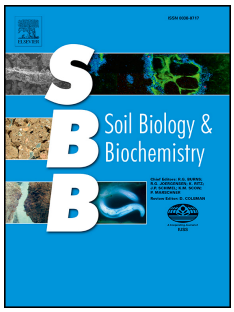

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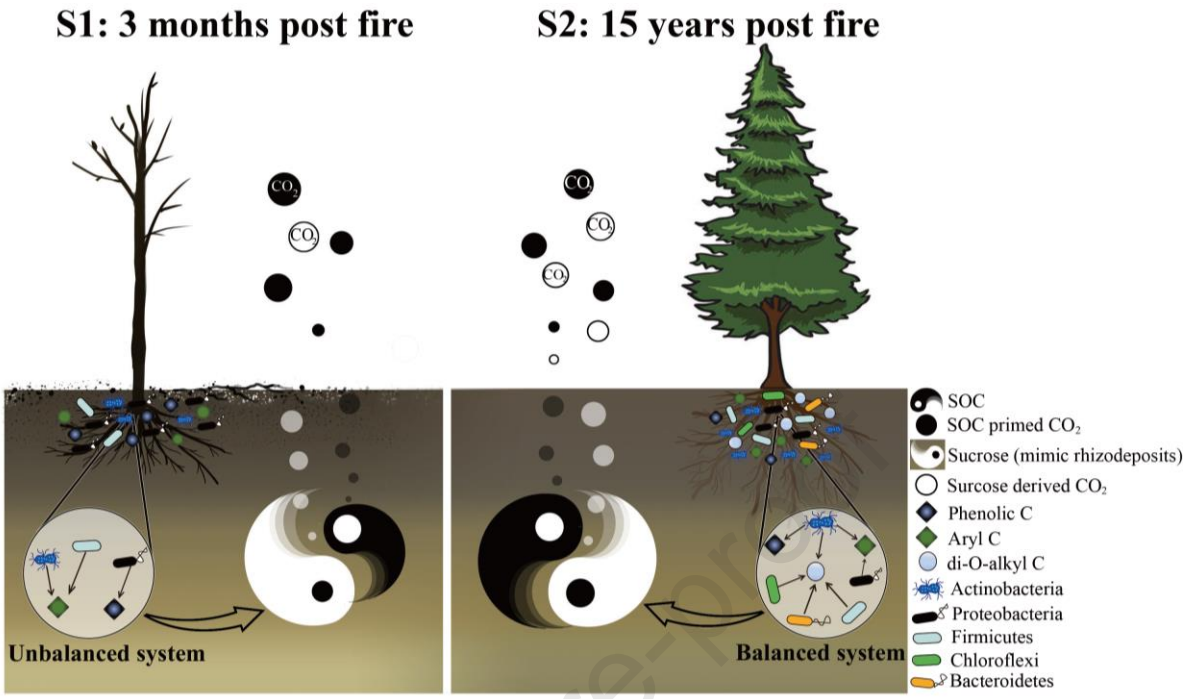
Graphical Abstract



Organic matter chemistry and bacterial community structure regulate decomposition processes in post-fire forest soils

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Abstract

Wildfires decrease forest aboveground biomass and have long-term legacy effects on carbon (C) stocks in soil via alterations of microbial communities and functions. However, the interactions between soil organic C (SOC) chemodiversity and bacterial communities that drive C decomposition remain unclear. Soils from two boreal forest sites, 3 months (S1) and 15 years (S2) after fire events, were incubated for 53 days to quantify the mineralization of sucrose (mimicking rhizodeposits, $\delta^{13}C$ = -11.97‰) and SOC priming. To reveal SOC-bacterial interactions that regulate SOC decomposition, the isotopic abundance, SOC chemical composition (^{13}C NMR), and associated bacterial community structure (16S rRNA gene sequencing) were analyzed. The best multivariate model (DISTLM) analysis indicated that aromatic C (phenolic-C and aryl-C) in S1 and di-O-alkyl C in S2 were the largest contributors to bacterial community structure. The co-occurrence network confirmed SOC-bacteria interactions, and revealed the highly co-occurrent groups, i.e. *Paenibacillus* in S1 and *Bacillus* in S2, both of which belong to the Firmicutes, correlated with recalcitrant C and labile C, respectively, and are potentially linked to decomposition. For example, Firmicutes (as well as Proteobacteria and Actinobacteria) were correlated with aryl-C

and phenolic-C in S1 and highly correlated with SOC priming intensity. The limited C resources (enriched refractory components, i.e. phenolic substances) in S1 favored oligotrophs to outcompete other bacterial groups, which likely aided decomposition of more recalcitrant SOC via co-metabolisms. The slow decomposition of sucrose and large soil priming effects observed in S1 suggested a faster SOC turnover via bidirectional processes of additional sucrose-C gain and native soil-C loss. Collectively, changes in SOC chemistry were coupled with an altered bacterial community, and their interactions might further correlate to decomposition, with implications for C sequestration in the post-fire boreal forest soils.

Keywords: *forest fire; C-microorganisms interactions; priming effect; C sequestration; core microorganisms*

1. Introduction

Wild fires modify the earth's land surface, particularly in the forest areas, which not only destroy vegetation but also cause huge carbon (C) losses from forest ecosystems (González-Pzrez et al., 2004; Certini, 2005; Balshi et al., 2009; Bowman et al., 2009). Increases in fire event frequency threaten the soil organic C (SOC) sink of boreal forests, with large CO_2 emissions that exceed boreal decadal uptake, turning forest soils from a net C sink to a CO_2 source (Walker et al., 2019). During forest fires, a proportion of aboveground biomass is incompletely combusted (Kasin et al., 2013). While aliphatic components (labile C) are lost (Czimczik et al., 2002; Abakumov et al., 2017), the produced pyrogenic C (PyC, recalcitrant C) resists degradation due to their aromatic nature (Czimczik et al., 2002; Kuzyakov et al., 2014). The formation of PyC and its incorporation into soil (wildfires transfer 0.06 to 0.4 Pg C $year^{-1}$) are important for long-term C storage in forests (Bird et al., 2015; Reisser et al., 2016). Forest ecosystem recovery after the fire, especially SOC restoration, normally takes decades (Moya et al., 2018). The legacy effects on C dynamics (mineralization of

SOC and recently input substrates, i.e. litter and rhizodeposits) during post-fire periods are an important determinant for C sequestration and restoration. However, this is rarely investigated, and the mechanisms underlying these C processes remain largely unknown.

Forest fire produced PyC in soil can: i) stabilize rhizodeposits and SOC (negative priming) via PyC-mineral interactions (Weng et al., 2017), or ii) cause stronger mineralization of rhizodeposits and SOC (positive priming), which are associated with changes in microbial community structure (Luo et al., 2017a, 2017b). Fires modify microbial biomass, activity, and community diversity by directly heating the soils (Dooley and Treseder, 2012; Luo et al., 2016; Pressler et al., 2019), or indirectly altering soil physicochemical properties, such as nutrient availability (Wan et al., 2001), pH (Luo et al., 2011), and SOC quantity (C content) (Neff et al., 2005; Hernandez-Soriano et al., 2016) and quality (C chemical composition), through the incorporation of PyC (Waldrop and Harden, 2010). SOC composition, namely the contents of alkyl-C, aryl-C, O-aryl-C, and carbonyl-C can explain more than 50% of the variations in microbial community composition (Ng et al., 2014). Despite intensive investigations of SOC chemical composition (Zhang et al., 2015; Abakumov et al., 2017) or microbial community structure (Docherty et al., 2012; Ferrenberg et al., 2013) only few studies have investigated the interactions between these two areas. In a recent study, SOC functional groups were associated with bacterial taxa (assessed by 16S rRNA gene sequencing) to assess how edaphic variables affect microorganism-C interactions (Bonanomi et al., 2019). However, there are still gaps in our understanding of associations between microorganisms and SOC, and the consequent effects of these associations on C decomposition.

Microbial utilization of organic substances and the consequent CO_2 emissions are determined not only by C availability and microbial community structure (Li et al., 2019a), but also by the affinity of the microbial community to different SOC sources (Bryanin et al., 2018). Labile organic compounds can be preferentially consumed by fast-growth microorganisms, r-strategists (Fontaine et al., 2003), which have high

nutritional requirements, and can maximize their growth when resources are abundant (Fierer et al., 2007). In contrast, microorganisms with K-strategy utilize recalcitrant C when populations are near carrying capacity and resources are limited (Fontaine et al., 2003). The signals of ^{13}C NMR in multiCP spectra indicate SOC chemical compositions by identifying the functional groups, which can be classified as labile (di-O-alkyl C: methoxyl C and alkyne C, carboxyl C) and recalcitrant (alkyl C, aryl C, and phenolic C) components (Li et al., 2017). Aryl-C, as a stable C form, strongly affects microorganisms and their traits, shifting bacterial community composition from r to K-strategy (Ng et al., 2014). Long-term application of manure (27-year field experiment) increased both aromatic component of SOC and the associated Acidobacteria and Bacillus (Li et al., 2018). Alkyl compounds were positively correlated with actinomycetes, indicating these microorganisms and their functional patterns are determined by the chemical nature of these C sources (Wang et al., 2017). Decreases in non-polar alkyl C (e.g., CH_3) and non-protonated aromatic-C underpin priming effects by enhancing microbial activity (Zhang et al. 2015). Recalcitrant and oxidation-resistant C in post-fire soils can have an inhibitory effect on both microbial growth and OC decomposition (Holden et al., 2015). However, the microbial community, especially the specific bacterial groups that are linked with SOC components and thus determine C decomposition, has rarely been investigated (Bonanomi et al., 2019). The mechanisms underpinning C decomposition processes require investigation as they are of great significance in terms of C sequestration in boreal forests (Walker et al., 2019).

