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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

Table 1
Colonizer-persister (cp) values, feeding habits (f–h) and average fresh weight of individuals (μg), based on n species, for families of soil nematodes. Weight data are provided only for families with data available for more than one species.

Nominal family[a]	Wt.					Nominal family[a]	Wt.				
	cp[b]	f–h[c]	μg[d]	SD[e]	*n*		cp[b]	f–h[c]	μg[d]	SD[e]	*n*
Achromadoridae	3	6	0.32	0.40	11	Iotonchidae	4	5	5.69	4.92	4
Actinolaimidae	5	5	9.56	3.98	5	Ironidae	4	5	5.55	4.52	8
Alaimidae	4	3	0.56	0.86	40	Isolaimidae	5	3	22.12	14.69	2
Alloionematidae	1	3	1.15	0.38	3	Leptolaimidae	3	3	0.35	0.22	5
Amphidelidae	4	3	0.25	0.21	2	Leptonchidae	4	2	1.07	0.60	29
Anatonchidae	4	5	8.54	8.04	30	Linhomoeidae	3	3	2.82		1
Anguinidae	2	1	9.39	21.51	26	Longidoridae	5	1	56.57	5.06	3
Aphanolaimidae	3	3	0.58	0.33	9	Mesorhabditidae	1	3	0.75	0.62	16
Aphelenchidae	2	2	0.25	0.06	7	Metateratocephalidae	3	3	0.17	0.11	6
Aphelenchoididae	2	1	0.21	0.20	44	Microlaimidae	3	3	0.15	0.01	2
Aporcelaimidae	5	8	44.27	48.83	35	Monhysteridae	2	3	0.43	0.50	33
Atylenchidae	2	1	0.11		1	Mononchidae	4	5	3.99	4.13	73
Aulolaimidae	3	3	0.43	0.28	9	Mydonomidae	5	8	11.34		1
Aulolaimoididae	4	2	0.79	0.47	3	Mylonchulidae	4	5	0.60	0.24	3
Bastianiidae	3	3	0.18	0.06	8	Myolaimidae	2	3	0.64	0.92	5
Bathyodontidae	4	3	1.42	0.73	10	Neodiplogasteridae	1	3	1.83	1.62	24
Belondiridae	5	1	2.62	3.04	33	Neotylenchidae	2	2	1.20	0.94	8
Brevibuccidae	1	3	0.24		1	Nordiidae	4	8	1.95	1.47	3
Bunonematidae	1	3	0.13	0.09	15	Nygolaimidae	5	5	5.39	9.58	27
Campydoridae	3	8	0.41	0.24	5	Odontopharyngidae	1	5	0.88		1
Cephalobidae	2	3	0.37	0.29	63	Onchulidae	3	5	2.82	2.61	4
Choanolaimidae	4	5	8.00		1	Opailaimidae	5		0.26		1
Chromadoridae	3	6	0.54	0.19	10	Osstellidae	2	3	0.10	0.04	2
Chronogastridae	3	3	0.35	0.22	5	Panagrolaimidae	1	3	1.13	1.24	25
Chrysonematidae	5	8	0.98		1	Paratylenchidae	2	1	0.06	0.02	16
Cobbonchidae	4	5	4.10	4.99	2	Peloderidae	1	3	7.44	5.27	29
Crateronematidae	4	8	1.43	0.67	2	Plectidae	2	3	0.89	0.95	55
Criconematidae	3	1	0.67	0.46	30	Pratylenchidae	3	1	0.23	0.25	24
Cyatholaimidae	3	6	0.66		1	Prismatolaimidae	3	3	0.49	0.74	6
Cylindrolaimidae	1	3	0.47	0.50	7	Protorhabditidae	1	3	0.28	0.21	6
Desmodoridae		6	0.26	0.15	4	Psilenchidae	2	1	0.49	0.24	5
Desmoscolecidae		3	0.07		1	Pterygorhabditidae	1	3	0.39		1
Diphtherophoridae	3	2	0.64	0.26	9	Qudsianematidae	4	8	2.00	1.82	49
Diplogasteridae	1	3	1.24	0.86	24	Rhabditidae	1	3	6.80	8.33	24
Diplogasteroididae	1	3	0.84	0.39	5	Rhabdolaimidae	3	3	0.09	0.02	5
Diplopeltidae	3		0.73		1	Rotylenchulidae	3	1	0.06		1
Diploscapteridae	1	3	0.30	0.25	3	Sphaerolaimidae		5	2.34		1
Discolaimidae	5	5	2.32	2.25	14	Sphaerulariidae		7	0.31		1
Dolichodoridae	3	1	0.18	0.04	5	Telotylenchidae	3	1	0.46	0.30	18
Dorylaimellidae	5	1	0.12		1	Teratocephalidae	3	3	0.09	0.03	6
Dorylaimidae	4	8	7.46	14.72	178	Thornenematidae	5	8	1.25	0.94	3
Ecphyadophoridae	2	1	0.03	0.02	3	Thorniidae	4	8	0.97		1
Elaphonematidae		3	0.56		1	Tobrilidae	3	5	7.12	6.12	19
Ethmolaimidae	3	3	0.74	0.36	2	Trichodoridae	4	1	0.65	0.47	19
Hemicycliophoridae	3	1	0.96	0.57	12	Tripylidae	3	5	2.50	3.14	18
Heteroderidae	3	1	0.13	0.04	13	Tylenchidae	2	1	0.15	0.14	66
Hoplolaimidae	3	1	0.51	0.40	19	Tylopharyngidae	1	3	0.66	0.02	2
Hypodontolaimidae	3	3	1.16	0.27	4	Xyalidae	2	3	1.93	2.17	7

