

5

Indices Developed Specifically for Analysis of Nematode Assemblages

HOWARD FERRIS¹ AND TOM BONGERS²

¹Department of Nematology, University of California, USA; ²Laboratory of Nematology, Wageningen University, The Netherlands

History

Back in the early 20th century, about 50 years into the era in which the diversity and abundance of nematodes became generally recognized, Cobb (1914) calculated that if the nematodes resident in one acre (0.4 ha) of soil near San Antonio, Texas, USA, were to proceed head-to-tail to Washington DC, some 3200 km distant, the first nematode would reach Washington before the rear of the procession left San Antonio! Eighty years later, Jairajpuri and Ahmad (1992) estimated that nematodes constitute nearly 90% of the world's multicellular animals while Platt (1994) asserted that four out of every five multicellular animals on the planet are nematodes.

Awareness of the seething hordes of worms was at first constrained by the microscopic nature of most of the phylum Nematoda. The study of human and animal parasites, usually larger than soil and aquatic forms and of immediate interest to their hosts, was first to develop (Dujardin, 1845; Baird, 1853). Besides patches of poor growth or 'tired soil' of undetermined cause, early recognition of the prevalence and impact of plant-parasitic nematodes was of those for which there are characteristic signs and symptoms in buds, seed heads, stems, foliage and roots (see examples in Christie, 1959 and Filipjev and Schuurmans Stekhoven, 1941). Around 1850, marine biologists began to recognize nematodes; there were, for example, studies on the nematodes of Iceland (Leuckart, 1849), the Mediterranean (Eberth, 1863), the English coast (Bastian, 1865), the coast of Brittany (Villot, 1875) and on nematodes collected by various expeditions (Von Linstow, 1876). Freshwater nematodes began to receive attention around 1890 with the papers of Daday (1897) on the Hungarian fauna. The development of information on free-living soil nematodes is well reviewed by Filipjev and Schuurmans Stekhoven (1941), Overgaard Nielsen (1949) and Paramonov (1962). Early work on the free-living nematodes included careful descriptions of *Enoplus*, *Oncholaimus*, *Rhabditis*

©CAB International 2009. *Nematodes as Environmental Indicators* (eds M.J. Willson and T. Kakouli-Duarte)

and *Dorylaimus* (Dujardin, 1845). That work was followed by a period of discovery during what Filipjev (1918) called 'the period from Bastian (1865) to de Man (1884-1893)' in which Bastian's studies on terrestrial, freshwater and marine nematodes were followed by further contributions to the knowledge of soil nematodes (e.g. Bütschli, 1873). Awareness of the diversity and abundance of nematodes was further accelerated with the impressive series of papers by de Man (see Karssen, 2006) and by Cobb (see Spenneman, 2003). Unfortunately, despite his legendary productivity, Cobb was sometimes unaware of the European literature, which resulted in a confusion of terminology, species descriptions and classification schemes (Overgaard Nielsen, 1949; Paramonov, 1962).

Further impetus to the study of nematology was provided by technological developments: advances in microscopy, biochemistry and molecular biology. Awareness of the impact of nematodes on plants increased as a result of the development and wide-scale use of nematicides; crop yields were improved in previously less-productive soils. Consequently, researchers and practitioners with varied backgrounds and interests were drawn into nematology. From the 1970s onwards, research on nematodes exploded following the fortuitous connections and interactions among Margaret Briggs, Ellsworth Dougherty, Warwick Nicholas and Sydney Brenner that resulted in the selection of *Caenorhabditis elegans* as a model organism for deciphering the genetic code (<http://plpnemweb.ucdavis.edu/Nemaplex>).

Prior to the eruption of research on *C. elegans*, other than the activities of a few taxonomists, most studies on soil nematodes centred on the biology and management of those that cause damage to higher plants. A milestone in the ecology of free-living soil nematodes was the seven-year study in Denmark by Overgaard Nielsen (1949) on nematode faunae of different soils, their physiological ecology and even their ecosystem services. Further notable ecological contributions emerged in the 1970s and 1980s (e.g. Nicholas, 1975). Centres of ecological study on nematodes developed in Sweden (e.g. Sohlenius, 1973), Poland (e.g. Prejs, 1970; Wasilewska, 1970), Italy (e.g. Zullini, 1976), Germany (e.g. Sudhaus, 1981), and Russia (e.g. Tsalolikhin, 1976). In the USA, there was a surge of activity in soil ecology at the National Resource Ecology Laboratory in Colorado Springs, led by Coleman and others (e.g. Yeates and Coleman, 1982), and similar activity at the Institute of Ecology of the University of Georgia, led by Crossley and colleagues (e.g. Stinner and Crossley, 1982). In the same time period, Yeates was developing a very productive programme on the ecology of soil nematodes in New Zealand (e.g. Yeates, 1979). A significant contribution was the publication of the PhD research of Ingham, with its accompanying review of preceding studies, in which the functional significance of bacterivore and fungivore nematodes was established by the demonstration that their excretion of nitrogen in excess of structural and metabolic needs stimulated plant growth (Ingham *et al.*, 1985).

