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# Trophic position of microbivorous and predatory soil nematodes in a boreal forest as indicated by stable isotope analysis

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## ABSTRACT

Nematodes of different trophic groups control distinct energy channels, though their exact trophic links remain little understood. Molecular data suggest that soil nematodes are readily consumed by a wide range of other soil animals, but the significance of these interactions remains unknown. We used stable isotope analysis to gain a better understanding of the trophic niches of soil nematodes in a boreal forest. We tested four taxonomic groups, Mononchida, Dorylaimida, Plectidae and Tylenchidae (mostly from the genus *Filenchus*), representing predators, omnivores, bacterivores and root-fungal feeders, respectively. To assess the trophic position of nematodes, we used a set of reference species including herbivorous, saprophagous and predatory macro-invertebrates, oribatid and mesostigmatid mites, and collembolans. The trophic position of the investigated groups of soil nematodes generally agree with common knowledge. All nematodes were enriched in <sup>13</sup>C relative to *Picea abies* roots and litter, as well as to fungal mycelium analyzed. Root-fungal feeders Tylenchidae had δ<sup>15</sup>N values similar to those of earthworms, enchytraeids and *Entomobrya* collembolans. In contrast, bacterivorous Plectidae were enriched in <sup>15</sup>N compared to saprophagous macroinvertebrates and most mesofauna species. Omnivorous Dorylaimida and predatory Mononchida were further enriched in <sup>15</sup>N and their isotopic signature was very similar to that of predatory arthropods. These data confirm a clear separation of nematodes into microbial feeders (Tylenchidae and Plectidae) and predators (Mononchida and Dorylaimida). They also suggest that the trophic position of soil animals is largely independent of their body size, the smallest soil predators like nematodes occupying the same trophic level as predatory macro-invertebrates. Our data failed to confirm that bacterivorous or predatory soil nematodes are important prey for oribatid mites or collembolans. The patterns of isotopic signatures indicate that soil nematodes and the bulk of soil animals depend on resources derived from a dominating upper-canopy tree (*P. abies*) via the detrital rather than mycorrhizal pathway. Herbaceous plants and dwarf shrubs do not contribute significantly to the energy budget of soil communities in the boreal forest studied.

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## 1. Introduction

Nematodes are among the most abundant groups of animals, also occupying key positions in soil food webs (Hunt et al., 1987; Berg et al., 2001; Ferris, 2010). According to morphological and anatomical traits, soil nematodes can be divided into several trophic groups including bacterivores, fungivores, herbivores, omnivores and predators (Yeates et al., 1993). Nematodes of different trophic groups are assumed to control distinct energy channels

within detrital food webs. For instance, bacterivorous nematodes and protozoans are the most important bacterial grazers, thus largely controlling the bacterial energy channel (Griffiths, 1990; Scheu et al., 2005; Mulder and Vonk, 2011; Zhao and Neher, 2013). Similarly, fungivorous nematodes are important regulators of the fungal energy channel, even though top-down control of fungal populations in the soil may be less efficient (Wardle and Yeates, 1993; Moore et al., 2005). This approach resulted in the use of nematodes for comparing the flows of energy and nutrients through the bacterial and fungal channels, e.g., by the fungal to bacterial feeder ratio (f/b) proposed by Freckman and Ettema (1993), or the channel index (CI) developed by Ferris et al. (2001). However, many aspects of trophic interactions of soil nematodes

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and their position in soil food webs are still little understood. For instance, bacterial-feeding nematodes may also feed on algae, slime molds and fungi (Gupta et al., 1979; Yeates et al., 1993; Ruess and Dighton, 1996; Newsham et al., 2004), omnivorous and predatory nematodes also consume bacteria and protozoans (Freckman, 1988), whereas root hair feeders may feed on fungal hyphae (Tiunov et al., 2001; Okada et al., 2005). Experimental evidence suggests that bacterial and fungal energy channels in detrital food webs are tightly interlinked (e.g. Crotty et al., 2011; Pollierer et al., 2012) while the above simplified trophic classification probably does not fully reflect actual trophic interactions of soil nematodes.

Besides controlling microbial populations, nematodes serve as prey for many soil animals. Direct experiments suggested that nematodes can readily be consumed by microbivorous soil animals like collembolans (e.g. Lee and Widden, 1996; Ruess et al., 2005). These observations were confirmed using molecular techniques as well (Heidemann et al., 2011). Regular predation of soil oribatids and collembolans on nematodes suggests that this interaction can be an important link in soil food chains (Heidemann et al., 2014a). On the other hand, DNA-detection methods remain qualitative or semi-quantitative, reflecting short-term interactions only (Heidemann et al., 2011). Thus, the extent and functional significance of such interactions in soil food webs remain unknown.

Stable isotope analysis (SIA) is widely used for investigating the structure of soil food webs (Scheu and Falca, 2000; Tiunov, 2007; Pollierer et al., 2009). Despite the growing importance of SIA in soil food web research, its application to the study of soil nematodes has been limited to only a few studies. Sampedro and Dominguez (2008) and Crotty et al. (2014) estimated the stable isotope composition of soil nematodes, but these were analyzed without separation into taxonomic or trophic groups. Darby and Neher (2012) identified isotopic signatures of Cephalobidae, Tylenchidae, Dorylaimida and a small subset of potential resources in a desert ecosystem. Finally, Sticht et al. (2009) reported the carbon isotope composition of several nematode trophic groups on two agricultural sites.