[a] Family assignments mainly according to Bongers [7] and Andrássy [2,3,4].
[b] cp values per Bongers and Bongers [10].
[c] Feeding habits per Yeates et al. [42]; feeding habit codes are: 1 = plant-feeding; 2 = hyphal-feeding; 3 = bacterial-feeding; 4 = substrate ingestion; 5 = animal predation; 6 = unicellular eucaryote feeding; 7 = dispersal/infective stages of animal parasites; 8 = omnivorous.
[d] Family average weights calculated per Andrássy [1] using data from Andrássy [2,3,4], Bongers [7], Goodey [17] and Jairajpuri and Khan [19].
[e] Standard deviation of family average weight.

from the molecular weights of C and O_2, as 12/44 or 0.273 of the mass of CO_2 evolved.

2.1.2.3. The metabolic footprint calculation. The expanded equation for the metabolic footprint of nematodes (F), as an index of C utilization of component taxa, is the sum of the production and respiration components, $F = P + R$, and expanded as:

$$F = \sum \left(N_t \left(0.1(W_t/m_t) + 0.273\left(W_t^{0.75}\right)\right)\right)$$

for each of the t taxa involved in the summation. Then, from the formula of Andrássy [1] and the L and a values each nematode species, the W_t parameter can be replaced by $(L^3/a^2)/(1.6 * 10^6)$.

2.1.2.4. Footprint form and function. The metabolic footprint is an estimator of nematode contribution to various ecosystem services and functions:

The **enrichment footprint** is the metabolic footprint of those nematodes most rapidly responsive to resource enrichment.
The **structure footprint** is the metabolic footprint of higher trophic levels which may have a regulatory function in the food web and which are indicative of the abundance of organisms of similar functions in non-nematode taxa [13,31].
The **functional footprint** is the total area of the two functional footprints (enrichment and structure) as illustrated in Figs. 1 and 2.

