

Soil Nematode Diversity: Species Coexistence and Ecosystem Function¹

CHRISTIEN H. ETTEMA²

Abstract: Soil nematode species diversity is often high, both at ecosystem and single soil-core scales. First, how can so many species coexist? There is evidence of niche partitioning, notably of physical space, but vast interspecific overlaps and trait plasticity seem equally common. It appears that coexistence of species with similar resource needs is made possible by small-scale disturbance and predation, which likely reduce local population sizes and interspecific competition. Regional processes such as dispersal, large-scale disturbance, and aggregation, which govern ecosystem level diversity, may also affect local species interactions and soil-core scale diversity. Second, what is the significance of having so many species, with so few trophic functions, for ecosystem processes? Focusing on bacterivore diversity, it is clear that species contributions to decomposition, likely to differ as a function of individual biologies, are concealed by the trophic group approach. However, considerable functional redundancy probably exists, which may explain why decomposition processes are maintained in highly disturbed soils despite the extinction of many species. Thus, soil nematode diversity is important for the long-term stability of soil functioning, and merits protection and further study.

Key words: biodiversity, disturbance, ecology, ecosystem function, functional redundancy, nematode, niche partitioning, soil, species coexistence, species diversity, trophic groups.

Terrestrial ecosystem fluxes of carbon, nutrients, leachates, and trace gases are regulated by the activities of hyperdiverse soil biotic communities (Anderson, 1995). In addition to tens of thousands of bacterial (Torsvik et al., 1994) and fungal (Domsch, 1975) types, a square meter of soil may contain several hundred to a thousand invertebrate species (Anderson, 1975). This striking diversity, for which soil has earned the title "poor man's tropical rainforest" (Usher et al., 1979), has raised two ecological questions. First, how can so many species with apparently low degrees of diet and habitat specialization coexist? Second, what is the function of this diversity for ecosystem

processes? Various soil ecologists have examined these questions in relation to the diversity of soil invertebrate orders and functional groups (Anderson, 1975, 1995; Beare et al., 1995; Brussaard et al., 1997; Ghilarov, 1977; Giller, 1996; Whitford, 1996), but fewer authors have specifically addressed the structure and function of species diversity within individual faunal groups (Foote, 1995; Heneghan and Bolger, 1996a; Lawton et al., 1996). The purpose of this review is to examine soil nematode species diversity and coexistence, and the relation between nematode diversity and soil ecosystem functioning.

SOIL NEMATODE SPECIES DIVERSITY

Soil nematode assemblages are often highly diverse, with species counts being rarely lower than 10, and frequently larger than 100 within a given ecosystem (Table 1; Bernard, 1992; Bloemers et al., 1997; Freckman and Virginia, 1997). Comparing between ecosystems is problematic because species diversity measurement depends on sampling intensity, which varies consider-

Received for publication 15 September 1997.

¹ Symposium paper presented at the 36th Annual Meeting of The Society of Nematologists, 19-23 July 1997, Tucson, Arizona.

² Institute of Ecology, University of Georgia, Athens, GA, 30602-2202.

E-mail: chettema@arches.uga.edu

This review could not have been written without the countless stimulating discussions with Soil Ecology Laboratory colleagues, particularly Liam Heneghan, Randi Hansen, and David Coleman. In addition, the comments of two anonymous reviewers and E. C. Bernard significantly improved the manuscript.

TABLE 1. Soil nematode species diversity in single and multiple soil cores, collected in various ecosystems.

