



Organic substitutions improve soil quality and maize yield through increasing soil microbial diversity

Hanwen Liu^{a,b}, Xiaofang Du^a, Yingbin Li^a, Xu Han^{a,b}, Bing Li^{a,b}, Xiaoke Zhang^a, Qi Li^{a,**}, Wenju Liang^{a,*}

^a Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, 110016, China

^b University of Chinese Academy of Sciences, Beijing, 100049, China

ARTICLE INFO

Handling Editor: Bin Chen

Keywords:

Organic substitution
Soil quality
Soil biota
Functional group
Maize yield

ABSTRACT

Organic substitution is beneficial to sustainable agricultural development. In order to determine the proper fertilization strategy, it is necessary to evaluate the effects of partial substitution of nitrogen fertilizer with organic amendments on soil quality and crop yield, as well as their decisive factors. A five-year organic substitution field experiment was set up to investigate the effects of partial substitution of chemical fertilizer with stover, cattle manure and biochar on soil quality, soil microbial and nematode diversities and crop yield in a maize (*Zea mays* L.) field of Northeast China. Our results showed that organic substitutions increased soil quality and manure substitution increased maize yield through changing the composition and functional group of soil biota. Bacteria played important roles in determining the maize yield, but the beneficial effects were contingent on the different types of organic substitution. Stover substitution improved soil quality through increasing bacterial diversity but may lead to the competition of nitrogen between microorganisms and crops. Compared with conventional fertilization, manure substitution provided resources with suitable C/N ratio (6.82) and resulted in the higher maize yield, but the soil quality improvement was weaker under manure substitution than under stover substitution. Biochar substitution reduced the relative abundance of plant-parasitic nematodes but caused an increasing of potential pathogenic fungi for maize. Comprehensively, stover substitution is the most promising fertilization regime for maize in Northeast China from the perspective of soil quality and soil biodiversity.

1. Introduction

Long-term heavy applications of chemical fertilizer have resulted in soil degradation due to acidification and the excess mineral nutrients accumulated in soil (Coolon et al., 2013; Zhao et al., 2018), and reduced the resistance of plants to diseases closely related to agricultural production (Peng et al., 2009). The development of sustainable agricultural practices can improve food security and the utilization efficiency of organic resources (Johnston and Poulton, 2018). Proper chemical fertilization replaced with organic amendments is important for the sustainability of agroecosystems (Ramanantenasoa et al., 2019). Organic amendments can improve soil quality and fertility with low environmental risk due to mitigating environmental pollution induced by long-term mineral fertilization (Mouratiadou et al., 2019; Duan et al., 2021; Sun et al., 2021; Song et al., 2021).

Soil quality can indicate the capacity of ecosystem functions provided by soil (Bünemann et al., 2018; Han et al., 2020). The assessment of soil quality index (SQI) can synthesize soil abiotic and biotic properties to reflect soil functions as a whole (Nannipieri et al., 2010; Bünemann et al., 2018; Schloter et al., 2018). Recently, the impacts of organic substitution on soil quality have been assessed in different agroecosystems. Chen et al. (2021) found that straw incorporation with nitrogen fertilizer increased SQI with increasing nitrogen application rate in semi-arid dryland farming system. Other researches in loamy soil and acidic red soil showed that the complete organic manure application reduced SQI compared with partial organic substitution (Tian et al., 2015; Ji et al., 2020). Therefore, the supplement of nitrogen fertilizer together with organic amendments is important in improving soil quality (Kuzakov and Xu, 2013). Aside from the supplement of chemical fertilizer, the type of organic amendments is another important

* Corresponding author.

** Corresponding author.

E-mail addresses: liq@iae.ac.cn (Q. Li), liangwj@iae.ac.cn (W. Liang).

<https://doi.org/10.1016/j.jclepro.2022.131323>

Received 9 November 2021; Received in revised form 24 February 2022; Accepted 10 March 2022

Available online 14 March 2022

0959-6526/© 2022 Elsevier Ltd. All rights reserved.

factor influencing soil quality. Li et al. (2020) compared four organic amendments (biochar, straw, manure and vermicompost) and found that pig manure substitution at 40% rate was beneficial for SQI and crop yield in the rapeseed-sweet potato rotation system. The above-mentioned researches showed that soil types and cropping system were important factors that influenced the effects of organic substitution. Therefore, it is necessary to choose the appropriate organic amendment based on site-specific conditions.

As important players in supporting soil quality, soil biota are also sensitive to organic substitution (Kou et al., 2018; Fan et al., 2020; Wang et al., 2020; Bello et al., 2021). The addition of organic amendments can alleviate the negative effects of mineral fertilization on soil biodiversity (Sun et al., 2016; Zhang et al., 2019; Liu et al., 2020; Lv et al., 2020). For instance, organic amendments with manure or biochar increased nematode diversity and microbivorous nematode abundance (Liu et al., 2016, 2020; Zhang et al., 2019). Even though, the benefits of organic substitution were obvious, researchers also found that some organic amendments could increase the pathogenic fungi with a potential risk of plant disease (Ji et al., 2020; Esmailzadeh-Salestani et al., 2021). Thus, a reasonable agricultural management practice is needed for further improving soil biodiversity and regulating the biotic disease in order to maintain sustainable crop production in Northeast China.

Increasing evidences suggest that the amount and composition of organic resources generally determine the effects of organic substitutions on soil quality (Bowles et al., 2014; van der Bom et al., 2018). Straw and manure, with H/C ratios of 1.5–1.6, are more easily decomposed by microbes than biochar (H/C ratio <1.0) (Krause et al., 2018; Shi et al., 2018; Siedt et al., 2021). As a fresh plant material, relatively higher C/N ratio for straw may result in the immobilization of N due to the competition between microorganisms and crops (Kuzyakov and Xu, 2013). The decomposed manure with a suitable C/N ratio was beneficial for nutrient release and could improve soil biodiversity (Liu et al., 2013). Alkaline and porous biochar can neutralize hydrogen ions to alleviate soil acidification (Cantrell et al., 2012; Gul et al., 2015) and enhance the capacity cation exchange and buffering in agroecosystems (Lehmann et al., 2020; Yang et al., 2020). A meta-analysis showed that straw substitution could increase soil nutrients such as N, P and K at Luvisol in Northeast China (Zhao et al., 2019). Fan et al. (2020) revealed that cow manure was beneficial to enhance wheat yield after chemical fertilizer substituted with straw or manure. Although many researches had tested the effects of organic substitutions on soil characteristics and crop yield, the response of soil biota and soil quality to different organic substitutions was still not clear. It is important to explore the influential mechanism of different types of organic substitution on soil quality and biodiversity in agroecosystems of Northeast China.

We conducted a five-year field experiment to investigate the effects of partial substitute chemical fertilizer with stover, cattle manure and biochar on soil quality, soil biodiversity (microbial diversity and nematode diversity) and crop yield in a maize (*Zea mays* L.) field of Northeast China. We hypothesized that five-year organic substitutions will increase soil quality and maize yield in comparison with the chemical fertilization alone (H1). Partial substitution of chemical fertilizer with stover and manure can improve soil biodiversity better than biochar due to their relatively higher available nutrients, and positively influence soil quality and crop yield (H2); while partial substitution of chemical fertilizer with biochar can reduce the abundance of plant pathogens and parasitic nematodes in soil due to their properties of alkalinity and stability (H3).

2. Materials and methods

2.1. Site description and experimental design

The organic substitution field experiment was established in 2016 at the National Field Observation and Research Station of Agro-ecosystems in Shenyang, Liaoning Province, China (41°31' N, 123°24' E). This area

has a humid and semi-humid continental monsoon climate. The annual mean temperature is 7.8 °C and precipitation is 700 mm (Lu et al., 2018). Soil type in the present study is Clay-loam mixed Fluvisol Cambisol (Gong et al., 2003) and crop system is maize continuous cropping systems.

The experiment area was a continuous cropping system of maize with conventional fertilization before this experiment was established. This experiment was a completely randomized block design with four replicates for each treatment (2.6 m² for each treatment plot). The four fertilization treatments included: (1) conventional urea with 220 kg N·ha⁻¹·y⁻¹ (Control); (2) 30% substitution rate of urea N with stover (FS); (3) 30% substitution rate of urea N with cattle manure (FM); and (4) 30% substitution rate of urea N with biochar (FB). The total amount of N applications was the same for all the fertilization treatments. All the organic fertilizers (stover, cattle manure and biochar) were mixed into soil as base fertilizer at one time before maize planting. The cattle manure has been decayed for balancing the content of carbon and nitrogen before application and biochar is the product of maize stover after thermal degradation. The basic properties of three organic amendments were shown in Table S1. The 30% organic substitution rate was calculated according to N content and all treatments at equal content of total nitrogen. The urea fertilizer was divided into two parts including base fertilizer (70%) and topdressing fertilizer (30%) for each treatment. The P and K fertilizers application rates were 80 kg P₂O₅ ha⁻¹ y⁻¹ and 60 kg K₂O ha⁻¹ y⁻¹ as base fertilizer in all treatments.

2.2. Soil sampling and crop yield

At maize ripening stages of 2019 and 2020, soil samples were collected from 0 to 20 cm depth using an auger (2.5 cm diameter; Eijkelkamp, the Netherlands). Nine subsamples in each plot were randomly collected and mixed to obtain a representative soil sample for each treatment. Total 32 soil samples (2 years × 4 treatments × 4 replicates) were taken in this study. All maize in each plot was collected at the ripening stage and the maize yield was indicated as dry weight of grains.

