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ORIGINAL ARTICLE

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Microbial communities and their genetic repertoire mediate the decomposition of soil organic carbon pools in revegetation shrublands in a desert in northern China

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Abstract

Revegetation using xerophytic plants in drylands can alter soil microbial community diversity and composition; however, information about the microbial communities and their genetic repertoires that are involved in soil organic carbon (SOC) processes in drylands remain unclear. This study aimed to characterize soil microbial genes and their potential to mediate SOC decomposition in three revegetation shrublands (*Artemisia ordosica*, *Salix psammophila* and *Caragana microphylla*) in the Mu Us Desert of northern China using an SOC mineralization experiment and shotgun metagenome sequencing. Among the three shrublands, the *S. psammophila* shrubland had the highest cumulative CO_2 emissions and highest rates of mineralization of the slow SOC pool. The mineralization rate of the slow SOC pool and the microbial taxonomic and functional composition displayed a significant correlation. Most C-degradation genes were assigned to three bacterial phyla, Actinobacteria, Proteobacteria and Acidobacteria. The relative abundance of microbial functional genes involved in degrading recalcitrant C-complexes was significantly higher in the *S. psammophila* shrubland, resulting in the slow accumulation of recalcitrant SOC. These results suggest that the microbial functional genes that regulate the decomposition of the SOC pool in dryland shrubland soils may be influenced by shrub species selection. These findings highlight the importance of understanding how microbial catabolic potential mediates the potential for SOC sequestration in different revegetation shrublands in drylands.

Highlights

- We studied SOC mineralization and soil microbial functional genes in three revegetation shrublands.
- *S. psammophila* shrubland had the highest CO_2 emissions and highest mineralization rates of the slow C pool.
- Slow SOC pool mineralization rate was related to microbial taxonomic and functional composition.

- Different dryland shrubs may mediate soil microbial functional genes that regulate SOC pool decomposition.

KEYWORDS

dryland, metagenomics, revegetation, shrubland, soil microbial functional genes, soil organic carbon mineralization

1 | INTRODUCTION

Soil stores more carbon (C) in the form of soil organic matter (SOM) than both terrestrial vegetation and atmospheric pools combined (Jobbágy & Jackson, 2000; Stockmann et al., 2013). In drylands, long-term anthropogenic activities and degradation of vegetation have resulted in massive soil C losses (Koerner & Klopatek, 2002; Z. Y. Zhou, Li, Chen, Zhang, & Li, 2011). Revegetation with xeric shrubs is a widely applied measure to rehabilitate ecological environments and improve the soil organic C (SOC) content (M. Cheng, Xue, Xiang, Darboux, & An, 2015). Variations in aboveground plant communities markedly affect the SOC pools by changing the quantity or quality of litters and by selecting for different soil microbial composition (Yan et al., 2018). It is widely accepted that the magnitude of the organic C reservoir in soils depends upon the activity of microorganisms (Liang, Schimel, & Jastrow, 2017). Thus, soil microbes significantly contribute to SOC turnover and the rate of C sequestration after revegetation of xerophytic shrubs in drylands.

Soil microorganisms contribute greatly to the C budget of ecosystems through their roles as decomposers, thereby influencing the longevity and stability of soil C pools (Bardgett, Freeman, & Ostle, 2008; P. Trivedi, Anderson, & Singh, 2013). Different SOC pools possess various stabilities and, consequently, display different turnover times (Schmidt et al., 2011), which ultimately regulate C emissions. For example, the labile soil C pool has a fast turnover rate and is vulnerable to environmental factors (Chen et al., 2016; X. Xu, Sherry, Niu, Zhou, & Luo, 2012), and increases in the labile C pool contribute proportionately more to soil CO_2 efflux, particularly in a short period (Gu, Post, & King, 2004). Although stable SOC has a slower turnover rate, its decomposition can also contribute substantially to soil CO_2 efflux (Cai, Feng, Zhang, & Xu, 2016). Soil microbes can mediate SOC decomposition via alterations in their diversity and composition, ultimately influencing the degree of SOC accumulation (Zheng et al., 2017). However, the decomposition of different SOC pools and mechanisms underlying the mediation of these phenomena by soil microbes with changes in plant species in drylands are yet unclear.

The stability of soil C stocks is traditionally speculated to be controlled by the recalcitrance of less reactive compounds and physical protection, whereas other studies have highlighted the important roles of soil microorganisms in the persistence of SOM (Canarini, Carrillo, Mariotte, Ingram, & Dijkstra, 2016; Rabbi, Wilson, Lockwood, Daniel, & Young, 2014; Rumpel, Kögel-Knabner, & Bruhn, 2002). Previous studies reported that vegetation characteristics can affect the diversity and composition of the soil microbial community and consequently influence ecosystem functioning (Schlatter, Bakkereeee, Bradeen, & Kinkel, 2015; Zak, Holmes, White, Peacock, & Tilman, 2003). However, taxonomic information regarding the microbial communities concerned is often not sufficiently robust to predict their functional capabilities, and the probing of microbial functional genes and the functional composition of microbial communities may help assess soil functions more efficiently (Barberán, Fernández-Guerra, Bohannan, & Casamayor, 2012; Yang et al., 2014).

In a plant–soil ecosystem, plant species govern the type and abundance of many organic substrates provided to soil microbial heterotrophs. As the complexity and amount of soil substrate differ among different plant species, microbial communities can alter their functional potentials to adjust their decomposition strategies (Feng et al., 2017; Jagadamma, Mayes, Steinweg, & Schaeffer, 2014). Changes in functional genes used to degrade labile or recalcitrant C can alter SOC decomposition and long-term soil C stability (J. Z. Zhou et al., 2012). Therefore, an understanding of the microbial functional potential for SOC degradation by targeting related genes involved in C cycling may help establish correlations between organic C cycling and changes in aboveground plant communities.

