

Original Research

# Soil Nematode Trophic Groups in Four Different Plantations in Southern China: Implications for Restoration

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## Abstract

Intensive anthropogenic disturbances have caused forest ecosystem degradation and soil erosion. Exotic fast-growing species are selected as pioneer species for restoration in degraded hilly lands of southern China. To better understand the potentials of the soil nematode trophic group composition in carbon sequestration, we investigated nematode trophic groups in *Acacia*, *Eucalyptus*, and *Schima* (native species as control) monoculture plantations in southern China after 23 years of reforestation. Our results showed that although total soil nematode abundance was not affected, the *Acacia* plantation significantly altered nematode trophic group composition over native species. Bacterivore and microbivore abundance, trophic diversity, and microbivore-driven soil organic carbon storage were higher in *Acacia mangium* than *Schima superba*. In contrast, plant parasitic nematode abundance and fungivore/bacterivore ratio were lower in *Acacia mangium* than *Schima superba*. As a result, *Acacia mangium* as a fast-growing pioneer tree species could be widely planted to maintain soil biodiversity and store carbon in restoring degraded forests in southern China. *Eucalyptus exserta* plantation enlarged the soil nematode community, including bacterivores, fungivores, and herbivores, suggesting that there is almost no allelopathy when eliminating anthropogenic disturbance in this study. Reasonable management is crucial for providing timber products and improving the ecological function of *Eucalyptus* plantations. Our results also highlight the critical roles of soil water and nutrient availability in regulating soil nematode trophic group composition and carbon sequestration.

**Keywords:** ecosystem restoration, soil biota, microbivore, *Acacia*, *Eucalyptus*

## Introduction

Plants are the source of life in a terrestrial ecosystem. They perform many ecological functions and shape the lives of living things in the environment where they live. Life is directly or indirectly dependent on plants [1-3]. The ability of plants to fulfill their functions primarily depends on the availability of appropriate climatic and edaphic conditions [4-5]. Therefore, soil is one of necessary conditions for a plant's existence, which is essential for living things. Soil, which has a complex structure, provides the basis for biological and biochemical processes. It is important to examine the changes in soil and its relationship with plants.

In the last few decades, intensive anthropogenic disturbances for economic development have greatly affected terrestrial ecosystems and caused a series of environmental problems such as forest degradation, biodiversity loss, and soil erosion. Forests, accounting for approximately 27% of the earth's land surface, play an important role in maintaining biodiversity, strengthening carbon sequestration capacity, and conserving water and soil [6-7]. Establishing forest plantation in degraded habitats is widely accepted as an effective approach to restore and rehabilitate the ecosystem through natural succession without anthropic disturbance [8]. Most previous studies focus on assessing vegetation recovery or soil organic matter accumulation during a degraded ecosystem's restoration [9-11]. Therefore, exploring how soil organisms respond to restoration is important for evaluating ecosystem restoration.

Soil organisms, including soil microorganisms and soil fauna, play a major role in organic matter decomposition and nutrient cycling [12]. Nematodes are the most abundant multi-cellular organisms in soil and are well adapted to a wide range of environmental conditions. Nematodes respond to disturbance rapidly and occupy key positions at all consumer trophic levels (bacterivore, fungivore, herbivore, omnivore, and predator) in the soil food web. Therefore, soil nematode trophic group composition can give insights into the structure and function of the soil ecosystem due to their crucial regulative roles in the microbial community [13]. Some previous studies have reported that nematodes are widely used as biotic indicators of conservation or disturbance, nutrient enrichment, and pollution of soils [14-17]. However, less attention has been paid to the application of soil nematodes as bio-indicators to evaluate the long-term natural recovery of degraded ecosystems.

