Conservation tillage regulates the assembly, network structure and ecological function of the soil bacterial community in black soils

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Abstract

Aims Traditional tillage represents a serious threat to the stability of soil ecosystems. Understanding the response mechanisms of soil microbial community assembly to different tillage practices is a major topic of soil ecological research.

Methods Here, we investigated the bacterial community structures and assembly in bulk and rhizosphere soils of soybeans grown under traditional tillage (moldboard plow, MP) and two conservation tillage practices, namely, no-tillage (NT) and ridge tillage (RT), using high-throughput sequencing methods.

Results Compared with MP, NT and RT increased the relative abundances of nitrifying bacteria of Nitrosospira sp. and the nitrogen-fixing bacteria of Mesorhizobium sp., Bradyrhizobium sp. and Burkholderia sp., but decreased the abundance of carbon-degrading bacteria, especially Blastococcus sp., Streptomyces sp. and Sphingomonas sp. The altered functional bacteria were mostly affiliated with biomarkers and keystone taxa in the NT and RT networks. For the results of network properties and assembly processes, we found that NT and RT habited a more stable bacterial network structure and a lower homogenizing dispersal value. Soil pH was the primary factor regulating both the bacterial community structures and assembly processes under the three tillage practices.

Conclusions The soil bacterial community structures and assembly processes were profoundly altered by tillage practices. The changes in functional bacteria indicated that conservation tillage might contribute to soil carbon sequestration, while stimulating nitrogen fixation and nitrification.
Keywords Tillage practices · Nitrogen fixation · Carbon degradation · Bacterial networks · Assembly processes

Introduction

Black soils (Mollisols) are highly productive and play key roles in ensuring food security in China (Liu et al. 2008). Tillage practice aims to improve crop production and agricultural sustainability through soil mechanical inversion and residue return (Dang et al 2015; Zuber and Villamil 2016). However, the intensive mechanical interference of traditional tillage, such as moldboard plows (MPs), leads to serious soil degradation, which is a major threat to the health of agricultural ecosystems (Montgomery 2007; Sainju et al. 2011; Zhang et al. 2012). In contrast, conservation tillage, such as no-tillage (NT), which minimizes soil erosion risks and input costs, is adopted to combat agricultural scourge (Busari et al. 2015; Zhao et al. 2017). Despite the benefits of NT, the key disadvantages are that it causes herbicide-resistant weeds to thrive and the soil surface to become compacted, which impedes normal root development, reduces the seed germination rate, and increases stubble-borne diseases (Dang et al. 2015; Steinkellner and Langer 2004; Sun et al. 2018). Therefore, compared with NT and MP, the conservation tillage practice of ridge tillage (RT) with low soil disturbance increases soil resilience and maximizes the positive impacts on soil quality (Alvear et al. 2005; Hobbs et al. 2008).

Tillage practices change soil properties and thus lead to variations in soil microorganisms, which play a considerable role in agroecosystems by mediating soil biogeochemical processes and plant nutrient uptake (Falkowski et al. 2008; Fierer 2017). Previous studies have revealed that conservation tillage significantly increased microbial diversity and biomass compared with traditional tillage (Chen et al. 2020a; Govaerts et al. 2007). In addition, it has been widely reported that tillage practices lead to obvious variations in soil microbial community structures (Li et al. 2021; Wang et al. 2017; Xia et al. 2019). However, a few studies have focused on the influences of tillage practices on the ecological functions of soil microbial communities. The results of long-term local experiments have revealed that conservation tillage enhances soil biological nitrogen fixation by increasing the abundances of Pseudomonas spp. and Agrobacterium spp. (Hoflich et al. 1999; Wang et al. 2020a), while other studies have found that conservation tillage increases denitrifiers, which in turn promotes soil nitrogen loss (Johnson and Hoyt 1999; Puerta et al. 2019). In addition, it is still not well understood how tillage practices impact soil carbon cycling with shifts in microbial communities between traditional and conservation tillage. For example, Wang et al. (2020b) has revealed that NT increases the abundance of anaerobes with low carbon utilization efficiency and reduces the abundance of cellulose-degrading groups, thus encouraging soil carbon sequestration. However, de Vries et al. (2015) documented that there is no obvious variation in cellulose-degrading genes among different tillage practices based on metagenomic analyses. Therefore, it is important to comprehensively understand the ecological functions of soil microorganisms under different tillage practices to improve the productivity and sustainable development of agricultural ecosystems.

