Responses of microbial community structure to land-use conversion and fertilization in southern China

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Article history:
Received 14 February 2015
Accepted 8 June 2015
Available online 26 June 2015

Keywords:
Land use
Fertilization
Microbial community structure
Phospholipid fatty acid (PLFA)
Soil physicochemical properties

A B S T R A C T

A short-term experiment was carried out in southern China to investigate the effects of land-use conversion from rice paddies to vegetable fields and fertilization on soil microbial community structure by analyzing soil phospholipid fatty acid (PLFA) profiles. A split-plot design with four replicates was adopted, in which land use (paddy and vegetable field) was the first-level treatment and fertilization (conventional fertilization and no fertilization) was nested as the second level. Our results showed that both land-use conversion and fertilization had significant effects on microbial community structure. After 2 years of land-use conversion, the total amount of PLFAs were 3.54 and 2.97 nmol g\(^{-1}\) for fertilized (V–F) and unfertilized (V–NF) vegetable fields, respectively, and 3.19 and 2.32 nmol g\(^{-1}\) for fertilized (R–F) and unfertilized (R–NF) rice paddies, respectively. Soil fungal PLFAs were 1.04 and 0.87 nmol g\(^{-1}\) for V–F and V–NF, respectively, which were significantly increased by 13.9 and 11.4 times compared with those of R–F and R–NF, respectively. The ratio of fungal to bacterial PLFAs significantly increased in vegetable fields compared with rice paddies. No significant differences were found in the total, bacterial, and actinomycetic PLFAs between vegetable fields and rice paddies. The application of fertilizer significantly increased the amount of total PLFAs and bacterial PLFAs. With land-use conversion and fertilization, soil physicochemical properties also changed, and microbial community structure showed a significant relationship with soil water content, N\(_\text{he-N}\), and pH, which explained the land-use conversion and fertilization effects on soil microbial community composition.

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1. Introduction

Soil microorganisms play a unique role in the processes of nutrient cycling [1], carbon and nitrogen turnover [2,3], and greenhouse gas emissions [4]. Agricultural management practices, such as cropping rotation, irrigation, and fertilization are known to have significant effects on microbial community structure in soils [5–9], which thereby influence the overall agroecosystem functions [10–12]. Land-use conversion, such as the conversion of rice paddies to uplands or vice versa, can significantly affect soil microbial communities [13,14]. Bossio et al. [15] found that flooded paddy soils had higher abundance of branched fatty acids, lower abundance of monounsaturated fatty acids, and lower abundance of fungi and actinomycetes than upland tomato fields. Sun et al. [16] found that land-use change from paddy to vegetables decreased bacterial diversity and soil microbial biomass despite an increase in the abundance of culturable microorganisms.

Although previous studies have reported that land-use conversion could alter soil microbial communities [17,18], the mechanisms of the effects of land-use conversion on soil microbial communities are poorly understood. It is commonly believed that the land-use-conversion-induced changes in soil physical and chemical properties result in the transformation of soil microbial communities, but no consistent relationships have been observed among various
studies. Soil water content has been shown to influence soil microbial communities directly and indirectly through impacts on soil aeration and nutrient availability [19]. Yang et al. [20] found that total phospholipid fatty acids (PLFAs) decreased significantly after land-use change from paddy to orchard, and soil moisture, organic matter, and nitrogen (N) were found to be the most important environmental factors affecting the variations in microbial community structure. Soil pH is another important factor that regulates soil microbial communities [21,22]. In the process of land-use conversion from paddy to upland, pH was one of the most important factors affecting soil microbial community structure [20].

Changes in fertilization often come with land-use change because different crops have different nutrient demands. The application of N fertilizer has been shown to have a significant influence on soil microbial community [23]. Yevdokimov et al. [24] found that N addition could increase the ratio of fungal to bacterial biomass and decrease the ratio of Gram-positive to Gram-negative bacteria using the PLFA technique. Li et al. [9] also found that the application of N fertilizer significantly increased soil microbial biomass, including bacteria, fungi, actinomycetes, Gram-positive bacteria, and Gram-negative bacteria. Fertilization can affect soil microbial communities through changing soil physico-chemical properties. Fertilization changes the soil C/N ratio, which further affects the microbial community and the decomposition rate [25]. Fertilization has been shown to be one of the drivers of soil acidification [26,27] and could affect microbial community structure indirectly by changing soil pH [28].

