

Nematode Indicators of Organic Enrichment

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Abstract: The organisms of the soil food web, dependent on resources from plants or on amendment from other sources, respond characteristically to enrichment of their environment by organic matter. Primary consumers of the incoming substrate, including bacteria, fungi, plant-feeding nematodes, annelids, and some microarthropods, are entry-level indicators of enrichment. However, the quantification of abundance and biomass of this diverse group, as an indicator of resource status, requires a plethora of extraction and assessment techniques. Soluble organic compounds are absorbed by bacteria and fungi, while fungi also degrade more recalcitrant sources. These organisms are potential indicators of the nature of incoming substrate, but current methods of biomass determination do not reliably indicate their community composition. Guilds of nematodes that feed on bacteria (e.g., Rhabditidae, Panagrolaimidae) and fungi (e.g., Aphelenchidae, Aphelenchoididae) are responsive to changes in abundance of their food. Through direct herbivory, plant-feeding nematodes (e.g., many species of Tylenchina) also contribute to food web resources. Thus, analysis of the nematode community of a single sample provides indication of carbon flow through an important herbivore channel and through channels mediated by bacteria and fungi. Some nematode guilds are more responsive than others to resource enrichment. Generally, those bacterivores with short lifecycles and high reproductive potential (e.g., Rhabditidae) most closely mirror the bloom of bacteria or respond most rapidly to active plant growth. The feeding habits of some groups remain unclear. For example, nematodes of the Tylenchidae may constitute 30% or more of the individuals in a soil sample; further study is necessary to determine which resource channels they portray and the appropriate level of taxonomic resolution for this group. A graphic representation of the relative biomass of bacterivorous, fungivorous, and herbivorous nematodes provides a useful tool for assessing the importance of the bacterial, fungal, and plant resource channels in an extant food web.

Key words: enrichment index, enrichment profile, faunal analysis, soil food web, structure index.

The community of soil organisms, also known as the soil food web, is dependent primarily on autotrophic input from plants or on subsidiary input from other sources and responds in characteristic ways to enrichment of its environment by organic matter. Primary consumers of the incoming substrate are the entry-level indicators of enrichment. They include bacteria, fungi, herbivorous nematodes, annelids, and arthropods. Quantification of abundance and biomass of this diverse group of organisms requires a plethora of extraction and assessment techniques. Bacteria, which absorb soluble organic compounds, and fungi, which derive their carbon and energy by degrading more recalcitrant organic sources, are among the most important participants in the initial acquisition of resources by the soil community. Through direct herbivory, plant-feeding nematodes also are important contributors to food web resources. Certain guilds of nematode predators are responsive to changes in the abundance of their bacterial, fungal, or nematode prey. Thus, a single nematode sample provides indication of resource flow through bacterial and fungal channels and through an important herbivore channel. At the proximal end of each channel, the flow of resources is indicated by the abundance and activity of nematodes characteristic of certain functional guilds (Fig. 1). With distal progres-

sion through the channels, the boundaries become less distinct as resources are dissipated among functional guilds of omnivorous nematodes and other organisms that are predators of the nematodes in all channels. Uncertainty regarding the feeding habits of certain nematode groups currently requires discrimination among the guilds selected as indicators.

Some nematodes are more responsive than others to resource enrichment. Generally, those bacterivores with short lifecycles and high reproductive potential most closely mirror the bloom of bacteria. Longer-lived and hardier fungivorous species are indicators of fungal abundance (Bongers, 1990; Ferris et al., 2001). While ambivalent as indicators, nematodes of the Tylenchidae may constitute 30% or more of the individuals in a soil sample. Clearly they are “entry-level” indicators, but in which resource channel do they participate? It is also possible that some soil nematodes are able to feed on, or absorb, soluble organic compounds because viable populations of many bacterivores can be maintained in axenic culture (Sulston and Hodgkin, 1988; De Ley and Mundo-Ocampo, 2004) and some animal parasites absorb hemolymph across the body wall (Munn and Munn, 2002). Further, the feeding apparatus of a few nematode groups are obscure and not clearly adapted to feeding on any organismal or particulate source. In other cases, the cuticle appears quite permeable and will swell in hypotonic solution.

Food webs are enriched when resources become available due to external input, disturbance, organism mortality, turnover, or shifts in the environment (Odum, 1985; Van Veen and Kuikman, 1990). An enrichment pulse is followed by heterotrophic succession, whereby the predominance of organisms changes through time depending on trophic roles, life course dynamics, and prevailing environmental conditions

Received for publication 5 June 2005.

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Symposium paper presented at the 43rd Annual Meeting of the Society of Nematologists, 7–11 August 2004, Estes Park, CO. The studies were supported in part by the Kearney Foundation of Soil Science, California Department of Food and Agriculture's Buy California Initiative and USDA Grant Agreement #02-0765, by California Federal Bay-Delta Program Agreement #ERP-02-P36, and by USDA Integrated Organic Program Grant #2004-05151.

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This paper was edited by G. W. Yeates.



