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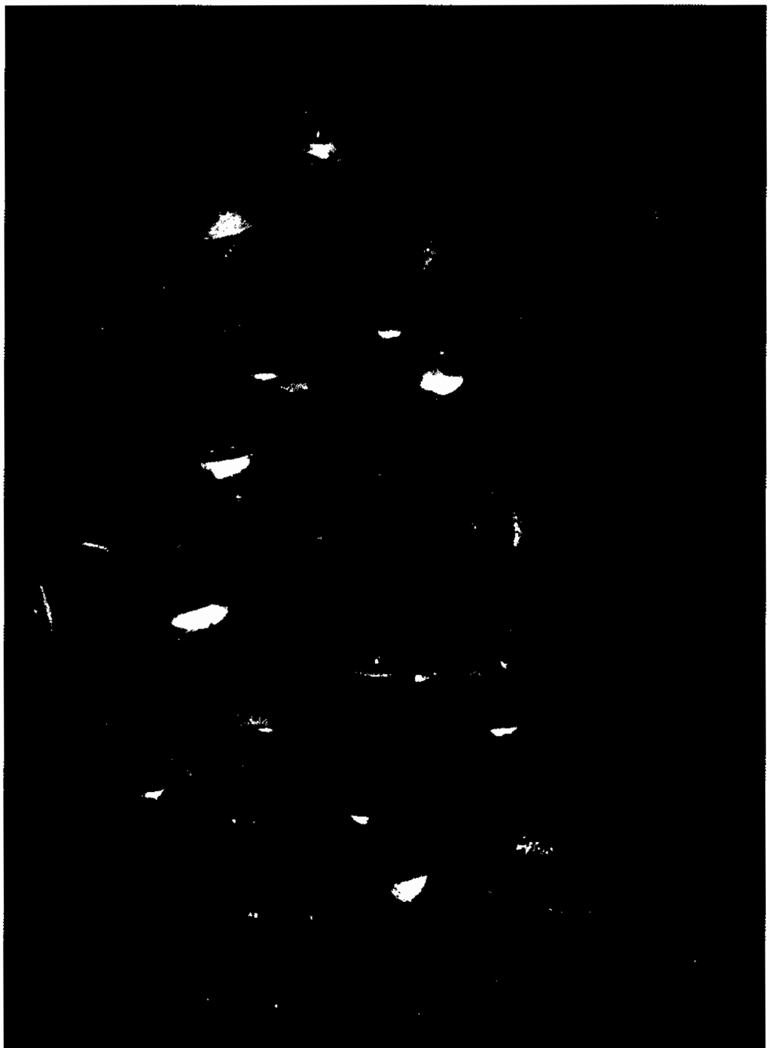

Armillaria mellea Photo Courtesy of John Menge

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The Structure and Functions of the Soil Food Web

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Abstract

Soils provide ever-changing environments for many life forms, including bacteria, protozoa, fungi, nematodes and arthropods. All organisms require carbon and energy. Unless, like plants, they are able to convert atmospheric carbon dioxide to simple sugars and then to more complex molecules, organisms obtain their carbon and energy from other organisms, either living or dead. The complex relationships among organisms in the soil are often described as soil food webs. Soil food webs have *structure*, determined by the life history and feeding habits of the component organisms. They also perform *functions* that are important in agricultural production and critical to the vitality of ecosystems.

Soil food webs are influenced by sources of carbon, including plant roots, detritus and composts, and they are altered by agricultural practices. We have determined that the nematode fauna provides a useful biological indicator system for assessment of the food web and its environment. Our research and observation on soil food web management demonstrates the fragile nature of this essential component of production systems.

Soil Food Web Functions

The soil food web is that community of organisms that utilize each other, either by predation or consumption of dead bodies, as sources of carbon and energy. The activities of these soil organisms results in a variety of ecological functions or services (see box) which are essential in the maintenance of crop production, soil fertility, and, indeed, in the continued existence of life on our planet.

