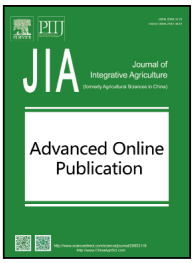
Journal of Integrative Agriculture 2020, 19(0): 2–11

Available online at www.sciencedirect.com

ScienceDirect



RESEARCH ARTICLE

Bacterial diversity and community composition changes in paddy soils that have different parent materials and fertility levels

MA Xin-ling[1, 2*], LIU Jia[3*], CHEN Xiao-fen[3], LI Wei-tao[4], JIANG Chun-yu[1, 2], WU Meng[1, 2], LIU Ming[1, 2], LI Zhong-pei[1, 2]

[1] *State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing 210008, P.R.China*

[2] *University of Chinese Academy of Sciences, Beijing 100049, P.R.China*

[3] *Soil and Fertilizer & Resources and Environment Institute, Jiangxi Academy of Agricultural Sciences, Nanchang 330200, P.R.China*

[4] *CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, P.R.China*

Abstract

Parent materials and the fertility levels of paddy soils are highly variable in subtropical China. Bacterial diversity and community composition play pivotal roles in soil ecosystem processes and functions. However, the effects of parent material and fertility on bacterial diversity and community composition in paddy soils are unclear. The key soil factors driving the changes in bacterial diversity, community composition, and the specific bacterial species in soils that are derived from different parent materials and have differing fertility levels are unknown. Soil samples were collected from paddy fields in two areas with different parent materials (quaternary red clay or tertiary sandstone) and two levels of fertility (high or low). The variations in bacterial diversity indices and communities were evaluated by 454 pyrosequencing which targeted the V4–V5 region of the 16S rRNA gene. The effects of parent material and fertility on bacterial diversity and community composition were clarified by a two-way ANOVA and a two-way PERMANOVA. A principal coordinate analysis (PCoA), a redundancy analysis (RDA), and multivariate regression trees (MRT) were used to detect changes in the studied variables and identify the factors affecting bacterial community composition. Co-occurrence network analysis was performed to find correlations between bacterial genera and specific soil properties, and a statistical analysis of metagenomic profiles (STAMP) was used to determine bacterial genus abundance differences between the soil samples. The contributions made by parent material and soil fertility to changes in the bacterial diversity indices were comparable, but soil fertility accounted for a larger part of the shift in bacterial community composition than the parent material. Soil properties, especially soil

Received 8 April, 2020 Accepted 14 July, 2020

MA Xin-ling, E-mail: maxl-scu@qq.com; LIU Jia, E-mail: liujia422@126.com; Correspondence LIU Ming, Tel: +86-25-86881337, E-mail: mliu@issas.ac.cn; LI Zhong-pei, Tel: +86-25-86881323, E-mail: zhpli@issas.ac.cn

[*] These authors contributed equally to this study.

doi: 10.1016/S2095-3119(20)63364-0

texture, were strongly associated with bacterial diversity. The RDA showed that soil organic carbon (SOC) was the primary factor influencing bacterial community composition. A key threshold for SOC (25.5 g kg^{-1}) separated low fertility soils from high fertility soils. The network analysis implied that bacterial interactions tended towards cooperation and that copiotrophic bacteria became dominant when the soil environment improved. The STAMP revealed that copiotrophic bacteria, such as *Massilia* and *Rhodanobacter*, were more abundant in the high fertility soils, but oligotrophic bacteria, such as *Anaerolinea*, were dominant in low fertility soils. The results showed that soil texture played a role in bacterial diversity, but nutrients, especially SOC, shaped bacterial community composition in paddy soils with different parent materials and fertility levels.

Keywords: microorganisms, soil biodiversity, soil fertility, soil texture, soil nutrients

1. Introduction

Microbial diversity and community composition play important roles in soil ecosystem processes and functions because they drive nutrient cycling, maintain soil structure, and transform organic carbon (Ibekwe *et al.* 2002; Brussaard *et al.* 2007). They are also important for agricultural sustainability (Bhat 2013).

The importance of the parent material impacts on bacterial diversity and community composition have been compared to soil depth (Sheng *et al.* 2015), land use (Deng *et al.* 2015), age of the plant stand (Guo *et al.* 2015), nutrient application, and straw return (Sun *et al.* 2016). Parent material has a considerable effect on microbial diversity indices (Deng *et al.* 2015). It is also considered to be the primary factor influencing microbial community composition (Guo *et al.* 2015; Sun *et al.* 2016). For example, a parent material has a stronger impact on the soil microbial community during the earlier stages of ecosystem development (Wagai *et al.* 2011). It is also thought that soils developed from the same parent materials usually accommodate similar microbial communities (Guo *et al.* 2015).

Soil properties have important effects on bacterial diversity and community composition. For example, soil pH has been generally shown to have crucial effects on bacterial community structure in many studies (Fierer and Jackson 2006; Lauber *et al.* 2009; Griffiths *et al.* 2011). Several studies have found that soil carbon (C), nitrogen (N), phosphorus (P), base ion and elemental ratios affect bacterial diversity and community composition (Faoro *et al.* 2010; Ramirez *et al.* 2010; Kuramae *et al.* 2012). Soil texture is known to influence microbial biomass (Müller and Höper 2004; Chodak and Niklinska 2010; Cao *et al.* 2016), enzymatic activity, and respiration (Melero *et al.* 2007; Chodak and Niklinska 2010; Józefowska *et al.* 2017). It also affects microbial diversity (Chau *et al.* 2011; Naveed *et al.* 2016) and community composition (Johnson *et al.* 2003).

