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Effects of tillage management on *cbbL*-carrying bacteria and soil organic carbon dynamics across aggregate size classes in the farmland of North China Plain

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ABSTRACT

Calvin-Benson-Bassham cycle (*cbbL*)-carrying bacteria in soil are essential to renew and circulate organic matter. However, the relation between *cbbL*-carrying bacteria and soil carbon dynamics under tillage managements, especially across the aggregate size remains unclear. Thus, in our study, soil organic carbon (SOC) storages, mineralization, and the *cbbL*-carrying bacterial community across five soil aggregate sizes were thoroughly investigated under four tillage treatments: conventional rotary tillage (CT), deep plowing (DP), subsoiling (SS), no-tillage (NT). We found macroaggregates (>2 mm) contributed most with regard to SOC stocks, whereas microaggregates (<0.25 mm) contributed the least among all the tillage managements (NT, DP, SS and CT). Macroaggregates (>1 mm) with the highest cumulative SOC mineralization were found in subsoiling, whereas microaggregates had the lowest cumulative mineralization under no-tillage. By physically protecting, no-tillage specifically inhibited carbon dioxide (CO_2) emissions in macroaggregates (>1 mm), whereas increased SOC levels and encouraged CO_2 releases across microaggregates. Shifts in the co-occurrence network demonstrated that subsoiling promoted the joint symbiotic function between *cbbL*-carrying bacteria, the efficiency of matter and energy, and information transfer. And the keystone species, the enhanced cooperation and stochastic processes of autotrophic microorganisms under subsoiling lead to increased carbon fixation and reduced CO_2 emissions in microaggregates with limited oxygen and nutrients. Overall, our work verified physical protection of large aggregates under no-tillage and improvement of microbial interaction efficiency under subsoiling. This may offer a theoretical foundation for the choice of tillage practices in fluvo-aquic soil regions.

1. Introduction

Soil organic carbon (SOC) is a crucial predictor of soil quality, and it affects soil biological health, crop production, and climate change (Alhameid et al., 2019; Bossio et al., 2020). Among mechanisms of SOC sequestration, soil aggregates are essential physical dimensions, with roughly 90% of SOC stabilization occurring in them (Kan et al., 2020). Six et al. (2002) reported that SOC is more active in macroaggregates and SOC may be protected in microaggregates with lower decomposition speed. Soil organic carbon pool in the farmland accounts for 8–10% of total global soil organic carbon pool (Zomer et al., 2021), which is most strongly affected by human activities. Developing a better understand of SOC dynamics in soil aggregates of agricultural soils can minimize carbon dioxide (CO_2) emissions and maximize SOC accumulation. Tillage management, as a relatively frequent occurrence of human activities, could exert influences on the formation, turnover, and stabilization of soil aggregates, and directly or indirectly alter SOC dynamics (Liu et al., 2022b). Conventional management, such as plow-based tillage, could substantially destroy soil aggregates and subsequently enhance SOC mineralization (Lichter et al., 2008; Qi et al., 2021). Reduced tillage improves soil structure, decreases nutrient loss, and enhances soil aggregate stability and SOC storage (Blanco-Canqui and Ruis, 2018; Liu et al., 2022c). No-tillage (NT) contributed to the macroaggregate formation and protected SOC from loss (Kabiri et al., 2016; Kan et al., 2020). However, promoting microbial growth caused by less distraction would boost the carbon-use efficiency (CUE) of the soil microbial community in turn (Sae-Tun et al., 2022; Sauvadet et al., 2018), and then promotes SOC decomposition. Consequently, changes

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in SOC dynamics based on various aggregates are not fully understood concerning tillage practices, which limits our prediction of the carbon storage capacity of agroecosystems and requires in-depth research.

CO_2-fixing microorganisms transform atmospheric CO_2 into organic matter, are essential to sequestrate atmospheric CO_2 and affect the regeneration and circulation of organic matter (Lynn et al., 2017). The Calvin-Benson-Bassham cycle is the primary way for photoautotrophs and chemical autotrophs to assimilate CO_2. The *cbbL* gene encodes the enzyme of I ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO), which regulates the rate of the Calvin-Benson-Bassham cycle (Liao et al., 2020). Therefore, the *cbbL* gene has been recently used to access autotrophic microbial diversity. By altering SOC, C/N, pH, bulk density, nitrogen availability, and phosphorus availability, tillage management substantially impact CO_2-fixing microorganisms (Liao et al., 2020; Lu et al., 2019; Qin et al., 2021; Wang et al., 2020c). Using a metagenomic approach to reveal soil microbial functional specificity under four tillage regimes, Wang et al. (2020c) found that organic mulching effectively increased the abundance of *cbbL* genes. Ge et al. (2016) suggested that in comparison to NT, conventional tillage treatment had lower levels of total and *cbbL*-carrying bacteria. But the other study reported that compared to no-tillage, conventional tillage could boost *cbbL* abundance, 16S rRNA, and RubisCO activity, the likelihood of CO_2 mitigation by tillage depended on the soil conditions (Lu et al., 2019). The long-term addition of organic or inorganic chemical fertilizers had no significant impact on *cbbL* genes in red sandy loam soil, the difference to previous study may be caused by soil types (Anandakumar et al., 2022). Though a large discrepancy existed in the abundance of *cbbL* genes caused by tillage management, relatively few studies have explored how tillage management modifies the structure and network of the soil autotrophic bacterial communities, notably the assembly processes.

Assembly theory holds that microbial community diversity is predominantly caused by deterministic processes like niche differentiation and stochastic processes like ecological drift (Stegen et al., 2012). The overall balance between deterministic and stochastic processes affects microbial communities and ecosystem functioning (Ernakovich et al., 2022). To assess the relative contributions of deterministic and stochastic processes, ecological processes are often categorized into homogeneous dispersion, dispersion restriction, homogeneous selection, non-dominated processes and variable selection. The balance between stochastic and deterministic processes may change as a result of variable tillage managements, but it is yet unclear how these ecological processes and the assemblage of autotrophic microorganisms will respond. Recently, microbial network analysis has been used to discover keystone taxa that have a substantial impact on microbial ecology, the response of the soil microbiome to environmental changes, and reveal processes linked to patterns of community construction (Liu et al., 2022c; Zheng et al., 2022). Previous studies revealed that tillage management affects the soil microbial symbiotic network differently, with rotary tillage and deep tillage complicating the bacterial network while simplifying the fungal network (Guan et al., 2022). Also, tillage management selects distinct microbial communities and shapes niches (Liu et al., 2018), no-tillage, conventional, and plow tillage enriched different keystone taxa, respectively. Unlike conventional tillage, no-tillage and reduced tillage were reported to have more stable bacterial network structures and lower homogeneous dispersion values (Liu et al., 2022c). Therefore, a thorough analysis of microbial networks and community assembly processes is also crucial to revealing the ecological functions of microbial communities and their connection with CO_2 emissions.

The fluvo-aquic soil areas, located in North China Plain, are momentous sources for food production in China. With increasing food demands, intensive agricultural practices led to adverse consequences such as soil degradation and increased greenhouse gas emissions (Kan et al., 2020). Thus, conducting proper tillage management is critical to sustainably develop local agriculture. To fully understand the SOC dynamics under different tillage management, separating soil into aggregates are necessary. Here, we combined a field experiment and an incubation experiment to explore the impacts of tillage managements on SOC stock, SOC mineralization and autotrophic bacterial communities. We hypothesized that: (i) SOC dynamics are related to the aggregate class and autotrophic bacterial communities; (ii) No-tillage decrease carbon mineralization of macroaggregates and increase the sequestration of SOC via physical protection; (iii) Subsoiling decrease carbon mineralization of microaggregates via the interaction of autotrophic microbes.

