

A framework for soil food web diagnostics: extension of the nematode faunal analysis concept

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Abstract

Nematodes, the earth's most abundant metazoa, are ubiquitous in the soil environment. They are sufficiently large to be identifiable by light microscopy and sufficiently small to inhabit water films surrounding soil particles. They aggregate around and in food sources. They include component taxa of the soil food web at several trophic levels. They can be categorized into functional guilds whose members respond similarly to food web enrichment and to environmental perturbation and recovery. Indices derived through nematode faunal analysis provide bioindicators for disturbance of the soil environment and condition of the soil food web. We enhance the resolution of faunal analyses by providing a weighting system for the indicator importance of the presence and abundance of each functional guild in relation to enrichment and structure of the food web. Graphical representations of food web structure, based on nematode faunal analyses, allow diagnostic interpretation of its condition. Simple ratios of the weighted abundance of representatives of specific functional guilds provide useful indicators of food web structure, enrichment, and decomposition channels. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

1.1. Soil food web structure and function

The many functions of soil food webs are defined in terms of key ecosystem processes or characterized relative to subjective perspectives (Table 1). At global, societal and ecosystem levels, organic matter decomposition, mineral and nutrient cycling, and carbon sequestration are major components of resource conservation, environmental maintenance and even

mediation of global climate change. The soil food web provides reservoirs of minerals and nutrients, detoxifies pollutants, modifies soil structure, and regulates abundance of pest and other opportunistic species (Doran and Parkin, 1994; Kennedy and Smith, 1995; van Straalen and van Gestel, 1998). Knowledge of the function of the soil food web in relation to the presence and abundance of its component organisms is a basic requirement for soil stewardship.

Since large amounts of the carbon and energy assimilated by each trophic guild are dissipated through metabolic activity (De Ruiter et al., 1998; Moore, 1994), the abundance and, perhaps, diversity of organisms in food webs may be regulated by the resource supply rate. The supply rate represents a "bottom-up"

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Table 1
Some important functions of the soil food web

Decomposition of organic matter
Cycling of minerals and nutrients
Redistribution of minerals and nutrients in space and time
Reservoirs of minerals and nutrients
Sequestration of carbon
Detoxification of pollutants
Modification of soil structure
Biological regulation of pest species

constraint on the size and activity of the web. Predation and competition among trophic levels provide “top-down” regulation of food web structure and function. Both regulators may control all, or different parts of, a food web (De Ruiter et al., 1995). Trophic cascade effects result from top-down regulation in a linear chain of trophic exchanges. In soil food webs, except at a local patch level or during successional recovery from extreme disturbance, there is probably sufficient connectance among guilds that trophic cascades are unlikely. More likely is that each guild

has more than one food source and that several guilds may share a common predator. The effects of change in abundance of a guild in such systems are much less predictable. The high degree of connectance provides functional redundancy and, consequently, functional resilience to perturbation, through many direct and indirect interactions (Menge, 1995; Strong, 1992; Wardle et al., 1995a,b; Yeates and Wardle, 1996).

To avoid contributing to the inconsistent usage of terminology in description of food webs (Wilson, 1999), we provide our working definitions (Table 2).

1.2. Food web evaluation

Alteration of the structure or function of the soil food web may be a consequence of environmental perturbation. It may also be an explicit management objective of environmental conservation and restoration programs, or of agricultural production practices. Evaluation of the state of the web may be

Table 2
Definition of terms^a

<i>Colonizer–persister (cp) scale</i> : Assignment of taxa of soil and freshwater nematodes to a 1–5 linear scale according to their <i>r</i> and <i>K</i> characteristics
<i>cp-1</i> : Short generation time, small eggs, high fecundity, mainly bacterivores, feed continuously in enriched media, form <i>dauerlarvae</i> as microbial blooms subside
<i>cp-2</i> : Longer generation time and lower fecundity than the <i>cp-1</i> group, very tolerant of adverse conditions and may become cryptobiotic. Feed more deliberately and continue feeding as resources decline. Mainly, bacterivores and fungivores
<i>cp-3</i> : Longer generation time, greater sensitivity to adverse conditions. Fungivores, bacterivores and carnivores
<i>cp-4</i> : Longer generation time, lower fecundity, greater sensitivity to disturbance. Besides the other trophic roles, smaller omnivore species
<i>cp-5</i> : Longest generation time, largest body sizes, lowest fecundity, greatest sensitivity to disturbance. Predominantly carnivores and omnivores
<i>Connectance</i> : The proportion of the potential links among nodes in a food web that are realized
<i>Faunal profile</i> : A graphical representation of the condition of a food web in relation to its structure and enrichment as indicated by weighted nematode faunal analysis
<i>Functional guild</i> : Nematode taxa with the same feeding habits, and inferred function, in the food web
<i>Ba_x, Fu_x, Ca_x, Om_x</i> (where <i>x</i> = 1–5): Functional guilds of nematodes that are bacterivores, fungivores, carnivores or omnivores where the guilds have the character indicated by <i>x</i> on the <i>cp</i> scale
<i>Functional stability</i> is the stability of a biological function to perturbation
<i>Guild</i> : An assemblage of species with similar biological attributes and response to environmental conditions
<i>Resilience</i> : The ability of the food web to recover from perturbation
<i>Resistance</i> : The ability of the food web to withstand the immediate effects of perturbation
<i>Stability</i> : Lack of change in a food web function following perturbation; it is the integral of both resistance and resilience
<i>Trophic role</i> : The observed or inferred food sources for a nematode guild

^a Adapted largely from Bongers (1990), Bongers and Bongers (1998), Ferris et al. (1999), Martinez (1992), and Wilson (1999).

accomplished by structural or functional analysis. In both cases, interpretation of the analysis involves knowledge of the relationship between the indicator and a characteristic of interest. Interpretation usually requires consideration of reliability, temporal and spatial variability, sensitivity and resolution of the measure, and technical sophistication (National Soil Survey Center, 1996).

Structural analysis of the soil food web through determination of the presence and abundance of individual taxa presents challenges. Sampling, capture, identification and assessment may be difficult for some taxa and technologically daunting for a whole fauna. Alternative measures are emerging; for example, biochemical analysis of microbial communities provides opportunities for indicating characteristic fatty acid or DNA fingerprints (Bossio and Scow, 1995; Pankhurst, 1997). Functional analysis of soil food web condition may include rates of soil respiration, organic matter decomposition, biologically-mediated mineralization, and other processes (e.g. Griffiths et al., 2001; Gunapala et al., 1998). Functional analysis may not indicate how those functions are being accomplished, or their sustainability.

