

RESEARCH ARTICLE

# Distributional patterns of soil nematodes in relation to environmental variables in forest ecosystems

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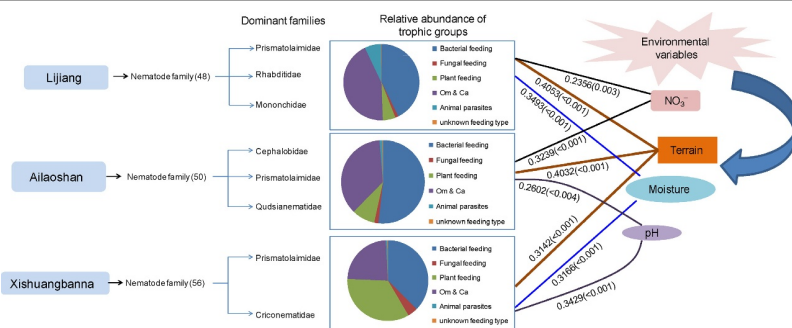
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## HIGHLIGHTS

- Relationships between environmental factors and nematode distributions at different spatial scales are assessed.
- Nematode diversity peaked in tropical forest ecosystem.
- Nematode diversity showed contrary patterns compared with their abundance.
- Factors most strongly affecting nematode communities changed across spatial scales.

## GRAPHICAL ABSTRACT



## ABSTRACT

Understanding biodiversity and biogeographic distribution of soil fauna is an important topic in ecology. While nematode communities have been compared among ecosystems, knowledge remains limited about how environmental factors and nematode distributions are linked at different spatial scales. Here, we employed high-throughput sequencing to compare nematode communities in tropical (Xishuangbanna), subtropical (Ailaoshan), and cold temperate spruce-fir (Lijiang) forest ecosystems with identical spatial sampling. Relationships between nematode communities and environmental factors were analyzed using redundancy analysis (RDA). Our results showed that nematode richness and diversity peaked in Xishuangbanna; however, no significant differences were observed in other two forest ecosystems. Bacterial feeders and Omnivores / Carnivores (Om & Ca) had the lowest relative abundance, but the highest diversity, in Xishuangbanna, with the opposite pattern being detected for fungal and plant feeders. Our data also demonstrated that, for forest ecosystems, climate factors drive nematode communities distributions at the regional scale, while terrain and soil characteristics (including pH and nutrients) drive nematode communities distributions at local scales. This study improves our current understanding of key factors (environmental parameters) responsible for the biogeographical distribution of forest nematode communities at different spatial scales.

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## 1 Introduction

A scientific understanding of biological distribution patterns across different spatial scales is required to explain relationships between aboveground and belowground biodiversity in terrestrial ecosystems (Wu et al., 2011). Global diversity patterns of plants and aboveground macroscopic vertebrates have been clarified (Porazinska et al., 2012). However, there is no evidence that the distribution patterns of belowground organisms, particularly microscopic soil animals (such as soil nematodes), are similar to aboveground organisms (Fierer et al., 2009; Decaëns, 2010; Bardgett and van der Putten, 2014). Our general understanding of distributional patterns of microscopic soil organisms and driving factors remains limited.

Nematodes are widely distributed, small-bodied soil metazoans that account for more than 80% of the abundance of animals on Earth (Fonseca et al., 2010). Their global species richness is tentatively predicted to exceed 1 million (Lamshead, 2004). Besides their huge numbers and diversity, they occur in all ecosystems, with various feeding types in food webs and functional diversity; consequently, they act as important bio-indicators, with key roles in mediating ecosystem processes (Bongers and Ferris, 1999; Neher, 2010). Therefore, by understanding the distributional patterns of soil nematodes, we could advance our knowledge of biogeography and ecology.

Soil nematodes often show high abundance and diversity at local scales (Boag and Yeates, 1998; Yeates, 1999). For example, Lawton et al. (1998) collected 374 species from a tropical forest in Cameroon, while Bloemers et al. (1997) reported 200 individuals and 89 nematode species in a single 1.9-cm diameter soil core. However, nematode distributions at larger scales have received relatively less attention (Nielsen et al., 2014; Song et al., 2017; van den Hoogen et al., 2019). Nielsen et al. (2014) showed the macro-ecological patterns and limited distribution of some nematode families at a global scale. A recent study showed that nematode abundance peaked in high-latitude zones rather than low-latitude zones in a global study (van den Hoogen et al., 2019). For nematode diversity study, Boag and Yeates (1998) found nematode communities to be less diverse in tropics than temperate ecosystems, while Powers et al. (2009) and Porazinska et al. (2010) obtained contrasting results. Other studies reported minimal differences in nematodes alpha diversity, even between Arctic and tropical regions (Kerfahi et al., 2016; Song et al., 2017). These inconsistent results demonstrate that knowledge of soil nematode distributions at large scales remains incomplete. Moreover, few comparisons of trophic groups and their driving factors have been completed at regional scales (Porazinska et al., 2012).

