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RESEARCH ARTICLE

Effects of environmental factors and tree species mixtures on the functional groups of soil organic carbon across subtropical plantations in southern China

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Abstract

Purpose There is a large area of coniferous plantations, such as *Cunninghamia lanceolata* and *Pinus massoniana*, in subtropics. Recent evidence has demonstrated that environmental factors and tree species mixtures have significant influences on soil organic carbon (SOC) storage in plantations. However, the diverse functional groups of SOC reveal different chemical stability. Therefore, the functional groups of SOC in subtropical plantations need to research.

Methods The SOC functional groups analyzed by ^{13}C nuclear magnetic resonance, and their distribution were compared among subtropical plantations from northern, middle, and southern latitudes, and between monospecific and conifer-broadleaf mixed plantations.

Results Compared to that of the northern and middle latitude subtropical plantations, the evenness of the four SOC functional groups was higher in the southern latitude subtropical plantations. The temperature and soil bacterial α-diversity were positively correlated, and the soil fungal α-diversity was negatively correlated with the evenness of the SOC functional groups. The proportion of the recalcitrant SOC functional group (alkyl C) was higher in the conifer-broadleaf mixed plantations than in the coniferous plantations, particularly in *C. lanceolata* plantations. The climatic factors, soil pH and soil microbial α-diversity, rather than the functional groups of leaf litter and fine root C, led to the differences in the SOC functional groups between the monospecific and mixed plantations.

Conclusion Our findings highlight that there is a minor risk of C decomposition in the southern subtropical plantations, and converting coniferous plantations to mixed plantations, which could improve the chemical stability of SOC in subtropical regions.

Keywords Plantation · Organic carbon functional group · Soil microbial community · Subtropical regions · Tree species mixture

Abbreviations

A/OA	Alkyl C/O-alkyl C
Arom/OA	Aromatic C/O-alkyl C
LMM	Linear mixed-effects model
NMR	Nuclear magnetic resonance
PCR	Polymerase chain reaction
RDA	Redundancy analysis
SEM	Structural equation model

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SOC	Soil organic carbon
VIF	Variance inflation factor

Introduction

The capacity of plantations to relieve the pressure of harvesting timber on wildwoods has been gradually recognized to facilitate CO_2 fixation and degraded soil restoration (Kelty 2006). There are strategies to grow the forest stock to 6.0×10^9 m^3 by 2030 to augment the national record of 2005, and ultimately to help achieve national carbon (C) neutrality by 2060 in China. Most of this C stock increase will rely on planted forest biomass and soil organic carbon (SOC) storage. It has been verified that East Asian monsoon subtropical forests contributed to large C uptakes in the 1990s and 2000s due to their young stand ages and high level of nitrogen deposition coupled with sufficient and synchronous water and heat availability (Yu et al. 2014). However, the two most widely distributed native coniferous tree plantations (i.e., *Cunninghamia lanceolata* and *Pinus massoniana*) in subtropical China are facing soil fertility degradation, productivity decline and frequent pests and diseases resulting from successive clear-cutting rotations (Liu et al. 2014). Native mixed-species forests, which can provide valuable timber, tree species diversity, and ecosystem services, (Bauhus et al. 2017) are progressively being deemed to be a potential forest management mode for replacing monospecific plantations. The size of the SOC stock has been extensively investigated in subtropical planted forests in recent studies (Li et al. 2020). Previous evidence in the southern subtropical region has demonstrated that the SOC functional groups differ among four monospecific plantations (Wang et al. 2010). The mixed plantations (i.e., *P. massoniana* and *Erythrophleum fordii* or *Eucalyptus urophylla* and *Acacia mangium*) have a higher proportion of recalcitrant SOC than the corresponding *P. massoniana* or *E. urophylla* monospecific plantations (Huang et al. 2017; Wang et al. 2019b). Existing evidence has shown ongoing and projected climatic warming scenarios in subtropical regions in China (IPCC 2021). However, the potential resistance of SOC storage to projected climate change, and whether there is greater SOC stability in the conversion of a plantation type from monospecific to mixed-species plantations across subtropical regions, remain to be further studied.

SOC is a compound of complex organic C functional groups (e.g., alkyl C, O-alkyl C, aromatic C, carbonyl C) (Crow et al. 2009). These complex C functional groups have diverse grades of stability and are resistant to decay in the ecosystem (Lorenz et al. 2007). Carbohydrates such as cellulose, contain abundant O-alkyl C components (Baldock et al. 1992). Lignin-derived aromatics become highly refractory during litter decomposition (Berg and Meentemeyer 2002), but aromatics do not always appear as recalcitrant in soils as initially thought (Cusack et al. 2018; Dignac and Rumpel 2006; Zhu et al. 2020). Several studies showed that alkyl C often accumulate in soil, thus contributing to increasingly stable SOC pools (Lorenz et al. 2007; Mikutta et al. 2006). However, the recent "soil continuum model" predicts that organic debris is continuously processed by the decomposer community into smaller polymers (Lehmann and Kleber 2015). Moreover, the newly proposed "ecosystem property theory" posits that biological and abiotic controls, rather than chemical structure, govern soil organic matter stability (Schmidt et al. 2011). These recent perspectives suggest that any C functional group, despite its chemical composition, would ultimately decay when the appropriate abiotic conditions and decomposer groups are present. Accordingly, we used these frameworks as a foundation to propose a novel concept of SOC functional group evenness; that is, if the evenness of SOC functional groups is reduced, the risk of C emission posed by any one SOM constituent having a huge impact due to climate change and other disturbances could rise, and thus the evenness of SOC functional groups could be used to represent the resistance of C to decomposition (Wang et al. 2019b). A similar perspective has been put forward; that is, the molecular diversity of the organic compounds, rather than the material properties of individual compounds, controls decomposition, because a greater diversity of molecules increases the cost of metabolism (Lehmann et al. 2020).

Many SOC functional groups are derived from plant residues that are transformed by soil bacterial and fungal activities (Kögel-Knabner 2002; Miltner et al. 2012; Simpson et al. 2007). Climatic factors (e.g., temperature and precipitation) are usually considered as the critical factors affecting SOC stocks, and frequently explain a large proportion of the variation in SOC stocks at regional and global scales (Jackson et al. 2017). Temperature is closely related to the microbial decomposition of soil organic matter, and thus loss of SOC (Wiesmeier et al. 2019). Most warming studies have shown that soil carbohydrates generally decrease with increasing temperature in subtropical and temperate forests (Feng et al. 2008; Pisani et al. 2015; Wang et al. 2019a). Rainfall controls forest structure, biodiversity, net primary productivity, and sources of plant-derived C (Clark et al. 2016), and thus influences SOC functional groups (Crow et al. 2009). Soil pH also regulates the capacity for SOC storage and nutrient supplies, and thereby regulates productivity (Chen et al. 2018; Slessarev et al. 2016). Recent studies have put forward that high soil acidity inhibits microbial activities, and increases SOC accumulation (Funakawa et al. 2014). However, the dominant factors controlling the SOC functional groups at the regional scale remain unknown.

