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Contribution of soil microbial necromass to SOC stocks during vegetation recovery in a subtropical karst ecosystem

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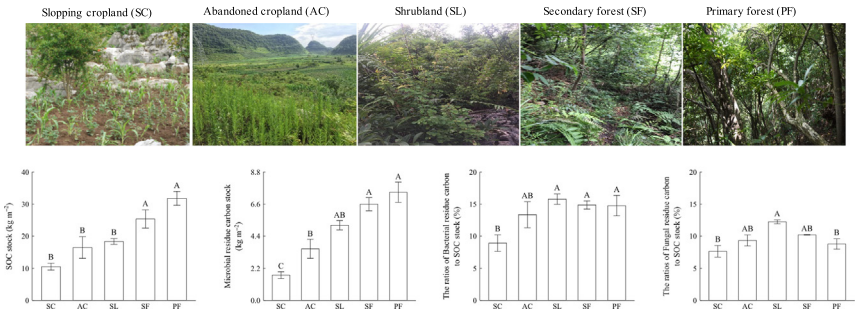
HIGHLIGHTS

- Fungal and bacterial residue carbon increased with vegetation recovery in karst landscape.
- Bacterial residue carbon contributes more to SOC stocks than fungal residue carbon.
- Gram positive bacteria PLFA has the largest abundance in microbial community composition.
- Gram positive bacteria increased in relative abundance with depth to the bedrock at all stages.

GRAPHICAL ABSTRACT



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ABSTRACT

Carbon sequestration is a key soil function, and an increase in soil organic carbon (SOC) is an indicator of ecosystem recovery because it underpins other ecosystem services by acting as a substrate for the soil microbial community. The soil microbial community constitutes the active pool of SOC, and its necromass (microbial residue carbon, MRC) contributes strongly to the stable SOC pool. Therefore, we propose that the potential for restoration of degraded karst ecosystems lies in the abundance of soil microbial community and the persistence of its necromass, and may be measured by changes in its contribution to the active and stable SOC pools during recovery. We investigated changes in SOC stocks using an established space-for-time chronosequence along a perturbation gradient in the subtropical karst ecosystem: sloping cropland < abandoned cropland < shrubland < secondary forest < primary forest. Microbial biomarkers were extracted from soil profiles from surface to bedrock and used to measure the contributions of the soil microbial community composition (using phospholipid fatty acids, PLFAs) and MRC (using amino sugars) to SOC stocks at each recovery stage. The results showed that the SOC stocks ranged from 10.53 to 31.77 kg m^{-2} and increased with recovery stage, with total MRC accounting for 17–28% of SOC. Increasing PLFAs and MRC abundances were positively correlated with improved soil structure (decreased bulk density) and organic carbon, nitrogen and phosphorus nutrient. Bacterial MRC contributes more to SOC stocks than fungal residue carbon during vegetation recovery. The PLFA analysis indicated that Gram positive bacteria were the largest microbial group and were relatively more abundant in deeper soils, and biomarkers for saprophytic and ectomycorrhizal fungi were more abundant in soils under woody vegetation. In conclusion, this study suggests that the soil microbial community in karst soils have the potential to adapt to changing soil conditions and contribute substantially to building SOC stocks after abandonment of agriculture in degraded karst landscapes.

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1. Introduction

Soil organic carbon (SOC) stocks have been observed to accumulate under ecosystem recovery, allowing regenerating ecosystems to act as net sinks for atmospheric carbon dioxide (CO_2) (Li et al., 2012; Liu et al., 2015; Tong et al., 2018). Whereas accumulating SOC has improved soil structure and fertility, recycling nutrients and retaining soil moisture and air content, thereby acting to promote further vegetation recovery (Tang et al., 2016). Microbial residue carbon (MRC), i.e. 'necromass', constitutes a persistent SOC pool (Liang et al., 2017; Zhu et al., 2020), so determining its contribution to SOC stocks may provide a useful indicator of carbon sequestration as a key ecosystem function. The abandonment of agriculture and vegetation was allowed to recover naturally in the degraded karst landscapes of subtropical region, providing a unique opportunity to investigate the contribution of the soil microbial necromass to rebuilding SOC stocks during karst ecosystem recovery.

The active soil microbial biomass constitutes a small (usually <5%) fraction of SOC stocks (Liang and Balser, 2011; Miltner et al., 2012; Liang et al., 2017). The accumulation and stabilization of microbial necromass is encouraged by its potential for physical and chemical protection via soil aggregation and mineral association in the stable SOC pool (Liang et al., 2017). Recently, the importance of MRC as a large microbially-derived SOC pool has emerged based on modeling and calculation of existing data and novel studies that report amino sugars (an important component from cell walls) as the indicative of bacterial and fungal MRC (Liang et al., 2019). For example, Shao et al. (2017) reported a strong relationship between MRC and the formation and subsequent sequestration of SOC during tropical forest restoration in China. In addition, Sun et al. (2016) estimated that MRC constituted 58% SOC in a ploughed cropland, and Khan et al. (2016) quantified that 50% SOC in arable and grassland soils and 30% SOC in saline arable and forest soils was derived from the microbial necromass. However, different microbial groups may play specific roles in SOC stocks under different environmental conditions. For example, fungi dominate in forests soils (Bahram et al., 2018) and may contribute more to SOC accumulation than bacteria (Kallenbach et al., 2016).