The geographical distributions of nematodes might be affected by many factors, including climate (temperature, rainfall), soil properties (pH, nutrients), and vegetation types (Harrison and Cornell, 2008). However, dominant controlling factors across spatial scales remain unclear (Bardgett and

van der Putten, 2014). This phenomenon impedes our ability to predict the structure of nematode communities following environmental shifts. Nielsen et al. (2014) showed that nematode distributional patterns were strongly related to mean annual rainfall and temperature at the global scale, van den Hoogen et al. (2019) found that soil resource availability is a dominant factor driving the distribution pattern of nematode abundance. At local scale, the dominant driving factors may be changed to factors including soil organic matters (Chen et al., 2015), pH (Liang et al., 2005), texture (Salame and Glazer, 2015) or other factors. Because spatial scale is inextricably linked with environmental heterogeneity, compared to small scales, larger spatial areas generally lead to greater environmental heterogeneity (Feaser et al., 2018). Thus, it is important to clarify the different driving factors at different spatial scales.

As molecular approaches have become an increasingly important tool to assess the diversity of soil fauna (Du et al., 2020), here, we employed the Illumina Miseq DNA platform to investigate the nematode communities of three distinct forest ecosystems. The first was a fast turn-over tropical forest (Xishuangbanna) that had little plant litter persisting on soil surfaces. The other two were humus-rich subtropical (Ailaoshan) and temperate forests (Lijiang) with high soil organic matter content (Chan et al., 2006; Qiao et al., 2014). We tested the hypothesis that nematode diversity is ordered tropical>subtropical>temperate, because aboveground plant species is highest in Xishuangbanna, followed by Ailaoshan and Lijiang (Lan et al., 2008; Huang et al., 2017; Wen et al., 2018). In addition we tested whether the relative abundance of different nematode trophic groups was closely related to their available resources. We also examined whether nematode distributions at regional scales corresponded to climatic differences (Nielsen et al., 2014), and whether those at local scales corresponded to soil properties. Specifically, we evaluated: 1) how the nematode community (diversity and trophic groups) differed among tropical, subtropical, and temperate forest ecosystems, 2) examined the distributional patterns of soil nematodes by analyzing the relationships between nematode community and environmental factors in forest ecosystems at both regional and local scales.

## 2 Materials and methods

### 2.1 Experimental design

We sampled soils from three CTFS forest plots in long-term ecological experimental stations of the Chinese Academy of Sciences in Yunnan Province, China; specifically: 1) 20-ha Xishuangbanna Forest Dynamics Plot (FDP) (21°36' N, 101°34' E), 2) 20-ha Ailaoshan FDP (24°32' N, 102°01' E), and 3) 25-ha Lijiang FDP (27°10' N, 100°13' E). Xishuangbanna is a typical Asian Monsoonal seasonal tropical rainforest that has two distinct climates; namely, the wet season (from May to October) and dry season (from November to April). The elevation ranges from 708 to 869

m, with a mean annual precipitation of 1493 mm, of which 1256 mm (84%) occurs in the wet season. The annual average temperature is 21.8°C (Cao et al., 2006). The Ailaoshan FDP is an evergreen broadleaved forest that has an annual mean precipitation of 1931 mm, of which 85% occurs between May and October. Elevation within the FDP ranges from 2490 to 2530 m, with an annual average temperature of 11.3°C (Gong et al., 2011). The Lijiang FDP is a cold temperate spruce-fir forest that has an annual mean precipitation of 1587 mm. The elevation within the FDP ranges from 3220 to 3344 m, with annual average temperature of 5.5°C (Huang et al., 2017).

At each forest dynamics plot, we established three 20 m × 20 m square sub-plots that were at least 50 m apart. At each station, one of the three 20 m × 20 m plots was on sloped land, while the other two were on flat ground and near ravines. Each plot was separated into sixteen 5 m × 5 m quadrats (Fig. S1). In each 5 m × 5 m quadrat, five soil samples were taken (one in the middle four at the corners) from 0 to 15 cm depth using a 5-cm diameter soil corer after removing surface plant litter. These cores were combined as independent replicates. Thus, in nine 20 m × 20 m plots, each plot had sixteen 5 m × 5 m quadrats, from which 144 separate soil samples were collected. Each of these soil samples was separated into two parts. One part was used to analyze physical and chemical properties (soil moisture, total C, N, and pH). The other part was used to extract soil nematodes. Soil nematodes were collected by combined sucrose centrifugation and Baermann funnels. In brief, 100 g fresh soil was weighed, and was then placed in Baermann funnels to extract soil nematodes for 48 h. After this, the soil was not discarded, rather 100 mL sucrose solution (454 g L<sup>-1</sup> of water) was added for additional centrifugation and further extraction (McSorley and Frederick, 2004). Finally, extracts were immediately used for subsequent DNA extraction.

