



Community composition, diversity and metabolic footprints of soil nematodes in differently-aged temperate forests



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ABSTRACT

Soil nematode communities can provide important information about soil food web structure and function. However, how soil nematode communities and their metabolic footprints change over time in temperate forests is not well known. We examined the changes in the composition, diversity and metabolic footprints of soil nematode communities in three differently-aged (young, mid and old) forests of the Changbai Mountains, China. Carbon flows through different nematode trophic groups were also quantified based on nematode biomasses. The results showed that the highest abundance and diversity of total nematodes was found in the mid forest. Nematode communities were characterized by the replenishment in abundance but not the replacement of dominant genera. A low enrichment footprint in the young forest suggests a decline in available prey, while a high enrichment footprint in the mid forest indicates an increase in resource entry into soil food web. The relationship between the carbon flows of omnivores-predators and fungivores was stronger than that among other trophic groups. Our study shows that bottom-up effects of the vegetation, the soil environment and the connectedness of nematode trophic groups are all important driving forces for nematode community structure in temperate forests.

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1. Introduction

Soil nematodes occupy a central position in the detritus food web and comprise a range of functional or trophic groups (Yeates et al., 1993). They can be used as indicators of the structure and functioning of soil food webs and of general ecosystem conditions (Neher, 2010; Sánchez-Moreno et al., 2011; Zhang et al., 2012). The contribution of soil nematodes to ecosystem processes and functions varies depending on the composition and diversity of the nematode community (Yeates et al., 2009; Costa et al., 2012; Porazinska et al., 2012). In forest ecosystems, the distribution and abundance of soil nematodes is determined by factors such as by plant species, soil type, soil fertility, litter depth and forest management (Yeates, 2007). Several studies have also shown that nematode community composition and diversity vary with forest

stand ages (Sohlenius, 2002; Williamson et al., 2005; Dickie et al., 2011). Feedbacks and interactions between plants and soil organisms can differ between forests of different ages (Kardol et al., 2005, 2009; van der Putten et al., 2009; Háněl, 2010). During forest succession, dominant plant species are replaced, and the identity and diversity of plants can greatly influence soil nematode communities (De Deyn et al., 2004; Cesarz et al., 2013). Changes in nematode communities could, therefore, be viewed as a consequence of the successional dynamics of plants (Thornton and Matlack, 2002; Biederman and Boutton, 2009). However, Yeates (2007) stated that the nematode population structure, especially the proportion of different nematode trophic groups, was similar across forest stands of different ages and he concluded that nematode contributions to ecosystem processes were similar in forests of different ages. Although the effects of plant community composition on soil nematodes are inconclusive, Yeates (2007) suggest soil nematode communities can provide important information about the role of forest species in structuring soil food webs during succession.

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Most studies performed so far on nematode diversity and functional indices have reflected soil food web composition. Recently, there has been a growing interest in the metabolic activity levels or so-called “energy channel” of soil nematode communities, which conveys information on the magnitude or nature of ecosystem functions (Ferris, 2010; Crotty et al., 2011). Ferris (2010) proposed using the nematode metabolic footprint to extend ecosystem assessments. This footprint provides additional descriptive information on the biomass, metabolic activity, and magnitudes of carbon (C) and energy flow in soil food webs. The nematode metabolic footprint consists of enrichment and structure footprints, which are representative for the carbon metabolism of lower and higher trophic levels, respectively (Ferris, 2010). Enrichment footprints place more emphasis on the C utilization of the enrichment opportunist nematodes such as *r*-strategist with lower trophic levels (Ferris et al., 2012). Nematode metabolic footprints provide an effective method for monitoring the available resources and estimating the contribution of nematodes to ecosystem services and functions. However, until now, relatively few studies have examined nematode metabolic footprints or carbon flow of different trophic groups in forests with different ages.

Therefore, we compared the community composition, diversity and metabolic footprints of soil nematodes in three forests that differ in age, quantified the carbon flow in each nematode trophic group, and determined the key driving factors of nematode communities. We hypothesized that total abundance, diversity and metabolic footprints of soil nematodes will increase with increasing forest age, and that the development of soil nematode communities will resemble the trajectory of the plant community.

2. Materials and methods

2.1. Experimental site

The research was conducted in the Changbai Mountain Nature Reserve (41°43′–42°26′ N, 127°42′–128°17′ E) of Jilin Province, Northeast China. The region is one of the largest biosphere reserves with minimal human disturbance in all of China. It was established in 1960 and joined the World Biosphere Reserve Network under the Man and the Biosphere Project in 1980 (Stone, 2006). The reserve is approximately 200,000 ha and its elevation ranges from 720 to 2691 m. The area has a typical temperate continental monsoon climate. The mean annual temperature varies from –7.3 °C to 2.8 °C, and the mean annual precipitation fluctuates between 750 mm and 1340 mm, most of which occurs from June to September (Wang et al., 2013).

