RESEARCH ARTICLE

Combining organic and inorganic fertilization increases rice yield and soil nitrogen and carbon: dissolved organic matter chemodiversity and soil microbial communities

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Abstract

Background and aims   Dissolved organic matter (DOM) is an active component of the soil organic carbon (SOC) and nitrogen (N) pool. However, the relationship between DOM chemodiversity and microbial communities, and their effects on the C and N in paddy fields under organic or inorganic fertilization, are poorly understood but important for sustainable agricultural production.

Methods   We conducted a six-year experiment in paddy fields under the following different organic and inorganic fertilizer treatments: no fertilizer (CK), chemical fertilizer (150 kg·hm^{-2} N; CF), 50% N from chemical fertilizer + 50% N from decomposed cattle manure (CMF50), and manure fertilizer (100% N from decomposed cattle manure; MF).

Results   CMF50 exhibited the highest yield (10.89% increase compared with CF). MF and CMF50 enriched the availability and content of soil N, which in turn exhibited a strong effect on net N mineralization and increased SOC and the amount of recalcitrant components of DOM. However, the continuous use of CF led to an increase in both soil bulk density and the number of anaerobic organisms *Anaerolinea* and *Bellilinea*. The fractions of DOM containing lignin-like and lipid-like compounds were strongly correlated with *Anaerolinea* and *Bellilinea* and contributed to net N mineralization and SOC. Continuous use of CF facilitated net N mineralization but decreased both DOC and SOC.

Conclusions   Continuous applications of CMF50 and MF improved the microbial communities and increased the recalcitrant components of DOM, thus highlighting the importance of the relationship between DOM composition and soil microbial communities while assessing the soil N and SOC.

Keywords   Paddy field · Fertilization treatment · Dissolved organic matter composition · Bacterial communities · Net nitrogen mineralization · Yield

Responsible Editor: Hans Lambers.

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Abbreviations

AI	Aromaticity index
AN	Alkali-hydrolysable N
CF	Chemical fertilizer

CK	No fertilizer
CMF50	50% N from chemical fertilizer + 50% N from decomposed cattle manure
DBE-O	Double bond equivalence minus oxygen value
DOC	Dissolved organic carbon
DOM	Dissolved organic matter
FT-ICR-MS	Fourier-transform ion cyclotron resonance mass spectrometry
MF	Manure fertilizer
OTU	Operational taxonomic units
SOC	Soil organic carbon
RDA	Redundancy analysis
SPE	Solid-phase extraction
TN	Total nitrogen

Introduction

Paddy fields are a major source of inland dissolved organic matter (DOM) (Bouman et al. 2007). DOM is an active component of the soil organic carbon (SOC) pool, playing a crucial role in biogeochemical cycles on a global scale (Li et al. 2018a; Weiwei et al. 2018). DOM provides soluble organic substrates that sustain microbial growth and activity (Guo et al. 2018). However, the complex molecular composition of DOM has made understanding its relationship with microbial communities challenging, particularly with regards to the carbon (C) and nitrogen (N) cycles in paddy fields under organic and inorganic fertilization (Li et al. 2018b; Yu et al. 2020).

Ultra-high-resolution Fourier-transform ion cyclotron resonance mass spectrometry (FT-ICR-MS) has provided unprecedented resolution of thousands of intact molecular components within DOM. This technique has been successfully applied to marine and terrestrial environments (Li et al. 2018a; Osterholz et al. 2016). However, few studies have focused on using FT-ICR-MS to analyze DOM composition and its association with microbial communities, SOC, and N mineralization in paddy fields (Li et al. 2018b, c). Chemical fertilizers can increase crop yields and soil N mineralization but can also deplete the SOC pool (Alam et al. 2019; Gai et al. 2018; Mulvaney et al. 2009). Organic fertilizer combined with chemical fertilizer may be a potential strategy to enrich soil N and SOC (Rong et al. 2016).

Soil N mineralization is generally limited by microbial N assimilation when microorganisms are exposed to substrates with N limitations (Fujii et al. 2018). In other words, increasing N-containing DOM in N-limited soil might be favorable for soil N mineralization. Therefore, DOM fractions that contain N might serve as a significant source of N to promote the net mineralization of N in paddy soil (Fujii et al. 2018; Wu et al. 2019). N fertilizer application in upland regions decreases the levels of recalcitrant lignin-like components; which may be attributed to the N-containing DOM obtained via microbial metabolism (Li et al. 2018b, d). The depletion of lignin-like components may also lead to an increase in lipid synthesis, which generally provides an energy source for microbes (Chong et al. 2018; He et al. 2022; Lee et al. 2019). However, the content of SOC and recalcitrant lignin-like components of DOM in upland soil can be increased by the long-term application of organic fertilizer (Ghosh et al. 2018; Li et al. 2018d).

N-mining bacteria decompose recalcitrant but N-rich soil organic matter (SOM) pools to obtain more mineralized N (Coonan et al. 2020; Moorhead and Sinsabaugh 2006; Yin et al. 2018). Hence, we hypothesized that the continuous application of organic fertilizer inhibits the decrease of recalcitrant lignin-like fractions, which may lead to a decrease in N-containing DOM fractions, including protein and amino sugar-like fractions that act as important N sources, and lipid-like fractions that may act as a core energy source to stimulate N mineralization by soil microbes when populations are near carrying capacity, thereby inhibiting soil net N mineralization while increasing soil C and N contents in paddy fields. We performed field experiments between 2015 and 2020 in a paddy field exposed to different organic and inorganic fertilizer treatments to test the above hypotheses.

Materials and methods

Study site

The field site was located at the experimental farm of the Foshan Institute of Agricultural Science, Guangdong Province, China (23.52886°N, 112.85709°E, Fig. S1). The region has a subtropical monsoon climate with a mean annual rainfall of 1688 mm and mean minimum and maximum temperatures in summer and winter of 28–34 °C

and 13–19 °C, respectively. The soil on the farm is classified as redogenic paddy soil developed from alluvial deposits. The 2015 soil properties were: pH 5.68, organic matter content 22.3 g·kg^{-1}, TN 1.11 g·kg^{-1}, alkali-hydrolyzable N (AN) 133.6 mg·kg^{-1}, available P 41.8 mg·kg^{-1}, and available K 141.0 mg·kg^{-1}.

