



## Frequency of stover mulching but not amount regulates the decomposition pathways of soil micro-foodwebs in a no-tillage system

Xinchang Kou<sup>a,b,1</sup>, Ningning Ma<sup>b,1</sup>, Xiaoke Zhang<sup>b,\*</sup>, Hongtu Xie<sup>b</sup>, Xudong Zhang<sup>b</sup>, Zhengfang Wu<sup>a,\*\*</sup>, Wenju Liang<sup>b</sup>, Qi Li<sup>b</sup>, Howard Ferris<sup>c</sup>

<sup>a</sup> School of Geographical Sciences, Northeast Normal University, Changchun, 130024, China

<sup>b</sup> Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, 110016, China

<sup>c</sup> Department of Entomology and Nematology, University of California Davis, One Shields Avenue, Davis, CA, 95616, USA

### ARTICLE INFO

#### Keywords:

Soil micro-foodweb  
Nematode communities  
Decomposition pathway  
Stover mulching

### ABSTRACT

In soil micro-foodwebs, resource-transfer links between bacteria, fungi and microbivorous nematodes govern the transformation and cycling of soil organic carbon and for the quality, productivity and sustainability of soil ecosystems. However, changing the amount and frequency of stover mulching affects the resources available for the bacterial versus fungal decomposition pathways of soil micro-foodwebs. Therefore, we investigated the responses of the soil micro-foodweb to maize stover mulching amounts (33% and 67% of the stover remaining at harvest) and frequencies (high frequency had continuous mulching every year; low frequency had mulch applied once every three years) during a 10-year mulching experiment in a no-tillage system. Soil microorganism and nematode communities were affected significantly by the frequency, but not the amount of stover mulching. Greater abundance of bacterial PLFAs that were correlated with bacterivores occurred in the high frequency mulching treatments. In the low frequency mulching treatments, the abundance of fungal PLFAs and their correlations with fungivores were higher. Greater nematode enrichment index in the high frequency mulching indicated more carbon flow from mulch into the soil micro-foodweb, whereas low frequency mulching tended to develop a relatively stable soil micro-foodweb. We conclude that trophic interactions regulate the binary coupling between bacteria and bacterivores with high frequency mulching and between fungi and fungivores with low frequency mulching. Consequently, the structure and activity of decomposition pathways in these soil micro-foodwebs are determined by the bottom-up effect of stover mulching.

### 1. Introduction

In many of the world's agricultural systems, exogenous organic materials play major roles in the maintenance of soil structure and providing nutrients for crop production (Pittelkow et al., 2015). Mismanagement of organic resources can have disastrous impacts on soil quality and productivity (Coleman et al., 2002; Poirier et al., 2014). Stover mulching is an important agricultural management practice for providing additional carbon and nutrients, channeled through decomposition pathways, to the soil micro-foodweb (Zhang et al., 2015b; Maarastawi et al., 2019). Soil microorganisms and nematodes are both facilitators and regulators of the decomposition pathway (Wardle, 1995; Neher, 2001; van den Hoogen et al., 2019). Bacteria and bacterivorous

nematodes participate in the bacterial channel, whereas fungi and fungivorous nematodes participate in the fungal channel (Thakur and Geisen, 2019). Bacterial and fungal energy channels are the main decomposition pathways in the soil; they differ in the substrates that they exploit and the rates at which they make minerals and nutrients available (Hunt et al., 1987; de Ruiter et al., 1993; Bardgett and Wardle, 2010). The complexity of the exploited substrates and the characteristics of the participating organisms, decomposition channels mediated by bacteria and fungi may be considered fast and slow with regard to rates of mineralization and nutrient turnover (Coleman et al., 1983; Moore and Hunt, 1988; de Vries and Caruso, 2016; Fabian et al., 2017). The channels also differ in the physical environment that they generate due to their impact on soil porosity and aggregate stability (Chivenge et al.,

\* Corresponding author. Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, 110016, China.

\*\* Corresponding author. School of Geographical Sciences, Northeast Normal University, Changchun, 130024, China.

E-mail addresses: [zxk@iae.ac.cn](mailto:zxk@iae.ac.cn) (X. Zhang), [wuzf@nenu.edu.cn](mailto:wuzf@nenu.edu.cn) (Z. Wu).

<sup>1</sup> These authors contributed equally to this work.

2007; Fabian et al., 2017). In comparison to bacterial decomposition, fungal decomposition generates more protected and stable carbon in a more structured soil (Six et al., 2006). Consequently, decomposition pathways play key roles in nutrient availability and soil organic carbon sequestration (Sul et al., 2013; Danger et al., 2016; Thakur and Geisen, 2019), which makes them important determinants of soil quality and of the productivity and sustainability of soil ecosystems (Filsler et al., 2016; Liu et al., 2016).

Exogenous inputs of organic materials can be designed to provide sufficient readily available and refractory nutrient resources for agricultural crop production (Fig. 1 A). Readily-available nutrient resources are most likely to be exploited by bacteria, which produce a rapid nutrient turnover within the soil foodweb. Alternatively, more recalcitrant nutrient sources are generally exploited by fungal decomposers with lower rates of metabolic nutrient demand and slower turnover (Danger et al., 2016), which amplifies soil organic carbon (SOC) accumulation (Fig. 1 B) (Six et al., 2006; de Vries et al., 2011). In various studies, stover mulching amounts and frequencies have influenced the quantity and quality of organic resources for primary decomposers and determined the composition and activity of the soil biota communities (Bossuyt et al., 2001; Kuzyakov, 2002; Zhou et al., 2018; Maarastawi et al., 2019). Wang et al. (2020) recently pointed out that the frequency of crop residue on the soil surface after harvest significantly influenced fungal community composition but had little effect on the bacteria ones in a no-tillage system. Also, Zhang et al., 2015 found that appropriate amount of straw mulch can increase bacterial quantity, whereas excessive mulching (15000 kg ha<sup>-1</sup>) has a negative effect on microbial communities in a field experiment. We therefore speculate that the effects of stover mulching will differ with the amount and frequency of material applied. However, few studies have attempted to explore the mechanistic responses of the soil foodweb to such differences in resource management and the current study is a contribution to filling that knowledge gap.

The function of decomposition pathways within the soil micro-foodweb such as resource-transfer between bacteria, fungi and microbivorous nematodes are extremely important for the transformation and cycling of SOC and for the quality, productivity and sustainability of soil ecosystems (Thakur and Geisen, 2019). Soil microorganisms are the primary players in nutrient cycling, and their activity and biomass are greatly affected by the resources available to them (bottom-up effects)

and to the abundance and diversity of organisms at higher trophic levels in the soil food web (top-down effects) (de Vries et al., 2013; Li et al., 2019). Free-living soil nematodes as major consumers in the soil microbiome feed on bacteria and fungi (Neher, 2010; Geisen et al., 2018). Bacterivore nematodes have been shown to enhance the turnover rates of soil bacterial communities, especially in copiotrophic environments where resources for bacteria are abundant (Jiang et al., 2017). By contrast, oligotrophic environments favor the growth of fungal communities with potential benefits to fungivorous nematodes (Thakur and Geisen, 2019). Therefore, the bottom-up effects from the stover mulching may regulate the trophic cascades between microbial communities and soil nematode assemblages (Moore and Hunt, 1988; Bardgett and Wardle, 2010; Sánchez-Moreno et al., 2011). A deeper understanding of how the frequency and abundance of exogenous resource applications influence the trophic cascades and the nature and activity of the decomposition pathway in the soil micro-foodweb is needed.

Therefore, we conducted an experiment with different frequencies and abundances of maize stover mulching applications in a 10-year no-tillage production system to explore the effects of stover mulching on the decomposition pathway within soil micro-foodweb. We hypothesized that the amount and frequency of stover applications would affect the abundance and connections between microbial and nematode communities, and consequently the dominant decomposition pathway. We anticipated that different channels within decomposition pathways would be activated by the amount and frequency that the organic resource (stover mulch) entered the no-tillage system.

