

# Soil energy pathways of different ecosystems using nematode trophic group analysis: a meta analysis

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**Summary** – We analysed 67 raw data sets of nematode genera from three types of ecosystems (grassland, cropland, and forest) to compare relative magnitude of energy pathways through the soil food web. Bacterial-, fungal- and herbivorous-based energy pathways were compared by percentages (in either abundances or biomass) of three soil nematode trophic groups (*i.e.*, bacterivore, fungivore and herbivore). The patterns of soil energy pathways were similar whether expressed as relative abundance or relative biomass. However, the percentage values of bacterivorous biomass in each type of ecosystem exceeded the percentage values of their abundance. Specifically, relative abundance of bacterivorous nematodes was similar among ecosystems but mean values of biomass were greatest in grassland and similarly less in cropland and forest ecosystems. By contrast, both relative abundance and biomass of fungivorous nematodes decreased progressively from forest to cropland and grassland ecosystems. The opposite pattern across ecosystems was observed for both relative abundance and biomass of herbivorous nematodes. We conclude that energy pathways are bacterial-dominated in all of the ecosystems whether expressed as abundance or biomass. Fungal and herbivorous pathways are second in dominance in forest and grassland ecosystems, respectively. The relative size of the fungal-based energy pathway suggests a gradient of resource quality among ecosystems. We suggest that herbivorous-based energy pathways are more important in grassland ecosystems than reported previously.

**Keywords** – cropland, decomposition pathway, energy, food web, forest, grassland, soil nematode trophic groups.

The soil food web includes three energy pathways, *i.e.*, root, bacterial and fungal (Moore & Hunt, 1998; Moore *et al.*, 2003). Energy flow *via* living roots through a grazing food chain depends on herbivores; energy flow *via* litter and detritus are through a decomposer food web depending on microorganisms and microbivores. Contrasting food chains or energy pathways impact ecosystem functions differently, *e.g.*, decomposition pathways dominated by bacteria tend to have faster rates of decomposition than those dominated by fungi (Wardle & Yeates, 1993). Bacteria tend to have lower C assimilation efficiency than fungi (Adu & Oades, 1978) and the amount of C storage by the bacterial pathway is less than by the fungal pathway (Suberkropp & Weyers, 1996). Furthermore, stored C that is mediated by the fungal pathway is more persistent than by the bacterial pathway (Bailey *et al.*, 2002).

Soil nematodes occupy key positions and most trophic levels in soil food webs, and can be identified easily to trophic group by morphological and anatomical characters. Three nematode trophic groups (*i.e.*, bacterivores, fungivores and herbivores) are key intermediaries each representing distinct energy pathways. Soil bacterivorous, fungivorous and herbivorous nematodes are mainly bottom-up controlled by food resources suggesting they respond proportionately to respective alteration of their food resources (*i.e.*, bacteria, fungi and plant roots) (Laakso & Setälä, 1999; Petersen, 2002; Scheu, 2002; Bonkowski, 2004). Therefore, we assume the relative abundance and/or biomass of bacterivorous, fungivorous and herbivorous nematodes represent their relative contribution to each of the three soil energy pathways. Many studies use nematode community to describe the decomposition pathways (Freckman & Et-

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tema, 1993; Ferris *et al.*, 2001; Ruess, 2003; Yeates, 2003). However, little is known about the relative magnitude of the three energy pathways in soil, particularly the herbivorous-based energy pathway. The objective of the present study was to compare the relative size of energy pathways of different ecosystems by analysing large amounts of raw data of soil nematode communities.

## Materials and methods

### DATA COLLECTION

The main criteria of data analysed in the present study were; *i*) soil samples from grassland, cropland or forest ecosystems; *ii*) internally consistent sampling methods across all sites of each study; *iii*) original values for each replicate; and *iv*) identification of nematode communities to genus. Neither ecosystem management practices nor treatments were distinguished in the present study. In total, 67 data sets met these criteria and were evaluated in this study (Table 1). Among these, there were 31 from grassland ( $n = 792$  soil samples), 17 from cropland ( $n = 1599$  soil samples), and 19 from forest ( $n = 743$  soil samples) (Table 1). Certainly, this collection of data is a small portion of published data for soil nematodes; this study represents an exploration of energy pathways based on available raw data. Due to its complexity, ecosystems can be recognised at many spatial scale levels and classified by various criteria including vegetation, climate/ecozone, site, sere, and human impact. In the present study, we define ecosystem by vegetation type (*i.e.*, grassland, cropland and forest ecosystems) (Ellenberg, 2009).