Experimental design

The continuous fertilization experiment began in 2015 with two *Oryza sativa* L. crops per year, comprising an early season crop (sown during early to mid-March and harvested between early July and mid-July) and a late season crop (sown during mid-July to late July and harvested between late October and early November). The field site was divided into 12 plots (6×4.5 m) with 50 cm buffer zones. Four treatments with three replicates were established in a randomized complete block design, comprising: no fertilizer (CK), chemical fertilizer (150 kg·hm^{-2} N; CF), 50% N from chemical fertilizer+50% N from decomposed cattle manure (CMF50), and manure fertilizer (100% N from decomposed cattle manure; MF). Both the early and late season crops were fertilized according to the treatments. The nutrient contents of decomposed cow manure provided are listed in Table S1. Two-thirds of the N, in the form of urea and decomposed cattle manure, was applied as the basal treatment 3 and 10 days before transplanting, respectively. The remaining N was split into two equal parts and applied at the tillering and differentiation stages. Potash and phosphate were applied to maintain the phosphorus (P) and potassium (K) contents in all fertilization treatments at the same level as those in the decomposed cattle manure treatments. A full dose of P and two-thirds of K were applied in the forms of Ca(H$_2$PO$_4$)$_2$·H$_2$O and KCl as basal treatments, with the remaining K applied at the differentiation stage. Irrigation water was applied as per the recommended agronomic practices for this area (Xu et al. 2021). Crop yield was calculated using the following formula:

$$\text{Rice yield}(\text{t}\cdot\text{hm}^{-2}) = \frac{Yield_p}{27} \times 10 \qquad (1)$$

Where $Yield_p$ was the yield (kg) of rice in each plot of the field site (6×4.5 m).

N mineralization

The fresh soil (10 g, dry weight) of each treatment in the paddy field was collected after harvest in the late season of 2020 and placed into 100 ml centrifuge tubes, mixed with distilled water at a ratio of 1:2 (w/v). The centrifuge tube was sealed and cultured at 28±1 °C. The net N mineralization was obtained by subtracting the initial inorganic N values of the initial samples from those of the samples after 60 days of incubation.

Sampling and analysis

In the 2020 late-season crop harvest, each plot was harvested manually to determine grain yields. Between 2015 and 2020, paddy soil samples were collected from five randomly selected sites in each plot after harvest in the late season by obtaining cores from the surface to a depth of 20 cm. A portion of each soil sample was sieved (< 2 mm) after air-drying, and before analysis, the remaining soil was stored in the refrigerator at -20 °C for further biochemical and molecular analysis within a week. The SOC and TN were measured with an elemental analyzer (multi-N/C 2100/2100S, Analytikjena Jena, Jena, Germany). Inorganic N (NH$_4^+$-N + NO$_3^-$-N) was determined in the subsamples after extraction with 2 M KCl using an automatic N analyzer (FUTURA, Alliance Instruments, Frépillon, France). AN was measured as described by Xiong et al. (2008). DOC was determined as described by Jones and Willett (2006).

Following a methodology used by Li et al. (2018c), DOM was extracted by shaking 60 g of fresh soil in 100 mL Milli-Q water on a reciprocal shaker (170 rpm) at room temperature (25 °C) for 8 h. The collecting samples and water samples were then centrifuged at 2800× g for 10 min, and the suspension was filtered through a 0.45-μm mixed cellulose ester membrane. Before the solid-phase extraction (SPE) procedure, SPE cartridges (Bond Elut PPL, 500 mg, 6 mL, Agilent Technologies, Palo Alto, CA, USA) were activated by sequentially rinsing with pure methanol (18 mL) and 0.01 M HCl (18 mL) (Lv et al. 2016). After the DOM samples were adjusted to pH 2, they were passed through the SPE cartridges, followed by Milli-Q water. Finally, the SPE cartridges were dried completely using ultra-pure N$_2$, after which DOM was eluted from the cartridges with

methanol (mass spectrometry grade, 10 mL) and stored at -20℃ for FT-ICR-MS analysis. The molecular species of the extracted DOM were analyzed using a 9.4 T Bruker Solarix-XR FT-ICR-MS (Bruker Daltonik, GmbH, Bremen, Germany), equipped with an electrospray ionization source in negative mode, as described by Fang et al. (2017). The sampling rate used was 180 μL/h, the ion accumulation time was 0.7 s, and the detection mass ranged from 150 to 1000 (m/z). The extraction blank and water samples were analyzed and removed from the obtained DOM samples. Mass peaks with S/N (the baseline signal intensity S divided by the noise width N) > 10 were considered; however, P was not included in the formula assignment since HCl was used in the SPE process, which may interfere with the FT-ICR-MS readings for P (Li et al. 2018b). Therefore, the molecular formula assignment for DOM only included elements C, hydrogen (H), oxygen (O), N, and sulfur (S), as P was not considered due to the potential interference from HCl used in the SPE process (Li et al. 2018b).

Total genomic DNA was extracted from each 0.5 g soil sample using an E.Z.N.A.® soil DNA kit (Omega Bio-tek, Norcross, GA, USA), following the manufacturer's protocols. The quality, integrity, and quantity of each DNA sample were determined by 1% agarose gel electrophoresis and a NanoDrop ND-2000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA). The V3-V4 region of the bacterial 16S ribosomal RNA gene was amplified by PCR using primers 341F (CCTAYGGGRBGCASCAG) and 806R (GGACTACNNGGGTATCTAAT). The PCR procedure was carried out as described by Caporaso et al. (2011). Raw sequence data were de-multiplexed, quality-filtered, and processed using QIIME software (Caporaso et al. 2012). Tags were clustered into operational taxonomic units (OTUs) at 97% sequence similarity by using VSEARCH (Rognes et al. 2016). The OTU table was used to calculate the alpha diversity and provide taxonomic profiles.

Statistics

For each DOM sample, the signal intensity of each identified molecule was normalized to the sum of all intensities of the spectrum obtained from FT-ICR-MS, and the relative intensities (relative abundance) were used for statistical analyses (Osterholz et al. 2016). Biomolecular compound groups of

DOM were categorized according to the stoichiometry of their molecular formulas using the aromaticity index (AI) and elemental ratios (H/C and O/C). The labile components (H/C ≥ 1.5) of DOM consist of lipid-like fractions (H/C = 1.5–2.0, O/C = 0–0.3), protein/amino sugar-like fractions (H/C = 1.5–2.2, O/C = 0.3–0.67, N/C ≥ 0.05), and carbohydrate-like fractions (H/C = 1.5–2.0, O/C = 0.67–1.2, comprising sugars CHO and sugars CHO_X). Recalcitrant components (H/C < 1.5) consist of lignin-like fractions (H/C = 0.7–1.5, O/C = 0.1–0.67, AI < 0.67, encompassing polyphenolic oligomers), tannin-like fractions (H/C = 0.5–1.5, O/C = 0.67–1.2, AI < 0.67), condensed aromatic-like fractions (H/C = 0.2–0.7, O/C = 0–0.67, AI ≥ 0.67), and unsaturated hydrocarbon-like fractions (H/C = 0.7–1, O/C = 0–0.1, comprising a mixture of aliphatic and aromatic or alkene structures with relatively little oxygen) (Ding et al. 2020; Feng et al. 2016; Huang et al. 2020; Li et al. 2018b; Šantl-Temkiv et al. 2013).