An alternative to complete structural analysis is provided by assessment of the presence and abundance of indicator guilds. There is considerable evidence that nematode faunal analysis provides a useful tool in assessing the structure, function, and probably the resilience of the soil food web (Ferris et al., 1999; Ritz and Trudgill, 1999; Wardle et al., 1995b). The characteristics of the nematode fauna that make it a good bioindicator have been well documented. In summary, nematodes are the most abundant of the Metazoa, occupy key positions at most trophic levels in soil food webs, can be captured and enumerated by standardized extraction procedures and are readily identified from morphological and anatomical characters. Further, since their feeding habits are clearly related to oral structure, their trophic roles are readily inferred. Each soil sample contains an abundance and diversity of nematodes and, consequently, has high intrinsic information value (Bongers, 1999; Bongers and Bongers, 1998; Bongers and Ferris, 1999; Yeates et al., 1993). In this paper, we develop a framework for weighted nematode faunal analysis as an indicator of the condition of the soil food web.

2. Methods and approaches

2.1. Background and rationale

Conceptual developments in the ecology of soil nematodes have progressed through several interesting and definable stages during the last few decades. Faced with the diversity and abundance of soil organisms, ecologists often resort to trophic or functional group categories based on feeding habit. The abundance and dynamics of nematode trophic groups have been described for various habitats and levels of disturbance. Results are often ambiguous, and conclusions few, since the trophic groups encompass an enormous diversity of life history and physiological characteristics (Ferris, 1993).

Application of community structure indices to nematode faunae has been an important step in the development of diagnostic tools for food webs (e.g. Freckman and Ettema, 1993; Gupta and Yeates, 1997; McSorley, 1997; Neher, 1999; Porazinska et al., 1998; Sohlenius and Sandor, 1987). A conceptual advance was the classification of nematode families along a colonizer–persister (cp) continuum (Bongers, 1990). This system recognizes that taxa of monophyletic families are adapted similarly to specific environmental conditions and food sources through anatomical and physiological commonalities. Taxa within a cp class are similar in their responses to disturbance (Table 2) (Bongers, 1999; Bongers and Ferris, 1999). The cp classification allows calculation of the index maturity (MI) of a nematode fauna as the weighted mean frequency of the cp classes (Bongers, 1990). It expresses the proportional representation of nematode families as an index of environmental condition.

Recent developments in nematode faunal analysis include the integration of nematode feeding groups (Yeates et al., 1993) and cp-scaling into a matrix classification of functional guilds (Table 2, Fig. 1) (Bongers and Bongers, 1998). Each guild represents a grouping of taxa of similar biology as envisioned in the use of trophic species in food web analysis (Cohen, 1989). The guild aggregation does not capture the exquisite biological variability of the species level, which represents the true detail of organism and community function in food webs (Polis, 1995; Wall and Moore, 1999), but it resolves, in part, the likely artefactual effects of trophic group composites (Ferris, 1993).

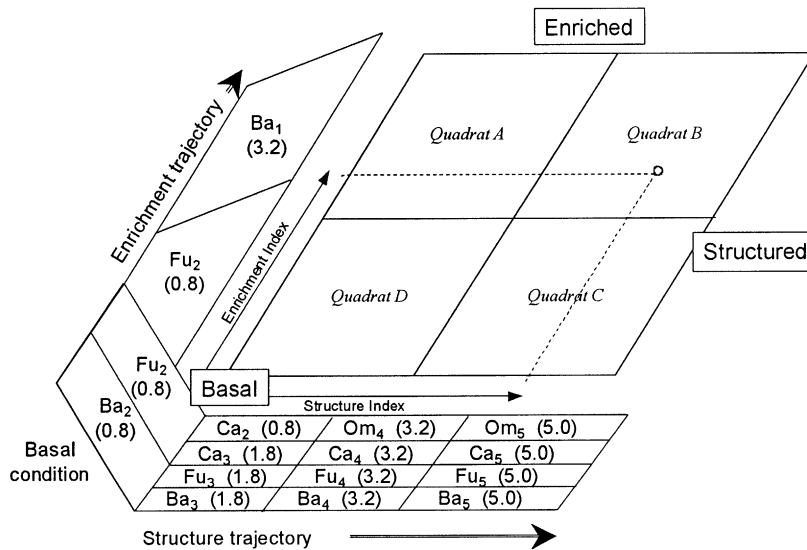


Fig. 1. Functional guilds of soil nematodes characterized by feeding habit (trophic group) and by life history characteristics expressed along a colonizer–persister (cp) scale (after Bongers and Bongers, 1998). Indicator guilds of soil food web condition (basal, structured, enriched) are designated and weightings of the guilds along the structure and enrichment trajectories are provided, for determination of the enrichment index (EI) and structure index (SI) of the food web.

Functional guilds, trophic species or trophic dynamic modules provide a manageable basis of organism aggregation in food web analysis and allow practical study of community dynamics (Johnson, 2000; Pahl-Wostl, 1995).

A progression of soil conditions from stressed or polluted to pristine is not exactly congruent with the continuum of nematode life history characteristics in the cp classification as defined by Bongers (1990). Rather, the most abundant nematode taxa under stressed conditions are those in cp-2, while the enrichment opportunists (cp-1) respond positively to disturbances that result in enrichment at any level of environmental quality (Bongers, 1999; Bongers and Ferris, 1999). A modified MI based on nematode taxa in cp classes 2–5 has proved useful in measuring pollution-induced stress (e.g. Korthals et al., 1996a). We believe that the cp-1 nematodes are important indicators of soil fertility. That was recognized by their inclusion in “cp triangles”, which accommodate an enrichment axis, as graphical representations of faunal composition (De Goede et al., 1993). Graphical representation of nematode faunal analysis provides an integral synopsis of the structure of the food web

and the state of its environment; it is a central theme of this treatise.

2.2. Nematode guild indicators of food web condition

As a framework for developing these concepts, we describe three qualitative conditions of food webs and identify the associated nematode indicator guilds (Fig. 1). We will describe as *basal*, a food web that has been diminished due to stress, including limitation of resources, adverse environmental conditions, or recent contamination. Resident or surviving organisms may be those with specialized physiological and behavioral adaptations. The nematode guilds present are those adapted to stress conditions and represented in the cp-2 class of the MI (Table 2). They appear to have wide ecological amplitude. Some have probolae that may be used to rasp food from surfaces, many are capable of prolonged cryptobiotic survival with undetectable metabolic activity, and they are more tolerant of polluted conditions than other nematode taxa. They are predominantly bacterial scavengers in the Cephalobidae (Ba₂) and fungal-feeders in the Aphelenchidae, Aphelenchoididae and Anguinidae (Fu₂).

Both the Ba₂ and the Fu₂ guilds are also present in all other food web classes and have been defined as general opportunists (Bongers, 1999).

