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Nitrogen addition mediates the effect of soil microbial diversity on microbial carbon use efficiency under long-term tillage practices

Mengni Zhang[1,2] | Shengping Li[1] | Xueping Wu[1,3] | Fengjun Zheng[1] | Xiaojun Song[1] | Jinjing Lu[1,2] | Xiaotong Liu[1] | Bisheng Wang[4] | Ahmed Ali Abdelrhmana[1] | Aurore Degré[2]

[1]Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, Beijing, PR China

[2]Terra Research Center, University of Liege, GxABT, Gembloux, Belgium

[3]Ministerial and Provincial Co-Innovation Centre for Endemic Crops Production with High-quality and Efficiency in the Loess Plateau, Taigu, PR China

[4]College of Agronomy, Qingdao Agricultural University, Qingdao, PR China

Correspondence
Shengping Li, Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, No. 12 Zhongguancun South Street, Haidian District, Beijing 100081, PR China.
Email: lishengping@caas.cn

Xueping Wu, Ministerial and Provincial Co-Innovation Centre for Endemic Crops Production with High-quality and Efficiency in Loess Plateau, Taigu, PR China.
Email: wuxueping@caas.cn

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Abstract

Tillage practices can influence soil microbial carbon use efficiency (CUE), which is critical for carbon cycling in terrestrial ecosystems. The effect of tillage practices could also be regulated by nitrogen (N) addition. However, the soil microbial mechanism relating to N fertilizer effect on microbial CUE under no-tillage (zero-tillage) is still unclear. We investigated how N fertilizer regulates the effect of tillage management on microbial CUE through changing microbial properties and further assessed the impact of microbial CUE on particulate (POC) and mineral-associated organic matter carbon (MAOC). For this we used a 16-year field experiment with no-tillage (NT) and conventional tillage (CT), both of which combined with 105 (N1), 180 (N2), and 210 kg N ha^{-1} (N3) N application. We found that microbial CUE increased with increasing N application rate. NT increased microbial CUE compared with CT in the 0–10 cm. The bacterial and fungal diversities of NT were higher than CT and N application decreased their diversities in 0–10 cm. The partial least squares path model showed that bacterial and fungal diversity had a significant influence on microbial CUE. Furthermore, POC and MAOC under NT were higher than CT and they also increased with increasing N application rate. It suggested that increasing microbial CUE induced by N application had the potential to increase POC and MAOC. Overall, this study highlights that N addition can alter the effect of soil microbial diversity on CUE, which further improves our understanding to explain and predict the fractions of SOC (i.e., POC and MAOC) in tillage systems.

KEYWORDS
microbial carbon use efficiency, microbial community, nitrogen, no-tillage, soil organic carbon

1 | INTRODUCTION

Soil biodiversity loss induced by agricultural practices threatened soil organic carbon storage (De Valença et al., 2017; Huang et al., 2019), which is crucial to the determination of carbon (C) cycling in ecological systems (Chen et al., 2017; Novara et al., 2017). The C stock is also susceptible to microbial carbon use efficiency (CUE) that is the fraction of C taken up by microbial cells and retained in biomass as opposed to being respired (Li et al., 2014, 2019; Zhou et al., 2020). Conservation tillage and nitrogen (N) addition are two common agricultural practices that could change soil microbial CUE by changing soil properties (e.g., temperature, moisture, and N availability;

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Domeignoz-Horta et al., 2020; Kallenbach et al., 2019; Manzoni et al., 2012; Widdig et al., 2020). Conservation tillage could induce N limitation because straw applied has a wide C/N ratio (Thierfelder et al., 2018) and needs more N to relieve N deficiency. However, conservation tillage and N addition have opposite effects on the diversity and structure of microbial community; for instance, no-tillage can increase the ratio of fungi to bacteria (F:B) and soil microbial diversity compared with conventional tillage, while N addition could decrease them (Dai et al., 2018; Liu et al., 2018; Zhang et al., 2012). When studying the combined effect of N addition and tillage practice, Li et al. (2020c) found that N addition in no-tillage system had higher soil microbial diversity than conventional tillage. These results indicate that tillage practice and N addition had interaction effect on microbial community. The microbial community could also influence microbial CUE (Nunes et al., 2020; Sinsabaugh et al., 2016; Wang et al., 2021). However, the combined impact of N addition and tillage practices on microbial CUE from the perspective of microbial community is lacking. Hence, it is essential to explore the soil microbial mechanism responsible for the effect of N application on microbial CUE to better understand carbon sequestration under tillage management.

No-tillage is a commonly used conservation tillage practice and numerous studies have investigated its effect on microbial CUE (Kallenbach et al., 2019; Mo et al., 2021; Yang et al., 2020a). Some studies have indicated that no-tillage increased microbial CUE compared with conventional tillage (Kallenbach et al., 2019; Mo et al., 2021; Sauvadet et al., 2018), but no effect was found by others (Van Groenigen et al., 2013). A possible reason for the different results is that N application could influence microbial CUE (Kallenbach et al., 2019; Mo et al., 2021; Van Groenigen et al., 2013) and its application rate is different among these studies. N application can also affect microbial growth and respiration by changing soil nutrient availability, particularly for N, because microbial cells need to balance C and N compositions (Manzoni et al., 2012). Moreover, the limitation of N increases over-flow respiration or C excretion rather than microbial growth, which further decreases microbial CUE (Qiao et al., 2019). Previous studies showed that no-tillage with straw retention could decrease soil N availability (Gentile et al., 2011; Thierfelder et al., 2018). These findings indicate that N application is a promising way to induce no-tillage systems to increase microbial CUE.

Microbial CUE can be influenced by microbial populations that have different rates of organic matter decomposition and absorption (Waldrop & Firestone, 2004). Adu and Oades (1978) found that fungi played a more important role than bacteria on microbial CUE. The main reason is that the C:N variation range of fungi is generally wider than that of bacteria and fungi have a higher demand for C element than bacteria (Keiblinger et al., 2010). However, other studies showed insignificant differences in the effect of microbial CUE induced by fungi and bacteria (Six et al., 2006; Thiet et al., 2006). One reason for these conflicting results is that N application could also influence microbial CUE by stimulating microbial activity and decreasing microbial respiration metabolism (Lee & Schmidt, 2014; Liu et al., 2018; Thiet et al., 2006) and the difference N application rates under these studies could contribute to the discrepancy. Another reason is that these studies only focused on the influence of microbial populations and biomass on microbial CUE (Keiblinger et al., 2010; Waldrop & Firestone, 2004) and ignored the key role of microbial diversity on microbial CUE (Domeignoz-Horta et al., 2020). Hence, studying the impact of N application on microbial CUE based on its effects on microbial diversity and community structure could provide a comprehensive perspective to reveal the influence of N application on C cycling.

Furthermore, the increase of microbial CUE is an effective means of increasing SOC sequestration (Bradford et al., 2013; Haddix et al., 2016). SOC fractions, especially for particulate (POC) and mineral-associated organic matter carbon (MAOC), are more sensitive to microbial CUE than total SOC (Averill & Waring, 2018; Chen et al., 2018; Ye et al., 2018). Averill and Waring (2018) found that substrate use efficiency can also directly affect C cycling through changing POC and MAOC. In addition, N addition significantly influenced soil POC and MAOC (Chen et al., 2019; Chen et al., 2020b; Ye et al., 2018). However, it remains unclear how N application regulates the effect of soil microbial CUE on POC and MAOC under tillage management. Therefore, studying the effects of N application is essential in understanding the role of soil microbial CUE on carbon sequestration potential.

Here we investigated the influence of N application on microbial CUE under tillage practices from a microbiological perspective. We hypothesized that: (a) the increase of microbial CUE induced by N application under no-till was higher than under conventional tillage; and (b) microbial diversity plays a more important role than microbial biomass in microbial CUE. The main objectives of this study were to: (1) evaluate the influence of tillage management and N application on soil microbial diversity, community compositions, and soil microbial CUE; (2) reveal how N application influences soil microbial CUE by regulating microbial diversity, community structure, and biomass; and (3) assess the influence of microbial CUE on soil POC and MAOC under tillage management with different N application rates.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted a continuous field experiment from 2003 to 2019 at Shouyang Experimental Station (113.11°E, 37.97°N), Jinzhong City, Shanxi Province, Northern China. The climate of the station is continental monsoon and its average annual potential precipitation and evaporation is 484 mm and 1750 mm, respectively (Wang et al., 2019). There were average 131 days about annual frost-free season. The soil type in the experimental site was sandy loam cinnamon soil developed from Calcaric-Fluvic Cambisols (Li et al., 2020b). Soil physical and chemical properties were initially presented in Table 1.

2.2 | Experimental design

The long-term experiment was conducted in 2003 using a randomized block design with three replicates. There were 18 plots and each plot

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TABLE 1 Soil physical and chemical properties in 0–25 cm layer in 2003

	Soil particle size distribution (%)			Available soil nutrient (mg kg^{-1})				
Soil layer (cm)	>0.020 mm	0.002–0.020 mm	<0.002 mm	N	P	K	SOC (g kg^{-1})	Bulk density (g cm^{-3})
0–10	58.5	35.7	5.8	58	8.3	96	22.7	1.06
10–25	59.6	34.6	5.8	52	6.9	93	19.8	1.2

was 5 m × 5 m in size. The continuous cultivated crop was spring maize that was planted in Mar and harvested in November.

