



Ecology of Plant and Free-Living Nematodes in Natural and Agricultural Soil

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Deborah A. Neher

Department of Plant & Soil Science, University of Vermont, Burlington, Vermont 05405; email: deborah.neher@uvm.edu (<mailto:deborah.neher@uvm.edu>)

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Abstract

Nematodes are aquatic organisms that depend on thin water films to live and move within existing pathways of soil pores of 25–100 μm diameter. Soil nematodes can be a tool for testing ecological hypotheses and understanding biological mechanisms in soil because of their central role in the soil food web and linkage to ecological processes. Ecological succession is one of the most tested community ecology concepts, and a variety of nematode community indices have been proposed for purposes of environmental monitoring. In contrast, theories of biogeography, colonization, optimal foraging, and niche partitioning by nematodes are poorly understood. Ecological hypotheses related to strategies of coexistence of nematode species sharing the same resource have potential uses for more effective biological control and use of organic amendments to foster disease suppression. Essential research is needed on nematodes in natural and agricultural soils to synchronize nutrient release and availability relative to plant needs, to test ecological hypotheses, to apply optimal foraging and niche partitioning strategies for more effective biological control, to blend organic amendments to foster disease suppression, to monitor environmental and restoration status, and to develop better predictive models for land-use decisions.

Key Words

ecological succession (/keyword/Ecological+Succession), optimal foraging (/keyword/Optimal+Foraging), biogeography (/keyword/Biogeography), food web (/keyword/Food+Web), niche partitioning (/keyword/Niche+Partitioning), ecosystem stability (/keyword/Ecosystem+Stability)

INTRODUCTION

André et al. (3) described soils as the final biotic frontier and suggested that we know more about outer space and the depths of the ocean than we do about the soil biology of our own backyard. This review covers advances in nematology since 1999 that pertain to the role of nematodes in the soil and rhizosphere (103, 165). Even with recent advances and the significant progress discussed in this review, the knowledge gap is vast, and discrepancies in basic ecology and biology of free-living nematodes and soil nematodes in natural ecosystems remain as they have for the past 25 years. Knowledge of plant-parasitic nematodes of economic or quarantine importance is orders of magnitude greater than that of free-living or beneficial nematodes that compose up to 60% to 80% of the soil nematode community. Consequently, studies of free-living nematodes and soil nematodes in natural ecosystems are several steps behind those of plant-parasitic nematodes and nematodes in agricultural ecosystems (53). Nematode ecologists are in initial stages of elucidating the taxonomy and systematics of free-living nematodes in agricultural systems and all soil nematodes in grassland, forest, and wetland systems, as well as life history strategies and the relationships between nematodes and their contribution to ecosystem function (10, 77). Evolutionary and geological evidence suggests that soil nematodes have considerably longer histories on Earth than organisms that have received more attention, such as mammals and vascular plants (70). This evolutionary history alone suggests that they play an essential role(s) in ecosystem structure and function.

Soil nematodes (typically 40 μm to 1.0 mm in length) are classified either as microfauna or mesofauna; their small size makes them unable to reshape soil and, therefore, they are forced to use existing pore spaces, water cavities, or channels for locomotion within soil. Most nematodes inhabit soil pores of 25–100 μm diameter. Nematodes depend on water films (1–5 μm thick), which coat and surround soil particles, to move through the soil system (61). The hierarchical and heterogeneous soil structure gives rise to a complex distribution of ephemeral water-filled pores and films that create many unique microhabitats. Habitable pore space, that is of sufficient size and connectivity to support nematodes, accounts for a small portion of total pore space (67). Within the habitable pore space, nematode activity is influenced by the balance between water and air (3). Saturation and drought both impact composition of nematode communities in soil because these conditions result in anaerobiosis and dehydration, respectively.

Definitions of Ecology

An increased public awareness of environmental problems has made ecology a common but often misused word. Ecology is the scientific study of the interactions of organisms with one another and with the physical and chemical environment. Ecological studies may focus on one or more scales: populations of a single species, an interacting community involving populations of many species, movement of matter and energy through a community within an ecosystem, large-scale processes within a biome, or global patterns within the biosphere. Research questions depend on the hierarchy of scale.

Several review articles have been published on basic biology and ecology of free-living (52) and plant-parasitic nematodes in agricultural (53, 165) and natural (35) ecosystems. Other reviews highlight the beneficial role of nematodes in ecological processes, including decomposition, nitrogen cycling (10, 77) and disease suppression (85, 135, 169). One of the first comprehensive reviews of agricultural and natural ecosystems was prepared by the Polish nematologist, Lucyna Wasilewska (159). Since then, comparative reviews have been published (103), and ecologists have begun to study diseases in natural ecosystems. Relatively well-studied natural systems are grasslands, coastal dune systems, and forests. This review focuses on the ecology of plant-parasitic (or root-feeding) and free-living nematodes that complete their entire life cycle within terrestrial soils or within plant roots. It will not include nematodes in aquatic ecosystems (144), nematode parasites of vertebrates, or nematodes affiliated with insects as pathogens or mutualists (84).

Historic Perspective

Application of ecological approaches and knowledge of biological suppression of disease in natural ecosystems is receiving more attention as environmental concerns mount for the longevity and quality of our natural resources. The field of nematology will be well served if it expands its attention to (a) biological and cultural approaches to enhance the habitat and effectiveness of natural enemies of plant-parasitic nematodes, and (b) the use of nematodes as biological indicators of soil quality.

Broad spectrum nematicides were shown to increase crop yields in the late 1940s and early 1950s, which increased an awareness of nematodes and increased the number of nematologists employed in the United States (166). Management of soilborne pathogens has relied historically on application of synthetic chemical biocides. Soil fumigation with general biocides decreases microbial populations and nearly eliminates nematodes. Fumigation of soil with general biocides results in a depauperate soil matrix that can only be inhabited by primary colonists. Although recovery occurs, population densities of beneficial soil nematodes may not return to pre-fumigation levels, even after five months (166). A progression of colonization by early successional species is followed by more-specialized, late-successional taxa (42). Several effective nematicides are being removed from the marketplace because of their impact on global climate as well as because of the ecological dysfunction that they trigger (56, 163). The consequences of other recent trends in management of arable lands that call for further research include (a) reducing cultivation in response to loss of soil by erosion and (b) the loss of resistance genes in crops caused by strong selective pressures created by extensive planting of monocultures. Crop yields may decrease unless alternative and equally effective strategies for management are adopted. For example, biological and cultural alternatives can be implemented to enhance the habitat and biology of natural enemies.