We apply the description *structured* to food webs in which resources are more abundant or where recovery from stress is occurring. Such webs are more speciose than the basal condition and there are more trophic links; the elements of community structure are apparent (Wardle and Yeates, 1993; Wardle et al., 1995a,b). With time, maturation and lack of perturbation, the degree of structure may increase, as indicated by a continuum of nematode guilds that represent cp classes 3–5 (Table 2). The indicator guilds of rudimentary community structure are the Ba₃ Pristomatolaimidae, the Fu₃ Diphtherophoridae and the Ca₃ Tripylidae. Generally, these nematodes have lower fecundity, longer life course and lower population levels than the cp-2 guilds. We include the Aphelenchid Ca₂ carnivores, which are able to tolerate basal conditions, with this group since their predaceous habit suggests some degree of structure. With greater structure in the community, more links in the food web, nematode predation and multitrophic interactions occur. The nematode guild indicators are the Ca₄ and Om₄ Mononchidae and Dorylaimidae (particularly, the smaller dorylaimids), and the Fu₄ Leptonchidae. Environmental stability and homeostasis results in the highest levels of community structure. Indicator guilds include the Ca₅ Discolaimidae and Om₅ Thornenematidae and Qudsianematidae (often considered larger dorylaimids). Nematodes in these guilds are large-bodied, and have the lowest fecundity and longest life courses of soil nematodes. They are susceptible to soil disturbance and are often absent from disturbed, polluted, or intensely-managed environments (Bongers, 1990, 1999). The biology of many of the taxa in cp classes 3–5 is not well known; further study may reveal physiological and behavioral characteristics that warrant some realignment of functional guilds. For example, *Aporcelaimellus* sp. (Om₅) can respond rapidly to unicellular algal blooms (Ettema and Bongers, 1993) and the predatory carnivores *Discolaimus* sp. (Ca₅) and *Clarkus* sp. (Ca₄) rapidly colonized defaunated soil (Shouse and Ferris, 1999; Yeates and van der Meulen, 1996).

Food webs become *enriched* when disturbance occurs and resources become available due to organism mortality, turnover, or favorable shifts in the environ-

ment (Odum, 1985). There is a flush of microbial activity and bacterial-feeding enrichment opportunists are enhanced. The Ba₁ guild includes the Rhabditiidae, Panagrolaimidae and Diplogasteridae. Many of its representatives survive periods of resource limitation in a metabolically-reduced *dauerlarva* alternative life stage (Table 2). Increased abundance of the Fu₂ guild may occur when complex organic material becomes available in the soil, either through natural or anthropogenic processes, or when fungal activity is enhanced under conditions less favorable for bacterial decomposition (Chen and Ferris, 2000). Nematodes in enrichment-indicating guilds often have phoretic relationships with insects, which enhances their invasive potential into newly enriched environments (Bongers, 1990, 1999; Bongers and Ferris, 1999). Of course, nematodes in the Ba₂ guild also increase with enrichment, but at a much slower rate than the Ba₁ guild (Ferris et al., 1996a).

The nematode guilds indicative of the designated food web conditions do not represent succession in the sense that one group is replaced by another as complexity of the food web increases. In many cases, they utilize different food resources, which become available as species richness increases. At each level of food web complexity, the nematode guilds representing lower complexity are also present, albeit proportionally less dominant, interacting at different nodes in the web.

In the reversal of complexity that occurs when a structured food web is subjected to environmental stress or disturbance, the cp-5 and cp-4 guilds, and all they represent through linkages in the food web, are most susceptible. They are followed by the cp-3 guilds. Ultimately, all that may remain are the cp-2 guilds and *dauerlarvae* stages of the Ba₁ guild. In many cases, the disturbance will result in enrichment, so there may be a period of resurgence of Ba₁ activity until the enrichment is depleted (Bongers and Bongers, 1998; Odum, 1985).

Herbivorous nematode families can also be arranged on the cp scale based on life history characteristics; they constitute guilds Pl₂ to Pl₅. Due to host-range specificities of these nematodes, and their response to the objective of maximized primary production in many managed systems, they may require separate analysis as indicators of environmental perturbation and the condition of the soil food web (Bongers, 1990;

Bongers and Korthals, 1995; Bongers et al., 1997; Yeates, 1994).

2.3. Indicator guild weightings

To develop a planar representation of food web condition, functional guilds of a nematode fauna are ordinated along a structure and an enrichment trajectory. Both trajectories have cp-2 guilds (indicators of basal conditions) as their origin (Fig. 1). The enrichment trajectory, calculated as the enrichment index (EI), is based on the expected responsiveness of the opportunistic non-herbivorous guilds (Ba_1 and Fu_2) to food resource enrichment. The structure trajectory, calculated as the structure index (SI), represents an aggregate of longevity, body size and disruption-sensitivity of functional guilds as captured in the cp classification of taxa (Table 2) (Bongers, 1990).

Distances along the structure trajectory are weighted according to the complexities of the food web indicated by the incumbent guilds. The enrichment trajectory is an indicator of the level of primary enrichment of the food web; that is, it indicates the abundance and activity of primary detrital consumers. A food web characterized at the proximal end of the structure trajectory would be considered basal and may indicate a stressed environment; one at the distal end would be considered structured and indicate a stable environment. Indication of environmental enrichment is independent of the food web position along the structure trajectory.

The indicator importance of the presence and abundance of different guilds varies with food web complexity. In structured food webs, the presence of cp-2

guilds is relatively unimportant since they are present in all food webs. However, the presence of Ca_5 and Om_5 guilds is a very important indicator since those nematodes are usually not found unless the environment is undisturbed. Consequently, we propose an indicator weighting system to reflect the importance of the presence of various guilds along the two trajectories. The structure weightings of guilds reflect the postulated degree of trophic connectance in food webs of increasing complexity as the system matures, or progressive food web simplicity as the system degrades.

The structure weighting system is loosely rooted in the hypothesis of constant connectance in community food webs. That hypothesis asserts that the number of trophic links (l), increases as a constant fraction of the square of the number of species (s), that is, $l = \alpha s^2$, where $\alpha < 0.5$ (Cohen, 1989; Martinez, 1992). We can only estimate the progression of numbers of nematode species in food webs of increasing complexity; at best, information is available only at the genus level and often only at the family level. To estimate relative taxon richness from available data (Table 3), we omit the herbivores (Bongers, 1990) and recognize that food webs of higher complexity contain representatives of food webs of lower complexity (Bongers and Bongers, 1998). In the absence of firmer data, we suggest that the relationship between relative taxonomic richness and food web complexity is roughly linear and increases by 0.5 with each increment in cp class number (n) along the structure trajectory. Relative taxonomic richness in the most speciose structured food webs, at the level of resolution of these data, is 2.5 times greater than that in basal food webs, so in structured food webs, $s^2 = 6.25$.

