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Differential soil microbial community responses to the linkage of soil organic carbon fractions with respiration across land-use changes

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ABSTRACT

Land-use change can modify terrestrial ecosystem processes with potentially important effects on below-ground carbon dynamics. Soil microbes are considered the rate-limiting factor in carbon decomposition. However, the effect of land-use change on soil microbial community and the mechanism of soil carbon dynamics remain unclear. In this study, soil samples were collected during four periods (April, June, August, and October) at sites in the Loess Plateau in China with different land- use types: *Robinia pseudoacacia* L. (RP) and abandoned land (AL); these areas were converted 10 years ago from similar farmlands, while the millet (*Setaria italica*) farmlands (FL) were selected as a control in our study. Quantitative PCR and Illumina sequencing of the 16S rRNA and ITS genes were performed to analyze the abundance, diversity, and compositions of the soil microbes (bacteria and fungi). Additionally, soil organic carbon fractions (soil organic carbon: SOC, dissolved organic carbon: DOC, microbial biomass carbon: MBC) and soil respiration components (soil respiration: SR, heterotrophic respiration: HR, autotrophic respiration: AR) were evaluated. The results showed that SOC fractions and soil respiration increased after land-use change, with significant correlation being observed. In particular, DOC was more related to SR and HR than to the other fractions. Moreover, the abundance and diversity of the microbes (bacteria and fungi) were greatly affected by the land- use change; both of them were significantly and positively correlated with soil organic carbon fractions and soil respiration components. For dominant bacterial phyla, both *Proteobacteria* and *Bacteroidetes* were significantly more abundant in the afforested soil than in the FL, while the abundances of *Actinobacteria* and *Chloroflexi* ranked as FL > AL > RP. For dominant fungal phyla, *Ascomycota* responded positively to land- use changes, whereas *Basidiomycota* responded negatively. Such changes in the abundances of microbial phyla were significantly correlated with the linkage of soil organic carbon fractions and respiration components. Altogether, these results suggest that the changes in components of soil respiration may be highly susceptible to soil organic carbon fractions, especially to DOC, and this linkage is largely modulated by microbial community across land-use changes.

1. Introduction

As the largest carbon pool in the terrestrial biosphere, soil contains much more carbon than that in either the vegetation or the atmosphere or their combination (Tarnocai et al., 2009). Thus, even a small shift in the soil organic carbon (SOC) pool can lead to significant changes in atmospheric CO_2 concentration, and further influence future climate change (Davidson and Janssens, 2006; Piao et al., 2012). Land-use change, particularly for afforestation, has the potential to alter the terrestrial carbon cycle (Davidson and Janssens, 2006). Despite the wealth of studies focusing on below-ground soil carbon dynamics across land-use changes (Li et al., 2012; Garcia-Franco et al., 2015), there is uncertainty in the magnitude or direction of carbon fluxes in the SOC pool (Post and Kwon, 2000; Tardy et al., 2015). Numerous studies have mainly focused on the theory that changes in soil carbon stocks are influenced by plant decomposition and physical protection (Davidson and Janssens, 2006; Lange et al., 2015). However, the microbial regulation for carbon cycling towards land-use change remains unclear.

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This uncertainty has greatly hindered the identification of soil carbon balances in afforested ecosystem. Therefore, to improve our predications of soil carbon balances, there is an urgent need for a better understanding of microbial community responses.

Soil microbes respond differently to soil carbon dynamics as a result of changing plant diversity and organic matter quality across land use changes (Li et al., 2012; Deng et al., 2016). However, the directions and magnitudes of these responses are uncertain. For instance, large amounts of plant residue inputs may decrease the efficiency with which microbes use carbon or decompose soil organic matter, and ultimately reduce soil carbon storage (Fontaine et al., 2007). Conversely, several studies have shown that high plant diversity or high amounts of plant residue inputs can increase the storage of soil carbon from fresh carbon by altering the growth of soil microbes (Lange et al., 2015; Tardy et al., 2015). Nevertheless, the contradicting results have suggested the critical role of microbial decomposition in regulating soil carbon dynamics in a changing environment. Moreover, some microbial taxa participate in the decomposition of soil organic matter, causing changes in SOC fractions, ultimately affecting soil CO_2 efflux (Tardy et al., 2015; Goldfarb et al., 2011). However, how changes in microbial compositions effectively explain the alterations in SOC fractions and soil respiration remains unclear, especially in afforested ecosystems (Deng et al., 2016; Xiao et al., 2017). Several recent studies of advanced microbial models showed that the incorporation of soil microbes into biogeochemical models substantially improved the model prediction of soil carbon dynamics (Allison et al., 2010; Hararuk et al., 2015). Therefore, understanding microbial carbon dynamics across land-use changes is likely not only to shed light on the ecological carbon cycle in afforested ecosystems, but also to improve the predication of the carbon balances when assessing the effects of land-use change on the SOC pool.

The Loess Plateau, which is located at the boundary of the arid and semiarid areas in China, has suffered from severe soil erosion and is characterized by low vegetation coverage (Bai and Dent, 2009). To rehabilitate the degraded lands, the Chinese government has implemented a series of environmental protection policies; one such policy is the Grain to Green Program (GTGP) (Fu et al., 2000). These policies result in increased net primary productivity and reduce the degree of soil disturbance; these effects have led to changes in above-ground and below-ground ecosystems (Ren et al., 2016a,b, 2017a). Numerous studies have been conducted to investigate the changes in soil carbon and nitrogen dynamics associated with the soil microbial community across land-use changes in an afforested ecosystem (Deng et al., 2016; Xiao et al., 2017; Ren et al., 2016a,b). However, most of these studies ignore the fact that below-ground carbon dynamics consist of a continuum of organic carbon fractions and CO_2 efflux (Garcia-Franco et al., 2015; Liang et al., 2015). Furthermore, traditional methods such as PLFA analysis or PCR-DGEE make it difficult to identify the effects of land-use changes on microbial communities at the species level and show limited phylogenetic or taxonomic resolution (Grayston et al., 2004; Frostegård et al., 2011). In contrast, the advent of next-generation sequencing has provided detailed information for soil microbial communities, and helped to clearly describe the soil microbial diversity and the processes structuring compositions (Biddle et al., 2008). Through using this method, we can gain a comprehensive understanding of the trends that characterize microbial community responses to land-use change, or the mechanisms governing the below-ground carbon cycling to disturbance in afforested ecosystems.