In southern China artificial forests have been established enormously in degraded hilly areas for ecological restoration during the past 50 years. Exotic fast-growing species such as *Acacia* and *Eucalyptus* are generally selected as pioneer species for reforestation due to their higher productivity and tolerance to barren and acidic soils [18]. In this study, reforestation with different tree species including *Acacia*, *Eucalyptus*, and *Schima* (native species as control) monoculture plantations have been conducted in degraded hilly lands of southern

China since 1983. To evaluate the soil restoration of different plantations and select an applicable pioneer species, we detected the changes in soil nematode trophic groups after 23 years of reforestation. Since *Acacia* as leguminous plants could fix nitrogen into soil due to its symbiosis with rhizobia, we hypothesized that *Acacia* soil would accumulate more nutrient substance and support a higher abundance of microbivorous nematodes. Given that *Eucalyptus* allelopathy is likely to inhibit understory plant growth, our second hypothesis is that *Eucalyptus* would suppress soil nematode abundance and diversity. We also hypothesized that soil nematode composition may vary with seasonal variability due to changes in water and nutrient availability.

## Materials and Methods

### Description of Study Site

The experimental site was located at Heshan National Field Research Station of Forest Ecosystem (22°34' N, 112°50' E, 80 m a.s.l.), Chinese Academy of Sciences, Guangdong, China. The climate is subtropical monsoon with a distinct dry (from October to March) and wet (from April to September) season. The mean annual precipitation is 1,700 mm with 80% of the precipitation occurring during the wet season. The mean annual temperature is 21.7°C, and the maximum and the minimum temperatures are 29.2°C in July and 12.6°C in January. Mean annual evaporation is 1600 mm. The soil is classified as Acrisol according to the United Nations Food and Agriculture Organization. The mean slope of the hilly land is 28°.

The zonal climax vegetation is subtropical monsoon evergreen broad-leaved forest. From 1950 to 1980 the forests were severely damaged due to excessive utilization, resulting in vegetation degradation and soil erosion. The dominant species were shrub and herbaceous species such as *Ischaemum indicum*, *Eriachne pallescens*, and *Baeckea frutescens*. In 1983, four experimental monoculture plantations were established to restore the degraded ecosystems. All plantations were left to develop naturally without anthropogenic disturbance [19].

### Soil Sampling and Analysis

The sampling sites were selected in the 12 catchment regions. Each catchment region, which occupied approximately 1 ha, was one of three replications of the four monoculture plantations: *Schima superba* (SS), *Acacia mangium* (AM), *Acacia auriculaeformis* (AA), and *Eucalyptus exserta* (EE). In each catchment region three 10 × 10 m<sup>2</sup> sampling blocks were randomly established on the upper slope, mid slope, and lower slope to eliminate the effect of slope. Soil samples were collected from the root and non-root zones, which were defined as close to trunk and far away from trunk in all the blocks. After the surface litter was removed carefully, five soil cores of 0-10 cm depth were randomly taken using a 3 cm diameter

auger in each plot, and combined to form one composite sample. Soil samples were collected on 9 November 2006 (dry season) and 11 May 2007 (wet season). Total soil sample numbers were 144. After passing through a 2 mm sieve and the removal of visible roots and stones by hand, subsamples were used for nematode extraction and identification, soil moisture, and dissolved organic carbon analyses. The other subsamples were air-dried for chemical analysis.

Gravimetric soil moisture was measured by oven-drying for 24 h at 105°C. Soil pH was determined in a soil water mixture of 1:2.5 (w/v) using a digital pH meter. Soil organic carbon was determined by the oxidation of  $\text{H}_2\text{SO}_4/\text{K}_2\text{Cr}_2\text{O}_7$  and titration with  $\text{FeSO}_4$ . Soil total nitrogen was measured using an ultraviolet spectrophotometer after Kjeldahl digestion. Dissolved organic carbon was extracted from moist 20 g soil samples after being shaken for 30 min in 60 ml of 0.5 M  $\text{K}_2\text{SO}_4$ . The extracts were filtered and measured by a total organic carbon analyzer (Elementar vario TOC, Elementar Co., Germany).