Table 3
Nematode taxonomic richness in food webs of differing complexity and calculated relative richness along the structure trajectory

Study	Food web condition			
	Basal (1) (cp-2)	Maturing (2) (\sum cp-2, 3)	Stable (3) (\sum cp-2–4)	Structured (4) (\sum cp-2–5)
Bongers and Bongers (1998)	13	21	26	29
McSorley (1997)	13	21	28	29
Yeates and van der Meulen (1996)	15	22	32	38
Ferris (farming systems, unpublished)	16	23	27	31
Ferris (prune orchards, unpublished)	11	20	24	26
De Goede and Bongers (1998b)	30	48	71	81
Relative richness: structure trajectory	1.0	1.5	2.0	2.5

For parallelism with the linear cp scale, we arbitrarily elect a maximum weighting (relative number of links in the food web) of 5.0, which requires α to be 0.8. So, the weighting of guilds along the structure trajectory is calculated as $0.8 \times (0.5(n + 1))^2$ (Fig. 1). As further data become available a possible refinement would be to provide differential weightings to the indicator value of functional guilds within each cp class.

The enrichment trajectory weighting system reflects responsiveness to increase in available resources. It is applied to the guilds that are the primary opportunistic indicators of environmental enrichment: the Ba₁ bacterial-feeders and the Fu₂ fungal-feeders. Using, as a reference, the fecundity and life-course characteristics of the Ba₂ guild, with a weighting of 0.8 (Fig. 1), the Ba₁ guild is more fecund and has a shorter life course. Under available resource conditions, the population increase rate is about four times as great as that of the Ba₂ guild (Ferris et al., 1996a,b). Consequently, they are assigned a weighting of 3.2. Presence of the Fu₂ guild, although also an indicator of basal conditions, suggests that fungal hyphae are being supported by an organic resource, consequently, it is included as an indicator of enrichment. The Fu₂ guild has similar reproductive potential to the Ba₂ guild, so it is weighted 0.8 (Chen and Ferris, 2000; Ferris et al., 1996a,b) (Fig. 1). As with the structure trajectory weightings, further research may suggest differential weighting among the guilds of enrichment opportunists.

Additional support for the weighting of guilds along the enrichment and structure trajectories is provided by correlations of the weights with individual nematode biomass. The correlation between average guild biomass and the structure trajectory weight series, based on number of food web links, yields $r^2 = 0.97$; that between average guild biomass and the enrichment trajectory weight series, based on reproductive potential, yields $r^2 = 0.90$. Using data from Bongers (1994), the relative average biomass of nematodes in the Ba₁ guild is 5.6 times that in the Ba₂ guild while the difference in proposed weights between the guilds is four-fold. Thus, the weighting system effectively integrates nutrient transfer during the life course, food availability, organism longevity, food web complexity, and individual biomass.

3. Applications in food web analysis

3.1. The faunal profile

A graphic representation of the “basal”, “structure” and “enrichment” condition of the soil food web, the faunal profile (Fig. 2A and B), is based on the relative weighted abundance of nematode guilds (Fig. 1). An earlier attempt at diagramming the nematode fauna was the cp triangle (De Goede et al., 1993) which depicts the proportional representation of unweighted cp-1, cp-2 and cp-3–5 groups (Fig. 2C). Disadvantages of that system were that the unweighted data did not provide satisfactory resolution to changes in the fauna, and that positions along the enrichment and structure axes were not independent. That is, an increase in enrichment opportunists in response to resource increase resulted in an apparent proportional decrease in the structure of the system. In the faunal profile, the enrichment and structure trajectories are calculated independently from the weighted abundance of nematodes in guilds representing basal (*b*), enrichment (*e*) and structure (*s*) food web components (Fig. 1). For example, the *b* component is calculated as $\sum k_b n_b$, where k_b are the weightings assigned to guilds that indicate basal characteristics of the food web (Ba₂, Fu₂) and n_b are the abundances of nematodes in those guilds. The *e* and *s* components are calculated similarly, using those guilds indicating enrichment (Ba₁, Fu₂) and structure (Ba₃–Ba₅, Fu₃–Fu₅, Om₃–Om₅, Ca₂–Ca₅), respectively. The EI provides location of the food web along the enrichment trajectory and is calculated as $100 \times (e/(e + b))$. Similarly, the SI provides location of the food web along the structure trajectory and is calculated as $100 \times (s/(s + b))$ (Fig. 1).

The faunal profile is constructed to indicate whether the soil community is basal (and inferred stressed), enriched, or structured and stable (e.g. Figs. 2A and B and 3). The weighting system allows separation of the condition of food webs at different sites or at different times, based on shifts in presence and abundance of nematode taxa, with greater resolution than through the use of unweighted cp triangles (compare Fig. 2B and C). The greater weight assigned to Ba₁ opportunists (which may represent <20% of nematode abundance even under enriched conditions) than to stress-surviving bacterial feeders (Ba₂) enhances sensitivity for detection of enrichment (e.g. Fig. 3).

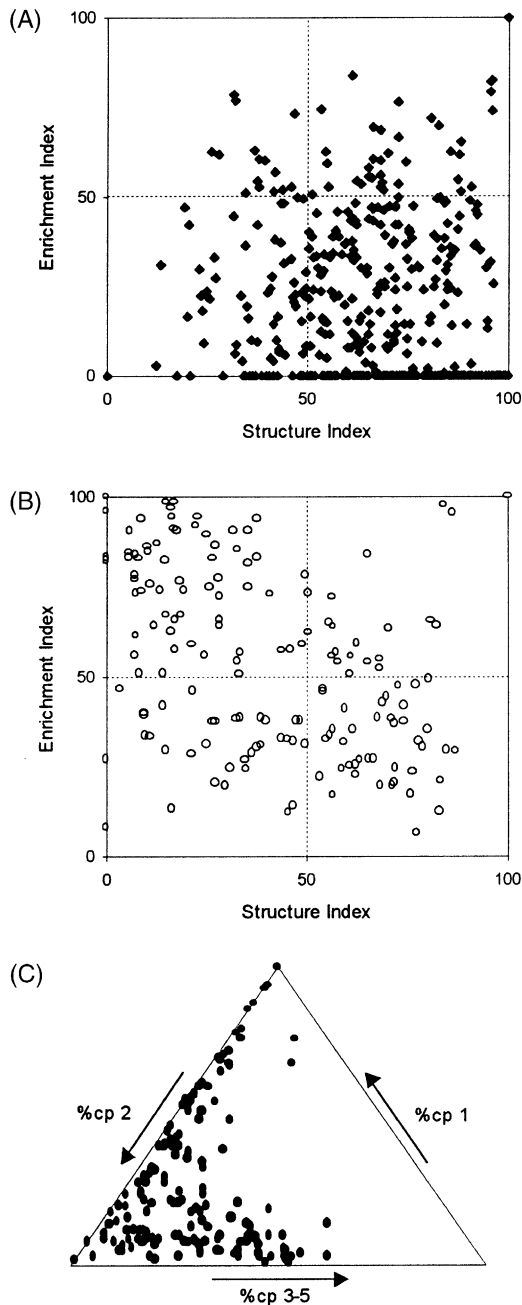


Fig. 2. Faunal profiles representing the structure and enrichment conditions of the soil food web for (A) natural undisturbed grasslands and (B) managed agricultural pastures throughout Europe (data from De Goede and Bongers, 1998a). The data for managed agricultural pastures are also plotted as (C), a cp triangle with unweighted proportional representation of cp-1, cp-2 and cp-3–5 groups of the nematode fauna (De Goede et al., 1993).