In this study, we hypothesized that soil respiration components may be changed synchronously with SOC fractions across land-use changes, and this alteration may be stimulated by the diversity and abundance of soil microbes (bacteria and fungi). In addition, we predicted that alterations in specific microbial taxa would account for the changing SOC fractions and components of soil respiration in an afforested ecosystem. Therefore, we focused on the following: (i) the changes in SOC fractions and soil respiration components, and (ii) the response of the abundance, diversity, and compositions of soil microbes to the linkage of SOC fractions with respiration components across land-use changes.

2. Method and material

2.1. Study area description

The study area is located in the Wuliwan watershed of Ansai County, Shaanxi Province, China (36°51′41.23″–36°52′50.87″N, 109°19′49.20″ –109°21′46.46″E), which is located in middle area of the Loess Plateau. This region is a temperate semiarid area with an average annual temperature of 8.8 °C and average annual precipitation of 510 mm (mainly from July to September). On average, there are about 157 frost-free days and 2415 h of total yearly sunshine. The present soil type is classified as Huangmian soil (Calcaric Cambisols, FAO) and is particularly susceptible to erosion.

Since 1973, the area has been used as a field experimental base to control soil erosion through wind and water by the Institute of Soil and Water Conservation, Chinese Academy of Sciences. The integrated management of vegetation restoration and soil and water conservation has been carried out gradually. In particular, all of the farmlands (FL) with slopes higher than 25° were converted to forestlands and abandoned lands. Currently, the forestlands with *Robinia pseudoacacia* L (RP). and abandoned land (AL) have become the main vegetation areas for rehabilitating ecology in the region. Moreover, RP is leguminous and has higher rates of net primary productivity than the former FL. AL was generated from previous FL due to their extremely low productivity and far distance from farmers' residences; thus, many farmlands have been abandoned for natural recovery without anthropogenic interference (i.e., cultivation, fertilization). For these three land-use types, the important values of each species in RP and AL were shown in Table S1. The averages of soil bulk density (BD) and clay content ranged from 1.1 to 1.2 and 8.9% to 9.6%, respectively. During the four periods, the averages of soil water contents and pH ranged from 7.1% to 20.2% and from 8.4 to 8.5, respectively (Table S2).

2.2. Experimental design, plant investigation and trenching

Sampling was carried out in April, June, August, and October of 2014. Two land-use types were selected based on the afforestation of former farmlands in the area: RP and AL, both of which had been afforested for 40 years. An adjacent FL was used as a reference site. All the study sites were located within the same area. These three land-use types have similar elevations and have been subjected to similar farming practices in the past. Moreover, their soils have developed from the same parent materials. Before afforestation, the main crops grown in these sites were millet (*Setaria italica*) and soybean (*Glycine* max), and their farming practices were similar. Experimental designs were described previously in detail (Ren et al., 2016a,b; Fig. S1). In brief, for each land-use type, we chose three 25 m × 50 m sites, which were considered the three independent replicates, since the distance between any two sites exceeded the spatial dependence (< 13.5 m) of most soil variables (Marriott et al., 1997); two 25 m × 25 m plots were established in each replicate site.

In addition, six quadrats (0.5 m × 0.5 m) (three trenched quadrats and three untrenched quadrats) were randomly established in each plot, and the trenches (0.5 m wide and 0.8 m deep) were excavated in October 2013. After covering the trenches with a 2-mm thick plastic sheet, we refilled them with soil, and the above-ground plants were carefully removed without any disturbance.

2.3. Soil respiration measurement and soil sampling

A total of six polyvinyl chloride (PVC) collars (16 cm inner diameter, 12 cm deep) were inserted to a depth of 10 cm. Three PVC collars of trenched quadrats were used to determine the soil HR, and another three PVC collars in untrenched quadrats were used to determine the

SR; accordingly, soil AR was the difference between SR and HR. During the periods in 2014 including April, June, August and October, soil respiration ratios (μmol CO_2 $m^{-2}s^{-1}$) were measured with a portable infrared analyzer (GXH-3010E1). To reduce the measuring error from weather conditions, the measurement time was selected as 09:00 and 11:00 am on days without rain, and the estimates of respiration were obtained from continuous 2- or 3- day measurements to represent the average monthly soil respiration. Finally, three data points of respiration ratios were averaged to obtain the results for a given plot, for both AR and HR.

Moreover, after removing the litter layer, 10 replicate samples (top 0–10 cm) were collected with an "S" shape using a soil auger (5 cm inner diameter) and then mixed thoroughly to provide one final soil sample per plot. During the process, in order to reflect the microbial response to respiration, soil samples were also collected around the designed quadrats. Overall, 72 samples (four periods × three land-use types × three sites × two plots) were collected. The samples were sieved through a 2-mm screen, and roots and other debris were removed. A portion of each soil sample was immediately transported to the laboratory to determine the soil water contents (SWC). Subsamples for molecular analysis were transported from the field to the laboratory on ice, and then stored at −80 °C. A portion of each soil sample was stored at 4 °C for analysis of dissolved organic matter and of microbial biomass, and soil subsamples were air- dried and stored at room temperature prior to chemical analysis.

2.4. Analysis of soil physicochemical properties

Soil moisture was assessed by oven drying to constant mass at 105 °C, soil temperature at 10 cm depth was measured adjacent to each respiration collar with a portable temperature probe. Soil pH and SOC were measured as described (Zhang et al., 2011). Concentration of dissolved organic carbon (DOC) was determined with a Shimadzu TOC-TN analyzer (Shimadzu Corp., Kyoto, Japan). Soil microbial biomass carbon (MBC) was estimated from fresh soil samples using a chloroform fumigation-extraction method as previously described (Vance et al., 1987). Soil clay was measured by the hydrometer method (Bouyoucos, 1962). Soil bulk density was calculated from the gravimetric weight of the core before and after oven drying at 105 °C for 24 h and considering the individual core volume (De Vos et al., 2005).