Isotopic signatures of heterotrophic organisms reflect an integrated isotope composition of their food sources. In food chains, both  $^{15}\text{N}$  and  $^{13}\text{C}$  contents increase with each trophic level due to the trophic fractionation, which is estimated as about 3–4‰ for  $\delta^{15}\text{N}$ , but only 0.5–1‰ for  $\delta^{13}\text{C}$  (Post, 2002; McCutchan et al., 2003). Besides differentiating trophic levels, SIA allows for identification of certain types of basal resources. For instance, in forest ecosystems carbon delivered into soil food webs by ground vegetation is depleted in  $^{13}\text{C}$  due to the so-called “canopy effect” (Brooks et al., 1997). The abundance of both  $^{13}\text{C}$  and  $^{15}\text{N}$  increases from the upper to the lower litter layers and down the soil profile (Wynn, 2007; Hobbie and Quimette, 2009). Mycorrhizal fungi are in general enriched in  $^{15}\text{N}$  and depleted in  $^{13}\text{C}$  compared to saprotrophs (Hobbie et al., 1999; Mayor et al., 2009). In turn, saprotrophic microorganisms are enriched in  $^{13}\text{C}$  compared to bulk SOM, which leads to strongly increased  $\delta^{13}\text{C}$  values in microbivorous soil animals (Potapov et al., 2013; Korobushkin et al., 2014). Finally, as non-vascular plants (lichens and algae) which receive N mainly from atmospheric deposits are depleted in  $^{15}\text{N}$  compared to other primary producers, phycophagous soil animals typically show low  $\delta^{15}\text{N}$  values (Maraun et al., 2011; Potapov et al., 2014).

Combined,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of soil animals delineate the “isotopic niches” that are distinct from actual trophic niches, but reflect them. SIA-based reconstructions of food web structure depend crucially on the correct estimation of the isotopic difference between main food sources and of the trophic fractionation factors. Considering a highly heterogeneous nature of soil organic matter and the great diversity of soil organisms, this information is difficult to obtain. On the other hand, trophic preferences and a typical

stable isotope composition of certain species and trophic groups of soil animals are relatively well known (Curry and Schmidt, 2007; Pollierer et al., 2009; Klarner et al., 2013). These species may thereby serve as reference points when estimating the trophic position of less well-studied soil organisms.

In this study, we used stable isotope analysis to gain a better understanding of the trophic links of soil nematodes in a boreal forest. Recent research shows a great importance of mycorrhizal fungi in the accumulation of soil organic matter in boreal forests (Godbold et al., 2006; Ekblad et al., 2013). Moreover, a significant proportion of root-associated fungi in boreal forests are represented by ericoid mycorrhizas (Clemmensen et al., 2013). “Root carbon” has been demonstrated to play a significant role in fueling the detrital food webs, but the information is still scarce and partly controversial (Pollierer et al., 2007, 2012; Remen et al., 2010). In particular, the significance of ericoid vegetation and associated mycorrhizal fungi in the diet of soil invertebrates in boreal forests remains virtually unknown.

To assess the trophic position of nematodes, we used a comparison against a set of reference species including herbivorous, saprophagous and predatory macro-invertebrates, oribatid and mesostigmatid mites, and collembolans. More specifically, we addressed two main questions: (1) Is the stable isotope composition of nematodes consistent with the conventional trophic classification? (2) Do SIA data support the view that nematodes play significant roles in the diet of saprophagous soil microarthropods? In addition, we aimed to obtain information on the role of mycorrhizal fungi in the diet of soil invertebrates, and the importance of ground vegetation in fueling the food webs in boreal forests.

## 2. Material and methods

### 2.1. Site description

The study was conducted in a spruce forest on albeluvisol, taiga zone of northwestern Russia (N 61°38.988, E 050°43.988). The mean annual air temperature is 0.5 °C, with an annual precipitation of about 620 mm. The stand is dominated by Norway spruce (*Picea abies*), but other species including *Betula pubescens* and *Populus tremula* are interspersed. There are sparse shrubs of rowan (*Sorbus aucuparia*) and dog rose (*Rosa canina*). The herbaceous layer is dominated by *Oxalis acetosella* and *Vaccinium uliginosum*. Less abundant herb species are *Maianthemum bifolium*, *Pyrola rotundifolia*, and mosses *Hylocomium splendens*, *Pleurozium schreberi*, *Rhytidiadelphus triquetrus*.

### 2.2. Sampling and processing of soil animals

Soil sampling was performed in late August. Three series of samples were taken randomly in an area of ca. 100 m<sup>2</sup>. For the assessment of the isotope composition of nematodes, twelve soil cores (10 cm in diameter, 5 cm deep) were used. Immediately after sampling soil cores were extracted using modified Baermann funnels (48 h). The nematodes collected were kept in water at 4 °C. Individual specimens were hand-picked using a dissecting microscope and dried at 60 °C. Four taxonomic groups were taken separately: Mononchida, Dorylaimida, Plectidae and Tylenchidae (mostly from the genus *Filenchus*), representing predators, omnivores, bacterivores and root-fungal feeders, respectively. In most cases, nematodes collected in several cores were pooled as one replication. Small-sized Tylenchidae were taken from five cores only, and the material obtained was pooled into two samples. All collecting procedures, from soil sampling to nematode drying, were accomplished within six days.

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