Microbial biomarkers are widely applied to quantify changes in different SOC pools (Kögel-Knabner, 2000). Changes in the soil microbial community can be measured directly by quantifying variations in the concentrations of specific compounds of known provenance (Boschker and Middelburg, 2002). Amino sugars and muramic acid are important constitutes of microbial cell walls and are widely used as microbial biomarkers to differentiate bacterial and fungal necromass in soils (Glaser et al., 2017; Liang et al., 2019). Muramic acid (MurN) exclusively originates from bacterial peptidoglycan, while glucosamine (GluN) occurs in fungal chitin and also in bacterial peptidoglycan bonded to MurN at a molar ratio of 2:1, while the origins of galactosamine (GalN) are non-specific. Phospholipid fatty acid (PLFA) biomarkers usually indicate broad groups of viable soil microorganisms including bacteria and fungi (Zhang et al., 2013; Maestre et al., 2015). The relative persistence of amino sugars in soil compared to PLFA biomarkers enables them to be used as time-integrating microbial biomarkers to quantify contributions of bacterial and fungal cell walls to soil organic matter (Liang and Balser, 2011; Liang et al., 2017; Ma et al., 2018). Ratios of fungal GluN and MurN are used to differentiate fungal versus bacterial MRC (Appuhn and Joergensen, 2006; Engelking et al., 2007). Fungal MRC is considered to be more chemically resistant to decomposition than bacterial MRC (Kallenbach et al., 2016; Shao et al., 2017), while bacterial MRC may be more likely to be physically protected from decomposition through interactions with soil microaggregates and clay minerals (Pronk et al., 2015). Recent studies using this approach reported that converting arable cropland to grassland increased MRC (Ding et al., 2017), mineral fertilization increased MRC (Ma et al., 2017; Zhang et al., 2018), and broad-leaved trees increased the contribution of MRC to SOC during subtropical forest restoration (Shao et al., 2017). Li et al. (2015) used a combination of amino sugars and PLFAs to determine that fungal necromass dominated microbial contribution to soil organic matter in a young mollisol under contrasting arable management in northeast China. Microbial biomarker approaches are, therefore, considered apt for assessing the changes in the function of the soil microbial community in regenerating karst landscapes.

The overall objective of this study was to qualify the contribution of the MRC to SOC stock during vegetation recovery. We hypothesized that MRC stock would increase with vegetation recovery making an increasing contribution to changes in SOC stock and we predicted that the ratio of fungal-to-bacterial MRC and PLFAs would increase with vegetation succession to woody types; and the contribution of MRC from different functional groups of fungi and bacteria changes with the different environmental conditions in soil profile at different stages of vegetation recovery. For example, Gram positive bacteria would be relatively more abundant in deeper soils, inputting more bacterial residue carbon to subsoil SOC stocks. A new Critical Zone Observatory was established in 2011 in a degraded karst catchment in southwest China to investigate the resilience and recovery of karst ecosystems subject to intense anthropogenic perturbation after abandonment of agriculture (Quine et al., 2017; Green et al., 2019). A space-for-time chronosequence was established along a perturbation gradient: sloping cropland < abandoned cropland < shrubland < secondary forest, and compared with nearby primary forest, to qualify the contribution of the MRC to SOC stock during vegetation recovery.

2. Material and methods

2.1. Study sites

The study sites were part of the Puding Karst Critical Zone Observatory (CZO) in Guizhou Province, southwest China, which is described in detail in Green et al. (2019) and the characteristics of the study sites are described in detail in Guo et al. (2019). In brief, the region is subject to a subtropical monsoon climate with annual mean precipitation of 1315 mm, and an annual mean temperature of ~15.1 °C (Liu et al., 2016). The soils are Mollic Inceptisols that originated from limestone bedrock of the Middle Triassic Guanling Formation (Lu et al., 2014). The natural climax vegetation community of the Chenqi catchment (26°15′37″–26°15′37″ N, 105°46′11″–105°46′29″E, 1100–1600 m a.s.l., area 1.29 km^2) is primary forest, i.e. mixed evergreen and broadleaved deciduous forest; but there is no natural vegetation remaining. Therefore, the primary forest 'end member' in the chronosequence is situated at Tianlong Mountain (26°14′44″–26°14′48″N, 105°14′40″–105°45′48″E, 1421–1503 m a.s.l.) and has no history of farming. Progressive phases of the abandonment of sloping cropland within the Chenqi catchment since the 1990s provide the different recovery stages of the chronosequence. The sloping cropland (SC) has been farmed since the 1960s and is intensively cultivated for staple crops such as *Zea mays*, *Glycine max* and *Brassica napus*. Farming was halted on the recently abandoned sloping cropland (AC) less than 3 years ago and is characterized by a low growing herbaceous plant community, e.g. *Conyza canadensis*, *Imperata cylindrica* and *Artemisia dubia*. The shrubland (SL), dominated by *Rubus parviflorus*, *Rubus sinopertus* and *Litsea rubescens*, is the next stage in plant succession and arises after about 5 years. Secondary forest, including species such as *Rhus chinensis*, *Populus adenopoda* and *Toona sinensis*, is fully established after 10 years (Fig. S1).

2.2. Soil sampling

In July 2016, twenty 10 × 20 m plots with 4 replicates were established on sloping cropland, abandoned cropland, shrubland and secondary forest in the Chenqi catchment, and in the primary forest on Tianlong Mountain. A soil auger with a diameter of 2 cm was used to collect soil samples from 0–10 cm, 10–30 cm, 30–50 cm, and 50 cm to bedrock. To account for spatial heterogeneity, soil profiles were sampled from four plots at least 30 m apart along one altitudinal transect,

and 10 soil cores were randomly collected within each plot and composited into a single soil sample. Each composite sample was sieved through a 2-mm mesh and stored at 4 °C prior to analysis.

Soil bulk density (D_b) was assessed using the core method: a 100 cm^3 volumetric cylinder and a solid ring were hammered into the face of each soil pit at each depth increment (Blake and Hartge, 1986). Samples were oven-dried at 105 °C for 2–3 days to constant weight before the mass of the dry soil sample was measured. Soil D_b was estimated as the oven-dried soil mass divided by the field volume of the sample.

2.3. Soil analyses

Soil chemical properties were analyzed using the methods described by Bao (2007). In brief, soil pH was measured in a 1:2.5 v:v soil-water suspension by glass electrode. Subsamples were air dried, homogenized and ground to 0.15-mm for SOC, total nitrogen (TN) and total phosphorus (TP) determination. SOC was determined by dichromate oxidation and titration with ferrous ammonium sulfate. Total N was determined by dry combustion method using an elemental analyzer (Elementar, Vario Max CN, Germany). Total P was measured spectrophotometrically with a continuous flow auto-analyzer (Bran Luebbe, AA3, Germany) after digestion with H_2SO_4-$HClO_4$.

Amino sugars (MurN, GluN and GalN) were determined according to the method described by Indorf et al. (2011). In brief, total amino sugars were extracted and derivatized using O-phthaldialdehyde (OPA), and the derivatives were separated by a high performance liquid chromatograph (Dionex Ultimate3000, Thermo Fisher Scientific, USA) equipped with an octadecylsilylated silica (ODS) gel column (Acclaim120 C18; 4.6 mm × 150 mm, 3 μm; Thermo Fisher Scientific, USA), and detected using a fluorescence detector with an excitation wavelength of 330 nm and an emission wavelength of 445 nm. The amino sugars were identified and quantified with reference to chromatograms of standard solutions containing mixed amino sugars.