2.5. Soil DNA extraction, PCR amplification, and Illumina sequencing

Microbial DNA was extracted from 0.5 g of fresh soil three times (for a total of 1.5 g of soil) with the E.Z.N.A soil DNA kit (OMEGA, USA). The concentration and quality of the DNA were assessed using a NanoDrop2000 spectrophotometer (Thermo Scientific, Wilmington, DE, USA). PCR amplification of bacterial 16S rRNA targeting the V4 region was conducted by using primers 515F (5′-GTGCCAGCMGCCG CGG-3′) and 907R (5′-CCGTC AATTCMTTTRAGTTT-3′) (Biddle et al., 2008). The fungal ITS-1 region was amplified by using primers ITS1F (5′-ACTTGGTCATTTAGAG- GAAGTAA-3′) and ITS2 (5′-BGCTGCGTTCTTCATCGATGC-3′) (Mukherjee et al., 2014). This primer set provided comprehensive coverage with the highest taxonomic accuracy for bacterial and fungal sequences. The PCR protocols that were used to amplify the 16S rRNA gene and ITS rRNA genes were described previously (Mukherjee et al., 2014; Ren et al., 2016a,b). Finally, an equal amount of PCR product from each sample was added into a single tube, and sent for analysis on Illumina's MiSeq platform at the Major Biological Institute in Shanghai, China.

Reads were demultiplexed, quality-filtered, and processed using QIIME (Caporaso et al., 2012). Sequence analysis was performed using the USEARCH v5.2.32 to filter out and eliminate noise from the data by clustering similar sequences with less than 3% dissimilarity. Finally, the complete dataset was sent to the Sequence Read Archive (SRA) database of the National Center for Biotechnology Information (NCBI) under the accession numbers of SRP056716, SRP058793 and SRP091677.

2.6. Quantitative PCR

Relative abundances of the 16S rRNA and fungal ITS-1 gene were amplified by using bacterial- and fungal-specific primer pairs, which were showed as above. The 20 μl qPCR reactions of bacteria contained 10 μl of EvaGreen 2X qPCR Master Mix (Applied Biological Materials Inc., Richmond, Canada), 0.5 μM of each primer (final concentration), an environmental and standard DNA template (1 μl per reaction) and sterile ddH_2O. The 20 μl qPCR reactions of fungi contained 10 μL EvaGreen 2 × qPCR MasterMix, 0.3 μM of each primer (final concentration), and environmental or standard DNA templates (2 μL per reaction). Then, quantitative PCR for bacteria and fungi were performed using a Bio-Rad C1000/CFX96 Thermocycler (Bio-Rad, Hercules, CA). In detail: for analysis of bacteria, thermal conditions were as follows: initial denaturation at 95 °C for 10 min, followed by 40 cycles of 95 °C for 15 s, 53 °C for 30 s, and 72 °C for 60 s; for analysis of fungi, thermal conditions were as follows: initial denaturation at 95 °C for 10 min, followed by 29 cycles of 95 °C for 15 s, 50 °C for 30 s, and 70 °C for 60 s. The copy numbers were tested by Bio-Rad CFX Manager Software which was installed in Bio-Rad C1000/CFX96 Thermocycler. All of the qPCR reactions were run in triplicate with each DNA template.

2.7. Statistical analyses

Taxonomic alpha diversity was calculated as estimated community diversity by the Shannon index using the Mothur software (v.1.30.1). Non-metric multi-dimensional scaling (NMDS) was selected to illustrate the clustering of different samples. Correlations among the soil microbial compositions, soil properties, and organic carbon fractions, as well as soil respiration components were determined using redundancy analysis (RDA) (Clarke et al., 2014). We also used the analysis of similarities (ANOSIM) to determine the significance of separation across land-use changes (Clarke et al., 2014). The relationships between the microbial characteristics (i.e., abundance, alpha diversity and beta diversity) and the soil properties and carbon fractions, as well as soil respiration components were performed by Spearman's correlation analysis.

Furthermore, we used the MetaWin (Sinauer Associates Inc., Sunderland, MA, USA) to test whether land-use change had a significant effect, and bootstrap 95% confidence intervals (CIs) were calculated for each categorical group (Ren et al., 2017b). If the bootstrap CI did not overlap with zero, the effects of land-use change on microbial phyla were deemed significant. In addition, changes in SOC fractions and respiration components, as well as microbial characteristics (alpha diversity, abundance, and phyla) induced by temporal variability and land use change were tested through one-way ANOVA using the R v.3.1.3 program.

3. Results

3.1. Effect of land-use changes on SOC fractions, soil respiration, and respiration components

Compared with FL, there were significant increases in MBC, SOC, and DOC by 43.8–570.8%, 21.2–334.0%, and 1.7–124.9%, respectively (Fig. 1; $p < .05$). During the growth season, SR, HR, and AR responded significantly to land-use changes (Fig. 1; $p < .05$). Compared with FL, SR increased significantly by 76.1% and 276.8% in AL and RP, respectively. HR and AR yielded average values of 0.6 μmol CO_2 $m^{-2}s^{-1}$ and 0.3 μmol CO_2 $m^{-2}s^{-1}$ in AL, and 1.3 μmol CO_2 $m^{-2}s^{-1}$ and 0.7 μmol CO_2 $m^{-2}s^{-1}$ in RP, respectively. Notably, Fig. 2 showed that SOC fractions were significantly related to soil respiration and respiration components, but with different slopes ($p < .05$). In contrast,