In this study, we aimed to determine variations in the decomposition of SOC and its constituents with changes in revegetated shrub species and to investigate the extent to which the microbial community functional potential (especially genes involved in soil C catabolism) can be altered by different xerophytic shrub species to regulate SOC decomposition. We hypothesized that (a) shrub species would differentially influence the structure and function of the soil microbiome and the decomposition of SOC pools and (b) the relative abundance of microbial catabolic genes specific to labile or recalcitrant C-complexes would regulate

the decomposition of SOC pools. To test these hypotheses, we performed laboratory incubation and shotgun metagenome sequencing to assay for SOC mineralization and microbial key genes for C degradation in three revegetation shrublands (*Artemisia ordosica*, *Salix psammophila* and *Caragana microphylla*) in the Mu Us Desert in northern China. In particular, our primary objectives were to determine the functions of microorganisms involved in decomposing SOC and its constituent compounds in three shrublands and to assess the selection of shrub species for ecological restoration in terms of the microbial catabolic potential for SOC.

2 | MATERIALS AND METHODS

2.1 | Study site and soil sampling

The study was conducted at the Yanchi Research Station (37°04′-38°10′N, 106°30′-107°47′E; 1,550 m above sea level) located at the southwestern edge of the Mu Us Desert in northern China (Figure 1). This site experiences a semi-arid continental monsoon climate, with an average annual temperature of 8.1°C. The average annual precipitation is 287 mm, with 62% of the rainfall falling between July and September (Jia et al., 2014). This site has quartisamment soil according to the US Soil Taxonomy (USDA, 1975). The dominant shrub species in this region are *A. ordosica*, *S. psammophila* and *C. microphylla.* Before vegetation rehabilitation, the study area comprised widespread bare sand-lands for decades. Since 1998, vegetation rehabilitation with *A. ordosica*, *S. psammophila* and *C. microphylla* has been simultaneously performed on bare sand-lands via aerial seeding, cutting propagation and seedling planting, respectively. Since then, the shrublands were fenced, grazing was prevented and no fertilizer was applied.

The *A. ordosica*, *S. psammophila* and *C. microphylla* shrublands selected for this study are located within a relatively narrow geographical range and have a similar developmental history. Their locations within the study site are illustrated in Figure 1. In August 2016, three 20 × 20 m sampling plots were established in each shrubland, at distances of 20 m away from each other. In each plot, all standard shrubs were selected and numbered, and five shrubs were randomly selected using a random number generator (https://www.random.org) for soil sampling. Soil samples were collected beneath the canopy of each shrub (at a central position between the trunk and the edge of the canopy) and in open areas between shrubs; 10 samples were obtained from each plot. Soil cores were obtained from a depth of 20 cm (excluding the litter layer) with a 4.5-cm-diameter soil auger. Thereafter, the 10 samples collected from each plot were mixed to create one composite sample, providing a total of nine composite samples (three shrub species × three replicates). Each composite soil sample was sieved through a 2-mm mesh to thoroughly homogenize the soil and eliminate roots and stones and then divided into three subsamples. One portion was air-dried for physico-chemical analysis, the second portion was stored at 4°C for subsequent assessment of the soil microbial biomass carbon (MBC) and laboratory incubation, and the third portion was subsequently stored at −80°C on dry ice and used for metagenomic analysis.

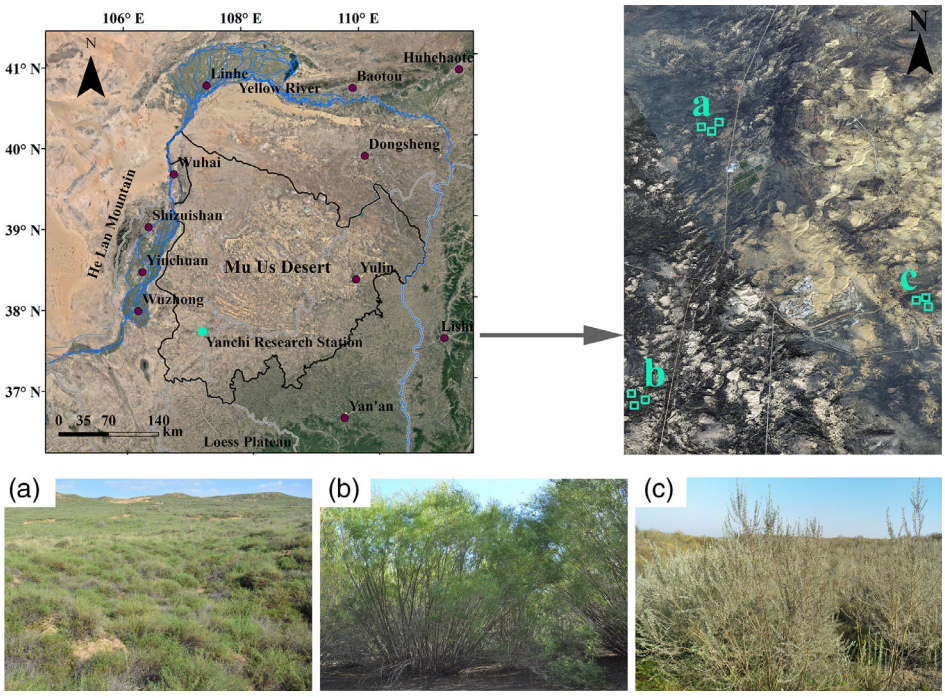

FIGURE 1 Location of the study site and the distribution of the three shrublands within the study area.
(a) *Artemisia ordosica* shrubland;
(b) *Salix psammophila* shrubland;
(c) *Caragana microphylla* shrubland

2.2 | Measurement of the physicochemical properties of the soil samples

Soil water content (SWC) was determined after oven-drying soil samples at 105°C for 24 hr. Soil pH was measured in a 1:2.5 soil/water suspension. Total SOC was measured using the potassium dichromate oxidation method (Bao, 2000). Total nitrogen (TN) content was analysed using the micro-Kjeldahl method (Jiang, 2000). Soil particle size was determined using a Mastersizer 2000 instrument (Malvern Instruments, Malvern, UK) and classified as clay (<0.002 mm), silt (0.002–0.05 mm) or sand (0.05–2.00 mm) in accordance with the criteria developed by the U.S. Department of Agriculture. Microbial biomass carbon was determined using a fumigation extraction method (Wu, Joergensen, Pommerening, Chaussod, & Brookes, 1990).

