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Berkeley, California
July 13, 14, & 15, 2004
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NEMATODES AND THE SOIL FOOD WEB: UNDERSTANDING HEALTHY SOILS

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ABSTRACT

Nematodes are partitioned into functional guilds based on feeding habit, opportunistic response to environmental enrichment and sensitivity to perturbation. Abundance within each guild is weighted by the indicator importance of that guild for the enrichment or structure characteristic of the system. Based on the analyses, soil foodwebs are categorized as enriched but unstructured, enriched and structured, resource-limited and structured, or resource-depleted with minimal structure. Differences can be detected in predatory regulation of opportunistic taxa, level and nature of enrichment, decomposition channels, and C:N of organic input. Differences can also be detected between annual-cropped agriculture with frequent disturbance, organically-driven, relatively undisturbed perennial systems, grasslands and forests with little disturbance or extrinsic enrichment, and systems by stressed resource depletion or extreme perturbation.

The functioning of the soil food web depends on its component organisms and the environment in which they exist. Assessment of the presence and abundance of individual taxa in the web is challenging. 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. 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). The analyses include recognition of an enrichment trajectory and a structure trajectory. The latter measures the abundance of trophic linkages in the food web and the probability of regulatory effects on opportunist populations through exploitation and competition. The enrichment trajectory reflects supply-side characteristics of the food web and increase or activity of primary consumers of incoming organic material (Ferris et al., 2001).

Plant-, bacterial- and fungal-feeding nematodes occupy the primary trophic channels through which energy and nutrients enter the soil food web. The relative abundance of these nematodes is considered an indicator of current or recent carbon flow through the respective channels. Some nematodes are relatively specialized predators of other nematodes while others are more generalist predators with prey at various trophic levels in the soil food web. The abundance of nematodes in various functional guilds at higher trophic levels are an indication of the degree of connectance in the web (Ferris et al., 2001). Life history strategies of enrichment indicators generally conform to the characteristics of opportunistic r-strategists; those of structure indicators to long-lived K-strategists (Bongers and Ferris, 1999).

Food webs are enriched when disturbance occurs and resources become available due to external input, organism mortality, turnover, or favorable shifts in the environment (Odum, 1985; Van Veen and Kuikman, 1990). Pulse enrichment is followed by heterotrophic succession whereby the predominance of organisms changes through time depending on trophic roles, life course dynamics, and prevailing environmental conditions (Ferris and Matute, 2003). Sustained enrichment may maintain a more consistent structure among functional guilds of soil organisms. 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 responses of certain guilds of nematodes, are more persistent and can be measured reliably (Ferris et al., 1996; Bongers and Ferris, 1999).

The enrichment-opportunist bacterivore nematode guild includes the families Rhabditidae, Panagrolaimidae and Diplogasteridae (Bongers and Bongers, 1998; Bongers and Ferris, 1999; Ferris et al., 2001). They are characterized by short generation time, small eggs and high fecundity. They appear to feed continuously in enriched media and then form metabolically-suppressed dauer larvae as resources are diminished. 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. The general opportunist nematodes, are predominantly bacterial scavengers in the Cephalobidae and fungal-feeders in the Aphelenchidae, Aphelenchoididae and Anguinidae.

Changes through time in the abundance of organisms in the soil community may be considered structural succession; the concurrent changes in food web function are considered functional succession. Fungivore and bacterivore nematodes are proving useful indicators of soil fungi and bacteria (e.g., Ferris et al. 2001; Ferris and Matute, 2003; Neher, 2001). Their abundance is presumed to mirror that of other important bacterivores (e.g. protozoa) and fungivores (microarthropods) and reflect the current or recent availability of their food. Fungal energy channels predominate when the organic material is of high C/N ratio and/or is placed on the soil surface rather than incorporated; bacterial decomposition channels predominate when the organic material is of low C/N ratio and is incorporated into the soil (Hendrix et al., 1986; Moore, 1994). Fungal- and bacterial-feeding nematodes, and other organisms that graze on primary decomposers, accelerate the decomposition of soil organic matter and increase mineralization, thus releasing nutrients for plant growth (Ingham et al., 1985; Ferris et al., 1996, 1997, 1998; Chen and Ferris, 1999; Neher, 2001).

Table 1
The value of nematode faunal analysis as bioindicators of the structure and function of the soil food web (adapted from Bongers & Ferris, 1999).

Millions of nematodes can occupy 1 m^2 of soil; there may be 50 different species in a handful of soil and yield sufficient individuals for reliable analysis.

Nematodes are among the simplest metazoa. They occur in any environment that provides a source of organic carbon. They occur in every soil type and under all climatic conditions, in habitats that vary from pristine to extremely degraded.

In soil, nematodes live in capillary water; their permeable cuticle provides direct contact with their microenvironment.

They do not rapidly migrate from stressful conditions and many species survive dehydration, freezing or oxygen stress; others are more sensitive. The community structure is indicative of local conditions to which they inhabit.