Phospholipid fatty acids (PLFAs) were quantified according to Bossio and Scow (1998). In brief, after mild alkaline methanolysis to form fatty acid methyl esters (FAMEs), samples were dissolved in hexane and analyzed by gas chromatography (Agilent 7890 B) with MIDI peak identification software (Version 4.5; MIDI Inc., Newark, DE). The PLFA used as biomarkers for total bacteria (i14:0, i15:0, a15:0, i16:0, i17:0, a17:0, 16:1ω7, 16:1ω9c, 17:1ω8c, cy 17:0, cy 19:0), Gram positive bacteria (i14:0, i15:0, a15:0, i16:0, i17:0, a17:0), Gram negative bacteria (16:1ω7c, 16:1ω9c, 17:1ω8c, cy 17:0, cy 19:0), Actinobacteria (10 Me16:0, 10 Me17:0, 10 Me18:0), total fungi (16:1ω5c, 18:3ω6c, 18:1ω9c and 18:2ω6,9c), saprophytic and ectomycorrhizal fungi (18:2ω6,9c) were identified according to Joergensen and Wichern (2008) and Willers et al. (2015). The PLFA 16:1ω5c was used to indicate arbuscular mycorrhizal fungi, but some caution is needed in this interpretation since this biomarker can also occur in Gram negative bacteria (Willers et al., 2015). When comparing the ratios of F:B with other studies, we recalculated these ratios according to their classification of the reference we cited.

2.4. Calculation of MRC content and stocks in soil

Fungal MRC content in soil (g kg^{-1}) on dry weight basis was calculated by subtracting bacterial GluN from total GluN, assuming that MurN and GluN are present at a ratio of 1:2 in bacterial cells, using Eq. (1) according to Appuhn et al. (2006), Appuhn and Joergensen (2006) and Engelking et al. (2007):

$$\text{Fungal MRC}\left(\text{g kg}^{-1}\right) = \left(\text{total GluN}\left(\text{g kg}^{-1}\right)/179.2\text{–}2 \times \text{MurN}\left(\text{g kg}^{-1}\right)/251.2\right) \times 179.2 \times 9 \quad (1)$$

where, the molecular weight of GluN is 179.2 g mol^{-1}, the molecular weight of MurN is 251.2 g mol^{-1}, and a value of 9 is used to convert fungal GluN to fungal MRC. Bacterial MRC content in soil (g kg^{-1}) on dry weight basis was calculated by multiplying the content of MurN (g kg^{-1}) by 45, according to Appuhn et al. (2006). Total MRC was calculated as the sum of fungal MRC and bacterial MRC.

SOC stocks (kg m^{-2}) were calculated using Eq. (2):

$$\sum_{i=1}^{4} SOC_i\left(\text{g kg}^{-1}\right)/1000 \times Db_i\left(\text{g cm}^{-3}\right) \times \text{soil depth(cm)} \times 10 \quad (2)$$

Soil inventories (kg m^{-2}) were calculated by substituting 1000 for SOC content in Eq. (2). Microbial residue carbon and nutrient (TN and TP) stocks were calculated by substituting MRC, TN and TP contents (g kg^{-1}) for SOC content in Eq. (2) respectively.

2.5. Statistical analyses

All statistical tests were performed using SPSS 21 software (IBM SPSS Statistics, USA). General linear mixed model with site as a fixed factor was used to test the potential effects of spatial heterogeneity (Table S2). One-way ANOVA and Tukey test for Post-Hoc comparisons were used to determine the differences of D_b, soil inventories, SOC and MRC stocks between vegetation types. The fits of second-order polynomial regression were conducted to assess the relationships between the soil microbial community composition and microbial residue carbon contents. The relationships between the soil microbial community composition, microbial residue carbon contents and the soil properties were assessed using Pearson correlations in SPSS. The figures were plotted in OriginPro 2017 (Originlab Corporation, USA).

3. Results

3.1. Soil properties

The soil stocks, i.e. total volume based on depth to bedrock and bulk density measurements, were significantly greater in the primary forest (89 ± 8.2 cm depth) compared to any of the managed vegetation types (range 49–69 cm depth) (Fig. S2; $p > 0.05$). Bulk density was increased in the abandoned cropland (1.19 g cm^{-3}) but decreased in the primary forest (0.89 g cm^{-3}) compared to the sloping cropland in the 0–10 cm soil depth, and increased with soil depth in the shrubland and secondary forest (Fig. S2). Soil pH values were similar between vegetation types and soil profile depths (Fig. S3b, $p > 0.05$). The SOC:TP ratios were increased in the shrublands and secondary forests compared to the other land use types throughout the soil profiles (Fig. S3f, $p < 0.05$).

The SOC stocks ranged from 10.53 to 31.77 kg m^{-2} and were 141–202% greater in the secondary (25.35 ± 2.84 kg m^{-2}) and primary forests (31.77 ± 3.94 kg m^{-2}) than the other vegetation types (Fig. 1a, $p < 0.05$). The TN stocks were larger in the primary forests (3.95 kg m^{-2}) than the other vegetation types (1.18–2.26 kg m^{-2}) ($p < 0.05$; Fig. 1b). The TP stocks were smaller in the shrublands and the secondary forests (0.12– 0.19 kg m^{-2}) than the primary forests (0.68 kg m^{-2}) ($p < 0.05$; Fig. 1c).

3.2. Soil microbial residue carbon stocks

The contents of MurN (bacterial MRC), GluN (fungal and bacterial MRC), GalN (non-specific MRC) and total amino sugars (MurN + GluN + GalN) were significantly affected by vegetation recovery stage ($p < 0.001$) and soil depth ($p < 0.001$) (Fig. S4). Total, fungal and bacterial MRC stocks increased substantially (181–397%) in the shrublands, secondary and primary forests compared with the sloping croplands (Fig. 2a, c and e, $p < 0.05$). The percentage contributions of total MRC to SOC stocks varied from 17 to 28% and were largest in the shrubland compared with the sloping cropland (Fig. 2b, d and f, $p < 0.05$).

