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Role of Nematodes in Soil Health and Their Use as Indicators[1]

Deborah A. Neher[2]

Abstract: The composition of nematode communities (plant-parasitic and free-living) may be used as bioindicators of soil health or condition because composition correlates well with nitrogen cycling and decomposition, two critical ecological processes in soil. Maturity and trophic diversity indices withstand statistical rigor better than do abundances, proportions, or ratios of trophic groups. Maturity indices respond to a variety of land-management practices, based largely on inferred life history characteristics of families. Similarity indices may be more useful than diversity indices because they reflect taxon composition. Improving existing indices or developing alternative indices refined by a greater understanding of the biology of key taxa may enhance the utility of nematodes as bioindicators.

Key words: biodiversity, biomonitor, ecology, integrity, maturity index, monitoring, nematode, soil, trophic diversity.

Biotic indicators of soil ecological health or condition can be used to assess the current status of vital ecological processes in soil and change in processes through time. Any indicator should reflect the structure and(or) function of ecological processes and respond to changes in soil condition that result from land-management practices. Furthermore, there must be sufficient taxonomic knowledge to identify organisms accurately and efficiently. For regional or national monitoring programs, additional criteria constrain choices of possible indicator taxa. For example, they must be applicable to all geographic locations, soil types, and vegetation types. For practical purposes, it is also desirable that costs for collecting samples by nonscientists be controlled, samples tolerate shipping to a central laboratory from remote locations, and frequent sampling not be required during the year (Neher et al., 1995).

Biologically, soil ecosystems support a diversity of microbes (fungi, bacteria, and algae), microfauna (protozoa), and mesofauna (arthropods and nematodes). Appropriate cautions are necessary when choosing organisms for use as bioindicators. For example, perspective may be narrowed by personal experience. An expert on a particular plant-pathogenic species, e.g., *Meloidogyne incognita,* may initially consider the species to be a good indicator because its presence and abundance are associated with development of economically important epidemics of root rot on cotton or tomato. However, individual species are not applicable across all plant species, soil types, or geographic climates. Caution must also be exercised on the other extreme—when choosing entire kingdoms for study, e.g., soil fungi and bacteria (sometimes pooled as the ''microbial community''). Although microbial communities are known to play critical roles in ecological processes, such as nutrient cycling, and also respond to environmental disturbances of soil, such as contamination by heavy metals (Duxbury, 1985; Nannipieri et al., 1990) and pesticides (Sims, 1990; Visser and Parkinson, 1992), there are inherent logistical and interpretative challenges. For example, microbial activity may fluctuate diurnally (Nannipieri et al., 1990), confounding time of day with site sampled in a regional monitoring program where hundreds of sites must be sampled within a 2-week period. Furthermore, it is tedious, indeed impossible, to identify all bacteria and fungi in a sample, and databases of biochemical profiles are either incomplete or inadequate, especially for free-living taxa.

Soil fauna have advantages over soil microbes as bioindicators. First, by being one or two steps higher in the food chain, they serve as integrators of physical, chemical, and biological properties related with their food resources. Second, their generation time (days to years) is longer than metabolically active microbes (hours to days), making them more stable temporally and not simply fluctuating with ephemeral nutrient flushes (Nannipieri et al., 1990). Nematodes (Bongers, 1990), Collembola (Frampton, 1997), and mites (Ruf, 1998) are three groups of mesofauna that have been considered for use as biological indicators. Of these three groups, nematodes have been evaluated most often for their use as indicators. Nematodes (free-living and plant-parasitic) may be the most useful group for community indicator analysis because more information exists on their taxonomy and feeding roles (Gupta and Yeates, 1997) than does for other mesofauna.

Nematodes possess several attributes that make them useful ecological indicators (Freckman, 1988). Soil nematodes can be placed into at least five functional or trophic groups (Yeates et al., 1993), and they occupy a central position in the detritus food web (Moore and de Ruiter, 1991). A small fraction of soil fauna depends directly on primary producers, feeding on plant roots and their exudates. The subgroups of these organisms that form parasitic relationships with plants and their roots are the best known of soil organisms because of the damage they cause to agricultural crops—such as decreasing plant production, disrupting plant nutrient and water transfer, and decreasing fruit and tuber quality and size (Brussaard et al., 1997; Yeates and Coleman, 1982). However, most of the soil nematode species ac-

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[2] Assistant Professor, Department of Earth, Ecological and Environmental Sciences, University of Toledo, Toledo, OH 43606.