2. Materials and methods

2.1. Experimental site and soil sampling

The field experiment was carried out in Qihe County, Shandong province, China (36°47′ N, 116°46′ E) in 2016, and the cropping system was winter wheat-summer maize rotation. The climate of Qihe is warm temperate subhumid monsoon climate with mean annual temperature of 13.4 °C, the precipitation of 622 mm, and the soil type of fluvo-aquic. Four field plots, each 10, 000 m^2 (100 m × 100 m), were established for various tillage managements. The experiment had four tillage managements: (1) conventional rotary tillage with straw returned (CT), deep plowing with straw returned (DP), subsoiling with straw returned (SS), no-tillage with straw returned (NT). The amount of corn straw returned to the field is about 2.25 kg• m^{-2} and the crop management measures carried out according to the local routine practice during the experiment.

Prior to the September 2019 maize harvest, soil samples (depth: 0–30 cm) were collected using a 5 cm diameter soil auger. For each tillage management, three plots (10 m × 10 m) were randomly chosen as three replicates, and 15 soil samples were collected from each plot according to the S-shape sampling approach and mixed into one sample. After removing visible the stones and residues, put them into hard plastic boxes to prevent extrusion, and transport back to the laboratory with ice boxes. Dry sieving is used to separate soil into the following particle sizes: >5 mm, 2–5 mm, 1–2 mm, 0.25–1 mm, and < 0.25 mm, with intact soil as control, which was kept no particle size divisions. One portion of the samples was stored at −80 °C for *cbbL* analysis, one was stored at 4 °C for the soil properties (soil water content, ammonium nitrogen, nitrate nitrogen, dissolved organic carbon and microbial biomass carbon) analysis, and the others were air-dried.

2.2. Soil properties

Soil water content (SM) was measured by the drying-weighing method. The glass electrode method (MP511 pH meter) was used to test soil pH at the ratio of 2.5:1(w/v). Ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) were determined using a flow analyzer (AA3, Bran + Luebbe Crop, Germany) after being extracted with $CaCl_2$. Soil total nitrogen (TN) was digested with concentrated sulfuric acid and measured with a flow analyzer. C/N was the ratio of soil organic carbon to total nitrogen. Related carbon indicators, including soil organic carbon(SOC), microbial biomass carbon (MBC), dissolved organic carbon (DOC), and Permanganate oxidizable carbon (POXC) were provided in our previous study (Shen et al., 2021). Soil carbon stocks were calculated as follows (Zhang et al., 2020; Zheng et al., 2022):

$$SOCstock = \frac{SOC}{100} \times bulkdensity \times soildepth \times 1000$$

$$SOCstock_{(fraction)} = Ai \times SOCstock$$

where Ai represents the proportion of five soil aggregates, and SOC stock $_{(\text{fraction})}$is the SOC stock in each fraction.

2.3. SOC mineralization incubation experiment

Briefly, 60 g air-dried soil samples of each size of aggregates were laid flat on the bottom of 250 mL incubation jars. The jars were plugged with rubber stoppers with a needle, and a three-way valve and glue were applied to the connections to prevent air leakage. We pre-cultivated the soil samples for 7 days after wetting the samples at 60% field water-holding capacity in a constant temperature incubator at 25 °C. The blank control was cultivated in the same condition. To determine the CO_2 released during incubation, about 20 mL gas in each jar was extracted by a syringe at 1, 3, 5, 7, 14, 21, 28, 35, 42, 49, 56, 63, 70, 77, 84, 133, 147, 161, 175, 196, 217, 238, 266, 294, 322, 350 and 378 days after the start of incubation. After each time of gas collection, the three-way valve was kept open for 30 min to ensure it equilibrated with the atmosphere. The CO_2 concentration was analyzed by gas chromatograph (Agilent, 7890B).

The first-order kinetic equation was used to fit the cumulative SOC mineralization of soil aggregates under different tillage management (Liu et al., 2022b).

$$C_m = C_o(1 - e^{-kt})$$

where k is the decomposition rate (d^{-1}), t is the incubation period (d), C_o is the potentially mineralizing C (mg kg^{-1}), and C_m is the cumulative C mineralization of soil aggregates (mg kg^{-1}).

Cumulative potential mineralization (CPM) of soil under distinct tillage managements was calculated as follows (Liu et al., 2022b):

$$CPM_i = \sum_{i=1}^{4} A_I \times C_o$$

where CPM_i is the cumulative potential mineralization (mg C kg^{-1} soil), and A_i denotes the proportion of five soil aggregates.

2.4. Illumina MiSeq sequencing of the cbbL gene

The DNA extraction and high-throughput sequencing of soil samples were conducted by Allwegene Technology Co., Ltd., Beijing, China. 1% agarose gel electrophoresis was used to detect the quality of DNA extraction, and NanoDrop2000 was used to determine the concentration and purity of DNA. Primers GACTTCACCAAAGACGACGA and TCGAACTTGATTTCTTTCCA for the first round of amplification of *cbbL*2 gene (Ji et al., 2016). The PCR amplification procedure is as follows: heating to 94 °C for 5 min, followed by 30 cycles (denaturation at 94 °C for 60 s, annealing at 52 °C for 60 s and elongation at 72 °C for 60 s) and fluorescence intensity was also acquired at 72 °C for 7 min. And primers CATCATGTTCGACCAGGACT and TCGAACTTGATTTCTTTCCA for the second round of amplification of *cbbL2* gene (Ji et al., 2016). The second amplification procedure is as follows: heating to 94 °C for 5 min, followed by 20 cycles (denaturation at 94 °C for 30 s, annealing at 52 °C for 30 s and elongation at 72 °C for 60 s) and fluorescence intensity was also acquired at 72 °C for 7 min. The PCR products were purified with Agencourt AMPure XP nucleic acid purification kit after being amplified by 1% agarose gel electrophoresis to determine the size of the amplified bands and Illumina MiSeq sequencing was performed on the MiSeq PE300 platform. Raw fastq files were quality-filtered by Trimmomatic (v 0.36) and merged by FLASH (v1.2.0). The chimera of the sequence and undesirable short sequence were removed using the UCHIME method according to the known database to manipulate the clean tags. The clean tags were clustered into OTUs (Operational Taxonomic Units) by vsearch (2.7.1) at a similarity level of 97%. The data sets were deposited on the NCBI Sequence Read Archive under accession numbers PRJNA932154.

2.5. Network construction and community assembly processes analyses

The network co-occurrence analysis was constructed in the integrated Network Analysis Pipeline (INAP, https://mem.rcees.ac.cn:8081/) (Feng et al., 2022b) using high-throughput sequencing data of autotrophic microorganisms and visualized on Geiph (Wang et al., 2022a). Only genera present in > 50% of all samples and with relative abundance>0.01% were chosen for network analysis to lower the number of pairings and increase network reliability (Zheng et al., 2022). The network in this work pooled the data of all soil aggregates in each tillage management, resulting in 15 replicates per treatment, because of the less variation of microbial community composition across soil aggregates compared to tillage management. The correlation matrix was constructed by Spearman, and the microbial molecular ecological network was built by setting the appropriate threshold based on the random matrix theory (RMT). Each edge denotes the association between two genera, while each node represents a particular genus. The degree of connection between a node and other nodes in the same module is represented by the Zi connection degree. The degree of connection between a node and other module nodes is represented by the Pi divergence degree. The complete ecological network is separated into four sections based on the Zi and Pi thresholds: peripheral nodes (Zi ≤ 2.5, Pi ≤ 0.62), module hubs (Zi > 2.5, Pi ≤ 0.62), connectors (Zi ≤ 2.5, Pi > 0.62), and network hubs (Zi > 2.5, Pi > 0.62). Typically, the module hubs and connections were regarded as keystone taxa (Shi et al., 2016).