In southern China, large areas of rice paddies have been converted to upland vegetable cultivation with the acceleration of urbanization and economic interests in the past decades. The vegetable cultivation area in China has grown from 3.5 to 17.9 million hectares, while the rice cultivation area has decreased from 33.3 to 26.5 million hectares since the 1980s [16]. Understanding the effects of land-use conversion on soil microbial communities is critical to elucidate the mechanisms and processes of greenhouse gas emissions and the potential for greenhouse gas management in China and beyond. And the influence of land-use conversion on soil conditions was undergoing a dynamic change. For example, Sun et al. [16] found that soil microbial community structure differed significantly between paddy and vegetable fields, and the soil microbial community structure of the new vegetable fields (10 years) was significantly different from that of the old vegetable fields (100 years). Thus, short-term, long-term and longer-term studies would give the findings a stronger underpinning. However, few studies have paid attention to the changes of microbial community structure in the early stage of land-use conversion. We hypothesize that two years of land-use conversion from paddy to vegetables and fertilization would significantly alter the soil microbial community structure and soil water content and pH could be important factors in shaping the soil microbial community structure. The current study used the PLFA method to examine: (1) the effects of land-use conversion from rice paddies to vegetable fields on soil microbial community structure; (2) the effects of fertilization on the soil microbial community structure; and (3) the environmental factors related to the changes in soil microbial community structure.

2. Materials and methods

2.1. Site description

The experimental fields were located at the Qianyanzhou Ecological Research Station (QYZ, 26°44′46″ N, 115°04′05″ E) in Jiangxi Province, southern China. The site is a typical, red soil hilly region with a subtropical monsoon climate. According to meteorological observations from 1989 to 2010 at QYZ, the mean air temperature is 18.0 °C with the coldest and warmest months in January and July, respectively. This area has abundant precipitation with an average annual precipitation of 1509.0 mm. Double cropping of paddy rice is the main cropping system in this area, but large areas of rice paddies have been converted to upland vegetable fields in past decades. Soil texture was sandy loam with 58% sand, 31% silt, and 11% clay. The topsoil (0–10 cm) has an organic carbon content of 9.40 g kg⁻¹ and total N content of 1.00 g kg⁻¹. The soil pH was 4.99 and the bulk density was 1.30 g cm⁻³.

2.2. Experimental design

The experimental fields had been continuously cultivating paddy rice for about 10 years. In July 2012, we converted a portion of the rice paddies to upland vegetable fields by draining the fields, with the remaining land continuing with rice cultivation. Each cropping system had two fertilization levels, e.g., conventional fertilization and no fertilization. Thus, the experiment included four treatments with four replicates in a split-plot design, in which the main plots were the cropping systems and each cropping system was split into subplots with and without fertilization. The treatments included vegetable fields with fertilization (V–F) and without fertilization (V–NF), and rice fields with fertilization (R–F) and without fertilization (R–NF). Each plot had an area of 120 m² (10 m × 12 m). In rice fields, rice was planted twice a year, with a fallow period in winter. In vegetable fields, vegetables were planted three times a year. The spacing was 17 cm × 25 cm for rice cultivation and 20 cm × 35 cm for vegetable cultivation. Compound fertilizer (N:P₂O₅:K₂O = 15%:15%:15%) and urea were applied at a rate of 358 kg N ha⁻¹ per year to the fertilized fields. The corresponding amount of phosphorus (P) and potassium (K) applied were 63 kg P ha⁻¹ and 119 kg K ha⁻¹ per year for paddy fields and 133 kg P ha⁻¹ and 254 kg K ha⁻¹ per year for vegetable fields, respectively. Conventional tillage was carried out at the beginning of each growing season.

2.3. Soil sampling

Soil samples were collected across the field at a depth of 0–20 cm using a corer device (diameter, 3 cm) in July 2014. In each plot, five soil cores were collected and pooled together as a composite sample. Composite samples were taken to the laboratory and plant residues and stones were removed from the soil samples. Each sample was sieved through 2-mm mesh and separated into three parts: one part was air dried for measurements of soil organic carbon (SOC), total N (TN), and pH, another part was preserved at −20 °C as fresh soil for measurements of soil NH₄⁺–N and NO₃⁻–N, and the third part was freeze-dried and preserved at −80 °C for determination of PLFAs.