Since 1988, there has been a tremendous increase in the emphasis on the use of nematodes as indicators of soil condition (52) and their predictive use in soil management (45). Formerly, focus in nematology was on the control of parasitic and harmful species, but now nematodes are more often seen as integral and potentially useful components of soil systems. As indicators, nematodes have advantages over other soil fauna. Protozoa may be more abundant but their lack of morphological characters makes taxonomic identification difficult. Moreover, conditions for encystment and excystment are not well synchronized with general disturbance, suggesting that population changes may not reflect levels of disturbance as readily as nematode populations (38). Although mites and collembolans are relatively large, with abundant characters for taxonomic identification, and are useful indicators in many habitats, these fauna are not always abundant in stressed and disturbed conditions. Complete community enumerations that include all microinvertebrates are more laborious to extract and taxonomically less approachable than focusing on nematode communities (3). In light of these advantages, the study of nematodes is most likely to contribute significantly to our understanding of biological processes in soil.

Ecology research spans a broad temporal and spatial scale of investigation. For the purposes of this review, the focus is on population, community, and ecosystem ecology, including basic and applied dimensions. Applications include environmental monitoring, restoration, and disease management in agricultural and natural ecosystems.

Population Ecology

Population ecologists focus on individual species and may ask questions regarding the interaction of morphological, physiological, and behavioral traits, plasticity of the traits (83), causes and consequences of dispersal (74) and dormancy (160), outcome of life-history adaptations (16), and/or impact of stress on population structure. Population ecology concepts examined in nematology include density-dependent regulation of populations (53), population dynamics (137), natural selection, and evolution. Population dynamics of nematodes have been modeled using logistic, negative binomial, stage-structured population growth, predator-prey equations, and simulation modeling (53).

Community ecologists examine interactions between species or trophic groups (sometimes referred to as guilds or functional groups), including spatial relationships and community assembly among different species that occur in the same habitat. Interactions between species include predation, competition, parasitism, and mutualism. At a single time point, communities can be described by their structure and composition. Change in community composition through time is a reflection of both seasonal dynamics (50) and ecological succession (42). Questions in community ecology address the dynamics of species interactions (53), the relationship between complexity and stability in ecosystems (91), the characterization of organisms as *r*- or *K*-selected in relationship to ecological succession (15), plant-herbivore coevolution (94), and energy (carbon) and nutrient fluxes through **food webs** (73). Indices of diversity, **evenness**, **similarity**, and ecological succession have been used to describe nematode community composition and structure (54, 117). Goals in community and ecosystem ecology include identifying sentinel or keystone taxa, quantifying the contribution of nematodes to nitrogen cycling, and defining lag effects between organisms and their impact on biogeochemical cycling (157; D.A. Neher & M.E. Barbercheck, unpublished data). Answers to these questions strengthen the justification to use nematode communities as biological indicators of soil quality because policy makers and government agencies prefer indicators that reflect ecological process and/or ecosystem function.

How Plants Affect Nematodes

Composition and structure of terrestrial communities vary among ecosystems because of contrasting plant composition and phenology, soil properties, and microclimates. Agricultural production fosters varietal selections for higher yields, generating a tradeoff in the root-to-shoot ratios that affect the quantity and quality of nutrients and energy flowing through soil food webs in both space and time. Root growth is more extensive and less ephemeral in perennial plants than with annual crops and supports a soil community with many omnivores and predators. Soil community composition with perennial crops resembles that of natural ecosystem soils more closely than with annual crops (54, 106, 159). Furthermore, perennial plants restore function in water infiltration and reduce compaction and, thus, increase rooting depth.

Plant species have greater effects on microbes and plant-parasitic nematodes, **trophic levels** with which they most intimately interact, than they do on predatory nematodes (158). Plants affect plant-parasitic nematodes at the species level (153) rather than at more coarse levels such as plant diversity (158) or plant functional group (154). However, functional groups of plants (i.e., legumes, forbs, grasses) have contrasting rooting patterns that create habitats more favorable to some species of nematodes than others. For example, mobile ecto- and semi-endo-parasites are more common under grasses, whereas sedentary ecto- and endo-parasites are more abundant under forbs where the soil tends to be fungal dominated (158). Communities of plant-parasitic nematodes can be complex within the rhizosphere of a single plant species. For example, the rhizosphere of marram grass (*Ammophila arenaria*) in coastal dune systems provides habitat to a community of plant-parasitic nematode species that are controlled by factors ranging from substrate resources, other organisms in the same position in the food chain, and predators in higher trophic positions (122).

Soil Food Webs

The concepts of population and ecosystem ecology integrate at the soil food web (13). A basic soil food web has a similar structure to food webs of other environments. Plants and organic debris provide habitat for soil flora and fauna. In grassland, desert, and forested ecosystems, about 5% of net carbon flow enters the above-ground grazing or consumer component, and the remainder enters the detrital food web (24). Three basic **energy pathways** exist in soil: plant tissue, bacterial, and fungal (98). The plant tissue pathway includes primary herbivores such as pathogenic nematodes and their consumers. These organisms decrease primary productivity of the plant by altering uptake of water and nutrients and may create abnormalities in root morphology and/or physiology. Energy and nutrients obtained by plants eventually become incorporated in detritus that support the bacterial and fungal pathways. The bacterial or fungal pathways include saprophytic and pathogenic bacteria or fungi and their respective nematode consumers (e.g., bacterivorous or fungivorous nematodes). The root, bacterial, and fungal pathways unite at levels higher in the food chain, i.e., omnivores and predators. Secondary and tertiary consumers graze on species in any of the trophic groups beneath them. For example, omnivorous nematodes feed on a variety of food sources, including algae, fungi, bacteria, small rotifers, enchytraeids, and small nematodes (167). This grazing activity regulates energy and nutrient flows more than their population dynamics and biomass suggest.

