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Nematode community structure as a bioindicator in environmental monitoring

Tom Bongers and Howard Ferris

Four of every five multicellular animals on the planet are nematodes. They occupy any niche that provides an available source of organic carbon in marine, freshwater and terrestrial environments. Nematodes vary in sensitivity to pollutants and environmental disturbance. Recent development of indices that integrate the responses of different taxa and trophic groups to perturbation provides a powerful basis for analysis of faunal assemblages in soil as *in situ* environmental assessment systems.

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Particles vary in size, nature and aggregation throughout the horizontal and vertical dimensions of the soil. Variability in the solid state affects volume, exchange, flow and diurnal and seasonal fluctuations of the liquid and gas phases of soil. The spatial and temporal heterogeneity provides myriad habitats for a vast diversity of organisms. Larger organisms live in natural channels in the soil or create tunnels and chambers. Smaller organisms, including nematodes, are primarily aquatic and live in the water films between soil particles. Their size allows movement through pore necks between particles or between aggregates of particles without tunneling activity. The ecological functions of soil organisms include organic matter decomposition, mineralization of nutrients, degradation of toxicants and population regulation of plant disease agents.

Soil organisms depend on each other for carbon and energy. The structure and function of below-ground food webs are disrupted by hydrocarbon and heavy-metal contaminants, mineral fertilizers and pesticides, and by physical disturbance. However, the results of such disruptions are unpredictable because they are influenced by the heterogeneity of the soil, fluctuations in abiotic conditions, chemical and physical buffering capacity, and by other biotic and abiotic interactions. Because nematodes occupy key positions as primary and intermediate consumers in soil food webs, evaluation and interpretation of the abundance and function of their faunal assemblages or community structure offers an *in situ* assessment of disruptive factors. An individual assessment at a site provides a snapshot of current conditions, whereas sequential assessments allow analysis of environmental degradation or remediation.

Nematodes were used in water quality assessment in the 1970s (Refs 1,2) during which the informational value of terrestrial nematode community structure became apparent[3]. During the 1980s, as concerns increased about the functioning and vulnerability of the soil ecosystem, researchers turned to assessment of *in situ* nematode faunae in environmental studies[4,5]. The characteristics of nematodes (Box 1) allow analysis of presence and abundance of individual taxa. Their faunal composition has emerged as a useful monitor of environmental conditions and ecosystem function in the soil[6–8].

Recent research indicates that simple analyses of *in situ* nematode faunae at family level provide a wealth of information on the nature of decomposition pathways and soil nutrient status[7,9] (Box 2). The analyses also indicate effects of agricultural practices and contaminants on the functioning of the soil food web[10–15]. They provide a basis for environmental management, remediation and conservation decisions.

Classification of nematodes by feeding behavior and life-history strategy

Nematodes are an evolutionarily successful group of organisms. They are ubiquitous in all habitats that provide available organic carbon sources; they are the planet's most abundant metazoa. In soil, some nematodes feed on higher plants, some on fungi or bacteria; others are carnivores or omnivores. They range in reproductive potential from explosive opportunists to conservative survivalists. They vary in sensitivity to pollutants and environmental disturbance. Recognition of the approximately 20 000 described species is based primarily on morphological and anatomical features supplemented by ecological function[16], although molecular markers are increasingly important for identification and classification[17–19]. Nematode form and function, especially concerning feeding behavior, are closely linked and consequently the feeding behavior of unknown species can be inferred from their morphology[20,21].

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The phylum Nematoda comprises the classes Secernentea and Adenophorea. The Secernentea are almost exclusively terrestrial, only rarely being freshwater or marine, whereas the Adenophorea occupy niches in all three habitats. The evolution of life-history strategy in these groups is a fertile area for ecological hypotheses[22] because they are so diverse. For example, the family Rhabditidae (Secernentea) tend to be relatively small (most are <1.5 mm length) bacterial-feeding nematodes with high metabolic activity and almost constant movement. They have voluminous gonads, produce many small eggs and respond rapidly to resource opportunities. Species in this family (*Caenorhabditis elegans* is probably the most famous representative) can form a non-feeding, inactive, survival stage known as a 'dauerlarva'. They are often linked in phoretic relationships with insects and are readily transported to new food resources. They flourish in habitats with high microbial activity and are frequently surrounded by potentially toxic microbial exudates; consequently, they have become relatively tolerant of pollutants. By contrast, the order Dorylaimida (Adenophorea) comprises taxa with individuals that are generally larger, have small gonads, produce fewer but larger eggs, do not form dauerlarvae and are sensitive to pollutants. Other taxa in the Secernentea and Adenophorea occupy intermediate positions on this continuum of r- to K-selected (*sensu lato*) features.