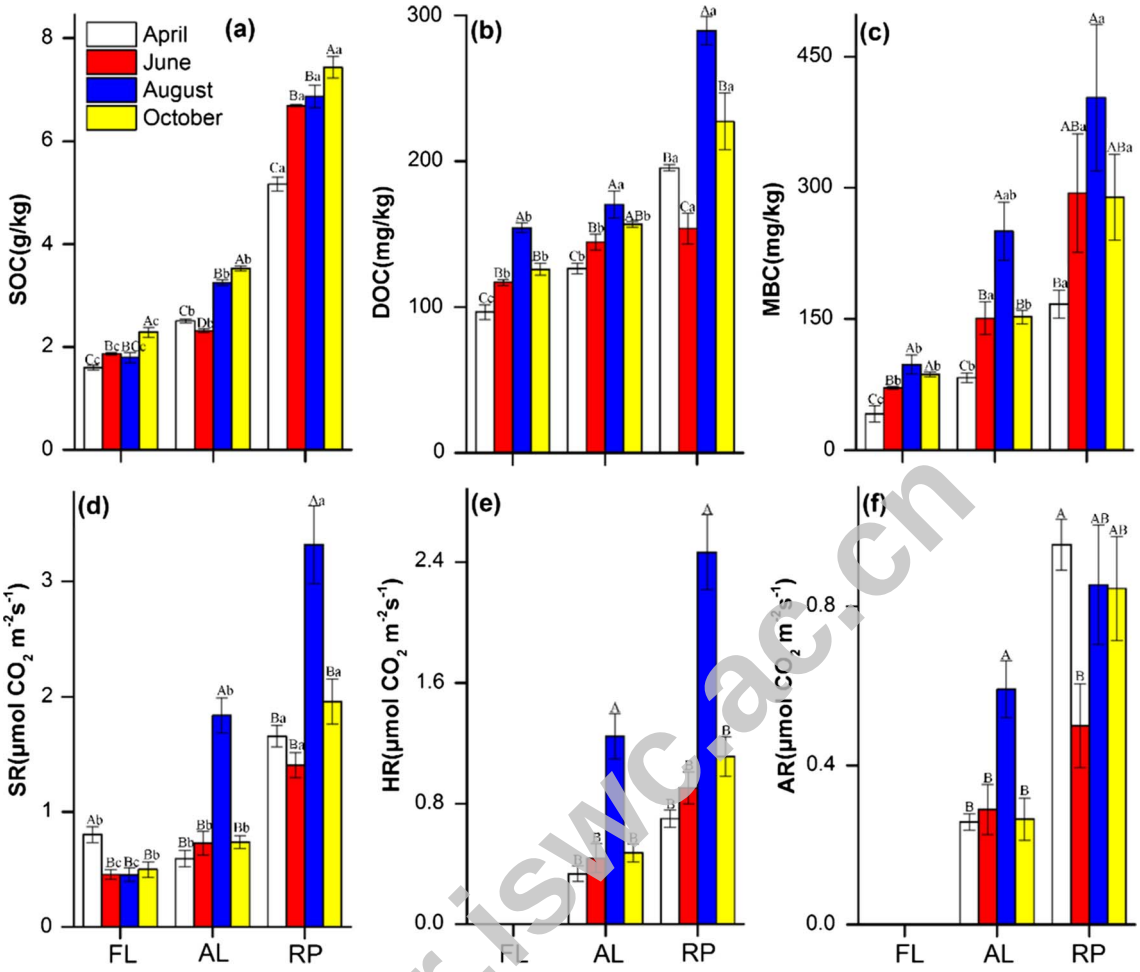

Fig. 1. Changes of soil organic carbon fractions (soil organic carbon: SOC, dissolved organic carbon: DOC, microbial biomass carbon: MBC) and soil respiration components (soil respiration: SR, heterotrophic respiration: HR, autotrophic respiration: AR) across land-use change during four periods. RP: *Robinia pseudoacacia* L.; AL: abandoned land; FL: farmland. Different uppercase letters indicate significant differences among different periods ($P < .05$) while different lowercase letters indicate significant differences among different land-use types; the error bars are the standard errors.

DOC was more related to soil respiration and its components than to other carbon fractions.

3.2. Effect of land-use changes on microbial abundance, diversity and compositions

After quality sequencing of 72 soil samples, both bacterial communities (a total of 935,682 sequences) and fungal communities (a total of 1,612,032 paired-end sequences) were obtained with the 515F/907R (bacterial 16S rRNA) and ITS1F/ITS2 (fungal ITS) primer sets across all soil samples. The number of bacterial sequences varied from 9649 to 25,143 per sample (mean = 12, 995), whereas the number of fungal sequences varied from 20,125 to 38,947 per sample (mean = 22,389). For the downstream analysis of bacteria, datasets were rarefied to 9500 sequences, whereas, for the downstream analysis of fungi, datasets were rarefied to 20,000 sequences.

An operational taxonomic unit (OTU) level approach was used to calculate the microbial diversity and abundance under different land-use changes and temporal variability (Fig. 3). With respect to the bacterial communities (Fig. 3a and b), in comparison with FL, the abundance and alpha diversity (Shannon index) increased by an average of 3.5% and 1.3% in AL, and 2.4% and 2.4% in RP, respectively. For the fungal communities (Fig. 3c and d), the abundance and alpha diversity (Shannon index) showed the same trend in the fungal communities in response to land-use change, and responded significantly to the temporal variability ($p < .05$). Moreover, Fig. 4 showed that soil bacterial and fungal communities in FL plots were distant from those in RP and AL. The assemblage compositions of soil bacteria and fungi differed significantly across land-use changes (ANOSIM: $R = 0.755$ for bacteria, $R = 0.905$ for fungi, $p < .001$ in all cases).

Considering all sequences, soil bacterial phyla (with relative abundance > 1%) were: Proteobacteria, Actinobacteria, Acidobacteria, Chloroflexi, Planctomycetes, Gemmatimonadetes, Bacteroidetes, Cyanobacteria, and Nitrospirae, with the average proportion of 31.6%, 25.4%, 17.6%, 6.7%, 6.5%, 2.4%, 3.2%, 1.7%, and 1.3%, respectively (Table S3). In detail, the abundances of Proteobacteria, Acidobacteria, and Bacteroidetes increased significantly after land-use change (Fig. 5a, b and Table S3). Both Proteobacteria (Qb = 35.5401, $p < .0001$) and Bacteroidetes (Qb = 6.4215, p = 0.01127) differed significantly. Furthermore, at the class level (Table S3), both Alphaproteobacteria and Gammaproteobacteria increased significantly after land-use change across four periods ($p < .05$), but Thermomicrobia and Bacil decreased significantly. At the order level, the Rhizobiales (branch of Alphaproteobacteria) and Xanthomonadales (branch of Gammaproteobacteria) were significantly higher in RP than these in FL across four periods ($p < .05$), while the Propionibacteriales, Acidimicrobiales, Micrococcales, and Frankiales showed the opposite trends (FL > AL or RP).