Three N fertilizer rates were applied under two tillage treatments in this study. The two tillage practices were NT (no-tillage with the maize straw mulching after harvesting, seeded with a no-till planter, N fertilizer was applied in small holes with 10 cm depth between two maize seeds/plants in each row, about 5 cm from the maize seed/maize plant in April) and CT (conventional tillage with maize straw removed, the plots were plowed twice to 0.25 m depth after harvesting and before seeding, respectively, and fertilized before ploughing in April) (Li et al., 2020b). The three N fertilizer rates were 105 kg N ha^{-1} (N1), 180 kg N ha^{-1} (N2), and 210 (N3) kg N ha^{-1} with urea. According to Fao (1999), the total use of chemical fertilizer in China ranks first in the world and the average N addition rate is 235 kg N ha^{-1}. However, the previous fertilization study in this study region showed that N uptake of maize plants, fertilizer N availability, and yield reached the maximum when N application rate was 105 kg N ha^{-1} (Wang et al., 2001). Hence, it is essential to explore the effect of high N addition under tillage practices due to the problem of high N addition in China. In addition, the row spacing was 0.6 m and plant spacing was 0.3 m.

2.3 | Soil sampling

The soil samples were collected from depths of 0–10 cm and 10–25 cm using a 10 cm diameter soil auger on August 1, 2019. The sampling date corresponded to the tasseling stage. During transport to the laboratory, all soil samples were stored in 4°C incubator. Plant tissues and rocks in soil samples were removed. The fresh soil was divided into several samples and put in a refrigerator at 4°C and soil subsamples for microbiological analysis were put in another refrigerator at − 80 °C before further analyses.

2.4 | Soil analysis

2.4.1 | Enzyme activities and microbial biomass

We determined the soil microbial biomass nitrogen (MBN) and carbon (MBC) by the chloroform fumigation-extraction method with an extraction efficiency of 0.45 (Cleveland & Liptzin, 2007; Jenkinson et al., 2004). The activities of β-1,4-N-acetyl-glucosaminidase (NAG), β-1,4-glucosidase (BG), and leucine aminopeptidase (LAP) in the soil samples were assayed with microplate-scale fluorometric procedures (Sinsabaugh et al., 1997). The BG, NAG, and LAP can produce assimilable nutrients from the major organic sources of C (e.g., β-linked glucans) and N (e.g., protein and amino polysaccharides) (Sinsabaugh et al., 2013). One gram of fresh soil sample was homogenized in 125 ml 50 mM Tris buffer. Buffer, soil sample solution, and substrate were dispensed into a 96-well microplate. Then, the microplates were cultured in a dark incubator for 4 hr at 25°C. Finally, we added 1 μl of 1 M NaOH to each well to stop the reaction. The microplates were determined using an automated fluorometer (BioTek Synergy H1 microplate reader, Winooski, VT) with excitation at 365 nm and emission at 450 nm (Saiya-Cork et al., 2002).

2.4.2 | Ecoenzymatic stoichiometry and CUE estimation

We used ecoenzyme activity, labile organic matter, and the C:N ratio of microbial biomass to calculate the CUE according to the stoichiometric modelling (Geyer et al., 2019; Sinsabaugh et al., 2016; Sinsabaugh & Shah, 2012). Labile organic matter was determined as the contents of DOC and N extracted from non-fumigated samples (Geyer et al., 2019). The CUE calculated from stoichiometric models was similar to it according to direct measurements of bacterial and fungal growth and respiration (Geyer et al., 2019; Sinsabaugh et al., 2016).

The microbial CUE was calculated according to the following equation:

$$\mathrm{CUE} = \mathrm{CUE}_{\mathrm{MAX}}[S_{\mathrm{C:N}}/(S_{\mathrm{C:N}} + k_{\mathrm{N}})] \quad (1)$$

Where: $S_{\mathrm{C:N}} = (1/\mathrm{EEA}_{\mathrm{C:N}})(B_{\mathrm{C:N}}/L_{\mathrm{C:N}})$, $S_{\mathrm{C:N}}$ is a scalar ratio that reflects the capability of the microbes to modify the disparity between the composition of microbial biomass and the basic composition of the available resources by the allocation of enzymatic activities. The value of half-saturation constant k_{N} is 0.5. According to the thermodynamic constraints, $\mathrm{CUE}_{\mathrm{max}}$ is set at 0.6. $\mathrm{EEA}_{\mathrm{C:N}}$ represents the ratio of C-acquiring activity to N-acquiring activity, $\mathrm{EEA}_{\mathrm{C:N}} = \mathrm{BG}/(\mathrm{NAG} + \mathrm{LAP})$. $L_{\mathrm{C:N}}$ represents the molar C:N ratio of labile substrate. $B_{\mathrm{C:N}}$ represents C:N of microbial biomass.

The threshold element ratios (TER) were calculated as follows:

$$\mathrm{TER}_{\mathrm{C:N}} = L_{\mathrm{C:N}} \times \mathrm{EEA}_{\mathrm{C:N}} \quad (2)$$

2.4.3 | PLFA analysis

We used phospholipid fatty acid (PLFA) analysis to assess microbial biomass and community structure. The modified Bligh and Dyer method

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was applied to extract PLFAs (Börjesson et al., 1998). We placed 5 g freeze-dried soil in a chloroform–methanol–citrate buffer mixture overnight and then extracted lipids from it. The lipids were poured into the SPE Tubes (DSC-Si, Discovery®, Sigma-Aldrich) and separated into neutral lipids, glycolipid, and phospholipid. In addition, we added PLFA 19:0 (Larodan Malmö, Sweden) to the phospholipid fraction as an internal standard. PLFAs were transesterified to fatty acid methyl esters by 1 ml 0.2 M methanolic-KOH (Chowdhury & Dick, 2012). We analyzed the extracts using an Agilent 6890 gas chromatograph furnished with a flame-ionization detector (Agilent Technologies, Palo Alto, CA). Fungal biomass was the sum of PLFAs 18:1ω9c and 18:2ω6c (Frostegård & Bååth, 1996; White et al., 1996). PLFAs (a15:0, a17:0, i14:0, i16:0, i15:0, and i17:0) were used as markers for gram-positive bacteria, whereas PLFAs (16:1ω11c, 16:1ω9c, 18:1ω7c, 18:1ω5c, cy19:0, and cy17:0) were used to markers Gram-negative bacteria (Brockett et al., 2012; Frostegård & Bååth, 1996). Actinomycetes biomass was the sum of 10Me16:0 and 10Me18:0 biomass (Willers et al., 2015). The sum of Actinomycetes, G^-, and G^+ biomass was total bacterial biomass.

2.4.4 | DNA extraction

The GMO food DNA Extraction Kit (Illumina MiSeq 250 PE, Auwigene Company, Beijing, China) was used to extract the microbial DNA of soil samples following the manufacturer's instructions. The total DNA concentration and quality were checked using a spectrophotometer (NanoDrop, ND2000, ThermoScientific) and agarose gel electrophoresis and the DNA samples were placed at −40°C for further analysis.

2.4.5 | 16S rRNA gene amplicon sequencing and ITS amplicon sequencing

The hypervariable bacterial V3–V4 region of 16S rRNA gene was amplified with the following forward/reverse primer 338F/806R (5′-ACTCCTACGGGAGGCAGCAG-3′)/(5′-GGACTACVVGGGTATCTAATC-3′) (Lee et al., 1993). The ITS2 region of fungi was amplified with the following forward/reverse primer set: ITS1F/ITS2R (CTTGGTCATTTAG AGGAAGTAA/GCTG-CGTTCTTCATCGATGC) (Luan et al., 2015). The thermal-cycling conditions were as follows: 95°C (3 min), followed by 30 cycles of 98°C (20 s), 58°C (15 s), 72°C (20 s) and final elongation at 72°C (5 min). The PCR products were detected using 1% agarose gel electrophoresis, then purified with an AxyPrep DNA gel Extraction Kit (Axygen Biosciences, Union City, CA). Amplicon libraries were quantified using a Fluorometer (Applied Biosystems 7500, Thermo Fisher Scientific), after which amplicons were sequenced (Illumina MiSeq PE250, Allwegene Technologies, China).

2.4.6 | Soil fractions separation

We used the soil wet-sieving method to separate different soil fractions (Curtin et al., 2019; Fang et al., 2019). To separate soil organic matter into labile C fraction and stable C fraction, we performed a combined density and particle size fractionation (Herath et al., 2014; Six et al., 1998). The two soil C fractions are as follows: light fraction, defined as f-POM, and the heavy fraction that contained aggregate protected organic matter (o-POM > 53 μm fraction) and mineral protected organic matter (MAOM < 53 μm fraction; Fang et al., 2019). The soil was isolated light fraction and heavy fraction by density fractionation using sodium polytungstate (SPT, IMBROS, Australia; Herath et al., 2014; Six et al., 1998).

All soil fractions were dried at 60°C. Soil fractions were acidified with 1.0 M HCl for decomposing the carbonate. Then, soil samples were dried for 8 hr at 60°C and sieved with a 0.149-mm sieve after drying. The SOC of soil sample was determined by using an elemental analyzer (Vario Macro C/N, Elementar, Germany).

