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Form and function: Metabolic footprints of nematodes in the soil food web

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ABSTRACT

Metabolic footprints provide metrics for the magnitudes of ecosystem functions and services provided by component organisms of the soil food web. Nematodes occupy various trophic roles and perform important functions within the web. They are convenient indicators of similar functions performed by other organisms in the web and are well-documented indicators of ecosystem condition. The generally vermiform shapes of nematodes, and the standardized morphometric characteristics used in their description, facilitate assessment of body volume and weight. Prescribed coefficients allow calculation of their carbon metabolism. Their production of body structure and eggs can be standardized for life course duration. Consequently, standardized metabolic activity levels, attributable to the abundance of nematodes performing various functional roles, can be calculated from existing and accessible morphometric data. Metabolic footprints of nematode assemblages provide measures of ecosystem services performed by each functional guild.

1. Introduction

There are many useful indices of ecosystem diversity; they measure species richness and relative abundance of component taxa (e.g. refs. [18,29,34,35]). Bongers [8] defined the Maturity Index for soil ecosystem analysis based on relative abundance of nematodes categorized, by life course characteristics, into a 1–5 colonizer-persister (cp) series ranging from extreme *r*- to extreme *K*-strategists. The concepts were extended to nematodes of aquatic systems [9]. A family of indices with different attributes has emerged based on the MI, including MI2–5, PPI, ΣMI, and others [12]. Building upon the Bongers [8] model, Ferris et al. [13] provided a framework for determining the enrichment (EI) and structure (SI) characteristics of food webs based on the relative weighted abundance of different functional guilds of nematodes.

Diversity and functional indices are useful descriptive tools for assessment of food web and ecosystem condition but they do not provide information on the magnitude or nature of ecosystem functions. For example, different assemblages with either an abundance of nematodes or with a few nematodes may have the same diversity indices, the same MI or the same SI and EI [12]. Documentation of metabolic activity levels of different indicator guilds of nematodes would convey more information on the importance of the food web or ecosystem attributes suggested by the indices.

While ecologists assess microbial abundance in soils in terms of biomass, assemblages of other soil organisms usually are expressed as abundance of individuals (e.g. ref. [14]). Yeates [39] suggested calculation of biovolume as a measure of the importance of nematodes in soil systems but that approach has not been widely adopted. In recognition of carbon (C) as the currency of ecosystems, Neher et al. [26] assessed the effects of elevated CO_2 in soil systems by calculating nematode biomass and respiration. The evolution of indices of food web structure and function (e.g. refs. [8,12,13]) and the accumulation of information on nematode biology and behavior, confer greater value on biomass and metabolism as measures of importance in ecological studies.

When other constraints are not limiting, carbon and energy are the resources that determine food web size and activity. Besides utilization of C in body and egg production, nematodes have size-dependent metabolic costs [14,21,22]. This paper extends the ecosystem assessments of Ferris et al. [14] to estimate the biomass and metabolic activity associated with each functional attribute of the food web. It builds on the evolving understanding that nematodes are indicators of abundance and activity of non-nematode taxa in their respective functional guilds [14,31,33] and demonstrates the concepts with selected data.

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2. Materials and methods

2.1. The model

2.1.1. Indices of ecosystem condition

The soil nematode assemblage has basal, enrichment and structural components. Trophic group prevalence indicates C and energy flow through herbivory, and through fungus- and bacteria-mediated decomposition channels. Functional guilds are designated based on feeding habits and cp classification and weighted according to their indicator characteristics [13]. Enrichment (EI), Structure (SI), Basal (BI), and Channel (CI) indices are calculated from weighted faunal components (*b, e, s*) of the nematode assemblage: $b = (Ba_2 + Fu_2) * w_2$; $e = (Ba_1 * w_1) + (Fu_2 * w_2)$; $s = (Ba_n * w_n + Fu_n * w_n + Pr_n * w_n)$, where the abundance of bacterial- and fungal-feeding nematodes is indicated by Ba and Fu, and that of higher predators (specialist nematode predators and generalist predators or omnivores) by Pr; *n* indicates the colonizer-persister assignment of the nematode taxa (*sensu* 11) and *w* the weighting assigned to nematodes in each functional guild. EI, SI, BI, and CI are calculated from the faunal components: $EI = 100 * e/(e + b)$; $SI = 100 * s/(s + b)$; $BI = 100 * b/(e + s + b)$; and $CI = 100\ Fu_2 * w_2/(Ba_1 * w_1 + Fu_2 * w_2)$ [6,12,13].

2.1.2. The metabolic footprint concept

The metabolic footprint has a production component and a respiration component. The production component is the lifetime amount of C partitioned into growth and egg production and the respiration component assesses C utilization in metabolic activity.

