

## The fate of soybean residue-carbon links to changes of bacterial community composition in Mollisols differing in soil organic carbon

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### Abstract

Quantifying residue carbon (C) incorporation into soil organic C (SOC) fractions, and underpinning microbial community in the decomposition process of crop residues are essential for improving SOC management in agricultural systems. However, the fate of residue-C and associated responses of microbial communities remain unclear in Mollisols in north-eastern China, where SOC varies geographically. A 150-day incubation experiment was conducted with <sup>13</sup>C-labelled soybean residue (4%) amended into two Mollisols differing in SOC (SOC-poor and SOC-rich soils). The <sup>13</sup>C abundances in SOC fractions and the CO<sub>2</sub>-C efflux from soil were determined, and bacterial community composition was analyzed with MiSeq sequencing. The amounts of residue-C incorporated into the coarse particulate organic C (POC), fine POC and mineral-associated C (MOC) fractions were 4.5-, 4.3- and 2.4-fold higher in the SOC-rich soil than in the SOC-poor soil, respectively. Residue amendment led to negative SOC priming before Day 50 but positive priming thereafter. The primed CO<sub>2</sub> per unit of native SOC was greater in the SOC-poor soil than in the SOC-rich soil. This indicates that the contributions of residue-C to the POC and MOC fractions were greater in the SOC-rich soil while residue amendment had stronger priming effect in the SOC-poor soil, stimulating the C exchange rate between fresh and native SOC. A principal coordinates analysis (PCoA) showed that the shift of bacterial community structure in response to residue amendment varied between the two soils. Genera *Verrucosipora*, *Xanthomonadales* and *Steroidobacter* were mainly enriched in the residue-amended SOC-poor soil while *Anaerolineaceae\_ uncultured* was dominant in the SOC-rich soil. The canonical correspondence analysis (CCA) revealed that the relative abundance of the bacterial operational taxonomic unit (OTU) among residue treatments was significantly associated with soil characteristics, especially C content in coarse POC and MOC fractions ( $p < 0.01$ ), implying that the shift of bacterial community composition in response to residue amendment contributes to the sequestration of residue-C in SOC fractions.

**Keywords:** SOC fractions; <sup>13</sup>C-labelled residue; Pyrosequencing; Bacterial community; Priming effect

### Introduction

As the largest pool of carbon (C) on Earth, soils contain approximately 2,344 Gt of C (Stockmann et al., 2013), and it is possible to substantially increase this amount (Macias and Arbestain, 2010). However, it is not fully understood how farming practise and soil properties affect the accumulation and mineralization of soil organic C (SOC) in agricultural fields (Comeau et al.,

2013). The return of crop residues to soil is an effective way to sustain the SOC content (Rui et al., 2009). For example, incorporation of crop residues for 43 years increased the SOC content by 21–29% in a wide range of soils (Pituello et al., 2016).

Physical fractionation of the SOC is a commonly-used approach to understand the impact of residue C on the SOC dynamics because various soil fractions play different roles in SOC stabilization (Shinjo et al., 2000; Six et al., 2004). The particulate organic C (POC) corresponds to relatively young transformed C, while the mineral-associated organic C (MOC) is more stable over time due to chemically binding with mineral constituents of the soil (Mazzilli et al., 2015). Using  $^{13}\text{C}$ -labelled materials allows the incorporation of the residue-C into various C fractions to be quantified (Buyanovsky et al., 1994; Hassink, 1997; Aita et al., 1997). For example, Aita et al. (1997) investigated the decomposition of  $^{13}\text{C}$ -labeled wheat plant residues in the field, and found that more residue-C was incorporated into the fine soil fraction in the topsoil than in the subsoil. The dynamics of crop residues has been studied in a number of soils including Argiudol and Cambisol (Balesdent and Balabane, 1996; Comeau et al., 2013; Mazzilli et al., 2015), but the information is limited for Mollisols, of which soil properties fundamentally differ from other soils.

Mollisols are important cropping soils in Northeast China and have a wide range of SOC contents, ranging from 9.5 to 58.1 mg g<sup>-1</sup> (Jin et al., 2013). The SOC contents of Mollisols have continuously decreased over the past decades (Fan et al., 2011; Liu et al., 2012), with an annual decline of about 0.9% in the 0- to 90-cm soil profile due to erosion, intensive tillage and burning of crop residues (Liu et al., 2006). In order to minimise or prevent this decline, the return of crop residues to the field is an important practice, especially the residue of soybean that is a major crop in rotation with cereal crops in Mollisols (Qin et al., 2010). A limited number of studies have shown that the return of crop residue could maintain or increase SOC in Mollisols (Liu and Herbert, 2002; Liu et al., 2012), but the effect of crop residues on SOC content and stability may vary between different Mollisols due to the biochemical variation in soils, which mediates the decomposition process (Lützow et al., 2006).

Microorganisms are the major driver of residue decomposition and turnover in soils, and play an important role in the incorporation of decomposed components into the SOC fractions (Rui et al., 2009; Marschner et al., 2011; Manjaiah et al., 2000). Residue chemistry and soil types can affect microbial populations and metabolisms (Kuzyakov et al., 2000; Semenov et al., 2012; Pascual et al., 2013). The effects of crop residue on microbial community have been studied in crop species such as wheat, maize and soybean (Bernard et al., 2007; Fan et al., 2014; An et al., 2015; Ramirez-Villanueva et al., 2015). For instance, the genus *Arthrobacter* belonging to Actinobacteria was found dominant as primary sequestrators in a Vertisol amended with soybean residue. However, such effects on C dynamics and associated microbial community in Mollisols remain largely unknown.

The objectives of this study were (1) to quantify the contribution of the soybean residues to various SOC fractions in two Mollisols differing in SOC content, and (2) to investigate the microbial community composition in response to residue amendment in the soils. A soybean residue labelled with  $^{13}\text{C}$  was used to track residue-derived C in soils during a 150-d incubation period. The MiSeq pyrosequencing technique of the 16S rRNA genes was employed to examine the effect of residue addition on microbial community. We hypothesized that the fate of residue-C in various SOC fractions of different soils is likely attributed to microbial accessibility to crop residues and community in response to residue amendment. With residue amendment, the specific selection of microbial community from the community reservoirs of the soils might affect residue-C turnover and its contribution to SOC fractions.

## Materials and methods

### Soil and residues preparation

The Mollisols used in this study were taken from the tillage layer to about 0.1-m depth at two

locations in northeast China. For each soil, 20 cores were collected from a farmer's paddock, bulked, air-dried and sieved through a 2-mm sieve. The SOC concentrations were 14 and 50 mg g<sup>-1</sup> for the SOC-poor and SOC-rich soils, respectively. The chemical characteristics of the two soils are listed in Table 1.

The technology of <sup>13</sup>CO<sub>2</sub> pulse-labelling was employed to produce the <sup>13</sup>C-labelled stalk residues of soybean. The plants were labelled for ten times across the growth stages and harvested at the fully matured stage. The details of <sup>13</sup>C labelling are referred to Lian et al. (2016). The δ<sup>13</sup>C value of the stalk was 1903.9‰. The shoot residues (stalk) were dried at 70 °C and ground through 2-mm and 0.25-mm sieves. The residues left in between were for the following incubation. The residue had 429 mg g<sup>-1</sup> of C, 13 mg g<sup>-1</sup> of N, 33.4 mg g<sup>-1</sup> of soluble sugar, 6.5 mg g<sup>-1</sup> of starch, 305 mg g<sup>-1</sup> of cellulose and 153 mg g<sup>-1</sup> of lignin.

### **Experimental setup and soil incubation**

An incubation experiment consisted of two soils (SOC-rich and SOC-poor Mollisols) and two residue treatments (with or without soybean residue). The soils were watered to 50% field capacity (FC) and pre-incubated at 25°C for 15 days to recover microbial activity and function (Butterly et al. 2016). The ground shoot residue (0.8 g) was mixed with 20 g of soil which was placed into each PVC core (4.5-cm height, 2-cm diameter) with nylon mesh bottoms. The soil was then compacted to a bulk density of 1.1 g cm<sup>-3</sup>. Each PVC core was placed into a 1-L mason jar together with a vial containing 10 mL of water to maintain the humidity inside the jar, and a 15-mL plastic vial containing 10 mL of 1 M NaOH as an alkali trap to capture evolved CO<sub>2</sub>. There were 15 jars per treatment for 5 sampling dates. Three of them were sampled at each time point. Through weighing and watering, the soil water content was maintained at 80% FC. All jars were kept in a dark incubator at a constant temperature of 25°C.

### **Respiration measurements and soil sampling**

The NaOH traps were sampled and then renewed on days 4, 8, 12, 16, 20, 24, 28, 32, 39, 46, 53, 60, 70, 80, 90, 100, 110, 120, 130, 140 and 150 after incubation was initiated. Soil respiration was estimated by measuring the amount of CO<sub>2</sub> absorbed in the NaOH trap. Carbonates in NaOH were precipitated using an excess 1 M SrCl<sub>2</sub> solution and filtered (Shahzad et al. 2015). HCl (0.1 M) was then used to neutralize the excess NaOH using phenolphthalein as an indicator (Blagodatskaya et al. 2011). The neutralized solutions together with SrCO<sub>3</sub> precipitate were centrifuged for three times at 2000 g for 10 min. The precipitate was washed in between with deionized and degassed water. Then, SrCO<sub>3</sub> precipitate was dried at 105 °C (Blagodatskaya et al. 2011). The δ<sup>13</sup>C value of carbonates (trapped CO<sub>2</sub>) was determined using Mat 253 isotope ratio mass spectrometer (Thermo Fisher, Germany).