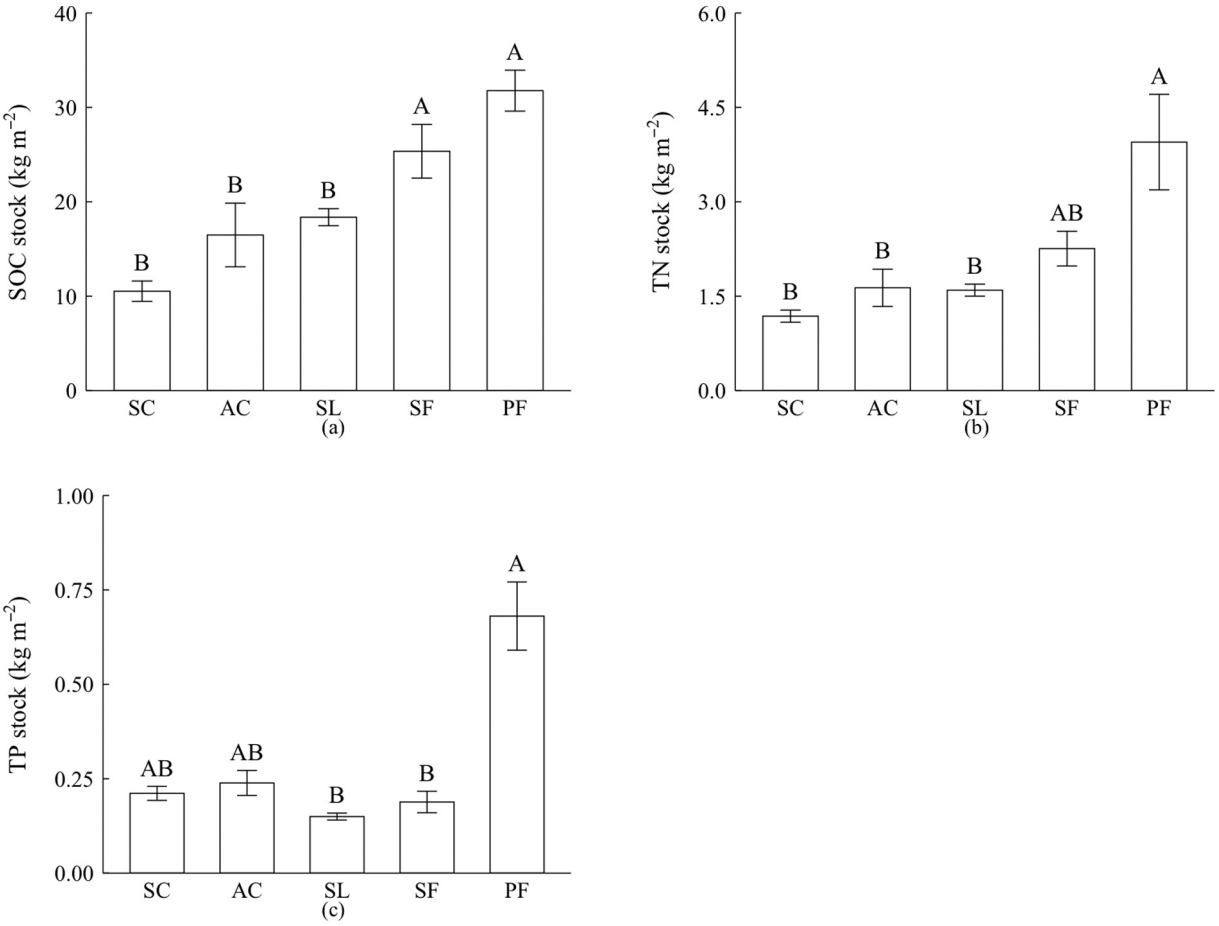


Fig. 1. Mean stocks (kg m^{-2}) for (a) soil organic carbon (SOC), (b) total nitrogen (TN), and (c) total phosphorus (TP) in the different vegetation recovery stages at the Chinese Karst CZO. SC, sloping cropland; AC, abandoned cropland; SL, shrubland; SF, secondary forest; PF, primary forest. Uppercase letters denote significant differences between the vegetation types. Error bars are ±1 s.e.

3.3. Soil microbial community composition

The effects of vegetation recovery stage ($p < 0.001$), soil depth ($p < 0.001$) and their interaction ($p < 0.01$) on the abundances of PLFA biomarkers were significant for all of the different groups of the soil microbial community indicated (Fig. S5). The contents of PLFA biomarkers declined with soil depth. The contents of biomarkers for total microbial, Gram positive bacteria (Fig. S5a), Gram negative bacteria (Fig. S5b), Actinobacteria (Fig. S5c), arbuscular mycorrhizal fungi (Fig. S5e) and saprophytic and ectomycorrhizal fungi (Fig. S5f) were larger from 0 to 50 cm depths in the shrublands, secondary and primary forests compared to the sloping and abandoned croplands. The ratios of biomarkers for fungi-to-bacteria ranged from 0.29 at 0–10 cm depth to 0.21 at >50 cm depth and decreased with soil depth in all vegetation types, and were larger in the abandoned croplands (0.29) and shrublands (0.28) than the other vegetation types. The ratios of Gram positive bacteria to Gram negative bacteria increased with soil depth from 1.21 to 2.45.

3.4. Relationships between soil microbial community composition, microbial residue carbon and soil properties

Both soil microbial community composition (fungal PLFAs, i.e. including arbuscular and saprophytic and ectomycorrhizal fungi; and, bacterial PLFAs, i.e. Gram positive and negative bacteria; total microbial PLFAs) and MRC contents (fungal, bacterial and total MRC contents) were positively related with soil nutrients (i.e. SOC, TN and TP) and nutrient ratios (i.e. SOC:TN, TN:TP and SOC:TP), and negatively related to pH and soil bulk density (Table S1, $p < 0.05$). The ratios of fungal-to-bacterial were positively related with SOC and TN. The ratios of Gram positive bacteria to Gram negative bacteria were negatively related with SOC, TN, SOC:TN, TN:TP and SOC:TP (Table S1, $p < 0.05$).