Ecological assembly processes are considered indispensable to coupling microbial community composition and the ecological functions they provide (Feng et al. 2018; Graham and Stegen 2017). It is widely accepted that stochastic (neutral theory) and deterministic (niche-based theory) processes both simultaneously influence microbial community assembly (Feng et al. 2018; Stegen et al. 2012). Nevertheless, the importance of stochastic and deterministic processes to microbial community assembly is still under debate. To partition the relative contributions of stochastic and deterministic processes, a conceptual framework dividing ecological processes into five fundamental processes, including homogenizing dispersal, dispersal limitation, homogeneous selection and variable selection, as well as “undominated processes”, has been developed and widely used to quantify the relative contributions of these processes (Stegen et al. 2015). Empirical evidence supports that microbial community assembly is driven by different combinations of these ecological processes (Feng et al. 2018; Jiao and Lu 2020; Stegen et al. 2015). However, the relative importance of these ecological processes on the assembly of soil bacterial communities under different soil tillage practices and their consequences for ecosystem functionality are still poorly understood.
Both abiotic environmental filtering and biotic interactions have a great influence on microbial community assembly (Jia et al. 2018; Zhou and Ning 2017). Many studies have proven that the assembly processes of microbial communities are driven by various soil factors, such as soil pH (Jiao and Lu 2020; Tripathi et al. 2018), total phosphorus (Xiong et al. 2010) and soil organic matter (Feng et al. 2018). In addition, biotic interactions (corporation and/or competition) were also one of the important determinants of microbial community assembly (Zhou and Ning 2017). Microbial networks can identify the complex biological interactions (Barberan et al. 2012), and may serve as linkages between ecological processes and microbial communities (Chen et al. 2020b). For example, the reduction in negative correlations among soil microbial communities was expected to decrease the relative importance of variable selection (Luan et al. 2020). In addition, microbial networks can also provide insights into the response of soil microbiomes to anthropogenic and environmental changes (Banerjee et al. 2019). Therefore, a comprehensive analysis of microbial networks and community assembly processes is essential to revealing the ecological function of microbial communities.

Herein, bulk and rhizosphere soils from soybean plants were collected to explore the composition, network structure and assembly process of bacterial communities under traditional tillage (MP) and conservation tillage (NT and RT) practices in Northeast China using high-throughput sequencing methods. We hypothesized that traditional tillage might reduce the stability of the microbial network and increase the relative contribution of stochastic processes, due to the lower microbial diversity and higher dispersal rates of MP in contrast to NT and RT. We then associated bacterial ecological networks and assembly processes to illuminate how the network properties and keystone taxa varied among NT, RT and MP, and to clarify the relative contribution of ecological processes shaping the assembly of bacterial communities under these three tillage practices.

Materials and methods

Experimental design and soil sampling collection

A long-term experimental station was established at the Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun, Jilin, China (44°59’N, 125°23’E) in the fall of 2013. The average yearly precipitation at the experimental site is 614 mm, and the mean annual temperature is 6.4 °C. The soil samples belong to black soil that is classified as Molisols according to the soil taxonomy system of the US.

The experiment was arranged with a completely randomized block design. Three tillage treatments were selected for this study: moldboard plow (MP), tillage, no-tillage (NT) and ridge tillage (RT). Except for sowing with a KINZE-3000 NT planter (Iowa, USA), the soil under NT was not disturbed. For RT, only ridging with a cultivator was conducted in June of each year. The MP was disturbed by moldboard plowing (0–20 cm) after the harvest of the maize harvest, secondary field cultivation in the spring by disking and the ridge-building process in June. For all treatments, a soybean and maize rotation was implemented and all soybean residues or maize straw of approximately 30 cm in length covered the soil surface after the annual harvest. For soybean cultivation, potassium (K), phosphorus (P) and nitrogen (N) fertilizers were applied as basal fertilizers at 80 kg ha⁻¹, 60 kg ha⁻¹, and 40 kg ha⁻¹, respectively. For maize cultivation, basal fertilizer was applied at 78 kg K ha⁻¹, 45.5 kg P ha⁻¹ and 100 kg N ha⁻¹, whereas an additional 50 kg N ha⁻¹ was used at the V6 stage as the top dressing.

A total of 48 soil samples (bulk and rhizosphere, three treatments × eight replicates) were collected at the soybean podding stage on July 25, 2017. Soil (0–20 cm) was randomly collected from each soybean plot (25 m × 7.8 m) as bulk soil samples. To collect the rhizosphere soil samples, ten soybean plants in each plot were shoveled out. After shaking off the loose adhesive soil on the root, the tightly bonded soil on the root surface was brushed down as rhizosphere soil (Philippot et al. 2013). The collected soils were kept in -80 °C and 4 °C refrigerators for soil DNA extraction and chemical property analysis, respectively.