Nematodes were extracted from 50 g of fresh soil using the Baermann funnel method. After fixation in 4% formaldehyde solution, nematodes were counted with an inverted microscope (Eclipse Ts100, Nikon). In each sample, the first 100 individuals were identified to four trophic groups, i.e., bacterivores, fungivores, herbivores, and omnivore-predators. All nematodes were identified

when the sample contained fewer than 100 individuals.

### Statistical Analysis

Nematode data were transformed using  $\ln(x + 1)$  to meet assumptions of normality and homogeneity of variance. Trophic diversity index (TDI) was calculated by  $\text{TDI} = 1/\sum p_i^2$ , where  $p_i$  is the proportion of individuals of the  $i$ th trophic group in the total community [20]. The effects of season, forest type, slope, root zone, and their potential interactions on soil and nematode properties were analyzed using four-way ANOVAs. Multiple comparisons were conducted to examine the effects of forest type on soil and nematode properties in both dry and wet seasons. Simple linear regressions were performed to assess the relationships of nematode properties and abiotic factors in dry and wet seasons. All statistical analyses were performed using SPSS 17.0 software (SPSS Inc., Chicago, USA). LSD was used to test differences among treatments.

## Results

### Soil Properties

Soil moisture varied with season (Table 1). Mean soil moisture in wet season (28.4%) was higher than that

Table 1. Results (F values) of four-way ANOVAs for the effects of season (S), forest type (F), slope (Sl), root zone (R), and their potential interactions on soil moisture (SM), soil pH, soil organic carbon (SOC), total nitrogen (TN), nematode abundance (N), trophic diversity index (TDI), bacterivore abundance (B), fungivore abundance (F), herbivore abundance (H), omnivore-predator abundance (O), fungivores/bacterivores ratio (F/B), and (fungivores+bacterivores)/herbivores ((F+B)/H).

Source of variation	SM	pH	SOC	TN	N	TDI	B	F	H	O	F/B	(F+B)/H
Season (S)	187.0***	92.6***	3.6	12.8***	8.7**	10.7***	64.2***	3.9*	0.0	0.0	4.7*	46.3***
Forest type (F)	38.8***	14.8***	37.6***	34.7***	5.5**	5.9***	9.1***	6.8***	5.0**	1.0	3.9*	2.1
Slope (Sl)	0.1	0.1	0.6	1.1	3.6*	3.9*	0.7	0.1	4.4*	1.8	0.6	2.2
Root zone (R)	1.4	12.6***	9.8**	5.7*	0.2	0.7	0.1	0.1	0.5	0.6	1.9	0.5
S × F	2.0	11.2***	1.9	2.5	7.1***	1.3	9.7***	1.8	4.9**	2.8*	3.8*	3.4*
S × Sl	0.9	0.1	0.7	0.8	0.4	0.9	0.5	0.2	0.5	1.4	0.3	0.2
S × R	0.0	5.4*	2.7	1.0	0.6	0.5	1.4	0.1	0.8	0.1	2.6	0.4
F × Sl	0.4	2.4*	0.5	0.7	0.7	5.4***	1.0	1.7	1.3	0.6	0.6	4.1**
F × R	0.2	2.6	1.1	1.2	0.2	0.2	0.6	1.6	0.2	0.2	1.7	1.0
Sl × R	0.1	3.7*	0.1	0.2	0.3	0.5	0.3	1.1	0.1	0.8	0.2	0.1
S × F × Sl	0.5	1.9	0.2	0.8	2.4*	2.4*	0.5	2.0	3.5**	1.1	0.7	2.2
S × F × R	0.9	0.2	0.2	0.3	0.3	0.8	0.0	0.3	0.5	0.6	0.9	0.5
S × Sl × R	0.2	1.6	1.8	0.9	0.2	1.1	0.3	1.6	0.2	1.3	0.0	0.7
F × Sl × R	0.8	0.6	1.0	0.8	1.1	0.2	0.9	0.1	1.0	1.1	0.8	0.6
S × F × Sl × R	0.4	0.8	1.3	1.4	1.0	0.5	0.6	0.7	0.9	0.3	0.6	0.9

