



Original article

Effects of crop species richness on the community of soil nematodes in an experimental agro-ecosystem

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ABSTRACT

Biodiversity losses in terrestrial ecosystems may negatively affect the functioning of underground ecosystems, especially in trophic interaction networks. These effects have mainly been found in grassland ecosystems. The responses of underground agro-ecosystems to biodiversity loss are largely unknown. Here, the relationships between crop species diversity and the abundance, diversity and functional indices of soil nematodes were examined in a 4-yr field experiment across five crop species richness levels (1, 2, 4, 8, and 16). The relationships between crop biomass and nematode abundance or ecological indices were also tested. Crop species richness had no significant effects on either total abundance nematode, nematode abundance within each trophic group, or nematode ecological indices. However, the plant parasitic nematodes, *Psilenchus* and *Partylenchus*, significantly differed among crop species diversity. Crop biomass significantly increased the abundances of total nematodes, plant parasites and omnivores/predators, and decreased that of fungivores. Furthermore, the responses of PPI (Maturity index of plant-parasitic nematode), EI (Enrichment index), and SI (Structure index) to crop biomass were positive, although CI (Channel index) was negatively affected. Redundancy analysis (RDA) further showed that crop species diversity and crop biomass account for 0.7% and 1.9% of the variation in nematode abundance, respectively. Our results clearly indicate that soil nematode abundance and community composition was more affected by crop biomass than by crop species diversity in agricultural systems.

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1. Introduction

A positive relationship between biodiversity and ecosystem functioning has been reported in many studies [1–3]. Generally, a higher plant biodiversity in terrestrial ecosystems has positive effects on ecosystem properties, such as productivity [4,5], nutrient cycling [6], and multi-trophic interaction networks [7–9]. However, most studies addressing the influence of plant species diversity on higher trophic level organisms have focused on aboveground invertebrates [7,8,10,11]. Belowground and

aboveground systems are intimately linked, and thus a combined above- and belowground approach should be used to enhance our understanding of the regulation and functioning of biodiversity [12,13]. Studies from grassland systems that examined both above- and belowground higher organisms reported that plant diversity had strong bottom-up effects on the multi-trophic interaction network, and belowground responses to plant diversity were relatively weaker than aboveground responses [9]. Given that there is high diversity of organisms belowground, the response of soil micro-organisms to plant diversity may be species-specific [14,15].

Nematodes are abundant and diverse invertebrates in belowground systems [16]. They play multiple roles in nitrogen mineralization and organic matter decomposition within the soil food web [17,18] and comprise a wide range of trophic groups including

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bacteria, fungi, and plant feeders, as well as predators and omnivores [19]. Nematode community structure can serve as an indicator for other soil biota and the soil food web as a whole [20]. Given the ease of recovering nematodes from soil and the ability to identify them to meaningful taxa or ‘functional groups’, soil nematodes offer great potential for their use as indicators of plant biodiversity in grasslands [9,14,15,21–25] and for assessing the impact of changing land use on soil conditions [26,27]. Plant diversity in grasslands has been shown to affect the relative abundance of soil nematode functional groups and changes in plant diversity can influence nematode community structure [9,14,15].

In contrast to grasslands, agricultural systems typically have much greater nutrient losses, partly due to removal of agricultural products from the landscape, and a higher frequency of disturbances due to farming practices such as tillage, fertilizer addition and pesticide treatment [27–29]. Agricultural production also commonly uses plant varieties selected for higher yield, which can generate a tradeoff in root-to-shoot ratios that affects the quantity and quality of nutrients and energy flow through soil food webs in both space and time [30]. As such, these key differences between grasslands and agro-ecosystem attributes may ultimately affect soil nematode abundance and community composition [26,27,31]. In multi-cropping production systems in which more than one plant variety or species is grown, soil biotic communities can be affected by crop diversity, with increases observed in the abundance, diversity, and activity of several functional groups [32]. However, these studies examined relatively low levels of crop species diversity (≤ 3 species). The effects of higher levels of crop diversity (> 5 species) on soil nematode communities remains to be considered. Therefore, a 4-yr field trial was carried out to explore the impacts of five crop species richness levels (1, 2, 4, 8, and 16) on abundance and community structure of soil nematodes. The goal of this study was to ascertain whether community structure of soil nematodes differed among different levels of crop species diversity, and to broadly compare the response of soil nematodes to plant species diversity between agricultural and grassland systems.

2. Materials and methods

2.1. Study region and experimental design

This study was conducted at the Experimental Farmland of Shandong Academy of Agricultural Sciences, located in Yishui, China. The region has a temperate maritime monsoon climate with cold winters and warm summers. The mean annual temperature and precipitation are 14.1 °C and 849 mm, respectively. The soils are Podzol E soil type.