Soil chemical analyses

The soil chemical properties were assayed according to the description by Lu (1999) after being passed through a 2 mm sieve. The specific data on soil pH, nitrate nitrogen (\(\text{NO}_3^-\)-N), ammonium nitrogen (\(\text{NH}_4^+\)-N), available phosphorus (AP), available potassium (AK), total nitrogen (TN), total carbon (TC), total
potassium (TK) and total phosphorus (TP) are shown in Table S1. Briefly, relative to the bulk soil, the rhizosphere soil had higher TC, TN and available nutrients (NO$_3^-$-N, NH$_4^+$-N, AK and AP). In addition, relative to NT and RT, MP significantly increased NO$_3^-$-N and pH in the bulk and rhizosphere soils and AP, TP and TC in the rhizosphere soils (Hu et al. 2020).

Soil DNA extraction and sequencing

Soil microbial total DNA was extracted (0.5 g fresh soil per sample) using the Fast DNA® Spin Kit for Soil (MP Biomedicals, USA). The primer pair 338F/806R (Castrillo et al. 2017), with a sample-specific barcode at the 5’ end, was used to amplify the V3-V4 region of the soil bacterial 16S rRNA gene. The PCR system and amplification conditions were described previously (Liu et al. 2020). The PCR products were further pooled and purified by an agarose gel DNA purification kit (TaKaRa, Dalian, China). The purified PCR products were sequenced on an Illumina MiSeq platform at Majorbio Bio-Pharm Technology Co., Ltd. (Shanghai, China).

Bioinformatic analyses

The QIIME pipeline (version 1.9.1) was used to perform raw FASTAQ data analysis (Caporaso et al. 2010). First, low-quality sequences with an average quality score < 20 and/or length < 200 bp were removed (Aronesty 2011). The UCHIME algorithm was used to filter chimeric sequences (Edgar et al. 2011). Then, the obtained high-quality sequences were clustered into operational taxonomic units (OTUs) with a 97% similarity level by UPARSE (Edgar 2010). The OTU representative sequences were identified taxonomically using the RDP classifier based on the SILVA database for bacterial species classification (Cole et al. 2005). Our raw sequences were submitted to the NCBI Sequence Read Archive (SRA) database with the accession number PRJNA644753.

Community assembly processes analyses

A null model was employed to evaluate the bacterial community assembly processes. Phylogenetic conservatism of communities was tested using the function ‘mantel.correlog’ in the “vegan” package of R (version 3.6.2) (R Development Core Team 2016) before building the null model (Stegen et al. 2013). To identify the bacterial community assembly processes within each sample, the standardized effect size measure of the mean nearest taxon distance (ses.MNTD) was calculated using the “picante” package in the R environment (‘taxa.labels’ function, 999 randomizations). The positive and negative values of ses.MNTD indicated phylogenetic overdispersion and phylogenetic clustering, respectively (Webb et al. 2002).

We quantified the influences of stochastic and deterministic processes on bacterial assembly by the nearest taxon index (βNTI) (‘comdistnt’ function, abundance.weighted = TRUE), which is the standard deviation of the between-community mean nearest taxon distance (βMNTD) (Stegen et al. 2012). Values of |βNTI| > 2 indicate a significant deviation between observed and expected phylogenetic turnover, which indicates the dominance of deterministic processes. βNTI values < −2 and > +2 denote homogeneous selection (lower phylogenetic turnover than expected) and variable selection (higher phylogenetic turnover than expected) processes, respectively (Stegen et al. 2012). Furthermore, we combined βNTI with the Bray–Curtis-based Raup-Crick (RC$_{bray}$) to quantify the effects of dispersal-based stochastic ecological processes (Stegen et al. 2013, 2015). RC$_{bray}$ values < −0.95 or > +0.95 denote distinct divergence from the null model expectation. The homogenizing dispersal and dispersal limitation processes were quantified by |βNTI| values < 2 but RC$_{bray}$ < −0.95 and RC$_{bray}$ > +0.95, respectively. Moreover, |βNTI| < 2 and |RC$_{bray}$| < 0.95 were considered undominated processes (Stegen et al. 2015). The “picante” package in the R environment was used to perform the above analyses (R Development Core Team 2016).

Co-occurrence network construction

To determine the bacterial species interactions, co-occurrence networks were constructed through the MENA pipeline based on random matrix theory (RMT) (Zhou et al. 2011; Deng et al. 2012). The OTUs with relative abundances less than 0.01% were removed to rule out spurious correlations. The topological indices of random empirical networks were summarized by 999 iterations to determine whether
network properties were error prone. Ten nodes with the highest degree were defined as hub nodes (Ma et al. 2020). The role of individual nodes was divided into four categories: network hubs, connectors, module hubs and peripherals (Olesen et al. 2007). Ecologically, peripheral nodes represent specialists while the other three represent generalists (Deng et al. 2012). The generalists and hub nodes together were considered keystone taxa in this study. Gephi (version 0.9.2) was applied to visualize the co-occurrence network.