Among the fungal taxa, the dominant phyla across all samples were: *Ascomycota* (71.2%), *Basidiomycota* (11.0%), and *Zygomycota* (14.6%) (Table S4). Compared with FL, land-use changes slightly increased

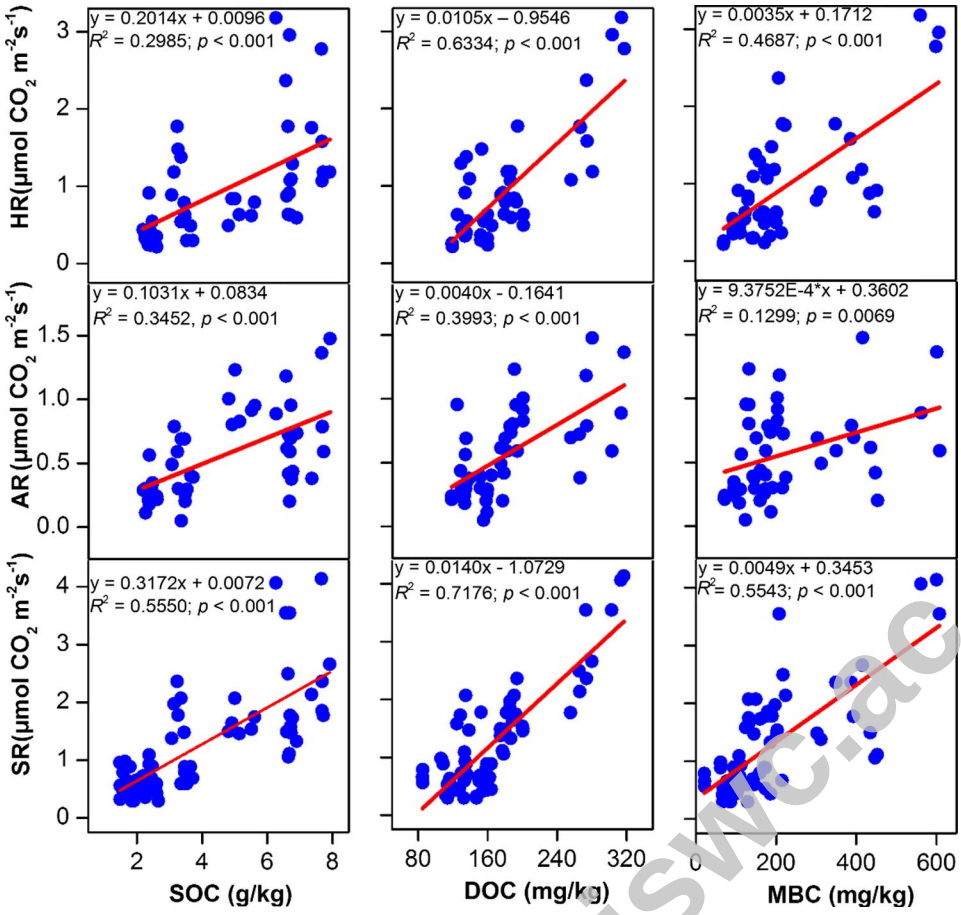

Fig. 2. The relationships between soil organic carbon fractions and soil respiration components following afforestation. Soil organic carbon (SOC); dissolved organic carbon (DOC); microbial biomass carbon (MBC); soil respiration (SR); heterotrophic respiration (HR); autotrophic respiration (AR).

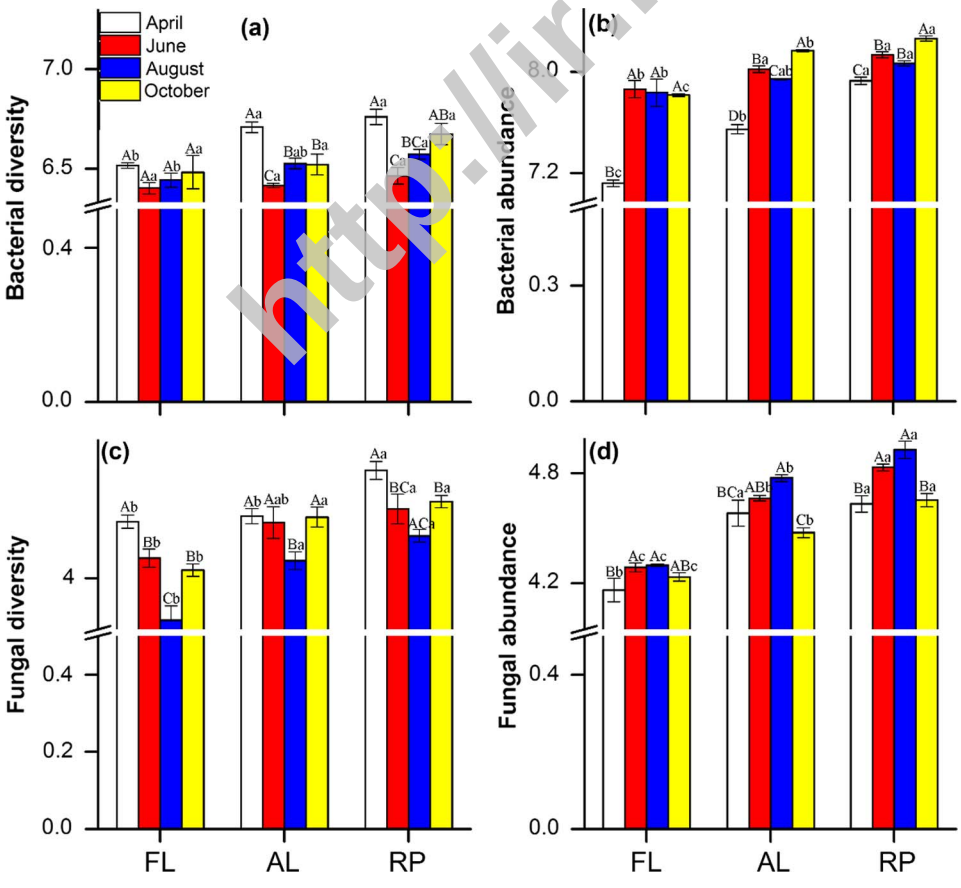

Fig. 3. Changes of microbial (bacterial and fungal) abundance and diversity (alpha diversity: Shannon index) across land-use change during four periods. RP: *Robinia pseudoacacia* L.; AL: abandoned land; FL: farmland. Different uppercase letters indicate significant differences among different periods ($P < .05$) while different lowercase letters indicate significant differences among different land-use types; the error bars are the standard errors.

