



# The effect of phosphorus addition, soil moisture, and plant type on soil nematode abundance and community composition

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## Abstract

**Purpose** Environmental variables such as soil moisture and phosphorus (P) might influence above- and below-ground biodiversity. In this study, we investigated the rarely reported individual and interactive multifactor effects of soil moisture and phosphorus addition with the type of above-ground tree species (biological interactions) on the soil nematode community structure. **Materials and methods** We established a completely randomized experimental design with two plant types (N<sub>2</sub>-fixer and non-nitrogen fixer) and different combinations of water treatments and P additions (i.e., water with P addition, water only, drought with P addition, and drought only) in a greenhouse and investigated their effects on the soil chemical properties and nematode community. Soil samples were collected at the end of the experiment and were analyzed for soil moisture content (SM), available phosphorus (aP), nitrate nitrogen (NO<sub>3</sub><sup>-</sup>-N), ammonium nitrogen (NH<sub>4</sub><sup>+</sup>-N), dissolved organic carbon (DOC), dissolved organic nitrogen (DON), and nematode community. The following trophic groups were assigned to the nematodes: bacterivores (Ba), fungivores (Fu), omnivores–predators (Op), and plant parasites (PP). The channel index (CI), enrichment index (EI), maturity index (MI), genus richness (GR), and Simpson dominance (Ig) were adopted to indicate the indices of the nematode food web. **Results and discussion** Phosphorus addition and its interaction with water treatments had no statistically significant effects on the soil nematode community, but there were significant decreasing ( $p < 0.05$ ) effects of P addition on the total density of nematodes of the N<sub>2</sub>-fixing tree under optimum water treatment. There were no significant interactive effects of P addition and water treatments on all the trophic groups, but plant type, water treatments, and their interactions significantly affected the density of most nematode trophic groups. The total nematode abundances of bacterivores, plant parasitic, omnivores, and enrichment index were significantly higher in the N<sub>2</sub>-fixers than in the non-nitrogen-fixing tree. **Conclusions** Soil nematode abundance and community composition were more affected by the plant type than by the P addition and its interaction with water treatments. Drought exerted adverse effects on the total density of soil nematodes, the dominant genera, and the trophic groups. This study demonstrated that the rate of drought impact hinges more on the type of tree and that

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N<sub>2</sub>-fixing tree could still maintain the soil food web structure irrespective of the environmental changes.

**Keywords** Biodiversity · Drought · Phosphorus · Microfauna · Nitrogen · Nematodes

## 1 Introduction

The diversity and composition of soil biota play an important role in ecosystem multifunctionality and exert vast influences on soil nutrient processes (De Vries 2012; Wagg et al. 2014). As a significant contributor to below-ground ecosystems, soil biota interconnect with the above-ground counterparts to create feedbacks that control ecosystem processes and properties (Hu et al. 2017; Salamun et al. 2017). Typically, among the soil biota, soil nematodes (e.g., bacterivores, fungivores, plant parasites, omnivores,

and predators) occupied critical positions in the primary, secondary and tertiary levels of the soil food web (Pan et al. 2016). Their activities regulate the size and function of fungal and bacterial populations in the soil, as well as the rates of carbon and nitrogen turnover (Biederman and Boutton 2009). Soil nematode communities are quite sensitive to the changes in soil nutrients (e.g., nitrogen (N) and phosphorus (P)), soil water content, and other management practices, and thus, they serve as useful ecological indicators of soil health (Sanaullah et al. 2011; Zhao et al. 2014; Cavagnaro 2016). They may respond favorably when the food supply is adequate, and a higher population size could occur when adverse soil environmental conditions (e.g., soil water deficit) do not obstruct growth and reproduction (Landesman et al. 2011). Because soil nematodes are moisture-dependent organisms, they can be directly affected by alterations in the soil water content, which can impede their migration towards their prey and indirectly by limiting effects of water on soil properties (Pan et al. 2016; Olatunji et al. 2018). However, experimental studies focusing on the impacts of nutrients, notably P addition and altered precipitation, on the soil nematode community are relatively limited (Liu et al. 2016a; Song et al. 2016).

As a result of climate change, a reduction in the number of precipitation events is predicted to increase abiotic and biotic stress on plants and soil biodiversity by limiting the quantity of nutrients available for soil biota and plant use (Cavagnaro 2016). There is increasing evidence that drought, as a driver of global climate change, may have intense effects on soils directly through changes in soil structure or indirectly through effects on soil organic matter turnover (Sun et al. 2016; Dam et al. 2017; Olatunji et al. 2018). These effects may subsequently affect the abundance and community composition of soil biota including nematodes and protozoa (Landesman et al. 2011; Pan et al. 2016; Sun et al. 2016; Dam et al. 2017). P addition can also exert significant effects on the soil nematode community by stimulating plant growth and increasing the below-ground translocation of photosynthates (Lei et al. 2015). However, recent studies have reported that a reduction in water availability to the soil environment can limit or aggravate the effects of P addition by enhancing its immobility in soil (Dong et al. 2014; Olatunji et al. 2018). In a P addition experiment in a secondary tropical forest, Zhao et al. (2014) reported that P addition significantly suppressed the total nematode density, the density of omnivores–predators, and some nematode indices. Despite the fact that the interactive effects of altered soil water content and P addition on soil fauna may be more complex than the effects of single factors, studies investigating the combined effects of these factors on soil nematodes are scarce. Additionally, soil modification induced by forest type, which is mainly related to plant identity and their rate of nutrient use, is another critical factor that can impact the composition of soil microbiota (Huang et al. 2013; Gao et al. 2017).