## 2. Materials and methods

### 2.1. Study site

The no-tillage system was established at the Lishu Conservation Tillage Research and Development Station of the Chinese Academy of Sciences (43°19'N, 124°14'E), Jilin Province, Northeast China. Prior to the no-tillage systems, the site was continuously cropped with maize (*Zea mays* L.) using conventional tillage practices. Application of exogenous materials and sampling for the current study commenced in 2007. The experimental site has a temperate subhumid continental monsoon climate. The mean annual temperature in the area is 6.9 °C, and the

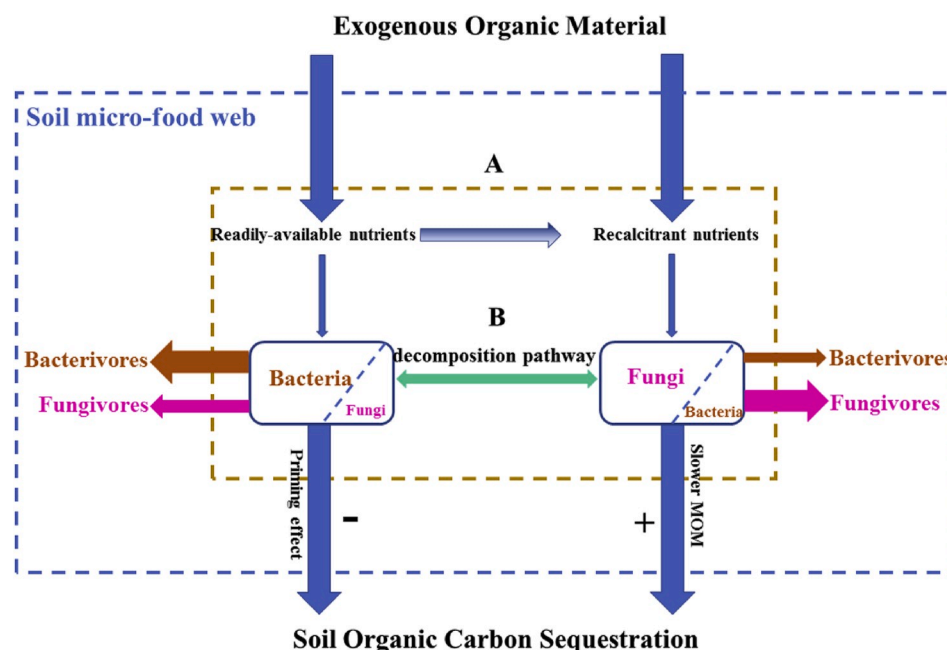


Fig. 1. Conceptual scheme of soil micro-foodweb response to the different forms' exogenous organic materials. MOM, microbially derived organic matter.

mean annual precipitation is 614 mm. The soil type is mollisol (IUSS working group WRB, 2007).

## 2.2. Experimental design and soil sampling

In the no-tillage system, 30-cm-high stubble was left after harvest and the remaining plant parts were crushed and applied to the soil surface at rates appropriate for the experimental treatments. The maximum application amount was designated 100% stover mulch and consisted of about 7500 kg ha<sup>-1</sup>. The four application treatments were 33% stover mulching every year (designated high frequency, low amount, HF-1/3), 67% stover mulching every year (high frequency, high amount, HF-2/3), 100% stover mulching in the first year only of each three-year cycle (low frequency, low amount, LF-1/3) and 100% stover mulching in the first two years of each three-year cycle (low frequency, high amount, LF-2/3) (Table A1). Between 2008 and 2016, there were three three-year stover mulching cycles. Therefore, we consider that there was an approximately equal amount of stover mulch applied in the HF-1/3 and LF-1/3 treatments in each three-year cycle and similarly in the HF-2/3 and LF-2/3 treatments. The experiment was a completely randomized block design with four replicates. The size of each plot was 261 m<sup>2</sup> (8.7 m × 30 m). Human disturbances in the no-tillage system was minimal except for sowing with a no-tillage machine (2BMZF-4). Mineral fertilizer (N–P<sub>2</sub>O<sub>5</sub>–K<sub>2</sub>O, 26%–12%–12%) was applied at sowing each year at a rate of 900 kg ha<sup>-1</sup>.

Soil samples were collected at a depth of 0–20 cm in June, August and October of 2016 (the end year of the third three-year cycle), which corresponded, respectively, to the seedling, heading and ripening stages of the maize crop. In total, there were 48 samples (4 treatments × 4 replicates × 3 growth stages). In each plot, eight soil cores were randomly collected with a 2.5 cm diameter auger and then uniformly mixed as a composite sample. The fresh samples were stored individually in plastic bags and kept at 4 °C in a refrigerator until further analysis.

A subsample of the fresh soil was used to extract soil nematodes and to analyze ammonium (NH<sub>4</sub><sup>+</sup>-N) and nitrate (NO<sub>3</sub><sup>-</sup>-N) nitrogen. A total of 20 g fresh soil was taken from each sample, plant roots were removed, and the soil was then frozen (–20 °C) and freeze-dried for extraction of microbial phospholipid fatty acids (PLFAs). Another subsample of the soil was air-dried and used for the analysis of SOC and total nitrogen (TN).

## 2.3. Analysis of soil physicochemical properties

Soil available nitrogen (NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N) was extracted with 2 mol L<sup>-1</sup> KCl. The filtrates were collected and determined using a flow analyzer (FIAstar 5000 Analyzer, Foss Tecator, Hillerød, Denmark). Soil organic carbon was determined by wet oxidation (K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub>) (Walkley and Black, 1934). Total soil nitrogen was analyzed using an automatic elemental analyzer (Elementar Analyzer System Vario MACRO cube, Germany). The chloroform fumigation-extraction method was used to determine microbial biomass carbon (MBC), and the MBC was calculated as the difference between fumigated and unfumigated samples (Jenkinson et al., 2004).

## 2.4. Analysis of phospholipid fatty acids (PLFAs)

The community composition of soil microorganisms was characterized using phospholipid fatty acid analysis (PLFAs) according to Bossio et al. (1998). Lipids were extracted from 6 g of freeze-dried soil using buffer that consisted of a mixture of citrate-chloroform-methanol (0.8:1:2). Solid-phase extraction columns (Supelco Inc., Bellefonte, PA, USA) were used to separate polar lipids from neutral lipids and glycolipids. The produced fatty acid methyl esters were extracted in hexane and dried under N<sub>2</sub>. Samples were analyzed with an Agilent 6850 series Gas Chromatograph equipped with MIDI peak identification software

(Version 4.5, MIDI Inc., Newark, DE).

The following biomarkers were used: total PLFAs (from C14 to C20), gram-positive (G<sup>+</sup>) bacteria PLFAs (i14:0, i15:0, i15:1ω6c, a15:0, i16:0, i17:0, a17:0, i18:0, a19:0), gram-negative (G<sup>-</sup>) bacteria PLFAs (16:1ω7c, 16:1ω9c, 17:1ω8c, cy17:0ω7c, 18:1ω5c, 18:1ω6c, 18:1ω7c, cy19:0ω7c), fungal PLFAs (18:2ω6c), arbuscular mycorrhizal fungi PLFAs (AMF, 16:1ω5c), and actinomycete PLFAs (10MeC16:0, 10MeC17:0, 10MeC17:1ω7c, 10MeC18:0, 10MeC18:1ω7c). The sum of the G<sup>+</sup>, G<sup>-</sup> and non-specific bacteria was used as total bacteria, and the sum of fungal PLFAs and AMF was used as total fungi (Briar et al., 2011; Dempsey et al., 2013; Zhang et al., 2013; Cui et al., 2018).

## 2.5. Soil nematode extraction and identification

A total of 100 g of fresh soil was used to extract soil nematodes using a modified cotton-wool filter method (Liang et al., 2009). Nematode abundance was expressed as individuals per 100 g dry soil and at least 100 nematodes from each sample were identified to genus level according to Bongers (1994) and Li et al. (2017). If the total number of nematodes was less than 100 individuals in a sample, all nematodes were identified. The nematodes were divided into the following four trophic groups by feeding habits and esophagus characteristics: bacterivores, fungivores, plant parasites and omnivores-predators (Yeates, 2003). The individual fresh weight of nematodes was estimated according to <http://Nemaplex.ucdavis.edu>. Nematode metabolic footprints values were calculated using the NINJA application (Sieriebriennikov et al., 2014).

## 2.6. Statistical analysis

Data were analyzed using SPSS19 statistical software (SPSS Inc., Chicago, IL, USA). Differences at the *P* < 0.05 level were considered statistically significant. The effect of maize growth stage, stover mulching amount and frequency on soil properties, microbial and nematode biomass were determined using three-way ANOVA. A Tukey's HSD test was used if the main effect was significant. The mantel test was used to analyze the effect of MBC, NO<sub>3</sub><sup>-</sup>-N, NH<sub>4</sub><sup>+</sup>-N and other soil characteristics on microbial and nematode community composition. Principal component analysis (PCA) was performed to explore soil biotic community composition based on the relative percentage of PLFAs and nematodes using CANOCO software, version 5.0 (ter Braak, 1988).

In order to determine the effects of the stover mulching amount and frequency on soil micro-foodweb associations, Spearman's rank correlation matrix based on biomass data of microorganisms and nematodes were depicted through network analysis using Cytoscape software, version 3.7.1 (Shannon et al., 2003; Morriën et al., 2017).

We used the organism biomass data to construct a piecewise Structural Equation Model (piecewise SEM) to explore the decomposition pathway within soil micro-foodweb under high or low frequency mulching. The piecewise SEM was based on our predictions and literature review (Shipley, 2000; Lefcheck, 2016) and the interactions among different trophic levels in the soil foodweb were assessed by Fisher C, *P*-value and AIC. Piecewise SEM was performed under the piecewise SEM package (Lefcheck, 2016; Liu et al., 2020).

