Soil Ecol. Lett. 2019, 1(3-4): 147–156
https://doi.org/10.1007/s42832-019-0010-1

RESEARCH ARTICLE

Organic amendment effects on nematode distribution within aggregate fractions in agricultural soils

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ARTICLE INFO

Article history:
Received June 19, 2018
Revised October 22, 2018
Accepted November 10, 2018

Keywords:
Organic amendment
Soil aggregate fractions
Nematode communities
Macroaggregate
Microaggregate

ABSTRACT

To evaluate the effect of organic amendments on soil nematode community composition and diversity within aggregate fractions, a study was initiated in agricultural soils with four-year organic amendments. Soil samples were collected from the plow layer (0–20 cm) under three cornfield management scenarios: 1) conventional cropping (CK, corn straw removal and no organic manure application); 2) straw retention (SR, incorporation of chopped corn stalk); and 3) manure application (MA, chicken manure input). The soil samples were fractionated into four aggregate sizes, i.e., >2 mm (large macroaggregates), 1–2 mm (macroaggregates), 0.25–1 mm (small macroaggregates), and < 0.25 mm (microaggregates, silt and clay fractions). The composition and diversity of soil nematode communities were determined within each aggregate fraction. The results showed that both SR and MA treatments significantly increased the percentage of macroaggregates (>1 mm) and only MA treatment strongly increased the mean weight diameter compared to the CK ($P < 0.05$). The abundance of total nematodes and four trophic groups were affected significantly by the aggregate fractions and their higher abundance occurred in the larger aggregates. The effects of aggregate size on most nematode genera were significant. Bacterivores in the small macroaggregates and microaggregates, and fungivores in the large macroaggregates were significantly different among treatments. The percentage of bacterivores increased after the application of organic materials, while that of fungivores decreased. It can be concluded that organic management significantly affects soil aggregation and soil characteristics within aggregates, and the aggregate size subsequently influences the distribution of nematode communities.

1 Introduction

Organic amendments have been recognized as a sustainable agricultural strategy to improve soil fertility and modify both soil aggregation and soil biotic community composition (Jiang et al., 2013; Zhang et al., 2016a; Hlava et al., 2017). Organic matter addition provide carbon substrate as cementing agent to involve in soil aggregation process and then enhance soil aggregate stability (Ahmad et al., 2008; Sarker et al., 2018). Soil organic amendment is also crucial for soil fauna due to the increase of nutrient availability and interaction between soil fauna and nutrient (Biederman et al., 2008).

Soil nematodes play essential roles in functioning of soil ecosystems (Wang et al., 2018). They live in water-filled pore spaces with different sizes and shapes, which largely depend on the size and arrangement of soil aggregates (Lebron et al.,

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2002). Therefore, the distribution of soil nematodes within different aggregates was likely driven by food distribution, living space and other factors induced by organic amendment (Briar et al., 2011a). Many studies showed that soil nematode community composition and diversity was affected by organic amendment practices such as the residue coverage of vetch, oat, cotton-gin and rye, and the application of swine manure, dairy cow or beef calf manure (Nahar et al., 2006; Hlava et al., 2017). However, the effects of organic amendment on the distribution of soil nematodes within different soil aggregate fractions are still not sufficiently understood. To understand the biological effect of organic amendment in agricultural soils, soil biotic communities should be explored at different spatial scales. Distribution of nematode communities within aggregates will provide a holistic measure of the biotic and functional status of soils (Briar et al., 2007; Hlava et al., 2017).

Some studies have concerned biological effect in soil aggregates, such as microbial patterns, i.e. inside and outside of soil aggregates, as influenced by agricultural management (Mummey et al., 2006; Briar et al., 2011a; Zhang et al., 2013a). Nielsen et al. (2010) found that spatial isolation at micro-scales within soil aggregates may have a stronger influence on the species richness of microorganisms than the small-scale heterogeneity. Due to the close interrelationships between nematodes and microbe, the addition of organic materials to soil can increase the microbial activity and then enlarge the food base for microbial grazers such as free-living nematodes (Briar et al., 2011b; Jiang et al., 2017). Briar et al. (2011a) found that nematode communities were more limited by habitable pore space for the soil fractions than by resource availability compared to microbial communities. Furthermore, the changes induced by organic input in soil nematode communities within aggregates may have important implications for the stability of soil food web. Most studies have primarily focused on the relationship between the distribution of soil microbes and soil aggregate fractions (Nielsen et al., 2010; Li et al., 2018; Liang et al., 2019). Relatively little is known about the effect of organic amendments on the distribution of nematodes within soil aggregates. It is important to assess nematode community composition in microhabitats for comprehensive insight into the structure and function of soil food web.

