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SHORT REPORT

Potential complementary functions among bacteria, fungi, and archaea involved in carbon cycle during reversal of desertification

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Abstract

Development of biological soil crusts (BSCs) on bare land is a sign of reversal of desertification, and microbial communities of BSCs are the biogeochemical engineers of desert ecosystems. However, regulation of different microbial groups involved in the carbon (C) cycle is not clear. This study investigated the correlation between bacteria, fungi, and archaea of BSCs involved in the C cycle during reversal of desertification through community abundance analysis by quantitative PCR and functional gene detection using GeoChip 5.0. Among the known C cycle genes found in BSCs, 84.5% of C degradation genes, 95% of C fixation genes, and all of methane oxidation genes were derived from bacteria owing to their highest proportion among the total microbial abundance of BSCs; some recalcitrant C degradation genes were derived from fungi; and other C fixation pathway and methanogenesis genes originated from archaea. The increased abundance of bacteria and fungi and decreased abundance of archaea during reversal of desertification, as well as the difference in C cycle genes of the three microbial groups, indicated the functional complementarity among these microorganisms involved in C cycle. At the early stage of BSC development, archaea, and bacteria provide available C sources by autotrophic CO_2 fixation pathway; bacteria play important roles in C degradation, C fixation, and methane oxidation during the entire BSC development process; and fungi mainly degrade lignin at the later stage of BSC development. Thus, cooperation among BSC microflora altered C cycle during reversal of desertification.

KEYWORDS

biological soil crusts, carbon degradation, carbon fixation, methane cycle, microbial functional group

1 | INTRODUCTION

Biological soil crusts (BSCs), known as restoration engineers of desert ecosystems, generally start with large filamentous cyanobacteria that stabilize the soil, followed by smaller cyanobacteria, green algae, lichens, and bryophytes (Colesie, Felde, & Büdel, 2016; Weber, Bowker, Zhang, & Belnap, 2016). Including archaea, bacteria, and microbial fungi, some microscopic algae and the photo-/myco-bionts of lichens are BSC microorganisms as well, and they constitute BSCs jointly (Maier, Muggia, Kuske, & Grube, 2016). Filamentous and mobile cyanobacteria, such as *Microcoleus* spp., are pioneer colonizers in sandy soil and help to bind soil particles to form BSCs in bare soil

(Büdel, Dulic, Darienko, Rybalka, & Friedl, 2016; Sancho, Belnap, Colesie, Raggio, & Weber, 2016; Weber et al., 2016). Lichens are prominent members of many BSCs and their thalli are often highly resistant to environmental fluctuations and extreme temperatures. The presence of lichens provides rich diversity in small niches for microorganisms, especially, fungi and bacteria (Maier et al., 2016; Rosentreter, Eldridge, Westberg, Williams, & Grube, 2016). In the later stages of BSC development, bryophytes arise as a conspicuous component, contributing to soil surface stabilization through water entrapment and facilitation of water infiltration (Colesie et al., 2016; Zhang et al., 2009); promoting soil formation through acceleration of chemical and physical weathering of soil and entrapment of mobile surface particulates (Belnap & Lange, 2001), enhancing carbon (C) and nutrient cycling through contributions of soil organic matter and nitrogen availability (Bowker, Maestre, & Escolar, 2010; Sancho et al., 2016); and providing habitats for invertebrates, algae, cyanobacteria, fungi, and lichens (Colesie et al., 2016). Therefore, BSCs are usually classified according to the dominant photoautotrophic organisms in different stages of the development process, such as cyanobacteria-, lichen-, or bryopgyte-dominated crusts (Colesie et al., 2016). Owing to their significance in improving soil stability and increasing species diversity of desert ecosystems, BSC development is regarded as an indication of reversal of desertification (Bowker, Belnap, Davidson, & Phillips, 2005). Furthermore, the important roles of BSCs are closely related to their microbial communities (Kheirfam, 2020), and shifts in the structure and function of BSC microbial communities are often used to assess the health and function of desert ecosystem as well as response and resiliency to environmental perturbations (Steven, Belnap, & Kuske, 2018; Wang, Liu, & Zhao, 2020). Rehabilitation of BSCs following disturbance of the drylands recovery process is mainly accomplished by the soil microbial community (Bowker, 2007; Molina-Montenegro et al., 2016).