In North America, short-grass prairie (*Bouteloua gracilis*), lodgepole pine (*Pinus contorta* subsp. *latifolia*), and mountain meadow (*Agropyron smithii*) have similar food web structure (76). They contain primary producers, consumers, and detritivores. The number and biomass per volume of soil organisms decline by orders of magnitude from bottom to top positions in the food chain. Although structure is conserved across ecosystems, relative abundance of organisms within trophic or functional groups may vary by ecosystem type (117). In Poland, bacterivorous and plant-parasitic nematodes are the most abundant nematodes in agricultural soils, omnivorous nematodes are more common in grasslands than agriculture, and fungivorous nematodes are relatively more abundant in forest than agricultural soils (117, 159). In contrast, relative numbers of nematodes in each functional group differ in Swedish soils. For example, ratios of organisms in fungal to bacterial pathways are greatest in fertilized barley (*Hordeum vulgare* L.), followed in descending order by meadow fescue (*Festuca pratensis* L.) and lucerne ley (*Medicago sativa* L.) (8).

A major question in soil ecology is whether soil food webs are regulated by resources (**bottom-up controlled**) or by predators (**top-down controlled**). Nematodes hold a central position in food webs and impact ecological processes both directly and indirectly, suggesting that they play a critical role in ecosystem function (73). Detritus-based food webs are thought to be bottom-up controlled because of their characteristically large number of species, complex structure, abundance of omnivores and resource generalists, long food chains, paucity of top predators, and spatial heterogeneity (12). These are characteristics associated with direct feeding interactions between links in the food chain. Nematodes disperse microbes residing on their body or in their gut, and slight to moderate grazing of nematodes on microbial populations is known to stimulate microbial growth (55). It is assumed that this type of grazing preference maintains a bacterial population in a youthful state and maintains decomposition activity. However, it has been suggested that soil food webs are not exclusively bottom-up controlled but sometimes regulated by top-down mechanisms associated with indirect interactions (89). For example, the presence of nematodes, sometimes looking for the serpentine soil, is associated with the abundance of microbial food sources (164). In some cases, nematodes, which may serve merely as a conduit by which resources pass from

the bottom to top trophic levels (156). However, top-down regulation of microbial- and plant-feeding nematodes by predatory nematodes has been reported by others (169). These mixed observations support the theoretical approach of de Ruiter et al. (34), who suggest control is both bottom up and top down (12).

PHYSICAL HABITAT

Ecologists discuss habitat structure in terms of accessible resource distribution. In soils, habitat structure is complex because of a combination of physical constraints imposed by pore structure, varying soil moisture, and resource distribution (plant roots and organic debris). Thus, natural selection is likely to act on consortiums of microorganisms within this physical matrix rather than on individuals (27). Typically, soil ecologists restrict considerations of pore or spatial structure to soil texture, i.e., grain size distributions (40, 67). Although soils with sandy texture are less porous than finer soils, the volume of pores large enough to be habitable for nematodes is greater in sandy soils than in finer soils. Fine soils provide more refuges for microbes that are inaccessible to their nematode grazers, thus diminishing the mineralization of microbial biomass by grazing. For these reasons, mineralization of microbial populations caused by nematode grazing is predicted to be greater in sandy than fine soils.

Aggregates as a Secondary Structure

In natural soils, soil particles are glued together by bacterial polysaccharides, interlaced by plant roots and fungal hyphae and other organic or mineral materials to form aggregates and provide a secondary structure. Therefore, formation and degradation of aggregates is linked to plant and fungal growth, decomposition, and soil water dynamics (140). Aggregates are organized hierarchically with smaller aggregates forming larger ones, creating habitat for nematodes. Distribution of nematode size is correlated with distribution of aggregate size (129). Different organisms may be associated with pore size refugia at different levels of aggregate organization. For example, bacterial density is greater inside than outside aggregates. As a result, nematode grazers that remain within aggregates may be more efficient than those that forage in space between aggregates. Under dry conditions, voids between aggregates may generate a network of isolated dry patches because generally water drains more quickly from the largest pores. Thus, bacterivorous nematodes are confined near their food source in aggregates after interaggregate spaces have drained (59, 116). The close proximity of nematode grazers and microbial prey connect ecological and biogeochemical processes, accelerating nutrient turnover and carbon mineralization (134). For enclosures to form, aggregates need to remain moist while becoming separated hydrologically from each other under unsaturated conditions. It has long been observed that aggregation lowers the water potential at which plants reach their permanent wilting point. Likewise, large populations of *Aporcelaimellus* nematodes have been observed at water potentials of 50 kPa where only pores $\leq 10 \mu\text{m}$ remain water-filled (116). Understanding the impacts of hierarchical soil structure is an important consideration for future investigations both in terms of **community structure** and function. Although aggregate structure modifies the relationship between soil fauna and texture, only a few ecologists and nematologists have considered aggregates as habitat for soil nematodes (165).

Foraging Patterns

Structure of physical habitat not only affects resource distribution, but also selects for the foraging and predation strategies of its inhabitants. Soil structure may affect foraging efficiency of nematodes directly by forcing them to follow paths longer and more tortuous than if no spatial partitions existed (1) or by confining them to isolated water-filled regions within aggregates. Within confined areas, compensatory growth of bacteria is stimulated by nematode feeding, thereby providing nematodes with more food. In homogenous environments, nematodes exhibit deliberate, **correlated movement** (66), which creates patterns that explore larger areas than simple random walks. When an attractant is present, nematodes rely on chemotaxis, making foraging more efficient (119). When structure is present, foraging becomes more of an avoidance strategy, allowing nematodes to escape structural traps such as dead-end pores (1). Bacterivorous nematodes appear to forage continuously on bacteria (171). However, individuals within populations differ in movement, with some moving fast and making large loops, whereas others move slowly and fluctuate between backward and forward movement (66). Given that entomopathogenic nematodes have contrasting interspecific foraging strategies within a trophic group (90), it is expected that free-living nematodes also vary in spectrum from generalist to specialist foraging strategies among species. Further, casual observations from life-history studies suggest that populations of mixed **age structure** (juvenile versus adult) may also exist in bacterivorous nematodes that contrast in foraging behavior (D.A. Neher & T.R. Weicht, unpublished data).