During incubation, three replicates in each treatment were destructively sampled on days 15, 30, 60, 90 and 150 after incubation. Each soil sample was separated into two or three parts: one part (approximately 2 g) was frozen immediately in liquid nitrogen, and then stored at -80 °C for DNA extraction and following pyrosequencing. This part was only collected on days 150. The second part (approximately 10 g) was maintained at 4 °C for measurements of microbial biomass and dissolved organic C. The remaining portion (approximately 8 g) was air-dried for the pH measurement and SOC fractionation. The pH was determined using a Wottler Toledo 320 pH meter in water (1:5 = w:v) after shaking the suspension for 30 min and centrifugation at 800 g for 5 min.

### **Microbial biomass C and dissolved organic C**

The chloroform-extraction method was employed to determine the microbial biomass C (MBC) in the soil (Vance et al. 1987). The organic C in the extracts was determined with a TOC analyser (Multi N/C 2100, Analytik Jena, Germany); MBC was calculated as the difference in the organic C concentrations in the extracts of the fumigated and non-fumigated soils and using a *k*<sub>EC</sub> of 0.37

(Joergensen, 1996). The amount of organic C for the non-fumigated soil samples corresponds to dissolved organic C (DOC) (Domanski et al., 2001).

### **SOC fractions**

The SOC of soil samples at the end of the incubation was separated into coarse POC, fine POC and MOC (Cambardella and Elliott, 1993). In brief, a 5-g sample was suspended in 35 mL of 1.7 g cm<sup>-3</sup> sodium iodide solution and centrifuged at 5000 rpm for 60 min. The free light fraction (soybean residues) was floated on the solution surface, and removed. A 0.5-mol L<sup>-1</sup> sodium hexametaphosphate solution was then added to the heavy fraction that was obtained from centrifugation for 18 h. The suspension was passed through 250- and 53- $\mu$ m sieves (Cambardella and Elliott, 1993; Gill et al., 1999). The organic C in the 250–2000  $\mu$ m, 53–250  $\mu$ m and < 53  $\mu$ m fractions were considered as coarse POC, fine POC, and MOC, respectively. All fractions were recovered and dried at 70 °C for 48 h. The  $\delta^{13}\text{C}$  value of each fraction was measured using the isotope ratio mass spectrometer. The C and N contents were determined using an Elementar III analyser (Hanau, Germany).

### **DNA extraction, 16S rRNA gene amplification, and pyrosequencing**

Soil DNA was extracted with a Fast DNASPIN Kit for Soil (Qbiogene Inc., Carlsbad, CA, USA) according to the manufacturer's instructions. DNA extracts were dissolved in 100  $\mu$ l of TE buffer (10 mM Tris-HCl, 1 mM EDTA, pH 8.0) and the quantity of the total DNA was determined with a NanoDrop spectrophotometer (Bio-Rad Laboratories Inc.). For pyrosequencing, primer 515F (5'-GTGCCAGCMGCCGCGGTAA-3') and 909R (5'-CCCCGYCAATTCMTTTRAGT-3') with 12 nt unique barcode was used to amplify the V4 hypervariable region of 16S rRNA gene. The PCR amplification program included initial denaturation at 94 °C for 3 min, followed by 30 cycles of 94 °C for 40 s, 56 °C for 60 s, and 72 °C for 60 s, and a final extension at 72 °C for 10 min. In order to minimize PCR bias, two PCR reactions for each sample were conducted, and PCR products from the reactions were combined. The amplicons from all samples were pooled with an equimolar concentration and pyrosequenced with the MiSeq sequencer (Caporaso et al., 2011, 2012).

After sequencing was completed, the raw sequences were sorted based on the unique sample barcodes, trimmed for sequence quality, and denoised using QIIME pipeline (version 1.17; <http://qiime.org/>). Any ambiguous bases were excluded from further analysis. Sequences with similarities of > 97% were clustered into one operational taxonomic unit (OTU). In total, 170,436 high quality and chimera-free reads with an average length of 434 bp were obtained. As the sequence number varied among samples ranging from 13,574 to 19,790, a randomly selected subset of 13,574 reads was applied to each sample for further analysis. Phylotypes were identified using Ribosomal Database Project (RDP) pyrosequencing pipeline (<http://pyro.cme.msu.edu>). All sequences have been deposited into the GenBank short-read archive SRP069728.

### **Calculations and statistical analyses**

The microbial metabolic quotient was calculated as soil respiration rate divided by microbial biomass C.

The residue-derived CO<sub>2</sub>-C was partitioned as follows (Balesdent and Balabane, 1992).

$$F_{residue} = (\delta_{mix} - \delta_{control}) / (\delta_{control} - \delta_{residue})$$

where  $\delta_{mix}$  is  $\delta^{13}\text{C}$ CO<sub>2</sub>-C at time t,  $\delta_{control}$  is  $\delta^{13}\text{C}$  of the no-residue soil, and  $\delta_{residue}$  is  $\delta^{13}\text{C}$  of the residue. Residue-derived CO<sub>2</sub>-C was calculated as the above,  $F_{residue}$  multiplied by the measured CO<sub>2</sub>-C. Soil-respired CO<sub>2</sub> was calculated as the difference between total respiration and residue-

derived respiration (Stewart et al., 2015).

In each SOC fraction, the proportion of C derived from residue C was calculated as excess  $\delta^{13}\text{C}$  in residue-amended soil divided by the excess  $\delta^{13}\text{C}$  of residue over the control soil (Poirier et al. 2013). The amount of residue C (in  $\text{mg C g}^{-1}$  soil) incorporated into the SOC fraction was calculated as this proportion multiplied by the C content in each SOC fraction.

UniFrac statistical analysis was performed online at <http://bmf.colorado.edu/unifrac/> to provide the index of community distances between each pair of samples (Lozupone and Knight, 2005; Hamady and Knight, 2009). Based on this, principal coordinates analysis (PCoA) was used to indicate patterns of similarity (Bray-Curtis similarity) in microbial community composition between treatments (Li et al., 2014). A canonical correlation analysis (CCA) was conducted to explore the association of the bacterial community composition with the soil characteristics. The PCoA and CCA were performed using the program R version 3.1.2 for Windows (R Development Core Team, 2010). The Chao estimator, Shannon's diversity index and evenness were obtained using the MOTHRUR program (<http://www.mothur.org>) (Chelius and Triplett, 2001).

With Genstat 13 (VSN International, Hemel Hempstead, UK), the analysis of variance (ANOVA) (Steel and Torrie, 1980) was performed to assess the effect of treatment on the residue C in SOC fractions, soil pH, DOC, respirations, and the relative abundance of the bacterial groups at the genus and OTU levels. Only genera and OTUs that had significant response ( $p < 0.05$ ) to treatments were presented. This was based on the least significant difference (LSD) at the significant level of  $p < 0.05$ .

## Results

### Incorporation of residue-C in the SOC fractions

The residue addition increased the SOC content in different fractions of soil C compared with the non-residue control (Table 2). Moreover, the magnitude of the increase was greater in the SOC-rich soil than SOC-poor soil, especially in the fine POC and MOC fractions.

After 150 days of incubation, the residue-C incorporated into SOC fractions differed between the soils (Table 3). In particular, the level of residue C input into the coarse and fine POC, and MOC in the SOC-rich soil was 1.95, 3.39 and 4.50  $\text{mg residue-C g}^{-1}$  soil, 4.5-, 4.3- and 2.4-fold greater than those in the SOC-poor soil, respectively.

### DOC and soil pH

The addition of residue significantly increased DOC in soil. After 15 days of incubation, DOC reached the peak of 2.2  $\text{mg g}^{-1}$  in the residue-incorporated SOC-rich soil, which was slightly higher than that in the SOC-poor soil. Thereafter, DOC declined steadily (Fig. 1). By the end of the incubation, there was no significant difference between the SOC-poor and SOC-rich soil, resulting in an average of 1.4  $\text{mg g}^{-1}$ . In the no-residue controls, the concentrations of DOC were, on average, only 0.68 and 0.64  $\text{mg g}^{-1}$  for the SOC-poor and SOC-rich soils, respectively.

The residue addition gradually increased soil pH over the incubation period (Fig. 2). An average 0.5 unit of increase in soil pH was observed in both soils by the end of incubation. The soil pH of the non-residue control was approximately 7.0 and 6.7 for the SOC-poor and SOC-rich soil, respectively.

### Microbial respiration

The addition of residue generally increased the soil respiration. Over the period of incubation,

the cumulative CO<sub>2</sub>-C derived from the residue in the SOC-poor soil was 10.1% greater than that in the SOC-rich soil (Fig. 3a). However, the cumulative CO<sub>2</sub>-C per unit of native SOC in the SOC-poor soil was 2.8-fold greater than that in the SOC-rich soil at the end of incubation (Fig. 3b). Although the residue addition increased CO<sub>2</sub>-C efflux from native SOC compared to the control at the end of incubation, the amounts of CO<sub>2</sub>-C derived from SOC under the residue treatment were smaller in the first 50 days of incubation, and this occurred in both soils.