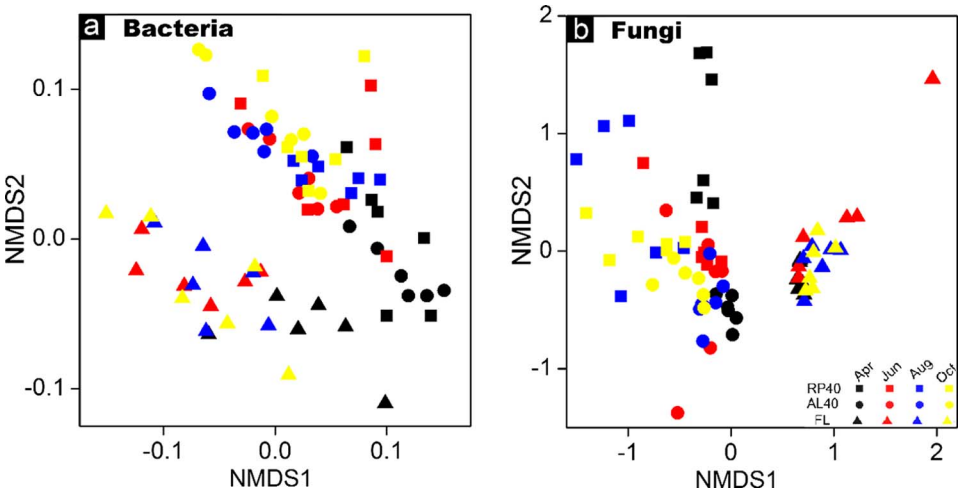

Fig. 4. Principle coordinates analysis of soil microbial (bacterial and fungal) communities across land-use change during four periods.

Ascomycota abundance and greatly decreased *Basidiomycota* abundance (Fig. 5c). Similarities, at the class level (Table S4), the abundances of *Dothideomycetes*, *Sordariomycetes*, and *Leotiomycetes* showed increased trends across four periods, but *Agaricomycetes* and *Tremellomycetes* declined significantly after land-use changes ($p < .05$). Moreover, at the order level, the *Pleosporales, Hypocreales, Sordariales, Xylariales, Helotiales, Chaetothyriales, Eurotiales,* and *Agaricales* were the dominant species but showed different trends across different periods.

3.2. Responses of the microbial community to the linkages of SOC fractions with respiration

The Spearman's correlation coefficients between the microbial characteristics (i.e., bacterial abundance: Babundance, bacterial alpha diversity: BShannon, bacterial beta diversity: BNMDS1, fungal abundance: Fabundance, fungal alpha diversity: FShannon, fungal beta diversity: FNMDS1) and the SOC fractions, as well as soil respiration components were estimated (Table 1). The results showed that the changes in microbial characteristics were significantly correlated with SOC, DOC, MBC, and soil respiration components ($p < .001$). Redundancy analysis and Spearman's analysis showed that SOC fractions (SOC, DOC, and MBC) and soil respiration were significantly correlated with the abundances of *Proteobacteria*, *Bacteroidetes*, *Actinobacteria*, *Chloroflexi*, and *Nitrospirae* in the bacterial compositions, and with abundances of *Ascomycota* and *Basidiomycota* in the fungal compositions (Fig. 6 and Table S5). Furthermore, at the class level (Table S6), SOC fractions and respiration were significantly correlated with the abundances of *Alphaproteobacteria, Gammaproteobacteria, Acidimicrobiia, Chloroflexia, Anaerolineae, Bacilli,* and *Cytophagia* in bacterial compositions, and with the abundances of *Dothideomycetes, Sordariomycetes Agaricomycetes*, and Tremellomycetes in fungal compositions. At the order level (Table S7), several species including *Rhizobiales, Solirubrobacterales, Xanthomonadales, Gaiellales, Sphingobacteriales, Acidimicrobiales, Cytophagales, Frankiales, Sordariales, Eurotiales* and *Agaricales* in microbial (bacterial and fungal) compositions were also significantly correlated with SOC fractions and respiration, but showed different responses.

4. Discussion

4.1. Linkages of SOC fractions with respiration across land-use changes

Land-use change could be represented in Earth system models (ESMs) and led to differential responses of soil carbon dynamics in

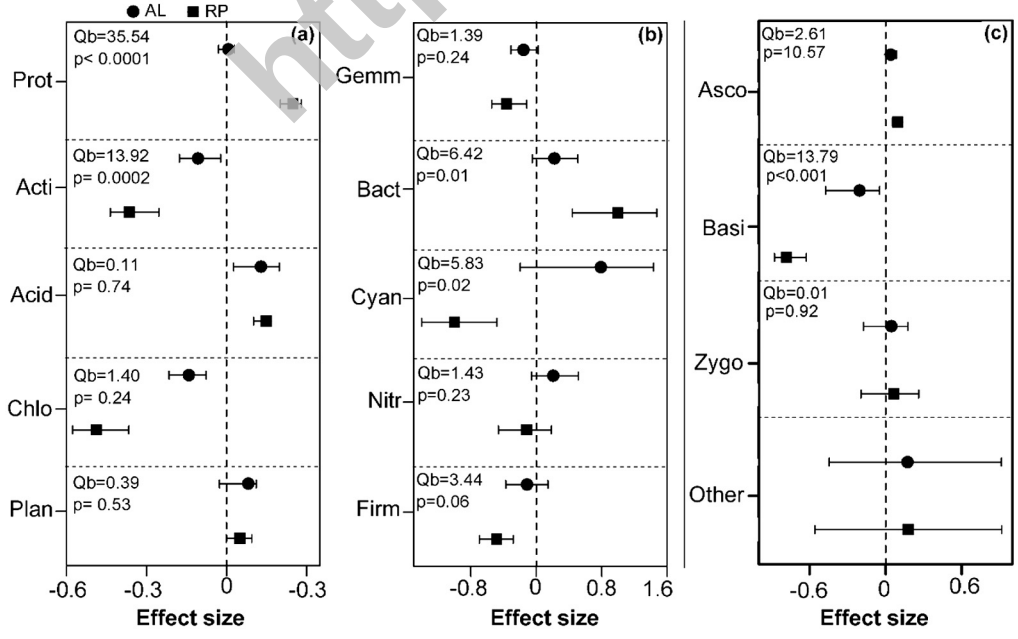

Fig. 5. The influence of land-use change on soil microbial (Bacterial and fungal) compositions. *Proteobacteria (Prot), Actinobacteria (Acti), Acidobacteria (Acid), Chloroflexi (Chlo), Planctomycetes (Plan), Gemmatimonadetes (Gemm), Bacteroidetes (Bact), Cyanobacteria (Cyan), Nitrospirae (Nitr), Firmicutes(Firm), Armatimonadetes (Arma), Verrucomicrobia (Verr). Ascomycota (Asco), Basidiomycota (Basi), Zygomycota (Zygo), Chytridiomycota (Chyt), Glomeromycota (Glom).*

Table 1
Spearman's rank correlation coefficients between the microbial (bacterial and fungal) characteristics (i.e., abundance, alpha diversity, beta diversity) and the soil properties and carbon fractions, as well as soil respiration components.