Niche Partitioning

The field of soil ecology encounters many contemporary challenges of ecological theory, such as resolving the apparent conflict between competitive exclusion, observed biodiversity, and functional redundancy within a heterogeneous environment (4). Individual taxa may have multiple functions, and several taxa appear to have similar functions (139). Functionally redundant species may represent a form of biological insurance against species loss by natural population cycles or disturbance (101). However, the impression of functional redundancy may be exacerbated by the scarce knowledge of basic biology and ecology of free-living nematodes, anonymity of most soil organisms, trophic position, and heterogeneous distribution of resources (102). Proponents of functional redundancy have been criticized for conclusions based on structurally simple microcosm experiments that contain far fewer species than field communities (5). In addition, redundancy within a trophic group fails to explain why contrasting species of bacterivores contribute differentially to nitrogen mineralization (49, 124) or coexist in riparian areas (43). Although species may appear to be functionally redundant, taxa performing the same function are often isolated spatially, temporally, or by microhabitat preference (9).

Ecologists have long been perplexed by the question of how so many species can coexist while using the same resource (75). This paradox can be resolved by assuming there are as many different resources as there are different species (91). Competing species can avoid competitive exclusion when individuals occupy resource patches that diverge in their physical, biological, and chemical nature. Moreover, distinct physiological and environmental requirements drive species of the same functional group to play contrasting roles in soil ecosystem processes. For example, three genera of bacterivorous nematodes respond to different soil types and moisture status in the same way, suggesting the diversity within nematode assemblages contributes to resilience in biologically mediated soil processes (168). As poikilotherms, nematode species

grow optimally over a limited temperature range. Therefore, communities exhibit a seasonal dynamic where the dominant species differs through time (50). Not only does temperature vary by season, but so does quantity and quality of plant litter as a food resource.

Soil pore size distribution may provide niche separation with each pore size category representing a niche for soil fauna of similar diameter. However, viewing pore size as a sole niche separator is simplistic. Other niche dimensions include diet, foraging strategy, and body size (53). Nematodes occupy existing pore spaces and respond to soil water dynamics as air-filled and water-filled pore size distributions oscillate. Soil moisture variation inhibits or encourages consumption by affecting habitat overlap between consumers and producers and by creating a dynamic partitioning of habitat within and among aggregates. Temperature and moisture affect rates of assimilation, respiration, and reproduction differently for each nematode species (48, 49, 99). Nematodes are sensitive to extreme temperatures, especially in moist soils where they are active (28). In hot, dry soils, nematodes can survive anhydrobiotically near roots or in interaggregate spaces. Species within a trophic group differ in sensitivity to temperature, which may reduce interspecific competition (2). Combinations of nematodes of different life strategies may lead to more thorough exploitation of a food source and, consequently, higher nitrogen mineralization.

Developmental stages of nematodes differ in relative survival. Infectivity of plants by nematodes can differ with life stage and nematodes have survival structures that operate at multiple life stages. For example, eggs are protected by thick-walled tissue or within cysts. Third-stage juveniles may convert to a dauer stage either as a survival or phoretic dispersal mechanism. Juvenile and adult stages may transition into anhydrobiosis with drought conditions. These physiological adaptations allow nematodes to invade and tolerate habitats in which few other animals can survive, and to avoid interspecific competition and many environmental selection pressures. Although nematodes have adaptive mechanisms to survive extremities of climate, their activity is stimulated by the return of more moderate conditions. For example, communities of nematodes are revived within minutes after rain in desert soils (28) or shift quickly between active and inactive states in response to small, diurnal changes of temperature or relative humidity in Antarctic soils (146).

ECOSYSTEM FUNCTION

Soil ecologists recognize that the structure of detrital **food webs** is reflective of ecosystem function, but few studies have explicitly explored these connections (12). Ecosystem functions include primary productivity (yield or plant growth), decomposition and nutrient cycling, disease suppression, and biological control. Mechanisms of these functions can be abiotic or biotic. For the management and development of sustainable ecosystems, it is probably most important to understand the relationships between energy and associated nutrients among functional groups.

Primary Productivity

Plant-parasitic nematodes decrease primary productivity of their hosts by consuming the cytoplasm of plant cells, triggering plant hormone responses that change source-sink relationships, and physically destroying roots. While feeding, the nematode may exist outside or inside the root and either remain sedentary or migrate through plant tissue. Negative effects of plant-parasitic nematodes are better documented than positive effects. However, an example of the latter is that low levels of below-ground herbivory of clover-by-clover cyst nematodes (*Heterodera trifolii*) increases root growth in grassland mixtures of white clover and *Lolium perenne* (7). Other studies show no net effect of total abundance of nematodes on tallgrass prairie (136) but do show a positive effect for short-grass prairie (77) or mid-successional grasslands (29).

Decomposition

Within the detrital community, bacterivorous nematodes play significant roles in regulating decomposer microflora composition (36), litter decay rates, and element cycles (6, 52). Rates of decomposition are affected by the number of **trophic levels** and their interactions (13, 138). Decomposition rates are sensitive to physical disturbances such as cultivation (110). For example, decomposition rates are 1.4 to 1.9 times faster in conventional than no-till soils with residues remaining on the surface (8). Fungi and fungivorous nematodes are more likely to regulate decomposition of surface residues in no-till soils, whereas bacteria and bacterivorous nematodes regulate decay rates in incorporated residues in conventional-till soils. The relative dominance of fungi and fungivorous nematodes in early stages of decay of surface residues can be explained by the initially high ratio of lignin to nitrogen. Bacteria and bacterivorous nematodes move in as secondary colonizers after decay is initiated.

Nutrient Cycling

Detrital pathways are responsible for the greatest proportion of nutrient mineralization in terrestrial ecosystems. Carbon and nutrients are inextricably linked in all food webs (61). Nematodes affect nitrogen availability both directly and indirectly (77). Directly, nematodes excrete ammonium as a byproduct because their prey generally has a lower ratio of carbon to nitrogen than nematodes need. Indirectly, they liberate nitrogen immobilized by microbes through metabolism and excretion and dispersal of microbes to more suitable substrates. 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 (8). Net nitrogen mineralization is tempered by immobilization by fungi (8) in Swedish forest soils and by bacterivorous nematodes in low fertility deserts soils in Utah (28).