2.5 | Statistics

The data were analyzed by two-way ANOVA to compare the effects of tillage management, N addition rates, and their interaction on enzyme activities, microbial CUE, PLFAs, microbial diversity and bacteria and fungi relative abundance in each soil depth. The Student's *t*-test was also applied to evaluate the significance of differences within two tillage treatments or two soil depths. The significance of differences within three N application rates was assessed by one-way ANOVA with the least significant difference (LSD) tests in each soil depth under the same tillage treatment. We used Shapiro–Wilk and Levene's test to detect the normality distribution and homoscedasticity of data before conducting ANOVA. Statistical analyses were conducted using SPSS software version 20.0 (SPSS Inc., Chicago, IL). We used Quantitative Insights Into Microbial Ecology (QIIME) version 1.9.1 to process the sequences (Caporaso., 2010). Operational taxonomic units clustering at 97% of identity were collected using Uclust in QIIME software. We used principal coordination analysis (PCoA) based on the Bray–Curtis distance in R (version 3.4.1) to evaluate changes in bacterial and fungal community structure. The statistical significance of differences was evaluated by permutational multivariate analysis of variance based on the Bray–Curtis distance metrics (with a significance level of $p < 0.05$). The relationships among agricultural practices, soil microbial diversity and community structure, microbial biomass, microbial CUE, and soil POC were explored using partial least squares path modeling (PLS-PM). In our path model, path coefficients and coefficients of determination (R^2) were confirmed by R (v.3.4.1) with the "plspm" package (Ai et al., 2018). The goodness of fit analysis (0.40 < GoF <1.00) was carried out to evaluate the model's fit (Wang et al., 2021). The value of Goodness of Fit was 0.69 in our study.

3 | RESULTS

3.1 | Changes in enzyme activities and microbial CUE

The interaction effect of tillage and N management on soil enzyme activities was significant ($p < 0.05$; Table S1). NT significantly

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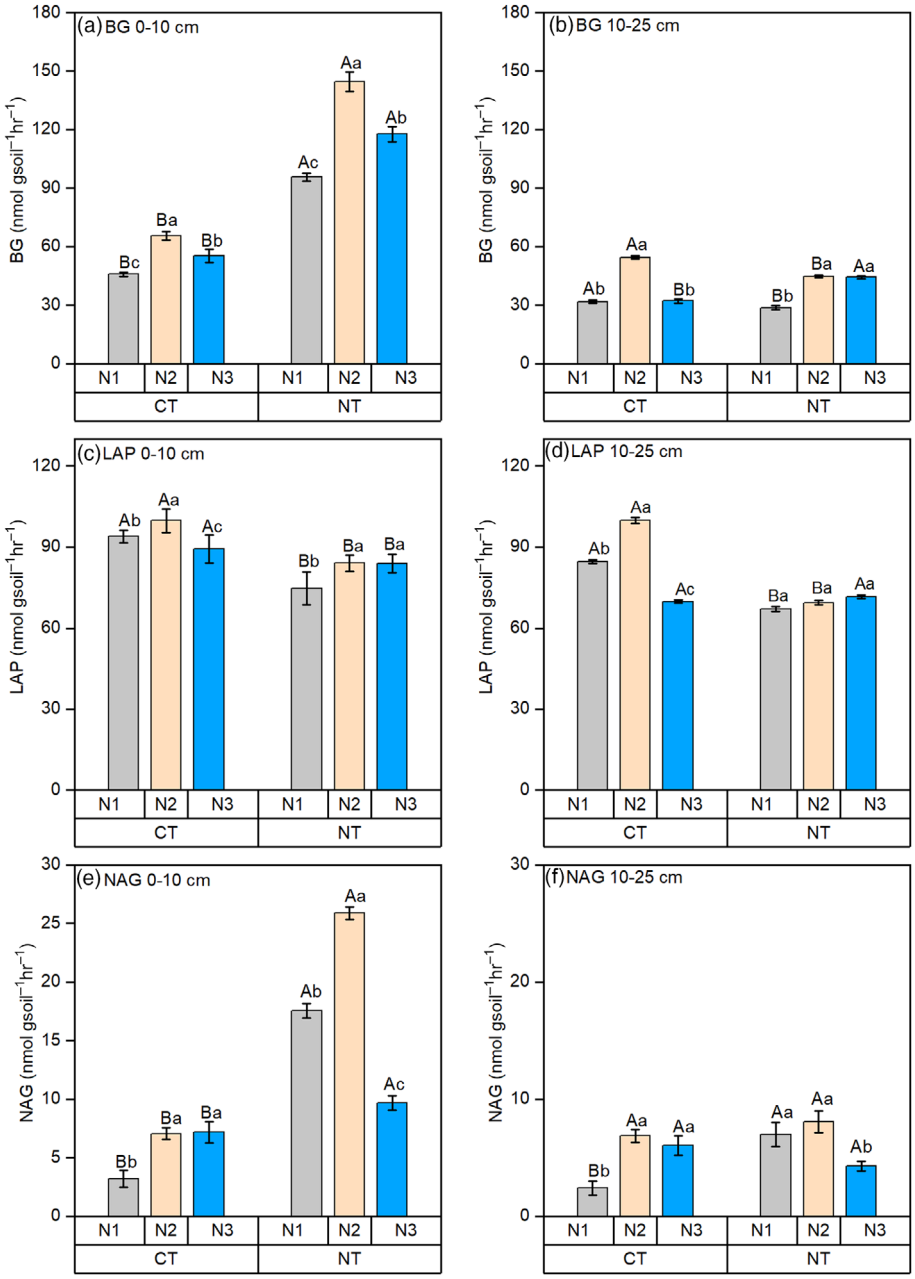

FIGURE 1 The effects of tillage (T) and nitrogen (N) on enzyme activity. Vertical bars indicate the standard error of means ($n = 3$). Different capital letters indicate significant differences ($p < 0.05$) between two tillage treatments under the same nitrogen addition rate; different lower-case letters indicate significant differences ($p < 0.05$) among nitrogen addition rates under the same tillage treatment. BG, β-glucosidase; NAG, N-acetyl-β-glucosaminidase; LAP, Leucyl aminopeptidase; N1, nitrogen addition at 105 kg N ha^{-1}; N2, nitrogen addition at 180 kg N ha^{-1}; N3, nitrogen addition at 210 kg N ha^{-1}; CT, conventional tillage; NT, no tillage [Colour figure can be viewed at wileyonlinelibrary.com]

increased BG and NAG activities under each N application rate relative to CT in 0–10 cm ($p < 0.05$; Figure 1). However, an insignificant difference was observed for BG between the two tillage treatments in the 10–25 cm soil layer (Table S1). There was an insignificant difference in the activities of BG and LAP under CT between different soil layers, while the two enzyme activities under NT in the 0–10 cm soil layer were significantly higher than that in the 10–25 cm soil layer ($p < 0.05$; Table S2). Moreover, the activities of BG and NAG of N2 were higher than of N1 and N3 under the two tillage treatments in the 0–10 and 10–25 cm soil layers (Figure 1). Moreover, the average value of LAP activity under CT treatment was higher than that of NT ($p < 0.05$) in 0–25 cm and it was higher under N2 than under N1 and N3 for CT treatment in the 0–10 cm layers (Figure 1).

The microbial CUE was significantly affected by tillage practice and N management, but their interaction effect was not significant (Table S3). The microbial CUE of NT under each N application rate was higher than CT in the 0–10 cm layers (Figure 2). The microbial CUE increased with increasing N application under two tillage treatments in 0–25 cm soil layers. These results showed that increasing N application rates under NT could enhance microbial CUE.

3.2 | Soil microbial community

The PLFA contents of the total and grouped soil microorganisms under tillage and N application treatments are shown in Figure 3. Total PLFAs, bacteria, fungi, and actinomycetes PLFAs in the 0–10 cm

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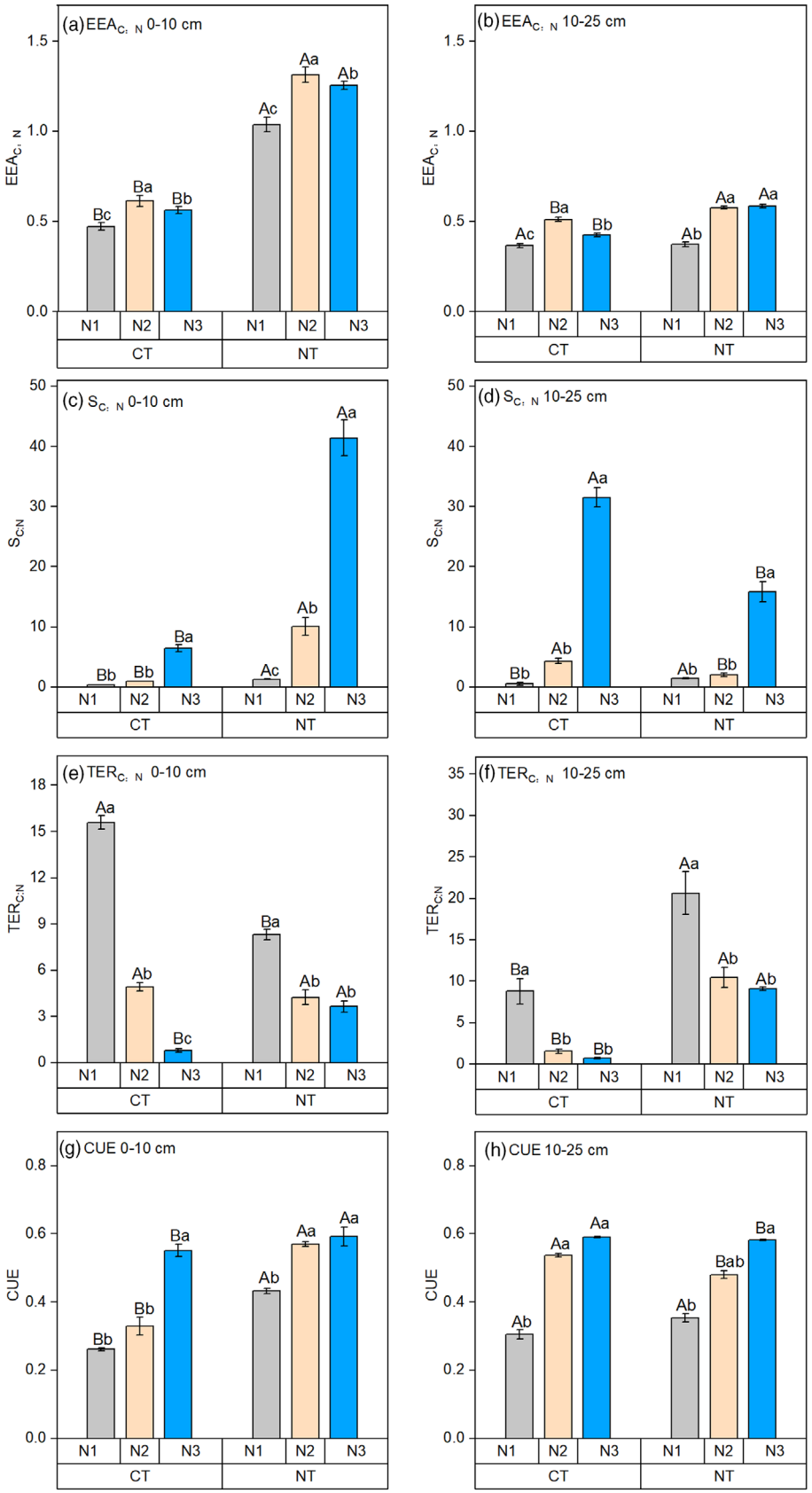