Ecosystem (Location)	Survey area (ha)	Sample dates	Sampling strategy				Species diversity			Literature citation
			Total samples	Cores per sample	Core depth (cm)	Core volume (cm ³)	Core weight (kg fw)	Total	Maximum per core	
Polar (Antarctica)	?	1	130	1	10	1,000	1.5	3	3	Freckman and Virginia (1997)
Subarctic (Sweden)	?	1	1	1	25	?	0.125	34	34	Ruess et al. (1998)
Agricultural (Tennessee)	?	3	30	10	?	50	?	100	?	Baird and Bernard (1984)
Hardwood forest (Indiana)	118	3	54	50	10	31	?	175	29	Johnson et al. (1972)
Pasture (Denmark)	?	5	25	1	5	5	?	226	35	Overgaard Nielsen (1949)
Prairie (Kansas)	259	3	61	1	15	?	1.5-2.5	228	45	Orr and Dickerson (1966)
Rainforest (Cameroon)	?	1	22	1	15	500	?	153	42	Price and Siddiqi (1994)
Rainforest (Cameroon)	24	1	24	1	30	84	?	431	89	Bloemers et al. (1997)

ably among surveys (Table 1). In addition, because of the tremendous effort required, records on diversity at the species level are so scarce that a valid ecosystem comparison of nematode species diversity is yet impossible. Based on this concern, and because of recent findings of vast tropical nematode diversity (Table 1), Procter's (1990) thesis that higher-latitude biomes maintain greater soil nematode diversity than lower-latitude systems must be questioned (Price and Siddiqi, 1994).

Critical for evaluating the structure and function of nematode diversity in different ecosystems is knowledge of the scale(s) at which diversity is expressed. With the exception of the impoverished fauna in the dry valleys of Antarctica (Freckman and Virginia, 1997), it appears that nematode assemblages are species-rich not only at the ecosystem scale but also at the scale of a single-soil core, which may contain dozens of species (Table 1). Similarity of species composition among soil cores taken within the same ecosystem is often low. For instance, Price and Siddiqi (1994) found only 9 (6% of total) species to be present in >50% of the cores collected, and Orr and Dickerson (1966) found only 7 (3% of total). Although Johnson et al. (1972) combined 50 cores into one sample, they found that still only half of total species occurred in >50% of the samples. These data suggest that nematode diversity has a significant local, soil core-scale component, and a patchy distribution at the ecosystem scale.

SPECIES COEXISTENCE

The first question raised by the great diversity of nematode assemblages, notably in small soil volumes, is how can so many species coexist? Although in a typical soil-core sample only a few species dominate while most other species have low abundances (Freckman and Ettema, 1993; Niles and Freckman, 1998; Overgaard Nielsen, 1949), the maintenance of high nematode species diversity, in light of their presumably low degree of diet and habitat specialization, appears to be an enigma (Anderson, 1975; Ghilarov, 1977; Giller, 1996).

To explain nematode species diversity in single soil cores and in whole ecosystems, it is important to consider both local and regional processes that may affect species coexistence at different scales (Huston, 1994). For instance, competitive interaction is a local process, which may influence how many species can coexist at the local (soil core) scale where nematodes interact directly. Regional processes such as dispersal, immigration, and large-scale disturbance may influence regional (ecosystem) as well as local nematode diversity.

Local processes

The classic local-scale model for species coexistence is the so-called equilibrium community, which is governed largely by interspecific competition for limiting resources. One of the predictions of the equilibrium competition model is that potential competitors should exhibit extensive niche partitioning to allow their coexistence (Giller, 1996). During the 1970s it became increasingly obvious that this theory failed to fully explain natural patterns of species distributions and coexistence, while the importance of climatic fluctuations, disturbances, and predation became more apparent (Huston, 1994). The latter set of processes governs the so-called non-equilibrium community, in which competition is weakened because disturbance and predation continuously limit competitor population sizes. Thus, species with highly overlapping resource requirements could coexist for a considerable, if not indefinite, time without competitive exclusion to occur (Huston, 1994). What is the relative importance of niche partitioning—principally of food, space, and time—and of disturbance and predation for the maintenance of local nematode species diversity?

