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Paddy soil microbial communities driven by environment- and microbe-microbe interactions: A case study of elevation-resolved microbial communities in a rice terrace

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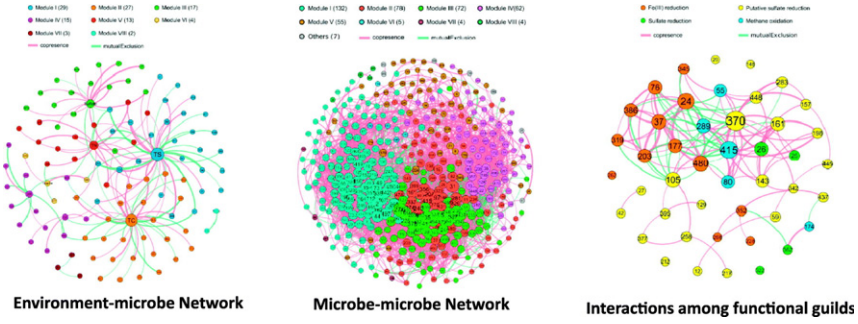
HIGHLIGHTS

- Microbial communities were characterized in rice paddy terrace.
- Sulfate may impact the innate microbiota and mitigate methane.
- Dynamic biotic interactions occurred in the paddy soils.
- Co-occurring of MOB and SRB/FeRB suggested associated communities.

GRAPHICAL ABSTRACT



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ABSTRACT

Rice paddies are a significant source of the greenhouse gas methane, which mainly originates from microbial activity. Methane generation in anaerobic systems involves complex interactions of multiple functional microbial groups. Rice paddies installed in hilly terrain are often terraced, providing multiple quasi-independent plots differing primarily in their elevation up a hillside. This represents an excellent study site to explore the influence of environmental factors on microbial communities and interactions among microbial populations. In this study, we used a combination of geochemical analyses, high-throughput amplicon sequencing, and statistical methods to elucidate these interactions. Sulfate, total nitrogen, total iron, and total organic carbon were determined to be critical factors in steering the ecosystem composition and function. Sulfate-reducing bacteria predominated in the rice terrace microbial communities, and Fe(III)-reducing and methane-oxidizing bacteria were abundant as well. Biotic interactions indicated by co-occurrence network analysis suggest mutualistic interactions among these three functional groups. Paddy-scale methane production may be affected by competition among methanogens and sulfate- and Fe(III)-reducing bacteria, or by direct methane oxidation by methane-oxidizing bacteria.
Capsule: Microbial communities were characterized in rice terrace. The environment- and microbe-microbe interactions indicated the mitigation of sulfate and Fe on methane production.

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1. Introduction

Rice is one of the most important food crops around the world, feeding >50% of the world's population. >75% of world's rice is produced in irrigated rice fields (Ma et al., 2010). The flood-and-drain cycles that occur in rice paddies create shifts of reduced and oxidized environments, which provide suitable habitats for a wide diversity of microbes. It has been proposed that complex organic matter can be utilized synergistically by various microbial guilds such as fermenters, denitrifiers, sulfate and Fe(III) reducers, methanogens, and methanotrophs in rice paddy soils (Liesack et al., 2000). Thus, rice paddies have been considered a major anthropogenic source of the greenhouse gas methane.

A number of soil, climate, and environmental factors have the potential to structure the rice paddy microbiota. For instance, Yang and Chang (1998) found that methane production and emission from rice paddies were governed by a suite of environmental factors such as temperature, organic matter supplementation, urea application, oxygen concentration, water content, soil pH, and light intensity (Yang and Chang, 1998). Soil characteristics may also impact the reduction of electron acceptors (e.g., sulfate, Fe(III), and nitrate) and methane production in rice paddy soils (Yao et al., 1999). Our previous study indicated that soil pH, nitrate, and sulfate concentrations shaped the innate soil microbial communities in rice paddy soils (M. Sun et al., 2015).

Synergistic, antagonistic, and neutral interactions between microorganisms influence the microbial community structure (Ho et al., 2016). For example, a methane-oxidizing bacterium *Methylomicrobium alcaliphilum* may exude substrates (e.g., acetate and succinate) that support heterotrophic microorganisms (Kalyuzhnaya et al., 2013). In some extreme environments, biotic interactions may become critical to sustain the function of the ecosystems. In acid mine drainage (AMD), acidophilic autotrophs produce organic substrates that facilitate the growth of heterotrophs, which in turn consume these compounds which would otherwise accumulate to levels that are toxic to autotrophs (Baker and Banfield, 2003; Sun et al., 2015b). Detailed investigation of such interactions will improve our understanding of microbial behaviors in rice paddy soils and their effect on biogeochemical processes, soil quality, and biodegradation of contaminants.

