

# New Frontiers in Nematode Ecology<sup>1</sup>

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*Abstract:* Future areas of emphasis for research and scholarship in nematode ecology are indicated by pressing agricultural and environmental issues, by new directions in applied nematology, and by current technological advances. Studies in nematode ecology must extend beyond observation, counting, and simple statistical analysis. Experimentation and the testing of hypotheses are needed for understanding the biological mechanisms of ecological systems. Opportunities for fruitful experimentation in nematode ecology are emerging at the ecosystem, community, population, and individual levels. Nematode ecologists will best promote their field of study by closely monitoring and participating in the advances, initiatives, developments, and directions in the larger field of ecology.

*Key words:* Approach, biodiversity, concept, ecology, level of organization, nematode, population regulation, scale, theory, trophic roles, variability.

Ecology is the study of relationships between organisms and their environment. Ecological relationships may be considered at and across various levels of biological organization, from the individual to the ecosystem. As in all fields of science, advances in ecology occur in surges as major ideas evolve and are verified in various systems and as new techniques that remove methodological constraints are developed.

In considering the status of nematode ecology, I am questioning i) whether the major ecological ideas and concepts have been tested in nematology, ii) whether nematode ecologists have capitalized on the technological advances in nematology and ecology, iii) whether the evolving sub-disciplines of ecology are being considered in relationship to nematodes, iv) whether important papers on nematode ecology are published in prominent ecological journals, and, finally, v) whether the evolving frontiers of nematology are being considered in the ecological context of genetic and environmental diversity, e.g., the importance of host-plant resistance and the development of transgenic plants and organisms.

The answers to these questions seem largely negative, or perhaps positive with

qualification, for a variety of reasons. First, nematode ecologists work with difficult systems: microscopic organisms in an often opaque environment. However, some nematodes are among the most tractable of animals to work with and provide distinct advantages to experimentation in soil systems because of the limitation of their immigration and emigration. Second, the concept of "nematode" ecologist tends to promote assembly of data vertically within the phylum, e.g., proportional distribution of the nematode community in various unlinked trophic groups, rather than horizontally across trophic exchanges among taxa. Third, in some research institutions there have been real or perceived constraints to interdisciplinary experimentation through reduced recognition in the merit and promotion process. Fortunately, this situation no longer remains in most institutions. Fourth, training in nematology often lacks appropriate breadth. Many agricultural nematologists are very familiar with plant-parasitic genera but are much less comfortable with the identification and biology of other groups. Finally, there is a need for the application of new technology, including diagnostic tools and markers of genetic diversity.

Ecologists have always wrestled with choosing suitable approaches in their research. Some, including Darwin, have argued for gathering all the facts and then looking for higher-order principles. Others have advocated hypothetico-deductive approaches (36). Clearly, a combination of

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rigorous analytical methodology with imaginative approaches and interpretations is needed. The understanding of nematode ecology will develop through the emergence of new theory, which will lead to additional falsifiable hypotheses as the basis for rational experimental design. Ecologists should ensure that they are completing the fundamental loop of the scientific method. Individually or collaboratively, they should participate in the complete sequence of observation-hypothesis-experiment, rather than remaining either theorists or empiricists.

Some major concepts in ecology have been explored in nematology, including the dynamics of species interaction (24,43), the relationship between complexity and stability in ecosystems (26), and the characterization of organisms as "r" or "K" selected (28). There has been some application of concepts of plant-herbivore coevolution (11) and density-dependent regulation of populations (3). However, more "recent" concepts such as metapopulations (17), optimal foraging theory (12,27) and evolutionarily stable strategies (29), and application of network theory to food webs (34) have received little attention.

Nematologists have often utilized new technology in their studies of nematode ecology, although the availability of equipment and expertise is sometimes a constraint. Currently, the tools of molecular biology are being applied in several significant areas, particularly to assess genetic diversity and to develop diagnostic tests (6). Collaborative efforts among scientists have led to the use of evolving technology for the measurement of diversity. There are tremendous opportunities for development of information-based resources for nematode management: e.g., databases of host ranges, specific biological antagonists, nematode-resistant cultivars, and optimization approaches to the selection of cropping sequences. Data analysis in nematology has occasionally included geostatistics, applied time-series analysis (31), and geographic information systems (18). How-

ever, these applications have often appeared preliminary or have been applied to inappropriate datasets.