The ecological functions of soil food webs include:

- Decomposition of organic matter
- Cycling of minerals and nutrients
- Reservoirs of minerals and nutrients
- Redistribution of minerals and nutrients
- Sequestration of carbon
- Degradation of pollutants, pesticides
- Modification of soil structure
- Biological regulation of pest species

As an example, in the course of consuming, digesting, assimilating, and metabolizing the bodies of their food sources, organisms convert complex organic molecules into new forms that are compatible with their own structural and metabolic needs. During this process, materials that are indigestible by the consumer are eliminated in simpler forms that are more accessible to other organisms. Component elements of the molecules that are digested may be in excess of the needs of the new owner and are excreted in mineral form, for example ammonia. Nitrogen in the form of ammonia is readily available to plants and to other soil organisms. The vast majority of the carbon and energy cycling through the soil organisms originates from photosynthetic activity of plants.

Food Web Structure

Soil organisms gain access to the carbon and energy fixed by plants through direct herbivory (some nematodes, arthropods, annelids, fungi), by consumption of soluble molecules exuded into the rhizosphere by plants (mainly bacteria), consumption of dead roots and leaf fall, and ultimately the dead plant (fungi and bacteria, often aided by maceration activities of arthropods and annelids). All of these "entry level" organisms have their predators; for example, bacteria are consumed by protozoa and nematodes, fungi by nematodes and microarthropods (Fig.1).

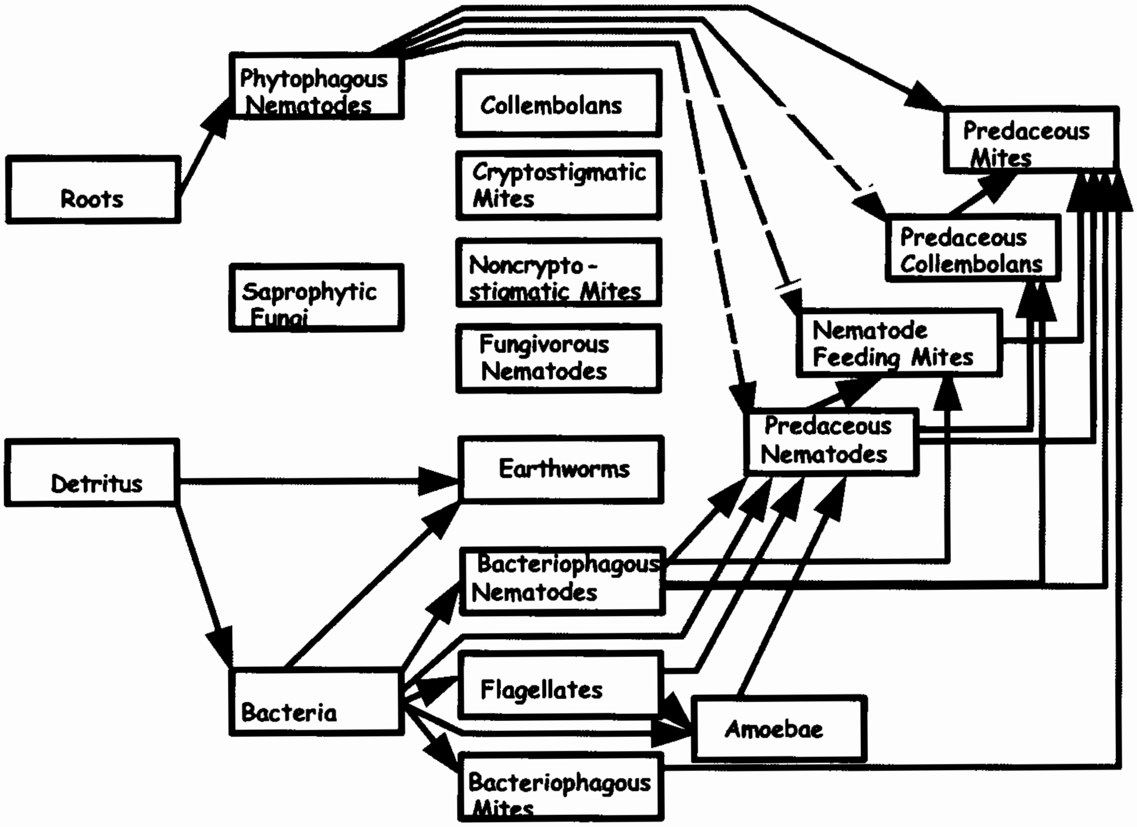
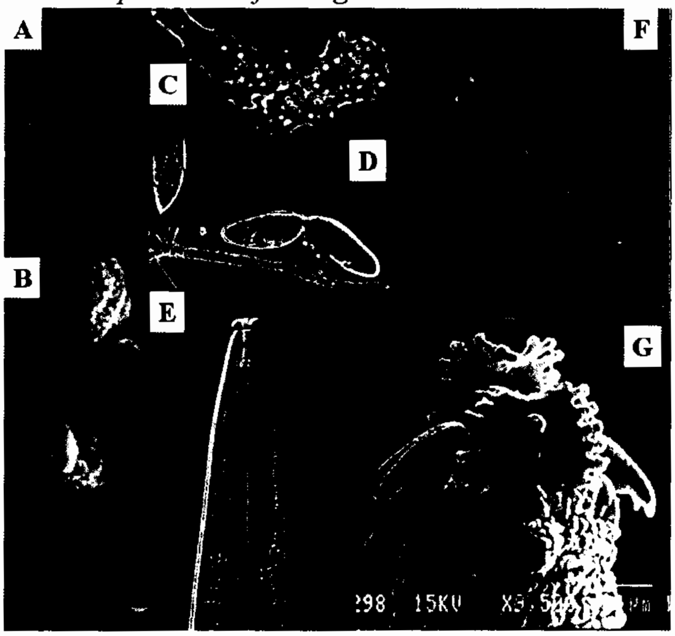