## 3. Results

### 3.1. Soil physicochemical properties

Three-way ANOVA revealed that the frequency effects of stover mulching on SOC was significant (*P* < 0.05), and the effects of growth stage on SOC, total nitrogen (TN) and available nitrogen (NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N) were significant (*P* < 0.05) (Table 1). At the same mulching amount, the value of SOC was higher in the low frequency (LF) than in the high frequency (HF) treatment (*P* < 0.05). The highest values of SOC, TN and NO<sub>3</sub><sup>-</sup>-N were at the maize seedling stage (*P* < 0.05).

**Table 1**  
Soil physicochemical properties in different stover mulching treatments (means  $\pm$  SE).

Stages	Treatments	SOC (g kg <sup>-1</sup> )	TN (g kg <sup>-1</sup> )	NO <sub>3</sub> <sup>-</sup> -N (mg kg <sup>-1</sup> )	NH <sub>4</sub> <sup>+</sup> -N (mg kg <sup>-1</sup> )
Seedling	HF-1/3	11.03 $\pm$ 0.74	1.65 $\pm$ 0.05	24.66 $\pm$ 2.45	5.37 $\pm$ 1.55
	LF-1/3	11.93 $\pm$ 0.76	1.63 $\pm$ 0.05	30.51 $\pm$ 1.51	2.49 $\pm$ 0.35
	HF-2/3	10.49 $\pm$ 0.08	1.68 $\pm$ 0.03	45.39 $\pm$ 11.51	3.01 $\pm$ 0.55
	LF-2/3	12.19 $\pm$ 0.44	1.68 $\pm$ 0.08	29.23 $\pm$ 5.60	4.29 $\pm$ 1.83
Heading	HF-1/3	9.01 $\pm$ 0.17	1.40 $\pm$ 0.04	13.32 $\pm$ 5.49	3.48 $\pm$ 0.74
	LF-1/3	10.03 $\pm$ 0.21	1.43 $\pm$ 0.03	18.99 $\pm$ 4.03	5.88 $\pm$ 1.04
	HF-2/3	9.13 $\pm$ 0.26	1.45 $\pm$ 0.09	9.59 $\pm$ 1.28	5.69 $\pm$ 1.17
	LF-2/3	10.67 $\pm$ 0.42	1.43 $\pm$ 0.03	23.89 $\pm$ 7.93	4.95 $\pm$ 0.54
Ripening	HF-1/3	10.09 $\pm$ 0.76	1.55 $\pm$ 0.03a	11.43 $\pm$ 0.74	4.27 $\pm$ 1.88
	LF-1/3	11.16 $\pm$ 0.47	1.65 $\pm$ 0.03a	11.22 $\pm$ 1.76	1.36 $\pm$ 0.37
	HF-2/3	10.04 $\pm$ 0.51	1.50 $\pm$ 0.04 ab	7.79 $\pm$ 1.57	3.86 $\pm$ 0.85
	LF-2/3	11.29 $\pm$ 0.22	1.38 $\pm$ 0.05b	7.19 $\pm$ 1.31	0.99 $\pm$ 0.09
F values of ANOVA					
Frequency (F)		20.28**	0.09	0.27	2.34
Amount (A)		0.12	1.39	0.58	0.01
Stage(S)		12.66**	22.58**	22.98**	4.89*
F $\times$ A		0.79	2.17	0.65	0.08
F $\times$ S		0.31	5.24*	1.97	0.28
A $\times$ S		0.03	0.22	2.48	3.01
F $\times$ A $\times$ S		0.11	1.71	2.56	2.89

SOC, soil organic carbon; TN, total nitrogen; NO<sub>3</sub><sup>-</sup>-N, nitrate nitrogen; NH<sub>4</sub><sup>+</sup>-N, ammonium nitrogen; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ .

### 3.2. Soil microbial communities

Soil total microbial PLFAs were significantly influenced by the plant growth stage ( $P < 0.01$ ) and mulching frequency ( $P < 0.05$ ) (Table 2), the highest value occurred at the heading stage (Fig. 2). The effect of the mulch amount on total PLFAs was not significant (Table 2). At the same stover mulching amount, total PLFAs were higher in high frequency applications than in low frequency treatments at all three growth stages of maize, especially for HF-2/3 and LF-2/3 at the heading stage ( $P < 0.05$ ). There was a similar trend in total bacterial PLFAs but the opposite trend in fungal PLFAs which were higher in low frequency treatments (Fig. 2). The principal component analysis (PCA) of microbial communities distinguished high frequency from low frequency treatments along the first axis (PC1), with bacteria being dominant in high frequency and fungi in low frequency treatments (Fig. 3a). Mantel test analysis suggested that the variations in microbial community

**Table 2**  
Three-way ANOVA on the effect of stover mulching frequency, amount and maize growth stage on microbial PLFAs and nematode biomass.

F values of ANOVA	Total PLFAs (n mol g <sup>-1</sup> )	Bacterial PLFAs (n mol g <sup>-1</sup> )	Fungal PLFAs (n mol g <sup>-1</sup> )	Nematode Biomass (μg 100g <sup>-1</sup> dry soil)	BF Biomass (μg 100g <sup>-1</sup> dry soil)	FF Biomass (μg 100g <sup>-1</sup> dry soil)
Frequency (F)	7.32*	9.82**	10.89**	29.36**	6.88*	27.39**
Amount (A)	0.53	0.61	0.50	0.97	0.11	0.21
Stage(S)	14.59**	13.50**	58.46**	54.78**	6.31*	23.87**
F $\times$ A	0.56	0.61	1.28	0.26	0.38	0.05
F $\times$ S	1.82	2.20	2.17	8.42**	3.21*	8.21**
A $\times$ S	1.67	1.84	1.05	1.21	0.39	0.17
F $\times$ A $\times$ S	0.72	0.85	0.48	1.23	0.13	3.19

Significant: \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ . BF, bacterivores; FF, fungivores.

composition were significantly correlated with MBC, NO<sub>3</sub><sup>-</sup>-N and SOC ( $P < 0.05$ ) (Table 3).

### 3.3. Soil nematode communities

Total nematode biomass was higher at the heading stage of maize than at other stages in all treatments ( $P < 0.05$ ) (Fig. 2). Three-way ANOVA showed that the mulching frequency, growth stage and their interactions have a significant effect on the bacterivores, fungivores and total nematode biomass ( $P < 0.01$ ). However, the mulching amount did not significantly affect nematode biomass (Table 2). The bacterivores, fungivores and total nematode relative abundance (Table A2) and biomass was higher in low frequency than in high frequency treatments with the same mulching amount at seedling (LF1/3 > HF1/3) and heading (LF1/3 > HF1/3 and LF2/3 > HF2/3) stages ( $P < 0.05$ ) (Fig. 4). High and low frequency treatments were separated in the principal component analysis (PCA) of nematode communities along the first axis (PC1), with bacterivores being dominant in high frequency treatments and fungivores prevailing in low frequency applications (Fig. 3b). Changes in nematode community composition were significantly correlated with MBC, TN and SOC ( $P < 0.01$ ) (Table 3).

The total nematode metabolic footprint, the total area of the enrichment and structure footprints, was significantly higher in LF 1/3 treatment than that in HF-1/3 and HF-2/3 treatments ( $P < 0.05$ ) (Fig. 4). Regardless of the amount of stover, a higher structure index of the nematode assemblage occurred in the low frequency and a higher enrichment index in the high frequency treatments ( $P < 0.05$ ).

### 3.4. Soil micro-foodweb relationships

Network analysis showed that the LF-1/3 and LF-2/3 treatments showed a strongly positive correlation among fungi, fungivores and predator-omnivores based on the biomass data with Spearman's rank correlation >0.9. However, HF-1/3 and HF-2/3 treatments showed a significantly positive correlation among bacteria, bacterivores and predator-omnivores. Moreover, an obviously positive correlation between plant-parasites and predator-omnivores was also found in HF-1/3, HF-2/3 and LF-2/3 treatments (Fig. 5).

Due to the non-significance of differences in nematode and microbial communities in treatments with different amounts of stover mulching, we constructed the piecewise SEM by only considering frequency of mulch applications (both HF-1/3 and HF-2/3 as high frequency treatments, and LF-1/3 and LF-2/3 as low frequency treatments). The piecewise SEM provided a good fit to the data for high frequency mulching treatments (Fisher C = 5.42;  $P$ -value = 0.49; AIC = 43.43) (Fig. 6a) and low frequency mulching treatments (Fisher C = 10.78;  $P$ -value = 0.09; AIC = 48.78) (Fig. 6b). Specifically, compared with high frequency mulching, low one increased the correlation among fungi, fungivores and predator-omnivores, and contributed to a higher SOC.