Statistical analyses

In this study, we randomly selected 23,914 bacterial sequences from each sample to compare the relative variation between samples. One-way ANOVA was conducted to test the divergences in the measured variables among the treatments using Statistical Product and Service Solutions (SPSS) software (version 19.0). The changes in the bacterial community composition and relative abundance at the phylum, genus and OTU levels among the tillage practices were determined with heatmaps, circles and ternary plots, which were displayed in the R environment with the “pheatmap”, “circlize” and “ggtern” packages, respectively (R Development Core Team 2016). In addition, non-parametric multivariate analysis of variance (Adonis) and principal coordinate analysis (PCoA) were carried out using the “vegan” package in the R environment to reveal the influence of different disturbance degrees on bacterial community structures. The correlation between bacterial communities and soil chemical properties was performed by the Mantel test and distance-based redundancy analysis (db-RDA) using the “vegan” package in the R environment.

Results

Bacterial community composition

In this study, 1,740,398 high-quality bacterial sequences were obtained from 48 soil samples (23,914–37,483 per sample), and they were clustered into 4,649 OTUs belonging to 38 phyla. The dominant bacterial phyla/classes (with average relative abundances higher than 5%) were Alphaproteobacteria (23.25%), Actinobacteria (20.07%), Acidobacteria (11.45%), Betaproteobacteria (9.95%), Chloroflexi (8.09%) and Bacteroidetes (6.13%) across all soil samples (Fig. 1, Table S2). In the bulk soils, compared with MP, NT and RT significantly increased ($P < 0.05$) the relative abundance of Nitrospirae while reduced the abundance of Saccharibacteria. Additionally, the relative abundances of Gemmatimonadetes and Actinobacteria were significantly lower ($P < 0.05$) in NT and RT than those in MP in the rhizosphere soils (Table S2).

Fifty-two genera were observed with mean relative abundances higher than 0.5% in at least one treatment. Among them, *Bradyrhizobium* (6.81%) and *Sphingomonas* (3.22%) were the most dominant genera. In the bulk soils, compared with MP, NT and RT significantly increased ($P < 0.05$) the relative abundances of three genera, including *Bacillus*, *Mesorhizobium* and *RB41*, while they decreased the abundances of 12 genera, including *Blastococcus*, *Sphingomonas* and *Methylobacterium*. In the rhizosphere soils, *Burkholderia*, *Mesorhizobium* and *Aquicella* obviously increased ($P < 0.05$), while nine genera, including *Mycobacterium*, *Methylotenera* and *Gemmatimonas*, decreased in NT and RT compared with those in MP (Table S2).

At the OTU level, the differences in the relative abundance of soil bacterial OTUs among the three tillage practices were further revealed by ternary plots (Fig. 1c and d). The results showed that there were more OTUs altered with specific tillage practices in the bulk soils (158 OTUs) than in the rhizosphere soils (72 OTUs). Specifically, compared with MP, NT and RT significantly increased ($P < 0.05$) the relative abundances of OTU2114 (*Mesorhizobium*) and OTU1206 (*Dehalogenimonas*) and decreased the abundances of seven OTUs, including *OTU1829* (*Blastococcus*), *OTU846* (*Sphingomonas*) and *OTU3866* (*Gemmatirosa*) in the bulk soils. Six OTUs, including *OTU4404* (*Bradyrhizobium*), *OTU2109* (*Rhizobium*) and *OTU3445* (*Burkholderia*), were remarkably increased ($P < 0.05$); and six OTUs, including *OTU1829* (*Blastococcus*), *OTU846* (*Sphingomonas*) and *OTU3141* (*Methylotenera*), were decreased in the rhizosphere soils of NT and
The bacterial taxonomic distribution at the phylum/class level were showed with circos plots in the bulk (a) and rhizosphere (b) soils under the different tillage practices. The thickness of each ribbon represents the relative abundances of bacterial phyla/classes. Ternary plot showed the enriched bacterial OTUs in the bulk (c) and rhizosphere (d) soils. Each circle represents one OTU, and the sizes of each circle represent its relative abundance. Green, red and orange circles mark OTUs significantly enriched in NT, RT and MP, respectively. The values in the brackets indicate the number of enriched OTUs. NT, RT and MP represent no-tillage, ridge tillage and moldboard plow tillage, respectively; B: bulk soil; R: rhizosphere soil. For example, NTB represents soil samples collected under no-tillage in bulk soils.

RT (Table S3). In addition, compared to MP, the relative abundances of OTU3343 (Streptomyces) and OTU3407 (Streptomyces) were lower in RT in bulk soils and in NT in rhizosphere soils, while OTU2806 (Nitrosospira) and OTU3942 (Nitrosospira) were enriched in RT in bulk soils and in NT in the rhizosphere soils, respectively.