There were strong correlations between the contents of fungal MRC (GluN) and the contents of biomarker PLFA for total fungi and all fungal groups; contents of PLFA biomarkers for saprophytic and ectomycorrhizal fungi were more strongly correlated ($R^2 = 0.79$) than for other fungal groups (Fig. 3, $R^2 = 0.70$– 0.77). There were strong correlations between the contents of bacterial MRC (MurN) and the biomarker PLFA for total bacterial and all bacterial groups; PLFA biomarkers for Gram positive bacteria were more strongly correlated with bacterial MRC ($R^2 = 0.69$) than for other bacterial groups (Fig. 3, $R^2 = 0.55$– 0.57).

4. Discussion

4.1. The contributions of microbial residue carbon to soil organic carbon stocks during vegetation recovery

As previously observed (e.g. Deng et al., 2014; Liu et al., 2015), the SOC stocks in the Chinese Karst CZO increased with natural vegetation recovery after cropland abandonment because organic inputs (litter and roots) from permanent vegetation and larger NPP increased over time (Liu et al., 2015; Tong et al., 2017, 2018). The effect of SOC loss during cultivation was measurable in all vegetation recovery stages,

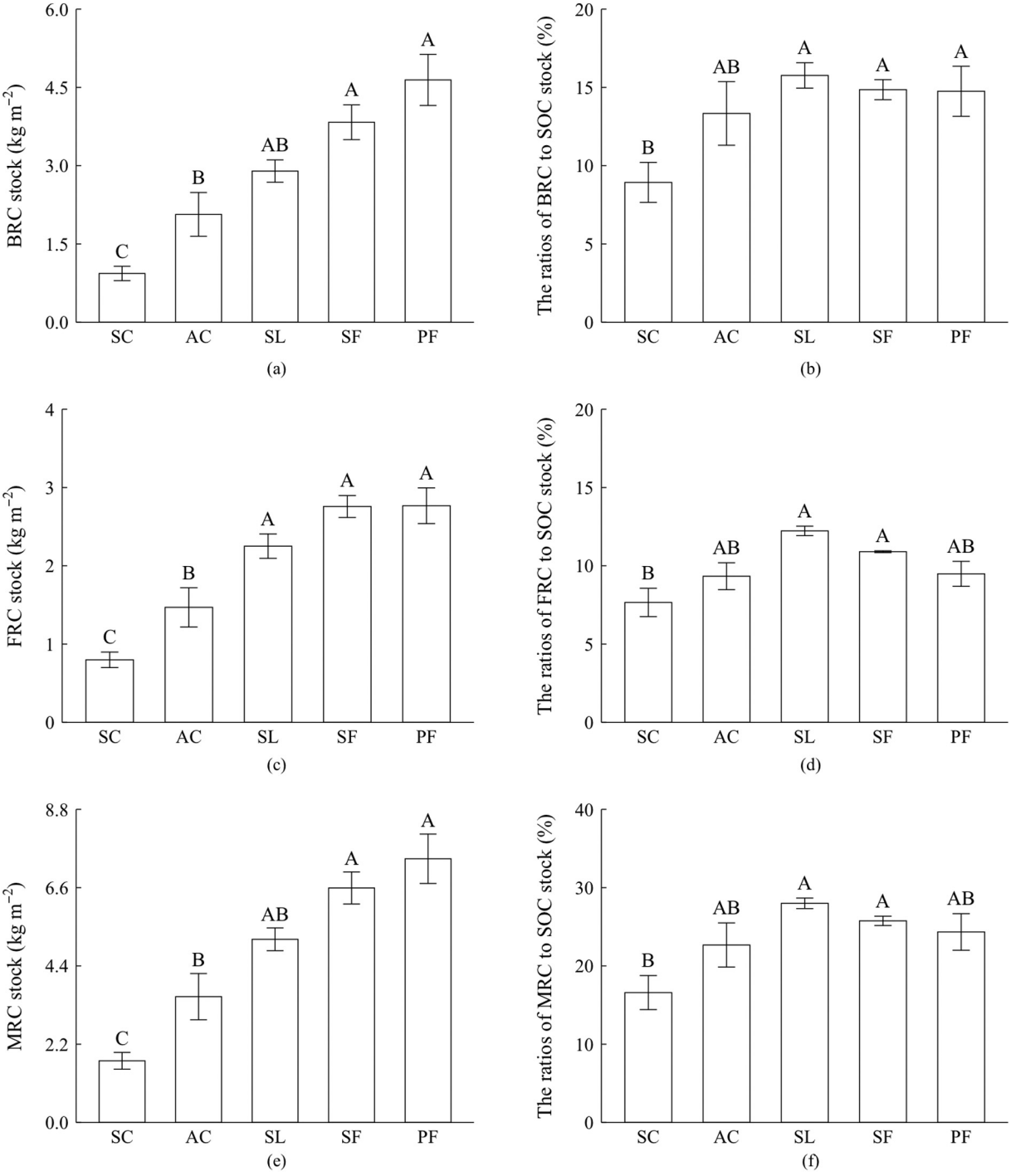
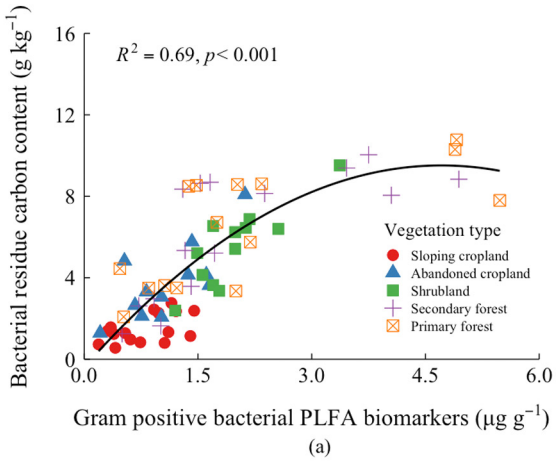


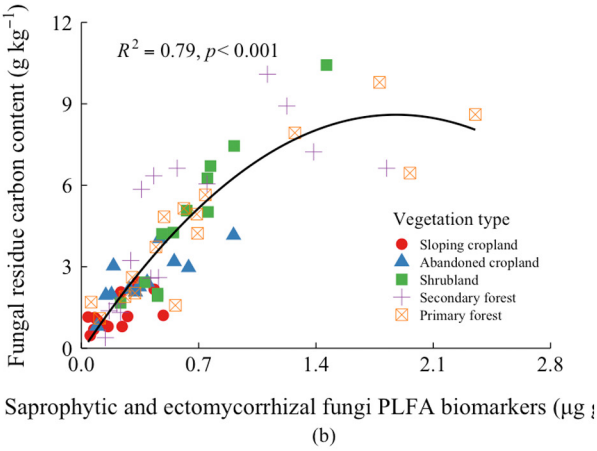
Fig. 2. Changes in the contribution (kg m^{-2}) of (a) bacterial (BRC), (c) fungal (FRC) and (e) total MRC (MRC) to soil; and ratios of (b) bacterial, (d) fungal and (f) total MRC to total SOC stock (%) in the full soil profile, at each vegetation recovery stage at the Chinese Karst CZO. SC, sloping cropland; AC, abandoned cropland; SL, shrubland; SF, secondary forest; PF, primary forest. Uppercase letters denote significant differences between the vegetation ($p < 0.05$).

including the secondary forest which had been allowed to regenerate naturally for several decades; consequently, the largest SOC stock was measured in the primary forest at Tianlong Mountain.