Principal coordinate analysis (PCoA) plots were utilized to evaluate the variations in the composition of microbial communities among treatments and to visualize any potential clustering of treatment effects. Cluster correlation heatmaps with signs and a correlation network (Pearson/Spearman Correlation Coefficient) were generated using the OmicStudio software (https://www.omicstudio.cn) to show correlations between DOM compositions and bacterial community compositions (where P-values < 0.05 and correlation thresholds ≥ 0.6 or ≤ -0.6 showed key linkages). Redundancy analysis (RDA) was used to identify the relationship between the soil N, C, microbial community, and DOM composition and their effects on net N mineralization. Structural equation modeling (SEM) was performed using IBM SPSS AMOS 21.0 to quantify the effects of soil environmental factors, key microorganism, and DOM composition on net N mineralization.

Results

Fertilization increased rice yield and changed soil properties

All the fertilization treatments increased the rice yield in 2020, and the continuous application of CMF50 led to a higher yield than that of the CF (10.89%) treatment (Table 1). For the soil properties, continuous

Table 1 Soil properties and rice yield of late season crop in paddy fields (2020) after six years of continuous experimental treatments

Treatments	Soil Bulk Density (g·cm^{-3})	pH	AN (mg·kg^{-1})	NO$_3^-$-N (mg·kg^{-1})	NH$_4^+$-N (mg·kg^{-1})	Net N mineralization (mg·kg^{-1})	Yield (t·hm^{-2})
CK	1.14 ± 0.01b	5.22 ± 0.03a	99.23 ± 0.72d	4.82 ± 0.38e	14.49 ± 2.14b	-7.59 ± 0.07c	3.50 ± 0.22c
CF	1.21 ± 0.03a	5.07 ± 0.03bc	103.71 ± 1.65 cd	7.11 ± 0.44d	18.07 ± 1.09ab	-6.09 ± 0.29d	4.50 ± 0.04b
CMF50	1.13 ± 0.02b	5.14 ± 0.03ab	112.22 ± 1.31b	9.24 ± 0.75bc	20.68 ± 0.90a	-9.66 ± 0.43b	4.99 ± 0.12a
MF	1.09 ± 0.01b*	5.22 ± 0.02a	128.99 ± 4.33a	11.33 ± 0.60a	23.66 ± 2.68a	-11.48 ± 0.76a	4.71 ± 0.12ab

Treatments: no fertilizer (CK); chemical fertilizer (150 kg·hm^{-2} N, CF); 50% N from chemical fertilizer + 50% N from decomposed cattle manure (CMF50); manure fertilizer (100% N from decomposed cattle manure; MF). Different lowercase letters indicate significant differences among treatments at $P < 0.05$. *Indicates the significant differences between the CK and other treatments $P < 0.05$

application of chemical fertilizer and decomposed cattle manure to the soil in paddy fields from 2015 to 2020 produced significant changes in SOC and TN levels, with a linear relationship between SOC and TN (regression analysis, $P < 0.0001$, Fig. S2). SOC decreased in the CF treatment compared to the control sample in 2020; however, it increased during the study period in the CMF50 and MF treatments compared to both the control sample and CF treatment (Fig. 1a). The CMF50 and MF treatments both increased TN levels (Fig. 1b). In 2020, soil bulk density levels decreased in the MF treatment, but increased in the CF treatment, which exhibited the lowest soil pH compared to the control sample (Table 1). High-dose application of decomposed cattle manure (CMF50 and MF) decreased net N mineralization; in contrast, the CF treatment enhanced net N mineralization. NO$_3^-$-N content following treatment with CF was significantly higher than that in the control sample. The CMF50 and MF treatments showed higher AN, NO$_3^-$-N, and NH$_4^+$-N content than the control sample, and higher AN and NO$_3^-$-N content than the CF treatment.

Change in DOM and bacterial composition

DOC varied among the different treatments in 2020. Soil DOC decreased in the CF treatment, whereas it increased significantly in the CMF50 and MF treatments, with the highest DOC value observed after the application of MF (Fig. 2a). The application of MF considerably increased the total number of compounds among DOM, but no significant differences were observed between the CMF50, CF, and control treatments (Fig. 2b). High-dose applications of decomposed cattle manure (CMF50 and MF) decreased

the labile DOM compound levels (Fig. 2c); however, CF application decreased levels of recalcitrant DOM components. In each treatment, DOM compound groups were dominated by lignin-like fractions, followed by lipid-like fractions (Fig. 2d). Application of CF decreased levels of condensed aromatic-like fractions while the application of CMF50 decreased levels of carbohydrate-like fractions. Application of MF decreased levels of carbohydrate-like and unsaturated hydrocarbon-like fractions, but increased levels of lignin-like fractions compared with the control sample. Application of CMF50 decreased levels of lipid-like and protein/amino sugar-like fractions, and application of MF decreased levels of unsaturated hydrocarbon-like, protein/amino sugar-like, and lipid-like fractions. However, the application of CMF50 and MF significantly increased levels of lignin-like fractions compared to the CF treatment.

Bacterial communities were influenced by different fertilization treatments in 2020 (Fig. 3a). Application of decomposed cattle manure enhanced the alpha diversity of the soil bacterial community (Shannon index), and the highest values occurred with the application of MF (Fig. S3). The dominant phyla among the treatments were Proteobacteria (20.0%), Chloroflexi (18.87%), Planctomycetes (11.61%), and Acidobacteria (8.85%). The CMF50 and MF application treatments increased the relative abundances of Proteobacteria, Firmicutes, Acidobacteria, Actinobacteria, Candidate.division.NC10 (in MF), and Bacteroidetes (in MF), but decreased the relative abundance of Chloroflexi and Verrucomicrobia compared with the control or CF (Fig. 3b and Table S2).