2.1.2.1. The production component. Nematode biomass is calculated by the Andrássy [1] formula $W = (L * D^2)/(1.6 * 10^6)$ where *W* is the fresh weight (μg) per individual, *L* is the nematode length (μm) and *D* is the greatest body diameter (μm). Nematodes, in general, have elongate cylindrical bodies tapering towards both ends with the anterior bluntly rounded and the posterior more acute. That simple shape provides conveniently for calculation of volume and biomass from available morphometric data. Andrássy [1] calculated nematode volume as the sum of the volumes of a series of complete and truncated cones. Since the method was measurement-intensive, he sought proxies and found that, for nematodes of different sizes, a formula for volume based on body diameter and length ($V = (L * D^2)/1.7$), where 1.7 is an empirically-determined constant, provided a volume estimate within 2% of that determined by the more intensive calculation.

The formulae of de Man [11] have been the standard morphometric descriptors for nematode taxa for over 50 years [36]. Among the standard parameters are *L*, the body length, and *a*, the ratio of length to maximum body diameter. Thus, from information available in the taxonomic descriptions of nematode species, the formula for nematode volume is restated as $V = (L^3/a^2)/1.7$. To calculate the weight of nematodes, Andrássy [1] determined their specific gravity as 1.082–1.086 (average 1.084) from the specific gravity of liquids in which they neither rose nor sank. From the product of specific gravity and volume, he determined the weight (*W*) of a nematode in terms of *L* and *D*. The formula can be rewritten to reflect available parameters as $W = (L^3/a^2)/(1.6 * 10^6)$ μg.

I developed a spreadsheet of 1368 nematode species for which morphometric data are provided in the texts of Goodey [17], Bongers [7], Jairajpuri and Khan [19] and Andrássy [2–4]. That allowed calculation of the weight of individuals of each species, the weight for a genus as the average weight of the species listed in that genus, and the weight for a family (Table 1) as the average for the known species of that family. At a high level of taxonomic resolution, the data for individual species can be used but, given the approximations involved in the metabolism calculations, and the time required for species identification, genus level averages are most practical and provide sufficient resolution; Table 1 is presented as evidence of data availability.

The nematode weight data are calculated from the body lengths and widths of adult nematodes; however, all individuals present in a sample are unlikely to be in the adult stage at the same time. If we assume that nematodes continue to assimilate resources at a rate indicated by their maximum body mass but, at some stage in their development, switch to partitioning assimilates into egg production rather than body structure, the biomass data, adjusted for life course duration, represents the rate of C utilization and the production component of the metabolic footprint.

Nematodes of different taxa complete their life courses at different rates. Opportunistic *r*-strategists in the cp-1 category may complete the life course in as little as 8 days (e.g. *Caenorhabditis elegans*) while those in the cp-5 category may have a life course of several months [8,14]. In reality, the life courses of larger nematodes in cp classes 3–5 are not well known but, based on estimated longevity and the body size and fecundity rates inferred by the cp classification [13] but, for current purposes, an approximately linear relationship between life course duration and cp class is assumed. The amount of C utilized in production is normalized for turnover rate by dividing by the cp value of each nematode group. That weights production (*P*) by the inverse of the life cycle length of the component taxa. Using the estimated dry weight of nematodes as 20% of fresh weight and the proportion of C in the body as 52% of dry weight [27,28], the weight of C is 0.1 of body fresh weight and $P_t = 0.1\ W_t/m_t$ where P_t, W_t and m_t are, respectively, the C used in production, the body weight, and the cp class of taxon *t*.

2.1.2.2. The respiration component. Nematode respiration rate per individual decreases with body size according to the allometric power dependence of basal metabolism and body weight observed in many organisms [20,38]. The relationship is described by $R = cW^b$, where *R* is the respiration rate, *W* is the fresh weight of the individual and *c* and *b* are regression parameters, such that *b* is close to 0.75 [5,22]. Thus, we can calculate the expected respiration rate and the total rate of CO_2 evolution for all nematodes in the system, for those taxa considered indicators of enrichment, those considered indicators of food web structure and connectance, and the taxa participating in various energy flow channels.

For each nematode species, the *c* values of the relationship $R = cW^b$, where $b = 0.75$, increase to maxima at soil temperatures between 20 and 30 °C and declines at higher temperatures [15]. For current purposes, the species and temperature-specific coefficient *c* is omitted from the relationships between respiration rates and body weight with the rationale, as documented in the allometric studies of Mulder et al. [24,25] and Reuman et al. [30], that species predominating at a point in time are similarly adapted to ambient conditions. At different points in time, with change in ambient conditions, different species will predominate. The sets of predominant species under one set of ambient conditions will have similar *c* values to each other but different from those of species predominating under alternate conditions, as observed by Ferris et al. [15,16]. Consequently, the cumulative respiration rate is calculated as $\Sigma R = N_t W^{0.75}$, where N_t is the number of individuals in each of the *t* taxa of interest.

Since we may be more interested in resource availability and C flow through the food web than CO_2 evolution, the weight of lifetime C mineralized by each taxon and, by summation, by each functional guild or the complete nematode assemblage, is derived