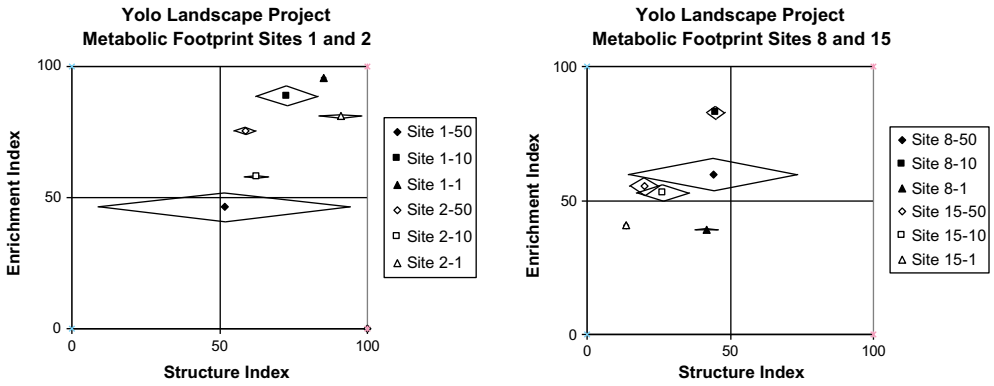

Fig. 1. Functional metabolic footprints of nematodes in soil food webs of the Yolo County landscape project. Vertical axis of each footprint represents the enrichment footprint and horizontal axis the structure footprint. Sites 1 and 2 are less-disturbed upland areas; sites 8 and 15 are areas of intensive agriculture. Suffixes to site designations, (50, 10, 1) indicate distances from the water channel at each site.

The **herbivore**, **bacterial** and **fungal footprints** are based on the nematode indicators of C and energy entering the soil food web through their respective channels.

The **composite footprint** is the metabolic footprint of the complete nematode assemblage, regardless of trophic role or ecosystem function.

2.1.3. Graphic display of the metabolic footprint for enrichment and structure indicators

The functional characteristics of the food web condition are depicted graphically as the intersection of the EI and SI per Ferris et al. [13] (e.g., Figs. 1 and 2). It is instructive to center the enrichment and structure components of the metabolic footprint on the intersection of the indices. However, the units of the indices are percentage and those of the footprint components (F) in C utilization per unit volume or weight of soil. In a spreadsheet calculation, F can be divided by an adjustable scalar, k. Then, the x-axis coordinates of the metabolic footprint are calculated as $SI - 0.5F_s/k$ and $SI + 0.5F_s/k$, where F_s is the sum of standardized C utilization by structure indicator taxa. Similarly, the y-axis coordinates are calculated as $EI - 0.5F_e/k$ and $EI + 0.5F_e/k$, where F_e is the sum of standardized C utilization by enrichment indicator taxa. The functional metabolic footprint is depicted by sequentially joining points: $SI - 0.5F_s/k$, EI; SI, $EI + 0.5F_e/k$; $SI + 0.5F_s/k$, EI; SI, $EI - 0.5F_e/k$; and $SI - 0.5F_s/k$, EI.

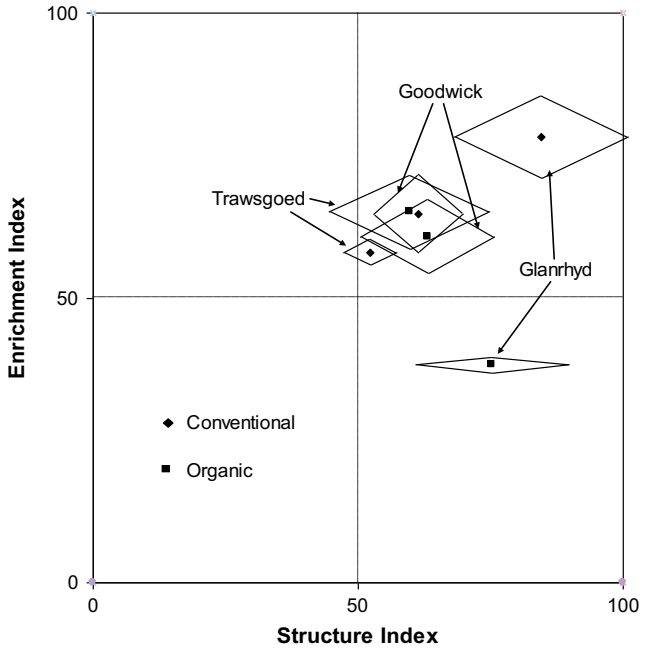

Fig. 2. Functional metabolic footprints of nematodes in Welsh grasslands subjected to conventional and organic management based on ten samples from each site. Data from Yeates et al. [41] and Yeates and Cook [43]; vertical axis of each footprint represents the enrichment footprint and horizontal axis the structure footprint.