At the genus level, 35 abundant genera were present at varying levels in the different treatments after

Fig. 1 SOC (**a**) and TN (**b**) in paddy soil under four continuous treatments at experimental sites (2015–2020). Treatments: no fertilizer (CK); chemical fertilizer (150 kg·hm^{-2} N, CF); 50% N from chemical fertilizer + 50% N from decomposed cattle manure (CMF50); manure fertilizer (100% N from decomposed cattle manure; MF). Different lowercase letters indicate significant differences among treatments at $P < 0.05$
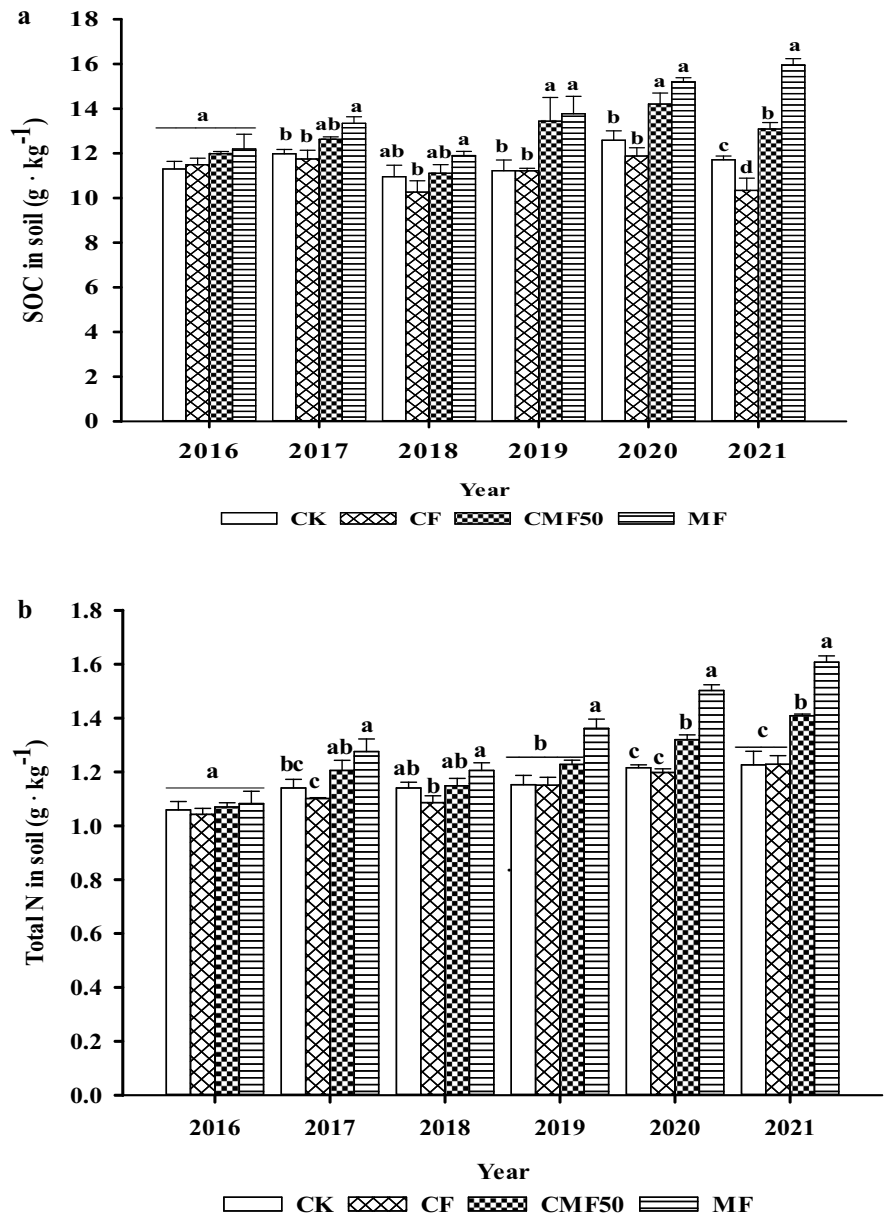
six years (Fig. 3c). CF treatment increased the abundance of *Anaerolinea* (Chloroflexi) compared with the control (Fig. 3c and Table S3). MF treatment decreased the abundance of *Anaerolinea*, *Bellilinea,* and *Desulfomonile*, but increased the abundance of *Anaeromyxobacter*, *Haliangium*, *Bryobacter*, *MND1*, *Sideroxydans*, *Pasteuria*, *Candidatus Nitrotoga*, *Occallatibacter*, *Gaiella,* and *Pedomicrobium* compared with CF treatment and the control sample. The CMF50 treatment increased the abundance of

Anaeromyxobacter, *Bryobacter,* and *Occallatibacter*, compared with the CF treatment and the control sample, but decreased the abundance of *Anaerolinea* and *Bellilinea* compared with the CF treatment.

The linkage between DOM composition and bacterial communities

To explore the correlations between DOM and bacterial taxonomic composition, the cut-off |R|≥0.6,
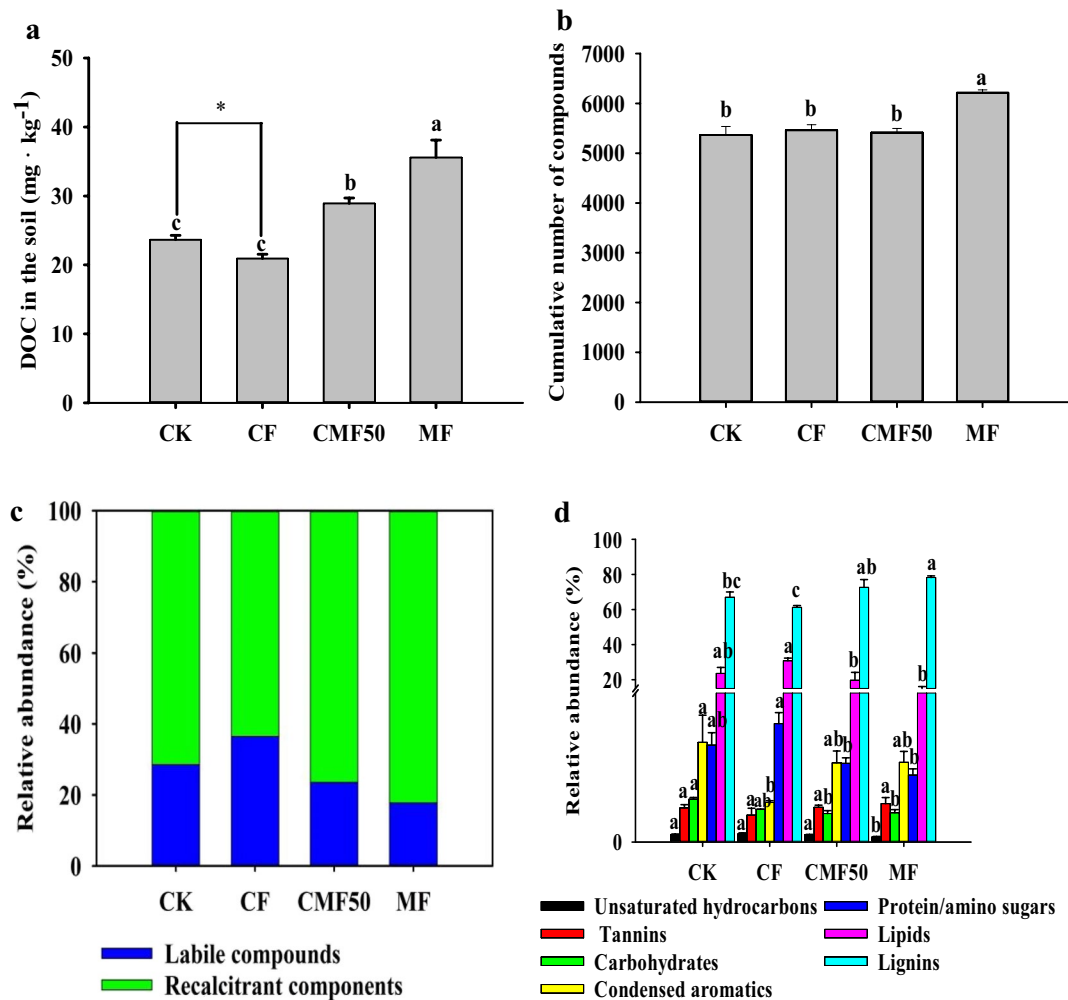
Fig. 2 Changes in DOC, DOM composition, and chemodiversity in paddy soils (2020) after six years of continuous experimental treatments. Treatments: no fertilizer (CK); chemical fertilizer (150 kg·hm^{-2} N, CF); 50% N from chemical fertilizer + 50% N from decomposed cattle manure (CMF50); manure fertilizer (100% N from decomposed cattle manure, MF). (**a**): DOC; (**b**): cumulative number of DOM compounds; (**c**): relative abundance of labile and recalcitrant components of DOM; (**d**): relative abundance of DOM compound groups. Different lowercase letters indicate significant differences among treatments at $P < 0.05$. *Indicates significant differences at $P < 0.05$, t-test