#### ECOLOGICAL STUDY AT VARIOUS LEVELS OF BIOLOGICAL ORGANIZATION

Ecology may be studied at various levels of biological organization, provided that processes, mechanisms, and theory are integrated across the levels. The following examination of areas and concerns at each level of ecological study suggests some of the many opportunities in nematode ecology. The review does not comprise an exhaustive list.

##### *Ecosystem level*

To understand ecology at the ecosystem level, the ecologist must study the behavior of whole systems in relation to environmental conditions and their perturbations. Responses at the ecosystem level result from the interaction of component parts of the system and from the impact of environment on these interactions. A basic tenet of systems ecology is that the behavior of the system as a whole may differ from that predicted by studying the independent behavior of components of the system. However, study of the component parts and their interrelationships is fundamental to analysis of the biological mechanisms that underlie systems ecology.

There are two important considerations in experimental design and ecological study at the systems level. One is the need for a synoptic approach. Rather than subsuming variability by experimental design, important information can be gained by characterizing relationships at discrete spatial or temporal distances as indicators of the performance of the system in different states. The other design consideration involves the powerful tools of systems analysis and systems research. The established protocols of the systems approach include initial definition of system boundaries, research objectives, state variables, extrinsic and intrinsic factors, and rates of flux. The second phase of the systems approach is to develop, verify, and validate a systems

model, and to conduct systems research using the model (22). Experience with systems models has established their value in revealing areas of ignorance. However, the coarse assumptions that are made to complete the model have often resulted in poor predictive abilities.

Because ecological models are scale-dependent, it is important to collect data at an effective scale of measurement. For example, spectral analysis may be a powerful tool for analysis of temporal or spatial data; however, it will be useful only if the data are collected at a finer scale than the interval between the critical spatial or temporal events (31).

In applied nematology, ecosystem-level studies are fundamental to understanding the behavior and design of cropping systems and to research and development in sustainable agriculture. Interdisciplinary team approaches, in which the experimental design, measurement, analyses, and interpretation cross disciplinary boundaries, and multidisciplinary participation, in which several investigators function independently in the same experimental environment, are vital to ecosystem-level research. Although modeling groups can form a useful core for interdisciplinary efforts, the research team must be structured so that all investigators are involved in design and experimental decisions.

I currently participate in a multi-investigator Low Input Sustainable Agriculture project, which involves a 30-acre long-term field site with three farming systems and appropriate crop rotations within those systems. The investigators frequently struggle with fundamental questions of experimental design and concept, management decisions, what to measure, what to compare, and the inadequacies of analytical procedures. The primary objective of the project is to study the response of the ecosystem to the farming systems, particularly as expressed through soil characteristics. This project exemplifies the challenges and opportunities of systems-level research. For example, appropriate analytical techniques must be ap-

plied to data from ecosystems in transition. Here there is opportunity for application of time series analyses and geostatistical approaches rather than comparison of variables at fixed points in time. There are problems in designing ecosystem level studies in a replicated experimental approach, e.g., decisions about which factors should be optimized and which should be controlled. It is difficult, if not impossible, to design small plot experiments with the diversity and companion plantings that could be developed on a whole farm. Approaches in field and ecosystems ecology may provide guidance.

Through 20 years of studying Canadian lakes, Odum (32) and Schindler (38) demonstrated that many properties of ecosystems cannot be studied at scales smaller than the ecosystem level. Based on theoretical ecology, Odum developed 18 ecosystem response-to-stress hypotheses. Schindler verified six of these hypotheses, partially verified six, and found three non-conformations in the community energetics of the lakes. Interestingly, functional properties (e.g., community metabolism) were more stable than structural properties (e.g., species composition). Furthermore, new species emerged in response to changes in stress that were not present at detectable levels before the stress.

Ecosystem-scale experiments would diminish in importance only if there were complete information on community composition, ecosystem function, and natural variation. Ecosystem experiments will continue to guide ecosystem management and theoretical developments, and will be especially important as a source of observations leading to controlled experiments that reveal the underlying mechanisms.