FIGURE 2 The effects of tillage (T) and nitrogen (N) on carbon use efficiency (CUE), element-requiring enzymatic activity ratio (EEAC:N), threshold element ratio (TERC:N), and scalar index (SC:N). Vertical bars indicate the standard error of means ($n = 3$). Different upper-case letters indicate significant differences ($p < 0.05$) between two tillage treatments under the same nitrogen addition rate; different lower-case letters indicate significant differences ($p < 0.05$) among nitrogen addition rates under the same tillage treatment. N1, nitrogen addition at 105 kg N ha^{-1}; N2, nitrogen addition at 180 kg N ha^{-1}; N3, nitrogen addition at 210 kg N ha^{-1}; CT, conventional tillage; NT, no-tillage [Colour figure can be viewed at wileyonlinelibrary.com]

layer were greater than in the 10–25 cm layer under two tillage treatments (Table S6). The average values of total PLFAs, bacteria, fungi, and actinomycetes PLFAs were higher under NT than CT in the 0–10 cm soil layer ($p < 0.05$; Figure 3). Moreover, only fungi and the F:B ratio were significantly affected by N application rates in the 0–25 cm layer and the interaction of tillage and N management also

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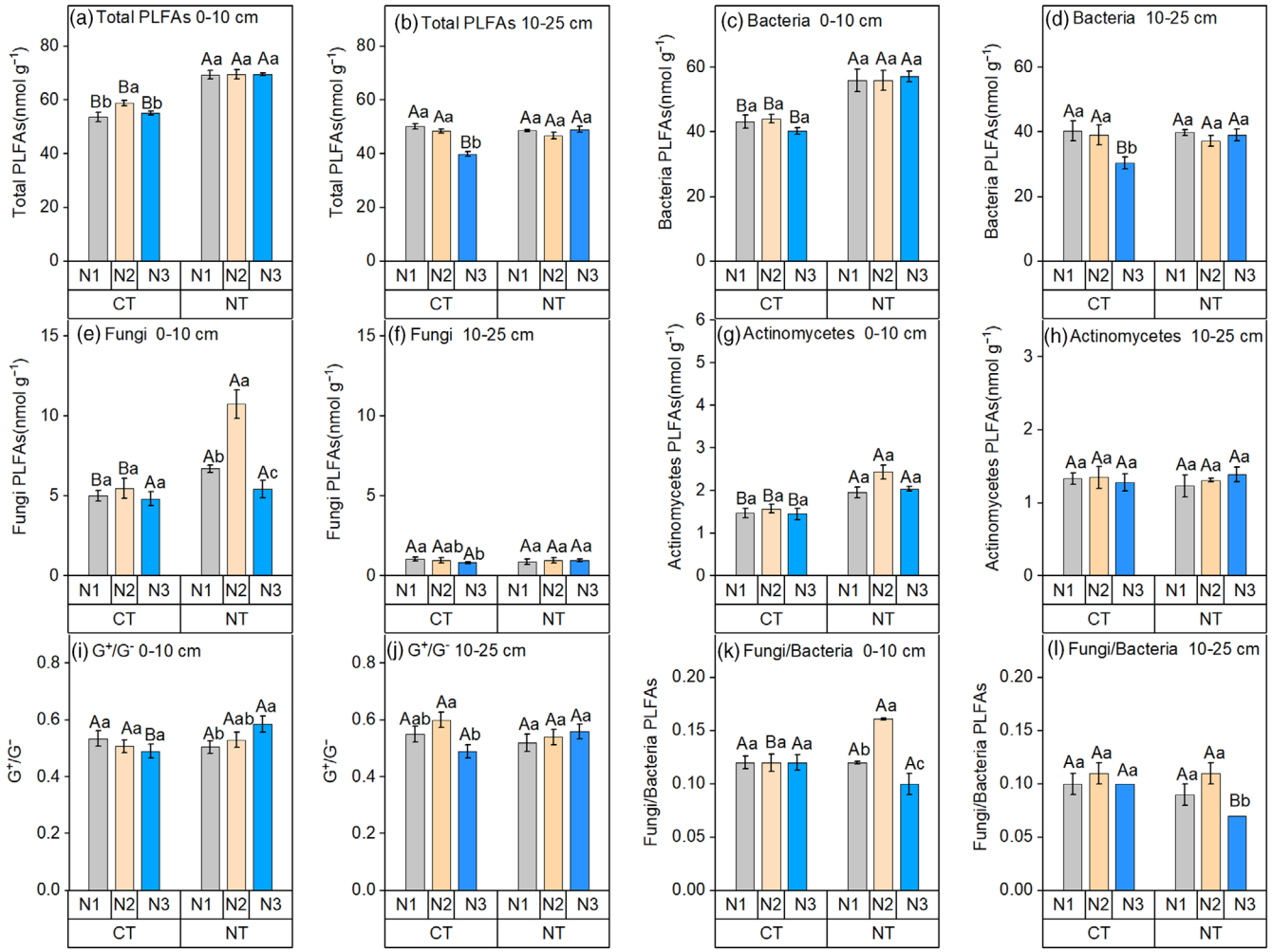

FIGURE 3 The effects of tillage (T) and nitrogen (N) on PLFAs. Vertical bars indicate the standard error of means ($n = 3$). Different upper-case letters indicate significant differences ($p < 0.05$) between two tillage treatments under the same nitrogen addition rate; different lower-case letters indicate significant differences ($p < 0.05$) among nitrogen addition rates under the same tillage treatment. N1, nitrogen addition at 105 kg N ha^{-1}; N2, nitrogen addition at 180 kg N ha^{-1}; N3, nitrogen addition at 210 kg N ha^{-1}; CT, conventional tillage; NT, no-tillage [Colour figure can be viewed at wileyonlinelibrary.com]

had a significant influence in 0–10 cm layer ($p < 0.05$; Table S5). Overall, the total PLFAs were increased by 19.2% under NT compared with CT in the 0–10 cm soil layer and not significantly affected by N level under NT in the 0–25 cm layer (Figure 3a,b). For each grouped soil microorganism, the average values of bacterial PLFAs and actinomycetes PLFAs under NT were increased by 21.2% and 24.4% in the 0–10 cm layer, respectively, compared with CT, but insignificantly affected by N level under each tillage treatment at both depths (Figure 3). The fungal PLFAs of N2 were the highest than N1 and N3 under NT, while there was no effect of N application rate under CT in the 0–10 cm layer (Figure 3e,f). Moreover, the G^+:G^- ratio was insignificantly affected by soil depth (Table S6), tillage treatments, and N application rates (Table S5). The G^+:G^- ratio increased with increasing N application rates under NT and there was no effect of N application rate under CT at 0–10 cm (Figure 3i). In addition, the F:B ratio was insignificantly affected by tillage management (Table S5). N2 produced a higher F:B ratio than N1and N3 under NT, whereas N application rate did not affect F:B ratio under CT in both depths (Figure 3k,l).

3.3 | Soil bacteria community compositions

According to 16S rRNA gene sequences, each sample ranged from 31,458 to 172,704 sequences at a 97% sequence identity threshold. Overall, a total of 8232 OTUs were identified. Actinobacteria (14.5%–32.6% relative abundance), Proteobacteria (16.5%–28.7% relative abundance), Acidobacteria (15.5%–37.1% relative abundance), Chloroflexi (10.5%–21.6% relative abundance), and Gemmatimonadetes (4.0%–6.9% relative abundance) were considered the dominant phyla associated with residue decomposition (Figure 4a,b). These five phyla accounted for 96.4% of all sequence reads (Figure 4).