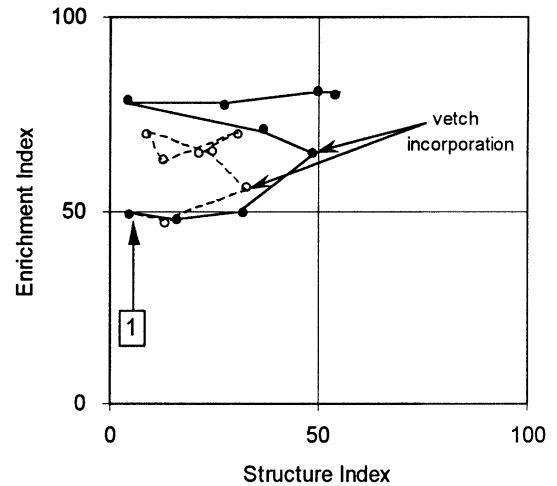


Fig. 3. Temporal progression of changes in the soil food web indicated by nematode faunal analysis in field plots receiving fall irrigation, a fall/winter cover crop, and spring-incorporation of the cover crop. Marker 1 indicates faunal structure before disturbance in August of year 1. The progression of changes in the fauna during the subsequent year is indicated in plots that were irrigated and were planted with a cover crop during the fall (solid markers) or were not irrigated and had no cover crop (open markers). Equal amounts of organic material (vetch) were incorporated into plots of both treatments in April. The final marker in each series indicates the final state of the nematode fauna at the final sampling in August of year 2. Data from Ferris (unpublished).

As a working and evolving model, we characterize soil food web condition (Table 4) based on the location of nematode faunal composition in the faunal profile (e.g. Fig. 2). Initially, the characterizations are somewhat subjective, integrating the authors' experience and interpretation of conventional wisdom and published information. With time and experience, we anticipate that they will become fine-tuned. From personal observations and analyses of published faunal structures, we propose the "usual" conditions for soil food webs in various natural and disturbed systems as a basis for faunal profile interpretation (Table 5).

3.2. Higher resolution diagnostics

Decomposition of organic matter may proceed through different channels in the soil food web. At one extreme, materials of high cellulose and lignin content and high C:N ratio are decomposed through fungal-dominated pathways; at the other extreme,

Table 4

Inferred condition of the soil food web and its environment based on weighted nematode faunal analysis^a

General diagnosis	Quadrat A	Quadrat B	Quadrat C	Quadrat D
Disturbance	High	Low to moderate	Undisturbed	Stressed
Enrichment	N-enriched	N-enriched	Moderate	Depleted
Decomposition channels	Bacterial	Balanced	Fungal	Fungal
C:N ratio	Low	Low	Moderate to high	High
Food web condition	Disturbed	Maturing	Structured	Degraded

^a Quadrats refer to faunal ordination in the faunal profile (Fig. 1).

moist, N-enrich tissues are decomposed through bacterial-dominated pathways (Wardle and Yeates, 1993). Where N is a constraining factor in primary production, it may be important to determine the level at which bacterial-dominated channels are functioning. Where N is in excess, it may be possible to enhance C levels in soil to promote immobilization. In perennial production systems, or natural systems, high C:N ratio of the organic material in soil may be necessary for long-term sustained production. In both cases, decomposition channels may be fungal-mediated. Nematode faunal analysis is readily applied to such higher resolution food web diagnostics.

The ratio of fungal- to bacterial-feeding nematodes has been proposed and used as an indicator of de-

composition pathways (e.g. Freckman and Ettema, 1993; Neher and Campbell, 1994; Sohlenius and Sandor, 1987; Todd, 1996; Twinn, 1974). We improve the resolution of this useful index by integrating the functional guild classification of the taxa. The three most abundant families of fungal-grazing nematodes are in the Fu₂ guild. Like taxa in the Ba₁ guild, several genera of the Fu₂ guild may be transported by insects (Maggenti, 1981). These cp-2 nematodes have relatively short generation times, on the order of 2–3 weeks (Chen and Ferris, 2000), have anhydrobiotic survival capabilities, and are tolerant of extreme conditions. Their survival capabilities allow them to succeed in basal systems where their food resources are available because fungal decomposition of organic matter often predominates (e.g. Hendrix et al., 1986; Jordan et al., 1995; Moore, 1994). Nematodes in the Fu₂ guild also are abundant under more stable environmental conditions such as woodlands and pastures where their food is abundant (e.g. Griffiths et al., 1997). The bacterial-feeding guild that characterizes basal food webs (Ba₂) are also present under all soil environmental conditions. Thus, they are not particularly useful as indicators of the level of bacterial decomposition. However, the enrichment opportunist Ba₁ guild are excellent indicators of bacterial response to low C:N ratio organic inputs and eutrophic conditions (Bongers and Bongers, 1998).

The percentage of the opportunistic nematode grazers on fungi and bacteria (Fu₂ and Ba₁), weighted by their fecundity and life course characteristics, that is represented by Fu₂, provides an interesting index of the nature of decomposition channels through the soil food web. We propose a channel index (CI), $100 \times (0.8Fu_2 / (3.2Ba_1 + 0.8Fu_2))$, where the coefficients are the k_e enrichment weightings for the respective guilds (Fig. 1).

Table 5

Guidelines for specific diagnostics and expected condition of soil food webs in different primary production systems^a

Primary production system	Quadrat	Normal food web condition
Grassland and pasture		
Natural	C	Structured
Managed	A–B	Disturbed–structured
Forest and woodland		
Natural	C	Structured–stable
Managed	C	Structured
Annual crop agriculture		
Conventional	D–A–B	Degraded–disturbed–structured
Low-input	B	Structured
Organic	A–B	Disturbed–structured
Perennial crop agriculture		
Conventional	B–C	Structured–stable
Low-input	C	Stable
Organic	B–C	Structured–stable

^a Quadrats refer to faunal ordination in the faunal profile (Fig. 1).