Differences among the above-ground tree species in terms of their identities (such as nitrogen-fixing, non-nitrogen-fixing, and fast-growing or slow-growing species) and their capacity to influence soil organic matter and soil nutrient availability (Rivest et al. 2015; Olatunji et al. 2018; Wang et al. 2018) can also impact the soil nematode community. For example, the literature has reported that, in addition to improving soil dissolved organic nitrogen (DON), dissolved organic carbon (DOC), and other elements (He et al. 2013), N<sub>2</sub>-fixing tree species (e.g., *Alnus cremastogyne* Burk) might also increase soil carbon (C), N, and omnivorous nematodes more than the non-nitrogen-fixing species (Huang et al. 2014; Qin et al. 2014). The N<sub>2</sub>-fixing tree can increase the abundance of bacterivorous nematodes, particularly the enrichment opportunists (such as *Rhabditis*) (Viketoft et al. 2009). Despite the significance of N<sub>2</sub>-fixing species, they are sometimes constrained by changes in soil water conditions and P additions (Tobita et al. 2016). To acclimatize, N<sub>2</sub>-fixing plants could adopt different strategies, including changes in plant growth and alterations in below-ground carbon input and resource allocation (Cleland et al. 2013), which in turn, may affect the structure of the nematode communities through changes in abiotic factors (Sanaullah et al. 2011). Changes in soil physical parameters, moisture content, and resource allocation may strongly affect the above-ground plant and can lead to changes in the abundance and diversity of soil fauna (Wang et al. 2018). However, studies focusing on the combined effects of multiple factors, such as plant types, altered soil water content, and P addition, on soil nematode community composition are scarce. Examining individual and interactive effects of plant types, soil water content, and P on soil nematode communities can improve our insights into how multifactor effects alter the soil food web structure and ecosystem processes.

This study aimed to investigate how the nematode community composition responds to individual and combined effects of plant type, P addition, and soil water content. We compared the nematode communities of soils vegetated with N<sub>2</sub>-fixing tree and non-nitrogen-fixing tree species. We hypothesized that (1) both P addition and altered soil water content and their interaction with plant type can significantly increase or decrease the abundance and community composition of soil nematodes, and (2) N<sub>2</sub>-fixing trees can independently provide more suitable environments that lead to larger soil nematode communities than do non-nitrogen-fixing species under reduced soil water content conditions.

## 2 Material and methods

### 2.1 Experimental design

A completely randomized experimental design of two plant types (N<sub>2</sub>-fixers and non-nitrogen fixers), two levels of water treatments (optimum watered and drought), and two levels of

P additions (with and without P) was established in a greenhouse (temperature range 18–32 °C; relative humidity range 50–85%) at the Center for Ecological Studies, Chinese Academy of Science, Sichuan Province, China. *Alnus cremastogyne* (N<sub>2</sub>-fixing tree) and *Eucalyptus grandis* (non-nitrogen-fixing tree) were used in this study. The two species were grown for approximately 2 years in the nursery section of Sichuan Agricultural University, Sichuan Province. We transplanted healthy and uniform (height) seedlings of each species into a total of 60 pots (10 L) filled with 4000 g of a homogenized soil sample 0.19% total nitrogen (TN), 2.67% total carbon (TC) and pH of 7.3. A total of 40 surviving and healthy plants were selected afterwards (20 pots for *Alnus cremastogyne* and 20 for *Eucalyptus grandis*), and these plants were subjected to four treatments. The four treatments included optimum water with P addition (WP), optimum water only (W), drought with P addition (DP), and drought only (D), and the treatments were assigned randomly to the tree species. The treatments were replicated five times. Before the addition of P, the total and available phosphorus of the soil was determined to be 0.89 g/kg and 27.6 mg/kg, respectively. P fertilization was supplied as sodium dihydrogen phosphate (NaH<sub>2</sub>PO<sub>4</sub>, 25.5% P) at the rate of 129.3 mg P per pot. The fertilizer was mixed with 200 ml of water per pot and supplied every 30 days for 3 months. Before the drought treatments, the soil relative water content (SRWC) was measured. The SRWC was sorted into two levels: optimum water (80–85%) and drought (30–35%). The SRWC was expressed as  $SRWC = [(W_{soil} - W_{pot} - DW_{soil}) / (W_{fc} - W_{pot} - DW_{soil})] \times 100$ , where  $W_{soil}$  was the current soil weight (soil + pot + water),  $W_{pot}$  was the weight of the empty pot,  $DW_{soil}$  was the dry soil weight, and  $W_{fc}$  was the soil weight at field capacity (soil + pot + water). The pots were weighed every day and watered up to their respective target SRWC by replacing the amount of water that was transpired and evaporated. We maintained a distance of 40 cm between the pots to avert shading by the leaves of neighboring plants.

## 2.2 Soil sampling and analysis

Six months following transplanting and treatments, the plants were removed, and the soils were collected from all the replicates for the determination of the chemical properties and nematode communities. Soil pH was measured in a deionized water suspension at a ratio of 25 ml water to 10 g of soil using a pH meter (PHS-25, INESA Instruments, China). Soil moisture content was measured gravimetrically from mass lost after oven drying 10 g of moist soil to a constant weight at 105 °C for 24 h. Soil nitrate (NO<sub>3</sub><sup>-</sup>-N) and ammonium nitrogen (NH<sub>4</sub><sup>+</sup>-N) were extracted using 50 ml of 2.0 M KCl and measured on a flow injection autoanalyzer (AutoAnalyzer3, Bran+Luebbe, Germany). Available phosphorus (aP) was extracted with 0.5 M NaHCO<sub>3</sub> (pH 8.2) and measured

colorimetrically by the molybdate–ascorbic acid (Olsen and Sommers 1982; Murphy and Riley 1962). DOC and DON were extracted from fresh moist soil with an addition of 2 M KCl at 20 °C and measured using a TOC/TN analyzer (Multi N/C® 2100(S), Analytik Jena AG, Germany) (Huang et al. 2011).

## 2.3 Extraction and analysis of soil nematode community

Nematodes were extracted from 100 g of fresh soil samples within 72 h using the modified cotton-wool filter method (Townshend 1963) and preserved in 5% formalin. All the nematodes in each sample were enumerated, and a total of 100 individual nematodes were randomly selected and identified to the genus level. The nematode populations were quantified as the number of nematodes per 100 g dry soil. Following Yeates et al. (1993), the nematodes were assigned into four trophic groups: (1) bacterivores (Ba), (2) fungivores (Fu), (3) omnivores/predators (Op), and (4) plant parasites (PP). Based on their life strategy, different colonizer–persister (*c-p*) values were assigned to each nematode using the report of Bongers (1990).