N application, tillage, and N × tillage interaction significantly influenced the bacterial (16S) community compositions (Table S7). For

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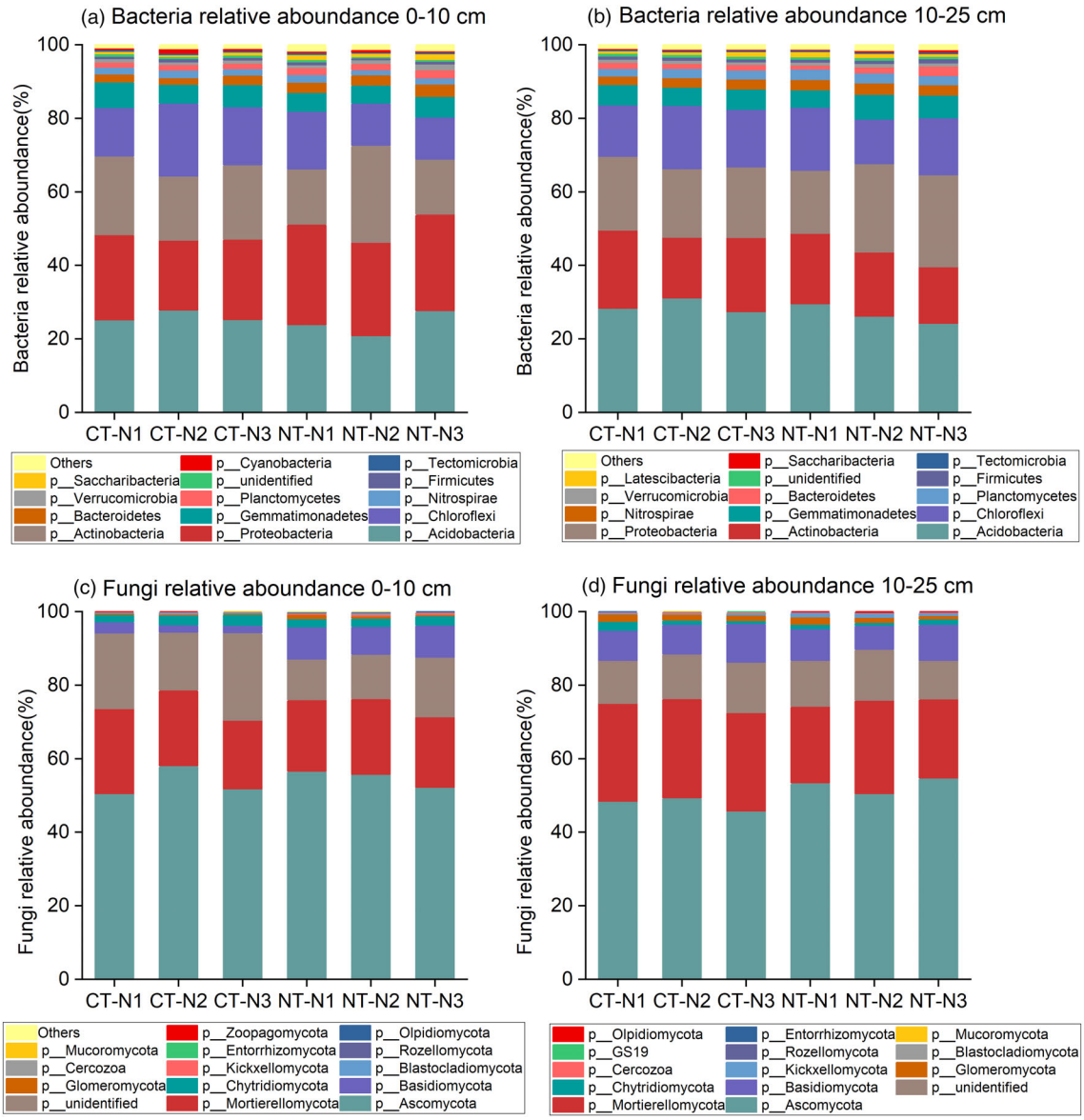

FIGURE 4 The effects of tillage (T) and nitrogen (N) on the relative abundance of bacteria and fungi. Relative abundance of bacterial and fungus for the taxonomic levels of the phylum. Values are means ($n = 3$) [Colour figure can be viewed at wileyonlinelibrary.com]

the dominant phyla, the relative abundances of Acidobacteria increased with soil depth, while the relative abundances of Proteobacteria, Bacteroidetes, and Actinobacteria declined with soil depth (Table S8). Compared with CT, NT increased the relative abundances of Bacteroidetes and Proteobacteria in the 0–25 cm layer (Figure S1). The relative abundances of Bacteroidetes increased with an increase in N application under two tillage treatments in the 0–10 cm soil layer. Furthermore, the relative abundances of Chloroflexi of N1 were higher than N2 and N3 under NT at both depths.

3.4 | Soil fungi community composition

The histogram of fungal community structure revealed structural and abundance differences among N application rates and tillage treatments (Figure 4c,d). Soil fungal communities included 2074 OTUs and there were five phyla of eumycota with an abundance >0.01%. Ascomycota and Mortierellomycota were the two most dominant, accounting for >60% of all phyla.

In more detail, the abundance of Basidiomycota and Glomeromycota was higher under NT than under CT in 0–10 cm layers (Figure S2). The relative abundances of Glomeromycota decreased with an increase in N application under NT in the 0–10 cm layers.

3.5 | Diversity of soil bacteria and fungi

The diversity of soil bacteria and fungi was significantly affected by tillage practice and N management in 0–10 cm layer. However, soil fungal diversity was only affected by their interactions in 0–10 cm

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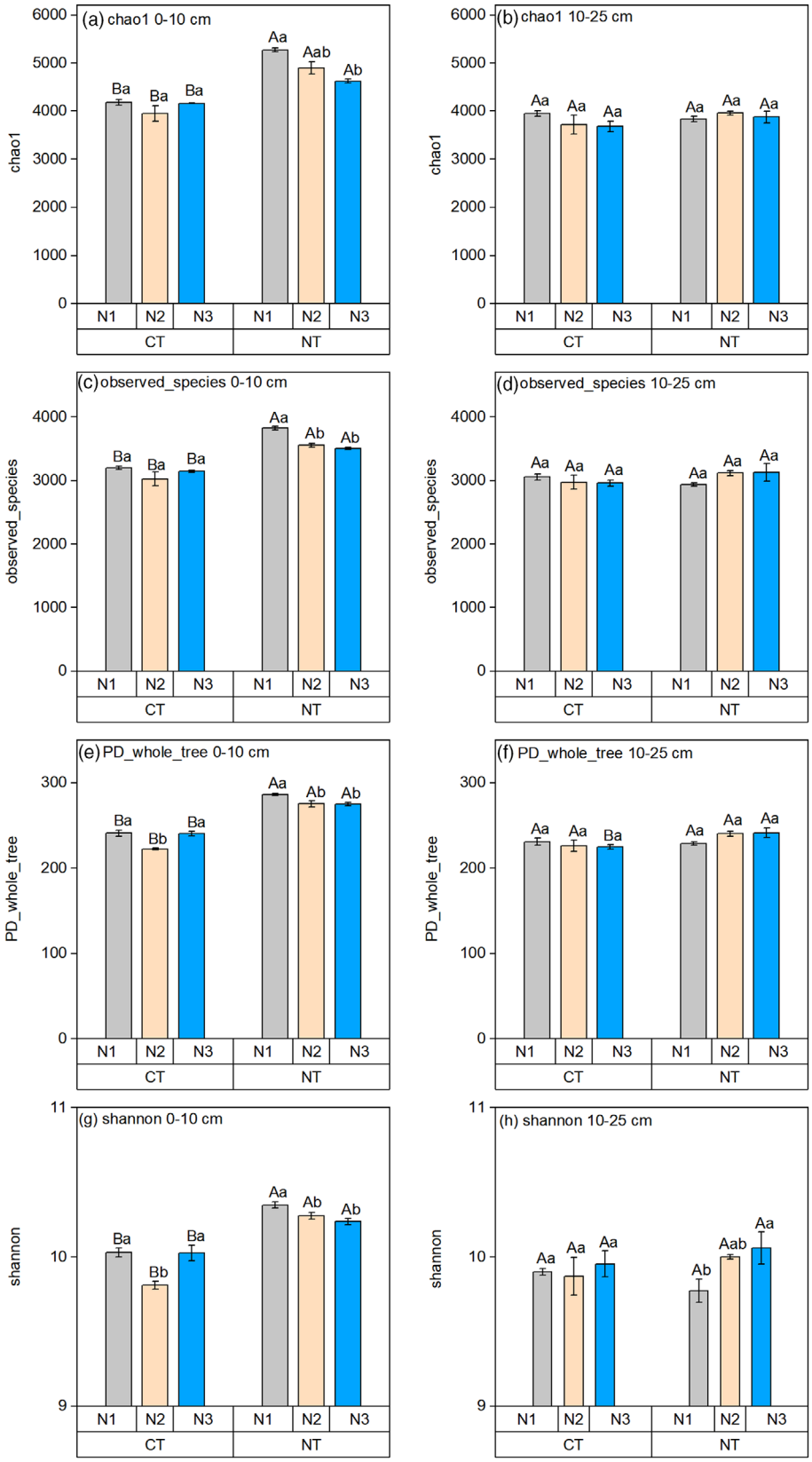