During the latter part of the 20th century, analyses of nematode communities in aquatic environments revealed that the incidence and prevalence of species in the community reflect the nature and quality of the environment

(e.g. Micoletzky, 1925; Prejs, 1970; 1977; Zullini, 1976; Callahan *et al.*, 1979). Many subsequent studies have expanded our understanding that various nematode species differ in response to degradation of aquatic environments. The nature and magnitude of changes in community structures of aquatic nematodes are recognized as excellent indicators of water and sediment quality in relation to pollution or enrichment (Beier and Traunspurger, 2001; Barbuta and Zullini, 2005).

So, interest in the role of nematodes in soil and aquatic ecosystems was established. In parallel, work continued in nematode taxonomy and systematics with understanding and interest accelerated by electron microscopy and molecular tools. In his oft-quoted passage reflecting that if all non-nematode matter was swept away, topography and land use patterns would be recognizable from the remaining nematodes, Cobb (1915) speculated that, had we sufficient knowledge, location and species of the various plants and animals would be decipherable by examination of their erstwhile nematode parasites. As documented above, we now have sufficient knowledge to concur with Cobb's speculation and, in fact, to expand on it in relation to environmental quality (Bongers and Ferris, 1999).

The development of nematodes as bioindicators in soil and aquatic systems required determination of appropriate ways to assess and quantify their contributions to ecological processes, and the validation of their utility as indicators of environmental condition. Several unique characteristics of nematodes facilitated those developments (see Yeates *et al.*, Chapter 1, this volume and Trett *et al.*, Chapter 12, this volume). Key among those characteristics is diversity, both taxonomic and functional, of nematodes.

Diversity Indices

Many indices have been developed and applied to assess the biodiversity of ecosystems (see Neher and Darby, Chapter 4, this volume for fuller explanation). In the purest sense, the indices are based on assessment of all organisms at the species level. In practice, they are usually applied at a resolution determined by available taxonomic knowledge and sometimes using data of differing taxonomic resolution, which confounds comparison among studies. They have seldom, if ever, been applied to an ecosystem in absolute terms; rather they are more likely applied to numbers of species of above-ground vertebrates, soil nematodes, etc.

Indices of taxonomic diversity have been described previously (Neher and Darby, Chapter 4, this volume); in summary they include: Species richness (S) (sometimes referred to as Hill's N_0 index (Hill, 1973)), Simpson's diversity index (D) (Simpson, 1951), Shannon's diversity index (H') (Shannon and Weaver, 1949), Hill's N_1 index (Hill, 1973) which is the exponential of the Shannon's index, Hill's N_2 index (Hill, 1973) which is the reciprocal of Simpson's index, and Pielou's J' evenness index (Pielou, 1966). These and other diversity indices provide assessment of organism heterogeneity in a system but no direct indication of organism or system function.

Table 5.1.
the same

Hoplitaimn
Pratylench
Aphelench
Cephalob
Plectidae
Rhabditid
Dorylaimi
Discolaim
Totals
Hill N_0
Simpson
Shannon
Hill N_1
Hill N_2
Pielou J'

p_i is the nu

Table 5.1. Diversity index calculations for two nematode assemblages (Samples A and B) of the same number of taxa and the same number of individuals.