To measure the soil C composition, soil samples were processed using a two-step hydrolysis procedure to separate the labile and recalcitrant C (Xue et al., 2016). Briefly, approximately 500 mg of ground soil was hydrolyzed with 20 mL of 2.5 mol L^{-1} H_2SO_4 at 105°C for 30 min. The hydrolysate was recovered via centrifugation and decantation. The residue was washed with 20 mL of water, the extract was added to the previous hydrolysate and the resulting solution was called "labile 1" (primarily polysaccharides). After drying at 60°C, the remaining residue was mixed overnight with 2 mL of 13 mol L^{-1} H_2SO_4 at 25°C, under continuous agitation. Thereafter, 24 mL water was added to dilute the acid to 1 mol L^{-1} and hydrolysis was carried out for 3 hr at 105°C. The hydrolysate and 20 mL water used to wash the residue were mixed and called "labile 2" (mostly cellulose). The labile 1 and 2 samples were quantitatively analysed individually using a Liqui TOC-Analyzer (Elementar, Jena, Germany). Finally, the value of labile C was obtained from a combination of labile 1 and 2 fractions. Recalcitrant C content was determined from the difference between the amounts of SOC and labile C.

2.3 | Measurement of plant biomass and litter

After soil sampling, five 1 × 1 m quadrats were placed around the soil sampling cores in each plot. For those subplots, the understory herbaceous plants were harvested and all surface litters were collected. Three 5 × 5 m quadrats were selected in each *A. ordosica* shrubland plot to harvest the *A. ordosica* aboveground part and root biomass. In each plot of the *S. psammophila* and *C. microphylla* shrublands, six standard shrubs were chosen, and their aboveground parts and root biomass were harvested. The dry weight of all plant and litter samples was measured after drying at 75°C for 48 hr.

2.4 | Incubation experiment

For each sample, 100 g of soil (dry weight) was weighed in a 500-ml jar. The water content of the soil in each jar was adjusted to 60% of the water-holding capacity with deionized water. A beaker containing 5 mL of 0.5 mol L^{-1} NaOH solution was placed in each jar to trap CO_2 emanating from the soil. After sealing, all jars were incubated at 25°C in the dark for 42 days. Three additional jars with a beaker containing NaOH solution were incubated in parallel. These jars served as controls to account for CO_2 trapped from the air. The NaOH solution in the beakers was changed after 1, 3, 5, 7, 10, 14, 21, 28, 35 and 42 days. Carbon dioxide evolved during the incubation period was trapped in the NaOH solution, and excess CO_2 was then titrated with 0.1 mol L^{-1} HCl after adding $BaCl_2$. Mineralized C was calculated as the cumulative CO_2-efflux rate (mg C kg^{-1} soil).

2.5 | Estimation of the sizes and mineralization rates of the SOC pools

The sizes and mineralization rate constants of SOC pools were estimated using a parallel first-order and zero-order model (Van Kessel, Reeves, & Meisinger, 2000). The coefficient adjusted R^2 and Akaike's information criterion (AIC) (Akaike, 1974) were used to select the best-fitting model (Table S1). This model assumes that SOC comprises an easily degradable (active) C pool mineralized exponentially in accordance with first-order kinetics and a slow cycling (slow) C pool mineralized in accordance with zero-order kinetics. The model is described by the following equation:

$$C_t = C_a\left(1 - e^{-k_a t}\right) + k_s t, \quad (1)$$

where C_t is the cumulative amount of mineralized C at time t, C_a is the size of the active C pool, and k_a and k_s represent the mineralization rate constants for the active and slow C pools, respectively. C_a, k_a and k_s were determined via nonlinear regression with SPSS software, version 20.0 (SPSS Inc., Chicago, IL, USA).

2.6 | Metagenomic shotgun sequencing, assembly and annotation

Soil DNA was extracted using the MoBio Power Soil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA) according to the manufacturer's instructions. The DNA was then examined electrophoretically on a 1% agarose gel. Each DNA concentration was determined using a NanoPhotometer spectrophotometer (Implen, Westlake Village, CA, USA) and measured using a Qubit dsDNA Assay Kit in a Qubit 2.0 fluorometer (Invitrogen, Carlsbad, CA, USA). After

analysing DNA samples, paired-end libraries were generated using the NEBNext Ultra DNA Library Prep Kit for Illumina (NEB, Ipswich, MA) following the manufacturer's instructions. The DNA in each sample was fragmented through sonication to generate ~350 base pair (bp) fragments and gel-purified. Sequencing was performed using the Illumina HiSeq 2,500 platform (Illumina, San Diego, CA, USA) at Novogene (Beijing, China).

The raw reads obtained from every metagenomics dataset were filtered by eliminating adaptor fragments and low-quality reads to generate clean data, which were then assembled using SOAPdenovo (Luo et al., 2012). The assembly with the longest N50 in every metagenome was selected for subsequent analysis. Scaftigs were generated after splitting into "N" sequences within the scaffolds, and scaftigs shorter than 500 bp were filtered out. USEARCH (Edgar, 2010) was used to select unique scaftigs from all metagenomic datasets. The abundance of unique scaftigs in every metagenome was calculated after mapping the corresponding clean data to unique scaftigs using SoapAligner (version 2.21) (Liu et al., 2011). The open reading frames (ORFs) contained in the scaftigs were predicted using MetaGeneMark (Zhu, Lomsadze, & Borodovsky, 2010). The predicted ORFs were clustered using CD-HIT (identity threshold of 95%) (Fu, Niu, Zhu, Wu, & Li, 2012) and selected for subsequent use for functional profiling. Relative gene abundance was defined as the ratio of the sum of the sequencing depth of every base in the predicated gene to the gene length. Functional annotation was performed using the Carbohydrate Active Enzyme Database (CAZy). For taxonomic analysis, the unique scaftigs were compared with reference microbial genomes in NCBI MicroNT datasets (including those of bacteria, fungi, archaea and viruses). The lowest common ancestor algorithm in MEGAN (Huson, Mitra, Ruscheweyh, Weber, & Schuster, 2011) was used to identify the taxon of every scaftig. Both functional and taxonomic annotation were performed using the best BLASTX hit with 50 bp as the minimum alignment length and $E < 1 \times 10^{-5}$ as the E-value cut-off. All raw sequence reads generated in this study were archived in the Sequence Read Archive database of the NCBI under accession number SRP149181.