The scalar (k), maintained constant for all footprints on a graph, is adjusted for acceptable visual representation and comparison of footprints of different locations or treatments. Then, each percentage point on the enrichment and structure axes represents k units of the standardized C utilization by the indicator taxa. The multifunctionality of the metabolic footprint is the area of the equilateral rhomboid centered on the intersection of the structure and enrichment indices, with diagonal dimensions F_s and F_e. The area of that shape is $(F_s \times F_e)/2$ with complex μg^2 units which may be best referred to as the standardized C units of the functional footprint. The functional metabolic footprint is maximized when the rhomboid shape becomes a square and one might consider, as a working hypothesis, that the productivity and turnover rates of the enrichment indicators, representative of the prey, are sufficient to maintain the needs of the predators (the structure indicators) so that the system is in metabolic balance.

The characteristics of the metabolic footprints are visually comparable within each faunal analysis chart. They may not be comparable between charts, except for comparisons of the ratios of enrichment and structure components, because of differences in the units of the data from which they are derived, differences in the k scalar used, and differences in nematode extraction methods, taxonomic resolution, and other sources of variation among datasets.

2.1.4. Resource flow

The magnitudes of C and energy flow through the fungal channel are represented as F_f, the C utilization coefficient, for fungal-feeding nematodes. Those of the bacterial and herbivory channels are the equivalent calculation for bacterial- and plant-feeding nematodes.

2.1.5. Statistical separation of metabolic footprint sizes

The metabolic footprints of various systems and treatments can be compared in terms of their enrichment dimensions (F_e) or structure dimension (F_s). Where appropriate replicate data are available, differences among enrichment footprints, structure footprints, functional footprints, fungal channel, bacterial channel, and herbivore channel footprints can be tested by analysis of variance. Since the multiplicative calculation of all these metrics

inflates variances, log transformations prior to analysis are appropriate.

2.2. Test of concept with selected datasets

2.2.1. Landscape project

In a study of biodiversity at larger spatial scales in Yolo County, California, plant biodiversity at both the field- and landscape-scale declined in relation to agricultural intensification. However, although plant diversity was greater in most riparian zones than in neighboring agriculturally-disturbed sites, the relationship between aboveground and belowground biodiversity was not strong, as also noted elsewhere [33,37]. Management effects on metabolic footprints of the nematode assemblages were determined at four of the sites, two in a valley with intensive agriculture and two in upland areas of less-intensive agriculture (Fig. 1). Faunal analysis of each nematode assemblage was conducted for three replicate soil samples, taken at distances 1, 10 and 20 m perpendicular to the edge of a water channel at each location.

2.2.2. Organic and conventional grasslands

Data of Yeates et al. [41] and Yeates and Cook [43] provide detailed nematode assemblages of conventional and organic grasslands in Wales. The data are from three sets of paired organic and conventional grasslands in similar geographic and climatic circumstances. Nematode assemblage data from three grassland sites were used to examine the metabolic footprints associated with the management strategies. Data were available for ten pseudo replicate soil samples from each field.

2.2.3. Farming systems study

An on-going long-term experiment at the University of California Davis compares three management strategies in an annually-cropped agricultural system. The strategies are “conventional” (conv), with a single economic crop each year and employing the use of mineral fertilizers as needed, “cover-cropped” (cc) in which the N requirements of the economic crop are at least partially supplied by a winter cover crop but can be supplemented by mineral fertilizers and permit the use of pesticides, and “organic” (org) in which pesticides are not used and nutrients are supplied through cover crops and manures. Superimposed on the farm management strategies are two tillage regimes, standard tillage (st) which may utilize up to 11 tillage operations per year, and conservation tillage (ct) in which in which soil disturbance is minimized except where needed for weed management and minor soil preparation prior to planting. Nematode assemblages were determined in tomato plots that had been in corn the previous cropping season. The plots were in a factorial design with three management systems (conv, cc and org) and two tillage regimes (st and ct) in three replications.