The maturity index

Natural taxa are composed of species with varying degrees of morphological and functional similarity; the lower the hierarchical level of the taxon, the higher the similarity. Nematode species in monophyletic families generally have similar r- or K-selected and other life-history characteristics. Consequently, species related at the family level exhibit similar responses to environmental perturbation[6].

Based on life-history syndromes (Box 3), families of nematodes can be ordered on a colonizer–persister (cp) scale. The scale ranges from one (early colonizers of new resources) to five (persisters in undisturbed habitats)[6]. The maturity index (MI) for a soil is the weighted mean cp value of the individuals in a representative soil sample (see www.spg.wau.nl/nema/MI_lit.htm for a recent overview of MI-literature). In practice, MI values for soil subjected to varying levels of disturbance range from less than 2.0 in nutrient-enriched disturbed systems to ± 4.0 in undisturbed, pristine environments. Agricultural practices, such as incorporating organic material (e.g. manure) into the soil, stimulate microbial activity and provide resources for opportunistic nematode species – consequently, there is a rapid decrease in the MI followed by a gradual increase during subsequent succession[13,23].

Nematodes that feed on higher plants, perhaps 10% of soil-inhabiting species, are omitted from the calculation of the MI because their occurrence and abundance is largely determined by the community structure, host status and vigor of plants growing in the soil. The more derived plant feeders, which have lower reproductive output than bacterial feeders, respond to enrichment of the host plant[9]. Species that are sensitive to disturbance and pollutants, such as plant feeders in the family Trichodoridae, can exhibit rapid resurgence in the presence of a vigorous host. Consequently, the equivalent of the MI for plant-feeding nematodes (the plant-parasite index, PPI) is calculated separately. The PPI tends to respond to environmental enrichment as the inverse of the MI (Ref. 9). An aggregate index that includes plant-feeding nematodes in the calculation of the MI might not clearly reflect a perturbation. For example, application of an aggregate index in Australian agroecosystems was not a useful indicator of disturbance[24]. However, recalculation of the MI in the original sense revealed differences among management systems[9].

Box 1. *In situ* soil ecological assessment based on nematode fauna: practical and applied aspects

- Almost 20 000 nematode species have been described and millions of nematodes can occupy 1 m^2 of soil. There can be 50 different species in a handful of soil and a 100-ml core of soil yields sufficient individuals for reliable analysis.
- Intensive repeated sampling is possible because the sample size of soil required is small and therefore relatively nondisruptive to a site.
- 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 to the family level using simple morphological characters.
- The large numbers of species and individuals recovered confer a high intrinsic information value on each sample.
- Nematode faunal composition analysis provides information on succession and changes in decomposition pathways in the soil food web, nutrient status, fertility and acidity of soil, and the effects of soil contaminants.
- Routine analysis of nematode fauna affords rapid assessment of response to management activity and levels of environmental stress, and provides decision criteria for conservation and remediation.

The MI as an indicator of enrichment

Opportunistic nematode species increase in numbers more rapidly than persister species in response to an increase in microbial activity caused by the addition of organic matter. An increase in the numbers of cp-1 nematodes is evident four days after manure is added to the soil and they become dominant in the community after two or three weeks. Over the next few weeks, cp-1 nematodes decrease and cp-2 species become dominant[23]. The MI increases during the succession and with decreasing microbial activity.

In agroecosystems, the MI has been used to differentiate between tillage regimes. The frequency of soil disturbance is inversely related to the magnitude of the MI but positively correlated with the PPI (Ref. 11). The inverse relationship between the PPI and the MI is apparent from their response to applications of ammonium, nitrate fertilizers and sewage sludge. The common factor in these studies is soil enrichment. Enrichment stimulates microbial activity and subsequent succession, which is reflected in an initial decrease in the MI followed by its gradual increase. Enrichment also increases carrying capacities of plants for

Box 2. Why nematodes make good bioindicators

- Nematodes are among the simplest metazoa. They occur in any environment that provides a source of organic carbon, in every soil type, under all climatic conditions and in habitats that vary from pristine to extremely polluted.
- 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 (although others are more sensitive). The community structure is indicative of conditions in the soil horizon that it inhabits.
- Nematodes occupy key positions in soil food webs. They feed on most soil organisms and are food for many others. They also influence vegetation succession.
- Because nematodes are transparent, their diagnostic internal features can be seen without dissection. They can therefore be identified without biochemical procedures.
- There is a clear relationship between structure and function: the feeding behavior is easily deduced from the structure of the mouth cavity and pharynx.
- Nematodes respond rapidly to disturbance and enrichment: increasing microbial activity leads to changes in the proportion of bacterial feeders in a community.