This study was carried out to investigate the effects of environmental factors and tree species mixtures on SOC functional groups, and their distributed evenness across subtropical plantations in China, and to clarify the direct and indirect influences of climate, soil pH, litter and fine root quality, and soil bacterial and fungal communities on the functional groups of SOC. We hypothesized that a) the evenness of SOC functional groups would be higher in the southern subtropics due to the lower temperature sensitivity of SOC in the high-temperature regions (Davidson and Janssens 2006), b) tree species mixtures would enhance the proportion of recalcitrant SOC functional groups and evenly distribute diverse functional groups of SOC based on our previous case studies in subtropical plantations (Huang et al. 2017; Wang et al. 2019b), and c) the functional groups of SOC would be determined by the soil bacterial and fungal communities since specific decomposers are expected to relate to specific SOC functional groups (e.g., saprotrophic fungi exclusively decomposing lignin, and bacteria preferentially utilizing carbohydrate) (Baldrian 2008; Wang et al. 2019a).

Materials and methods

Study site

In this study, nine planted forest sites across subtropical China were selected along a latitudinal gradient from 22°03’N to 32°10’N (Fig. 1). Based on climate regionalization in China (Bian et al. 2013), these nine planted forest sites were divided into three subtropical regions (i.e., northern, middle, and southern) (Table 1). There were nine types of plantations in this study: (1) The *P. massoniana* monospecific plantation, (2) *C. lanceolata* monospecific plantation, (3) other coniferous monospecific plantation, (4) broadleaved monospecific plantation, (5) *P. massoniana*-broadleaf mixed plantation, (6) *C. lanceolata*-broadleaf mixed plantation, (7) other conifer-broadleaf mixed plantation, (8) broadleaved species mixed plantation, and (9) coniferous species mixed plantation. For each site, the mean annual temperature (MAT) and the mean annual precipitation (MAP) were recorded from local forest ecological research stations. The MAT of the transect ranges from 14.9 to 22.0 °C, and the MAP ranges from 839 to 1761 mm. Additional details for MAT and MAP are available in Table 1.

Soil, litter, and root samplings

In total, 163 plots were selected in the nine plantation sites, and the field inventories were conducted in 2020. Standardized sampling and measurement protocols were applied across the study. At each site, each plot (each 20 m × 20 m) was randomly established in an individual type of planted forest. In the field surveys, all stems ≥3 cm in DBH (diameter at breast height = 1.3 m) in each plot were individually recorded, measured, and identified to the species level. The main tree species present at the individual sites are shown in Table S1. Besides the trees in the 20 m × 20 m plot, two 5 m × 5 m quadrats and four 1 m × 1 m quadrats were selected for shrubs and herbs, respectively, to investigate and calculate the vegetation Shannon’s index (Spellerberg and Fedor 2003). The Shannon diversity index $(H')=-\Sigma p_i \log_2 p_i$, where $p_i=ni/N$, n_i is the abundance of $_{i}^{th}$ plant species, and N is the total abundance (Shannon and Weaver 1949).

In each plot, ten mineral soil (A horizon) cores (3.5 cm diameter) were randomly collected to a depth of 0-10 cm after removal of the organic horizon to determine soil chemical properties. The soil types are classified as Red soil or Yellow soil in China’s classification system, which are equivalent to a Ferralsol or

GS(2019)1674

Fig. 1 Location of the nine sample sites (red dots). Map source: National Platform for Common Geospatial Information Services (https://www.tianditu.gov.cn/), Check of Drawings Number: GS (2019)1674. Abbreviations of sample sites: PX, Pingxiang; GLM, Jiulian Mountain; LC, Lechang; JPM, Jinpen Mountain; QYZ, Qianyanzhou; ETH, Elephant Trunk Hill; YC, Yichang; JY, Jinyang; PZ, Pengzhou

Table 1 The latitude, longitude, mean annual temperature (MAT), mean annual precipitation (MAP), soil pH (mean ± SE), soil type, and climate region of the nine sample sites

Variables	Latitude	Longitude	MAT (°C)	MAP (mm)	Soil pH	Soil type	Subtropical region
PX (19)	22°03’N	106°51′E	22.0	1328	4.09 ± 0.73	Ferralsol	Southern
GLM (17)	24°35’N	114°26′E	18.5	1761	4.58 ± 0.17	Ferralsol	Middle
LC (27)	25°06’N	113′21’E	19.2	1515	4.54 ± 0.25	Ferralsol	Middle
JPM (15)	25°17’N	115°11′E	18.6	1673	4.47 ± 0.12	Ferralsol	Middle
QYZ (30)	26°44’N	115°03′E	18.9	1458	4.53 ± 0.4	Ferralsol	Middle
ETH (12)	28°10’N	112°51′E	17.7	1386	4.16 ± 0.17	Luvisol	Middle
YC (12)	31°04’N	110°56′E	16.9	1215	4.88 ± 0.22	Ferralsol	Northern
PZ (18)	31°15’N	103°47′E	15.1	1025	4.18 ± 0.18	Luvisol	Northern
JY (13)	32°10’N	104°19′E	14.9	839	5.12 ± 0.71	Luvisol	Northern

Abbreviations of the nine sample sites: *PX* Pingxiang, *GLM* Jiulian Mountain, *LC* Lechang, *JPM* Jinpen Mountain, *QYZ* Qianyanzhou, *ETH* Elephant Trunk Hill, *YC* Yichang, *JY* Jinyang, *PZ* Pengzhou. The numbers in parentheses indicate the number of plots a Luvisol, respectively, according to the World Reference Base for Soil Resources (ISSS–ISRIC–FAO 1998) (Table 1). Each soil sample was transferred to a disposable sterile bag, and all the samples were taken to the laboratory immediately in coolers. The ten cores from each plot were combined and sieved through a 2 mm sieve to carefully remove the roots, plant material, and gravel and to minimize the influence of plant residues on chemical analyses. Each sample was divided into two parts: one was stored at 4 °C for soil chemistry measurements, and the other was stored at −40 °C for DNA extraction. The live root residues (diameter ≤ 2 mm) were separated by visual inspection (Vogt and Persson 1991), and then combined in each plot.

Soil, litter, and root chemical analyses

The soil pH was measured from homogenized samples by a 1:2.5 soil to deionized water ratio using a glass electrode (Table. 1). The organic C functional groups of soil, litter, and fine root samples were analyzed by solid-state ^{13}C nuclear magnetic resonance (NMR) spectroscopy, together with the cross-polarization/total sideband suppression (CP/TOSS) technique (Wang et al. 2019b; Zhang et al. 2015). Before NMR spectral analysis, the soil samples were pretreated with 10% (v/v) hydrofluoric acid to remove Fe^{3+} and Mn^{2+} from the soil, and to concentrate the organic C of a whole soil sample, thus improving the signal-to-noise ratio (Schmidt et al. 1997). The ^{13}C NMR ranges were separated into four common chemical shift areas: carbonyl C (165-210 ppm), aromatic C (110-165 ppm), O-alkyl C (45-110 ppm), and alkyl C (0-45 ppm) (Kögel-Knabner 2002). Alkyl C/O-alkyl C (A/OA) has previously been used as an indicator of soil C quality as a substrate for microbes as well as of the extent of soil organic matter decomposition (Chen et al. 2004; Huang et al. 2008). The ratio of aromatic C/O-alkyl C (Arom/OA) was used to describe the extent of aromatization of SOC during decay (Ono et al. 2013).