$P < 0.05$ was selected to identify the important correlations (Fig. 4). Significant correlations were identified between the OTUs of bacterial phyla and the DOM compound groups. Lipid-like and unsaturated hydrocarbon-like fractions were negatively correlated with Firmicutes, Acidobacteria, Bacteroidetes, and Proteobacteria, and unsaturated hydrocarbon-like fractions were positively correlated with Chloroflexi. Protein/amino sugar-like fractions were negatively correlated with Proteobacteria, Acidobacteria, and Firmicutes, but positively correlated with Nitrospirae

and Chloroflexi. Tannin-like fractions were positively correlated with Rokubacteria. Lignin-like fractions were significantly positively correlated with Actinobacteria, Proteobacteria, Firmicutes, Acidobacteria, and Bacteroidetes but negatively correlated with Chloroflexi. The OTUs of bacteria at the genus level showed opposite relationships between labile compounds and recalcitrant DOM components (Fig. 4b). *Bryobacter*, *Pasteuria*, *Haliangium*, *Sideroxydans*, *Occallatibacter*, *Candidatus Nitrotoga*, *Gaiella*, *Steroidobacter*, *Pseudolabrys*, *Opitutus*,
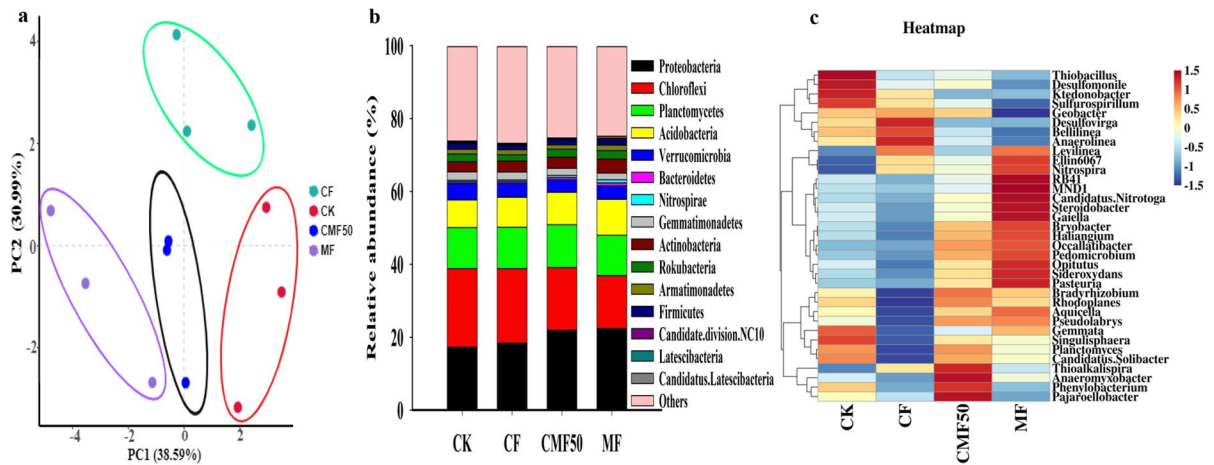
Fig. 3 Distribution of bacterial communities under different fertilizer management treatments in paddy soils (2020) after six years of continuous experimental treatments. (**a**) Principal coordinate analysis of the structure of bacterial communities. (**b**) Bacterial composition at phylum level in different treatments. (**c**) Heat map showing the trend in changes in genera under different fertilization management treatments. Treatments: no fertilizer (CK); chemical fertilizer (150 kg·hm^{-2} N, CF); 50% N from chemical fertilizer + 50% N from decomposed cattle manure (CMF50); manure fertilizer (100% N from decomposed cattle manure; MF)

and *Pedomicrobium* were positively correlated with lignin-like fractions but negatively correlated with labile DOM compounds (such as protein/amino sugar-like and lipid-like fractions). *Anaerolinea* and *Bellilinea* were strongly negatively correlated with lignin-like fractions but positively correlated with

unsaturated hydrocarbon-like, lipid-like, and protein/amino sugar-like fractions (*Anaerolinea*).