Residue amendment increased the microbial metabolic quotient, but the magnitude of this increase decreased with incubation time (Fig. 4). After 15 days of incubation, the microbial metabolic quotient in the SOC-poor soil was 0.36 µg g<sup>-1</sup> day<sup>-1</sup>, which was 71% higher than that in the SOC-rich soil. However, after 150 days of incubation, there was no significant difference between the two soils, resulting in 0.04 µg g<sup>-1</sup> day<sup>-1</sup> on average.

### Microbial community composition

In general, the average OTU number was in a range of 455 to 597 across the treatments. There was no difference between the two soils without residue amendment in the Alpha diversity indices of bacteria such as Chao1 richness, Shannon's diversity and evenness. The residue amendment significantly decreased these indices of bacterial diversity in the SOC-poor soil, but not in the SOC-rich soil (Table 4).

The Beta diversity indices, i.e. principal coordinate analysis (PCoA), showed that the residue treatments clustered separately from the no-residue controls, and bacterial community in the residue-amended SOC-poor soil clustered separately from that in the residue-amended SOC-rich soil (Fig. 5). The CCA revealed the strong relationship between community composition and the environmental variables that were mainly SOC-associated (Fig. 6). In particular, total C ( $r=0.823$ ;  $p < 0.01$ ) and N ( $r=0.913$ ;  $p < 0.01$ ), C/N ( $r=0.910$ ;  $p < 0.01$ ), C content in coarse POC ( $r=0.842$ ;  $p < 0.01$ ) and MOC ( $r=0.901$ ;  $p < 0.01$ ), DOC ( $r=0.762$ ;  $p < 0.05$ ), pH ( $r=0.808$ ;  $p < 0.01$ ), and NO<sub>3</sub><sup>-</sup> ( $r=0.768$ ;  $p < 0.05$ ) appeared to be strongly linked to microbial community composition.

The effects of residue amendment and soil on bacterial community occurred mainly in 39 genera affiliated to 8 phyla (Fig. 7). Positive responses to the residue amendment, resulting in increases of relative abundance, were observed in a number of genera including *Mycobacterium*, *Xanthomonadales-uncultured*, *Steroidobacter*, *Anaerolineaceae-uncultured*, *Niastella*, and *Phyllobacteriaceae-unclassified*, while negative responses occurred in other genera such as *Arthrobacter*, *Blastococcus*, *Gaiellales-cultured*, *Phycococcus*, *Intrasporangiaceae-unclassified*, *Actinobacteria-norank*, *Sphingomonas*, *Gemmatimonas*, *Gemmatimonadaceae-uncultured*, and *KD4-96-norank*. In addition, the genera abundances differed between the two soils amended with residue. For instance, *Arthrobacter*, *Blastococcus*, *Gaiellales-cultured*, *Phycococcus*, *Actinobacteria-norank*, *Gemmatimonas*, *Gemmatimonadaceae\_uncultured*, *KD4-96\_norank*, *Anaerolineaceae\_uncultured* and *Niastella* had greater abundances in the SOC-rich soil compared to the SOC-poor soil. However, an opposite trend was observed for *Verrucosipora*, *Mycobacterium*, *Xanthomonadales\_uncultured* and *Steroidobacter*. Table S1 provided the abundance of each OTU in different experimental treatments.

## Discussion

### The contribution of residue-C to SOC fractions

The addition of soybean residue favoured fresh C sequestration in the SOC fractions in the 150-d period, and the magnitude of this contribution was greater in the SOC-rich than SOC-poor Mollisol (Table 3). This, however, is inconsistent with the observation by Stewart et al. (2008) who found that soils with low C contents could store greater proportion of added residue than those with greater C contents. The inconsistency is likely attributed to the SOC saturation point

in the SOC-rich soil being not reached with the amount of amended residue in this study, as soil C saturation greatly affects the amount of new C stabilized (Six et al., 2002).

The greater accumulation of the residue-derived C in the fine POC fraction of the SOC-rich soil (Table 3) is likely due to POC-associated properties. The POC consists of organic materials that are likely occluded in aggregates (Six et al., 2002; Bajgai et al., 2014). Mollisols with high SOC have large amounts of aggregates which contribute to a larger number of bonding sites enabling to trap partially decomposed plant fragments to prevent further decomposition (Six et al., 2002; Li et al., 2010). Interestingly, the greater contribution of residue-C to MOC in the SOC-rich Mollisol implies that more plant-derived organic compounds physically bind sorption sites in the fine fraction, which is considered as the main sites of long-term sequestration of C in soil (Plante et al., 2006; Chivenge et al., 2011; Puttaso et al., 2013). These compounds, particularly polysaccharides, fatty acids and phenolic compounds, have been found in the MOC fraction by tracking these <sup>14</sup>C-labeled compounds (Jagadamma et al., 2014), and the physicochemical properties of these compounds influenced the binding efficiency in the fraction. Thus, the different processes of residue decomposition between soils greatly affect the fresh C incorporation into SOC fractions.

Although residue addition to the soils resulted in greater SOC stocks, the mineralization of native SOC was stimulated by the residue amendment. This was evident that CO<sub>2</sub>-C derived from SOC markedly increased in the residue-amended treatments compared to the control over the period of incubation (Fig. 3). The priming effect induced by freshly added C was also observed in various soils such as Calcarosol and Calcic Haploxeroll (Bell et al., 2003; Blagodatskaya and Kuzyakov, 2008; Bernard et al., 2009). However, in this study, the priming effect in residue-amended soils was negative in the first 50 days before it turned to positive afterwards. This indicates that microbes exhibit a preference to the residue substrates. This is probably because plants residues comprise glucose from cellulose, and xylose and arabinose from hemi-cellulose, which primarily provide source of energy in soil, and thereby are readily decomposed at the initial stages of residue decomposition (Paul, 2016). These organic compounds in residues might dominantly drive the microbial processes instead of facilitate their accessing native SOC. McMahon et al. (2005) also reported that Gram-native bacteria were most active in utilizing wheat straw at earlier incubation. Nevertheless, the stimulated microbes switched to decompose native SOC later probably because of increasing demand for N (Shahzad et al., 2015). The C/N in SOC (Table 1) was much lower than that in residues (33). The switching time point for accelerating the mineralization of native SOC might depend on soluble N in soils, and microbial activity.

It is for the first time to observe that the residue-induced priming effect of CO<sub>2</sub> efflux per unit SOC was greater in the SOC-poor soil compared to the SOC-rich soil. Given that the increase of C content due to residue amendment in the SOC-poor soil was much less than the SOC-rich soil (Table 2) and the metabolic quotient was greater in the SOC-poor soil compared to the SOC-rich soil (Fig. 4), the C exchange rate in this soil was faster. This is likely attributed to the lack of physical protection against SOC decomposition, such as fewer aggregates in the SOC-poor soil (Jin et al., 2013). On the other hand, the C-metabolizing functions of soil microbes in response to the residue input would also affect the intensity of the priming effect (Pascault et al., 2013). The different effects of soil microbes on the priming effect between the two soils were further addressed below.

### **Effect of residue on bacterial community linking to SOC turnover**

The transformation of SOC depends on the activity of soil microbial decomposers (Pascault et al. 2013; Ramirez-Villanueva et al. 2015). The greater contribution of fresh C to SOC fractions in the SOC-rich than SOC-poor soil was closely associated with the microbial community composition in response to the residue amendment. In the PCoA analysis, the residue-amended SOC-rich soil was separated from the SOC-poor soil, indicating that microbial responses to the

residue amendment vary between the soils.

The amendment of plant residues usually increases the relative abundance of bacterial groups, particularly in the nutrient-rich environments, such as Actinobacteria, Proteobacteria and Bacterioidetes (Fierer et al., 2007; Ramirez-Villanueva et al., 2015). In this study, a few genera such as *Verrucosipora* and *Mycobacterium* belonged to Actinobacteria were markedly enriched in the residue-amended SOC-poor soil while non-genus in this phyla was enriched in the residue-amended SOC-rich soil (Fig. 7). As the amount of CO<sub>2</sub>-C derived from residues and SOC in this soil were greater than that of the SOC-rich soil, the two genera were likely to contribute to the turnover of fresh C and the mineralization of native SOC. This is because many species affiliated to this phylum enable to produce extracellular enzymes for decomposition of macromolecules, such as cellulose, chitin and starch (Suela-Silva et al., 2013). Actinobacteria are often enriched in materials where organic materials are degraded (Schäfer et al., 2010).

In the phylum of Proteobacteria, the increased abundance of *Xanthomonadales* and correspondent OTU in response to residue amendment (Fig. 7; Table S1) might contribute to the degradation of various organic compounds, especially in the SOC-poor soil. This is consistent with the findings by Eichorst and Kuske (2012) that *Xanthomonadales* was enriched with <sup>13</sup>C-cellulose across geographically and edaphically different soils. Interestingly, the greater increase in the abundance of *Steroidobacter* in the residue-added SOC-poor soil compared to the SOC-rich soil might be associated with C and N cycling, because this genus utilizes only a narrow range of organic substrates with nitrate as the electron acceptor (Fahrbach et al., 2008). As the concentration of available N in the SOC-poor soil was much lower than that in the SOC-rich soil (Table 1), the enriched *Steroidobacter* in the SOC-poor soil would favor SOC decomposition for N demand in this soil.