Addressing our hypothesis (a) that tree species richness affected the proportion of the various SOC functional groups, we used an evenness index to characterize the organic C functional groups distribution in litter, roots, and soil in this study. The evenness of C functional groups was represented by Pielou's evenness index (J'): $J' = H'/H_{max}$, where H' is the Shannon diversity index, and H_{max} is the maximum possible value of H', which is equal to Ln S, where S is the total number of C functional groups. The Shannon diversity index $(H') = -\Sigma p_i \log_2 p_i$, where $p_i = ni/N$, n_i is the abundance of $_i^{th}$ C functional groups, and N is the total abundance. In this study, there were four C functional groups targeted in this analysis (namely, alkyl C, O-alkyl C, aromatic C, and carbonyl C), and therefore $S = 4$, and $\text{Ln } S = 1.386$; n_i is the percentage of the $_i^{th}$ organic C functional group in the total SOC calculated by the relative intensities for each C functional group region in ^{13}C NMR spectra; and N is the total proportion of various organic C functional groups (Wang et al. 2019b). A higher Pielou's evenness index means that the different C functional groups were distributed more evenly; a lower Pielou's evenness index means that the proportion of individual C functional groups was especially relatively high or low.

Soil bacterial and fungal α-diversity

Shannon diversity Index was used to represent the soil bacterial and fungal α-diversity. Additional details for obtained data of soil microbial community are available in Appendix S1.

Statistical analyses

A linear mixed-effects model (LMM) was used to evaluate the differences in the evenness of SOC functional groups and the individual SOC functional groups in all 163 plots among the three subtropical regions, where the region was treated as a fixed factor, and the forest type was treated as a random factor, to diminish the influence of different forest types. Multiple comparisons of the evenness of SOC functional groups and the individual SOC functional groups among the three subtropical regions were examined by Tukey's HSD test.

The correlation heatmaps were calculated between the SOC functional groups and other variables (Fig. S1). The candidate models for SOC functional groups were investigated for multicollinearity of predictors and assumptions of normality and heteroscedasticity by calculating variance inflation factors (VIFs) and graphically examining plots of residuals (Hall et al. 2020). The criterion $\text{VIF} < 3$

was used to select suitable fixed effects variables in the mixed effects models to remove strongly multicollinear variables (Ouyang et al. 2019). Therefore, structural equation models (SEMs) were used to tease apart the potential direct and indirect effects of abiotic and biotic factors on SOC functional groups among the three subtropical regions. The optimum models for SOC functional groups were selected by comparing Akaike information criterion values among nested models (Hall et al. 2020).

LMM was also used to evaluate the differences in the organic C functional groups in soil, litter and fine roots and the soil microbial community between the monospecific plantations and conifer-broadleaf mixed plantations, where forest type was treated as a fixed factor, and the forest site was treated as a random factor, to diminish the influence of different sampling sites. In total, 100 plots from *P. massoniana* monospecific plantations, *C. lanceolata* monospecific plantations, broadleaved monospecific plantations, *P. massoniana*-broadleaf mixed plantation, and *C. lanceolata*-broadleaf mixed plantation were selected.

We compared the relative importance of different variables using standardized regression coefficients from the LMM. In this LMM, climate, soil pH, the functional groups of litter and fine root C, and soil microbial α-diversity were treated as fixed factors, and forest site was treated as a random factor.

A redundancy analysis (RDA) was used to partition the variation in SOC functional groups (alkyl C, O-alkyl C, aromatic C, and carbonyl C) into fractions explained by the climate, soil, plant C groups and soil microbial community, in which the vectors of the explanatory variables (MAT and MAP, soil pH, litter and fine root C functional groups, soil bacterial α-diversity and soil fungal α-diversity) were taken into consideration. The region and tree species mixing effect on the distribution pattern of the chemical compositions of SOC was assessed using permutational multivariate ANOVA (PERMANOVA).

SEMs were performed using the piecewise SEM package version 4.0.2 in R (Lefcheck 2016). The LMMs were used with the lme4 package in R (https://cran.r-project.org/web/packages/lme4/) (Zuur et al. 2009). RDA and PERMANOVA were performed with the vegan package in R. 4.0.2 (RCoreTeam 2019). All data were standardized before analysis to achieve a normal distribution. Statistical analyses were performed using the R program (version 4.0.2) (RCoreTeam 2019). All significant differences were assessed at a level of $p < 0.05$.

Results

Differences in SOC functional groups of plantations among the three subtropical regions

The overall distribution of the SOC functional groups of the subtropical plantations shifted significantly among the northern, middle, and southern subtropical regions (Table 2). The evenness of the four main SOC functional groups (i.e., alkyl C, O-alkyl C, aromatic C, and carbonyl C) was higher in the southern subtropical plantations than in the northern and middle subtropical plantations (Fig. 2). Among the four main SOC functional groups, the proportion of soil O-alkyl C in total organic C was significantly lower in the southern subtropical plantations than in the

Table 2 Statistical significance (*p values*) and analysis (R^2) of the differences in the distribution of SOC functional groups among the northern, middle, and southern regions ($N = 163$), and between the mono-and mixed-species plantations in subtropical China, based on one-way PERMANOVA

The distribution of SOC functional groups	F. Model	R^2	*p* value
Among the northern, middle, and southern regions	250.7	0.61	**0.001**
Between northern and middle subtropical	129.6	0.48	**0.003**
Between northern and southern subtropical	981.6	0.94	**0.003**
Between middle and southern subtropical	84.8	0.42	**0.003**
Between the mono- and mixed-species plantations	206.3	0.68	**0.001**
Between coniferous and broadleaf plantations	60.9	0.48	**0.001**
Between coniferous and mixed plantations	202.1	0.73	**0.001**
Between broadleaf and mixed plantations	66.8	0.56	**0.001**
Between *C. lanceolata* and mixed plantations	195.1	0.76	**0.001**
Between *Pinus massoniana* and mixed plantations	9.1	0.43	**0.001**

Bold numbers represent statistically significant differences ($p < 0.05$)

northern and middle subtropical plantations, and the proportion of soil aromatic C in total organic C was significantly higher in the southern subtropical plantations than in the northern and middle subtropical plantations (Fig. 3a). The soil Arom/OA was significantly higher in the southern subtropical plantations than in the northern and middle subtropical plantations (Fig. 3b).