The experiment was established in 2007. The crop species used were selected from a pool of 20 crop species commonly grown in North China [10] that included cotton (*Gossypium* spp.), maize (*Zea mays* L.), soybean (*Glycine max* (L.) Merr.), tomato (*Solanum lycopersicum* L.), wild cabbage (*Brassica oleracea* L.), millet (*Setaria italica* (L.) Beauv), sweet sorghum (*Sorghum bicolor* (L.) Moench), ryegrass (*Lolium perenne* L.), adzuki bean (*Vigna angularis* (Willd.) Ohwi et Ohashi), peanut (*Arachis hypogaea* L.), mungbeans (*Vigna radiata* (L.) R. Wilczek), alfalfa (*Medicago sativa* L.), eggplant (*Solanum melongena* L.), celery (*Apium graveolens* L.), clover (*Trifolium repens* L.), wheat (*Triticum aestivum* L.), rape (*Brassica campestris* L.), sunflower (*Helianthus annuus* L.), kidney bean (*Phaseolus vulgaris* L.), sesame (*Sesamum indicum* L.). Five crop richness levels (1, 2, 4, 8, and 16) were designed by randomly selecting the species to be grown in each plot from the species pool listed above. Detailed species composition information for each plot is provided in [Supplementary Table S1](#). There were 10 replications for each crop richness level. The field contained 50 plots (each 9 m \times 9 m), with a

5-m walkway between any two plots. Each plot contained 22 rows and 22 columns of crop plants, with the same crop species within each row but potentially different crop species in adjacent rows. The same experiment designs continued four years until 2010, although crops were harvested in each year. No pesticides and chemical fertilizers were used during the course of study. Weed species in the plots were removed by hand and herbicide application was used to control weeds in the walkway.

2.2. Nematode sampling

Soil samples were collected from each plot at 0–20 cm depth at the early, middle, and late stages of crops in 2010, which was in accord with seeding stage, blooming stage, and maturing stage of crop. Five soil samples were taken from each plot along the diagonal and pooled. Pooled samples were stored at 4 °C until extraction. Nematodes were extracted from 100 g of fresh soil from each pooled sample by the method of centrifugal flotation in sucrose solutions [33–35]. Nematode abundance was measured as individuals per 100 g dry soil, and at least 100 nematodes from each sample were identified to genus according to Bongers [36] using an inverted compound microscope. The nematodes were ascribed to four trophic groups [19]: plant parasites (Pp_x), bacterivores (Ba_x), fungivores (Fu_x), and omnivores/predators (OP_x) (where $x = 1-5$) [20,37]. x represent the colonizer–persister (cp) scale according to their r and K characteristics [20]. Nematodes in cp-1 have short generation duration, high fecundity, and are regarded as “enrichment opportunists” and tolerant to disturbance and can be ascribed to r -strategists. In contrast, cp-5 nematodes produce few large eggs, have a long life cycle combined with a long generation time and are generally intolerant of disturbance and inhabit stable, mature ecosystems [20,38].

2.3. Nematode community index

To characterize community responses of soil nematode to crop species richness, the following community indices were calculated: (1) species richness S , the number of taxa; (2) Shannon–Wiener diversity index (H'), $H' = -\sum p_i \times \ln p_i$, where p_i is the proportion of the i th taxon [39]; (3) Maturity index of free-living nematode (MI), $MI = \sum v_i \times f_i$, where $v_i = c-p$ value of the i th taxon, $f_i =$ frequency of that taxon in a sample [37]; (4) Maturity index of plant-parasitic nematode (PPI), $PPI = \sum v_i \times f'_i$, $f'_i =$ frequency of that taxon i in a sample [37]; (5) Channel index (CI), $CI = 100 \times (0.8 \times Fu_2) / (3.2 \times Ba_1 + 0.8 \times Fu_2)$ [20]; (6) Enrichment Index (EI), $EI = 100 \times e / (e + b)$, where $e = (Ba_1 \times W_1) + (Fu_2 \times W_2)$, $b = (Ba_2 + Fu_2) \times W_2$, $W_1 = 3.2$ and $W_2 = 0.8$ [20]; (7) the structure index (SI), $SI = 100 \times s / (s + b)$, where $s = Ba_x \times W_x + Ca_x \times W_x + Fu_x \times W_x + OP_x \times W_x$, $x = 3-5$, $W_3 = 1.8$, $W_4 = 3.2$, $W_5 = 5.0$ [20].

2.4. Biomass determination

Three plants were randomly collected for each species in each plot at each sampling date, and the dry organic matter biomass of whole plant (both above- and belowground parts together) was determined for each species after drying at 60 °C for 72 h. Then, the total biomass of each plot was represented by summing these weights for 22 plants in the central row in each plot.

2.5. Data analysis

We used two-way ANOVA (SAS 9.13, SAS Institute Inc., Cary, NC, USA) to test for effects of crop species diversity, sampling date and their interaction on abundance and ecological indices of soil

nematodes. The relationships between crop biomass and nematode abundance or nematode ecological indices were tested over all plots across sampling dates using Pearson correlation based on software R 3.03 [40]. Redundancy analysis (RDA) was also performed to explore nematode community composition in relation to environmental factors (crop species diversity, crop biomass and sampling date) using the CANOCO 4.5 software [41]. Nematode abundances and crop biomass were $\ln(x + 1)$ transformed to normalize data prior to statistical analysis. Differences at $P < 0.05$ level were considered as statistically significant.

3. Results

3.1. Nematode abundance and community composition

Thirty-four nematode taxa were identified during the course of study (Table 1). The abundances of total nematodes, plant parasites, fungivores, and omnivores/predators, but not bacterivores, were significantly affected by sampling date ($P < 0.05$, Table 2). However, crop species richness and the interactions between crop species diversity and sampling date had no significant effects on the abundances of total nematodes and those within each trophic group (Table 2 and Fig. 1). Regarding the numerical dominance of each trophic group, plant parasites comprised the highest percentage, followed by bacterivores, omnivores/predators, and fungivores in each crop species level.