The CAZy database includes six CAZy classes, auxiliary activity (AA) redox enzymes, carbohydrate-binding modules (CMB), carbohydrate esterase (CE), glycoside hydrolase (GH), glycosyl transferase (GT) and polysaccharide lyase (PL). To estimate the SOC degradation potentials of soil microbial communities, we specifically focused on CAZy genes responsible for the catabolism of various C-complexes with varying decomposability, ranging from labile C (e.g., monosaccharides and polysaccharides) to recalcitrant C (e.g., phenols). All CAZy genes detected herein and their potential substrates are listed in Table S2.

2.7 | Data analyses

One-way analysis of variance (ANOVA) was performed to examine differences in plant and soil properties, SOC mineralization and the relative abundance of microbial functional genes among the three shrublands. The normality of residuals and the homogeneity of variances were assessed using the Shapiro–Wilk and Levene tests, respectively. Log/sqrt-transformation was used when data were not normally distributed. Fisher's least significant difference (LSD) analysis was performed for multiple comparisons of means. Correlations between the soil properties and the relative abundance of CAZy genes that degrade five categories of organic compounds and SOC mineralization parameters were evaluated using the Spearman method. The Mantel test was performed to analyse the correlations between microbial taxonomic and functional composition and SOC mineralization parameters. Differences in the taxonomic and functional composition of microbial communities among the shrublands were assessed via permutational multivariate ANOVA (PERMANOVA) and visualized using principal component analysis (PCA). Linear regression analysis was used to determine the relationships between the PCA axes. Statistical analyses, correlation analyses and linear regression analyses were performed using SPSS software, version 20.0. The Mantel test, PERMANOVA and PCA were implemented using the Vegan package in R software, version 3.3.1 (R Core Team, 2016). Results are presented as mean values ± standard error (SE). Statistical significance was determined at a level of $p < 0.05$.

3 | RESULTS

3.1 | Plant and soil C properties

Plant characteristics differed markedly among the three shrublands (Figure 2a; $p < 0.05$). Above-ground and below-ground biomasses were the largest in the *S. psammophila* shrubland and the smallest in the *A. ordosica* shrubland. The *S. psammophila* shrubland also had the largest litter biomass. Regarding soil C, total SOC content was significantly larger in the *S. psammophila* and *A. ordosica* shrublands ($p < 0.05$). Recalcitrant C content was the largest in the *A. ordosica* shrubland and labile C content was the largest in the *S. psammophila* shrubland (Figure 2b).

3.2 | SOC mineralization

Cumulative CO_2 emission resulting from SOC mineralization from the *S. psammophila* shrubland was significantly larger than that from the other two shrublands (Figure 3; $p < 0.05$). According to the modelling results, the mineralization rates of the active C pool did not differ significantly

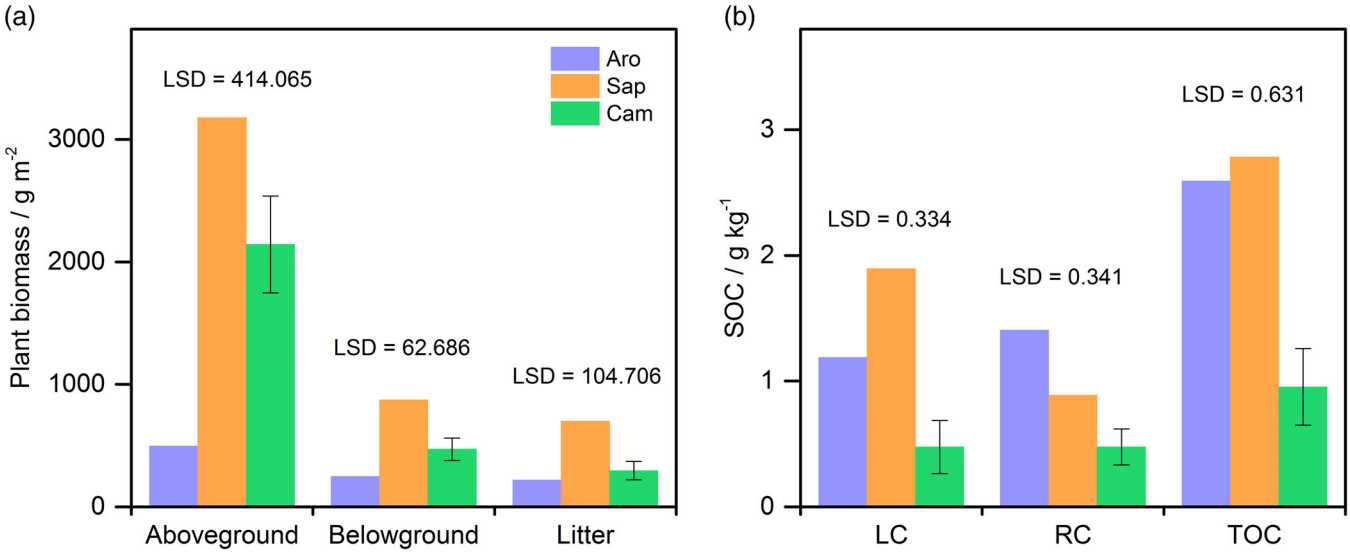

FIGURE 2 Plant and soil variables in the three shrublands. (a) Aboveground plant, belowground root and litter biomass. (b) Soil C, including total organic C (TOC), labile C (LC) and recalcitrant C (RC) pools. Error bars represent standard errors ($n = 3$). The LSD represents the least significant difference value at significance $p < 0.05$. Aro: *Artemisia ordosica*; Cam: *Caragana microphylla;* Sap: *Salix psammophila*

among the three shrublands (Table 1); however, those of the slow C pool were significantly higher in the *S. psammophila* shrubland (Table 1; $p = 0.012$).

3.3 | Differences in microbial functional genes related to C degradation

Genes mediating the catabolism of various C-complexes were identified in each of the three shrublands (Figure 4).