Therefore, our objectives were to investigate the effects of organic amendments on the distribution of soil nematode communities within different aggregate fractions. We hypothesize that the effects of organic amendment on soil nematode communities vary at the level of soil aggregates, and macroaggregates benefit the multiplication of nematodes due to the increase of nutrient and space.

2 Materials and methods

2.1 Experimental site

This experiment was set up in April 2007 at a soil amendment site (42°27′ N, 122°28′ E), which was located in Zhangwu county of Liaoning province, China, where corn (*Zea mays* L.) was the main crop. This region lies in the northern temperature zone and is characterized by a continental monsoon climate, with a mean annual temperature of 7.1°C, mean annual precipitation of 510 mm and mean annual evaporation of 1832 mm. The maximum average wind speed is 25 $m \cdot s^{-1}$ in April. The soil is classified as Cambisol (IUSS working group WRB, 2014) with 1.23% soil organic matter, 840 $mg \cdot kg^{-1}$ total N, 77.00 $mg \cdot kg^{-1}$ available N (exchangeable ammonium-N and nitrate-N), 4.10 $mg \cdot kg^{-1}$ available P, 78.00 $mg \cdot kg^{-1}$ available K, pH (H_2O) 8.20 at 0–20 cm depth in 2007 (Liang et al., 2011). Before the experiment, corn was planted in the field for more than 20 years. The agricultural activities consisted of rotary tillage followed by sowing corn in the spring, and inter-tillage and artificial weeding in the jointing stage of corn. No herbicide was applied during the experimental process.

2.2 Experimental design

The experimental design was a randomized complete block of nine plots (three treatments with three replicates, 30 m^2 each). The plots were separated from each other by a 1-m-wide alley. The three treatments included a conventional cropping system (CK, corn straw removal and no application of organic manure), a straw retention system (SR, application of 9000 $kg \cdot ha^{-1}$ chopped corn stalks) and a manure application system (MA, inputs of 15000 $kg \cdot ha^{-1}$ chicken manure) (Liang et al., 2011; Zhang et al., 2014). The above-mentioned application rates were in accordance with routine practices in the study site. The corn stover was chopped to about 3–5 cm and applied on the surface after harvest. And manure was applied before sowing together with other chemical fertilizers as base fertilizers. For each treatment, the application rates of N (urea), P_2O_5 (diammonium phosphate), and K_2O (potassium chloride) were the same, which were 210, 60, and 60 $kg \cdot ha^{-1}$, respectively. Chemical fertilizer and organic amendments were applied during each growing season from 2007 to 2011 (Liang et al., 2011).

2.3 Soil sampling

Before corn sowing, soil samples were collected from the plow layer (0 – 20 cm) of the nine plots (three treatments with three replicates) in April 2011. In the central rows of each plot, two pits were dug. After removing the surface residue, one undisturbed soil block (10 cm length × 10 cm width × 20 cm height) was taken from each pit. The soil samples from two pits of each plot were homogenized roughly and sorted out as one replicate, and then stored at 4°C and used for the separation of aggregates.

2.4 Aggregate-size separation

Dry-sieving of soil may reduce the disruption of physical habitat of soil microbial communities (Schutter and Dick, 2002). Thus, the dry-sieving method was considered to be

better than wet-sieving for studying biological communities within the aggregates (Gartzia-Bengoetxea et al., 2009). Field-moist soils were dried at 4°C until the gravimetric water content decreased to approximately 80 $g \cdot kg^{-1}$ soil. At this moisture level, soils could be passed through finer sieves for aggregate-size separation (Zhang et al., 2014). One part was used to determine soil nematodes of bulk soil, and the other part continued to be sieved. After the removal of visible plant residues and stones, the soil samples were passed through a 5 mm sieve (Schutter and Dick, 2002).

For each time, soil aggregates were separated by placing 100 g of cool-dried sub-samples (< 5 mm) into a nest of sieves mounted on a Retsch AS200 Control (Retsch Technology, Düsseldorf, Germany) and mechanically shaken (amplitude 1.5 mm) for 2 min to divide the soils into the following four aggregate-size classes: >2 mm (large macroaggregates), 1–2 mm (macroaggregates), 0.25–1 mm (small macroaggregates) and < 0.25 mm (microaggregates and silt and clay fractions) (Gartzia-Bengoetxea et al., 2009; Briar et al., 2011a; Zhang et al., 2012a). Small aggregates passing through a 0.25 mm sieve are considered too small for nematode to enter and this fraction will thus referred to as inter-aggregate soil and space (Briar et al., 2011a). The sieving was conducted several times until the amount of the smallest faction was greater than 50 g. Then fractionated samples for each aggregate-size class from each sieving were combined to make composite samples to determine mean weight diameter and composition of nematode communities. Mean weight diameter, MWD = Σ (percentage of sample weight on sieve $\times$ the mean diameter of the size classes), was calculated as an index for characterizing the structure of the bulk soil (Van Bavel, 1950).