Food partitioning: Like many other soil animals, nematodes do not appear to partition food resources to a great extent; only 5 to 8 feeding habits are recognized (Yeates et al., 1993). Strong competition among plant feeders may limit diversity in this feeding group (Eisenback and Griffin, 1987; Freckman and Caswell, 1985; Sikora et al., 1979),

but observations of such interactions among species within other feeding groups are scarce. Before concluding that nematodes lack extensive diet specialization, it must be kept in mind that feeding habits of many species have been morphologically or taxonomically inferred rather than experimentally assessed (Yeates et al., 1993). In addition, diet definitions such as “bacteria” or “fungi” could be too general, as nematodes may be selective within these categories. For instance, Grewal and Wright (1992) found in petri dish studies that *Caenorhabditis elegans* was significantly more attracted to *Serratia* and *Enterobacter* species than to a *Bacillus* species. Similarly, Ruess and Dighton (1996) found that *Aphelenchoides saprophilus* reproduced significantly better on some mycorrhizal fungal species than on others. Yet it is far from clear whether coexisting nematode species would show different preferences, and whether under field conditions nematodes could afford to maintain such selectivity. In fact, diet plasticity, the crossing of trophic category lines, has been noted for several species (Yeates et al., 1993). Such diet shifts are sometimes part of ontogenetic development, but probably more often are a survival strategy in the typically heterogeneous and ephemeral soil habitat, and may be a means to avoid competition. Clearly, the large uncertainty regarding feeding habits in situ remains a serious problem that nematologists need to address.

Space partitioning: Soil harbors an immense diversity of pore, channel, and aggregate sizes; countless microsites with different microclimates; and several biological domains such as rhizospheres, detrituspheres, and drilospheres (Beare et al., 1995). Throughout this matrix, soil nematodes live in water-filled pores or in water films covering aggregates, roots, organic debris, and walls of earthworm burrows. Partitioning of this porous, watery world among nematode species could result primarily from the great variation in nematode body dimensions (Yeates, 1986). Because active movement is constrained by pore diameter and water-film depth, body width is particularly critical (Wallace, 1963). For example, the coexist-

ence of the bacterial feeders *Plectus parietinus* and *Paramphidelus uniformis* in a wetland soil in southern Georgia, USA (C. Ettema, unpubl.), can potentially be explained by body-width differences: Although they have equal average adult body length, *P. parietinus* is almost four times wider, which effectively separates its foraging range from that of *P. uniformis*. Boag and Robertson (1983) used thin sections of resin-impregnated soil to demonstrate such microdistribution differences between the large plant-feeder *Longidorus elongatus* and the smaller *Rotylenchus robustus*. Yeates (1987) provided experimental evidence of spatial partitioning by body-size variation among mononchid predators. In pastures that through earthworm introduction had increased average pore size, the large *Iotonchus stockdilli* was more abundant compared to control pastures, at the expense of the smaller *Clarkus propapillatus* and *Cobbonchus australis*, which were more abundant in control plots. Further inference of spatial partitioning by body-size variation has come from large-scale correlative patterns between nematode species and soil textures (De Goede and Bongers, 1994; Goodell and Ferris, 1980; Jones et al., 1969; Norton, 1979; Wallace et al., 1993; Yeates et al., 1997). Soil texture not only determines the physical structure of nematode space but also affects its temperature and moisture dynamics (Wallace, 1963). Microclimatic preferences may vary substantially between nematode species. For example, in pine forest soil incubations, Sohlenius (1985) found that population growth of coexisting bacterivorous species greatly varied with soil temperature and moisture. Numbers of *Chronogaster* sp. increased in warm and wet conditions, *Monhystera* sp. populations expanded in moist conditions regardless of temperature, while *Alaimus* sp. reproduced best in warm conditions regardless of moisture. *Acrobeloides* sp. thrived at almost all temperature-moisture combinations, including the hot, dry treatment. Temperature and moisture gradients, and vertical changes in root and organic matter content, spatially separate species within the soil profile (Alphay, 1985; De

Goede et al., 1993; Freckman and Virginia, 1989; Sohlenius, 1997; Yeates, 1980, 1981). As pore-size distribution, soil microclimate, root density, and organic matter content are interrelated by multiple connections, it is difficult to isolate species relations to single factors (Norton, 1979). Therefore, the answer to the question of whether nematode species partition space remains necessarily obscure in detail. However, considering the ample potential for partitioning provided by vast soil heterogeneity and nematode body-size variation, the overall answer is plausibly positive.