Table 1
Proportional contribution (%) of various nematodes to the nematode assemblage under different crop species diversity treatments across the whole experiment.

Genus	Guild ^a	Crop species richness level				
		1	2	4	8	16
<i>Panagrolaimus</i>	Ba ₁	7.71	6.93	6.76	6.97	7.03
<i>Rhabditis</i>	Ba ₁	3.19	3.28	3.53	4.78	3.76
<i>Monhystera</i>	Ba ₂	0.94	0.65	0.46	0.50	0.30
<i>Acrobeles</i>	Ba ₂	0.10	0.28	0.36	0.39	0.14
<i>Cervidellus</i>	Ba ₂	0.05	0.08	0.16	0.05	0.02
<i>Cephalobus</i>	Ba ₂	2.98	2.33	2.20	2.47	3.44
<i>Anonchus</i>	Ba ₂	0.00	0.00	0.04	0.00	0.00
<i>Eucephalobus</i>	Ba ₂	0.08	0.03	0.17	0.09	0.33
<i>Punctodora</i>	Ba ₃	1.07	0.80	0.19	0.41	0.89
<i>Prismatolaimus</i>	Ba ₃	1.55	2.06	1.27	1.02	0.62
<i>Prochromadora</i>	Ba ₃	0.00	0.00	0.00	0.05	0.00
<i>Alaimus</i>	Ba ₄	0.04	0.10	0.09	0.05	0.02
<i>Nothotylenchus</i>	Fu ₂	0.04	0.00	0.00	0.18	0.00
<i>Aphelenchus</i>	Fu ₂	8.83	8.24	8.80	7.09	9.50
<i>Proleptonchus</i>	Fu ₄	0.00	0.00	0.00	0.00	0.02
<i>Mononchus</i>	OP ₄	3.08	2.25	2.27	2.29	1.94
<i>Dorylaimus</i>	OP ₄	11.45	9.73	8.61	8.48	10.58
<i>Mesodorylaimus</i>	OP ₄	0.82	0.25	0.76	0.41	0.49
<i>Tylenchus</i>	PP ₂	8.21	8.02	8.86	6.85	5.94
<i>Aphelenchoides</i>	PP ₂	0.05	0.00	0.03	0.02	0.03
<i>Psilenchus</i>	PP ₂	0.46	0.95	0.35	0.39	0.47
<i>Boleodorus</i>	PP ₂	0.22	0.13	0.34	0.26	0.42
<i>Paratylenchus</i>	PP ₂	0.21	0.21	0.26	0.30	0.22
<i>Tylenchorhynchus</i>	PP ₃	1.77	2.60	1.97	3.04	2.90
<i>Pratylenchus</i>	PP ₃	8.85	11.49	12.94	11.27	9.44
<i>Brachyderus</i>	PP ₃	0.37	1.19	0.47	0.38	0.22
<i>Scutellonema</i>	PP ₃	0.00	0.00	0.00	0.00	0.02
<i>Criconema</i>	PP ₃	0.75	0.08	0.06	0.08	0.30
<i>Criconemoides</i>	PP ₃	3.43	5.21	4.54	2.10	3.40
<i>Helicotylenchus</i>	PP ₃	8.40	8.77	8.77	10.76	9.83
<i>Rotylenchus</i>	PP ₃	12.69	11.93	11.71	16.31	13.59
<i>Longidorella</i>	PP ₅	4.21	4.99	5.94	5.10	6.39
<i>Xiphinema</i>	PP ₅	1.91	1.46	1.78	2.10	1.78
<i>Longidorus</i>	PP ₅	6.51	5.96	6.30	5.84	5.97

^a Functional guilds of soil nematodes characterized by feeding habits and life history characters. Ba, bacterivores; Fu, fungivores; PP, plant-parasites; OP, Omnivores/predators; numbers following the functional groups indicate the cp values [20,37].

Table 2

Statistical results of effects of crop diversity, sampling date, and their interactions on the abundance of specific trophic group.

Factors	Crop diversity			Sampling date			Interactions		
	F	df	P	F	df	P	F	df	P
Total nematode	1.37	4	0.249	3.42	2	0.036	0.71	8	0.680
Bacterivores	0.29	4	0.883	1.78	2	0.172	0.77	8	0.627
Fungivores	1.01	4	0.403	7.50	2	0.001	0.34	8	0.948
Omnivores/Predators	0.99	4	0.414	16.58	2	<0.001	0.96	8	0.471
Plant parasites	1.64	4	0.167	4.10	2	0.019	0.83	8	0.581

At genera level, the most abundant genera were *Rotylenchus*, *Pratylenchus*, and *Dorylaimus* (relative abundance > 8%, Table 1). A significant crop species richness effect was observed on the abundances of *Psilenchus* and *Pratylenchus* ($P < 0.05$), and there were significant sampling date effects on 20 genera ($P < 0.05$) (Table 3).

3.2. Nematode ecological indices

The nematode ecological indices were showed in Table 4. No significant effect of crop species diversity on each nematode ecological index was detected ($P > 0.05$). However, sampling date had significant effects on the PPI, CI, EI, and SI, and PPI, EI, and SI increased, and CI decreased from early stage to late stage of crop.

