different forest ages. The angle between the arrow line and the sorting axis indicates the correlation between a soil indicator and the sorting axis; the smaller the angle, the higher the correlation. SOC, soil organic carbon; TN, total nitrogen; $\text{NH}_4^+\text{-N}$, ammonium nitrogen; $\text{NO}_3^-\text{-N}$, nitrate nitrogen; AP, available phosphorus; AN, available nitrogen; BD, bulk density; SWC, soil water content.

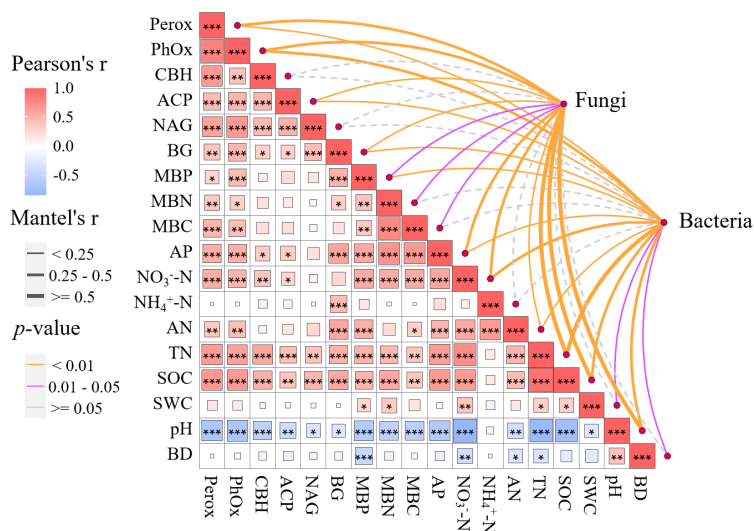


Fig. 4. Correlation of soil fungi and bacteria contents with soil properties, enzyme activities, and microbial biomass C, N, and P. BD, bulk density; SWC, soil water content; SOC, soil organic carbon; TN, total nitrogen; AN, available nitrogen; $\text{NH}_4^+\text{-N}$, ammonium nitrogen; $\text{NO}_3^-\text{-N}$, nitrate nitrogen; AP, available phosphorus; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; MBP, microbial biomass phosphorus; ACP, acid phosphomonoesterase activity; BG, β -glucosidase activity; NAG, N-acetylglucosaminidase activity; PhOx, phenol oxidase activity; Perox, peroxidase activity; CBH, cellobiohydrolase activity. *** $p<0.001$; ** $p<0.01$; * $p<0.05$.

software. Redundancy analysis (RDA) was performed using R Studio 4.4.2 (*vegan* and *tidyverse* packages). Pearson's correlation analysis and Mantel's test were performed using R Studio 4.4.2 (*hmisc*, *corrplot*, *vegan*, *dplyr*, *ggcor*, and *ggplot2* packages). The structural equation model was performed using R Studio 4.4.2 (*piecewiseSEM*, *QuantPsyc*, and *lme4* packages).

Results

Characterization of Total PLFAs, Fungi, Bacteria, and Fungi-to-Bacteria Ratio

Soil total phospholipid fatty acids (total PLFAs) and fungi PLFAs were not significantly affected by stand age in the *C. hystrix* plantation forest (Fig. 1). There were no significant differences between the fungi PLFAs of six stand ages. In the 10–20 cm soil layer, the fungi-to-bacteria ratio (F:B ratio) of the 34-year-old stand was significantly higher than that of the other stand stages ($p<0.05$). In the 20–30 cm soil layer, the F:B ratio of the

34-year-old stand was significantly higher than the 6-, 10-, 15-, and 30-year-old stands ($p < 0.05$).

Characterization of Microbial Community

In the 0-10 cm soil layer, G⁺ bacteria: G⁻ bacteria ratio (G⁺:G⁻ ratio) in the 6-year-old stand was significantly higher ($p < 0.05$) than the other stands (Fig. 2). In the 10-20 cm soil layer, the G⁺:G⁻ ratio in the 34-year-old stand was significantly lower ($p < 0.05$) than the 6-, 10-, and 30-year-old stands. In the 20-30 cm soil layer, the G⁺:G⁻ ratio in the 34-year-old stand was significantly lower ($p < 0.05$) than in the 6- and 30-year-old stands.

Redundancy Analysis of Soil Microbial Community and Soil Properties

Redundancy analysis (RDA) was used to analyze the interrelationships between soil microbial communities and soil properties in different stand ages of *C. hystrix* plantation forests (Fig. 3). Results showed that the explanatory rates of RDA1 and RDA2 were 52.63% and 27.25%, respectively, with a cumulative explanatory rate of 79.88%. The soil pH was negatively correlated with the soil NO₃⁻-N, NH₄⁺-N, AN, TN, AP, and SOC.