Fig. 1. The flow of carbon and energy through herbivore, fungal and bacterial channels in a soil food web (from Moore et al, 2003).

A food web diagram (e.g., Fig. 1) is a representation of the hypothesized flow of carbon and energy among organisms. The size and activity of the food web is limited by the amount of carbon and energy available. Links drawn between organisms are the known or conjectured feeding relationships and indicate the direction of flow of resources. Carbon and energy obtained by consumers at the entry level of the food web are utilized by those organisms for growth, reproduction and respiration. Carbon dioxide lost from the soil is the product of respiration of soil organisms and represents a net loss in resources to the consumers of those organisms, that is, the next trophic (feeding) level. The loss of carbon at each trophic level limits the abundance of predators that can be supported by any group of prey. The proportion of the total possible links among organisms in the web that are actually realized is termed the connectance of the web. Potential links among organisms in the web will not be realized if those organisms are separated in space or time due their individual physiology and the nature of the environment.

Molecules that are taken up by bacteria and then pass on to the organisms that consume bacteria are considered to be in the "bacterial decomposition channel" (Fig. 2). The organisms in this channel are generally metabolically very active and the passage of molecules through and from the bacterial channel is rapid. Materials decomposed and digested by fungi are often more complex and their flow through the "fungal decomposition channel" (Fig. 3) may be slower.

Fig. 2. Some organisms of the bacterial decomposition channel of a soil food web. A. Bacteria photographed at the limit of resolution of a light microscope; B. Bacteria visualized with a scanning electron microscope; C. and D Amoeboid and ciliated protozoa; E Opportunistic bacterial-feeding nematodes; and F and G Bacterial-feeding nematodes with more specialized feeding structures.



