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Changes in the composition of soil microbial communities and their carbon-cycle genes following the conversion of primary broadleaf forests to plantations and secondary forests

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Abstract

The soil organic carbon (C) cycle is primarily mediated by soil microorganisms and their genes that function in the C cycle (C-cycle genes), both of which are strongly affected by land cover disturbance. However, the mechanism underlying microbially mediated soil C loss after conversion of primary natural broadleaf forests (BF) to plantation forests (PF) and secondary forests (SF) remains unknown. Here, we measured soil physicochemical properties and soil microbial community properties, and examined their linkages with microbial C-cycle genes. Forest conversion dramatically decreased the richness of the soil fungal community but not of the bacterial community, and altered the composition of both communities. Analysis of C-cycle genes revealed that the abundance of genes associated with C fixation, methane metabolism, and C degradation decreased by 51.3%, 57.9%, and 67.0%, respectively with the conversion of BF to PF; and by 6.3%, 4.1%, and 15.6%, respectively, with the conversion of BF to SF. The reductions in the abundance of C-cycle genes, especially the reduction of hemicellulose- and lignin-degradation genes, were primarily associated with the declines in the abundance of forest conversion-sensitive microbes indexed by operational taxonomic units (*fs*OTUs, $\beta = 0.41$). *fs*OTUs were taxonomically diverse and included members frequently co-occurring with numerous other microbes in the microbial communities, indicating that the manipulation of *fs*OTUs by forest management could improve soil fertility and soil C sequestration. Forest conversion-induced shifts in *fs*OTUs abundance were associated with changes in soil potassium permanganate oxidizable organic carbon (PXC) concentration, dissolved organic carbon (DOC) concentration, and soil pH. Our results indicate that alterations in soil substrate supply (e.g., DOC and PXC) and soil pH induced by forest conversion may strongly shape *fs*OTUs structure and decrease the abundance of hemicellulose and lignin degradation genes, and consequently increase C loss.

KEYWORDS
carbon cycling genes, forest conversion, microbial co-occurrence, network analysis, soil microbiomes

1 | INTRODUCTION

Soil organic carbon (SOC) plays a vital role in maintaining soil fertility (Six et al., 2000), and the dynamic of SOC affects the global carbon (C) cycle (Wang et al., 2021). Land-use change affects soil C dynamics by influencing C inputs, stability, and turnover via the soil microbial community (Wei et al., 2014). Globally, forest-related land use changes can cause soil C emissions as high as 2.8 Pg C yr^{-1} (Pan et al., 2011) and can reduce the soil as a C sink for greenhouse gases (Lauber et al., 2013). Such undesirable effects can be reduced by sustainable forest management, which focuses on meeting environmental quality standards and protecting the organisms that provide ecosystem services (Hartman et al., 2018; Paula et al., 2014). Deforestation or forest conversion from natural forest to other land uses, generally decreases soil fertility and the soil C stock by reducing the activities of soil microorganisms (Drake et al., 2019; Schwendenmann & Pendall, 2006). Soil microorganisms and their associated C cycling functional genes mediate key ecosystem processes such as litter decomposition and soil organic C mineralization and thus may cause the loss of soil C during the conversion of natural forest to other land uses (Bennett et al., 2012; Liu et al., 2020). Therefore, an improved understanding is needed of how forest conversion causes soil C loss associated with soil microorganisms and their C cycling functional genes.

Soil microorganisms and their genes that function in C cycling ('C-cycle genes,' hereafter) largely determine the forest soil C cycle (Paula et al., 2014). Decomposition of plant biomass by soil bacteria and fungi results in the retention of a part of the plant-derived C in the soil in the form of stable organic matter (Trivedi et al., 2013). Decomposition generally involves the interaction of soil microorganisms (Hartmann & Widmer, 2006). Microbial co-occurrence network analysis is the best tool for understanding the direct and indirect interaction among members of the soil microbial community (Faust & Raes, 2012; Schlaeppi & Bulgarelli, 2015). Network analyses have been increasingly used to identify the specific microorganisms that frequently affect soil microbial community structure, and to determine the patterns of microbial community assembly and the responses of microbial groups to land-use change (Agler et al., 2016; Hartman et al., 2018). To date, the shifts in the compositions and co-occurrence patterns of soil-specific microorganisms caused by forest conversion remain inadequately unexplored.

Managing the soil microbial community as part of sustainable forest management requires that we understand whether soil microorganisms, which are sensitive to forest conversion, have specific network properties. Certain microorganisms are regarded as keystone taxa when they frequently co-occur with large numbers of other microorganisms and when they significantly affect community dynamics and microbial functions (Banerjee et al., 2016). Ecosystem processes (e.g., the soil C cycle) are affected not only by the richness and composition of the soil microbial community but also by the related C-cycle genes (Paula et al., 2014). However, it remains unclear whether the keystone taxa and the corresponding functional genes in soil-specific microbial communities are sensitive to forest conversion. More importantly, little is known about whether microorganisms that are sensitive to forest conversion act alone or with other microorganisms in affecting C-cycle genes. Such information is needed to implement sustainable forest management via the enhancement of those microorganisms that contribute to soil C sequestration.

Researchers have previously studied the effects of land-use change on plant biodiversity (Fang, 2001) and have focused on either the fungal or bacterial community (da C Jesus et al., 2009; Lan et al., 2020; Wang et al., 2021), or microbial genes related to soil C and nitrogen (N) cycling (Paula et al., 2014). Our laboratory previously reported that conversion of primary natural broadleaf forests (BF) to plantation forests (PF) and secondary forests (SF) altered soil chemical properties by decreasing the soil C stock and the activities of soil C-degrading enzymes (hydrolase and oxidase) and reducing new C inputs (Luo et al., 2019, 2020). However, little is known about how specific soil microorganisms and microbial C-cycle genes together regulate the loss of soil C with the conversion of BF to PF and SF due to the shifts of soil physicochemical properties.

In the current study, we used amplicon sequencing, high-throughput quantitative-PCR-based chip (QMEC) technique, and network analysis and structural equation model (SEM) to determine the mechanisms by which soil microorganisms contribute to the loss of soil C with forest conversion of BF to PF and SF. We tested two hypotheses: (1) changes in the structure of soil microbial community, and the reduction in the abundance of C-cycle genes, and especially those that contribute to C degradation would help explain the loss of soil C with forest conversion; and (2) the effects of specific soil microorganisms and of C-cycle genes are coupled in causing the deterioration of soil physicochemical properties and the decline in nutrient availability with forest conversion.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in the Conghua region (113°17′–114°04′E, 23°22′–23°56′N) in Guangdong Province, China (Figure S1). The native vegetation is subtropical and tropical monsoon broadleaf forests (Luo et al., 2020; Zeng et al., 2016). The mean annual temperature is about 21°C, and the mean annual precipitation is about 1900 mm. The average altitude of this region is 590 m and the average slope is 31°. The soils are lateritic red Ferralsols (FAO-UNESCO, 1974) developed from granite.