Time partitioning: Nematode coexistence may be further facilitated by temporal divergence in activities of species. Differences between trophically similar species have been noted at small temporal scales (minutes to hours), for instance, related to ingestion and metabolic rate, and at larger scales (weeks to months), such as in generation time and length of the reproductive period (Anderson and Coleman, 1982; Ferris et al., 1995, 1996, 1997; Robinson et al., 1986; Schiemer, 1983). Such rate differences, further modified by temperature, contribute to seasonal patterns and successional sequences after disturbance (Ettema and Bongers, 1993; Venette and Ferris, 1997; Yeates et al., 1985) and may lead to at least partial temporal separation of competing species (Anderson and Coleman, 1982; Sohlenius, 1985). Although *r*-selected species may be adapted to consume resources before others, potentially leading to competitive exclusion and reduced species diversity, tradeoffs in other life-history characteristics often preclude such outcomes. For instance, *Rhabditis* s. l. has significantly faster reproduction and metabolism than *Acrobeloides* sp. (Bongers, 1990; Ferris et al., 1995, 1996) but is more susceptible than *Acrobeloides* to fungal predators such as *Drechmeria coniospora* (Bouwman et al., 1996; Van den Boogert et al., 1994), and is more dependent on the presence of ample food resources (Ettema and Bongers, 1993; Schiemer, 1983).

Small-scale disturbance: Microclimatic and other small-scale disturbances may influ-

ence local nematode diversity by limiting overall nematode abundance and competitive pressure. Although soil generally is considered a favorable, stable habitat buffered from large changes in temperature and moisture (Coleman and Crossley, 1996; Giller, 1996), at the small spatiotemporal scales of nematodes it is a transient environment, particularly in the top few centimeters where most nematodes live. A case in point is the profusion in many soils of opportunist taxa suited for exploiting ephemeral habitats, such as *Acroboloides* spp. and *Aphelenchoides* spp. (Ettema and Bongers, 1993). Local species populations, restricted in their movement range, must cope with severe disturbances in habitat (water films, pore distribution) and food resources (e.g., microbial populations) as dry-wet and freeze-thaw cycles elapse, pulses of root exudates pass, and earthworms reassemble the soil profile. Although direct experimental evidence is not yet available, it seems likely that these small-scale disturbances facilitate local species coexistence by limiting overall nematode abundance and competitive pressure.

Predation: A similar effect may be expected from predation, since nematode abundances are significantly lowered by predators such as fungi (Bouwman et al., 1996), microarthropods (Hyvönen and Persson, 1996), and numerous other soil organisms (reviewed by Yeates and Wardle, 1996). Predation may particularly facilitate species coexistence if it primarily affects the dominant competitors (Huston, 1994), which is likely the case in nematode assemblages. Although many nematode predators are generalists, their primary victims may be among the dominant nematode species because predation rates in soil are largely dependent on chance encounters (Yeates and Wardle, 1996). For example, Hyvönen and Persson (1996) found that in humus incubations the populations of the dominant bacterivores *Acroboloides* and *Wilsonema* were more than halved in the presence of various predatory arthropods, while the less abundant *Alaimus* and *Teratocephalus* were unaffected compared to the predator-free control. While this density-dependent predation effect also

was expected for the abundant *Plectus*, this species was unaffected possibly because of evasive behavior (Hyvönen and Persson, 1996; Small, 1987). Similarly, Bilgrami (1993) found in petri dish studies that several bacterial feeding species greatly suffered from predation by *Aporcelaimellus nivalis*, except *Rhabditis* sp., which evaded predation by rapid undulatory movements. In this particular situation, where a strong competitor such as *Rhabditis* is less affected by predation than weaker competitors (the other bacterivores), predation may reduce rather than enhance diversity. However, assuming that every nematode species is susceptible to some predators, and given that in soils many different predator species operate simultaneously, it is likely that predation often reduces overall crowding and generally enhances local nematode diversity.