Box 3. Colonizer–persister (cp) groupings of nematode taxa

Nematodes are assigned to cp groups on the basis of character sets that rank them along a colonizer–persister continuum on a one to five scale. The most rapid colonizers (cp-1) are bacterial-feeding, enrichment opportunists with short generation times, large gonad volume, high rates of egg production, high rates of mobility and metabolic activity, and almost constant ingestion of the microbial suspension in soil solution. These nematodes have the ability to enter a non-feeding, inactive 'dauerlarva' survival stage when resources are limited or under stressed conditions.

The productivity characteristics of general opportunists (cp-2) are less extreme than those of cp-1. Feeding on bacteria appears more deliberate and the bacterial-feeding cp-2 taxa do not have a dauerlarva stage.

Productivity characteristics are less pronounced in higher cp groups and bacteria are less likely to be the primary food resource. Species in higher cp-groups produce fewer eggs than those in lower groups; they are also the most susceptible to environmental disturbance and change. Interestingly, the ability to reproduce parthenogenetically, ostensibly a high-productivity character, is not a useful criterion for cp grouping because it occurs in representative taxa across all groups.

Species in different cp classes differ in ecological amplitude; lower cp groups are represented in terrestrial, freshwater and marine environments, whereas nematode taxa in higher cp groups generally have a narrower ecological amplitude.

plant-feeding nematodes, resulting in higher PPI levels. The PPI, MI and the ratio of the two are valuable measures with which to assess the state of agroecosystems[9,11–13,25–28].

The MI under conditions of stress

Pollution induces a shift in community structure towards dominance by opportunistic species[29]. For nematodes, the MI decreases as a result of the disappearance of taxa that are higher on the cp scale. These taxa, which are composed mainly of predators and omnivores, are assumed to play a regulating role both in the soil food web and in buffering outbreaks of soil-borne plant diseases. Under conditions of light to moderate pollution, the abundance of sensitive species is reduced, whereas the abundance of tolerant species is unaffected or increases. However, even the tolerant species decrease under heavily polluted conditions, either because of toxic effects or because of a decrease in microbial activity[30,31].

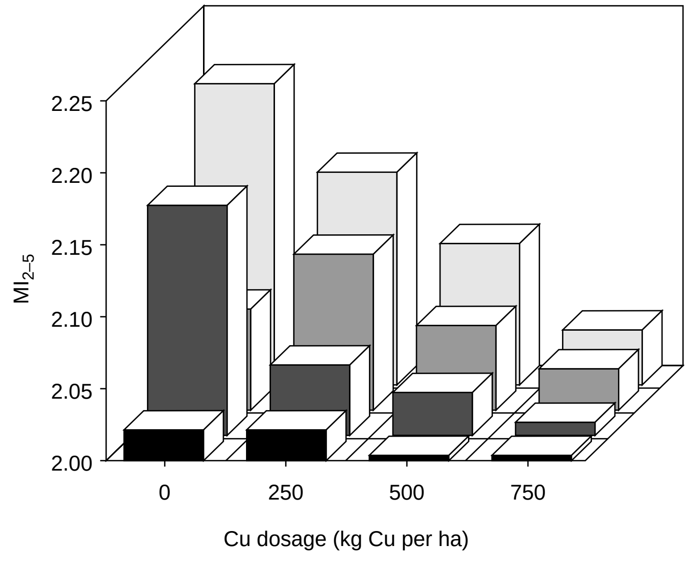

Fig. 1. Relationship between the maturity index (MI) based on cp groups 2–5 ($MI_{2–5}$), pH and dosage of copper (Cu) ten years after adding copper sulfate ($CuSO_4$) to a soil buffered at different pH levels (represented by shading, which increases with increasing acidity: palest = pH 6.1 then pH 5.5, 4.7 and 4.0, respectively). Cp groups 2–5 represent nematode taxa classified into four of five classes along a colonizer (one) to persister (five) continuum by omitting the enrichment opportunists (cp-1). *Redrawn, with permission, from Ref. 31.*

The MI is a convincing indicator of the degree of heavy metal contamination in marine sediment[32] and in terrestrial systems[33–35]. However, in agricultural soils, which are already highly disturbed, the relationship between the MI and heavy-metal stress is obscured by the high abundance of Rhabditidae (cp-1). The sensitivity of the MI to abundant opportunists is being increasingly recognized. Indeed, a recent review has questioned the usefulness of including opportunists in the index[31].