In the 1950s, large areas of primary native BF were clear-cut and replaced by PF in some cases and by naturally developed SF with the recovery of the natural vegetation. At present, the PF and SF forests have developed without human disturbance for about 70 years due to the closing of the land to achieve reforestation in China (Fang et al., 2001; Zeng et al., 2016). Different parts of PF are planted with *Cunninghamia lanceolata*, *Eucalyptus* sp., *Phyllostachys heterocycle*, or *Pinus massoniana*. In BF, native broadleaf species are dominant, and SF consists of a mixture of broadleaf and plantation species.

In the current study, the comparison of the three forest types was reasonable for two reasons. First, all of the selected study sites have similar geography and climate (Luo et al., 2019). Second, the PF and SF were both covered by the same climax vegetation (i.e., the primary native broadleaf forests, BF) before their establishment, such that all three forest types have varied only in forest management (Zeng et al., 2016). Details on the stand characteristics and geography of the three forest types are provided in Appendix S1.

2.2 | Experimental design and sampling

The 42 selected study sites included 14 sites for PF, 14 sites for SF, and 14 sites or BF (Figure S1). Each site was represented by three plots, each of which measured 30 m × 40 m, 30 m × 30 m, and 30 m × 20 m in the BF, SF, and PF, respectively.

In September 2018, five soil cores (one core from the centre and one from 5 m within each corner) at a depth of 0–10 cm were collected from each of the 126 plots. The soil cores from three plots at the same site were combined and mixed to yield one soil sample per site. Each of the 42 soil samples was passed through a 2-mm-sieve. One part of each sample was air-dried for 2 weeks and then ground and used to determine soil chemical and physical properties as described in the Supplemental methods. A second part was stored at −80°C for the measurement of microbial communities, microbial biomass C, and C-cycle genes. A third part was oven-dried at 105°C to constant weight for the measurement of moisture content.

2.3 | Microbial community analyses

DNA was extracted from approximately 0.5 g of fresh bulk soil of each soil sample (including 14 samples from BF, 14 samples from SF, and 14 samples from PF) using an MN NuceloSpin 96 Soi DNA kit (Gene Company Ltd., Beijing, China) according to the manufacturer's instructions. DNA quality and concentration were assessed using a spectrophotometer-SynergyHTX (Gene Company Limited, Beijing, China). To identify the bacterial and fungal communities, PCR amplicons of the bacterial 16S rRNA gene and fungal ITS2 region were obtained using the primers 338F (5′-ACTCCTA CGGGAGGCAGCA-3′), and 806R (5′-GGACTACHVGGGTWTCTAAT-3′), as well as ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) -ITS2 (5′-GCTGCGTTCTTCATCGATGC-3′). The amplicons were sequenced using the Illumina Hiseq 2500. Taxonomy was assigned to OTUs for bacteria and fungi using UPARSE and FLASH with a phylotype clustered at 97% sequence similarity (Edgar, 2013; Hartman et al., 2018). Taxonomic classification was conducted with SILVA (version 119; http://www.arb-silva.de) and UNITE (version 7.0; http://unite.ut.ee/index.php) databases for bacteria and fungi, respectively. All raw sequence data in this study have been deposited in the National Center for Biotechnology Information Sequence Read Archive under the accession number PRJNA703767 for fungi, and PRJNA703468 for bacteria.

2.4 | Quantification of microbial C-cycle genes

A total of 29 C-cycle genes and one 16S rRNA gene were quantified using a high-throughput QMEC and validated primers to evaluate the potential of the microorganisms to contribute to C cycling (Chen et al., 2020). A detailed account of the methods and processes was provided by Zheng et al. (2018). A threshold cycle (C_T) of 31 was used as the detection limit. Multiple melting peaks with amplification efficiencies beyond the range (0.9–1.1) were discarded. The total relative abundance of each gene category or family was calculated using the approach of Paula et al. (2014).

2.5 | Statistical analysis

Using one-way ANOVAs analysis and Pearson analysis with least significant difference test (LSD) using R version 4.0.2, we determined the effect of forest type on microbial α or β-diversity, the abundance of microbial communities, the abundance of C function genes, and soil properties; significance was set at <0.05. Fungal OTUs (fOTUs) were filtered to eliminate OTUs clustered as a whole phylum or kingdom unassigned or protist or plant. Similarly, bacteria OTUs (bOTUs) clustered as mitochondria and chloroplasts were removed.

We normalized the filtered OTU sequence counts as relative abundance counts per million (CPM) for the general analysis using the BioConductor package *edgeR* (Robinson et al., 2010). We then analyzed the significant various components of β-diversity in each kingdom using unconstrained principal coordinates analysis (PCoA) based on Bray–Curtis dissimilarities (Hartman et al., 2018). Ordination analyses were conducted using the R package *phyloseq* (McMurdie & Holmes, 2013). The effect of forest type on community dissimilarity was evaluated using permutational analysis of multivariate dispersions (PERMANOVA) with the functions *betadisp* and *adonis* in the package *vegan* (Anderson & Willis, 2003; Oksanen et al., 2015). Pairwise differences among the forest types were assessed with the function pairwise.perm.manova in RVAideMemoire package (Hervé, 2016).

To identify *fs*OTUs, we calculated the point-biserial correlation coefficient (r) of OTUs that were linked to one or a combination of forest types based on indicator species analysis using the *indicspecies* package (De Cáceres et al., 2010. Figures S6–S8). The analysis was considered with 10^4 permutations and with significance set at $p < 0.05$ value. OTUs were inferred to be sensitive to forest conversion when their abundances differed among the forest types at a false discovery rate corrected value of $p < 0.05$. After confirmation by both indicator species analysis and likelihood ratio tests with the *edgeR* package (Robinson et al., 2010), *fs*OTUs were identified.