This study we used solid-state ^{13}C NMR spectroscopy and next-generation sequencing to link SOC chemical composition with bacterial community composition in post-fire soils, of 3 months (S1) and 15 years (S2), at depths of 0-5 cm, 5-20 cm, and 20-40 cm. The soils were incubated for 53 days following the input of sucrose (to mimic rhizodeposits, with $\delta^{13}C$ = -11.97‰). The aims of this study were to investigate: 1) the bacterial community composition, SOC chemical composition, and their relationships, and 2) SOC-bacteria interactions and their link to C decomposition, i.e.

sucrose mineralization and sucrose-induced priming effects. We hypothesized that: i) bacterial community diversity would be lower in S1 due to lower content of labile organic compounds after fire compared to S2, and ii) SOC mineralization would be stronger in S2 as compared to S1, due to higher bacterial activity, and more positive connections between the bacterial community and SOC chemical components.

2 Materials and Methods

2.1. Soil samples

The soils were sampled from a pine forest in New Shuguang Country (S1: 50°12'46.512"N, 127°15'57.528"E) and Forest Center (S2: 52°7'48.252"N, 125°55'37.920"E), Heilongjiang province, China. Coniferous forests represent ~60% of the boreal forest and ~65% of the burned areas in North China (http://www.forestdata.cn/index.html). The boreal forest is widely and evenly distributed in these areas, and the soils are characterized as Phaeozem. Though geographically distant from each other, these two sites possessed similar vegetation type, age, soil types, and horizon depths. Both sites experienced a severe fire that burned the majority of aboveground plant biomass. Soils were collected in August 2015, that is, after 3 months (S1) and 15 years (S2) after the respective fire events. From each site, three independent field replicates were collected, and each replicate was a mixed sample from a random five independent points. By digging pits, the soils were collected from 0-5 cm (humus layer, O horizon), 5-20 cm (topsoil, A horizon) and 20-40 cm (illuvial, B horizon). Unburned areas adjacent (within 20-100 m) to the burned sites were sampled as unburned soils (US1 and US2, SI Table 1). Stones and plant residues were removed by hand, and the soil samples were stored at 4 ℃ before the incubation study.

Prior to the incubation experiment, the soil samples were passed through a 2 mm sieve, homogenized, and adjusted to 40% of water-holding capacity (WHC), and then pre-incubated at 25 ℃ for 7 days (Luo et al., 2011). Basic soil properties, including

dissolved organic C (DOC), total C, total N, pH, and $\delta^{13}C$ (‰) were measured for all samples, and the composition of SOC functional groups before incubation was determined by solid-state ^{13}C-NMR spectra.

2.2. Experimental design

After pre-incubation, soils (100 g, $\delta^{13}C$ = -26 ~ -24‰) were thoroughly mixed with 1% sucrose (w/w, 4200 mg C kg^{-1} soil, $\delta^{13}C$ = -11.97 ± 0.12‰) solution (the content of added water was accounted for (reach 40% WHC), and used 1/3 added water to dissolve sucrose and spraying into soils, beaker was rinsed with the remaining water several times and added to the soils). The un-amended soils were treated in the same way without sucrose. Soil (30 g) was incubated in a 100-mL beaker placed inside a 1000 mL glass jar for 53 days. The evolved CO_2 was absorbed into 20 mL of 1.0 M NaOH, that was renewed after 1, 3, 7, 14, 28, and 53 days and used to determine total soil CO_2 emission and the CO_2 derived from SOC or added sucrose based on $\delta^{13}C$ analysis. Deionized water (10 mL) was placed in the base of the glass jar to maintain humidity during the incubation. Three jars with only deionized water and NaOH were incubated as blanks. All jars were sealed with a rubber bung, randomized, and incubated (25 °C) for 53 days. Soils (0.5 g) were destructively sampled to investigate changes in bacterial community structure for 16S rRNA gene sequencing after incubation. Graphic design of the experiment can be found in SI Fig. 1.

2.3. Chemical and biological analyses

Soil pH was measured at the ratio of 1:2.5 (w/w) of soil-to-deionized water using a pH electrode. Total C and N in air-dried soils (milled < 200 μm) were determined by dry combustion (LECO CNS 2000, LECO Corporation, Michigan, USA). Microbial biomass C (MBC) was determined by chloroform fumigation-extraction (Wu et al., 1990; Durenkamp et al., 2010) and measured by using a total organic carbon (TOC) auto-analyzer (Shimadzu, Analytical Sciences, Kyoto, Japan). MBC was calculated as the difference in DOC concentrations between the fumigated and unfumigated soil

samples and multiplied by a factor of 2.22 (K_{EC}). The natural $\delta^{13}C$ (‰) signature of the soils (air-dried, milled < 2 mm) and sucrose were determined using an elemental analyzer-coupled-isotope ratio mass spectrometer (EA-IRMS) (Sercon Ltd, Crewe, UK). Soil characteristics are shown in Table 1.

2.4. Total CO_2 emission and partitioning of CO_2 fluxes

The total CO_2 emission during the soil incubation was determined by trapping CO_2 in 1 M NaOH (20 mL) (Tinsley et al., 1951). NaOH solution (5 mL) was mixed with water (10 mL) and titrated with 0.05 M HCl using a TIM840 auto titrator (Radiometer Analytical, Villeurbanne Cedex, France). To measure $\delta^{13}C$ (‰) in the trapped CO_2 solution, a 5 mL aliquot was combined with 1 M $BaCl_2$ (10 mL) in a centrifuge tube (Aoyama et al., 2000). The $BaCO_3$ precipitates were filtered and collected on glass fiber filters (90 mm, Whatman GF/A, UK), rinsed three times with distilled water, and dried at 60 °C overnight. Precipitates (5 mg) were placed in tin capsules and analyzed for $\delta^{13}C$ via EA-IRMS (elemental analyzer-isotope ratio mass spectrometer) (Sercon Ltd, Crewe, UK).

2.5. Calculation of CO_2 derived sources

The differences between $\delta^{13}C$ values of SOC and sucrose enabled the separation of soil-derived and sucrose-derived CO_2 according to Balesdent et al. (1996):

$$F_{CO_2\text{-}C,\ sucrose} = (\delta^{13}{}_{sample}CO_2 - \delta^{13}{}_{soil}CO_2) / (\delta^{13}{}_{sucrose}CO_2 - \delta^{13}{}_{soil}\,CO_2) \quad \text{(Eq 1)}$$

where $F_{CO_2\text{-}C,sucrose}$ was the fraction of CO_2 released from sucrose in sucrose-amended soil. $\delta^{13}{}_{sucrose}CO_2$ was the $\delta^{13}C$ value of the sucrose, $\delta^{13}{}_{sample}CO_2$ and $\delta^{13}{}_{soil}CO_2$ were the $\delta^{13}C$ value of the total CO_2 released from the sucrose-amended soil and the soil without sucrose, respectively.

The fraction of SOC mineralization from total CO_2 ($F_{CO_2\text{-}C,soil}$) was calculated as

$$F_{CO_2\text{-}C,soil} = 1 - F_{CO_2\text{-}C,\ sucrose} \quad \text{(Eq}$$

2)

To calculate the priming effect (PE), the following equation was used to estimate the absolute amount of the PE and its relative magnitude:

$$PE = [F_{CO_2\text{-}C,soil} \times (CO_2\text{-}C_{sample})] - (CO_2\text{-}C_{soil}) \quad \text{(Eq 3)}$$

where, CO_2-C_{sample} and CO_2-C_{soil} were the total CO_2 released from sucrose-added soil and non-added soil, respectively.

2.6. Chemical structure of soils by ^{13}C NMR

Dry soil samples (4 g) were weighed into centrifuge tubes (50 mL), hydrofluoric acid (HF) (10% v/v; 25 mL) was added, and the tubes were shaken for 1 h. Subsequently, the samples were centrifuged at 3000 rpm for 10 min. The supernatant was discarded, and the residual soil was treated with HF again. The HF treatment was repeated 8 times. For the first four times, tubes were shaking for an hour each time, the following three treatments were shaken for 12 hours, and the final treatment was shaken for 24 hours. The remaining soil material was washed with deionized water (25 mL) and centrifuged (four times); each time, the supernatant was discarded. The remaining soil material was oven-dried (40 °C) and then milled to < 0.3 mm. The ^{13}C NMR spectra of SOC were measured using a Bruker Advance 400 spectrometer at 400 MHz for ^{13}C with a 3.2 mm double-resonance MAS probe head (at a spinning speed of 15 kHz, with a 90° pulse-length of 4 μs). The referenced material of ^{13}C chemical shifts was tetramethylsilane.