2.3. Determination of soil abiotic and biotic properties

Soil pH was analyzed through vibrating slurry at a water-to-soil ratio of 2.5:1 (v/w) and measured using pH meter (Mettler-Toledo FE28, Switzerland). Soil organic carbon (SOC) and total nitrogen (TN) were determined by the Elementar Analyzer System (Vario MACRO cube, Germany). Soil NH₄⁺-N and NO₃⁻-N were measured by continuous flow analyzer (FIAStar5000 Analyzer, Foss Tecator, Hillerød, Denmark). Available nitrogen (AN) was the sum of NO₃⁻-N and NH₄⁺-N. Microbial biomass carbon (MBC) and nitrogen (MBN) were determined according to Brookes et al. (1985) and Vance et al. (1987). The β-glucosidase (BG) and N-acetyl-β-D-glucosaminidase (NAG) activities were measured using incubation methods reported by Tabatabai (1994) and Parham and Deng (2000). Soil mixtures with and without substrates (β-glucoside for BG and p-nitrophenyl-N-acetyl-β-D-glucosaminide solution for NAG) were cultured at 37 °C for 1 h. The color intensity of the filtrate was measured at 405 nm with a spectrophotometer. Soil BG and NAG activities were calculated by subtracting control absorbance from sample absorbance (see Table 1).

2.4. Soil microbial and nematode DNA analysis

High-throughput sequencing was used to characterize the soil microbial and nematode community by Illumina MiSeq platform. Soil microbial DNA was extracted using the method provided by Fast DNA SPIN Kit (MP Biomedicals, USA) from 0.5 g fresh soil. The bacterial 16S rRNA gene was profiled based on the primer pairs 515F (5'-GTGCCAGCMGCCGCGG-3') and 907R (5'-CCGTCGAATTCMTT-TRAGTTT-3') (Biddle et al., 2008), and fungal ITS region was amplified using primer pairs ITS86F (5'-GTGAATCATCGAATCTTTGAA-3') and ITS4R (5'-TCTCCGCTTATTGATATGC-3') (De Beeck et al., 2014). Soil

Table 1
Soil properties (mean (SE), n = 8) in different fertilizer treatments.

Treatments	Control	FS	FM	FB
pH (H ₂ O)	5.18(0.04)b	5.43(0.1)a	5.36(0.06)	5.46(0.08)a
SOC (g kg ⁻¹)	10.3(0.24)b	11.14(0.21)	11.38(0.21)	13.9(0.71)a
TN (g kg ⁻¹)	1.31(0.03)	1.31(0.04)	1.36(0.03)	1.31(0.02)
NO ₃ ⁻ -N (mg kg ⁻¹)	4.85(0.78)	4.15(0.92)	3.39(0.57)	3.34(0.58)
NH ₄ ⁺ -N (mg kg ⁻¹)	50.37(15.36)	48.13	48.45	48.8(16.22)
AN (mg kg ⁻¹)	55.22(15.51)	52.29	51.84(16.7)	52.13
MBC (mg kg ⁻¹)	82.83(3.33)	108.68	90.17(5.87)	74.16(4.18)
MBN (mg kg ⁻¹)	13.98(1.15)	14.16(0.95)	12.36(0.96)	11.29(0.81)
NAG (mg kg h ⁻¹)	28.14(1.11)b	38.63(4.67)	29.52(3.32)	28.09(2.87)
BG (mg kg h ⁻¹)	34.87(1.48)c	55.01(2.82)	46.58(1.97)	41.58(1.2)b
C/N ratio	7.88(0.26)b	8.51(0.19)b	8.37(0.21)b	10.62(0.58)
MBC/MBN ratio	6.1(0.35)b	7.83(0.38)a	7.46(0.46)	6.71(0.43)
BG/NAG ratio	1.25(0.06)b	1.54(0.16)	1.75(0.23)a	1.58(0.15)

The differences between treatments were tested using mixed linear model with the year as random factors. Different lower-case letters indicate the significant differences of variable means among different treatments. SOC, soil organic carbon; TN, total nitrogen; AN, available nitrogen; BG, β -glucosidase activity; NAG, N-acetyl- β -D-glucosaminidase activity; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; Yield, the dry weight of maize grains. Control, 100% conventional urea; FS, 30% substitution rate of urea N with stover; FM, 30% substitution rate of urea N with cattle manure; FB, 30% substitution rate of urea N with biochar.

nematodes were extracted using the modified cotton-wool filter method from 100 g soil and the total number was determined under a microscope (Liang et al., 2009). Nematode suspension was transferred to a test tube and removed supernatant and retained 2 ml suspension carefully for subsequent DNA extraction. Soil nematode DNA was extracted using DNeasy Blood & Tissue Kit (Qiagen) and the primer pairs were NF1F and 18Sr2bR (Porazinska et al., 2009). The detailed extraction method of nematode DNA, the PCR reactions and thermal cycling conditions of nematodes followed the method reported by Du et al. (2020). The high-throughput sequencing process was performed by Shanghai Majorbio Bio-pharm Technology Co. Ltd. The representative sequences of bacteria, fungi and nematodes annotated against the Silva 138, UNITE 8.0 and NCBI NT_v202006004 database, respectively (Quast et al., 2013; Nilsson et al., 2018). In our study, 7555 OTUs for bacteria, 741 for fungi, 87 for nematodes were obtained after screening and randomly selecting. Then the 'Faprotax' and 'FUNGuild' were used to parse the ecological guilds of the bacterial and fungal OTUs, respectively (Louca et al., 2016; Nguyen et al., 2016).

2.5. Soil quality measurement

The minimum data set (MDS) was used to calculate soil quality index (Doran and Parkin, 1996). Firstly, principal components (PCs) with eigenvalues more than 1 and total explained variation more than 5% were selected (Brejda et al., 2000a; Andrews et al., 2002a). Secondly, the variables having absolute values within 10% of the highest factor loading were selected into the MDS within each PC (Andrews et al., 2002a). When multiple variables were retained in one PC, we calculated the linear correlations and cut off the redundant variable from the MDS with correlation coefficient higher than 0.60 (Andrews et al., 2002a, 2002b). In our study, soil abiotic and biotic properties (SOC, TN, NH₄⁺-N, NO₃⁻-N, AN, pH, MBC, MBN, BG, NAG) were used to calculate

soil quality index (SQI) and then SOC, NH₄⁺-N, MBC and BG were selected as the key indicators using MDS method. Thirdly, using the following curve to normalize and score the MDS indicators (Brejda et al., 2000b; Andrews et al., 2002a).

$$NL-SF(Y) = 1 / [1 + (x / x_0)^b]$$

Where NL-SF (Y) is the nonlinear transformation score of each indicator with the ranging from 0 to 1, x and x₀ are the value and the mean value of corresponding indicator. Each indicator was termed in two opposite directions, b is the slope of the equation, b = -2.5 for 'more is better' functions and b = 2.5 for 'less is better' functions. Finally, the following weighted additive equation was used to calculate SQI (Andrews et al., 2002a, 2002b).

$$SQI = \sum_i W_i S_i$$

Where W indicates the weighting factor of the soil properties that equals the percentage of each PC's explanation. S is a nonlinear (NL-SQI) score, i is the number of PC.

2.6. Network analysis

For exploring the co-occurrence pattern between microbial and nematode taxa in the micro-food web, we analyze the co-occurrence network based on the Spearman correlation matrix. Before constructing the network, we only retained the top 10% OTUs of bacteria and fungi (Soliveres et al., 2016), and classified the nematode OTUs on genus level. The 'corrplot' and 'igraph' packages in R program were used to determine the Spearman correlation and the topological properties of the network, respectively. In order to obtain a strongly co-occurring network, we focused on the correlation which Spearman's absolute r > 0.65 and P < 0.01 (Fan et al., 2020), then the network was visualized using 'Gephi' software (<https://gephi.org/>). The complexity of each network was calculated as the ratio of edges to nodes. The following equation was used to calculate Modularity (Newman, 2010).

$$Q = [\sum_{ij}(A_{ij} - k_i k_j / 2m) \delta(c_i, c_j)] / 2m$$

Where m is the number of edges, A_{ij} equals 1 or 0 indicating OTUs i and j are connected or not. k_i and k_j are the number of taxa that have significant correlations with taxa i and j, respectively, and $\delta(c_i, c_j)$ is 1 or 0 indicating i and j are in the same module or not.

The relative abundance-weighted community degree (RACD) was calculated to compare the associations of soil biotic community in different fertilization treatments. And the RACD was defined as: $\sum N \times RA$, where N and RA indicate the degree and the relative abundance of the OTUs (bacteria, fungi and nematode) (Sun et al., 2020).

2.7. Structural equation model analysis

The structural equation model (SEM) was used to identify how organic substitution indirectly or directly affected soil quality and maize yield. The organic substitutions (Control and all organic treatments were assigned values of 0 and 1, respectively) were regarded as an exogenous variable. Prior to SEM analysis, we used the PC1 of PCoA and functional groups PCA to represent biotic community composition and the functional indicator, respectively (Veen et al., 2010), including bacterial functional groups parsed from 'Faprotax', fungal functional groups parsed from 'FUNGuild' and nematode trophic groups. Finally, we used Amos 18.0 (IBM, SPSS, New York, USA) software to fit models and visualize the diagram.

2.8. Statistical analysis

The mixed linear model was used to test the differences among treatments of different organic substitution with the year as random factor to ignore interannual effect. The multiple comparisons among

different treatments were conducted using Tukey HSD and performed by 'multcomp' package in the R software (version3.5.1). The alpha and beta diversities were determined using the 'vegan' package in R software. We measured the microbial and nematode community compositions using Principal Co-ordinates Analysis (PCoA, Bray-Curtis dissimilarity) (Bray and Curtis, 1957). The diagrams were visualized using the 'ggplot2' package in the R program.

3. Results

3.1. Effects of organic substitution on soil quality and maize yield

The organic substitutions (FS, FM and FB) significantly increased the soil quality index (SQI) after five years, with the highest value of SQI found in FS treatment (0.645) (Fig. 1a; $P < 0.05$). Compared with Control, FM treatment significantly increased grain yield of maize (11788 kg ha⁻¹) (Fig. 1b; $P < 0.05$).