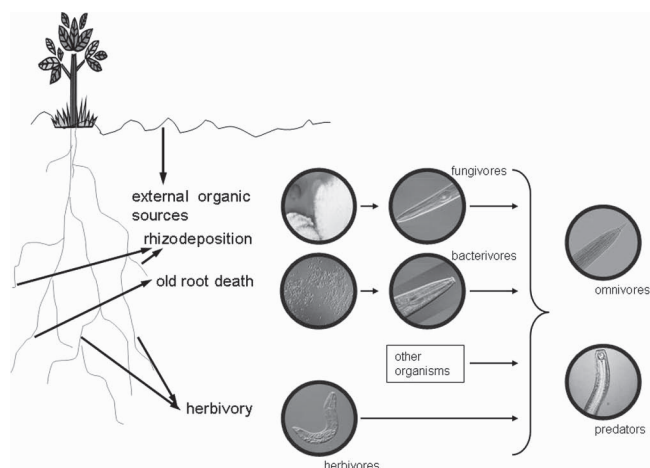


FIG. 1. Nematode indicators of resource flow through carbon channels of the soil food web.

(Sachs, 1950; Sudhaus, 1981; Ferris et al., 1996b; Ferris and Matute, 2003). Changes through time in the abundance and type of organisms in the soil community may be considered structural succession; changes in food web function, not necessarily concurrent with community composition, are considered functional succession. Sustained organic enrichment may halt the succession and maintain a consistent structure among functional guilds of soil organisms. However, in some cases the succession is not mediated by availability of resources but by life history factors, including dispersal opportunities through phoretic associations with emerging insects (Sudhaus et al., 1988). The mass of available C diminishes with each trophic interchange, effectively dictating the abundance and biomass of organisms at each trophic level. Some of the organism responses to enrichment are ephemeral; others, including those of certain guilds of nematodes, are more persistent and can be measured reliably (Ferris et al., 1996b; Bongers and Ferris, 1999).

The nematode guilds most responsive to organic enrichment are the cp-1 nematodes (*sensu* Bongers 1990), which have been termed *enrichment opportunists*. Under conditions conducive to their activity and survival, nematodes other than the enrichment opportunists also respond quite rapidly to organic amendment. Aphelenchid nematodes (cp-2) increase in abundance after enrichment with high C/N organic material, green algal blooms at the soil surface are colonized by small Dorylaimida (Ettema and Bongers, 1993), and organically amended chambers buried in an agricultural soil were colonized by *Discolaimus* sp. (Shouse, 2000). Similarly, the increased supply of resources to the food web through direct herbivory is indicated by increase in the more r -selected plant-feeding nematodes. So, we distinguish between organisms that increase rapidly in number following an enrichment event and those that are already present but are attracted to a new resource; all are indicators, but with differing mechanistic bases. We

consider the term *enrichment indicators* to be more inclusive of all nematodes that respond to organic amendment. The enrichment opportunists are relatively well known and characterized; recognition of the colonizers may be more of a challenge.

In undisturbed food webs, the abundance of higher trophic level organisms, and the number of trophic links among them, is greater than after disturbance (Wardle and Yeates, 1993). For higher trophic levels to be sustained there must be some conservation of resources in the lower trophic levels. A smaller portion of the carbon assimilated by a nematode with a high metabolic rate will be available to predators than that assimilated by a nematode with a low metabolic rate. Reduced resources available to higher trophic levels may decrease predation pressures on opportunistic species at lower trophic levels (Ferris et al., 2001; Berkelmans et al., 2003).

HISTORICAL DEVELOPMENT OF THE CONCEPTS

Örley (1880) provided an ecological classification of nematodes, unencumbered by phylogenetic considerations, by dividing the Nematoda into the Parasita, comprising the parasitic forms; the Rhabditiformae, comprising those living in decomposing organic substances or the surrounding soil; and the Anguillulidae, comprising the remainder of the free-living soil and aquatic nematodes. Potts (1910) noted that the Rhabditiformae (specifically mentioning *Rhabditis* and *Diplogaster*) could be maintained in a flask of bacteria in which other free-living nematodes would soon succumb. He observed that Örley's Rhabditiformae are apparently absent from dry soils and, even in soils rich in humus, are found in quantity only when fresh organic material is introduced. Substrates rich in labile carbon may be deficient in nitrogen or another essential mineral and so favor the fungal rather than the bacterial decomposition channel (Ruess and Ferris, 2004). If the carbon form is not conducive to bacterial decomposition, addition of minerals will increase activity in the fungal channel (Ruess et al., 2002).

Understanding of the rapid response of certain nematodes to organic enrichment progressed through the observations and studies of Schneider (1866), Örley (1880), and Maupas (1899). Metcalf (1903) described the rapid increase of rhabditid nematodes feeding on bacteria in various rotting plant material. Both he and Potts (1910) reported that the Maupas (1899) technique of placing scraps of meat in soil resulted, 5 or 6 d thereafter, in very large numbers of rhabditids and diplogasterids. They noted that before the remains of the meat have disappeared, other species become dominant and replace the enrichment opportunists. Briggs (1946) concluded that any material suitable as a substrate for soil bacteria will result in enrichment of certain nematode species when added to soil. The tech-



nique of enrichment amplification for detection of rhabditid nematodes has continued to be an important tool (Dougherty, 1960; De Ley and Mundo-Ocampo, 2004).

The existence of a life stage of rhabditid nematodes with a cuticle differing from that in other stages was reported by Schneider (1866), who considered this form to be a molting stage but was uncertain of its role. According to Maupas (1899), Pérez (1866) recognized an “encysted” stage in *Rhabditis teres* and indicated that larvae easily encysted at the end of the second stage. Experimentally, Maupas (1899) determined that always the same life stage entered encystment when nutrients were lacking. He showed that emergence from the encysted stage occurred with enrichment and noted that encysted nematodes survive for weeks and are often a dispersal stage. Later, Fuchs (1915), in his description of rhabditids associated with bark beetles, coined the term dauer larva for the persistent or enduring stage of these nematodes. We now know that dauer larva induction in *Caenorhabditis elegans* is mediated by the ratio between a dauer-inducing pheromone, which is produced constantly by the nematode, and the magnitude of a carbohydrate signal from the bacterial prey. The ratio constitutes a net measure of population size in relation to food availability. When the dauer-inducing pheromone is significantly greater than the food signal, dauer formation commences (Riddle, 1988). The term dauer larva is sometimes applied more broadly to recognize persistence of nonfeeding life stages across a broad range of Nematoda (Bird and Opperman, 1998).