To compare the solid-state ^{13}C-NMR spectra among samples, Bruker TopSpin (v3.5) was used to calculate the peak areas and integrated to estimate their relative proportions (Li et al., 2017). The choice of spectral regions and identification of C functional groups (chemical structures) was performed (Bonanomi et al., 2013). The following seven groups were targeted: 0 - 45 ppm, alkyl C; 45 - 110 ppm, O-alkyl C (with 45 - 60 ppm for methoxyl C, 60 - 90 ppm for alkyne C, and 90 - 110 ppm for

di-O-alkyl C); 110 - 160 ppm, aromatic C (with 110 - 142 ppm for aryl C and 142 - 160 ppm for phenolic C); 160-220 ppm, carboxyl C (with 160 - 190 ppm for carboxy C and 190 - 220 ppm for carbonyl C). The peaks of chemical composition in soils were 22.5, 52.5, 76.5, 101.5, 126, 151 and 175 ppm for alkyl C, methoxyl C, alkyne C, di-O-alkyl C, aryl C, phenolic C, and carboxyl C, respectively.

2.7. 16S rRNA gene sequencing

DNA was extracted from fresh soil (0.5 g) using FastDNA Spin Kits for Soil (Catalog Number: 116560200, MP Biomedicals, Santa Ana, CA, USA). The extracted DNA was purified using UltraClean DNA purification kits (MoBio, Carlsbad, CA, USA). The isolated DNA was eluted in 50 μL TE buffer (10mM Tris-HCl, 1 mM EDTA, pH 8.0). The DNA quality was verified by a NanoDrop 2000 spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). The 16S rRNA gene amplification and sequencing were done as follows. The V4–V5 region of the bacterial 16S rRNA gene was amplified using the primer pair 515F (5'-GTGCCAGCMGCCGCGG-3')/907R(5'-CCGTCAATTCMTTTRAGTTT-3') (Biddle et al., 2008). To discriminate each sample, a unique 5-base-pair (bp) sequence was inserted into the reverse primer. The PCR amplification of each sample was performed in triplicate with 50 μL reaction mixtures containing 0.5 μL (125 pmol) of each forward/reverse primer, 1 μL (approximately 50 ng) of genomic DNA, 23 μL of double-distilled water, and 25 μL of Premix Taq (Takara, Shiga, Japan). The PCR program was conducted as follows: 3 min of denaturation at 94 °C; followed by thirty-five thermal cycles of 30 s at 94 °C, 30 s at 54 °C and 45 s at 72 °C; and a final extension for 10 min at 72 °C with a thermocycler PCR system. The PCR products were purified, mixed, and submitted to Novogene for single-end sequencing on the IonS5TMXL platform (Novogene, Beijing, China).

2.8. Statistical analyses

Raw DNA sequences were processed to remove low-quality ($Q < 25$) and short sequences (< 200 bp), including ambiguous base calls or homopolymers (> 6 bp), by

using Cutadapt (Martin, 2011). The following analysis excluded chimeric and singleton sequences. Uparse (Edgar, 2013) was used to cluster high-quality reading into operational taxonomic units (OTU) with 97% sequence similarity threshold, and compared with the Silva database (v132) using Mothur v1.39.5 (Wang et al., 2007). 1403938 valid sequences (min sample sequences: 51351, max: 84485, average: 77997) were obtained in total. The sequence data were submitted to the National Center for Biotechnology Information (NCBI) Sequence Read Archive (http://trace.ncbi.nlm.nih.gov/Traces/sra/) with bioproject number PRJNA664958.

Alpha diversity (picante function in the vegan package of R) of soil bacterial community were calculated after rarefying all samples to the same sequencing depth. A principal coordinate analysis (PCoA) based on Bray-Curtis distance (vegdist function in vegan) from all samples was used to differentiate bacterial community structure for all three depths of the two sites (S1 and S2) (Zhang et al., 2007). PERMANOVA (Adonis function in vegan) was used to quantify these effects. The characterization of bacterial community features (taxa) for recovery times and at the three soil depths was performed using the linear discriminant analysis (LDA) effect size (LEfSe) method (http://huttenhower.sph.harvard.edu/lefse/) for biomarker discovery. Circos (http://mkweb.bcgsc.ca/tableviewer/visualize/) was used to facilitate the identification and analysis of similarities and differences arising from comparisons the relative abundance of phyla (Krzywinski et al., 2009), which emphasizes the statistical significance and biological relevance (Segata et al., 2011). Distance-based linear model multivariate analysis (DISTLM) was used to evaluate the relative effects of environmental factors on the soil bacterial community (Mcardle and Anderson, 2001).

For the construction of co-occurrence networks for bacterial communities and environment factors, all OTU taxa from the two sites were used to run the networks by setting the same indexes (dissimilarity threshold for the maximum value of the KLD matrix and the Spearman's correlation threshold to 0.8). For each edge and measure, permutation and bootstrap distributions were generated with 100 iterations.

Measure-specific *p* values were computed as the area of the mean of the permutation distribution under a Gauss curve generated from the mean and standard deviation of the bootstrap distribution. The *p* values were adjusted using the Benjamini-Hochberg procedure (Benjamini and Hochberg, 1995; 2000). Finally, only edges supported by two measures and adjusted *p*-values below 0.05 were retained. The nodes and diamonds in the constructed networks represent OTUs and environment factors, respectively, and edges represent strong and significant correlations between OTUs and SOC functional groups. Network visualization was conducted using Gephi 0.9.1 and Cytoscape 3.6.1 (Smoot et al., 2010). OTUs (assigned to phyla and genera) with the highest betweenness centrality scores were considered as keystone species (González et al. 2010). The data are shown in SI Table 2. The calculated topological characteristics of networks included the following: positive and negative correlations, nodes, edges, graph density, and modularity (SI Table 3). Indicated by PERMANOVA ($R^2 = 0.54$, $p < 0.001$, SI Table 4) and ANOSIM analysis ($R = 0.62$, $p < 0.001$, Fig. 2b, SI Table 4), the difference between soil layers was relatively smaller compared with the time post-fire. Therefore, samples from different depths were combined to run the network analysis for these two sites.

Structural equation modeling (SEM) was conducted in AMOS software (AMOS 18.0 version, IBM, Chicago, IL, USA) (Bowker et al., 2008). Path analyses were conducted to evaluate relationships among soil chemistry, soil microbial communities, and total CO_2, and soil primed CO_2.

The effects of soil site and soil depth on the sucrose-derived CO_2 and primed CO_2 in sucrose-amended treatments were analyzed by mixed effect ANOVA (SPSS Statistics 23) at $p < 0.05$, following the Tukey post-hoc test.

3. Results

3.1. Soil properties and SOC chemical composition

SOC chemical composition and other soil properties (except pH) were dependent on the soil site and depth (Table 1). The pH of S2 was lower than S1, while water-holding capacity in S2 was higher (Table 1, SI Table 5). Microbial biomass C in S2 was 50% and 20% higher than that in S1 for soil horizons A and B, respectively (Table 1, SI Table 5). In addition, the content of labile SOC components, such as carbonyl-C, were higher in S2 compared to S1 (SI Fig. 2, SI Table 6). The aromatic-C (aryl-C and phenolic-C) decreased with the depth in S1, while it nearly unchanged along depths of S2 (SI Fig. 2, SI Table 6).

3.2. Soil CO_2 emission and source partitioning

The amounts of mineralized sucrose and primed SOC were determined by soil site and depth (SI Table 7), with the largest magnitude of mineralization in the O horizon, as compared to the A and B horizons (Fig. 1, SI Fig. 3, SI Table 8). The total CO_2 and sucrose-derived CO_2 were higher in S2 than S1, and decreased with soil depth (Fig. 1, SI Fig. 3, SI Table 8). The sucrose-derived CO_2 released from S2 was three times as much as that from S1. The ratio of primed SOC to the total CO_2-C mineralization was higher in S1 than S2 (Fig. 1), although the total primed C was similar in both sites (Fig. 1, SI Fig. 3, SI Table 8). The rates of primed CO_2 emission peaked on day 3 for both sites, and thereafter the mineralization of both sucrose and SOC remained at a relatively low level (Fig. 1, SI Fig. 3, SI Table 8).

3.3. Effects of fire on bacterial community composition

Bacterial diversity based on the Shannon and Chao1 indices decreased with soil depth (Fig 2a, SI Table 9). The taxa with different abundances among the three horizons (O: 0-5, A: 5-20, and B: 20-40 cm) of the two sites are shown in SI Fig. 5. Rare species (< 5% relative abundance), such as Bacteroidetes, Acidobacteria, Gemmatimonadetes, and Verrucomicrobia, were higher in the topsoil than deeper layer in both sites. Compared to the topsoil, the relative abundance of Firmicutes increased in deeper layers (SI Fig. 4, SI Table 10).