The EI assesses food web response to available resources and the CI indicates the predominant decomposition pathways. The two indices, in combination, provide a powerful basis for assessing soil fertility levels, nutrient availability, nutrient leaching potential, and necessary adjustments of C or N to alter these conditions. They have the appealing feature that they do not require total faunal analysis or identification of nematodes in all functional guilds. The indices are based solely on the abundance of the Ba₁ guild (primarily Rhabditidae, Panagrolaimidae and Diplogasteridae), the Fu₂ guild (primarily Aphelenchidae, Aphelenchoididae and Anguinidae) and the Ba₂ guild (primarily Cephalobidae).

The SI can also be used independently of the faunal profile to represent time course progressions in the structure of the soil food web in response to disturbance and during remediation.

4. Results and discussion

Ecological weighting of indicator species is commonly used in freshwater biology but has seldom been applied in terrestrial ecology. Exceptions are the MI for nematodes (Bongers, 1990) and the weighted coenotic index (WCI) developed with testate and ciliate protozoa but applicable to other potential indicator groups (Wodarz et al., 1992). The WCI collapses an enormous amount of both community and species level information, including species richness, dominance, abundance and ecological weightings of individual species into a single value. However, in both these indices, and in others, the integration of information into a single value masks the signals available in the component proportions of the community.

Like the WCI, the MI is a weighted index; the weights are a linear progression, from 1 to 5, with increment of the cp classes of the nematode taxa. It has long been recognized that the presence in the soil of nematode guilds of successively higher cp classes does not represent unit increases in informational importance (Bongers and Ferris, 1999). The weights were not applied in cp triangles of nematode faunae (Fig. 2C) (Bongers et al., 1995; De Goede et al., 1993; Ettema and Bongers, 1993). For food web diagnostic purposes, we have used a weighting system based on the structure and enrichment in the food web that is

represented by the presence and abundance of different functional guilds. Rather than a linear series, the weights reflect an exponential increase in species linkages along one trajectory and in reproductive potential along the other.

Nematode faunal analysis of irrigated agricultural field plots demonstrates an annual progression of changes in the soil food web (Fig. 3). The data are from an experiment to generate an abundance of bacterial-feeding nematodes in the spring by enhancing soil food web activity in September and October, prior to the winter months (Ferris et al., 1998). Marker 1 indicates nematode faunal analysis in August, when the soil was very dry, prior to management. A progression of changes in the nematode fauna occurred in plots that either remain dry (open markers) or were managed (received irrigation and a leguminous cover crop — solid markers). In the spring the vegetation was removed from the managed plots, an equivalent amount of green organic material (vetch) was incorporated into all plots, and 2 weeks later tomatoes were planted. Increase in enrichment opportunists in the nematode fauna of the managed plots indicated response of the food web. That response was reflected by increase in available mineral N and increased crop yield. The faunal structure in both treatments stabilized in the mid- to late-summer but indicated greater structure in the managed plots than in the dry plots.

4.1. Representation of food web diagnostics

Since it may be cumbersome to develop a faunal profile for every analysis, a useful alternative is to present the EI and SI for each web as a bar chart or table. The quadrat of the faunal profile can be indicated above each bar (Fig. 4).

Faunal analysis in the late summer suggests a more structured, and perhaps less active, food web in agricultural field plots under conventional than organic management criteria (Fig. 4). However, all components of the food web are well-represented under both management systems, consistent with the conclusion by Jaffee et al. (1998) of similarity between the systems in this experiment. When the same soils were supplied with organic matter under standardized conditions, microbial activity and decomposition rates in the conventional soil lagged only slightly behind those in the organic soil and, within a week, activity

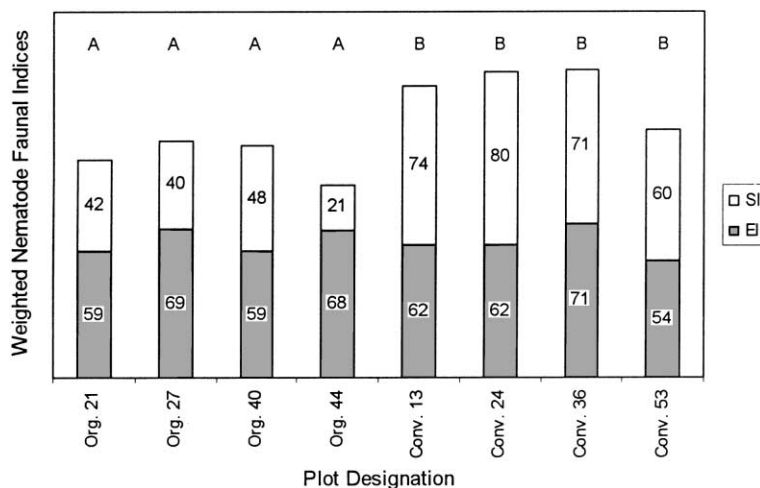


Fig. 4. Enrichment indices (EI) and structure indices (SI) for field plots in which beans were grown under organic (plots 21, 27, 40 and 44) or conventional (plots 13, 24, 36 and 53) production practices. Plots were sampled at harvest of the bean crop in August. Food web diagnostic quadrats (see Fig. 1) are indicated above each bar. Data from Jaffee et al. (1998).

levels in the two were indistinguishable (Gunapala et al., 1998).

4.2. Applications

High cellulosic and lignified organic matter fuels the soil food webs of grassland and forest systems; their soils often have a high C:N ratio and low pH. They exhibit fungal dominated decomposition pathways. Nematode secondary decomposers in such systems may be predominantly fungal-feeders (Fu₂, Fu₃ and Fu₄). An example is provided by nematode faunal analyses from a comparison of several hundred natural, undisturbed grasslands with managed, disturbed grasslands (De Goede and Bongers, 1998a) (Fig. 2A and B).

The natural grasslands have food webs predominantly in Quadrat C of the faunal profile, indicating structured food webs and relatively low primary productivity. Many of the disturbed grasslands reflect the effect of management. Some appear to be highly disturbed and nutrient enriched so that opportunistic nematodes predominate (Quadrat A). Such effects may result from the application of manures and fertilizers. In some cases, the food webs of the managed grasslands have attained some structure (Quadrat B), while still exhibiting a high level of primary productivity. Other grasslands have Quadrat C food webs similar to

those in the natural grasslands. As a caveat, it should be noted that there may be some temporal effects in these data sets, depending on the sampling strategy. In many systems, soil food web enrichment is characteristic of the microbial activity that occurs in the spring and a maturation occurs by the end of the summer.

In another example, the nematode faunae of paired samples, two sets from pasture and one from forest, were assessed 52 months after the soil in one of each pair had been defaunated with methyl bromide. The food webs of the pasture sites appear to have recovered from the perturbation and regained their structure (Quadrats B and C). Analysis of the forest site, however, suggests that residual differences in enrichment remained between the food webs of the treated (Quadrat B) and untreated (Quadrat C) plots (Table 6, data from Yeates and van der Meulen, 1996).