	Sample A	Sample B	Sample A Diversity calculations			Sample B Diversity calculations		
			p_i	p_i^2	$\log(p_i)$	p_i	p_i^2	$\log(p_i)$
Hoplolaimidae	5	15	0.045	0.002	-3.109	0.134	0.018	-2.010
Pratylenchidae	5	15	0.045	0.002	-3.109	0.134	0.018	-2.010
Aphelenchidae	15	5	0.134	0.018	-2.010	0.045	0.002	-3.109
Cephalobidae	15	5	0.134	0.018	-2.010	0.045	0.002	-3.109
Plectidae	2	15	0.018	0.000	-4.025	0.134	0.018	-2.010
Rhabditidae	5	50	0.045	0.002	-3.109	0.446	0.199	-0.806
Dorylaimidae	50	5	0.446	0.199	-0.806	0.045	0.002	-3.109
Discolaimidae	15	2	0.134	0.018	-2.010	0.018	0.000	-4.025
Totals	112	112						
Hill N_0	8	8						
Simpson	0.26	0.26						
Shannon	1.66	1.66						
Hill N_1	5.24	5.24						
Hill N_2	3.85	3.85						
Pielou J'	0.80	0.80						

p_i is the number of individuals of a taxon as a proportion of the total number of individuals.

The indices do not assess or measure the abundances or proportions of organisms that are food or feeders, prey or predators (Table 5.1). Rather, ecosystem function is inferred, for example, in the expectation that if there are many different types of organisms feeding on each other, the system has some internal regulation and therefore overall stability. While that conclusion may bear weight in Sample A with high proportions of omnivores (Dorylaimidae) and predators (Discolaimidae), it would be less valid for Sample B. In Sample B there are greater proportions of opportunists, including bacterial-feeding Rhabditidae, and plant feeders (Hoplolaimidae and Pratylenchidae) which may be responding to enhanced host vigor in the more enriched environment.

Indices of Ecosystem Function

While there are several indices of community and ecosystem structure (Table 5.1), there are fewer indicators of ecosystem function. Certainly, it is a common observation that a preponderance of herbivores in the nematode assemblage of soil is an indicator that management practices have diminished *functional diversity* in the soil food web. The first papers on the effect of disturbances on soil nematode assemblages appeared around 1960 with studies on the effect of liming and fertilization (Bassus, 1960, 1967), on nematodes of regenerating woodland and grassland (Yuen, 1966), in sand dunes, forests

and grasslands (Yeates, 1968, 1972, 1974). Wasilewska (1974) noted that omnivorous dorylaimids of forest soil were most sensitive to disturbance. In the same period, Johnson *et al.* (1972, 1973, 1974), also studying nematode assemblages of forests, similarly concluded that dorylaimids are very sensitive to disturbance and should be considered K-strategists.

The potential for macrofauna to indicate water quality has a long history; the use of nematodes as indicators of water pollution was initiated in rivers by Zullini (1976) and in lakes by Prejs (1977). Zullini's focus on nematodes as bioindicators in freshwater systems emerged when he was appointed as an ecological expert in a lawsuit on river pollution and asked if he could prove that pollution affected the river biology (A. Zullini, 2007, personal communication). The early indicator work was followed by several studies on the relationships between water quality and nematode assemblages (e.g. Cantelmo and Rao, 1978; Boucher, 1980; Tietjen, 1980; Lamshead, 1986; Vranken *et al.*, 1988). The use and formalization of nematodes as bioindicators in freshwater systems has continued to expand (e.g. Hodda and Nicholas, 1986; Samoiloff, 1987; Yeow *et al.*, 1999; Bazzanti, 2000; Beier and Traunspurger, 2001, 2003; Barbuta and Zullini, 2005).

In the early 1980s, concerns regarding soil pollution and its impact on the functioning of soils were increasing. In The Netherlands, the Dutch National Institute for Public Health and the Environment (RIVM) started a search for groups of organisms with potential as bioindicators of soil quality similar to those used in biological water quality assessment. Nematodes and bacteria appeared to be the most promising organisms. In 1984, not having experience with nematodes, RIVM officials asked the second author of this chapter to bridge the gap between nematode taxonomists and soil ecologists by composing a user-friendly identification key in 'De Nematoden van Nederland' (Bongers, 1988), and to study the relation between soil type, vegetation type and nematode assemblages (Bongers *et al.*, 1989). One project of the RIVM soil ecology group monitored the biological recovery of contaminated soils after heat sterilization and amendment with organic material (Kappers and van Esbroek, 1988). Building on studies of ecological succession in cow dung (Sudhaus, 1981; Sudhaus *et al.*, 1988) and on the ecological studies of Johnson *et al.* (1972, 1973, 1974), Wasilewska (1970, 1974); Zullini (1976), Zullini and Peretti (1986) in a variety of ecosystems, Bongers *et al.* (1989) arranged nematode taxa into five categories along an r-K scale. That arrangement evolved into the Maturity Index for terrestrial and marine nematodes (Bongers, 1990; Bongers *et al.*, 1991).