Soil bacterial community structure

The PCoA plot based on the Bray–Curtis distance clearly showed that the bacterial communities were mainly divided into two major groups based on the bulk and rhizosphere soils (Adonis tests, P < 0.001) (Fig. 2a). In addition, the separated PCoA plots based on the bulk and rhizosphere soils individually showed that the three tillage treatments significantly altered the bacterial communities (Adonis tests, P < 0.01) (Fig. 2b and c, Table S4).

The results of the Mantel test revealed that the soil pH, C/N, TC, TN, AP, KK, NH₄⁺-N and NO₃⁻-N were significantly correlated with the bacterial community structures (P < 0.05) (Fig. S1). After variance inflation factor (VIF) screening, db-RDA showed that NH₄⁺-N played the most important role (R² = 0.740, P < 0.001) regulating the bacterial community structures under the three tillage practices in combination with the bulk and rhizosphere soils (Fig. 2d, Table S5). Furthermore,
the separated db-RDA plots revealed that soil pH contributed the most to the variations in the bacterial community structures under different tillage practices in both the bulk ($R^2 = 0.728$, $P < 0.001$) and rhizosphere ($R^2 = 0.698$, $P < 0.001$) soils (Fig. 2e and f, Table S5).

Functional annotation and biomarker identification

In this study, FAPROTAX annotation indicated that three dominant functional groups (mean relative abundances higher than 1%) were associated with the carbon cycles, namely, aerobic chemoheterotrophy,
chemoheterotrophy and aromatic compound degradation. The relative abundance of the aforementioned groups was significantly decreased in RT compared with that in NT and MP in bulk soils. Compared with MP, NT and RT distinctly reduced the relative abundance of aromatic compound degradation in the rhizosphere soils (Fig. 3). In addition, the dominant functional groups involved in the nitrogen cycles included nitrogen fixation, ureolysis, nitrification, nitrate reduction and aerobic ammonia oxidation. Compared with MP, NT and RT significantly increased the relative abundances of nitrification, aerobic ammonia oxidation and nitrate reduction in the bulk soils, and the abundance of nitrogen fixation in the rhizosphere soils (Fig. 3).

Tenfold cross-validation was performed to assess the importance of biomarkers. The error rate of cross-validation tended to stabilize when the 10 most relevant genera were selected. Ten genera were defined as biomarkers: *Methylotenera*, *Gemmatimonas*, *Burkholderia*, *Segetibacter*, *Gemmatirosa*, *Luteibacter*, *Noviherbaspirillum*, *Methylobacterium*, *Blastococcus*, and *Mycobacterium* (Fig. 4a). The relative abundance of the biomarkers in the different treatments was further illustrated by a heatmap, which showed that most of the biomarkers, such as *Methylotenera*,

![Fig. 3 Functional prediction of bacterial communities in the bulk and rhizosphere soils under the different tillage practices using FAPROTAX.](image-url)

- NT, RT and MP represent no-tillage, ridge tillage and moldboard plow tillage, respectively; B: bulk soil; R: rhizosphere soil
**Blastococcus** and **Gemmatimonas**, had lower relative abundance, while only **Burkholderia** had a higher relative abundance in the rhizosphere soils of NT and RT than in those of MP (Fig. 4b).

**Network analysis**

The bacterial co-occurrence networks displayed differences in network structures and topological properties among the different tillage practices (Fig. 5, Table S6). The edge number of NT was higher than that of RT and MP in the bulk and rhizosphere soils. The node number of NT and RT was higher in the bulk and rhizosphere soils, respectively, than that of MP. Additionally, the average clustering coefficient (avgCC) and average connectivity (avgK) of the network were greater in NT than in RT and MP, whereas compared with NT and MP, RT resulted in greater modularity (M) and average path distance (GD) (Fig. 5, Table S6).

We observed that the degree of hub nodes and the number of generalists were higher in NT than in RT and MP in both the bulk and rhizosphere soils. In the bulk soils, most of the hub nodes were affiliated with Acidobacteria under the three tillage practices. The majority of the hub nodes detected in MP belonged to Acidobacteria, while the hub nodes of Actinobacteria and Proteobacteria (Alpha-, Beta- and Gamma-) were dominant in the rhizosphere soils in NT and RT (Table S7). Intriguingly, some functional OTUs, such as OTU2160 (**Brevundimonas**) and OTU3445 (**Burkholderia**) in NT and OTU2736 (**Rhizobacter**) and OTU2500 (**Nitrospirae**), were shared by hub nodes and generalists in RT in the rhizosphere soils. The other OTUs that were shared by hub nodes and generalists belonged to Acidobacteria, including OTU2346 (**Stenotrophobacter**) in the rhizosphere soils of MP, and OTU2900 (**Vicinamibacter**), OTU567 (**Stenotrophobacter**) and OTU3322 (**Unclassified**) in the bulk soils in NT, RT and MP, respectively (Tables S7 and S8).