We developed bipartite networks by visualizing the significant ($p < 0.05$) correlation between OTU and one or more of the forest types using the indicator species analysis with the *igraph* package (Csardi & Nepusz, 2006). Spearman rank correlations were assessed between OTUs and normalized CPM counts. The main ecological clusters of strongly associated OTUs were identified based on the constructed co-occurrence networks with all samples. We calculated all

pair-wise Spearman correlations between OTUs and visualized the significant and positive correlations ($p > 0.7$ and $p < 0.001$) with the function Fruchterman–Reingold layout in the *igraph* package. This analysis enabled us to focus only on the OTUs that were likely to interact with each other and that strongly co-occurred.

We subsequently performed in-depth analyses of soil microbial bipartite and co-occurrence networks. We then calculated network characteristics, including the degree of co-occurrence (number of direct correlations to a node), the total number of edges (connections between nodes representing positive, significant correlations between OTUs), and the total number of network nodes (representing OTUs). The main modules (i.e., ecological clusters of soil microorganisms) in the network were visualized in the *igraph* package (Clauset et al., 2004). The relative abundance of each module was calculated by averaging the relative abundances of species in each forest type. We then defined keystone OTUs as those nodes within the top 1% of node degree values of the soil co-occurrence network.

A SEM was used to evaluate the potential direct and indirect effects of the soil C fractions, soil physicochemical properties, and the relative abundance of the main modules of soil microorganisms (modules 1, 2, and 3) on the C-cycle genes. Before constructing SEM, we conducted principal component analysis (PCA) within each group to reduce collinearity. The first component (PC1), which explained 49.5%–98.7% of the total variance of these following factors, was then introduced into a model using AMOS version 24.0 (IBM SPSS, USA). We reduced the soil clay content and moisture content into one variable (Edaphic variables); reduced SOC, dissolved organic carbon (DOC), microbial biomass carbon (MBC), and potassium permanganate oxidizable organic carbon (PXC) into one variable (Soil C); reduced microbial module 1, module 2, and module 3 (Figure 4) into one variable (module abundance); and reduced C fixation, methane metabolism, and C degradation genes into one variable (C-cycle genes). We calculated the standardized total effects of forest type, soil C, soil properties, and module abundance on the C-cycle genes to aid in the interpretation of the SEM. We also evaluated the fit of our model using the root mean squared error of approximation and the model test.

3 | RESULTS

3.1 | Microbial richness decreases with forest conversion

Soil bacterial richness was greater than soil fungal richness, and soil fungal richness but not soil bacterial richness was significantly affected by forest type, that is, fungal richness was higher in BF than in PF and was intermediate in SF (Table 1). Pairwise tests also revealed significant differences in soil fungal communities among the three forest types (Table S2). Among soil bacteria, relative abundance was highest for Proteobacteria (30.6%–32.6%), Acidobacteria (29.3%–33.7%), Actinobacteria (12.3%–13.8%), Chloroflexi (5.7%–10.9%), Verrucomicrobia (4.5%–6.9%), Planctomycetes (3.7%–4.2%), and Gemmatimonadetes (0.8%–1.1%). Among soil fungi, relative abundance was highest for Ascomycota (45.8%–50.5%), Basidiomycota (14.9%–28.0%), Mortierellomycota (5.9%–12.9%), and Mucoromycota (0.4%–2.0%). With forest conversion of BF to SF and PF, the relative abundance of bacteria (Acidobacteria and Actinobacteria) and fungi (Basidiomycota) significantly decreased (Figure 1). Unconstrained PCoA separated the soil fungal communities of the three forest types along axis 1 (Figure 2). The discrete outlier in the bacterial community in PF was associated with a low soil pH value (Figure 2). We did not observe significant differences in the dispersion of soil bacterial and fungal communities (Table S2).

3.2 | Identifying forest conversion sensitive OTUs

The bipartite network with indicator species analysis showed that the abundances of the identified individual fungal and bacterial OTUs (*fs*OTU and bOTUs, respectively) in soil communities varied among

TABLE 1 OTU numbers and α-diversity of soil fungal and bacterial communities as affected by forest types

		Richness		α Diversity	
Forest types	OTUs	Chao1	ACE	Shannon	Simpson
Fungi					
BF	389 ± 16a	459.6 ± 19.1a	449.9 ± 18.6a	3.82 ± 0.10	0.061 ± 0.008a
SF	374 ± 15ab	449.4 ± 21.0ab	433.8 ± 19.3ab	3.49 ± 0.14	0.094 ± 0.014b
PF	332 ± 19b	387.8 ± 19.8b	392.2 ± 14.3b	3.52 ± 0.12	0.085 ± 0.016b
Bacteria					
BF	997 ± 12	1053.4 ± 9.9	1041.0 ± 10.0	5.45 ± 0.04	0.011 ± 0.001
SF	987 ± 17	1044.1 ± 16.2	1029.4 ± 16.4	5.47 ± 0.03	0.011 ± 0.001
PF	976 ± 21	1043.7 ± 19.2	1025.0 ± 18.5	5.40 ± 0.04	0.011 ± 0.001

Note: values are means ± standard error ($n = 14$). For fungi or bacteria, means followed by different letters are significantly different ($p < 0.05$) with least significant difference test (*LSD* test).

BF, SF, and PF indicate natural broadleaf forests, secondary forests, and plantation forests, respectively.