In our experience so far, food webs from annual cropping systems usually map in the left side of the faunal profile while those from perennial cropping systems and forests usually map on the right, unless stressed or recently enriched.

4.3. Higher resolution food web diagnostics

The degree of fungal participation in the primary decomposition channels of soil food webs is suggested

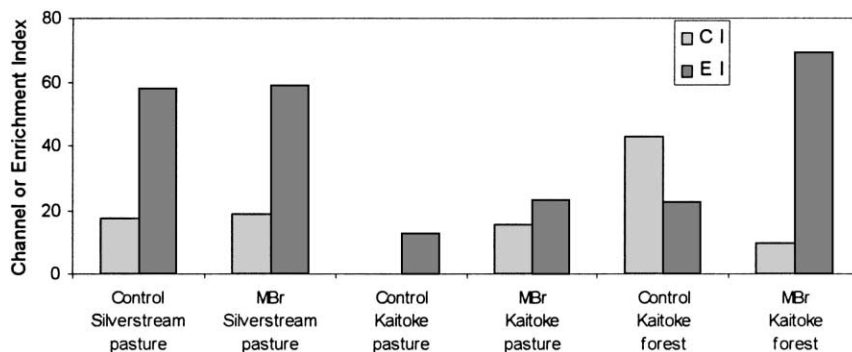


Fig. 5. Decomposition channel indices (CI) and enrichment indices (EI) for forest and pasture food webs 52 months after soil fumigation with methyl bromide. Data from Yeates and van der Meulen (1996).

Table 6

Food web condition analysis of soil 52 months after treatment with methyl bromide, compared to untreated soil, at three sites^a

Location	Treatment	EI	SI	Quadrat ^b
Silverstream pasture	Control	57.9	92.0	B
	Methyl bromide	58.8	94.2	B
Kaitoke pasture	Control	12.3	94.3	C
	Methyl bromide	23.1	90.5	C
Kaitoke forest	Control	22.9	82.0	C
	Methyl bromide	69.1	95.9	B

^a Data are from Yeates and van der Meulen (1996).

^b Quadrats refer to faunal ordination in the faunal profile (Fig. 1). The percentages of the weighted faunal analysis indicating those characteristics of the food web.

by the CI. On a cautionary note, it would be misleading to imply that the CI provides a quantitative measure of the component flow of C and energy through the fungal and bacterial decomposition channels. That degree of calibration of the index has not been conducted and may not be technically possible. However, if the CI is higher at one site than at another, we infer that the proportion of fungal decomposition occurring at the first site is higher than at the second. For example, in the methyl bromide recovery study (Yeates and van der Meulen, 1996), the predominant decomposition pathways of these forest and pasture sites might be expected to be fungal-mediated. However, several of the sites have a low CI and appear to be considerably enriched (high EI), suggesting bacterial decomposition (Fig. 5). In fact, one site (the Kaitoke

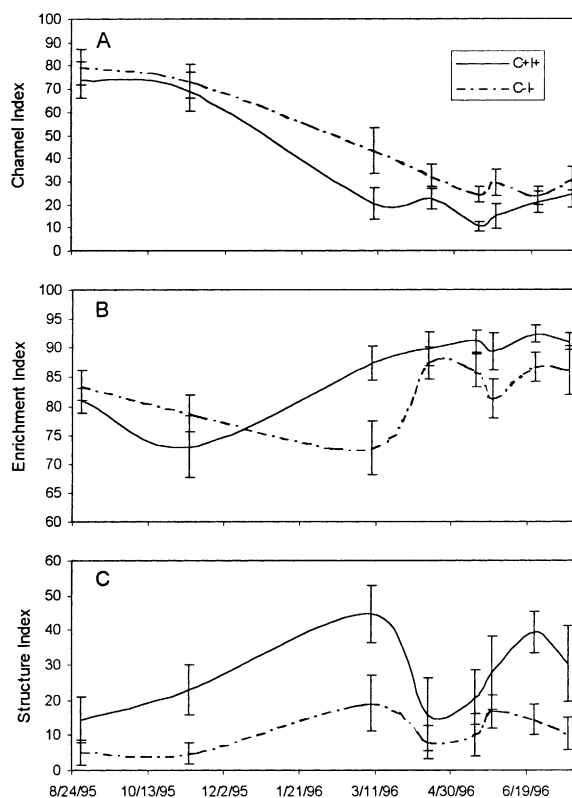


Fig. 6. Higher-resolution diagnostics of data presented in Fig. 3. (A) Fungal proportion of primary decomposition (CI), (B) food web enrichment (EI) and (C) food web structure (SI), in response to environmental management (fall irrigation and fall/winter cover crop, C+I+, or no fall irrigation and cover crop, C-I-). Data from Ferris (unpublished).

pasture control plot) was apparently devoid of cp-2 level fungal-feeders. At the Kaitoke forest site, where faunal analysis indicated that recovery was not complete, the higher EI and lower CI suggest greater bacterial activity in the treated plot than in the control plot.

Greater insight into the dynamic balance between fungal and bacterial decomposition is provided by time course data from a single site in which the nature and abundance of the decomposing material was changing over time. In the agricultural field experiment partially portrayed in Fig. 3, the effect of two soil food web management strategies on the CI, EI and SI is demonstrated (Fig. 6). In the C+I+ treatment, a leguminous cover crop was established in late August and grown, with irrigation, during a climatically dry period between August and November. During this period, soil temperatures are conducive to microbial and nematode activity but lack of moisture is a constraint. In the C–I– treatment, the soil remained dry and there was no cover crop. The following spring equal amounts of organic material were incorporated into each plot

to fuel the food web during the summer growing season.

Bacterial decomposition apparently increased in the C+I+ plots and the CI was lower than in soil of the C–I– plots (Fig. 6A). We infer that any decomposition occurring in the dry C–I– soil was mediated predominantly by fungi. The effect of the manipulations on enrichment of the soil food web is demonstrated by the EI (Fig. 6B). Clearly, the EI was greater during the winter and spring months where, during the previous fall, a carbon source had been provided and favorable conditions created for bacterial decomposition. An important caveat here is that the soils were not severely stressed in either treatment; rather, the food web in some plots was inactivated by a constraining factor (availability of soil moisture). Yields of the subsequent summer crop were greater in treatments that generated high EI in March and April, presumably associated with enhanced levels of N mineralization due to nematode grazing on the microbial biomass (Fig. 7A) (Ferris et al., 1998).