Relationship between Soil Microbial Communities and Environmental Factors

Soil pH showed a highly significant negative correlation ($p < 0.001$) with SOC, TN, NO₃⁻-N, AP, MBC, MBN, MBP, CBH activity, PhOx activity, and Perox activity, while SOC and TN showed a significant positive correlation ($p < 0.01$) with soil enzyme activities (BG, NAG, ACP, CBH, PhOx, and Perox) as well as microbial biomass C, N, and P. The soil NO₃⁻-N and AP content were significantly and positively correlated ($p < 0.001$) with MBC, MBN, and MBP. The Mantel's test revealed that the bacteria content was significantly correlated with soil BD, pH, SWC, SOC, TN, AN, NO₃⁻-N, AP, MBP, BG activity, ACP activity, PhOx activity, and Perox activity ($p < 0.05$, Fig. 4). There was a significant correlation ($p < 0.05$) between fungi content and soil pH, SOC, TN, AN, NO₃⁻-N, AP, MBC, MBN, MBP, BG activity, ACP activity, PhOx activity, and Perox activity.

Furthermore, the study underscores that total PLFAs showed a highly significant positive correlation ($p < 0.05$) with enzyme activities (BG, NAG, ACP, CBH, PhOx, and Perox), and soil properties (SOC, AN, NH₄⁺-N, NO₃⁻-N, TN, TP, DOC, and AP) in the 0-10 cm soil layer (Fig. 5).

Discussion

PLFAs reflect the transient state of microbial changes and are rapidly decomposed after cell death [18, 19]. In this study, the total PLFAs, fungi, and bacteria content

in the 0-10 cm soil layer were higher than the 10-20 cm soil layer and the 20-30 cm soil layer, which may be due to the input of litter to the topsoil (0-10 cm layer), which may stimulate the proliferation of microorganisms [20-22].

A study on *Cunninghamia lanceolata* plantations revealed that total PLFAs, bacteria, fungi, actinomycetes, G⁺ bacteria, and G⁻ bacteria in the topsoil (0-10 cm) were higher in the middle-aged plantation (12-) than in the young plantation (6-) and mature plantation (25-) [21]. Another study revealed that the number and abundance of PLFAs were higher in 13-year-old *Eucalyptus* than those in other younger plantations (3-, 7-, and 10-) in subtropical China [22]. With the increase in forest age, the total PLFAs content in the topsoil showed a trend of decreasing, increasing, and then decreasing, among which the highest PLFAs content was found in the 30-year-old *C. hystrix* forest, which may be attributed to the elevation of soil nutrients. Additionally, bacteria prefer better soil fertility, while fungi are more able to survive in poorer soil fertility, and the F:B ratio can reflect soil quality conditions and ecosystem stability [15, 22]. The highest F:B ratio was found in the 34-year-old *C. hystrix* plantation forest, which indicated that soil fungi dominated in the 34-year-old *C. hystrix* plantation forest, while fungi dominated the decomposition of difficult-to-degrade organic matter and formed slow-releasing humus, which was conducive to long-term carbon storage [9]. Besides, the G⁺:G⁻ ratio can also characterize the changes in soil organic matter and fertility [22]. This study found that the G⁺:G⁻ ratio of the 34-year-old *C. hystrix* plantation forest was relatively lower than that of the other forest ages, which indicated that soil G⁻ bacteria gradually dominated in the 34-year-old *C. hystrix* plantation forest, probably due to G⁻ bacteria were more likely to reproduce in environments rich in organic matter (e.g., apoplastic litter, fertilizer, and plant residues) [21]. The increase of apoplastic litter biomass with stand age in *C. hystrix* plantations could also explain the increase in soil organic matter [9].

Soil fungi and bacteria contents are linked with soil pH, SOC, TN, AN, NO₃⁻-N, AP, BG activity, ACP activity, PhOx activity, Perox activity, and MBP, further confirming that soil properties and enzyme activities are important factors influencing microbial community under different forest ages [23]. Notably, SOC as a major energy source required by microorganisms is considered a key factor in regulating soil microbial biomass and community structure [15, 24-26]. Additionally, soil AN content related to fungi and bacteria content indicated that the soil AN content could influence microbial activity and reproduction capacity.

In this study, the SOC and TN contents of 30-year-old and 34-year-old *C. hystrix* plantation forests were higher than those of other forest ages, also indicating that SOC and TN contents improved after *C. hystrix* plantation forests from middle-aged forest (15-) to the mature forest stage (30- and 34-), which may be due to the increase of apoplastic litter biomass [9-12, 27].