2.2.4. Metabolic footprints of an arid desert

Nematode assemblages associated with creosote bush (*Larrea tridentata*), rabbit brush (Ericameria paniculata) and bare soil in the Mojave Desert of California were used to examine food web condition and metabolic footprint sizes. Five replicate samples to a depth of 20 cm represented each environment (Ferris et al., 2004).

3. Results and discussion

3.1. Tests of concept with selected datasets

3.1.1. Landscape project

The less-disturbed upland agriculture sites (sites 1 and 2) had very different food web and metabolic footprint characteristics than the more intensive valley agricultural sites (sites 8 and 15). While SI was greater at 1 m than it was further from the edge of the water channel in the upland sites, that was not the case in the valley sites where the riparian strip at the canal edge was much reduced. (Fig. 1, Table 2). The EI varied inconsistently with distance from the creek or canal edge, probably related to the amount of disturbance that had taken place in preparation for crop planting. The significant enlargements of the enrichment, bacterial and fungal channel footprints at sites 1 and 8 were in the disturbed cultivated areas and coincided with earlier commencement of tillage activities at those sites. Univariate analyses across the four sites revealed a significantly lower enrichment footprint at site 2 than at the other sites but no differences in structure or total functional footprints among sites.

3.1.2. Organic and conventional grasslands

The enrichment footprint was greater in conventional than organic grasslands at Glanrhyd, and the opposite at Trawsgoed (Table 3). Similarly, the structure footprint was lower in the conventional grassland at Trawsgoed than at the other locations.

Table 2
Landscape project, Yolo County, California – statistical separation of descriptive food web indices and log-transformed metabolic footprint sizes, (efoot = enrichment footprint, sfoot = structure footprint, tfoot = functional footprint, bactfoot = bacterivore footprint, fungfoot = fungivore footprint, pltfoot = plant-feeder footprint). Distances, (m) are from the nearest water channel. In each row, means followed by the same letter do not differ ($P = 0.05$).

	50 m	10 m	1 m
Site 1			
BI	32.3 a	7.7 b	3.6 b
SI	51.6 a	72.6 ab	85.0 b
EI	46.3 a	88.7 bc	95.5c
Ln efoot	5.1 a	4.7 a	2.8 b
Ln sfoot	7.1 a	5.5 a	2.6 b
Ln tfoot	11.6 a	9.6 a	4.7 b
Ln pltfoot	3.0 ns	3.5 ns	2.4 ns
Ln bactfoot	5.4 a	4.6 a	1.5 b
Ln fungfoot	4.1 a	3.4 a b	2.4 b
Site 2			
BI	17.6 a	24.5 a	6.6 b
SI	58.6 a	62.6 ab	90.9 b
EI	75.5 a	58.0 b	80.9 a
Ln efoot	3.8 ns	2.6 ns	3.0 ns
Ln sfoot	4.6 ns	4.8 ns	5.1 ns
Ln tfoot	7.8 ns	6.7 ns	7.5 ns
Ln pltfoot	3.5 ns	2.7 ns	2.9 ns
Ln bactfoot	3.1 ns	2.7 ns	2.2 ns
Ln fungfoot	3.9 ns	3.0 ns	3.6 ns
Site 8			
BI	30.6 b	15.2 a	42.8 b
SI	44.0 ns	44.9 ns	41.2 ns
EI	59.5 b	82.7 c	39.1 a
Ln efoot	5.4 a	4.4 a	2.3 b
Ln sfoot	7.1 a	4.8 b	4.6 b
Ln tfoot	11.8 a	8.5 b	6.2 b
Ln pltfoot	3.5 a	4.3 a	0.3 b
Ln bactfoot	5.2 a	3.0 b	2.8 b
Ln fungfoot	4.0 a	4.2 a	1.9 b
Site 15			
BI	39.7 a	39.2 a	54.5 b
SI	20 ns	26.5 ns	13.6 ns
EI	55.2 ns	52.9 ns	40.6 ns
Ln efoot	4.8 ns	4.3 ns	3.9 ns
Ln sfoot	4.4 ns	4.7 ns	3.2 ns
Ln tfoot	8.5 ns	8.3 ns	6.3 ns
Ln pltfoot	3.5 ns	1.5 ns	1.7 ns
Ln bactfoot	4.4 ns	3.9 ns	4.2 ns
Ln fungfoot	4.3 ns	4.0 ns	3.3 ns

Table 3
Statistical separation of log-transformed metabolic footprints of nematodes in Welsh grasslands subjected to conventional (conv) and organic (org) management, based on ten samples from each site. Data from Yeates et al. [41] and Yeates and Cook [43]; efoot = enrichment footprint, sfoot = structure footprint, tfoot = functional footprint, bactfoot = bacterivore footprint, fungfoot = fungivore footprint, pltfoot = plant-feeder footprint. In each column, means followed by the same letter do not differ ($P = 0.05$).