The phylum of Chlorflexi was also considered to degrade compounds such as starch, long-chain sugars, and pyrogallol in plant residues (Hug et al., 2013). The significantly increased abundance of the genus *Anaerolineaceae\_uncultured* (Fig. 7) in response to the residue amendment implies the importance of the relevant species in the transformation of plant-derived organic C in Mollisols. Moreover, due to the greatest abundance among genera in the residue-amended SOC-rich soil, *Anaerolineaceae\_uncultured* and correspondent OTUs are likely to be the major contributors to the transformation of fresh C into and the sequestration of these transformed compounds in the SOC fractions as the CCA analysis indicated a strong association of the bacterial community composition with SOC and MOC (Fig. 6). This highlights that the various responses of bacterial community to residue addition in different soils may possess different ecological functions, especially C sequestration.

The addition of soybean residue significantly decreased the abundances of three genera in Acidobacteria in the SOC-poor soil in this study. It could be attributed to the increased soil pH (Fig. 2) which might constrain the abundance of Acidobacteria after residue amendment. Liu et al. (2016) recently showed that pH was a main factor structuring acidobacterial communities, and had a negative association with Acidobacteria subgroup 1 and 3, that *Candidatus*, *Solibacter* and *Bryobacter* in this study were affiliated to. Although the residue amendment led to the increase of pH of the SOC-rich soil as well, the extent of this increase was lower than that of the SOC-poor soil. As these genera did not significantly respond to residue amendment in the SOC-rich soil (Fig. 7), there might have a threshold in pH to effectively influence their abundances.

## Conclusion

This study showed that the amendment of the soybean residue increased C content in POC and MOC fractions in Mollisols. The residue-C contribution to SOC fractions in the SOC-poor soil was less than that in the SOC-rich soil. This was likely attributed to the fast decomposition of the residue and strong priming effect in the SOC-poor soil. The residue amendment enriched the abundances of Genera *Verrucosipora*, *Xanthomonadales* and *Steroidobacter* in the SOC-poor soil, while *Anaerolineaceae\_uncultured* in the SOC-rich soil. This change in bacterial

community was associated with the incorporation of residue-C into various SOC fractions. The further interpretation on the soil microbial functional genes associated with the turnover of fresh C will be useful to clarify the microbial feedback to residue return in term of soil C sequestration.

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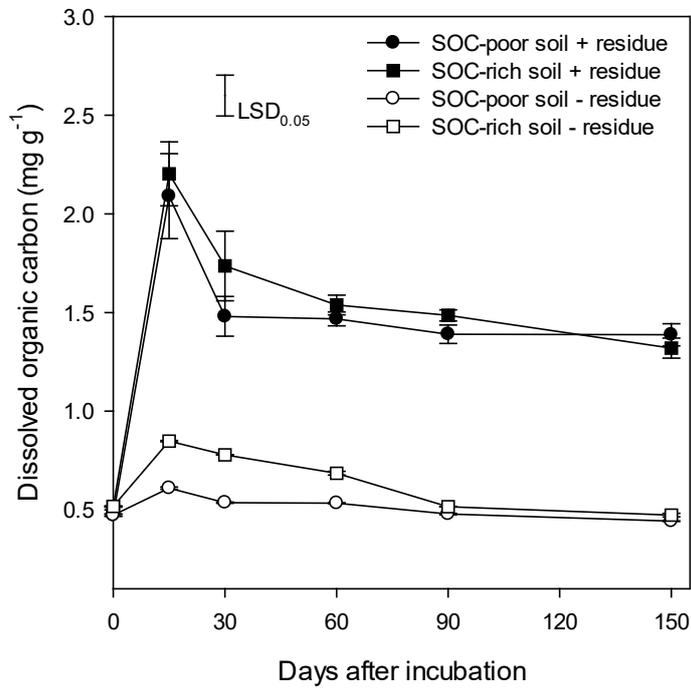
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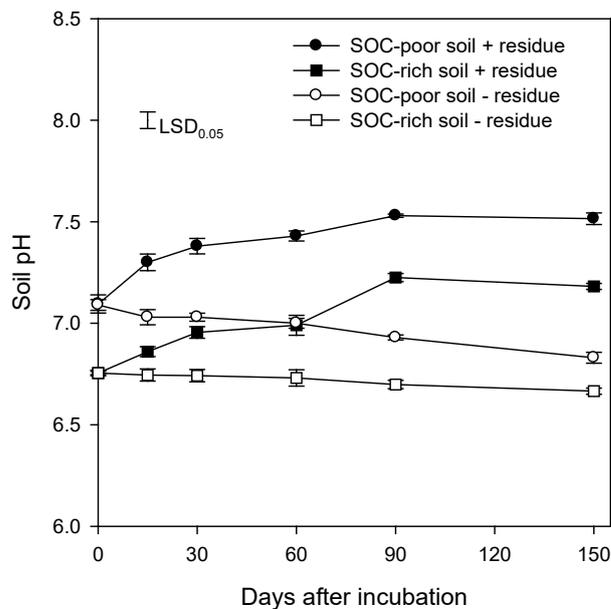
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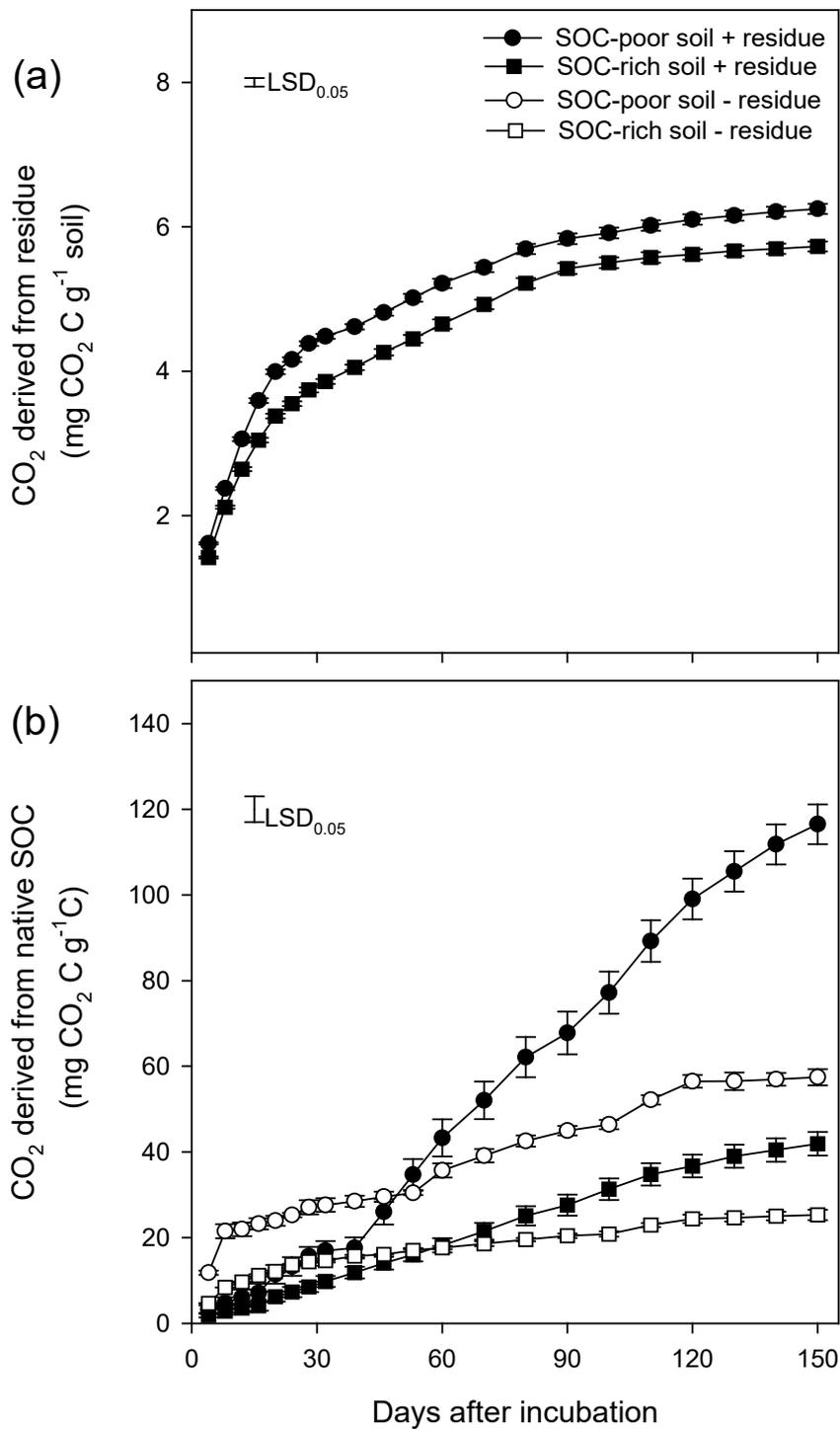
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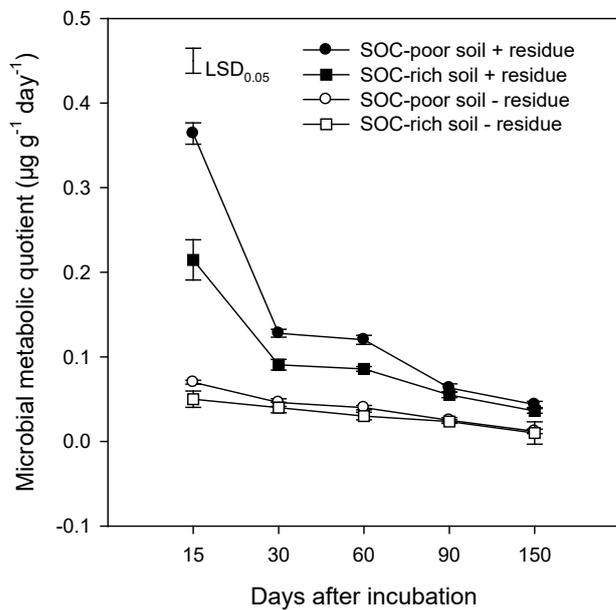
**Figure 1.** Changes of dissolved organic carbon in the soil organic C (SOC)-poor and SOC-rich Mollisols amended with (+) or without (-) soybean residue and incubated at 25°C for 150 days. Vertical bars on datum points represent the standard error of the mean (n=3).