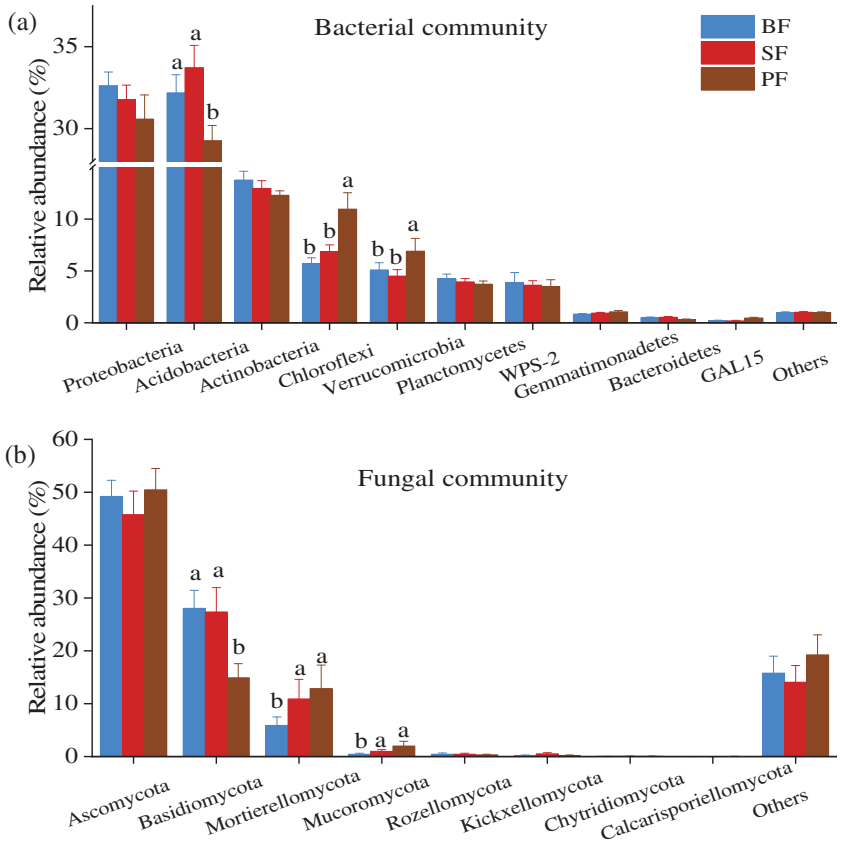

FIGURE 1 Relative abundances of the abundant soil bacteria (a) and soil fungi (b) at the phylum level. 'Others' represents unclassified groups. Values are means ± standard error ($n = 14$). Means with different letters among the three forest types are significantly different at $p < 0.05$. BF, SF, and PF indicate natural broadleaf forests, secondary forests, and plantation forests, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

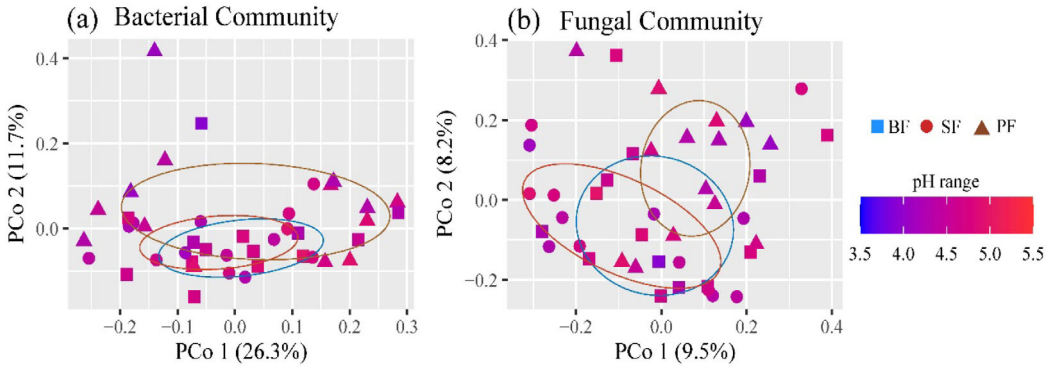

FIGURE 2 Unconstrained PCoA ordinations of bacteria (a) and fungi (b); and forest types are clustered, and point colors indicate soil pH values. Forest type presented the major driver of community variation. The proportion of variation given on each axis refers to the explained fraction of total variation in the community. BF, SF, and PF indicate natural broadleaf forests, secondary forests, and plantation forests, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

the forest types (Figure 3). Many bOTUs were shared by BF and SF but fewer by BF or SF and PF. These relationships at the OUT level indicate a close clustering between BF and SF, but not with PF samples in the ordination analyses. We observed weak clustering of BF fOTUs with both SF and PF.

We then defined the OTUs that were identified by both indicator species and edgeR analysis as *fs*OTUs. In soil, we detected a total of 96 bacterial and 35 fungal *fs*OTUs; these accounted for 5.1% and 9.3% of the total soil bacterial and fungal sequences, respectively (Figure 3a,b). Specific phyla of bacteria (Chloroflexi and Acidobacteria) and fungi (Basidiomycota) varied among the forest types (Figures 1 and 3c,d). Numbers of Acidobacteria and Basidiomycota OTUs were greater in BF and SF than in PF, while numbers of Chloroflexi OTUs were lower in BF and SF than in SF (Figure 1). We also examined the taxonomic assignment and mean relative abundances of the individual *fs*OTUs across the three forest types (Figure S6). Relative abundances were higher for Acidobacteria bOTU1435 and bOTU51 (family Acidobacteria) and for Agaricomycetes fOTU1, fOTU139, fOTU293, and fOTU486 (family Basidiomycota) in BF and SF than in PF, which was consistent with patterns seen at the phylum level (Figures S6–