Location	System	efoot	sfoot	tfoot	bactfoot	fungfoot	pltfoot
Glanrhyd	conv	6.3 b	7.1 b	12.7 c	6. 4b	4.2 c	4.4 a
Goodwick	conv	5.9 b	6.4 b	11.7 b	6.3 b	2.2 a	5.0 bc
Trawsgoed	conv	5.0 a	5.8 a	10.1 a	5.2 a	3.5 b	4.8 ab
Glanrhyd	org	4.5 a	6.9 b	10.6 a	5.1 a	4.5 c	5.3 cd
Goodwick	org	6.1 b	6.7 b	12.1 bc	6.3 b	4.4 c	5.7 d
Trawsgoed	org	6.2 b	6.9 b	12.4 bc	6.3 b	4.2 c	5.6 d

There were no consistent relationships between management strategies and the total functional footprint. The higher fungal/bacterial footprint ratio in the organic field at Glanrhyd might indicate a lower quality of organic matter, or depleted organic matter, consistent with the lower EI at that location (Fig. 2). The higher enrichment footprint and bacterial-feeding nematode abundance at several of the sites suggests a higher quality or a recent application of labile organic matter. The fungal-feeding nematode footprint was generally higher in organic grasslands than in the paired conventional fields, as recognized by Yeates et al. [41]. Similarly, the metabolic footprint of plant-feeding nematodes was generally greater in organic grasslands, suggesting greater flow of resources into the food web through herbivory channels. Glanrhyd conventional, the site with the highest EI (Fig. 2), also had the greatest total functional footprint and the lowest herbivore footprint.

3.1.3. Farming systems study

In the California farming system experiment, the structure footprints of all the farming systems and tillage levels were rather low (Fig. 3), although typical for disturbed annually-cropped agricultural situations. Elsewhere [23,32], we have speculated that, after changes in management strategies, higher trophic level nematodes in such systems may require considerable time to become re-established. The enrichment footprint was generally greater in the farming systems with resources supplied by cover crops and manures rather than by mineral fertilizers. There impact of tillage regime was only apparent in differences between the organic conservation tillage system and the other systems (Fig. 3).

In the farming systems project, the Channel Index (not shown), an indicator of fungal the ratio of fungal to bacterial activity in the food web, was significantly greater in the conventional farm management system under either tillage regime than in the cover crop and manure driven systems. A comparison of the C-mineralization coefficients of the bacterial and fungal channels suggests that the differences were associated with greater resource flow through the bacterial channels in the organically-amended systems while the magnitude of the C flow though fungal channels was similar across treatments.

3.1.4. Metabolic footprints of an arid desert

The enrichment and structure indices of soil samples from the Mojave Desert were indicative of a depleted system in which there are insufficient resources remaining after transition through the entry-level organisms to support higher trophic levels (Fig. 4) [13]. The system is depauperate and climatically constrained. However, there is a clear influence of the abundance, albeit meager, of resources available around the seasonally-active desert vegetation in comparison to bare soil.