A null model was used to evaluate the underlying driving mechanisms of *cbbL*- carrying bacterial community assembly processes. Based on the nearest taxon index (βNTI) and Raup-Crick index (RCbray), the assembly processes were divided into deterministic process and stochastic process specifically including homogeneous selection (deterministic process, βNTI < -2), homogeneous dispersal (stochastic process, |βNTI| < 2 and RC < -0.95), undominated (stochastic process, |βNTI| < 2 and |RC| < 0.95), dispersal limitation (stochastic process, |βNTI| < 2 and RC > 0.95), and variable selection (deterministic process, βNTI > 2). The null model analysis was performed on the platform https://www.cloudtutu.com/#/index.

Niche breadth could reflect microbial community adaptability to the environment and resource utilization capacity. The microbial community with a wider niche breadth may perform more diverse soil ecology functions. The "Spaa" package in R was used to calculate the Levins' niche breadth index of the *cbbL*-carrying bacterial community under four tillage management (Wang et al., 2022b).

2.6. Statistical analysis

Data were analyzed using SPSS 24, origin, and R. One-way analysis of variance (ANOVA) with Duncan's Multiple Range test was used to examine significant differences between treatments. The effect of tillage management and soil aggregates on soil properties was analyzed by two-way analysis of variance (ANOVA). The differences of autotrophic bacteria communities in aggregates under different tillage measures were determined by principal coordinate analysis (PCoA) based on the Bray-Curtis. Permutation multivariate variance (PERMANOVA) analysis was performed using the "adonis" function in the "vegan" package to quantitatively assess the effects of tillage management and aggregate size on microbial communities. The bacterial taxa composition in phylum and genus levels were performed on the Tutools platform https://www.cloudtutu.com/#/index. And the differential species among distinct treatments were assessed by Stamp software. Based on the spearman correlation coefficient, the Mantel test determined the correlation among different environmental variables, carbon dynamics characteristics, and autotrophic microbial communities. Random forest using "rfPermute" package in R was to assess the significant predictors of SOC emissions, and the relevant predictors were further chosen for structural equation modeling (SEM) to analyze the potential mechanisms of carbon emissions under different tillage management using Amos 26.

3. Results

3.1. Effect of tillage management on soil properties across aggregate size class

Among the distinct treatments, soil properties varied differently (Table 1). The soil moisture (SM) of the aggregates showed an increasing trend as the aggregate size became small. pH significantly differed across diverse soil aggregates, with the highest in NT. Compared to CT, DP and SS significantly increased TN contents in large macroaggregates (>5 mm, 2–5 mm) while decreasing those in the other soil aggregates (0.25–1 mm, <0.25 mm). TN content of soil aggregates increased with the decreased aggregate size. Soil NO_3^-N contents differed among tillage management and ranged as follows: NT > CT > DP > SS. Soil NH_4^+-N in each aggregate decreased with the soil aggregate size reduced, while the content of NO_3^-N increased with the reduced soil aggregate size. NT significantly increased C/N compared to others, and the highest C/N was observed in the macroaggregates>5 mm under NT treatment.

We found that tillage management, agglomerate size, and their interactions could significantly affect SM, TN, NH_4^+-N, and NO_3^--N (**Table S1**). The effect of tillage management on C/N was insignificant, but the interaction between tillage management and agglomerate size could greatly influence the ratio of TC and TN.

3.2. Effect of tillage management on aggregate-associated SOC mineralization

At the beginning of the incubation experiment, SOC mineralization rates in soil aggregates decreased rapidly (**Fig. S1**). The highest mineralization rates across five aggregate size classes were found in < 0.25 mm aggregates among all tillage treatments. After 14 days, SOC mineralization rates gradually climbed, then declined, eventually remained steady. DP, SS, and NT treatments showed higher SOC mineralization rates than CT treatment in larger-size (>5 mm, 2–5 mm) soil aggregates, while the SOC mineralization rates in NT treatment were lower than CT after 84 d. However, NT showed significantly higher mineralization rates in soil aggregates (1–0.25 mm, <0.25 mm).

The cumulative SOC mineralization in soil aggregates among all the treatments increased with the extension of cultivation time (Fig. 1). In general, the highest cumulative SOC mineralization was obtained in the microaggregates. In large-size soil aggregates, DP, SS, and NT showed higher cumulative SOC mineralization than CT in the early incubation period. However, the cumulative mineralization in NT increased slowly after 100 days and finally showed lower values than CT. At the final stage of incubation, the highest cumulative SOC mineralization was found in DP in macroaggregates. Regarding microaggregates, NT treatment showed the highest cumulative SOC mineralization.

3.3. Effect of tillage management on aggregate-associated SOC storage and cumulative potential SOC mineralization

We found that large macroaggregates (>5 mm, 2–5 mm) contributed most with regard to SOC stocks, whereas microaggregates (<0.25 mm) accumulated the least (Fig. 2**A**). The highest SOC stock (18.34 Mg ha^{-1}) was recorded in macroaggregates (>5 mm) under DP treatments, and higher 58.98%, 45.98%, and 22.29% than CT, SS, and NT, respectively. Meanwhile, under SS treatment, microaggregates (<0.25 mm) retained more SOC stock.

The cumulative mineralization of SOC in soil aggregates could be well fitted to the first-order kinetic model to assess SOC stability (**Table S2**). For the soil macroaggregates (>5 mm, 2–5 mm, 1–2 mm), DP and SS treatment had higher values of C_o and mineralization quotient, but for the microaggregates (<0.25 mm), NT and CT treatment

Table 1
Soil properties under different tillage managements.