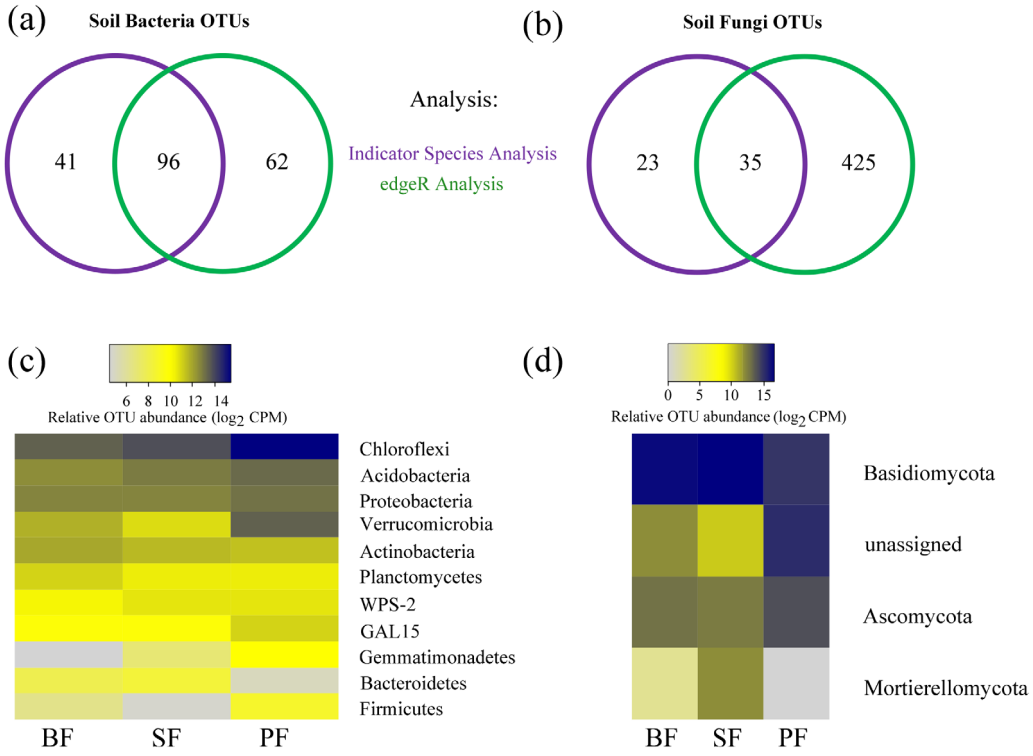

FIGURE 3 Forest conversion-sensitive microbes. Numbers of forest conversion-sensitive bacterial OTUs (a) and fungal OTUs (b) in soil samples, and mean relative abundances (counts per million, CPM; log2 scale) of forest conversion-sensitive OTUs of bacteria (c) and fungi (d). Venn diagrams show the number of OTUs responding to forest conversion identified by indicator species analysis (purple) and by edgR (green). OTUs identified by both methods were defined as forest conversion sensitive OTUs (*fs*OTUs). BF, SF, and PF indicate natural broadleaf forests, secondary forests, and plantation forests, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

S8). Taken together, the results indicate that although most members of the microbial communities were shared among the three types, each forest type supported a specialized cluster of soil fungi and bacteria.

3.3 | Forest conversion alters microbial co-occurrence patterns

We constructed co-occurrence networks for soil fungal and bacterial communities, and calculated their properties (the total number of edges, total number of network nodes, and degrees of co-occurrence; Figure S9). Consistent with the α-diversity analyses (Tables 1 and 2, and Figure S5), the soil bacterial network included a greater number of significant co-occurring OTUs, connections, and *fs*OTUs than the soil fungal network (Figure S9). We also mapped the *fs*OTUs (Table 2 and Figure 3) into the microbial networks, and found that they agglomerated according to forest type, especially PF (Figure S9).

For an in-depth analysis, we investigated the distribution patterns of *fs*OTUs in meta co-occurrence patterns of bacterial and fungal communities (Figure 4 and Table 2). We found that the abundance patterns of inter-kingdom microbial associations varied among the different forest types. In the soil meta-networks, three modules (module 1, module 2, and module 3) contained a relatively high proportion of *fs*OTUs (Figures 4 and S10). The distribution of these sensitive module members in the network partially revealed the potential drivers of community dissimilarity detected in the PCoA ordinations (Figure 2). For instance, the effect of forest conversion on the soil microbial communities was obvious with a discrete module 1 in the soil network, including *fs*OTUs specific to forest type. Module1 was separated from modules 2 and 3, and the separation was largely based on the grouping of *fs*OTUs according to forest types (Figure 4a,b). The forest conversion responsive modules in soil contained a taxonomically broad set of bacteria and fungi (Figure 4c), showing that the different forest types do not target specific microbial lineages.

The *fs*OTUs were identified among highly abundant and low count soil taxa (Figure S11). They had low to medium degrees of co-occurrence, and most keystone OTUs were sensitive to forest conversion (Tables 2 and S3). Taken together, the results indicate that forest conversion substantially altered the co-occurrence patterns of many keystone OTUs, and also affected the independence of their connectivity and abundance of microorganisms.

3.4 | Abundance of C-cycle genes decreases with forest conversion

The total relative abundance of the C-degradation genes (Figure S12b) was significantly higher in BF and SF than in PF ($p < 0.05$), that is, conversion of BF to PF greatly reduced the numbers

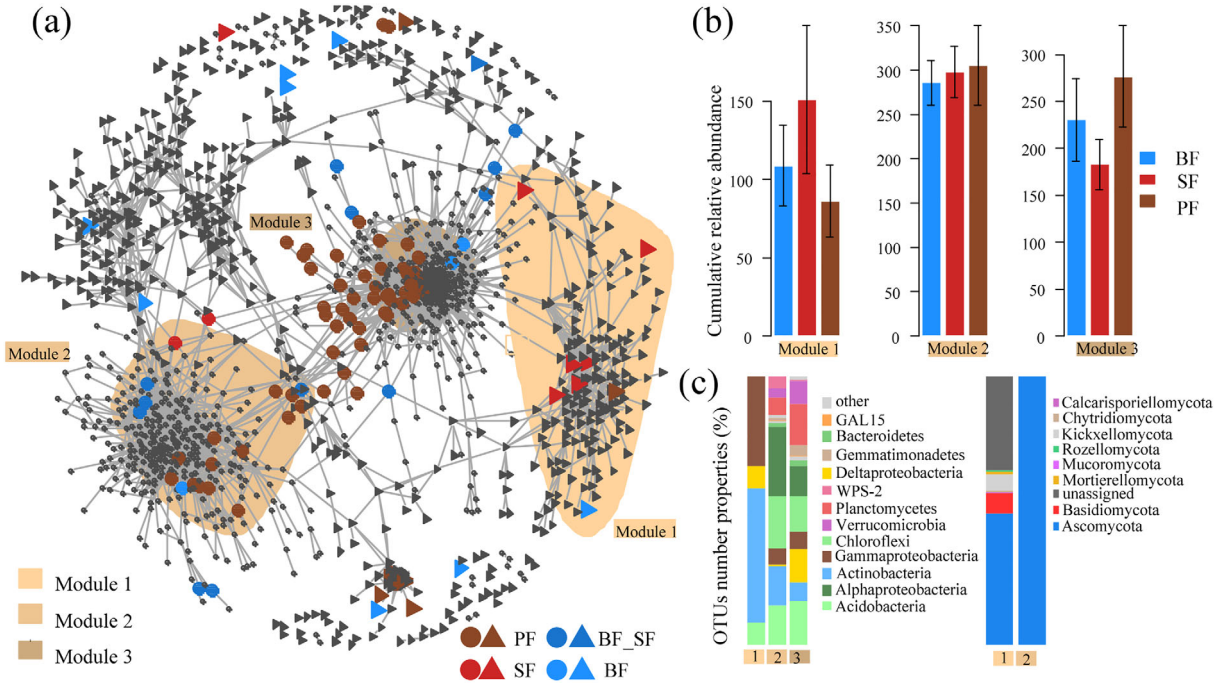

FIGURE 4 Co-occurrence patterns of forest conversion-sensitive OTUs. (a) Co-occurrence networks visualizing significant correlations ($p > 0.7$, $p < 0.01$; indicated with gray lines) between fungi and bacteria OTUs in soil communities. Triangles and circles and represent fungal and bacterial OTUs, respectively. *fs*OTUs are colored according to their association with the different forest types (as defined in Figure 3), and gray OTUs are insensitive to forest conversion. Shared areas represent the network modules (module 1, module 2, module 3) containing *fs*OTUs as defined in Figure S10. (b) Cumulative relative abundance (as counts per million, CPM; *y*-axis in *1000) of all fungi and bacteria of the forest conversion sensitive modules in soil co-occurrence networks. The cumulative relative abundance in samples of BF, SF, and PF forest types indicates the overall response of forest conversion-sensitive modules to the different forest types. (c) Taxonomic composition of forest conversion sensitive modules (reported as the proportional number of OTUs per class of fungi and bacteria, respectively). BF, SF, and PF indicate natural broadleaf forests, secondary forests, and plantation forests, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Properties of soil meta co-occurrence networks