Two types of nematode opportunists can be distinguished: enrichment opportunists and general opportunists[23,36]. Enrichment opportunists colonize food-enriched conditions and are classified as cp-1; general opportunists are classified as cp-2 (Refs 23,37). The response of enrichment opportunists to almost any kind of disturbance suggests two alternative calculations of the MI. One is to omit enrichment opportunists if the MI is a measure of pollution-induced stress under enriched conditions, the other is to use a graphical representation of the MI. In an agroecosystem, where copper sulfate ($CuSO_4$) was applied ten years previously to soil fixed at different pH levels, the MI based on cp-2–5 decreased with both decreasing pH and increasing Cu. There was also a synergistic interaction between the two stressors[31] (Fig. 1). A graphical approach[38] allows the response of enrichment opportunists (cp-1), general opportunists (cp-2) and persisters (cp-3–5) to be distinguished. Greater dominance of cp-1 types indicates 'enrichment'; increase of cp-2 (decrease of cp-1 and cp-3–5) indicates 'stress'; and increase of cp-3 to cp-5 indicates natural succession mediated by increased environmental stability[31,37] (Fig. 2). The graphical representation of nematode community structure provides an integral synopsis of the state of the environment and is much easier to interpret than a list of incumbent species.

Why are persisters more sensitive than colonizers to chronic pollution? There are several possible explanations: cumulative effects in long-lived species, high genetic variability of opportunists accelerating the selection of tolerant genotypes, and rapid recovery of opportunists during fluctuations in stress concentration. In addition, acute toxicity is highly correlated with cp rating, suggesting that the effect of pollutants is not only on reproductive potential[22,30,39].

The MI in relation to nematode community succession

Each sere in a vegetation succession has a characteristic nematode community, which reflects the biotic and abiotic characteristics of each successional stage[40] and influences the vegetation succession[41]. If the nematode faunae of two stable successional stages differ in their MI, it is probably a result of differences in rhizosphere ecology, soil nutrient status, pH or soil pollution.

Primary succession in the nematode community of a nutrient-deficient habitat has not been studied, but it is unlikely to be reflected by an increasing MI. If the first successional stage of a nutrient-deficient environment consists of algae or mosses, the first nematode colonizers will be omnivorous Dorylaimida and general opportunists[23]. Nematode succession of nutrient-rich habitats, such as cow dung, with high microbial abundance and activity, is initiated by enrichment opportunists carried by insects[42]. The enrichment opportunists are slowly followed by nematodes with higher cp values[23]. During secondary succession, in the recovery of disturbed habitats, enrichment opportunists or general opportunists initially dominate, depending on the level of microbial activity.

Once soil fertility is enhanced with manure, the MI decreases rapidly and enrichment opportunists predominate. The first colonizers are replaced by general opportunists as microbial activity decreases and the MI gradually increases with decreasing soil fertility. During further succession, the general opportunists are replenished – but not replaced – by persisters that are not necessarily dependent on the same resources[43,44]. Therefore, species richness increases but general opportunists remain dominant.

Recent studies in New Zealand[45] and Cameroon[46] suggest that the MI reaches much higher values in those countries than it does in comparable habitats in Europe[47]. Perhaps protozoa or other organisms replace general opportunist nematodes as primary grazers in the soil food web under certain conditions.

The structure of nematode communities in sediments of flowing freshwater is inconsistent and variable. Community structure might be the result of frequent introductions of species rather than trophic interactions among species. Although the presence of enrichment opportunists clearly indicates microbial grazing by nematodes[2,48], the analysis of nematode community structure and the use of MIs in freshwater sediments require further study.