Further catalytic activities followed, including evolution and testing of the ideas (De Goede *et al.*, 1993; Ettema and Bongers, 1993; Korthals *et al.*, 1996a, b, c) and cataloging of the feeding habits of soil nematodes (Yeates *et al.*, 1993). A testament to the biological insights underpinning the r-K scale is that, over the years, there have been few adjustments. One example of a change is based on the notion that opportunists can be distinguished as enrichment or general opportunists and that the former are characterized by having a dauerlarva stage. Since Monhysteridae do not have a dauerlarva stage and are tolerant of unfavorable conditions, the family was moved to the 'general opportunist' category (Bongers *et al.*, 1995).

Basics of t

For
col
'Co
me
ato
ity
info
sam
terr

c-p1

Nem
occu
und
bact
and
tuni

c-p2

Nem
rates
respo
tode
in w
They
bacte

c-p3

Nem
sensi
and s

c-p4

Small
body
permi
nema
seek
and s

c-p5

Large
low m

Basics of the c-p series and the maturity index family

For calculation of maturity indices, soil nematodes are categorized into a 1-5 colonizer-persister series; ranging from extreme r- to extreme K-strategists. 'Colonizer' nematodes at the lower end of the c-p scale are considered enrichment opportunists and therefore indicate resource availability; 'persister' nematodes at the high end of the scale indicate system stability, food web complexity and connectance. Each nematode taxon, usually at family level, is classified into one of the five c-p classes. Genera and species within a taxon have the same c-p value as their family, or genus in the case of some marine taxa. For the terrestrial and freshwater taxa, the following groups can be distinguished:

c-p1

Nematodes with a short generation time and a large proportion of the body occupied by gonads which produce many small eggs. Population growth under food-enriched conditions is explosive. The nematodes are primarily bacterial feeders with high metabolic activity. They are tolerant of pollutants and of products of organic matter decomposition. These enrichment opportunists form dauerlarvae when microbial biomass and activity decreases.

c-p2

Nematodes with a short generation time and relatively high reproduction rates, although lower than those in c-p1, consequently, they are slower to respond to environmental enrichment than c-p1 nematodes. These nematodes do not form dauerlarvae and occur in all environments, including those in which resources are abundant and those in which resources are scarce. They are very tolerant of pollutants and other disturbances. They include bacterial feeders, fungal feeders and a few predators.

c-p3

Nematodes with longer generation time than c-p2 nematodes and greater sensitivity to disturbances. They include bacterial feeders, fungal feeders and some predators.

c-p4

Small dorylaims and the large non-dorylaimids with a low ratio of gonad to body volume. These nematodes are characterized by a long generation time, permeable cuticle and high sensitivity to pollutants. The non-carnivorous nematodes in this group are relatively sessile whereas the carnivores actively seek prey. The group is composed of larger carnivores, smaller omnivores and some bacterial feeders.

c-p5

Large dorylaimid nematodes with a long life span, low reproduction rates, low metabolic activity and slow movement. The gonads are small relative to

the body volume and produce a small number of large eggs. They have a permeable cuticle and are very sensitive to pollutants and other disturbances. This group is composed of the larger omnivores and predators.

As recognized early in the development of the c-p series (Bongers, 1990; Bongers *et al.*, 1991), a c-p classification at the genus or species level would be more informative. However, early attempts to assign c-p values at the genus level (Bongers *et al.*, 1989) proved difficult due to lack of information on the biology and sensitivity of the individual genera. Consequently, family level assignments to c-p classes were used in the formal introduction of the MI (Bongers, 1990). The relevance of the family level assignments has been justified on the basis that nematodes with similar morphology and feeding habits, and with similar life history traits, have a high probability of similar sensitivity and responsiveness to environmental change (Bongers and Ferris, 1999). As information emerges on the biology and sensitivity of individual genera and species, greater resolution in c-p assignments will be possible. The most recent descriptions of c-p class assignments for families of terrestrial nematodes is Bongers and Bongers (1998) and of marine nematodes is Bongers *et al.* (1991).

Calculation and use of the Maturity Index family

All the indices are based on the weighted proportion of nematodes in the fauna that meet the index criteria. A generic formula for calculation of indices in the MI family is:

$$XI = \sum_{i=1, f} v_i n_i / \sum_{i=1, f} n_i$$

where XI is the index of interest, v_i is the colonizer-persister (c-p) value assigned to taxon i , and n_i is the number of nematodes in each of the f taxa that meet the criteria of the index.