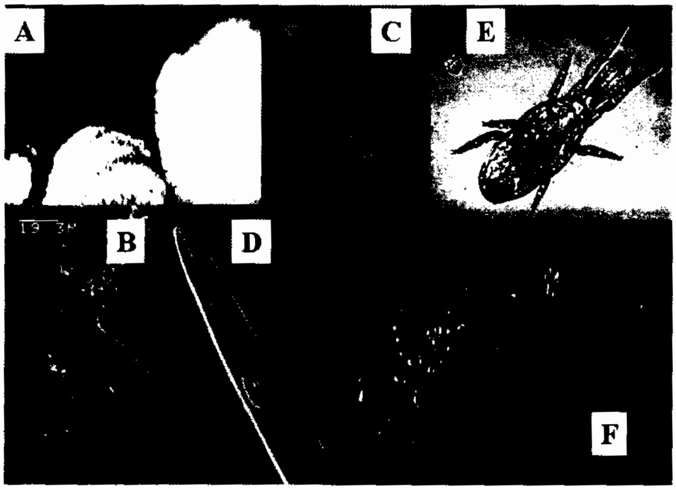


Fig. 3. Some organisms of the fungal decomposition channel of a soil food web. A. Fungi photographed with a light microscope; B. Fungi visualized with a scanning electron microscope; C and D. Fungal-feeding nematodes; E and F. Fungal feeding mite and collembolan.

A diversity of soil organisms in the food web is generally considered beneficial. When organisms perform ecological functions such as regulation of pest species or mineralization of nutrients, redundancy in the number of species performing the function may compensate for seasonal dynamics of the species, differential effects of the environmental conditions, or abundance of their predators. Functional redundancy may promote relative consistency of important functions. Considerable ecological theory addresses relationships between the connectance of the food web and its stability or its ability to recover after disturbance (resilience). Redundancy is a measure of the number of links in the web that perform the same function. It is an indicator of the functional stability of the web if one or more organism guilds are reduced or removed, or if links are broken between guilds due to spatial or temporal patterns.

One simple view of food web structure is the trophic (or feeding) cascade; a linear chain of trophic exchanges that results in predictable consequences when the abundance of organisms in a trophic guild changes. Assume that population levels of an herbivore guild are regulated by a carnivore guild, and that the carnivore guild is prey for a top predator. Then, if the top predator guild is decimated by some perturbation, numbers of organisms in the carnivore guild should increase and, in turn, numbers in the herbivore guild will be reduced to lower levels by greater predation pressure. Depending on the resolution level at which they are considered, however, most food webs are not this simple (Strong, 1992), although trophic cascades have been observed in some rather unlikely systems (Pace *et al.*, 1999).

A more common organization of the food web is that of a trophic network where each guild may have several sources of food and several guilds may share a common predator. The effects of change in abundance of a guild in such systems are much less predictable. Decrease in the abundance of a particular predator group at one trophic level may have little impact on its prey abundance if the event is accompanied by increase in abundance of a competing predator guild. Increase in abundance of a guild that exploits the same resource as another may result in an enhancement rather than a competitive effect if the resource is rendered more accessible by the activity. A series of direct and indirect interactions among organism guilds has been characterized (Menge, 1995).

While food web processes can be studied and understood relatively easily in laboratory microcosms, the environment of soil organisms is spatially complex. The supply of food to the community comes from sources that are often spatially separated; litter at the soil surface, roots that may differ in their accessibility and attractiveness to soil organisms with specific morphotypes. The environment differs with depth with regard to physical conditions and their daily and seasonal fluctuations, including temperature, moisture, gaseous exchange and availability. It also differs physically in terms of soil texture, aggregation, restrictive layers, rocks, old root channels, organism burrows, etc. (Fig. 4). Additionally, organisms are patchy in their distribution, determined by their reproductive and locomotion patterns. The patches differ in their species composition so that predators and prey may be co-distributed in some areas but not in others. Some predators are very specific in their prey selection, others are omnivorous. Even where co-distributed, predator and prey ratios may not be stable which can result in locally chaotic oscillations of the respective populations.