BSC microorganisms are the biogeochemical engineers of desert ecosystems, and the biological mechanism of elemental cycling is largely driven by microbially catalyzed redox reactions (Falkowski, Fenchel, & Delong, 2008). C is a major component of biological and mineral compounds, and C-based molecules (such as organic compounds, saccharides, fats, proteins, and vitamins) are crucial for all living forms. However, the complexities of BSC microbial communities and their effects impede our understanding of the microbial mechanism that regulates C cycle during the process of reversal of desertification. The explosion of microbial genome sequence data and increasingly detailed analyses of the functions of a specific soil microbiome have yielded useful insights into the role of microorganisms in C cycle (Anantharaman et al., 2016; Parks et al., 2018). For instance, Bahram et al. (2018) analyzed the structure and function of the topsoil microbiome on a global scale. In these studies, culture-independent approaches have provided deeper insights into the diversity and function of BSC microbial community in various deserts or soil types (Abed, Al-Sadi, Al-Shehi, Al-Hinai, & Robinson, 2013; Castillo-Monroy et al., 2011; Liu et al., 2018; Liu, Liu, Hui, & Xie, 2017; Soule, Anderson, Johnson, Bates, & Garcia-Pichel, 2009; Steven, Hesse, Gallegos-Graves, Belnap, & Kuske, 2015), including regulation of C and N cycles (Zhao et al., 2020). Nevertheless, a major challenge is to decipher the main microbial functional groups in BSCs that are involved in different processes of the C cycle and their interactions, and understand the mechanisms regulating their operation and contribution to desert ecosystems.

In this study, we selected BSCs of different ages to clarify the regulation mechanism of C cycle mediated by various microbial groups (bacteria, fungi, and archaea). Our objectives were to (a) identify the main functional species among bacteria, fungi, and archaea involved in C cycle, (b) quantify the functional genes in different functional groups and their contribution to C cycle, and (c) generalize the interaction mechanism among the three microbial groups in C cycle during the reversal of desertification. The findings of this study could improve our understanding of desertification management or desertification reversal indicators.

2 | MATERIALS AND METHODS

The study areas are located in Shapotou and are restored vegetation enclosures on the southeast edge of the Tengger Desert, China (Figure S1). The selected revegetation systems were established in a chronosequence in 1956, 1964, 1973, 1987, and 2000, and different types of BSCs (cyanobacteria-, lichen-, and/or moss-dominated) were formed from the vegetation (Figure S1). According to the age of BSCs (61, 53, 44, 30, and 17 years old, respectively), the samples were named as 61Y, 53Y, 44Y, 30Y, and 17Y, respectively. The five BSCs of different ages with various macroscopic compositions and soil physicochemical properties (Table S1) were collected in June 2017. Triplicate composite BSC samples were collected for each revegetation time using our previously described methods (Liu et al., 2018). The samples were quickly transported to the laboratory, sieved using sterilized steel screen (1 mm), homogenized, and stored at −80°C. The DNA was extracted from duplicated 1-g aliquots of each BSC sample using the E.Z.N.A Soil DNA Kit (Omega Bio-tek, Norcross, GA) within 1 week. The eukaryotic ITS rRNA gene, bacterial 16S rRNA gene, and archaeal 16S rRNA gene were amplified using primer sets ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2 (5′-GCTGCGTTCTTCATCGATGC-3′), 338F (5′-ACTCCTACGGGAGGCAGCA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′), and 524F10-extF (5′-TGYCAGCCGCCGCGGTAA-3′) and Arch958R-modR (5′-YCCGGCGTTGAVTCCAATT-3′), respectively. The compositional structures of bacterial, fungal, and archaeal communities were determined as described previously (Liu et al., 2017; Zhao et al., 2020) using Illumina MiSeq sequencing. After the raw FASTQ files were demultiplexed and quality-filtered using QIIME (version 1.17), operational taxonomic units (OTUs) were clustered with 97% similarity using UPARSE (version 7.1) (Liu et al., 2017). The raw reads were deposited in the NCBI Sequence Read Archive database (Accession No. SRP091312 for bacteria and fungi, Accession No. SRP118745 for Archaea). Quantitative real-time PCR (qPCR) was used to quantify the bacterial, fungal, and

archaeal abundance, and their gene copy numbers were employed to calculate their relative percentages in microbial communities. GeoChip 5.0 was selected to identify the key functional genes and main microbial species involved in C cycle, and the ratio of the average signal intensity of each gene category to the total genes involved in C cycle in bacteria, fungi, and archaea was used to express their relative percentage contributions. The study sites, sampling methods, soil treatment, DNA extraction, qPCR, and GeoChip analysis are described in detail in the Supplementary methods.