Significance levels: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$

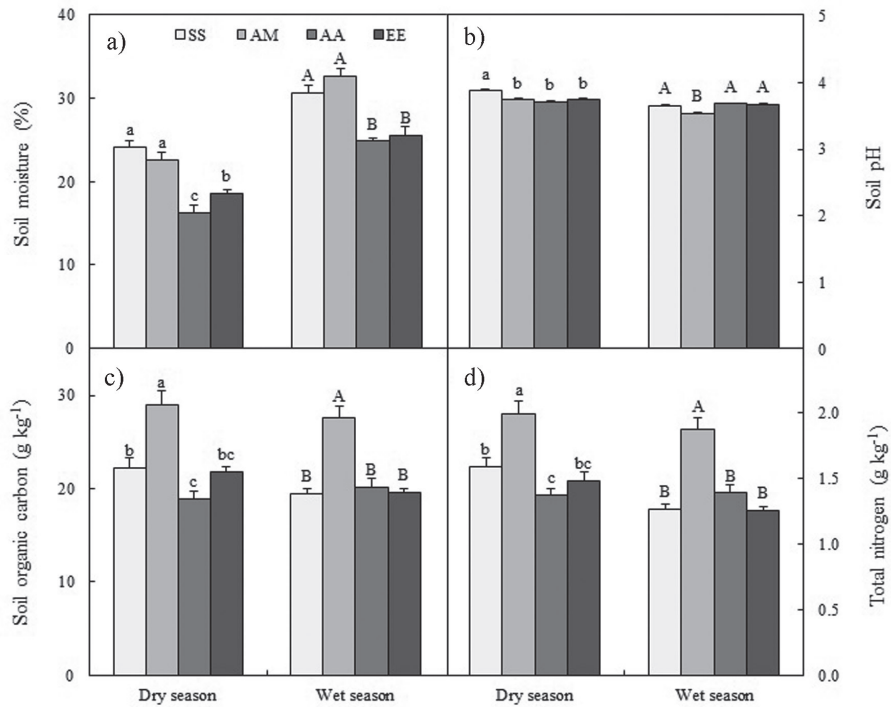


Fig. 1. Soil moisture a), soil pH b), soil organic carbon c), and total nitrogen d) as affected by forest type in dry and wet seasons. Bars indicate standard errors of means (n = 18). SS, AM, AA, and EE represent *Schima superba*, *Acacia mangium*, *Acacia auriculaeformis*, and *Eucalyptus exserta*, respectively. Data in the columns with the same lowercase letter (dry season) or capital (wet season) are not significantly different ( $P > 0.05$ ).