E-mail: deborah.neher@utoledo.edu

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tually have beneficial roles in ecosystem processes and are not parasites or pests. For example, microbial-grazing mesofauna, such as nematodes, affect growth and metabolic activities of microbes and alter the microbial community, thus regulating rates of decomposition (Seastedt, 1984; Trofymow and Coleman, 1982; Wasilewska et al., 1975; Whitford et al., 1982; Yeates and Coleman, 1982) and nutrient mineralization (Seastedt et al., 1988; Sohlenius et al., 1988). Unlike earthworms, nematodes are ubiquitous and certain species are frequently the last animals to die in polluted or disturbed areas (Freckman, 1988; Samoiloff, 1987), partly because they can survive desiccation and revive with moisture. Relative to other soil fauna, trophic or functional groups of nematodes can be separated easily, primarily by morphological structures associated with their various modes of feeding (Freckman, 1988; Yeates and Coleman, 1982). The relative abundance and size of nematodes typically make sampling and extraction easier and less costly than for other soil fauna.

Role of Nematodes in Soil Health

Nematodes play an important role in essential soil processes. The direct contribution of nematodes to nitrogen mineralization and distribution of biomass within plants has been demonstrated in controlled experiments. In petri-dish experiments, more nitrogen is available in the ammonium form when bacterivorous and fungivorous nematodes are present than when they are absent (Trofymow and Coleman, 1982). Nitrogen mineralized through microbial grazing is available subsequently to plants (Seastedt et al., 1988; Sohlenius et al., 1988) and has been demonstrated to affect biomass allocation in plants. In a microcosm experiment with buffalo grass (*Bouteloua gracilis*), Ingham et al. (1985) demonstrated that plant shoots grow larger in soils with bacteria, fungi, and their respective grazers than in soils with less complex soil food webs. Root biomass may also increase in the presence of microbial-grazing nematodes.

Under field conditions, bacterivorous and predatory nematodes are estimated to contribute (directly and indirectly) about 8% to 19% of nitrogen mineralization in conventional and integrated farming systems, respectively (Beare, 1997). Nematodes contribute to nitrogen mineralization indirectly by grazing on decomposer microbes, excreting ammonium, and immobilizing nitrogen in live biomass (Beare, 1997; Ferris et al., 1998; Ingham et al., 1985). Predatory nematodes also regulate nitrogen mineralization by feeding on microbial-grazing nematodes, a conduit by which resources pass from bottom to top trophic levels (Wardle and Yeates, 1993). Although plants depend on nitrogen for their survival and growth, ecological disruptions such as cultivation or additions of mineral fertilizer increase nitrogen availability, sometimes in excess of, or asynchronous with, plant needs. Increased availability of nitrate and ammonium is associated inversely with successional maturity of nematode communities in cultivated mineral soils for agricultural purposes (Neher, 2001).

Use of Nematodes as Indicators

Nematodes have several biological features that reinforce their use as indicators. First, nematodes have a permeable cuticle, which allows them to respond with a range of reactions to pollutants and correspond with the restorative capacity of soil ecosystems (Šály and Rágala, 1984; Wasilewska, 1979, 1989). Second, some nematodes have resistant stages such as cryptobiosis or cysts that allow them to survive inactively during environmental conditions unfavorable to growth and(or) development. However, some nematode taxa such as Dorylaimidae have no resistant stages, which may make them more sensitive to environmental change (Bongers, 1999). Finally, nematodes have heat shock proteins that are highly conserved (Hashmi et al., 1997). Expression of these proteins is enhanced when exposed to stresses such as heat, metal ions, or organic toxins (Kammenga et al., 1998). Perhaps these proteins could serve as biomarkers for ecotoxicological assessment of soils (Guven et al., 1994, 1999; Kammenga et al., 2000).