Regional processes

For many organisms, species coexistence and diversity is not only influenced by local processes, like those discussed above, but also may be affected by regional processes such as large-scale disturbance, dispersal and immigration, and aggregation (Huston, 1994). These processes appear to also affect nematode diversity, at ecosystem and soil core-scale.

Large-scale disturbance: In contrast to the punctuated events of soil microenvironmental variability, large-scale disturbances are typically long-lasting and often negatively affect nematode diversity, although it is sometimes surprising how many species survive environmental insults (Bloemers et al., 1997; Niles and Freckman, 1998). For instance, species reductions have been noted as a result of tillage and pesticide use (Freckman and Ettema, 1993), heavy-metal pollution (Korthals et al., 1996a, 1996b), acidification (Ruess and Funke, 1992; Ruess et al., 1996), and forest clearance (Bloemers et al., 1997). While these studies were not designed to test the effects of disturbances on species coexistence, they are relevant to the coexistence debate because their results have furthered the insight, sparked by Bongers (1990), that species within feeding

groups can have quite different life histories and environmental tolerances.

Dispersal and immigration: Dispersal and immigration may prevent competitive exclusion and enhance local diversity by subsidizing the local populations of inferior competitors through the regional species pool. Or, if competitive exclusion did occur, immigration may re-establish the extinct population (Huston, 1994). It is quite likely that dispersal and immigration processes play a role in the maintenance of local nematode diversity. Although active dispersal of nematodes may be limited, passive dispersal by wind and phoresis is significant. For instance, Orr and Newton (1971) collected 28 nematode genera, representing all feeding groups, from dust traps that caught nematodes dispersed by wind. Poinar (1983) reported numerous genera that travel short or long distances on or in various insects. Transport by other organisms such as earthworms, birds, and humans is likely important, as well. The result of dispersal, immigration, and extinction processes is a landscape mosaic of patches, where each patch is at a different stage of succession, close to or far away from competitive equilibrium (Huston, 1994). Such asynchronous patch dynamics may be one explanation for the low similarity in nematode species composition between soil cores taken within the same ecosystem.

Aggregation: A second spatially explicit process is population aggregation. In the equilibrium competition model, species populations are randomly distributed in a homogeneous environment, which maximizes the number of interspecific encounters and thus competitive pressure. However, in reality, species distributions often are aggregated because of population processes and in response to environmental heterogeneity (Legendre, 1993). Thus, the number of confrontations between competitors and the pressure to partition resources may be less than expected. Recent models (Hanski, 1987; Shorrocks and Rosewall, 1987) suggest that species with highly overlapping resource requirements can coexist if their resources are ephemeral and patchily

distributed, as long as they aggregate in different resource islands. Soil, with its high degree of spatiotemporal heterogeneity, clearly could accommodate such a mechanism (Giller, 1996), as has been demonstrated for coexisting soil mite species (O'Connell and Bolger, in press). Similarly, field studies of soil nematodes have shown that nematode distributions can be highly aggregated, with potential competitors (i.e., of similar feeding category) aggregating in partly or wholly separate patches, several square decimeters (Delaville et al., 1996; Rossi et al., 1996) to tens of meters squared in size (Ettema et al., in press; Wallace et al., 1993; Webster and Boag, 1992). Potentially, such island effects also occur at smaller scales, where nematode foods such as microbial colonies or root hairs are scattered in a labyrinth of pore channels, forming minute islands that each have different colonizing species. Species colonization of such resource islands may be partly deterministic (i.e., predictable because of species traits such as mobility and foraging behavior), but clearly colonization also has a major stochastic component. Small-scale aggregation effects likely form one more explanation for the high diversity of trophically similar species recovered from single core-soil samples.