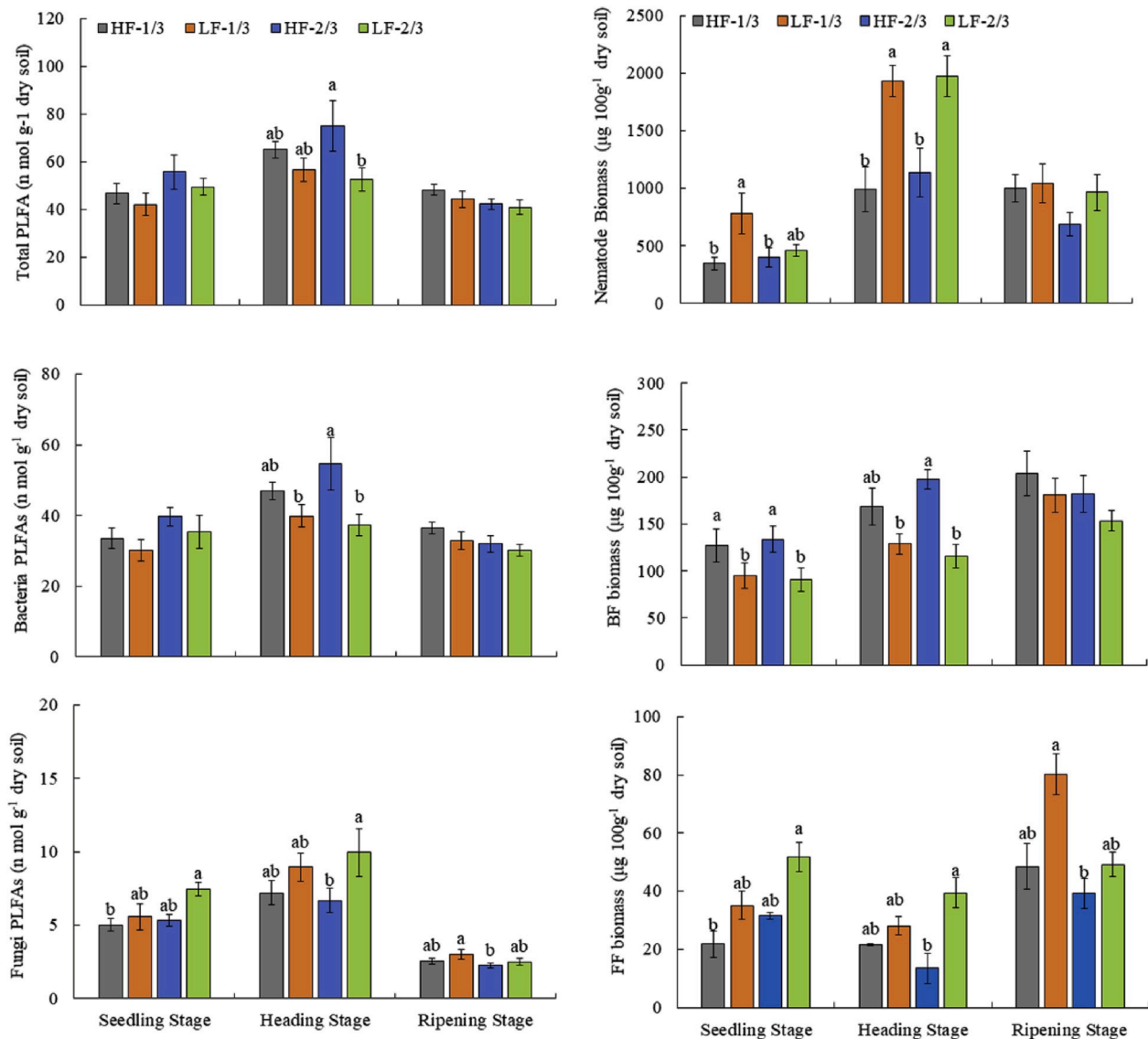


Fig. 2. Total, bacterial and fungal PLFAs biomass, and total, bacterivorous and fungivorous nematode biomass in different stover mulching treatments at the three growth stages of maize. Different lower-case letters represent significant differences at  $P < 0.05$  among treatments at the same growth stage as determined by a Tukey's post-hoc test. HF-1/3: 33% stover mulching every year; HF-2/3: 67% stover mulching every year; LF-1/3: 100% stover mulching in the first year only of each three-year cycle; LF-2/3: 100% stover mulching in the first two years of each three-year cycle. BF, bacterivores; FF, fungivores.

## 4. Discussion

### 4.1. Effects of stover mulching amount and frequency on microorganism and nematode communities

Contrary to our hypothesis, the amount of mulch did not affect soil microbial and nematode community composition. In the previous studies, microbial and nematode abundance and biomass were greater with increasing amounts of mulch from 3000 to 12000  $\text{kg ha}^{-1}$  (Zhang et al., 2012; Hua et al., 2014; Zhang et al., 2015b), which seems to be the intuitive expectation. However, in our experiment, the difference between stover mulch amounts were 33% and 67%, i.e. 2475 and 4950  $\text{kg ha}^{-1}$ , and the relatively smaller differences in mulching amount were not sufficient to influence soil biota communities. Zhang et al. (2016) also proposed that there is a threshold (over 5000  $\text{kg ha}^{-1}$ ) for crop residue return to increase soil microbial biomass. In addition, another possible reason is that the significant effect of stover mulching amount on soil microbe and nematode communities may be weakened after 10-year period. However, as expected, the frequency of mulching with

the same mulching amount in a three-year cycle had a greater impact on microbial and nematode communities. The frequency of mulching affects not only the quantity but the quality of organic input, and then soil properties and biota communities (Cesarano et al., 2017; Zheng and Marschner, 2017). In our study, the low frequency (LF) treatments had a higher fungal PLFAs than that in the high frequency (HF) ones with the same mulching amount. Fungal decomposers with lower metabolic demand (Six et al., 2006; Zheng and Marschner, 2017; Kou et al., 2018) and wider enzymatic capabilities than bacteria can mineralize recalcitrant substrates (high C/N) (Bossuyt et al., 2001; Gusewell and Gessner, 2009; de Vries et al., 2012; Fabian et al., 2017). High frequency stover addition maintained a continuous supply of easily available organic substances (Elmajdoub and Marschner, 2015), which is beneficial for the fast-growing microorganisms such as bacteria, and had a positive priming effect to accelerate the decomposition of SOC (Kuzyakov, 2010; Huo et al., 2017). The principal component analysis showed that bacteria were dominant in high frequency treatment, which suggested that the bacterial community, characterized by fast turnover rates, exploits and metabolizes most of the readily-available organic substances

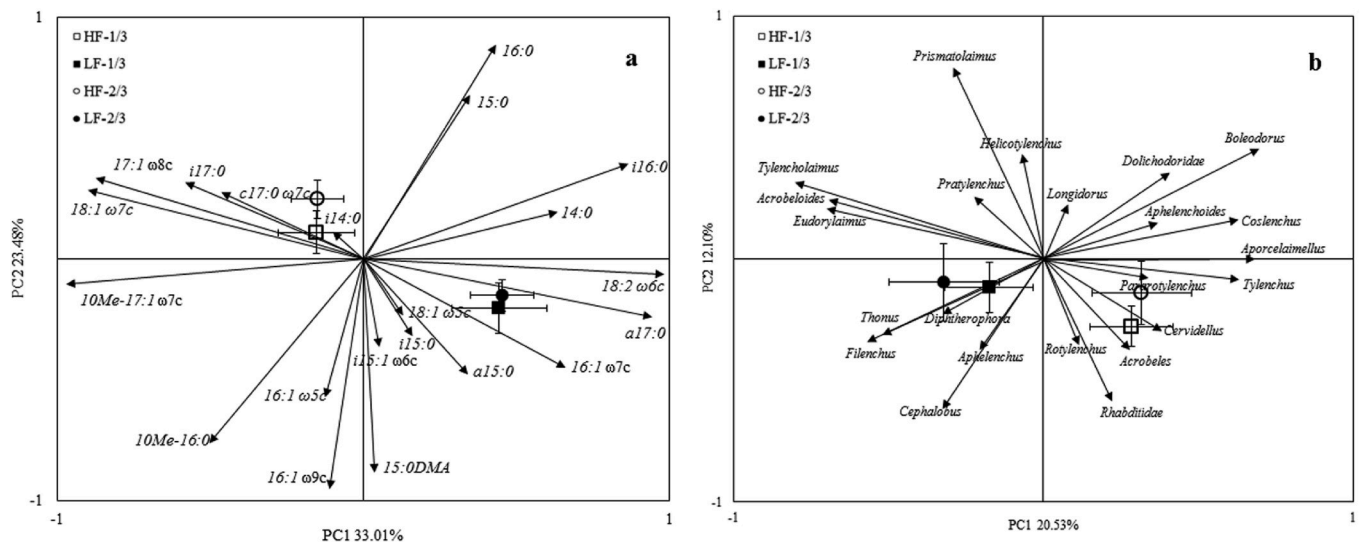


Fig. 3. Principle components analysis (PCA) of soil microbial (a) and nematode (b) communities in the different stover mulching treatments.