3 | RESULTS AND DISCUSSION

During the development of BSCs, the total microbial abundance significantly increased with the increase in the abundance of bacteria and fungi, whereas the abundance of archaea gradually decreased (Liu et al., 2018; Table S2). In particular, bacteria accounted for the highest percentage along the chronosequence, while fungi only formed a certain proportion in the later stages of BSC development (53Y-61Y) (Figure 1), possibly owing to the changes of macroscopic compositions of BSCs and the improved soil physicochemical properties following stabilization of dunes (Table S1). Bacteria are the core components of BSC microbial community, while fungi can produce a wide range of enzymes that can degrade recalcitrant substrates (such as chitin, cellulose, and lignin) that cannot be degraded by other microorganisms (Warren et al., 2019). Hence, accumulation of BSC macroscopic compositions and soil organic matter content at the later stage of BSC development can increase fungal abundance. Besides, during the early stage of BSC development, microorganisms may utilize more energy to survive (Fiere et al., 2012), and the adaptability of different microorganisms to the soil environment is different. For instance, archaea can live in extremely harsh environments with low nutrients content (Konings, Albers, Koning, & Driessen, 2002), such as during the early stage of BSC development, whereas increased nutrients content is more beneficial to bacteria and fungi, especially for some fungal groups in arid land (Allen, 2007; Jin, Schaeffer, Ziegler, & Evans, 2015). Moreover, competition between microorganisms may occur owing to limited internal resources at later stage of BSC development (Feng et al., 2017), and archaea may be at disadvantage in competition with bacteria or fungi (Bates et al., 2011).

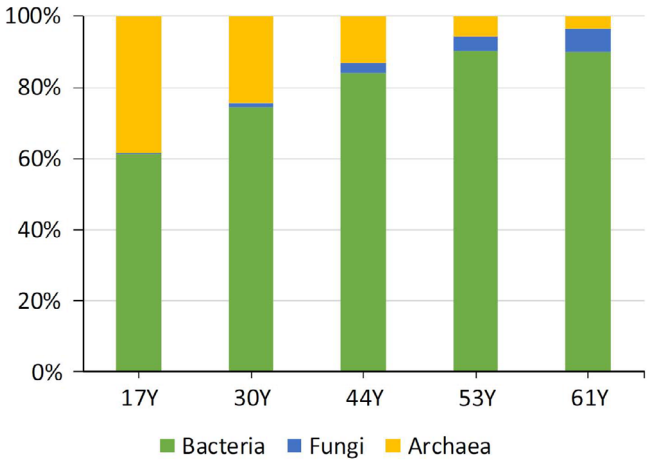

FIGURE 1 The relative percentages of bacterial, fungal, and archaeal abundance during BSC development. 17Y, 30Y, 44Y, 53Y, and 61Y represent 17-, 30-, 44-, 53-, and 61-year-old BSCs sampled from sand-fixing revegetation of 2000, 1987, 1973, 1964, and 1956, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

Comparison of the dominant community compositions and functional groups of C cycle at the phylum level showed that all the C cycle functional groups were dominant species in the composition structure during BSC development, including Actinobacteria and Proteobacteria (bacteria) (Figure S2A), Ascomycota and Basidiomycota (fungi) (Figure S2B), and Thaumarchaeota and Euryarchaeota (archaea) (Figure S2C). This finding indicated that C cycle is the main function of BSC microbiota (Liu et al., 2018), and that all the dominant species participate in C cycle. However, bacterial and archaeal functional species with highest relative abundance were not the most dominant phyla in their respective groups. For example, Actinobacteria presented the highest relative abundance in the bacterial group, whereas Proteobacteria, an extremely diverse phylum with a wide range of functions (Campbell, Engel, Porter, & Takai, 2006), was the most dominant C cycle functional group. In addition, the proportion of functional components at the phylum level was relatively constant during BSC development, while the relative percentages of the dominant microbial phyla significantly changed (Figure S2), indicating that the functional groups of the selected BSC samples were mostly stable at different development stages.