2.5 Soil nematode identification

Nematodes were extracted with a modified cotton–wool filter from a 50 g soil sample from each aggregate-size class after dry-sieving or from bulk soil without sieving (Verschoor and De Goede, 2000). Nematode populations were expressed as the number of nematodes per 100 g of dry soil. Using an inverted compound microscope (100 $\times$ magnification), at least 100 nematodes from each sample were identified to the genus level. If the population was less than 100 individuals, all individuals were identified. The trophic groups of soil nematodes were assigned according to their feeding habits and life-history characteristics (Yeates et al., 1993). Most genera belonging to Tylenchidae and Nordiidae were assigned to plant parasites and omnivores-predators, respectively, except for *Filenchus* and *Longidorella*, which were classified as fungivores and plant parasites, respectively, as supported by recent evidence (Okada et al., 2005; Erum and Shahina, 2010).

2.6 Nematode community analyses

The following ecological indices for soil nematodes were calculated: Trophic diversity, TD = $1/\Sigma p_i^2$; Simpson's dominance index, $\lambda = \sum p_i^2$; Shannon diversity, $H' = -\sum p_i \ln p_i$, where p_i is the percentage of individuals in the *i*th taxon; Maturity index, $MI = \Sigma v(i) \cdot f(i)$, where $v(i)$ is the *c-p* value of taxon *i*, $f(i)$ is the frequency of taxon *i* in a sample (Bongers and Ferris, 1999; Zhang et al., 2013b); Nematode channel ratio, NCR = $B/(B + F)$, where *B* and *F* are the percentages of the nematode fauna allocated to bacterivorous and fungivorous groups (Yeates, 2003); Enrichment index, $EI = 100 \times e/(b + e)$; Structure index, $SI = 100 \times s/(b + s)$; Basal index, $BI = 100 \times b/(b + e + s)$ and channel index, $CI = 100 \times (0.8Fu_2/(3.2Ba_1 + 0.8Fu_2)$ (Ferris et al., 2001), where b, e and s is the abundance of individuals in guilds in the basal component, enrichment component and structural component weighted by their k_b, k_e and k_s values, respectively. k_b is the weighting assigned to guilds Ba_2 and Fu_2, k_e to guilds Ba_1 and Fu_2, and k_s to guilds Ba_3–Ba_5, Fu_3–Fu_5, Op_3–Op_5. Ba_x, Fu_x, Op_x, Pp_x (where x = 1–5) represent the functional guilds of nematodes that are bacterivores (Ba), fungivores (Fu), omnivores-predators (Op) or plant parasites (Pp) where the guilds have the character indicated by x on the colonizer–persister (cp) scale (1–5) according to their *r* and *K* characteristics and nematodes in the same functional guilds respond similarly to food web enrichment and to environmental perturbation.

2.7 Statistical analysis

Nematode abundances were ln (x + 1) transformed to normalize data prior to statistical analysis. All statistical analyses were run with SPSS statistical software (SPSS Inc., Chicago, IL). To test the main effects and interactions of organic treatment and aggregate effects, general linear model analysis of variance designed for split plot was performed with organic treatment and aggregate class as fixed factors and replicates as random factors. Treatment was considered the main factor and aggregate-size class a sub-plot factor. One-way ANOVA was used to analyze the treatment effect on each aggregate fraction and the aggregate-size effect on each treatment. Comparisons of the means for aggregate fraction and management systems were made using Tukey's honestly significant difference. Differences at $P < 0.05$ were considered statistically significant.

3 Results

3.1 Aggregate-size distribution and mean weight diameter

For each treatment, aggregate-size percentage varied significantly with aggregate-size classes (Table 1). Small macroaggregates (0.25 – 1 mm) dominated and their percentages were higher than those of other aggregate sizes. Compared with the CK, both SR and MA treatments significantly increased the percentage of macroaggregates (>2 mm and 1 – 2 mm) ($P < 0.01$), and only MA treatment significantly increased the values of mean weight diameter (MWD) ($P < 0.05$).

Table 1 Aggregate-size distribution and mean weight diameter under different treatments.

Treatment	Aggregate proportion in size class (%)				MWD
	< 0.25 mm	0.25–1 mm	1–2 mm	>2 mm	
CK	26.60	40.12	13.80	19.47	1.17
SR	23.91	36.42	17.01	22.66	1.31
MA	20.01	37.19	18.32	24.47	1.39

CK, conventional cropping system; SR, incorporation of chopped corn straw; MA, inputs of chicken manure; MWD, mean weight diameter.