Paddy fields cover 30% of the arable land in China and 90% of them are distributed in tropical or subtropical China (Jia *et al.* 2010). Parent materials in subtropical China vary considerably (Xu and Cai 2007). The different parent materials and their weathering stage determine soil texture, clay mineral contents, and nutrient availability to biota (Ulrich and Becker 2006), all of which affect soil microorganisms (Deng *et al.* 2015). Fertilization regimes, crop exudations, and residue return also make fertility highly variable across paddy soils in this region. However, the contributions made by different parent materials and fertility to bacterial diversity and community composition in paddy soils are unclear. In this study, it was hypothesized that both the parent materials and soil fertility affect soil properties and ultimately determine the bacterial diversity and community composition of paddy soils. Therefore, soil samples were taken from paddy fields with different parent materials and fertility in a red soil region of subtropical China. Bacterial diversity and community composition were measured with 454 pyrosequencing. The objectives of this study were to: (1) clarify the critical soil factors driving the changes in bacterial diversity and community composition, and (2) identify the dominant bacterial species in paddy soils that were specific to certain parent materials and fertility levels.

2. Materials and methods

2.1. Site description and soil collection

The sampling sites were located in Yingtan City (28°12′–28°13′N, 116°55′E), Jiangxi Province, subtropical China. The climate in this region is typical subtropical monsoon, and has an annual precipitation of 1 795 mm, an annual evaporation of 1 318 mm, and a mean annual temperature of 17.6ºC. Quaternary red clay and tertiary sandstone were identified as typical parent materials in this region. All the paddy fields belonged to a state farm and double rice was continuously cultivated before the sampling period. The agronomic practices, such as flood irrigation and fertilizer application, have been almost identical across the sampling

plots in recent years. The fertilizer application rates were approximately 300 kg N ha^{-1} yr^{-1}, 66 kg P ha^{-1} yr^{-1}, and 248 kg K ha^{-1} yr^{-1} for each plot. After consulting local experts, low- and high-fertility soils derived from quaternary red clay were sampled from newly cultivated (about 5 years) and old (>100 years) paddy fields. Low- and high-fertility soils derived from tertiary sandstone were also sampled from newly cultivated (about 15 years) and old (>80 years) paddy fields. As a result, there were four soil groups, namely quaternary red clay parent materials and high fertility (RCH), quaternary red clay parent materials and low fertility (RCL), tertiary red sandstone parent materials and high fertility (RSH), tertiary red sandstone parent materials and low fertility (RSL). For each soil group, three paddy fields (~0.2 ha each) that were about 100 m apart were selected as replicated sampling plots. Five surface soil subsamples (0–15 cm) were collected from each sampling plot immediately after late rice cultivation at the end of October, 2014. They were collected using a soil auger (3 cm in diameter) and a zigzag sampling pattern. Then the subsamples were thoroughly mixed and the composite soil samples were used for the chemical-physical property and microbial analyses. The average soil chemical-physical properties and rice yields for each soil group are shown in Appendix A.

2.2. Chemical property measurements

The soil pH was measured by a potentiometer, and the SOC was determined by the potassium dichromate oxidation method (Mebius 1960). The soil samples were digested with 0.8 mol L^{-1} $K_2Cr_2O_4$ and concentrated H_2SO_4 (v/v, 1:1) at 150°C for 30 min. Then the SOC was titrated against 0.5 mol L^{-1} ferrous iron solution. The total N (TN) was determined using the Kjeldahl method (Kjeldahl 1883). The soil sample was heated and boiled with concentrated H_2SO_4. Then, the TN was absorbed by 2% boric acid solution and titrated against 0.1 mol L^{-1} sulfuric acid. The available N (AN) was hydrolyzed by 1 mol L^{-1} sodium hydroxide and measured using micro-diffusion methods (Conway 1948). After the soil had been melted with anhydrous sodium carbonate or extracted with 0.5 mol L^{-1} sodium bicarbonate, the total P (TP) and available P (AP) were determined by the molybdenum-blue colorimetric method (Dickman and Bray 1940). Soil total K (TK) and available K (AK) were determined by the modified flame emission spectrometric method after the soil had been digested in concentrated $HF/HClO_4$ (v/v, 2:1) or extracted using 1 mol L^{-1} ammonium acetate, respectively (Pansu and Gautheyrou 2006). Another set of soil samples were dispersed in 0.5 mol L^{-1} sodium hydroxide and soil texture was determined using the pipette method (Pansu and Gautheyrou 2006).

2.3. DNA extraction, PCR amplification and 454 pyrosequencing

Soil microbial genomic DNA was extracted from 0.5 g fresh soil using a FastDNA™ SPIN Kit (MP Biomedicals, Santa Ana, CA, USA), and the quantity and quality of the extracted DNA were measured by an Eppendorf BioSpectrometer Basic (Eppendorf Corporate, Hamburg, Germany). The DNA concentration was >100 ng μL^{-1} and the OD_{260}/OD_{280} was >1.6 for each DNA sample, which meant that they could be used in the following analyses. The primers (F515 and R907) and target regions of the bacterial 16S rRNA genes were described in Shen *et al.* (2013). The PCR cycling conditions were 94°C for 5 min, 33 cycles of 94°C for 30 s, 55°C for 30 s. and 72°C for 45 s. There was a final extension at 72°C for 10 min. The PCR products were purified using an E.Z.N.A. Cycle-Pure Kit (Omega, Norcross, GA, USA) and run on a Roche FLX 454 pyrosequencing platform (Roche Diagnostics Corporation, Branford, CT, USA). About 4 175 high-quality 16S rRNA reads for each sample were obtained after sequencing. The raw data produced by the sequencing were analyzed according to Caporaso *et al.* (2010). About 1 630 high-quality sequences were screened out for each sample after short sequences (<200 bp), ambiguous bases, barcodes, homopolymers and low quality sequences (quality score Q<25) were eliminated. Sequences with ≥97% similarity were assigned to the same operational taxonomic unit (OTU) by UCLUST (Edgar 2010). The most abundant sequence in each OTU was selected as the representative sequence. Then, the representative OTU sequences were classified by RDP classifier with a confidence threshold of 80% and the taxonomic information was annotated (Wang *et al.* 2007). The sequence data was submitted to the Sequence Read Archive (SRA) of the NCBI and the accession number was SRP267058.