Due to the significant correlations between compound groups and bacterial genera, the interconnections between the compositions of each DOM compound group and genera taxa (OTUs) were explored
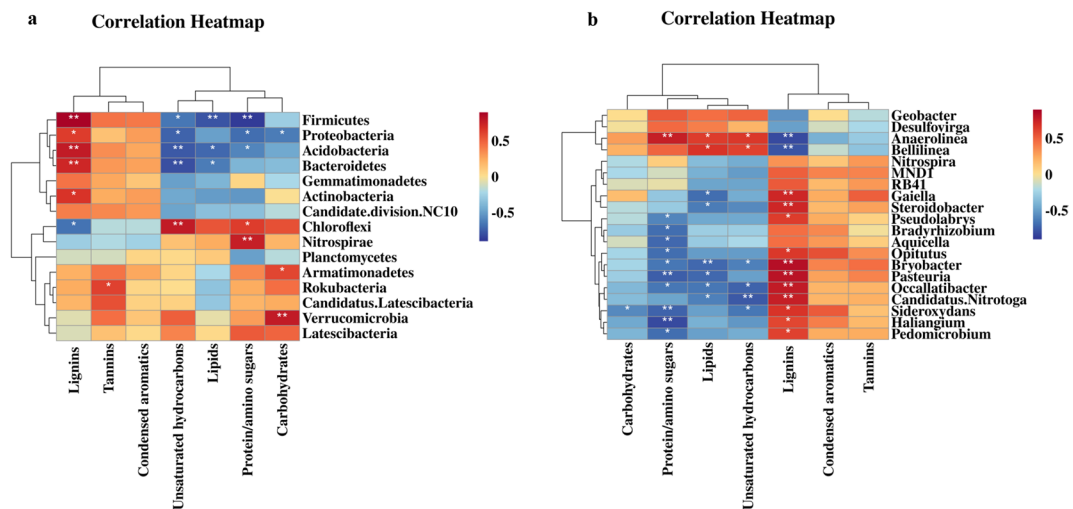

Fig. 4 Clustering correlation heatmap showing significant correlations between DOM composition and bacterial taxa in paddy soils after six years of continuous experimental treatments: (**a**) phylum level, (**b**) genus level. *: $P < 0.05$, **: $P < 0.01$
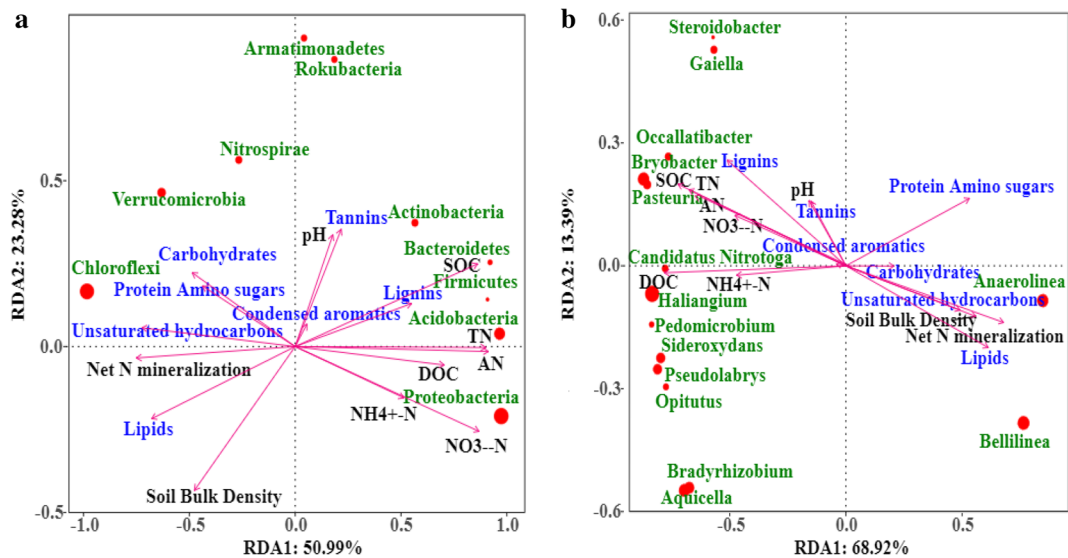
Fig. 5 RDA of soil properties and bacterial communities with respect to net N mineralization in paddy soils after six years of continuous experimental treatments: (**a**) phylum level, (**b**) genus level

using correlation network analysis (Fig. 4S). The 35 most abundant genera and the 100 most abundant DOM molecules of each compound group were considered for the correlation network analysis. At |R|≥0.6, $P < 0.05$, there were 52 candidate top DOM molecules of lignin-like fractions that were significantly correlated with 13 top genera. *Anaerolinea* and *Bellilinea* were correlated with the 40 top molecules, accounting for 80% of the total top molecules of lignin-like fractions. Interestingly, most of the lignin-like molecules with high numbers of C atoms (C≥15) were negatively correlated with the top genus *Anaerolinea* but positively correlated with *Halliangium* and *Pasteuria*. Most of the lignin-like molecules with several C atoms less than 14 were positively correlated with *Anaerolinea* but negatively correlated with *Haliangium, Pasteuria, Sideroxydans*, and *Bryobacter* (Fig. S4a). Unsaturated hydrocarbon-like molecules containing N, with a high double bond equivalence minus oxygen value (DBE-O), showed strong positive correlations with *Anaerolinea* and *Bellilinea,* but strong negative correlations with *Bryobacter* (Fig. S4b and Table S4). Of the labile DOM compounds, protein/amino sugar-like molecules showed negative correlations with the 10 top genera, especially *Haliangium, Pasteuria,* and *Sideroxydans.* However, 16 of the 31 protein/amino sugar-like molecules were positively correlated with *Anaerolinea*

(Fig. S4c). The top 35 lipid-like molecules exhibited negative correlations with *Bryobacter*, *Pasteuria, Occallatibacter, Gaiella,* and *Steroidobacter,* whereas 23 of these 35 top molecules exhibited strong positive correlations with *Bellilinea,* especially *Anaerolinea* (Fig. S4d).

Soil properties and bacterial communities with respect to net N mineralization

The redundancy analysis (RDA) plot revealed a negative correlation between net N mineralization and NO_3^--N, NH_4^+-N, TN, AN, DOC, and SOC, but a positive correlation with soil bulk density (Fig. 5). Unsaturated hydrocarbon-like fractions and labile DOM compounds, including carbohydrate-like, protein/amino sugar-like, and most notably lipid-like fractions, showed positive effects on net N mineralization; however, the recalcitrant DOM components, especially the lignin-like fractions with a strong positive correlation with SOC, presented a negative correlation with net N mineralization. At the phyla level, Nitrospirae, Verrucomicrobia, and especially the dominant phylum Chloroflexi (which was positively correlated with soil bulk density), exerted a positive effect on net N mineralization, while Actinobacteria, Bacteroidetes, Firmicutes, and the dominant phyla Acidobacteria and Proteogacteria, exerted a negative

effect on net N mineralization (Fig. 5a). At the genera level, *Anaerolinea* and *Bellilinea*, both with a strong positive correlation with soil bulk density and unsaturated hydrocarbon-like, protein/amino sugar-like and lipid-like fractions, were strongly positively correlated with net N mineralization, while *Haliangium*, *Candidatus Nitrotoga*, *Pasteuria*, *Bryobacter, and Occallatibacter* were strongly negatively correlated with net N mineralization (Fig. 5b).