#### *Community level*

Community ecology is the ecology of a group of organisms of different species that occur in the same habitat and interact through trophic and spatial relationships. In the plant nematology literature, "community ecology" is often loosely used to describe the ecology of only the nematodes in

the system, particularly their trophic organizations. However, this use of "community" is misleading: The nematodes may be only distantly linked in trophic relationships and may not be spatially proximate in the soil. Furthermore, each nematode species interacts in a community of organisms at the same and related trophic levels, most of which are not nematodes. Thus the community must be defined in terms of all its components and their interactions, as implied in the definition of community ecology. Without such a definition, nematode "community ecology" will remain at the level of trophic group summations.

As with systems-level studies, the design of replicated experiments for hypothesis testing at the community level is often difficult. Simple statistical descriptions of observations are not sufficient. Again, there are opportunities in approaches that capitalize on spatial or temporal variability among components of the system, rather than assigning variability as "error." Equally important are geostatistical methods that measure relative magnitude of populations and (or) environmental conditions at discrete points in space, and thus make use of spatial variability. Similarly, techniques such as LOESS (locally weighted scatterplot smoothing) may be useful in revealing underlying trends in spatially variable data that would otherwise be lost as "variance" (8,14).

*Trophic roles in communities:* Because of their lack of training in the taxonomy of free-living nematodes, ecologists have categorized nematodes into trophic groups, based largely on oral structure and assumptions of feeding habits (15,30,33). Although descriptively appealing, aggregating nematode species with very different biologies into a single trophic group fails to acknowledge the quantitative contribution or significance of each species in the system. In addition, because metabolic and respiratory energetics have been studied for only a few species of nematodes, extrapolations of those data to the energetics

of trophic level groupings may result in questionable estimates. Grouping of species of similar biology into "trophic species" is an acceptable intermediate compromise (9), with an attendant requirement of greater knowledge of the biology, metabolic rates, and lifetable characteristics of the organisms. The categories used for nematodes by Bongers (4) provide a useful framework. Greater knowledge of individual species energetics and progress in the equally deficient area of substrate suitability and preference for each species are critical. A few comprehensive inventories of changes in species composition and abundance through time have been compiled (e.g., 1) and, when combined with further study of individual species energetics and feeding habits, will provide valuable datasets for understanding community dynamics.

An important area of ecological study is the role and management of nematodes in the health and productivity of sustainable soils. There is substantial evidence of the importance of nematodes as agents in mineral and nutrient cycling (16,19,20). Unfortunately, over the last 50 years, the training of students in plant nematology has focused on primary consumers. In contrast, many earlier nematologists were generalists in understanding and approach. Plant nematologists must communicate with ecologists and keep apprised of recent developments and evolving concepts.

One potential application of nematology and ecology is based on the importance of microbial degradation in the recovery of polluted soil and water and in the decomposition of wastes. Because nematodes are among the primary grazers on microbes, we need to determine the extent to which such grazing enhances or reduces microbial activity. Which nematode species are adapted or adaptable to bioremediation of polluted environments? There are already some examples of pioneering studies in this area (2,4,40,41).

Another potential application arises out

of research on aquatic systems, which are often open communities. The effects of extrinsic forces, for example, tides or stream flow, delivering food sources into a community will be an interesting area of investigation (1). Such "supply-side" ecological processes may be less dynamic, but still important, in their influence on soil nematodes. Here the system will be fueled less regularly by organic matter incorporation and pulses of rainfall or irrigation.

*Biodiversity:* We have only scratched the surface in developing inventories of nematode species in different habitats, disturbed or undisturbed (e.g., 1). Nematode species composition or the presence or absence of key species may be useful ecological and environmental indicators (4,37).

A rich field of investigation is the potential success of organisms entering and becoming established in systems in transition. These studies may provide information on the potential for introducing organisms such as biocontrol agents or high-turnover mobile microbivores to create a food substrate that would augment levels of a nematode-parasitic fungus.

*Community structure in biological control:* Community ecology involves the study of multitrophic interactions. Several organisms may participate in host-parasite interactions, predator-prey interactions, and decomposition food webs. Studies at this biological level must be collaborative to ensure appropriate taxonomic expertise.