Consistent with our hypothesis, microbial residue carbon made an increasing contribution to changes in the SOC stock during vegetation recovery. However, the MRC stocks accounted for 17–28% of the SOC stocks across all vegetation types, which is less than reported in some previous studies (Khan et al., 2016; Sun et al., 2016; Liang et al., 2019), and presumably because of the lower fungal-to-bacterial MRC ratios (0.60–0.86) compared to other ecosystems (0.9–4.5) (Ding et al., 2015; Liang et al., 2019; Khan et al., 2016; Zhang et al., 2016). Fungal MRC (GluN) constitutes 49 mg g^{-1} biomass dry matter, compared with 13.9 mg g^{-1} MurN in Gram positive bacteria and 3.7 mg g^{-1} in Gram negative bacteria (Liang et al., 2019). For example, Khan et al. (2016) reported that the soil microbial communities of alkaline and neutral soils tended to be dominated by bacteria and had low ratios of fungal-to-bacterial MRC that varied between 0.22 and 0.29. Furthermore, Kallenbach et al. (2016) suggested that bacterial residue C had a relatively rapid turnover rate compared to fungal residue C contributing to smaller observed total MRC contributions to SOC stocks.


Bacterial residue carbon content (g kg^{-1})
R^2 = 0.69, p< 0.001
Vegetation type
Sloping cropland
Abandoned cropland
Shrubland
Secondary forest
Primary forest
Gram positive bacterial PLFA biomarkers (μg g^{-1})

(a)


Fungal residue carbon content (g kg^{-1})
R^2 = 0.79, p< 0.001
Vegetation type
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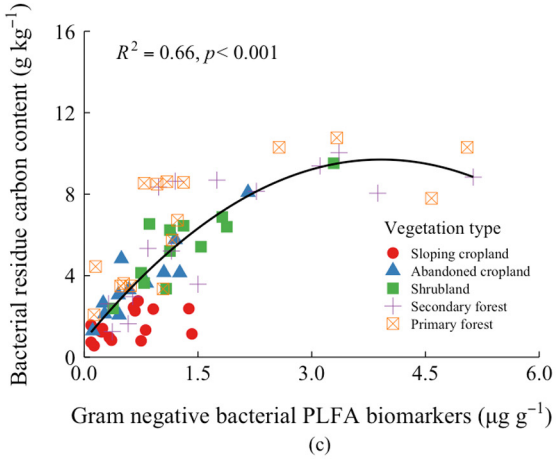
Abandoned cropland
Shrubland
Secondary forest
Primary forest
Saprophytic and ectomycorrhizal fungi PLFA biomarkers (μg g

(b)


Bacterial residue carbon content (g kg^{-1})
R^2 = 0.66, p< 0.001
Vegetation type
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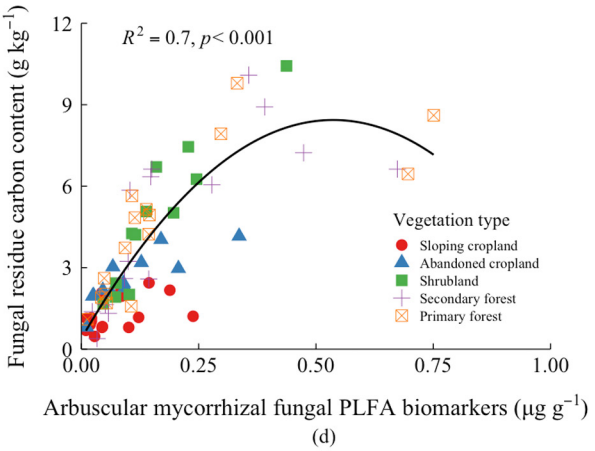
Abandoned cropland
Shrubland
Secondary forest
Primary forest
Gram negative bacterial PLFA biomarkers (μg g^{-1})

(c)


Fungal residue carbon content (g kg^{-1})
R^2 = 0.7, p< 0.001
Vegetation type
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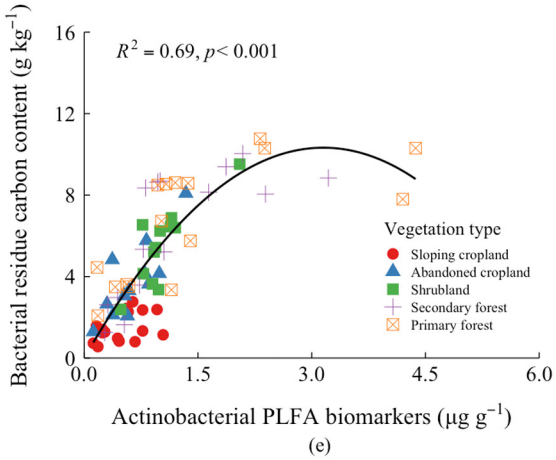
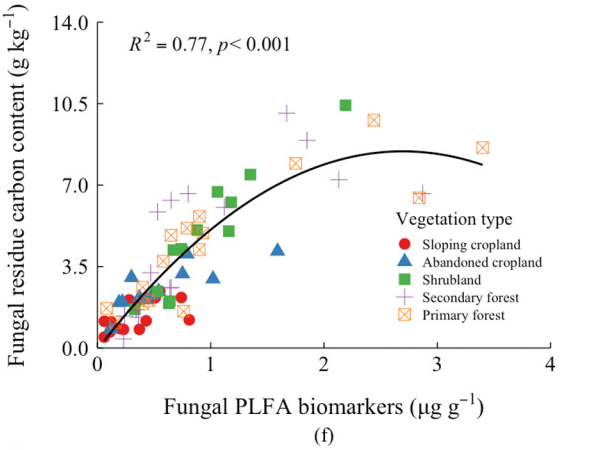
Abandoned cropland
Shrubland
Secondary forest
Primary forest
Arbuscular mycorrhizal fungal PLFA biomarkers (μg g^{-1})