2.4. Soil property measurements

Soil water content was automatically recorded by an automatic data logging system through wireless technology. The soil NH₄⁺–N and NO₃⁻–N were extracted from 20 g fresh soil with 1 mol L⁻¹ KCl (soil:extract, 1:5) and analyzed using a flow-injection autoanalyzer ((CFA)-AA3, SEAL, Germany). Soil pH was measured at a soil:water ratio of 1:2.5 using a pH meter. SOC and TN were measured using a C/N analyzer (Elementar, Vario Max CN, Germany) with the combustion temperature of 900 °C.

2.5. PLFA analysis

PLFAs were analyzed using the method described by Bååth and Anderson [29]. Lipids were extracted from freeze-dried soil (8 g) in
a single-phase mixture of chloroform:methanol:phosphate buffer (1:2:0.5). After extraction, the lipids were separated into neutral lipids, glycolipids, and polar lipids (phospholipids) on a silicic acid column. The samples were analyzed using a Thermo ISQ gas chromatography-mass spectroscopy system (TRACE GC Ultra ISQ). Helium was used as the carrier gas. The fatty-acid methyl esters extracted by the buffer were then injected in splitless mode and resolved via a DB-5 column (30 m × 0.25 mm ID × 0.25 mm) using an initial temperature of 150 °C for 4 min, after which the temperature was ramped to 250 °C at 4 °C min⁻¹ and held for 5 min. The concentrations of the individual compounds were obtained by comparing the peaks with an internal standard (nonadecanoic acid methyl ester 19:0). Thirteen PLFAs ([i]15:0, [a]15:0, 15:0, [i]16:0, 16:1ω7c, i17:0, cy17:0, cy19:0, 17:0, 18:1ω9c, 18:2ω6, 10Me16:0, 10Me18:0) were used for data analysis. The fatty-acid signatures 15:0, 17:0, [i]15:0, [a]15:0, [i]16:0, i17:0, 16:1ω7c, cy17:0, and cy19:0 were used as bacterial biomarkers. The fatty acids 18:1ω9c and 18:2ω6 were used as fungal indicators and 10Me16:0 and 10Me18:0 were used as indicators for the actinomycetes. The fatty acids [i]15:0, [a]15:0, [i]16:0, and i17:0 were used to represent Gram-positive (G⁺) bacteria, while 16:1ω7c, cy17:0, and cy19:0 were used to represent Gram-negative (G⁻) bacteria [30,31].

2.6. Statistical analysis
A general linear model for univariate analysis of variance for split plots was used to evaluate the significant differences in soil properties and microbial community structure from the land-use and fertilization treatments (P < 0.05). Data shown were means of the four replicates. Principal component analysis (PCA) was used to analyze soil microbial community structure. The relationship between soil microbial community structure and microbial properties was analyzed using redundancy analysis (RDA), in which microbial lipids were used as dependent variables and soil properties were explanatory variables [20]. The environmental factors affecting microbial community structure were detected by a permutation test (999 permutations). PCA and RDA were conducted with CANOCO for Windows 4.5. General linear model analysis was performed using SPSS 19.0 (SPSS Inc., Chicago, IL, USA). Figures were generated using the Origin 8.6 package (Origin Lab Corporation, USA) and CANOCO for Windows 4.5.

3. Results

3.1. Soil physicochemical properties

Land-use conversion from paddy rice to upland vegetables significantly changed the soil physicochemical properties (Table 1). The concentrations of NH₄⁻-N and NO₃⁻-N in the vegetable fields increased by 3.6 and 1.2 times, respectively, compared with the concentrations in paddy soils. Soil pH decreased with the conversion. When fertilizer was applied, soil pH significantly decreased from 5.00 to 4.56, and when fertilizer was not applied, the change in soil pH with land-use conversion was not significant. No significant differences in the SOC and TN concentrations were found between vegetable fields and rice paddies (P > 0.24). The land-use conversion significantly decreased the average soil water content of the two years regardless of fertilizer application.