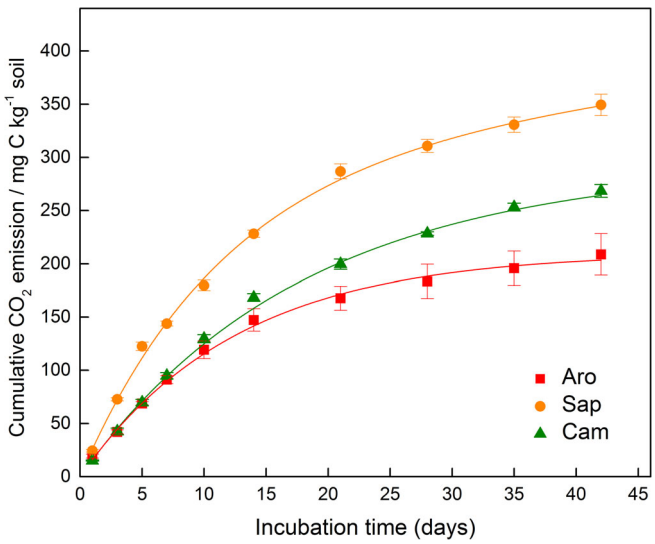

FIGURE 3 Cumulative CO_2 emissions from the soil samples from the three shrublands during the 42-day incubation. Solid lines represent model fits using a parallel first- and zero-order kinetic model. Error bars represent standard errors ($n = 3$). Aro: *Artemisia ordosica*; Cam: *Caragana microphylla;* Sap: *Salix psammophila*

The total relative abundance of genes promoting C degradation was approximately 9% of the assembled metagenomes. Overall, C-degradation genes were significantly more abundant in the *A. ordosica* and *S. psammophila* shrublands than in the *C. microphylla* shrubland, regardless of the catabolism of labile or recalcitrant C pools ($p < 0.05$). Differences in C-degradation genes between *A. ordosica* and *S. psammophila* shrublands were primarily reflected in the relative abundance of catabolic genes specific to recalcitrant C-complexes (such as carboxylic acids and phenols). The relative abundances of recalcitrant C-degradation genes, especially genes responsible for acetylxylan, pectate, alginate and lipids catabolism, were generally greater in *S. psammophila* shrubland ($p < 0.05$).

3.4 | Taxonomic profiles of the microorganisms involved in soil C degradation

The taxa of microbes catabolizing divergent C-complexes were identified in accordance with the CAZy genes. The composition of C-degradation microbes differed across the three shrublands (Figure S1; PERMANOVA, $F = 8.35$, $p = 0.0035$) and was associated with the mineralization rate of the slow C pool (Table S3). The primary phyla of the putative C-degradation microbes identified in the present soil samples were Actinobacteria, Proteobacteria and Acidobacteria (Figure 5). The relative abundance of Actinobacteria and Acidobacteria was significantly higher during the catabolism of recalcitrant C than for labile C, especially in the *S. psammophila* shrubland ($p < 0.05$). Further taxonomical classification at the genus level revealed

TABLE 1 Parameters and R^2 values of the first- and zero-order kinetic model fitted with the cumulative C mineralization data ($n = 3$)

Shrublands	C_a / mg C kg^{-1}	k_a / day^{-1}	k_s / mg C kg^{-1} day^{-1}	R^2
Aro	176.205	0.100	0.805	0.997
Sap	308.038	0.085	1.184	0.997
Cam	252.649	0.065	0.790	0.998
F	18.950	4.549	10.150	–
P	0.003	0.063	0.012	–
SE	20.566	0.066	0.732	–
LSD	52.620	–	0.242	–

C_a is the size of the active C pool. k_a and k_s are the mineralization rates for the active and slow C pools, respectively.
Aro: *Artemisia ordosica*; Cam: *Caragana microphylla*; LSD: least significant difference at $p < 0.05$; Sap: *Salix psammophila*; SE: standard errors calculated from ANOVA.

that C-degradation genes were mainly distributed in genera *Solirubrobacter*, *Rubrobacter*, *Streptomyces* and *Conexibacter*, which belong to the Actinobacteria phylum (Figure S2).

3.5 | Linking SOC mineralization parameters to the soil microbial taxonomic and functional composition

Different shrub species exerted significant effects on soil microbial taxonomic composition and functional composition (PERMANOVA, $F = 28.81$, $p = 0.004$ and $F = 8.58$, $p = 0.0035$, respectively; Figure 6a and b). According to the Mantel test results, both the soil microbial taxonomic composition and functional composition correlated significantly with the cumulative CO_2 emission levels following SOC mineralization and the mineralization rate of the slow C pool ($p < 0.05$). However, the active C pool size and the mineralization rate were not significantly associated with the microbial taxonomic or functional composition (Table 3). The microbial genes involved in the degradation of carboxylic acids and phenolic compounds were positively correlated with the mineralization rate of the slow C pool (Table 4, $p < 0.05$).

4 | DISCUSSION

4.1 | SOC mineralization in different revegetation shrublands

The results of this investigation support the hypothesis that the decomposition of SOC pools differs in the three