## 2.2 Genetic sequencing

High-throughput sequencing was performed as follows: first, nematode genomic DNA was extracted using a Power Soil<sup>®</sup> DNA Isolation Kit (MO BIO) according to the supplied instructions. Primers (NF1:5'GGTGGTGCATGGCCGTCT-TAGTT3' 18sr2b:5'TACAAAGGGCAGGGACGTAAT3'; Porazinska et al., 2012), including an eight base index, were synthesized. PCR involved an initial 4 min denaturing step at 94°C, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 30 s, extension at 72°C for 45 s, with a final extension at 72°C for 5 min. The target PCR amplified product size was about 400 bp. Purified PCR products were used to build the library, followed by sequencing with Illumina Miseq (Read Length 2 × 300 bp). Bidirectional sequences generated by Miseq were spliced by FLASH software. After removing chimeras with QIIME, high-quality sequences were assigned to each sample by split\_libraries.py program in QIIME. Finally, these sequences were blasted in the SILVA 119SSUParc (www.arb-silva.de) database (Quast et al., 2013). We chose this database because our primers were

SSU rRNA loci flanked. In addition, this database has more than four million high-quality eukaryotic 16/18S rRNA sequences, including nearly 20 000 nematode reference sequences. The closest matching sequence contained in the database, for which taxonomic information was documented, was used for the subsequent analysis.

All matched sequences in the SILVA 119SSUParc database were assigned a species identity. For more accuracy, we used Statistical Assignment Package (SAP) to evaluate taxonomic accuracy (Munch et al., 2008). This method is used to assign posterior probabilities at each taxonomic level. Here, we set it to 85% to estimate reliability at each taxonomic level. For 1000 randomly selected nematode sequences, SAPs were successfully assigned all sequences at 34%, 55%, 86%, and 99% for species, genus, family, and order taxonomic levels, respectively. This result suggests that SILVA assignments below the family level should be treated with low confidence (< 85% posterior probability). Thus, only family and order taxonomic information were used for further analysis. We only used family taxonomic information for the analysis. Nematode families were grouped according to trophic status (bacterial-feeders, fungal-feeders, plant feeders, omnivores, and carnivores) following Yeates et al. (1993) and the website nemaplex.ucdavis.edu.

## 2.3 Statistical analysis

A linear mixed-effects model was used to analyze the effects of terrain and sites on nematode diversity (Shannon–Wiener diversity index  $H' = -\sum p_i (\ln p_i)$ , where  $p_i$  is the proportion of reads in the  $i$ th taxon) and richness among Xishuangbanna, Ailaoshan, and Lijiang FDPs. Duncan's test was used to determine if differences were significant, with significance being set at  $P < 0.05$ . Soil moisture, pH, C:N, NH<sub>4</sub><sup>+</sup>, and NO<sub>3</sub><sup>-</sup> was used to construct a soil property and terrain matrix for redundancy analysis (RDA) in the vegan package (Oksanen et al., 2010) of R v. 1.17-3 project (R Development Core Team, 2013). Detrended correspondence analysis (DCA) indicated that axis length was less than three; thus, redundancy analysis (RDA) was appropriate to analyze relationships between nematode communities and edaphic factors. The function adonis in R was used to compare differences in the nematode community among Xishuangbanna, Ailaoshan, and Lijiang FDPs, and among plots in each FDP. The function envfit was used to detect correlative significance between each environmental variable and the nematode community.

## 3 Results

### 3.1 BLAST results of sequences

The 144 soil samples yielded a total of 2 240 769 high-quality sequences, of which 643 119 sequences were from Xishuangbanna FDP, 607 128 sequences were from Ailaoshan FDP, and 990 522 sequences were from Lijiang FDP. For Xishuangbanna FDP, only 137 245 (21.3%) sequences were identified

as soil nematodes. For Ailaoshan FDP, 368 647 (60.7%) sequences were identified as soil nematodes. For Lijiang FDP, 638 314 (64.4%) sequences were identified as soil nematodes, based on BLAST results. All nematode sequences combined represented 56 families from 15 orders. In addition to soil nematodes, other sequences were identified as eukaryotic taxa, representing nine phyla (Table S1)

The trophic groups of soil nematodes differed among the three forests. The relative abundance of bacterial-feeding (37.37%) and plant-feeding groups (34.53%) was similar in Xishuangbanna FDP, with both groups being dominant, followed by omnivores and carnivores and fungal feeders (Table S2). However, in Ailaoshan FDP, the bacterial-feeding group (51.78%) was overwhelmingly dominant, followed by omnivores and carnivores, plant feeders, and fungal feeders (Table S2). Both bacterial-feeding group (42.73%) and Omnivores & Carnivores (Om & Ca) (43.46%) were dominant in Lijiang FDP, followed by animal parasites, plant feeders, and finally fungal feeders (Table S2).