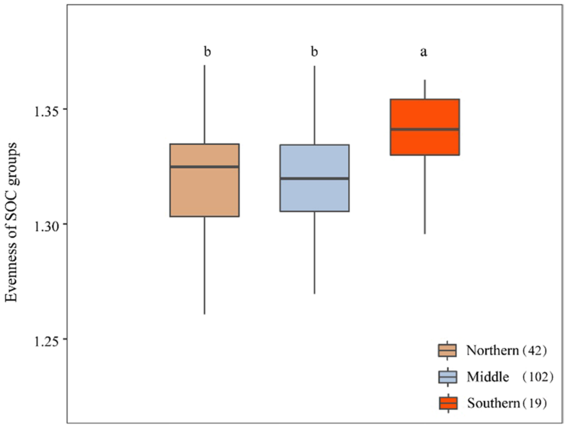
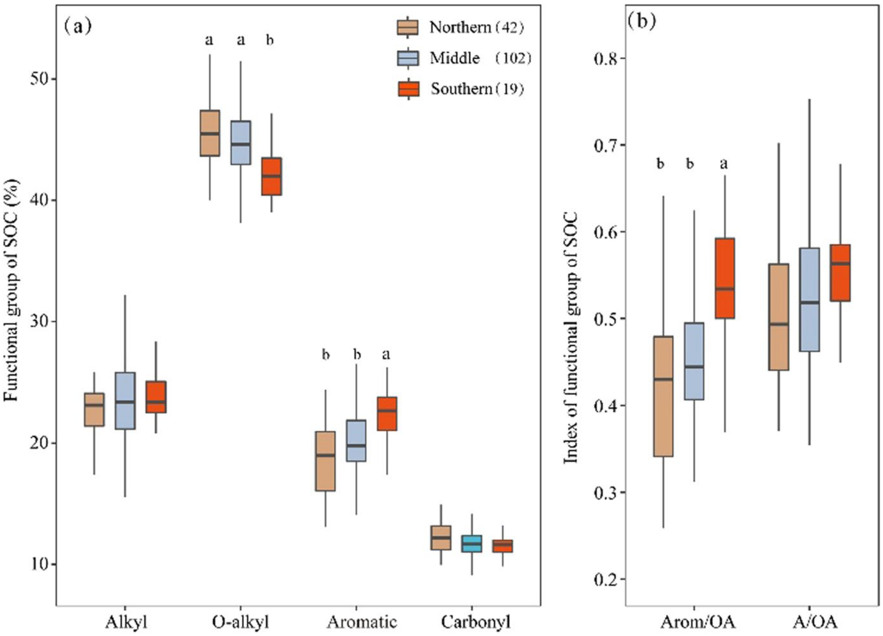


Fig. 2 Differences in the evenness of SOC functional groups among the northern, middle, and southern subtropical plantations, with the forest type variable as a random factor. Boxplots represent the median, the first and third quartiles, and 1.5 × the inter-quartile range. Different lowercase letters of the same category represent statistically significant differences ($p < 0.05$; Tukey-HSD test). The numbers in parentheses indicate the number of plots. ($N = 163$)

Differences in SOC functional groups between the monospecific and mixed plantations

The overall distribution of SOC functional groups also differed significantly between the monospecific and mixed plantations (Table 2). The proportion of soil alkyl C was higher in the conifer-broadleaf mixed plantations than in the monospecific plantations ($p < 0.05$) (Fig. 4a), in the conifer-broadleaf mixed plantations than in the coniferous plantations ($p < 0.01$) (Fig. 4c), in the *C. lanceolata*-broadleaf mixed plantations than in the *C. lanceolata* plantations ($p < 0.05$) (Fig. 4e), and in the *P. massoniana*-broadleaf mixed plantations than in the *P. massoniana* plantations ($p < 0.05$) (Fig. 4g). The proportion of soil aromatic C was lower in the conifer-broadleaf mixed plantations than in the monospecific plantations ($p < 0.01$) (Fig. 4a), in the conifer-broadleaf mixed plantations than in the coniferous plantations ($p < 0.05$) (Fig. 4c), and in the *C. lanceolata*-broadleaf mixed plantations than in the *C. lanceolata* plantations ($p < 0.05$) (Fig. 4e). The soil Arom/OA was lower in all the conifer-broadleaf mixed plantations than in the monospecific plantations ($p < 0.05$) (Fig. 4b), and in the conifer-broadleaf mixed plantations than in the coniferous plantations ($p < 0.05$) (Fig. 4d).

Fig. 3 Differences in the functional groups of SOC (**a**), and aromatic/O-alkyl C (**b**) among the northern, middle and southern subtropical plantations, with the forest type variable as a random factor. Boxplots represent the median, the first and third quartiles, and 1.5 × the inter-quartile range. Different lowercase letters of the same category represent statistically significant differences ($p < 0.05$; Tukey-HSD test). The numbers in parentheses indicate the number of plots. ($N = 163$)