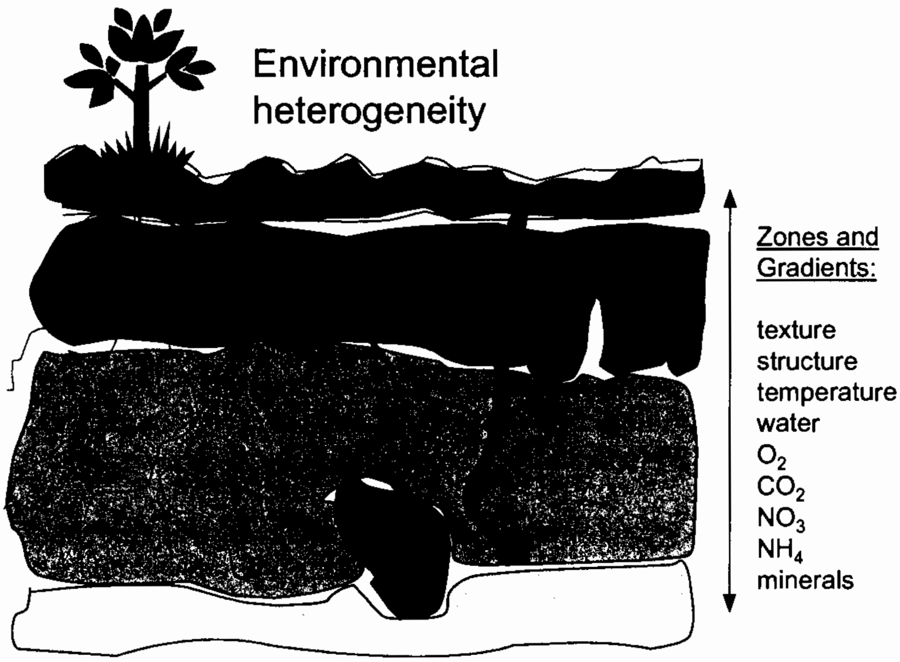


Fig. 4. Spatial heterogeneity of the soil environment as a determinant of habitat quatilty of soil organisms.

Food Web Management

Management of the soil food web may be the consequence of environmental conservation or restoration programs, or of agricultural production practices. Usually, the management objective is to enhance one or more of the functions of the web. By increasing soil moisture levels in the fall, while soil temperatures were still sufficiently high for biological activity, we increased the size of the microbial biomass and that of its predator guilds, including bacterivore nematodes and protozoa. The consequence was that the bacterivore guilds were at high abundance the following spring when the microbial biomass responded to incorporation of a winter cover crop. Grazing of the bacterivores enhanced mineralization of nutrients that would otherwise have been immobilized in the microbial biomass with the result that nutrient deficiencies were eliminated in the summer crop (Ferris *et al.*, 2004).

Beyond the diversity and patchiness imposed by food sources, population attributes, co-distribution of predators and prey, there is trophic bias in the effect of disturbance of the soil community. Theory and experiment suggest that for specialist predators to have a consistent regulatory effect on the abundance of their prey it is necessary for prey and predator population densities to be under equilibrium conditions (Turchin, 1995). Higher predators are often larger organisms. Their environment is readily destroyed by physical disturbance of the soil; they are slow to recover from toxic or environmental perturbations, their life cycles are longer and their reproductive potential lower than opportunistic organisms at the entry level of the food web. Consequently, in disturbed agricultural soils, equilibrium conditions of predator and prey densities seldom occur. Is it possible that where soil disturbance is minimized, biological regulation of pest species in the soil food web is more likely to occur?