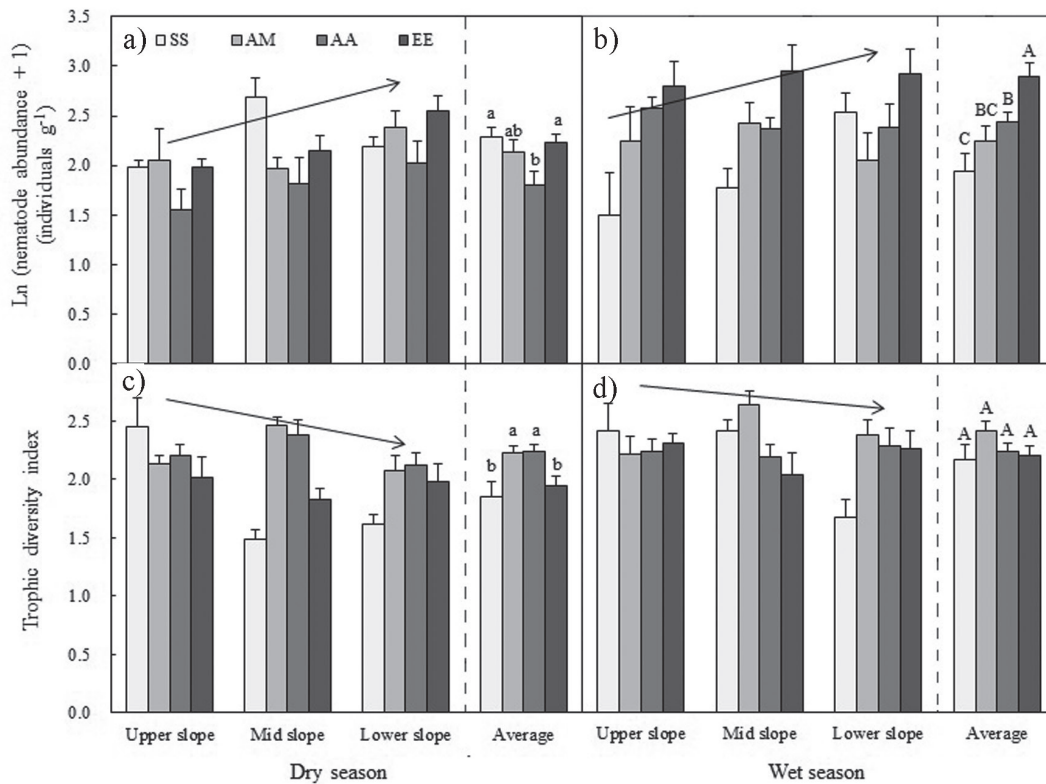


Fig. 2. The effects of forest type and slope on nematode abundance (a, b) and trophic diversity index (c, d) in dry and wet seasons. Bars indicate standard errors of means (n = 6 for upper slope, mid slope, and lower slope; n = 18 for average). SS, AM, AA, and EE represent *Schima superba*, *Acacia mangium*, *Acacia auriculaeformis*, and *Eucalyptus exserta*, respectively. Data in the columns with the same lowercase letter (dry season) or capital (wet season) are not significantly different ( $P > 0.05$ ).