An important concept in population regulation by natural enemies is that of density dependence, which has proven useful in interpreting the regulation of plant nematode populations by their parasites (21). Population regulation is a community attribute, however, and not merely a two-species interaction. Thus we need to study the density dependence of nematode population regulation at the community level. Nematode-suppressive soils have been documented, but the mechanisms of suppression have been determined in only a few studies (e.g., 45). Detailed categorization of these mechanisms will necessarily

involve development of multiple-decrement life tables (7) that include mortality resulting from exploitation, competition, and antibiosis.

#### *Population level*

Population ecology is that of a group of organisms of one species occupying a given area. It is the study of all the processes that generate the adaptation of organisms to their biotic and abiotic environments and includes demography, population dynamics, population genetics, and population regulation. As at other levels of ecological study, an important consideration is that of variability, including the range of genetic variability, the maintenance of genetic variation, and the interaction of variation and selection that results in evolutionary change.

Again, ecologists face the problem of definition of appropriate experimental or observational scale. The concept of metapopulations recognizes that what we consider to be a "population" may actually be a composite of individual populations that are in demographic and genetic disequilibrium but stable as a whole (17). Most population studies in the field in nematology are actually conducted at the metapopulation level. The concept is especially applicable to populations of soil nematodes, which form isolated aggregates in the soil matrix. The concept is also applicable to parthenogenic organisms that are reproductively restricted from genetic recombination. Generally, ecological investigations of soil nematodes have not utilized a scale appropriate for a population of interacting individuals in a consistent environment. The size of the unit for selection of an appropriate scale is unknown. In both biotic and abiotic environments, the differences between the soil surface and 50-cm depth are enormous.

Considerable demographic data need to be gathered at the population level, especially on generation times and the variability of life-table parameters such as stage-specific development rates, survivorship,

and fecundity. Again, variance is a challenge, but a wealth of information can be gained by measuring it, determining its underlying mechanisms, and considering its contribution to the success of nematodes in various ecosystems.

Spatial patterns and nematode population dynamics are other areas where appropriate scale of measurement is important. For reasonable use of geostatistical analyses, the spatial scale of measurement should be smaller than the probable scale at the spatial level of interest. Applied time-series analysis (e.g., spectral or cospectral analysis) may be extremely data intensive, requiring observations to be taken frequently enough so that cycles can appear in the analysis. Estimation of life-table parameters for *Paratrichodorus minor* by "reverse simulation" was successfully achieved from observations at 12-hour intervals. However, lifetable parameters could not be determined from field data obtained at a larger time scale (39).

#### *Individual level*

At the individual level, ecology is the study of the relationship of the physiological processes of organisms to their environmental conditions. These relationships constitute the underlying mechanisms of ecology. There are many sublevels of individual ecology, which are mechanistically linked.

An area rich in potential for nematology is that of behavioral ecology, the study of the behavior of an organism in relation to its environment. Concepts in this area include that of the Evolutionarily Stable Strategy; the optimal strategy is the one that maximizes the chance of current survival and future reproductive success (29). A component of this strategy is Optimal Foraging Theory (12,27), which involves, for example, determination of the distance within which a plant-parasitic nematode should respond to a host root stimulus to maximize survival. The optimal strategy is a function of the behavioral and survival attributes of the species, the location of an individual in the soil profile, the danger of

movement into a physically or biologically unfavorable habitat, and the probability of non-encounter with the food source.

Another area of individual ecology with exciting potential in nematology is chemical ecology; i.e., the origins and nature of chemical cues in the environment and the response of organisms to those cues. Nematodes invariably respond to CO<sub>2</sub> gradients, which may orient them generally toward a rhizosphere, but there must be species-specific signals (10). Advancing techniques in chemical analysis will be useful. The potential alteration of the behavioral ecology of plant-parasitic nematodes through attraction, repellence, and confusion provides interesting opportunities in nematode management (10,13).

#### INTEGRATION ACROSS THE HIERARCHY OF ECOLOGICAL ORGANIZATION

Ecologists struggle to explain observations at one level of organization based on biological understanding of a lower level. Theory reduction may be defined as the interpretation of higher-level phenomena in terms of lower-level processes or mechanisms (23). The desire for such interpretation emphasizes the importance of documenting the descriptive biology and seeking its underlying mechanisms.

Ecophysiology is the bridge between population level parameters and cellular or subcellular biology. The cellular and subcellular biology of one nematode system, *Caenorhabditis elegans*, is extremely well understood. The challenge remains to extend this understanding to other nematode systems and to bridge the gap between cellular, individual, and population levels of biology (35).