2.4. Data analysis

Bacterial diversity and community were analyzed by R version 3.2.3 (R Core Team 2014). The phyloseq package was used to calculate the Bacterial Chao1 and Shannon indices. The vegan package in R was used to perform a principal coordinate analysis (PCoA) and a redundancy analysis (RDA). Removal of the autocorrelation variables and significance testing of the soil factors followed Liu *et al.* (2018) when the RDA was carried out. The mvpart package was used to generate multivariate regression trees (MRT) (De'Ath 2002). Any significant effects of parent material and fertility on bacterial diversity and community composition were determined with two-way ANOVA and two-way PERMANOVA using Past 3 (Hammer *et al.* 2001). Significant differences among soil groups were determined

at $P<0.05$. Correlations between soil properties and bacterial diversity indices were also determined with two-tailed Pearson correlation statistic using Past 3. A co-occurrence network analysis of bacterial genera and specific soil properties was carried out using the plugin CoNet in Cytoscape 3.5.1 (Shannon *et al.* 2003). Strong correlations between two genera or between genera and soil properties were defined as having Spearman's correlation coefficients >0.75 at $P<0.01$. The topology parameters of the network were determined by Cytoscape 3.5.1 using NetworkAnalyzer (Shannon *et al.* 2003), and bacterial genus abundance differences among soil groups were determined by a statistical analysis of metagenomic profiles (STAMP) (Parks *et al.* 2014).

3. Results

3.1. Bacterial diversity and community composition in soils with different parent materials and fertility levels

Both parent material and fertility significantly affected bacterial richness and the diversity indices. The order for the Chao1 and Shannon index changes was as follows: RSL~RCH>RSH>RCL. The parent material contributed 23.0 and 24.4% to the total variation in the Chao1 and Shannon indices, respectively (Table 1), whereas fertility explained 22.8 and 24.0% of the total variation in the Chao1 and the Shannon indices, respectively (Table 1).

For the same parent material, the relative abundances of Proteobacteria, Acidobacteria, Actinobacteria, Chlorobi, Bacteroidetes, Planctomycetes, and Gematimonadetes in high-fertility soils were significantly higher than those in low-fertility soils (Fig. 1). On the contrary, Chloroflexi and Nitrospirae were remarkably lower in high-fertility soils than in low-fertility soils (Fig. 1). At the same soil fertility level, the relative abundances of Chloroflexi and Acidobacteria in red clay soils were significantly higher than those in red sandstone soils (Fig. 1). In contrast, Proteobacteria, Chlorobi, Bacteroidetes, Gematimonadetes, and Spirochaetae were significantly lower in red clay soils than in red sandstone soils (Fig. 1).

Axes 1 and 2 of the PCoA assigned 35.6 and 16.1% of the variation to bacterial community composition, respectively (Fig. 2). The bacterial communities in soils with different parent materials and fertility levels could be separated (Fig. 2). The two-way PERMANOVA also indicated a significant difference in community composition between the different parent materials ($P<0.01$) and fertility levels ($P<0.001$) (Appendix B). Soil fertility explained about 45.4% of the total variation in bacterial community composition, whereas parent material explained 23.9% (Appendix B).

Table 1 Bacterial diversity indices for paddy soils with different parent materials and fertility levels[1)]

	Chao1	Shannon
Soil		
RCH	3 341 a	6.64 a
RCL	1 928 b	5.62 c
RSH	3 069 a	6.45 b
RSL	3 344 a	6.64 a
F-value		
Parent material	5.76*	134***
Fertility	5.71*	132***
Interaction	12.55**	284***
Percentage of total variance		
Parent material	23.0	24.4
Fertility	22.8	24.0
Interaction	50.2	51.5
Error	4.00	0.182

[1)] RCH, soils with quaternary red clay parent materials and high fertility; RCL, soils with quaternary red clay parent materials and low fertility; RSH, soils with tertiary sand stone parent materials and high fertility; RSL, soils with tertiary sand stone parent materials and low fertility; Chao1, richness index; Shannon, diversity index.
Different lowercase letters in the same column indicate a significant difference at $P<0.05$. *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

3.2. Impact of soil properties on bacterial diversity and community composition

The bacterial Chao1 and Shannon indices were negatively related to soil pH and clay content, but positively associated

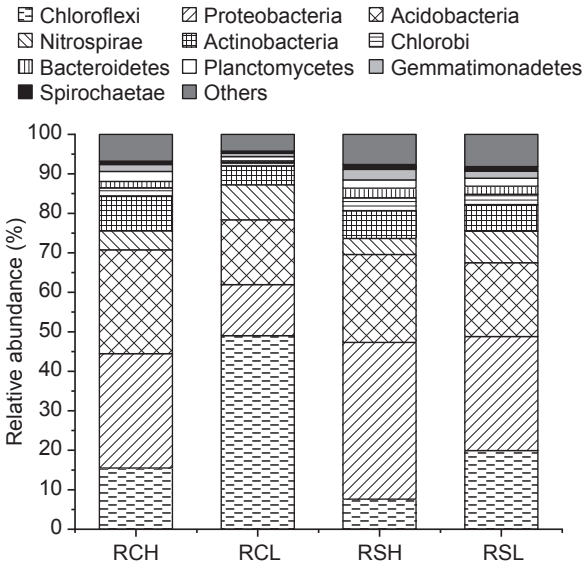


Fig. 1 Relative abundances of the major bacterial phyla in paddy soils with different parent materials and fertility levels. RCH, soils with quaternary red clay parent materials and high fertility; RCL, soils with quaternary red clay parent materials and low fertility; RSH, soils with tertiary sand stone parent materials and high fertility; RSL, soils with tertiary sand stone parent materials and low fertility.