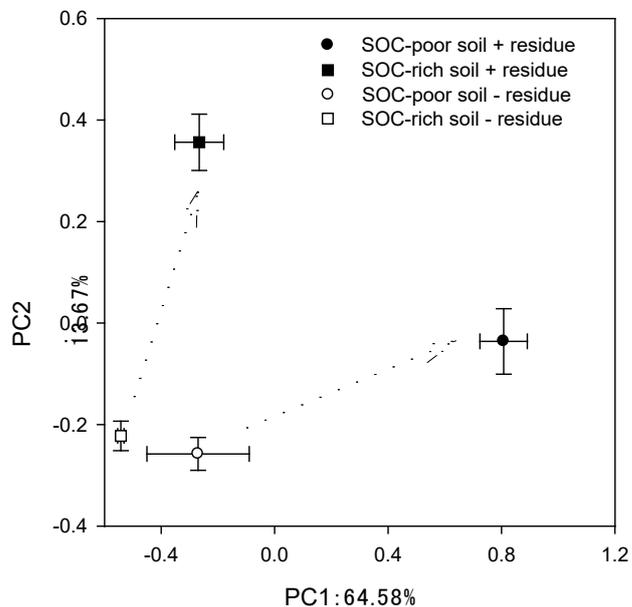
**Figure 2.** Changes over time of soil pH in the soil organic C (SOC)-poor and SOC-rich Mollisols amended with (+) or without (-) soybean residue and incubated at 25°C for 150 days. Vertical bars on datum points represent the standard error of the mean (n=3).



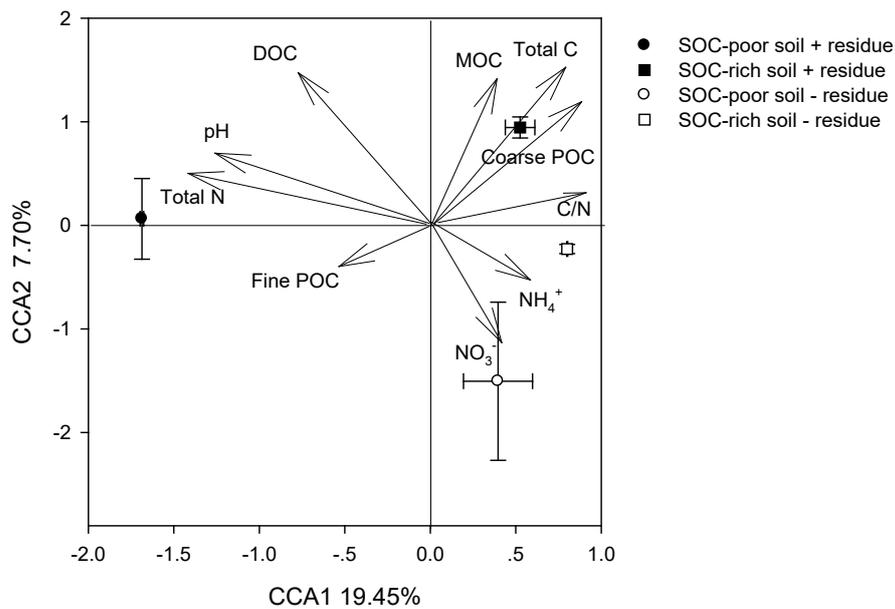
**Figure 3.** The cumulative CO<sub>2</sub>-C derived from residues (a), and native SOC as calculated on a basis of SOC (b) in the soil organic C (SOC)-poor and SOC-rich Mollisols amended with (+) or without (-) soybean residue and incubated at 25°C for 150 days. Vertical bars on datum points represent the standard error of the mean (n=3).



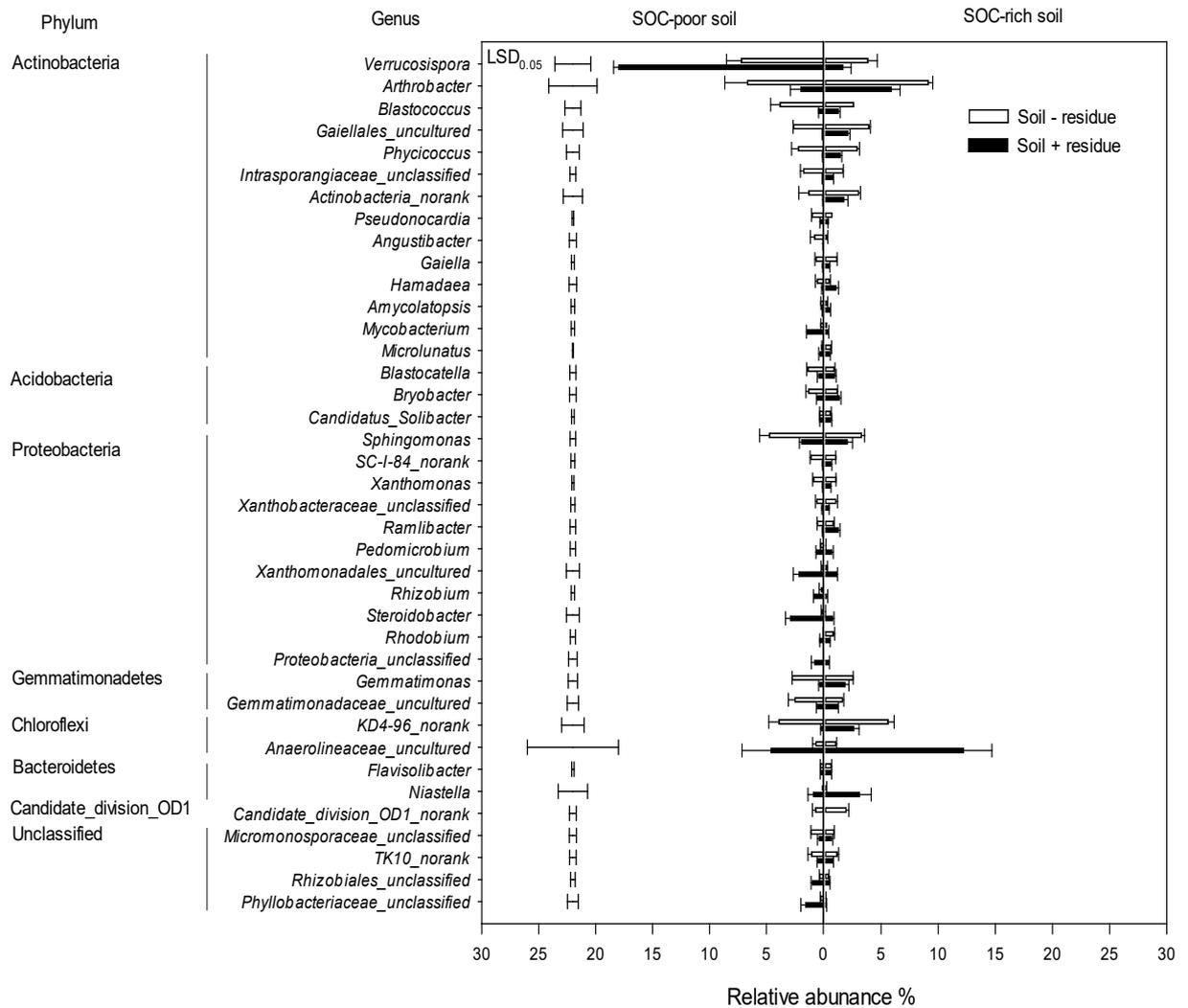
**Figure 4.** Microbial metabolic quotient in the soil organic C (SOC)-poor and SOC-rich Mollisols that were amended with (+) or without (-) soybean residue and incubated at 25°C for 150 days. Vertical bars on datum points represent the standard error of the mean (n=3).



**Figure 5.** Principal coordinates analysis (PCoA) of soil bacterial community in the soil organic C (SOC)-poor and SOC-rich Mollisols that were amended with or without soybean residue and incubated at 25°C for 150 days. Error bars on data points represent the standard error of the mean (n=3). PCoA score plot based on weighted Uni Fracmetrics.



**Figure 6.** Canonical correspondence analysis (CCA) considering the relative abundance of bacteria at the operational taxonomic units (OTUs) level and soil total C and N, C/N ratio, concentrations of  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , pH, dissolved organic C (DOC), particulate organic C (POC) and mineral organic C (MOC). The soil organic C (SOC)-poor and SOC-rich Mollisols were incubated with (+) or without (-) amended-residue at 25°C for 150 days. Error bars on datum points represent the standard error of the mean (n=3).



**Figure 7.** The relative abundances of bacteria at the genus level in the soil organic C (SOC)-poor and SOC-rich Mollisols that were amended with (+) or without (-) soybean residue and incubated at 25°C for 150 days. Horizontal error bars on datum points represent the standard error of the mean (n=3). Only genera with significant ( $p < 0.05$ ) responses to the treatments were presented.

