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Effect of Organic Amendment Amount on Soil Nematode Community Structure and Metabolic Footprints in Soybean Phase of Soybean-Maize Rotation in Mollisols

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ABSTRACT

In order to assess the effect of the amount of organic amendments on soil nematode community structure and metabolic activity, the community composition, abundance, and metabolic footprints of soil nematodes were determined in a long-term experiment field with various amounts of organic amendments in Northeast China. Fertilization treatments included (1) an unfertilized control (CK), (2) chemical fertilizer without manure amendment (OM_0), (3) manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer (OM_1), and (4) manure applied at 22.5Mg ha^{-1} plus chemical fertilizer (OM_2). A total of 46 nematode genera were found in the present study. The treatments with higher organic amendments had the smallest number of genera of plant parasites (5), but larger number of dominant genera (7). Total soil nematodes, bacterivores and fungivores were most abundant in OM_2, followed by OM_1, and lowest in both OM_0 and CK. Organic amendments increased enrichment index (EI). High amount of organic amendments increased bacterivore metabolic footprint (Baf), fungivore metabolic footprint (Fuf), and enrichment footprint (Ef). The relationships between metabolic footprint of bacterivores or fungivores and increments of soil organic carbon (△SOC) or total soil nitrogen (△TN) were stronger than that between abundance of bacterivores or fungivores with exception of the relationship between bacterivores and △SOC. The EI and Ef were positively correlated with △SOC and △TN. These findings suggest that organic amendment amount affect activity or function of soil nematodes at entry levels in food web, and that metabolic footprints of soil nematodes may be better indicators than their abundances in assessing their relationships with nutrients.

Key Words: function, long-term, metabolic activity, soil food web, trophic group

INTRODUCTION

Soil nematodes are relatively abundant invertebrate, occupy key positions at different trophic levels in soil food web (Ferris *et al*., 2001; Zhang *et al*., 2015a) and possess important functional diversity in soil ecosystem (Neher, 2001; Ferris and Bongers, 2006). Studies have shown that soil nematodes are involved in a variety of soil processes (Coleman *et al*., 2004; Zhao *et al*., 2014), and their abundance, food web indices, and metabolic activity provide insight into the ecological structure and functions of the soil food web (Ferris *et al*., 2001; Ferris, 2010; Sánchez-Moreno *et al*., 2011). Since the nematode metabolic footprint was derived by Ferris (2010) as a metric of metabolic activity and ecosystem function, it has been applied to estimate the activity and contribution of soil nematodes to different ecosystems, such as cropland (Ferris *et al*., 2012; Zhang *et al*., 2015b) and woodland (Hodson *et al*., 2014; Zhang*et al*., 2015a; Zhao *et al*., 2014).

Soil nematodes as a part of soil biology are influenced by their food resources and soil food web (Sánchez-Moreno *et al*., 2006; dos Santos *et al*., 2009). Organic matter amendments can improve soil structure, nutrient status and provide food resources for soil microorganisms which in turn provide food of bacterivores or fungivores (Fu *et al*., 2005; Xiao *et al*., 2014), and thus influence activity or diversity of soil nematodes in soil food web (Magdoff, 2001; Carter, 2002; Fontaine *et al*., 2003; Smukler*et al*., 2008). Applying organic manure influences soil nematode community structure, diversities, and activities (Ferris and Matute, 2003; Liang *et al*., 2009). Organic manure increases the abundance of bacterivores, fungivores, and omnivores/predators (Yeates*et al*., 1997; Wang *et al*., 2006; Biederman*et al*., 2008; Li *et al*., 2010; Tabarant*et al*., 2011), but reduces the abundance of plant parasites (Rodriguez-Kabana *et al*., 1987;Abawi and Widmer, 2000; Briar *et al*., 2007; Buena *et al*., 2007; Tabarant*et al*., 2011; Korthals*et al*., 2014). There is no doubt that organic amendments have an effect on the abundance of bacterivores. However, some studies have shown contrary results on other trophic groups, such as plant parasites (Thoden*et al*., 2011). McSorley*et al*. (1998) and Bulluck III *et al*. (2002) reported that organic amendments had no suppressive effects on plant parasites and *Meloidogyne incognita*. Organic amendments can even increase the abundance of plant parasites (Biederman*et al*., 2008). Some studies also found that organic amendments had no influence on fungivores (Biederman*et al*., 2008; Ferris *et al*., 2012) and omnivores/predators (Pan *et al*., 2010). Most previous studies focused on effects of organic matter on soil nematode fauna, but only a few studies investigated the effect of the amount of organic matter on soil nematodes. Wang *et al*. (2006) and Zhang *et al*. (2012) found that amount of organic matter (sunn hemp hay or wheat residues) affected the abundance and biomass of soil nematodes. However, Biederman*et al*. (2008) and Ferris *et al*. (2012) reported that the abundance of total nematodes or bacterivores and fungivores were not affected by amount of organic matter (urban wood waste and green-waste compost). These studies were both conducted in the soil with low levels of organic matter. The effect of organic amendment on soil nematodes was associated with the type of organic matter or soil properties (Ferris and Matute, 2003; Sánchez-Moreno *et al*., 2008). Therefore, it is very important to study the effect of the amount of organic amendments on soil nematodes in the soil with high organic matter content, such as Mollisols where the organic matter content is typically greater than 5%.

The effect of organic amendments on soil nematodes community structure also depends on crop types and rotation systems (Sánchez-Moreno *et al*., 2008; Ferris *et al*., 2012; Zhong*et al*., 2015). Most studies of effect of organic amendments on soil nematodes were conducted in vegetables (tomato, cucumber) (Bulluck*et al*., 2002; Li *et al*., 2010), sunn hemp/oats (Wang *et al*., 2006), sorghum

(Villenave*et al*., 2010), millet (Villenave*et al*., 2003), banana (Tabarant*et al*., 2011) and maize with continuous cropping (Liang *et al*., 2009), etc. Soybean is a leguminous crop that fixes nitrogen. The effects of litter, metabolites, secretions, stubble, and soybean roots on soil biology, especially parasites, were different from those of vegetables and graminaceous crops (Li *et al*., 2015). Crop rotations with soybean are the main cropping systems in Northeast China.

Northeast China is the key base of grain production in China. The typical soil in this area is Mollisols that are fertile, have high organic matter content, and support a high abundance and diversity of soil biology. The soybean-maize rotation is a representative cropping system. In our previous study, we found that application of organic manure increased the abundance of bacterivores, Shannon-Weaver index (H′) and species richness (SR) in soybean fields (Pan *et al*., 2010). However, there is still a lack of information on the amount effects of organic amendments on soil nematodes under the soybean-maize rotation in the soil with high organic matter content. The objectives of this study were to 1) determine the responses of the soil nematode community structure and function to different amounts of organic amendments in soybean phase of soybean-maize rotation and 2) evaluate the contribution of soil nematodes to C utilization under different organic amendment amounts in Mollisols. It was hypothesized that increasing the amount of added organic amendments would benefit the soil nematode community structure and activity in soil food web and accelerate the contribution of soil nematodes to C utilization.

MATERIALS AND METHODS

Experimental site

The study was carried out in a long-term fertilization experiment established in 2001 at National Observation Station of Hailun AgroecologySystem, Chinese Academy of Sciences, Heilongjiang province, China (47° 26′ N, 126° 38′ E). The mean annual rainfall is approximately 550 mm, with approximately 65% occurring from June to August. The region has a typical temperate continental monsoon climate, with hot summers and cold winters.