Synthesis

In ecology, there is a longstanding tension between those who see every species as different and unique, and those who seek unifying patterns (Lawton, 1992, 1995). Traditionally, the coexistence debate focused on species differences, explaining the diversity of coexisting species by their differential use of resources. The equilibrium competition model formed the background against which Anderson (1975) termed the coexistence of soil faunal species with apparently low degrees of resource specialization "enigmatic." In the preceding review on food, space, and time partitioning among nematode species, it was found that there is in fact considerable evidence for niche partitioning among nematodes, most notably of spatial and temporal niche dimensions. These differences are interesting because they re-

fute the general notion that species within the same feeding group are biologically similar and functionally redundant. However, many of the cited studies not only include observations of differences but also report strong similarities among taxonomically and trophically related species, as well as potentially high plasticity of traits. Some of these studies may have lacked the level of resolution required to distinguish at the nematode-scale significant differentiation, or may have failed to address differences in other requirements and the persistence of traits in a complex field reality. Nonetheless, it becomes apparent that the equilibrium competition model alone is inadequate to explain the often high local nematode diversity. Although supporting data for nematodes are yet scant, it seems likely that alternative processes, such as small-scale disturbance, predation, and small-scale aggregation, play an important role in lessening local competitive pressure and allowing coexistence of species with similar resource needs. In addition, regional processes such as dispersal, immigration, and large-scale aggregation and disturbance, which determine ecosystem scale diversity, also may influence the outcome of local species interactions and resulting soil-core scale diversity.

A dynamic equilibrium community concept, where fluctuating local diversity results from an approximate balance among opposing regional and local processes (Huston, 1994), could provide the framework for future nematode ecological research. According to this model, solving the nematode coexistence puzzle clearly requires more than natural history studies of single species in petri dishes, or experiments with mixed species in homogeneous soil microcosms under controlled climate, even if innovative molecular, microscopic, or other sensitive techniques are used. It additionally demands non-equilibrium and spatially explicit thinking in designing experiments, which may, for instance, measure the effects of microclimatic variability, predation, and resource patchiness on nematode species coexistence in laboratory microcosms, and quantify

nematode community responses to natural or manipulated spatial patchiness, from soil core to ecosystem scale.

ECOSYSTEM FUNCTION

A second major question raised by soil nematode diversity is, what is the significance of having so many species, with so few trophic functions, for ecosystem processes? Will primary production and decomposition processes proceed differently if fewer microbivorous, herbivorous, or predaceous nematode species were involved, even if trophic group biomass were maintained? Given the nematode species loss that often occurs due to agricultural practices and environmental pollution, these questions are not just purely of academic interest. Unfortunately, it is easier to ask than to answer them, as experimental data are lacking and various ideas are difficult to test in the field (Lawton et al., 1996). Yet, since the question is primarily the definition of interspecific differences and similarities in nematode functions, it is possible to infer some general predictions from the data reviewed above on species coexistence. For brevity, the next discussion is focused on the function of bacterivorous nematode diversity for decomposition processes.