Compared to the effect of soil depth, the bacterial community was more

influenced by site location, with larger community variation between S1 and S2 (Adonis = 0.32, $p < 0.01$), but relatively small variation between the three depths in S2, as well as A and B horizons in S1 (Fig. 2a, b). The PERMANOVA ($R^2 = 0.54$, $p = 0.001$) and ANOSIM (R = 0.62, $p = 0.001$) analyses also confirmed higher variation of bacterial communities between the two sites relative to depth (SI Table 4). Circos analyzed the similarities and differences of the relative abundance of phyla among treatments (Fig. 2c). Proteobacteria in S1 and Actinobacteria in S2 had the highest abundance (SI Table 10). The greatest difference observed at the genus level in S1 and S2 were *Streptomyces*, *Actinoallomurus* (Actinobacteria), *Afipia* (Proteobacteria) and *Bacillus* (Firmicutes) (SI Fig. 6).

3.4. Correlation of SOC chemical composition and bacterial communities

Co-occurrence network analysis revealed the interconnections between soil chemical properties and bacterial community composition (Fig. 3). 24 nodes and 99 edges were present in the S1 network, and 38 nodes and 130 edges in the S2 network (SI Table 3). At the phylum level, Actinobacteria, Proteobacteria, and Firmicutes were negatively correlated with phenolic-C and aryl-C, and there were more negative correlations (94.2%) than positive among them in S1. In S2, the diversity and abundances of Chloroflexi, Gemmatimonadetes and Verrucomicrobia were higher compared to S1. Similarly, the abundances of these phyla, as well as those of Actinobacteria, Proteobacteria, and Firmicutes were correlated with di-O-alkyl-C, DOC, aryl-C, phenolic-C, alkyl-C, and carbonyl-C. The S2 network showed a balanced system that the positive (54%) and negative (46%) correlations between microorganisms and C chemical compositions were nearly equal (Fig. 3, SI Table 3).

Firmicutes were the key phylum for both sites, based on the co-occurrence network analysis (Fig. 3, SI Table 2). The modules that were most important to the network structure were determined based on betweenness centrality (BC) score. *Paenibacillus* (Firmicutes), *Massilia* (Gammaproteobacteria), *unidentified_Rickettsiales* (Alphaproteobacteria), and *Solirubrobacter* (Actinobacteria) were designated as the highly co-occurrent groups in S1, while in S2, *Alicyclobacillus*

and *Bacillus* (Firmicutes), *Streptomyces* (Actinobacteria), and *Microvirga* (Alphaproteobacteria) were the key genera (SI Table 2). The variation of bacterial communities between S1 and S2 was attributed to contributions of phenolic-C (68%), pH (8%) in S1, and di-O-alkyl-C (41%) and aryl-C (23%) in S2, as indicated by DISTLM analysis (Table 2). The contribution of recalcitrant C (i.e. phenolic-C and aryl-C) to bacterial community (Firmicutes, Actinobacteria, Proteobacteria and Bacteroidetes) was greater than 50% in S1. In contrast, labile C (di-O-alkyl-C) in S2 contributed to Firmicutes, Chloroflexi, Actinobacteria, and Proteobacteria more than that of S1 (Fig. 3, 4; Table 2).

3.5. Bacterial communities in relation to C dynamics

To identify the relationship among basic soil properties, SOC chemistry, bacteria, and priming effect, the model factors were selected based on the following conditions for S1 and S2, respectively. First, soil properties and chemistry ($p < 0.05$) were selected through the best multivariate model (DISTLM) analysis (Table 2). Second, microorganisms were selected for the relative abundance (higher than 5%) and the significant correlation ($p < 0.05$) between phyla and priming effect (Fig. 2c, 3, SI Table 12). Based on the analysis of the relationship among basic soil properties, SOC chemistry, bacteria, and priming effect, the abiotic factors in S1 were pH, phenolic C, and aryl C, while those in S2 were pH, di-O-alkyl C, and aryl C. The biotic variables were Proteobacteria, Actinobacteria, Firmicutes, and Bacteroidetes in S1 and Proteobacteria, Actinobacteria, Firmicutes, and Chloroflexi in S2.

Through Pearson correlation of bacteria (phylum level) and primed CO_2 of the two sites, Bacteroidetes were correlated ($R^2 = -0.686$, $p < 0.05$) with the PE in S1, while Chloroflexi correlated with PE in S2 ($R^2 = -0.929$, $p < 0.01$) (SI Table 12). The SEM also revealed the relevance among abiotic factors, major phylum level microorganisms, total CO_2, and primed CO_2. Proteobacteria, Actinobacteria, Firmicutes, and Bacteroidetes were negatively correlated to phenolic-C and aryl-C, which were linked with soil priming in S1 (Fig. 4). Labile compounds (di-O-alkyl-C) were negatively correlated with the abundance of Firmicutes and Proteobacteria in S2,

417 while recalcitrant C (aryl-C) had negative associations with the abundance of
418 Chloroflexi. Furthermore, Actinobacteria and Proteobacteria were positively
419 correlated to soil total CO_2 and primed CO_2 (Fig. 4).

420

421 **4. Discussion**

422 *4.1 Bacterial community in post-fire soils*

423 Soil bacterial taxa that have been identified as aromatic C-degraders (i.e.
424 *Massilia*, *Burkholderia*, and *Bacilli*) are viewed as positive fire-responders
425 (Ferrenberg et al., 2013; Whitman et al., 2019). After establishing themselves in
426 post-disturbance soil, these microorganisms can adapt to stress, i.e. limitation of
427 available C, and thus degrade complex carbohydrates, such as aromatic C and chitin
428 to maintain their metabolism (Mataix-Solera et al., 2009). Firmicutes are viewed as
429 either copiotrophic or oligotrophic bacteria, able to change trophic strategy depending
430 on the nutritional status (Fierer et al., 2007). Not only are they able to withstand
431 resource stress (S1 in this study) via formation of endospores (Yeager et al., 2005;
432 Galperin et al., 2012), but also adapt to resource-rich conditions (Fierer et al., 2007;
433 Bonanomi et al., 2019). The genus *Paenibacillus* in S1 and *Bacillus* in S2 (both
434 Firmicutes) were the co-occurrent groups (Fig 3, SI Table 2). *Bacillus* is not only a
435 spore-forming taxon but a phenotypically heterogeneous group, with members that
436 exhibit a wide range of nutritional requirements and growth conditions (Ash et al.,
437 1991; Fierer et al., 2007). *Paenibacillus,* as a spore-forming taxon, has been found to
438 colonize and thrive in burned soils of forest ecosystems due to their spores ability to
439 resist heat and toxic compounds, i.e. fire produced phenol (Yeager et al., 2005).
440 Moreover, the relative abundance of Firmicutes increases with soil depth, reflecting
441 their adaptation to oligotrophic environments (Hansel et al., 2008; Li et al., 2014).

442 Depth is another factor that can shape microbial community structure (Fierer et
443 al 2003; Pérez-Valera et al., 2019). Bacterial diversity was lower in the A and B
444 horizons compared to O horizon (Fig. 2a), which was attributed to the decline in
445 organic C and nutrient availability with soil depth (Table 1). However, the responses

of phyla to soil depth were not consistent. The relative abundance of most phyla, such as Bacteroidetes and Acidobacteria decreased, whereas the relative abundance of Firmicutes increased (relatively enriched) with soil depth (Fig. 2c). Bacteroidetes are copiotrophic microorganisms, enriched in soils that have a high labile C content, whereas Firmicutes cannot be adequately predicted by changes in C availability or soil nutritional conditions due to their ability to adapt to a range of ecosystems by distinct trophic strategy (Fierer et al., 2007). Thus, the whole bacterial community apart from Firmicutes, shifted to lower abundance with increasing depth and oligotrophic conditions, i.e. lower content of TC, TN and DOC (Dooley and Treseder, 2012).

Soil pH and chemical composition of SOC, such as phenolic-C, aryl-C, and di-O-alkyl-C, were the most influential factors explaining bacterial community structure as based on the DISTLM analysis (Table 2). First, soil pH can be linearly correlated with the amount of microbial biomass and activity (Rousk et al., 2009), and increased pH is often found in post-fire forests because of alkaline reaction from ash (Pereira et al., 2014). In addition, SOC properties modulate bacterial community not only via C content, but also by its chemical composition. For instance, phenolic-C in S1 and di-O-alkyl C in S2 contributed 68% and 41% to bacterial community structure, respectively (Table 2), indicating their strong interrelation between each other (Ng et al., 2014; Bonanomi et al. 2019; Li et al., 2019ab). However, previous studies focused on the change in either soil organic matter chemistry (Näthe et al., 2017) or microbial community (Mataix-Solera et al., 2009), disregarding their interactions.