One aspect of the interface between individual organisms and the dynamics of populations is that of genetic and physiological variability. For example, eggs of the sugarbeet cyst nematode, *Heterodera schachtii*, exhibit four types of dormancy. All four types may be present simultaneously in eggs of a single population (44). The explanation of population level phe-

nomena from the biology of individuals requires appreciation and measurement of the diversity among individuals.

The interface between populations and communities involves considerations of scale and universe size addressed earlier. The complexity of interactions at the community level often requires simplification through development of multitrophic models. Such models may be phenomenological in that they use, for example, regression techniques to describe observed response of the system to measured perturbation. Alternatively, they may be mechanistic in that they synthesize the expected behavior of the system from the prediction of the response of its components to the perturbation. Both approaches have merit; the simplicity and precision of phenomenological approaches can provide useful descriptors of community level processes. For other purposes, including descriptive realism and the transfer of the model to other environments, the mechanistic approach is appropriate.

Theory is the pathway to extrapolation when predictions of system behavior are made without benefit of prior experimentation. As such, theory provides a basis for formulating testable hypotheses. Development of a theoretical basis also provides a crude guide for management actions without the benefit of prior site-specific studies.

#### RESEARCH PRIORITIES FOR BIOSPHERE SUSTAINABILITY

Nematode ecologists will promote their field of study by closely monitoring and participating in the advances, initiatives, developments, and directions in the larger field of ecology. A current thrust in the United States is the development of a Sustainable Biosphere Initiative (25), which emphasizes three primary research areas: i) global change, i.e., the ecological causes and consequences of climatic change and land- and water-use patterns; ii) biological diversity, i.e., expansion of the biological

inventory and elucidation of the ecological causes and consequences of diversity and its changes; and iii) sustainable ecological systems, i.e., stress detection, stress restoration, systems management, and the interface of ecological and human social systems.

Within these areas of emphasis, specific research topics include the following: the study of patterns of diversity; the interaction of morphological, physiological, and behavioral traits and the plasticity of the traits; the causes and consequences of dispersal and dormancy; the population-level consequences of life-history adaptations; the mediation of changes in population size at the level of the individual; the effect of the structure of a population on its response to stress; the effect of landscape fragmentation on populations; the factors that govern assembly of communities; feedback mechanisms between biotic and abiotic factors; the effect of patterns and processes at one spatial or temporal scale on those at another; and the consequences of spatial and temporal environmental variability. These defined research areas will channel ecological thinking and will generate research funding opportunities. Nematode ecologists have the potential to make significant contributions to these initiatives.

#### RECOMMENDATIONS

*i.* Review and consider the Van Gundy (42) admonition to "take off our blinders" and to monitor and incorporate the advances of related areas of science.

*ii.* Seek sabbatical leave opportunities with basic biologists or animal and plant ecologists to avoid the inbreeding of thought inherent in professional interactions limited to disciplinary peers.

*iii.* Participate in and ensure *interdisciplinary* rather than *multidisciplinary* research in sustainable agriculture and integrated pest management projects.

*iv.* Endeavor to bridge departmental and other institutional boundaries in establishing professional and collaborative liaisons.

v. Publish results of nematological studies that address current issues in ecology in ecological journals.

vi. Diversify academic lineages and experience in nematology units through hiring practices, sabbatical leave opportunities, and postdoctoral appointments.

vii. Consider the strengths of the biological system underlying nematode ecology. Nematode molecular biology, development, genetics, and physiology are better known than for most other organisms; populations are quantifiable and individuals are distinguishable; migration is minimal; and the habitat is definable and buffered.

viii. Adhere rigorously to the scientific method in research approach; complete the loop of observation, theory, hypothesis, experiment, new theory or alternative hypothesis. Always incorporate at least two phases of this process; for example, observation, theory, hypothesis, experiment or hypothesis, experiment, alternative hypothesis.

ix. Avoid the pitfall of trying to find some application for new technology, an approach that usually leads to being stuck in the loop of observation, collecting data, and trying to relate it to theory. This approach is unlikely to advance knowledge in nematode ecology. Rather, define the research problem (based on theory and hypothesis) and devise innovative approaches for testing the hypothesis using all available techniques.