To illustrate the opportunistic responses of certain nematode groups, we enriched samples taken from the interface of organic and mineral layers of soil with slices of banana. Abundance of various nematode groups was determined 2 wk after enrichment (Fig. 2). By that time the resource was already depleted, and the enrichment opportunists were beginning to form dauer larvae (Fig. 3). Observations of this type and reports by diverse researchers on the responsiveness of certain nematode groups to organic enrichment led to placement of rhabditid, diplogasterid, and panagrolaimid nematodes in the cp-1 group (Bongers, 1990) as a functional guild of bacterial-feeding enrichment opportunists (Bongers and Bongers, 1998) with a metabolically depressed specialized survival stage.

FUNCTIONAL GUILDS

The functioning of the soil food web depends on its component organisms and the environment in which they exist. Sampling, capture, identification, and assessment may be difficult for some taxa and technologically daunting for a whole fauna. An alternative to complete structural analysis of the food web is provided by assessment of the presence and abundance of indicator guilds. Bailey et al. (2004) adopted the approach of

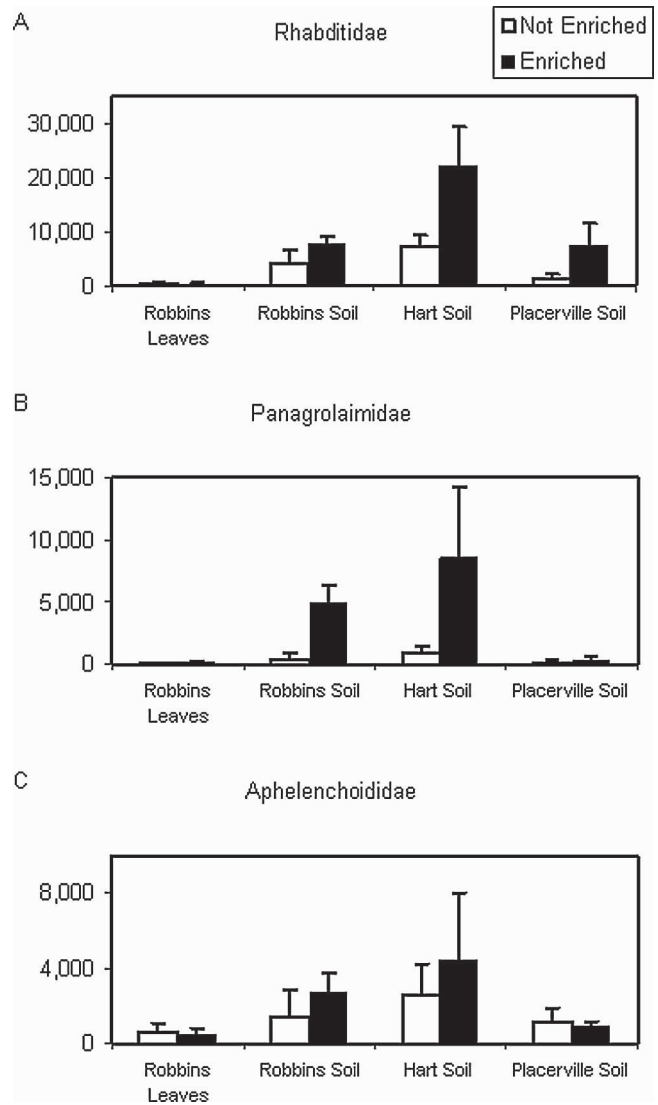


FIG. 2. Response of selected nematode groups to organic enrichment, abundance 2 wk after enrichment with a slice of banana in soil samples maintained moist and at 22°C. Numbers per liter soil. Error bars indicate 1 s.d.

Gitay and Noble (1997) in assigning species to a functional guild if they used the same resources in the same way. We adopt a more restrictive resource-based defini-

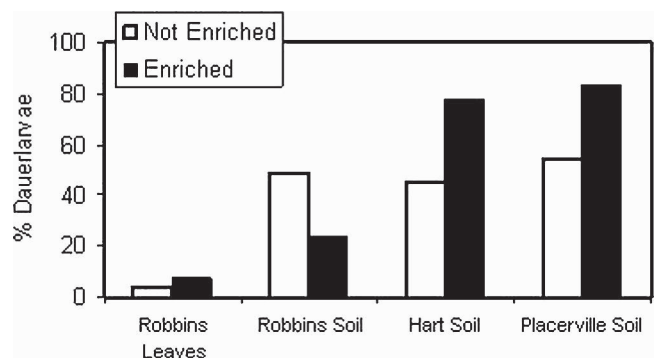


FIG. 3. Response of selected nematode groups to organic enrichment. Proportion of dauer larvae after decline of the organic resource, 2 wk after the beginning of the experiment illustrated in Fig. 2.