## 2.4 Community indices of soil nematode

The nematode parameters of channel index (CI), enrichment index (EI), maturity index (MI), genus richness (GR), and the Simpson dominance (I<sub>g</sub>) were adopted to indicate the functional diversity and maturity indices of the nematode food web. The (CI), (EI), and (MI) were calculated according to the following formulas:  $CI = 100 \times 0.8 \times Fu_2 / (3.2 \times Ba_1 + 0.8 \times Fu_2)$ ;  $EI = 100 \times (e / (e + b))$ ;  $MI = \sum v_i f_i$ , where  $b$  is the basal food web component ( $Ba_2, Fu_2$ ),  $e$  is the enrichment component ( $Ba_1, Fu_2$ ) of the bacterivores (Ba) and fungivores (Fu),  $v_i$  is the *c-p* value of free-living nematodes to the  $i$ th genus and  $f_i$  is the proportion of the genus in the nematode community (Bongers 1990; Ferris et al. 2001; Yeates 2003). The GR and the I<sub>g</sub> were calculated as follows:  $GR = (S - 1) / \ln(N)$ ; and  $I_g = \sum p_i^2$ , where  $S$  represents the number of taxa,  $N$  is the number of individuals identified and  $p_i$  is the proportion of the  $i$  taxon (Simpson 1949; Pielou 1966).

## 2.5 Statistical analysis

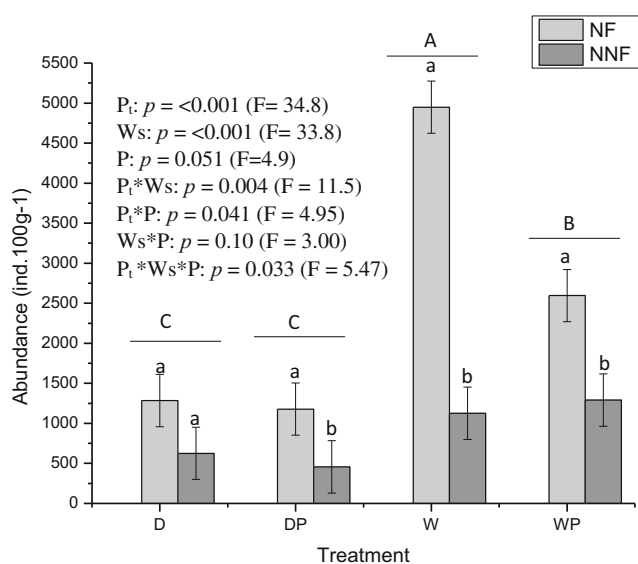
Obtained data were tested for the assumptions of normality and homoscedasticity using the Shapiro–Wilk's test. Analysis of variance (three-way ANOVA) was used to test the main and interactive effects of plant species, water, and P addition on the soil chemical properties, the abundance, and the nematode community indices. The least significant difference (LSD) test was used to test differences among treatment means with a significance level of  $p < 0.05$ . Paired sampled *t* test was used

to compare differences in the abundance and ecological indices of the soil nematodes between the two-tree species, and differences at  $p < 0.05$  were considered to be statistically significant. SPSS version 18.0 (SPSS Inc., Chicago, IL, USA) was used to perform the analyses. Figures were prepared using SigmaPlot 12.5 (Systat Software, Inc.). Partial redundancy analysis (RDA) was used to examine the relationship between the soil nematode community and the soil chemical properties. The best-fitting nematode genera with a proportion higher than 1 in one or all treatments were used as the variable to better explain the relationship between the nematode community and chemical properties better.

### 3 Results

#### 3.1 Soil nematode community composition and abundance between plant type

The total nematode abundance differed among the plant species (Fig. 1). The total density of nematodes in the soil vegetated with the  $N_2$ -fixing tree was higher (1285 individuals per 100 g soil in drought with P addition to 4,948 individuals per 100 g soil in optimum water treatment) than that of the non-nitrogen fixer (456 individuals per 100 g soil in drought with P addition to 1290 individuals per 100 g soil in optimum water with P addition). A total of 28 nematode genera were



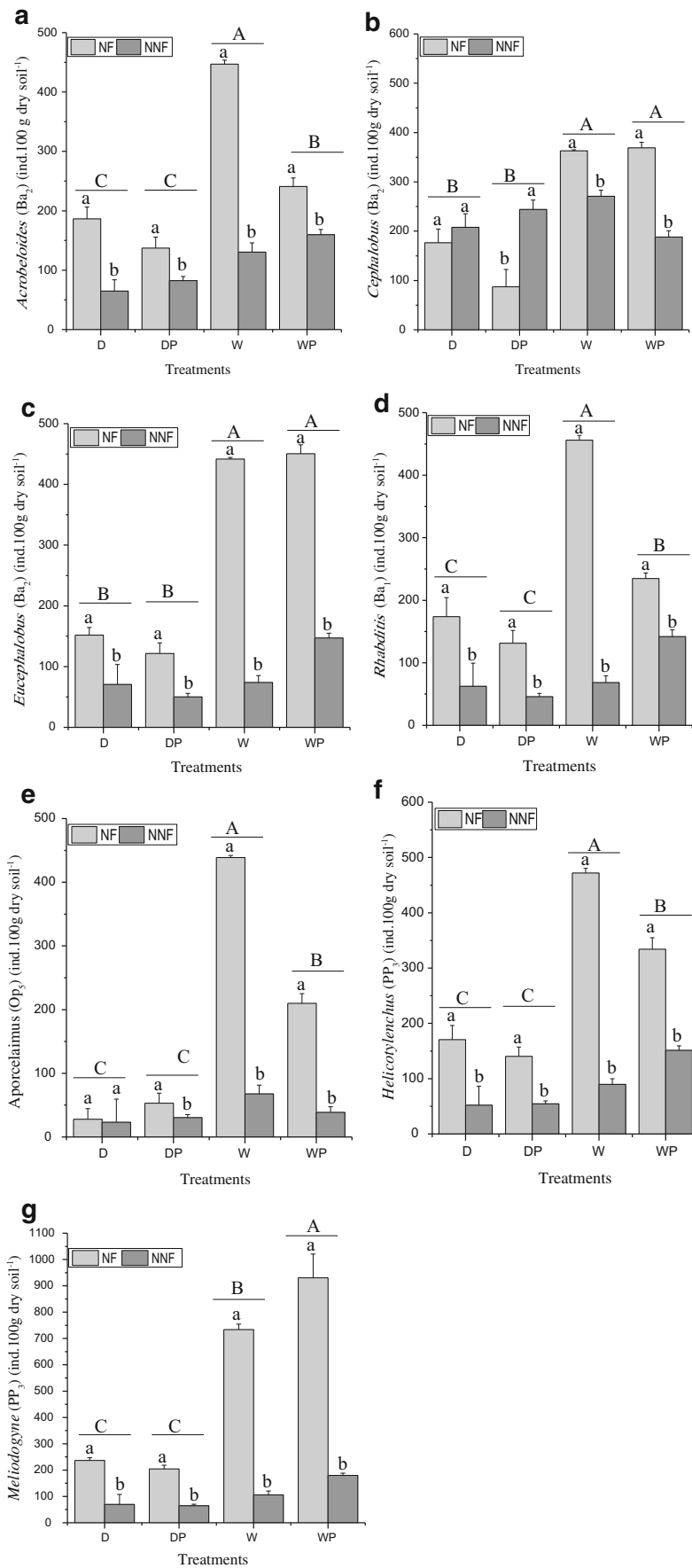
**Fig. 1** Responses of soil nematode abundance to P addition and water treatments. NF, nitrogen-fixing tree; NNF, non-nitrogen-fixing tree; WP, water + phosphorus; W, water only; DP, drought + phosphorus; D, drought only;  $P_t$ , planting types, water treatments;  $P_s$ , phosphorus treatments. Dissimilar uppercase letters denote significant differences among the treatments; different lowercase letters indicate significant differences between the NF and NNF. Significant at  $p < 0.05$ . The error bar represents SE