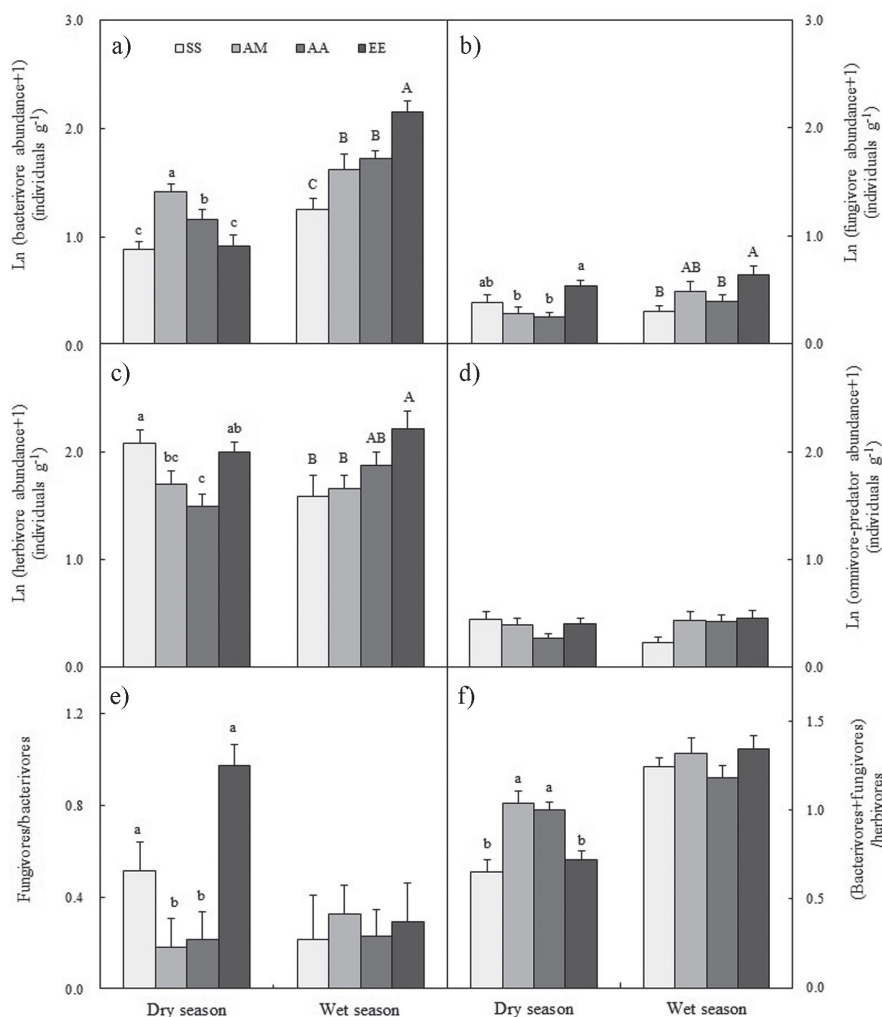


Fig. 3. Bacterivore abundance a), fungivore abundance b), herbivore abundance c), omnivore-predator abundance d), fungivores/bacterivores e), and (bacterivores+fungivores)/herbivores f) as affected by forest type in dry and wet seasons. Bars indicate standard errors of means ( $n = 18$ ). SS, AM, AA, and EE represent *Schima superba*, *Acacia mangium*, *Acacia auriculaeformis*, and *Eucalyptus exserta*, respectively. Data in the columns with the same lowercase letter (dry season) or capital (wet season) are not significantly different ( $P > 0.05$ ).

in dry season (20.4%; Fig. 1a). Forest type significantly affected soil moisture (Table 1). Soil moisture in AA and EE were lower than that in SS in both seasons (Fig. 1a). Soil pH responded significantly to season, forest type, and root zone (Table 1). Mean pH in wet season were lower than that in dry season (Fig. 1b). Forest type significantly influenced soil organic carbon and total nitrogen (Table 1). Both soil organic carbon and total nitrogen in AM were higher compare with SS both in dry and wet seasons (Figs 1c-d). Both soil organic carbon and total nitrogen of root zone were significantly higher than the non-root zone.

### Nematodes and Trophic Groups

Both nematode abundance and TDI responded significantly to season, forest type, and slope (Table 1). Mean nematode abundance in the wet season was higher than in the dry season (Figs 2a-b). Nematode

abundance in AA was lower than that in SS in the dry season average over all slopes (Fig. 2a). In wet season, nematode abundance in AA and EE were higher than that in SS (Fig. 2b). Mean nematode abundance was greater in mid than upper slope, and reached the maximum in the lower slope (Figs 2a-b). Mean TDI in wet season was higher than that in dry season (Figs 2c-d). TDI in AM and AA were higher than that in SS in the dry season average over all slopes (Fig. 2c). Mean TDI was lower in the mid than upper slope, and reached the minimum in the lower slope (Figs 2c-d).