Fertilization significantly influenced soil physicochemical properties (Table 1). Fertilization significantly increased NH₄⁻N and NO₃⁻-N by 8.0 and 1.3 times, respectively, compared with the no-fertilization treatments. Specifically, V–F had significantly higher NH₄⁻N and NO₃⁻-N contents than V–NF, while no significant difference in mineral N content was found between R–F and R–NF. Land use and fertilization had a significant interactive effect on soil NH₄⁻-N and NO₃⁻-N content (P < 0.05). Fertilization significantly decreased soil pH, especially in upland vegetable fields. Fertilization also significantly increased SOC and TN (P < 0.05), but had no interaction with land use type.

3.2. Soil microbial community

The microbial biomass represented by total PLFAs was higher in the vegetable soil than in the paddy soil, but the difference was not statistically significant (P = 0.14; Table 2). Fertilizer PLFAs and actinomycetic PLFAs did not change significantly with land-use conversion (P > 0.12). Soil fungal biomass significantly increased with land-use conversion from rice paddies to vegetable fields (P < 0.01). Fungal biomass of V–F and V–NF increased by 13.9 and 11.4 times compared with that of R–F and R–NF, respectively. The fungal/bacterial PLFAs ratio of V–F and V–NF reached 0.45 ± 0.04 and 0.44 ± 0.08, respectively, which were significantly higher than those of the paddy soil (P < 0.01). Land-use conversion had little impact on the ratio of Gram-negative bacteria to Gram-positive bacteria (G⁻/G⁺; P = 0.89; Table 2).

In addition to the land-use conversion effects, we also found that fertilization had considerable impacts on soil microbial community structure (Table 2). Fertilization significantly increased the total PLFAs by 37.5% in paddy fields and 19.2% in vegetable fields, especially the bacterial biomass. The soil bacterial biomass of R–F was 1.4 times that of R–NF, and the bacterial biomass of V–F was 1.2 times that of V–NF. Fertilization had little impact on soil fungal biomass (P = 0.36), actinomycete biomass (P = 0.61), G⁻/G⁺ (P = 0.76), and fungal/bacterial ratio (P = 0.998; Table 2). Land-use conversion and fertilization had no significant interactive effect on soil microbial community composition (P > 0.34; Table 2).

The effects of land-use conversion and fertilization on soil microbial communities were investigated by principal component analysis (PCA; Fig. 1A). The first and second principal components (PC1 and PC2) explained 56.2 and 36.3% of the total variance in PLFAs. The effect of land-use conversion was reflected in PC1 with positive values for the vegetable fields (square symbols in Fig. 1A) and negative values for the rice paddies (circular symbols in Fig. 1A), while PC2 carried some information on the effects of

### Table 1

<table>
<thead>
<tr>
<th></th>
<th>NH₄⁻-N mg kg⁻¹</th>
<th>NO₃⁻-N mg kg⁻¹</th>
<th>pH</th>
<th>SOC g kg⁻¹</th>
<th>TN g kg⁻¹</th>
<th>Water content %</th>
</tr>
</thead>
<tbody>
<tr>
<td>R–F</td>
<td>27.88 ± 8.61ab</td>
<td>6.75 ± 3.10ab</td>
<td>5.00 ± 0.13*</td>
<td>11.13 ± 0.45ab</td>
<td>1.09 ± 0.03ab</td>
<td>24.48 ± 2.33*</td>
</tr>
<tr>
<td>R–NF</td>
<td>9.39 ± 1.62a</td>
<td>4.95 ± 1.72a</td>
<td>5.21 ± 0.15*</td>
<td>10.27 ± 0.47a</td>
<td>1.14 ± 0.03a</td>
<td>24.48 ± 2.32a</td>
</tr>
<tr>
<td>V–F</td>
<td>160.68 ± 14.80a</td>
<td>19.07 ± 1.99a</td>
<td>4.56 ± 0.08ab</td>
<td>11.92 ± 0.57a</td>
<td>1.21 ± 0.06a</td>
<td>18.05 ± 1.00a</td>
</tr>
<tr>
<td>V–NF</td>
<td>11.56 ± 3.98b</td>
<td>6.16 ± 1.62b</td>
<td>4.94 ± 0.06a</td>
<td>10.56 ± 0.18b</td>
<td>1.04 ± 0.05b</td>
<td>17.68 ± 0.97b</td>
</tr>
<tr>
<td>Land-use (L)</td>
<td>P &lt; 0.01</td>
<td>P &lt; 0.01</td>
<td>P = 0.01</td>
<td>P = 0.25</td>
<td>P = 0.24</td>
<td>P &lt; 0.01</td>
</tr>
<tr>
<td>Fertilization</td>
<td>P &lt; 0.01</td>
<td>P &lt; 0.01</td>
<td>P = 0.02</td>
<td>P = 0.03</td>
<td>P = 0.03</td>
<td>P = 0.92</td>
</tr>
<tr>
<td>L × F</td>
<td>P &lt; 0.01</td>
<td>P &lt; 0.03</td>
<td>P = 0.25</td>
<td>P = 0.59</td>
<td>P = 0.22</td>
<td>P &lt; 0.02</td>
</tr>
</tbody>
</table>