OTUs[a]		Connectivity[b]	Connections[c]			Keystone[d]		*fs*OTUs[e]	
Bacteria	Fungi	Network wide	Bac-Bac	Fun-Fun	Bac-Fun	Bacteria	Fungi	Bacteria	Fungi
864	623	15.2	9964	1578	47	15	0	81 (0)	26 (0)

[a]Number of network nodes.
[b]Mean number of connections per node.
[c]Number of network edges.
[d]Number of keystone OTUs.
[e]Number of forest conversion sensitive OTUs present in the network (number of keystone OTUs).

of genes that contribute to C degradation. The abundance of the following C-cycle genes was substantially decreased by conversion of BF to SF or PF: *acsE*, *accA*, *aclB*, and *acsB*, which are involved in C fixation; *mxa* and *emGDH*, which are involved in methane production; *pmoA* and *mmoX*, which are involved in methane oxidation, *abfA*, *manA*, and *xylA*, which are involved in hemicellulose, and *manp*, which are involved in lignin degradation (Figure 5). In summary, these results suggested that conversion of BF to PF and SF decreased genes involved in C-fixation, methane production, and degradation of recalcitrant C compounds (e.g., hemicellulose and lignin), which would substantially reduce organic matter decomposition.

3.5 | Linkage of soil microbial communities with C-cycle genes under forest conversion

The relative abundance of module 1 and module 2 were significantly associated with the abundance of soil C-cycle genes (e.g., C degradation genes; $p < 0.05$; Table S4). MBC and DOC were negatively related to the relative abundance of module 2 and were positively related to the relative abundance of module 3 ($p < 0.05$; Table S4). We then used SEM to increase our understanding of the direct and indirect potential effects of forest conversion on the soil C cycle. Our SEM explained 50% of the variation in the abundance of soil C and

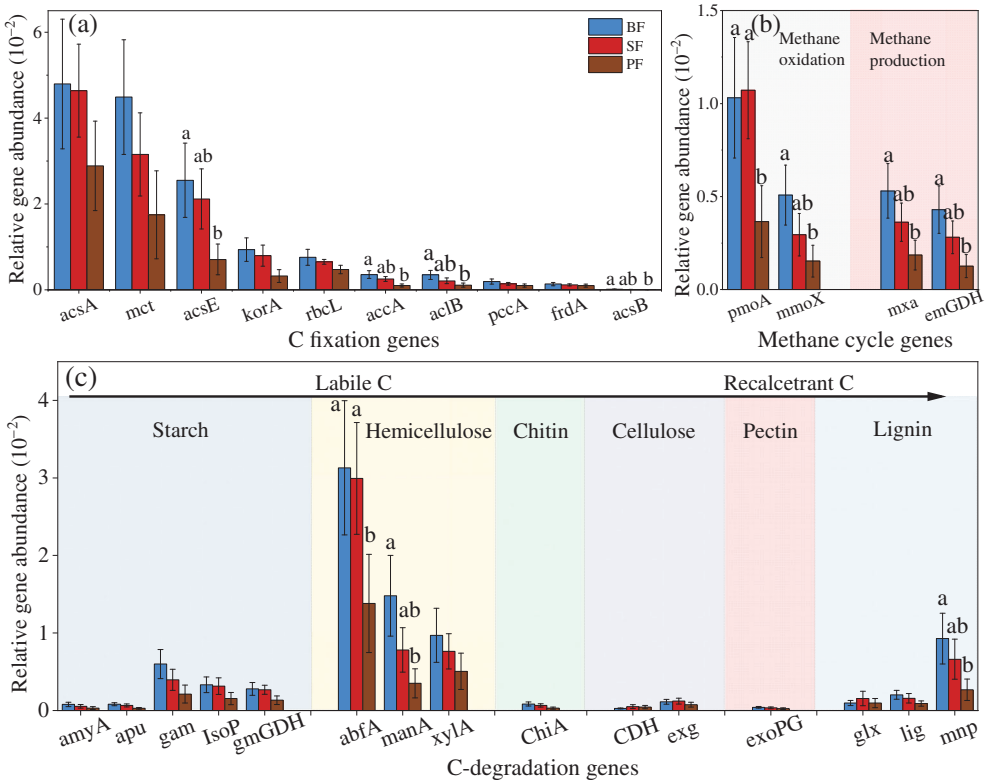

FIGURE 5 Forest conversion effects on microbial C-cycle genes. Relative gene abundances in C fixation (a), in methane metabolism (b), and in C degradation (c) among forest types. Values are means ± standard error ($n = 14$). Among forest types, means with different letters are significantly different ($p < 0.05$) with *LSD* test. *abfA*, arabinofuranosidase; *accA*, acetylCoA carboxylase carboxyl transferase; *aclB*, sucinyl-coA synthetase; *acsA*, carbonmonoxide dehydrogenase; *acsB*, 5-methyltetrahydrofolate corrinoid/iron-sulfur protein methyltransferase; *acsE*, 5-methyltetrahydrofolate corrinoid/iron-sulfur protein methyltransferase; *amyA*, alpha-amylase; *apu*, amylopullulanase; *CDH*, carveol dehydrogenase; *ChiA*, endochitinase; *emGDH*, methanol dehydrogenase; *exg*, exoglucanase; *exoPG*, extraconucleated polygalacturonase; *frdA*, fumarate reductase flavoprotein subunit; *gam*, glucoamylase; *glx*, glyoxal oxidase; *gmGDH*, glucose dehydrogenase; *Isop*, Isopullulanase; *korA*, 2-oxoglutarate ferredoxin oxidoreductase; *lig*, lignin peroxidase; *manA*, Mannanase; *mct*, mesaconyl CoA C1C4 CoA transferase; *mmoX*, ammonia monooxygenase subunit; *mnp*, manganese peroxidase; *mxa*, methanol dehydrogenase (cytochrome c) subunit; *pccA*, propionylCoA carboxylase alpha; *pmoA*, methane/ammonia monooxygenase subunit A; *rbcL*, rubisCO large chain; *xylA*, xylose isomerase. BF, SF, and PF indicate natural broadleaf forests, secondary forests, and plantation forests, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

32% of the abundance of soil C-cycle genes (Figure 6a). The relative module abundance has direct and positive effects on C-cycle genes. However, a negative and significant relationship was found between soil C and the relative abundance of C-cycle genes (Figure 6). This indicated that conversion of BF to PF and SF reduced the relative abundance of C-cycle genes (e.g., hemicellulose- and lignin-degradation genes) by decreasing the relative abundance of module 1 and module 2, and by decreasing PXC (Figure 6 and Table S4).