3.2 Total nematode abundance and trophic groups within aggregates

The effect of organic treatments on the total nematode abundance was not significant and the aggregate effect was significant ($P < 0.01$). The average values of total nematode abundance (100 g^{-1} dry soil) across agricultural treatments were significantly higher in macroaggregates (>2 and 1 –2 mm) and lower in microaggregates compared with bulk soil ($P < 0.05$) (Fig. 1). For each treatment, the total nematode abundance increased significantly with increasing aggregate size ($P < 0.05$) (Fig. 1). Total nematode abundance was negatively correlated with the percentage of aggregates ($r = 0.40$, $P < 0.05$).

The aggregate effects on the abundances of four trophic groups ($P < 0.01$) and the treatment effects on those of bacterivores and fungivores ($P < 0.05$) were significant (Fig. 1). The highest abundances of the four trophic groups all appeared in the large macroaggregates or macroaggregates, and the lowest in the microaggregates (Fig. 1). Bacterivores and fungivores made up 64%–88% of the total nematode abundance. Bacterivores in the small macroaggregates and microaggregates, and fungivores in the large macroaggregates were significantly different among treatments ($P < 0.05$), with highest values occurring in the MA or SR treatments. In the bulk soil, no significant treatment effects on four trophic groups were observed.

3.3 Nematode community composition

Forty-two genera belonging to 20-one families were identified (Table 2). The effects of aggregate size on all genera, except for *Paraphelenchus* and *Rotylenchus*, were significant ($P < 0.05$) (Data not shown in Table 2). The effects of organic treatments on 13 genera, such as *Cephalobus*, *Plectus* and *Tylencholaimus*, were significant ($P < 0.01$). Some rare genera, such as *Aporcelaimellus*, *Longidorella*, *Macroposthonia*, *Panagrolaimus* and *Thornia* were found in only one or a few sample(s), and generally showed no significant responses to organic amendments.

3.4 Nematode ecological indices

With increasing aggregate size, the values of TD, H' and MI increased significantly, and λ and BI decreased significantly ($P < 0.01$) (Table 3). The values of TD, H', MI and CI significantly decreased in the MA treatment compared with

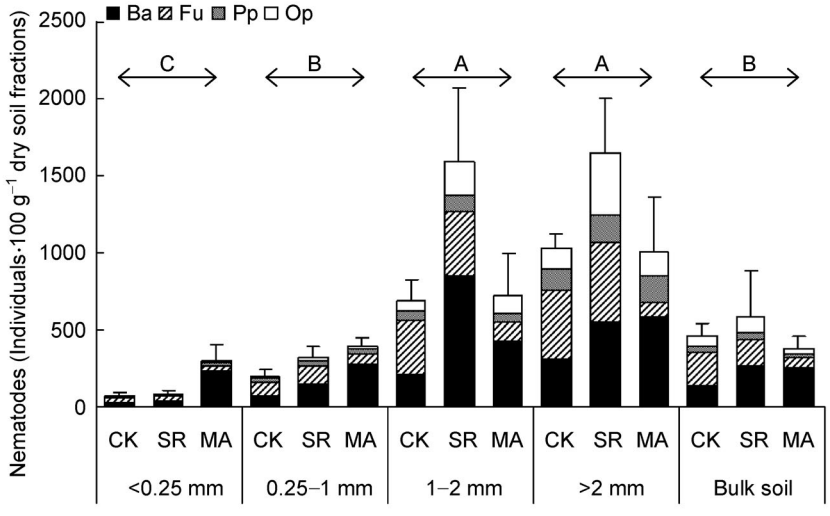

Fig. 1 Total nematode abundance (individuals ·100 g^{-1} dry soil) within four soil aggregate fractions under different treatments. Error-bars represent the standard error. Grouped means designated by inclusion line with different capital letters indicated significant differences among aggregate fractions determined using Tukey's HSD ($P < 0.05$). CK, conventional cropping system; SR, incorporation of chopped corn straw; MA, inputs of chicken manure. Ba, bacterivores; Fu, fungivores; Pp, plant-parasites; Op, omnivores-predators.

Table 2 Percentage contribution (%) of various nematode genera to the nematode assemblage within aggregates.