3.2. Effects of organic substitution on soil biodiversity and community composition

The response of soil biodiversity varied with different types of organic substitutions (Fig. 2; $P < 0.05$). Compared with Control, the FS and FB treatments significantly increased the Shannon index and decreased the Simpson index of bacteria ($P < 0.05$). In contrast, the lower Shannon index and higher Simpson index of fungi were found in FS treatment ($P < 0.05$). The Shannon index of nematodes was significantly lower in FB treatment than in other treatments ($P < 0.05$). No differences were observed in the Ace and Chao indices.

Organic substitutions significantly influenced the microbial community composition (Fig. 3). The PCoA showed that two canonical axes explained 31.61%, 31.13% and 38.68% of all variations in bacterial, fungal and nematode communities, respectively. Soil bacterial communities in organic substitution treatments (FS, FM, FB) were clearly separated from Control (Fig. 3a). Soil fungal communities in Control, FM and FB treatments were clearly separated with FS treatment along the first axis, indicating that the community compositions of fungal communities were distinctly different from those in FS treatment (Fig. 3b). The organic substitution significantly affected the *Abditibacteriota*, *Firmicutes*, *Gemmatimonadota*, *Halanaerobiaeota*, *WPS-2*, *Sumerlaeota*, *Basidiomycota*, *Ascomycota*, *Zoopagomycota*, *Aphelenchoides*, *Ditylenchus*, *Cephalobidae*, *Helicotylenchus* and *Proleptonchus* (Table S2; $P < 0.05$).

The organic substitutions increased the relative abundance of chitinolytic bacteria and microbivorous nematodes (*Rhabditidae*, *Cephalobidae*, *Aphelenchoides*, *Ditylenchus* in FS treatment, *Cephalobidae*,

Ditylenchus, *Proleptonchus* in FM treatment and *Proleptonchus* in FB treatment), while decreased the relative abundance of bacterial functional groups (including bacteria associated with degradation of aromatic hydrocarbons, oxygenic photoautotrophy and human pathogens) and the symbiotic fungi (*Glomeraceae*) (Fig. 4). Compared with Control, FS and FB treatments increased fungal pathogen (*Piptocephalidaceae* in FS treatment; *Leptosphaeriaceae*, *Plectosphaerellaceae* and *Olpidiaceae* in FB treatment). Organic substitutions also decreased the relative abundance of plant-parasitic nematodes (*Basiria*, *Helicotylenchus*). In comparison with FM treatment, FB treatment also reduced the relative abundance of *Pseudhalenchus* and *Pratylenchus* (Fig. 4; $P < 0.05$).

3.3. Effects of organic substitution on soil biotic network

We constructed co-occurring networks for each treatment to identify soil taxa that highly co-occurring with each other (Fig. 5a). Species with high degrees in FS and FM treatments were distinct from Control and FB treatments (Fig. S1). Compared with the Control, FM treatment increased the modularity metric of network ($Q = 0.53$), and FS treatment promoted the positive associations (73%) and increased the network complexity (9.7) of soil biota (Fig. 5b). In addition, FS and FM treatments improved the relative abundance of soil microbes and nematodes with high degree (>40 with microbes and >30 with nematodes) (Fig. S2). Organic substitution significantly increased the bacterial RACD index compared with Control ($P < 0.05$). While nematode RACD index was lower in FB than in other treatments (Fig. 5c; $P < 0.05$).

3.4. Contribution of soil biota to soil quality and maize yield

Structural equation model (SEM) analysis indicated that the effects of organic substitutions on soil quality or maize yield were indirect rather than direct (Fig. 6). Specifically, organic substitution increased soil quality by inducing the changes in bacterial diversity, the associations among taxa and functional groups of soil biota. Organic substitution improved maize yield through changing functional groups of bacteria. The biotic diversity, functional groups and associations of soil biota explained 73% of the total variance in SQI, and the functional groups of soil biota explained 32% of the total variance in crop yield.

4. Discussion

4.1. Organic substitution improved soil quality and biodiversity

The 30% substitution rate of chemical fertilizer with organic amendments improved soil quality and manure substitution increased

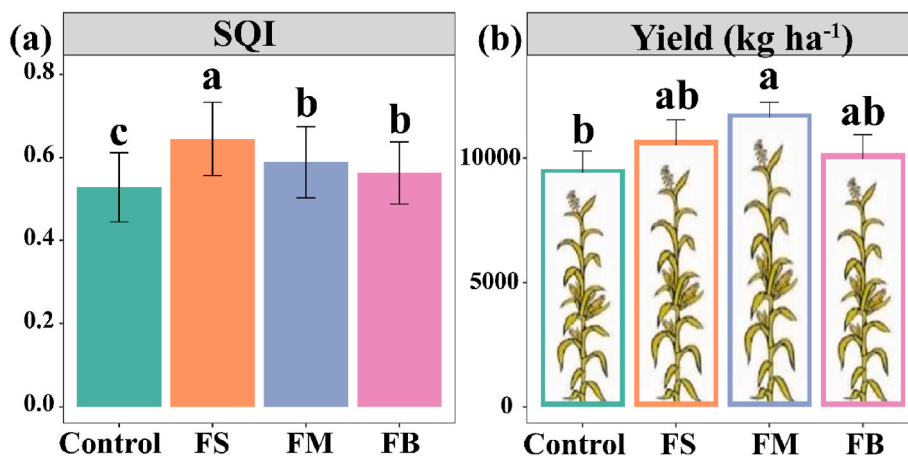


Fig. 1. Soil quality index (SQI) (a) and maize yield (b) in different fertilizer treatments (mean \pm SE, $n = 8$). Different lower-case letters indicate the significant differences of variable means among different treatments. Yield, the dry weight of maize grains. Control, 100% conventional urea; FS, 30% substitution rate of urea N with stover; FM, 30% substitution rate of urea N with cattle manure; FB, 30% substitution rate of urea N with biochar.

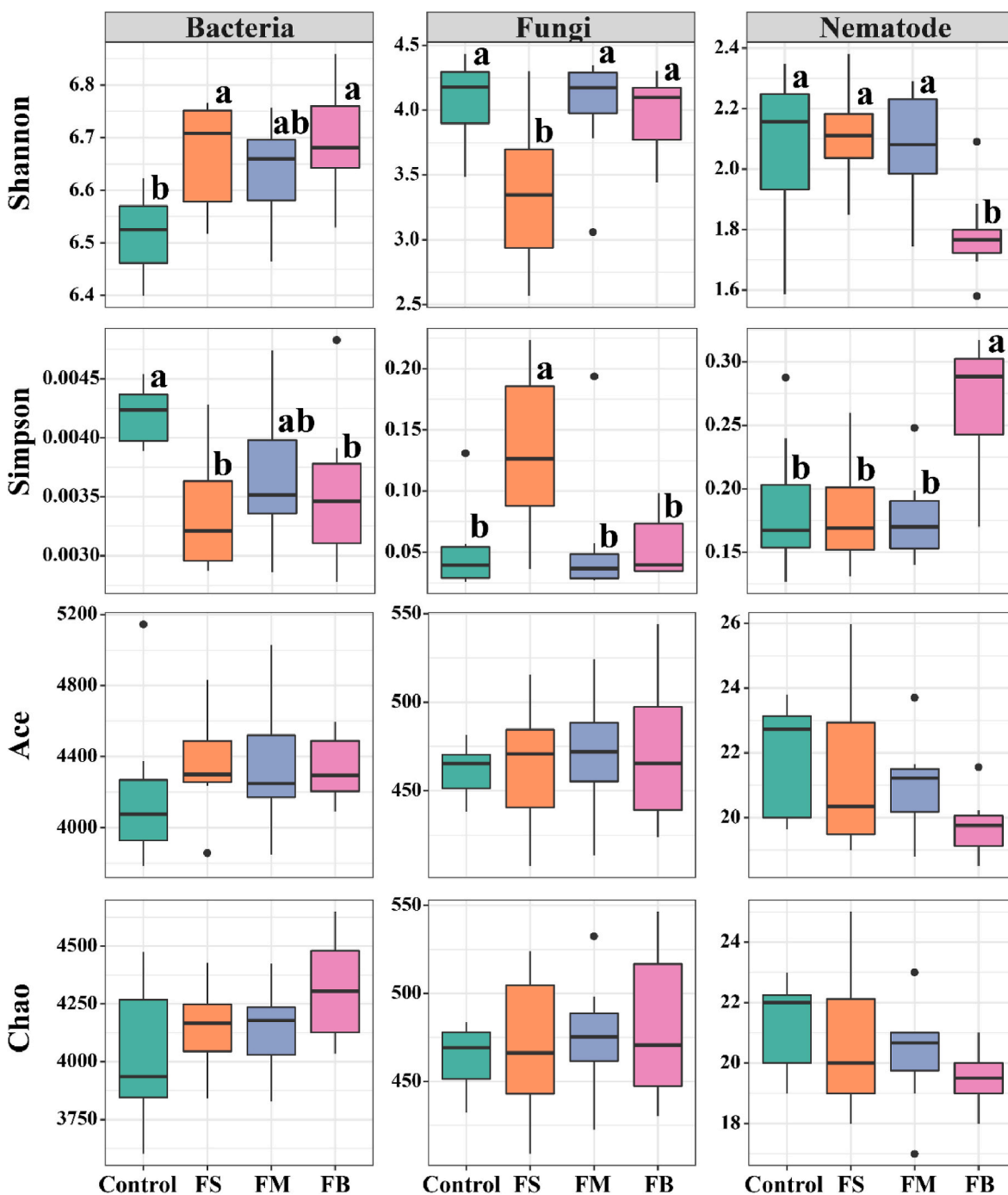


Fig. 2. Diversity and richness of bacteria, fungi and nematodes in different fertilizer treatments (mean \pm SE, $n = 8$). Different lower-case letters indicate the significant differences of variable means among different treatments. Control, 100% conventional urea; FS, 30% substitution rate of urea N with stover; FM, 30% substitution rate of urea N with cattle manure; FB, 30% substitution rate of urea N with biochar.