Nematodes occupy key positions in soil food webs. They feed on most soil organisms and are food for many others.

The functions of nematodes in soil food webs are apparent; their food source is easily deduced from the structure of the mouth cavity and pharynx.

Community structure can be determined from a small sample, which is relatively non-disruptive to a site so that intensive repeated sampling is possible.

Extraction of nematodes from soil is standardized through efficient, routine procedures. Extracted nematodes can be preserved and stored for future analyses. Nematodes can be identified using simple morphological characters.

The large numbers of species and individuals recovered confer a high intrinsic information value on each sample.

Nematode faunal profile analysis provides information on succession and changes in decomposition pathways in the soil food web, nutrient status and soil fertility, and the effects of soil contaminants.

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). As time progresses, the degree of structure may increase, as indicated by nematode guilds with lower fecundity, longer life course and lower population levels. With greater structure in the community, more links in the food web, nematode predation and multitrophic interactions occur. The nematode guild indicators are in families that contain smaller-bodied predators and omnivores, including the Mononchidae and Dorylaimidae. Environmental stability and homeostasis results in the highest levels of community structure; indicator guilds include the Discolaimidae, Thornenematidae and Qudsianematidae. 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; Bongers and Bongers, 1998; Bongers et al., 2001).

A graphic representation of enrichment and structure condition of the soil food web is based on the relative weighted abundance of nematode guilds. The faunal profile is constructed to indicate whether the soil community is enriched but unstructured (Quadrat A), enriched and structured (Quadrat B), resource-limited and structured (Quadrat C), or resource-depleted with minimal structure (Quadrat D) (Fig. 1).

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" 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 many soil food webs, except at a local level or during successional recovery from extreme disturbance, there is the probably sufficient connectance amongst guilds that trophic cascades are unlikely. More likely, is that

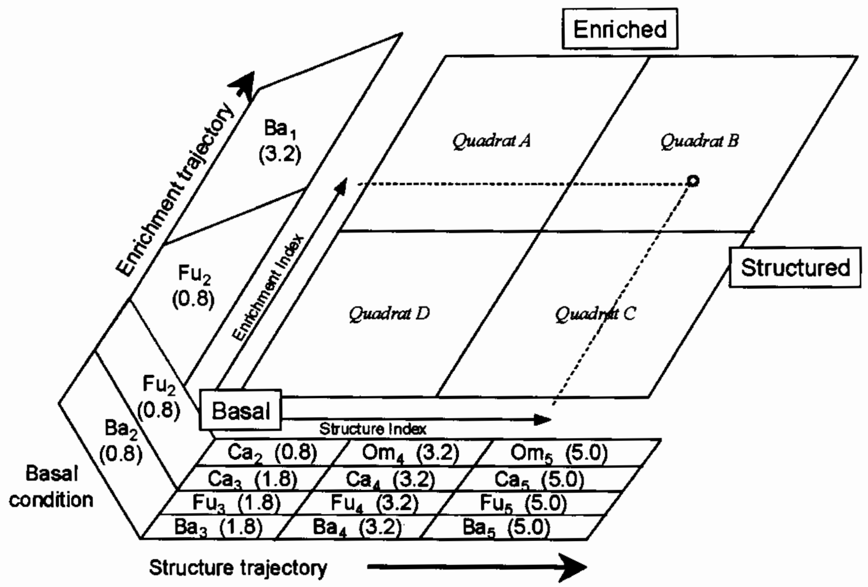

Fig. 1 Functional guilds of soil nematodes characterized by feeding habit (trophic group) and by life history characteristics, after Bongers and Bongers, 1998. Indicator guilds of soil food web condition (basal, structured, enriched) are designated and weightings of the guilds along the structure and enrichment trajectories are provided, for determination of the Enrichment Index and Structure Index of the food web.

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 (Yeates and Wardle, 1996).

Some soils are characterized as being biologically suppressive to pest populations. A population may indeed be suppressed (driven to very low numbers), or regulated (amplitude of population cycles dampened) by one or many other organisms that use it among their food resources. From observation and anecdote, suppressive soils often have a diversity of organisms in several trophic and functional groups of the food web. When such soils are defaunated, the suppressiveness often disappears. From food web theory, the number of trophic linkages among organisms increases as a constant fraction of the square of the number of species in the web (Cohen, 1989; Martinez, 1992). Consequently, for a species in a speciose food web, at least one linkage, and probably more depending on feeding specialization, will constitute resource acquisition. Those remaining constitutes resource provision to other species in the web. Of course, soil biotas are not uniformly dispersed in a single homogeneous community. Rather, there are in spatially separated patches that differ in resource availability, species composition, and abiotic factors. The concept of a metacommunity (Wilson, 1992) is useful to consider the movement of predators among patches of prey and the potential for predator-prey relationships to regulate their 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 dynamics and enhance the functional stability of the system (Warren, 1996).

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