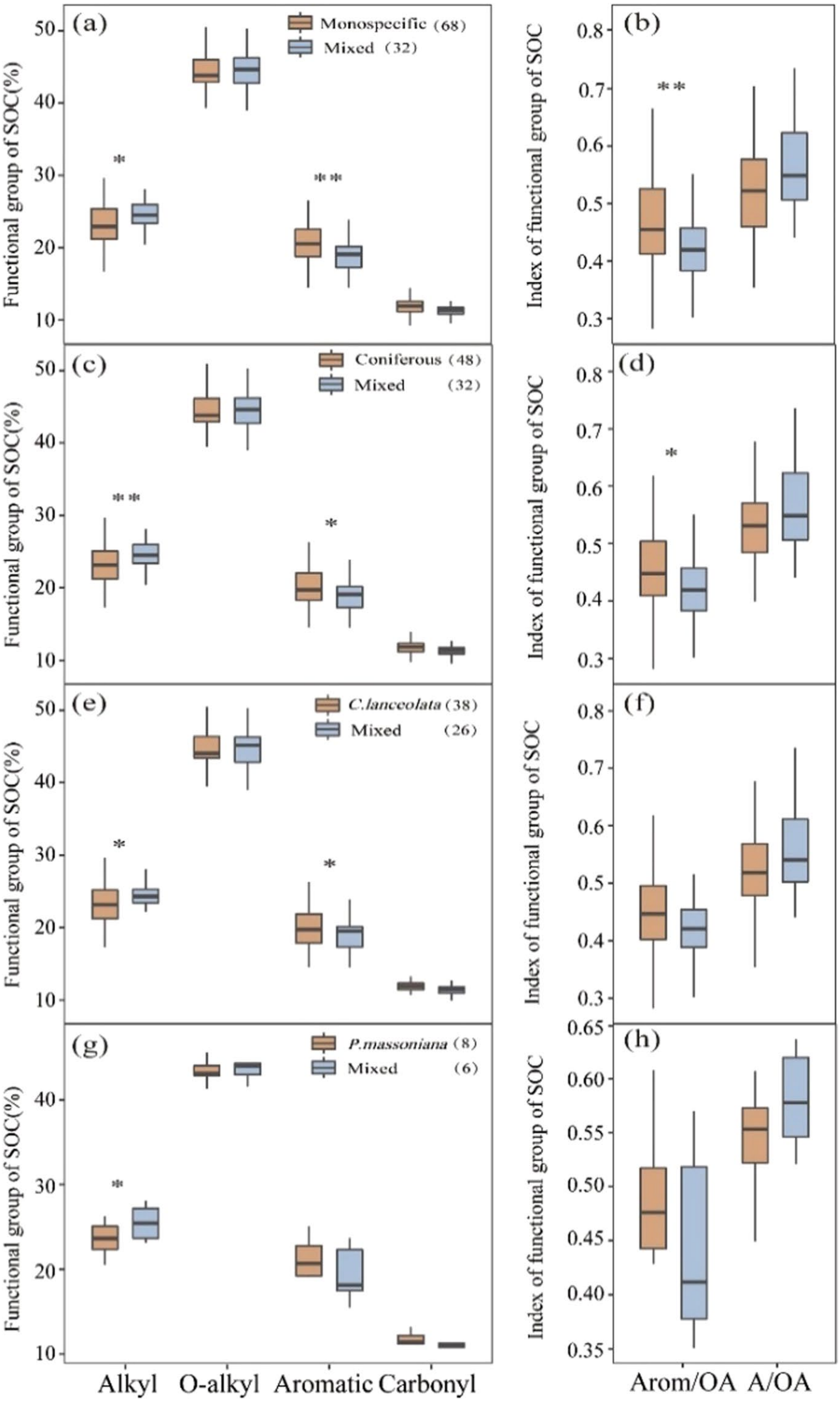


Fig. 4 Differences in the functional groups of SOC and the ratios of the functional groups of SOC between the monospecific and conifer-broadleaf mixed plantations (**a** and **b**), between the coniferous and conifer-broadleaf mixed plantations (**c** and **d**), between the *C. lanceolata* and *C. lanceolata*-broadleaf mixed plantations (**e** and **f**), and between the *Pinus massoniana* and *P. massoniana*-broadleaf mixed plantations (**g** and **h**), with the variable of sampling site as a random factor. Boxplots represent the median, the first and third quartiles, and 1.5 × the inter-quartile range. Asterisks indicate a significant effect. *Corrected significance at $p < 0.05$; **corrected significance at $p < 0.01$. The numbers in parentheses indicate the number of plots. ($N = 100$)

The relationships of abiotic and biotic factors and SOC functional groups across the plantations

MAT had a direct positive influence on the evenness of SOC groups, whereas MAP and soil pH did not have a significant influence on the evenness of SOC groups (Fig. 5a, Fig. S2a). Soil bacterial α-diversity was directly positive, and soil fungal α-diversity was directly negative on the evenness of SOC groups (Fig. 5a, Fig. S2a). The climatic factors (MAT and MAP) had negative and positive effects on soil pH, respectively, and then soil pH affected the soil microbial α-diversity (Fig. 5a). MAT had negative effect on soil fungal α-diversity (Fig. 5a). Vegetation diversity did not have a significant influence on the evenness of the SOC groups, although the MAT and MAP had a significant influence on the vegetation diversity (Fig. 5a, Fig. S2a).

MAT had a direct positive influence, and MAP had a direct negative influence on the soil Arom/OA, whereas soil pH did not have a significant influence on the soil Arom/OA (Fig. 5b, Fig. S2b). Soil bacterial α-diversity had a direct positive influence, and soil fungal α-diversity had a direct negative influence on the soil Arom/OA (Fig. 5b, Fig. S2b). Vegetation diversity did not have a significant influence on soil Arom/OA, although MAT and MAP had a significant influence on vegetation diversity (Fig. 5b, Fig. S2b). Soil pH had a negative effect on soil A/OA (Fig. 5c, Fig. S2c).

The relationships of abiotic and biotic factors and SOC functional groups between the monospecific and mixed plantations

The proportion of alkyl C in litter was higher in the monospecific than in the conifer-broadleaf mixed plantations ($p<0.05$) (Fig. 6a). The proportion of O-alkyl C in fine roots was higher in the monospecific than in the conifer-broadleaf mixed plantations ($p<0.05$) (Fig. 6c). The proportion of aromatic C in litter was lower in the monospecific than in the conifer-broadleaf mixed plantations ($p<0.001$) (Fig. 6a). The proportions of carbonyl C in litter ($p<0.05$) and fine roots ($p<0.01$) were lower in the monospecific than in the conifer-broadleaf mixed plantations (Fig. 6a, c). The Arom/OA ($p<0.001$) in litter C was lower in the monospecific than in the conifer-broadleaf mixed plantations (Fig. 6b).

There were significant differences in soil fungal α-diversity ($p<$ 0.05) and soil bacterial α-diversity ($p<$ 0.01) between the monospecific and conifer-broadleaf mixed plantations (Fig. 7). Soil Arom/OA was positively correlated with MAT (Fig. 8a), and soil A/OA had a negative correlation with MAP (Fig. 8b). Soil pH had a negative influence on soil A/OA (Fig. 8b). The litter and fine root C functional groups, and soil bacterial and fungal community did not respond to soil Arom/OA and A/OA (Fig. 8a, b). Redundancy analysis showed that the MAT, soil pH, and soil fungal α-diversity were the best explanatory variables for the observed changes in the overall SOC functional groups (Fig. 9).

Discussion

Patterns of SOC functional groups in subtropical plantations across regions

This study is the first report on the patterns of SOC functional groups in plantations across regions, as most studies on SOC storage have been carried out at the regional scale (Jia et al. 2021; Li et al. 2019; Liu et al. 2018). Recently, the concept of the diversity and functional complexity of organic C fractions determining the decomposability of soil C (Lehmann et al. 2020), and the high evenness of organic C functional groups minimizing the risk of C decomposition posed by any one SOC constituent having a huge impact during disturbances (Wang et al. 2019b), were consecutively proposed. Hence, the higher evenness of SOC functional groups in the southern subtropical plantations than in the middle and northern subtropics in this study, indicated that the potential resistance of SOC against decay in plantations in subtropical low-latitude climate regions would be larger. The forecast results show that the MAT will continue to increase, and drought will become more frequent in subtropical China (IPCC 2021). Numerous studies have shown that SOC storage generally decreases with increased temperature when controlling for precipitation, which is mainly due to stimulated labile SOC decomposition (Koven et al. 2017; Wang et al. 2019a). The strong negative effect of temperature on SOC storage was also revealed in subtropical forests (Li et al. 2020). Combined with the findings in this study, the potential resistance of forests in high-temperature regions to projected climate warming could be high. Future research needs to further focus on the differences in storages of different SOC functional groups among climate regions.