Disease Suppression/Biological Control

Although some nematodes are the causal agent of disease and, thus, the target of biocontrol, others are predators that can control a disease caused by a bacteria or fungus (169). Mechanisms suggested to control plant-parasitic nematodes include competition, arbuscular mycorrhizal fungi, endophytic fungi, and plant resistance (151). Mechanisms originating with the plant are called bottom-up interactions because they are driven by limitation of resource availability. Coastal dune systems exemplify all of these mechanisms (122). The root zone of marram grass (*Ammophila arenaria*) contains a mixture of plant-parasitic nematode species that each respond in a different manner. For example, the cyst nematode *Heterodera arenaria* is

controlled by host nutrients and soil microbes, whereas the lesion nematode *Pratylenchus penetrans* is suppressed by prior colonization of roots by arbuscular mycorrhizal fungi (32, 131). Fungi can also alter competition between species of plant-parasitic nematodes within a single rhizosphere (71).

Plant-parasitic nematodes can also be controlled by predators or parasitic soil organisms (85) such as soil microbes, predator nematodes, microarthropods, and tardigrades. Bacterial species of *Pasteuria* and the nematode trapping fungus *Hirsutiella rhossiliensis* parasitize root-knot and cyst nematodes (81, 127). Diplogasterid nematode predators (e.g., *Odontopharynx longicaudata*) are well suited for biocontrol of nematodes, because they are easy to culture and have short life cycles, prey-specificity, and resistance to adverse conditions (86). Mononchidae (e.g., *M. fortidens*, *M. longicaudatus*, *M. gaugleri*) have been considered to be unsuccessful for biocontrol because of their scarcity, long life cycle, and sensitivity to environmental disturbance. In infertile natural areas, abundances of *Discolaimus*, *Tripyla*, and *Prionchulus* nematodes have been observed to suppress root-knot nematodes (133). Physical or chemical properties of soil that influence disease suppression of plant-parasitic nematodes include pore structure, pore connectivity, water-air balance, organic matter, and pH (57). Subsistence agriculture has relied on traditional knowledge to favor beneficial organisms by cultivation methods and appropriate use of soil amendments, sanitation, crop rotation, fallow, adjusting planting time, including antagonistic and trap crops, artificial and natural flooding, and burning stubble (18). These practices were not necessarily based on scientific knowledge but were empirically determined due to the prohibitive cost of nematicides.

ECOLOGICAL THEORY

Ecological theory developed from the study of above-ground and aquatic systems has been applied to soil communities but incompletely tested. Soil communities are unique because omnivory is more prevalent than in other communities. Above-ground predators are usually larger than their prey, whereas this is not true in the soil, as soil pores constrict size differences between predator and prey. Omnivory is an advantage in a heterogenous distribution of uncertain food items (37). Perhaps, the prevalence of omnivory in soil communities negates the existence or role of keystone taxa (123) because it produces complex interactions, making it impossible to make broad trophic-level generalizations. Further, omnivory may be prevalent because soil physical partitioning disrupts trophic interactions. Moore et al. (97) demonstrated that soil food webs can be stable in the presence of omnivory because the resource base is greater than that consumed.

Even though soil habitats are unique for their spatial constraints, similarities with other habitat types should not be ignored. One possible similarity is that the optimal foraging strategy among bacterivorous nematodes in soil is synonymous with the “green world” hypothesis (“The world is green because it is prickly and tastes bad”) proposed by Hairston et al. (65). Generalist herbivores seek a varied diet to tolerate or dilute exposure to plant defense chemicals, whereas specialists have coevolved tolerance to these chemicals. Like plants, microbes produce multitudes of defense compounds that could be detrimental to their grazers. Bacterivorous nematodes are likely generalists with varied diets to reduce the impact of microbial toxins. Some fungivores are specialists that exhibit contrasting growth rates on different fungal species (118).

Ecologists debate whether measures of biodiversity are directly proportional to ecosystem stability (93). One explanation is that soils are the largest reservoir of biodiversity. Therefore, soil function has been demonstrated to be resilient to disturbance. Nematode communities offer a model system to evaluate ecological theory in soils. Ecological succession of nematode communities have been studied but many questions remain relating to where, how, and why particular species are present, what they eat, and the type of interaction they have with other species in the food web.

Biodiversity and Ecosystem Stability

One can hypothesize that in a stable system each microhabitat is occupied by organisms that were first present and/or best able to colonize the niche and become established, and niche overlap is relatively small. Understanding the relationship of biodiversity to ecosystem function and stability is of importance to scientists involved in environmental monitoring, ecological restoration, and sustainable agriculture. Stability is defined as the ability to withstand or to recover from a disturbance. This definition is sometimes used synonymously with that of resilience or resistance. Resilience is the ecological memory or capacity of a system to absorb disturbances, reorganize, and maintain adaptive capacity before shifting to another **stability domain** (63, 120). A sufficient reservoir of community members remain so that a system can be recolonized and return to its original equilibrium, reestablishing ecosystem function. A combination of two scenarios may facilitate ecosystem resilience: (a) local, internal, or within-patch organisms that survived the disturbance and (b) external sources of organisms that can disperse and recolonize a system.

Many grass-roots conservation and restoration groups promote greater diversity as a means to achieving ecosystem stability (141) because species richness may preserve function (72). However, many ecologists claim that biodiversity itself (number of species or species richness) is not a good predictor of stability, (79, 93) and controversy remains. Gross et al. (62) suggest food web stability is enhanced when species at intermediate trophic levels are fed upon by multiple predator species.

Index values of species richness simply represent the number of taxa, not the identity or ecological diversity of species. Consequently, a community of invasive taxa could have the same **diversity index** as a community of native taxa. A diversity index is simply a mathematical value that represents an inseparable integration of species numbers and equality or evenness of abundance among species (80). Nematode diversity can be assessed at the species, genus, or trophic level (111). At the trophic level, it is a measure of food chain length and **food web** complexity. A trophic diversity index assumes that greater diversity of trophic groups in soil food webs, and longer food chains reflect improved ecosystem function (95). Generally, diversity assessed at the genus or trophic resolution of soil nematodes is greater in perennial and natural systems than annual cropping systems, with or without cultivation (54). In contrast, Neher (104) found little difference in trophic diversity (food web complexity) between conventional and organic farms, neither of which was fumigated with general biocides. Reducing the frequency of cultivation (68) and including perennial crops in agricultural systems (54, 106, 159) are two ways to increase trophic diversity in arable soils.