Rice terraces consist of a series of flat fields cut into sloping land for rice production. Differences in elevation down the mountainside and may create shifts in physicochemical and geochemical conditions between paddies, making the rice terrace a better model than conventional rice paddies to study the abiotically driven factors (i.e. environmental factors that modulate the composition of microbial communities) and biotic factors. In this study, we selected the Gaoyao rice terrace, Southwest China, to investigate these interactions. A series of 15 small rice fields were selected along a ridge. This rice paddy soil was analyzed by high-throughput amplicon sequencing, physiochemical analyses, as well as statistical methods. We investigated (i) the detailed taxonomic inventory within the rice paddies; (ii) the effect of environmental conditions on the microbial communities; and (iii) the interaction between microbial populations within communities as influenced by environmental factors.

2. Materials and methods

2.1. Sites and soil sampling

Our study was conducted in Gaoyao paddy terrace covering an area of 100 ha in Guizhou province, southwest China (N: 26°8′32.55″; E: 107°50′18.40″). A total of 60 paddy soil samples were collected from 15 flooded paddy fields from the top (elevation: 840 m) to bottom (elevation: 803 m) of the terrace (Fig. 1), with ~2.5 m elevation difference between each plot. Two rhizosphere soils and 2 bulk soils were collected from each paddy. Bulk soils were defined as the soil that does not adhere to the rice roots, while the soil adhering to the roots after shaken vigorously were carefully scrapped from the roots as rhizosphere soil. Each sample was coded as <field number>-<soil type><replicate>. For example, sample 4-R2 would be replicate #2 of rhizosphere soil (R) from filed number four while 5-B1 would be replicate #1 of bulk soil (B) from field number five.

2.2. Geochemical analysis

All 60 soil samples were freeze-dried under vacuum (Scientz, Ningbo, China) for 48 h. Leaves, plant roots, and gravel were removed by passing the lyophilized sample through a 2-mm sieve. Rice paddy soil was thoroughly ground using a mortar and pestle and passed through a through a 200-mesh sieve. Ten grams of soil samples were mixed with 25 ml distilled water for 5 min and settled for another 20 min. The soil samples were then subjected for pH and oxidation-reduction potential (Eh) measurement using a HACH HQ30d pH meter (HACH, Loveland, USA).

An additional five grams of each soil sample was shaken with 25 ml distilled water for 5 min, followed by 4 h of equilibration. Then the mixture was centrifuged (rcf = 8000 × *g*) for 25 min, and the supernatant was collected and analyzed via ion chromatography for nitrate and sulfate (DIONEX ICS-40, Sunnyvale, CA, USA).

Total sulfur, carbon, hydrogen, and nitrogen in the soils were measured directly and total organic carbon and soluble sulfur were measured after removing inorganic carbon by digesting with 5% HCl (AR grade, Kemiou, Tianjing) by an elemental analyzer (Vario MACRO cube, Elementar, Hanau, Germany). Total Fe and Fe(II) were measured as described previously (Liu et al., 2015; Yu et al., 2016). Briefly, 1 g of soil was shaken with 10 ml 1 M HCl for 30 min, followed by centrifugation at 8000 rpm for 25 min. The supernatant was then collected and iron species (Fe(II) and Fe(III)) were measured using spectrophotometric methods with 1,10-phenanthroline at 510 nm (Tamura et al., 1974).

2.3. High-throughput sequencing of the V4 region of 16S rRNA genes

Total genomic DNA was extracted from 0.4 g of well-mixed soil using the MO BIO Soil Isolation Kit (MO BIO, Carlsbad, USA) in accordance with the manufacturer's specifications. Total genomic DNA was subjected to high-throughput sequencing of the 16S rRNA amplicons using an Illumina MiSeq platform at the Novogene Cooperation (Beijing, China). Bacterial/archaeal communities were analyzed using a variety of bioinformatics tools and pipelines. A detailed procedure regarding 16S rRNA amplicon sequencing can be found in the supplemental information.

2.4. Numerical analyses

Canonical correspondence analysis (CCA) was performed to investigate the influence of selected environmental parameters on soil microbial communities as described previously (Sun et al., 2016a; Sun et al., 2016b). Multivariate regression tree (MRT) analysis was performed using the mvpart package (with default parameters) in R to correlate the relative abundances of microbial taxa at class level and the environmental parameters (De'Ath, 2007).

The co-occurrence network analysis was performed to investigate the biotic interactions between populations. This method describes how the taxa (operational taxonomic unit (OTUs) in this study) of a soil microbial community interact by exhibiting the positive or negative Spearman correlations. We constructed a correlation matrix by calculating all pairwise Spearman's correlation coefficients (r) among top 500 most abundant OTUs. A connection indicates a strong ($|r| > 0.6$) and significant ($p < 0.05$) Spearman's correlation. A positive correlation may suggest a mutualistic interaction while a negative correlation may indicate competition or predation (Lupatini et al., 2014). All statistical analyses were performed using igraph package in R (Csardi and Nepusz, 2006). The co-occurrence networks were visualized and the topological properties (i.e., clustering coefficient, shortest average path length and

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