In this study, the evenness of functional groups increased primarily due to the decrease in the proportion of soil O-alkyl C, and the increase in the

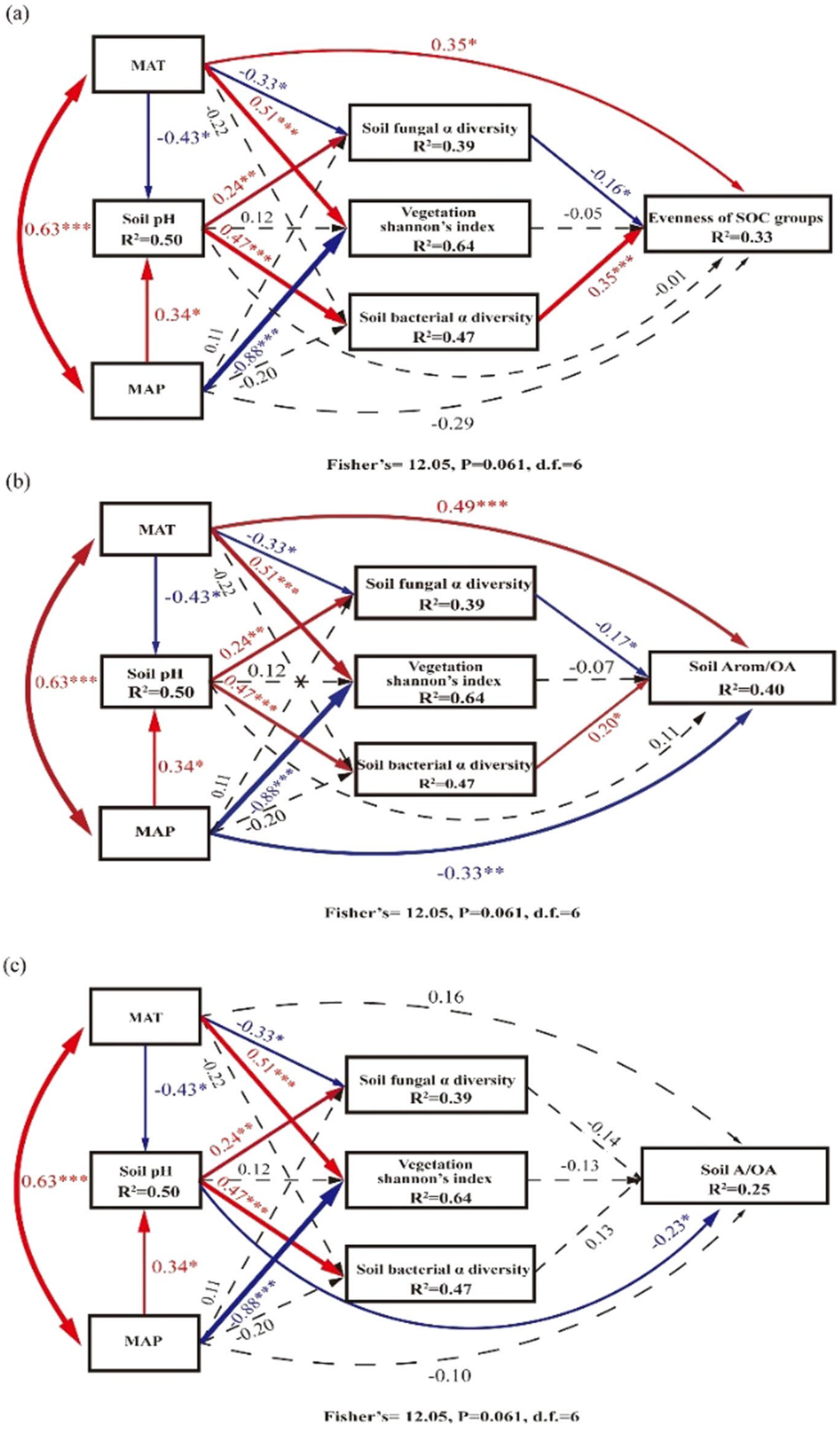


Fig. 5 Structural equation modeling (SEM) analysis depicting the regulatory pathway of the controls of evenness of SOC functional groups, soil Arom/OA, and soil A/OA under the conditions of MAT, MAP, soil pH, soil fungal α-diversity, soil bacterial α-diversity, and vegetation Shannon's index across subtropical plantations in southern China. Numbers adjacent to arrows represent the standardized path coefficients. Solid lines indicate significant positive (red) or negative (blue) piecewise relationships between variables ($p < 0.05$), and dotted lines indicate nonsignificant relationships ($p > 0.05$). R^2 indicates the total variation of the dependent variable explained by all independent variables. Fisher's C statistic refers to the test of the overall model fit, where high p values indicate plausibility of the overall model. $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). ($N = 163$)

Fig. 6 Differences in the functional groups of litter C (**a**), the ratios of the functional group of litter C (**b**), differences in the functional groups of fine root C (**c**), and the ratios of the functional group of fine root C (**d**) between monospecific and conifer-broadleaf mixed plantations, with the variable sampling site as a random factor. The symbols indicate a significant effect, $p<0.05$ (*), $p<0.01$ (**), and $p<0.001$ (***). Boxplots represent the median, the first and third quartiles, and 1.5 × the inter-quartile range. The numbers in parentheses indicate the number of plots. ($N=100$)