4.2. Interactions between SOC chemistry and microbiome

SOM and microbiome interactions in S1 soil

Co-occurrence network analyses showed the changes of SOC chemical composition (i.e. enriched recalcitrant-C vs depleted labile-C) in S1, led to a stronger negative connection with the relative abundance of Proteobacteria, Actinobacteria, and Firmicutes (Fig. 3). Path analysis confirmed that these bacterial phyla were associated with more recalcitrant C components, i.e. phenolic-C and aryl-C in S1 (Fig.

475 4a). These compounds, such as aryl-C, reflect relatively stable forms of SOC, and the
476 strong association with microbiome indicated the large contributions of recalcitrant
477 components to bacterial community establishment in the early period after fire (Fig.
478 4a). Similarly, the high content of aryl-C in soil with addition of green waste derived
479 PyC strongly influenced microbial community composition via large recalcitrant
480 components (Ng et al., 2014).

481 Specifically, the phylum Proteobacteria is associated with recalcitrant
482 components of aryl-C (Li et al., 2019b). Litter chemistry parameters, including
483 proximate cellulose and lignin/N ratio, have primarily been linked with Proteobacteria
484 (Bonanomi et al., 2019). For example, *Sphingomonadalaes* (class of
485 Alphaproteobacteria) was found to utilize lignin (Goldfarb et al., 2011). The addition
486 of ^{13}C-labelled wheat residue favored the development of Gammaproteobacteria
487 (genera *Massilia* and *Pseudomonas*), which are known to degrade recalcitrant organic
488 compounds (Bernard et al., 2007). In addition, the phylum Actinobacteria was
489 associated with the content of O-aromatic fraction, which was explained by a better
490 adaptation of this phylum to soil enriched with aryl-C alike components, such as
491 PAHs (Ortega-González et al., 2015). This phylum is also adapted to soils enriched
492 with PyC aromatic components (Luo et al., 2013; Luo et al., 2017a).
493 *Solirubrobacterales* (Actinobacteria) may be involved in the degradation of various
494 aromatic hydrocarbons and PAHs (e.g., C4-C16 alkane and fluoranthene) by
495 producing extracellular enzymes (Page et al., 2015). Moreover, Actinobacteria, as
496 K-strategists, can out-compete other organisms by utilizing recalcitrant C, most likely
497 via their extended mycelium (Jeewani et al., 2020). Thus, these specific microbial
498 groups were observed in soils shortly after a fire, and able to survive in presence of
499 recalcitrant C compounds, e.g., PyC generated by the burning.

500 *SOM and microbiome interactions in S2 soil*

501 Several years after a fire, SOC is composed of a wider range of labile and
502 recalcitrant fractions, which led to a higher diversity in the microbial community with
503 different microbial life-history strategies (Waldrop and Harden, 2010; Holden et al.,
504 2015). The SOC chemical compositions, including di-O-alkyl-C and aryl-C in S2, in

S2 were correlated to several bacterial phyla (Fig. 3b and 4b). In particular, Chloroflexi, corresponding to K-strategy, was correlated with aryl-C, while the relative abundance of Firmicutes were mostly associated with labile carbohydrates, i.e. di-O-alkyl-C (Bonanomi et al. 2019). Li et al. (2019b) also confirmed the correlation between Firmicutes and di-O-alkyl C/O-alkyl C. Easily-degradable SOC, such as -OCH, in organic compost was utilized by *Bacillus* (belong to phylum of Firmicutes) via cellulases, chitinases, and proteases (Li et al., 2018). Firmicutes were considered a highly co-occurrent microbe in both sites (Fig. 3), and linked to aryl-C and di-O-alkyl-C in S1 and S2, respectively (Fig. 4), suggesting their ability to adapt both copiotrophic and oligotrophic conditions. *Alicyclobacillus* (Firmicutes) was generally capable of degrading polycyclic aromatic hydrocarbons (PAHs) in crude-oil contaminated soil (Yang et al., 2014). A higher abundance of Firmicutes after forest fire has been previously reported (Ferrenberg et al., 2013), and these microorganisms might dominate post-fire forest ecosystems through different succession stages: i) survive after the fire and out-compete the majority of copiotrophs in stressed condition via spores (Yeager et al., 2005; Galperin et al., 2012), ii) take advantage of labile C to maintain their fast growth and metabolisms (Verastegui et al., 2014; Bonanomi et al., 2019), while additional C/nutrients are offered by recovering plants, and iii) degrade complex C, such as chitin, for survival when available labile resources are depleted (Ng et al., 2014; Devpura et al., 2017; Bonanomi et al., 2019).

The classes of Betaproteobacteria and Gammaproteobacteria, regarded as opportunists, were highly correlated with the easily-degradable compounds (Di Lonardo et al., 2017). We found the phylum Proteobacteria had negative correlations with carbonyl-C and alkyne-C (Fig. 3). The decreased proportion of O-alkyl-C and di-O-alkyl-C, that are associated with sugars and cellulose, respectively, mirrored a reduction of relative abundance of Proteobacteria during litter decomposition (Bonanomi et al. 2019). However, Proteobacteria have not only been linked with labile carboxylic C, but also with recalcitrant components (aryl-C) (Li et al., 2019b). This contradiction requires detailed classification at lower phylogenetic levels. For instance, Betaproteobacteria (i.e. *Burkholderiales*) and Gammaproteobacteria (i.e.

535 *Enterobacteriales, Alteromonadales, Pseudomonadales*) responded quickly to labile C
536 (Di Lonardo et al., 2017), while taxa within the class of Alphaproteobacteria (i.e.
537 *Sphingomonadalaes*) adapted to both labile sucrose and recalcitrant lignin (Goldfarb
538 et al., 2011). *Microvirga* (Alphaproteobacteria) was enriched in nutrient-poor and
539 heavy metal contaminated soils (Lgwe and Vannette, 2019). Thus, similar to the
540 phylum Firmicutes, the variations of corresponding C fractions associated with
541 Proteobacteria suggested this phylum can adapt to C substrates of varying chemical
542 recalcitrance, i.e. C availability (Goldfarb et al., 2011).

543 *4.3. Biological and chemical interactions on soil organic C decomposition*

544 Despite the chemical composition of SOC being one of the major driving forces
545 shaping microbial communities, few studies have linked SOC chemodiversity with
546 biodiversity to assess their interactive effects on SOC dynamics (Bonanomi et al.,
547 2019). Previous studies indicated that Actinobacteria could be enriched in PyC
548 enriched soils (labile C limited), and responsible for the positive soil priming effects
549 via their extended mycelium (Luo et al., 2013; Luo et al., 2017a). Actinobacteria
550 dominated the oligotrophic environments of S1, that were enriched with refractory
551 organic C components, and were linked to soil priming (Fig. 2c, 4a). In addition,
552 Proteobacteria and Firmicutes, which were positively correlated to SOC priming in S1
553 (Fig. 4a), might be involved in decomposition of recalcitrant components due to their
554 wide nutritional niches (discussed above). Comparably, the aromatic compounds
555 remaining in forest soils shortly after fire (S1) might depress microbial activity and
556 function in C decomposition. These inhibitory effects of toxic compounds, i.e.
557 phenolic-C produced from burning, not only retarded bacterial utilization but also
558 caused stress for microorganisms (Fig. 4a). For example, Bacteroidetes, as
559 S-strategists that release polysaccharides and reduce growth yield to resist toxic
560 stresses (Manzoni et al., 2014; Malik et al., 2019), had a relatively small influence on
561 SOC priming (Fig. 4a). Overall, the dominant phyla (apart from Bacteroidetes)
562 modulated by oligotrophic conditions displayed relatively large SOC decomposition
563 as compared to sucrose (Fig. 1; SI Fig. 3).

The phyla Firmicutes and Chloroflexi were negatively associated with SOC mineralization in S2 (Fig. 4b), indicating small effects by these phyla on C decomposition. This agrees with previous research that has shown these phyla make relatively small contributions to SOC priming (Trivedi et al., 2013; Di Lonardo et al., 2017). Although both phyla were activated by enriched di-O-alkyl-C and aryl-C in S2, the lower magnitude of SOC priming caused by the same phylum, e.g., Firmicutes, in S2 compared to S1, might be due to: i) higher diversity leading to stronger competition with other microbial groups, thus having lower activity and redundant functions in SOC decomposition and, ii) preferential utilization of labile components, i.e. di-O-alkyl-C, to maintain their metabolisms and growth, instead of exploiting SOC for nutrients and energy (Kuzyakov et al., 2000).

Actinobacteria and Proteobacteria showed strong correlations to SOC decomposition (Fig. 4b). However, these phyla were not strongly correlated to either soil pH or chemicals (either labile di-O-alkyl-C or recalcitrant Aryl-C), indicating that both Actinobacteria and Proteobacteria had not been constrained by specific edaphic variables, affinity to soil resources (i.e. C/energy), or stresses (i.e. acidity). Additionally, the enhanced C bioavailability and community diversity in S2 decreased the significance of individual phyla in SOC priming. Instead of highly co-occurrent microorganisms, the overall community, or say, average microorganisms, were the contributors to SOC priming in S2, but with much less magnitude compared to S1 (Fig. 1, SI Table 8).