**Fig. 2** Density of the dominant soil nematodes by genera under P and water treatments. **a** *Acrobeloides*, **b** *Cephalobus*, **c** *Eucephalobus*, **d** *Rhabditidae*, **e** *Aporcelaimus*, **f** *Meloidogyne*, and **g** *Helicotylenchus*. WP, water + phosphorus; W, water only; DP, drought + phosphorus; D, drought only. Dissimilar uppercase letters denote significant differences among the treatments; different lowercase letters indicate significant differences between the NF and NNF. Significant at  $p < 0.05$ . The error bar represents SE

identified under the two-tree species (Table S1, Electronic Supplementary Material), of which *Acrobeloides*, *Aporcelaimus*, *Cephalobus*, *Eucephalobus*, *Helicotylenchus*, *Meloidogyne*, and *Rhabditidae* were the most dominant genera occurring in all the treatments. Plant type had a significant influence on the density of the dominant genera (Table S2, Electronic Supplementary Material). The density of the most dominant genera was significantly higher ( $p < 0.05$ ) in the soil planted with the  $N_2$ -fixing tree than in that with the non-nitrogen-fixing trees (Fig. 2a–d). However, the density of *Cephalobus* was significantly higher ( $p < 0.05$ ) in the non-nitrogen-fixing tree than in the  $N_2$ -fixing tree (Fig. 2b). The bacterivores and plant-parasitic nematodes in the soil vegetated with  $N_2$ -fixing trees were higher than those of non-nitrogen-fixing trees, irrespective of the P additions under optimum water and drought treatments (Fig. 3a, c). The channel index of the soil vegetated with the  $N_2$ -fixing trees was significantly lower ( $p < 0.01$ ) than that of the non-nitrogen-fixing tree (Table 1). The enrichment index of the soil vegetated with the  $N_2$ -fixing trees was significantly higher ( $p < 0.01$ ) than that of the non-nitrogen-fixing trees.

#### 3.2 Effects of phosphorus addition on soil nematode community structure

The ANOVA results showed that P addition had no significant independent effects on the total abundance of soil nematodes ( $F = 4.9$ ,  $p = 0.051$ ) (Fig. 1) and all nematode community indices (Table 2). At the genus level, the density of *Acrobeloides*, *Rhabditidae*, *Aporcelaimus*, and *Helicotylenchus* in P-treated soils under the optimum water condition were significantly lower ( $p < 0.01$ ) than those in the soils without the P treatment (Fig. 2a, d–f). P addition had no statistically significant effects on the abundance of the trophic groups, except for the omnivores–predators (Table S3, Electronic Supplementary Material). Compared to the soil samples without P treatment, the densities of all the trophic groups in P-treated soil were lower under the optimum water treatments (Fig. 3a–d). Although P addition had no significant independent effects on the nematode community indices (Table 2), its addition significantly increased ( $p < 0.01$ ) the channel index but decreased the enrichment index of the soil vegetated with the  $N_2$ -fixing tree (Table 1).



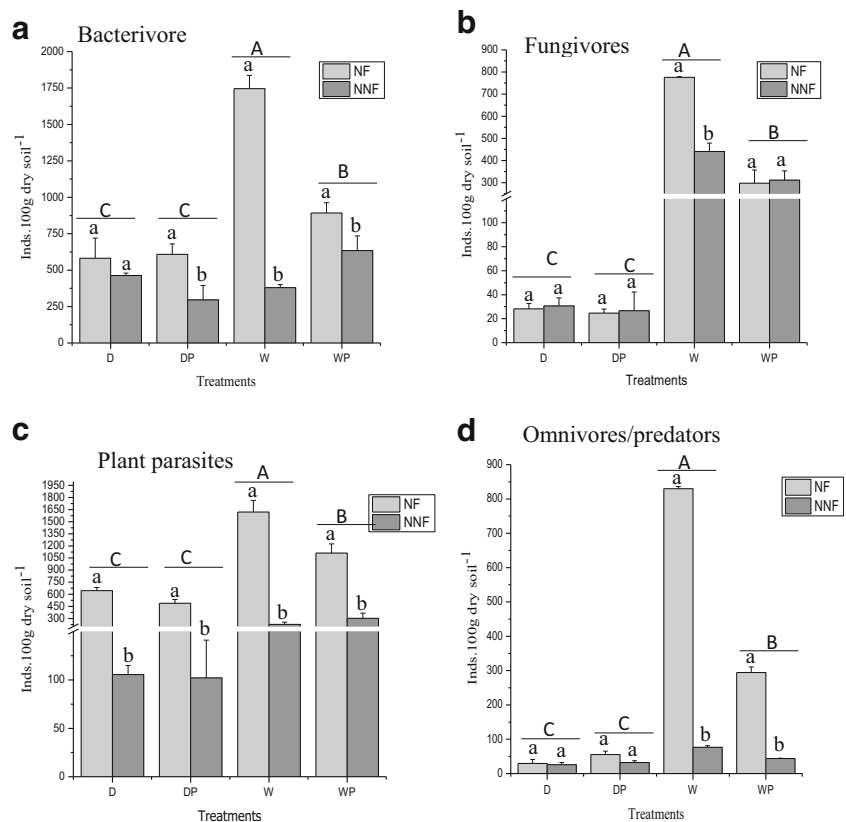
### 3.3 Effects of soil water contents on soil nematode community structure