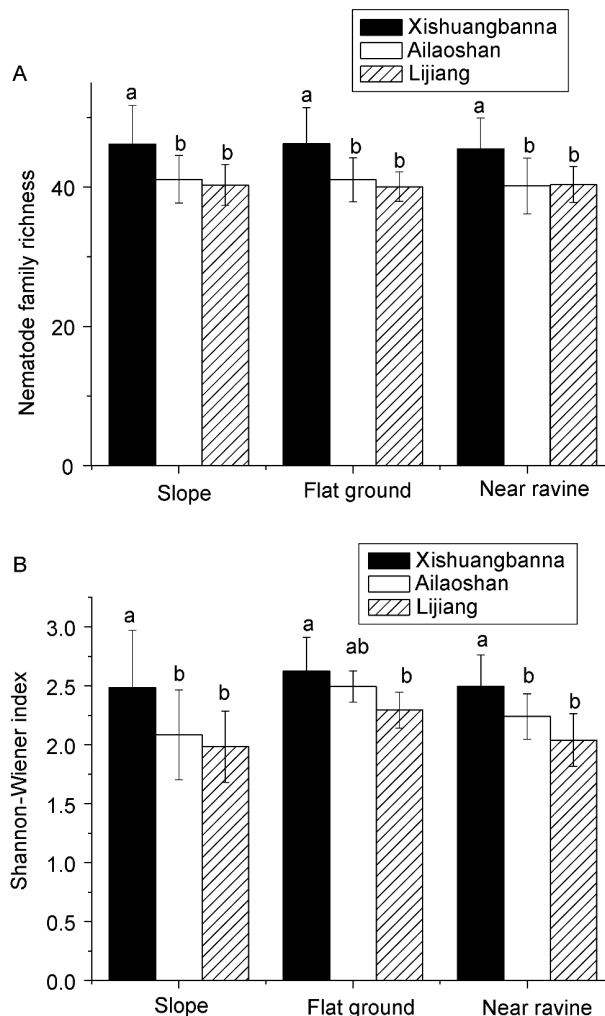
### 3.2 Diversity of soil nematodes

A total 56, 50, and 48 nematode families were detected in Xishuangbanna, Ailaoshan, and Lijiang FDP, respectively. Pristomatolaimidae and Criconematidae were the dominant (more than 10%) families in Xishuangbanna; Cephalobidae, Pristomatolaimidae, and Qudsianematidae were the dominant families in Ailaoshan FDP; and Pristomatolaimidae, Rhabditiidae, and Mononchidae were the dominant families in Lijiang FDP (Table S2). Significant differences in nematode family richness were detected in these three forest ecosystems ( $F_{sites} = 32.083^{**}$ ), of which Xishuangbanna FDP had the highest diversity; however, no significant difference was observed between Ailaoshan and Lijiang FDP (Fig. 1A). Nematode diversity showed a very similar pattern to richness ( $F_{sites} = 29.225^{**}$ , Fig. 1B). The high diversity in Xishuangbanna FDP was mostly generated by bacterial-feeding soil nematodes (Fig. 2).

### 3.3 Communities of soil nematodes within forest dynamic plot (FDP)

At the regional scale, significant nematode community differences were observed among Xishuangbanna, Ailaoshan, and Lijiang FDP ( $F_{sites} = 54.196^{***}$ ,  $F_{terrain} = 4.863^{***}$ , Fig. 3). Soil C:N and moisture were the main drivers that influence the nematode community composition (Table S3).

At the local scale of each FDP (Fig. 4), different factors affect the nematode distribution in different plot. In the Xishuangbanna FDP, pH, moisture, and terrain were the main factors that influence the nematode community composition (Table S4). In the Ailaoshan FDP, terrain,  $\text{NO}_3^-$  and pH were the main factors (Table S4). In the Lijiang FDP, moisture, terrain and  $\text{NO}_3^-$  were the main factors that influence the nematode community composition (Table S4).