3.3. Relationships between nematode abundance or ecological indices and treatments

The relationships between crop biomass and nematode abundance or nematode ecological indices are presented in Table 5. There were significant positive effects of crop biomass on the abundances of total nematodes, plant parasites, and omnivores/predators, as well as the PPI, EI, and SI. In contrast, the abundances of fungivores and CI were negatively related to crop biomass. The crop biomass had no significant impacts on the density of bacterivores and MI.

Results from redundancy analysis (RDA) showed that eigenvalues were 0.068 ($F = 10.3$, $P = 0.002$) and 0.016 for axis 1 and axis 2, respectively, and the first two axes explained 8.42% of the total species-environment variation (Fig. 2). Crop species diversity explained 0.7%, while crop biomass and sampling date explained 1.9% and 4.0% of the variation in soil nematode abundance, respectively.

4. Discussion

The present study revealed an impact of crop biomass, but not crop species diversity, on soil nematode abundance and community composition. Crop biomass significantly increased the density of total nematodes, plant parasites and omnivores/predators, whereas it reduced the relative abundance of fungal feeders (Table 5). These results are consistent with several previous reports [42–44], which showed that abundance of plant parasites and omnivores/predators increased with increasing residue quantity, indicating that residue quantity was an important factor determining the abundance of soil nematodes at the trophic level. Higher biomass input implies not only a greater plant resource for specific plant-feeding nematodes, but also increased microbial biomass which contributes to nutrient cycling, and larger populations of nematodes feeding upon them [12,26,45]. However, the higher abundance of omnivores/predators can likely reduce the population density of fungal feeders. The lower abundance of fungal feeders may also attribute to the reduced density of resources available to them (fungal communities) if, for example,

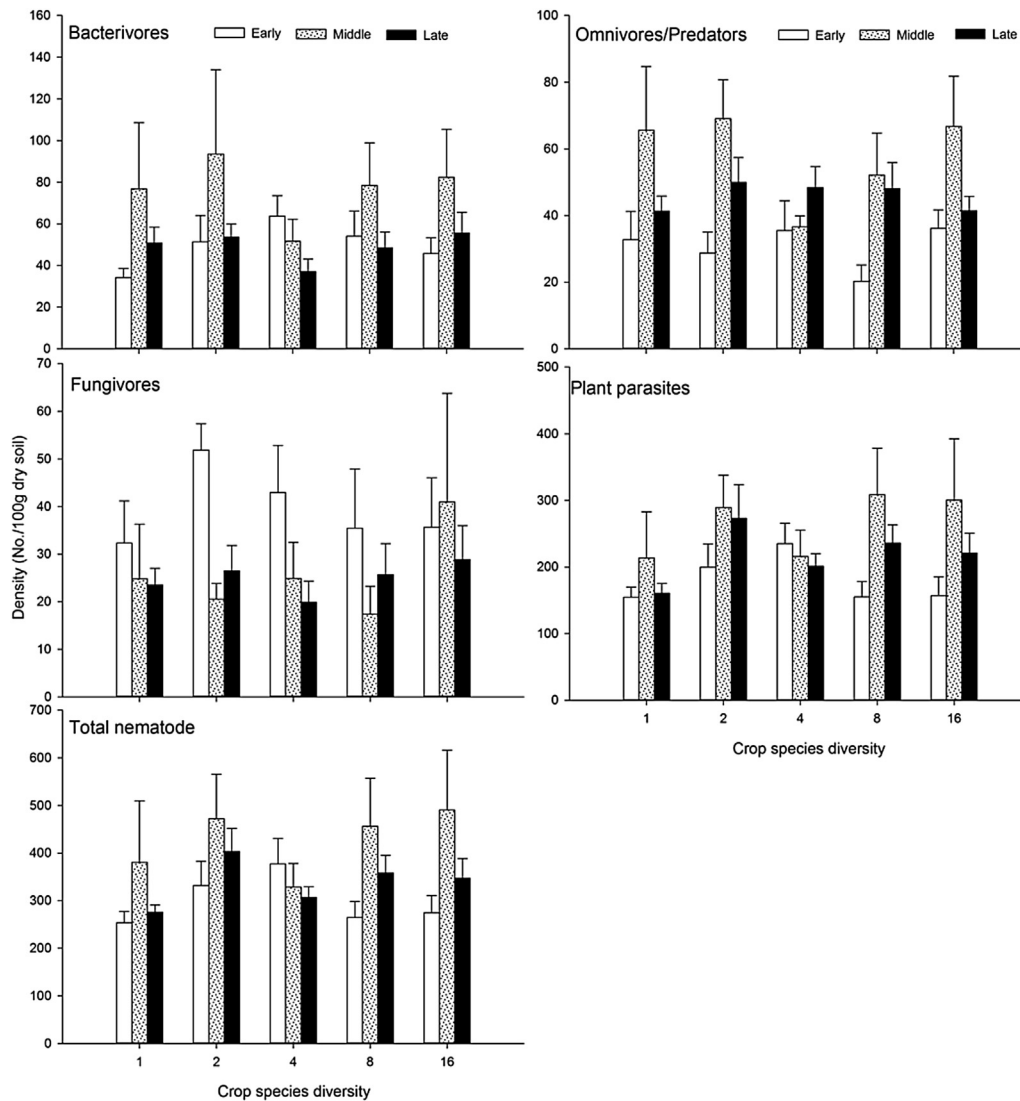


Fig. 1. Total nematode abundance and abundance of different trophic groups in each crop species richness level at different sampling dates. The data are Means \pm S.E. (standard error) individuals/100 g dry soil ($n = 10$). There were no significant differences in variable means among crop diversity treatments at each sampling date.

there were antagonistic interactions between bacterial and fungal taxa competing for increased biomass. The underline mechanism needs further to be studied in future.