Soil tillage effectively mixes organic matter throughout the tilled zone so that products of its decomposition are available to plant roots. However, that disturbance disrupts the higher trophic levels of the food web. In the absence of such disturbance, there is a need for intrinsic distribution systems within the soil profile. Such systems are provided by the proliferation and morphology of the plant root system; note that plants selected for conventional agricultural systems may not have optimum root structure and function for no-till system. Fungal hyphae ramify through the soil profile, effectively coupling decomposing carbon sources at the soil surface with mineral sources released or leached deeper in soil. Mycorrhizal fungi extend the exploratory and absorptive capacity of the root system. Arthropods at the soil surface macerate the organic matter into finer particles that allows physical sifting to deeper regions, burrowing organisms, including annelids achieve vertical redistribution of organic materials.

Achieving this ideal of a functioning food web may require a time-consuming transition after conventional agricultural practices have been used. It undoubtedly will require modifications in equipment and other technology. Managing the delivery system of resources into the food web without disturbing its structure in the process, and at the same time optimizing crop growth, may be the greatest challenge of conservation tillage systems. Management of weeds is always a major consideration. In irrigated agriculture, the use of delivery systems such as buried drip lines may minimize water availability for weed seed germinationat the soil surface. Such drip lines may provide a vehicle for distribution of mineral nutrients during, and even after, the transition.

Finally, the soil food web is a functioning, hopefully active, biological system. Organisms at all trophic levels are using carbon and energy, releasing carbon dioxide and dissipating energy. Unless the available resources are continuously replenished, the food web will decrease in activity and the abundance of the component organisms will diminish, the more sensitive groups first. Coupled with efforts to preserve the stability of their environment, it will be necessary to continue to supply food to the soil system. In food webs where carbon and energy is not subsidized by external sources or by the production of cover crops and green manures, the herbivory channel into the soil food web is likely to predominate, with negative effects on crop production (Fig. 5). We believe that management of the soil food web to regulate populations of herbivore species below pest levels will require rotation of crop species, use of resistant cultivars and the preservation of activity of their regulatory predators of the pest species.

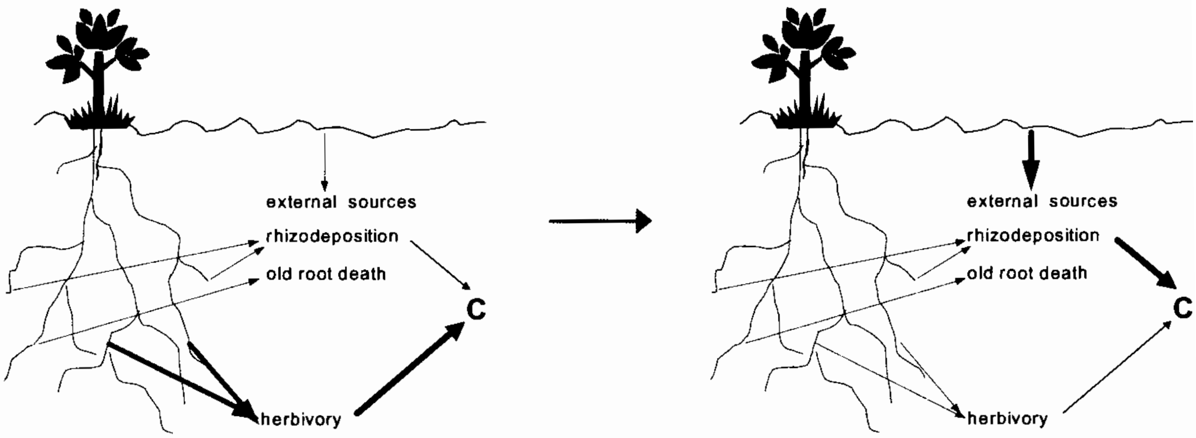


Fig. 5. A management goal in sustainable production systems: to maximize carbon (C) flow into the soil food web through detritivore rather than herbivore channels (from Ferris, 2004).