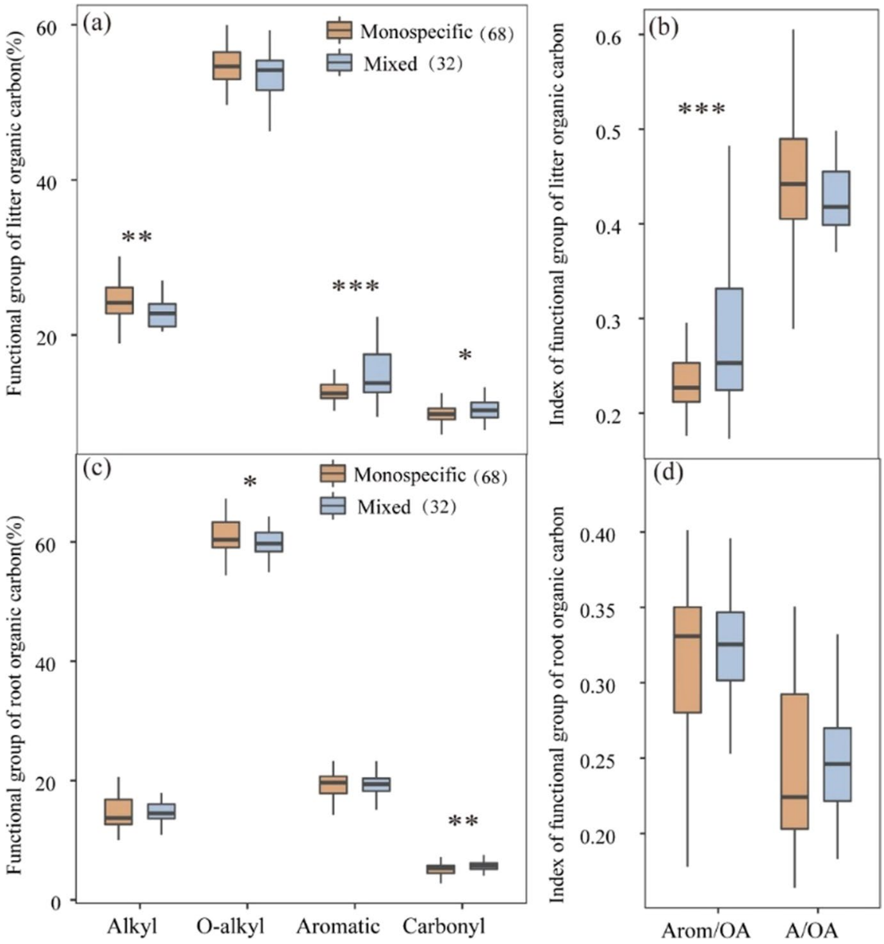
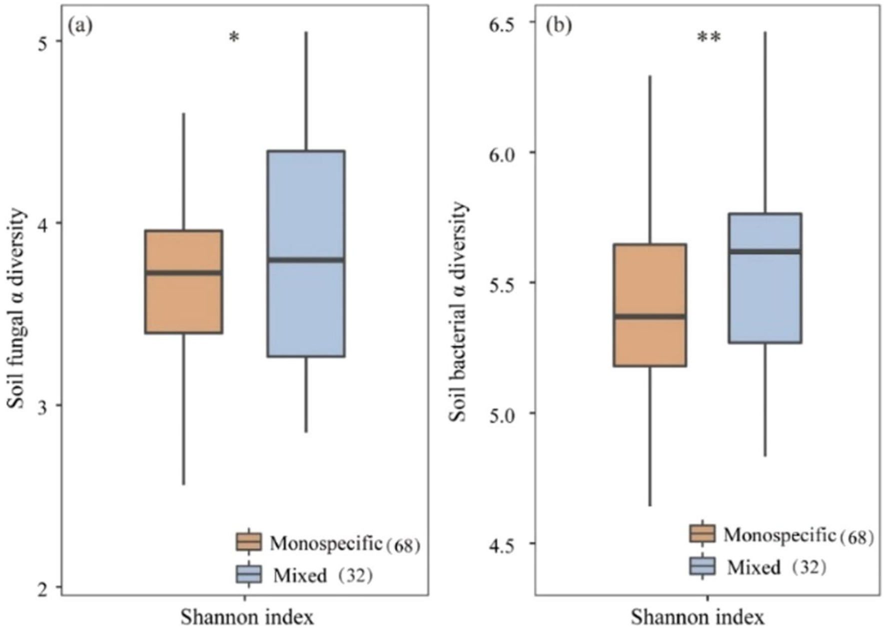


Fig. 7 Differences in soil fungal diversity (**a**), and soil bacterial diversity (**b**) between monospecific and conifer-broadleaf mixed plantations, with the variable of sampling site as a random factor. The symbols indicate a significant effect, $p<0.05$ (*) and $p<0.01$ (**). Boxplots represent the median, the first and third quartiles, and 1.5 × the inter-quartile range. The numbers in parentheses indicate the number of plots. ($N=100$)



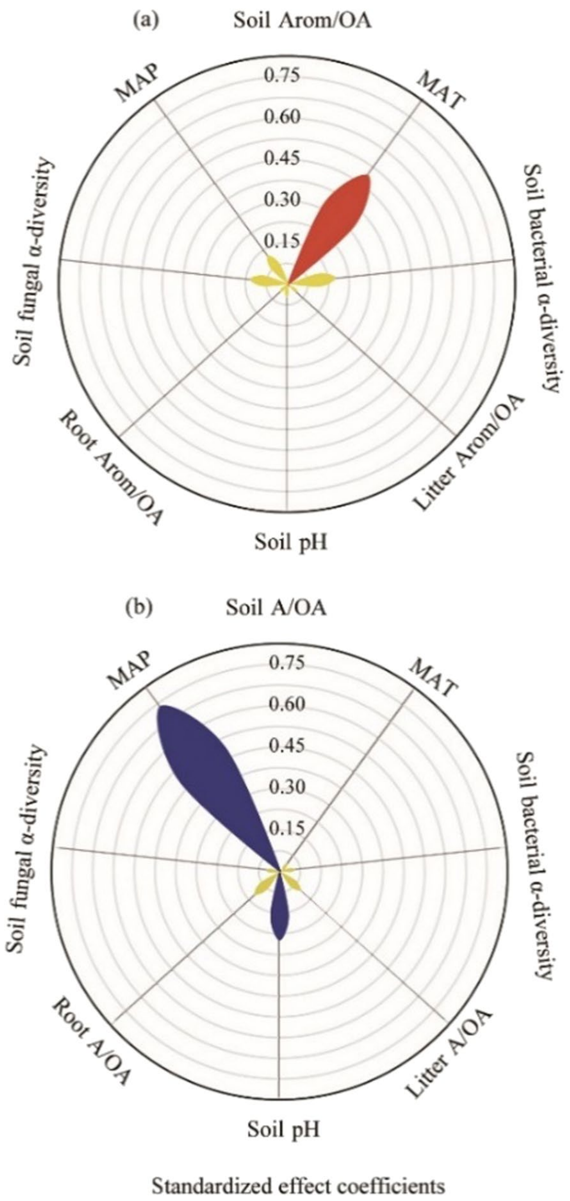


Fig. 8 Standardized effect coefficient of MAT, MAP, soil pH, litter Arom/OA, fine root Arom/OA, soil bacterial α-diversity, and soil fungal α-diversity on soil Arom/OA (**a**), and standardized effect coefficient of MAT, MAP, soil pH, litter A/OA, fine root A/OA, soil bacterial α-diversity, and soil fungal α-diversity on soil A/OA (**b**), among the *Pinus massoniana* monospecific plantations, *C. lanceolata* monospecific plantations, broadleaved monospecific plantations, *P. massoniana*-broadleaf mixed plantations, and *C. lanceolata*-broadleaf mixed plantations. The lengths of the 'petals' in these flower diagrams reflect the effect sizes for the relationships in the models. Red indicates a positive relationship ($p<0.05$), blue indicates a negative relationship ($p<0.05$), and yellow indicates a nonsignificant relationship ($p>0.05$). ($N=100$)

proportion of aromatic C (Fig. 3a); and the soil bacterial α-diversity was positively correlated with the soil Arom/OA, and the soil fungal α-diversity was negatively correlated with the soil Arom/OA (Fig. 5b). Warming preferentially reduced the proportion of soil O-alkyl C by increasing soil bacterial diversity in our previous study in a subtropical plantation, as well as the observed results in the 20-year, long-term, warmed site in Harvard Forest (DeAngelis et al. 2015; Wang et al. 2019a). Except bacteria, soil fungi represent another major part of the microbial population and predominant decomposers of SOC (Miura et al. 2013). Saprotrophic fungi, especially basidiomycetes, are generally effective at and are mainly responsible for lignin decomposition (Baldrian 2008; Martinez et al. 2009). When soil fungal diversity increases, the fungi typically dominating the degradation of lignin, possibly are emerged, and soil aromatic C decomposition may increase. Further studies could quantify the functional gene activity at the mRNA level to improve the understanding of the decomposition and mineralization processes driven by the fungal community in the soil (Li et al. 2017). Soil microbial residues are also important sources of soil organic matter and play a very important role in the accumulation of SOC (Yang et al. 2022; Zhang et al. 2020). For example, soil bacterial and fungal necromass C, which have highly specific muramic acid and glucosamine contents, respectively (Joergensen and Georg 2018; Wang et al. 2021), contribute to the persistent components of SOC (Buckeridge et al. 2022). However, there is still a large uncertainty about soil microbial residues as part of persistent organic matter due to the lack of quantitative assessments of the processes of SOC formation through microbial necromass (Liang et al. 2019).