Since the 1970s, nematodes have been used as environmental biomonitors for aquatic systems. For example, *Panagrellus redivivus* has been used as a biomonitor to detect toxin concentrations that affect molting and organism size through stimulation, inhibition, or lethality, and provides a rapid bioassay that costs less than 10% of a *Salmonella* bioassay. The nematode has been used to determine toxic effects of about 400 single chemicals (Samoiloff, 1987). Also in the 1970s, the use of a nematode: copepod ratio (Raffaelli and Mason, 1981) was popular for monitoring of aquatic ecosystem condition. Both nematodes and copepods are abundant in aquatic systems but differ in their sensitivity to stress. Generally, nematodes are less sensitive to environmental stress or pollution than are copepods. Therefore, a high ratio indicates pollution, such as oil spills, sewage, and increasing organic enrichment (Amjad and Grey, 1983; Raffaelli and Mason, 1981). The nematode: copepod ratio is, however, fraught with problems. First, pollution has already occurred by the time the ratio shift is obvious. Second, a positive correlation between copepod populations and sand grain size makes it impossible to separate the effects of pollution from those of sediment particle size, thereby reducing statistical rigor (Coull et al., 1981). Finally, copepods are noted to consume nematodes of different trophic groups (Lehman and Reid, 1993), rendering the ratio unreliable.

In the 1980s, interest increased for using nematode communities as indicators for environmental monitoring of terrestrial communities (Bongers, 1990; Freckman, 1988). Initially, simple indices of abundance, proportions, or ratios of nematodes by trophic group were proposed. Subsequently, diversity indices were employed and a Maturity Index (MI) was developed for terrestrial nematodes (Bongers, 1990; Yeates, 1970, 1984). Later, the application of the MI was extended successfully to marine and brackish sediments (Bongers et al., 1991). Rigorous statistical analyses reveal that maturity and trophic diversity indices better differentiate the ecological condition of soils on a regional scale than do individual or ratios of trophic groups (Neher and Campbell, 1996; Neher et al., 1995).

Diversity indices are popular because they are easy to calculate. However, significant semantic, conceptual, and technical problems limit their usefulness as indicators of soil condition. Computationally, they represent summations of taxon proportions without differential weight for qualitative differences among taxa, which render them insensitive to taxon composition. Therefore, soils with 100% exotic or 100% native species could have identical diversity values. Alternatively, similarity indices, such as the Jaccard and Sørensen indices, are sensitive to taxon composition (Jongman et at., 1995; Topham et al., 1991) and would give a value of zero for a comparison of 100% exotic vs. 100% native taxa.

Diversity has been equated with numbers of taxa, and the popular press has perpetuated this misconception. Rather, diversity integrates numbers of taxa (i.e., richness (S)) and equitability among taxa (i.e., evenness (E)). Although Shannon (H') (Shannon and Weaver, 1949) and Simpson (λ) (Simpson, 1949) indices are most popular, there are many diversity indices—each having relative strengths. For example, the Camargo index may be more sensitive for assessing structural alterations in aquatic communities than the H' and MacArthur indices, which are sensitive to the number of taxa present and the whole spectrum of taxon proportions (Camargo, 1992). Typically, the H' index is sensitive to rare taxa, and the λ index weights common taxa. Jackknife methods can be applied to skewed data (Potvin and Roff, 1993). Hill's family of diversity numbers is easiest to interpret ecologically because the indices define units as taxa but they are not necessarily superior from a statistical perspective (Heip et al., 1988; Ludwig and Reynolds, 1988). Hill's diversity numbers N0, N1, and N2 are defined as numbers of all taxa, abundant taxa, and very abundant taxa, respectively (Ludwig and Reynolds, 1988). N1 equates with an antilog of a Shannon index ($e^{H'}$), and N2 equals the reciprocal of a Simpson index ($1/\lambda$).

Even though diversity is most often equated with species, it can be applied at various taxonomic levels of resolution, such as genus, family, and trophic group. For free-living nematodes, it is more common to apply a diversity index to taxonomic levels above species because species identifications based on morphology are difficult. In addition, functional groups are a practical necessity because the effect of each species on ecosystem processes has not been determined (Chapin et al., 1992).