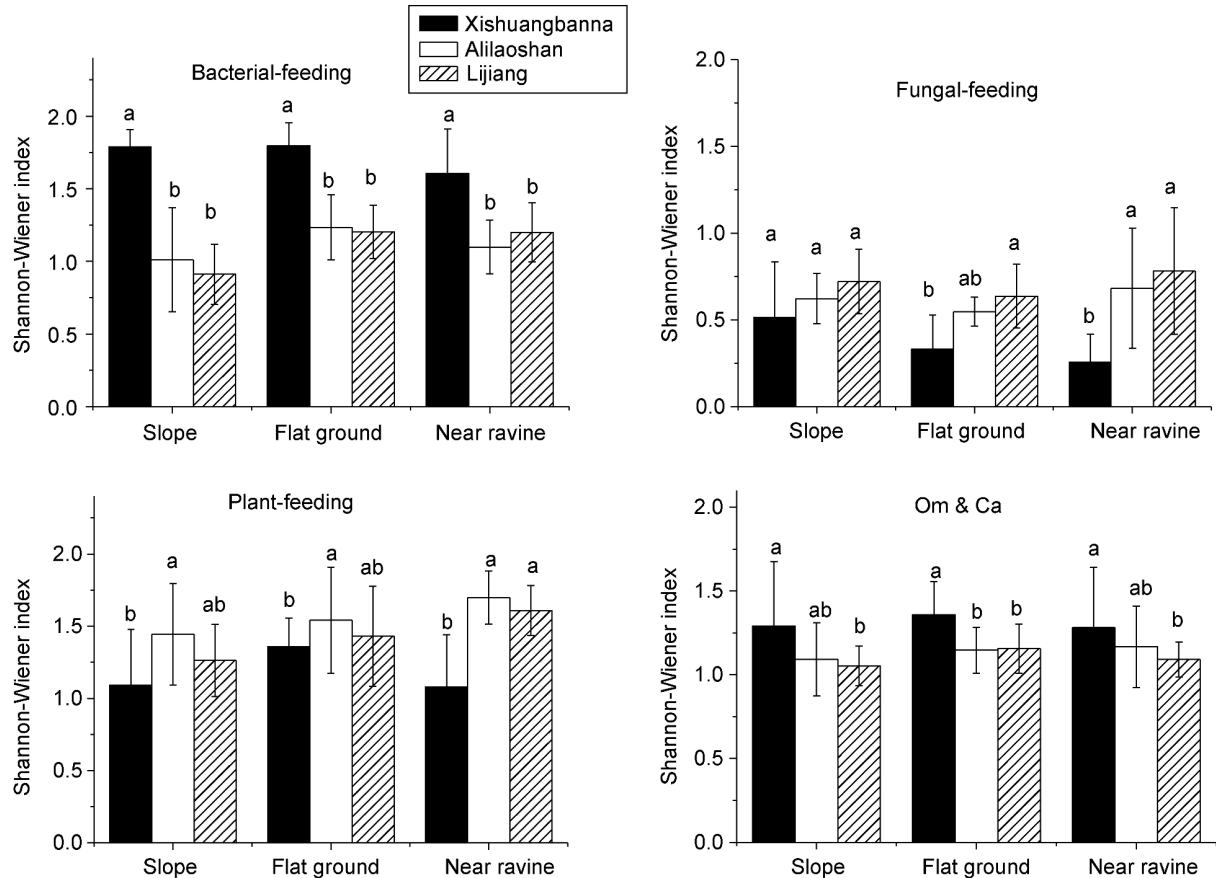


**Fig. 1** Nematode family richness (A) and diversity (B) at different terrain conditions in Xishuangbanna, Ailaoshan and Lijiang FDPs. Error bars represent standard deviation ( $n = 16$ ). Lower case letters indicate significant differences ( $P < 0.05$ , Duncan's test) among Xishuangbanna, Ailaoshan and Lijiang FDPs.

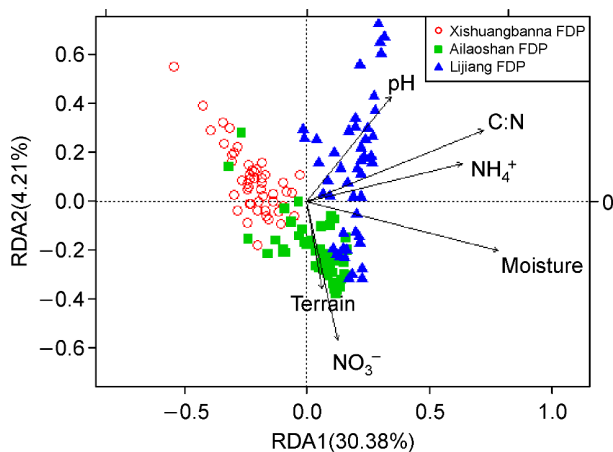
## 4 Discussion

### 4.1 Nematode richness and diversity

Previous studies on soil nematode richness and diversity detected two contrasting trends. Some studies in the 1980s and 1990s found that nematode diversity was augmented by increasing latitude (Procter, 1984; Boucher, 1990; Boucher and Lamshead, 1995); however, studies in the 2000s showed that nematode richness and diversity follow no definite trend along a latitudinal gradient (Boag and Yeates, 1998; Fonseca and Netto, 2015; Song et al., 2017). Our findings were consistent with those of by Yeates (1999), with soil nematodes exhibiting greater diversity at lower latitudes. Our study showed that soil nematode richness and the Shannon–Wiener diversity index were higher in tropical forest



**Fig. 2** Shannon-Wiener Index of different soil nematodes feeding types at different terrain conditions in Xishuangbanna, Ailaoshan and Lijiang FDPs. Error bars represent standard deviation ( $n = 16$ ). Lower case letters indicate significant differences ( $P < 0.05$ , Duncan's test) among Xishuangbanna, Ailaoshan and Lijiang FDPs.