maize yield in comparison with chemical fertilization alone, which was consistent with our first hypothesis. The main reasons for the beneficial effects of organic substitution on soil quality and maize yield are the supplying of organic substrates and concomitant changes in soil biotic composition and functional groups. Previous studies have confirmed the positive effects of organic substitution on soil nutrients and soil quality (Ji et al., 2020; Liu et al., 2021). Organic substitution promoted the beneficial functional groups of soil biota, such as chemoheterotrophic bacteria, saprophytic fungi and microbivorous nematodes, which was conducive to the improvement of soil fertility (Wal et al., 2013; Kou et al., 2018; Ning et al., 2021). The changes in soil microbial functional

group rely on the variation of abiotic factors caused by fertilizations (Zhao et al., 2020). Our result of SEM showed that bacterial functional groups played important roles in determining the maize yield, especially the increase of bacteria related to nitrogen cycling (nitrate reduction, chitinolysis). The easily decomposed substrates (stover and manure) increased the bacteria associated with chemoheterotrophy and chitinolysis while the high decomposition resistance substrate (biochar) caused the increase of bacteria associated with fermentation and nitrate reduction. Chemoheterotrophic bacteria are considered as decomposers, which are in charge of organic resource recycling in soil ecosystems (Kämpfer et al., 1993), while fermentation can promote carbon cycling

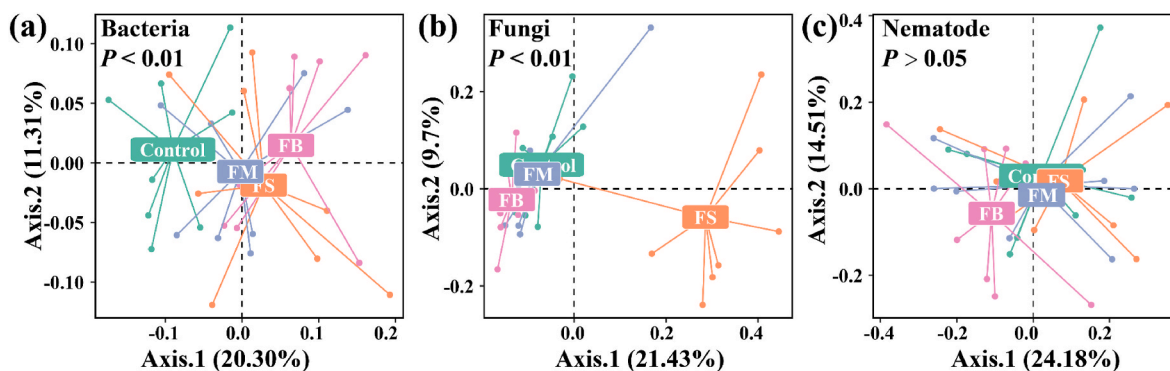


Fig. 3. Principal Co-ordinates Analysis (PCoA) plot of bacteria, fungi and nematodes (a, b, c). Control, 100% conventional urea; FS, 30% substitution rate of urea N with stover; FM, 30% substitution rate of urea N with cattle manure; FB, 30% substitution rate of urea N with biochar.

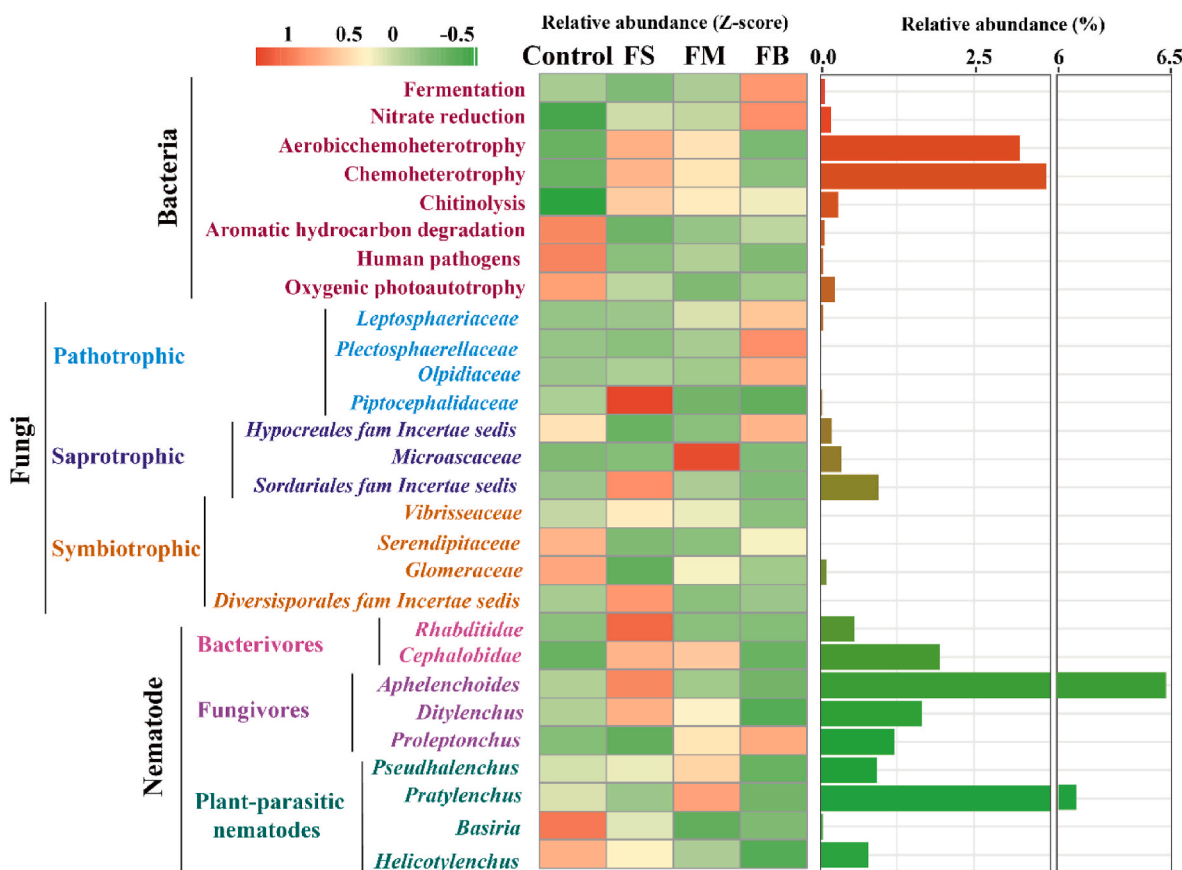


Fig. 4. Functional groups of bacterial, fungal and nematode (left), relative abundance of each functional groups (right). The heatmap showed the Z-score of relative abundance. Control, 100% conventional urea; FS, 30% substitution rate of urea N with stover; FM, 30% substitution rate of urea N with cattle manure; FB, 30% substitution rate of urea N with biochar.

due to metabolizing glucose. The increase of these functional groups indicated that organic amendments can provide abundant organic resources and stimulate the vigorous metabolism of soil biota.

4.2. Effects of organic substitution on soil quality and biodiversity depending on the type of organic amendment

Both stover and manure substitutions increased bacterial diversity and strengthened the interspecific associations of soil biota. Stover substitution significantly improved soil quality through increasing soil microbial diversity and interspecific associations of soil biota. Meanwhile, the high microbial activity indicated by BG and NAG activities

also indirectly supported that stover substitution accelerated nutrient cycling and led to the highest SQI. Bacteria and fungi had different responses to stover substitution. This is because bacterial and fungal communities vary in their resource preferences and tactics for nutrient-acquisition, for instance, bacteria prefer resources that are easily decomposition compared with fungi (Six et al., 2006). The decrease of fungal Shannon diversity indicated that the greater selective impact of stover on fungal taxa, which further restricted the ecological functions of fungi. In stover substitution treatment, the higher positive connections suggested that more species were symbiotic or with similar niche in the network (Zelezniak et al., 2015; Duran et al., 2018). The decrease in abundance of species belonging to positive feedback loop will result in