Table 3

Mantel-test of environmental variables on microbial and nematode communities.

Environmental variable	Microbial community		Nematode community	
	r	P	r	P
MBC	0.25	<0.01	0.16	<0.01
NO <sub>3</sub> <sup>-</sup> -N	0.27	<0.01	0.06	0.19
NH <sub>4</sub> <sup>+</sup> -N	0.06	0.19	0.06	0.15
TN	0.15	<0.05	0.14	<0.01
SOC	0.21	<0.01	0.19	<0.01

MBC, microbial biomass carbon; NO<sub>3</sub><sup>-</sup>-N, nitrate nitrogen; NH<sub>4</sub><sup>+</sup>-N, ammonium nitrogen; TN, total nitrogen; SOC, soil organic carbon.

(Paterson et al., 2007; Moore-Kucera and Dick, 2008). Thus, high frequency mulching frequently provided fresh organic substrates which stimulated bacterial growth and, at the same time, decreased SOC sequestration through the priming effect (Kuzaykov, 2010). In that case, and perhaps counter-intuitively, frequent stover mulching may accelerate SOC mineralization and have negative impacts on soil C sequestration (Fontaine et al., 2004; Wang et al., 2011; Shahbaz et al., 2017).

Changes in the quantity and quality of stover induced by mulching frequency have been reported to stimulate soil microbial communities dominated by bacteria or fungi, and indirectly influenced microbivorous nematodes, their main predators, through bottom-up effects (Dupont et al., 2009; Richter et al., 2019; Thakur and Geisen, 2019). Our study also proved that the bacteria or fungi predator groups increased when soil bacteria (or fungi) communities were enhanced by resource application. Moreover, a higher fungivores and total nematode biomass was observed in low frequency mulching than in high ones, which suggested that low frequency mulching with less soil disturbance provided stable survival conditions for nematodes, especially for K-strategist nematodes with bigger size, and then the corresponding total nematode biomass increased (Ferris, 2010; Sul et al., 2013). Additionally, we calculated the nematode metabolic footprint based on nematode biomass, as the index of nematode carbon metabolism, indicates the response ability of the nematode communities to resources (Ferris, 2010). A greater nematode metabolic footprint was also shown in low frequency treatments than in high ones, which indicated that a larger quantity of carbon flow went through the soil foodweb decomposition pathway (Zhang et al., 2015a; Zhang et al., 2017), and eventually made a contribution to sequestration of SOC.

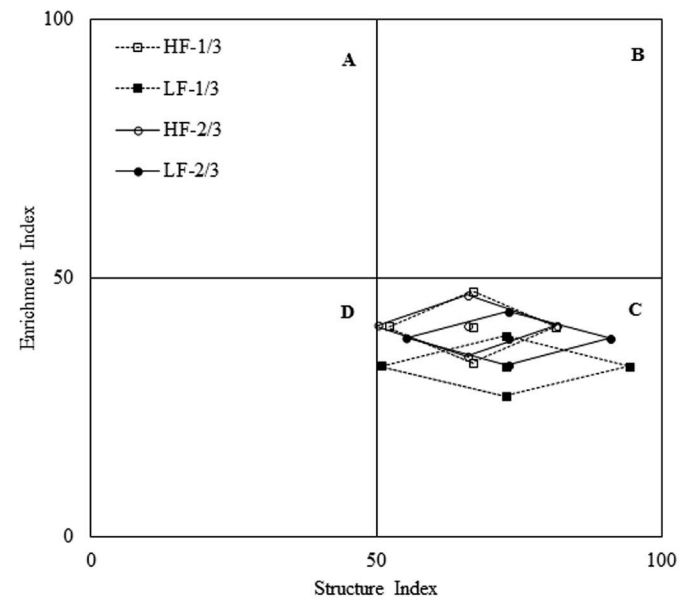
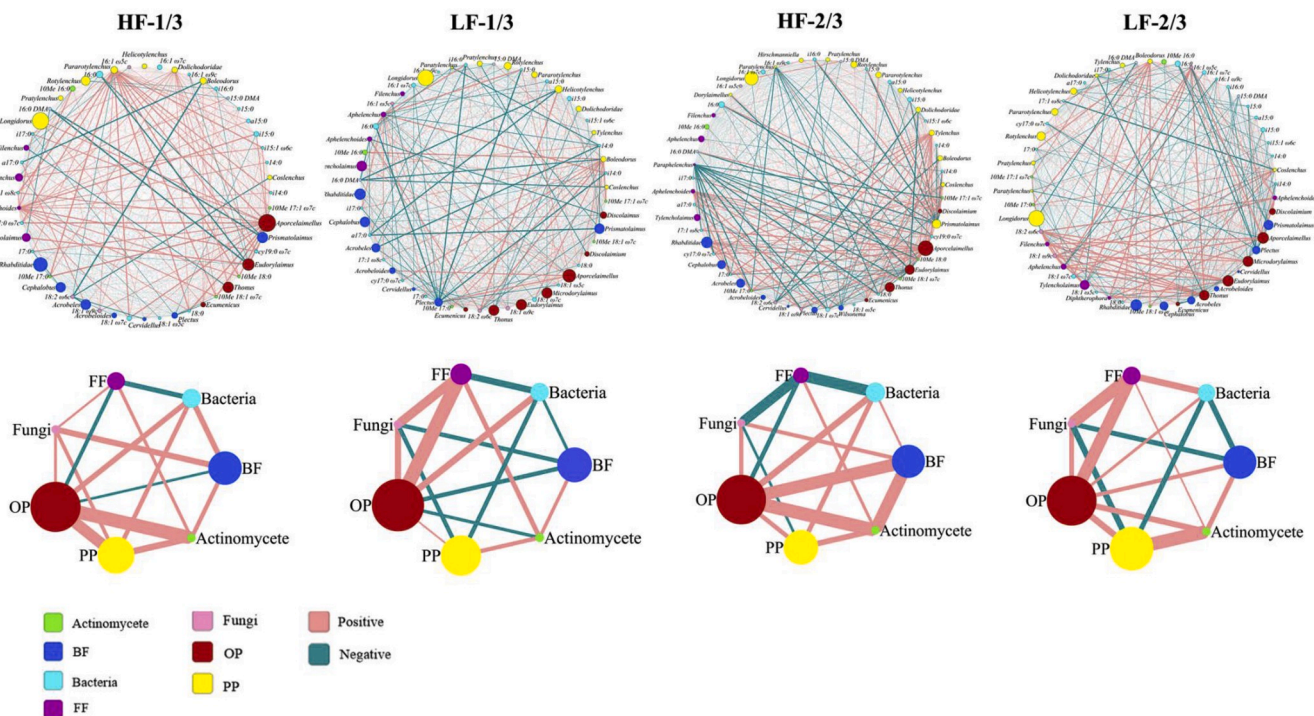


Fig. 4. Functional metabolic footprints of nematode communities under different stover mulching treatments. The vertical axis represents the enrichment footprint and the horizontal axis represents the structural footprint. The x-axis coordinates of the metabolic footprints are calculated as  $SI-0.5F_s/k$  and  $SI+0.5F_s/k$ , and the y-axis coordinates as  $EI-0.5F_e/k$  and  $EI+0.5F_e/k$ . The functional metabolic footprint is depicted by sequentially joining points:  $SI-0.5F_s/k$ ,  $EI$ ;  $SI$ ,  $EI+0.5F_e/k$ ;  $SI+0.5F_s/k$ ,  $EI$ ;  $SI$ ,  $EI-0.5F_e/k$ ; and  $SI$ ,  $EI$  (central point).  $F_s$  (structure footprint) is the sum of the standardized C utilization from the structural indicator taxa and  $F_e$  (enrichment footprint) from the enrichment indicator taxa (Ferris, 2010), and the k value is 8.