Season significantly impacted bacterivore and fungivore abundance (Table 1). Both bacterivores and fungivores in wet season were higher than those in dry season (Figs 3a-b). Bacterivores in AM and AA were higher compare with SS in dry season (Figs 3a-b). In wet season, bacterivores in all AM, AA, and EE were higher than SS (Fig. 3a). Only fungivores in EE were higher than SS (Fig. 3b). Although no seasonal difference, herbivores

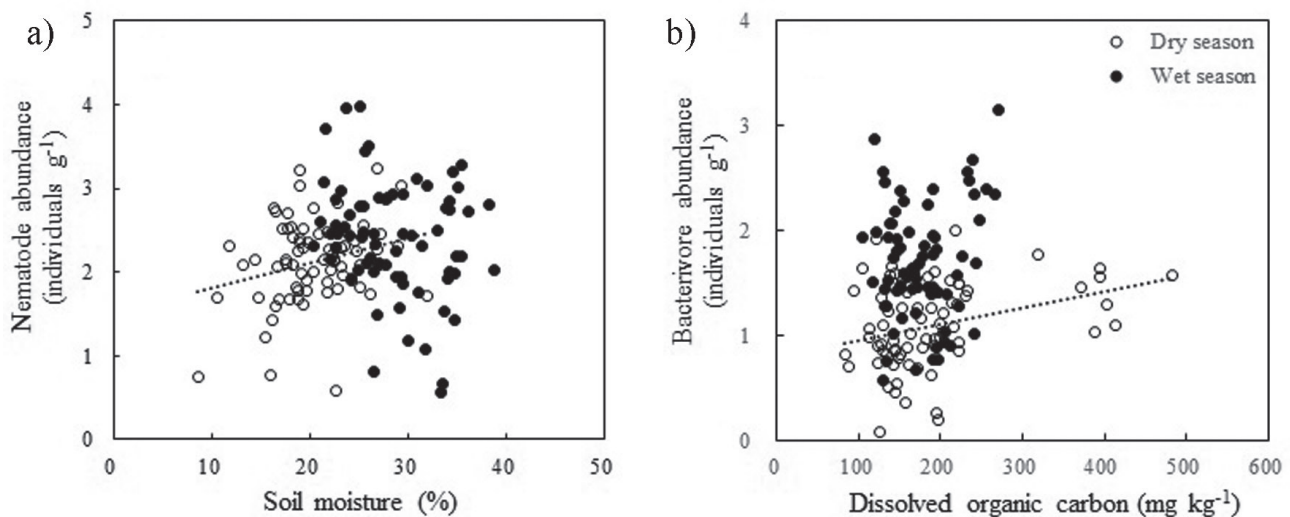


Fig. 4. Positive dependence of nematode abundance on soil moisture and positive dependence of bacterivore abundance on dissolved organic carbon across all the plots in dry season.

varied with forest type (Table 1). Herbivores in AM and AA were lower than that in SS in dry season (Fig. 3c). In wet season, herbivores in EE were higher compare with SS (Fig. 3c). No effect of season or forest type on omnivore-predator abundance was detected (Table 1, Fig. 3d). Season and forest type significantly affected the fungivore/bacterivore ratio (Table 1). Fungivores/bacterivores in wet season were lower than those in the dry season, and Fungivores/bacterivores in AM and AA were lower than SS in dry season (Fig. 3e). In contrast, (fungivores+bacterivores)/herbivores in wet season were higher than in dry season, and (fungivores+bacterivores)/herbivores in AM and AA were higher than SS in dry season (Fig. 3f).

#### Relationships of Nematode with Abiotic Factors

Nematode abundance linearly increased with soil moisture in dry season ( $r = 0.26$ ,  $P < 0.05$ ; Fig. 4a). Bacterivore abundance have a positive relationship with dissolved organic carbon in dry season ( $r = 0.32$ ,  $P < 0.01$ ; Fig. 4b).

### Discussion

#### Effect of Forest Type

Although our results showed that total soil nematode abundance was not obviously amplified in AM and AA, AM and AA increased bacterivore abundance in both dry and wet seasons. In addition, AM and AA enhanced trophic diversity and microbivore abundance, and depressed herbivore abundance and fungivore/bacterivore ratio in the dry season (Figs 2-3), indicating that *Acacia* significantly alter nematode trophic group composition. These findings support our first hypothesis.