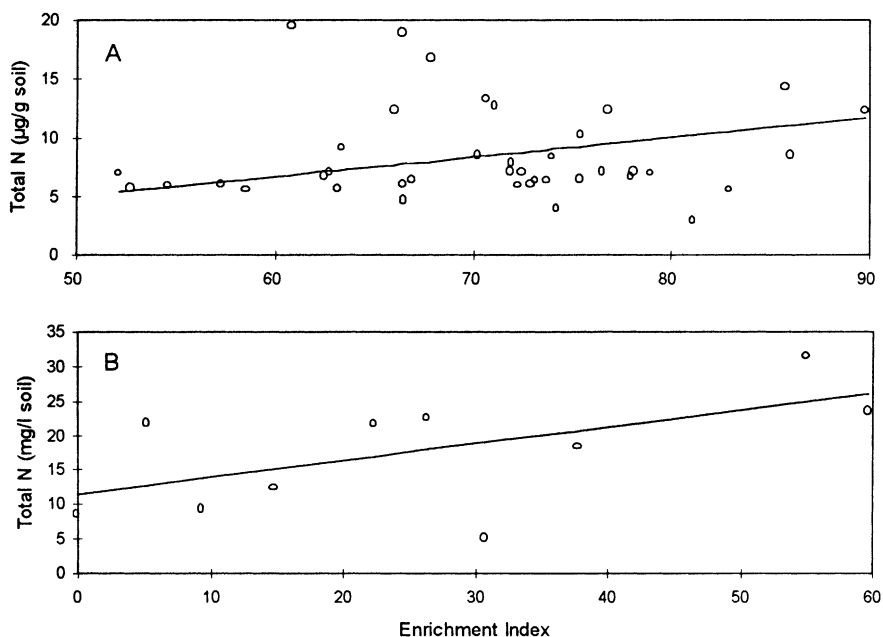


Fig. 7. Relationship between mineral N and EI of the soil food web as indicated by nematode faunal analysis. (A) Low-input agricultural plots in California. Soil mineral N at the end of May in relation to the EI 2 weeks earlier ($P < 0.05$) (data from Ferris (unpublished)). (B) Grasslands in The Netherlands ($P < 0.05$) (data from De Goede and Bongers, 1998b).

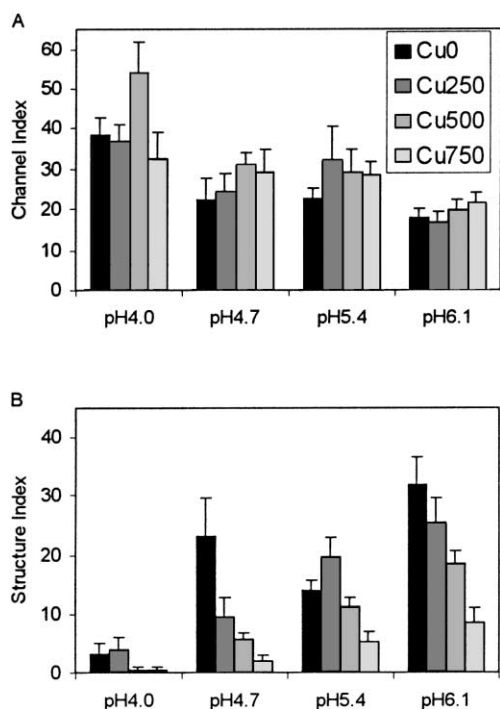


Fig. 8. Decomposition CI for soil food webs 10 years after application of Cu at different pH levels, as indicated by nematode faunal analysis. Data from Korthals et al. (1996b).

Another example of the relationship between available N and the EI of the soil food web, as indicated by nematode faunal analysis, is provided by data from 13 grassland sites (De Goede and Bongers, 1998b) (Fig. 7B). However, high EI values are not necessarily always associated with high levels of available mineralized nutrients. An active food web recently enriched with organic material, depending on the C:N ratio of the input, may immobilize N rather than enhance its availability (Chen and Ferris, 2000).

As evidenced by the data of Korthals et al. (1996b), fungal decomposition channels were apparently more active (higher CI) in soil where the pH was low (Fig. 8A). Ten years after application, there was no detectable effect of residual Cu on the CI at any pH level. However, there was a continued effect on food web structure at low pH, and a strong interaction effect of pH and Cu level on the SI (Fig. 8B). The conclusions regarding residual effects of the treat-

ments are consistent with those of the original data analyses (Korthals et al., 1996b).

Food web structure analysis for two manipulation levels of the irrigation and cover crop experiment indicates greater food web diversity and structure (higher SI) in plots maintained biologically active during the fall and winter months than in unplanted dry soil (Fig. 6C). In early March, cover crop material was incorporated into all plots and the soil was tilled in preparation for a summer tomato crop. The higher SI of the C+I+ plots suggests more linkages in the food web, greater resilience, and greater buffering of population increases in opportunistic guilds. Such buffering may have a regulatory effect on the dynamics of herbivorous species in the system.

5. Summary and conclusion

Nematode faunal analysis provides a powerful tool for diagnosis of the complexity and status of soil food webs (Ritz and Trudgill, 1999; Wardle et al., 1995b). The functional diversity of soil nematodes includes activities at many nodes and at many trophic levels in the web. Consequently, the presence and abundance of specific taxa is an indicator of the complexity of the web at the trophic levels indicated by those taxa. Since related taxa, with similar morphological, anatomical and physiological attributes, have similar feeding habits, useful faunal analyses can be obtained by identification to the family level (Bongers, 1990, 1999; Bongers and Ferris, 1999), which allows separation of taxa into trophic dynamic modules (Pahl-Wostl, 1995) or functional guilds (Bongers and Bongers, 1998).

We have ascribed characteristics of food webs that map into the quadrats graphical representations of the faunal profile. We reiterate that such divisions are approximations, but that they form a basis for interpretation of the likely conditions of food webs and the soil environment in different ecosystems. They are based on the collective experience and observations of many biologists as captured in much of the literature cited. Food webs, at the level of nematode indicators, may not respond instantly to disturbances or enrichment. There may be a lag of 1 to several weeks, determined by the reproductive biology of the organisms, before changes in nematode abundance are

measurable. Further, food webs are dynamic features of the soil environment as suggested by the temporal examples provided in this document (Figs. 3 and 6). It may be unwise to assess and interpret the biological condition of the soil from a sample at a single point in time.

We have suggested and described analyses for higher resolution interpretation of food web and environmental condition based on taxa that are relatively easily identified. These tools are potentially important for soil resource managers, both for diagnostic purposes and as a basis for management decisions.

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We acknowledge and appreciate the vision of researchers who recognizing that their data sets may be invaluable resources for addressing a range of ecological questions, have published nematode faunal analyses in toto. We thank Dr. Gerard Korthals for supplying the complete data set from the pH/Cu study and Bart Verschoor for his insights on the relationship of nematode biomass to the weighting system.

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