At all levels of ecology, we should be dissatisfied with limiting our studies to observations and simple statistical analyses. We must take the further step of understanding the biological mechanisms of the system. This step will include hypothesis proposal and testing as well as experimentation on components of ecological systems in microcosm. Generally, this approach is easiest to accomplish at the population and physiological levels. Perturbation and response experiments are valuable to delineate the function of system components. Ecosystem-level experiments are important as a basis for understanding the whole

system response. Replicated experimentation is more difficult at the community and systems level, and measurements and analyses may involve techniques from other disciplines, such as engineering and sociology.

#### LITERATURE CITED

1. Algoni, D. M. 1990. Community dynamics of free-living nematodes in some tropical mangrove and sandflat habitats. *Bulletin of Marine Science* 46:358–373.
2. Amjad, S., and J. S. Gray. 1983. Use of the nematode–copepod ratio as an index of organic pollution. *Marine Pollution Bulletin* 14:178–181.
3. Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. Chicago: University of Chicago Press.
4. Bongers, T. 1990. The maturity index: An ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83:14–19.
5. Bongers, T., and G. W. Yeates. 1988. Report on workshop: Nematodes in natural systems; the use of nematodes in environmental studies. *Pedobiologia* 32:88.
6. Caswell-Chen, E. P., V. M. Williamson, and F. F. Wu. 1992. Random amplified polymorphic DNA analysis of *Heterodera cruciferae* and *H. schachtii* populations. *Journal of Nematology* 24:343–351.
7. Carey, J. R. 1989. The multiple decrement life-table: A unifying framework for cause of death analysis in ecology. *Oecologia* 78:131–137.
8. Cleveland, W. S., and S. J. Devlin. 1988. Locally weighted regression: An approach to regression analysis by local fitting. *Journal of the American Statistical Association* 83:596–610.
9. Cohen, J. E. 1989. Food webs and community structure. Pp. 181–202 in J. Roughgarden, R. M. May, and S. A. Levin, eds. *Perspectives in ecological theory*. Princeton: Princeton University Press.
10. Dusenbery, D. B. 1987. Prospects for exploiting sensory stimuli in nematode control. Pp. 131–135 in J. A. Veech and D. W. Dickson, eds. *Vistas on nematology*. Society of Nematologists.
11. Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: A study in coevolution. *Evolution* 18:586–608.
12. Emlen, J. M. 1966. The role of time and energy in food preference. *American Naturalist* 100: 611–617.
13. Ferris, H. 1992. Biological approaches to the management of plant-parasitic nematodes. Pp. 112–172 in J. P. Madden, ed. *Beyond pesticides: Biological approaches to pest management in California*. Berkeley: University of California Press.
14. Ferris, H., and J. C. Prot. 1991. Interpreting crop yield–nematode and nematode–nematode relationships from field data. *Journal of Nematology* 23: 528–529 (Abstr.).
15. Freckman, D. W., and R. Mankau. 1986.

Abundance, distribution, biomass and energetics in a northern Mojave Desert ecosystem. *Pedobiologia* 29: 129–142.

16. Griffiths, B. S. 1990. A comparison of microbial-feeding nematodes and protozoa in the rhizosphere of different plants. *Biology and Fertility of Soils* 9:83–88.

17. Hanske, I., and M. Gilpin. 1991. Metapopulation dynamics—Brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3–16.

18. Haslett, J. R. 1990. Geographic information system: A new approach to habitat definition and the study of distributions. *Trends in Ecology and Evolution* 5:214–216.

19. Hunt, H. W., D. C. Coleman, E. R. Ingham, R. E. Ingham, E. T. Elliott, J. C. Moore, S. L. Rose, C. P. P. Reid, and C. R. Morley. 1987. The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils* 3:57–68.

20. Ingham, R. E., J. A. Trofymow, E. R. Ingham, and D. C. Coleman. 1985. Interactions of bacteria, fungi and their nematode grazers: Effects on nutrient cycling and plant growth. *Ecological Monographs* 55: 119–140.

21. Jaffee, B., R. Phillips, A. Muldoon, and M. Mangel. 1992. Density-dependent host–pathogen dynamics in soil microcosms. *Ecology* 73:495–506.

22. Kitching, R. L. 1983. *Systems ecology: An introduction to ecological modelling*. New York: University of Queensland Press.