Data labeled with different letters indicated soil properties were significantly different at P < 0.05. Treatments: R–F: rice paddies with fertilization; R–NF: rice paddies with no fertilization; V–F: vegetables with fertilization; V–NF: vegetables without fertilization. Variables: NH₄⁻-N: ammonium nitrogen; NO₃⁻-N: nitrate nitrogen; SOC: soil organic carbon; TN: total nitrogen.

Table 1 Soil physicochemical properties after 2 years of land-use conversion from paddy rice to upland vegetables (Values presented are means ± SE).
Treatments: R

Data labeled with different letters indicated soil microbial community structure were significantly different at \( P < 0.05 \). Treatments: R–F: rice paddies with fertilization; R–NF: rice paddies with no fertilization; V–F: vegetables with fertilization; V–NF: vegetables without fertilization.

fertilization (filled versus open symbols in Fig. 1A) on microbial communities. Specifically, the vegetable soil was more abundant in 18:1w9c, while the paddy soil was more abundant in 17:0 and cy17:0 (Fig. 1B). As indicated by PC2, fertilization favored the a15:0 and i15:0 PLFAs, while the non-fertilized soils favored 18:2w6 (Fig. 1B).

3.3. Relationships of microbial community structure with soil properties

Soil microbial community structure was significantly influenced by changes in environmental factors associated with land-use conversion and fertilization. Redundancy analysis (RDA) showed that the first (RD1) and second axes (RD2) explained 54.5 and 8.1% of the total variance in the PLFA profiles, respectively (Fig. 2). Soil water content, NH4\(^+\)-N, and pH were the key factors in shaping the soil microbial communities (Fig. 2). This was also demonstrated by simple linear regression analysis, which showed that soil water content, NH4\(^+\)-N, and pH explained 51.6, 22.4, and 19.6%, respectively, of the variance in soil microbial community structure (Table 3).

4. Discussion

4.1. Effect of land-use conversion on microbial community structure

In this study, we found that land-use conversion from rice paddies to vegetable fields significantly altered the fungal PLFAs and the fungal/bacterial PLFA ratio (Fig. 1, Table 2). Further analyses showed that the effect of land-use conversion on soil microbial communities mainly resulted from its impacts on environmental factors, such as soil water content, NH4\(^+\)-N, and soil pH. After the land-use conversion, the soil environment turned from anaerobic to aerobic, and the abundance of PLFA cy17:0, which is indicative of...
Table 3
Results of the simple linear regression analysis between soil physicochemical properties and microbial community structure.

<table>
<thead>
<tr>
<th></th>
<th>R²</th>
<th>P</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water content</td>
<td>0.52**</td>
<td>&lt;0.01</td>
<td>14.91</td>
</tr>
<tr>
<td>NH₄⁻N</td>
<td>0.22*</td>
<td>0.02</td>
<td>4.05</td>
</tr>
<tr>
<td>pH</td>
<td>0.20*</td>
<td>0.03</td>
<td>3.41</td>
</tr>
<tr>
<td>NO₃⁻N</td>
<td>0.14</td>
<td>0.10</td>
<td>2.34</td>
</tr>
<tr>
<td>SOC</td>
<td>0.03</td>
<td>0.64</td>
<td>0.49</td>
</tr>
<tr>
<td>TN</td>
<td>0.02</td>
<td>0.67</td>
<td>0.49</td>
</tr>
</tbody>
</table>

*Significant at P < 0.05, **significant at P < 0.01.
Variables: NH₄⁻N: ammonium nitrogen; NO₃⁻N: nitrate nitrogen; SOC: soil organic carbon; TN: total nitrogen.