Factor	Particle size of soil aggerates	CT	DP	SS	NT
SM (%)	Intact soil	18.54 ± 0.05Ab	19.17 ± 0.72Ab	18.85 ± 0.40Aa	19.52 ± 0.71Aa
	>5 mm	20.80 ± 0.07Aa	21.53 ± 1.44Aa	19.21 ± 0.40Ba	20.78 ± 0.24Aa
	2–5 mm	19.11 ± 0.65ABab	18.60 ± 0.54Bb	18.98 ± 0.26ABa	19.76 ± 0.27Aa
	1–2 mm	17.68 ± 0.43Bb	17.98 ± 0.50ABbc	19.37 ± 0.39Aa	18.90 ± 1.31ABa
	0.25–1 mm	17.36 ± 0.41Ab	16.69 ± 1.31Ac	18.56 ± 0.77Aa	18.80 ± 1.82Aa
	<0.25 mm	13.76 ± 2.32Bc	14.31 ± 0.93Bd	17.60 ± 0.12Ab	16.18 ± 1.21ABb
pH	Intact soil	7.93 ± 0.03Ba	8.00 ± 0.01Ba	7.98 ± 0.07Bab	8.40 ± 0.06Aa
	>5 mm	7.97 ± 0.07Ba	8.02 ± 0.04Ba	8.07 ± 0.10Ba	8.36 ± 0.16Aa
	2–5 mm	7.96 ± 0.03Ba	8.00 ± 0.04Ba	8.01 ± 0.07Ba	8.42 ± 0.09Aa
	1–2 mm	7.93 ± 0.02Ba	8.01 ± 0.04Ba	7.99 ± 0.06Bab	8.47 ± 0.05Aa
	0.25–1 mm	7.90 ± 0.04Ba	8.00 ± 0.06Ba	7.92 ± 0.08Bab	8.42 ± 0.04Aa
	<0.25 mm	7.81 ± 0.01Bb	7.89 ± 0.04Bb	7.86 ± 0.08Bb	8.12 ± 0.18Ab
TN ($g \bullet kg^{-1}$)	Intact soil	1.44 ± 0.03Ad	1.49 ± 0.02Abc	1.44 ± 0.02Ac	1.47 ± 0.03Ad
	>5 mm	1.10 ± 0.02Bf	1.43 ± 0.08Ac	1.29 ± 0.06BAd	1.09 ± 0.11Bc
	2–5 mm	1.27 ± 0.01Ce	1.48 ± 0.05Abc	1.35 ± 0.07BCd	1.37 ± 0.04Bd
	1–2 mm	1.51 ± 0.01Bc	1.49 ± 0.22Bbc	1.43 ± 0.02Cc	1.62 ± 0.04Ac
	0.25–1 mm	1.76 ± 0.02Ab	1.55 ± 0.04Bb	1.56 ± 0.03Bb	1.78 ± 0.04Ab
	<0.25 mm	2.00 ± 0.03Ba	1.69 ± 0.01Ca	1.70 ± 0.02Ca	2.40 ± 0.07Aa
NH_4^+-N ($mg \bullet kg^{-1}$)	Intact soil	4.98 ± 0.10Bab	4.76 ± 0.02Cb	5.25 ± 0.08Ab	4.98 ± 0.04Ba
	>5 mm	5.16 ± 0.24Aa	4.87 ± 0.09Aab	5.26 ± 0.21Ab	4.99 ± 0.08Aa
	2–5 mm	5.11 ± 0.20Aab	5.04 ± 0.14Aa	5.33 ± 0.17Ab	5.04 ± 0.08Aa
	1–2 mm	5.03 ± 0.20Aab	4.52 ± 0.02Cc	4.76 ± 0.13Bc	4.94 ± 0.04ABa
	0.25–1 mm	4.62 ± 0.13Cc	4.57 ± 0.17Cc	5.60 ± 0.12Aa	4.93 ± 0.15Ba
	<0.25 mm	4.79 ± 0.12Abc	4.15 ± 0.04Bd	4.83 ± 0.15Ac	4.99 ± 0.15Aa
NO_3^--N ($mg \bullet kg^{-1}$)	Intact soil	29.63 ± 0.46Bab	24.01 ± 1.59Cb	20.36 ± 2.70Dab	36.84 ± 1.74Ac
	>5 mm	26.98 ± 1.48ABb	23.73 ± 2.00Bb	17.37 ± 2.75Cb	28.57 ± 1.37Ad
	2–5 mm	30.08 ± 1.17Ba	23.24 ± 1.50Cb	19.81 ± 2.45Cab	36.76 ± 3.79Ac
	1–2 mm	29.88 ± 0.81Bab	23.54 ± 1.00Cb	20.27 ± 3.90Cab	37.91 ± 1.44Ac
	0.25–1 mm	30.63 ± 0.96Ba	24.06 ± 1.25Cb	22.46 ± 2.49Cab	42.73 ± 1.65Ab
	<0.25 mm	32.57 ± 3.12Ba	28.80 ± 3.20BCa	23.22 ± 2.89Ca	56.15 ± 3.67Aa
C/N	Intact soil	7.50 ± 0.26Bab	6.97 ± 0.20Cbc	7.12 ± 0.13BCab	7.97 ± 0.23Ab
	>5 mm	7.97 ± 0.07Ba	7.39 ± 0.24Bab	6.90 ± 0.56Bb	9.48 ± 0.48Aa
	2–5 mm	7.39 ± 0.10Aab	6.90 ± 0.62Abc	7.34 ± 0.27Aab	7.41 ± 0.56Abc
	1–2 mm	6.65 ± 0.10Bc	6.70 ± 0.16Bc	7.26 ± 0.19Aab	6.71 ± 0.24Bc

(continued on next page)

Table 1 (*continued*)

Factor	Particle size of soil aggerates	CT	DP	SS	NT
	0.25–1 mm	7.11 ± 0.22Abc	6.49 ± 0.10Bc	7.19 ± 0.22Aab	6.93 ± 0.28Ac
	<0.25 mm	7.49 ± 0.13Aab	7.91 ± 0.12Aa	7.64 ± 0.11Aa	6.67 ± 0.55Bc

SM, soil moisture; TN, total soil nitrogen, g·kg^{-1}; NO_3^-N, nitrate nitrogen, mg·kg^{-1}; NH_4^+-N, ammonium nitrogen, mg·kg^{-1}; C/N, the ratio of soil organic carbon to the total nitrogen. CT: rotary tillage, DP: deep ploughing, SS: subsoiling, NT: no tillage, the same below. Mean ± SD (standard deviation) is shown (n = 3). Different capital letters indicate the significant differences between different tillage managements in the same agglomerate sizes, and different lowercase letters indicate the significant differences between different agglomerate sizes of the same tillage managements ($P < 0.05$).

had higher C_o values. The mineralization quotient and C_o value for various soil aggregates revealed a distinct pattern with respect to various tillage practices. Under DP treatment, C_o and mineralization quotient values were significantly higher in large macroaggregates (>5 mm, 2–5 mm), which implied that DP affected soil mineralization potential and promoted SOC loss. However, C_o and mineralization quotient showed lower values in macroaggregates (>5 mm, 2–5 mm) of NT treatment.

The CPM calculated from C_o was significantly different among distinct tillage management ($P < 0.05$) (Fig. 2**B**). Significantly higher CPM was under DP treatment ($P < 0.05$), while the lowest CPM was under CT treatment. Under distinct tillage management, aggregate size classes contribute differently to cumulative potential mineralization (**Table S3**). Under DP and SS treatments, soil macroaggregates > 5 mm had the highest contribution rate, whereas soil macroaggregates 2–5 mm had the highest contribution rate in the CT and NT treatments. The contribution rates of 1–2 mm soil macroaggregates under CT and SS treatments and < 0.25 mm soil microaggregates under DP and NT treatments were relatively lower, ranging from 5.25% to 8.52 and 5.72%-8.81%, respectively.

3.4. Effect of tillage management on abundance and structure of cbbL-carrying bacterial communities across aggregate class size

Compared to other treatments, DP showed a significantly higher abundance of *cbbL* gene OTUs in 2–5 mm macroaggregates (**Table S4**).

Tillage management insignificantly affected the taxonomic diversity (i.e., Chao1 and Shannon index) but affected phylogenetic diversity (PD index) and Observed species **(Fig. S2)**. Among SS and NT treatments, macroaggregates with size between 2 and 5 mm showed decreased phylogenetic diversity relative to CT and DP treatments. Macroaggregates with size of 1–2 mm under NT treatments had lower phylogenetic diversity than DP treatments.

PCoA analysis implied the *cbbL*-carrying bacterial community composition could be well separated by tillage management **(**Fig. 3**)**. Overall, the front two axles explained 21.61% and 16.17% variation in the bacterial community, respectively. Furthermore, an Adonis analysis discovered the significant difference among tillage management (R^2 = 0.40, $P < 0.001$), while the difference among soil aggregates were insignificant ($R^2 = 0.05$, $P = 0.872$). At the phylum level, the majority of the *cbbL*-carrying bacteria across all treatments, accounting for > 99% of the detected community, belonged to *Proteobacteria*. **(Fig. S3A, B)**. At the genus level, *Hydrogenophaga*, *Brevirhabdus*, and *Alkalilimnicola* were the dominant *cbbL*-carrying bacteria (**Fig. S4A**). Particularly, the abundance of Thiobacillus enhanced under SS treatments in microaggregates (<0.25 mm) (**Fig. S4B**). SS increased *Alkalispirillum* abundance in 1–2 mm macroaggregates.