(d)


Bacterial residue carbon content (g kg^{-1})
R^2 = 0.69, p< 0.001
Vegetation type
Sloping cropland
Abandoned cropland
Shrubland
Secondary forest
Primary forest
Actinobacterial PLFA biomarkers (μg g^{-1})

(e)


Fungal residue carbon content (g kg^{-1})
R^2 = 0.77, p< 0.001
Vegetation type
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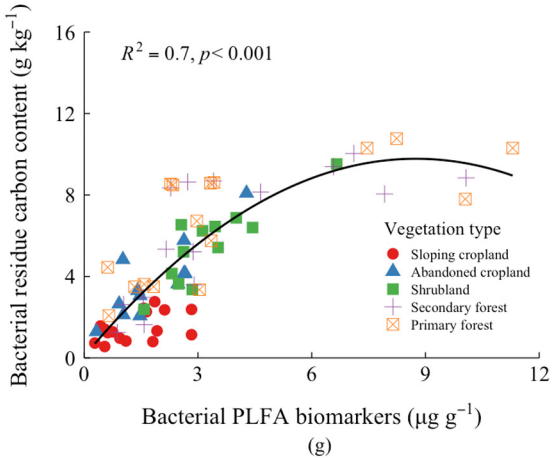
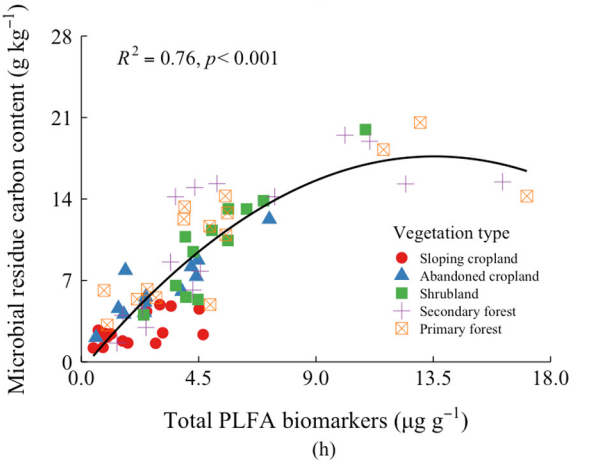
Abandoned cropland
Shrubland
Secondary forest
Primary forest
Fungal PLFA biomarkers (μg g^{-1})

(f)


Bacterial residue carbon content (g kg^{-1})
R^2 = 0.7, p< 0.001
Vegetation type
Sloping cropland
Abandoned cropland
Shrubland
Secondary forest
Primary forest
Bacterial PLFA biomarkers (μg g^{-1})

(g)


Microbial residue carbon content (g kg^{-1})
R^2 = 0.76, p< 0.001
Vegetation type
Sloping cropland
Abandoned cropland
Shrubland
Secondary forest
Primary forest
Total PLFA biomarkers (μg g^{-1})

(h)

Unlike the MRC stock that was increased during vegetation recovery, the proportion of MRC to SOC stock was firstly increased to the maximum in the shrubland stage then decreased in secondary and primary forests stage. As woody plant species proliferate and plant litter becomes more lignified and diversified, relatively more carbon goes towards acquiring energy and nutrient (i.e. higher metabolic activity and larger respiration rate) rather than biomass carbon synthesis (i.e. lower anabolic activity and lower carbon use efficiency) (Kallenbach et al., 2016; Zhu et al., 2020), potentially reducing the amount of residue carbon input and slowing its accumulation in soils of secondary and primary forest. Whereas, plant litter with a significant input into forest soils accelerates SOC accumulation compared to grassland and shrubland (Liang et al., 2019). Therefore, microbial residue carbon contributes proportionately less to SOC stocks when recovering to forest stages compared to shrubland stage. The contribution of fungal biomass to SOC is widely reported as greater than that from bacteria in forest soils (Bailey et al., 2002). However, we observed that the relative proportion of bacterial MRCs was always greater overall and the ratio of fungal to bacterial MRC was invariant with time. Saprophytic fungal populations, e.g. white and brown rot fungi, are assumed to increase in topsoil as woody plant species proliferate and plant litter becomes more lignified (Merila et al., 2010; Tang et al., 2015; Tobiasova, 2011). A trophic cascade develops as fungi decompose woody plant litter releasing carbon and nutrients to the rest of the soil food web including bacteria (Crotty et al., 2012; Williams et al., 2016), and the more stable soil conditions allow the development of all mycelial fungi including mycorrhizae (Lladó et al., 2017). In this study, fungal-to-bacterial ratios based on PLFA biomarkers during vegetation recovery were similar to recent investigations using PLFA analysis in other forests in subtropical China (0.21–0.27 vs 0.19–0.24) (Huang et al., 2013).

4.2. Relationships between microbial necromass and viable microbial community

Improving soil structure, indicated by decreasing D_b and increased contents of SOC and nutrients with progressive vegetation recovery increased microbial biomass C and N (Liu et al., 2012) and led to the increase in the contribution of MRC to the SOC stock (Murugan et al., 2014; Liang et al., 2019; Shao et al., 2018). Although we did not measure changes in the quality of the SOC in this study, we previously determined that the activity of C-, N- and P-hydrolase enzymes increased with vegetation recovery and suggested that near-to-natural biological function was restored in the shrubland and secondary forest, relative to the primary forest (Guo et al., 2019). Bacterial communities are broadly described as more sensitive to the availability of fresh and high-quality organic substrates and the variations in soil pH, whereas fungal communities are more predominant in acid soils with poor nutrients and substrate quality (i.e. high C:N ratios and lignin content; Li et al., 2015; Bahram et al., 2018). Because of the strong buffering capacity of the base-rich karst soils, there was no significant difference in pH between vegetation types or with soil depth (Guo et al., 2019), so we assume that the driving factor for change in microbial community structure was the quantity and quality of available substrates and coincident improved soil structure caused by increased soil organic matter.