#### 4.2. Effect of stover mulching frequencies on decomposition pathways within soil micro-foodweb

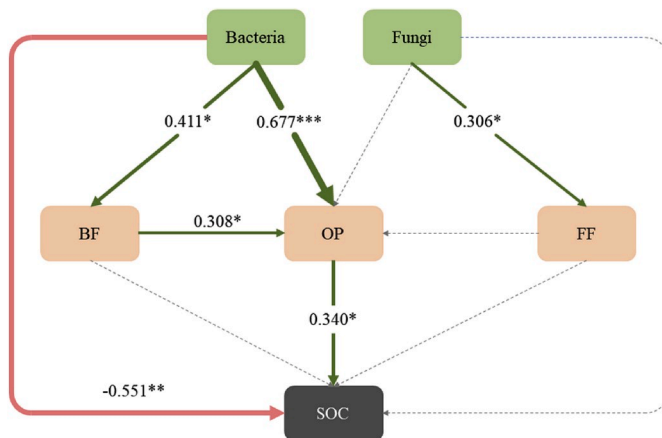
Piecewise SEM showed that low frequency mulching has a positive correlation among fungi, fungivores and predator-omnivores, but not between bacteria and bacterivores, which might be inferred that a stronger fungal decomposition pathway in low frequency than in high frequency mulching. Bacteria and fungi have distinct metabolic capabilities to break down substrates with different qualities. The shift of decomposition pathway within the soil foodweb plays an important role



**Fig. 5.** Network visualization of the interaction strengths within soil micro-foodweb. The size of the circles represents the amount of biomass, and the different filled colors represent different groups. BF, bacterivores; FF, fungivores; PP, plant parasites; OP, predators-omnivores. HF-1/3: 33% stover mulching every year; HF-2/3: 67% stover mulching every year; LF-1/3: 100% stover mulching in the first year only of each three-year cycle; LF-2/3: 100% stover mulching in the first two years of each three-year cycle.

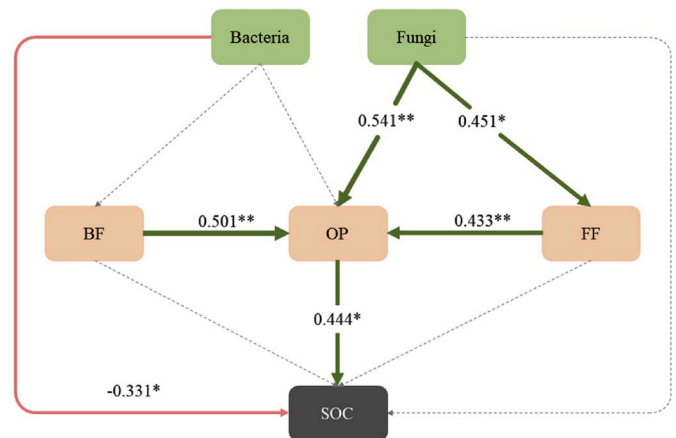
**a High Frequency Mulching**

Model: Fisher C = 5.42, AIC = 43.43, P-value = 0.49



**b Low Frequency Mulching**

Model: Fisher C = 10.78, AIC = 48.78, P-value = 0.09



**Fig. 6.** Piecewise structural equation modeling of decomposition pathway within soil micro-foodweb in high frequency (a) (Fisher C = 5.42; P-value = 0.49; AIC = 43.43) and low frequency (b) (Fisher C = 10.78; P-value = 0.09; AIC = 48.78) treatments. The width of arrows is proportional to the strength of path coefficients (standardized correlation coefficients). Continuous green and red arrows indicate positive and negative relationships, respectively, whereas dashed black arrows indicate no significant relationship. BF, bacterivores; FF, fungivores; PP, plant parasites; OP, predator-omnivores.

in determining soil carbon loss rates, in which the bacterial decomposition pathway favors a rapid nutrient turnover, but does not benefit soil carbon and nitrogen sequestration compared to the fungal decomposition pathway (de Vries et al., 2011). The quality of easily-available and refractory substrates played a leading role in influencing the shifts between bacteria and fungi decomposition pathways of soil foodweb and thereby carbon turnover (Fabian et al., 2017). In our study, high frequency mulching treatments with new stover input every year provided

enough easily-available carbon resource, which made bacterial decomposition pathway dominant in soil food web. However, low frequency mulching applied once in the first or first two years of the three-year cycle, substrates became refractory with the development of decomposition process and might more utilizable for the fungi (Bossuyt et al., 2001). Hence, with the same mulching amount in a three-year cycle, low frequency organic input might fuel a community succession trend from bacteria to fungi (Moore-Kucera and Dick, 2008; Don et al., 2017).

Furthermore, we observed that low frequency treatments with a relative strong fungal decomposition pathway increase the SOC, which has been implied in previous studies that fungi have a bigger protected carbon pool and retain a greater proportion of carbon than bacteria, and this can improve the physical environment for carbon stabilization and enhance the accumulation of microbially derived organic matter (Six et al., 2006; Danger et al., 2016).

Carbon and nitrogen mineralization are often accelerated due to the presence of grazers (Six et al., 2006; Ferris et al., 2012). Similarly, our results suggest that the decomposition pathway in our study continued to be driven by the bottom-up effects of bacteria and fungi on microbivorous nematodes. Variation in bacterivores and fungivores was fueled by the nature of resource input and by microbial communities, and depend on their life history characteristics (Ferris and Matute, 2003). With the same amount of mulch, we found a strong positive correlation between fungi, fungivores and predator-omnivores in low frequency and a strong positive correlation between bacteria, bacterivores and predator-omnivores in high ones (Fig. 5), which powerfully supported our views that low and high frequency enhanced fungal and bacterial decomposition pathways, respectively (Rooney et al., 2006; Andrés et al., 2016; Guan et al., 2018). It must be noted that bacterial and fungal decomposition pathways within the soil foodweb are not distinctly separated, but that both pathways operate simultaneously, and that different carbon transfer and utilization processes occur between them (Ruess and Ferris, 2004; Cui et al., 2018). Organic carbon input with different amounts and frequencies regulated the microbial and nematode community composition and the corresponding decomposition pathway differently.

Certainly, there are many objectives for, and benefits of mulching. Besides SOC sequestration, they generally improve weed suppression, soil moisture retention, soil texture improvement and soil health. In this case, we demonstrated that considering the frequency of applications is necessary to enhance the soil biological activities underlying SOC accumulation in the specific cropping system, those were the residues of the maize crop. However, the application of such studies must consider the availability of potential mulch sources in a given biogeographic region. They include sorghum, wheat, pea, etc., which differ in C/N ratios have been shown to have quite different effects on soil foodweb structure and function (Ferris and Matute, 2003; Dupont et al., 2009). In addition to amount and frequency of application, such exogenous materials, alone or in combination, could provide an important set of input variables in future experiments with the same or different overall objectives as the current study.

## 5. Conclusions

Although organic inputs can alter the abundance of bacteria (and bacterivores) and fungi plus fungivores in soil micro-foodweb decomposition pathways, the frequency of stover mulch was more influential in this regard than the amount of stover mulch. The bacterial decomposition pathway was strengthened by the high frequency mulching while the fungal pathway was favored with the low frequency mulching. Higher fungal biomass with low frequency mulching could lead to more SOC sequestration. The trophic interactions between soil microbial and nematode communities are a main driver for carbon flows in the decomposition pathway. In conclusion, no-tillage systems that receive mulch with varying frequency merit further study to understand the metabolic processes and transformations of carbon that occur in the decomposition pathways of soil micro-foodwebs.

## 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 National Key Research and Development Plan, China (2017YFD0200602), National Natural Science Foundation of China (No. 41771280), National Science and Technology Fundamental Resources Investigation Program of China (No. 2018FY100304) and K.C. Wong Education Foundation (GJTD-2019-10). We also would like to thank Prof. T. Martijn Bezemer (Netherlands Institute of Ecology) and Prof. Joann K. Whalen (Chief Editor) for insightful advice of the manuscript.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2020.107789>.