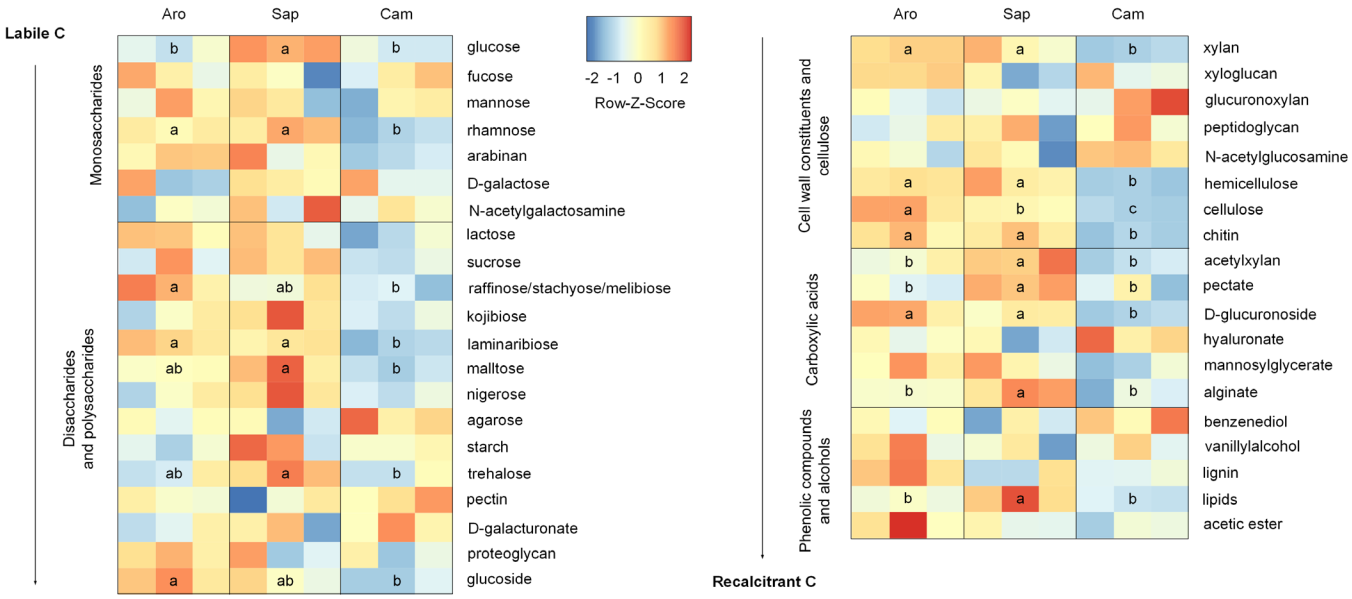

FIGURE 4 Distribution of selected C-complexes' degradation pathways in the three shrublands. The heat map shows the scaled relative abundance of each pathway (normalized and centred Z-scores). Each shrubland column contains the result of adjacent single replicates ($n = 3$). Different letters indicate significant differences ($p < 0.05$). Aro: *Artemisia ordosica*; Cam: *Caragana microphylla;* Sap: *Salix psammophila*

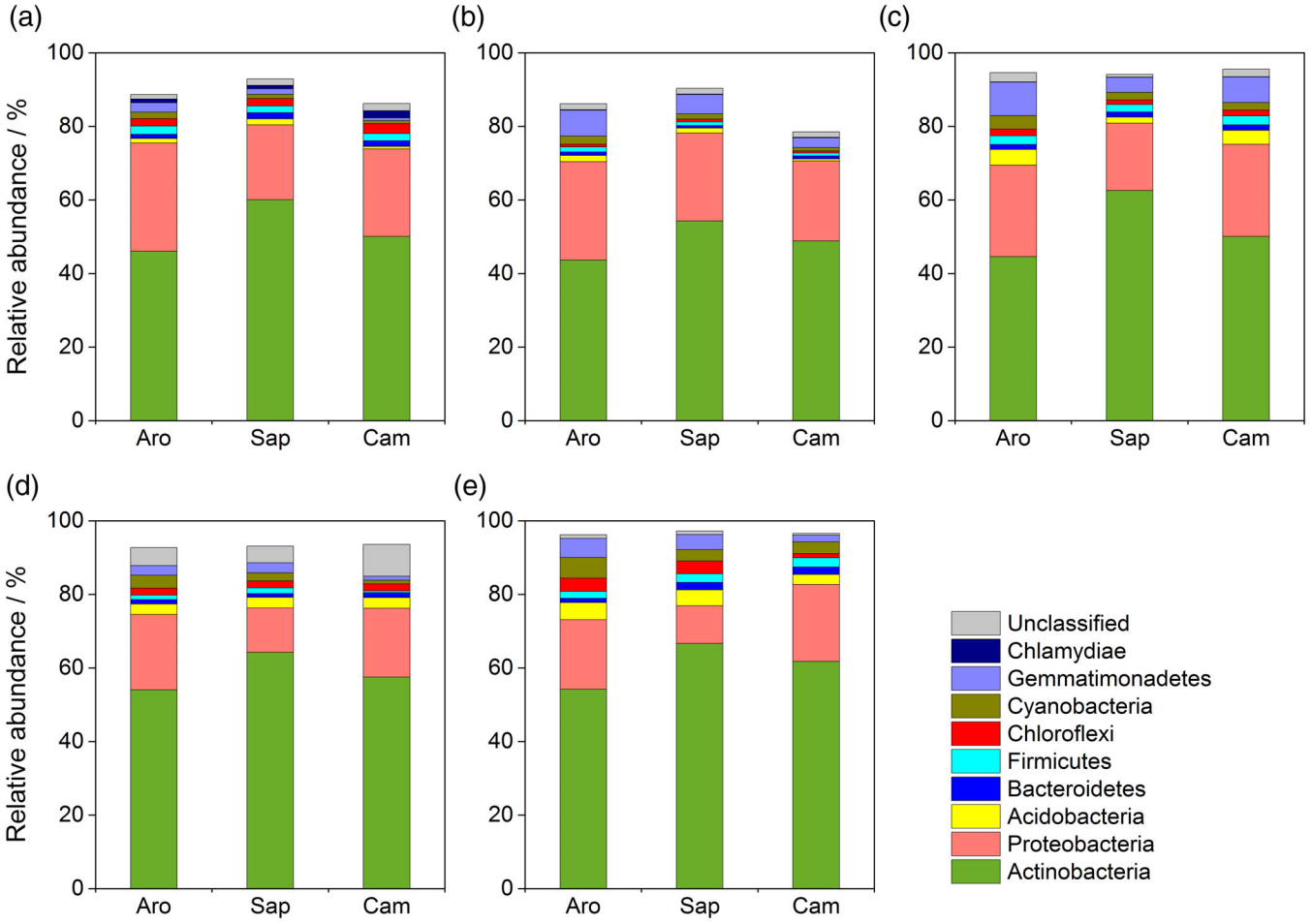

FIGURE 5 Relative abundance of the major phyla of C-degradation microbes in the three shrublands. (a)–(e) Represent the degradation pathways of monosaccharides, disaccharides and polysaccharides, cell wall constituents and cellulose, carboxylic acids, phenolic compounds and alcohols, respectively. Aro: *Artemisia ordosica*; Cam: *Caragana microphylla;* Sap: *Salix psammophila*

shrublands. The differences were mainly reflected in the mineralization rate of the slow C pool, which was highest in the *S. psammophila* shrubland (Table 1). Generally, the labile C pool responds rapidly to changes in the C supply, and the mineralization rate affects the SOC content (Mi, Li, Chen, Xie, & Bai, 2015; X. Xu et al., 2012). In the present study, no significant differences were observed in the mineralization rate of labile C among the three shrublands