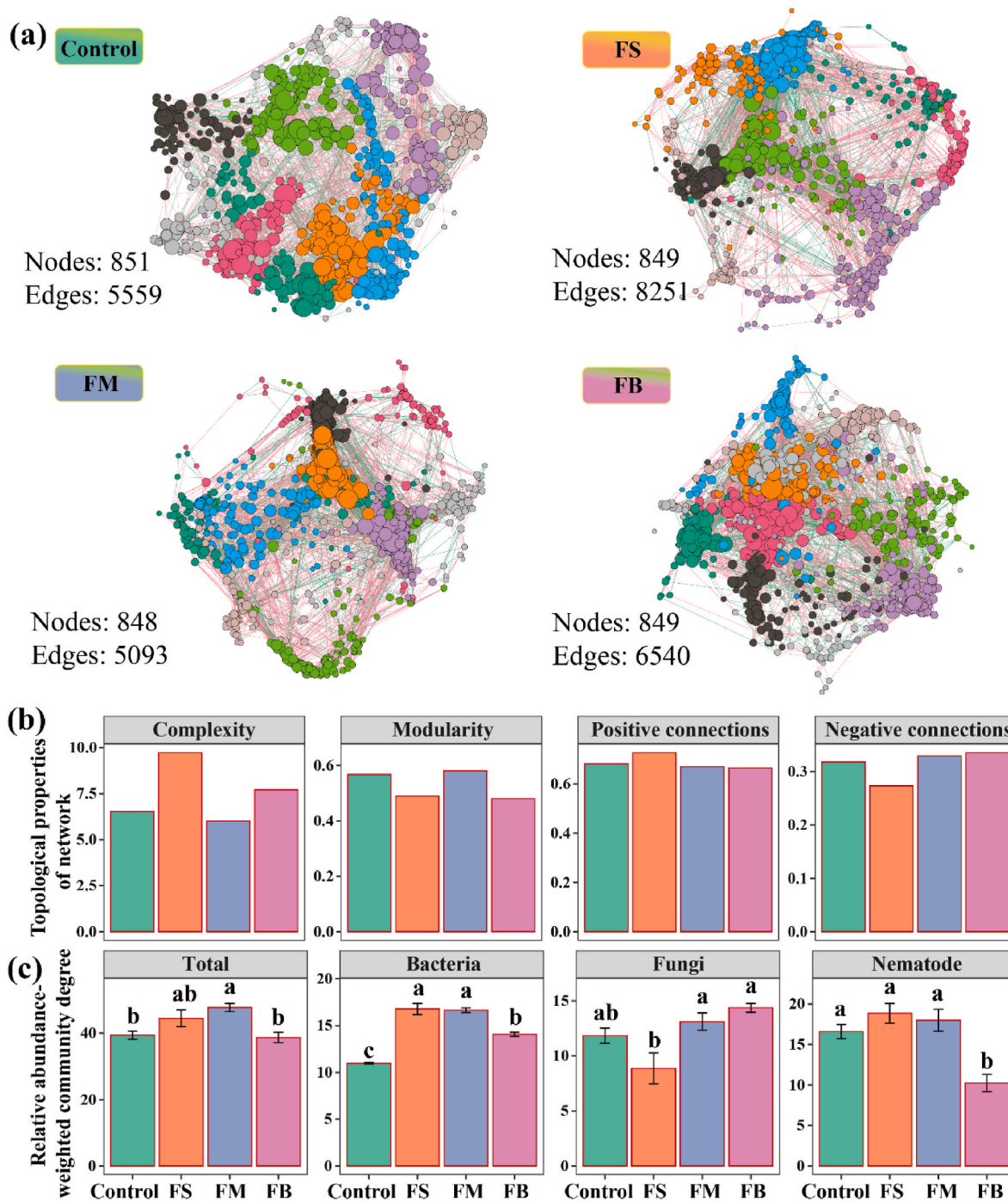


Fig. 5. Network diagram based on modularity in four treatments (a); Network topology properties in four treatments (b). Relative abundance-weighted community degree (RACD) of total biota, bacteria, fungi and nematodes in four treatments (c). Nodes indicate soil biotic taxa (bacteria and fungi at OTU levels, nematodes at genus levels); Edges indicate the correlation between taxa; red and blue color indicate the negative and positive correlations, respectively; The size of nodes indicate the numbers of correlation between one species and other species; the color of nodes indicate different modules; Control, 100% conventional urea; FS, 30% substitution rate of urea N with stover; FM, 30% substitution rate of urea N with cattle manure; FB, 30% substitution rate of urea N with biochar.

negative impact on fitness of other taxa within feedback loop (Coyte et al., 2015). The increase of positive connections may result from the limitation of nitrogen in soil (Hernandez et al., 2021). Since the C input from stover provides more available C but insufficient available nitrogen for soil microorganisms. So stover substitution may lead to the competition of nitrogen between the assimilation of microorganisms and the uptake of plants (Kuzyakov and Xu, 2013).

Manure substitution may provide suitable resources for microorganisms and weaken the competition between microorganisms and

plants caused by stover application, which may result in higher maize yield in manure substitution compared with conventional fertilization. Meanwhile, the partially negative connections and high modularity in soil network suggested manure substitution better maintain the stability of soil food web (Herren and McMahon, 2017). The high modularity suggested that ecological clusters were independent of each other in chemical fertilizer and manure treatments. The impact of losing a taxon would be restricted to its own module rather than involving others, which supported a stable network (Stouffer and Bascombe, 2011). In

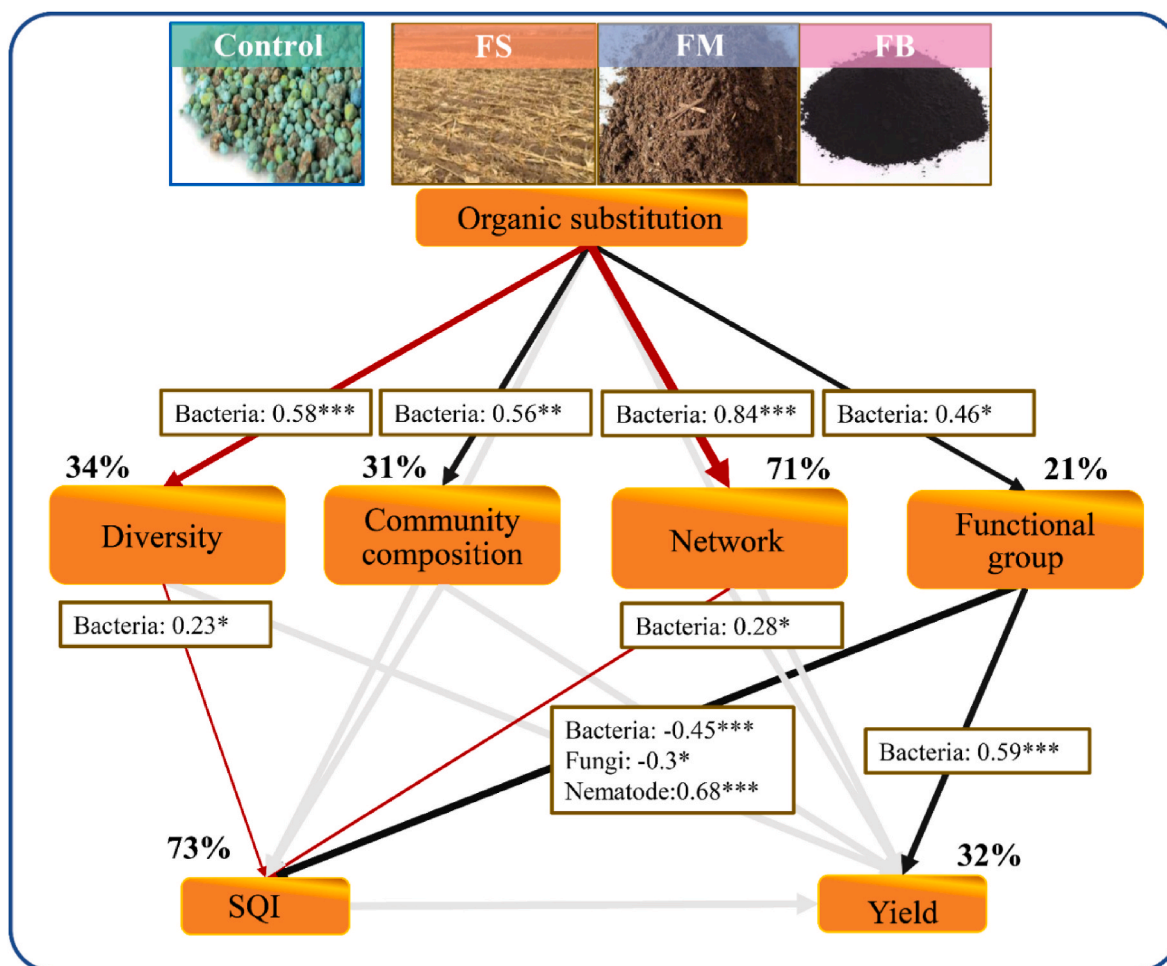


Fig. 6. Structural equation model analysis illustrating the effects of changes in soil biota due to organic substitution on soil quality and maize yield ($\chi^2 = 26.438$, $df = 25$, $P = 0.385$, $NFI = 0.892$, $CFI = 0.993$, $RMSEA = 0.043$). Path coefficients (correlation coefficients) along arrows are standardized by the mean of each parameter. Arrow width is proportional to the coefficients of the relationship. Red line, significant positive correlation; grey line, no significant; black line, significant correlation. A mediation variable is a collection of variables, Alpha diversity including bacterial, fungal and nematode Shannon-diversity, community composition including PC1 of bacterial, fungal and nematode PCoAs, network including bacterial, fungal and nematode RACD, function groups including bacterial and fungal function groups and nematodes trophic groups.

our five-year fertilization system, manure substitution can restore the balance of the network more quickly. Thus, the balance of carbon and nitrogen is very important in organic amendments.

Biochar substitution significantly increased soil pH due to the characteristic with high pH (Graber et al., 2010), which was more suitable for acid soil. The total amount of C input from biochar was as much as 15 t ha^{-1} after five years, soil carbon storage was significantly increased because of the resistance to decomposition. In addition, biochar substitution decreased the abundance of plant-parasitic nematodes, which is consistent with the result of Liu et al. (2020). Contrast to our hypothesis, although with the low relative abundance, the pathogenic fungi increased after biochar application. This was consistent with the result of Ji et al. (2020) who suggested organic substitution has a risk of fungal disease. The change of antagonistic taxa and pH were two important factors (Chen et al., 2020), so the occurrence of pathogenic fungi with biochar amendment was worthy to attention under specific conditions (types of climate, crops and soil) in maize continuous cropping systems.