FIGURE 5 The effects of tillage (T) and nitrogen (N) on bacterial diversity. Vertical bars indicate the standard error of means ($n = 3$). Different upper-case letters indicate significant differences ($p < 0.05$) between two tillage treatments under the same nitrogen addition rate; different lower-case letters indicate significant differences ($p < 0.05$) among nitrogen addition rates under the same tillage treatment. N1, nitrogen addition at 105 kg N ha^{-1}; N2, nitrogen addition at 180 kg N ha^{-1}; N3, nitrogen addition at 210 kg N ha^{-1}; CT, conventional tillage; NT, no-tillage [Colour figure can be viewed at wileyonlinelibrary.com]

layer ($p < 0.05$). NT significantly increased soil bacterial diversity compared with CT in 0–10 cm under each N addition rate ($p < 0.05$; Figure 5). Soil bacterial diversity decreased with soil depth under NT ($p < 0.05$; Table S12). N application also significantly affected bacterial diversity under NT, whereas N application had no effect under CT in the 0–10 cm layer (Figure 5). Bacterial diversity decreased with an

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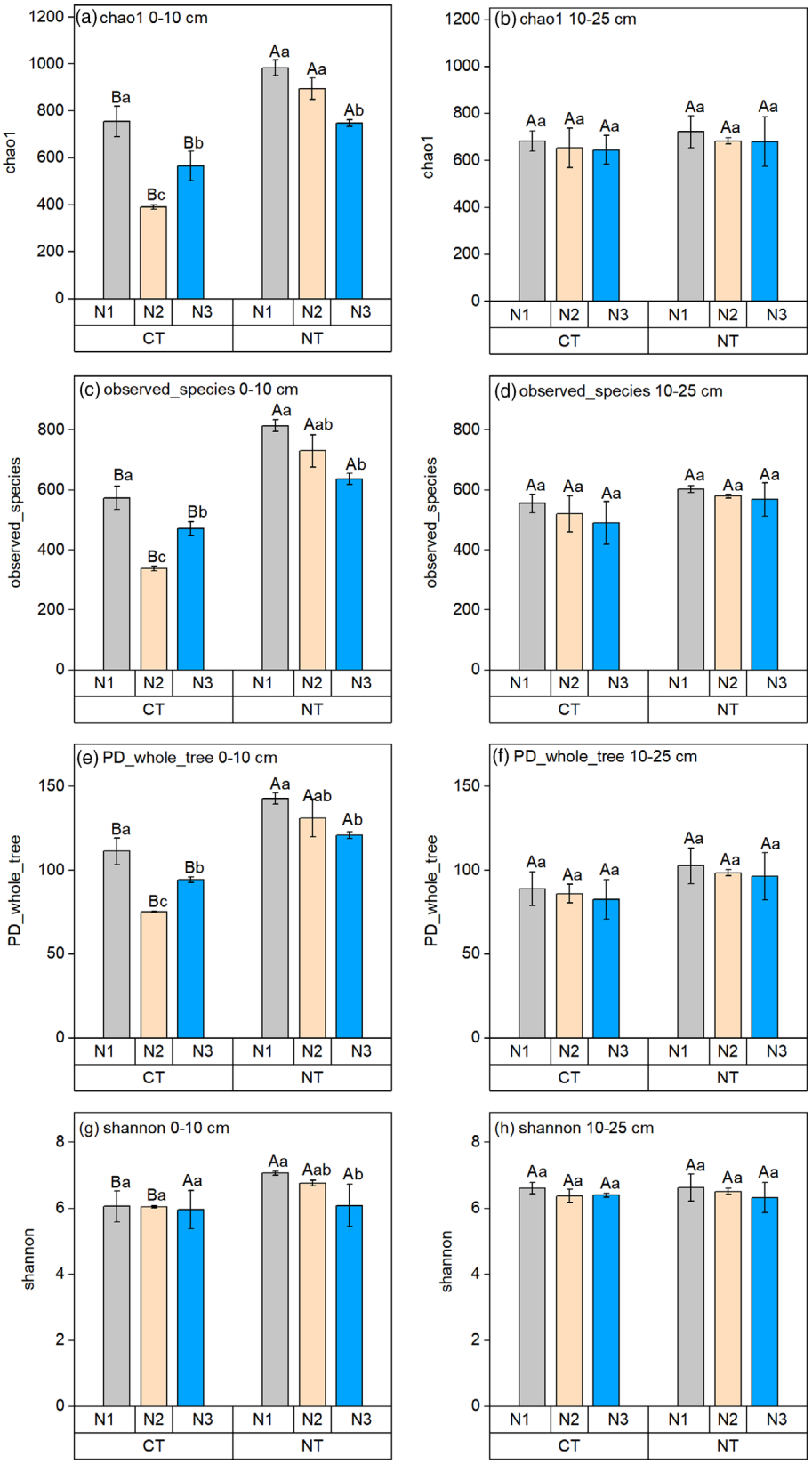

FIGURE 6 The effects of tillage (T) and nitrogen (N) on fungal diversity. Vertical bars indicate the standard error of means ($n = 3$). Different upper-case letters indicate significant differences ($p < 0.05$) between two tillage treatments under the same nitrogen addition rate; different lower-case letters indicate significant differences ($p < 0.05$) among nitrogen addition rates under the same tillage treatment. N1, nitrogen addition at 105 kg N ha^{-1}; N2, nitrogen addition at 180 kg N ha^{-1}; N3, nitrogen addition at 210 kg N ha^{-1}; CT, conventional tillage; NT, no-tillage [Colour figure can be viewed at wileyonlinelibrary.com]

increase in N application rates under NT in the 0–10 cm layer, while N application had no influence on bacterial diversity under two tillage treatments in the 10–25 cm layer. Similarly, NT significantly enhanced the average value of soil fungi diversity compared with CT in 0–10 cm layer (Figure 6). Soil fungal diversity decreased as the soil depth under NT and decreased with an increase in N application rates under NT in

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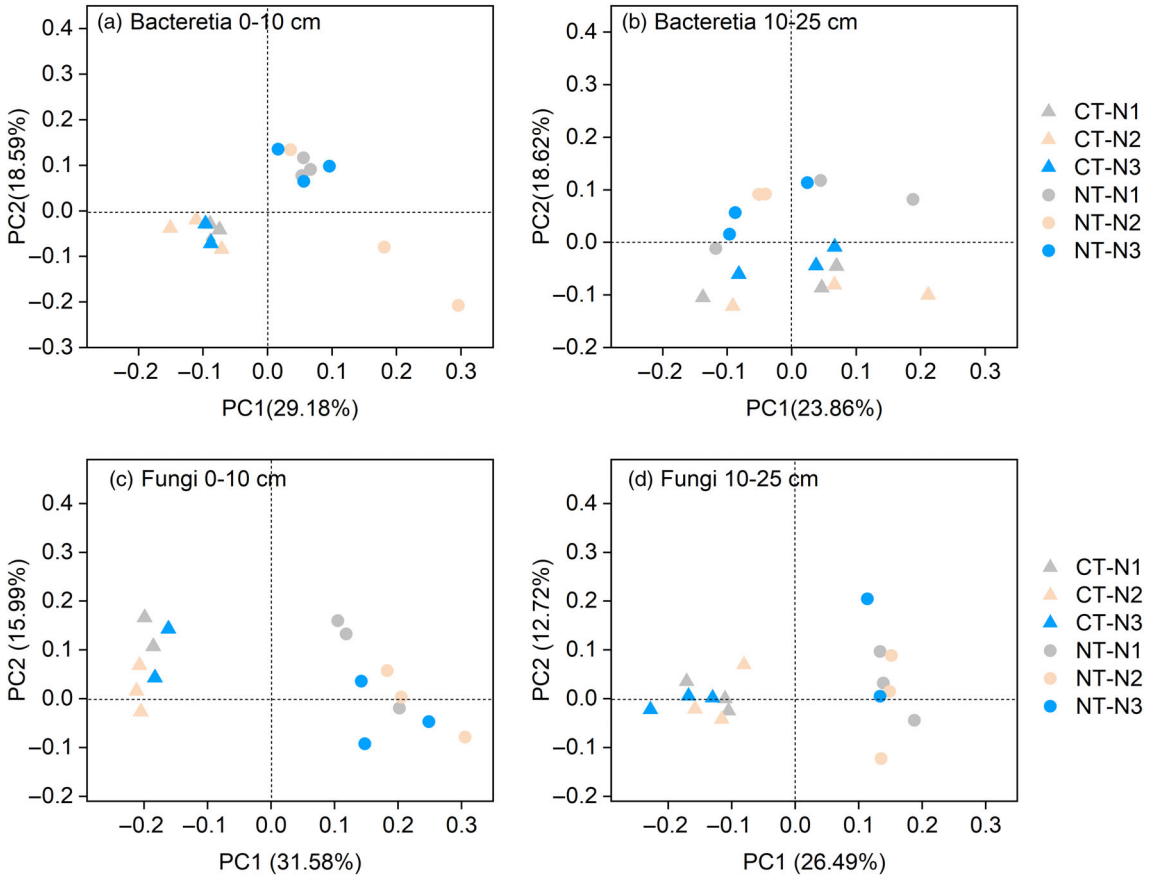

FIGURE 7 Principal coordinate analysis (PCoA) of the bacterial and fungal compositions among tillage (T), nitrogen (N), and soil depth (D). N1, nitrogen addition at 105 kg N ha^{-1}; N2, nitrogen addition at 180 kg N ha^{-1}; N3, nitrogen addition at 210 kg N ha^{-1}; CT, conventional tillage; NT, no-tillage [Colour figure can be viewed at wileyonlinelibrary.com]

0–10 cm layer (Table S14 and Figure 6). However, the fungal diversity of CT was not influenced by soil depth. N application also had no influence on fungal diversity under two tillage treatments in 10–25 cm soil layer.