TABLE 1. Functional guild classification matrix for soil nematodes. Example taxa, based on current knowledge of life-history characteristics and feeding behavior, are indicated for each guild. (For further detail, see Bongers and Bongers, 1998; Ferris et al., 2001.).

Feeding Habit	Life-history characteristics (Colonizer-persister classification)				
	1	2	3	4	5
Plant-feeding	Pf1	Pf2 Tylenchidae	Pf3 Pratylenchidae	Pf4 Trichodoridae	Pf5 Longidoridae
Hyphal-feeding	Fu1	Fu2 Aphelenchidae	Fu3 Diphtherophoridae	Fu4 Tylencholaimidae	Fu5
Bacterial-feeding	Ba1 Panagrolaimidae	Ba2 Cephalobidae	Ba3 Teratocephalidae	Ba4 Alaimidae	Ba5
Animal-predation	Ca1 some Diplogasteridae	Ca2 Seinuridae	Ca3 some Tripylidae	Ca4 Mononchidae	Ca5 Discolaimidae
Unicellular-feeding	Un1 Monhysteridae	Un2 Microlaimidae	Un3 Achromadoridae	Un4	Un5
Omnivorous	Om1 some Diplogasteridae	Om2	Om3	Om4 Qudsianematidae	Om5 Thornenematidae
Some key features	<i>Enrichment opportunists</i> High fecundity Small eggs Short lifecycle Dauer stage High gonad:body ratio	<i>Basal fauna</i> Small nematodes Anhydrobiosis Lower metabolic activity Feeding adaptations	<i>Rudimentary food web structure</i> Sensitivity to chemical stressors More food web links (predators and omnivores)	<i>Greater food web structure</i> Greater sensitivity to disturbance Larger body size Fewer eggs Longer life-cycle	<i>Highest food web structure</i> Undisturbed conditions Large nematodes Long-lived Narrow ecological amplitude Lowest gonad:body ratio

tion applied to nematodes by Bongers and Bongers (1998) by also requiring that the nematodes assigned to a functional guild have similarities in life-history dynamics, responsiveness to resource enrichment, and sensitivity to disturbance. The cp scaling introduced by Bongers (1990) provides the life-history ordinate for the functional guild matrix of nematodes; the known or inferred feeding habits (around six clearly defined categories per Yeates et al., 1993) provide the abscissa (Table 1). As a caveat we recognize that, as argued by Yeates (2003), there may be enormous diversity in the response to environmental conditions of individual taxa assigned to a functional guild (for examples, see Ferris et al., 1995, 1996a, 1997). Reliability of indices may require species-level resolution of functional guild assignments.

After an enrichment event, panagrolaimids may respond in one environment or localized patch and rhabditids in another (Fig. 2). Both have responded to the resource and are indicative of the enrichment. Soil biotas are not uniformly dispersed in a single homogeneous community; rather, they are in spatially separated patches that differ in resource availability, abiotic influences, species composition, and dynamic synchrony (Fig. 4). The concept of a metacommunity (Wilson, 1992) is useful in considering the movement of predators among patches of prey and in assessing the potential for predator-prey relationships to regulate prey levels. Essentially, the soil food web comprises a series of spatially structured open communities, with migration of organisms among patches and mass-flow processes that constitute ecosystem subsidy of resources across community boundaries. The resource subsidies and organism migrations perhaps stabilize patch dy-

namics and enhance the functional stability of the system (Warren, 1996).

Despite the conceptual appeal of the metacommunity model, it is difficult to observe or monitor the soil community at a patch level appropriate for soil nematodes. A sampling device may pass through a patch, through several patches, or through none. The rationale for assigning nematodes to functional guilds such that the organisms within a guild, based on feeding habit and similarity of biology, might be expected to respond similarly to environmental perturbation has been well developed (Bongers and Bongers, 1998; Bongers and Ferris, 1999). The functional redundancy represented in the enormous taxonomic diversity of nematode faunas creates a high probability that the absence of a guild is a reliable indicator of disturbance

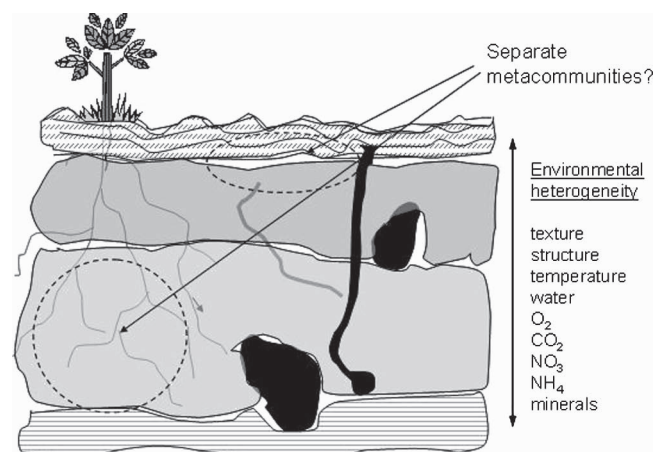


FIG. 4. Resource distribution and structure of the environment contribute to the metacommunity nature of biotic patches in the soil.

and that the presence of a guild is a reliable indicator of lack of perturbation or of recovery from perturbation. In the case of organic enrichment of soil, opportunistic guilds (r -strategists) respond reliably. Considering soil nematode taxa as representatives of functional guilds generates an indicator profile not constrained by population distribution patterns and microenvironment effects. The challenge, we believe, is to improve the resolution of assignment of taxa, or even of regional biotypes of those taxa, to appropriate indicator guilds.