4 | DISCUSSION

In considering the effects of the conversion of BF to PF and SF on soil C dynamics, previous studies have separately explored plant diversity (Fang, 2001), soil chemical properties, the soil C stock, and related enzyme activities (Luo et al., 2019), or have focused on either the fungal or bacterial communities (da C Jesus et al., 2009; Wang et al., 2021). In the current study, we assessed the relationships between the abundances of soil microorganisms (both bacteria and fungi) and C-cycle genes with the loss of soil C caused by the conversion of BF to PF and SF. We also determined whether and how these relationships were associated with changes in soil physicochemical properties caused by forest conversion. Our findings indicate that management that fosters certain *fs*OTUs in specific forest types may increase soil fertility and C sequestration in subtropical forests.

4.1 | Divergent responses of soil microbial members to forest conversion

We found that forest conversion had different effects on the soil bacterial and fungal communities. That there was no significant difference in the variance of soil bacterial and fungi among forest types suggested that differences among forest types were mainly driven by true biological differences, rather than an artifact of difference of within-group variances (Hartman et al., 2018). Conversion of BF to PF

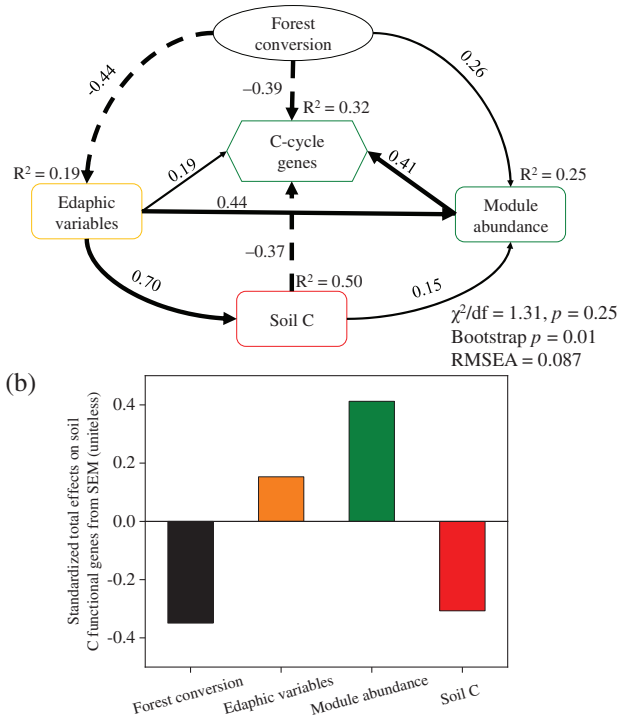

FIGURE 6 A structural equation model describing the potential effects of forest conversion, edaphic variables, soil C, and the relative abundance of main ecological clusters on soil C-cycle genes. For soil edaphic variables, 49.5% of the variation was explained by the first component from a PCA conducted with soil clay content, moisture content, and pH; for soil C, 52.1% of the variation was explained by the first component from a PCA conducted with SOC, DOC, MBC, and PXC; for soil module abundance, 64.4% of the variation was explained by the first component from a PCA conducted with module 1, module 2, and module 3 from Figure 4; for soil C function genes, 98.7% of the variation was explained by the first component from a PCA conducted with C fixation, methane metabolism and C degradation genes. Soil C-cycle genes include soil C fixation genes, soil C degradation genes, and soil methane metabolism genes. Soil potassium permanganate oxidizable carbon (PXC), soil dissolved carbon (DOC), and soil microbial biomass carbon (MBC) [Colour figure can be viewed at wileyonlinelibrary.com]

and SF did not significantly affect the diversity or richness of the soil bacterial community but decreased the diversity and the richness of the soil fungal community. Researchers have previously reported differences in the responses of soil bacterial communities vs. soil fungal communities to land use (da C Jesus et al., 2009) or afforestation (Liu et al., 2020). In the current study, the different responses of soil bacteria vs. soil fungi may be due to the decreases in nutrient content and increases in soil pH with forest conversion of BF to PF and SF (Luo et al., 2019).

Consistent with our first hypothesis, we found a significant effect of forest conversion on the composition of the soil bacterial community (Figures 1 and S2–S5), because bacteria with high degrees of co-occurrence were only found in the soil microbial networks in PF. However, forest conversion had substantial effects on the α-diversity of fungi but not bacteria (Figures S3 and S5; Table 1). Therefore, forest types had a smaller effect on the species richness to a smaller degree than on the composition of the bacterial community. This result was consistent with previous observations that bacterial species richness was less variable than species composition in response to environmental factors (e.g., land-use change) (Liu et al., 2020). Shifts in microbial community composition may not necessarily result in changes in richness or diversity because univariate measures of richness and diversity mask the relationship between groups and individual taxa (Wu et al., 2007) and because the changes of some taxonomic groups may be compensated by changes in others (Hartmann & Widmer, 2006).

We found that forest conversion-sensitive *fs*OTUs (identified in Figure 3) in the soil microbial community could be regarded as indicator taxa with respect to the effect of forest conversion on β-diversity. For instance, the higher relative abundance of bacteria *fs*OTUs from the Chloroflexi and Acidobacteria in BF than in SF and PF (Figure S6) was consistent with the separation by forest types in the PCoA analysis of soil microbial communities. The multiple tree species and high soil organic matter content of BF may help explain why Acidobacteria OTUs were abundant in that type of forest. In contrast, the presence of a single tree species and the low soil organic matter content may help explain why Chloroflexi OTUs were abundant in PF (Ren et al., 2016). Consistent with the latter study, we found that OTUs representing three families within the Chloroflexi, *TK10* (bOTU67), *AD3* (bOTU31 and bOTU70), and *Ktedonobacteria* (bOTU151, bOTU472) were significantly more abundant in PF than in BF or SF (Figure S7). We also noted that OTUs representing the *Acidobacteria* (bOTU1435, bOTU51) family within the Acidobacteria were significantly more abundant in BF and SF than in PF. Because bacteria in these families are sensitive to changes in soil organic matter content and pH, the conversion-induced changes in the relative abundance of these bacteria may be explained by the effects of the conversion of these soil properties (Fierer et al., 2007; Ward et al., 2009).