4.3. Rational fertilization regimes for maize

Stover substitution had the highest soil quality index. As a kind of organic resource, stover was the best of three organic amendments for

maize. But 30% stover substitution rate of chemical fertilizer may cause competitions between microorganisms and plants for nitrogen nutrient, resulting in the difficulty of nitrogen uptake by maize (Kuzakov and Xu, 2013; Fan et al., 2020). Therefore, the suitable stover substitution rate may be less than 30% and need to be further studied. Manure effectively reduced the competitions between microbes and plants for nitrogen nutrient, thus supporting the highest grain yield of maize. Animal organic fertilizer has suitable C/N ratios (about 6.8–21) and active microorganisms, which are more conducive to the release of soil nutrients and the increase of biodiversity (Liu et al., 2013; Siedt et al., 2021). The improvement of manure substitution on soil quality was weaker than stover substitution. Stover substitution accelerated nutrient cycling by providing more carbon sources and resulted in the increasing of soil quality. Biochar substitution was beneficial to weaken soil acidification and soil carbon sequestration (Graber et al., 2010; Lévesque et al., 2020). However, biochar substitution led the increase of fungal pathogen in this study. Properties of biochar feedstock and pyrolysis temperature may also influence our results, so the characteristics of different biochar should be further studied for better selection suitable organic amendments for maize in Northeast China.

5. Conclusion

Partial organic substitution of chemical fertilizer with stover, manure and biochar increased soil quality. Manure substitution weakened the competition between soil biota and plants through providing resources with suitable C/N ratio and improved the maize yield through stabilizing the soil biotic network. Biochar substitution can reduce the relative abundance of plant-parasitic nematodes, but there is still a potential risk of increasing pathogenic fungi for maize. Taken together, Stover substitution is the most promising fertilization regime for both increasing soil quality and soil biodiversity. The proper application rate of stover substitution should be further studied to relieve the competition between microorganisms and crops for nitrogen and for the improvement of crop yield.

CRedit authorship contribution statement

Hanwen Liu: Data curation, Formal analysis, Writing – original draft. **Xiaofang Du:** Methodology, Writing – review & editing. **Yingbin Li:** Data curation, Formal analysis, Writing – review & editing. **Xu Han:** Formal analysis, Methodology. **Bing Li:** Data curation, Formal analysis. **Xiaoke Zhang:** Writing – review & editing. **Qi Li:** Conceptualization, Writing – original draft, Writing – review & editing. **Wenju Liang:** Conceptualization, Writing – review & editing.

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.

Acknowledgements

This research was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (Grant Nos. XDA28020202, XDA28090100 XDA28090200), the National Natural Science Foundation of China (Grant Nos. 41977054 and 31330011), and the Shenyang Plan Project of Science and Technology (Grant No. 213552), China.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jclepro.2022.131323>.

References

- Andrews, S.S., Karlen, D.L., Mitchell, J.P., 2002a. A comparison of soil quality indexing methods for vegetable production systems in Northern California. *Agric. Ecosyst. Environ.* 90, 25–45. [https://doi.org/10.1016/S0167-8809\(01\)00174-8](https://doi.org/10.1016/S0167-8809(01)00174-8).
- Andrews, S.S., Mitchell, J.P., Mancinelli, R., Karlen, D.L., Hartz, T.K., Horwath, W.R., Pettygrove, G.S., Scow, K.M., Munk, D.S., 2002b. On-farm assessment of soil quality in California's central valley. *Agron. J.* 94, 12–23. <https://doi.org/10.2134/agronj2002.0012>.
- Bello, A., Wang, B., Zhao, Y., Yang, W., Ogundej, A., Deng, L., Egbeagu, U.U., Yu, S., Zhao, L., Li, D., Xu, X., 2021. Composted biochar affects structural dynamics, function and co-occurrence network patterns of fungi community. *Sci. Total Environ.* 775, 145672. <https://doi.org/10.1016/j.scitotenv.2021.145672>.
- Biddle, J.F., Fitz-Gibbon, S., Schuster, S.C., Brechnley, J.E., House, C.H., 2008. Metagenomic signatures of the Peru Margin seafloor biosphere show a genetically distinct environment. *Proc. Natl. Acad. Sci. Unit. States Am.* 105, 10583–10588. <https://doi.org/10.1073/pnas.0709942105>.
- Bowles, T.M., Acosta-Martinez, V., Calderon, F., Jackson, L.E., 2014. Soil enzyme activities, microbial communities, and carbon and nitrogen availability in organic agroecosystems across an intensively-managed agricultural landscape. *Soil Biol. Biochem.* 68, 252–262. <https://doi.org/10.1016/j.soilbio.2013.10.004>.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27, 326–349. <https://doi.org/10.2307/1942268>.
- Brejda, J.J., Karlen, D.L., Smith, J.L., Allan, D.L., 2000a. Identification of regional soil quality factors and indicators: II. Northern Mississippi Loess Hills and Palouse Prairie. *Soil Sci. Soc. Am. J.* 64, 2125–2135. <https://doi.org/10.2136/sssaj2000.6462125x>.
- Brejda, J.J., Moorman, T.B., Karlen, D.L., Dao, T.H., 2000b. Identification of regional soil quality factors and indicators: I. Central and southern high plains. *Soil Sci. Soc. Am. J.* 64, 2115–2124. <https://doi.org/10.2136/sssaj2000.6462115x>.
- Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biol. Biochem.* 17, 837–842. [https://doi.org/10.1016/0038-0717\(85\)90144-0](https://doi.org/10.1016/0038-0717(85)90144-0).
- Bünemann, E.K., Bongiorno, G., Bai, Z., Creamer, R.E., De Deyn, G., de Goede, R., Flesskens, L., Geissen, V., Kuyper, T.W., Mäder, P., Puleman, M., Sukkel, W., van Groenigen, J.W., Brussaard, L., 2018. Soil quality – a critical review. *Soil Biol. Biochem.* 120, 105–125. <https://doi.org/10.1016/j.soilbio.2018.01.030>.
- Cantrell, K.B., Hunt, P.G., Mu, B., Jm, A., Ksr, A., 2012. Impact of pyrolysis temperature and manure source on physicochemical characteristics of biochar. *Bioresour. Technol.* 107, 419–428. <https://doi.org/10.1016/j.biortech.2011.11.084>.
- Chen, A.L., Zhang, W.Z., Sheng, R., Liu, Y., Hou, H.J., Liu, F., Ma, G.H., Wei, W.X., Qin, H.L., 2021. Long-term partial replacement of mineral fertilizer with in situ crop residues ensures continued rice yields and soil fertility: a case study of a 27-year field experiment in subtropical China. *Sci. Total Environ.* 787, 147523. <https://doi.org/10.1016/j.scitotenv.2021.147523>.
- Chen, D.L., Wang, X.X., Zhang, W., Zhou, Z.G., Ding, C.F., Liao, Y.W.K., Li, X.G., 2020. Persistent organic fertilization reinforces soil-borne disease suppressiveness of rhizosphere bacterial community. *Plant Soil* 452, 313–328. <https://doi.org/10.1007/s11104-020-04576-3>.
- Coolon, J.D., Jones, K.L., Todd, T.C., Blair, J.M., Herman, M.A., 2013. Long-term nitrogen amendment alters the diversity and assemblage of soil bacterial communities in tallgrass prairie. *PLoS One* 8, e67884. <https://doi.org/10.1371/journal.pone.0067884>.
- Coyte, K.Z., Schluter, J., Foster, K.R., 2015. The ecology of the microbiome: networks, competition, and stability. *Science* 350, 663–666. <https://doi.org/10.1126/science.aad2602>.
- De Beeck, M.O., Lievens, B., Busschaert, P., Declerck, S., Vangronsveld, J., Colpaert, J.V., 2014. Comparison and validation of some ITS primer pairs useful for fungal metabarcoding studies. *PLoS One* 9, e97629. <https://doi.org/10.1371/journal.pone.0097629>.
- Doran, J.W., Parkin, T.B., 1996. Quantitative indicators of soil quality: a minimum data set. *Methods Assessing Soil Quality* 49, 25–37. <https://doi.org/10.2136/sssaspecpub49.c2>.
- Duan, Y., Chen, L., Zhang, J.B., Li, D.M., Han, X.R., Zhu, B., Li, Y., Zhao, B.J., Huang, P., 2021. Long-term fertilisation reveals close associations between soil organic carbon composition and microbial traits at aggregate scales. *Agric. Ecosyst. Environ.* 306, 107169. <https://doi.org/10.1016/j.agee.2020.107169>.
- Duran, P., Thiergart, T., Garrido-Oter, R., Agler, M., Kemen, E., Schulze-Lefert, P., Hacquard, S., 2018. Microbial interkingdom interactions in roots promote arabidopsis survival. *Cell* 175, 973. <https://doi.org/10.1016/j.cell.2018.10.020>.
- Du, X.F., Li, Y.B., Han, X., Ahmad, W., Li, Q., 2020. Using high-throughput sequencing quantitatively to investigate soil nematode community composition in a steppe-forest ecotone. *Appl. Soil Ecol.* 152, 103562. <https://doi.org/10.1016/j.apsoil.2020.103562>.
- Esmaeilzadeh-Salestani, K., Bahram, M., Ghanbari Moheb Seraj, R., Gohar, D., Tohidfar, M., Eremeev, V., Talgre, L., Khaleghdoust, B., Mirmajlessi, S.M., Luik, A., Loit, E., 2021. Cropping systems with higher organic carbon promote soil microbial diversity. *Agric. Ecosyst. Environ.* 319, 107521. <https://doi.org/10.1016/j.agee.2021.107521>.
- Fan, K.K., Delgado-Baquerizo, M., Guo, X.S., Wang, D.Z., Zhu, Y.G., Chu, H.Y., 2020. Microbial resistance promotes plant production in a four-decade nutrient fertilization experiment. *Soil Biol. Biochem.* 141, 107679. <https://doi.org/10.1016/j.soilbio.2019.107679>.
- Gong, Z.T., Chen, Z.C., Zhang, G.L., 2003. World reference base for soil resources (WEB): establishment and development. *Soils* 35, 271–278. <https://doi.org/10.13758/j.cnki.tr.2003.04.002>.
- Gul, S., Whalen, J.K., Thomas, B.W., Sachdeva, V., Deng, H., 2015. Physico-chemical properties and microbial responses in biochar-amended soils: mechanisms and future directions. *Agric. Ecosyst. Environ.* 206, 46–59. <https://doi.org/10.1016/j.agee.2015.03.015>.
- Graber, E.R., Harel, Y.M., Kolton, M., Cytryn, E., Silber, A., David, D.R., Tschansky, L., Borenshtein, M., Elad, Y., 2010. Biochar impact on development and productivity of pepper and tomato grown in fertigated soilless media. *Plant Soil* 337, 481–496. <https://doi.org/10.1007/s11104-010-0544-6>.
- Han, X., Li, Y.B., Du, X.F., Li, Y.H., Wang, Z.W., Jiang, S.W., Li, Q., 2020. Effect of grassland degradation on soil quality and soil biotic community in a semi-arid temperate steppe. *Ecol. Process.* 9, 63. <https://doi.org/10.1186/s13717-020-00256-3>.
- Hernandez, D.J., David, A.S., Menges, E.S., Searcy, C.A., Afkhami, M.E., 2021. Environmental stress destabilizes microbial networks. *ISME J.* 15, 1722–1734. <https://doi.org/10.1007/s00374-020-01470-z>.
- Herren, C.M., McMahon, K.D., 2017. Cohesion: a method for quantifying the connectivity of microbial communities. *ISME J.* 11, 2426–2438. <https://doi.org/10.1101/112391>.
- Ji, L.F., Ni, K., Wu, Z.D., Zhang, J.W., Yi, X.Y., Yang, X.D., Ling, N., You, Z.M., Guo, S.W., Ruan, J.Y., 2020. Effect of organic substitution rates on soil quality and fungal community composition in a tea plantation with long-term fertilization. *Biol. Fertil. Soils* 56, 633–646. <https://doi.org/10.1007/s00374-020-01439-y>.
- Johnston, A.E., Poulton, P.R., 2018. The importance of long-term experiments in agriculture: their management to ensure continued crop production and soil fertility; the Rothamsted experience. *Eur. J. Soil Sci.* 69, 113–125. <https://doi.org/10.1111/ejss.12521>.