**Table 1.** General chemical characteristics of two Mollisols differing in the concentration of soil organic C (SOC)

Mollisols	Locations	SOC (mg g <sup>-1</sup> )	Total (mg g <sup>-1</sup> )			Available (µg g <sup>-1</sup> )			C/N	pH
			N	P	K	N	P	K		
SOC-poor	43°20' N, 124°28' E	14	1.6	0.64	12.6	97	64	145	8.8	7.1
SOC-rich	48°17' N, 127°15' E	50	4.9	2.43	15.6	366	57	163	10.2	6.8

**Table 2.** Carbon content in the coarse particulate organic C (POC), fine POC and mineral-associated organic C (MOC) fractions in the soil organic C (SOC)-poor and SOC-rich Mollisols that were amended with (+) or without (-) soybean residue and incubated at 25°C for 150 days. Values are the means ± SE (n=3).

Treatments	Coarse POC	Fine POC	MOC
	(mg C g <sup>-1</sup> soil)		
SOC-poor soil + residues	1.7±0.36	2.6±0.40	10.0±2.31
SOC-rich soil + residues	7.8±0.50	18.8 ±0.65	28.1±1.64
SOC-poor soil - residues	1.1±0.11	2.7±0.17	8.6±0.70
SOC-rich soil - residues	6.8±0.16	15.9±1.56	23.8±1.60
LSD ( <i>p</i> = 0.05)	1.18	2.32	3.72

**Table 3.** Residue-derived C retained in the coarse particulate organic carbon (POC), fine POC and mineral-associated organic carbon (MOC) fractions in the SOC-poor and SOC-rich Mollisols that were amended with soybean residue and incubated for 150 days at 25°C. Values are the means ± SE (n=3).

Treatment	Coarse-POC	Fine-POC	MOC
	(mg residue-C g <sup>-1</sup> soil)		
SOC-poor soil	0.43±0.05	0.79±0.15	1.84±0.59
SOC-rich soil	1.95±0.23	3.39±0.16	4.50±0.09
LSD ( <i>p</i> = 0.05)	0.39	0.50	1.89

**Table 4.** Number of operational taxonomic units (OTUs) and alpha diversity indices of bacteria (at 97% sequence similarity) in the soil organic C (SOC)-poor and SOC-rich Mollisols that were amended with (+) or without (-) soybean residue, and incubated at 25°C for 150 days. Values are the means ± SE (n=3).

Treatments	Number of OTUs <sup>a</sup>	Chao1 estimator of richness	Shannon's diversity index	Shannon's evenness
SOC-poor soil + residues	455±52 <sup>b</sup>	554 ± 57	4.5 ± 0.28	0.046 ± 0.009
SOC-rich soil + residues	597 ± 45	687 ± 36	5.3 ± 0.28	0.012 ± 0.004
SOC-poor soil - residues	542 ± 33	616 ± 4	5.1 ± 0.07	0.017 ± 0.020
SOC-rich soil - residues	575 ± 5	642 ± 21	5.3 ± 0.04	0.013 ± 0.001
LSD ( <i>p</i> = 0.05)	68	65	0.36	0.010

<sup>a</sup>All sequence datasets were aligned with equal number of reads (13,574 reads) for downstream analysis.<sup>b</sup>Values are means of three replicate pyrosequencing datasets.



## Supplementary

**Table S1.** Abundance of bacterial operational taxonomic units (OTUs) represented as individual counts in the soil organic C (SOC)-poor and SOC-rich Mollisols that were amended with (+) or without (-) soybean residue, and incubated at 25°C for 150 days. Values are the means  $\pm$  SE (n=3). Only OTUs with significant ( $p < 0.05$ ) responses to the treatments were presented.

<i>Genus</i>	OTU code	Number of reads				LSD
		SOC-poor soil + residues	SOC-poor soil - residues	SOC-rich soil + residues	SOC-rich soil - residues	
<i>Verrucosipora</i>	OTU738	1657 $\pm$ 73	663 $\pm$ 211	150 $\pm$ 119	353 $\pm$ 133	290
<i>Arthrobacter</i>	OTU460	1 $\pm$ 1	42 $\pm$ 42	34 $\pm$ 2.5	84 $\pm$ 4.2	38
	OTU567	177 $\pm$ 145	460 $\pm$ 163	410 $\pm$ 125	522 $\pm$ 75	297
<i>Blastococcus</i>	OTU778	36 $\pm$ 2.5	348 $\pm$ 136	114 $\pm$ 27	238 $\pm$ 0	128
<i>Gaiellales_uncultured</i>	OTU31	0.3 $\pm$ 0.6	20 $\pm$ 18	33 $\pm$ 8.6	52 $\pm$ 5.7	20
	OTU246	0.3 $\pm$ 0.6	2 $\pm$ 1.4	1.3 $\pm$ 0.6	0.5 $\pm$ 0.7	1.8
	OTU367	1.7 $\pm$ 2.1	50 $\pm$ 61	3.7 $\pm$ 1.2	13 $\pm$ 5.0	55
	OTU404	N.D.	2.5 $\pm$ 3.5	1.7 $\pm$ 1.5	4 $\pm$ 1.4	4.0
	OTU413	N.D.	0.5 $\pm$ 0.7	0.7 $\pm$ 0.6	3.5 $\pm$ 3.5	3.4
	OTU445	1 $\pm$ 1	37 $\pm$ 12	40 $\pm$ 4	80 $\pm$ 13	17
	OTU474	N.D.	3.5 $\pm$ 5.0	9.3 $\pm$ 3.2	22 $\pm$ 5.0	7.6
	OTU549	N.D.	18 $\pm$ 25	0.3 $\pm$ 0.6	1.5 $\pm$ 0.7	23
	OTU595	N.D.	14 $\pm$ 16	17 $\pm$ 10	32 $\pm$ 7	21
	OTU589	2.7 $\pm$ 3.1	32 $\pm$ 0.7	43 $\pm$ 7.2	69 $\pm$ 7	12
	OTU592	0.3 $\pm$ 0.6	17 $\pm$ 13	9.3 $\pm$ 0.6	29 $\pm$ 7.8	14
	OTU634	N.D.	15 $\pm$ 15	10 $\pm$ 3.2	27 $\pm$ 2.8	14
	OTU641	0.7 $\pm$ 1.2	13 $\pm$ 11	1.7 $\pm$ 2.1	1.5 $\pm$ 0.7	11
OTU668	0.7 $\pm$ 1.2	17 $\pm$ 18	20 $\pm$ 3.2	25 $\pm$ 1.4	17	
OTU700	N.D.	3 $\pm$ 4.2	1 $\pm$ 1	3.5 $\pm$ 0.7	4.2	

<i>Phycoccus</i>	OTU44	5±2	199±100	128±28	266±37	104
	OTU478	8±2.7	159±46	70±14	154±5.7	46
<i>Actinobacteria_norank</i>	OTU21	0.3±0.6	3.5±0.7	3±2.7	6.5±6.4	6.8
	OTU33	0.7±0.6	5.5±5.0	2±1	0.5±0.7	4.8
	OTU53	N.D.	8.5±12.0	12±1.5	24±14	17
	OTU93	0.7±1.2	7.5±7.8	7.7±5.0	16±6.3	11
	OTU97	N.D.	6±5.7	9.7±6.0	20±2.1	9.5
	OTU215	1±1	30±35	31±8.7	59±4.2	34
	OTU228	2.3±1.5	2±2.8	N.D.	N.D.	3.2
	OTU295	4.3±1.2	35±6	30±3.5	58±1.4	7.1
	OTU379	N.D.	9.5±13	12±8.2	24±7.1	17
	OTU557	0.3±0.6	5±7.1	N.D.	N.D.	6.5
	OTU644	0.7±0.6	4±4.2	1±1	1±1.4	4.3
	OTU720	2±2	6.5±6.4	2.3±2.1	6±4.2	7.9
	OTU742	N.D.	2.5±2.1	0.3±0.6	2.5±0.7	2.2
	<i>Pseudonocardia</i>	OTU415	1±0	4.5±3.5	4.7±1.5	6±2.8
OTU458		5.7±1.2	16±6	12±2.5	16±7.8	9.5
OTU710		12±0	36±21	15±2.5	18±5.0	20
OTU747		2.7±3.8	3.5±3.5	0.3±0.6	N.D.	5.9
<i>Angustibacter</i>	OTU565	N.D.	17±5	7±1	11±7.1	7.9
	OTU812	3.3±2.1	53±66	2.3±0.6	15±2.1	61
<i>Gaiella</i>	OTU167	0.3±0.6	5±1.4	6±2.7	22±2.8	4.6
	OTU278	N.D.	10±10	10±4.2	23±2.8	11
	OTU530	0.3±0.6	16±16	16±2.1	33±3.5	15
<i>Hamadaea</i>	OTU577	3.7±1.5	27±9	9.7±4.6	26±2.1	10
	OTU132	9.7±7.4	40±18	94±40	42±17	57
<i>Amycolatopsis</i>	OTU135	N.D.	8±11	N.D.	N.D.	10
	OTU391	1.3±1.2	31±11	46±2	28±11	29
<i>Mycobacterium</i>	OTU58	N.D.	2.5±3.5	2.7±1.2	6±4.2	5.3