3.5. Effect of tillage management on the cbbL-carrying bacterial co-occurrence networks and assembly processes

Networks were generated to evaluate *cbbL*-carrying bacterial community co-occurrence patterns under the distinct tillage managements (Fig. 4). The autotrophic bacterial network exhibited more positive than negative correlations under four tillage managements. The order of positive correlation ratio was as follows: SS (77.05%) > NT (74.67%) > DP (65.00%) > CT (64.65%). Compared to SS and NT, DP and CT treatments promoted a negative correlation among bacterial networks. DP increased the total nodes and edges compared to other treatments (**Table S5**). SS and NT had higher average clustering coefficients and network density relative to CT and DP. Nevertheless, the average length path in SS and modularity in NT were lower. Using the zi-pi plot (**Fig. S5)**, we found the keystone taxa in different tillage managements, including *Brevirhabdus*, *Alkalispirillum*, *Sulfurifustis*, *Cyanobium*, *Thiocystis*, *Bradyrhizobium*, and *Thioalkalivibrio*. More details were shown in **Table S6.** The combined results of βNTI and RCbray demonstrated homogeneous selection, dispersal limitation, and undominated processes primarily governed the structure of *cbbL*-carrying bacterial communities (Fig. 5, S6). Overall, stochastic processes contributed the most to all tillage management. SS treatments increased the relative importance of stochastic processes, and DP treatments increased the relative importance of dispersal limitation. Specifically, stochastic processes dominated the bacterial community assembly processes under CT, DP, and SS treatments in > 5 mm macroaggregates, while deterministic processes are involved more under CT, DP, and SS treatments in microaggregates. Furthermore, the value of habitat niche breaths showed no significantly different under distinct tillage managements (**Fig. S7**).

3.6. Correlations among soil properties, cbbL-carrying bacterial communities and CO_2 emissions

A Mantel test revealed TN significantly correlated with other soil properties and under CT treatment, the *cbbL*-carrying bacterial community was positively correlated with MBC, NH_4^+, and NO_3^- (Fig. 6**A**). There was a significant relationship between keystone *cbbL*-carrying bacteria, soil properties, and CO_2 emissions (**Fig. S8**). *Brevirhadus* was positively correlated with CO_2 emissions. Additionally, there was a strong positive link between CO_2 emissions and *Sulfuritustis* abundance. Random forest modeling (**Fig. S9**) explained the 75.57% variance of CO_2 emissions and revealed that SOC (16.44%, $P < 0.01$), TN (14.23%, $P <$ 0.01), DOC (11.62%, $P < 0.01$), NO_3^- (10.51%, $P < 0.01$), POXC (6.90%, $P < 0.05$), MBC (5.68%, $P < 0.05$), pH (5.22%, $P < 0.05$) and C/N (4.75%, $P < 0.05$) were the primary predictors for CO_2 emissions. Structural equation modeling (SEM) further indicated CO_2 emissions were substantially affected by soil properties and *cbbL*-carrying bacterial communities (Fig. 6**B** $\chi^2 = 8.990$, df = 9, $P = 0.438$, RMSEA = 0.000, GFI = 0.960).

4. Discussion

4.1. Aggregate-associated SOC dynamics under distinct tillage managements

SOC can represent soil carbon sequestration potential, and carbon input is the main factor for SOC storage (Rui and Zhang, 2010). Compared to microaggregates, macroaggregates contribute more to SOC stock in all tillage management (Fig. 2**A**). The aggregate hierarchy model suggests that macroaggregates are cemented by organic matter and microaggregates, and SOC storage should increase with the size of aggregate (Six et al., 2000). Also, the straw returned to the field, entered the macroaggregates, and was converted into organic carbon (Wang et al., 2021), increasing the SOC storage in the macroaggregates. A wheat–peanut rotation study also highlighted the positive correlation between macroaggregate-associated C storage and soil TOC storage

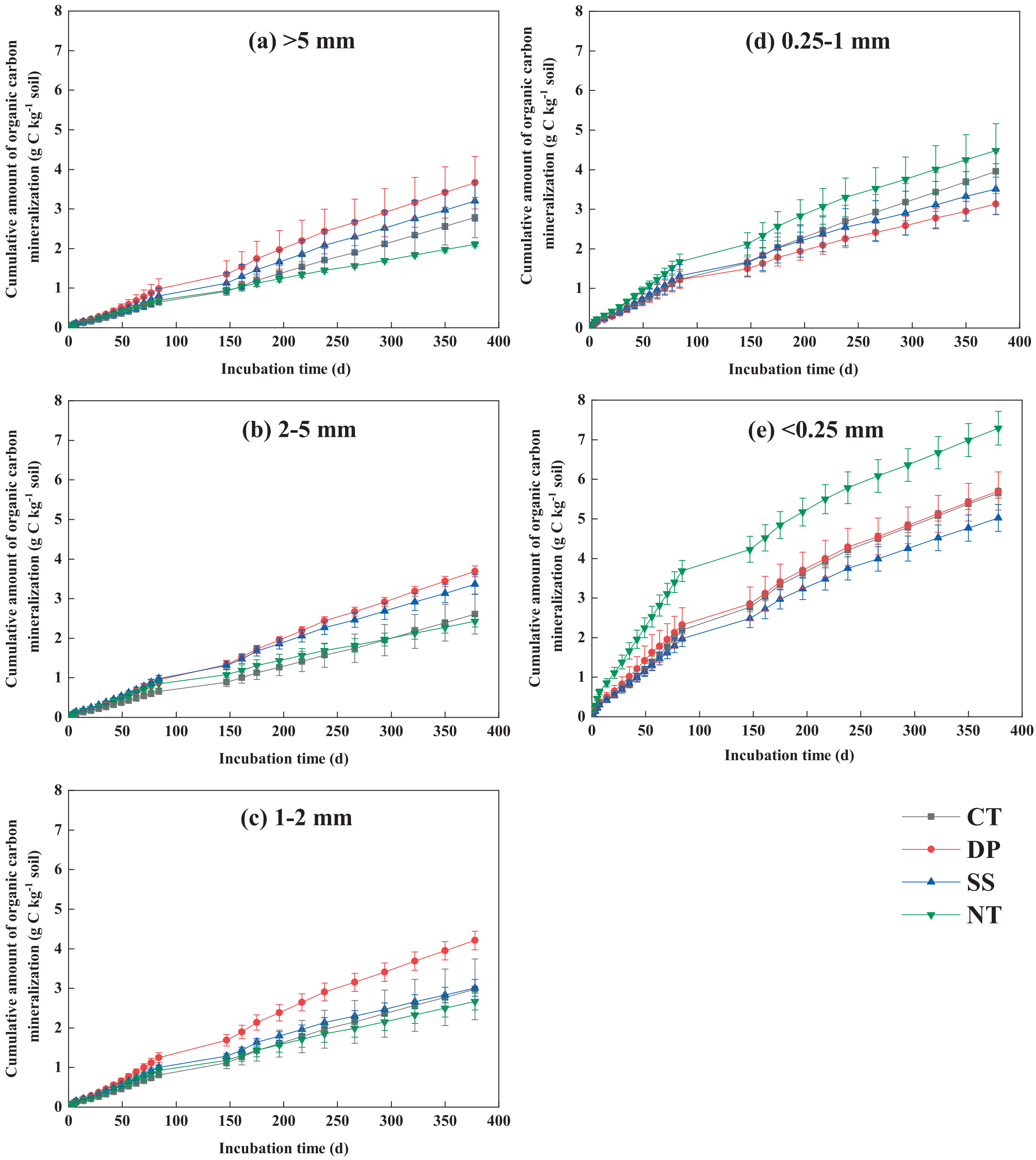

Fig. 1. Cumulative mineralization of SOC across aggregates under tillage managements. The figure (a), (b), (c), (d), (e) refers to cumulative organic carbon mineralization across > 5 mm, 2–5 mm, 1–2 mm, 0.25–1 mm and < 0.25 mm soil aggregates, respectively. The same below. Error bar means standard deviation (SD) (n = 3).

(Zhao et al., 2022). Tillage management is another factor affecting SOC storage. The order of SOC storage in this study is as follows: NT > SS > DP > CT, which is similar to previous studies (Liu et al., 2021a; Liu et al., 2022a; Liu et al., 2022b; Wang et al., 2020a). The less disturbance caused by NT protects macroaggregates, thus promoting SOC storage (Liu et al., 2022a). Furthermore, a *meta*-analysis revealed NT and conventional tillage enhance root growth and crop residue accumulation on the soil surface, therefore, SOC storage increased (Li et al., 2020).