Further applications and prospects

One objective of environmental policy is the conservation and management of areas that provide habitat for rare plants or animals. Even agroecosystems can be unique in their combination of soil characteristics. Nematodes are potentially useful as indicators and for setting management priorities in unique and valuable habitats. It is difficult, and perhaps unimportant, to calculate how many species are present when determining the biodiversity of an area. The relative rareness of indicator species could provide useful information more readily. Enrichment-opportunist nematodes are not useful as indicators because they occur whenever microbial activity increases. When changes in the soil system are monitored over time, seasonal influences on the nematode community become apparent[13]. As decomposition rates change in relation to temperature and substrate, and as plants progress through an annual cycle of competition for nutrients with fungi and bacteria, there are short-term changes in nematode community structure. Such changes predominantly involve opportunists (cp-1 and cp-2). The types and abundance of persister species with narrow ecological amplitudes are indicative of unique combinations of soil habitat characteristics that might require priority preservation or intervention[49].

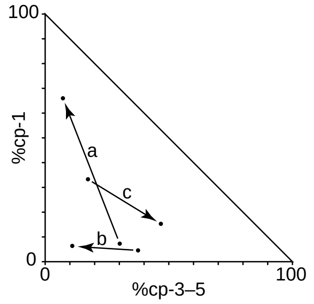

Fig. 2. Shifts in the percentage representation in the nematode fauna of taxa classified into five cp groups along a colonizer (one) to persister (five) continuum in response to (a) environmental enrichment, (b) acidification and (c) succession. Arrows indicate the direction of change: %cp-1 is the percentage of the fauna represented by enrichment opportunists (group 1); %cp-3–5 is the percentage of the fauna represented by taxa of persister species with K-selected characteristics (groups 3–5). *Redrawn, with permission, from Ref. 37.*

There are many examples of the use of community structure analysis for environmental monitoring; a few (e.g. those using protozoa[50] and mites[51]) have taken a cp-classification approach. The advantage of the MI based on nematode community structure is in the ubiquity of nematodes, the relationship between form and function, the variability among families in sensitivity to environmental disturbance, the ease with which assessments can be made and the consistent response of taxonomic groups to different forms of environmental perturbation. In The Netherlands, the National Institute of Public Health and the Environment (RIVM), the largest agency responsible for monitoring and managing polluted soils, routinely employs the MI as a monitoring tool. In the USA, the MI approach is being evaluated for large-scale regional monitoring of the ecological health of agricultural soils[12].

Life-strategy-based ecosystem parameters using nematode faunal assemblages are new. Calibration of the cp-classification at taxonomic levels below the family might increase sensitivity of the MI but will require further research on the response of individual genera to disturbance. In a few cases, divergent functions, such as fungal-feeding, predation and insect parasitism in the Aphelenchina, occur within a taxonomic level. Where there is functional divergence within a family, identification at the genus or species level might be necessary.

Future research challenges concerning the MI include characterization of seasonal effects, isolation techniques, identification of stressors, statistical properties and reference criteria. For example, the presence of a few cp-5 nematodes in a sample might have considerable impact on the magnitude of the MI because of the weighting factor. However, the probability of detecting such rare occurrences might differ from that of detecting more abundant organisms. Furthermore, the functional biology of some of the nematodes in higher cp classes is less well known than that of cp-1 and cp-2 nematodes. We are still in a period of development and testing, but new opportunities for practical application are continually emerging (Box 4).

Box 4. Past and future vision

In 1914, Cobb[52] wrote:

> …if all the matter in the universe except the nematodes were swept away, our world would still be dimly recognizable, and if, as disembodied spirits, we could then investigate it, we would find its mountains, hills, vales, rivers, lakes, and oceans represented by a film of nematodes. The location of towns would be decipherable, since for every massing of human beings there would be a corresponding massing of certain nematodes. Trees would still stand in ghostly rows representing our streets and highways. The location of various plants and animals would still be decipherable, and, had we sufficient knowledge, in many cases even their species would be determined by an examination of their erstwhile nematode parasites.

As we approach the millennium, we can provide further detail to Cobb's pictorial prose by adding that fields in which the soils have been managed in a sustainable manner would also be apparent and distinguishable from those in which the soils are damaged by misuse of pesticides or irreversibly polluted with heavy metals. Areas in which the soils have increased in salinity, acidity and eutrophication would be evident, as would those with undisturbed and pristine habitats that warrant the highest priority for protection. Our synthesis of the ecological function of nematodes in soil ecosystems has progressed to the extent that we can assess nematode faunal assemblages to measure the impact of stressors that threaten the functioning of soils. We can predict crop losses and can provide advice on cropping sequences and soil management practices so that sustainable optimal yields can be attained.

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