*Acacia*, which produce a great quantity of litterfall of  $1.11 \text{ kg m}^{-2} \text{ y}^{-1}$  and develop larger belowground biomass, could support more decomposers, including bacteria, fungi, and microbivores [21]. Extensive roots of *Acacia* also form symbioses with soil nitrogen-fixing bacteria [22-23], resulting in bacterial enrichment and subsequent dominance of bacterial energy channel controlled by bottom-up effects [24-25]. The above two ecological processes facilitate the accumulation of soil organic carbon. Lower herbivore abundance in *Acacia* could be attributed to spatial competition between bacterivores and herbivores. Increasing bacterivore abundance would limit the growth of herbivores.

Soil nematode abundance and some trophic groups, including bacterivores, fungivores, and herbivores, in EE was identical with SS in dry season and higher than SS in wet season (Figs 2-3). In addition, EE did not affect trophic diversity index regardless of season (Fig. 2), suggesting that that of *Eucalyptus* allelopathy do not inhibit soil nematodes in this study. The results are inconsistent with our second hypothesis. A previous study suggested that *Eucalyptus* allelopathy would impact understory vegetation, soil microorganisms, and soil fauna through aboveground volatilization, precipitation eluviation, root secretion, and litter deposition releases [26]. However, no obvious reduction of understory vegetation diversity was found in *Eucalyptus* plantation without human disturbance (data not shown), suggesting that the allelopathic effect of *Eucalyptus* is weak in this study. Higher nematode abundance and their trophic groups in *Eucalyptus* could be interpreted in two ways. On the one hand, some insoluble secondary metabolites from *Eucalyptus*, such as phenolic acid compounds at lower concentrations, may provide an additional carbon source that stimulates soil microbial biomass, microbivore abundance, and herbivore abundance [27-29]. On the other hand, *Eucalyptus* litter decompose much more rapidly [30]. More available nutrients release will be

helpful for expansion of the soil nematode community in *Eucalyptus*.

### Effect of Season and Interaction with Forest Type

Total nematode density, bacterivores, and fungivores all showed significantly seasonal variation (Table 1, Figs 2-3), which is in support to our last hypothesis. In the wet season, plants grow quickly and develop greater fine root biomass and litterfall quantity. Higher water and nutrient availability in the wet season is conducive to the expansion of the soil nematode community [31]. Positive effects of soil moisture on nematode abundance and effects of dissolved organic carbon on bacterivore abundance in the dry season have been shown in our results (Fig. 4), which could explain higher nematode abundance in the lower slope due to surface water and nutrient runoff. This is consistent with findings of some previous studies in arid regions [32-33]. However, interactive effects of season and forest type make total and bacterivore nematode abundance independent of soil moisture or dissolved organic carbon in the wet season (Table 1, Fig. 4). For instance, *Eucalyptus* need to consume a large amount of water through root uptake to support their rapid aboveground biomass accumulation [34], resulting in lower soil moisture (Fig. 1). In tropical and subtropical areas with plenty of rain, especially in the wet season, lower soil moisture will accelerate organic matter decomposition and soil fauna aggregation through increasing oxygen supply and microbial activity [35-36].

### Conclusions

With artificial forests established in degraded hilly area, this study investigated the effects of different monoculture plantations on soil nematode trophic groups. *Acacia*, particularly *Acacia mangium*, improve the dominance of bacterial energy channel and suppress plant parasitic nematodes, consequently facilitating soil carbon sequestration, indicating that *Acacia mangium* as a fast-growing pioneer tree species could be widely planted in restoring degraded forests in southern China. Plantations of *Acacia* mixed with native species are also encouraged. A *Eucalyptus*-enlarging soil nematode community suggests that there is almost no allelopathy in *Eucalyptus* plantations in this study. Reasonable management of *Eucalyptus* plantations is helpful for maximizing economic and ecological value in the meantime. This study provides data and theoretical support for tree species selection in restoring degraded ecosystems in southern China.

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