In agricultural soils, greater diversity of trophic groups is correlated with an increase in the frequency of generally-less-abundant trophic groups (i.e., fungivorous, omnivores, and predators) relative to that of generally-more-abundant trophic groups (i.e., bacterivorous and plant-parasitic groups) (Wasilewska, 1979). Appropriate caution must be taken when applying indices at the family or trophic group levels. Diversity is linked artificially to the taxonomic resolution an investigator employs. Unfortunately, ambiguity in trophic classification of nematodes usually occurs because it is inferred by morphology rather than actual experiments on feeding preferences (Yeates et al., 1993). Furthermore, feeding-habit groupings may be ambiguous and(or) not mutually exclusive in some cases. For example, abundant populations of *Aphelenchoides, Tylenchus, Tylencholaimus,* and *Ditylenchus* can be classified as "plant/fungal feeding" nematodes (Sohlenius et al., 1977), or some "predaceous" *Mesodorylaimus* sp. can grow and reproduce by feeding on bacteria (Russell, 1986). *Tylenchus* spp. are often considered fungal-feeders in ecological studies, but the basis of the judgment is dubious because several species feed and reproduce on roots. In other cases, some species may always be placed in one category and may have developmental stages or generations that fit in another category. Finally, another disadvantage of relying on trophic groups for regional or national monitoring programs is that the method of extraction affects the proportion of each trophic group obtained. For example, a modified Cobb's sifting-and-gravity method with multiple sievings is more time-consuming but recovers a larger proportion of total nematodes and a greater representation of all trophic groups than does elutriation with one sieving (McSorley and Walter, 1991; Neher et al., 1995).

Maturity indices are used as a measure of the ecological successional status of a soil community. They are based on the principle that different taxa have contrasting sensitivities to stress or disruption of the successional sequence because of their life-history characteristics. Because succession can be interrupted at various stages by common agricultural practices, such as cultivation and applications of fertilizer and pesticides (Ferris and Ferris, 1974; Wasilewska, 1979) (Table 1), the successional status of a soil community may reflect the history of disturbance. Therefore, smaller index values are indicative of a more disturbed environment and larger values may indicate a less disturbed environment (Freckman and Ettema, 1993).

Bongers' original MI proposal had separate indices for free-living (MI) and plant-parasitic nematodes

TABLE 1. Maturity Index variations.

Index	Groups[a]	CP[b]	Citation(s)
MI	FL	1-5	Bongers, 1990
MI25	FL	2-5	Bongers et al., 1995; Neher and Campbell, 1994; Popovici, 1992
PPI	PP	2-5	Bongers, 1990
ΣMI	FL + PP	1-5	Yeates, 1994
ΣMI25	FL + PP	2-5	Neher and Campbell, 1996

[a] FL = free-living, PP = plant-parasitic.

[b] CP = colonizer-persister values (Bongers, 1990).

(PPI). The index is represented by a colonizer-persister (CP) value that ranges from a colonizer (CP = 1) to a persister (CP = 5) with the index values representing life-history characteristics associated with *r*- and *K*-selection, respectively. Those with a CP = 1 are *r*-selected or colonizers, with short generation times, large population fluctuations, and high fecundity. Those with a CP = 5 are *K*-selected or persisters, produce few offspring, and generally appear later in succession (Bongers and Bongers, 1998; Bongers and Ferris, 1999). Small and large CP weights correspond with taxa relatively tolerant and sensitive to ecological disturbance, respectively. Two modifications to the MI include one proposed by Yeates (1994) and a second proposed by both Popovici (1992) and Bongers et al. (1995). Yeates' (1994) proposed modification of the index is based on merging free-living and plant-parasitic nematodes in a soil community (ΣMI). Popovici (1992) was the first to suggest removing the nematode families with CP = 1 from the index (MI25). In Bongers et al. (1995), opportunistic taxa (CP = 1) are re-evaluated because they are considered enrichment opportunists and their population densities increase rapidly in response to additives of nutrients to soil and may not necessarily reflect long-term changes in soil ecological condition. Those with CP values between 2 and 5 are more stable temporally and may provide long-term information about environmental conditions.

Maturity indices have the strength that observed values vary with land management practices (Table 2) among plant species, soil types, and seasons (Neher et al., 1995). Nematode community structure and function are known to change in response to land-management practices such as nutrient enrichment through fertilization by organic or inorganic nitrogen, cultivation, liming, drainage, plant community composition and age, and toxic substances such as heavy metals, pesticides, and polycyclic aromatic hydrocarbons.

Despite such useful attributes, maturity indices are also subject to serious limitations. Notably, CP values are inferred by morphology rather than confirmed by feeding preference experiments (Bongers, 1990; Yeates et al., 1993). Consequently, the CP values established for particular taxa will be modified through time as detailed life-history information becomes available (e.g., Wasilewska, 1995a; Bongers et al., 1995). Secondly, maturity indices were proposed for implementation using the family level of resolution. However, the index may be improved by increasing resolution through application to genera (Ettema, 1998) to overcome problems associated with genera within a family, or species within a genus, having contrasting life-history characteristics and, also, the incongruent rules for taxo-

TABLE 2. Direction of response of maturity indices to various kinds of disturbance. If an index is not listed for a particular type of land-management practice, it was either not significant or mentioned in a publication.