The successional status of a soil community may reflect the history of disturbance. Succession in cropped agricultural fields after cultivation and clearing of native vegetation shifts a community to an earlier stage of succession that favors a relative abundance of opportunistic species, such as bacteria and their predators, who colonize the soil. The communities are dominated by organisms with short generation times, small body size, rapid dispersal, and generalist feeding habits such as bacteria and bacterivorous nematodes (10). Subsequently, relative abundance of fungi and fungivorous nematodes increase in the area. Secondary and tertiary consumers or predators establish later. Macrofaunal diversity is hypothesized to be greatest at intermediate stages of succession where early- and late-staged taxa coexist (69, 121). This intermediate disturbance hypothesis could explain why some groups of organisms are more abundant in no-till (i.e., intermediate disturbance) than either conventionally tilled (i.e., extreme disturbance) or old-field (i.e., no disturbance) systems (155). If disturbance is common or harsh, only a few taxa that are resistant to disruption will persist (121). If disturbance is mild or rare, soil communities will approach equilibrium and be dominated by a few taxa that can outcompete all other taxa. However, attainment of steady-state equilibrium in agricultural or natural ecosystems is rare. Succession of nematode communities has also been well described for a pine forest (33), during formation of compost (142), and after application of compost (42).

Succession can be interrupted at various stages by disturbances. Two major types of disturbance in agricultural systems, physical and chemical, are often intertwined in managed ecosystems (51). Physical disturbance includes cultivation and compaction by repeated passes of heavy machinery. Such cultivation shifts agricultural soils to an early stage of succession (106, 155). Alternatively, reduced tillage leaves most of the previous crop residue on the soil surface, and this results in changes in the physical and chemical properties of the soil (68). Surface residues retain moisture, dampen temperature fluctuations, and provide a continuous substrate that promotes fungal growth. Chemical disturbance includes amendments for fertility and addition of organic matter and/or pesticides, all of which are substrates for bacteria. Therefore, these amendments favor the bacterial channel (165) and provide a general enrichment phenomenon (103). High levels of fertility and naturally saline soils generate osmotic stress that is detrimental to the survival of many nematode species (145). A combination of cultivation and fertilizer reduce the flow through the fungal channel and decouple the regulation of nitrogen mineralization and decomposition by organisms higher in the food chain compared to grassland ecosystems (17, 96).

Disturbance can also be characterized by intensity and duration, expressed as acute or chronic, pulse or press (11, 152). Chronic or press disturbance can lead to gradual species extinction and eventually decreases resiliency of an ecosystem to disturbance or disruption (79, 120). Monoculture agriculture or long-term exposures to soil polluted with heavy metals are types of chronic disturbance.

Measures of ecological succession of nematode communities include the fungivore to bacterivore ratio, as well as maturity, channel, and structure indices (15, 47). The fungivore to bacterivore ratio reflects the successional stage of the decomposer community. The nematode **maturity index** (15) is based on relative sensitivity of various taxa to stress or disruption of the successional pattern. Originally, the maturity index was based separately on community composition of free-living and plant-parasitic nematodes (15, 54), but there is debate on whether that is necessary (107, 164). Recommendations for environmental monitoring on large geographic scales are to calibrate these nematode community indices by ecoregion (112) and ecosystem type (117). Indices that describe associations within nematode communities, such as the maturity index, are less variable than measures of abundance of a single nematode taxonomic or functional group, and are more reliable statistically as measures of ecosystem condition (107, 113).

BIOGEOGRAPHY

Since Charles Darwin, ecologists have been intrigued with how and why community assemblages vary among habitat patches, geographic regions, or islands. Explanations have ranged from latitudinal differences in climate (128), habitat heterogeneity, and niche partitioning (75), to island biogeography theory (IBT). IBT predicts that isolation by island or habitat area drives species richness and suggests a positive association between species richness and land area because large areas attract more immigrants, hold larger populations, and decrease the risk of stochastic extinction (91). Geographic isolation also accounts for species isolation and evolution and reduces potential colonists. IBT was developed for plant and vertebrate species and has yet to be tested thoroughly for invertebrate taxa, especially those residing in soil (82). Only recently are nematode community assemblages being examined from an IBT perspective. For example, nematodes have been studied for island systems in the Antarctic (92) and Hawaii (14), for lake islands in the boreal forests of northern Sweden (82), and for epiphytes as islands of different sizes and on different tree species in New Zealand rainforests (158). To date, ecosystem attributes (e.g., decomposition or respiration rate, nitrogen or phosphorus loss), plant associates, interactions of temperature and moisture regimes, and niche partitioning appear to be better predictors of species richness than IBT (82, 158).

Latitudes differ in patterns of temperature and precipitation, resulting in contrasting biomes. The latitudinal gradient hypothesis predicts that biodiversity of biota will be greater in tropics than temperate zones, although nematodes may be an exception. Procter (128) attributes the relatively low tropical nematode biodiversity to an inability to compete with more specialized organisms in the tropics, and suggests that nematodes are more adaptable and tolerate climate-induced stress typical of higher latitudes. However, this interpretation of latitudinal gradients was based on soil samples that are relatively thin in tropical systems. When litter and understory habitats are sampled in addition to mineral soil, nematode species richness in a Costa Rican tropical rainforest is comparable or exceeds that of temperate latitudes (126). Detritus and root substrates are more abundant above than below ground in tropical rainforests.

Colonization of new patches depends on the ability to move between patches, permeability of corridors, distance between patches, and accessibility of patches. These parameters are structural in nature. Nematodes can be dispersed to new habitats by wind, water, and biotic vectors. Under climax conditions, nematodes are constantly supplied, but the lack of suitable niches generally prevents population establishment. If soil aggregates are resources, interaggregate spaces define the minimal distance that organisms need to travel from one patch to the next. Accessibility to patches depends on the pore sizes leading into an aggregate. Pore sizes at the surface of an aggregate may determine the vulnerability of organisms within

the aggregate to predation from the outside. Colonization sequence and recruitment in soil patches may depend on soil moisture because it determines patch connectivity and corridor permeability for animals of different body sizes and locomotion modes.

Many soil-dwelling micro- and mesofauna can reproduce parthenogenically. Parthenogenesis is an **r-selected** trait, allowing colonization in the absence of mates and usually results in faster population growth rates, potentially accelerating energy and matter fluxes through the food web.