The community indices we quantified reflect changes in the composition of soil nematode communities and indicate functional changes in the soil food web [46]. PPI was proposed for nematodes feeding on higher plants and seems to be positively correlated with plant primary production [37]. EI could reflect the availability of resources to the soil food web and the response of primary decomposers to the resources [47], whereas SI is primarily determined by omnivorous and predatory nematode populations, and is sensitive to disturbance. CI is considered to indicate whether the “fast” bacterial channel or “slow” fungal channel of energy transformation prevails in an ecosystem [20]. Our results showed that crop biomass had significant positive effects on the PPI, EI, and SI, but decreased the CI, indicating that the increase in crop biomass increased food resources for the soil food web, and this in turn increased the abundance of higher trophic groups. The CI values indicate that the “fast” bacterial channel was the dominant decomposition pathway in this experimental agro-ecosystem. Furthermore, higher PPI values indicate that increased nutrient

was absorbed by plants, and short-stylect ectoparasites are replaced or replenished by plant parasites feeding at more nutrient-rich cells in the deeper root zones [48].

Crop species richness had no effects on the abundance of any of the nematode functional groups or the ecological indices we quantified. This finding was in accordance with roughly 30 other previous studies [49], suggesting plant diversity had no or weak effects on soil organisms. However, the duration of these studies was very short and as such, the conclusions obtained represented only the short-term effects of plant diversity. In contrast, significant plant diversity effects on soil organisms are known to increase with experimental duration and have been observed 4–6 y after initiation of the field trails in some studies [50]. More recently, long-term experiments (≥ 6 y) reported that plant diversity had positive effects on the soil organisms, but that neither plant functional group nor plant identity were important [9,14,15]. Thus, the lack of an effect of crop species richness on nematode community in our study could potentially be attributed, at least in part, to the slightly shorter term of our experiments (4 yr in the present study).

Our results indicate that the effects of plant diversity on soil organism communities in grassland ecosystems cannot be simply

Table 3
Changes in the abundances of nematode genera associated with crop species diversity at different sampling dates.