Experimental design

A randomized block design was used in this experiment, with three replicates and four treatments. A 2-year rotation of soybean (*Glycine max* (Merrill.) L.) and maize (*Zea mays* L.) was established in 2001. The treatments included (1) CK, unfertilized control; (2) OM_0, only chemical fertilizers, no manure amendment; (3) OM_1, manure applied at 7.5 Mg ha^{-1} plus chemical fertilizers; (4) OM_2, manure applied at 22.5Mg ha^{-1} plus chemical fertilizers. Chemical fertilizers were applied in the same amount in the same crop phase for all treatments, except CK where no fertilizers were applied. Fertilizers were applied at rates of 20.5 kg N ha^{-1}, 16.6 kg P_2O_5 ha^{-1} and 30 kg K_2O ha^{-1} as diammonium phosphate, urea and potassium sulfate for soybean and 75.7 kg N ha^{-1}, 14.7 kg P_2O_5 ha^{-1}, and 30 kg K_2O ha^{-1}as diammonium phosphate, urea and potassium sulfate for maize. Pig manure was collected from the same source every year, with 265 g C kg^{-1}, 21 g N kg^{-1}, 5.95 g P_2O_5 kg^{-1} and 2.89 g K_2O on dry weight basis.The C, N, P_2O_5 and K_2O manure nutrient rates were, respectively, 1990, 158, 44.6 and 22.7 kg ha^{-1} for the 7.5 Mg ha^{-1} manure rate, and 5960, 473, 134 and 65 kg ha^{-1} for the 22.5 Mg ha^{-1} manure rate. The pig manure was applied in the previous fall after maize or soybean harvest and fertilizers were applied with soybean or maize sowing in spring. There were a total of 12 plots, and each plot was 12 m × 5.6 m. All of aboveground crop residues were removed from the field plots. All plots were fall tilled (mouldboard ploughed) after harvest. More detailed information on crop husbandry practices is given by Ding *et al*. (2012).

Soil sampling and measurement of soil properties

Soil samples were collected during the soybean phase of the soybean-maize rotation in 2014. A steel trowel was used to collect soil samples from the top 20 cm in May, August and October. Nine soil samples were collected from each plot and mixed thoroughly by hand. Plant roots and stones were manually removed from soil samples. One part of the soil samples collected in spring was used for the analysis of total soil organic C and total N using a VarioEL CHN elemental analyzer (HeraeusElementarVarioEL, Hanau, Germany).Soil moisture was determined by drying samples at 105 ℃ to stable weight.

Nematode extraction, identification and community analysis

Nematodes were extracted from 100 g of wet soil using the Baermann tray method modified from the Baermann funnel method (Barker, 1985), for 72 h. The collected nematodes were heat-killed (60 ℃) and fixed with a 4% triethanolamine formaldehyde (TAF) solution. One-quarter of each nematode suspension was observed under an Olympus microscope (200 x or 400 x), and each nematode was identified to the genus using diagnostic keys (Yin *et al*., 1998; Anonymous, 2014). Nematode taxa were assigned to four trophic groups based on Yeates et al. (1993): plant parasites (PP), fungivores (Fu), bacterivores (Ba) and omnivores/predators (OP). The abundance of total nematodes and each taxonomic group were adjusted to the number of nematodes per 100 g of dry soil. In the rest of the nematode suspension, 100 specimens per sample were randomly selected and measured for length (L) and maximum body diameter (D) using an ocular micrometer. If the selected specimens did not include all genera for a corresponding sample, we deviated from the random selection and intentionally selected and measured unrepresented genera.

The enrichment index (EI), structure index (SI) and channel index (CI) were calculated to estimate the soil condition and soil food web state (Ferris *et al*., 2001). The EI indicates enrichment of available resource in soil environment; the SI indicates complexity and stability of food webs, and CI indicates whether organic matter decomposition is dominated by bacterial or fungal pathways. The metabolic footprints of nematodes (F) indicating C utilization in the soil food web based on nematode biomass (W) was computed for each sample (Ferris, 2010). These indices were calculated as follows:

$$CI = 100 \times 0.8Fu2/(3.2Ba1 + 0.8Fu2)$$

$$EI = 100 \times (e/(e + b))$$

$$SI = 100 \times (s/(s + b))$$

$$e = \sum(3.2\ Ba1 + 0.8Fu2)$$

$$b = \sum 0.8(Ba2 + Fu2)$$

$$s = \sum(1.8Ba3 + 3.2Ba4 + 3.2Ca4 + 5.0Ca5)$$

The numeric after Ba, Fu, Om and Ca is the respective colonizer-persistor (c-p) value and is used to represent the functional guilds of bacterivores, fungivores, omnivores and predators, respectively (Ferris *et al*., 2010); for example, Fu2 is fungivores with a c-p value of 2.

$W = (D^2 \times L) / (1.6 \times 10^6)$

where W is the nematode fresh weight (μg), D is the greatest body diameter (μm) and L is the nematode length (μm).

$F = \sum (N_t (0.1 (W_t / m_t) + 0.273 (W_t^{0.75})))$

where N_t, W_t and m_t represent the number, fresh weight (μg) and c-p value of *t* taxa, respectively.

Metabolic footprints of plant parasites, bacterivores, fungivores and omnivores/predators were abbreviated as PPf, Baf, Fuf and OPf, respectively, and they were summed to provide different metrics of ecosystem functions. Enrichment footprint (Ef) and structure footprint (Sf) were calculated by summing enrichment component (bacterivores with cp1 and fungivores with cp2) and structure component (cp3, cp4 and cp5) (Ferris, 2010; Hodson*et al*., 2014).

Data analysis

The nematode abundance and metabolic footprint were ln (x+1) transformed to meet normality criteria prior to statistical analyses. Repeated measures ANOVA was used to test the overall effects of fertilizer treatments and samplingtimes on the abundance, metabolic footprint and food web index of soil nematodes. Post hoc mean tests LSD were performed to assess the effects of fertilizer and organic amendment treatments on the abundance, metabolic footprint and food web index of soil nematodes at each sampling time. Regression analysis was conducted to evaluate the relationship between increments of SOC (△SOC) or TN (△TN) and the abundance or metabolic footprints of nematodes. The increments are difference values between treatment and CK in SOC or TN; we took △SOC and △TN of CK as zero. All statistical analyses were performed at a significance level of 0.05 using the software package SPSS 16.0 (SPSS, Chicago, IL).

RESULTS

Community structure

The nematodes included 46 taxa in this study (Supplementary Table I). Bacterivores were most abundant with 17 taxa, followed by omnivores/predators with 12 taxa, plant parasites with 10 taxa, and fungivores with 7 taxa. A genus with relative abundance over 10% was defined as a dominant genus. The treatments with higher organic amendments had the smallest number of genera of plant parasites (5 genera), but larger number of dominant genera. Treatments listed in descending order of genera were OM_2 (7 genera) > OM_1 or OM_0 (5 genera) > CK (4 genera). Genus *Heterodera* was dominant in all treatments in August, except OM_2. *Eucephalobus* was dominant in all treatments in May, August and October.

SUPPLEMENTAL TABLE I

Relative abundance (%) of nematode genera in the treatments[a)] with different amounts of organic amendment.

Genus	CK			OM_0			OM_1			OM_2		
	May	Aug.	Oct.	May	Aug.	Oct.	May	Aug.	Oct.	May	Aug.	Oct.
Heterodera	9.5	20.7	3.2	8.6	17.6	4.7	6.1	15.5	3.2	6.0	9.7	1.1
Helicotylenchus	-	-	-	0.7	0.2	0.5	-	0.4	-	-	-	-
Pararotylenchus	0.9	1.9	1.5	1.4	-	2.6	2.7	0.4	0.5	0.8	0.1	0.5
Rotylenchus	0.5	-	1.3	0.2	0.4	-	0.4	0.4	0.2	-	-	-
Paratylenchus	-	-	-	-	-	0.5	-	-	0.2	-	-	-
Paratrichodorus	-	0.5	0.7	-	-	-	-	-	-	-	-	-
Aglenchus	-	-	0.7	-	-	-	-	-	-	-	-	-
Boleodorus	1.4	-	4.4	-	-	0.9	1.7	-	0.3	-	-	1.5
Tylenchus	-	-	-	0.5	0.4	1.4	0.4	-	-	0.3	0.1	-
Trichodorus	-	-	0.3	-	-	-	-	-	-	-	-	-
Juveniles of Hoplolaimidae	0.9	0.2	0.8	0.9	0.4	1.7	-	-	0.8	0.1	-	-
Alaimus	0.7	2.4	2.3	1.8	0.9	4.7	0.6	2.8	8.3	2.3	2.0	4.6
Acrobeles	-	0.2	-	-	-	0.2	-	-	0.1	-	1.0	0.1
Acrobeloides	12.3	8.9	10.6	12.2	11.3	11.6	9.7	6.9	2.2	10.9	3.0	4.8
Cephalobus	0.5	-	-	-	-	-	0.4	-	0.1	-	-	-
Cervidellus	1.4	0.5	0.2	-	-	1.2	1.7	0.4	0.3	0.3	0.4	0.7
Chiloplacus	-	-	1.8	-	0.2	0.7	-	-	0.1	-	0.1	0.2
Eucephalobus	25.5	17.4	17.8	26.2	19.8	21.2	24.8	21.7	25.7	28.2	17.5	27.2
Monhystera	-	0.2	0.5	-	0.2	0.2	-	-	0.1	-	0.4	0.9
Prismatolaimus	0.7	1.4	2.5	-	0.2	3.5	-	1.4	1.6	0.3	1.3	2.0
Anaplectus	-	3.8	1.8	1.8	7.2	1.7	1.3	5.2	8.9	2.7	10.5	8.1
Plectus	-	0.2	-	-	-	0.5	0.4	-	-	-	0.3	0.2
Mesorhabditis	-	8.0	7.4	1.4	5.7	8.0	1.5	11.9	7.0	1.8	17.7	8.9
Protorhabditis	3.5	0.5	0.7	5.4	0.7	1.0	6.3	1.4	2.9	12.9	1.2	2.3
Diplolaimelloides	-	0.2	0.2	1.1	-	2.3	-	-	2.3	-	0.6	1.5
Chromadorita	-	-	-	-	-	-	-	0.4	0.5	-	1.2	0.1
Wilsonema	-	0.2	-	-	-	-	-	-	-	-	-	-
Rhabditidae	-	0.7	1.2	-	9.4	-	-	2.7	0.8	-	1.3	6.8
Ditylenchus	5.3	4.5	7.0	10.4	5.9	4.5	16.4	4.6	18.5	14.1	12.8	10.9
Aphelenchoides	0.7	0.9	1.3	-	6.3	0.3	-	3.9	1.0	0.8	1.3	0.9
Aphelenchus	5.1	1.9	3.7	4.5	3.5	4.9	3.4	1.2	1.1	2.8	1.0	0.9
Filenchus	16.0	4.0	9.0	22.3	2.8	13.2	19.3	5.0	5.2	12.3	7.4	9.0
Malenchus	-	7.5	1.5	-	1.5	2.6	-	4.1	0.7	-	3.0	1.5
Tylencholaimellus	3.9	-	-	-	-	0.2	-	0.2	0.6	1.1	-	-
Tylencholaimus	-	0.2	-	-	0.7	1.6	-	2.7	0.7	-	0.4	1.0
Aporcelaimus	3.9	0.7	2.7	-	0.7	0.7	1.7	0.5	0.7	1.9	0.3	0.8
Mesodorylaimus	-	-	-	-	-	-	0.4	-	0.1	-	-	0.2
Prodorylaimus	-	2.4	2.3	-	2.0	0.9	-	0.9	1.1	0.4	1.3	0.9

Doryllium	7.2	5.6	-	0.7	-	0.5	-	-	-	-	-	-
Dorylaimoides	-	-	0.5	-	-	-	-	-	-	-	-	0.1
Mononchus	-	2.6	1.7	-	0.9	0.7	0.4	2.8	1.2	-	0.3	0.4
Discolaimium	-	-	-	-	-	-	-	-	0.1	-	-	-
Eudorylaimus	-	0.9	5.9	-	1.1	0.9	0.4	2.5	1.5	-	2.3	1.5
Longidorella	-	-	0.8	-	-	-	-	-	-	-	-	-
Microdorylaimus	-	0.7	2.0	-	-	-	-	-	-	-	0.7	-
Torumanawa	-	-	0.3	-	-	-	-	-	-	-	0.6	-
Dorylaimidae	-	-	1.3	-	-	-	-	0.2	1.1	-	-	0.6

[a] CK = no chemical fertilizer or manure; OM_0 = chemical fertilizer, no manure; OM_1 = manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer; OM_2 = manure applied at 22.5 Mg ha^{-1} plus chemical fertilizer.

Soil nematode abundance

The amount of organic amendments significantly affected the abundance of total soil nematodes, bacterivores, fungivores and omnivores/predators (Table I). Soil nematodes, bacterivores, and fungivores were most abundant in OM_2, with the highest amount of organic amendment, followed by OM_1, and lowest in both OM_0 and CK, without organic amendment (Figs. 1 and 2). For bacterivores and fungivores, the abundance of *Anaplectus*,*Mesorhabditis*, *Ditylenchus* and *Filenchus* increased by 202%, 150%, 278% and 148%, respectively, in OM_2 compared with OM_1 in August (data not shown). The abundance of plant parasites was slightly higher in CK and OM_0 than in OM_2 in August and October. The abundance of omnivores/predators was largest in CK, followed in decreasing order by OM_2, OM_1 and OM_0.

TABLE I

Repeated measure analysis for effects of treatments with different amounts of organic amendment and sampling time on soil nematode abundance.

Soil nematodes	Treatment		Time		Treatment x time	
	F value	df	F value	df	F value	df
Total soil nematodes	24.1**[a]	3	47.0**	2	0.7	6
Plant parasites	3.5	3	12.8**	2	0.1	6
Bacterivores	13.0**	3	61.8**	2	1.5	6
Fungivores	27.7**	3	4.1*[b]	2	0.2	6
Omnivores/predators	17.8**	3	37.0**	2	1.8	6

[a]Data is significant at $P< 0.05$.

[b]Data is significant at $P< 0.01$.

Fig.1

Fig. 1 Abundance of total soil nematodes (ln (individuals per 100 g dry soil + 1))in the treatments with different amounts of organic amendment.CK = no chemical fertilizer or manure; OM_0 = chemical fertilizer without manure, OM_1 = manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer; OM_2 = manure applied at 22.5 Mg ha^{-1} plus chemical fertilizer.

Fig. 2

Fig. 2 Abundance of nematode trophic groups (ln (individuals per 100 g dry soil + 1)) in the treatments with different amounts of organic amendment. CK = no chemical fertilizer or manure; OM_0 = chemical fertilizer without manure, OM_1 = manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer; OM_2 = manure applied at 22.5 Mg ha^{-1} plus chemical fertilizer.

Food web condition

Repeated measures analysis showed that the amount of organic amendment was significantly affected SI and the sampling time had a significant effect on all food web indices, CI, EI and SI (Table II). The CI value decreased with soybean growth and was higher in May than in August and October. Post hoc means tests showed a clear decreasing trend in the CI value with increasing amount of organic amendments in May and October (Fig. 3a). EI increased with an increase in the amount of organic amendments (Fig. 3b). The EI value was highest in $OM_{2,}$ followed by OM_1 and OM_0, and lowest in CK at all three sampling times. SI tended to increase with soybean growth, and it was highest in CK and significantly higher than in OM_0, OM_1 and OM_2.

TABLE II

Repeated measure analysis for effect of treatments with different amounts of organic amendment and sampling time on soil nematode food web indices.

Ecological index[a]	Treatment		Time		Treatment x time	
	F value	df	F value	df	F value	df
CI	2.6	3	9.1**[b]	2	0.6	6
EI	4.0	3	4.5*[c]	2	0.3	6
SI	10.3**	3	23.5**	2	0.8	6

[a] CI = channel index; EI = enrichment index; SI = structure index.

[b] Data is significant at $P< 0.01$.

[c] Data is significant at $P< 0.05$.

Fig. 3

Fig. 3 Food web indices of soil nematodes in the treatments with different amounts of organic amendment.CK = no chemical fertilizer or manure; OM_0 = chemical fertilizer without manure, OM_1 = manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer; OM_2 = manure applied at 22.5 Mg ha^{-1} plus chemical fertilizer. CI = channel index; EI = enrichment index; SI = structure index. 'f', 's' and 't' following treatment abbreviations represent that samples were collected in May, August and October, respectively.

Nematode metabolic footprint

The amount of organic amendments significantly influenced nematode metabolic footprints calculated for different trophic groups and functional indices, including Baf, Fuf and Ef (Table III, Fig. 4). The sampling time had a significant effect on PPf, Baf, Opf, Ef, and Sf (Table III). All of the nematode metabolic footprints shifted with sampling time, and they were higher in August and lower in May and October (Fig. 4). The metabolic footprints of bacterivores and fungivores tended to be higher in the treatments with high amount of organic amendments than in the treatments with low amount of organic amendments or CK (Fig. 4). The metabolic footprint of omnivores/predators was slightly higher in CK than in the treatments with organic amendments and lowest in OM_0. Ef tended to rise with the increase in the amount of organic amendments, and it was lowest in CK (Fig. 5). Sf was lowest in OM_0 and higher in CK, OM_1 and OM_2.

TABLE III

Repeated measure analysis for effect of treatments with different amounts of organic amendment and sampling time on soil nematode metabolic footprint.

Metabolic footprint[a)]	Treatment		Time		Treatment x time	
	F value	df	F value	df	F value	df
PPf	3.5	3	12.5**	2	0.2	6
Baf	10.7**[b)]	3	54.0**	2	1.2	6
Fuf	31.0**	3	2.0	2	0.4	6
Opf	13.7**	3	37.9**	2	0.9	6
Ef	26.6**	3	13.8**	2	0.1	6
Sf	8.6**	3	53.3 **	2	1.3	6

[a)]PPf = metabolic footprint of plant parasites; Baf = metabolic footprint of bacterivores; Fuf = metabolic footprint of fungivores; Opf = metabolic footprint of omnivores/predators; Ef = enrichment footprint; Sf = structure footprint.

[b)] Data is significant at $P< 0.01$.

Fig.4

Fig. 4 Metabolic footprint of each nematode trophic group (ln (μg per 100g dry soil + 1)) in treatments with different amounts of organic amendment.CK = no chemical fertilizer or manure; OM_0 = chemical fertilizer without manure, OM_1 = manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer; OM_2 = manure applied at 22.5 Mg ha^{-1} plus chemical fertilizer. PPf = metabolic footprint of plant parasites; Baf = metabolic footprint of bacterivores; Fuf = metabolic footprint of fungivores; OPf = metabolic footprint of omnivores/predators.

Fig. 5

Fig. 5 Functional metabolic footprint (ln (μg per 100g dry soil + 1)) in treatments with different amounts of organic amendment.CK = no chemical fertilizer or manure; OM_0 = chemical fertilizer without manure, OM_1 = manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer; OM_2 = manure applied at 22.5 Mg ha^{-1} plus chemical fertilizer. Ef = enrichment footprint; Sf = structure footprint.

Changes of soil nematode in relation to increments of SOC and TN

Linear regressions presented that the abundance and metabolic footprints of bacterivores or fungivores were significantly and positively related to △SOC and △TN (Fig. 6). The adjusted determination coefficients (R^2) for the abundance or metabolic footprints of bacterivores with △TN were higher than those with △SOC, while the values of R^2 for the abundance or metabolic footprints of fungivores with △SOC were higher than those with △TN. The R^2 for the abundance of bacterivores was lower than the footprint of bacterivores with △TN, and the R^2 for the abundance of fungivores was lower than the footprints of fungivores for both △SOC and △TN. Food web indices, EI and CI, were both strongly related to △SOC and △TN, but their correlation was opposite; EI was positively and CI was negatively related to △SOC and △TN (Fig. 7). The slopes of the linear regressions of enrichment footprint with △SOC and △TN were both significantly positive, and the R^2 for Ef was larger than that of EI with △SOC and △TN.

Fig. 6

Fig. 6 Relationship between abundance (ln (individuals per 100 g dry soil + 1)) or footprint (ln (μg per 100g dry soil + 1)) of each nematode trophic group and increments of soil organic carbon or total soil nitrogen level. Ba = bacterivores; Fu = fungivores; Baf = metabolic footprint of bacterivores; Fuf = metabolic footprint of fungivores; SOC = soil organic carbon; TN = total soil nitrogen. R^2 is the adjusted determination coefficient of linear regression. '*' and '**' indicate significance at p<0.05 and p<0.01, respectively. Circles with and without fill represent abundance and footprint respectively of each nematode trophic group.

Fig. 7

Fig. 7 Relationship between food web indices or functional footprints (ln (μg per 100g dry soil + 1)) and increments of soil organic carbon or total soil nitrogen level. EI = enrichment index; CI = channel index; Ef = enrichment footprint; SOC = soil organic carbon; TN = total soil nitrogen. R^2 is the adjusted determination coefficient of linear regression. '*' and '**' indicate significance at p<0.05 and p<0.01, respectively. Circles with and without fill represent food web index and functional footprint, respectively.

DISCUSSION

Many previous findings have reported the effect of organic amendments on soil nematode community or food web (Liang *et al*., 2009; Tabarant*et al*., 2011; Jiang *et al*., 2013). In the present study, we focused on understanding the changes of soil nematode fauna caused by long-term different application amounts of pig manure. Our results supported the hypothesis that the amount of organic amendments affects the soil nematode community structure and metabolic footprint. The treatments with higher organic amendments had smallest number of genera of plant parasites but largest number of dominant genera. It is likely that organic amendments can produce antagonistic soil organisms, stimulate the competitive status of the non-pathogenic organisms, or have toxic effects during decomposition (Wang *et al*., 2001). Some plant parasite species are hard to be observed because they are least abundant or extinct when the negative effects exist for a long term. However, some genera were closely related to the amount of organic amendment, such as*Anaplectus*,*Mesorhabditis*, *Ditylenchus* and *Filenchus*, their abundances increased by 2.0, 1.5, 2.8 and 1.5 times in August, respectively, when the amount of organic amendment was increased 3 fold from 7.5 to 22.5 Mg ha^{-1} (data not shown). The dominant genera in OM_2 were all bacterivores and fungivores. Organic amendments favor the organism entry into soil food web, especially bacteria and fungi which provide food resources of bacterivores and fungivores (Yeates*et al*., 1993), which may explain why high amount of organic amendments had larger dominant genera.

High amount of organic amendment decreased the abundance of plant parasites but increased the abundance of total soil nematodes, bacterivores and fungivores. However, low amount of organic amendment did not show a significant effect on the abundance of soil nematodes, suggesting that the effect of organic amendments on soil nematodes is related to the amount of organic manure. Organic amendments can suppress the abundance of plant parasites by promoting antagonistic soil organisms, by stimulating the competitive status of the non-pathogenic organisms, or by producing toxic compounds during decomposition (Thoden*et al.*, 2011). Organic amendments increase biomass of bacteria and fungi which bacterivores and fungivores feed on, and consequently support higher abundance of bacterivores and fungivores (Ingham *et al*., 1985). Our results were in disagreement with the findings of Biederman*et al*. (2008), who observed that neither the amount nor the location of organic amendments influenced the abundance of total nematodes, and Ferris *et al*. (2012), who found that the abundance of bacterivores and fungivores did not show a relationship with the level of soil organic matter. This is likely due to different types or amounts of organic matter used across the experiments: Biederman*et al*. (2008) used three rates of untreated urban wood waste, Ferris *et al*. (2012) used two rates of green-waste compost, and we used three rates of pig manure. Different organic matter amendments possess different C:N ratios that influence the abundance of soil nematodes (Ferris and Matute, 2003; Villenave*et al*., 2010).

Most previous studies reported that organic amendments can increase EI or decrease CI (Ferris *et al*., 2001; Li *et al*., 2010; Villenave*et al*., 2010). There were trends of increased EI and decreased CI with increased amount of organic amendments, suggesting the trends of enhanced available resources and organic matter decomposition dominated by bacterial pathways. However, the effects of amount of pig manure on these two functional indices were not significant, likely because a range of amounts of added pig manure were not enough to cause differences in EI and CI. Another reason for this observation may be that the amount of manure in the OM_1 treatment was already at the upper threshold to affect EI and CI in the fertile Mollisols; the organic C input from organic amendment was about 1990 kg ha^{-1} in MO_1. SI was decreased by organic amendments, but it was not related to the amount of organic amendments referring to the graph of EI *vs*. SI. This result suggests that organic amendments disturb the structure or complexity of soil food web. Organic amendments usually have negative effects on the value of SI (Liang *et al*., 2009; Villenave *etal*., 2010). This is mainly due to organic amendments increasingthe abundance of soil nematodes belonging to lower c-p guilds, ratherthan omnivores-predators (Liang *et al*., 2009; Pan *et al*., 2010); the SI index is primarilydetermined by higher c-p guilds of soil nematodes (Ferris *et al*., 2001).

Since the metabolic footprint is based on the biomass and metabolic activity of soil nematodes, it can provide information about function or contribution of soil nematodes in soil food web (Ferris, 2010). The metabolic footprints of bacterivores and fungivores were higher in the treatments with high pig manure than in those with low or without pig manure, suggesting that the amount of organic amendment affects activity or function of bacterivores and fungivores. This is likely due to organic amendments enhancing the biomass of bacteria and fungi, and then indirectly influencing the Baf and Fuf. Christensen *et al*. (2012) found that organic amendment increased both fungal biomass and fungivores. We did not observe any effect of organic amendment on the metabolic footprint of plant parasites. This is inconsistent with the finding of Zhang *et al*. (2016) who reported that organic amendment increased the carbon biomass of plant parasites. The different findings are likely due to differences in soil fertility; the experiment of Zhang *et al*. (2016) was conducted in Henan province in central China, where the soil is much poorer than Mollisols in northeast China and barely provides enough nutritions for plants. Organic amendments can enhance the plant root growth in the soil of Henan province and thus increase the abundance and metabolic footprint of plant parasites. Another reason is likely due to different crops; the experiment in the presenct study was conducted in the soybean phase of a soybean-maize rotation and soybean is the host of *Heterodera* which was the main plant parasite through all treatments in our study. The existence of soybean host for the main plant parasite may weaken the amount effect of organic amendment on metabolic footprint of total plant parasites.

The Ef tended to rise with the increased amount of organic amendments. This suggests that amount of organic amendments influence activity or ecosystem service of soil nematodes at low trophic levels in soil food web. Zhang *et al*. (2016) found that cattle manure compost and maize straw had no effects on Ef in a maize crop, but maize straw increased the Ef in a wheat crop. The effect of organic amendments on the metabolic footprint of soil nematodes may be influenced by the type of organic matter and crops. Although structure metabolic footprint (Sf) differed among treatments, the amount of organic amendment did not present clear effect on it, which may due to the effect of chemical fertilizer. Chemical fertilizer can decrease the relative abundance of predators/omnivores (Li *et al*., 2012), while the Sf mainly reflects their activity (Ferris, 2010). Based on the amount effect of organic amendments on metabolic footprints of soil nematodes, we conclude that amount change of organic amendment directs the activity or function of soil nematodes at entry levels in food web.

In previous studies, the abundance of bacterivores or fungivores were significantly correlated with soil organic C or soil N (Savin*et al*., 2001;Liang *et al*., 2007; Postma-Blaauw*et al*., 2005; Pan *et al*., 2010). In this study, we found that the abundance and metabolic footprint of bacterivores and fungivores were positively related to △SOC and △TN, suggesting bacterivores and fungivores play a role in C and N cycles in the soil food web. The comparison of their relationships with △SOC and △TN suggests that bacterivores were more closely related to N than to C and fungivores were more closely related to C than to N, which might be related to their specific roles as decomposers of labile/recalcitrant organic matter. The metabolic activity of bacterivores and fungivores can increase soil mineral N by about 20% in microcosm experiments (Ferris *et al*., 1998; Chen and Ferris, 1999). Albers *et al*. (2006) also found that about 50% of the C in the body of bacterivores is likely due to recent plant material amendments. However, our results contradicted the observations of Cheng *et al*. (2008), who reported that nitrogen had no effects on the abundance of these two trophic groups in turf soils in Ohio, USA. These different findings may be attributed to various climates, plants or nematode genus compositions, as nematode genera or functional guilds have different responses to the soil N level (Todd *et al*., 2006; Sánchez-Moreno *et al*., 2008; Liang *et al*., 2009). The relationships between metabolic footprint of bacterivores or fungivores and △SOC or △TN were stronger than that between abundance of bacterivores or fungivores and △SOC or △TN (except relationship between bacterivores and △SOC), indicating a closer relationship of metabolic footprints of soil nematodes with nutrients than the abundance with nutrients. Nematode enrichment indicators, EI and Ef, were strongly related to △SOC and △TN, suggesting available resources and activity of soil nematodes at lower trophic levels of soil food webs were correlated with increments of SOC and TN. In previous studies, the values of EI and Ef usually correlated with SOC levels (Ferris *et al*., 2012; Ito *et al*., 2015). Ferris *et al*. (2012) found the Ef was related to SOC levels in spring but not at the end of summer. This finding supported our result; the SOC was consumed and △SOC disappeared over the growing season, thus, the Ef was no longer related to SOC levels at the end of summer.

CONCLUSIONS

In the conditions of soybean-maize cropping system and the soil with high organic matter content, long-term application of different amounts of organic amendments affects the soil nematode community structure and metabolic footprint. Higher amount of organic amendments reduced the genera of plant parasites but increased dominant genera. The abundances of total soil nematodes, bacterivores and fungivores were enhanced by higher amount of organic amendments. The genera, *Anaplectus*,*Mesorhabditis*, *Ditylenchus* and *Filenchus* were closely related to the amount of organic amendments. The metabolic footprints of bacterivores and fungivores also increased with the increase in the amount of organic amendments.Ef was higher in the treatments with higher amount of organic amendments than those with lower amount of organic amendments or control with no organic amendment. Based on the effect of amount of organic amendments on metabolic footprints of soil nematodes, we conclude that the amount of organic amendments directs the activity or function of soil nematodes at entry levels in food web. Comparison of the relationships between metabolic footprint and abundance of bacterivores or fungivores and changes in soil organic carbon (△SOC) or total nitrogen (△TN)suggest changes in soil nutrients may have a greater effect on metabolic footprints of soil nematode than their abundances. Nematode indicators of enrichment, EI and Ef, were strongly related to △SOC and △TN, indicating the available resource and activity of soil nematodes at lower trophic levels of soil food web were correlated with increments of SOC and TN.

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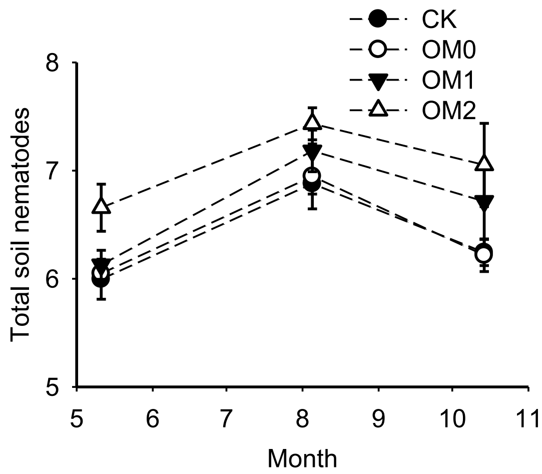

Fig. 1 Abundance of total soil nematodes (ln (individuals per 100 g dry soil + 1))in the treatments with different amounts of organic amendment.CK = no chemical fertilizer or manure; OM_0 = chemical fertilizer without manure, OM_1 = manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer; OM_2 = manure applied at 22.5 Mg ha^{-1} plus chemical fertilizer.

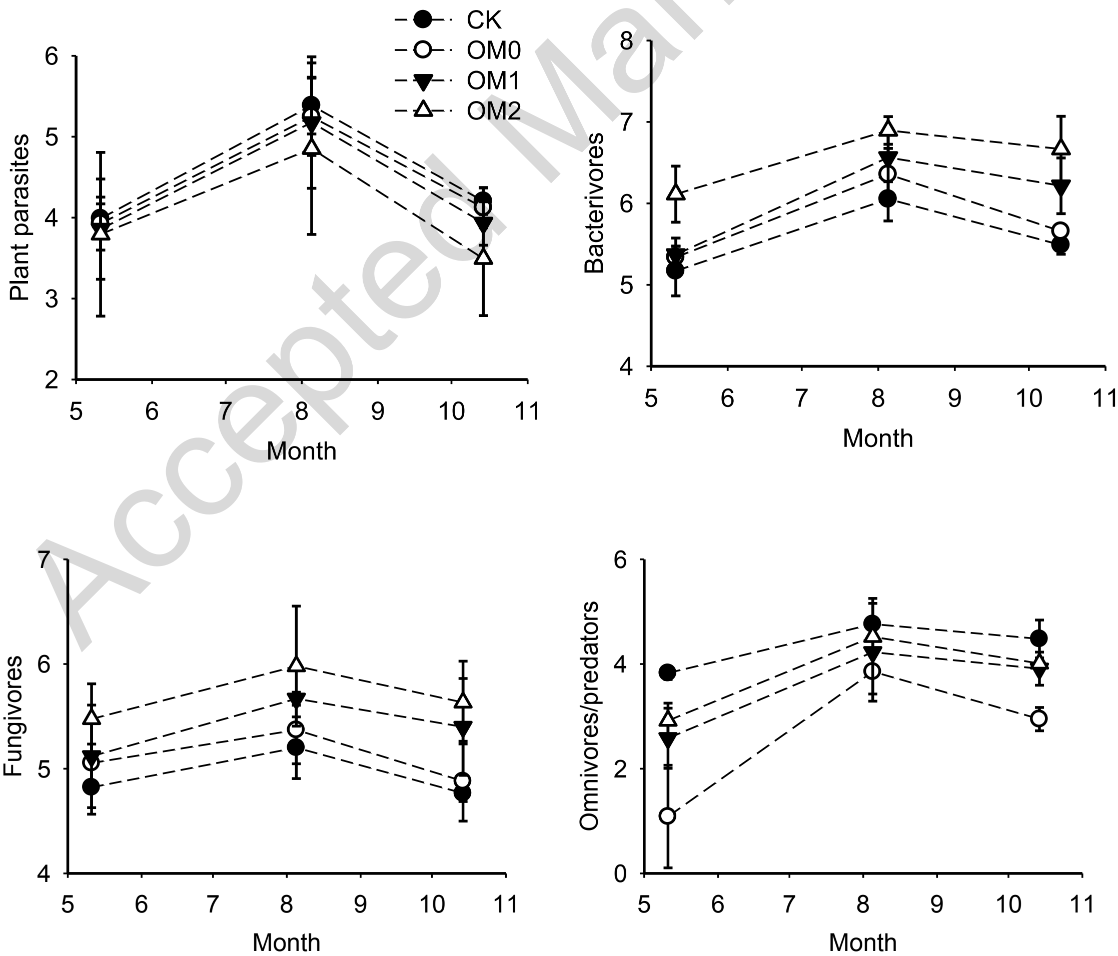

Fig. 2 Abundance of nematode trophic groups (ln (individuals per 100 g dry soil + 1)) in the treatments with different amounts of organic amendment. CK = no chemical fertilizer or manure;

OM_0 = chemical fertilizer without manure, OM_1 = manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer; OM_2 = manure applied at 22.5 Mg ha^{-1} plus chemical fertilizer.

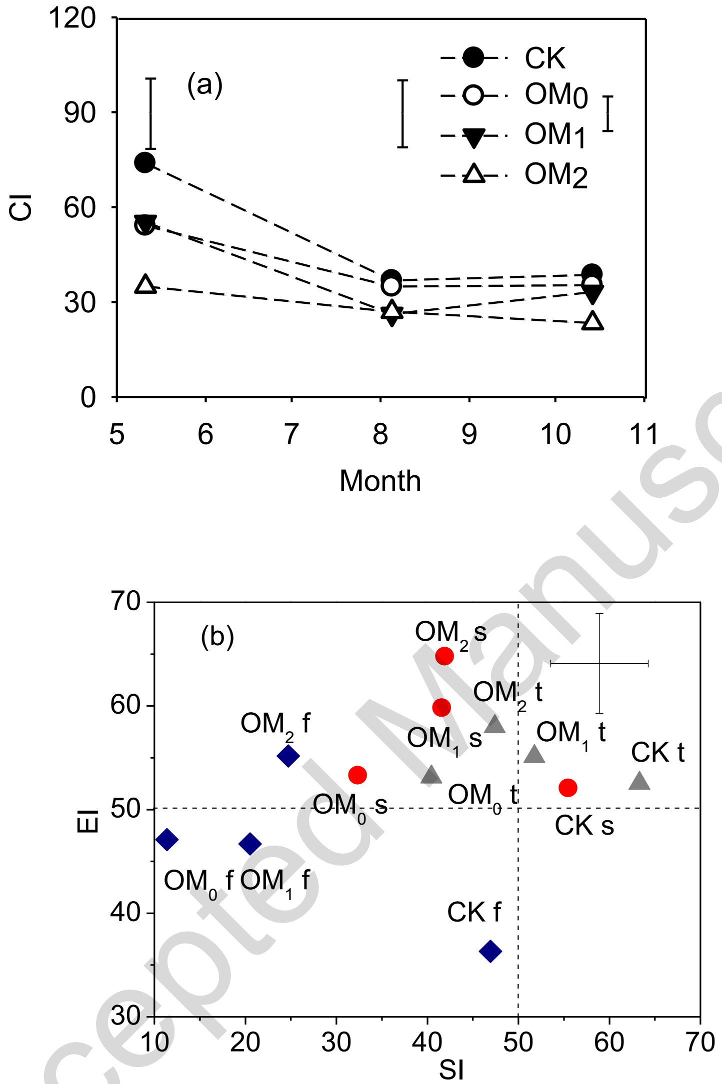

Fig. 3 Food web indices of soil nematodes in the treatments with different amounts of organic amendment.CK = no chemical fertilizer or manure; OM_0 = chemical fertilizer without manure, OM_1 = manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer; OM_2 = manure applied at 22.5 Mg ha^{-1} plus chemical fertilizer. CI = channel index; EI = enrichment index; SI = structure index. 'f', 's' and 't' following treatment abbreviations represent that samples were collected in May, August and October, respectively.

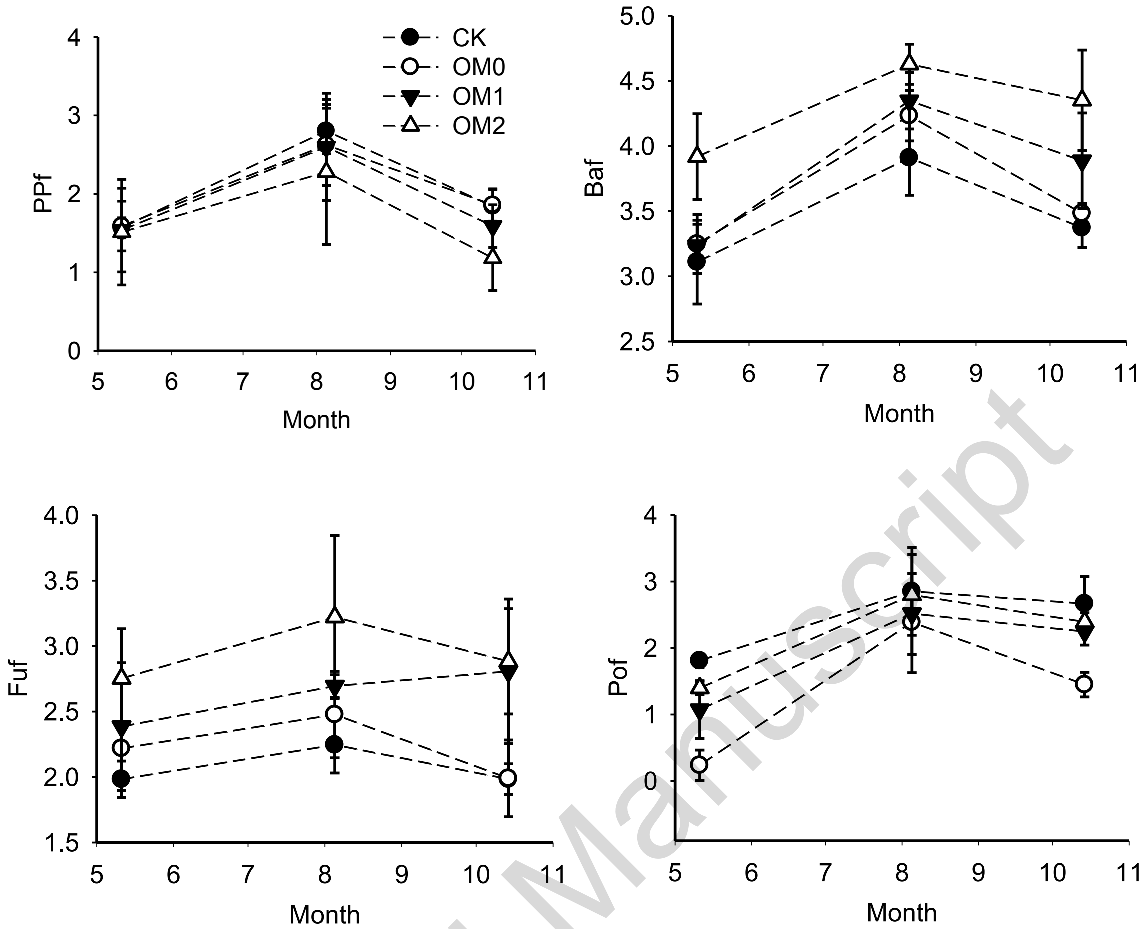

Fig. 4 Metabolic footprint of each nematode trophic group (ln (μg per 100g dry soil + 1)) in treatments with different amounts of organic amendment.CK = no chemical fertilizer or manure; OM_0 = chemical fertilizer without manure, OM_1 = manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer; OM_2 = manure applied at 22.5 Mg ha^{-1} plus chemical fertilizer. PPf = metabolic footprint of plant parasites; Baf = metabolic footprint of bacterivores; Fuf = metabolic footprint of fungivores; OPf = metabolic footprint of omnivores/predators.

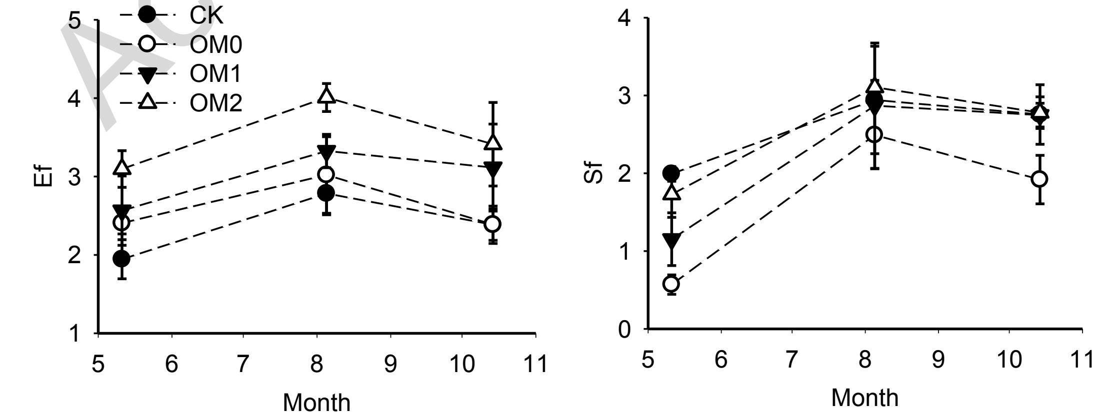

Fig. 5 Functional metabolic footprint (ln (μg per 100g dry soil + 1)) in treatments with different amounts of organic amendment.CK = no chemical fertilizer or manure; OM_0 = chemical

fertilizer without manure, OM_1 = manure applied at 7.5 Mg ha^{-1} plus chemical fertilizer; OM_2 = manure applied at 22.5 Mg ha^{-1} plus chemical fertilizer. Ef = enrichment footprint; Sf = structure footprint.

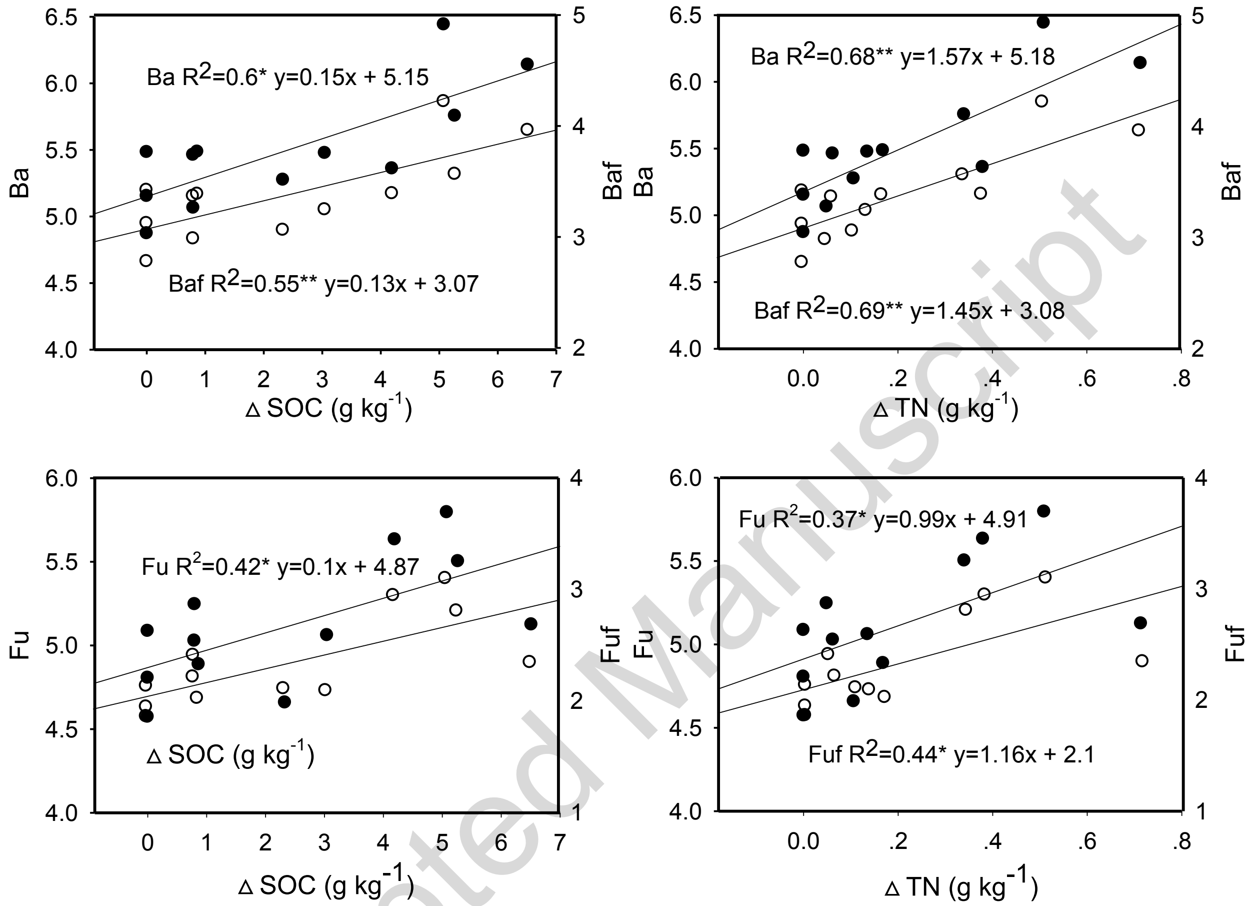

Fig. 6 Relationship between abundance (ln (individuals per 100 g dry soil + 1)) or footprint (ln (μg per 100g dry soil + 1)) of each nematode trophic group and increments of soil organic carbon or total soil nitrogen level. Ba = bacterivores; Fu = fungivores; Baf = metabolic footprint of bacterivores; Fuf = metabolic footprint of fungivores; SOC = soil organic carbon; TN = total soil nitrogen. R^2 is the adjusted determination coefficient of linear regression. '*' and '**' indicate significance at $p<0.05$ and $p<0.01$, respectively. Circles with and without fill represent abundance and footprint respectively of each nematode trophic group.

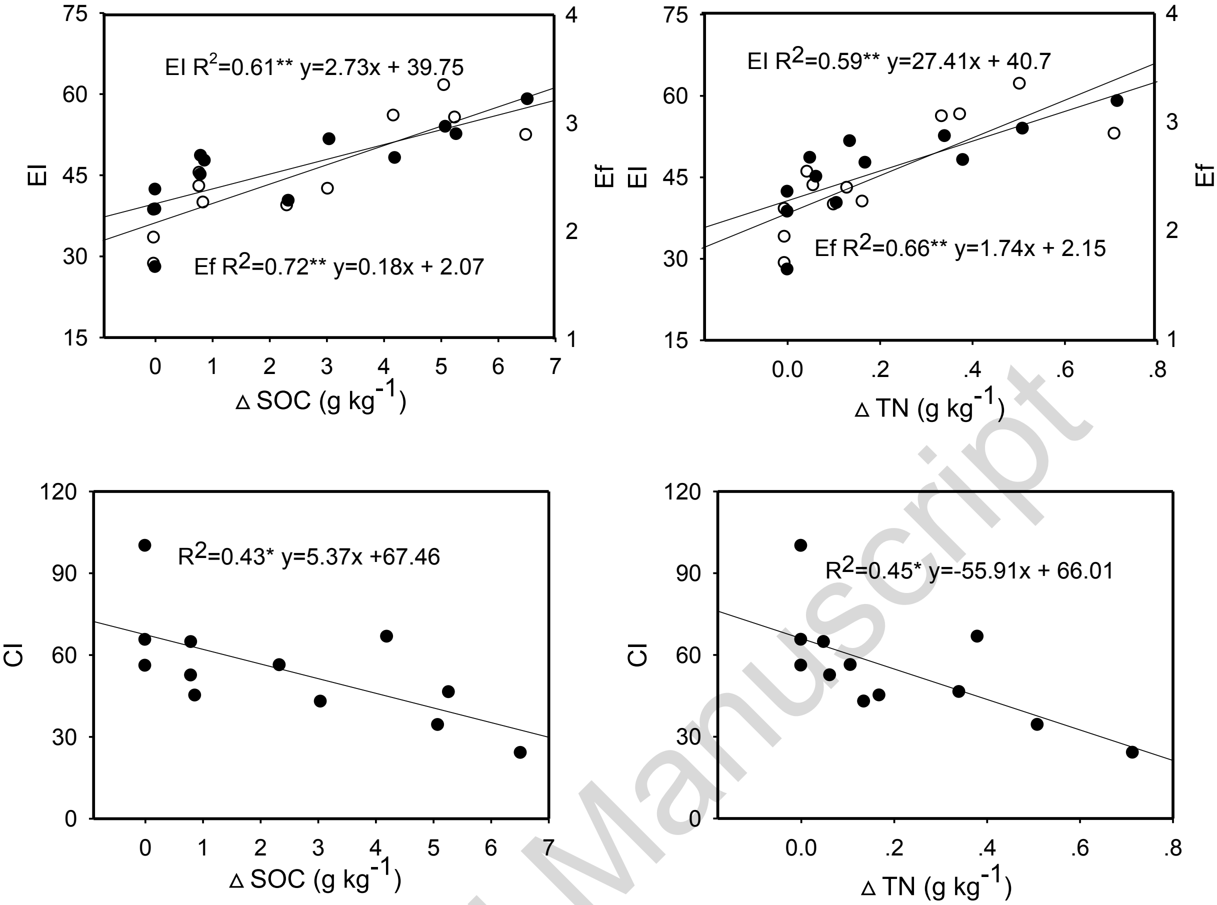

Fig. 7 Relationship between food web indices or functional footprints (ln (μg per 100g dry soil + 1)) and increments of soil organic carbon or total soil nitrogen level. EI = enrichment index; CI = channel index; Ef = enrichment footprint; SOC = soil organic carbon; TN = total soil nitrogen. R^2 is the adjusted determination coefficient of linear regression. '*' and '**' indicate significance at p<0.05 and p<0.01, respectively. Circles with and without fill represent food web index and functional footprint, respectively.