With regard to the total C cycle genes, 84.5 and 13.6% of the C degradation genes originated from bacteria and fungi, respectively (Figure 2a). The bacterial genes were mainly involved in degrading starch, hemicellulose, chitin, and aromatics, whereas fungal genes were involved in pectin, cellulose, and lignin degradation. It has been reported that prokaryotes can rapidly degrade simple substrates, whereas fungi are the main decomposers of recalcitrant organic matters through long-term degradation process (Boer, Folman, Summerbell, & Boddy, 2005; Schneider, Keiblinger, Schmid, Sterflinger-Gleixner, & Riedel, 2012). The main C fixation pathways were all derived from bacteria, with Calvin cycle detected in most of the bacterial phyla, while decarboxylate/4-hydroxybutyrate cycle originated from archaea (Figure 2b). Thus, genes involved in C degradation and C fixation in BSCs were mainly derived from bacteria on the whole, owing to their highest abundance in the BSCs. The methanogenesis genes were derived from archaea, whereas CH_4 oxidation genes were only observed in bacteria (Figure 2c). These results suggest that the functional genes from bacteria, fungi, and archaea are perfectly complementary in the C cycle process.

Among the C cycle genes, the total abundance of C degradation genes was the highest, when compared with that of C fixation and CH_4 cycle genes (Figure 3). The dominant key gene involved in degrading labile C (such as starch) was amyA, which was mainly derived from Actinobacteria, whereas the proportion of genes involved in degrading recalcitrant C (such as chitin and aromatics) was

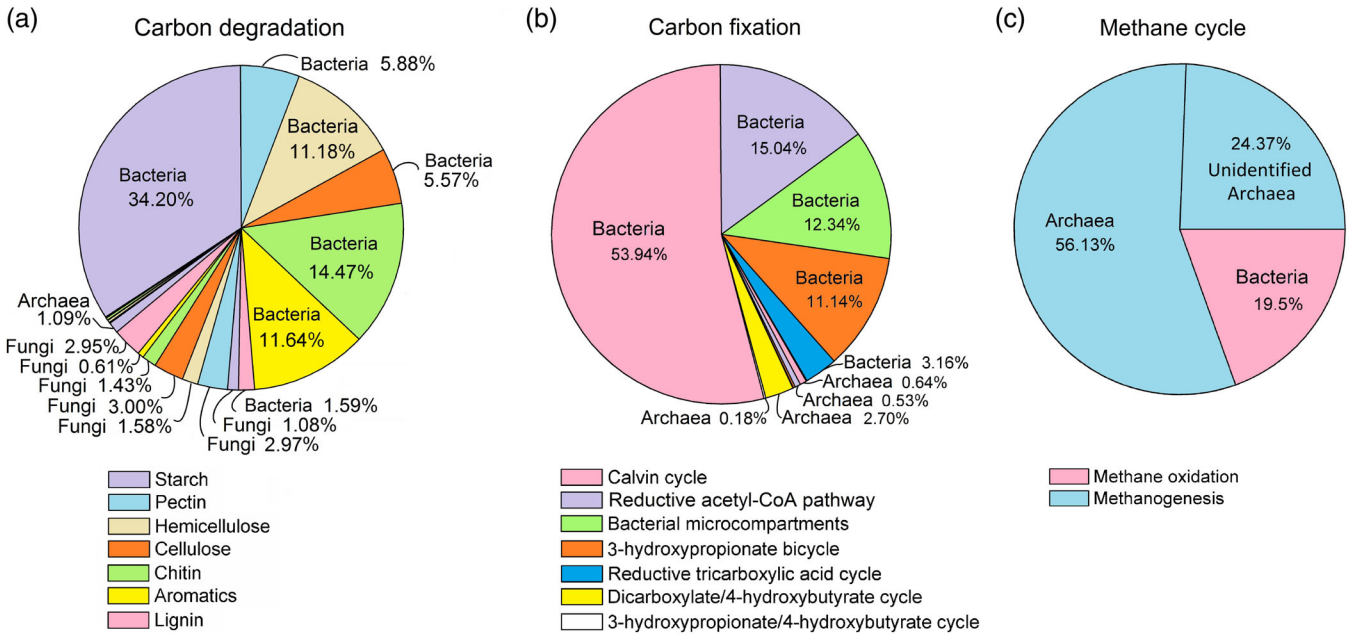

FIGURE 2 Relative contribution of functional genes of bacteria, fungi, and archaea to different processes of C cycle (a, C degradation; b, C fixation; c, CH_4 cycle) in BSCs. Owing to the similar relative percentages of the contribution of bacteria, fungi, and archaea to different C cycle processes during BSC development, only data of 61-year-old BSCs are presented as a special case [Colour figure can be viewed at wileyonlinelibrary.com]

higher than those of labile C degrading genes in Proteobacteria (Figure 3a). Furthermore, the abundance of recalcitrant C degrading genes (such as those encoding cellobiase, endoglucanase, chitinase, and phenol oxidase) was higher than that of labile C degrading genes in Ascomycota. Thus, combined with the observation of higher abundance of C degrading genes in 61-year-old BSCs, it can be concluded that Actinobacteria and Proteobacteria were primarily involved in C degradation, and that Ascomycota might be important for improving soil available C through decomposition of recalcitrant C substrates at the later stage of BSC development.