TG	Nematode family	Treatment	CK				SR				MA			
		Aggregate (mm)	< 0.25	0.25 – 1	1 – 2	>2	< 0.25	0.25 – 1	1 – 2	>2	< 0.25	0.25 – 1	1 – 2	>2
Ba	Cephalobidae	*Acrobeles*	9.7	2.6	1.2	3.1	0.0	3.8	2.0	1.9	1.3	1.6	1.6	2.9
		Acrobeloides	0.0	0.0	0.9	1.8	6.3	0.0	1.6	3.3	1.7	0.3	4.5	4.8
		Acrobelophis	1.5	1.7	0.6	0.0	2.3	2.9	3.3	0.0	4.4	4.5	5.4	0.0
		Cephalobus	8.5	7.8	4.7	4.1	9.8	9.7	11.3	6.9	16.1	26.0	23.1	18.7
		Cervidellus	1.5	5.0	4.6	3.1	2.7	1.0	1.3	0.3	2.2	10.4	1.9	0.3
		Chiloplacus	1.6	0.0	0.0	0.3	0.0	0.0	0.3	0.0	1.3	0.0	0.3	0.3
		Eucephalobus	5.2	0.9	0.9	2.6	1.1	1.7	0.6	4.7	0.0	0.6	1.0	2.3
		Heterocephalobus	1.9	0.9	0.6	0.0	2.1	1.0	2.3	2.2	5.3	2.2	1.6	0.0
	Alaimidae	*Alaimus*	0.0	2.8	3.4	6.8	0.0	6.5	10.0	8.4	0.3	1.3	3.8	15.6
	Plectidae	*Plectus*	0.0	9.2	7.1	4.5	2.3	13.1	14.2	0.3	0.0	0.0	0.6	0.0
		Wilsonema	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0		
		Panagrolaimus	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Prismatolaimidae	*Prismatolaimus*	1.5	3.3	2.5	0.8	0.0	0.3	1.0	0.0	0.0	0.7	0.6	0.0
	Rhabditidae	*Rhabditis*	7.9	5.5	2.5	1.0	17.8	7.7	3.2	2.8	34.9	23.3	14.3	12.8
Fu	Aphelenchoididae	*Aphelenchoides*	5.0	7.6	7.4	3.9	1.0	2.9	1.3	0.6	0.0	1.0	0.0	0.0
		Rhadinaphelenchus	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Aphelenchidae	*Aphelenchus*	4.8	6.9	8.2	4.2	10.5	2.6	5.8	2.4	3.3	2.6	1.0	2.4
		Paraphelenchus	3.5	3.9	2.7	7.1	15.2	12.0	4.2	8.6	6.3	6.1	5.9	2.6
	Diphtherophoridae	*Diphtherophora*	0.0	1.4	1.6	3.2	0.0	1.3	5.1	6.4	0.3	0.0	0.0	1.5
	Anguinidae	*Ditylenchus*	1.3	2.4	2.4	2.2	3.4	4.2	3.9	0.6	1.5	2.3	0.6	1.0
	Tylenchidae	Filenchus	7.1	3.3	6.4	2.4	7.6	8.7	6.2	3.7	0.9	2.6	2.2	0.0
	Leptonchidae	*leptonchus*	8.2	0.0	4.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Dorylaimoides	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
		Tylencholaimus	6.3	15.5	19.2	21.6	0.6	3.6	2.3	10.1	1.3	2.3	6.7	2.9
Pp	Tylenchidae	*Boleodorus*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0
		Malenchus	1.5	5.3	2.7	10.1	0.6	0.6	1.6	0.6	0.0	0.0	3.5	3.1
	Dolichodoridae	*Dolichorhynchus*	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Belondiridae	*Dorylaimellus*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.2	0.0	0.0	0.6	5.2
	Hoplolaimidae	*Helicotylenchus*	3.2	1.0	0.9	0.8	1.6	3.3	2.3	5.1	3.0	1.6	0.6	1.0
		Rotylenchus	14.6	6.3	4.9	0.9	6.7	0.6	1.6	3.1	13.4	5.0	4.8	5.5
	Nordiidae	*Longidorella*	0.0	0.0	0.0	0.3	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0
	Criconematidae	*Macroposthonia*	1.6	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
	Pratylenchidae	*Pratylenchoides*	3.0	0.4	0.3	0.0	5.1	4.5	1.9	0.6	0.9	1.6	0.0	1.2
		Tylenchorhynchus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Op	Aporcelaimidae	*Aporcelaimellus*	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
	Discolaimidae	*Discolaimium*	0.0	0.5	0.6	0.8	0.0	0.3	0.7	3.8	0.0	0.0	0.0	0.6
		Discolaimus	0.0	0.0	0.6	0.0	0.0	0.6	0.0	0.0	0.0	0.0	1.3	0.0
	Qudsianematidae	*Dorydorella*	0.0	0.0	0.9	2.4	1.1	2.3	0.0	1.9	0.6	0.0	7.1	0.3
		Microdorylaimus	0.0	0.0	0.6	2.6	0.0	1.6	4.2	3.2	0.0	0.3	1.0	0.3
		Thonus	0.0	4.4	6.8	5.7	0.0	0.6	7.5	14.1	0.3	2.5	6.0	14.6
	Longidoridae	*Longidorus*	0.0	0.3	0.3	1.3	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
	Nordiidae	*Thornia*	0.6	0.3	0.0	1.0	2.1	1.0	0.0	0.0	0.0	0.9	0.0	0.0

TG, trophic group; CK, conventional cropping system; SR, incorporation of chopped corn straw; MA, inputs of chicken manure. Ba, bacterivores; Fu, fungivores; Pp, plant-parasites; Op, omnivores-predators.

the CK and SR treatments regardless of aggregate sizes ($P < 0.05$). The values of λ, NCR and BI were also significantly different among treatments regardless of aggregate sizes ($P < 0.05$).