Microbe	Index		Soil properties and carbon fractions						Soil respiration components		
			pH	SWC	ST	SOC	DOC	MBC	SR	HR	AR
Bacteria	Abundance	R	−0.396**	−0.121	0.055	0.697**	0.603**	0.683**	0.448**	0.286*	0.124
		p	0.001	0.311	0.649	< 0.001	< 0.001	< 0.001	< 0.001	0.049	0.403
	Alpha diversity	R	−0.307**	0.412**	−0.375**	0.376**	0.291*	0.168	0.335**	−0.043	0.356*
	(Shannon)	*p*	0.009	< 0.001	0.001	0.001	0.013	0.159	0.004	0.774	0.013
	Beta diversity	R	0.448**	0.09	−0.141	−0.691**	−0.613**	−0.733**	−0.567**	−0.601**	−0.279
	(BNMDS1)	*p*	< 0.001	0.45	0.238	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.054
	Abundance	R	−0.447**	0.456**	0.299*	0.752**	0.642**	0.763**	0.748**	0.703**	0.324*
		p	< 0.001	< 0.001	0.011	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.025
Fungi	Alpha diversity	R	−0.299*	0.387**	−0.394**	0.453**	0.308**	0.327**	0.335**	−0.235	0.134
	(Shannon)	*p*	0.011	0.001	0.001	0	0.009	0.005	0.004	0.107	0.363
	Beta diversity	R	−0.588**	0.410**	−0.055	0.734**	0.540**	0.588**	0.658**	0.500**	0.445**
	(FNMDS1)	*p*	< 0.001	< 0.001	0.645	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.002

Soil water contents (SWC); soil temperature (ST); soil organic carbon (SOC); dissolved organic carbon (DOC); microbial biomass carbon (MBC); soil respiration (SR); heterotrophic respiration (HR); autotrophic respiration (AR).

** Correlation is significant at the 0.01 level.

* Correlation is significant at the 0.05 level.

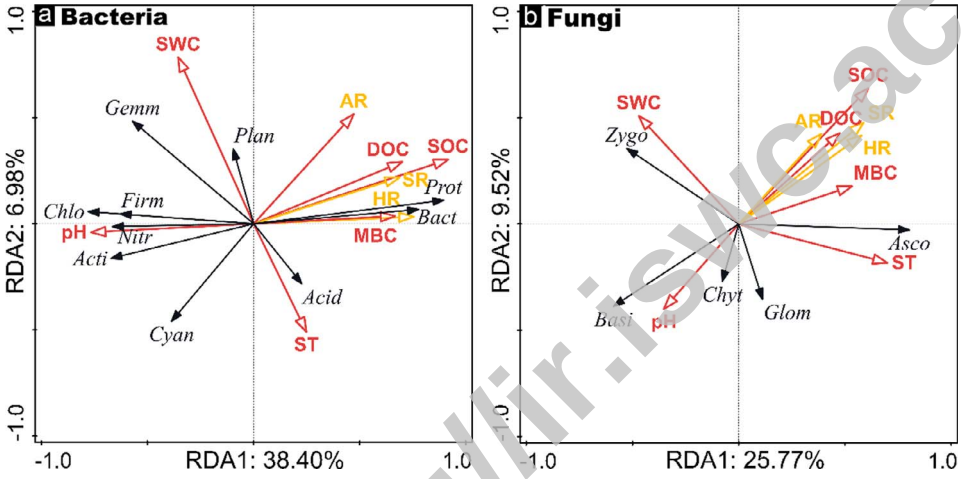

Fig. 6. Ordination plots of the results from the redundancy analysis (RDA) to identify the relationships among the microbial populations (Black arrows) and the soil properties and organic carbon fractions (Red arrows), as well as soil respiration components (Yew arrows) across land-use change. *Proteobacteria (Prot), Actinobacteria (Acti), Acidobacteria (Acid), Chloroflexi (Chlo), Planctomycetes (Plan), Gemmatimonadetes (Gemm), Bacteroidetes (Bact), Cyanobacteria (Cyan), Nitrospirae (Nitr), Firmicutes(Firm), Armatimonadetes (Arma), Verrucomicrobia (Verr). Ascomycota (Asco), Basidiomycota (Basi), Zygomycota (Zygo), Chytridiomycota (Chyt), Glomeromycota (Glom).* (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

terrestrial ecosystem (Luo et al., 2016). The magnitudes and directions of such differential responses were associated with SOC fractions (Iqbal et al., 2010; Liang et al., 2015). Present study confirmed that there were increases in soil respiration and components in response to land use change (Fig. 1), and this increases were positively correlated with SOC fractions (Fig. 2). This may be because higher plant diversity and complex plant compositions in afforested lands can import carbon to soil in the form of litter and root exudates, and further accelerate the decompositions and accumulations of SOC (Dube et al., 2009; Lange et al., 2015). Such linkages were suggested by several recent studies (Zheng et al., 2009; Rui et al., 2016) and highlighted by soil carbon models (Liang et al., 2015; Luo et al., 2016). However, depending on microbial decomposition of SOC (Jenkinson and Rayner, 1977), soil carbon fractions may hold different carbon turnover times (Liang et al., 2015; Rui et al., 2016). Consequently, SOC fractions responded differently to changes in soil respiration (Fig. 2). Among these three carbon fractions, DOC, in particular, was considered the most active form of fresh carbon and can stimulate CO_2 emission (Straathof et al., 2014) and showed a closer relation with soil respiration and heterotrophic respiration (Fig. 2). Previous studies identified that DOC has been considered as an indicator of the availability of soil carbon for microbial processes, which in turn control CO_2 emission from the soil to the atmosphere (Iqbal et al., 2010; Straathof et al., 2014). Overall, these results suggest that land-use changes in the afforested ecosystem can increase the SOC fractions, especially DOC, further altering CO_2 emission from the soil to the atmosphere.