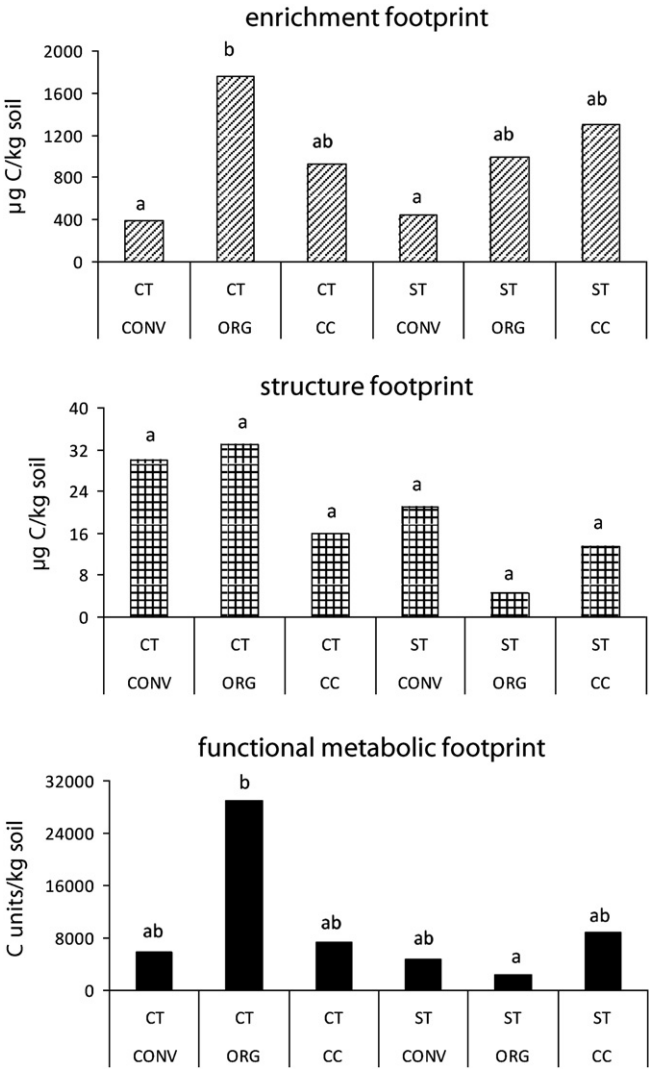

Fig. 3. Metabolic footprints of nematodes in the soil food webs in the California Farming Systems Project comparing crops managed under conventional (CONV), organic (ORG) or cover cropped (CC) systems in plots subjected to intensive standard tillage (ST) or reduced conservation tillage (CT).

3.2. Expanded food web analysis and testable hypotheses

Metabolic footprint analysis provides additional descriptive information on food web form and function (Table 4). Two hypothetical family level assessments of nematode assemblages (A and B) have the same number of individuals but distributed differently among families with varying functional attributes. Assessment C has the same proportional distribution of individuals among taxa as assessment B but at ten-fold abundance. The differences between the three samples are not revealed by Shannon's or Simpson's Diversity Indices [34,35]. Further, the quantitative differences between samples B and C are not detected by the Maturity Index or by BI, EI, SI, or CI [8,12,13]. They are, however reflected in the magnitude of the metabolic footprints, based on C utilization for production and respiration.

The enrichment footprint, which represents C utilization of the supposed prey of the structure indicator nematodes is, in some cases (Figs. 1 and 2), smaller than the structure footprint. This seemingly unsustainable state does not support the working hypothesis, that in a system which is in metabolic balance, the productivity and turnover rates of the enrichment indicators

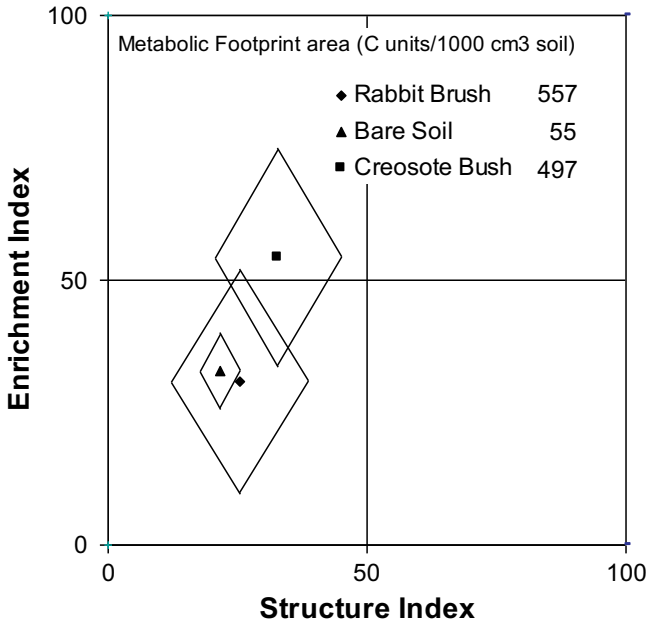

Fig. 4. Functional metabolic footprints of depauperate and climatically constrained soil food webs of the Mojave Desert of California. Vertical axis of each footprint represents the enrichment footprint and horizontal axis the structure footprint.