**Fig. 3** Redundancy analysis (RDA) of the nematode family communities and relationships between nematode communities and environmental variables with symbols coded by study sites in Yunnan Province, China.

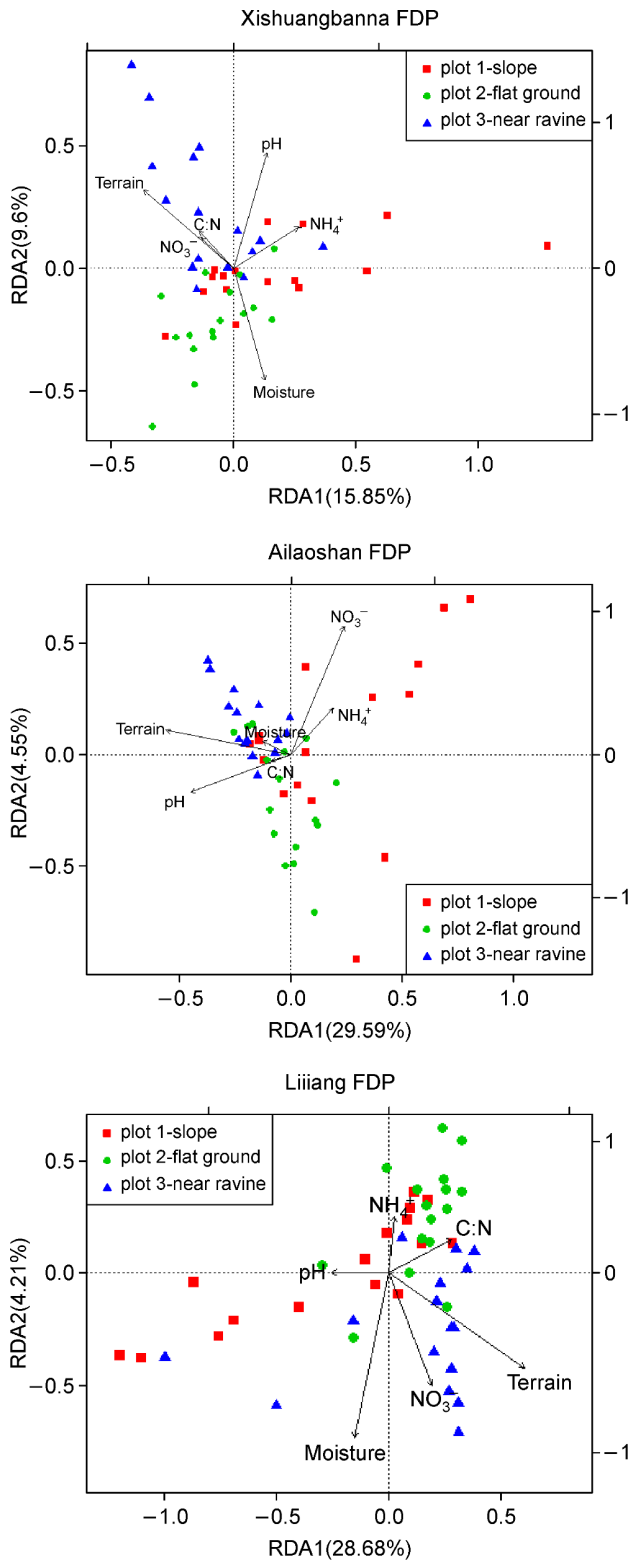
(Xishuangbanna FDP) compared to the other two ecosystems viz. subtropical (Ailaoshan FDP) and temperate forest (Lijiang FDP). This result supports previous studies and demonstrated that tropical forests had higher soil nematode diversity than

temperate forests (Porazinska et al., 2010; Porazinska et al., 2012).

Despite Xishuangbanna (tropical site) having the highest richness and diversity of nematodes, no significant difference was observed between Ailaoshan and Lijiang. Although different climate conditions was observed between Ailaoshan and Lijiang FDP (annual average temperature is 10.7°C and 5.5°C in Ailaoshan and Lijiang FDP respectively; Huang et al., 2017; Wen et al., 2018), both of them have thick humus and high organic carbon content (Table 1). Similar soil characteristics may be an important reason for the lack of significant differences in nematode richness and diversity. The pattern of belowground richness and diversity such as soil nematodes is very complex, and is strongly influenced by soil physico-chemical properties, rather than climate variables (Bardgett and van der Putten, 2014).