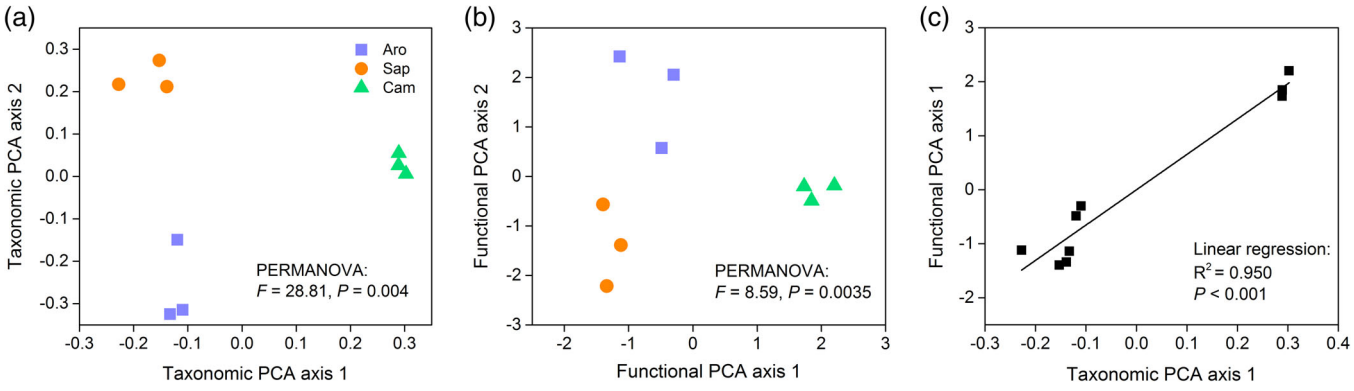

FIGURE 6 Soil microbial taxonomic (a) and functional (b) composition in the three shrublands, and the relationship between the taxonomic and functional compositions (c). $n = 3$. The proportion of variation explained by taxonomic PCA axes 1 and 2 is 69.0 and 18.5%, respectively. The proportion of variation explained by functional axes 1 and 2 is 44.9 and 23.6%, respectively. Aro: *Artemisia ordosica*; Cam: *Caragana microphylla*; Sap: *Salix psammophila*

TABLE 2 Correlations between the soil organic carbon (SOC) mineralization parameters and soil properties ($n = 3$)

Soil properties	C_a	k_a	k_s
SWC	−0.117	0.533	0.167
C/N	0.567	0.150	0.650
MBC	−0.233	**0.933*****	0.167
TN	−0.167	0.552	0.134
Clay	−0.583	0.633	−0.333
Silt	−0.217	0.583	0.083
Sand	0.433	−0.500	−0.067

C/N: the ratio of soil organic carbon (C) to total nitrogen; C_a: the size of the active C pool; C_{min}: the amount of total mineralized C at the end of incubation experiment; k_a: the mineralization rate for the active C pool; k_s: the mineralization rate for the slow C pool; MBC: microbial biomass C; SWC: soil water content; TN: total nitrogen.
***Bold represents $p < 0.001$.

(Table 1). A 3-year incubation study showed that CO_2 emissions from the decomposition of resistant C can account for the majority of total cumulative CO_2 emission and that the decomposition rate can be beneficial for accurate analysis of soil C decomposition (Feng et al., 2017). In our short-term incubation experiment, although most CO_2 emissions resulted from labile C pool mineralization, mineralization of the slow C pool was mostly responsible for the differences between SOC mineralization rates in the three shrublands.

Soil organic carbon mineralization is affected by many factors. Soil properties, such as the clay content, water-holding capacity and C:N ratio, are considered important factors regulating SOC decomposition (X. Xu et al., 2016). In the present study, few clear associations were found between the soil properties and SOC mineralization, for either the labile C pool or the slow C pool (Table 2), the exception being that the MBC content affected the mineralization rate of the labile C pool. The mineralization rate in the initial phases of the incubation process depends on

TABLE 3 Correlations between soil organic carbon (SOC) mineralization parameters and the microbial taxonomic and functional composition, as shown by the Mantel test ($n = 3$)

SOC decomposition parameters	Taxonomic composition	Functional composition
	r	*r*
C_{min}	**0.289***	**0.383***
C_a	0.177	0.200
k_a	0.270	0.221
k_s	**0.295***	**0.468***

C_{min} is the amount of total mineralized C at the end of incubation experiment. C_a is the size of the active C pool. k_a and k_s are the mineralization rates for the active and slow C pools, respectively.
*Bold represents $p < 0.05$.

TABLE 4 Relationships between soil organic carbon (SOC) mineralization parameters and the relative abundance of microbial C-degradation genes ($n = 3$)

Categories of C-degradation genes	C_a	k_a	k_s
Monosaccharides	0.467	0.500	0.600
Disaccharides and polysaccharides	0.250	0.617	0.517
Cell wall polymers including cellulose	0.450	**0.917****	0.001
Carboxylic acids	0.417	0.583	**0.638***
Phenolic compounds and alcohols	0.433	0.633	**0.767***

C_{min} is the amount of total mineralized C at the end of the incubation experiment. C_a is the size of the active C pool. k_a and k_s are the mineralization rates for the active and slow C pools, respectively.
*$p < 0.05$.; **$p < 0.01$.

intense microbial activity in the rapidly oxidizable organic C pool (Carvalho, Mendonça, La Scala, & Reis, 2013). Therefore, microbial biomass might be a key factor influencing SOC mineralization in the initial phase. In addition to MBC content, the taxonomic composition of the soil microbial community contributed to changes in SOC mineralization (Table 3). Shifts in the bacterial or fungal community composition towards certain groups potentially greatly contribute to SOC mineralization because of differing capabilities in degrading carbohydrates or complex organic compounds (Zheng et al., 2017). Microorganisms degrading complex organic compounds may differ among the three shrublands, resulting in diverging slow C pool mineralization rates. Although variations in the soil properties in the three shrublands did not directly affect the mineralization of the SOC pool, they might have caused indirect effects by modifying the soil microbial community composition.