Soil aggregates, sensitive to tillage management, are the pivotal reservoir of SOC retention and mineralization (Pulleman and Marinissen, 2004). Generally, soil aggregates size class are negatively correlated with SOC turnover time (Liu et al., 2022b; Six et al., 2002). In our study, large macroaggregates (>2 mm) were the major contributors to SOC mineralization, accounting for 50.92%-71.89% of the CPM (**Table S3**), which is similar to other studies (Liu et al., 2022b). This is because the high SOC storage in large soil macroaggregates and physical protection of large macroaggregates to SOC are more susceptible to microbial action (Wang et al., 2020b), while microaggregates improve the adsorption of organic substances through robust ligand exchange and cationic bridging, thus lower CPM (Razafimbelo et al., 2008). In addition, we detected the highest SOC and TN contents in microaggregates, which may be due to the high soil respiration and shorter turnover time of aggregate-associated SOC in large soil macroaggregates (Liu et al., 2020; Liu et al., 2022b; Six et al., 2002). SOC mineralization

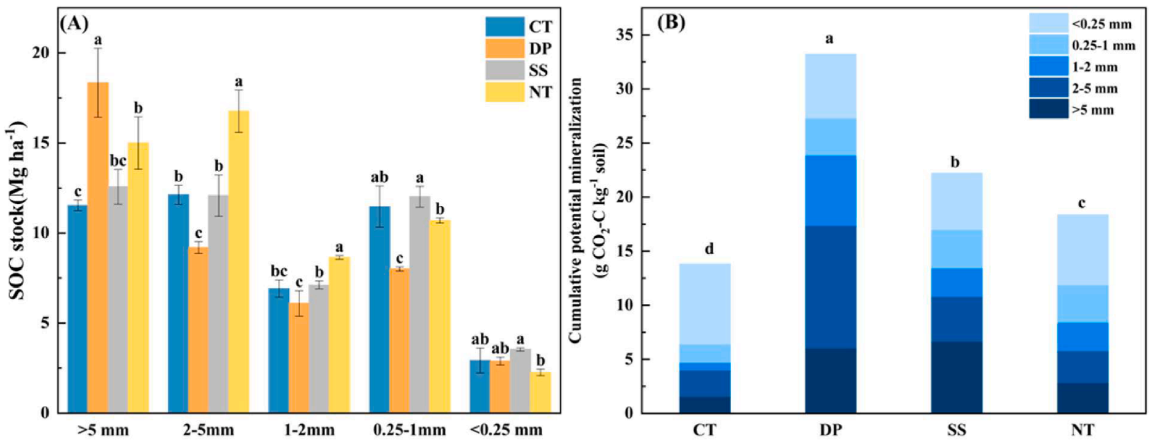

Fig. 2. **(A)** SOC stock across soil aggregates under different tillage managements. (B) Cumulative potential mineralization across soil aggregates under different tillage managements. Lowercase letters mean significant difference ($P < 0.05$) among tillage management. Error bar means standard deviation (SD) (n = 3).

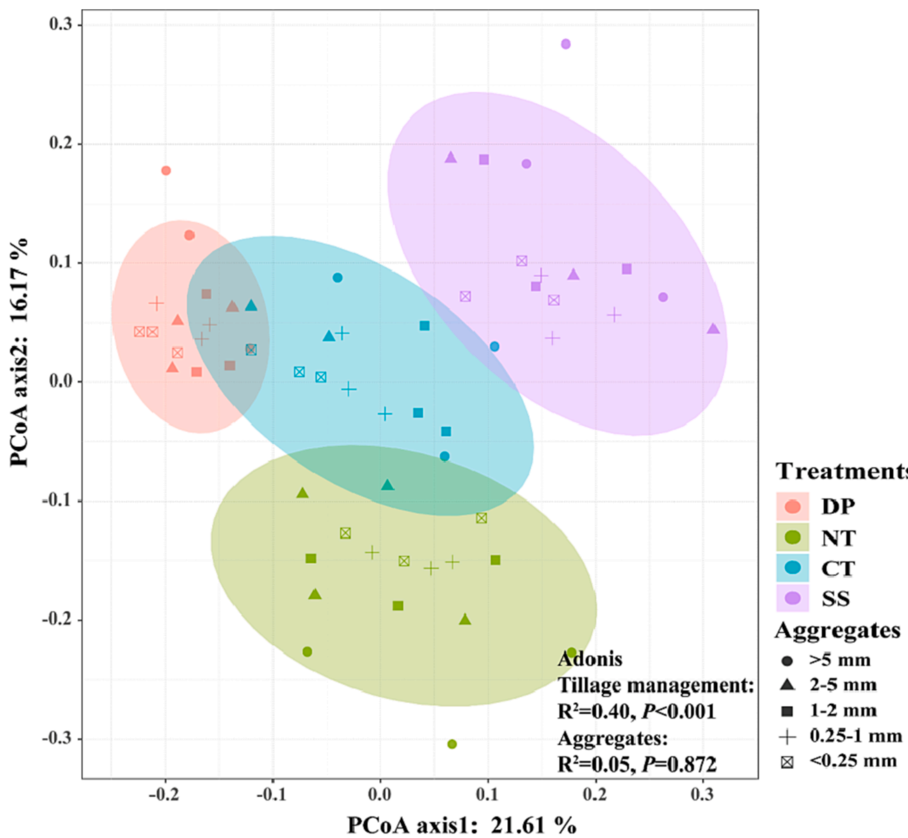

Fig. 3. The *cbbL*- carrying bacterial community compositions were assessed by the principal coordinate analysis (PCoA) based on Bray-Curtis distance and Adonis based on PERMANOVA.

potential (C_o) is active and decomposable SOC and reflects soil carbon fixation capacity. The lowest C_o was observed in macroaggregates under the NT treatment (**Table S2**), implying the inert carbon pool and higher SOC sequestration under NT. By reducing soil disturbance, NT maintains nutrients and water and promotes the formation and stability of soil aggregates (Liu et al., 2021b).

Different tillage management had various impacts on the mineralization rate and cumulative mineralization of SOC in soil aggregates (Fig. 1). In large macroaggregates (>2 mm), DP and SS treatments showed a higher SOC mineralization rate and cumulative mineralization than CT treatment. The reason may be that deep plowing and subsoiling were conducive to exogenous organic carbon from straw decomposing and entering the large-size aggregates. The SOC mineralization rate under NT treatment was higher than that of CT treatment in the early incubation stage. However, it turned out to be lower than that of CT treatment from the 84th day of incubation, indicating that soil aggregates (>1 mm) in NT treatment contained lower content of easily mineralized organic carbon than that in CT. In other words, no-tillage improved the stability of organic carbon in soil aggregates (>1 mm). In microaggregates (<0.25 mm), NT treatment showed the highest organic carbon mineralization rate in the early stage of incubation. Meanwhile, the most increased cumulative SOC mineralization may be related to the highest organic carbon content in microaggregates under NT treatment.