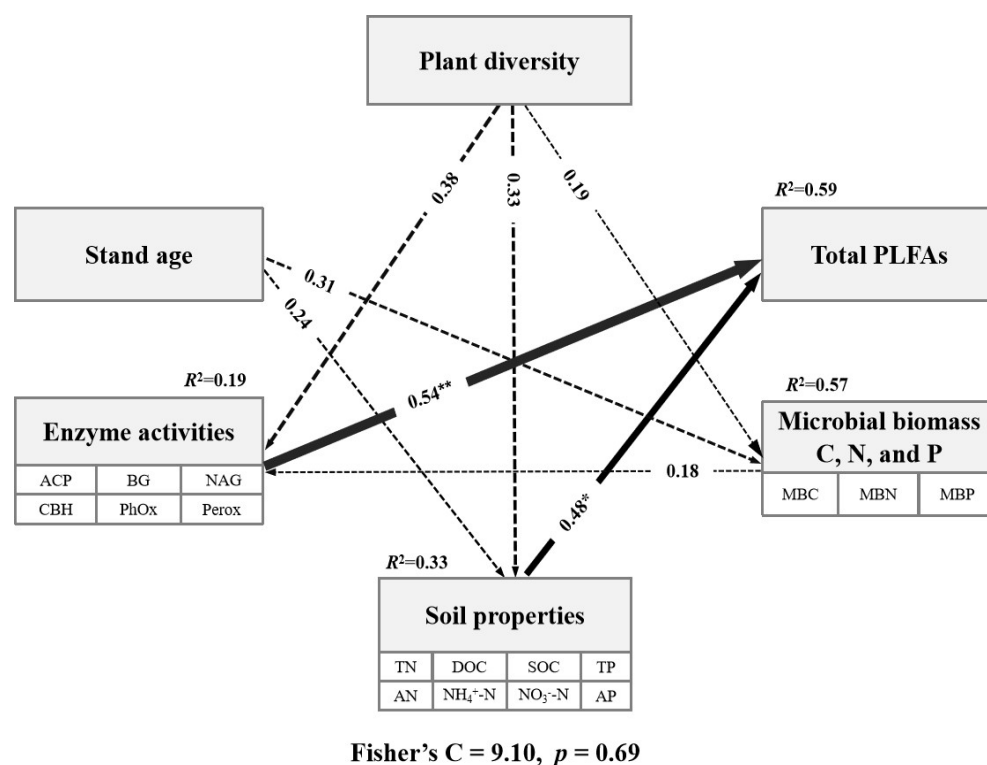


Fig. 5. The structural equation model of stand age, soil properties (TN, DOC, SOC, TP, AN, NH₄⁺-N, NO₃⁻-N, and AP), plant diversity (species richness, Simpson dominance, Shannon-Wiener diversity, Pielou dominance, and Margalef richness), microbial biomass C, N, and P (MBC, MBN, and MBP), enzyme activities (BG, NAG, ACP, CBH, PhOx, and Perox), and total PLFAs in *Castanopsis hystrix* forests of six stand ages (6a, 10a, 15a, 25a, 30a, and 34a). ** $p < 0.01$; * $p < 0.05$. Numbers near the lines represent the standard path coefficients. Solid arrows indicate positive flows of causality ($p < 0.05$); dashed lines indicate non-significant ($p > 0.05$) pathways; arrow widths denote the magnitude of these effects.

Furthermore, the dynamics of soil nutrients and soil microorganisms had the same trend, which indicates that soil nutrients may drive microbial activity [16].

Soil enzyme activity plays multiple roles in forest ecosystems, including promoting organic matter decomposition and participating in soil nutrient cycling [12, 16]. This study underscores that the total PLFAs were positively correlated with enzyme activities (BG, NAG, ACP, CBH, PhOx, and Perox) and soil properties (SOC, DOC, AN, TN, NH₄⁺-N, NO₃⁻-N, TP, and AP) in the 0-10 cm soil layer. Plant communities tend to input more easily decomposable low-molecular organic matter into the soil through leaf litter, root systems, and leaf secretions, thereby increasing soil nutrient content and providing soil microorganisms with a better quality food source, thus promoting microbial growth [22, 27]. Therefore, it is suggested that fertilization can be used to accelerate the community evolution of *C. hystrix* plantation forests in southern subtropics, improve soil fertility, and accelerate the promotion of soil nutrient cycling. Enhance soil microbial activity by monitoring and regulating soil nutrients, such as TN, SOC, AN, NO₃⁻-N, and AP.

Conclusions

This study showed that total PLFAs, fungi, and bacteria content in the topsoil (0-10 cm soil layer) showed a decreasing, increasing, and then decreasing trend with the increase of forest age. The total PLFAs, fungi, bacteria, arbuscular mycorrhizal fungi, and ectomycorrhizal fungi contents in the 0-10 cm soil layer were higher than those in the 10-20 cm soil layer and the 20-30 cm soil layer. Soil fungal and bacterial contents showed significant correlations with SOC, pH, AP, NO₃⁻-N, AN, TN, BG activity, ACP activity, PhOx activity, Perox activity, and MBP. The dynamics of microorganisms are consistent with the dynamics of soil nutrients, and it may be that soil nutrients drive microbial activity. Notably, the microbial content declined as the stand age increased to 10 years, and fertilizers should be reasonably applied to improve soil fertility in future *C. hystrix* plantation forests operated up to 10 years.

Acknowledgments

This study was jointly funded by the National Natural Science Foundation of China (Grant Nos 41991285, 32101342, and 42207158), the Science and Technology Program of Guangdong (Grant No. 2024B1212080005).

and No. 2024B1212070012), the Guangdong Flagship Project of Basic and Applied Basic Research (Grant No. 2023B0303050001), and the Science and Technology Projects in Guangzhou (Grant No. E33309).

Conflict of Interest

The authors declare no conflict of interest.

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