The water treatments significantly impacted the nematode abundance ( $F=33.8$ ,  $p\leq 0.001$ ) (Fig. 1). The total density of nematodes under drought stress was significantly lower ( $p < 0.05$ ) than that under the optimum water treatment (Fig. 1). The densities of the dominant genera were significantly higher ( $p < 0.05$ ) in the optimum water treatment than in the drought treatments (Fig. 2a–g). There was an apparent decreasing effect of drought treatments on the abundance of each trophic group (Fig. 3a–d). The abundances of fungivores and omnivores were not significantly different between the two plants under the drought treatment (Fig. 3b, d). The genus richness and Simpson dominance values were significantly higher in the optimum water treatments than in the drought treatments in the soil vegetated with the  $N_2$ -fixing tree (Table 1). However, in the soil vegetated with the non-nitrogen-fixing trees, the g genus richness was significantly higher in the drought treatments than in the optimum water treatments. There were no significant differences in the maturity index and Simpson dominance between the tree species under the drought treatments, but under the optimum water treatments, the maturity index and Simpson dominance values of the soil vegetated with the  $N_2$ -fixing tree were significantly higher than those of the non-nitrogen-fixing tree (Table 1).

### 3.4 Combined effects of P addition and water treatments on the soil nematode community composition and abundance

Although the interaction of the P addition and water treatments had no significant impact on the total nematode abundance, there were significant decreasing ( $p < 0.05$ ) effects of P addition with optimum water on the total density of nematodes of the soil with the  $N_2$ -fixer (Fig. 1). The P addition and water treatments had no statistically significant interactive effects on the abundances of most dominant genera (Table S2, Electronic Supplementary Material). However, the addition of P to the drought-treated soil significantly ( $p < 0.05$ ) increased the abundance of *Cephalobus* in the non-nitrogen fixer (Fig. 2b). P addition with optimum water treatments significantly decreased the abundances of the trophic groups (Fig. 3a–d), though there was no significant statistical interaction of the P addition and water treatments on all the trophic groups (Table S3, Electronic Supplementary Material). The water treatments and their interaction with P addition significantly impacted ( $p < 0.001$ ) the genus richness and channel index. The genus richness values in the P-treated optimum water and drought soil were higher than their non-P counterparts (Table 1).

**Fig. 3** Trophic structure of soil nematode under the influence of P and water treatments. **a** Bacterivores, **b** fungivores, **c** plant parasites, **d** omnivore–predator. WP, water + phosphorus; W, water only; DP, drought + phosphorus; D, drought only. Dissimilar lowercase letters indicate significant differences between the NF and NNF. Significant at  $p < 0.05$ . The error bar represents SE



**Table 1** Soil nematode community indices of the two-tree species under P and water treatments

Index	Treatment	NF	NNF
GR	D	2.78 ± 0.04Bb	4.05 ± 0.11Aa
	DP	2.75 ± 0.03Bb	3.68 ± 0.03Aa
	W	3.42 ± 0.00Aa	3.38 ± 0.02Aa
	WP	3.79 ± 0.19Aa	3.51 ± 0.01Aa
Ig	D	0.30 ± 0.06Ba	0.38 ± 0.06Aa
	DP	0.28 ± 0.02Ba	0.32 ± 0.04Aa
	W	0.48 ± 0.06Aa	0.19 ± 0.01Bb
	WP	0.49 ± 0.15Aa	0.21 ± 0.01Bb
MI	D	2.86 ± 0.64Aba	1.87 ± 0.24Aa
	DP	1.51 ± 0.19Ba	1.36 ± 0.07Aa
	W	3.84 ± 0.55Aa	1.63 ± 0.07Ab
	WP	3.06 ± 0.59Aa	1.14 ± 0.03Ab
CI	D	0.39 ± 0.03Cb	90.47 ± 9.52Aa
	DP	6.66 ± 0.66Bb	42.06 ± 4.82Aa
	W	7.84 ± 2.83Bb	70.74 ± 3.70Aa
	WP	27.47 ± 18.10Ab	86.17 ± 8.26Aa
EI	D	47.25 ± 17.84Aa	5.35 ± 3.48Bb
	DP	31.16 ± 11.65Aa	8.88 ± 1.97Bb
	W	44.32 ± 11.65Aa	27.16 ± 2.93Ab
	WP	28.34 ± 8.33Aa	23.28 ± 1.69Ab

Values are mean ± SE. Dissimilar lowercase letters denote significant differences among the treatments under each plant species. Different lowercase letters at each treatment indicate significant differences in the variable mean between the tree species. Different uppercase letters under each tree species indicate significant differences in the variable mean among the treatments. WP, water + phosphorus; W, water only; DP, drought + phosphorus; D, drought only. GR, genus richness; Ig, Simpson dominance; MI, maturity index; CI, channel index; EI, enrichment index.

**Table 2** The ANOVA of the effects of planting types (P<sub>t</sub>), phosphorus addition (Ps), water treatment (Ws), and their interactions on soil nematode indices

	Nematode indices				
	GR	Ig	MI	CI	EI
P <sub>t</sub>	< 0.001	0.039	< 0.001	< 0.001	0.007
Ws	0.003	0.594	0.076	0.043	0.221
Ps	0.654	0.815	0.101	0.772	0.276
P <sub>t</sub> × Ws	0.001	0.003	0.014	0.874	0.091
P <sub>t</sub> × Ps	0.024	0.920	0.310	0.026	0.179
Ws × Ps	0.001	0.617	0.584	0.005	0.869
P <sub>t</sub> × Ws × Ps	0.695	0.763	0.625	0.062	0.928

P<sub>t</sub>, planting types, water treatments; Ps, phosphorus treatments; GR, genus richness; Ig, Simpson dominance; MI, maturity index; BAI, bacterial index; CI, channel index; EI, enrichment index; ns, not significant. Values shown in italics are significant at *p* < 0.05