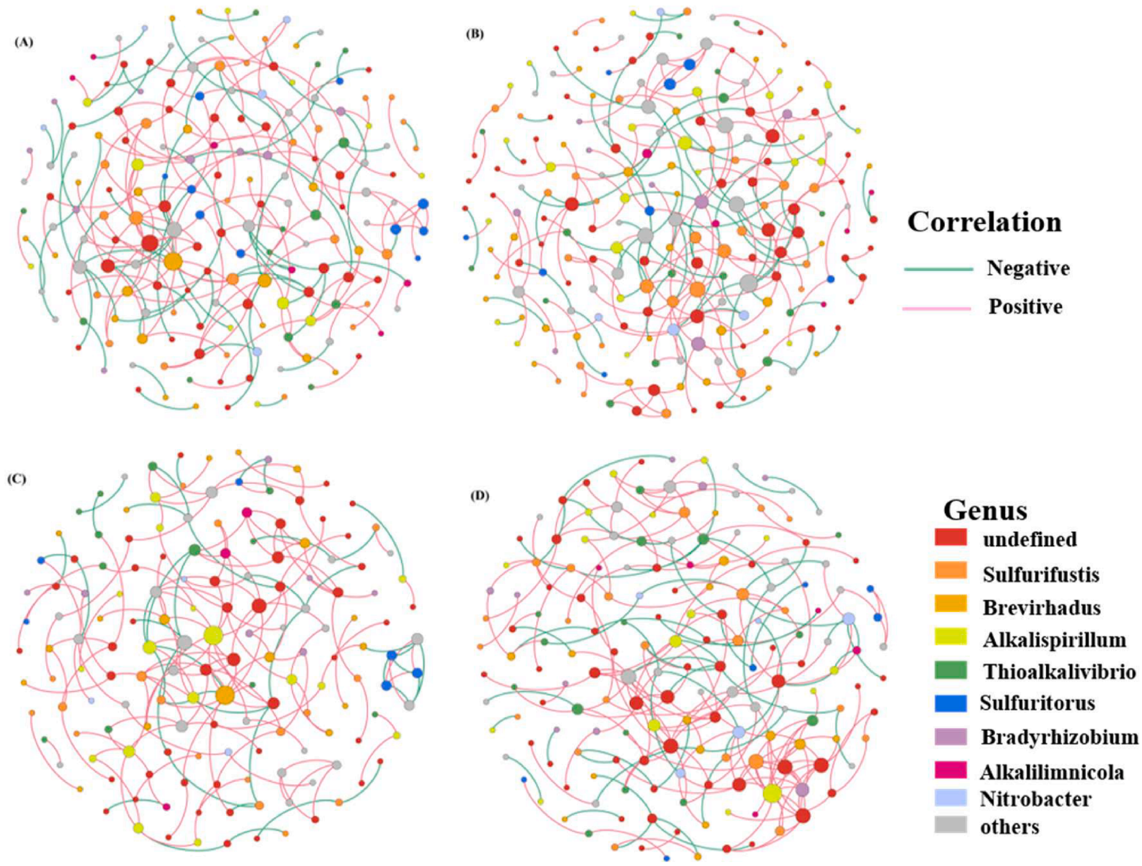

Fig. 4. *cbbL*-carrying bacterial co-occurrence networks under different tillage management. (A)CT, (B)DP, (C)SS, (D)NT.

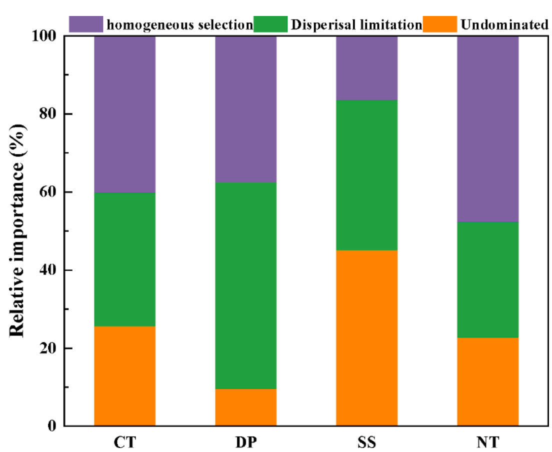

Fig. 5. Contributions of ecological assembly processes governing *cbbL*-carrying bacterial community under different tillage management.

4.2. The effects of tillage management on microbial community traits

The abundance and diversity of autotrophic microorganisms could indirectly characterize the C sequestration potential (Yuan et al., 2012). This study showed that in 2–5 mm aggregates, DP treatment increased the abundance of *cbbL* gene OTUs and *cbbL* species compared to other treatments. Extensive abundance observation in 2–5 mm aggregates was probably derived from the high level of total nitrogen and active carbon, such as DOC and permanganate oxidizable carbon (Shen et al., 2021). The high available nutrients may provide spatially adaptive living microhabitats for *cbbL*-carrying microbes and facilitate the growth and colonization of microbes (Wang et al., 2022a; Yuan et al., 2013).

In this study, tillage management rather than aggregate sizes was the major contributor to regulating *cbbL*-carrying microbial communities (Fig. 3), which may be due to the more substantial effect of tillage management on soil properties concealed the variation among aggregate sizes. Understanding the *cbbL*-carrying microbial composition may enhance predictions of SOC fixation. Most *cbbL*-carrying bacteria are called *Proteobacteria* (Fig. S3**A**)*,* which are facultative autotrophs and can sequester carbon and degrade organic carbon compounds. *Proteobacteria* are nutrient-rich with abundant species and genetic diversity, such as aerobic and anaerobic, autotrophic and heterotrophic, phototrophic and chemotrophic, and their metabolic versatility makes them easier to successfully compete with resources under tillage effects (Feng et al., 2022a; Horner-Devine et al., 2004; Li et al., 2022; Xiao et al., 2019). In our study, NT treatment increased *Proteobacteria* in 2–5 mm aggregates, which was driven by the higher nutrient content. Other dominant phylums such as *Streptophyta*, *Cyanobacteria,* and *Chlorophyta* were photoautotrophic microorganisms and limited to topsoil growth, with fewer abundance (Yuan et al., 2012). The increase in the abundance of *Streptophyta* under DP treatments was likely related to the fact that DP destroyed soil structure, allowing more light to the soil (Wu et al., 2014).

The co-occurrence network analysis of *cbbL*-carrying bacteria could provide deeper insight into complex interactions among microorganisms under different tillage management (Barberán et al., 2012). Our study discovered the effects of tillage management on bacterial network structure and complexity. Although NT treatments had fewer nodes than other management, the edges in NT were the highest, indicating a more complex microbial structure. The complexity of the network often manifests as coordinated variability in microbial abundance. Previous studies found the number of associations rather than taxa determined the complexity of the microbial network (Banerjee et al., 2019). Another interesting finding is that SS and NT treatments increased the positive

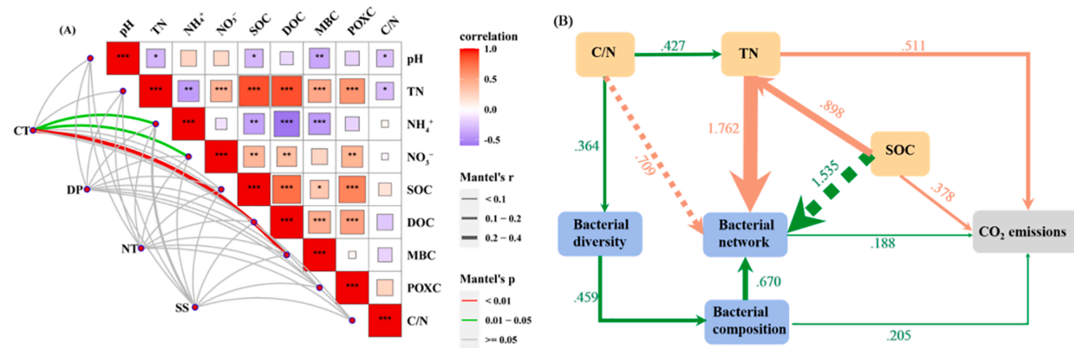

Fig. 6. (A) Soil properties influencing *cbbL*-carrying bacterial communities under four tillage managements. Pairwise comparisons between environmental factors are shown in a color gradient, with individual boxes containing Spearman's correlation coefficient and indication of level of significance: *$P < 0.05$, ** $P < 0.01$ and ***$P < 0.001$. (B) The interaction among soil properties, *cbbL*-carrying bacterial communities and CO_2 emissions based on structural equation modeling (SEM) analysis. The arrow width in the figure indicates the strength of the path coefficients. Continuous arrow indicates the path is significant, while discontinuous arrow indicates the path is not significant. The red and green arrow indicates the positive and negative correlation respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