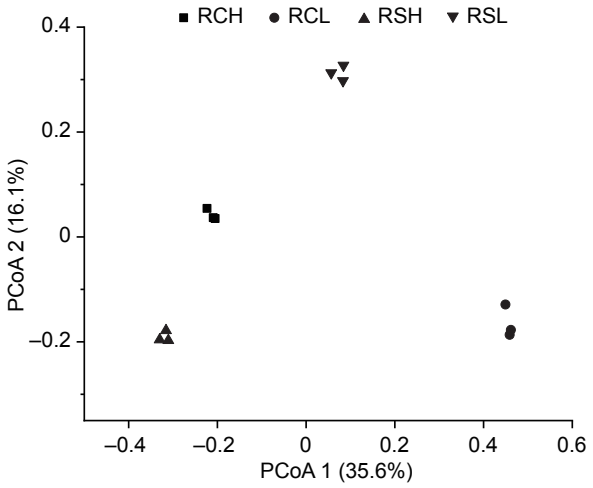


Fig. 2 Principal coordinate analysis (PCoA) of the variation in bacterial community composition, based on the Bray-Curtis distance, for paddy soils with different parent materials and fertility levels. RCH, soils with quaternary red clay parent materials and high fertility; RCL, soils with quaternary red clay parent materials and low fertility; RSH, soils with tertiary sand stone parent materials and high fertility; RSL, soils with tertiary sand stone parent materials and low fertility.

with sand content (Table 2). The Shannon diversity index was particularly positively associated with AP and the carbon: nitrogen (C:N) ratio (Table 2).

The redundancy analysis results showed that axes 1 and 2 accounted for 42.2 and 16.8% of the variation in bacterial community composition between the parent materials and fertility, respectively (Fig. 3). Bacterial community composition was significantly influenced by SOC, AP, and pH (Fig. 3). In particular, SOC explained 28.5% of the changes in bacterial community composition and separated the different soils along axis 1. The bacterial community compositions in the different soils were divided by the SOC thresholds derived from the multivariate regression tree analysis (Fig. 4). These were SOC<25.5 g kg^{-1} and ≥25.5 g kg^{-1} for the low-fertility soils (RCL and RSL) and high-fertility soils (RCH and RSH), respectively (Fig. 4).

The co-occurrence network analysis showed there were 21 nodes and 114 edges in the network (Fig. 5). The average clustering coefficient (avgCC), betweenness centrality, and closeness centrality of the network values were 0.774, 4.52, and 0.703, respectively (Appendix C). The *Massilia*, *Rhodanobacter*, *Tumebacillus*, *Rhodomicrobium*, *Gemmata*, *Haliangium*, *Marmoricola*, *Nevskia*, *Tahibacter*, *Mucilaginibacter* and *Candidatus Planktophila* genera were positively related to SOC (Fig. 5). The proportions of positive and negative edges for the above genera were about 33.0 and 26.6%, respectively (Appendix C). Genera of *Anaerolinea*, *Leptolinea*, *Kedonobacter*, *Actinospica*, *Desulfovibrio*, *Geobacter*, *Sinomonas* and *Acidothermus* were negatively related to SOC (Fig. 5). Their proportions of positive and negative edges were about 16.0 and 21.3%, respectively (Appendix C).

Table 2 Correlations between bacterial diversity, and soil chemical and physical properties[1)]

	pH	AP	Sand	Clay	C:N
Chao1	–0.707*	NS	0.572*	–0.832**	NS
Shannon	–0.912**	0.579*	0.652*	–0.938**	0.631*

[1)] AP, available phosphorus; Sand, 0.02–2 mm; Clay, <0.002 mm; C:N, carbon to nitrogen ratio.
*, $P<0.05$; **, $P<0.01$; NS, not significant.

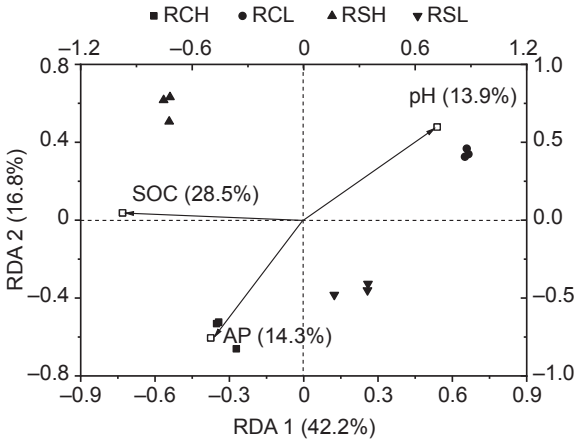


Fig. 3 Redundancy analysis (RDA) of the soil property effects on the composition of bacterial communities in paddy soils with different parent materials and fertility levels. RCH, soils with quaternary red clay parent materials and high fertility; RCL, soils with quaternary red clay parent materials and low fertility; RSH, soils with tertiary sand stone parent materials and high fertility; RSL, soils with tertiary sand stone parent materials and low fertility; SOC, soil organic carbon; AP, available phosphorus.

3.3. Differences in bacterial genus abundance between high- and low-fertility soils

The multivariate regression tree results divided the bacterial communities in the different soil samples into two groups. The bacterial communities in RCH and RSH soils belonged to group 1, and those in RCL and RSL soils were classified as group 2. The STAMP analysis indicated that three bacteria genera were significantly different in abundance between groups 1 and 2. *Massilia* and *Rhodanobacter* were dominant in group 1, whereas *Anaerolinea* were much more abundant in group 2 (Fig. 6).

4. Discussion

In the current study, the contribution made by parent material to bacterial richness and diversity index variations was comparable to soil fertility. Parent material and soil

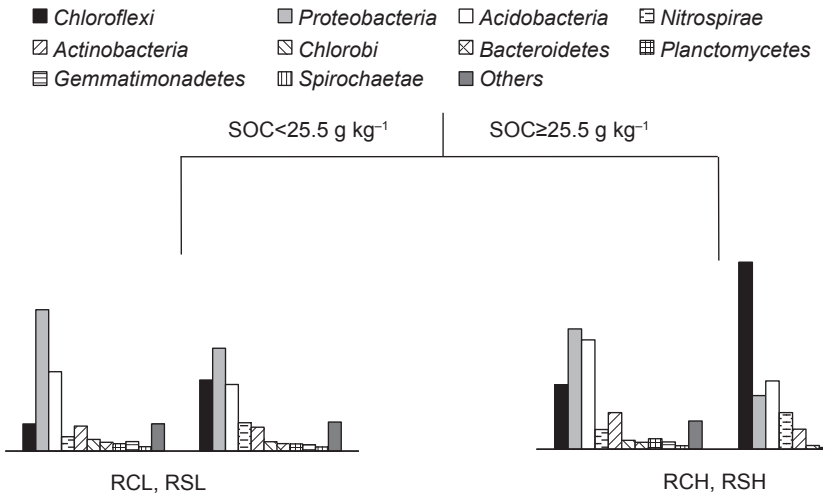


Fig. 4 Multivariate regression tree for bacterial community compositions in paddy soils with different parent materials and fertility levels when partitioned by soil organic carbon. Bar plots indicate relative abundances of the bacterial phyla. SOC, soil organic carbon; RCH, soils with quaternary red clay parent materials and high fertility; RCL, soils with quaternary red clay parent materials and low fertility; RSH, soils with tertiary sand stone parent materials and high fertility; RSL, soils with tertiary sand stone parent materials and low fertility.