To quantify the relative importance of the soil bulk density, DOM composition, SOC, soil N, and key microorganism, SEM analysis was performed to simultaneously assess and quantify the relative contributions of major factors on the net N mineralization (Fig. S5). Soil TN and AN indirectly or directly affected the abundance of genera *Anaerolinea* and *Bellilinea* among Chloroflexi. Notably, the soil bulk density played the most important role in affecting the abundance of genera *Anaerolinea* and *Bellilinea*, which affected the accumulation of different compositions of DOM. *Anaerolinea* and *Bellilinea*, with a direct negative effect (-0.74) on the levels of lignin-like fractions, exhibited direct positive effects on the levels of lipid-like (0.88), protein/amino sugar-like (0.54), and unsaturated hydrocarbon-like fractions (0.62), but showed no significant direct effects on the levels of carbohydrate-like fractions (0.24). Compared with carbohydrate-like fractions, lignin-like, lipid-like, protein/amino sugar-like, and unsaturated hydrocarbon-like fractions exhibited stronger direct effects on net N mineralization. Notably, lipid-like (0.84) and lignin-like (-0.74) fractions exhibited a dominant effect on net N mineralization. Net N mineralization exhibited a strong effect (-0.77 to -0.60) on the content of SOC, which in turn exhibited a strong effect (0.79 to 0.86) on the content of TN.

Discussion

Variation of soil properties and rice yield

Continuous application of CMF50 and MF increased TN (ranging from 1.07 to 1.41 g·kg^{-1} and 1.08 to 1.61 g·kg^{-1}, respectively) and SOC (ranging from 11.12 to 14.21 g·kg^{-1} and 11.90 to 15.95 g·kg^{-1}, respectively) in paddy soil considerably during the study period (Fig. 1). These findings are consistent with those of previous studies that reported

that organic fertilizer, either alone or combined with chemical fertilizer, continuously enhanced the capacity of soil to retain carbon and supply N in paddy fields (Bai et al. 2018; Coonan et al. 2020; Gai et al. 2018). Moreover, the application of high doses of decomposed cattle manure (CMF50 and MF) enhanced the AN and NO_3^--N content of soil compared with the control sample and CF treatment (Table 1). A possible explanation is that the addition of decomposed cattle manure reduced N losses (Hou et al. 2018). These findings also explained why the CMF50 exhibited a higher rice yield than the CF treatment.

Continuous application of CF decreased the soil pH, which was consistent with the findings of Jin et al. (2019). The application of CF increased net N mineralization but decreased SOC in paddy soils, which might be attributed to microbial degradation in native SOM to obtain more mineralized N (Alam et al. 2019; Roba 2018). The application of MF decreased soil bulk density, but the application of CF increased soil bulk density. This finding might be associated with organic components, which have a dilution effect on bulk density (Celik et al. 2010).

Effects on DOM and bacterial composition

DOM is the most active part of the SOC pool. The application of CMF50 and MF significantly increased the content of soil DOC; by 2020, the application of MF notably enhanced the cumulative number of identified DOM compounds (Fig. 2a and b). This can be attributed to the decomposed cattle manure increasing the total organic matter reservoirs, resulting in higher DOM composition (Li et al. 2018d, 2019). However, the decrease in DOC and recalcitrant DOM components, including condensed aromatic-like fractions, in the CF treatment might result from the higher mineralization of organic materials compared with the control sample (Alam et al. 2019).

Based on microbial substrate preferences and trophic strategy, the increase in Proteobacteria, Acidobacteria, Firmicutes, and Bacteroidetes (in MF) in the CMF50 and MF treatments were shown previously to conform with the characteristics of fast-growth microorganisms and r-strategists (Jeewani et al. 2020; Mickan et al. 2019). Application of CMF50 and MF increased the alpha diversity of the soil bacterial community (Fig. S3) and especially increased the

abundance of genera among the r-strategists Proteobacteria and Actinobacteria, such as *MND1, Sideroxydans, Haliangium, Pedomicrobium*, and *Candidatus Nitrotoga* in MF, and *Anaeromyxobacter, Bryobacter,* and *Occallatibacter* in CMF50 and MF, respectively. Therefore, r-strategists need to take advantage of labile C to maintain their fast growth rate and metabolism, thus resulting in the reduced relative abundance of labile DOM compounds (such as carbohydrate-like fractions) after the application of MF and CMF50 compared with the control sample (Ling et al. 2021; Razanamalala et al. 2018). However, the abundance of unsaturated hydrocarbon-like fractions containing N (Fig. 2d and S4) decreased in the MF treatment, suggesting that unsaturated hydrocarbon-like fractions among recalcitrant DOM components might be relatively vulnerable to microbial decomposition. It has been reported that Chloroflexi, as K-strategists, can grow on lignocellulosic substrates and are replete with aromatic compound degradation genes to degrade recalcitrant DOM compounds (Colatriano et al. 2018; Wong et al. 2016). Application of CMF50 and MF suppressed the growth of Chloroflexi, in particular, the anaerobic organisms *Anaerolinea* and *Bellilinea*, which led to higher levels of recalcitrant DOM components in paddy soils compared with CF application or the control sample (Fig. 3b). This finding indicates that *Anaerolinea* and *Bellilinea* could be the dominant genera among Chloroflexi that cause recalcitrant C degradation. We suggest that stoichiometrically-balanced, supplementary, decomposed cattle manure, either alone or combined with CF, could cut fertilizer use while enhancing the sequestration of C into SOM in paddy soil.

We observed an increase in the abundance of protein/amino sugar-like, lipid-like, and unsaturated hydrocarbon-like (compared with MF) fractions and a decrease in the abundance of lignin-like fractions following continuous application of CF, compared with the application of CMF50 and MF. This might be due to continuous chemical-N input allowing the growth of K-strategist bacteria, which in turn may increase the consumption of recalcitrant lignin-like fractions while synthesizing and supporting more lipid-like, protein/amino sugar-like or unsaturated hydrocarbon-like substrates when populations are near carrying capacity (Devi et al. 2012; He et al. 2022; Li et al. 2018b; Shi et al. 2017; Yin et al. 2018). Therefore, the protein/amino sugar-like, unsaturated

hydrocarbon-like, and lipid-like fractions might act as important N sources or energy for K-strategists.