#### 4.2 Trophic distribution patterns of soil nematodes

Most existing studies identified nematode trophic groups based on microscopic identification, which is very time consuming and labor intensive when large samples must be analyzed, and requires professional expertise for identification. Molecular methods allowed us to estimate the relative



**Fig. 4** Redundancy analysis (RDA) of the nematode family communities and relationships between nematode family communities and environmental variables with symbols coded by terrain in Xishuangbanna and Ailaoshan FDPs, Yunnan Province, China.

abundance of nematodes from large sample sizes rapidly, however, limitations exist. For instance, Molecular methods cannot do quantitative analysis. In addition, blast results tend to have low taxonomic resolution. Soil nematodes of larger body size also tend to be overestimated, as they have more cells and gene copies per individual, increasing their component in DNA-sequence analyses (Griffiths et al., 2006). Even so, using the number of sequences to reflect the relative abundance of nematode species has potential. For instance, Porazinska et al. (2010) showed that the number of individuals per nematode species was closely correlated with read abundance. Du et al. (2000) compared morphological and high-throughput sequencing methods and found that the two methods reached consistent conclusions in the nematode community composition and trophic structure.

The trophic abundance of soil nematodes is generally best explained by substrate resources. Our data (C and N) supported previous studies, showing that subtropical (Ailaoshan FDP) and temperate forest (Lijiang FDP) had much more soil organic matter and, hence, likely to support more microbial biomass (Chan et al., 2006; Qiao et al., 2014), and it is also confirmed by other evidence. For example, Qiao et al. (2004) found that microbial biomass carbon in subtropical forest (Ailaoshan FDP) was approximately five times greater than that in tropical forest (Xishuangbanna FDP). Interestingly, Chan et al. (2006) showed that the total microbial biomass of the surface organic layer at Ailaoshan FDP ( $4.33 \pm 1.64 \text{ g C kg}^{-1}$  dry soil) was approximately twofold greater than that of surface mineral soil ( $2.16 \pm 0.88 \text{ g C kg}^{-1}$  dry soil) in Xishuangbanna FDP. However, the surface mineral soil of Xishuangbanna FDP contained three times less microbial biomass ( $0.63 \pm 0.17 \text{ g C kg}^{-1}$  dried soil) than that at Ailaoshan FDP. Therefore, it is reasonable for Ailaoshan and Lijiang FDP support a higher relative abundance of bacterial-feeding nematodes (Table S2). Likewise, the higher relative abundance of plant-feeding nematodes at Xishuangbanna FDP might reflect the high plant diversity, because certain plant roots are susceptible to soil nematodes feeding on them (Liu et al., 2002; Zheng et al., 2006; De Deyn et al., 2008; Xiao et al., 2014; Zhang et al., 2015; van den Hoogen et al., 2019). For example, Zhang et al. (2015) showed that tropical rainforests have the highest root biomass than other forest types in China. The relative abundance of plant-feeding and bacterial-feeding nematodes in this study was consistent with that of Nielsen et al. (2014), who found that plant-parasitic dominate warm sites, while bacterial feeders dominate colder sites. This distribution pattern could be explained by the fact that more plant biomass resources are available for parasites to exploit in tropical forests. Alternatively, colder sites might be more disturbed, allowing opportunistic bacterial feeders to dominate (Bongers and Ferris, 1999; Nielsen et al., 2014). Our results also showed that the abundance of Om & Ca was relatively higher in sub-tropical and temperate forest (Ailaoshan and Lijiang FDPs) compared to tropical forest

ecosystem (Xishuangbanna FDP). This phenomenon might be related to more humus or organic matter accumulating in sub-tropical and temperate forest, as organic C is an important growth factor determining nematode body size, especially for large-bodied Om & Ca (Liu et al., 2015). In addition, more large-bodied soil nematodes were observed in sub-tropical and temperate forest (Ailaoshan and Lijiang FDPs) than in tropical forest (Xishuangbanna FDP) when we extracted soil nematodes from soil samples. Of note, we cannot rule out that this high proportion of Om & Ca in sub-tropical and temperate forest may be caused by their larger body size.

For nematode trophic diversity (Fig. 2), all four trophic types showed contrasting patterns to the relative trophic abundance of soil nematodes for tropical forest versus the other two forest ecosystems. Thus, higher abundance does not necessarily indicate higher diversity. For example, in the current study, tropical forest (Xishuangbanna FDP) had the highest relative abundance (34.12%) but the lowest diversity of plant feeders than the other two forest ecosystems. This contrasting trophic diversity of soil nematodes implies that available food resources differ across forest ecosystems.