### DATA ANALYSIS

Nematode genera were assigned to one of three trophic groups (*i.e.*, bacterivores, fungivores, herbivores) (Yeates *et al.*, 1993; Okada *et al.*, 2005); predators and omnivores were not included in this study. To evaluate the soil energy pathways of each type of ecosystem, percentage of abundance and percentage of biomass of the bacterivorous, fungivorous and herbivorous nematodes were calculated. The sum of the percentages of the three trophic groups of each soil sample equals 100%. The calculation of mean nematode biomass (fresh weight,  $\mu\text{g}$ ) of each genus in each sample was as follows:

$$B = \left( \frac{D^2 L}{1.6 \times 10^6} \right),$$

where  $B$  is the mean biomass per individual,  $D$  is the greatest body diameter ( $\mu\text{m}$ ) and  $L$  is the nematode length ( $\mu\text{m}$ ) (Andrássy, 1956). The values of  $D$  and  $L$  were measured directly or obtained from Bongers (1988), a book containing taxonomic descriptions of nematode genera. The mean nematode biomass of a genus was assigned the mean biomass of the respective taxonomic family when the genus dimensions were not described in Bongers (1988). The mean biomass of nematode families was given in Ferris (2010). The biomass of the three trophic groups of each soil sample was calculated. As the units for soil nematodes differ (*i.e.*, individuals ( $\text{g dry soil}$ )<sup>-1</sup>, individuals ( $\text{g fresh soil}$ )<sup>-1</sup>, individuals  $\text{m}^{-2}$  or individuals ( $\text{l soil}$ )<sup>-1</sup>) in the 67 collected data sets, nematode biomass could not be unified in this study. To make data comparable across studies, the biomass of nematodes of the three trophic groups was transformed to relative biomass (percentage) before analysis. This

**Table 1.** Descriptions of data source, number of study sites, number of samples of different ecosystems.

Ecosystem	No. of sites	No. of samples	Reference
Grassland	31	792	De Goede & Bongers (1998)*; Yeates <i>et al.</i> (1997, 2003); Neher <i>et al.</i> (2005); Villenave <i>et al.</i> (2011); Zhao & Neher (2013)
Cropland	17	1599	Scow <i>et al.</i> (1994); Korthals <i>et al.</i> (1996); de Goede & Bongers (1998); Neher <i>et al.</i> (1998, 2003, 2005); Yeates <i>et al.</i> (1999b); Ferris <i>et al.</i> (2004); Blanchart <i>et al.</i> (2006); Sanchez-Moreno <i>et al.</i> (2006, 2009); Okada & Harada (2007); Villenave <i>et al.</i> (2009, 2010); Treonis <i>et al.</i> (2010); Li <i>et al.</i> (2010); Liang <i>et al.</i> (2009); Hou <i>et al.</i> (2010); Zhang <i>et al.</i> (2011); Zhao & Neher (2013)
Forest	19	743	de Goede & Dekker (1993); de Goede (1996); Sohlenius (1996, 1997, 2002); Sohlenius & Boström (2001); Zhao <i>et al.</i> (2011, 2012, 2013); Zhao & Neher (2013); Zhao <i>et al.</i> (unpubl.)

\* Book including many raw data sets of soil nematode communities.