### 3.5 Soil chemical properties and their relationships with soil nematode communities

P addition significantly increased the DOC and aP of both the N<sub>2</sub>-fixing trees and the non-nitrogen-fixing trees, irrespective of the water treatments (Table 3). However, the DOC content of the N<sub>2</sub>-fixing trees was higher (234.1 mg/kg dry soil) than that of the non-nitrogen-fixing trees (216.73 mg/kg dry soil) under the drought treatment. The NO<sub>3</sub><sup>-</sup>-N and DON concentrations significantly increased under the drought treatment, irrespective of P addition, but the NO<sub>3</sub><sup>-</sup>-N and DON concentrations in soil vegetated with the N<sub>2</sub>-fixing tree were higher than those of the non-nitrogen-fixing tree (Table 3). There was a significant interaction of planting type and water treatment on all the chemical variables. The results of partial RDA indicated that the soil nematode community structures under the two-tree species were distinctly separated from each other (Fig. 4). The first two axes together explained 64.0% of the total variation observed in the soil nematode communities. The first RDA axis was driven mainly by NO<sub>3</sub><sup>-</sup>-N, NH<sub>4</sub><sup>+</sup>-N, SM, DON, and aP, while DOC, SM, and pH drove the second axis. The bacterivores nematodes included *Eucephalobus*, *Acrobeloides*, and *Cephalobus*; fungivorous nematodes included *Aphelenchus*; the plant-parasitic nematodes *Ditylenchus* was positively related to DON, aP, and NO<sub>3</sub><sup>-</sup>-N. Similarly, omnivores–predators including *Thonus*, *Aporcelaimus*, and *Mesodorylaimus*; the plant-parasitic nematodes including *Aphelenchoides*, *Criconemoides*, and *Tylenchus*; and the bacterivores Rhabditidae were positively associated with NH<sub>4</sub><sup>+</sup>-N, DOC, and SM (Fig. 4).

## 4 Discussion

### 4.1 Variation in soil nematode community composition and abundance between plant type

The soil nematode community is a useful ecological indicator that provides information about the effects of different management practices on soil health (Zhao et al. 2014). The diversity and abundance of soil fauna and their trophic groups can be significantly affected by the type of above-ground plant species (Olatunji et al. 2018; Wang et al. 2018). The present study revealed the influence of plant type on the soil nematode abundance, trophic groups, and community indices. Previous studies had reported that N<sub>2</sub>-fixing tree species might improve the abundance of soil fauna, including bacterivorous and omnivorous nematodes more than non-nitrogen fixers (Huang et al. 2014; Qin et al. 2014). Similarly, in this study, the total density of nematodes was higher in the soil vegetated with the N<sub>2</sub>-fixing tree (Fig. 1), likely due to there being more food resources under N<sub>2</sub>-fixing trees, which favor the increase in the abundance of opportunistic bacterivores and those of

**Table 3** Effects of P addition and water treatments on soil chemical properties

Plant species	Treatment	NO <sub>3</sub> <sup>-</sup> -N	NH <sub>4</sub> <sup>+</sup> -N	DOC	DON	PH	SM	aP
NF	D	5.08a	0.45a	234.18b	115.59a	7.57a	9.83c	27.66c
	W	0.73b	0.13a	215.92c	63.91d	7.63a	10.74b	19.33d
	DP	5.70a	0.33a	277.92b	98.46b	7.53a	9.42d	50.00b
	WP	1.13b	0.23a	297.17a	71.84c	7.81a	11.88a	76.66a
NNF	D	2.89a	0.18b	216.73c	73.40b	7.61a	9.34b	14.66d
	W	0.47c	0.80a	238.41b	63.96 d	7.50a	13.64a	23.33c
	DP	2.01b	0.16b	239.76b	80.32a	7.69a	8.30b	105.3a
	WP	0.34c	0.12b	366.99a	71.22c	7.44a	11.93a	80.00b
Analysis of variance ( <i>p</i> values)								
Planting (Pt)		< 0.001	ns	ns	< 0.001	ns	ns	< 0.001
Water (Ws)		< 0.001	ns	0.005	< 0.001	ns	0.001	< 0.001
Phosphorus (Ps)		ns	ns	0.001	ns	ns	ns	0.004
Pt*Ws		0.001	0.018	0.006	< 0.001	0.005	0.01	< 0.001
Pt*Ps		ns	ns	ns	0.001	ns	ns	< 0.001
Ws*Ps		ns	ns	0.007	0.004	ns	ns	< 0.031
Pt* Ws*Ps		ns	0.034	ns	0.001	ns	ns	0.001

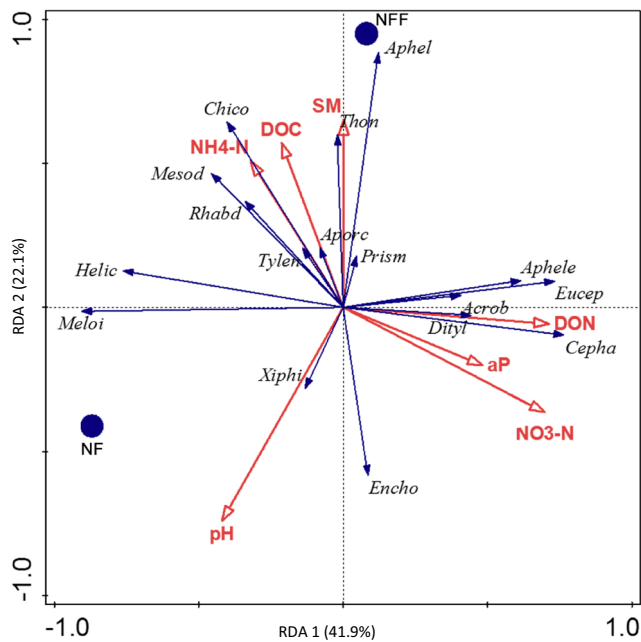
Each value is the mean ( $n = 5$ ). *NF*, nitrogen-fixing tree; *NNF*, non-nitrogen-fixing tree; *D*, drought; *W*, optimum water; *DP*, drought plus phosphorus addition; *WP*, optimum water plus phosphorus addition; *SM*, soil moisture (%); *pH*, soil pH; *DOC*, dissolved organic carbon (mg/kg dry soil); *DON*, dissolved organic nitrogen (mg/kg dry soil); *NH<sub>4</sub><sup>+</sup>-N*, soil ammonium nitrogen (mg/g); *NO<sub>3</sub><sup>-</sup>-N*, soil nitrate nitrogen (mg/g); *aP*, available phosphorus (mg P kg<sup>-1</sup> soil); *ns*, no significant effect. Significant *p* values ( $p < 0.05$ ) are shown in bold face type. Different letters indicate significant differences among the treatments under each tree species