Principal component analysis of bacterial composition at the phylum level showed that two principal components accounted for 47.7% and 42.4% of the overall variances among these treatments in the 0–10 and 10–25 cm layers, respectively (Figure 7). We also found that PCoA of the fungal composition showed that two principal components accounted for 46.5% and 39.2%, respectively. We revealed that the two fractions (CT and NT) formed their clusters separated by PC1 in both soil layers. For fungi, the samples under the three N application rates of CT clustered closely, while samples within the NT differed more distinctly in both soil layers.

3.6 | Soil fractions

Tillage practice, N management, and their interaction had a significant influence on soil POC and MAOC contents in 0–25 cm layer ($p < 0.05$; Table S15). The POC and MAOC contents decreased with depth (Table S16). NT increased the POC and MAOC contents by 12.1% and 10.1% compared with CT in the 0–10 cm layer, respectively (Figure 8). The POC and MAOC contents increased with increasing N addition and the rate of increase under NT was higher than under CT in the 0–10 cm layer. However, tillage and N treatment had no influence on MAOC in the 10–25 cm layer (Figure 8d).

3.7 | PLS-PM analysis

We established a partial least squares path model to better integrate the interrelationships among N application, tillage practices, microbial communities, soil enzyme activities, soil microbial CUE, POC, and MAOC (Figure 9). The indirect effect of tillage treatments (0.38) on soil microbial CUE was larger than that of N application (0.13). We further found that tillage management and N application affected microbial CUE through changing soil bacterial diversity, fungal community structure, and fungus diversity more than bacterial and fungal biomass. The responses of microbial CUE to bacterial and fungal diversity were also different (Figure 9). Moreover, the results showed that microbial CUE and soil enzyme activities had a direct effect on soil POC.

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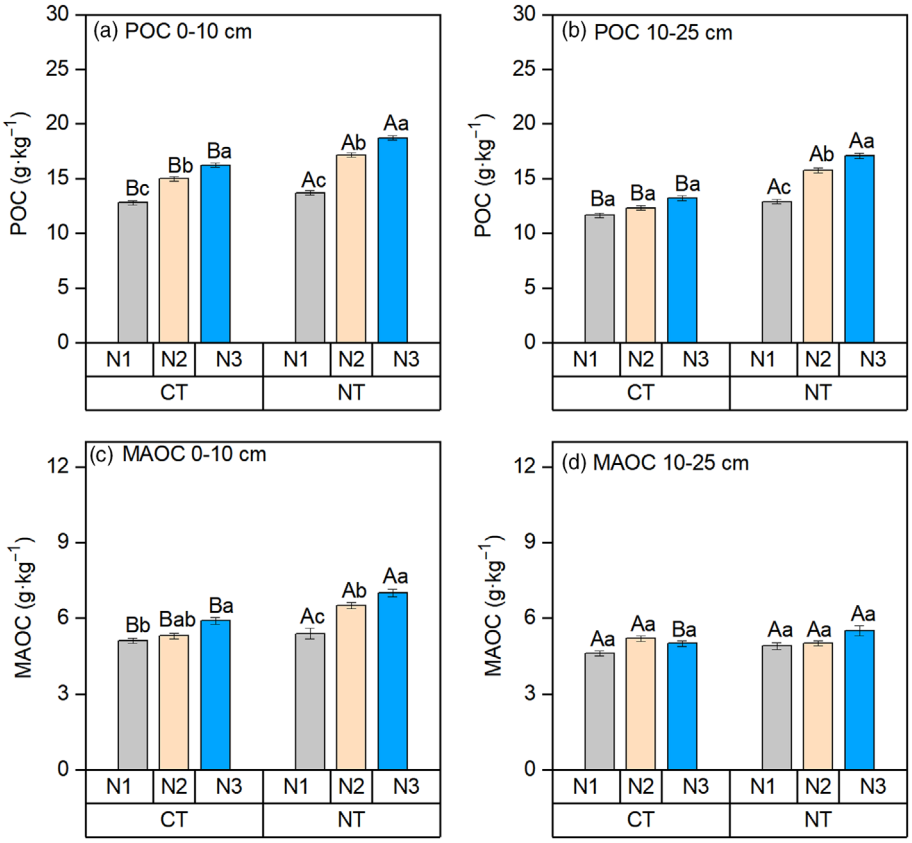

FIGURE 8 The effects of tillage (T) and nitrogen (N) on soil POC and MAOC. Vertical bars indicate the standard error of means ($n = 3$). Different upper-case letters indicate significant differences ($p < 0.05$) between two tillage treatments under the same nitrogen addition rate; different lower-case letters indicate significant differences ($p < 0.05$) among nitrogen addition rates under the same tillage treatment. N1, nitrogen addition at 105 kg N ha^{-1}; N2, nitrogen addition at 180 kg N ha^{-1}; N3, nitrogen addition at 210 kg N ha^{-1}; CT, conventional tillage; NT, no-tillage [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

4.1 | Effect of tillage and N addition on soil microbial diversity and community structure

Soil microbial communities are essential to maintaining soil ecosystem function and can be affected by tillage and N application (Bärlocher & Boddy, 2016; Keszthelyi et al., 2008). We found that NT treatment increased bacterial and fungal diversity in 0–10 cm layer compared to CT treatment (Figures 5 and 6). The difference between CT and NT could be due to the decrease of soil physical disturbance and protection from fungal hyphae and their mycelial network under the no-tillage system (Ceja-Navarro et al., 2010; Verbruggen & Toby, 2010; Wang et al., 2017). Another reason is that no-tillage with straw mulching could increase soil microbial diversity by increasing soil organic matter and carbon source inputs in surface soil (Li et al., 2020c). However, straw mulching less affected soil microorganisms in 10–25 cm than in 0–10 cm depth under no-tillage (Sun et al., 2016), which could lead to an insignificant difference in the bacterial and fungal diversity in 10–25 cm layer between NT and CT treatments. This is the main reason why the effect of the two tillage practices on microbial diversity is inconsistent in 0–10 and 10–25 cm soil layers.

Furthermore, soil fungal and bacterial diversity decreased with increasing N application rates in the 0–10 cm layer and was higher under NT treatment than under CT (Figures 5 and 9). One possible reason is that the straw in no-tillage has a wide C/N ratio (Thierfelder et al., 2018), which leads to an N limitation under this tillage system because microbe needs more N under this condition. A previous meta-analysis showed that appropriate N addition (<100 kg N ha^{-1} year^{-1}) is essential to stimulate microbial growth in no-tillage systems because it regulates soil C/N (Thierfelder et al., 2018; Zhou et al., 2017). However, excessive N fertilization suppresses the diversity of soil microbes because of the toxic effect of urea (Omar & Ismail, 1999; Wang et al., 2018). In this study, the highest N application rate (210 kg N ha^{-1}) could induce toxicity, resulting in lesser microbial diversity. In addition, CT had lower soil SOC (Li et al., 2010; Liu et al., 2021) and C/N ratio compared with NT (Fiorini et al., 2020), which leads to carbon limiting for microorganisms. Hence, the effect of N application had a smaller effect on microbial diversity under CT than NT. The previous study also showed that the N application level (100–200 kg N ha^{-1}) decreased soil microbial diversity under no-tillage (Li et al., 2020c), which confirms our conclusion under the N application level (105–210 kg N ha^{-1}) (Figures 5 and 6). In addition, increasing N application rates under no-tillage practice had a negative effect on some dominant flora such as Chloroflexi (Figure S1) that plays a vital role in the decomposition of refractory C compounds (Li et al., 2019b; Piazza et al., 2019). These results further indicate that N application needs to be considered when studying the effect of tillage management on SOC from the perspective of microbial properties.

Tillage management could also influence the vertical distribution of soil microbial communities (Nunes et al., 2020). We found no difference in enzyme activities, total PLFAs, and bacterial and fungal diversity among soil layers under CT treatment (Figures 1, 3, 5, and 6).