	OTU120	54±22	9.5±3.5	4.3±1.5	5±0	28
	OTU147	56±9	7±1.4	23±12	11±5.0	20
	OTU374	17±15	N.D.	1.3±0.6	0.5±0.7	19
<i>Microthumatus</i>	OTU601	6±3.6	22±0	43±4.6	54±2.1	7.8
	OTU127	2.7±2.5	7±0	15±8.5	4.5±0.7	12
	OTU155	N.D.	5±4.2	0.3±0.6	2±1.4	4.1
	OTU321	9.3±14	32±19	20±5.7	32±7.1	27
	OTU434	4±5.2	11±9	3.3±2.5	4.5±2.1	11
	OTU442	0.3±0.6	6±8.4	8.7±2.9	12±2.8	9.0
	OTU513	2±2.7	24±32	N.D.	1±1.4	29
	OTU534	N.D.	6±8.5	7.8±1.2	10±1.4	7.9
	OTU537	3.3±3.2	9.5±11	1.7±0.6	1±1.4	10
	OTU539	8.7±6.4	13±10	16±15	11±3.5	22
	OTU622	4±3.6	9±13	5±2	3±1.4	12
	OTU655	N.D.	2.5±3.5	3±2	1±0	4.1
<i>Bryobacter</i>	OTU151	3.7±2.1	1.5±2.1	7.7±1.5	3.5±0.7	3.9
	OTU238	N.D.	3.5±5.0	8.3±1.5	9.5±3.5	5.9
	OTU250	1±1	6.5±3.5	7±1	9±0	3.7
	OTU352	1±1	13±18	0.33±0.6	2±1.4	16
	OTU420	16±10	62±42	50±11	56±7.8	43
	OTU488	14±9.1	0.5±0.7	2.7±2.9	1.5±0.7	12
	OTU499	2.3±2.5	N.D.	2.7±2.1	N.D.	4.2
	OTU515	0.7±0.6	13±17	20±11	16±5.7	21
	OTU597	0.3±0.6	8.5±11	N.D.	N.D.	9.7
	OTU635	0.67±0.6	5.5±5.0	N.D.	N.D.	4.6
	OTU693	N.D.	1±1.4	0.7±0.6	1±1.4	1.9
	OTU792	4.3±2.1	4±5.7	22±7	9±0	10
<i>Candidatus_Solibacter</i>	OTU259	N.D.	1±1.4	2.7±2.1	1.5±0.7	3.0
	OTU342	6.7±7.2	N.D.	0.3±0.6	N.D.	9.3

	OTU450	6.3±3.5	28±10	34±14	31±8.5	22
	OTU583	N.D.	2.5±0.7	2.3±2.5	3±1.4	3.6
	OTU588	N.D.	3.5±2.1	0.7±0.6	5.5±3.5	3.8
	OTU590	1±0	7±7.1	5.3±0.6	5±1.4	6.6
	OTU718	N.D.	5±0	4±2	5±1.4	2.9
<i>Sphingomonas</i>	OTU32	67±23	327±187	93±36	178±22	180
	OTU76	48±26	54±27	52±19	57±11	49
	OTU270	43±35	19±6	9±2.7	28±2.8	45
	OTU546	16±9	35±12	32±18	40±14	31
<i>SC-I-84_norank</i>	OTU207	N.D.	3±1.4	1.7±2.1	2.5±2.1	3.6
	OTU264	N.D.	5±7.1	N.D.	N.D.	6.4
	OTU658	0.7±0.6	6.5±0.7	2.3±1.5	7±1.4	2.5
	OTU682	3.7±0.6	45±23	33±18	58±1.4	31
	OTU695	N.D.	4.5±6.4	0.3±0.6	N.D.	5.8
	OTU721	0.3±0.6	8±9.9	4±1	14±4.2	9.9
	OTU734	1.7±0.6	26±5	9.3±2.1	13±0.7	5.3
<i>Xanthomonas</i>	OTU186	6±1.7	78±15	52±9	96±2.1	17
<i>Xanthobacteraceae_unclassified</i>	OTU115	10±5	50±23	38±6	94±28	34
<i>Ramlibacter</i>	OTU6	3.3±2.1	25±13	33±2	34±5.7	14
	OTU211	1±1	9.5±12	30±12	19±2.1	18
	OTU331	3±1	14±8	49±18	22±8.5	26
<i>Pedomicrobium</i>	OTU37	17±6	1.5±0.7	7±3.6	4±1.4	8.7
	OTU221	8.7±3.8	1±1.4	14±8	3.5±0.7	11
	OTU320	35±17	2±0	40±16	5.5±3.5	30
<i>Xanthomonadales_uncultured</i>	OTU65	30.±14	6±4.2	12±2	7.5±0.7	19
	OTU169	85±60	5.5±6.4	27±8	1.5±2.1	79
	OTU172	3.3±3.2	0.5±0.7	7±2.7	3.5±2.1	5.7
	OTU230	N.D.	1±1.4	1.7±1.5	6±2.8	3.4
	OTU454	54±37	1±1.4	33±10	2±2.8	48

	OTU502	4±3	N.D.	N.D.	N.D.	3.9
	OTU613	20±8	3±0	18±5	4±2.8	12
<i>Rhizobium</i>	OTU779	29±4.6	8.5±0.7	9±4	3.5±0.7	7.9
	OTU789	49±21	5.5±5.0	7.7±2.1	4±0	27
<i>Steroidobacter</i>	OTU164	59±49	1±0	4.3±2.9	0.5±0.7	63
	OTU242	12±4.4	4.5±2.1	5±5.6	2.5±2.1	9.5
	OTU414	123±16	5±7.1	49±15	5±0	29
	OTU529	57±21	2±1.4	7.7±3.8	4±0	27
	OTU726	11±12	N.D.	N.D.	N.D.	28
<i>Rhodobium</i>	OTU77	2.3±0.6	7.5±6.4	9±3	10±7.1	9.5
	OTU808	1.7±1.2	27±37	37±6	64±12	36
<i>Proteobacteria_unclassified</i>	OTU36	0.3±0.6	4±4.2	1.3±1.5	3±0	4.4
	OTU43	11±5	N.D.	5.7±8.1	1.5±0.7	12
	OTU49	24±6.7	7±0	7.7±3.8	9±0	9.9
	OTU175	1.3±1.5	9±7.1	9.7±3.1	11±4.2	8.7
	OTU241	0.7±0.6	N.D.	1.3±1.5	2.5±0.7	2.2
	OTU277	1.3±1.2	6±5.7	1.7±0.6	0.5±0.7	5.5
	OTU314	5.7±1.5	8±0	16±3	13±6.4	7.3
	OTU330	6±6.6	2.5±3.5	7.7±2.1	8.5±0.7	9.5
	OTU349	62±19	4±2.8	3±2.7	2±1.4	25
	OTU351	N.D.	2.5±2.1	2.3±2.1	3.5±2.1	3.8
	OTU385	1.3±0.6	9±8.5	3.3±0.6	13±2.8	8.2
	OTU405	N.D.	0.5±0.7	0.7±1.1	1±1.4	2.1
	OTU418	N.D.	N.D.	0.3±0.6	2±1.4	1.5
	OTU449	47±34	3.5±3.5	3.3±3.1	3±1.4	44
	OTU456	66±53	0.5±0.7	36±9.9	N.D.	69
	OTU477	2.7±3.8	0.5±0.7	0.3±0.6	0.5±0.7	5.1
	OTU521	71±28	9±9.9	4.3±3.1	2±1.4	38
	OTU527	5±1	9±4.2	2.7±1.2	4±0	4.3

*Gemmatimonas*

OTU630	16±4.4	5.5±5.0	13±5	11±7.8	12
OTU647	3±3.5	18±2.8	31±3	29±7.8	9.4
OTU777	6.3±11	5±7.1	N.D.	N.D.	15
OTU781	N.D.	N.D.	7±5.3	N.D.	6.8
OTU7	N.D.	1.5±2.1	3.3±1.5	2±1.4	3.0
OTU110	0.3±0.6	1.5±2.1	5.7±4.7	1±0	6.4
OTU114	N.D.	2±1.4	3±5.2	3±1.4	6.9
OTU165	1.3±1.5	9.5±9.2	5±6.1	15±5.0	12
OTU212	3±5.2	15±9	0.3±0.6	11±0.7	11
OTU298	5.7±2.5	1±0	4.7±5.5	N.D.	7.8
OTU343	6.7±6.7	1.5±0.7	1±1	0.5±0.7	8.7
OTU353	N.D.	2.5±2.1	1.3±1.5	3.5±0.7	2.8
OTU360	N.D.	1±1.4	2.7±2.5	1±0	3.5
OTU387	N.D.	3.5±5.0	4±2	6.5±0.7	5.2
OTU465	N.D.	17±10	N.D.	1.5±0.7	18
OTU506	N.D.	4±4.2	3.7±1.5	5.5±0.7	4.4
OTU517	N.D.	1±1.4	0.3±0.6	2.5±0.7	1.6
OTU525	N.D.	18±18	2±1	31±0	17
OTU566	N.D.	1.5±2.1	0.7±0.6	1±0	2.1
OTU627	N.D.	2±2.8	N.D.	N.D.	2.6
OTU681	1.3±1.2	22±25	5±1.7	6±1.4	22
OTU683	2.3±0.6	33±5	28±5	29±0.7	8.1
OTU714	N.D.	11±2	12±10	9.5±0.7	13
OTU725	2.3±3.2	68±25	41±9	63±2.1	26
OTU737	N.D.	5.5±3.5	7±2.7	4.5±2.1	5.1
OTU743	1.7±1.5	11±4	14±9	12±1.4	13
OTU775	N.D.	2.5±3.5	N.D.	N.D.	3.2
OTU776	0.3±0.6	6.5±9.2	7±6	16±2.8	12
OTU783	N.D.	5±4.2	8.7±3.1	6±0	5.5