4.4. Implications

Short-term fire history creates an unbalanced condition (S1), which referred to soils with limited resources of C and nutrients, lower microbial diversity, and negative correlation between microbial groups (Fig. 5). Domination by K-strategists might lead to decreased mineralization of new substrates and, instead, increased priming of native SOC (Fig. 1 and 5). High stabilization of newly input substrate C (indicated by less loss via mineralization) and large loss of native SOC by accelerated SOC turnover (Fig. 5). This suggested that forest soil shortly after fire is a vulnerable C pool (disturbed ecosystem), with the potential for high loss of native SOC but, also for

the accumulation and stabilization of new substrate C input, i.e. rhizodeposits, restoring the SOC pool in the following years. Several years after fire in S2 the SOC pool displayed a greater chemical diversity that relieved microorganisms from stress in terms of resource limitation, and consequently fostered the development of well-structured and highly diverse microbiome community (Fig. 5). This led to more equal mineralization between new (additional sucrose) and old (native soil) C in S2 (comparably, it had much larger soil priming intensity but less substrate decomposition in S1, Fig. 1).

It should be noted that fire history might not be the only driver of soil microbial properties and C decomposition between S1 and S2. Although the sampling sites of S1 and S2 have the same soil type with identical parent materials as well as similar weather in terms of precipitation and temperature, the observed differences in the microbial community and consequent soil processes could still be explained by some other unknown variable that generated not by fire. Also, the causation of microbe-C interaction and consequent decomposition cannot be fully predicted by correlation analysis, and requires exquisite experiment design and solid data to support. Here, we concluded that the forest ecosystem decades after a fire is comprised of more diversified chemicals (e.g., with both labile and recalcitrant) and better structured microbial communities (e.g., dominated by both r and K strategists), and their interactions consequently balance decomposition of plant derived C and SOC (Fig. 5).

5. Conclusions

Through a combination of 16S rRNA gene sequencing and ^{13}C NMR, the current study revealed the correlation of SOC chemical composition with bacterial community composition, and the links of bacteria-C interactions to decomposition of SOC and sucrose, in post-fire forest soils. Recalcitrant components of SOC shaped microbiome community in S1: phenolic-C correlated to the oligotrophic bacteria, while both labile di-O-alkyl C and aromatic-C shaped the whole community in S2. The dominant oligotrophic organisms in S1, including Actinobacteria (e.g.,

623 *Solirubrobacterales*) and Firmicutes (e.g., *Bacillus*), were well adapted to stressed and
624 resource-limited environments, thus potentially linked with SOC priming. In
625 comparison, the bacterial guilds in S2 were more evenly distributed across phyla and
626 less constrained by individual abiotic variables. The abundance of the phylum
627 Proteobacteria was positively correlated to SOC priming in S2, but the overall effects
628 on soil priming were more limited. This study elucidated the interactions between
629 SOC chemical composition and bacterial community, and their link to C
630 decomposition.

631

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Table 1. Basic soil properties of the two sites (S1: 3 months post-fire and S2: 15 years post-fire) at three depths (O: 0-5 cm, A: 5-20 cm and B: 20-40cm). Data are mean ± SD. The significant differences between means are shown in SI Table 2.

Treatment	pH	WHC (%)	Total C (%)	Total N (%)	C/N	DOC (mg kg^{-1})	MBC (mg kg^{-1})	$\delta^{13}C$ (‰)
S1-O	5.74±0.33	64.0±6.78	5.07±1.21	0.29±0.03	17.69±2.35	224.29±20.04	664.65±11.37	-25.99±5.7
S1-A	5.11±0.43	36.0±9.78	1.05±0.11	0.06±0.01	18.97±0.43	80.43±5.20	324.08±21.5	-24.74±6.7
S1-B	5.42±0.29	35.0±4.33	0.36±0.01	0.02±0.01	17.72±0.29	49.63±1.25	288.67±21.84	-24.25±3.78
S2-O	5.54±0.21	70.0±5.13	8.92±1.21	0.54±0.01	17.35±5.13	328.85±46.28	607.91±33.65	-25.91±3.74
S2-A	5.40±0.12	62.0±3.24	2.44±1.21	0.16±0.01	15.73±0.17	242.65±52.51	475.62±37.03	-25.02±6.58
S2-B	5.47±0.17	55.3±4.35	1.33±0.21	0.08±0.01	16.19±4.35	163.95±4.44	348.31±10.15	-24.16±3.78

WHC: water-holding capacity, DOC: dissolved organic C, MBC: microbial biomass C

Table 2. The best multivariate model (DISTLM) analysis of the two sites

S1 (3 months post-fire)				S2 (15 years post-fire)			
Soil properties	**prop**	***p***	**Cumulative**	**Soil properties**	**prop**	***p***	**Cumulative**
Phenolic C	0.68	0.00	0.68	Di-O-alkyl C	0.41	0.00	0.41
pH	0.08	0.02	0.76	Aryl C	0.23	0.00	0.65
Di-O-alkyl C	0.06	0.13	0.82	pH	0.07	0.37	0.71
Methoxyl C	0.04	0.33	0.86	Carbonyl C	0.06	0.50	0.77
Alkyne C	0.03	0.49	0.89	Alkyl C	0.04	0.69	0.81
C/N	0.04	0.48	0.93	WHC	0.04	0.65	0.85
Total C	0.04	0.44	0.97	C/N	0.09	0.37	0.94

WHC - water holding capacity; C/N - the ratio of total C to N.

S1: 3 months post-fire, S2: 15 years post-fire

Fig. 1. Partitioning of CO_2 emission after the addition of sucrose into samples from three horizons (O: 0-5, A: 5-20, B: 20-40 cm) of two soils (S1: 3 months post-fire and S2: 15 years post-fire) during a 53-day incubation. "Primed C" is CO_2 evolved from native SOM primed by sucrose. "Sucrose-derived C" is CO_2 evolved from sucrose mineralization, and "Basal soil derived C" is total CO_2 evolved from the control soil without substrate addition. "0-1, 1-3, 3-7, 7-14, 14-28, and 28-53" represent the incubation period of 0-1, 1-3, 3-7, 7-14, 14-28, and 28-53 days, respectively. Data represent mean (n=3) and bars represent standard errors of the means.

Fig. 2. (a) Histogram of Shannon diversity based on 97% similarity level for the three horizons (O: 0-5, A: 5-20 and B: 20-40 cm) of two soils (S1: 3 months post-fire and S2: 15 years post-fire). Significance differences were detected by *t*-test. Asterisk indicates significant differences (*: $p < 0.05$; **: $p < 0.01$). (b) Principal co-ordinates analysis (PCoA) of the structure of bacterial communities based on Bray-Curtis distance in two soils consisting of three horizons. PERMANOVA (Adonis function in vegan package of R) was used to quantify these effects. (c) Distribution of bacterial communities for the three horizons (O: 0-5, A: 5-20, and B: 20-40 cm) of two soils (S1: 3 months post-fire and S2: 15 years post-fire) at the phylum level was visualized by Circos.

Fig. 3. Co-occurrence networks of bacterial communities in two soils (3 months (S1) and 15 years (S2) post-fire). A connection stands for a strong (Spearman's $\rho > 0.8$) and significant ($p < 0.01$) correlation (degree > 6). The size of each node is proportional to the number of connections (that is, degree). The size of each edge is proportional to the weight of the connection (orange and blue lines represent positive negative connections, respectively).

Fig. 4. A structural equation model (SEM) used to assess multivariate effects on the

total CO_2 and primed CO_2 (red lines, positive connections; green lines, negative connections; gray line, not significant) in two soils (3 months (S1) and 15 years (S2) post-fire). Line size represents the strength of correlation.

Fig. 5. Conceptual graph of C sequestration in 3 months (S1) and 15 years post-fire (S2) soils, via the balance of input (stabilization of sucrose in incubation to mimic rhizodeposits in forest) and output (mineralization of sucrose and SOC), driven by interaction of SOM chemistry and microbiome diversity. Yin and Yang, as inseparable and contradictory opposites, represent new C input of sucrose (sucrose derived CO_2) and old native SOC (SOC derived CO_2), respectively. The two opposites of Yin (SOC) and Yang (rhizodeposits) complement each other while, as a whole, indicate total C in soil. The small circle (core) inside indicates C loss via mineralization from soil to atmosphere.

The limited C resources (i.e. phenolic and aryl C) in S1 (3 months post-fire, low microbial diversity, and unbalanced system) favored oligotrophs microorganisms, which in turn decomposed more recalcitrant SOM via co-metabolisms. The small sucrose decomposition and large priming in S1 suggested faster SOC turnover via bidirectional processes of newer substrate-C gain and older C loss via priming. While in S2 (15 years post-fire, high microbial diversity and balanced system), the more balanced C resources (i.e. phenolic and di-O-alkyl C) favored both copiotrophs and oligotrophs, which lead to the equivalent sucrose decomposition and priming. This suggested newer sucrose-C gain and older C loss were balanced in post-fire soils at decadal scale.