Disturbance	Response	Citation(s)
Cultivation	↑ or ↓PPI, ↓MI, ↓ΣMI, ↓ΣMI25	Freckman and Ettema, 1993; Yeates, 1994; Yeates and van der Meulen, 1996
Organic nitrogen: manure or urea	↑PPI, ↓MI	de Goede and Dekker, 1993; Ettema and Bongers, 1993; Ferris et al., 1996; Neher, 1999; Neher and Olson, 1999
Mineral fertilizer: nitrate or ammonium	↑PPI, ↓MI, ↓ΣMI25	Neher, 1999
Liming	↓MI	de Goede and Dekker, 1993
Fumigants: methyl bromide or metamsodium	↓MI, ↓ΣMI, ↓PPI	Ettema and Bongers, 1993; Yeates and van der Meulen, 1996
Herbicides and(or) insecticides	↓MI25	Neher and Olson, 1999
Replacement of annual crops by perennial crops	↑PPI, ↑MI, ↑ΣMI	Freckman and Ettema, 1993; Neher and Campbell, 1994; Yeates, 1994
Increasing age of meadows	↑MI	Wasilewska, 1994
Conversion of grass monoculture to mixed culture	↑MI	Wasilewska, 1995b
Drainage of fen peat soils	↓MI, ↓ΣMI	Wasilewska, 1995a
Heavy metals	↓MI, ↓MI25, ↓ΣMI, ↓ΣMI25	Korthals et al., 1996a, 1996b[a], 1998[b]; Nagy, 1999[c]; Yeates, 1994[d]
Polycyclic aromatic hydrocarbons: phenanthrene	↓ΣMI	Blakely, 1999
Benzo[a] pyrene	↑ΣMI25	Blakely, 1999

[a] Cu, Zn, Ni.

[b] Cu, Zn.

[c] Cr, Cd.

[d] Cu, Cr, Ar.

nomic nomenclature. Third, calibration of indices by quantitative levels of disturbance, ecosystem type (Neher, 2001), and major land resource regions (Neher et al., 1998) is necessary for interpretation. Fourth, regional or national environmental surveys span 98-107 genera in 43-50 families (Neher et al., 1998) that require comprehensive knowledge of nematode taxonomy among all groups. Currently, a major limitation in implementation of maturity indices is the general lack of persons and commercial laboratories with the knowledge and personnel, respectively, to handle large numbers of samples for identification of free-living nematodes.

Improving the indices may increase the utility of nematodes as bioindicators, employing a suite of complementary indices, or developing alternative indices. Biotic similarity indices may be more useful than diversity indices because they are sensitive to taxon composition. An Index for Biotic Integrity (IBI) (Karr et al., 1986) or Weighted Coenotic Index (WCI) (Wodarz et al., 1992) provides the advantage of integrating the strengths of several indices including components of taxon richness, taxon evenness, taxon composition based on habitat, life-history traits, trophic composition, abundance, exotics, and disease. Interpretation of IBI and WCI requires reference to some putatively undisturbed, baseline/reference community for interpretation or comparison (Karr, 1991, 1995) for each implementation. Unfortunately, undisturbed or pristine reference bases are scarce. The IBI was developed originally for fish communities (Karr et al., 1986) and has since been adapted for benthic (Kerans and Karr, 1994) and avian (Moors, 1993) communities in freshwater ecosystems. Indices for Biotic Integrity have been applied successfully in a variety of contexts including mine drainage, sewage effluent, and habitat alteration, and in a diversity of geographic areas (Karr, 1991). Fiscus (1997) attempted to adapt the IBI concept to nematodes but found it incapable of differentiating levels of disturbance caused by a variety of land-management practices. Its limited utility was attributed to ambiguity among trophic group assignments, paucity of empirical evidence for life-history traits, distinction between exotic and native species, and characterization of the health of individual nematodes. The WCI has been applied to protozoans (testate, amoebae, and ciliates), earthworms (Wodarz et al., 1992), and nematodes (Yeates et al., 1997).