We inspected the *fs*OTUs for taxa with potentially important functions for sustainable forest management. Among soil fungi, we found OTUs representing *Agaricomycetes* (fOTU1, fOTU139, fOTU293, and fOTU486) within Basidiomycota and representing *Sordariomycetes* (fOTU424 and fOTU515) within Ascomycota had higher abundance in BF and SF than in PF. Species of Basidiomycota contribute to lignin decomposition, while species of Ascomycota contribute to hemicellulose and cellulose decomposition (Bastida et al., 2013). These examples suggest that conversion of BF to PF and SF may result in the decreased abundance of taxa related to hemicellulose and lignin decomposition.

In our soil meta-networks, *fs*OTUs clustered in distinct modules that reflected the different forest types (Figures 4 and S10). These results suggested that many groups of microbes responded uniformly to specific forest types and therefore grouped together in the soil microbial networks. The soil *fs*OTUs exhibited low to medium degrees of co-occurrence in the soil network, indicating that forest conversion did not influence the highly co-occurring soil microbes, which may be regarded as 'core microbiome' members (Shade et al., 2012). This suggests that when sustainable forest management is implemented, only

the non-core or "accessory" of the soil microbial community (the *fs*OTUs) could be manipulated.

We found that forest conversion affected the network patterns, β-diversity, and keystone taxa of soil microbial community (Tables 2 and S3). Keystone taxa frequently interact with other taxa, significantly affecting the overall community (Ma et al., 2016). This finding suggests that conversion of BF to PF and SF mainly affected the soil microorganisms with keystone functions. Most importantly, this finding suggests that the relative abundance of keystone taxa identified by co-occurrence networks can be manipulated by forest management to increase soil fertility and soil C sequestration (Faust & Raes, 2012; Schlaeppi & Bulgarelli, 2015).

4.2 | Responses of C-cycle genes to forest conversion

Our first hypothesis also concerned how C-cycle genes were affected by forest conversion and whether the changes in their abundance were associated with the abundance of keystone soil microbes and soil physicochemical properties. The conversion of BF to PF and SF decreased the relative abundance of 29 C-cycle genes (see Discussion section in Appendix S2). In particular, conversion of BF to PF and SF significantly reduced the abundance of lignin-degradation genes, which was consistent with a previous finding that the abundance of many C and N genes involved in decomposition decreased with change in land use from forest-to-pasture (Paula et al., 2014). In both the later study and our study, these changes suggested that conversion reduced the decomposition of litter or root C in soil. This result was consistent with the finding that conversion of BF to PF and SF significantly reduced new C inputs by 13.1% and 34.0%, respectively (Luo et al., 2020).

Consistent with our second hypothesis, our SEM provided further evidence that conversion of BF to PF and SF reduced the abundance of soil microbial C-cycle genes by reducing the relative abundance of keystone and phylogenetically grouped bacteria and fungi within module 1 and module 2 (which were significantly associated with C-degradation genes). Modules 1 and 2 contain bacterial families within the dominate Acidobacteria and Actinobacteria and fungal families with the dominant Ascomycota and Basidiomycota; these families are known to be organic matter decomposers, that is, they metabolize organic substrates (e.g., polysaccharides) provided by the litter and roots (Bastida et al., 2013; da C Jesus et al., 2009). These results suggest that the decrease in the abundance of Acidobacteria, Actinobacteria, Ascomycota, and Basidiomycota might explain the reduction in the abundance of C-cycle genes (e.g., genes contribute to hemicellulose and lignin degradation).

Our SEM also showed that forest conversion indirectly reduced soil microbial C-cycle genes by decreasing the concentration of soil C (e.g., MBC, DOC, and PXC) and soil edaphic properties (e.g., soil pH, soil moisture content, and soil clay content). These soil properties were previously found to be key factors associated with changes in bacterial and fungal communities during forest conversion because microbial abundance and composition depend on soil nutrient availability and soil physicochemical properties (da C Jesus et al., 2009). Our results showed that soil MBC, DOC, pH, and moisture content were negatively associated with the relative abundance of soil microbial communities within module 2, and were negatively correlated with soil C-degradation genes. Soil DOC is thought to be the most available C substrate for microorganisms, and soil pH and moisture content regulate the composition of the soil bacterial community (Liu et al., 2020). Our unconstrained ordination analyses also revealed that changes in pH with conversion affected the variation in the properties of the soil fungal and bacterial communities (Figure 2). These results suggest that the decreases in soil DOC, PXC, and pH alter the response of forest conversion-sensitive microbes (especially bacteria within the Acidobacteria and Actinobacteria and fungi within the Ascomycota and Basidiomycota), and thereby reduce the relative abundance of genes that contribute to the degradation of hemicellulose and lignin.

5 | CONCLUSIONS

Conversion of BF to PF and SF dramatically decreased the abundance of both bacterial (Acidobacteria and Actinobacteria) and fungal (Ascomycota and Basidiomycota) *fs*OTUs, and of soil C-cycle genes (e.g., hemicellulose and lignin degradation genes). The reduction of C-cycle genes with forest conversion suggests that the preservation of BF and the establishment of a PF with a mixture of suitable native broadleaf species (similar to those in BF) would increase the abundance of C-cycle genes, and consequently increase soil C inputs and soil C sequestration. We also found that the reductions in the abundance of C-cycle genes, especially those involved in hemicellulose and lignin degradation, were primarily related to the declines in the abundance of *fs*OTUs within bacteria (Acidobacteria and Actinobacteria) and fungi (Ascomycota and Basidiomycota). Such effects suggest that particular members of the soil microbial community (and especially *fs*OTUs) and their C-cycle genes are coupled in their regulation of C loss from soil. Overall, our study suggests that enhancement of *fs*OTUs may improve soil quality in subtropical plantation and SF by increasing decomposition rates and accelerating soil C sequestration.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used to support the findings of this study are available from the corresponding author upon request.

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