Responses of bacterial communities to DOM composition

We found correlations between DOM molecular distribution and bacterial taxonomy under various continuous fertilization treatments (Fig. 4). Recalcitrant lignin-like fractions showed strong negative correlations with Chloroflexi, consistent with the findings of Li et al. (2021). Chloroflexi can utilize recalcitrant C, such as aryl-C, which is found in lignin (Boye et al. 2017; Colatriano et al. 2018). *Anaerolinea* and *Bellilinea* were correlated with 80% of the 52 top lignin-like molecules (Fig. 4Sa), which suggests that they may be the dominant genera decomposing lignin-like fractions among all Chloroflexi in the paddy soil. Interestingly, most lignin-like molecules with high numbers of C atoms showed negative correlations with the relative abundance of *Anaerolinea*, while having a positive correlation with lignin-like molecules with < 14 C atoms. This indicates that *Anaerolinea* might prefer to decompose high-molecular-weight lignin-like molecules into low-molecular-weight molecules. Unsaturated hydrocarbon-like fractions containing N and labile DOM compounds, including lipid-like and protein/amino sugar-like fractions, showed positive correlations with both *Anaerolinea* and *Bellilinea* (Fig. 5b, c, e, and S4). This could be attributed to *Anaerolinea* and *Bellilinea* favoring lignin-like decomposition, and thus taking advantage of labile C and organic N as their energy and growth sources, respectively (Kirk et al. 1976; Moorhead and Sinsabaugh 2006). Although Actinobacteria, Proteobacteria, Firmicutes, Acidobacteria, and Bacteroidetes have been characterized as r-strategists, some strains within these phyla are well known for their ability to decompose or grow in lignin (Lee et al. 2019). *Bryobacter*, *Occallatibacter* (Acidobacteria), *Pasteuria* (Firmicutes), *Haliangium, Sideroxydans, Candidatus Nitrotoga* (Proteobacteria), *Gaiella (Actinobacteria), Steroidobacter, Pseudolabrys, Opitutus,* and *Pedomicrobium (Proteobacteria)* were positively correlated with lignin-like fractions, reflecting that some genera within Actinobacteria, Proteobacteria, Firmicutes, and Acidobacteria are capable of growing in lignin-like fractions (Li et al. 2019; Ling et al. 2021). Our results suggested that DOM composition

influenced the change of bacterial composition; thus, labile and recalcitrant C utilization by bacteria.

Soil properties and bacterial communities associated with net N mineralization

RDA and SEM analyses showed that soil N availability and TN exhibited a strong effect on net N mineralization and was strongly positively correlated with SOC, DOC, lignin-like fractions, and some bacterial communities. These findings revealed that soil N in paddy soils might be an important factor influencing the microbial community by utilizing C as an energy source to mineralize DOC and obtain inorganic N (Coonan et al. 2020; Craine et al. 2007). Notably, soil bulk density was one of the dominant factors that influenced the bacterial community; specifically, *Anaerolinea*, *Bellilinea* (anaerobic organisms, Chloroflexi), *Haliangium*, *Candidatus Nitrotoga* (Proteobacteria), *Pasteuria* (Firmicutes), *Bryobacter, and Occallatibacter* (Acidobacteria) were found to have strong correlations with soil bulk density and net N mineralization. The net N mineralization exhibited a strong direct effect (-0.77 to -0.60) on the content of SOC, which exhibited a strong direct effect on the content of TN (0.79 to 0.86). These findings indicated that the soil N and C content were influenced by the net N mineralization condition in the paddy fields.

Lignin-like fractions were the dominant component of recalcitrant C under anoxic conditions (paddy fields) and exhibited a dominant negative effect (direct effect: -0.74) on net N mineralization (O'Donnell et al. 2016; Wang et al. 2016). These findings indicated the lignin-like fractions might be the dominant component of DOM that inhibit the net N mineralization in paddy soils. However, the lignin-like fractions showed a negative correlation with protein/amino sugar-like, unsaturated hydrocarbon-like, and most notably lipid-like fractions, which was consistent with the findings of Ly and Hur (2018). These findings indicated that the decrease in lignin-like fractions could lead to an increase in protein/amino sugar-like, unsaturated hydrocarbon-like, and lipid-like fractions. Genera *Anaerolinea* and *Bellilinea* exhibited a strong direct effect on protein/amino sugar-like and unsaturated hydrocarbon-like fractions. Both of them exhibited a strong effect on the net N mineralization of soil N. However, the levels of NO_3^--N, NH_4^+-N, TN, and AN exhibited a negative

effect on the net mineralization of soil N. These findings indicated that protein/amino sugar-like, and unsaturated hydrocarbon-like fractions containing N (Fig. S4d), might be important sources of organic N, while the content and availability of soil N were the main factors stimulating bacteria to favor soil organic N (Ekenler and Tabatabai 2004; Fujii et al. 2018). *Anaerolinea* and *Bellilinea* exhibited no significant direct effects (0.24) on carbohydrate-like fractions but showed a strong direct effect (0.88) on lipid-like fractions. Carbohydrate-like fractions exhibited a weak positive effect (direct effect: 0.47) on net N mineralization, whereas lipid-like fractions showed a strong positive contribution (direct effect: 0.84) to net N mineralization. These findings indicated that lipid-like fractions might become a major source of C, acting as an energy source for N-mining bacteria (Chong et al. 2018; Sebastián et al. 2016). Our data supports the microbial N mining hypothesis, where the availability and content of soil N cause a priming effect to decompose recalcitrant DOM components but allow more energy sources and the availability of more N-rich DOM for N mining by bacteria.

Conclusion

The continuous application of CMF50 for six years resulted in the highest rice yield. The applications of both MF and CMF50 increased the soil N content and availability but decreased the net N mineralization. MF and CMF50 increased SOC, whereas CF decreased SOC, which was associated with the labile and recalcitrant components of DOM. The decrease in lignin-like fractions led to an increase in the levels of lipid-like fractions and the fractions of DOM containing N, which were strongly correlated with *Anaerolinea* and *Bellilinea* and contributed to net N mineralization and SOC.

The findings of this study suggested that the composition of DOM, soil N-driven bacterial carbon-acquisition strategy, and net N mineralization in paddy fields respond to fertilization treatments. These findings have the potential to aid in predicting soil's ability to retain C and supply N, as well as its capacity to support rice production.

Author contributions Yanggui Xu: Methodology, Formal analysis, Investigation, Writing—Original Draft, Writing—Review & Editing. Zhiping Peng: Conceptualization, Validation, Investigation, Resources. Yuting Tu: Formal analysis, Investigation. Jichuan Huang: Conceptualization, Validation, Resources, Writing—Review & Editing. All authors read and approved the final manuscript.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests 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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