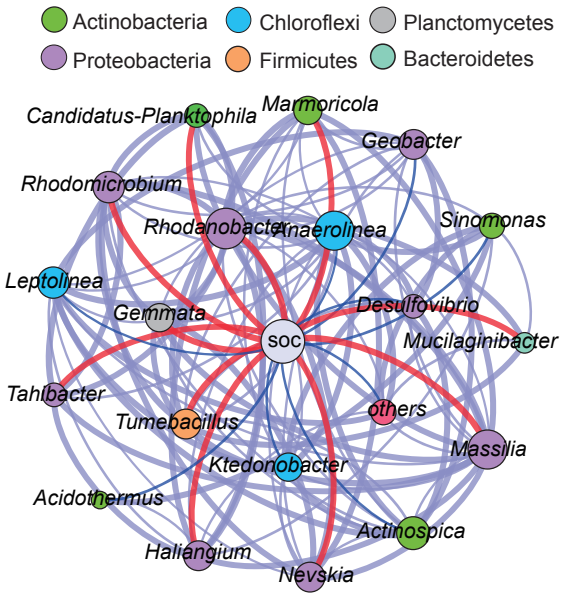


Fig. 5 Co-occurrence network analysis of the bacterial communities at the genus level. The node colors are based on bacterial taxonomic information at the phylum level. Edges that are directly related to soil properties are shown in order to visualize the potential effects of soil properties on bacterial co-occurrence patterns. The red lines represent positive interrelationships, the blue lines represent negative interrelationships, the grey lines represent interrelationships between genera. The size of the node represents the connecting degree, and the width of the lines represents the strength of the correlation.

fertility also significantly affected the relative abundances of major bacterial phyla. However, parent material explained less of the variation in bacterial community composition than fertility. The influence of parent material on bacterial diversity and community composition is usually restricted by nutrient availability (Sheng *et al.* 2015). For example, in paddy field surface soils, fertilizer application, and crop exudation increase soil C, N, P, and K availability and soil fertility, both of which lead to improved microbial growth and shape community structure (Sheng *et al.* 2015). Different rice cultivation times contributed to the discrepancies in soil fertility recorded in this study, which was in agreement with Chen X F *et al.* (2018). The significant interaction effect in this study of parent material and fertility on bacterial diversity and community composition also indicated that the impact of parent material might be moderated by soil fertility.

Generally, bacterial richness and diversity increase in acidic to neutral soils (Fierer and Jackson 2006). In the current study, there were apparently negative relationships between soil pH and the bacterial diversity indices. However, the path analysis suggested that pH positively and directly affected bacterial richness and diversity. The negative effect was probably caused by the indirect influence of other soil factors (Appendices D and E). The results also showed that bacterial diversity was positively associated with soil nutrients, such as AP and the C:N ratio. Similarly, a previous study also found that bacterial diversity was closely related to soil nutrients, such as soil ammonium N (Sun *et al.* 2015). Previous reports have also shown that soil texture is more stable than other soil properties and has important effects on soil microorganisms (Deng *et al.* 2015; Cao *et al.* 2016). For example, bacterial richness indices increase when the sand (Chau *et al.* 2011) or coarse soil (Carson *et al.* 2010) contents are higher. Bacterial richness and diversity were

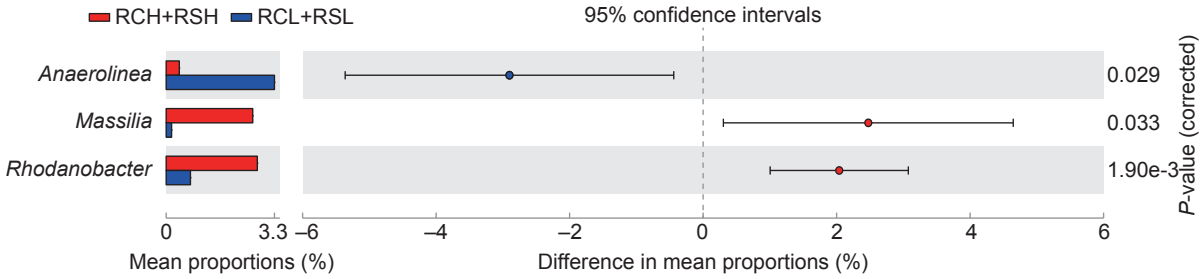


Fig. 6 Differentially abundant bacterial genera in paddy soils with different fertility levels. Significant differences between groups were calculated by Welch's test and the corrected *P*-value were calculated by the Bonferroni multiple test correction. The error bars indicate the standard deviation of triplicated samples and the circles represent 95% confidential intervals. RCH, soils with quaternary red clay parent materials and high fertility; RCL, soils with quaternary red clay parent materials and low fertility; RSH, soils with tertiary sand stone parent materials and high fertility; RSL, soils with tertiary sand stone parent materials and low fertility.

positively correlated to soil sand content, but negatively correlated with clay content in this study. A possible reason is that the coarser soil had more isolated water films than the fine-textured soil. Therefore, the coarser soil had more isolated micro-habitats and less competitive pressure than the finer soil, which means that it can harbor more species (Chau *et al.* 2011).