should be sufficient to maintain the needs of the predators. Besides the possibility that those systems are not in metabolic balance, there are several alternative explanations. For example, there may be other prey available to the predators so that their footprint is larger than anticipated based on that of their prey. Further, a large proportion of juvenile stages of long-lived predator nematodes would result in inflation of footprint sizes based on adult dimensions.

In the examples presented (Figs. 1–4), nematodes were identified to the genus level. Taxonomic resolution at the family level is problematic for biomass measurements. Although other families of nematodes have a smaller size range, the Dorylaimidae, as an extreme, has family average weight of 7.5 μg with a standard deviation of 14.7 for a coefficient of variation of almost 200% (Table 1). Clearly, the mean is not a good predictor of the weight of many of the genera and species. If the dominant taxon in a sample is of a size lower than the mean, biomass calculations based on average-sized individuals will be inflated; if greater, they will be depressed. That argues for taxonomic resolution below the family level. A similar case has been made for variability in the functional attributes of genera within nematode families [40].

One might argue that the information embodied in metabolic footprints could be provided, as a proxy, by nematode abundance data. However, nematode abundance data do not account for respiratory attributes, body size or longevity of nematodes with different functional characteristics. Metabolic footprints provide a quantitative component to nematode faunal analyses of ecosystem structure and function. The calculations require some additional computation but are based on accessible data on nematode dimensions and respiration. They have some embedded assumptions regarding life course duration, temperature effects on metabolic rates, and life stage structures of populations. However, I believe that the additional information provided by the analyses provides an opportunity for more detailed interpretation of ecosystem structure and function, and the roles of nematodes therein.

Table 4
Nematode assemblages of three hypothetical soil samples (A, B and C) with associated diversity indices, functional indices and metabolic footprints. The three samples include representatives of the same families, which have various functional attributes, but with different abundance.

	A	B	C	cp[a]	f–h[b]	Wt.[c]	$R+P$[d]
Hoplolaimidae	5	15	150	3	h	0.51	0.18
Pratylenchidae	5	15	150	3	h	0.23	0.10
Aphelenchidae	15	5	50	2	f	0.25	0.11
Cephalobidae	15	2	20	2	b	0.37	0.15
Plectidae	2	15	150	2	b	0.89	0.29
Rhabditidae	2	50	500	1	b	6.80	1.83
Dorylaimidae	50	5	50	4	p	7.46	1.42
Qudsianematidae	15	2	20	5	p	2.00	0.51
Total	109	109	1090				
Simpson's Index	0.3	0.3	0.3				
Shannon's Index	1.6	1.6	1.6				
Maturity Index	3.4	1.6	1.6				
Basal Index	9	8	8				
Enrichment Index	33	90	90				
Structure Index	87	91	91				
Channel Index	65	2	2				
Enrichm. footprint[e]	4	91	915				
Structure footprint[f]	79	8	81				
Functional footprint[g]	144	371	37,105				
Herbivory footprint[h]	1	4	42				
Composite footprint[i]	88	109	1091				

[a] Colonizer-persister values of Bongers [8] and Bongers and Bongers [10].
[b] Feeding habit codes per footnote of Table 1.
[c] Fresh weights of adult nematodes per Table 1.
[d] Carbon respiration (R) and production (P) coefficients.
[e] Metabolic footprint of nematodes rapidly responsive to resource enrichment.
[f] Metabolic footprint of higher trophic levels.
[g] Total area of the enrichment and structure footprints.
[h] Metabolic footprints based on the nematode indicators of C and energy flowing through herbivory.
[i] Metabolic footprint of the complete nematode assemblage.

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