The SI was significantly affected by the organic treatment and the aggregate size ($P < 0.01$), while the EI was not. The soil nematode faunal analysis (Fig. 2) showed a shift that plots from quadrat C at the large macroaggregates and macroaggregates to quadrat A and D at the microaggregates, which indicated that the less disturbed or relative undisturbed stable environment in >1 mm macroaggregates compared to other fractions. This shift was more obvious in the organic amendment treatments (SR and MA) than the CK.

4 Discussion

4.1 Effect of organic amendments on soil nematode communities

The effect of organic amendments on the trophic group within the aggregate fractions was significant. Organic amendments affected the densities of opportunistic bacterivores and fungivores not only by increasing the supply of nutrient resources, but also by changing soil habitat (Biederman et al., 2008; Wang et al., 2018). For example, the corn stalk application increase soil carbon and nitrogen, soil moisture and soil temperature, which are all important factors being related to soil nematode communities (Thakur et al., 2014; Zhang et al., 2016a; Sun et al., 2018). Additionally, organic amendment with a high level of available nutrient source influenced microbial community structure, activities and functions, and then soil nematode communities, especially for bacterivores and fungivores, were affected through predator–prey interactions (Zhang et al., 2016b; Cesarano et al., 2017; Zheng and Marschner, 2017). Bacteria and fungi have distinct metabolic abilities to break down substrates with different qualities. Bacteria prefers to easily-available and fungi prefers to refractory substrates (Fabian et al., 2017), which explain a different response to organic treatments between bacterivores and fungivores in our study. Bacterivores as the opportunists of nematodes were more sensitive to higher nutrient resources (García-Álvarez et al., 2004). Significant increases in the NCR also supported that organic matter decomposition was achieved primarily through the bacterial-based energy pathway, which was faster than the fungal-based channel (Ruess and Ferris, 2004; Ferris and Bongers, 2006). This opposite trend between bacterivores and fungivores was also the reason for no significant organic amendment effect on the total nematode abundance. Nahar et al. (2006) and Jiang et al. (2013) also proved that there were high numbers of bacterivores and low diversity indices in