**Bacterial community assembly processes**

The values of ses.MNTD of all samples were significantly less than zero, with a lower value in the bulk soils than in the rhizosphere soils \( (P < 0.05) \) (Fig. 6a), suggesting that the bacterial communities were more phylogenetically clustered in the bulk soils. Additionally, a significant phylogenetic signal was observed across short phylogenetic distances by the phylogenetic mantel correlogram (Fig. 6b).
The combined results of βNTI and R_Cbray showed that no homogeneous selection was observed in the deterministic processes, while only homogenizing dispersal and undominated processes were detected for the stochastic processes (Fig. 6c). Variable selection dominated the bacterial community assembly processes across all the tillage practices, although it played a greater role in the bulk soils than in the rhizosphere soils. Homogenizing dispersal contributed more to the bacterial community assembly processes in the bulk and rhizosphere soils of MP than in those of NT and RT. Compared with RT, NT increased the importance of stochastic processes in the bulk and rhizosphere soils. Additionally, the Mantel test showed that soil pH was significantly correlated (P < 0.05) with βNTI (Fig. S1).

Discussion

Bacterial community structures significantly affected by tillage practices

In this study, irrespective of the tillage practice, soil bacterial communities were divided into two major groups according to the bulk and rhizosphere soil samples, suggesting that rhizosphere effort rather than tillage practice was the dominant factor in regulating the bacterial communities (Fig. 2a). We observed that the variations in the bacterial community structures in the bulk soils were larger than those in the rhizosphere soils, which were likely because the stronger determinant of root exudates released from the roots onto the bacterial communities concealed the variation between tillage practices (Philippot et al. 2013). In addition, the bacterial communities

![Fig. 5 Bacterial ecological networks displayed at the OTU level in the bulk and rhizosphere soils under the different tillage practices. A connection indicates a strong (Spearman’s ρ > 0.6) and significant (P < 0.01) correlation. Each node represents a unique OTU. The nodes colored by phyla/classes and the keystone taxa are magnified. NT, RT and MP represent no-tillage, ridge tillage and moldboard plow tillage, respectively; B: bulk soil; R: rhizosphere soil.](image-url)
were also significantly affected by the tillage practices in the bulk and rhizosphere soils (Fig. 2b and c). This finding is corroborated by Tyler (2019) and Xia et al. (2019), who observed that the underlying soil properties varied under different tillage practices and were the dominant factors in shifting microbial communities.

Soil chemical properties had a significant relationship with the bacterial community structure in the bulk and rhizosphere soils (Fig. S1). Soil NH$_4^+$-N played a dominant role in driving differentiation across all soil samples (Fig. 2d). Soil available nitrogen observably affects plant growth, and its uptake by plants is strongly dependent on rhizosphere microbial guilds (Moreau et al. 2019). In this study, the NH$_4^+$-N content ranged from an average of 1.75 mg kg$^{-1}$ in the bulk soils to 4.36 mg kg$^{-1}$ in the rhizosphere soils (Table S1); thus, it is reasonable that a large variation in soil NH$_4^+$-N contributed the most to shaping the bacterial community structures of all the samples across the bulk and rhizosphere soils. Additionally, soil pH contributed the most to regulating the bacterial community structures in the bulk and rhizosphere soils (Fig. 2e and f), although soil pH varied by only 0.3 units among the three tillage practices. This finding suggested that even a small pH range change induced by tillage practices was still the most important factor determining soil bacterial community composition (Degrange et al. 2015). This result is associated with the narrow optimum soil pH range for bacteria, and when the pH value exceeds a certain range, a physiological constraint on soil bacteria is observed that changes the competition outcomes or decreases the net growth of the individual groups, which cannot survive (Lauber et al. 2009).

**Fig. 6** Relative impacts of ecological processes on bacterial community assembly under the different tillage practices in the bulk and rhizosphere soils. The standardized effect size measure of the mean nearest taxon distance (ses.MNTD) was shown in the bulk and rhizosphere soils within the different tillage practices (a), n.s. represent no significant difference ($P > 0.05$). Mantel correlograms between the phylogenetic distances of two OTUs and their niche distances. Solid points indicate significant correlations ($P < 0.05$) (b). The relative contributions of five ecological assembly processes with the three tillage practices (c). NT, RT and MP represent no-tillage, ridge tillage and moldboard plow tillage, respectively; B: bulk soil; R: rhizosphere soil.
Variations in soil bacterial community composition induced by different tillage practices