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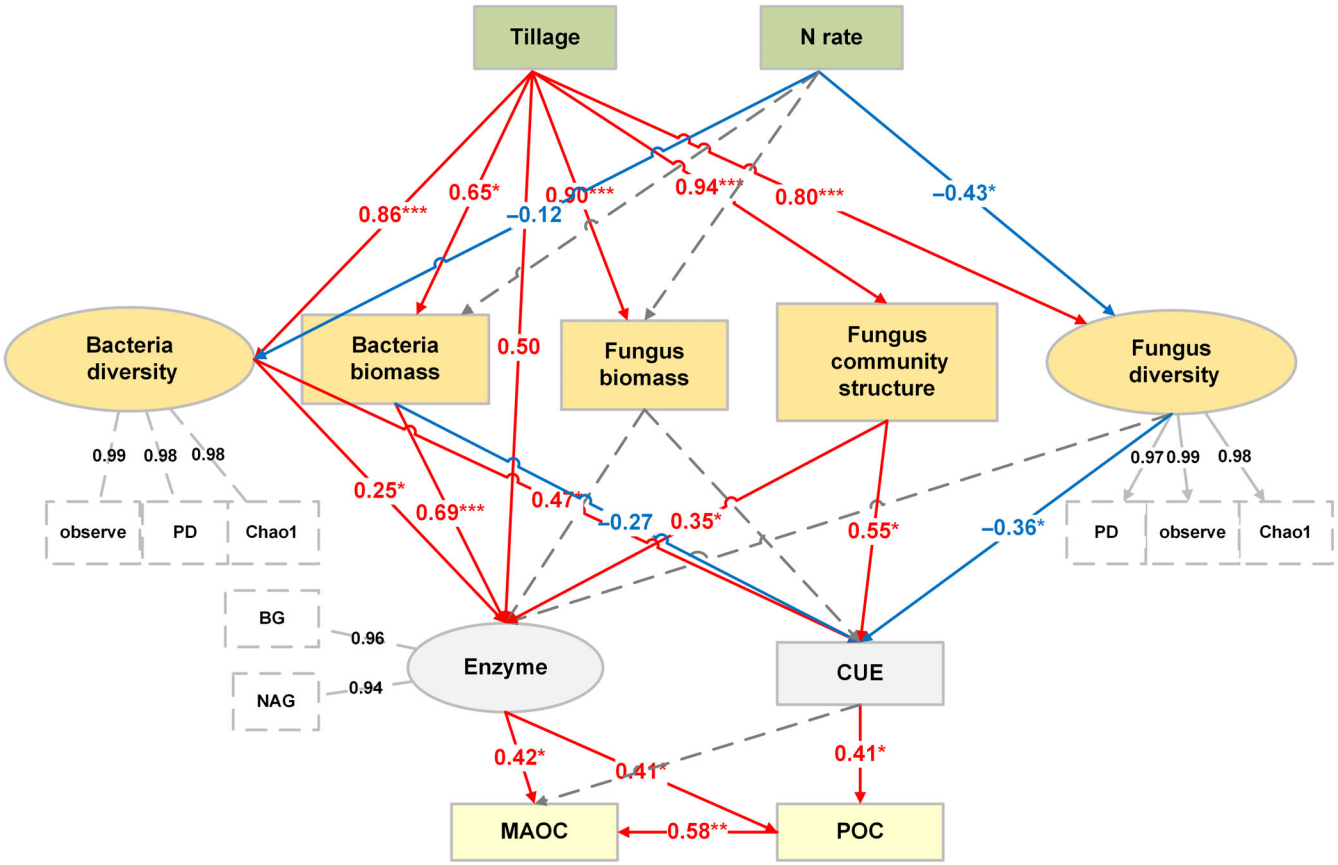

FIGURE 9 Directed graph of the partial least squares path model (PLS-PM). Each box represents an observed (i.e., bacteria biomass) or each oval represents a latent variable (e.g., bacteria diversity). The loading of bacteria diversity, fungus diversity, and enzyme activities that create the latent variables are shown in the dashed rectangle. Path coefficients are reflected by the widths of the arrows and the numbers next to the arrows. Red and blue arrows indicate positive and negative effects, respectively. Dashed arrows indicate that coefficients do not differ significantly ($p > 0.05$) [Colour figure can be viewed at wileyonlinelibrary.com]

The main reason was that soil microbial communities in different soil layers would be similar to each other after homogenization induced by plowing under CT (Sun et al., 2018). However, fungal and bacterial diversity decreased as soil depth increased under NT (Tables S12 and S14), which was supported by the previous study (Jumpponen et al., 2010). This was likely because no-tillage creates heterogeneous soil (Sun et al., 2018). Our previous study in this experiment site showed that soil depth had a significant influence on soil moisture, bulk density, porosity, and aggregate stability in 0–20 cm soil depth (Li et al., 2020a), which could lead that microbial properties are different with changing in topsoil depth. In addition, some previous studies also showed the difference in enzyme activities and microbial properties under different topsoil depths (Fierer et al., 2003; Mathew et al., 2012). Hence, altered soil physicochemical properties under conservation tillage created significantly different habitats for microbe and resulted in the change of soil microbial community structure and diversity (Mathew et al., 2012).

Moreover, the decrease rate of fungal and bacterial diversity with increasing soil depth was higher under N1 than N2 and N3 for NT treatment (Figures 5 and 6), indicating that a low N rate can enhance topsoil bacterial and fungal diversity under NT. Hence, it is not sufficient to only consider the surface layer when investigating bacterial and fungal diversity response to N application rates in no-tillage systems.

4.2 | Relationship of soil microbial characteristic and microbial CUE

Soil microbial CUE can affect soil C cycling (Spohn et al., 2016). We found that NT increased the soil microbial CUE compared with CT in the 0–10 cm layer (Figure 2). One possible reason was that NT could decrease soil temperature by surface mulching and further increase microbial CUE (Apple et al., 2006; Wetterstedt & Agren, 2011). We also found that NT decreased average soil temperature in the two soil layers (Table S17). The second reason could be that NT continuously supplied labile organic substrates for microbial biomass by residue application, resulting in higher CUE of NT than CT (Álvaro-Fuentes et al., 2013). POC is a labile organic substrate and NT increased POC compared with CT treatment (Figure 8). In addition, bacteria diversity had positive relationships with microbial CUE (Figures 9). NT could also increase microbial CUE by increasing bacteria diversity. Microbial

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CUE increased with increasing N application under both tillage treatments in 0–25 cm (Figure 2). The reason is that N addition can reduce microbial respiration metabolism (Liu et al., 2018; Spohn et al., 2016; Thiet et al., 2006) and increase microbial biomass (Jha et al., 2020), resulting in higher microbial CUE. Moreover, although N fertilizer was only applied at 10 cm depth under no-tillage in our study, N addition had a significant influence on the microbial CUE in deeper soil layer (10–25 cm). The main reason is that nitrate nitrogen can transport with soil water movement, resulting in nitrogen leached into deeper soil depth (Li et al., 2021). In addition, our previous study showed that NT increased the soil porosity of >55 μm diameter pores compared to the CT treatment, which indicated that NT could increase soil water infiltration and nitrogen leaching (Li, et al., 2020a).

Furthermore, although a recent study showed that microbial diversity drives CUE in artificial soil (Domeignoz-Horta et al., 2020), to the best of our knowledge, few experimental studies have directly demonstrated the interaction effect of tillage management and N application on microbial CUE in a field experiment. In our study, the PLS-PM showed that bacteria diversity, fungal diversity, and fungal community structure could play more critical roles than their biomass in increasing microbial CUE (Figures 9, S3,S4,). We also found that the bacterial and fungal diversity had different influences on microbial CUE under two tillage and these relationships were regulated by N application under no-tillage (Figures 9 and S4). Bacterial diversity positively influenced microbial CUE, whereas fungal diversity had an adverse impact on microbial CUE (Figure 9). The difference points to the importance of studying the diversity of fungal and bacterial communities separately for predicting soil C cycling. In addition, microbial network complexity drives carbon cycling with direct feedback effects on multiple ecosystem functions (Morriën et al., 2017; Wagg et al., 2019; Zhou et al., 2010), which could also influence microbial CUE. Further research should be undertaken to explore the effect of bacterial and fungal networks on microbial CUE.

4.3 | The influence of microbial CUE on soil POC and MAOC fractions

POC is a functional soil component for stable soil organic carbon (Witzgall et al., 2021). In contrast to POC, MAOC is more protected (physically or chemically), making it not easy to mineralize (Abramoff et al., 2018). We found that high N application (210 kg N ha^{-1}) increased POC and MAOC content under two tillage practices (Figure 8), which is similar to the previous study (Ye et al., 2018). The possible reason was that plant biomass (Stewart et al., 2016; Thomas et al., 2010; Wang et al., 2018) and microbial residues (Chen et al., 2020a) increased with increasing N application. However, some discrepant findings showed that N addition decreased (Ye et al., 2018) or had no significant influence on MAOC (Yuan et al., 2020). The main reason for the inconsistent results could be that microbial residues controlled the variation of soil MAOC pool and the microbial residues were different due to different N application rates (Averill & Waring, 2018; Chen et al., 2020a; Su et al., 2020; Yang et al., 2020b).

Microbial CUE increased with increasing POC and MAOC due to the increment of N application rates (Figure S5) and N addition also increased microbial CUE, POC, and MAOC content in some previous studies (Chen et al., 2019; Liu et al., 2018; Ye et al., 2018). These findings suggested that increasing N application rates is an efficient measure to increase POC and MAOC by enhancing microbial CUE under CT and NT practices. However, the increasing rate of POC or MAOC with microbial CUE under NT was higher than under CT because of the regulation of N addition (Figure S5). A possible reason was that there was N limitation under NT (Zhou et al., 2017) because the straw applied in this tillage system has a wide C/N ratio and microbe needs more N (Thierfelder et al., 2018). Therefore, this study further highlights the critical role of N addition in regulating the effect of microbial CUE on soil organic carbon fractions under tillage practices.

5 | CONCLUSIONS

N application could alter the effects of tillage practices on soil microbial diversity, community composition, biomass, and CUE. Bacterial and fungal diversities were more responsible for soil microbial CUE than their biomass. Although microbial CUE was more susceptible to tillage management than N application, it increased with an increase in N application rate under the two tillage practices. Furthermore, soil microbial CUE increased soil POC and MAOC contents and N application also increased the two SOC fractions. This research underscores the importance of N application to reveal the effect of tillage management on POC and MAOC from the perspective of soil microbial properties, which contributes to understanding the potential C sequestration benefits of increasing N addition under no-tillage.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Shengping Li https://orcid.org/0000-0001-6940-9179
Xueping Wu https://orcid.org/0000-0002-7772-0773
Xiaotong Liu https://orcid.org/0000-0001-9393-933X
Ahmed Ali Abdelrhmana https://orcid.org/0000-0002-7243-7338

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