Designing Agricultural Systems with Community Approaches

Modern agricultural methods have relied heavily on nonrenewable natural resources, especially soil and ancient groundwater (44). Petroleum products for fuel, pest management, and fertility have replaced or substituted natural and seasonal patterns of ecological processes with synthetic materials. Designing agricultural systems that more closely mimic natural ecosystems will rely on a greater working knowledge of ecology and evolution. Natural ecosystems, whose components are the results of natural selection, are sustainable; most are productive, responsive to pests, and retentive of nutrients (44). Agricultural soils would more closely resemble soils of natural ecosystems if management practices reduced or eliminated cultivation, including use of heavy machinery and general biocides, and incorporated perennial crops and organic material (41, 103). Uncultivated soil typically has greater aggregate structure, higher organic matter, and more tilth than cultivated soil (58). Generally, research shows that physical disturbance is more disruptive than chemical disturbance (103, 105), although general biocides kill many nontarget predators of the pest or pathogen target (42, 108). Perennial crops have larger root systems than annuals and, thus, provide larger rhizosphere habitats to support complex soil food webs and help to reduce soil erosion because of a longer growing season, fewer inputs of pesticides and fertilizers, fewer passes of farm machinery, and greater carbon sequestration (58). Organic amendments have numerous benefits, including improved soil tilth, retention of water and nutrients, and providing a substrate to support beneficial organisms that allow natural competitive, antagonistic, and mutualistic relationships to occur (85). Organic matter includes microbes as well as bacterivorous and fungivorous nematodes that enhance ecosystem processes such as decomposition, nutrient mineralization, and disease suppression. Although it is difficult to separate their individual effects, concurrent addition of organic matter and elimination of general biocides have the benefit of allowing omnivores and predaceous species to increase in prevalence, which promotes natural disease suppression (147).

Essential Research

Ecological research on nematodes is more than simple observation, enumeration, and identification (45, 130). Given their central role in the soil food web and linkage to ecological processes, nematodes can be a tool for testing ecological hypotheses and understanding biological mechanisms in soil. A limited number of ecological hypotheses have been tested using soil nematodes. However, many other hypotheses that are not yet tested have potential applications for contributing to more sustainable agricultural systems, including improved strategies for biological control and disease suppression, and environmental monitoring. These studies may ultimately lead to development of improved soil ecological theory to understand the impacts that soil fauna have on system processes.

Synchronizing nutrient release and availability relative to plant needs is critical for improving nutrient use efficiency and limiting pollution by excess nutrients. Nematode abundance and environmental properties are often measured simultaneously for practical reasons. However, time lags exist between relative abundance of nematodes and subsequent availability of nitrogen (170; D.A. Neher & M.E. Barbercheck, unpublished data). The need for better resolution of these time lags has practical consequences for designing sampling schedules to test ecological hypotheses related to herbivore-host, pathogen-host, and grazer-food resource questions. Failure to consider time lags may lead to potentially erroneous interpretation of these relationships.

We need to understand ecological theory to better manage our soils. Within the past 20 years, useful tools have emerged in molecular biology (132), stable isotopes (20), complex systems modeling, and in situ techniques to quantify pore networks in soil. These tools offer some exciting possibilities to identify ecological mechanisms related to niche partitioning (169), optimal foraging (30), and biogeochemical cycling (156, 161).

Monitoring and Restoration

Currently, a major limitation in implementation of maturity indices is the lack of public and commercial laboratories with the knowledge and personnel to handle large numbers of samples for identification of free-living nematodes (105). Identification of sentinel taxa that predictably respond to specific disturbance types and respond quantitatively to intensity of disturbance will allow development of molecular-based tool kits that can be used by nonspecialists. For example, Neher & Stürzenbaum (114) developed a general biomarker approach that quantifies DNA damage of nematode species that are relatively sensitive to toxic chemicals and/or unable to repair their DNA to its original sequence (potentially creating lethal mutations) when exposed to relatively high doses of polycyclic aromatic hydrocarbons, but are unresponsive when exposed to a heavy metal. Briefly, this approach performs PCR on relatively long (12K bp) fragments of DNA followed by quantitative PCR. Long sequences are needed to increase the probability that they contain misreads and will not amplify properly. Unfortunately, primers developed for *Caenorhabditis elegans* do not work for other bacterivorous nematodes, including members of the families Cephalobidae and Panagrolaimidae, and the genus *Plectus* (D.A. Neher, unpublished data). Sequence determination of extended lengths of DNA is needed for the free-living nematodes recognized as sentinel taxa. To date, sequence information has been biased toward plant-parasitic nematodes of economic concern (125). Before discontinuing traditional morphological identification of sentinel taxa, it will be necessary to link extensive morphological features to diagnostic DNA sequences. Sequence knowledge will be especially useful for taxa that are morphologically similar and/or for identification of juveniles, which have fewer diagnostic features. Such molecular operational taxonomic units (MOTUs) have enormous potential to become useful for biodiversity surveys (126).

Indicator taxa must correlate or predict ecosystem function to be of value for implementation at regional or national scales.

Linkage of taxa to ecosystem function is necessary to convince other biologists and monitoring programs of the utility of nematode communities as indicators. Nematologists are only beginning to identify sentinel taxa (39, 46, 51, 143) that represent a subset of nematode communities. Identification of the most appropriate taxa will require knowledge of species

assemblage patterns under different scenarios of management practices, often representing a complicated mixture of abiotic and biotic factors (5, 51). Newer computational techniques such as Artificial Neural Networks (88) and null models (60) in conjunction with current multivariate statistical techniques may help to link individual taxa with habitat conditions. Subsequent studies are needed to verify the sentinel status of specific taxa and to determine the geographic or ecological range of their utility. These experiments should be conducted to quantify impacts of multiple and interacting management practices on biodiversity, nutrient cycling, pest populations and plant productivity.

Microbial complexity also increases positively with chemical complexity of the substrates (100). If optimal foraging of bacterivorous and fungivorous nematodes occurs, then one would expect that at least a portion of the food web is **donor controlled** because diversity of lower trophic nematodes would increase with complexity of organic substrates and the microbial decomposer community. This hypothesis assumes many microbial species exude toxic compounds for defense. Nematodes must forage on a varied diet to reduce toxicity and increase nutrition.