4.2 | Effects of microbial functional genes on the decomposition of SOC pools

As hypothesized, soil microbial functional genes had a significant effect on SOC decomposition. Gene abundance is a good predictor of soil element-cycling rates because it integrates information regarding both environmental history and recent process activity (Petersen et al., 2012). In the present study, microbial functional genes, especially those for the metabolism of carboxylic acids and phenolic compounds, were significantly correlated with the mineralization rate of the slow C pool (Tables 3 and 4). Similarly, a previous study revealed potential associations between soil microbial functional genes and the decomposition of SOC constituents (Feng et al., 2017). Furthermore, a study on the associations between soil microbial functional genes and enzyme activity indicated that gene relative abundance is an adequate predictor of the associated enzyme activity (Trivedi et al., 2016).

Thus, although microbial enzyme activities involved in C-degradation were not measured directly, the highest relative abundance of catabolic genes for recalcitrant C-complexes in the *S. psammophila* shrubland was associated with the microbial utilization of recalcitrant C-complexes. Together, the higher microbial degradation rate and activity for recalcitrant C in the *S. psammophila* shrubland versus those of the other two shrublands might retard the accumulation of the recalcitrant C pool in soil, although the largest plant biomass and quantity of litter were measured in the soil in this shrubland type (Figure 2a,b). Numerous studies on other ecosystems, including grasslands, the Tundra and forest ecosystems, have demonstrated that warming or watering can enhance microbial functions in terms of recalcitrant C-degradation (L. Cheng et al., 2017; Hopkins, Torn, & Trumbore, 2012; Xue et al., 2016; Zhang, Johnston, Li, & Konstantinidis, 2017). Dryland microbes are considered particularly sensitive to global environmental changes (Nie et al., 2013). Thus, microbes in the *S. psammophila* shrubland potentially drive accelerated decomposition of recalcitrant C-complexes with environmental changes.

Labile C-complexes are utilized more efficiently by microbes than recalcitrant C-complexes (Cotrufo, Wallenstein, Boot, Denef, & Paul, 2013). In the present study, no significant correlation was observed between the microbial functional genes and the mineralization rate of the active C pool (Table 3). Differences in microbial functional gene abundance in the three shrublands did not result in differences in the decomposition rate of the active C pool. Owing to robust correlations between enzyme activities with functional genes (P. Trivedi et al., 2016), these results suggest similar microbial utilization of labile C-complexes, particularly in the *A. ordosica* and the *S. psammophila* shrublands. However, higher accumulation of labile C was observed in the *S. psammophila* shrubland (Figure 2). It is likely that partial degradation products from recalcitrant C-complexes contribute to the labile C pool, as detected by Pires et al. (2017). Compared to the *A. ordosica* shrubland, the higher degradation of recalcitrant C-complexes by soil microbes in the *S. psammophila* shrubland might, therefore, result in a relatively increased accumulation of the labile C pool. In addition, not only can microorganisms promote the release of C into the atmosphere through their catabolic activities but also synthesize labile C into a stable form by their anabolic functions (Cotrufo et al., 2013; Liang et al., 2017). We speculate that microbial anabolic activities were smaller in the *S. psammophila* shrubland; however, further studies are required to investigate the contribution of microbial-derived C to SOC sequestration in the three shrublands. In the *C. microphylla* shrubland, although the relative abundance of C-degradation genes was the lowest (Figure 4), the accumulation of the C pool was also the smallest. The poorest soil water content (Table S4) may have restricted microbial catabolic and anabolic activities and resulted in equal accumulation of labile and recalcitrant C pools.

In this study, both microbial taxonomic and functional compositions were significantly correlated with the decomposition of SOC pools (Table 3). Changes in the microbial taxonomic composition may not alter the capacity of the soil to facilitate ecosystem functions because of functional redundancy resulting from different taxonomic groups with a common function (Cardenas et al., 2015). However, PCA results in the present study showed that the axes of the taxonomic and functional composition shared significant linear relationships with each other ($p < 0.001$; Figure 6c). These findings indicate that the divergent microbial taxonomic composition in the three shrublands could alter the capacity of those communities to degrade SOC. Similarly, a study of a temperate forest ecosystem showed that variations in the soil microbial community structure can lead to differential soil microbial functions, including soil C transformation and turnover among contrasting forest types (You et al., 2016). The number of genes involved in the degradation of various C sources is reported to differ between different microbial groups (Trivedi et al., 2013; Zhao, Liu, Wang, & Xu, 2013). Actinobacteria and Acidobacteria, which are classified as oligotrophs and thrive on moderately labile and recalcitrant forms of C (Fierer, Bradford, & Jackson, 2007; Trivedi et al., 2013), were more abundant and related to the catabolism of carboxylic acids and phenolic compounds (Figure 5). Those microbial groups have a higher potential to generate enzymes involved in C-degradation in comparison with other groups and can be used to predict enzyme activity (Trivedi et al., 2013; Trivedi et al., 2016). Analysis of genetic diversity and functional microorganisms involved in SOC utilization are important for establishing further associations between microbial composition and ecological functions during SOC mineralization (Brookes et al., 2017). Therefore, the composition of C-degradation genes can reflect the ability of microbes to utilize various C-complexes, thereby affecting the accumulation of SOC pools in different shrublands in recovering dryland environments. However, further studies are required to determine the association between soil microbial genomic information and dynamic SOC decomposition processes.

5 | CONCLUSIONS

In summary, our results demonstrate that the soil microbial communities utilized divergent decomposition strategies for different SOC pools in different shrublands. Instead of soil properties, the soil microbial taxonomic and functional composition shared significant relationships with SOC mineralization, especially for the mineralization rate of the slow soil

C pool. The microbial communities directly affected SOC decomposition, primarily by mediating degradation changes in the slow C pool in soil in different shrublands. In the *S. psammophila* shrubland, the highest mineralization rate of the slow C pool and highest relative abundance of genes for the degradation of recalcitrant C-complexes might limit the accumulation of the recalcitrant C pool. However, further studies on microbial anabolic functions are necessary to completely explain differences in SOC sequestration in revegetation shrublands. Overall, the present findings highlight the important role of the microbial functional potential in decomposing SOC and its constituents after revegetating different shrub species in a dryland, indicating that an understanding of this role may provide more comprehensive information regarding the mechanism underlying microbial SOC sequestration and may provide evidence for the selection of appropriate ecological management practices in drylands.

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CONFLICT OF INTEREST

There are no conflicts of interest to declare.

DATA ACCESSIBILITY

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

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