Reasons for the differences in SOC functional groups between monospecific and mixed plantations

In this study, we found that the proportion of soil alkyl C was higher, and the proportion of soil aromatic C was lower in the conifer-broadleaf mixed plantations than in the conifer monospecific plantations, although there was no significant difference in the evenness of SOC functional groups between the mixed-species and monospecific plantations. These results indicated that the mixture of conifer-broadleaf

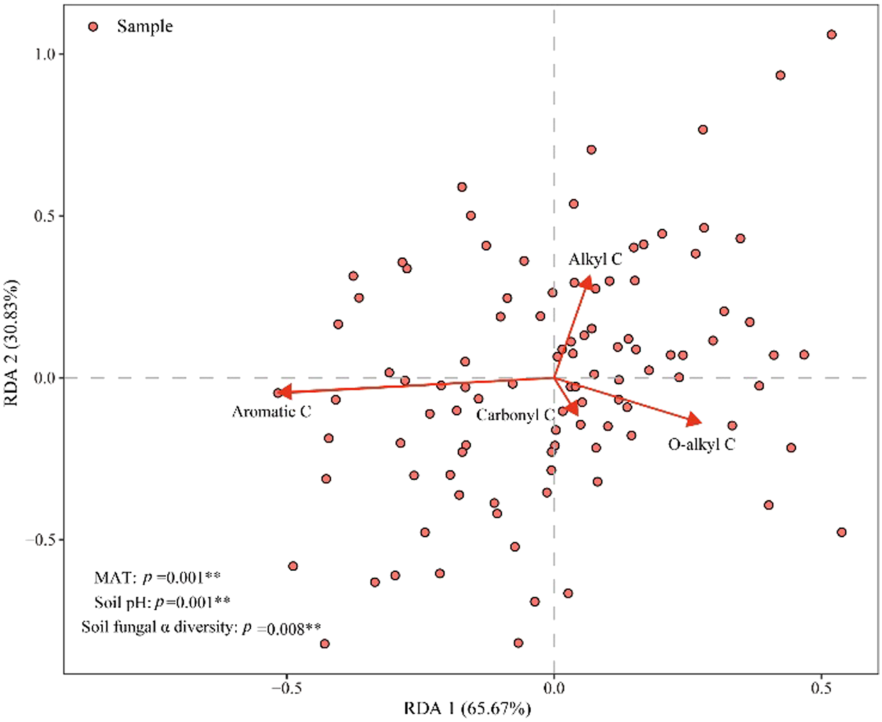


Fig. 9 Ordination biplot diagrams for the redundancy analysis (RDA) displaying the effect of environmental factors on the variance in the chemical composition of soil organic carbon (SOC) among the *Pinus massoniana* monospecific plantations, *C. lanceolata* monospecific plantations, broadleaved monospecific plantations, *P. massoniana*-broadleaf mixed plantations, and *C. lanceolata*-broadleaf mixed plantations. Red arrows represent dependent variables: SOC functional groups (alkyl C, O-alkyl C, aromatic C, and carbonyl C). The symbols indicate a significant effect, $p < 0.01$ (**). ($N = 100$)

tree species, particularly the *C. lanceolata*-broadleaf species mixture, could improve the proportion of recalcitrant alkyl C composition in SOC, and reduce the aromatic degree of SOC in subtropical plantations. Previous studies have shown that the proportion of the soil alkyl C functional group increased after mixing the coniferous species *P. massoniana* and the broadleaved species *Epicrates fordii*, as well as mixing *Eucalyptus urophylla* and the nitrogen-fixing species *A. mangium* (Huang et al. 2017). Here, we further showed a significant increase in the recalcitrant C functional group by converting conifer plantations to conifer-broadleaf mixed plantations, particularly from *C. lanceolata* plantations to *C. lanceolata*-broadleaf mixed plantations, in the subtropics at the regional scale. Moreover, lignin-rich litter residues decrease with the reduction in the proportion of coniferous tree species through mixed-species forest management (Krishna and Mohan 2017). Recent evidence has shown that the conifer-broadleaf tree species mixture accelerates the decomposition of the aromatic C functional group in conifer needles (Cotrufo et al. 2013; Wang et al. 2018). These results suggest possible reasons for the decline in the aromatic C functional group in soils when converting conifer plantations to mixed-species plantations.

The MAT, MAP, soil pH and soil fungal diversity were the influencing factors on the difference in the functional groups of SOC between the coniferous monospecific and conifer-broadleaf mixed plantations in this study (Figs. 8 and 9). As we demonstrated in the above discussion, temperature facilitated the decomposition of soil O-alkyl C (Wang et al. 2019a), and soil fungal community dominating the degradation of lignin accelerated the decomposition of soil aromatic C (Baldrian 2008; Martinez et al. 2009). The proportion of alkyl C increased with the abundance of *Actinobacteria* (Zhang et al. 2018). Under drought condition, the gram-positive *Actinobacteria* display their competitive advantages (Bouskill et al. 2013). These results could explain the significant negative relationship between MAP and soil A/OA in the subtropical plantations in this study. The reducing soil pH increased the soil alkyl C in an acid rain simulation and in a vegetation conversion experiment in subtropical plantations (Guo et al. 2016; Wu et al. 2020). This could be the explanation for the significant negative relationships between the soil pH and soil A/OA and soil alkyl C in the subtropical plantations in this study.

Conclusions

In this study, we found that the various SOC functional groups were distributed more evenly in the southern subtropical plantations than in the northern and middle subtropics, and that the higher MAT promoted the evenness of SOC functional groups. The decrease in soil O-alkyl C with the increase in the diversity of the soil bacterial community, and the increase in aromatic C with the decrease in the diversity of the soil fungal community, contributed to the increasing evenness of the SOC functional groups. The previous findings that the higher proportion of recalcitrant SOC functional groups in the conifer-broadleaf mixed plantations in case studies of the southern subtropics were verified at the subtropical regional scale. Our results suggest that the southern subtropical plantations have a minimized risk of C decomposition due to the projected increase in MAT, and decrease in MAP. These results highlight that the conversion of monospecific conifer to mixed-species plantations in the subtropics could be an effective silviculture method of improving the chemical stability of SOC.

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Declarations

Conflict of interest The authors declare that they have no competing interests.

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