## References

- Andrés, P., Moore, J.C., Simpson, R.T., Selby, G., Cotrufo, F., Deneff, K., Haddix, M.L., Shaw, E.A., de Tomasel, C.M., Molowny-Horas, R., Wall, D.H., 2016. Soil food web stability in response to grazing in a semi-arid prairie: the importance of soil textural heterogeneity. *Soil Biology and Biochemistry* 97, 131–143.
- Bardgett, R.D., Wardle, D.A., 2010. *Aboveground-belowground Linkages*. Oxford University Press, United Kingdom.
- Bongers, T., 1994. De nematoden van Nederland. In: *Vormgeving en technische realisatie*. Uitgeverij Pirola, Schoorl, Netherlands.
- Bossio, D.A., Scow, K.M., Gunapala, N., Graham, K.J., 1998. Determinants of soil microbial communities: effects of agricultural management, season, and soil type on phospholipid fatty acid profiles. *Microbial Ecology* 36, 1–12.
- Bossuyt, H., Deneff, H., Six, J., Frey, S.D., Merckx, R., Paustian, K., 2001. Influence of microbial populations and residue quality on aggregate stability. *Applied Soil Ecology* 16, 195–208.
- Briar, S.S., Fonte, S.J., Park, I., Six, J., Scow, K., Ferris, H., 2011. The distribution of nematodes and soil microbial communities across soil aggregate fractions and farm management systems. *Soil Biology and Biochemistry* 43, 905–914.
- Cesarano, G., Filippis, F.D., Storia, A.L., Scala, F., Bonanomi, G., 2017. Organic amendment type and application frequency affect crop yields, soil fertility and microbiome composition. *Applied Soil Ecology* 120, 254–264.
- Chivenge, P.P., Murwira, H.K., Giller, K.E., Mapfumo, P., Six, J., 2007. Long-term impact of reduced tillage and residue management on soil carbon stabilization: implications for conservation agriculture on contrasting soils. *Soil and Tillage Research* 94, 328–337.
- Coleman, D.C., Reid, C.P.P., Cole, C.V., 1983. Biological strategies of nutrient cycling in soil systems. *Advances in Ecological Research* 13, 1–51.
- Coleman, D.C., Fu, S.L., Hendrix Jr., P., D., C., 2002. Soil foodwebs in agroecosystems: impacts of herbivory and tillage management. *European Journal of Soil Biology* 38, 0–28.
- Cui, S.Y., Liang, S.W., Zhang, X.K., Li, Y.B., Liang, W.J., Sun, L.J., Wang, J.K., Bezemer, T.M., Li, Q., 2018. Long-term fertilization management affects the C utilization from crop residues by the soil micro-food web. *Plant and Soil* 429, 335–348.
- Danger, M., Gessner, M.O., Bärlocher, F., 2016. Ecological stoichiometry of aquatic fungi: current knowledge and perspectives. *Fungal Ecology* 19, 100–111.
- de Ruiter, P.C., Vanveen, J.A., Moore, J.C., Brussaard, L., Hunt, H.W., 1993. Calculation of nitrogen mineralisation in soil food webs. *Plant and Soil* 157, 263–273.
- de Vries, F.D., Liiri, M.E., Bjørnlund, L., 2012. Land use alters the resistance and resilience of soil food webs to drought. *Nature Climate Change* 2, 276–280.
- de Vries, F.T., Caruso, T., 2016. Eating from the same plate? Revisiting the role of labile carbon inputs in the soil food web. *Soil Biology and Biochemistry* 102, 4–9.
- de Vries, F.T., Van Groenigen, J.W., Hoffland, E., Bloem, J., 2011. Nitrogen losses from two grassland soils with different fungal biomass. *Soil Biology and Biochemistry* 43, 997–1005.
- de Vries, F.T., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjørnlund, L., Jørgensen, H.B., Brady, M.V., Christensen, S., De Ruiter, P.C., d'Hertefeldt, T., Frouz, J., Hedlund, K., Hemerik, L., Gera Hol, W.H., Hotes, S., Mortimer, S.R., Setälä, H., Sgardelis, S.P., Uteseny, K., van der Putten, W.H., Wolters, V., Bardgett, R. D., 2013. Soil food web properties explain ecosystem services across European land use systems. *Proceedings of the National Academy of Sciences of the United States of America* 110, 14296–14301.
- Dempsey, M.A., Fisk, M.C., Yavitt, J.B., Fahey, T.J., Balsler, T.C., 2013. Exotic earthworms alter soil microbial community composition and function. *Soil Biology and Biochemistry* 67, 263–270.
- Don, A., Böhme, I.H., Dohrmann, A.B., Poeplau, C., Tebbe, C.C., 2017. Microbial community composition affects soil organic carbon turnover in mineral soils. *Biology and Fertility of Soils* 53, 1–12.
- Dupont, S.T., Ferris, H., Horn, M.V., 2009. Effects of cover crop quality and quantity on nematode-based soil food webs and nutrient cycling. *Applied Soil Ecology* 41, 157–167.
- Elmajdoub, B., Marschner, P., 2015. Response of microbial activity and biomass to soil salinity when supplied with glucose and cellulose. *Journal of Soil Science and Plant Nutrition* 15, 816–832.