- Kämpfer, P., Steiof, M., Becker, P.M., Dott, W., 1993. Characterization of chemoheterotrophic bacteria associated with the in situ bioremediation of a waste-oil contaminated site. *Microb. Ecol.* 26, 161–188. <https://doi.org/10.1007/BF00177050>.
- Kou, X.C., Su, T.Q., Ma, N.N., Li, Q., Wang, P., Wu, Z.F., Liang, W.J., Cheng, W.X., 2018. Soil micro-food web interactions and rhizosphere priming effect. *Plant Soil* 432, 129–142. <https://doi.org/10.1007/s11104-018-3782-7>.
- Krause, H.M., Huppi, R., Leifeld, J., El-Hadidi, M., Harter, J., Kappler, A., Hartmann, M., Behrens, S., Mader, P., Gatteringer, A., 2018. Biochar affects community composition of nitrous oxide reducers in a field experiment. *Soil Biol. Biochem.* 119, 143–151. <https://doi.org/10.1016/j.soilbio.2018.01.018>.
- Kuzakov, Y., Xu, X., 2013. Competition between roots and microorganisms for nitrogen: mechanisms and ecological relevance. *New Phytol.* 198, 656–669. <https://doi.org/10.1111/nph.12235>.
- Lehmann, J., Cowie, A., Masiello, C.A., Kammann, C., Woolf, D., Amonette, J.E., Cayuela, M.L., Camps-Arbestain, M., Whitman, T., 2020. Biochar in climate change mitigation. *Nat. Geosci.* 14, 883–892. <https://doi.org/10.1038/s41561-021-00852-8>.
- Lévesque, V., Rochette, P., Hogue, R., Jeanne, T., Ziadi, N., Chantigny, M.H., Dorais, M., Antoun, H., 2020. Greenhouse gas emissions and soil bacterial community as affected by biochar amendments after periodic mineral fertilizer applications. *Biol. Fertil. Soils* 56, 907–925. <https://doi.org/10.1007/s00374-020-01470-z>.
- Li, P., Wu, M.C., Kang, G.D., Zhu, B.J., Li, H.X., Hu, F., Jiao, J.G., 2020. Soil quality response to organic amendments on dryland red soil in subtropical China. *Geoderma* 373, 114416. <https://doi.org/10.1016/j.geoderma.2020.114416>.
- Liang, W.J., Lou, Y.L., Li, Q., Zhong, S., Zhang, X.K., Wang, J.K., 2009. Nematode faunal response to long-term application of nitrogen fertilizer and organic manure in Northeast China. *Soil Biol. Biochem.* 41, 883–890. <https://doi.org/10.1016/j.soilbio.2008.06.018>.
- Liu, E.K., Yan, C.R., Mei, X.R., Zhang, Y.Q., Fan, T.L., Shah, V., 2013. Long-term effect of manure and fertilizer on soil organic carbon pools in dryland farming in northwest China. *PLoS One* 8, 56536. <https://doi.org/10.1371/journal.pone.0056536>.
- Liu, T., Chen, X.Y., Hu, F., Ran, W., Shen, Q.R., Li, H.X., Whalen, J.K., 2016. Carbon-rich organic fertilizers to increase soil biodiversity: evidence from a meta-analysis of nematode communities. *Agric. Ecosyst. Environ.* 232, 199–207. <https://doi.org/10.1016/j.agee.2016.07.015>.
- Liu, T., Yang, L.H., Hu, Z.K., Xue, J.R., Lu, Y.Y., Chen, X.Y., Griffiths, B.S., Whalen, J.K., Liu, M.Q., 2020. Biochar exerts negative effects on soil fauna across multiple trophic levels in a cultivated acidic soil. *Biol. Fertil. Soils* 56, 907–925. <https://doi.org/10.1007/s00374-020-01436-1>.
- Liu, J.A., Shu, A.P., Song, W.F., Shi, W.C., Li, M.C., Zhang, W.X., Li, Z.Z., Liu, G.G., Yuan, F.S., Zhang, S.X., Liu, Z.B., Gao, Z., 2021. Long-term organic fertilizer substitution increases rice yield by improving soil properties and regulating soil bacteria. *Geoderma* 404, 115287. <https://doi.org/10.1016/j.geoderma.2021.115287>.
- Louca, S., Parfrey, L.W., Doebeli, M., 2016. Decoupling function and taxonomy in the global ocean microbiome. *Science* 353, 1272–1277. <https://doi.org/10.1126/science.aaf4507>.
- Lu, C.Y., Chen, H.H., Teng, Z.Z., Yuan, L., Ma, J., He, H.B., Chen, X., Zhang, X.D., Shi, Y., 2018. Effects of N fertilization and maize straw on the dynamics of soil organic N and amino acid N derived from fertilizer N as indicated by ¹⁵N labeling. *Geoderma* 321, 117–126. <https://doi.org/10.1016/j.geoderma.2018.02.014>.
- Lv, M.R., Li, J.J., Zhang, W.X., Zhou, B., Dai, J., Zhang, C., 2020. Microbial activity was greater in soils added with herb residue vermicompost than chemical fertilizer. *Soil Ecol. Lett.* 2, 209–219. <https://doi.org/10.1007/s42832-020-0034-6>.
- Mouratiadou, I., Stella, T., Gaiser, T., Wicke, B., Nendel, C., Ewert, F., van der Hilst, F., 2019. Sustainable intensification of crop residue exploitation for bioenergy: opportunities and challenges. *GCB Bioenergy* 12, 71–89. <https://doi.org/10.1111/gcbb.12649>.
- Nannipieri, P., Ascher, J., Ceccherini, M.T., Landi, L., Renella, G., 2010. Microbial diversity and soil functions. *Eur. J. Soil Sci.* 68, 12–26. <https://doi.org/10.1111/ejss.4.12398>.
- Newman, M., 2010. *Networks: an Introduction*. Oxford University Press, Oxford, p. 784.
- Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecol.* 20, 241–248. <https://doi.org/10.1016/j.funeco.2015.06.006>.
- Nilsson, R.H., Larsson, K.H., Taylor, A.F.S., Bengtsson-Palme, J., Jeppesen, T.S., Schigel, D., Kennedy, P., Picard, K., Glöckner, F.O., Tedersoo, L., Saar, I., Kõljalg, U., Abarenkov, K., 2018. The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Res.* 47, D259–D264. <https://doi.org/10.1093/nar/gky1022>.
- Ning, Q., Chen, L., Zhang, C.Z., Ma, D.H., Li, D.M., Han, X.R., Cai, Z.J., Huang, S.M., Zhang, J.B., 2021. Saprotrophic fungal communities in arable soils are strongly associated with soil fertility and stoichiometry. *Appl. Soil Ecol.* 159, 103843. <https://doi.org/10.1016/j.apsoil.2020.103843>.
- Parham, J.A., Deng, S.P., 2000. Detection, quantification and characterization of β -glucosaminidase activity in soil. *Soil Biol. Biochem.* 32, 1183–1190. [https://doi.org/10.1016/S0038-0717\(00\)00034-1](https://doi.org/10.1016/S0038-0717(00)00034-1).
- Peng, S.B., Tang, Q.Y., Zou, Y.B., 2009. Current status and challenges of rice production in China. *Plant Prod. Sci.* 12, 3–8. <https://doi.org/10.1626/ppp.12.3>.
- Porazinska, D.L., Giblin-Davis, R.M., Faller, L., Farmerie, W., Kanzaki, N., Morris, K., Powers, T.O., Tucker, A.E., Sung, W., Thomas, W.K., 2009. Evaluating high-throughput sequencing as a method for metagenomic analysis of nematode diversity. *Mol. Ecol. Resour.* 9, 1439–1450. <https://doi.org/10.1111/j.1755-0998.2009.02611.x>.
- Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glockner, F.O., 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res.* 41, D590–D596. <https://doi.org/10.1093/nar/gks1219>.
- Ramanantenasoa, M.M.J.A., Genermont, S., Gilliot, J.M., Bedos, C., Makowski, D., 2019. Meta-modeling methods for estimating ammonia volatilization from nitrogen fertilizer and manure applications. *J. Environ. Manag.* 236, 195–205. <https://doi.org/10.1016/j.jenvman.2019.01.066>.
- Schlöter, M., Nannipieri, P.L., Sorensen, S.J., van, Elsas, J.D., 2018. Microbial indicators for soil quality. *Biol. Fertil. Soils* 54, 1–10. <https://doi.org/10.1007/s00374-017-1248-3>.
- Shi, X.C., Guo, X.L., Zuo, J.N., Wang, Y.J., Zhang, M.Y., 2018. A comparative study of thermophilic and mesophilic anaerobic co-digestion of food waste and wheat straw: process stability and microbial community structure shifts. *Waste Manag.* 75, 261–269. <https://doi.org/10.1016/j.wasman.2018.02.004>.
- Siedt, M., Schaffer, A., Smith, K.E.C., Nabel, M., Ross-Nickoll, M., van Dongen, J.T., 2021. Comparing straw, compost, and biochar regarding their suitability as agricultural soil amendments to affect soil structure, nutrient leaching, microbial communities, and the fate of pesticides. *Sci. Total Environ.* 751, 141607. <https://doi.org/10.1016/j.scitotenv.2020.141607>.
- Six, J., Frey, S.D., Thiet, R.K., Batten, K.M., 2006. Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil. Sci. Soc. Am. J.* 70, 555–569. <https://doi.org/10.2136/sssaj2004.0347>.
- Soliveres, S., Manning, P., Prati, D., Gossner, M.M., Alt, F., Arndt, H., Baumgartner, V., Binkenstein, J., Birkhofer, K., Blaser, S., Bluthgen, N., Boch, S., Boehm, S., Boerschig, C., Buscot, F., Diekötter, T., Heinze, J., Hoelzel, N., Jung, K., Klaus, V.H., Klein, A.M., Kleinebecker, T., Klemmer, S., Krauss, J., Lange, M., Morris, E.K., Mueller, J., Oelmann, Y., Overmann, J., Pasalic, E., Renner, S.C., Rillig, M.C., Schaefer, H.M., Schlöter, M., Schmitt, B., Schoening, I., Schrupf, M., Sikorski, J., Socher, S.A., Solly, E.F., Sonnemann, I., Sorkau, E., Steckel, J., Steffan-Dewenter, I., Stempfhuber, B., Tschapka, M., Tuerke, M., Venter, P., Weiner, C.N., Weisser, W.W., Werner, M., Westphal, C., Wilcke, W., Wolters, V., Wubet, T., Wurst, S., Fischer, M., Allan, E., 2016. Locally rare species influence grassland ecosystem multifunctionality. *Philos. Trans. R. Soc. B-Biol. Sci.* 371, 20150269. <https://doi.org/10.1098/rstb.2015.0269>.
- Song, A.L., Li, Z.M., Liao, Y.L., Liang, Y.C., Wang, E.Z., Wang, Sai, Li, X., Bi, J.J., Si, Z.Y., Lu, Y.H., Nie, J., Fan, F.L., 2021. Soil bacterial communities interact with silicon fraction transformation and promote rice yield after long-term straw return. *Soil Ecol. Lett.* 3, 395–408. <https://doi.org/10.1007/s42832-021-0076-4>.
- Stouffer, D.B., Bascompte, J., 2011. Compartmentalization increases food-web persistence. *Proc. Natl. Acad. Sci. Unit. States Am.* 108, 3648–3652. <https://doi.org/10.1073/pnas.1014353108>.
- Sun, G., Sun, M., Luo, Z.C., Li, C., Xiao, X.P., Li, X.J., Zhong, J.J., Wang, H., Nie, S.A., 2021. Effects of different fertilization practices on anammox activity, abundance, and community compositions in a paddy soil. *Soil Ecol. Lett.* 99, 103206. <https://doi.org/10.1007/s42832-021-0103-5>.
- Sun, R.B., Chen, Y., Han, W.X., Dong, W.X., Zhang, Y.M., Hu, C.C., Liu, B.B., Wang, F.H., 2020. Different contribution of species sorting and exogenous species immigration from manure to soil fungal diversity and community assemblage under long-term fertilization. *Soil Biol. Biochem.* 151, 108049. <https://doi.org/10.1016/j.soilbio.2020.108049>.
- Sun, R.B., Dsouza, M., Gilbert, J.A., Guo, X.S., Wang, D.Z., Guo, Z.B., Ni, Y.Y., Chu, H.Y., 2016. Fungal community composition in soils subjected to long-term chemical fertilization is most influenced by the type of organic matter. *Environ. Microbiol.* 18, 5137–5150. <https://doi.org/10.1111/1462-2920.13512>.
- Tabatabai, M.A., 1994. Soil enzymes. In: Weaver, R.W., Angle, S., Bottomley, P., Bezdicek, D., Smith, S., Tabatabai, A., Wollum, A. (Eds.), *Methods of Soil Analysis. Part 2: Microbiological and Biochemical Properties*. Soil Sci. Soc. Am. J. Madison, WI, pp. 775–833.
- Tian, W., Wang, L., Li, Y., Zhuang, K.M., Li, G., Zhang, J.B., Xiao, X.J., Xi, Y.G., 2015. Responses of microbial activity, abundance, and community in wheat soil after three years of heavy fertilization with manure-based compost and inorganic nitrogen. *Agric. Ecosyst. Environ.* 213, 219–227. <https://doi.org/10.1016/j.agee.2015.08.009>.
- Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. *Soil Biol. Biochem.* 19, 703–707. [https://doi.org/10.1016/0038-0717\(87\)90052-6](https://doi.org/10.1016/0038-0717(87)90052-6).
- van der Bom, F., Nunes, I., Raymond, N.S., Hansen, V., Bonnicksen, L., Magid, J., Nybroe, O., Jensen, L.S., 2018. Long-term fertilisation form, level and duration affect the diversity, structure and functioning of soil microbial communities in the field. *Soil Biol. Biochem.* 122, 91–103. <https://doi.org/10.1016/j.soilbio.2018.04.003>.
- Veen, G.F., Olff, H., Duyts, H., van der Putten, W.H., 2010. Vertebrate herbivores influence soil nematodes by modifying plant communities. *Ecology* 91, 828–835. <https://doi.org/10.1890/09-0134.1>.
- Wal, A., Geydan, T.D., Kuyper, T.W., Boer, W.D., 2013. A thready affair: linking fungal diversity and community dynamics to terrestrial decomposition processes. *FEMS Microbiol. Rev.* 37, 477–494. <https://doi.org/10.1111/1574-6976.12001>.
- Wang, Y., Chen, G.W., Sun, Y.F., Zhu, K., Jin, Y., Li, B.G., Wang, G., 2020. Different agricultural practices specify bacterial community compositions in the soil rhizosphere and root zone. *Soil Ecol. Lett.* 4, 18–31. <https://doi.org/10.1007/s42832-020-0058-y>.
- Yang, W., Feng, G., Miles, D., Gao, L.H., Jia, Y.L., Li, C.J., Qu, Z.Y., 2020. Impact of biochar on greenhouse gas emissions and soil carbon sequestration in corn grown under drip irrigation with mulching. *Sci. Total Environ.* 729, 138752. <https://doi.org/10.1016/j.scitotenv.2020.138752>.