Food Web Evaluation

Its connectance, redundancy and resilience determine the structural and functional resilience of the soil food web. Guilds vary in their sensitivity to environmental disturbance; often guilds at higher trophic levels in the web are more sensitive than those at lower trophic levels. Disturbance of the web may decrease the abundance of predators of opportunistic species. Consequently, upon enrichment through plant growth or organic matter incorporation, opportunistic herbivore and decomposer species may undergo unregulated increase. That may result in damage to the primary producer (plant), immobilization of nutrients or other examples of functional instability.

Evaluation of the state of the soil food web may be accomplished by structural or functional analysis. Structural analysis of the web is very difficult if it requires inventory and assessment of all participants. It may be simplified if reliable indicator species or guilds are identified. Functional analysis may calibrate specific functions of the web but may not indicate how those functions are being accomplished or their sustainability.

Nematode faunal analysis provides a useful tool in assessing the structure, function, and probably the resilience, of the soil food web. Nematodes are the most abundant of the Metazoa, occupy key positions in soil food webs, can be captured and enumerated by standardized extraction procedures, and their identification is based on morphological and anatomical characters. Further, since there is a clear relationship between structure and function, their trophic roles are readily inferred. Consequently, since each soil sample contains an abundance and diversity of nematodes it has high intrinsic information value (Bongers and Ferris, 1999).

Functional guilds of soil nematodes identified at the family level provide adequate resolution to indicate the state of the soil environment and the condition of the resident food web. The realization that nematode families can be categorized according to their response to environmental disturbance or enrichment (Bongers, 1990) evolved into the concept of indicator guilds (Bongers and Bongers, 1998). Essentially the guilds represent a matrix classification of nematode taxa based on feeding habit and response to disturbance or opportunity. Since the indicator guilds are distributed throughout the food web, they are indicators of the presence and abundance of other organisms in similar trophic niches.

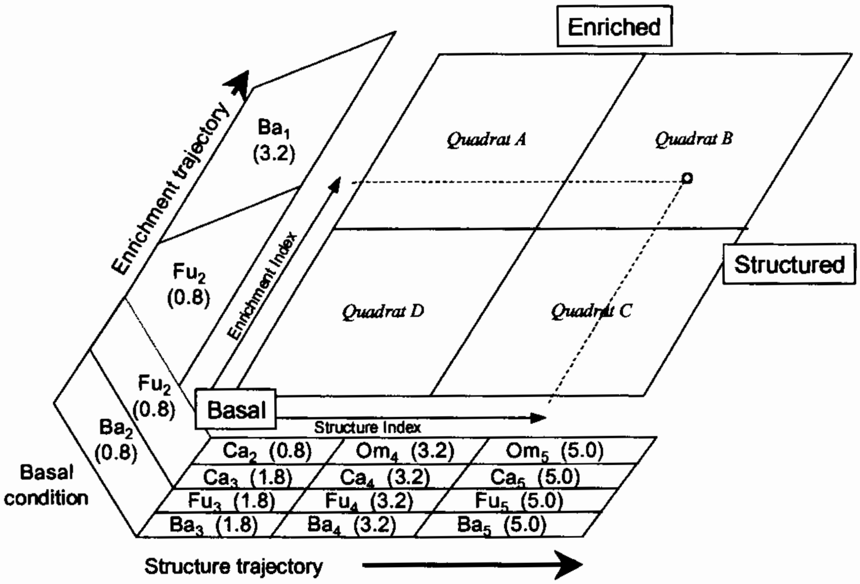


Fig. 6. Functional guilds of soil nematodes characterized by feeding habit (trophic group) and by life history characteristics, after Bongers and Bongers, 1998. Indicator guilds of soil food web condition (basal, structured, enriched) are designated and weightings of the guilds along the structure and enrichment trajectories are provided, for determination of the Enrichment Index and Structure Index of the food web.

By weighting the abundance of nematodes in a guild by the indicator importance of that guild with regard to the maturity, basal condition, or enrichment of the food web, the condition of the food web with regard to those three trajectories can be plotted on a