Nematode faunal analysis is evolving as a powerful bioindicator of the soil condition and of structural and functional attributes of the soil food web (Table 1) (Bongers and Ferris, 1999; Neher, 2001), and it will improve with greater resolution (Yeates, 2003). The analyses include recognition of an enrichment trajectory and a structure trajectory. The enrichment trajectory reflects supply-side characteristics of the food web and increase in primary consumption of incoming organic material (Ferris et al., 2001). As microbial blooms fade, enrichment opportunist microbivores are replaced by general opportunists with specialized morphological, physiological, and behavioral adaptations for more deliberate feeding on less available resources. Fungal energy channels predominate when the organic material is of high C/N ratio; bacterial decomposition channels predominate when the organic material is of low C/N ratio (Hendrix et al., 1986; Moore, 1994; Ruess, 2003; Ruess and Ferris, 2004).

Because large amounts of the carbon and energy assimilated by each trophic guild are dissipated through metabolic activity (Moore, 1994; De Ruiter et al., 1998), 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” 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 (Strong, 1992). In many 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, each guild has more than one food source and 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 (Yeates and Wardle, 1996).

THE ENRICHMENT PROFILE

In relatively closed systems, e.g., forests and natural environments, carbon and energy are internally gener-

ated by plant autotrophs and supplied to the soil through litter, water, wind, and atmospheric deposition, rhizodeposition, and direct herbivory (Fig. 5A). In more managed systems, besides the input from autotrophs and the atmospheric sources, carbon is also supplied by organic subsidies delivered by animals and farmers. The soil and its food web become enriched by substrates that include materials of greater complexity than the low C/N ratio putrefying animal and vegetable matter used in the experiments of Maupas (1899), Metcalf (1903), Potts (1910), and Briggs (1946).

A graphic representation of entry-level nematode indicators may be a useful tool for assessing the importance of the bacterial, fungal, and plant resource channels in an extant food web; however, the exercise also challenges the knowledge base with regard to feeding habits and nematode biomass. Here we introduce, in concept, the “Enrichment Profile” as a means of visualizing the amount of carbon and the relative metabolic activity in each channel (Fig. 5B). The profile is based on the proportional contribution to total nematode biomass of nematodes in the three channels. At present, due to the data gaps in knowledge of feeding habits, the profile must be considered conceptual and a demonstration of potential.

If the Enrichment Profile is implemented with current data, the functional guild structures should include only taxa with a high degree of feeding-habit certainty. So, for example, at this time we can with some certainty assert the bacterial-feeding habits of families in the Rhabditida, the fungal-feeding habits of many families in the Aphelenchina, and the plant-feeding habits of most families, other than the Tylenchidae, in the Tylenchina. Although restriction of the analyses to these groups may result in under-representation of one or more of the resource-flow channels, the bias may be relatively consistent across all analyses. The Enrichment Profile provides a tool for management of the organismal guilds of the soil food web to achieve a desired functional outcome.

Benefits of activity in the fast-cycle bacterial channel (Table 2) to the autotrophic producer include amplification of rates of mineralization by bacterivorous nematodes and protozoa. A potential downside of the fast cycle is that the food web may be bottom heavy with organisms that have high rates of metabolic and respiratory activity so that relatively small amounts of carbon transfer to higher trophic levels. In that case, the system may support only low abundance of predators, and biotic regulation of herbivorous opportunists may be limited. For a food web to develop greater levels of connection, carbon must be conserved through multiple trophic transfers. At the same time, the environment must be conducive to survival and increase of the higher-order trophic levels. When the slow-cycle fungal channel predominates, respiratory loss of carbon and metabolic rates are slower, and there is opportunity for