Fig. 1.

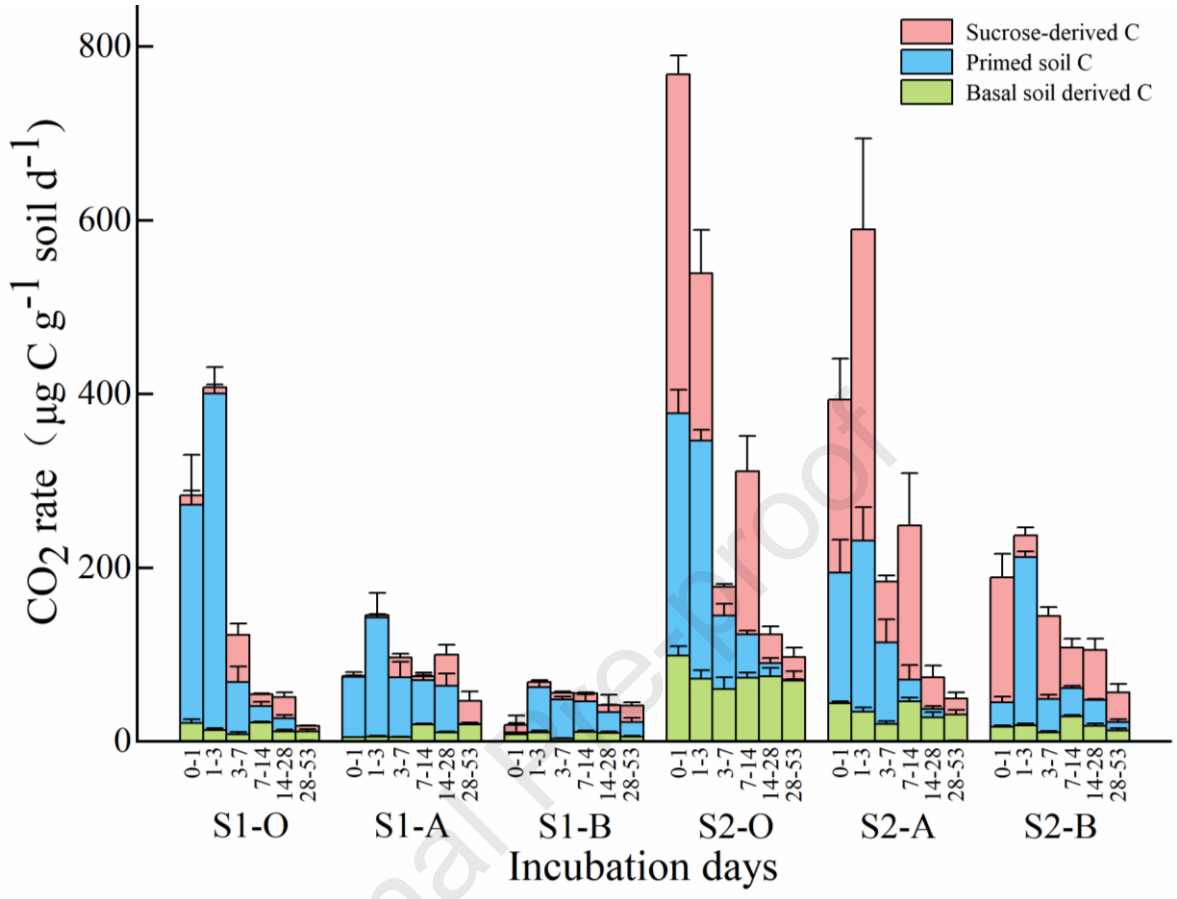


Fig. 2.

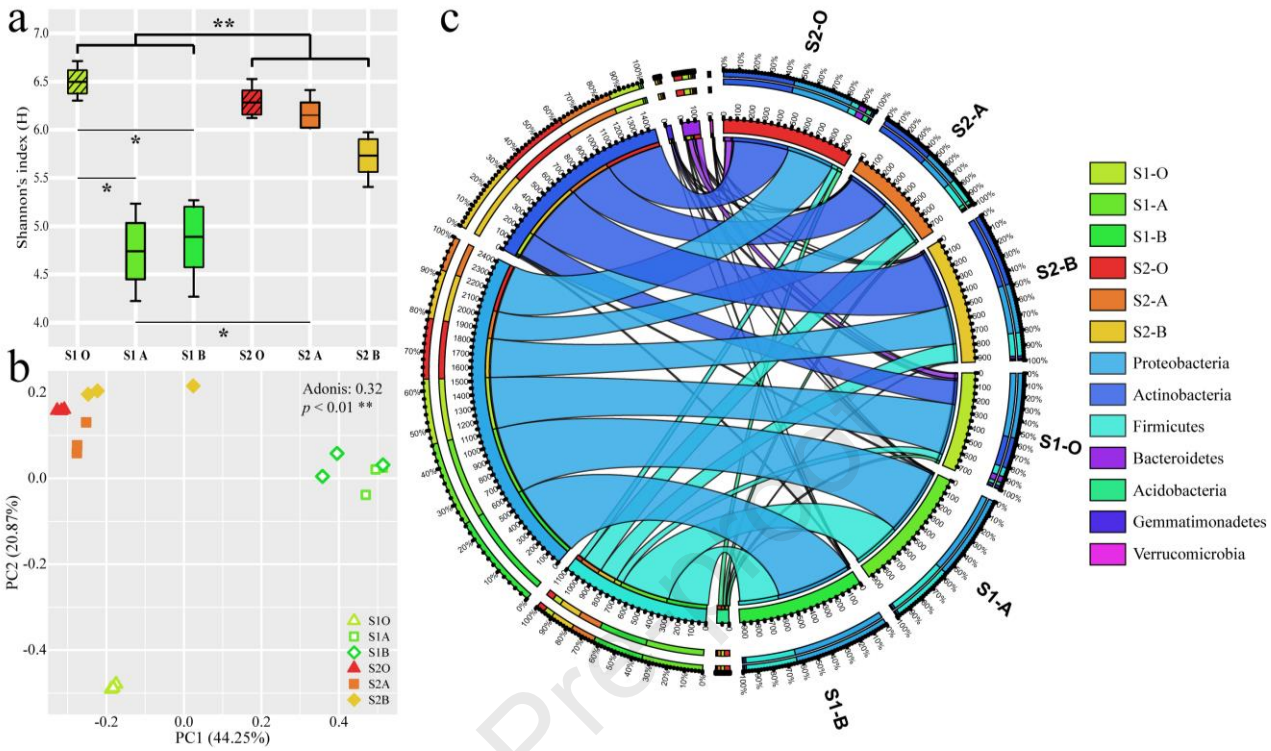


Fig. 3.

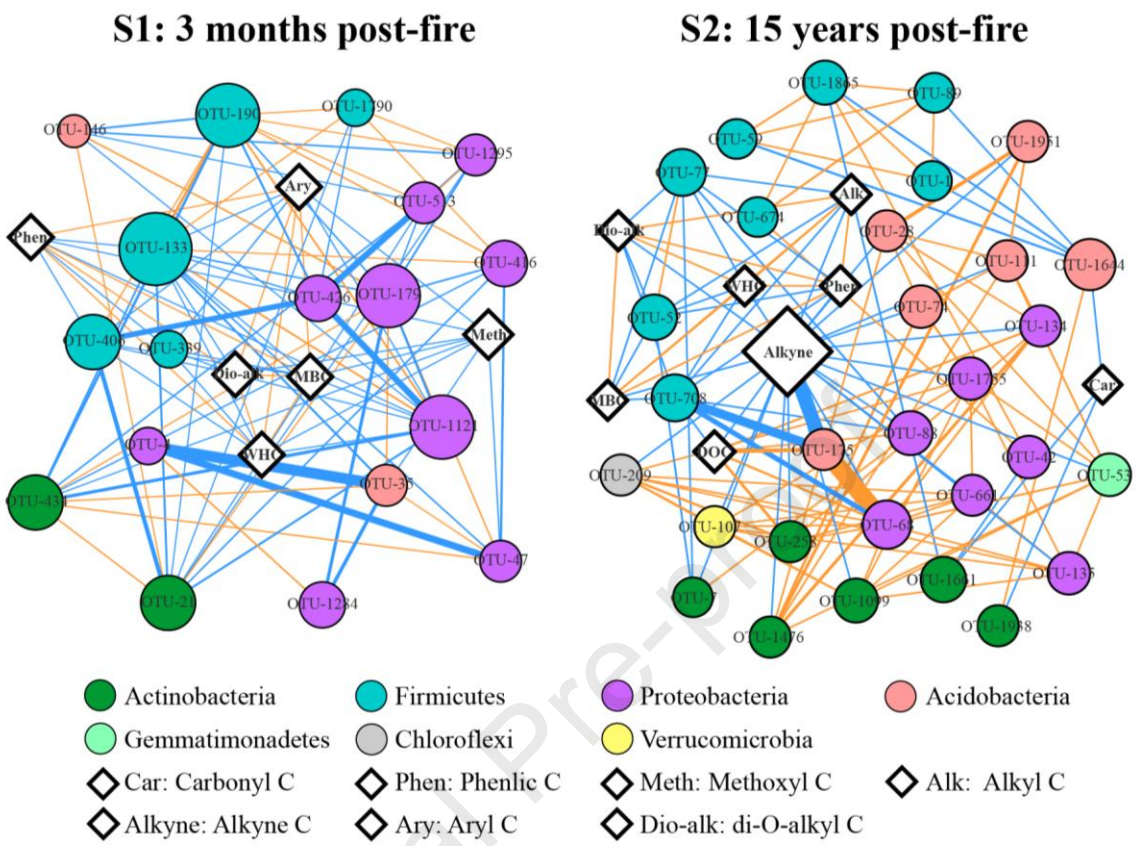


Fig. 4.