#### 4.3 The factors driving variation of soil nematode community at different spatial scales

The nematode community is related to environmental factors at different scales (Boag and Yeates, 1998; Nielsen et al., 2014). Similarly, our data showed small overlaps that indicated significant differences to the nematode community among the three forest types (Xishuangbanna, Ailaoshan and Lijiang FDPs) (Fig. 3). Both C:N and moisture were the strongest factors contributing to this difference (Table S3). The higher latitude and elevation at Ailaoshan FDP (approximately 2500 m) and Lijiang FDP (approximately 3200 m) compared to Xishuangbanna FDP (approximately 800 m) resulted in these two sites having lower temperatures and slower decomposition rates, with greater humus accumulation (Huang et al., 2007; van den Hoogen et al., 2019). This humus accumulation inevitably causes higher organic C and C:N in these two forest ecosystems (Table 1). In addition, the surface soils of these two systems are less dense with higher water content (up to 60%–70%, Table 1) than in Xishuangbanna FDP (approximately 30%). Given that C:N and soil moisture are important factors affecting nematode communities, they are also the strongest factors driving differences in nematode communities (van den Hoogen et al., 2019). Differences in C:N and soil moisture among the three studied forest ecosystems was driven by differences in temperature; thus, climate factor likely determine the composition of

nematode communities at regional scales. However, the influences of climate on soil nematodes are not direct, but act indirectly by changing soil conditions (van den Hoogen et al., 2019).

The current study delineated three distinct groups within each forest dynamic plot (FDP), which were based on terrain dimensions *viz.* slope, flat ground, and proximity to ravines (Fig. 4). Thus, environmental heterogeneity caused by spatial distance (at least 50 m between plots in this study) significantly contributes toward determining patterns in the spatial distribution of the nematode community at the habitat scale (Bardgett and van der Putten, 2014). Of importance, this terrain-based pattern was similar at all the three study sites (Lijiang, Ailaoshan, and Xishuangbanna FDPs). Terrain was the only factor that significantly drove differences in the nematode community at all three FDPs (Fig. 4). This phenomenon was probably caused by soil nematodes responding to variation in soil properties that was reflected by terrain rather than a response to terrain, *per se*. For example, more litterfall accumulates on flat ground compared to slopes, and is considered to have an important impact on soil nutrients (Xia et al., 2015), which affect nematode communities. Furthermore, soil pH was the main factor determining differences to the nematode communities between tropical forest (Xishuangbanna FDP) and subtropical forest (Ailaoshan FDP). In comparison,  $\text{NO}_3^-$  determined differences in the nematode communities between subtropical forest (Ailaoshan FDP) and temperate forest (Lijiang FDP). Thus, terrain and soil properties, rather than climate factors (like temperature) drive the distribution of soil nematodes at local scales. This phenomenon is consistent with our hypothesis, and supports the conclusions of Bardgett and van der Putten (2014); specifically, at large spatial scales, climatic and topographic factors strongly influence the distribution of biodiversity in soils, the physical and chemical properties of soils are more important factors at smaller scales.

## 5 Conclusions

The current study confirmed that the diversity and patterns of distribution of small invertebrates do not completely follow that of above-ground plants or large animals; however, invertebrate diversity was highest in the low latitude tropical forest. The relative abundance of nematode trophic groups showed contrasting patterns with diversity in this study. Lower temperatures (which reduce decomposition rates) and accumulated surface organic matter were dominant factors

**Table 1** Forest topsoil (0–15 cm) total C, N, pH and water content in Xishuangbanna, Ailaoshan and Lijiang FDP±represent deviation ( $n = 48$ ).

Sites	Total carbon ( $\text{g kg}^{-1}$ )	Total nitrogen ( $\text{g kg}^{-1}$ )	pH	Water content (%)
Xishuangbanna	18.26±2.79	2.05±0.24	5.03±0.30	29.87±2.54
Ailaoshan	64.87±4.72	6.40±0.51	4.84±0.15	66.26±2.49
Lijiang	85.64±5.97	6.9±0.63	5.44±0.47	74±2.91

affecting the distribution of soil nematodes in these three FDPs. Therefore, climate appears to be the most important factor influencing the distribution of soil nematodes at regional scales. However, at local scales, terrain and soil properties were the most important factors; therefore, the factors that have the strongest effect on nematode communities vary across different spatial scales. In conclusion, this study clarifies how soil nematodes are distributed in forest ecosystems across large spatial scales, and could be applied to predictions in other regions.

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## Data accessibility

The nematode SSU RNA gene sequences recovered in this study were deposited in the NCBI GenBank Sequence Read Archive (SRA) under accession number SRP074446.

## Electronic supplementary material

Supplementary material is available in the online version of this article at <http://dx.doi.org/10.1007/s42832-020-0069-8> and is accessible for authorized users.

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