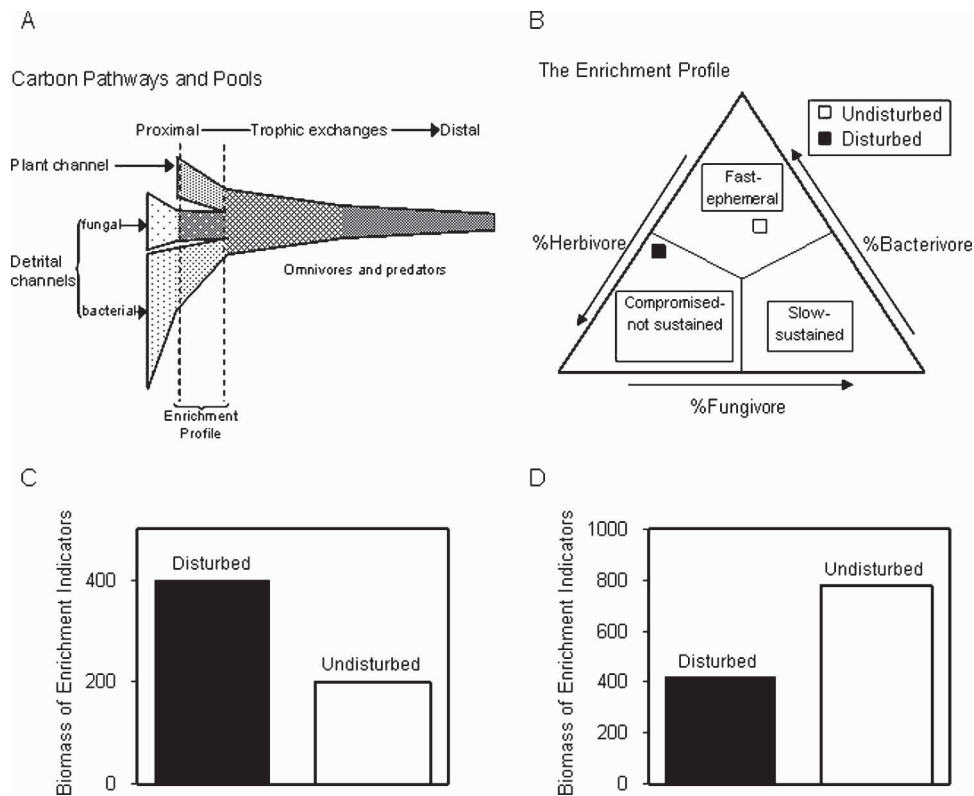


FIG. 5. (A) Sources of carbon and channels of carbon flow through the soil food web indicating the portion of the nematode fauna used for enrichment profile analysis. (B) The enrichment profile and interpretation of the nature of food web enrichment. C-D) Biomass of enrichment indicators where enrichment of the undisturbed soil is advised (C) and for a productive state of the undisturbed soil (D).

greater transfer of resources to higher trophic levels, although such transfer will probably occur over a longer time frame. When coupled with decrease in environmental perturbation, the subsequent enhancement of predator guilds should increase regulatory pressure on opportunistic guilds, including opportunistic and plant-damaging herbivores.

Most soil microbial communities are carbon-limited (Alden et al., 2001), so addition of high C/N organic matter can result in immobilization of nutrients. In that case, the system will often respond to addition of fertilizer (e.g., Ruess et al., 2002). In a managed system, the challenge is to select enrichment material of appropriate constitution so that carbon is conserved for higher

trophic levels while maintaining nutrient sufficiency that does not constrain plant growth. The Enrichment Profile provides a tool for monitoring the structure and function of the soil food web in response to the frequency of organic input and the C/N ratio of the substrate relative to a hypothetical target zone (Fig. 5B).

While the Enrichment Profile provides analysis of the proportional biomass in each channel, it does not indicate the absolute activity of the channel. It is instructive to consider the Enrichment Profile in conjunction with the total biomass of bacterivorous, fungivorous, and herbivorous nematodes. In hypothetical examples provided, the biomass of enrichment indicators in an undisturbed site is lower than that in a disturbed site

TABLE 2. General characteristics of major carbon and energy channels in soil food webs (Ruess and Ferris, 2004).

	Channel designation		
	Bacterial	Plant	Fungal
Turnover rate	Fast	Intermediate	Slow
Environment	Moist	Moist-Dry	Dry-Moist
Substrate C/N	Low	Low	Medium to high
Ecological considerations	Successional shifts unless resources resupplied	Damage to producer	Food web structure
Functional characteristics	Mineralization-immobilization cycles Carbon depletion rate high.	Immobilization and mineralization Carbon depletion rate intermediate	High C levels may result in immobilization of nutrients Slow mineralization and carbon depletion rates.
Predators	Protozoa and nematodes	Fungi and nematodes	Microarthropods and nematodes

(Fig. 5C), suggesting that addition of organic matter or alleviation of nutrient constraints may be necessary to enhance productivity in undisturbed soil (Fig. 5D).

ORGANIC ENRICHMENT EFFECTS: EXPERIMENT AND OBSERVATION

The organisms of the soil food web are dependent on resources from plants or amendment from other sources. A tempting hypothesis is that elevated atmospheric CO₂ will result in greater root exudation, which will be reflected in the size and activity of the soil food web. Changes in litter quality may result in under-elevated CO₂ (Bazzaz, 1990; Cotrufo et al., 1998), with consequent effects on structure and activity of microbial communities (Klironomos et al., 1997; Marilley et al., 1999; Islam et al., 2000). However, changes in rhizosphere microbial communities can be subtle or undetectable. At the Facilitated Ambient CO₂ Experiment (FACE) in Switzerland, there was no change in the total heterotrophic and autotrophic rhizosphere bacteria, but there was a change in the distribution of genotypes within soil populations of *Rhizobium leguminosarum* (Montealegre et al., 2000). Nematode Enrichment Profiles from that site (Ferris and Moore, unpub.) and from another FACE site (Neher et al., 2004) did not detect enrichment effects from elevated CO₂ (Fig. 6).

Direct application of organic matter and mineral fertilizers to the soil clearly affects the abundance and activity of soil organisms. For example, Enrichment Profile analyses of nematode data from grasslands managed under conventional or organic protocols (Yeates and Cook, 1998) strongly suggest greater productivity of the conventional system and minimal effect of the conventional practices on food web structure (Fig. 7A). In those grasslands, there was proportionally greater herbivory in the organic soil, and the conventional soil was more bacterial (Fig. 7B). The total biomass of indicators of activity in the bacterivore, herbivore, and fungivore channels was greater in the conventional soil (Fig. 7C). The data suggest a speculative and untested

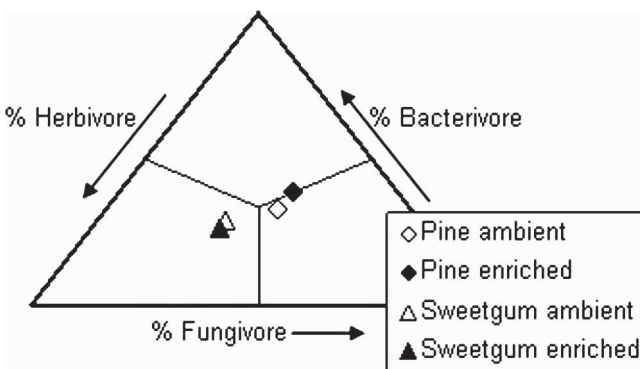


FIG. 6. Lack of effect of atmospheric CO₂ enrichment in relation to ambient CO₂ on the soil food web of pine and sweetgum plantations as indicated by nematode faunal analysis (Data from Neher et al., 2004).