23. Loehle, C. 1988. Philosophical tools: Potential applications to ecology. *Oikos* 51:97–104.

24. Lotka, A. 1925. *Elements of physical biology*. Baltimore: Williams and Williams.

25. Lubchenco, J., A. M. Olson, L. B. Brubaker, S. R. Carpenter, M. M. Holland, S. P. Hubbell, S. A. Levin, J. A. MacMahon, P. A. Matson, J. M. Melillo, H. A. Mooney, C. H. Peterson, H. R. Pulliam, L. A. Real, P. J. Regal, and P. G. Risser. 1991. The sustainable biosphere initiative: An ecological research agenda. *Ecology* 72:342–371.

26. MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533–536.

27. MacArthur, R. H., and E. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603–609.

28. MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton, NJ: Princeton University Press.

29. Maynard Smith, J. 1976. Evolution and theory of games. *American Scientist* 64:41–45.

30. Niblack, T. L. 1989. Applications of nematode community structure research to agricultural production and habitat disturbance. *Journal of Nematology* 21:437–443.

31. Nielsen, D. R., and M. H. Alemi. 1989. Statistical opportunities for analyzing spatial and temporal heterogeneity of field soils. Pp. 261–272 in M. Clarholm and L. Bergstrom eds. *Ecology of arable land—*

*Perspectives and challenges*. Boston: Kluwer Academic Publishers.

32. Odum, E. P. 1990. Field experimental tests of ecosystem-level hypotheses. *Trends in Ecology and Evolution* 5:204–205.

33. Parmelee, R. W., and D. G. Alston. 1986. Nematode trophic structure in conventional and no-tillage agroecosystems. *Journal of Nematology* 18: 403–407.

34. Patten, B. C., R. W. Bosserman, J. T. Finn, and W. G. Cale. 1976. Propagation of cause in ecosystems. Pp. 457–479 in B. C. Patten, ed. *Systems analysis and simulation in ecology*, vol 4. New York: Academic Press.

35. Riddle, D. L., and L. L. Georgi. 1990. Advances in research on *Caenorhabditis elegans*: Application to plant parasitic nematodes. *Annual Review of Phytopathology* 28:247–269.

36. Roughgarden, J., R. M. May, and S. A. Levin. 1989. Introduction. Pp. 3–10 in J. Roughgarden, R. M. May, and S. A. Levin, eds. *Perspectives in ecological theory*. Princeton, NJ: Princeton University Press.

37. Samoiloff, M. R. 1987. Nematodes as indicators of toxic environmental contaminants. Pp. 433–439 in J. A. Veech and D. W. Dickson, eds. *Vistas on nematology*. Society of Nematologists.

38. Schindler, D. W. 1990. Experimental perturbation of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* 57:25–41.

39. Schneider, S. M., and H. Ferris. 1986. Estimation of stage-specific developmental times and survivorship from stage frequency data. *Researches on Population Ecology* 28:267–280.

40. Tietjen, J. H., and J. J. Lee. 1984. The use of free-living nematodes as a bioassay for estuarine sediments. *Marine Environmental Research* 11:233–251.

41. Van Kessel, W. H. M., R. W. B. Zaalberg, and W. Seinen. 1989. Testing environmental pollutants on soil organisms: A simple assay to investigate the toxicity of environmental pollutants on soil organisms using CdCl<sub>2</sub> and nematodes. *Ecotoxicology and Environmental Safety* 18:181–190.

42. Van Gundy, S. D. 1980. *Nematology—Status and prospects: Let's take off our blinders and broaden our horizons*. *Journal of Nematology* 12: 158–163.

43. Volterra, V. 1926. *Variazioni e fluttuazioni del numero d'individui in specie animali conviventi*. *Memorie Accademia Nazionale del Lincei* (Ser. 6) 2: 31–113.

44. Zheng, L., and H. Ferris. 1991. Four types of dormancy exhibited by eggs of *Heterodera schachtii*. *Revue de Nématologie* 14:419–426.

45. Zuckerman, B. M., M. B. Dicklow, G. C. Coles, R. Garcia, and N. Marban-Mendoza. 1989. Suppression of plant parasitic nematodes in the Chinampa agricultural soils. *Journal of Chemical Ecology* 15: 1947–1955.