With regard to the C fixation pathways of BSCs, Calvin cycle, reductive acetyl-CoA pathway, and 3-hydroxypropionate bicycle were the main pathways (Figures 2b and 3b) during BSC development. The major common microbial functional groups involved in these pathways were Proteobacteria, Cyanobacteria, Firmicutes, and Actinobacteria. These three main pathways by which autotrophic organisms fix C (Thauer, 2007), along with another autotrophic CO_2 fixation pathway used by some of the earliest organisms on Earth—the dicarboxylate/4-hydroxybutyrate cycle (Berg, Kockelkorn, Buckel, & Fuchs, 2007) in archaea—accomplished by Thaumarchaeota in BSCs, provide available C sources for BSC system. Moreover, a high relative abundance (12.34%) of bacterial microcompartments (such as protein ccml, CsoS1, CsoS2, and CsoSCA), a unique C fixation organelle known as the carboxysome, which compartmentalizes the enzymes RuBisCO (ribulose-1,5-bisphosphate carboxylase/oxygenase) and carbonic anhydrase (Sutter, Wilson, Deutsch, & Kerfeld, 2013), was observed. These carboxysomes can effectively increase the local CO_2 concentration at the active site of RuBisCO and decrease its relatively unproductive side reaction with oxygen (Kerfeld, Heinhorst, & Cannon, 2010), thus also playing an important role in C fixation of BSCs. The genes *tktA*, *pcc*, and *fthfs*, encoding *Rhodobacter capsulatus* transketolase, propionyl-CoA carboxylase, and formyltetrahydrofolate synthetase, respectively, were the key C fixation genes in the microbial community and their potential roles increased in the later stage of BSC development (Figure 3b).

With regard to the CH_4 cycle genes, all of methanogenesis genes were derived from Euryarchaeota. The *mcrA* gene encoding methyl-CoM reductase presented the highest abundance in BSCs (Figure 3c), showing higher activity under anoxic than oxic/oxygenic conditions (Angel, Matthies, & Conrad, 2011). In contrast, majority of the CH_4 oxidation genes (*mmoX* and *pmoA*) were derived from Proteobacteria, with some CH_4 oxidation genes also derived from unclassified bacteria, indicating that many unidentified species of Proteobacteria are present in BSCs. The total abundance of the key genes involved in CH_4 production (*hdrB*, *mcrA*, and others) as well as *pmoA* and *mmoX* involved in CH_4 oxidization was the lowest, when compared with that of C degradation and fixation genes, resulting in low net CH_4 efflux in the desert ecosystems. Methanogenesis performed by anaerobic archaea represents the largest biogenic source of CH_4 on Earth (Angel et al., 2011), and desert soils covered by BSCs are more active than their bare counterparts (Aschenbach et al., 2013). A previous study reported that methane uptake was only detected in undisturbed soils in arid areas (>90 mm yr^{-1}), but not in hyperarid soils (<20 mm yr^{-1}) (Angel & Conrad, 2009), suggesting that the contribution of desert ecosystems to global CH_4 amount is less.