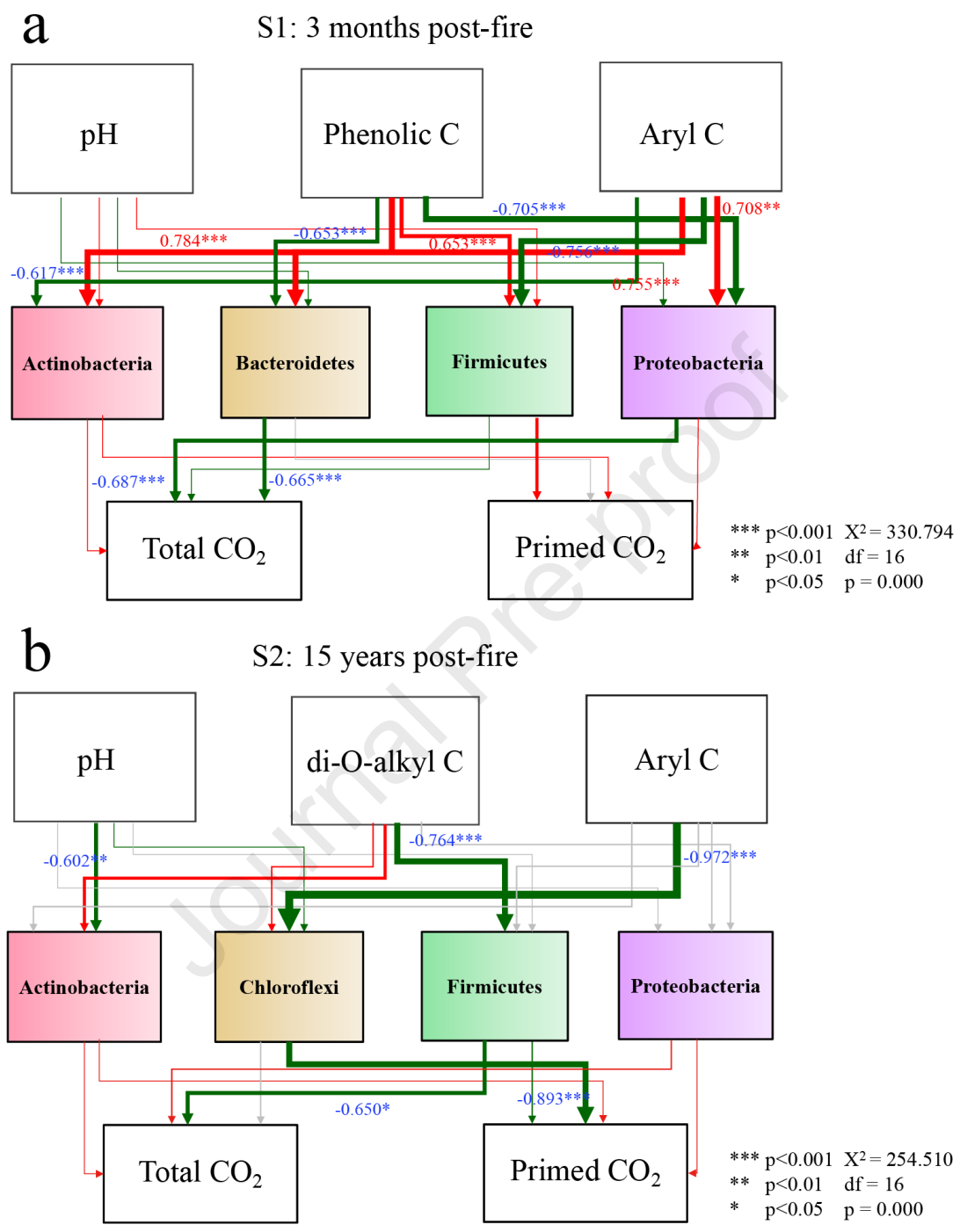
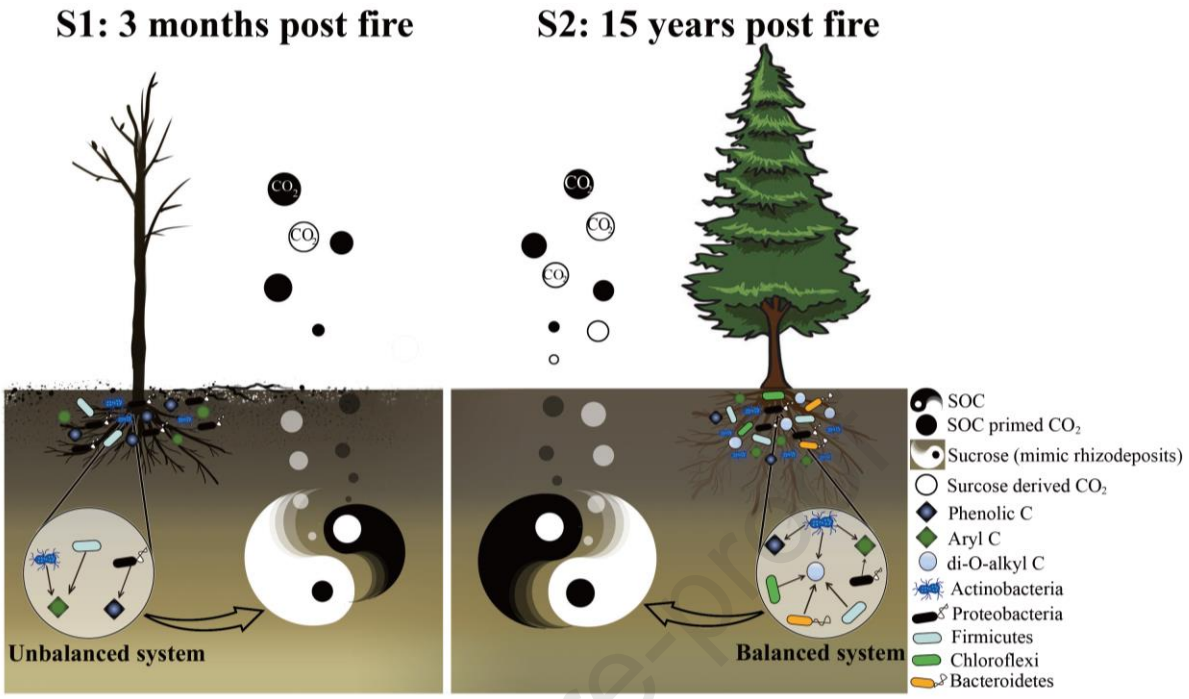

a
S1: 3 months post-fire
pH
Phenolic C
Aryl C
-0.705***
0.708**
0.784***
-0.653***
0.653***
-0.756***
-0.617***
0.755***
Actinobacteria
Bacteroidetes
Firmicutes
Proteobacteria
-0.687***
-0.665***
Total CO2
Primed CO2
*** p<0.001 X2 = 330.794
** p<0.01 df = 16
* p<0.05 p = 0.000
b
S2: 15 years post-fire
pH
di-O-alkyl C
Aryl C
-0.764***
-0.602**
-0.972***
Actinobacteria
Chloroflexi
Firmicutes
Proteobacteria
-0.650*
-0.893***
Total CO2
Primed CO2
*** p<0.001 X2 = 254.510
** p<0.01 df = 16
* p<0.05 p = 0.000

Fig. 5



Organic matter chemistry and bacterial community structure regulate decomposition processes in post-fire forest soils

Highlight:

1. We investigated soil priming effects in post-fire forest soils.
2. Soil microbial diversity decreased with soil depth.
3. NMR and sequence analyses were utilized to understand C-microbe interactions.
4. Positive association between aromatic-C and Firmicutes was correlated to SOC loss.

December/January 17th, 2021

Submission Letter to,

Dear Editor,

All the authors declare that there are no competing and conflict interests.

With best regards

Yuo Luo

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: