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Original article

Tillage and rotation effects on community composition and metabolic footprints of soil nematodes in a black soil

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ABSTRACT

Understanding the response of soil biota to tillage and rotation practices is useful for evaluating the effect of agricultural management. We investigated soil physiochemical properties, nematode community structure and composition and their metabolic footprints in different tillage and crop rotation systems in a 12-year old field experiment in a black soil. The experiment was based on a split-plot design with conventional tillage (CT) and no-tillage (NT) as main plots and corn-soybean rotation (CS) and continuous corn (CC) treatments as subplots. Soil samples were taken at 0–5 cm and 5–15 cm depths. The results showed that in comparison with CT, NT increased total soil organic carbon, soil moisture and microbial biomass carbon at 0–5 cm depth regardless of rotation system. Rotation effect on total nematode abundance was significant. The abundance of fungivores was significantly influenced by the tillage effect, with higher abundance found in CT systems. In total, fifty-eight nematode genera were identified. *Acrobeloides* dominated under CS and *Filenchus* under CC. In NT system, a bacterial-dominated decomposition pathway was dominant under CS, and fungal-based channel under CC at 0–5 cm depth. The interactive effect of tillage and rotation changed the decomposition channel. Under CS system, lower structure index (SI) and higher channel index (CI) were found in CT than in NT at 0–5 cm depth. At both depths, functional metabolic footprint was greater under CS than under CC in both tillage systems. Footprint of fungivores also suggested a greater flow of resources into the food web through fungivorous channels under CC. Redundancy analysis (RDA) showed that tillage and rotation influenced soil nematodes by changing soil physiochemical properties. Nematode community analysis indicated that corn-soybean rotation system increased nematode abundance and their functional metabolic footprint, and favored a more diverse residue resource entry into soil food webs.

1. Introduction

In agroecosystems, agricultural practices such as conservation tillage and crop rotation are beneficial for sustainable crop production due to their positive influences on the soil environment. Furthermore, tillage and crop rotation generally affect soil physicochemical properties and biological activities [1–4]. For example, no-tillage involving surface crop residue application has been adopted as a means to promote soil aggregate stability and fertility, while simultaneously increase the abundance and activity of soil biota [5–8]. In addition, crop rotation can also increase the input of organic C and N into the soil, which enhances soil fertility [9]. When high amounts of crop residues are returned to the soil, crop rotation can influence the soil microbial habitat, improve soil structure, and increase the activity and diversity of soil fauna [10–12].

Among soil fauna, soil nematodes are one of most important metazoa due to their abundance and functional diversity [13]. Plant-parasitic nematodes interact directly with plants and microbiovorous nematodes act as consumers of microflora, and thereby indirectly regulate decomposition and release of nutrients in agroecosystems [14]. Many studies have also documented that soil nematode communities can be used as bioindicators for different ecosystems [15–19]. For example, the relative abundance of fungal-feeding and bacterial-feeding nematodes may be regarded as sensitive indicators of management changes [20]. The decline in diversity of nematode fauna with increasing levels of

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management reflects not only physical disturbance but also the changes in the quantity and quality of organic matter returned to the soil. Considering these indicative functions, many researchers have reported how soil nematodes respond to agricultural practices. Okada and Harada [21], for example, observed that nematode diversity indices, maturity, structure and channel indices were higher in a no-tillage system than in a conventional tillage system. Overstreet et al. [22] showed that in comparison with conventional tillage, soil nematode abundance increased significantly in conservation tillage such as strip tillage, while Zhang et al. [23] showed that the responses of nematode trophic diversity, the enrichment index and the channel index were all sensitive to the tillage effect. Crop rotation sequences including different crop varieties can also influence nematode abundance, diversity and community structure. Rhaman et al. [3], for example, reported that free-living nematodes were more abundant in a wheat-lupin rotation system than in a continuous wheat system, while Postma–Blaauw et al. [24] found that maize monocultures were characterized by plant-parasitic nematodes and a barely-potato rotation system was dominated by bacterivorous and fungivorous nematodes.

Until now, most studies on soil nematode communities have been focused either on the effects of different tillage practices or on the effects of crop rotation. How rotation and tillage interactively affect soil nematode communities is relatively unknown. However, tillage and rotation are two important agricultural practices that are usually applied together in the crop fields of many countries [2,3,25]. Therefore, studies that examine on the interactive effect of tillage and rotation on soil nematode communities are needed. Additionally, from nematode ecology point of view, previous studies have focused on nematode ecological indices to analyze nematode community composition and diversity in different agricultural management systems. These indices of nematode communities do not provide much information on the magnitude or nature of the ecosystem functions these nematode communities provide [26]. To gain insight into the metabolic activity levels of various indicator guilds of nematodes, Ferris [26] proposed the nematode metabolic footprint which provides a quantitative component of ecosystem structure and function based on carbon utilization [27]. Ferris [26] and Zhang et al. [23] showed that the nematode metabolic footprint can provide insight into the structure and function of soil food webs. In this study, we use the nematode metabolic footprint to indicate how crop rotation and tillage influence ecosystem function and service of soil food web.

The objectives of our study were to analyze the interactive effect of tillage and rotation on soil nematode community composition and soil physiochemical properties, to quantify the nematode metabolic footprint in different tillage and rotation practices, and to evaluate which kinds of agricultural management practices are more favorable for agroecosystem stability and sustainability in terms of soil biota in a black soil.

2. Materials and methods

2.1. Site description

The study was conducted at the Experimental Station (44°12′ N, 125°33′ E) of the Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, in Dehui County, Jilin Province, China. The soil at this site is classified as black soil (Typic Hapludoll according to the USDA Soil Taxonomy) with a clay loam texture consisting of 36.0% clay, 24.5% silt and 39.5% sand. Before the establishment of the experiment, the field was used for corn production using a conventional tillage management (see below) for more than 20 years [28].

2.2. Experimental design and management practices

The experiment was a split-plot design with four replicates, initiated in the fall of 2001 with tillage system as the main plot and rotation management as the sub-plot [28]. Tillage systems included a conventional tillage (CT) and a no-tillage (NT) treatment. Rotation management treatments were corn-soybean rotation (CS) (one year corn and one year soybean) and continuous corn (CC).

The practices in CT consisted of mouldboard plowing (20 cm depth) after harvest in October, and disking (7.5–10 cm depth) and harrowing for the secondary seedbed preparation in about May of the next year. All aboveground crop residues in CT were incorporated into the soil. There were minimal human disturbances in NT except for planting using a KINZE-3000 NT planter (Williamsburg, Iowa). After harvest, all the corn straws were collected and cut into pieces of roughly 30 cm leaving a 30–35 cm stubble stand, and the pieces were then returned to the soil surface. Soybean residues were directly returned to the soil surface. The size of each individual subplot was 5.2 m × 20 m. Crops were sown in May and harvested in October. A fallow period (about seven months) was followed after each harvest.

Each year, in the corn field, 100 kg N ha^{-1}, 45.5 kg P ha^{-1} and 78 kg K ha^{-1} were applied as starter fertilizer during the sowing period and 50 kg N ha^{-1} as top dressing at the V-6 stage (6 leaves with collars). During the sowing period of soybean, 40 kg N ha^{-1}, 60 kg P ha^{-1} and 80 kg K ha^{-1} were applied as starter fertilizer [28].

2.3. Soil sampling

Soil samples were collected in April 2012, which was at the end of fallow period following corn harvest in 2011. In each subplot, composite samples of five random sub-samples were collected with a soil auger (2.64 cm diameter). Soil samples were taken at the depths of 0–5 cm and 5–15 cm. In total, 32 soil samples were collected. The fresh samples were placed in the plastic bags and kept at 4 °C until processed and analyzed. Bulk density was determined at 0–5 cm and 5–15 cm depth using a 100 cm^3 cylinder (5 cm height × 5 cm diameter).

2.4. Soil physiochemical properties

Soil organic carbon (SOC) was determined by dichromate oxidation and titration with ferrous ammonium sulfate [29]. Total nitrogen (TN) was determined by Kjeldahl method [30]. Soil NO_3^--N and NH_4^+-N were detected by using a flow injection auto analyzer (FIAstar 5000 Analyzer, Denmark). Microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were extracted using the chloroform fumigation and extraction method and measured using a TOC analyzer (Multi C/N 3000, Analytik Jena, Germany) [31]. Soil moisture (SM) was determined gravimetrically by drying samples at 105 °C.

2.5. Soil nematode identification

Nematodes were extracted from 50 g fresh soil by a modified cotton-wool filter method [32]. After counting the total abundance of nematodes in each sample, 100 individuals were randomly selected and identified to genus level using an inverted compound microscope [33]. If the total nematodes did not reach 100 in a sample, all the nematodes in the sample were identified. Nematode abundance was expressed as individuals per 100 g dry soil. Nematodes were assigned to the following the trophic groups according to their feeding habits: bacterivores (BF), fungivores (FF), omnivores-predators (OP) and plant-parasites (PP) [34].

2.6. Data analysis

The following nematode ecological indices were calculated: trophic diversity (Td) [35], Shannon–Weiner index (H′), Simpson index (λ) [20], generic richness (GR) [36], nematode channel ratio (NCR), enrichment (EI), structure (SI), basal (BI) and channel (CI) indexes according to Ferris et al. [37]. Nematode average fresh body mass by genus (W) was estimated based on http://plpnemweb.ucdavis.edu/nemaplex/Ecology/nematode_weights.htm. The nematode metabolic footprint (NMF) was then calculated as $NMF = \sum(N_t\ (0.1W_t/m_t + 0.273\ (W^{0.75})))$, where W_t and m_t represent the body weight and colonizer-persister (cp) values of genus t respectively. The enrichment footprint (efoot) is the metabolic footprint of lower trophic levels (cp 1–2) while the structure footprint (sfoot) represents the metabolic footprint with the higher cp value (3–5) [23,26]. Functional metabolic footprint (FMF) was calculated as $(F_s \times F_e)/2$ with complex μg^2 units [26].

Prior to statistical analysis, nematode abundances and different trophic metabolic footprints were $\ln(x + 1)$ transformed to achieve normality. The software package SPSS 16.0 for Windows (SPSS Inc., Chicago, IL, USA) was used for data analysis. Effects of tillage and rotation on measured variables were analyzed using the general

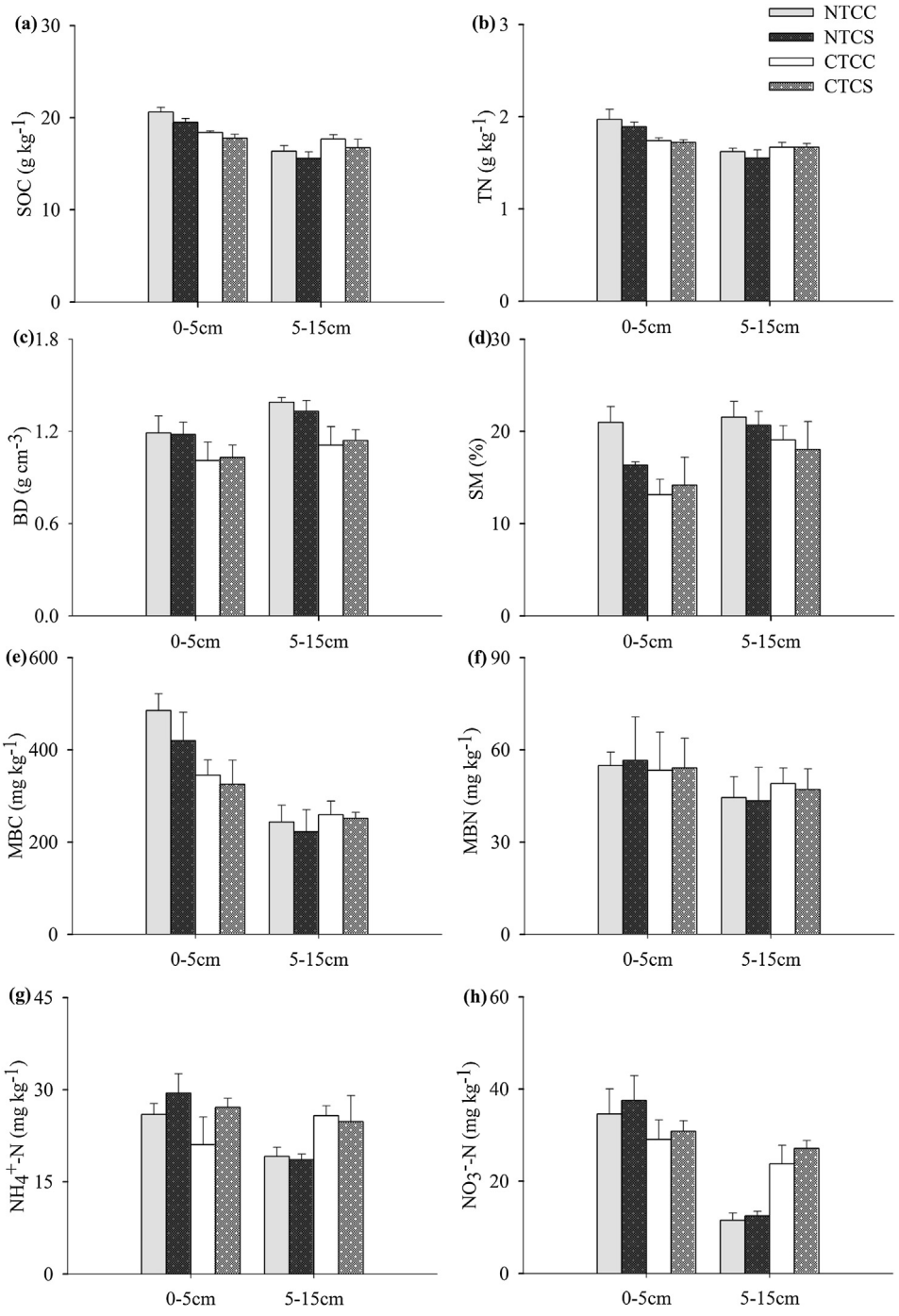

Fig. 1. Soil physicochemical properties in different tillage and rotation systems. Bars indicate standard error ($n = 4$). SOC, total soil organic carbon; TN, total nitrogen; SM, soil moisture; BD: bulk density; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen.

linear model (GLM) procedure for split-plot designs. Differences at $P < 0.05$ level were considered to be statistically significant. When their interactions were significant, individual comparisons were based on an independent-samples *T* test. The relationship between nematode genera and environment factors was examined based on redundancy analysis (RDA) using the CANOCO software, version 4.5 [38]. Tillage treatments (NT and CT), rotation treatments (CC and CS) and soil depth (0–5 cm and 5–15 cm) were included as dummy (1, 0) environment variables. A Monte Carlo permutation test (499 permutations) was used to test the significance of first and all canonical axes.

3. Results

3.1. Soil physiochemical properties

At 0–5 cm depth, the values of SOC, TN, BD, SM, MBC and NO_3^-–N were significantly higher in NT than in CT regardless of rotation system ($P < 0.05$, Fig. 1a–e and h). The contents of SOC were 5.74% and 3.37% greater under CC than under CS at 0–5 cm depth in both NT and CT systems, respectively ($P < 0.05$). The rotation effect on NH_4^+-N and the interaction of tillage and rotation effect on SM were significant at 0–5 cm depth ($P < 0.05$). At 5–15 cm depth, tillage significantly influenced SOC, NH_4^+-N and NO_3^-–N, with greater values found in CT than in NT regardless of rotation system ($P < 0.05$). And BD showed the opposite trend, with higher values found in NT ($P < 0.05$). The values of soil properties such as SOC, TN and SM were higher at 0–5 cm than at 5–15 cm depth in NT system ($P < 0.05$).

3.2. Nematode abundance and community composition

At 0–5 cm depth, total nematode abundance, bacterivorous and plant-parasitic nematodes were higher in the CS than in the CC treatment regardless of the tillage system ($P < 0.01$, Table 1). Fungivores were significantly affected by the tillage treatment at both depths (Table 1), with higher abundance being in CT. The interaction of tillage and rotation also influenced fungivores, with higher abundance being under CC than under CS in NT systems ($P < 0.05$) at 0–5 cm depth. At 5–15 cm depth, the abundance of total nematodes and fungivores were significantly higher in the CT than in the NT treatment regardless of rotation system ($P < 0.05$; $P < 0.01$) (Table 1).

In total, fifty-eight nematode genera were identified and only genera with more than 1% relative abundance were listed in Table 2. *Acrobeloides* was the most abundant genus (relative abundance > 10%) under CS while *Filenchus* under CC. *Rotylenchus* dominated in NT at 5–15 cm depth. At 0–5 cm depth, the relative abundance of *Cephalobus* was greater under CS than under CC system regardless of the tillage system ($P < 0.05$) (Table 2). Omnivores-predators such as *Aporcelaimellus* and *Discolaimium* were strongly affected by tillage, rotation and their interactions with the highest relative abundances being in NTCC and in NTCS, respectively ($P < 0.05$) (Table 2). At 5–15 cm depth, the bacterivores including *Acrobeloides* and *Rhabditis* were strongly influenced by rotation effects with relatively higher abundances under CS than under CC (Table 2). And the relative abundance of the *Discolaimium* was significantly higher in CTCC, than in CTCS ($P < 0.05$). No significant tillage, rotation and their interaction effect were found on other genera.

3.3. Nematode ecological indices

Tillage effect at both depths, and rotation and their interaction at 0–5 cm depth on NCR were significant ($P < 0.05$) (Table 3). In NT systems, higher value of NCR was found under CS than under CC at 0–5 cm depth. Tillage effect on SI value was significant at 0–5 cm depth. The EI was significantly affected by rotation with higher value being in CS than in CC ($P < 0.05$) only at 5–15 cm. At 0–5 cm depth, the NTCC treatment was mostly located in quadrat C, NTCS and CTCC in quadrat A and D, and CTCS in quadrat D. At 5–15 cm depth, most plots were located in quadrat C, which indicated relatively less disturbed environments. Remarkably, BI responded to rotation with greater values under CS than under CC regardless of tillage but only at 0–5 cm depth. Rotation effect at 5–15 cm depth and the interaction effect of tillage and rotation at both depths on CI were significant. In NT system, CI was higher in CC than in CS at both depths ($P < 0.05$) (Table 3).

3.4. Nematode metabolic footprints in different tillage and rotation systems

At 0–5 cm depth, the interactive effect of tillage and rotation significantly influenced BFfoot, FFfoot and sfoot (Table 4). In NT system, higher values of FFfoot and lower BFfoot were observed under CC than under CS ($P < 0.05$). In CT system, FFfoot was greater under CS than under CC ($P < 0.05$). At 5–15 cm depth, rotation effect on BFfoot and efoot, tillage effect on FFfoot, and the interaction of tillage and rotation on efoot were all significant ($P < 0.05$). Nematode functional metabolic footprint (FMF) is the total area of the

Table 1
Total abundance (individuals per 100 g dry soil) and abundances of nematode trophic groups in different tillage and rotation treatments (mean ± SE, $n = 4$).

Soil depth	Tillage (T)	Rotation (R)	Total abundance	BF	FF	PP	OP
0–5 cm	NT	CC	242.39 ± 20.46	80.50 ± 21.90	94.41 ± 12.37	38.87 ± 6.26	28.61 ± 4.31
		CS	322.21 ± 44.22	163.03 ± 36.63	53.79 ± 5.23	74.58 ± 20.38	30.81 ± 9.95
	CT	CC	254.14 ± 24.63	76.51 ± 13.33	105.65 ± 24.46	45.80 ± 15.19	26.18 ± 2.29
		CS	549.31 ± 88.66	188.56 ± 45.29	231.10 ± 47.71	90.94 ± 4.31	38.71 ± 7.19
	ANOVA		*P* value				
	T		ns	ns	<0.05	ns	ns
	R		<0.01	<0.01	ns	<0.05	ns
	T × R		ns	ns	<0.01	ns	ns
5–15 cm	NT	CC	275.87 ± 72.78	97.63 ± 39.88	46.27 ± 15.12	104.38 ± 36.79	27.59 ± 4.28
		CS	305.66 ± 46.66	153.58 ± 38.31	56.44 ± 7.34	53.54 ± 8.25	42.10 ± 6.66
	CT	CC	401.58 ± 85.77	129.07 ± 34.25	139.80 ± 31.34	86.07 ± 27.20	46.64 ± 7.36
		CS	595.02 ± 99.64	191.89 ± 36.02	202.82 ± 36.13	160.52 ± 43.37	39.79 ± 8.45
	ANOVA		*P* value				
	T		<0.05	ns	<0.01	ns	ns
	R		ns	ns	ns	ns	ns
	T × R		ns	ns	ns	ns	ns

T, Tillage; R, Rotation; BF, bacterivores; FF, fungivores; PP, plant-parasites; OP, omnivores-predators.

Table 2
The relative abundance (%) of nematode genera in different tillage and rotation treatments (mean ± SE, $n = 4$).

Genus	Abbr.	0–5 cm		5–15 cm					
		NT		CT		NT		CT	
Bacterivores		CC	CS	CC	CS	CC	CS	CC	CS
Acrobeles	*Acr*	3.89 ± 1.63	0.96 ± 0.38	2.29 ± 1.08	0.67 ± 0.24	0.29 ± 0.21	1.26 ± 0.96	3.33 ± 2.01	0.33 ± 0.24
Acrobeloides	*Acd*	8.30 ± 1.03	15.60 ± 3.22	7.69 ± 2.59	14.95 ± 0.82	2.03 ± 0.70	13.13 ± 2.10	8.00 ± 1.78	12.18 ± 3.86
Cephalobus	*Cep*	0.59 ± 0.42	7.66 ± 0.51	5.38 ± 1.19	3.99 ± 0.01	6.98 ± 2.84	11.15 ± 3.10	6.67 ± 2.09	6.98 ± 1.43
Chronogaster	*Chr*	0.41 ± 0.29	2.60 ± 0.56	1.68 ± 1.00	1.33 ± 0.62	12.32 ± 6.12	3.67 ± 1.33	4.33 ± 2.39	5.32 ± 2.02
Heterocephalobus	*Het*	5.88 ± 1.31	9.68 ± 6.49	6.52 ± 2.82	6.98 ± 1.48	5.86 ± 1.92	3.94 ± 2.31	2.33 ± 0.47	3.29 ± 1.23
Mesorhabditis	*Mes*	4.09 ± 2.06	4.20 ± 1.51	0.71 ± 0.43	0.00 ± 0.00	0.29 ± 0.21	1.82 ± 1.41	2.00 ± 1.08	1.32 ± 0.23
Rhabditis	*Rha*	0.00 ± 0.00	5.25 ± 3.03	7.92 ± 5.59	1.66 ± 0.47	0.00 ± 0.00	6.76 ± 2.10	1.33 ± 0.47	3.96 ± 1.40
Wilsonema	*Wil*	1.23 ± 0.87	0.00 ± 0.00	1.00 ± 0.58	0.00 ± 0.00	1.58 ± 0.73	0.25 ± 0.25	0.67 ± 0.47	0.33 ± 0.24
Fungivores									
Aphelenchoides	*Apd*	8.18 ± 5.17	2.25 ± 0.86	9.91 ± 3.34	10.65 ± 4.41	0.29 ± 0.21	0.34 ± 0.34	5.33 ± 0.47	6.22 ± 4.05
Aphelenchus	*Aps*	1.85 ± 0.27	9.67 ± 3.78	3.40 ± 1.03	7.65 ± 2.96	3.06 ± 0.70	6.73 ± 3.20	4.33 ± 2.01	9.92 ± 1.43
Ditylenchus	*Dit*	6.93 ± 2.60	0.67 ± 0.47	2.81 ± 1.95	3.66 ± 1.65	0.80 ± 0.57	0.74 ± 0.74	3.33 ± 0.85	0.99 ± 0.00
Dorylaimoides	*Dor*	1.65 ± 1.16	0.31 ± 0.22	1.26 ± 0.50	1.66 ± 0.85	1.73 ± 0.29	0.25 ± 0.25	1.67 ± 0.85	7.67 ± 3.52
Filenchus	*Fil*	14.46 ± 1.66	5.78 ± 1.96	17.64 ± 5.94	11.60 ± 3.43	13.61 ± 5.73	5.38 ± 4.18	15.33 ± 1.70	5.95 ± 1.86
Nothotylenchus	*Not*	4.13 ± 1.82	0.00 ± 0.00	5.61 ± 4.58	2.00 ± 1.41	1.94 ± 1.04	1.49 ± 1.49	1.67 ± 0.47	0.00 ± 0.00
Tylencholaimus	*Tyl*	0.00 ± 0.00	1.38 ± 0.67	0.52 ± 0.30	0.99 ± 0.70	0.92 ± 0.36	1.08 ± 0.71	3.00 ± 0.82	0.67 ± 0.47
Omnivores-Predators									
Aporcelaimellus	*Apo*	9.39 ± 1.15	0.98 ± 0.41	2.14 ± 1.19	1.99 ± 0.00	2.40 ± 1.36	6.20 ± 1.26	5.67 ± 1.18	1.98 ± 0.40
Discolaimium	*Dis*	0.41 ± 0.29	1.67 ± 0.24	0.23 ± 0.23	0.00 ± 0.00	1.99 ± 0.37	1.93 ± 0.39	3.33 ± 0.85	0.33 ± 0.24
Microdorylaimus	*Mid*	3.66 ± 2.16	1.96 ± 0.82	1.47 ± 0.63	1.66 ± 0.24	2.02 ± 0.36	1.43 ± 0.59	1.00 ± 0.41	1.99 ± 0.71
Plant-parasites									
Aglenchus	*Agl*	2.00 ± 0.74	0.67 ± 0.47	0.00 ± 0.00	1.65 ± 0.84	0.00 ± 0.00	0.92 ± 0.64	0.33 ± 0.24	1.00 ± 0.41
Boleodorus	*Bol*	1.42 ± 0.12	4.29 ± 2.40	0.44 ± 0.44	0.33 ± 0.24	1.33 ± 0.94	2.83 ± 1.27	1.33 ± 0.94	4.31 ± 1.03
Helicotylenchus	*Hel*	2.06 ± 1.45	2.31 ± 0.18	1.25 ± 0.78	4.98 ± 0.70	6.52 ± 3.26	4.27 ± 2.26	4.00 ± 0.41	3.65 ± 0.86
Miculenchus	*Mil*	0.00 ± 0.00	1.25 ± 0.88	3.18 ± 1.07	1.32 ± 0.62	0.29 ± 0.21	0.00 ± 0.00	2.00 ± 1.41	0.33 ± 0.24
Pararotylenchus	*Par*	1.83 ± 0.25	10.66 ± 4.72	5.43 ± 3.70	8.30 ± 0.46	6.09 ± 1.71	6.25 ± 2.58	7.00 ± 3.54	5.97 ± 0.83
Rotylenchus	*Rot*	1.23 ± 0.87	6.86 ± 2.14	5.67 ± 3.61	4.30 ± 1.68	17.72 ± 4.61	13.13 ± 4.66	6.00 ± 0.41	6.64 ± 1.26

The total percent of genera with <1% relative abundance is less than 5% and not listed in Table 2.

enrichment and structure footprints as illustrated in Fig. 2. At both depths, the FMF was greater under CS than under CC in both NT and CT systems.

3.5. Redundancy analysis on nematode genera responses to soil physiochemical properties

Redundancy analysis (RDA) revealed that NTCC and the other three treatments were clearly discriminated by the first principal component (Fig. 3a). The eigenvalues were 0.127 ($F = 3.942$, $P = 0.0060$) and 0.272 ($F = 2.252$, $P = 0.0020$) for the first canonical axis and all canonical axes, respectively. The first axis explained 46.8% of the species-environment variation and the second axis explained 36.9% of the variation. Redundancy analysis (RDA) showed that BD, SM and NO_3^-–N were relatively important factors which influenced the distribution of nematode genera (Fig. 3b). The eigenvalues were 0.157 ($F = 4.282$, $P = 0.006$) and 0.350 ($F = 1.547$, $P = 0.0160$) for the first canonical axis and all canonical axes, respectively, and the first two axes could explain 62.9% of the variation.

4. Discussion

4.1. Tillage and rotation effects on soil physiochemical properties

Soil physiochemical properties such as SOC and MBC were higher in NT than in CT at 0–5 cm depth in this study. Conservation tillage such as NT had a positive influence on the sequestration of soil organic matter and reduced the fluctuation in the surface temperature and moisture, which were all beneficial for soil biota [39]. In both NT and CT systems, lower values of SOC were found under CS compared with CC. Huggins et al. [2] indicated that less C inputs in corn-soybean rotation system than in continuous corn system tends to decrease the accumulation of SOC. In our study, compared with 5–15 cm soil depth, higher content of SOC were found at 0–5 cm depth among the four treatments ($P < 0.05$). Residues covering on the surface soil might enhance soil moisture, prevent C and N mineralization and maintain the soil fertility [10].

4.2. Tillage and rotation effects on soil nematode abundance and community composition

The total nematode abundance was greater under CS than under CC at 0–5 cm soil depth in our study. This finding was in agreement with the studies of Freckman and Ettema [14] and Rahman et al. [3], who also reported that nematodes were more abundant in the rotation system. In comparison to the monoculture system, crop rotation can cause changes in the substrate utilization patterns and may offer greater diversity of organic matter inputs by incorporating diverse crop residues, thus facilitating the increase of soil biota abundance and diversity [3,22,40]. In our study, in contrast with corn residues, soybean residues are rich in easily-utilizable sugars and proteins but poor in cellulose and hemicelluloses [5]. Thus crop rotation provided the easily-utilizable resource for soil nematodes.

The abundance of fungivores was higher in CT than in NT. Similarly, Fu et al. [25] and Liphadzi et al. [41] also found a greater abundance of fungivores in conventional tillage. The similar phenomenon was not found in the abundance of bacterivores in our study. This could be due to the trophic groups of nematodes playing different roles in different ecological processes. Yeates and Bongers [20] reported that bacterial-feeding nematodes tend to dominate at early stages of decomposition and that fungal-feeding nematodes contributed at later stages. Fu et al. [25] also concluded that the change from bacterivores to fungivores was a common feature in organic matter decomposition.

The responses of soil nematodes to tillage and rotation in our study were genus-dependent. For example, *Acrobeloides* only

Table 3
Nematode ecological indices (mean ± SE, $n = 4$) in different tillage and rotation treatments.

Soil depth	Indices	NT		CT		Tillage (T)	Rotation (R)	T × R
		CC	CS	CC	CS			
0–5 cm	Td	3.02 ± 0.30	2.56 ± 0.18	2.64 ± 0.22	2.98 ± 0.11	ns	ns	ns
	λ	0.09 ± 0.01	0.14 ± 0.02	0.12 ± 0.01	0.10 ± 0.01	ns	ns	ns
	H′	2.64 ± 0.11	2.37 ± 0.12	2.48 ± 0.12	2.61 ± 0.09	ns	ns	ns
	GR	4.38 ± 0.48	3.96 ± 0.37	4.26 ± 0.47	4.18 ± 0.30	ns	ns	ns
	NCR	0.44 ± 0.07B	0.70 ± 0.02A	0.43 ± 0.04	0.40 ± 0.05	<0.05	<0.05	<0.05
	EI	47.68 ± 5.88	54.11 ± 5.78	50.56 ± 6.74	40.25 ± 0.39	ns	ns	ns
	SI	61.90 ± 5.33	44.33 ± 4.61	41.57 ± 1.64	38.09 ± 6.84	<0.05	ns	ns
	BI	28.03 ± 3.55	33.79 ± 4.49	37.56 ± 2.63	43.34 ± 3.29	ns	<0.05	ns
	CI	72.21 ± 15.04A	30.51 ± 4.13B	66.65 ± 14.49	89.02 ± 5.64	ns	ns	<0.01
5–15 cm	Td	2.90 ± 0.33	2.88 ± 0.21	3.08 ± 0.25	3.18 ± 0.12	ns	ns	ns
	λ	0.12 ± 0.02	0.10 ± 0.01	0.10 ± 0.02	0.10 ± 0.02	ns	ns	ns
	H′	2.55 ± 0.10	2.51 ± 0.13	2.62 ± 0.19	2.70 ± 0.11	ns	ns	ns
	GR	4.77 ± 0.43	3.93 ± 0.52	4.36 ± 0.52	5.10 ± 0.48	ns	ns	ns
	NCR	0.55 ± 0.13	0.74 ± 0.10	0.43 ± 0.06	0.45 ± 0.08	<0.05	ns	ns
	EI	37.34 ± 2.34	50.67 ± 1.09	43.76 ± 3.88	46.17 ± 2.80	ns	<0.05	ns
	SI	64.19 ± 6.00	60.93 ± 6.08	60.40 ± 4.62	70.83 ± 0.25	ns	ns	ns
	BI	31.42 ± 6.19	27.62 ± 3.36	37.00 ± 7.56	28.19 ± 4.74	ns	ns	ns
	CI	97.50 ± 2.50A	26.65 ± 10.84B	75.34 ± 11.79	60.26 ± 14.11	ns	<0.01	<0.05

Td, trophic diversity; λ, Simpson index; H′, Shannon–Weiner index; GR, generic richness; NCR, nematode channel ratio; EI, enrichment index; SI, structure index; BI, basal index; CI, channel index. When significant interaction occur, only significant differences among CC and CS were labeled with different letters with each tillage system and at each soil depth as determined by an independent-samples T test, $P < 0.05$.

Table 4
Log-transformed metabolic footprints of different trophic groups in different treatments (mean, $n = 4$).

Soil depth	Tillage (T)	Rotation (R)	ln BFfoot	ln FFfoot	ln PPfoot	ln efoot	ln sfoot
0–5 cm	NT	CC	2.38B	2.37A	1.41	3.01	3.98
		CS	3.62A	1.81B	3.01	3.75	3.43
	CT	CC	3.45	2.40b	1.72	3.59	3.27
		CS	3.33	3.25a	2.98	3.94	3.76
	ANOVA						
	T		ns	<0.05	ns	ns	ns
	R		ns	ns	<0.01	<0.05	ns
	T × R		<0.05	<0.01	ns	ns	<0.05
5–15 cm	NT	CC	2.26	1.83	2.96	2.57B	3.74
		CS	3.86	1.74	2.76	3.98A	3.99
	CT	CC	3.16	2.86	2.68	3.64	4.13
		CS	3.92	3.30	3.00	4.05	4.38
	ANOVA						
	T		ns	<0.01	ns	ns	ns
	R		<0.01	ns	ns	<0.01	ns
	T × R		ns	ns	ns	<0.05	ns

BFfoot, bacterivore footprint; FFfoot, fungivore footprint; PPfoot, plant-parasite footprint; efoot, enrichment footprint; sfoot, structure footprint. When significant interaction occur, only significant differences between CC and CS were labeled with different capital letters in NT and lowercase letters in CT, respectively, as determined by an independent-samples T test, $P < 0.05$.

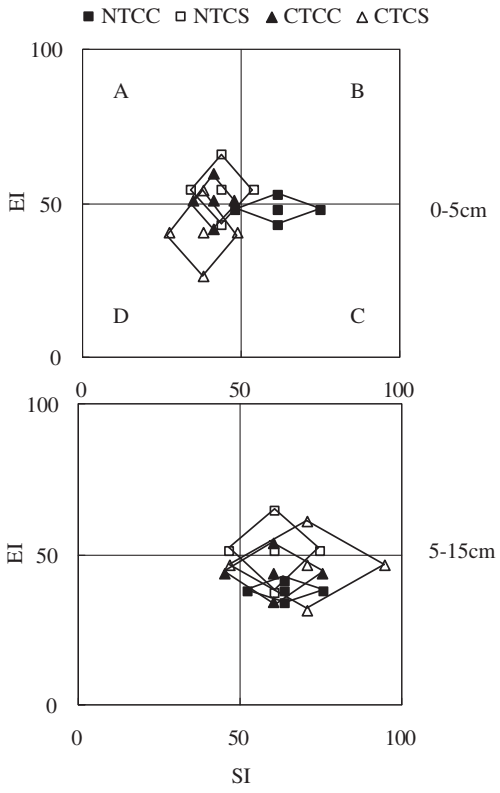

Fig. 2. Functional metabolic footprint of nematodes subjected to tillage and rotation effects at different soil depths. The vertical axis and horizontal axis of each footprint represent enrichment footprint and structure footprint respectively. The functional metabolic footprint is described by the sequentially joining points: (SI-0.5F_s, EI); (SI, EI + 0.5F_e); (SI + 0.5F_s, EI); (SI, EI-0.5F_e). F_s and F_e represent structure footprint and enrichment footprint, respectively. The nematode functional metabolic footprint is the total area of the two functional (enrichment and structure) footprints (Ferris 2010).

dominated under CS systems (Table 2). DuPont et al. [12] concluded that *r*-strategists such as *Acrobeloides* were often found in highly disturbed cropping systems compared with *K*-strategists. In addition, *Filenchus* was dominant under CC systems with high soil organic carbon in our study. Okada et al. [42] reported that *Filenchus* was more likely to occur in soils with abundant organic matter. The RDA analysis showed that soil nematode genera were clearly separated by tillage and rotation treatments. The use of nematode communities as bioindicators to determine the impact of agricultural management practices relies on the discrimination of nematodes at the genus level [43]. Our study also showed that different nematode genera had different preferences for soil microhabitats. For example, *Chronogaster* and *Discolaimium* were positively correlated to soil moisture (Fig. 3b). Many researches have reported that *Chronogaster* [44] and *Discolaimium* [45] are observed in the area saturated with water. Additionally, NTCC with higher content of SOC, SM and MBC distinguished from the other three treatments at the first axis (Fig. 3a). In this study, NTCS, CTCC and CTCS had the similar soil properties. Jiang et al. [46] suggested that soil environment might directly influence soil nematode

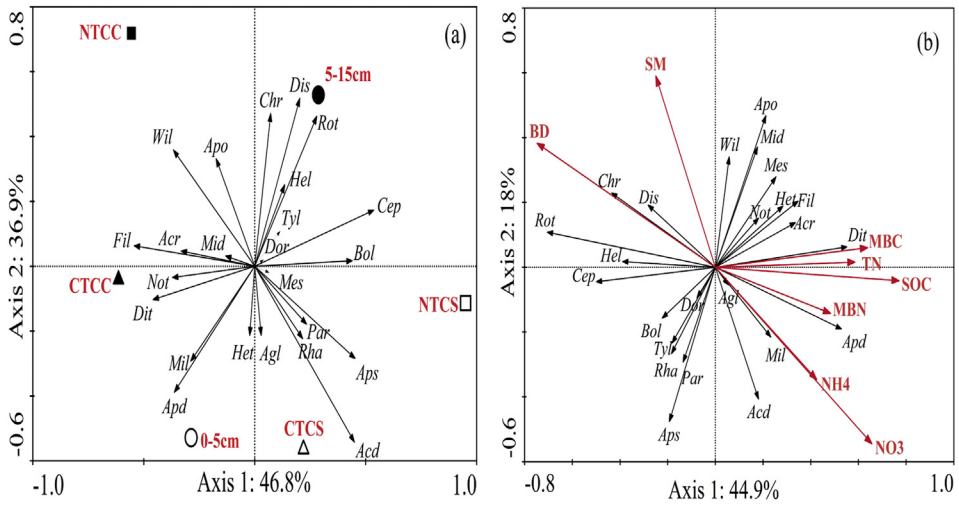

Fig. 3. Redundancy analysis (RDA) of the relationship between nematode genera and environment factors (a) as well as nematode genera and soil physiochemical properties (b) at 0–15 cm soil depth. Nematode genus abbreviations were shown in Table 2. SOC, total soil organic carbon; TN, total nitrogen; SM, soil moisture; BD: bulk density; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; NO3, NO_3^--N; NH_4, NH_4^+-N.

communities. Therefore, we also agreed that the soil properties played an important role in determining the distribution pattern of nematodes.

4.3. Tillage and rotation effects on nematode ecological indices

In NTCC treatment, the fungal-based channel was at 0–5 cm soil depth and bacterial-based channel at 5–15 cm depth. Our results reconfirmed the observations of Ding et al. [47] who found that NT led to a fungal dominant system and this phenomenon was more significant in the 0–5 cm layer. The changes of decomposition channel from fungal channel to bacterial channel might due to the anaerobic environment in the deeper layer in NT system. It is known that fungi are aerobic organisms [47]. Higher bulk density and soil moisture in our study in NTCC treatment at 5–15 cm soil depth might lead to lower soil porosity and resisted air flow. It might have negative effects on fungi accumulation which indirectly influenced fungivores at deeper layer.

The higher value of NCR indicated that the bacterial-dominated decomposition pathway was dominant only in NTCS. In contrast, many other studies reported that the fungal decomposition channel dominated in no-tillage [21,48]. Our results suggest that the interactive effect of tillage and rotation changed the decomposition channel. The addition of residues with different quality and quantity in rotation systems can lead to the variations in nematode community structure [49]. In our study, soybean residues with N-rich tissues tend to be decomposed through bacterial-dominated "fast" pathways [50,51]. Therefore, we consider that crop residue quality in the rotation system may have contributed to the changes in the NCR.

The nematode faunal analysis on structure index (SI) and enrichment index (EI) can provide information about the status of the soil food web [37]. Under both CC and CS systems, greater SI was found in NT than in CT, which indicates that soil food webs in no-tillage with relatively few disturbances tend to be a more stable and structured. Sánchez–Moreno et al. [52] also showed that the soil food web was more complex in an organic no-tillage system with the high SI value. At 0–5 cm soil depth, under the CS system, relatively lower value for SI and higher value for CI in CT than in NT, which suggested that soil food web was disturbed by the conventional tillage practices [37,53]. Therefore, we suggested that the soil food web in the conventional tillage treatment was unfavorable for the development and stability of the soil ecosystem.

4.4. Tillage and rotation effects of nematode functional metabolic footprint

In our study, nematode metabolic footprints provided information about the structure and function of soil food webs with different agricultural management practices. The nematode trophic footprints indicated the C and energy following into the soil food web through their respective trophic channels [26]. In NT system, higher FFfoot but lower BFfoot were found under CC, which also suggested a greater flow of resources into the food web through fungivorous channels than bacterivorous channels. The Enrichment footprint (efoot) can be regarded as an indicator of C and energy flow through *r*-strategists [27]. Relatively higher enrichment footprints (efoot) were found under CS than under CC, which suggested the enhancing productivity and turnover rates of the enrichment indicators in the rotation system to maintain metabolic balance [26].

At both depths, we found a similar variation trend that the functional metabolic footprint was larger under CS than under CC in both tillage systems. A greater functional footprint suggested that higher amounts of C were used for nematodes production [23]. Diverse resource of organic matter in rotation system increased the input and improved the quality and quantity of residues, which was therefore more beneficial for soil nematodes to utilize resources. On one hand, cover crop quality and quantity were important determinants of the nature and magnitude of soil food web services [12]. On the other hand, soil nematodes as significant regulators of food web have influence on residue decomposition and nutrients in ecosystems [25].

5. Conclusions

In conclusion, our study shows that no-tillage practice promotes soil organic carbon accumulation and increases soil microbial biomass carbon. Nematode trophic footprints respond differently to the tillage and rotation effects, and offer more information on carbon and energy entering the soil food webs. Nematode abundance and functional metabolic footprint all increase at 0–5 cm soil

depth in rotation system. The application of rotation practices in a no-tillage system may result in a bacterial-dominated decomposition pathway at both depths. Nematode community analysis indicates that a no-tillage system is beneficial for soil ecosystem stability and sustainability, and that a corn-soybean rotation system provides a more diverse residue resource entry into soil food webs.

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