- Fabian, J., Zlatanovic, S., Mutz, M., Premke, K., 2017. Fungal–bacterial dynamics and their contribution to terrigenous carbon turnover in relation to organic matter quality. *The ISME Journal* 11, 415–425.
- Ferris, H., Matute, M.M., 2003. Structural and functional succession in the nematode fauna of a soil food web. *Applied Soil Ecology* 23, 93–110.
- Ferris, H., 2010. Form and function: metabolic footprints of nematodes in the soil food web. *European Journal of Soil Biology* 46, 97–104.
- Ferris, H., Sánchez-Moreno, S., Brennan, E.B., 2012. Structure, functions and interguild relationships of the soil nematode assemblage in organic vegetable production. *Applied Soil Ecology* 61, 16–25.
- Filser, J., Faber, J.H., Tiunov, A.V., Brussaard, L., Frouz, J., De Deyn, G., Alexei, V.U., Matty, P.B., Patrick, L., Michel, L., Diana, H.W., Pascal, Q., Herman, E., Juan, J.J., 2016. Soil fauna: key to new carbon models. *Soils* 2, 565–582.
- Fontaine, S., Bardoux, G., Abbadie, L., Mariotti, A., Eacute, 2004. Carbon input to soil may decrease soil carbon content. *Ecology Letters* 7, 314–320.
- Geisen, S., Snoek, L.B., ten Hoover, F.C., Duyts, H., Kosteenko, O., Bloem, J., Martens, H., Quist, C.W., Helder, J., van der Putten, W.H., 2018. Integrating quantitative morphological and qualitative molecular methods to analyze soil nematode community responses to plant range expansion. *Methods Ecol. Evol.* 9, 1366–1378.
- Guan, P.T., Zhang, X.K., Yu, J., Cheng, Y.Y., Li, Q., Andriuzzi, W.S., Liang, W.J., 2018. Soil microbial food web channels associated with biological soil crusts in desertification restoration: the carbon flow from microbes to nematodes. *Soil Biology and Biochemistry* 116, 82–90.
- Güsewell, S., Gessner, M.O., 2009. N:P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. *Functional Ecology* 23, 211–219.
- Hua, C., Wu, P.F., He, X.J., Zhu, B., 2014. Effects of different amounts of straw returning treatments on soil nematode community in purple soil. *Biodiversity Science* 22, 392–400.
- Hunt, H.W., Coleman, D.C., Ingham, E.R., Ingham, R.E., Elliott, E.T., Moore, J.C., Rose, S. L., Reid, C.P.P., Morley, C.R., 1987. The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils* 3, 57–68.
- Huo, C.F., Luo, Y.Q., Cheng, W.X., 2017. Rhizosphere priming effect: a meta-analysis. *Soil Biology and Biochemistry* 111, 78–84.
- IUSS Working Group WRB, 2007. World Reference Base for Soil Resources 2006, First Update 2007. World Soil Resources Reports No. 103. FAO, Rome.
- Jenkinson, D.S., Brookes, P.C., Powlson, D.S., 2004. Measuring soil microbial biomass. *Soil Biology and Biochemistry* 36, 5–7.
- Jiang, Y.J., Liu, M.Q., Zhang, J.B., Chen, Y., Chen, X.Y., Chen, L.J., Li, H.X., Zhang, X.Y., Sun, B., 2017. Nematode grazing promotes bacterial community dynamics in soil at the aggregate level. *The ISME Journal* 11, 2705–2717.
- 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 and Soil* 432, 129–142.
- Kuzyakov, Y., 2002. Review: factors affecting rhizosphere priming effects. *Journal of Plant Nutrition and Soil Science* 4, 66–70.
- Kuzyakov, Y., 2010. Priming effects: interactions between living and dead organic matter. *Soil Biology and Biochemistry* 42, 1363–1371.
- Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573–579.
- Li, Q., Liang, W.J., Zhang, X.K., Mohammad, M., 2017. *Soil Nematodes of Grasslands in Northern China*. Zhejiang University Press, Hangzhou; published by Elsevier Inc, London, United Kingdom.
- Li, X.P., Zhu, H.M., Geisen, S., Bellard, C., Hu, F., Li, H.X., Chen, X.Y., Liu, M.Q., 2019. Agriculture erases climate constraints on soil nematode communities across large spatial scales. *Global Change Biology* 1–12, 00.
- 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 Biology and Biochemistry* 41, 883–890.
- Liu, T., Chen, X., Hu, F., Ran, W., Shen, Q., Li, H., 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.
- Liu, T., Yang, L.H., Hu, Z.K., Xue, J.R., Lu, Y.Y., Chen, X., 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. *Biology and Fertility of Soils*. <https://doi.org/10.1007/s00374-020-01436-1>.
- Maarastawi, S.A., Frindte, K., Bodelier, P.L.E., Knief, C., 2019. Rice straw serves as additional carbon source for rhizosphere microorganisms and reduces root exudate consumption. *Soil Biology and Biochemistry* 135, 235–238.
- Moore, J.C., Hunt, H.W., 1988. Resource compartmentation and the stability of real ecosystems. *Nature* 333, 261–263.
- Moore-Kucera, J., Dick, R.P., 2008. Application of  $^{13}\text{C}$ -labeled litter and root materials for in situ decomposition studies using phospholipid fatty acids. *Soil Biology and Biochemistry* 40, 2485–2493.
- Morriën, E., Hannula, S.E., Snoek, L.B., Helmsing, N.R., Zweers, H., de Hollander, M., Soto, R.L., Bouffaud, M.L., Buée, M., Dimmers, W., Duyts, H., Geisen, S., Girlanda, M., Griffiths, R.I., Jørgensen, H.B., Jensen, J., Plassart, P., Redecker, D., Schmelz, R.M., Schmidt, O., Thomson, B.C., Tisserant, E., Uroz, S., Winding, A., Bailey, M.J., Bonkowski, M., Faber, J.H., Martin, F., Lemanceau, P., de Boer, W., van Veen, J.A., van der Putten, W.H., 2017. Soil networks become more connected and take up more carbon as nature restoration progresses. *Nature Communications* 8, 14349.
- Neher, D.A., 2001. Role of nematode in soil health and their use as indicators. *Journal of Nematology* 33, 161–168.
- Neher, D.A., 2010. Ecology of plant and free-living nematodes in natural and agricultural soil. *Annual Review of Phytopathology* 48, 371–394.
- Paterson, E., Gebbing, T., Abel, C., Sim, A., Telfer, G., 2007. Rhizodeposition shapes rhizosphere microbial community structure in organic soil. *New Phytologist* 173, 600–610.
- Pittelkow, C.M., Liang, X., Linquist, B.A., Lee, K.J., van Groenigen, J., Lundy, M.E., van Gestel, N., Six, J., Venterea, R.T., van Kessel, C., 2015. Productivity limits and potentials of the principles of conservation agriculture. *Nature* 517, 365–368.
- Poirier, V., Angers, D.A., Whalen, J.K., 2014. Formation of millimetric-scale aggregates and associated retention of  $^{13}\text{C}$ - $^{15}\text{N}$ -labelled residues are greater in subsoil than topsoil. *Soil Biology and Biochemistry* 75, 45–53.
- Richter, A., Kern, T., Wolf, S., Struck, U., Ruess, L., 2019. Trophic and non-trophic interactions in binary links affect carbon flow in the soil micro-food web. *Soil Biology and Biochemistry* 135, 239–247.
- Rooney, N., McCann, K., Gellner, G., Moore, J.C., 2006. Structural asymmetry and the stability of diverse food webs. *Nature* 442, 265–269.
- Ruess, L., Ferris, H., 2004. Decomposition pathways and successional changes. *Nematology* 2, 547–556.
- Sánchez-Moreno, S., Ferris, H., Young-Mathews, A., Culman, S.W., Jackson, L.E., 2011. Abundance, diversity and connectance of soil food web channels along environmental gradients in an agricultural landscape. *Soil Biology and Biochemistry* 43, 2374–2383.
- Shahbaz, M., Kuzyakov, Y., Heitkamp, F., 2017. Decrease of soil organic matter stabilization with increasing inputs: mechanisms and controls. *Geoderma* 304, 76–82.
- Shannon, P., Maillet, A., Ozier, O., Baliga, N.S., Wang, J.T., Ramage, D., Amin, N., Schwikowski, B., Ideker, T., 2003. Cytoscape: a software environment for integrated models of biomolecular interaction networks. *Genome Research* 13, 2498–2504.
- Shipley, B., 2000. A new inferential test for path models based on directed acyclic graphs. *Structural Equation Modeling: A Multidisciplinary Journal* 7, 206–218.
- Sieriebriennikov, B., Ferris, H., de Goede, R.G.M., 2014. NINJA: an automated calculation system for nematode-based biological monitoring. *European Journal of Soil Biology* 61, 90–93.
- Six, J., Frey, S.D., Thiet, R.K., Batten, K.M., 2006. Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Science Society of America Journal* 70, 555–569.
- Sul, W.J., Asuming-Brempong, S., Wang, Q., Turlou, D.M., Penton, C.R., Deng, Y., Rodrigues, J.L.M., Adiku, S.G.K., Jones, J.W., Zhou, J.Z., Cole, J.R., Tiedje, J.M., 2013. Tropical agricultural land management influences on soil microbial communities through its effect on soil organic carbon. *Soil Biology and Biochemistry* 65, 33–38.
- ter Braak, C.J.F., 1988. CANOCO-A Fortran Program for Canonical Community Ordination by (Partial) (Detrended) (Canonical) Correspondence Analysis, Principal Components Analysis and Redundancy Analysis (version 2.1). Agricultural Mathematics Group, Wageningen. Technical Report LWA-88-02.
- Thakur, M.P., Geisen, S., 2019. Trophic regulations of the soil microbiome. *Trends in Microbiology* 27, 771–780.
- van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., de Goede, R.G.M., Adams, B.J., Ahmad, W., Andriuzzi, W.S., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., de Brito Caixeta, L., Chen, X.Y., Costa, S.R., Creamer, R., da Cunha Castro, J., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutiérrez, C., Høberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q., Liang, W.J., Magilton, M., Marais, M., Martín, J.A.R., Matveeva, E., Mayad, E.H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Rius, J.E.P., Pan, K. W., Peneva, E., Pellissier, L., da Silva, J.C.P., Pitteloud, C., Powers, T.O., Powers, K., Quist, C.W., Rasmann, S., Sánchez Moreno, S., Scheu, S., Setälä, H., Sushchuk, A., Tiunov, A.V., Trap, J., van der Putten, W., Vestergård, M., Villenave, C., Waejenber, L., Wall, D.H., Wilschut, R., Wright, D.G., Yang, J., Crowther, T.W., 2019. Soil nematode abundance and functional group composition at a global scale. *Nature* 572, 194–198.
- Wang, H.H., Guo, Q.C., Li, X., Li, X., Yu, Z.H., Li, X.Y., Yang, T.T., Su, Z.C., Zhang, H.W., Zhang, C.G., 2020. Effects of long-term no-tillage with different straw mulching frequencies on soil microbial community and the abundances of two soil-borne pathogens. *Applied Soil Ecology* 148, 103488.
- Walkley, A., Black, I.A., 1934. An examination of the Degtjareff method for determining soil organic matter and proposed modification of the chromic titration method. *Soil Science* 37, 29–38.
- Wang, J.B., Chen, Z.H., Chen, L.J., Zhu, A.N., Wu, Z.J., 2011. Surface soil phosphorus and phosphatase activities affected by tillage and crop residue input amounts. *Plant Soil and Environment* 57, 251–257.
- Wardle, D.A., 1995. Impacts of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices. *Advances in Ecological Research* 26, 107–185.
- Yeates, G.W., 2003. Nematodes as soil indicators: functional and biodiversity aspects. *Biology and Fertility of Soils* 37, 199–210.
- Zhang, X.Q., Qian, Y.L., Cao, C.F., 2015. Effects of straw mulching on maize photosynthetic characteristics and rhizosphere soil micro-ecological environment. *Chilean Journal of Agricultural Research* 75, 481–487.
- Zhang, B., Xu, S.Q., Tian, C.J., 2016. Long-term effect of residue return and fertilization on microbial biomass and community composition of a clay loam soil. *Journal of Agricultural Science* 154, 1051–1061.
- Zhang, S.X., Li, Q., Lü, Y., Sun, X.M., Jia, S.X., Zhang, X.P., Liang, W.J., 2015. Conservation tillage positively influences the microflora and microfauna in the black soil of Northeast China. *Soil and Tillage Research* 149, 46–52.
- Zhang, S.X., Li, Q., Lü, Y., Zhang, X.P., Liang, W.J., 2013. Contributions of soil biota to C sequestration varied with aggregate fractions under different tillage systems. *Soil Biology and Biochemistry* 62, 147–156.

- Zhang, X.K., Li, Q., Zhu, A.N., Liang, W.J., Zhang, J.B., Steinberger, Y., 2012. Effect of tillage and residue management on soil nematode communities in North China. *Ecological Indicators* 13, 75–81.
- Zhang, X.K., Ferris, H., Mitchell, J., Liang, W.J., 2017. Ecosystem services of the soil food web after long-term application of agricultural management practices. *Soil Biology and Biochemistry* 111, 36–43.
- Zheng, B., Marschner, P., 2017. Residue addition frequency influences respiration, microbial biomass and nutrient availability in soil amended with high and low C/N residue. *Journal of Soil Science and Plant Nutrition* 17, 1–13.
- Zhou, D.X., Su, Y., Ning, Y.C., Rong, G.H., Wang, G.D., Liu, D., Liu, L.Y., 2018. Estimation of the effects of maize stover return on soil carbon and nutrients using response surface methodology. *Pedosphere* 28, 411–421.