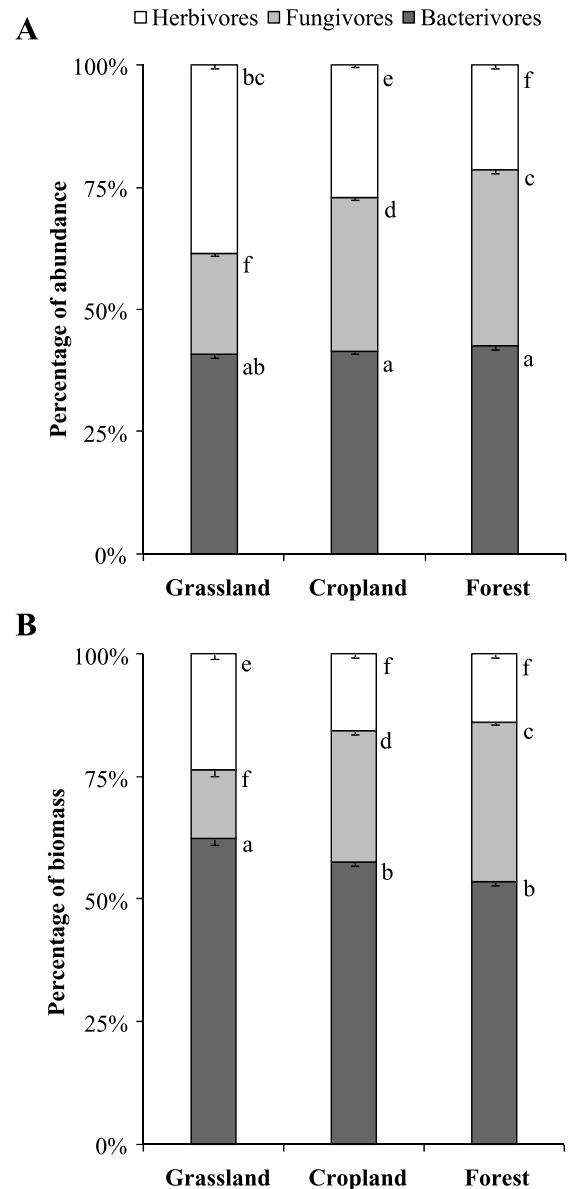
generated a potential shortcoming of the present study because we determined the relative size, rather than actual magnitude, of soil energy pathways. Using biomass measures might improve our insight on the magnitude of energy flux flows through different energy pathways. However, mean biomass of a given family or genus used in this study may not match the actual value of the identified taxon in the family or genus of each soil sample (Ferris, 2010). Therefore, there is still room for improvement of using biomass of nematodes as an indicator for determination of soil energy pathways.

Percentages of the abundance and biomass of bacterivorous, fungivorous and herbivorous nematodes of the ecosystems were analysed separately by one-way ANOVA. Briefly, differences of nine treatments or variables (3 trophic groups  $\times$  3 ecosystems) were compared. Statistical significance was determined at  $P < 0.05$ . All statistical analyses were performed using SPSS software. Because the variances were unequal (even after natural log, square root, arcsine or rank transformation), Tamhane's T2 was used to test differences among treatments.

## Results

### PERCENTAGE OF ABUNDANCE OF THE BACTERIVOROUS, FUNGIVOROUS AND HERBIVOROUS NEMATODES IN DIFFERENT TYPE OF ECOSYSTEMS

The percentages of abundance of bacterivorous nematodes were 40.8%, 41.3% and 42.7% in grassland, cropland and forest ecosystems, respectively (Fig. 1A). Percentages of bacterivorous nematode abundance were similar among the three ecosystem types (Fig. 1A). The percentages of fungivorous nematode abundance were greatest in forest (36.0%), and decreased progressively to cropland (31.6%) and grassland (20.7%) (Fig. 1A). The percentages of herbivorous nematode abundance decreased progressively from grassland (38.5%) to agriculture (27.1%) and forest (21.4%) (Fig. 1A). In cropland and forest ecosystems, the percentages of abundances of the three trophic groups differed from each other; the percentage of bacterivore abundance was the greatest and the percentage of herbivore abundance was the smallest (Fig. 1A). In grassland ecosystems, there was no remarkable difference between the percentages of bacterivore and herbivore nematode abundance (Fig. 1A). Addition-



**Fig. 1.** The percentages of abundance (A) and biomass (B) of the bacterivorous, fungivorous and herbivorous nematodes of grassland ( $n = 792$ ), cropland ( $n = 1599$ ) and forest ( $n = 743$ ) ecosystems. Bars represent means  $\pm$  standard error. Values of bacterivorous, fungivorous or herbivorous nematode percentages with contrasting letters differ statistically at the  $P < 0.05$  level (Tamhane's T2 test).

ally, the percentage of fungivore abundance was the smallest among the three trophic groups in grassland ecosystems (Fig. 1A).

#### PERCENTAGE OF BIOMASS OF THE BACTERIVOROUS, FUNGIVOROUS AND HERBIVOROUS NEMATODES IN DIFFERENT TYPE OF ECOSYSTEMS

The percentage of bacterivorous biomass in grassland (62.4%) ecosystems was greater than that in cropland (57.5%) and forest (53.6%) ecosystems (Fig. 1B). The percentage of fungivorous biomass was greatest in forest (32.6%), and decreased progressively to cropland (26.7%) and grassland (13.9%) (Fig. 1B). The percentage of herbivorous biomass decreased progressively from grassland (23.7%) to cropland (15.8%) or forest (13.8%) (Fig. 1B). In grassland ecosystems, the percentage of herbivorous nematode biomass was greater than the percentage of fungivorous nematode biomass (Fig. 1B). The opposite rank order of herbivorous and fungivorous nematodes occurred in cropland and forest ecosystems (Fig. 1B).