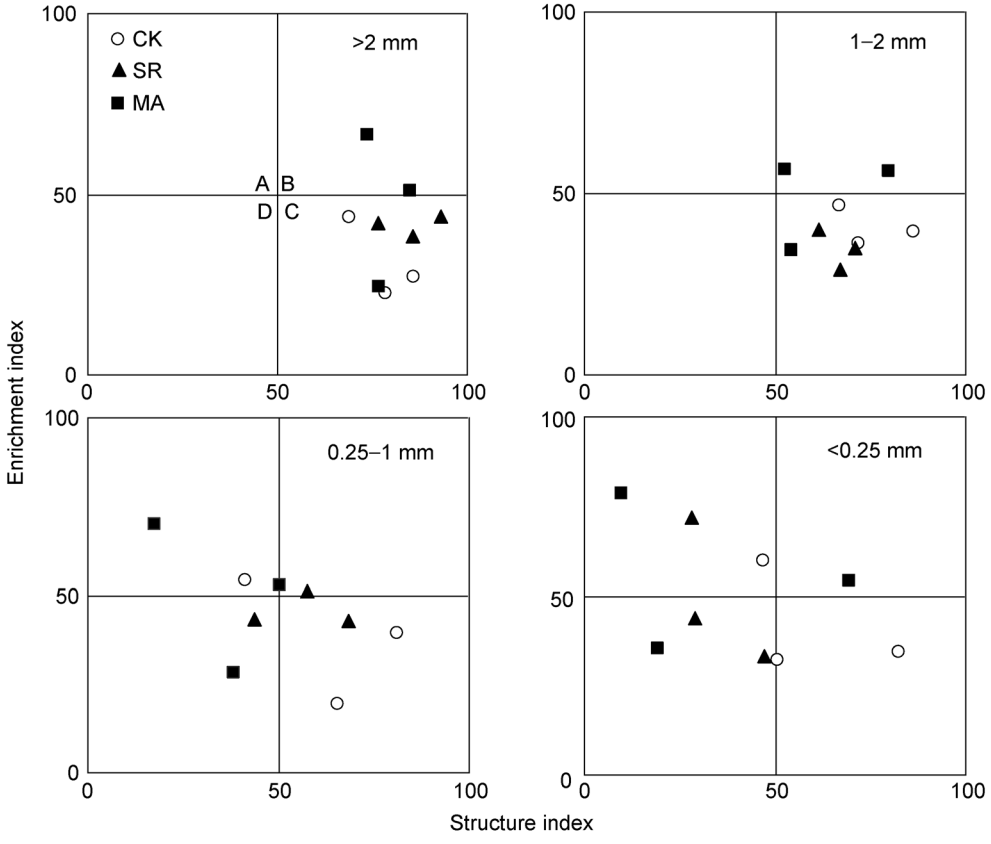

Fig. 2 Nematode faunal analysis within four soil aggregate fractions under different organic treatments. CK, conventional cropping system; SR, incorporation of chopped corn straw; MA, inputs of chicken manure.

manure-amended plots. However, Griffiths et al. (2010) considered that the bacterial:fungal ratio or decomposition pathway measured from bacterivores and fungivores gave conflicting results in many respects. Measuring multiple indicators so as not to rely on a single attribute was needed to identify the mechanisms responsible for the organic improvement.

4.2 Effect of aggregate fractions on soil nematode communities

Although the small macroaggregate was the dominant class, higher nematode abundances were observed in the macroaggregates (>2 mm and 1–2 mm fractions). The change of total nematode abundance increased with increasing aggregate size but not percentage of the aggregate fractions. Being consistent with the total nematode abundance, a significant increase in the four trophic groups was found as aggregate size increased. Not only the abundance but also the diversity of soil nematodes increased significantly by increasing aggregate size, as indicated by the TD and H'. Nematode faunal analysis showing by SI and EI indicated that habitats in macroaggregates provided free-living nematodes with a relatively stable living environment relative to small aggregates. A relatively higher abundance of omnivores-predators resulted in a lower BI in the large macroaggregates. Probably the small space of aggregates fractions might be one of the important limiting factors for nematodes such as the omnivores-predators with relatively large body. Briar et al. (2011a) considered that nematode distribution depended largely on not only their body size, but also their feeding habits and the availability of nutrient materials within aggregate fractions. The macroaggregates provided more intra-aggregate pore space for nematodes survival and more nutrients than microaggregates (Briar et al., 2011a). Additionally, the rarity of roots, small pore size and low pore volume, and physical constraints within and between the microaggregates were also the causes of nematode sparseness (Bonkowski et al., 2009).

4.3 Effect of organic amendments on soil aggregate fractions

Organic amendments significantly increased the percentage of macroaggregates (>1 mm) and mean weight diameter (MWD). Celik et al. (2010) and Jiang et al. (2017) found that applications of organic materials significantly increased the values of MWD and promoted the formation of macroaggregates. Kushwaha et al. (2001) showed that in a tropical dryland agroecosystem of Varanasi in India, residue retention increased the percentage of soil in the >4.75 mm water-stable soil aggregate fraction. Organic residue could be a catalyst for biological activity and induce binding of soil particles onto macroaggregates (Zhang et al., 2013a). Organic amendment measures, such as crop residue or manure application, enhanced soil aggregate stability through the positive effects on soil binding agents (Zhang et al., 2014). Therefore, organic amendment is an available strategy for increasing aggregation and reducing soil degradation (Ahmad et al., 2008).

4.4 The relationships among organic amendments, soil aggregate fractions and nematode communities

The organic amendment provided organic resources and aggregate binding agents to soil, which can bind small macroaggregates or microaggregates into large macroaggregates, then strengthened aggregate stability (Zhang et al., 2012a). The effect of organic amendments on soil nematodes resulted primarily from the change of nutrient resources (Zhao et al., 2013; Zhang et al., 2014), whereas the influence of aggregate fractions on soil nematodes mainly resulted from the soil physical structure change (Briar et al., 2011a). Since organic amendments affected the distribution of aggregates, and aggregation influenced the availability of organic material inputs, it is difficult to separate their concurrent effect on soil nematode communities. For example, many of the studied nematode genera were sensitive to both the aggregate size and organic amendment treatment. The alteration of soil nematode genera might be due to a concurrent effect of soil microclimate change and bottom-up control produced by organic amendments and aggregate size (Zhao et al., 2014). The effects of the two types of organic amendments were different. Straw retention increased the total nematode abundance and diversity in larger aggregates and was an important driver of soil nematode communities (Okada and Harada, 2007; Zhang et al., 2012b). The manure treatment tended to decrease the total abundance and diversity of nematodes compared with the control. This may depend on that the manure treatment increased the intensity and frequency of extreme disturbances of the soil ecosystem, thus negatively affecting nematode communities. MI was negatively related to disturbance and their low values in MA treatment also proved that more disturbance from manure application.