The soil chemical and physical properties also influence the bacterial community in soils with different parent materials (Chodak and Niklinska 2010; Chau *et al.* 2011; Guo *et al.* 2013; Sheng *et al.* 2015; Cao *et al.* 2016). For example, as the terminal restriction fragment length polymorphism analysis showed, bacterial composition was significantly correlated with soil pH and available Mn in the top soil (Sheng *et al.* 2015). Sun *et al.* (2015) suggested that, in addition to soil pH, SOC and AP also significantly contribute to bacterial community variation. This study also found that SOC, AP, and pH significantly affected bacterial community composition, which confirmed the results reported by Sun *et al.* (2015) and Sheng *et al.* (2015). In particular, SOC was the primary factor affecting the variation in bacterial community composition. A threshold of 25.5 g kg^{-1} SOC led to significant variations in the bacterial community between the high- and low-fertility soils. Sun *et al.* (2015) found that 10.1 g kg^{-1} of soil total C significantly contributed to changes in the bacterial communities found in lime concretion black soils. The different thresholds for SOC between previous studies and this study were probably due to the different soil types, fertilities, and fertilizer application rates.

The network analysis indicated that the bacterial genera positively correlated with SOC had more positive edges. In contrast, the proportion of negative edges was higher among the bacterial genera negatively related to SOC. The positive edges suggested that there was mutual cooperation rather than competition within the bacterial assembly (Li *et al.* 2020), whereas negative edges implied that inter-competitive exclusion occurred within the bacterial community (Feng *et al.* 2017). The results from this study indicated that bacterial interaction tended towards cooperation when the soil environment (SOC and fertility level) improved, which confirmed the results of previous studies (Li *et al.* 2019; Xie *et al.* 2019). The network analysis also revealed that most of the genera positively related to SOC were copiotrophic bacteria. Furthermore, the STAMP analysis showed the *Massilia* and *Rhodanobacter* were rich in soils with high fertility levels (SOC≥25.5 g kg^{-1}), whereas *Anaerolinea* dominated in the low-fertility soils (SOC<25.5 g kg^{-1}). Some species of *Massilia* can use a wide range of sugars, organic acids, and amino acids as their single carbon for growth (Zul *et al.* 2008), and *Rhodanobacter* are often isolated from the rhizosphere of many types of plants (Madhaiyan *et al.* 2014; Won *et al.* 2015). *Massilia* and *Rhodanobacter* belong to the phylum Proteobacteria, which generally contains copiotrophic bacteria. This means that they thrive where available nutrient levels are elevated, such as in high-fertility soils. *Anaerolinea* belong to phylum Chloroflexi, which are oligotrophic bacteria. A large number of *Anaerolinea* are found in paddy soils and can decompose diverse C substrates under anaerobic conditions (Zhang *et al.* 2019). *Anaerolinea* have also been shown to have a cellulolytic capacity (Xia *et al.* 2016). Therefore, we can conclude that *Anaerolinea* might have proliferated in the low-fertility soils in our study because they could utilize recalcitrant C.

In our study, the rice yields were about 16 500 and 10 500–12 000 kg ha^{-1} yr^{-1} in the high- and low-fertility paddy fields respectively. The differences in rice yield might indicate variations in the amounts of easily degradable carbon, e.g., root exudates. The different crop yields had an indirect influence on the bacterial community by favoring different copiotrophic or oligotrophic microbial life strategies in soil (Cederlund *et al.* 2014). In contrast, the soil microbial community drives the decomposition of organic matter and nutrient cycling, which affect soil fertility

and agrosystem sustainability (García-Orenes *et al.* 2016; Chen H *et al.* 2018). For example, it has been shown that microbial communities have a considerable influence on soil sustainability when maize (Ramírez *et al.* 2017) or soybean (Meriles *et al.* 2009) are grown. One possible reason is that the microbes may regulate the mineralization of and competition for nutrients that sustain plant productivity (Heijden *et al.* 2008). Therefore, future studies should focus on the relationship between changes of bacterial trophic type and rice production sustainability in red paddy soils with specific parent materials and fertility levels.

5. Conclusion

The effects of parent materials and soil fertility on bacterial diversity were approximately comparative in paddy soils in our study. But soil fertility contributed greater to the variation of bacterial community composition. Soil texture was the primary factor determining bacterial richness and diversity in soils with different parent materials and fertility levels. However, nutrients, especially SOC, determined bacterial community variations. Differences in SOC content led to changes of bacterial interactions and the growth and decline of specific copiotrophic and oligotrophic bacteria. Future work should focus on the relationship between shifts of bacterial trophic type and rice production sustainability in red paddy soils.

Acknowledgements

This work was supported by the National Key Research and Development Program of China (2018YFD0301104-01), the National Natural Science Foundation of China (41201242 and 41907041), the Major Research and Development Program for Science and Technology of Jiangxi Province, China (20182ABC28006), and the “135” Plan and the Field Frontier Project, China (ISSASIP1642). We thank International Science Editing (http://www.internationalscienceediting.com) for language editing. In addition, we are grateful to the anonymous reviewers and editors for their helpful comments.

Appendices associated with this paper can be available on http://www.ChinaAgriSci.com/V2/En/appendix.htm

References

Bhat A K. 2013. Preserving microbial diversity of soil ecosystem: A key to sustainable productivity. *International Journal of Current Microbiology and Applied Sciences*, **2**, 85–101.

Brussaard L, Ruiter P, Brown G. 2007. Soil biodiversity for agricultural sustainability. *Agriculture Ecosystems & Environment*, **121**, 233–244.

Cao Y, Li Y, Li C, Huang G, Lu G. 2016. Relationship between presence of the desert shrub *Haloxylon ammodendron* and microbial communities in two soils with contrasting textures. *Applied Soil Ecology*, **103**, 93–100.

Caporaso J G, Kuczynski J, Stombaugh J, Bittinger K, Bushman F D, Costello E K, Fierer N, Pena A G, Goodrich J K, Gordon J I, Huttley G A, Kelley S T, Knights D, Koenig J E, Ley R E, Lozupone C A, McDonald D, Muegge B D, Pirrung M, Reeder J, *et al.* 2010. QIIME allows analysis of high-throughput community sequencing data. *Nature Methods*, **7**, 335–336.