<i>Gemmatimonadaceae_uncultured</i>	OTU806	4±3.6	13±11	7.7±5.5	11±2.8	13
	OTU212	3±5.2	15±9.2	0.3±0.6	11±0.7	11
	OTU247	N.D.	9.5±5.0	14±9	12±5.7	13
	OTU303	N.D.	3.5±2.1	2±2	3.5±0.7	3.3
	OTU346	12±5.8	75±52	31±2	40±9.2	49
	OTU493	4.7±4.0	0.5±0.7	3±1	1±1.4	5.6
	OTU524	0.7±0.6	N.D.	6±2.7	1±0	3.5
	OTU637	N.D.	4±1.4	1.3±1.2	6.5±0.7	2.1
	OTU639	3.3±4.9	N.D.	0.3±0.6	N.D.	6.4
	OTU697	3.3±3.2	71±25	17±4	40±2.1	24
	OTU708	N.D.	N.D.	1.3±1.5	2±0	1.9
	OTU804	17±8	48±29	27±5	26±0.7	29
	OTU816	0.3±0.6	3±4.2	7.7±3.8	7±2.8	6.8
	<i>KD4-96_norank</i>	OTU24	0.3±0.6	10±14	0.3±0.6	N.D.
OTU166		0.7±0.6	31±33	29±17	71±4.2	37
OTU198		N.D.	7±7.1	5±3.6	19±2.1	8.2
OTU382		1.3±1.5	25±1	15±8	26±6.4	12
OTU487		2.7±1.5	101±2	56±10	114±33	33
OTU547		1.7±2.1	24±7	13±4	40±2.8	9.3
OTU633		N.D.	22±18	17±8	30±5.7	20
OTU676		9.7±6.0	134±97	102±29	212±34	101
OTU698		N.D.	3.5±2.1	2.7±0.6	4.5±2.1	2.8
OTU770		0.3±0.6	1.5±0.7	0.7±0.6	1±1.4	1.8
<i>Anaerolineaceae_uncultured</i>	OTU19	N.D.	N.D.	1±1	N.D.	1.3
	OTU20	13±15	4±4.2	2.3±0.6	1±0	20
	OTU22	57±55	N.D.	N.D.	N.D.	71
	OTU48	2±2	8.5±11	131±65	20±4.2	84
	OTU55	N.D.	1.5±2.1	9±10.2	3±0	13
	OTU60	N.D.	0.5±0.7	9±5.3	1±0	6.8

OTU124	21±34	N.D.	3±2.7	N.D.	44
OTU125	N.D.	6.5±3.5	7±3	5.5±2.1	5.4
OTU126	40±45	N.D.	16±9	N.D.	60
OTU163	3±5.2	N.D.	6.7±3.2	N.D.	7.9
OTU176	0.3±0.6	1.5±0.7	6.7±3.2	1.5±0.7	4.3
OTU185	0.3±0.6	0.5±0.7	7.3±7.0	0.5±0.7	9.1
OTU191	0.3±0.6	1±1.4	9.7±7.8	N.D.	10
OTU200	N.D.	N.D.	10±9	1±0	12
OTU220	N.D.	N.D.	0.7±1.2	0.5±0.7	1.6
OTU229	N.D.	5.5±6.4	4.7±4.6	8.5±6.4	10
OTU233	4.7±5.7	N.D.	0.7±1.2	N.D.	7.5
OTU234	5±6.2	0.5±0.7	5.7±4.7	N.D.	10
OTU293	4.3±6.7	N.D.	93±69	1.5±0.7	89
OTU305	N.D.	N.D.	13±5	1±0	6.6
OTU337	N.D.	N.D.	9.3±7.5	0.5±0.7	9.7
OTU361	49±67	5.5±7.8	229±85	21±5.7	140
OTU376	0.7±1.2	N.D.	1±1	N.D.	1.9
OTU400	N.D.	N.D.	2.7±2.9	N.D.	3.7
OTU422	6±5	N.D.	3.6±5.5	N.D.	9.6
OTU428	N.D.	3±4.2	7.7±5.7	4±1.4	8.4
OTU438	0.3±0.6	N.D.	22±8	0.5±0.7	11
OTU444	N.D.	1±1.4	1.7±2.1	0.5±0.7	3.0
OTU484	1.7±1.5	2±2.8	5±4	2±0	6.1
OTU508	6±10	N.D.	N.D.	N.D.	13
OTU536	19±18	N.D.	N.D.	N.D.	23
OTU543	N.D.	N.D.	2.7±3.8	N.D.	4.9
OTU544	N.D.	N.D.	9±16	N.D.	20
OTU596	0.7±1.2	N.D.	12±4	N.D.	5.4
OTU643	60±71	0.5±0.7	15±24	N.D.	96

	OTU646	24±40	N.D.	N.D.	N.D.	52
	OTU652	4.3±5	2.5±3.5	0.7±1.2	N.D.	7.5
	OTU722	87±118	4.5±6.4	233±103	10±2.8	202
	OTU732	0.7±1.2	0.5±0.7	1.3±1.5	N.D.	2.6
	OTU739	1.3±2.3	6.5±6.4	213±182	3.5±3.5	205
	OTU772	N.D.	N.D.	1.3±1.5	2.5±0.7	2.1
	OTU790	0.7±1.2	2±0	10±4	2.5±2.1	5.7
	OTU793	5.3±8.4	N.D.	3±2.7	0.5±0.7	11
	OTU821	1.3±2.3	N.D.	7.3±6.8	N.D.	9.3
<i>Flavisolibacter</i>	OTU25	3±3.6	18±0.7	24±11	19±2.8	15
	OTU210	0.7±1.2	4±1.4	2.3±0.6	3.5±2.1	2.9
	OTU316	2.3±2.5	17±0.7	14±1	14±1.4	3.8
	OTU511	N.D.	1.5±2.1	4±3	7.5±0.7	4.4
	OTU528	N.D.	7±8.5	4±1	7.5±5.0	9.1
	OTU579	N.D.	3±4.2	6±2.7	2±1.4	5.3
	OTU800	N.D.	1±1.4	1±1	1.5±0.7	1.9
<i>Niastella</i>	OTU288	27±44	N.D.	71±31	9.5±0.7	70
	OTU430	6±3.6	N.D.	9±1.7	1±1.4	5.3
	OTU430	6±3.6	N.D.	9±1.7	1±1.4	5.3
	OTU453	3±1	2±1.4	67±39	2.5±2.1	50
	OTU541	17±29	N.D.	N.D.	N.D.	37
	OTU609	17±10	N.D.	1.3±1.2	N.D.	14
<i>Candidate_division_ODI_norank</i>	OTU201	N.D.	5±4.2	N.D.	3±1.4	4.1
	OTU582	N.D.	N.D.	0.3±0.6	7.5±2.1	2.1
	OTU605	N.D.	2.5±0.7	2±3.5	6.5±2.1	4.9
	OTU774	N.D.	53±52	N.D.	161±37	58
<i>Micromonosporaceae_unclassified</i>	OTU157	N.D.	2.5±3.5	4.3±1.5	7.5±0.7	3.8
	OTU315	29±9.1	81±59	42±20	45±16	63
	OTU324	0.3±0.6	2±0	3±2	5.5±0.7	2.8

<i>TK10_norank</i>	OTU621	0.7±0.6	11±3	6.7±4.7	22±7.1	9.3
	OTU8	2±1	6.5±9.2	1±1	0.5±0.7	8.6
	OTU67	0.3±0.6	4.5±2.1	4.7±2.1	4±1.4	3.6
	OTU107	33±21	38±12	29±9	51±3.5	32
	OTU159	1±1.7	2.5±3.5	1.7±1.2	1.5±0.7	4.2
	OTU162	0.7±0.6	1.5±2.1	2±1.7	1.5±0.7	3.1
	OTU197	3.7±2.5	5.5±2.1	9±2.7	13±0.7	5.1
	OTU226	1.3±0.6	1±0	2.7±2.3	7±2.8	4.0
	OTU304	0.7±0.6	N.D.	0.3±0.6	N.D.	0.9
	OTU362	N.D.	0.5±0.7	N.D.	0.5±0.7	0.9
	OTU406	N.D.	8±5.7	9.3±5.0	15±3.5	8.9
	OTU486	N.D.	6.5±7.8	N.D.	N.D.	7.1
	OTU512	2±2.7	14±9	7±5.2	10±1.4	11
	OTU526	N.D.	0.5±0.7	N.D.	0.5±0.7	0.9
	OTU785	1.3±2.3	5.5±7.8	2.7±0.6	1.5±2.1	7.9
	<i>Rhizobiales_unclassified</i>	OTU175	1.3±1.5	9±7.1	9.7±3.1	11±4.2
OTU314		5.7±1.5	8±0	16±3.1	13±6.3	7.3
OTU349		62±19	4±2.8	3±2.7	2±1.4	25
<i>Phyllobacteriaceae_unclassified</i>	OTU630	16±4.4	5.5±5.0	13±5	11±7.8	12
	OTU49	24±6.7	7±0	7.7±3.8	9±0	9.9
	OTU449	47±34	3.5±3.5	3.3±3.1	3±1.4	44
	OTU521	71±29	9±9.9	4.3±3.1	2±1.4	38

N.D. indicates not detected.