Probably the small size of soil nematodes (typically 40 μm to 1.0 mm in length) made them unable to reshape soil, which forced them to use existing pore paces, water cavities, or channels for locomotion within soil (Neher, 2010). The effect of soil nematodes on aggregates may be indirect through regulating soil nutrient cycling and availability and then contribute to the development of improved soil structure (Biederman et al., 2008). Therefore, the effect of aggregate fractions on soil nematodes was greater than that of soil nematodes on aggregate fractions.

Physical and resources constraints of soil habitats were the main factors responsible for the distribution of nematodes within soil aggregates: (1) the porosphere (inter-aggregate pores) and aggregatusphere (intra-aggregate pores) are important microhabitats for soil nematodes; large aggregates have more intra-aggregate pore space with immobile water where soil fauna preferred to reside and prey on microbes (Jiang et al., 2013; Wang et al., 2018), but the small aggregate increased the inter-aggregate pores with mobile water. (2) Another possible explanation of more nematodes living in macroaggregates than microaggregates was resource con-

Table 3 Effect of treatments and aggregate sizes on nematode ecological indices.

Indices	Treat	< 0.25 mm	0.25–1mm	1–2 mm	>2 mm	
TD	CK	2.44±0.25	2.62±0.08	2.53±0.33	2.93±0.07	A
	SR	2.51±0.32	2.65±0.13	2.62±0.30	3.38±0.13	A
	MA	1.82±0.41	1.85±0.24	2.50±0.44	2.52±0.02	B
		B	B	AB	A	
λ	CK	0.13±0.01	0.10±0.01	0.11±0.03	0.12±0.04	AB
	SR	0.20±0.05	0.08±0.01	0.09±0.01	0.09±0.01	B
	MA	0.38±0.18	0.21±0.05	0.13±0.02	0.14±0.01	A
		A	B	B	B	
H'	CK	2.20±0.02	2.61±0.02	2.63±0.13	2.57±0.19	A
	SR	1.98±0.22	2.70±0.06	2.72±0.04	2.66±0.04	A
	MA	1.61±0.48	2.12±0.22	2.41±0.15	2.27±0.06	B
		B	A	A	A	
MI	CK	2.25±0.39	2.56±0.27	2.85±0.20	3.03±0.21	A
	SR	1.88±0.23	2.33±0.13	2.57±0.06	3.07±0.18	A
	MA	1.68±0.29	1.91±0.23	2.45±0.19	2.70±0.15	B
		B	B	A	A	
NCR	CK	0.55±0.16	0.48±0.11	0.36±0.11	0.38±0.10	C
	SR	0.54±0.12	0.57±0.06	0.64±0.08	0.48±0.09	B
	MA	0.83±0.09	0.81±0.07	0.78±0.06	0.85±0.01	A
		A	A	A	A	
BI	CK	28.45±6.90	27.56±5.59	20.60±4.14	19.40±3.42	B
	SR	37.48±6.26	31.44±4.14	28.25±1.70	13.32±3.83	AB
	MA	33.20±11.46	36.79±6.61	27.33±6.09	17.22±2.43	A
		A	A	AB	B	
CI	CK	56.71±22.11	70.43±17.67	77.08±11.46	72.55±7.03	A
	SR	63.11±27.50	51.39±8.15	66.38±13.27	63.73±10.08	A
	MA	22.47±15.38	31.21±22.52	19.22±10.47	17.26±8.22	B
		A	A	A	A	

Capital letters in lines and rows indicate significant differences among aggregate fractions and organic treatments determined using Tukey's HSD, respectively ($P < 0.05$).

straints. The abundance of free-living nematodes was consistent with the presence of large amounts of bacteria (Jiang et al., 2017). The inter-aggregate pores is a transient niche, and nematodes preferentially migrate where the food resource is located. However, intra-aggregate pore can form aggregate enclosures, a narrow but possibly resource-rich search area, of which were more facilitative for nematodes survival and predation (Jiang et al., 2018).

5 Conclusions

Organic amendments increased the proportion of macroaggregates, mean weight diameter and stimulated the bacterivores. The effect of organic treatments appeared to be more evident on community composition than the total abundance of nematodes. The effects of organic amendment on soil nematode communities vary with the different soil aggregate fractions. More nematodes prefer to live in macroaggtegates. In conclusion, the soil physical structure, resource constraints and predator–prey interaction associated with organic amendments play important roles in the distribution of soil nematode communities within different aggregate fractions.

Acknowledgments

This research was supported by the National Key Research & Development Plan of China (No. 2016YFD0300204).

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