Carson J K, Gonzalez-Quiñones V, Murphy D V, Hinz C, Shaw J A, Gleeson D B. 2010. Low pore connectivity increases bacterial diversity in soil. *Applied and Environmental Microbiology*, **76**, 3936–3942.

Cederlund H, Wessén E, Enwall K, Jones C M, Juhanson J, Pell M, Philippot L, Hallin S. 2014. Soil carbon quality and nitrogen fertilization structure bacterial communities with predictable responses of major bacterial phyla. *Applied Soil Ecology*, **84**, 62–68.

Conway E J. 1948. Microdiffusion analysis and volumetric error. *Nature*, **161**, 583.

Chau J F, Bagtzoglou A C, Willig M R. 2011. The effect of soil texture on richness and diversity of bacterial communities. *Environmental Forensics*, **12**, 333–341.

Chen H, Xia Q, Yang T, Shi W. 2018. Eighteen-year farming management moderately shapes the soil microbial community structure but promotes habitat-specific taxa. *Frontiers in Microbiology*, **9**, 1776.

Chen X F, Liu M, Kuzyakov Y, Li W T, Liu J, Jiang C Y, Wu M, Li Z P. 2018. Incorporation of rice straw carbon into dissolved organic matter and microbial biomass along a 100-year paddy soil chronosequence. *Applied Soil Ecology*, **130**, 84–90.

Chodak M, Niklinska M. 2010. Effect of texture and tree species on microbial properties of mine soils. *Applied Soil Ecology*, **46**, 268–275.

De’Ath G. 2002. Multivariate regression trees: a new technique for modeling species–environment relationships. *Ecology*, **83**, 1105–1117.

Deng H, Yu Y J, Sun J E, Zhang J B, Cai Z C, Guo G X, Zhong W H. 2015. Parent materials have stronger effects than land use types on microbial biomass, activity and diversity in red soil in subtropical China. *Pedobiologia*, **58**, 73–79.

Dickman S R, Bray R H. 1940. Colorimetric determination of phosphate. *Industrial and Engineering Chemistry*, *Analytical Edition*, **11**, 665–668.

Edgar R C. 2010. Search and clustering orders of magnitude faster than BLAST. *Bioinformatics*, **26**, 2460–2461.

Faoro H, Alves A C, Souza E M, Rigo L U, Cruz L M, Al-Janabi S M, Monteiro R A, Baura V A, Pedrosa F O. 2010. Influence of soil characteristics on the diversity of bacteria in the southern Brazilian Atlantic forest. *Applied and Environmental Microbiology*, **76**, 4744–4749.

Feng K, Zhang Z J, Cai W W, Liu W Z, Xu M Y, Yin H Q,

Wang A J, He Z L, Deng Y. 2017. Biodiversity and species competition regulate the resilience of microbial biofilm community. *Molecular Ecology*, **26**, 6170–6182.

Fierer N, Jackson R B. 2006. The diversity and biogeography of soil bacterial communities. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 626–631.

García-Orenes F, Roldán A, Morugán-Coronado A, Linares C, Cerdà A, Caravaca F. 2016. Organic fertilization in traditional mediterranean grapevine orchards mediates changes in soil microbial community structure and enhances soil fertility. *Land Degradation & Development*, **27**, 1622–1628.

Griffiths R I, Thomson B C, James P, Bell T, Bailey M, Whiteley A S. 2011. The bacterial biogeography of British soils. *Environmental Microbiology*, **13**, 1642–1654.

Guo H C, Wang W B, Luo X H, Wu X P. 2013. Variations in rhizosphere microbial communities of rubber plantations in Hainan island, China. *Journal of Rubber Research*, **16**, 243–256.

Guo H C, Wang W B, Luo X H, Wu X P. 2015. Characteristics of rhizosphere and bulk soil microbial communities in rubber plantations in Hainan island, China. *Journal of Tropical Forest Science*, **27**, 202–212.

Hammer Ø, Harper D A T, Ryan P D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol Electron*, **4**, 1–9.

Heijden M G A V D, Bardgett R D, Straalen N M V. 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*, **11**, 296–310.

Ibekwe A, Kennedy A, Frohne P, Papiernik S, Yang C H, Crowley D. 2002. Microbial diversity along a transect of agronomic zones. *FEMS Microbiology Ecology*, **39**, 183–191.

Jia J, Li Z, Liu M, Che Y. 2010. Effect of glucose addition on N transformations in paddy soils with a gradient of organic C content in subtropical China. *Agricultural Sciences in China*, **9**, 1309–1316.

Johnson M J, Lee K Y, Scow K M. 2003. DNA fingerprinting reveals links among agricultural crops, soil properties, and the composition of soil microbial communities. *Geoderma*, **114**, 279–303.

Józefowska A, Pietrzykowski M, Woś B, Cajthaml T, Frouz J. 2017. Relationships between respiration, chemical and microbial properties of afforested mine soils with different soil texture and tree species: Does the time of incubation matter. *European Journal of Soil Biology*, **80**, 102–109.

Kjeldahl J. 1883. Neue méthode zur bestimmung des stickstoffs in organischen Körpern. *Zeitschrift für Analytische Chemie*, **22**, 366−382. (in German)

Kuramae E E, Yergeau E, Wong L C, Pijl A S, Veen J, Kowalchu G A. 2012. Soil characteristics more strongly influence soil bacterial communities than land-use type. *FEMS Microbiology Ecology*, **79**, 12–24.

Lauber C L, Hamady M, Knight R, Fierer, N. 2009. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. *Applied and Environmental Microbiology*, **75**, 5111–5120.

Li P F, Liu M, Ma X Y, Wu M, Jiang C Y, Liu K, Liu J, Li Z P. 2020. Responses of microbial communities to a gradient of pig manure amendment in red paddy soils. *Science of the Total Environment*, **705**, 135884.

Li W T, Liu M, Wu M, Jiang C Y, Kuzyakov Y, Gavrichkova O, Feng Y Z, Dong Y H, Li Z P. 2019. Bacterial community succession in paddy soil depending on rice fertilization. *Applied Soil Ecology*, **144**, 92−97.