similar *c-p* guilds (e.g., *c-p*, 3 and 5, respectively). Therefore, the vegetation of the soil with the N<sub>2</sub>-fixing tree could increase the food resources for soil nematodes. Additionally, this study revealed that some nematode genera were more closely related to similar environmental variables but under distinct plants species (Fig. 4), suggesting there is a species-specific partitioning of nematode genera that is irrespective of the management practices for their preference in biochemical variables. We observed that *Eucephalobus*, *Acrobeloides*, *Cephalobus*, *Aphelenchus*, and *Ditylenchus* genera were positively correlated with DON, aP, and NO<sub>3</sub><sup>-</sup>-N; furthermore, *Thonus*, *Aporcelaimus*, *Mesodorylaimus*, *Aphelenchoides*, *Criconemoides*, *Tylenchus*, and *Rhabditidae* were positively associated with NH<sub>4</sub><sup>+</sup>-N, DOC, and SM. The correlation with different chemical properties indicated that nematode genera within the same trophic group responded differently to environmental variables (Sun et al. 2016). Consistent with the observation of Song et al. (2016), the higher density of bacterivores in the soil vegetated with the N<sub>2</sub>-fixing tree than in the soil with the non-nitrogen-fixing tree was mainly due to the higher abundances of *Acrobeloides*, *Cephalobus*, *Eucephalobus*, and *Rhabditis* and correspond to the higher soil NO<sub>3</sub><sup>-</sup>-N and DON under the N<sub>2</sub>-fixer. Hence, there was a more enriched soil food web in the soil vegetated with the N<sub>2</sub>-fixer. The bacterivores among the nematode trophic groups play a crucial role in the soil detritus food web, and an increase in their abundance often improves plant nutrient

mineralization (Liu et al. 2016b). Our results contrasted with the suggestion of Liu et al. (2016b), who stated that higher N levels could cause physiological changes in a plant that may prevent the multiplication of plant-feeding nematodes. We observed that despite the higher level of NO<sub>3</sub><sup>-</sup>-N and DON in the soil vegetated with the N<sub>2</sub>-fixing tree than in the soil with the non-nitrogen-fixing tree (Table 3), the density of plant-parasitic nematodes under the N<sub>2</sub>-fixing tree was higher than that of the non-nitrogen-fixing tree. These results indicated that the N<sub>2</sub>-fixing tree provides a greater plant resource and likely increased microbial biomass (Pan et al. 2016), which contributed to nutrient cycling and the higher abundance of herbivorous nematodes that feed upon them. Although the biomass input of either the N<sub>2</sub>-fixing or the non-nitrogen-fixing tree was not quantified in this study, similar to Lu et al. (2016), the higher density of omnivores/predators in the soil vegetated with the N<sub>2</sub>-fixing tree than in the soil with the non-nitrogen-fixing tree might be because the N<sub>2</sub>-fixing tree contributed residue quantities that favored their abundance more than the non-nitrogen-fixing tree.

The soil nematode community indices measured in this study reflect changes in the soil nematode communities and indicate differences in the soil food web of N<sub>2</sub>-fixing tree compared to that of non-nitrogen-fixing trees. Consistent with the findings of Liu et al. (2016a), the enrichment index in the soil vegetated with the N<sub>2</sub>-fixing tree was significantly higher than that of the non-nitrogen-fixing tree. Conversely, the CI of the non-nitrogen-





**Fig. 4** Redundancy analysis (RDA) ordination biplot of soil nematode genera and soil chemical properties. NF, nitrogen-fixing tree; NFF, non-nitrogen-fixing tree, DOC, dissolved organic carbon, DON, dissolved organic nitrogen; SM, soil moisture,  $\text{NH}_4^+\text{-N}$ , ammonia nitrogen;  $\text{NO}_3^-\text{-N}$ , nitrate nitrogen; aP, available phosphorus and soil pH; *Aphel*, *Aphelenchoides*; *Thon*, *Thonus*; *Chico*, *Criconemoides*; *Mesod*, *Mesodorylaimus*; *Rhabd*, *Rhabditidae*; *Tylen*, *Tylenchus*; *Aporc*, *Aporcelaimus*; *Prism*, *Prismatolaimus*; *Aphele*, *Aphelenchus*; *Eucep*, *Eucephalobus*; *Acrob*, *Acrobeloides*; *Cepha*, *Cephalobus*; *Dityl*, *Ditylenchus*; *Helic*, *Helicotylenchus*; *Encho*, *Enchodelus*; *Xiphi*, *Xiphinema*; *Meloi*, *Meloidogyne*

fixing tree was significantly higher than that of the  $\text{N}_2$ -fixing tree. The differences in the enrichment index and channel index of the  $\text{N}_2$ -fixers compared to the non-nitrogen fixers could be explained mainly by the observed variations in the abundances of bacterivores and fungivores between the tree species. The enrichment index could reflect the availability of resources to the soil food web and the response of the primary decomposers to the resources (Song et al. 2016), while the channel index is considered to indicate the decomposition pathways in an ecosystem (Lu et al. 2016). The higher enrichment index and the lower channel index indicated that the  $\text{N}_2$ -fixing tree, likely due to its nitrogen-fixing mechanism, could drive the soil food web to the bacterial decomposition channel by increasing the soil  $\text{NO}_3^-\text{-N}$  and DON (Table 3). The high maturity index value indicates that the structure of the nematode community is stable and the complexity of the soil food web could increase under the  $\text{N}_2$ -fixing trees.

#### 4.2 Influence of P addition on soil nematode community structure

Studies examining the effects of P addition on soil nematode communities are relatively limited (Liu et al. 2016b; Song et al. 2016). Hence, the response of the soil nematode

community composition and structure to P addition is not very clear. In the present study, the ANOVA results showed that P addition had no significant independent effects on the total nematode abundance, dominant genera, trophic groups, and community indices. However, the addition of P under optimum water conditions decreased the total nematode and the density of the most dominant genera of the soil vegetated with the  $\text{N}_2$ -fixer. The results also indicated that members of the dominant genera *Acrobeloides*, *Rhabditidae*, *Aporcelaimus*, and *Helicotylenchus* were sensitive to P addition and did not increase in the P with optimum water treatment soil despite the higher DOC and aP contents. Similarly, fungivores, plant parasitic, omnivore/predator nematode, and bacterivores decreased with P addition under the optimum water treatments. A previous study had suggested that plants efficiently and economically shift resources from nutrient acquisition so they can directly obtain enough resources from the soil in the condition of nutrient addition (Olatunji et al. 2018). Thus, the resource input from plants to soil organisms will be reduced (Treseder and Vitousek 2001). Zhao et al. (2014) also reported that an increase in the soil P could result in the reduction of the resources input from plants to soil organisms in the short term. P addition significantly increased the soil P content in this study. Therefore, the decrease in the total nematodes and the density of the most dominant genera might be due to the increased soil aP after P addition. The significant increase in the value of channel index with P addition compared to the no-P treatment suggested that although the  $\text{N}_2$ -fixer could drive the soil food web to the fast-bacterial channel, the fungal-mediated decomposition pathway also existed with the P addition treatments (Lu et al. 2016).