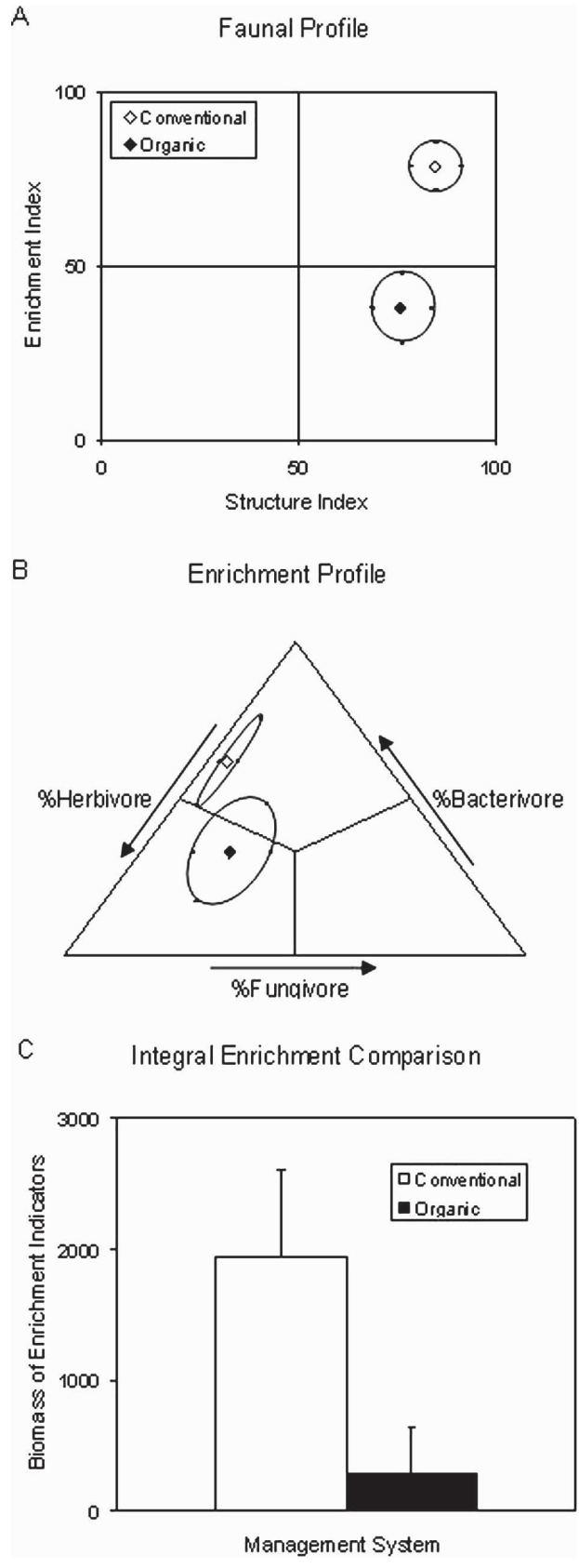


FIG. 7. Effects of two management systems on the faunal and enrichment profiles of the soil food web in a grassland. Data points are means of 10 replicate samples and are surrounded by one standard deviation (Data from Yeates and Cook, 1998).

management interpretation that mineral fertilizer applications in the conventional pasture stimulated the bacterial channel at the expense of the fungal channel. Reduction of fertilizer inputs would proportionally enhance fungal activity and, with the lower respiratory loss of carbon, increase regulation of herbivore species. Although fungivore activity is greater in the organic soil, the system is probably limited by mineral nutrient availability. Application of an acceptable source of mineral nutrients or mineral-rich composts would probably enhance productivity of that system.

DISCUSSION AND CONCLUSIONS

A general concept is emerging of the effects on the soil food web of amendment with organic matter of different C/N ratio on the rate of decline in availability of resources to higher trophic levels (Fig. 8). The resultant changes are reflected in food web enrichment, structure indices, and other community metrics. The impact of organic amendment on the food web is complicated by spatial factors. Physical incorporation of organic material into the soil profile delivers the material to its consumers but is differentially deleterious to their predators. On the other hand, mulching organic material on the soil surface without incorporation preserves the structure of the food web but may not enhance its

enrichment except for in a limited zone at the organic-mineral interface of the soil profile. Herein lies the dilemma of reduced-tillage production systems, the problem of nutrient availability in the root zone. Recent cultivars of most crop species have been selected using conventional practices, including incorporation of mineral fertilizers, and they have evolved root morphology and physiology appropriate to those practices. For organically driven reduced-tillage systems, it may be necessary to select cultivars with root systems that explore resources at the soil surface and that have a greater relative investment in root biomass. Delivery of carbon and nutrients through the profile of a physically and chemically undisturbed soil system will be enhanced by hyphal networks and organisms that burrow; however, such transport systems will take time to develop.

The nature of the organic substrate changes with time. Readily decomposed components are utilized rapidly by bacteria, and more recalcitrant components are resources for fungi. A succession of soil organisms mirrors the changes in the resource (Ferris and Matute, 2003; Ruess, 2003; Ruess and Ferris, 2004). As that organismal succession occurs, there is a concomitant change in food web function, and rates of decomposition and mineralization decline. Consequently, maintenance of a highly active soil food web that provides the desired functions for an agricultural production system may require repeated input of organic material designed to engineer the desired state of food web structure and function (Fig. 8).