Spatially explicit concepts of population dynamics based on the interaction between individuals are a new approach to look at complex systems. In soils, spatially explicit models have to function within a spatially partitioned and diverse environment. Quantitative models of age-structured populations that are scale-appropriate, three-dimensional estimations of hierarchical soil structure would improve predictions of the impact of soil nematodes on their contribution (direct or indirect) to ecological processes such as nitrogen mineralization. These models require more detailed life history experiments that quantify feeding, respiration, and biomass (115), as well as reproduction dynamics at the level of genus and species and population **age structure**. Spatially explicit models will enhance existing soil models that relate **trophic structure** to ecosystem function but fail to treat soil heterogeneity at scales relevant to soil microbes (2–4 µm) and microfauna (5–100 µm) and thus misrepresent the contribution of different taxa. Because spatially explicit models are required on the pore-scale of soils, there are current limitations in existing instrumentation, media resolution, and computer capacity. Emerging models will be required to incorporate efficient computational techniques to adjust observation from life-history studies with observation at the field and microcosm scales.

Relatively little is known about nematode community assemblages and species in natural terrestrial ecosystems. These natural systems can be valuable as reference points for environmental monitoring or ecological restoration efforts (117). They can also be study sites to learn biological mechanisms for disease suppression and host-pathogen relationships. Resulting models are useful to generate and test hypotheses of the attenuation of interactive strength in soil food webs of controlled and field settings.

Nematodes are important components of the soil community with substantial effects on soil ecosystem processes and plant **community structure** (6, 31, 130, 150). Soil nematodes affect the composition of natural vegetation and may cause dramatic shifts in vegetation dynamics through time (29). Herbivory and disease caused by plant-parasitic nematodes rarely kill the host plant but can reduce competitiveness of affected plants. Changes in competitive relationships among plant species can influence direction and rate of succession. Effects of above-ground herbivory on plant competition are relatively well studied, but the role of below-ground herbivory is gaining recognition, especially in its role as a constraint to net primary productivity in grassland systems where plant-parasitic nematodes are numerically abundant as root herbivores (78). Furthermore, selective grazing by plant-parasitic nematodes can affect competition between crop and weed species (22), establishment of clover in rye grass (26), and establishment of dune ecosystems (149). Further knowledge of these types of biotic interactions in soil has applications in the restoration and conservation of plant species diversity.

Plant-parasitic nematodes and plant hosts in natural ecosystems have coevolved longer than crop-nematode systems (19). Understanding the mechanisms of the widespread resistance and tolerance of wild plants could be useful to improving crop protection against plant-parasitic nematodes (94, 148).

Finally, facilitative and inhibitory interactions between plants and nematodes require further study to better understand below-ground plant defense (162). Plant exudates are not always beneficial for plant-parasites. For example, root exudates of *Leucanthemum vulgare*, *Ranunculus acris* and clover (*Trifolium pretense*) decrease populations of plant-parasitic nematodes in the rhizosphere (154). Some plant species contain and exude nematicidal compounds (23) and harbor nematode-suppressive microbes in their rhizosphere (87). For example, *Plantago* is a nematode suppressing plant genus (30). The mechanism is not clear, but greater concentrations of glucose and fumaric acid occurred in root exudates of *Plantago* (162) and barley (*Hordeum vulgare*) in the presence of *Pratylenchus penetrans* and *Meloidogyne incognita*, respectively (64). These effects were isolated from those of other rhizosphere microbes in a controlled experiment.

SUMMARY POINTS

1. Historically, nematology primarily addressed research questions related to disease management by general biocides. Contemporary concerns about environmental degradation and global climate change provide incentives to revisit nematodes as pivotal ecological players in soil communities of agricultural and natural ecosystems.
2. Ecology is a branch of biology and contributes to our understanding of evolution, and may focus on one or more scales, such as population, community, or ecosystem.
3. Nematodes are aquatic organisms that depend on thin water films to live and move within existing pathways of soil pores of 25–100 µm diameter.
4. Soils provide a complex hierarchical scaling of structure that includes pore distribution and aggregates. Habitable pore space oscillates in response to soil water dynamics. Few nematologists or ecologists include physical

5. Given their central role in the soil food web and linkage to ecological processes, nematodes can be a tool for testing ecological hypotheses and understanding biological mechanisms in soil.
6. Ecological succession is one of the most tested community ecology concepts, and a variety of indices have been proposed for purposes of environmental monitoring. In contrast, theories of biogeography, colonization, optimal foraging, and niche partitioning are poorly understood.
7. Ecological hypotheses related to strategies of coexistence of species sharing the same resource have potential uses for more effective biological control and use of organic amendments to foster disease suppression.
8. Indicator taxa must correlate or predict ecosystem function to be valued for implementation on regional or national scales. It is the linkage to ecosystem function that is necessary to convince other biologists and programs of the utility of nematode communities as indicators.

FUTURE ISSUES

1. Release and availability of nutrient amendments synchronized to the timing of plant needs would improve nutrient use efficiency and limit pollution of excess nutrients.
2. Biological control and use of organic amendments to foster disease suppression can be made more effective by applying ecological concepts related to nematode strategies of coexistence of nematode species sharing the same resource.
3. Tools are needed to explicitly identify dietary preferences to allow for a greater understanding of nematode ecology at a species or genus level.
4. Sentinel nematode taxa that predictably respond to specific disturbance types need to be identified and verified to develop relatively simple molecular-based tool kits for nonspecialists.
5. Interpretation of nematodes as biological indicators of soil depends on quantifiable linkages between indicator taxa and ecosystem function.
6. Quantitative models of age-structured populations that are scale-appropriate, three-dimensional estimations of hierarchical soil structure would improve predictions of the impact of soil nematodes and their contribution to ecological processes.
7. Discovering community assembly patterns of soil nematodes under different scenarios of management practices will provide a reference for interpretation of nematode indicators used for environmental monitoring, conservation, and restoration.

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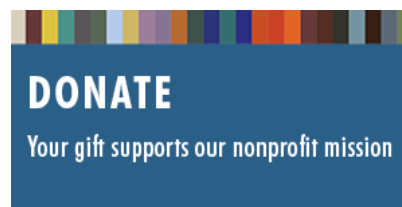
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