- Zelezniak, A., Andrejev, S., Ponomarova, O., Mende, D.R., Bork, P., Patil, K.R., 2015. Metabolic dependencies drive species co-occurrence in diverse microbial communities. *Proc. Natl. Acad. Sci. Unit. States Am.* 112, 6449–6454. <https://doi.org/10.1073/pnas.1421834112>.
- Zhang, X.K., Wu, X., Zhang, S.X., Xing, Y.H., Liang, W.J., 2019. Organic amendment effects on nematode distribution within aggregate fractions in agricultural soils. *Soil Ecol. Lett.* 1, 147–156. <https://doi.org/10.1007/s42832-019-0010-1>.
- Zhao, X., Liu, B.Y., Liu, S.L., Qi, J.Y., Wang, X., Pu, C., Li, S.S., Zhang, X.Z., Yang, X.G., Lal, R., Chen, F., Zhang, H.L., 2019. Sustaining crop production in China's cropland by crop residue retention: a meta-analysis. *Land Degrad. Dev.* 6, 694–709. <https://doi.org/10.1002/ldr.3492>.
- Zhao, Y.C., Wang, M.Y., Hu, S.J., Zhang, X.D., Ouyang, Z., Zhang, G.L., Huang, B., Zhao, S.W., Wu, J.S., Xie, D., Zhu, B., Yu, D., Pan, X., Xu, S., Shi, X., 2018. Economics- and policy-driven organic carbon input enhancement dominates soil organic carbon accumulation in Chinese croplands. *Proc. Natl. Acad. Sci. Unit. States Am.* 115, 4045–4050. <https://doi.org/10.1073/pnas.1700292114>.
- Zhao, Z.B., He, J.Z., Quan, Z., Wu, C.F., Sheng, R., Zhang, L.M., Stefan, G., 2020. Fertilization changes soil microbiome functioning, especially phagotrophic protists. *Soil Biol. Biochem.* 148, 107863. <https://doi.org/10.1016/j.soilbio.2020.107863>.