#### Discussion

The patterns of soil energy pathways were similar whether expressed as relative abundance or relative biomass. However, the percentage values of bacterivorous biomass in each type of ecosystem exceeded the percentage values of their abundance. Specifically, both the percentages of nematode abundance and biomass results suggest that energy pathways are bacterial-dominated in all of the ecosystems. Moreover, herbivorous-based energy pathways were greater than fungal-based energy pathways in grassland ecosystems and the reverse rank order in forest ecosystems. Some of the difference in values of abundance or biomass is attributed to contrasts in body size among individual taxa within trophic groups. For example, the biomass of some common (or even dominant) herbivorous (*e.g.*, *Lelenchus*, *Malenchus* and *Tylenchus*) and fungivorous (*Filenchus*, *Ditylenchus*, *Aphelenchoides* and *Aphelenchus*) nematodes are less than the biomass of some common bacterivorous nematodes (*e.g.*, genera in Rhabditidae, Panagrolaimidae, Cephalobidae and Plectidae) (Neher *et al.*, 2004; Ferris, 2010). In general, herbivorous nematodes are large compared with bacterivorous nematodes. Based on current available methodology of calculations of average nematode biomass at family or genus level, the biomass of some common bacterivorous genera (*e.g.*, *Rhabditis*) exceed the biomass of most of the herbivorous genera (Ferris, 2010).

The relative magnitude of energy pathways among grassland, cropland and forest ecosystems, indicated by either relative abundance or biomass, does not represent

the absolute energy flow through this energy pathway in these three ecosystems. In this study, dominance of the bacterial-based energy pathway is consistent with previous studies (Wasilewska, 1979; Sohlenius, 1980; Yeates & Bird, 1994; Popovici & Ciobanu, 2000; Hanel, 2003; Ruess, 2003; Zhao *et al.*, 2013). Fungal-dominated decomposition pathways tend to occur in habitats with substrates of high cellulose and lignin content and high C:N ratio; bacterial-dominated decomposition pathways tend to occur in habitats with N-rich substrates (Wardle & Yeates, 1993). Therefore, the significant difference of fungal-based energy pathways among the three ecosystems indicates a gradient of resource quality among these ecosystems. Substrates with greater quantities of lignin decompose more slowly (*e.g.*, Meentemeyer, 1978; Kogel, 1986; Gholz *et al.*, 2000) than substrates with primarily cellulose or simple sugars. Given that lignin is decomposed primarily by fungi, especially the white-rot fungi (Kirk & Farrell, 1987; Valli *et al.*, 1992), this implies that there is a positive correlation in the dominance of the fungal energy pathway and lignin:cellulose content in detritus.

The novelty of this study is the additional consideration of the herbivorous-based pathway. We suggest that this is a third major pathway not only in cropland but also grassland and forest ecosystems. For example, the herbivorous-based energy pathway was greater than the fungal-based energy pathway in grassland ecosystems. The high relative size of herbivorous-based energy pathways in grassland ecosystems may reflect the high density of fine roots that favour herbivorous nematodes. Many previous studies reported that (live) fine root biomass was greater in grassland ecosystems than in forest and cropland ecosystems at both local and global scales (Jackson *et al.*, 1997; Tufekcioglu *et al.*, 1998; Reich *et al.*, 2001). In addition, topsoils are typically deeper and soil organic carbon is usually greater in grassland ecosystems than in forest and cropland ecosystems (Evrendilek *et al.*, 2004) and land use changes from grassland to cropland or forest decrease soil carbon stocks (Guo & Gifford, 2002).

In summary, we documented the rank order of bacterial-, fungal- and herbivorous-based energy pathways of grassland, cropland and forest ecosystems. In those ecosystems, the relative magnitude of energy through bacterial-based energy pathway exceeded both fungal- or herbivorous-based energy pathways. However, there were significant differences of the relative sizes of fungal- or herbivorous-based energy pathway among those ecosystems. Moreover, our results suggest that the below-ground

herbivorous-based energy pathway accounted for a major percentage of below-ground energy pathways. Nematode parasitism can increase translocation of photosynthate to soil microbial biomass (Bardgett *et al.*, 1999; Yeates *et al.*, 1999a). Therefore, below-ground free-feeding herbivory effects should be considered in future studies, as well as other organisms that feed on fungi and bacteria, such as protista and microarthropods. This information will improve our insight of how much energy flux flows through different energy pathways in soil foodwebs.

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