4.2. Trends in soil microbial community as drivers of soil carbon dynamics across land-use changes

It has been generally accepted that microbes are the most active components of the soil ecosystem, and they are thought to be the rate-limiting step in SOC decompositions (Hararuk et al., 2015). However, such responses may differed with changing plant compositions (Lange et al., 2015) and climatic conditions (Luo et al., 2016; Ren et al., 2018). In our study area, the annual cycle of cultivating and harvesting crops were replaced by the much longer forest cycle. Consequently, it enabled the development of large net primary productivity and produced quantity of carbon input into soil (Lai et al., 2016; Ren et al., 2017a). Considerable changes of carbon inputs can influence the utilization by microbial community, and finally affect the composition and distribution of SOC pools and their decomposability (Baumann et al., 2013; Tardy et al., 2015). These results were observed in present study that soil microbial diversity and abundance showed significant relationships with SOC fractions and respiration across land-use changes (Table 1). Together with the above-stated discussion regarding the linkage of SOC fractions with soil respiration, these results suggested that the responses of soil respiration and its components to land-use change may mainly depend on organic carbon fractions (DOC) being mediated by soil microbes (Hararuk et al., 2015; Zhang et al., 2016). Some studies showed

that change in DOC, caused by microbial properties, was the potential predicator for microbial respiration in response to re-vegetation (Xiao et al., 2017). Therefore, land-use changes in afforested ecosystem can help to improve soil microbial diversity and abundance, thereby contributing to increases SOC fractions, particularly DOC, and enhancing soil respiration.

The positive responses of soil microbial diversity to SOC fractions and respiration were discussed above; however, this raised the question- do such responses represent a community-wide response, or are they accompanied by changes in certain microbial taxa? After further analysis, we found that microbial (bacterial and fungal) compositions provided indications about the environmental filters that may have driven the ecosystem carbon cycling in the afforested ecosystem (Fig. 6 and Table S4).

Bacterial community compositions differed due to the enriched relative abundances of the major phyla *Proteobacteria, Bacteroidetes*, and *Cyanobacteria (*Fig. 5 and Table S3*)*, which showed strong correlations with SOC fractions and respiration (Fig. 6a and Table S4). In detail, *Proteobacteria* favored the soil with rich carbon availability (Fierer et al., 2007); thus this phylum may promote the increases in SOC fractions and respiration. In addition to the abundance of *Proteobacteria* discussed above, another possible explanation might be related to the compositions of *Proteobacteria* (Tables S6 and S7). For example, at the class and order levels, both *Rhizobiales* (branch of *Alphaproteobacteria*) and *Xanthomonadales* (branch of *Gammaproteobacteria*) were significantly correlated with SOC fractions and respiration, further supporting the variations of *Proteobacteria* and their response to SOC fractions and respiration across land-use changes. Moreover, the variations of *Bacteroidetes* were stimulated by plant roots and are well adapted to labile carbon in soil (Goldfarb et al., 2011); thus an higher in *Bacteroidetes* might lead to increases in soil organic carbon (Xiao et al., 2017) (Fig. 6). The *Sphingobacteriales*, the branch of *Bacteroidetes*, increased significantly after land-use changes and showed mostly closed to changes of SOC fractions and respiration (Table S6). The positive impacts of increased concentrations of organic matter on the growth of *Proteobacteria* and *Bacteroidetes* were also observed previously (Stevenson et al., 2004; He et al., 2012). Also, other specific taxa, especially for *Actinobacteria* and *Chloroflexi,* decreased significantly across land-use changes and drove the negative responses of SOC fractions and respiration, suggesting a possible balance of soil carbon dynamics being mediating by these two phyla (Fierer et al., 2007; Goldfarb et al., 2011). It has been well established that *Actinomycetales*, an order of *Actinobacteria*, was more abundant in cultivated lands with lower content of organic matter than in the afforested land (Lee-Cruz et al., 2013); thus this phylum showed a negative correlation with soil carbon dynamics in our study. Altogether, land-use changes in the afforested ecosystem greatly influenced the dominant bacterial communities, such as *Proteobacteria, Bacteroidetes, Actinobacteria,* and *Chloroflexi;* the functions of these changing bacterial species can then feedback to help maintain the carbon balance.

As for the fungal community compositions, both *Ascomycota* and *Basidiomycota* accounted for 69.62% of the dissimilarities among treatments and were significantly correlated with SOC fractions and soil respiration (Fig. 6b and Table S4); this phenomenon can be explained by the functions of these two phyla. In detail, both *Ascomycota* and *Basidiomycota* metabolized the organic matter in rhizodeposits, and the abundances of these two fungal phyla were influenced by soil organic matter dynamics as a result of the decomposition of plant residues (Hannula et al., 2012; Bastida et al., 2013). Land-use change in the restored ecosystem provided suitable environment for both phyla, where they utilized the easily degradable fraction of plant residues better, and facilitated carbon accumulation and respiration. The results were consistent with those of a study (Carson et al., 2010), showing that changes in the structure of fungal communities were clearly correlated with changes in carbon fractions. However, in our study, we found that these two phyla and their branches responded differently to the belowground carbon cycle (Fig. 6b, Tables S5–S7). In detail, both *Dothideomycetes* and *Sordariomycetes*, the branches of *Ascomycota*, were positively correlated with SOC fractions and respiration, but *Agaricomycetes* and *Tremellomycetes*, the branches of *Basidiomycota*, were negatively correlated with SOC fractions and respiration (Table S6). These differential responses were because the competitions between these classes resulted in changes in the soil carbon dynamics (Fierer et al., 2007; Rosling et al., 2011). Therefore, together with their functions, these results suggest that the dominant fungal species can be responsible for the changes in SOC and ultimately affect soil respiration across land-use change in the afforested ecosystem.

5. Conclusion

These results have demonstrated that increases in soil respiration components (HR and AR) were coupled with the corresponding changes in SOC fractions, particularly DOC. Such changes depended on alteration of the microbial (bacterial and fungal) communities. In detail, increases in microbial abundance and alpha diversity as well as changes in microbial beta diversity increased the SOC fractions and respiration components across land-use changes. Certain microbial taxa, such as *Proteobacteria, Bacteroidetes, Actinobacteria, Chloroflexi,* belonging to bacterial compositions and *Ascomycota*, *Basidiomycota* belonging to fungal compositions in afforested ecosystems could modulated the linkage of SOC fractions and respiration components. Collectively, our results highlight the importance of microbes for regulating belowground carbon dynamics, and suggest that soil microbes altered the components of soil respiration by affecting SOC fractions, especially DOC.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.11.011.

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