Liu M, Liu J, Chen X F, Jiang C H, Wu M, Li Z P. 2018. Shifts in bacterial and fungal diversity in a paddy soil faced with phosphorus surplus. *Biology and Fertility of Soils*, **54**, 259–267.

Madhaiyan M, Poonguzhali S, Saravanan V S, Kwon S W. 2014. *Rhodanobacter glycinis* sp nov., a yellow-pigmented gamma proteobacterium isolated from the rhizoplane of field-grown soybean. *International Journal of Systematic and Evolutionary Microbiology*, **64**, 2023−2028.

Mebius L J. 1960. A rapid method for the determination of organic carbon in soil. *Analytica Chimica Acta*, **22**, 120−124.

Melero S, Madejon E, Herencia J F, Ruiz J C. 2007. Biochemical properties of two different textured soils (loam and clay) after the addition of two different composts during conversion to organic farming. *Spanish Journal of Agricultural Research*, **5**, 593–604.

Meriles J M, Vargas G S, Conforto C, Figoni G, Lovera E, March G J, Guamán C A. 2009. Soil microbial communities under different soybean cropping systems: characterization of microbial population dynamics, soil microbial activity, microbial biomass, and fatty acid profiles. *Soil & Tillage Research*, **103**, 271–281.

Müller T, Höper H. 2004. Soil organic matter turnover as a function of the soil clay content: Consequences for model applications. *Soil Biology & Biochemistry*, **36**, 877–888.

Naveed M, Herath L, Moldrup P, Arthur E, Nicolaisen M, Norgaard T, Ferre T P A, Jonge L W. 2016. Spatial variability of microbial richness and diversity and relationships with soil organic carbon, texture and structure across an agricultural field. *Applied Soil Ecology*, **103**, 44–55.

Pansu M, Gautheyrou J. 2006. *Handbook of Soil Analysis*: *Mineralogical*, *Organic and Inorganic Methods*. Springer, Berlin Heidelberg, Berlin.

Parks D H, Tyson G W, Hugenholtz P, Beiko R G. 2014. STAMP: Statistical analysis of taxonomic and functional profiles. *Bioinformatics*, **30**, 3123–3124.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [2019-09-10]. http://www.R-project.org/

Ramirez K S, Lauber C L, Knight R, Bradford M A, Fierer N. 2010. Consistent effects of nitrogen fertilization on soil bacterial communities in contrasting systems. *Ecology*, **91**, 3463–3470.

Ramírez M, López-Piñeiro A, Peña D, Nunes J R, Albarrán Á, Muñoz A, Gama J, Loures L. 2017. Seasonal and

interannual fluctuation of the microbial soil community in a maize field under long-term conservation agriculture management. *Sustainability*, **9**, 778.

Shannon P, Markiel A, Ozier O, Baliga N S, Wang J T, Ramage D, Amin N, Schwikowski B, Ideker T. 2003. Cytoscape: A software environment for integrated models of biomolecular interaction networks. *Genome Research*, **13**, 2498–2504.

Shen C, Xiong J, Zhang H, Feng Y, Lin X, Li X, Liang W, Chu H. 2013. Soil pH drives the spatial distribution of bacterial communities along elevation on Changbai Mountain. *Soil Biology & Biochemistry*, **57**, 204–211.

Sheng R, Qin H, O'Donnell A G, Huang S, Wu J, Wei W. 2015. Bacterial succession in paddy soils derived from different parent materials. *Journal of Soils and Sediments*, **15**, 982–992.

Sun L, Xun W, Huang T, Zhang G, Gao J, Ran W, Li D, Shen Q, Zhang R. 2016. Alteration of the soil bacterial community during parent material maturation driven by different fertilization treatments. *Soil Biology & Biochemistry*, **96**, 207–215.

Sun R, Zhang X X, Guo X, Wang D, Chu H. 2015. Bacterial diversity in soils subjected to long-term chemical fertilization can be more stably maintained with the addition of livestock manure than wheat straw. *Soil Biology & Biochemistry*, **88**, 9–18.

Ulrich A, Becker R. 2006. Soil parent material is a key determinant of the bacterial community structure in arable soils. *FEMS Microbiology Ecology*, **56**, 430–443.

Wagai R, Kitayama K, Satomura T, Fujinuma R, Balser T. 2011. Interactive influences of climate and parent material on soil microbial community structure in Bornean tropical forest ecosystems. *Ecological Research*, **26**, 627–636.

Wang Q, Garrity G M, Tiedje J M, Cole J R. 2007. Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. *Applied and Environmental Microbiology*, **73**, 5261–5267.

Won K, Singh H, Ngo H T T, Son H M, Kook M C, Kim K Y, Yi T H. 2015. *Rhodanobacter koreensis* sp. nov., a bacterium isolated from tomato rhizosphere. *International Journal of Systematic and Evolutionary Microbiology*, **65**, 1180−1185.

Xia Y, Wang Y B, Wang Y, Chin F Y L, Zhang T. 2016. Cellular adhesiveness and cellulolytic capacity in *Anaerolineae* revealed by omics-based genome interpretation. *Biotechnology for Biofuels*, **9**, 111.

Xie L, Zhang Q J, Cao J L, Liu X F, Xiong D C, Kong Q, Yang Y S. 2019. Effects of warming and nitrogen addition on the soil bacterial community in a subtropical Chinese fir plantation. *Forest*, **10**, 861.

Xu Y B, Cai Z C. 2007. Denitrification characteristics of subtropical soils in China affected by soil parent material and land use. *European Journal of Soil Science*, **58**, 1293–1303.

Zhang Y, Li Q, Chen Y L, Dai Q G, Hu J. 2019. Dynamic change in enzyme activity and bacterial community with long-term rice cultivation in mudflats. *Current Microbiology*, **76**, 361−369.

Zul D, Wanner G, Overmann J. 2008. *Massilia brevitalea* sp. nov., a novel beta proteobacterium isolated from lysimeter soil. *International Journal of Systematic and Evolutionary Microbiology*, **58**, 1245−1251.

Executive Editor-in-Chief ZHANG Wei-li
Managing editor SUN Lu-juan