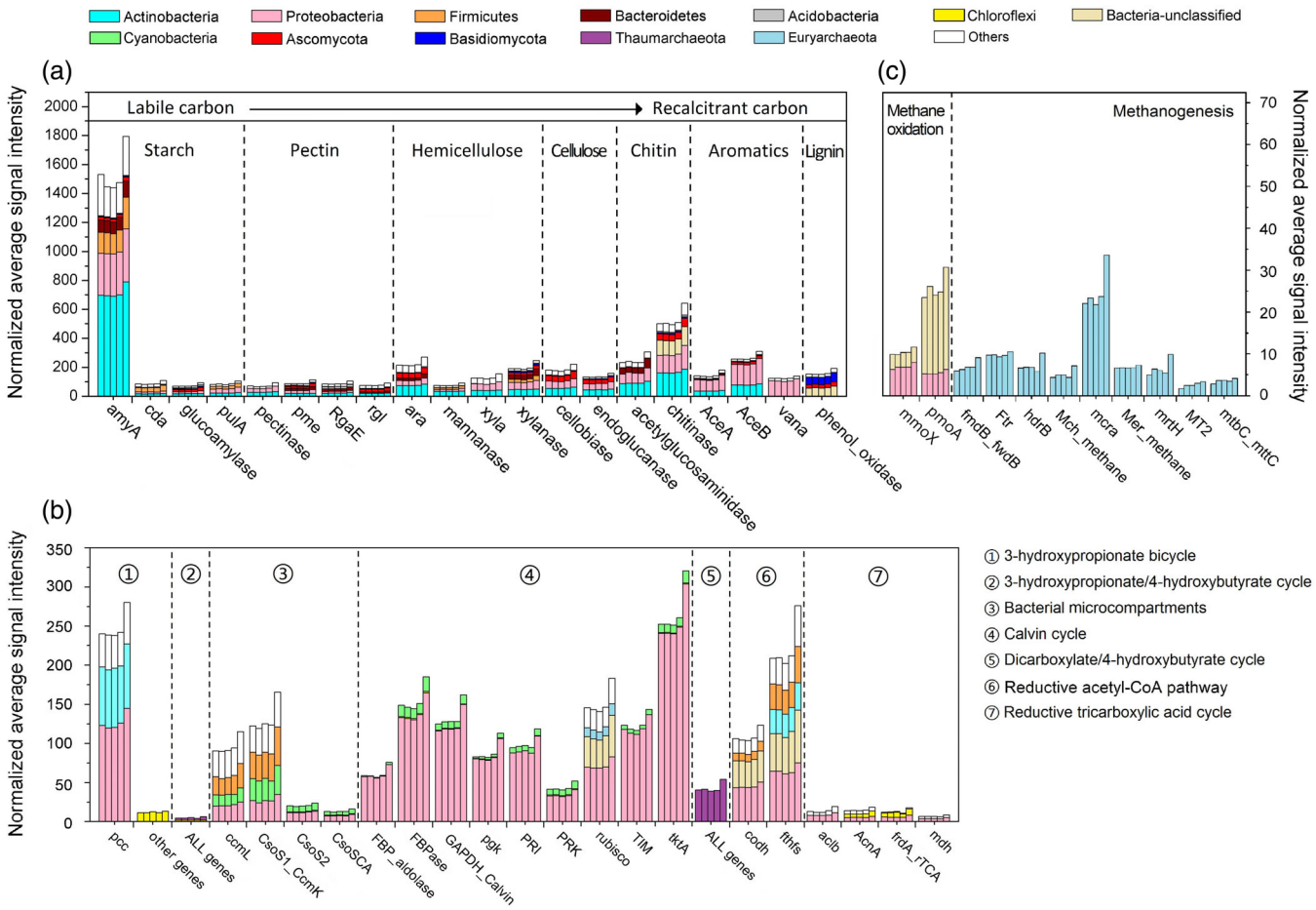

FIGURE 3 Changes in the key functional genes of the main functional phyla involved in (a) C degradation, (b) C fixation, and (c) CH_4 cycle during BSC development. From left to right, five columns represent 17-, 30-, 44-, 53-, and 61-year-old BSCs, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

4 | CONCLUSION

In conclusion, our findings unveiled the key functional genes and main functional groups involved in the C cycle among bacteria, fungi, and archaea in BSCs. Although these three groups competed for common resources, they were complementary in function, suggesting an important 'synergistic relationship' among different microorganisms. During the early stage of BSC development, archaea and bacteria provide available C sources by autotrophic CO_2 fixation pathway; bacteria play important roles in C degradation, C fixation, and methane oxidation during the entire BSC development process; and fungi mainly degrade lignin at the later stage of BSC development. The cooperation among the three microbial groups altered the C cycle during reversal of desertification. The investigation of microbial functional genes involved in the C cycle of BSCs, which has not been explicitly considered in C metabolism models, revealed that a higher abundance of fungi and bacteria is a desertification reversal indicator. With continuing research on microbial communities and their functions of BSCs using a combination of culture-independent methods (various microbiomics technologies) and culture-based approaches, addressing questions, such as desertification management and reversal of desertification, could clarify the significance of these microbial communities for healthy and sustainable function of desert ecosystems.

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DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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