The responses of the functional bacteria involved in carbon and nitrogen cycling to different soil disturbances were diverse (Tables S2 and S3). OTU1829 and OTU846 were affiliated with *Blastococcus* and *Sphingomonas*, and their relative abundances were significantly lower in NT and RT than in MP in the bulk and rhizosphere soils. Studies have shown that *Blastococcus* can degrade soil organic matter (Wang et al. 2020c) and *Sphingomonas* may play a key role in the degradation of polycyclic aromatic hydrocarbons (Macchi et al. 2018). In addition, OTU3343 (*Streptomyces adustus*) and OTU3407 (*Streptomyces yanglinensis*) can effectively degrade lignocellulose (Noda et al. 2012), which had lower abundances in the bulk soils with RT and in the rhizosphere soils with NT. These results indicate that intensive disturbance may accelerate the decomposition of carbon sources (Wang et al. 2020c) because the increased disturbance would increase the soil surface area by forming more microaggregates (Six et al. 2000). In contrast, NT and RT slowed down the decomposition rate of soil organic matter compared with MP, and thus led to an increase in soil carbon sequestration (Powlsion et al. 2016).

The representative sequences of OTU3445 and OTU2114 had 97.12% and 99.53% similarity to *Burkholderia singularis* and *Mesorhizobium gobiense*, respectively. *Burkholderia* and *Mesorhizobium* have been widely reported to have nitrogen fixation capabilities (Fan et al. 2019; Soe et al. 2020), and their abundances were significantly higher in the rhizosphere soils in NT and RT than in MP. Similarly, OTU4404 (*Bradyrhizobium japonicum*) and OTU2109 (*Rhizobium etli*) are widely documented to facilitate nodulation and biological nitrogen fixation of legumes (Kalita and Malek 2020; Rivas et al. 2009; Roper et al. 2020), and these bacteria were obviously increased in the rhizosphere soils of NT. Additionally, OTU2806 (*Nitrosospira multiformis*) and OTU3942 (*Nitrosospira tenuis*), which play a pivotal role in the nitrification process (Lin et al. 2018), were enriched in the bulk soils of RT and rhizosphere soils of NT. This finding was consistent with the results of Holland (2004) and Torabian et al (2019), who stated that conservation tillage increased soil nitrogen loss by enhancing nitrification, since nitrate nitrogen is easily leached out from soil (Levy-Booth et al. 2014). This phenomenon is due to increased soil moisture and reduced soil pH and oxygen content in NT and RT, which led to higher nitrifier abundance and activities (Johnson and Hoyt 1999; Torabian et al 2019).

Given the changes in the relative abundances of the bacterial taxa associated with carbon and nitrogen cycling in NT and RT compared with MP, we speculate that conservation tillage might enhance soil nitrogen cycling in nitrogen fixation and nitrification, while contributing to soil carbon sequestration by weakening soil carbon degradation. This concept was reconfirmed by FAPROTAX annotation analysis (Fig. 4). The increase of soil carbon sequestration leads to the reduction of CO₂ emissions, slows global warming, and contributes to improving soil organic carbon levels (Chevallier et al. 2010; Lopez-Garrido et al. 2011). The enhancement of biological nitrogen fixation can substantially improve agricultural systems, which has both environmental and economic costs associated with the nitrogen supply (Torabian et al., 2019). Additionally, higher potential nitrification increases the content of nitrate nitrogen that can be absorbed and utilized by plants, thus promoting plant growth despite increasing the risk of nitrogen loss (Beeckman et al. 2018; Chen et al. 2008; Luo et al. 2019).

Tillage practices affect the stability of the soil bacterial network and the ecological function

Network analysis offers deep insights into the complex interactions of bacterial communities under soil perturbations (Barberan et al. 2012). Our study observed that tillage practices had impacts on bacterial network structures (Fig. 5, Table S6). The network of NT with the largest edge displayed more complex interactions in the bulk and rhizosphere soils, although the NT network possessed relatively fewer nodes than the MP and RT networks in the rhizosphere soils. This finding was in line with the results of Banerjee et al. (2019), who observed that the complexity of microbial networks is determined by the number of associations rather than the number of taxa. Additionally, the highest avgK of the NT network in the bulk and rhizosphere soils also demonstrated that compared with MP, NT created a higher density of interactions among OTUs (Ma...
et al. 2020). Bouizgarne et al. (2014) showed that closely coupled OTUs share the same habitat preferences, and their simultaneous occurrence markedly alleviates environmental stresses and stimulates crop growth. Additionally, a network with a greater average path distance (GD) can enable environmental fluctuations to propagate more slowly to the whole network, thus playing a better role in buffering environmental perturbations (Wang et al. 2014). Simultaneously, higher modularity (M) was conducive to enhancing the stability of network structures (Kitano 2004; Krause et al. 2003). Therefore, the higher values of GD and M in the bulk and rhizosphere soils of the RT network indicated that compared with MP, RT was more robust to environmental disturbances.