As described at the end of the last section, the widely reported change in the predominance of fungi to bacteria in soil that is often used to indicate a key change in ecosystem recovery (e.g. Bailey et al., 2002; Karhu et al., 2014; Malik et al., 2016) was not observed in this study, using either amino sugar (MRC) or PLFA analysis. However, the use of PLFAs allowed us to probe further the responses of specific groups of bacteria and fungi to change during vegetation recovery. Like the fungal MRC, PLFA biomarkers for fungi were present in larger contents in the secondary and primary forest soils. With regard to bacterial groups, carbon quality/availability in soils is indicated by the ratio of opportunistic K-strategist Gram positive bacteria to r-strategist Gram negative bacteria (Dungait et al., 2013; Fanin et al., 2019). In this study, the ratios of Gram positive bacteria to Gram negative bacteria were negatively related to SOC, TN, SOC:TN, TN:TP and SOC:TP, and increased with depth in the karst soils, indicating the functional niche of Gram positive bacteria as slow-growing and persistent spore-forming ecotypes that are better able to use complex substrates (Dungait et al., 2011). Furthermore, the Gram positive bacteria have a peptidoglycan cell wall that is 3.75 times thicker than Gram negative bacteria (Joergensen, 2018; Liang et al., 2019), so a proliferation of Gram positive types may explain a larger input of MRC to subsoil SOC stocks that can be explained by other measurements.

Mycorrhizal fungi play a pivotal role in the mobilization and solubilization of nutrients including N and P (Lladó et al., 2017). Plants that naturally colonise characteristically nutrient-poor karst soils are assumed likely to establish mycorrhizal associations to help them to exploit the limited available resources (Green et al., 2019). Phosphorus is a strongly limiting nutrient in karst systems because of the paucity in the parent rock and strong P adsorption to calcium, while the N limitation in abandoned agricultural landscapes is caused by immediate strong N leaching that was not replaced by natural vegetative regeneration (Li et al., 2018a, 2018b; Guo et al., 2019). Moreover, because of the change in plant litter quantity and quality (discussed above), we hypothesized that the contribution of MRC from different functional groups of fungi and bacteria would change at different stages of vegetation recovery. Indeed, we only have evidence to partially accept this hypothesis because we observed an increase in both total fungal MRC and total fungal and mycorrhizal PLFA biomarkers in the shrubland soils (0– 30 cm) that was similar to the primary forest. Furthermore, the succession to woody vegetation was predicted to be associated with an increased incidence of biomarkers indicating saprophytic and ectomycorrhizal rather than arbuscular mycorrhizal associations (Clemmensen et al., 2013; Dickie et al., 2014). Both ectomycorrhizal and saprophytic fungi can produce a wide range of enzymes that release N and P from soil organic matter (Averill et al., 2014). Due to their saprotrophic capabilities, the promotion of saprophytic fungi has been shown to lower SOC contents while a arbuscular mycorrhizal fungi have positive effects to SOC contents (Khan et al., 2016), but saprophytic and ectomycorrhizal fungi may be more competitive for nutrients when C-availability is not limiting (Bödeker et al., 2016; Phillips et al., 2013); accordingly we quantified a greater abundance of PLFA biomarkers indicating a larger saprotrophic and ectomycorrhizal fungal population, contributing more fungal biomass C inputs to SOC stocks under this alkaline karst soil with higher SOC contents. Nevertheless, the predominance of bacteria over fungi in all soils indicated by bacterial MRC at each stage of vegetation recovery was confirmed by PLFA biomarkers for Gram positive bacteria, Gram negative bacteria and Actinobacteria, suggested strong competition for nutrients within the microbial community in later stages of vegetation recovery.

The importance of microbial-derived organic matter in subsoil horizons has been widely discussed (e.g. Rumpel and Kögel-Knabner, 2011). Recent research using PLFA analysis suggested that acidic subsoils under natural subtropical forest vegetation are dominated by large populations of r-strategist bacteria due to the availability of labile C (Chen et al., 2016). However, in this study in base-rich karst soils, both necromass (MRC) and viable microbial groups (PLFAs) contents were greater in the topsoil and became less with depth, consistent with a previous study (Shao et al., 2017). The largest abundance of Gram positive

Fig. 3. The relationship between soil microbial community biomass and soil microbial residue carbon contents in each vegetation recovery stage at the Chinese Karst CZO. The fitnesses of second-order polynomial regression are shown in black solid lines.

bacteria identified across the vegetation recovery gradient was also observed to decreased with soil depth, coincident with the increase in D_b and exponential depletions in SOC and nutrient content. These and other factors, including the reduced availability of oxygen and the relative stability of the subsoil environment, drive a shift in microbial community structure to bacterial dominance that is widely reported (e.g. Wang et al., 2014; Banfield et al., 2017). Moreover, the selection for K-strategist, oligotrophic Gram positive bacteria with depth under the conditions observed in this study is consistent with theories of microbial functional ecology (De Vries and Shade, 2013).

5. Conclusions

The SOC stocks after abandonment of agriculture have increased as vegetation recovered naturally in the subtropical karst ecosystem. The contributions of total MRC to SOC stocks varied from 17– 28% with the largest values in the shrublands that were similar to primary forests. Despite the increase in woody plant type inputs, bacterial MRC contributed more to SOC stocks than fungal MRC overall during vegetation recovery. The increasing MRC contents were mainly attributed to the improvements of SOC, TN and TP after the abandonment of sloping croplands. We also found Gram positive bacteria was the largest group of bacterial population, and the ratios of Gram positive bacteria to Gram negative bacteria increased along the soil profiles as C availability decreased. Whereas saprophytic and ectomycorrhizal fungi contributed more to the total fungal abundance in the secondary and primary forests. These results provide the relationships between the living microbial community and microbial necromass in regenerating karst soils, and suggest different microbial groups have the potential to adapt to nutrient limitations and play different roles in SOC accumulation in different phases of vegetation recovery.

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CRediT authorship contribution statement

Zhiming Guo: Investigation, Writing – original draft, Visualization. **Xinyu Zhang:** Conceptualization, Writing – review & editing, Supervision. **Jennifer A.J. Dungait:** Conceptualization, Writing – review & editing. **Sophie M. Green:** Writing – review & editing. **Xuefa Wen:** Supervision. **Timothy A. Quine:** Writing – review & editing, Supervision.

Declaration of competing interest

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

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