anaerobic bacteria [32], decreased significantly. Meanwhile, the abundance of a fungal biomarker, 18:1ω9c, significantly increased, suggesting the converted vegetable fields favored fungal growth. Indeed, we found that the fungal biomass and the ratio of fungi/bacteria dramatically increased with the land-use conversion from rice paddies to vegetable fields (Table 2). Our results were in line with previous studies [15,20]. For example, Yang and Zhang [20] found that land-use conversion from paddy to orchard significantly increased the relative abundance of fungi. In an incubation experiment using polycarbonate pots, Tian et al. [33] found that the fungi/bacteria ratio of the continuously flooded treatment was 1.4 times lower than the non-flooded treatment, which supports our result that water regimes could alter the fungi/bacteria ratio. It was noted that the higher ratio of fungi/bacteria might indicate better sustainability of the vegetable fields, because fungi have greater growth yield efficiency than bacteria. That is, for each unit of substrate C used, fungi invest a greater proportion into biomass and metabolite production than bacteria [34]. Thus, fungi-dominated soils might have greater C storage and slower C turnover [34]. De Vries et al. [35] found that fungi-dominated soil might result in lower N mineralization as fungi have higher C/N ratios than bacteria. However, our result that the land-use conversion had little effect on bacterial biomass does not support other studies in the literature. For example, Li et al. [13] found that soil bacterial biomass significantly decreased 5 years after land-use conversion from paddy to vegetable field in Jiangsu Province.

In this study, we found that the most significant factor affecting the structure of soil microbial communities was soil water content (Fig. 2, Table 3), which was significantly decreased by the conversion from paddy to vegetables (Table 1). Previous studies also concluded that soil water content was one of the major determinants of soil microbial community composition [9]. Land-use-conversion-induced changes in soil microbial community were also related to soil pH and NH₄⁻N content. A previous study also concluded that soil pH and nutrient status, not specifically land-use type, could best predict shifts in microbial community composition [21]. We found that soil pH significantly decreased after 2 years of conversion from the rice paddies to vegetable fields. Our result was similar to a previous study where pH decreased after conversion to upland from paddy fields in acidic soil [36]. This decreased soil pH might play an important role in shaping the soil microbial community under land-use conversion. Rousk et al. [37] found that bacterial growth decreased and fungal growth increased with lower pH.

4.2. Effect of fertilization on microbial community structure

Soil microbial community structure was influenced by fertilization. In our study, fertilization exerted a significant impact on the bacterial biomass (Table 2), which agrees with a previous study that the effect of fertilizer amendment on bacterial communities was more dramatic than land use change [6]. The total PLFAs in this study increased with N fertilization, which was consistent with previous studies [9]. Most soil microbes are heterotrophic and use organic C as C and energy sources. Therefore, fertilization could not only stimulate microbial growth by providing a N source but also promote plant growth, providing root exudates as C sources for microbial growth [9,38,39].

In this study we found that fertilization significantly increased soil NH₄⁻N, NO₃⁻N, SOC, and TN, and decreased soil pH (Table 1). Liebig et al. [40] also found that fertilization decreased soil pH and increased SOC and TN. Soil acidification through nitrification of ammoniacal fertilizer was responsible for the pH decrease, which further altered the soil microbial community composition. Earlier studies also found that soil total PLFAs were highly correlated with SOC and TN [41]. In this study, fertilization increased SOC and TN as well as total PLFAs, although SOC and TN had no significant effect on soil microbial community structure.

5. Conclusions

After land–use conversion from paddy to vegetable fields, fungal PLFAs and the fungal/bacterial ratio significantly increased. Bacterial PLFAs did not change significantly. Similarly, fertilization enhanced the total PLFAs and bacterial PLFAs in both rice paddies and vegetable fields. Land use and fertilization had no interactive effect on soil microbial community composition. Soil microbial community structure was affected by soil physicochemical properties, which were subject to land–use conversion and fertilization. Soil water content, NH₄⁻N, and pH were the three most important factors in shaping the soil microbial community structure. These findings contribute towards an understanding of the changes in soil microbial communities in response to agricultural management practices and land–use conversion trends in China and beyond.

Acknowledgments

This work was financially supported by the National Basic Research Program of China (973 Program, 2012CB417103) and the National Natural Science Foundation of China (41001179). Authors also thank the academic editor and anonymous reviewers for their constructive comments, which helped in improving the manuscript.

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