Genus	Sampling date	Crop species richness level					Statistics (<i>P</i> -values)	
		1	2	4	8	16	Crop diversity	Time
<i>Panagrolaimus</i>	Early	13.08 ± 1.82a	25.96 ± 6.85a	25.15 ± 4.82a	13.25 ± 2.94a	20.45 ± 4.06a	0.854	0.045
	Middle	25.30 ± 5.04a	26.08 ± 4.74a	18.32 ± 3.39a	25.53 ± 4.31a	27.58 ± 6.59a		
	Late	32.23 ± 12.66a	31.39 ± 11.15a	24.54 ± 4.51a	36.40 ± 12.66a	30.41 ± 5.66a		
<i>Monhystera</i>	Early	0.70 ± 0.70a	0.24 ± 0.24a	0.60 ± 0.60a	0.00 ± 0.00a	0.23 ± 0.23a	0.258	<0.001
	Middle	3.98 ± 1.73a	2.53 ± 1.12a	1.06 ± 0.77a	2.52 ± 0.80a	1.14 ± 0.76a		
	Late	4.01 ± 1.53a	5.06 ± 3.60a	2.96 ± 1.29a	2.83 ± 1.23a	1.99 ± 0.96a		
<i>Cervidellus</i>	Early	0.20 ± 0.20a	0.93 ± 0.63a	1.56 ± 1.18a	0.00 ± 0.00a	0.18 ± 0.18a	0.856	0.039
	Middle	0.32 ± 0.30a	0.00 ± 0.00a	0.00 ± 0.00a	0.55 ± 0.55a	0.00 ± 0.00a		
	Late	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a		
<i>Cephalobus</i>	Early	10.56 ± 4.44a	10.92 ± 4.13a	12.88 ± 3.59a	13.59 ± 3.60a	11.60 ± 3.64a	0.721	0.007
	Middle	5.62 ± 1.73a	5.09 ± 1.68a	3.27 ± 1.28a	2.54 ± 0.62a	6.54 ± 1.75a		
	Late	10.72 ± 4.27a	11.72 ± 3.59a	5.42 ± 0.99a	10.51 ± 4.43a	19.62 ± 10.07a		
<i>Eucephalobus</i>	Early	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.196	0.010
	Middle	0.40 ± 0.40a	0.35 ± 0.35a	0.89 ± 0.59a	0.44 ± 0.44a	0.59 ± 0.59a		
	Late	0.36 ± 0.36a	0.00 ± 0.00a	0.87 ± 0.51a	0.51 ± 0.51a	3.01 ± 1.63a		
<i>Punctodora</i>	Early	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.227	<0.001
	Middle	3.58 ± 1.65a	3.50 ± 2.42a	0.00 ± 0.00a	4.07 ± 1.95a	3.07 ± 1.27a		
	Late	6.25 ± 6.05a	6.23 ± 5.03a	1.84 ± 1.84a	0.32 ± 0.32a	6.77 ± 5.98a		
<i>Prismatolaimus</i>	Early	1.05 ± 1.05a	3.97 ± 2.03a	2.18 ± 1.49a	0.00 ± 0.00a	2.56 ± 0.94a	0.368	0.004
	Middle	3.83 ± 1.91a	6.37 ± 2.27a	4.86 ± 1.94a	3.67 ± 1.43a	1.48 ± 0.82a		
	Late	9.15 ± 5.92a	14.36 ± 10.82a	6.03 ± 2.46a	7.39 ± 2.94a	2.79 ± 1.81a		
<i>Aphelenchus</i>	Early	32.30 ± 8.85a	51.88 ± 5.53a	42.98 ± 9.88a	33.52 ± 12.28a	35.65 ± 10.41a	0.369	<0.001
	Middle	23.53 ± 3.48a	26.46 ± 5.37a	19.87 ± 4.44a	25.69 ± 6.53a	28.59 ± 7.17a		
	Late	24.46 ± 11.50a	20.49 ± 3.35a	24.90 ± 7.56a	17.33 ± 5.93a	40.97 ± 22.82a		
<i>Dorylaimus</i>	Early	12.90 ± 1.98a	16.86 ± 3.22a	26.08 ± 6.47a	11.74 ± 2.58a	23.36 ± 4.65a	0.570	<0.001
	Middle	36.36 ± 4.56a	40.68 ± 6.98a	34.01 ± 4.93a	39.41 ± 6.00a	36.52 ± 5.00a		
	Late	55.50 ± 19.83a	60.11 ± 10.14a	28.66 ± 1.69a	40.34 ± 8.40a	57.73 ± 15.09a		
<i>Mesodorylaimus</i>	Early	4.92 ± 1.78a	2.35 ± 1.15a	5.24 ± 2.01a	3.18 ± 1.27a	4.93 ± 0.89a	0.255	<0.001
	Middle	0.90 ± 0.45a	0.35 ± 0.35a	2.07 ± 0.79a	0.26 ± 0.26a	0.00 ± 0.00a		
	Late	1.53 ± 0.77a	0.28 ± 0.28a	0.37 ± 0.37a	0.94 ± 0.49a	0.30 ± 0.30a		
<i>Tylenchus</i>	Early	29.17 ± 4.93a	33.91 ± 11.29a	34.64 ± 6.51a	20.01 ± 4.63a	20.69 ± 3.67a	0.371	0.040
	Middle	28.66 ± 5.21a	36.44 ± 7.99a	30.77 ± 5.68a	35.44 ± 6.28a	19.94 ± 3.80a		
	Late	17.50 ± 6.83a	26.88 ± 7.57a	25.05 ± 5.76a	18.48 ± 6.92a	25.41 ± 7.26a		
<i>Psilenchus</i>	Early	3.12 ± 1.83b	7.29 ± 2.74a	3.09 ± 1.06ab	3.64 ± 1.00ab	4.86 ± 1.756ab	0.024	<0.001
	Middle	0.69 ± 0.45a	1.57 ± 1.13a	0.30 ± 0.30a	0.00 ± 0.00a	0.28 ± 0.28a		
	Late	0.36 ± 0.24b	2.41 ± 0.71a	0.00 ± 0.00b	0.53 ± 0.53b	0.00 ± 0.00b		
<i>Boleodorus</i>	Early	1.91 ± 0.86a	1.55 ± 1.07a	2.88 ± 1.29a	2.37 ± 1.00a	4.49 ± 3.16	0.793	<0.001
	Middle	0.00 ± 0.00a	0.00 ± 0.00a	0.41 ± 0.41a	0.44 ± 0.44a	0.00 ± 0.00a		
	Late	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a		
<i>Paratylenchus</i>	Early	1.16 ± 0.87a	1.41 ± 0.95a	2.00 ± 0.91a	2.70 ± 1.07a	1.89 ± 1.03a	0.956	<0.001
	Middle	0.00 ± 0.00a	0.20 ± 0.20a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a		
	Late	0.69 ± 0.46a	0.87 ± 0.62a	0.52 ± 0.52a	0.53 ± 0.53a	0.52 ± 0.52a		
<i>Tylenchorhynchus</i>	Early	4.88 ± 1.35a	13.18 ± 4.95a	3.96 ± 1.18a	3.05 ± 0.76a	6.00 ± 2.01a	0.573	<0.001
	Middle	3.34 ± 1.63a	4.64 ± 2.22a	5.18 ± 2.46a	10.31 ± 4.36a	4.41 ± 1.89a		
	Late	7.72 ± 2.41a	12.98 ± 3.49a	10.64 ± 2.97a	19.50 ± 5.23a	21.26 ± 8.56a		
<i>Pratylenchus</i>	Early	29.11 ± 10.20b	49.17 ± 14.24ab	55.35 ± 7.21a	29.42 ± 5.19ab	24.22 ± 5.05b	0.033	0.934
	Middle	27.23 ± 7.28a	27.05 ± 6.52a	35.93 ± 7.82a	52.06 ± 11.32a	45.88 ± 17.79a		
	Late	24.55 ± 5.90b	60.55 ± 12.99a	39.01 ± 7.23ab	40.17 ± 7.71ab	36.21 ± 6.45ab		
<i>Brachyderus</i>	Early	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.395	<0.001
	Middle	0.60 ± 0.40a	11.78 ± 10.07a	1.30 ± 0.93a	0.82 ± 0.56a	0.66 ± 0.45a		
	Late	2.69 ± 1.53a	3.29 ± 1.57a	3.47 ± 1.31a	3.26 ± 2.09a	1.78 ± 1.26a		
<i>Criconema</i>	Early	6.62 ± 3.81a	0.88 ± 0.66a	0.54 ± 0.36a	0.00 ± 0.00a	2.80 ± 2.27a	0.502	0.004
	Middle	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.88 ± 0.88a	0.47 ± 0.47a		
	Late	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a		
<i>Criconemoides</i>	Early	8.20 ± 3.78a	13.69 ± 8.76a	18.25 ± 12.14a	7.96 ± 3.68a	6.64 ± 3.35a	0.230	0.003
	Middle	20.58 ± 14.11a	36.74 ± 11.10a	18.66 ± 5.22a	11.48 ± 2.20a	13.95 ± 3.15a		
	Late	3.58 ± 1.81a	14.04 ± 4.25a	10.02 ± 5.21a	3.20 ± 1.27a	17.41 ± 5.59a		
<i>Helicotylenchus</i>	Early	14.78 ± 3.04a	17.65 ± 3.61a	34.20 ± 13.80a	32.61 ± 9.98a	22.42 ± 11.71a	0.938	0.010
	Middle	13.47 ± 3.14a	38.02 ± 21.40a	16.79 ± 5.14a	22.62 ± 8.77a	28.99 ± 8.06a		
	Late	47.27 ± 18.65a	50.45 ± 18.00a	35.82 ± 13.31a	60.87 ± 17.82a	57.43 ± 27.82a		
<i>Rotylenchus</i>	Early	16.98 ± 3.58a	20.04 ± 9.26a	27.92 ± 10.47a	27.66 ± 9.01a	28.64 ± 12.20a	0.677	<0.001
	Middle	33.98 ± 11.92a	75.54 ± 19.22a	45.39 ± 9.50a	56.05 ± 13.77a	62.20 ± 11.11a		
	Late	64.53 ± 29.90a	51.22 ± 9.62a	47.15 ± 18.36a	92.26 ± 36.26a	61.78 ± 30.40a		
<i>Longidorus</i>	Early	17.75 ± 3.54a	15.01 ± 3.10a	15.43 ± 4.23a	8.84 ± 2.61a	11.43 ± 2.34a	0.943	<0.001
	Middle	14.17 ± 1.62a	17.61 ± 5.61a	25.89 ± 4.16a	24.12 ± 5.34a	15.18 ± 2.86a		
	Late	27.03 ± 12.49a	38.64 ± 8.79a	23.78 ± 3.48a	30.11 ± 6.62a	39.26 ± 13.61a		