As gatekeepers of ecosystem function, keystone species provide important contributions to biogeochemical cycling (Banerjee et al. 2018; Jiang et al. 2017). It has been widely reported that generalists with important topological roles and hub nodes with the highest degree exert a considerable influence on microbial network structure and function (Banerjee et al. 2019; Herren and McMahon 2018; Shi et al. 2020). In this study, it was common for Acidobacterial OTUs to be identified as keystone taxa because Acidobacteria can occupy a broad niche and have traits related to degrading soil organic carbon (Jiang et al. 2017; Mannisto et al. 2013). Additionally, half of the biomarkers were also tied to the soil carbon cycle, including *Methylotenera*, *Gemmatimonas*, *Methylobacterium*, *Blastococcus* and *Mycobacterium* (Guo et al. 2016; Kalyuzhnaya et al. 2012; Ren et al. 2017; Sanjenbam et al. 2020; Wang et al. 2020c). More notably, some keystone taxa were simultaneously identified by generalists and hub nodes, which might be explained by their particularly important ecological functions. For instance, the keystone taxa OTU2160 (*Brevundimonas*) and OTU3445 (*Burkholderia*) in rhizosphere soils of NT have been reported to be diazotrophic and can enhance crop growth and root colonization (Fan et al. 2019; Naqqash et al. 2020). OTU2500 and OTU2736 in the rhizosphere soils of RT were classified as *Nitrosospira* and *Rhizobacter*, respectively, and these bacteria are well known to play a crucial role in nitrification and nitrogen fixation (Lin et al. 2018; Tong et al. 2020). We also found that the nitrogen-fixing bacterium *Burkholderia* was identified as a biomarker based on random forest analysis (Fig. 4). Overall, the soil bacteria closely involved in soil carbon and nitrogen cycling were integrated as keystone taxa and biomarkers, indicating that tillage practices changed microbial-mediated carbon and nitrogen cycling, thereby affecting the ecological functions.

Assembly of soil bacterial communities influenced by tillage practices

In this study, we observed that stochastic and deterministic processes played a crucial role in the assembly of bacterial communities by null models (Ofiteru et al. 2010). Soil bacterial communities were more closely phylogenetically clustered in the bulk soils than in the rhizosphere soils (Fig. 6a). The weak phylogenetic clustering in the rhizosphere soils might be tied to the reduced relative contribution of deterministic processes because of the lower variable environmental filtering in the rhizosphere soils, which can cause phylogenetic overdispersion of bacterial communities (Fan et al. 2017; Gobena et al. 2014). Additionally, the increasing relative importance of stochastic processes in rhizosphere soils was well associated with higher soil fertility, which can weaken niche selection by promoting the growth of soil microorganisms and reducing competition for resources (Chen et al. 2017; Zhou et al. 2014). We found that stochastic processes, especially homogenizing dispersal, had a higher relative contribution to bacterial community assembly processes in the bulk and rhizosphere soils of MP than in those of NT and RT (Fig. 6c). This could be explained by the strong soil disturbance in MP, which could have led to high dispersal rates and thus tended to be more similar to the soil bacterial communities (Stegen et al. 2015; Zaneveld et al. 2017).

The results of the Mantel test also showed that soil pH was markedly correlated with bacterial community assembly processes (Fig. S1), which was consistent with previous reports (Tripathi et al. 2018). The closer to neutral pH of both the bulk and rhizosphere soils of MP may have reduced the selection pressure from environmental filters (Tripathi et al. 2018) since a neutral pH environment is more suitable for the growth of most bacteria (Madigan 2012). Moreover, niche-based processes are influenced by not only abiotic factors (environmental filtering) but also biotic interactions (e.g., competition, predation...
and mutualism) (Zhou and Ning 2017). Therefore, the soil nutrients and soil pH in NT were not significantly higher than those in RT, although the relative importance of stochastic processes was increased in NT because more microbial interactions in NT could alleviate environmental selection pressure (Bouizgarne et al. 2014; Jiao et al. 2020).

Conclusions

Our study showed that the composition, structure and assembly process of bacterial communities in the bulk and rhizosphere soils were significantly affected by tillage practices. Specifically, the relative abundance of nitrifying bacteria and nitrogen-fixing bacteria increased, while the bacteria associated with carbon degradation were decreased in NT and RT compared with those in MP. Additionally, the soil bacterial networks in NT and RT were more robust to environmental disturbances than those in MP. The deterministic processes played a predominant role in the assembly of bacterial communities under the three tillage practices, and the relative contribution of MP to the homogenizing dispersal process was greater in both the bulk and rhizosphere soils than that of NT and RT. Soil pH played a major role in mediating bacterial community structures and assembly processes under different tillage practices. Overall, this study provides a variety of evidence that conservation tillage practices were more conducive to soil carbon sequestration, nitrogen fixation and nitrification compared with traditional tillage practices, which provides a new perspective for the application of agricultural management practices in agroecosystems.

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Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

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