correlation and average clustering coefficient among *cbbL*-carrying bacteria, which implied a more collaborative relationship and buffered against environmental fluctuations (Liu et al., 2022c; Zhang et al., 2018). The enhanced collaboration among *cbbL*-carrying bacteria under NT and SS treatments might be caused by inconsistent factors. NT may increase the niche width by increasing the nutrient content of the soil, thus reducing bacterial competition (Banerjee et al., 2016; Chen et al., 2018). However, under SS treatments, large aggregates were destroyed, and the proportion of microaggregates was increased (Shen et al., 2021). The smaller the size of aggregates, the lower the availability of matter, and more potent synergism and shorter average path length are needed to overcome the stubborn soil environment and promote substance, energy, and information transfer (Wang et al., 2021). Additionally, the increased network density under SS and NT treatments indicated a closer relationship and reduced environmental stress (Kitano, 2004). Keystone taxa, regarded as network hubs, connectors, and modular hubs, are essential for maintaining ecosystem function by facilitating nutrient exchange and resource utilization (Shi et al., 2016). Meanwhile, the keystone taxa under SS treatments are all obligate autotropic microorganisms, also explaining the stronger synergism and carbon fixation capacity (Wu et al., 2014). Other nitrogen-fixing bacteria such as *Bradyrhizobium* and *Burkholderiales* (Fan et al., 2019; Hu et al., 2021) were defined as keystone taxa in the *cbbL*-carrying network because carbon and nitrogen cycle processes are coupled, implying tillage management altered micro-mediated carbon and nitrogen cycling and affected the ecological functions (Guo et al., 2015).

Microbial assembly couple community composition and ecosystem function, including stochastic and deterministic processes, both of which occur simultaneously and their relative importance vary with environmental conditions (Chase and Myers, 2011). Tillage management changes the taxonomic and phylogenetic composition of microorganisms by affecting soil environmental heterogeneity (Wang et al., 2022b). In this study, microbial community assembly is dominated by stochastic processes under four tillage managements indicating that the environment is relatively stable, and microorganisms follow natural processes and maintain a high community diversity (Xun et al., 2019). Compared to other treatments, SS significantly increased the relative importance of stochastic processes, which could be explained by that solid collaborative relationship between *cbbL*-carrying bacteria under SS, weakening the presses of environment (Jiao and Lu, 2020). Our microbial assembly analysis also found that DP treatment increased the relative importance of dispersal limitation processes, and (Liu et al., 2022c) reported that the strong soil disturbance led to high dispersal rates of microbes.

4.3. Correlation among soil properties, cbbL-carrying bacterial communities and CO_2 emissions

Both soil properties (SOC, TN, C/N) and *cbbL*-carrying bacterial communities could affect CO_2 emissions, and soil properties contributed the most in this study (Fig. 6**B**). One previous study demonstrated that the different C mineralizability was dominated by abiotic factors among tillage managements (Qi et al., 2021), which verified this result. SOC, TN, and C/N could impact plant growth, carbon input and microbial activity by affecting nutrient availability (Zheng et al., 2022), thus CO_2 emissions.

Meanwhile, previous research has highlighted the importance of autotrophic microorganisms (facultative autotrophic and obligate autotrophic microorganisms) for carbon sequestration in farmlands (Ge et al., 2016; Lu et al., 2019; Yuan et al., 2012). Among them, obligatory autotrophic microorganisms only use CO_2 as the only carbon source and are more prominent contributors to carbon fixation (Wu et al., 2014). Here in our study, SEM results also confirmed the importance of *cbbL*-carrying bacterial communities to SOC dynamics, and the change in soil properties may indirectly affect carbon emissions by altering the *cbbL* community. An interesting theory holding the lower the organic carbon content, the stronger the carbon sequestration potential of autotrophic microorganisms (Bhattacharya et al., 2016; Chen et al., 2016; Stewart et al., 2008), highlight the strong interaction between SOC, *cbbL*-carrying bacterial communities and SOC dynamics. Additionally, changes in other physicochemical properties such as bulk density and porosity due to tillage effects can result in CO_2 fixation triggered by autotrophic microorganisms, as the changed bulk density and porosity affected light transmittance, gas diffusivity, and contact between microorganisms and substrate (Lu et al., 2019).

Although microbial diversity was suggested to play a crucial role in predicting terrestrial ecosystem function (Lynn et al., 2017; Wang et al., 2022a), here we did not find a direct link between microbial diversity and carbon dioxide emissions in this study (Fig. 6**B**). Diverse *cbbL*-carrying bacterial communities exhibit a high degree of functional redundancy (Birge et al., 2015), indicating microbial community diversity is not the dominant factor of microbial function. However, microbial diversity may affect carbon emissions by affecting the microbial community composition, especially the proportion of obligate and facultative autotrophic microorganisms. Microorganisms with different metabolic modes have distinct carbon fixation abilities and highly similar microorganisms suppress carbon metabolism by sharing similar microhabitats (Wang et al., 2022a).

Additionally, soil properties affected by tillage management can alter the efficiency of material cycling, energy transfer, and information exchange among autotrophic microbial networks, thereby changing CO_2

emissions. The average path length in the co-occurrence network inhibited CO_2 emissions (Fig. 6**B**). There are three roles for the carbon fixed by autotrophic microorganisms, one is to be mineralized again to CO_2, the other is to be reduced to methane by homeotropic microorganisms, and the third is to form SOC, DOC, and MBC (Wu et al., 2014). Therefore, a stronger fixation of CO_2 does not always mean fewer emissions. Notably, the impact of average path length of *cbbL* genes on C mineralization is mainly based on statistical analysis. Further carbon isotope labeling experiment should be conducted to get empirical evidence to examine this finding in the future.

5. Conclusion

Tillage management strongly impacted SOC dynamics via changing soil properties (SOC, TN and C/N) and *cbbL*-carrying bacterial community structure across aggregate sizes. Soil properties contributed the most while microbial community composition and network interaction may be the biological leading factors affecting carbon emissions. Also, our study confirmed that the macroaggregates were the main component of the SOC sequestration pool, while microaggregates were the main component of SOC loss pool from mineralization. Subsoiling management increased the proportion of obligate autotrophic bacteria, cooperative interaction between *cbbL*-carrying bacteria, the relative importance of stochastic processes, and reduced the environmental pressure, thus decreasing CO_2 emissions in microaggregates while it increased CO_2 emissions in macroaggregates. However, no-tillage inhibited CO_2 emissions in macroaggregates>1 mm by physically protecting due to no disturbance, while it increased CO_2 emissions due to higher SOC contents in microaggregates. Overall, our study implies that NT could promote SOC storage, and SS could promote the interaction of soil *cbbL*-carrying bacteria community, leading to the carbon emission alleviation in fluvo-aquic soil regions. Further research should combine isotopic techniques to deeply explore carbon flow in agroecosystems and provide new insights into the relationship between farming practices and greenhouse gas emissions.

CRediT authorship contribution statement

Yao Yao: Investigation, Data curation, Visualization, Writing – original draft. **Xiaolin Shen:** Methodology, Data curation, Writing – original draft. **Lili Wang:** Conceptualization, Supervision, Writing – review & editing, Funding acquisition. **Jianning Zhao:** Methodology. **Lingxuan Gong:** . **Su Wang:** Visualization. **Linyi Wu:** Visualization. **Gang Li:** . **Weiming Xiu:** . **Guilong Zhang:** Project administration.

Declaration of Competing Interest

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110213.

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