In the Changbai Mountains, three forests (70, 300 and 400 years of age, hereafter called ‘young, mid and old’ forests), were selected for this study. The original vegetation in all forests was classified as mixed broad-leaved and Korean pine, which is the typical zonal vegetation in the Changbai Mountains. The soil is classified as Albi-Boric Argosolsand and the original soil characteristics of three forests were similar (Xu et al., 2004; Li et al., 2010; Shen et al.,

2013). The basic characteristics of the three forests are listed in Table 1.

2.2. Soil sampling

For each forest, six plots (20 m × 20 m for each) were selected randomly as sample replicates and the minimal distance between two plots was about 100 m. Strictly speaking these should be considered as pseudoreplicates. In each plot, composite samples of 5 random sub-samples were collected as one soil sample. After removing the surface plant litter, a total of 36 soil samples at both 0–10 cm and 10–20 cm depths (6 plots × 3 forests × 2 depths) were taken with a 2.5-cm-diameter auger in June of 2012. After collection, the fresh soil samples were stored in individual plastic bags and immediately brought to the laboratory. The samples were kept at 4 °C in a refrigerator until further analysis and processed within one week. Fresh soils were used to extract soil nematodes and to analyze soil moisture (SM), NO₃-N, NH₄-N, dissolved organic carbon (DOC), and microbial biomass carbon (MBC). Air-dried samples were used to analyze other soil properties.

2.3. Nematode community analysis

Soil nematodes were extracted from 100 g of fresh soil using a modified cotton-wool filter method (Liang et al., 2009). Nematode populations were expressed as the number of individuals per 100 g of dry soil, and at least 100 specimens per sample were randomly selected and identified to genus level using an inverted compound microscope according to Bongers (1994) and Ahmad and Jairjuri (2010). Soil nematodes were assigned to the following trophic groups characterized by feeding habits: bacterivores (BF), fungivores (FF), plant parasites (PP) and omnivores-predators (OP) (Yeates et al., 1993). The Shannon diversity (H') index was calculated and used as an indication of the diversity of the soil nematodes (Shannon, 1948). The enrichment index was $EI = 100 \times e / (b + e)$ and the structure index was $SI = 100 \times s / (b + s)$ (Ferris et al., 2001), where b , e and s are the abundance of individuals in guilds in the basal component, enrichment component and structural component weighted by their k_b , k_e and k_s values, respectively. k_b is the weighting assigned to guilds Ba₂ and Fu₂, k_e is the weighting assigned to guilds Ba₁ and Fu₂, and k_s is the weighting assigned to guilds Ba₃–Ba₅, Fu₃–Fu₅, and Op₃–Op₅. Ba_{*x*}, Fu_{*x*}, Op_{*x*}, and Pp_{*x*} (where $x = 1$ –5) represent the functional guilds of nematodes that are bacterivores (Ba), fungivores (Fu), omnivores-predators (Op) or plant parasites (Pp), respectively, where the guilds have the character indicated by x on the colonizer–persister (cp) scale (1–5) according to their r and K characteristics, and nematodes in the same functional guilds respond similarly to food web enrichment and to environmental perturbation.

Following identification, the length (L) and maximum body diameter of all identified adult nematodes were determined using an ocular micrometer. Nematode biomass was calculated using the formula $W = (L^3/a^2)/(1.6 \times 10^6)$, where W is the fresh weight (μg)

Table 1
Main characteristics of the three forests.

| Age | Location | Stand age (a) | Altitude (m) | Canopy density | No. of tree species | Tree DBH (cm) | Dominant tree species |
|-------|-----------------------|---------------|--------------|----------------|---------------------|---------------|---|
| Young | 42°22′ N 128°00′ E | 70 | 796 | 0.7 | 28 | 7.4 | <i>Betula platyphyll</i> and <i>Populus davidiana</i> |
| Mid | 42°23′ N 128°05′ E | 300 | 801 | 0.85 | 39 | 10.5 | <i>Pinus koraiensis</i> and <i>Tilia amurensis</i> |
| Old | 42°22′ N 128°06′ E | 400 | 878 | >0.85 | 25 | 13.2 | <i>Pinus koraiensis</i> and <i>Betula costata</i> |

DBH, diameter at breast height. Data from Li et al. (2010).

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