Bacterivorous nematodes, which feed on primary decomposers, have considerable leverage on decomposition rates (Freckman, 1988). In food web-based decomposition models (Bengtsson et al., 1996), their influence is dependent on trophic group biomass but not species composition, a pragmatic assumption that reflects the extreme redundant species hypothesis (Walker, 1992). A shortcoming of this hypothesis is that it systematically ignores the biologies of species. The wide range of life histories, fragmentarily reviewed above, demonstrates that bacterivorous species may differ considerably in their feeding activity, not only in magnitude and rate (related to ingestion, metabolic rates, and fecundity) but also in locale (soil horizons), timing (diurnal, seasonal patterns), and persistence under disturbance and predation pressures. For in-

stance, Ferris et al. (1997) found that during a growing season in an agroecosystem there were significant differences between the contributions of individual bacterivorous species to nitrogen mineralization, as a function of individual species abundances and temperature-influenced metabolic and development rates.

A second shortcoming of the redundant-species approach is that it limits species function to direct trophic relationships (Beare et al., 1995), ignoring the many indirect, feedback mechanisms that constitute the core of bacterivorous nematode function in decomposition (Bengtsson et al., 1996). Grazing, though directly limiting bacterial numbers, stimulates bacterial activity and decomposition rates as it leads to recycling of immobilized nutrients, transportation of microbial propagules to new substrates, and bioturbation-enhanced diffusion of oxygen. Again, it may be expected that bacterivores differ considerably in these contributions, given different metabolic efficiencies, body sizes, activity ranges, and movement patterns among species. In sum, the trophic group approach is pragmatically justified in large-scale soil food web analyses but generally inappropriate in nematode ecology studies (Ferris, 1993; Whitford, 1996).

Accepting that species, not just trophic group biomass, are important, the question remains whether each and every species matters functionally. Will decomposition rates inalterably change when a single, or several, bacterivorous species drop out? Considering the apparently uninterrupted continuation of decomposition processes in disturbed soil with reduced nematode diversity, it does not seem likely that each species is crucial. In fact, some or many bacterivores may be functionally redundant. Regardless of the interspecific differences outlined above, the surviving species may have enough in common with the lost species that the former can compensate for the loss of the latter, both in density and function. Disturbance studies have provided many examples of density compensation among bacterivores. For instance, Ruess et al. (1996)

reported that soil acidification led to bacterivorous species loss but not to significantly different total bacterivore abundance, as the extinction of 6 species and the reduction of 13 more was compensated for by density increases of 8 other bacterivores. Similarly, Korthals et al. (1996a) noted that, at low levels of copper pollution in arable soil, increases of *Chiloplacus* sp. compensated for decreases in *Acrobeloides* sp., though at high levels of pollution this compensation was not complete. Unfortunately, both studies did not measure functional properties, so it cannot be concluded whether the compensated species were functionally redundant. In general, experiments to specifically address nematode functional redundancy are difficult to realize, as there are no specific nematicides to manipulate species composition in the field (Lawton et al., 1996), and realistic microcosm assemblages are hard to build because many species are unculturable. However, it is possible to compare functional properties of disturbed and pristine nematode assemblages that have different species composition, as Heneghan and Bolger (1996b) showed for soil microarthropods. For such comparisons, it is important that functional response be measured at appropriate scales, relevant to domains of species activities (Anderson, 1995).

In conclusion, the answer to the question of whether bacterivorous nematode diversity is a form of functional complexity, in which each species plays a unique role in decomposition, or includes a high degree of functional redundancy, with many species able to substitute for each other, can perhaps never be fully answered with experimental data. However, when focusing on patterns of species similarities instead of differences, at least some degree of functional redundancy is likely. In fact, functional redundancy is a feature of many complex systems, including ecosystems (Schulze and Mooney, 1993) and genetic systems (Pickett and Meeks-Wagner, 1995; Tautz, 1992), and is built into man-made business operation systems to safeguard systems reliability (Ushakov, 1994). Functional redundancy in soil communities may explain why decomposition

processes are maintained in highly disturbed soils, despite the extinction of many microbivorous species (Lawton et al., 1996). Thus, even if the detailed functions of each and every nematode species may never be fully understood, and regardless of how many species are functionally redundant, nematode diversity is likely important for the long-term stability of soil ecosystem functioning and therefore merits protection and further study.

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