The data are Mean ± S.E. (standard error) individuals/100 g dry soil. (*n* = 10). The same letters at each sampling date represent no significant differences in variable means among crop diversity treatments. Only the genera with significant responses to crop diversity or sampling date were listed (Significance level, *P* ≤ 0.05).

applied to agricultural systems. Agricultural systems typically receive many more disturbances (e.g., tillage, fertilizer addition, and pesticide spray) than relatively undisturbed grasslands

[27–29]. In general, annual crops have shorter growing periods, shallower rooting depths, lower root densities and less root biomass than perennial grasslands [51,52]. The larger and deeper

Table 4
Changes in the values of nematode ecological indices associated with crop species diversity at different sampling dates.

Indices	Sampling date	Crop species richness level					Statistics (<i>P</i> -values)	
		1	2	4	8	16	Crop diversity	Time
S	Early	16.30 ± 0.56a	15.40 ± 0.87a	15.90 ± 0.97a	15.50 ± 0.93a	17.20 ± 0.49a	0.667	0.775
	Middle	16.67 ± 0.47a	15.89 ± 0.73a	17.00 ± 0.57a	15.90 ± 0.55a	16.11 ± 0.54a		
	Late	16.20 ± 0.66a	16.90 ± 0.43a	15.80 ± 0.49a	15.60 ± 0.56a	15.70 ± 0.67a		
<i>H'</i>	Early	3.47 ± 0.10a	3.30 ± 0.14a	3.38 ± 0.10a	3.29 ± 0.18a	3.53 ± 0.07a	0.632	0.744
	Middle	3.39 ± 0.10a	3.37 ± 0.10a	3.51 ± 0.08a	3.42 ± 0.09a	3.45 ± 0.06a		
	Late	3.45 ± 0.07a	3.53 ± 0.07a	3.45 ± 0.08a	3.34 ± 0.10a	3.43 ± 0.11a		
MI	Early	0.94 ± 0.08a	0.91 ± 0.08	0.78 ± 0.06a	0.78 ± 0.07a	0.99 ± 0.10a	0.089	0.313
	Middle	1.04 ± 0.09a	0.91 ± 0.12a	0.96 ± 0.08a	0.91 ± 0.10a	0.89 ± 0.06a		
	Late	1.13 ± 0.11a	0.98 ± 0.10a	0.89 ± 0.09a	0.82 ± 0.10a	0.97 ± 0.09a		
PPI	Early	1.90 ± 0.07a	1.88 ± 0.11a	2.10 ± 0.09a	1.92 ± 0.17a	1.85 ± 0.10a	0.098	0.013
	Middle	1.89 ± 0.12a	2.07 ± 0.12a	2.16 ± 0.07a	2.11 ± 0.07a	2.09 ± 0.09a		
	Late	1.95 ± 0.08a	2.17 ± 0.08a	2.16 ± 0.08a	2.25 ± 0.13a	2.08 ± 0.13a		
CI	Early	24.97 ± 4.80a	36.17 ± 7.87a	19.15 ± 2.39a	20.92 ± 4.67a	21.89 ± 4.18a	0.408	0.002
	Middle	17.06 ± 2.65a	16.32 ± 2.33a	18.12 ± 4.57a	16.14 ± 2.66a	16.47 ± 5.16a		
	Late	16.02 ± 6.66a	16.69 ± 4.06a	13.64 ± 3.36a	11.65 ± 5.14a	14.11 ± 5.68a		
EI	Early	74.76 ± 4.27a	71.88 ± 3.30a	78.72 ± 1.81a	76.43 ± 3.34a	78.07 ± 2.71a	0.610	0.014
	Middle	81.44 ± 1.53a	80.94 ± 1.23a	80.44 ± 2.74a	82.77 ± 2.60a	83.45 ± 3.51a		
	Late	81.85 ± 4.59a	80.97 ± 3.41a	83.27 ± 2.23a	85.59 ± 3.79a	81.34 ± 2.91a		
SI	Early	68.96 ± 7.14a	59.23 ± 6.84a	67.64 ± 3.61a	59.51 ± 8.60a	75.10 ± 3.34a	0.807	<0.001
	Middle	84.16 ± 2.05a	84.22 ± 2.14a	86.27 ± 3.62a	86.16 ± 2.22a	83.01 ± 3.52a		
	Late	88.42 ± 2.42a	89.24 ± 1.43a	83.35 ± 2.81a	84.70 ± 4.05a	82.41 ± 4.15		