#### 4.3 Effects of soil water contents on soil nematode community structure

Previous studies have reported that changing water availability can significantly impact the soil fauna community abundance (Song et al. 2016; Wang et al. 2018). Similarly, water treatments significantly influenced the total nematode abundance, the density of the dominant genera, and the trophic groups. Contrary to Savin et al. (2001), but consistent with the exclusion hypothesis (Gorres et al. 1999; Landesman et al. 2011), drought significantly decreased the total density of soil nematodes compared to the optimum water treatment. The decrease appeared to hinge more on the identity of each tree, as a higher density of nematodes could still be observed under the  $\text{N}_2$ -fixing tree than under the non-nitrogen-fixing tree. The observed general decreases in the total nematode density, the dominant genera, and the trophic groups due to drought indicate that little individual growth was conceivable, likely due to restrictions in the movement towards food resource (Zhao et al. 2014). However, a study has suggested that in response to the drought stress, nematodes could survive by migrating

below the sampling depth (Landesman et al. 2011). This assertion is unlikely in the present study because ours is a pot experiment, which captured the whole organic horizon. However, it is possible that drought stress led to nematode mortality and that surviving individuals, particularly of the dominant genera, entered anhydrobiosis.

The energy flow in the soil food web occurs mainly via feeding and interactions among soil biota, and the feeding relationship is linked to the availability of food, predator species, and soil environments (Xiao et al. 2014). Given the high sensitivity of fungivores and omnivores/predators to drought (Fig. 3b, d) compared to the other trophic groups (Fig. 3a, c), our results suggest that changes in the soil water content likely alter the feeding relationship by increasing the fungivorous grazing. Except for the GR and CI, we do not observe significant responses of the nematode community indices to the water treatments. Studies have reported the negative influence of an increase in soil nitrogen availability on soil nematode generic richness (Song et al. 2016; Wei et al. 2012). Similarly, in this study, the  $\text{NO}_3^-$ -N and DON in the soil vegetated with the  $\text{N}_2$ -fixers was significantly higher under the drought treatment and subsequently led to a decline in the generic richness of the nematodes. The result of this study indicates that changes in the soil water contents could result in an altered soil food web.

#### 4.4 Combined effects of P addition and water treatments on the soil nematode community structure

Previous findings have reported that alterations in the soil water content due to climate change scenarios and nutrient additions (e.g., P and N) contribute to variations in the soil nematode community structure (Zhao et al. 2014; Cavagnaro 2016; Pan et al. 2016; Sun et al. 2016). Contrary to our first hypothesis, we do not find statistically significant interactive effects of soil water content and P addition for the dominant genera and the trophic groups. Nevertheless, the addition of P to drought-treated soil increased the density of the *Cephalobus* genus in the soil vegetated with non-nitrogen fixers more than in the soil of the nitrogen fixers. Unfortunately, we could not find any studies that investigated the effects of P when added to soil under drought on the soil nematode community, either in a pot experiment or in the field. We suggested that the present observation might be that the positive effects of combining drought and P are higher than the individual effects, and the P addition could help stabilize some nematode genera of the soil vegetated with the non-nitrogen fixer under the drought condition. Further study is required in this regard, as the difference in the complexity of the plant and soil biota assemblages could also regulate the responses of the soil nematodes to varying resource availability and microenvironments (Raty and Huhta 2003).

Omnivore–predator can be used as an indicator of soil condition, and a higher population indicates a lesser disturbed soil environment with excellent living conditions (Pan et al. 2016). Similar to the observation of Zhao et al. (2014), the density of omnivore–predator in the soil vegetated with  $\text{N}_2$ -fixers was significantly higher than that of the soil vegetated with non-nitrogen fixers, irrespective of P interaction with optimum water condition. These apparent differences indicated that P addition might not be necessary for the stability of soil nematodes under the  $\text{N}_2$ -fixing tree, and its addition is of minor disturbance to the food webs of the  $\text{N}_2$ -fixing tree. Overall, the data of this study indicated that there were adverse effects of drought on the soil nematode community and that the interaction of P and water addition had no impact on the soil nematode abundance and most of the community structure. This study points to the positive influence of the  $\text{N}_2$ -fixing tree on the soil nematode abundance and community composition. It is important to mention that this study is restricted to only *A. cremastogyne* ( $\text{N}_2$ -fixer) and *E. grandis* (non-nitrogen fixer). Therefore, the findings should be viewed in this context, and further studies considering other tree species of specific identity should be carried out. These studies would allow testing the generality of the patterns found here.

## 5 Conclusions

Our results indicate that the soil nematode community structure has a higher density in the soil vegetated with the  $\text{N}_2$ -fixing tree than in the soil with the non-nitrogen-fixing tree. The total nematodes and the density of bacterivores, plant parasitic, and omnivores/predators in the soil vegetated with the  $\text{N}_2$ -fixing tree were significantly higher than those of the non-nitrogen-fixing tree. Notably, the higher density of bacterivores, soil  $\text{NO}_3^-$ -N, and DON in the soil vegetated with the  $\text{N}_2$ -fixer than in the soil with the non-nitrogen fixer indicated a more enriched soil food web existed under the  $\text{N}_2$ -fixing tree. The present findings further demonstrated that the soil nematode abundance and community composition was more affected by the type of trees and water treatments than by the P addition or its interaction with the water treatments. Neither P addition nor its interaction with water had statistically significant effects on the total nematode abundance, dominant genera, trophic groups, and community indices. However, we found that with P addition, the total nematode abundance of the soil vegetated with the  $\text{N}_2$ -fixer decreased under the optimum water condition. Although drought exerted adverse effects on the total density of soil nematodes, dominant genera, and trophic groups, this study demonstrated that the rate of impact appeared to hinge more on the identity of each tree; furthermore, the  $\text{N}_2$ -fixer could still maintain its ecological function irrespective of the environmental changes.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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