There are many reasons that nematodes are excellent indicators of food web and environmental condition (Bongers and Ferris, 1999). Among them are the natural abundance and diversity of nematodes that potentially provide enormous information from a single extraction of the nematode community of a single soil sample. The tools provided by faunal analysis appear to be powerful, but there are some data gaps and leaps of faith. Categories along the life history ordinate of the functional guild matrix are based largely on body size. An enormous amount of work remains in determining the longevity, fecundity, and sensitivity to specific environmental disturbances for the structure indicator nematodes.

Currently, because it is prohibitively time consuming to measure all nematodes in a sample for biomass determination, we calculate nematode biomass as an indicator of enrichment channel activity using Andr assy's (1956) formula and the published widths and lengths of adult nematodes (e.g., from Bongers, 1988). Of course, not all nematodes in the soil fauna are adults, so some overestimation is inherent in our data. In lieu of biomass data, we find that weighting the abundance of enrichment indicators as in Ferris et al. (2001) provides similar general patterns in the Enrichment Profile to those obtained with biomass data. An argument could

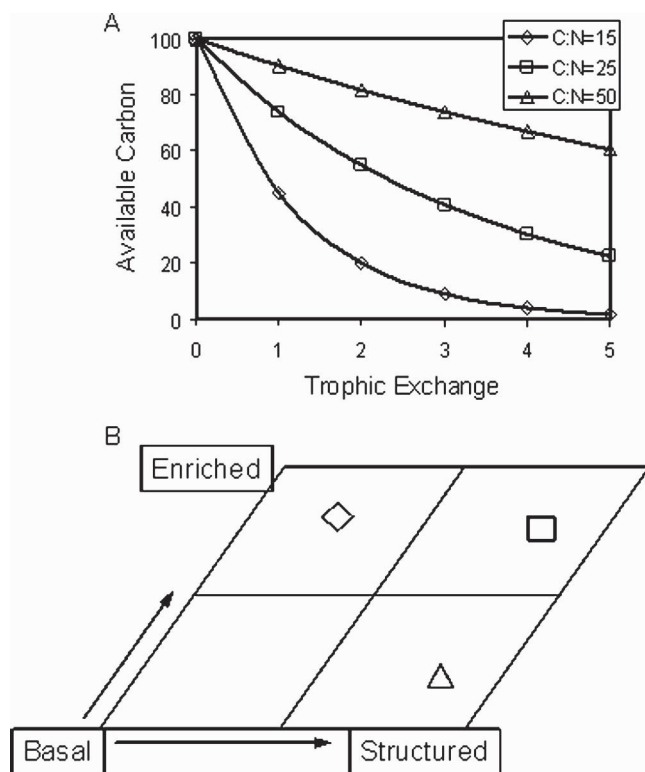


FIG. 8. Soil food web structure by design of input. (A) Hypothesized rates of decline of available carbon from organic materials of different C/N ratio with successive trophic transfer. (B) The consequent effect on the Enrichment and Structure Indices of a soil food web.



be made that metabolic rates would provide greater resolution in indicating biotic activity in the enrichment channels. However, we are uneasy about application across the whole phylum of the coefficients for converting biomass to respiratory rates developed by Klekowski et al. (1972) because we have found considerable variability in the coefficients among species within a single family (Ferris et al., 1995).

In some cases, feeding habits of nematodes have been determined by observation; in others, they are inferred from stomal structures. The excellent compilation of observed and inferred feeding habits by Yeates et al. (1993) is now more than a decade old; additional data should be available. However, revision at this time may be premature, given the frequency with which new information is emerging, e.g., the fungal-feeding habit of the diplogasterid nematode, *Tylopharynx foetida* (Von Lieven and Sudhaus, 2000; Wu et al., 2001). Another consideration is that taxonomic classification has changed. The cp-scaling (Bongers, 1990) followed the classification scheme used by Bongers (1988) in *Nematoden van Nederland*. In that publication, the family Dorylaimidae contained only *Dorylaimus*. Because *D. stagnalis* tolerates polluted conditions, Dorylaimidae was assigned cp value 4. Since that time, Jairajpuri and Ahmad (1992) synonymized Prodorylaimidae and Thornenematidae (both cp 5) with Dorylaimidae, and consequently a single family contains representatives of more than one putative cp group, underscoring the need for higher-resolution diagnostics.

Omnivory is a real and appropriate concept; however, it is particularly difficult in our analyses when life stages may be in different trophic groups, e.g., juvenile mononchids as bacterivores (Yeates, 1987a,b) or aphelenchids as fungivores and herbivores. The feeding habits of that predominant family of soil nematodes, the Tylenchidae, remain a research challenge. Emerging reports on the fungal-feeding habits of *Filenchus* (Okada and Kadota, 2003) are useful, but much more work remains. Characterization of the opportunistic colonizers that constitute the other component of the enrichment indicators will be important. It seems highly probable that these species will have the characteristics of successful invaders, including wide ecological amplitude and genetic diversity (Ferris et al., 2003).

Despite the work yet to be done, soil nematodes are beginning to fulfill their promise as environmental indicators, and nematode faunal analyses are providing potential tools for soil food web management. Continued validation of the inferences derived from such analyses and investigation of their sensitivity will enhance their reliability.

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