The data are Mean ± S.E. (standard error, $n = 10$). The same letters at each sampling date represent no significant differences in variable means among crop diversity (Significance level, $P \leq 0.05$). *H'*: Shannon–Wiener diversity index; MI: Maturity index of free-living nematode; PPI: Maturity index of plant-parasitic nematode; CI: Channel index; EI: Enrichment index; SI: Structure index.

Table 5
The relationships between crop biomass and nematode trophic group abundance or ecological indices using Person correlation.

	Total nematode	Ba	Fu	OP	Pp	<i>H'</i>	MI	PPI	CI	EI	SI
<i>r</i>	0.1896	0.1191	-0.3168	0.3198	0.245	0.0332	-0.0111	0.2959	-0.3085	0.3112	0.5015
<i>P</i>	0.0224	0.1538	0.0001	<0.0001	0.0003	0.6916	0.8951	0.0003	0.0002	0.0001	<0.0001

r = Person correlation coefficient. Ba: Bacterivores; Fu: Fungivores; OP: Omnivores/Predators; Pp: Plant parasites; *H'*: Shannon–Wiener diversity index; MI: Maturity index of free-living nematode; PPI: Maturity index of plant-parasitic nematode; CI: Channel index; EI: Enrichment index; SI: Structure index. Different letters denote difference at $P < 0.05$.

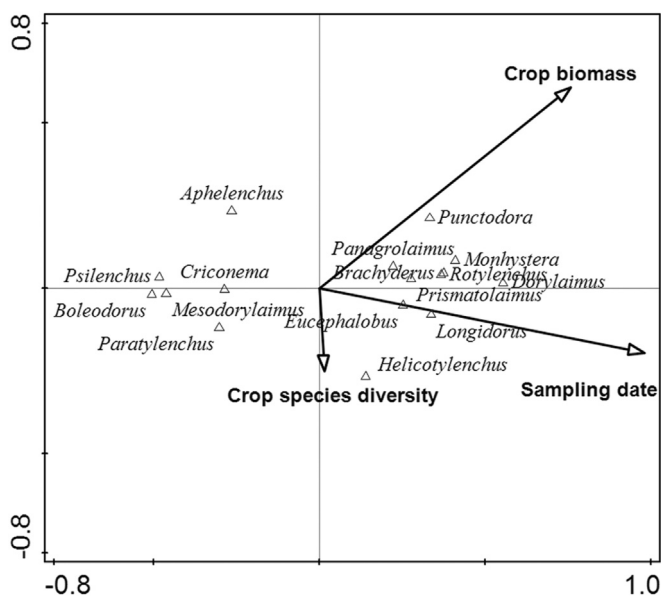


Fig. 2. Redundancy analysis (RDA) of the abundance of soil nematode and treatment variables (crop species diversity, crop biomass and sampling date).

root systems may improve soil physical and biological properties in perennial grasslands in ways that favor soil organisms. These factors can help perennial roots maintain soil organic carbon [53,54]

and more complex soil food webs that regulate the nutrient cycle and important ecological process [55,56]. This, in turn, supports higher diversity and abundance of soil microorganisms in perennial grasslands than that in annual crops [51,55,57]. Thus, the differential response of soil nematodes to plant diversity in these two ecosystems may relate to the root functional traits.

5. Conclusions

Our findings indicate that crop biomass significantly altered soil nematode abundance and community composition, while crop species richness had no significant impacts on these parameters. These results are in contrast to those obtained in studies conducted in grassland ecosystems. Thus, the effects of plant diversity on soil organism communities in grassland ecosystems cannot be simply applied to agricultural systems. Differences in the frequency of disturbance and resulting effects on root functional traits may help explain the differential response of soil nematodes to plant diversity in these two ecosystems.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.ejsobi.2016.01.003>.

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