Given the limitations and pitfalls of various indices, one asks whether it is reasonable to expect a global nematode index of soil condition (e.g., Yeates and van der Meulen, 1996). A single nematode index may be useful for regional or national surveys that summarize findings to non-scientists such as political leaders. However, research efforts may be better directed toward elucidating genera or species that are especially sensitive or tolerant to impact of specific land-management practices for implementation at local scales. Identification of these key taxa would be useful as individual biomonitors or for streamlining numbers of operational taxonomic units (OTUs) necessary for use in composite indices, such as maturity indices, IBI, or WCI. Yeates and van der Meulen (1996) mention that indexing ''key populations'' may prove more useful than a single nematode index.

Environmental disturbances in agroecosystems can be classified into two major categories—chemical and physical—that can alter nematode communities in qualitatively different ways (Fiscus and Neher, 2002). Chemical disturbances include nutrient enrichment and chemical pollutants; physical disturbances include cultivation. Nematode taxa may be sensitive to disturbance directly and(or) indirectly. Patterns of nematode taxon sensitivity to direct and indirect effects of management practices can be detected using analytical tools such as canonical correspondence (CCA) and partial CCA (ter Braak, 1986, 1988, 1995), respectively. Sensitivity and insensitivity are defined as a respective decrease and increase in abundance when exposed to a disturbance. Indirect effects are defined as changes in nematode abundance due to secondary, physical or chemical effects of a management practice. For example, an indirect effect may be a nematode community response associated with decreased organic matter, presumably caused primarily by cultivation. Decreased organic matter would be a direct effect, and the secondary community or population response of nematodes would be an indirect effect. Taxa considered relatively sensitive or insensitive to particular types of disturbance may be considered for further evaluation as ''key taxa.'' Fiscus and Neher (2002) propose such a set of taxa based on analysis of data from sites with contrasting cultivation and chemical disturbance intensities (Table 3) (McQuaid and Olson, 1998; Neher and Olson, 1999). Caution must be exercised in selecting groups of key taxa because management practices often employ a combination of disturbance and nutrient enrichment, confounding two categories. For example, soils may be cultivated followed by applications of mineral fertilizer and herbicides. Generally, cultivation might be considered a negative disturbance and chemical/nutrient-driven enrichment a positive effect. Negative and positive infer decreasing and increasing populations of certain taxa, respectively. In management practices that combine these two opposing effects—one decreasing and one increasing populations of certain taxa—it is difficult to link an indicator based on nematode community structure directly to changes in ecological process.

In conclusion, it makes ecological sense to use nematodes as bioindicators of soil condition. Nematodes represent a central position in the soil food web and correlate with ecological processes such as nitrogen cycling and plant growth. Although there are few persons

TABLE 3. Genera sensitive to physical and chemical disturbances either directly or indirectly. Sensitivity (S) and insensitivity (I) are defined as increased and decreased abundance in response to a disturbance, respectively (adapted from Fiscus and Neher, 2002).

	Physical		Chemical	
Genus	Direct	Indirect	Direct	Indirect
Achromadora	I	S		
Acrobeles		I		I
Acrobeloides		I		
Alaimus			S	S
Anatonchus	I	I		
Aphelenchoides	S	S		I
Aporcelaimus				I
Cephalobus	I	S	I	
Chiloplacus	I	I		
Clarkus	I	I		I
Cylindrolaimus			S	
Diphtherophora			I	
Discolaimus	S	S	S	S
Enchodelus				I
Eucephalobus	S	S	I	I
Eudorylaimus	S	S		S
Eumonhystera		S		S
Heterocephalobus	S	S		
Mesorhabditis			S	
Monhystera		S	I	
Mylonchulus	I	I	I	
Panagrolaimus		S		I
Plectus	I	I	I	
Prismatolaimus	I	S	S	
Tylencholaimellus	I	I		I
Wilsonema	S	S		

trained and few commercial laboratories available to identify free-living nematodes in large numbers of samples, nematode taxonomy is more extensively developed than the taxonomy for other soil fauna such as mites, protozoa, and collembolans. Priority research areas for implementation of nematodes as indicators of soil condition across large geographic scales include verification of life-history characteristics, feeding preferences, identification of key taxa, correlation of key taxa to disturbance, and calibration of indices relative to ecosystem, climate, and soil type.

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