MI

The Maturity Index is based on non-plant-feeding taxa and considered a measure of environmental disturbance; low MI values indicate a disturbed and/or enriched environment, high MI values a stable environment (Bongers, 1990). In essence, the MI is an ecological indicator of the state of succession of a system whereby disturbance and its consequent enrichment effects result in a setback of succession to an earlier state (Odum, 1985). In the case of the nematode assemblage, the successional setback is reflected in a lower MI (Bongers *et al.*, 1997).

The dauerlarvae of enrichment opportunists, animal parasites such as mermithids, and entomopathogenic nematodes are excluded from the calculation of MI (Bongers and Bongers, 1998) as their presence does not provide information about the present functioning of the soil food web. An abundance

of dauerlarvae indicates a system that has been enriched and has now declined to a less enriched phase. The ratio of dauerlarvae to active stages of rhabditids, as an indicator of resource availability, was introduced and tested by Sohlenius (1969, 1973) and comparisons of that ratio over time may provide insights into the resource dynamics of the system. However, a difficulty with such an approach would be the problem of identifying dauerlarvae of different nematode taxa. For example, dauerlarvae of entomopathogenic nematodes often are found in soil but are not indicators of food web enrichment.

PPI

The Plant Parasite Index, is comparable to the MI but computed only for the plant-feeding nematodes with the rationale that their abundance is determined by the vigor of their host plants which, in turn, is determined by system enrichment. Consequently, under nutrient poor conditions of natural ecosystems, often associated with a high proportion of Tylenchidae (c-p2) in the nematode assemblage, the PPI is lower than under enriched agricultural conditions, the inverse of the response of the MI to enrichment (Bongers, 1990; Bongers *et al.*, 1997). The reports that *Filenchus misellus* feeds on fungi (Brzeski, 1998; Okada *et al.*, 2002, 2005) underscores the need for further study on the feeding habits of the many genera and species in this ubiquitous Tylenchidae.

PPI/MI

The PPI/MI ratio is lower under nutrient poor conditions than under nutrient rich conditions. It is a sensitive indicator of enrichment in agroecosystems (Bongers and Korthals, 1995; Bongers *et al.*, 1997).

MI2-5

This index is identical to the MI but excludes the c-p1 enrichment opportunists. The index was derived during studies of the relationship between MI and copper concentration under agricultural conditions. In those studies, it was apparent that there was a strong relationship between decrease in higher c-p value nematodes and pollution-induced stress while the c-p1 nematodes responded to the presence of decomposing organic material. In some cases, the pollutant may become a resource for a component of the microbial community which, in turn, acts as a resource for the c-p1 nematodes. The MI2-5 was first discussed at the Crop Protection Symposium in Ghent (Bongers and Korthals, 1993).

ΣMI

This was proposed by Yeates (1994) and is equivalent to the Total MI of Wasilewska (1994). The index is the MI for all nematodes in the system, including plant feeders, based on the assertion that the complete assemblage provides integral information with regard to disturbance and environmental condition. If a soil ecosystem receives nutrient input, opportunistic

bacterial- and fungal-feeding nematodes respond rapidly to the corresponding increase in their resources. Plant parasites do not respond in the short term but may increase later as a result of higher plant vigor. Since many are c-p3 or higher, the expected decrease of MI in response to enrichment is offset by inclusion of plant parasites in ΣMI . Further, many plant feeders, such as the c-p3 Pratylenchidae, are tolerant of pollutant stress (Korthals *et al.*, 1996a, b) which, in ΣMI , offsets the impact of pollution registered by the MI or MI2-5 (Bongers and Bongers, 1998; Bongers, 1999).

$\Sigma MI2-5$

This index computes the MI for all nematodes in the c-p2-5 range (Neher and Campbell, 1996). The index recognizes that the higher c-p value plant-feeding species also provide information of environmental stress but bears some of the burden of the ΣMI in situations of nutrient enrichment.

In all cases, the indices of ecosystem function in the Maturity Index family show differences between the two samples of identical species richness and abundance (Table 5.2) that were not apparent in the diversity and evenness indices calculated for the same data (Table 5.1).

Sometimes the Maturity Index has been expressed as

$$MI = \sum_{i=1,f} v_i p_i$$

which has led to some unfortunate miscalculations in manuscripts submitted for publication. The errors commonly arise when the proportions of all taxa present are calculated in a spreadsheet, as for the calculation of ΣMI , and then the same proportions, excluding those that are not relevant, are used to calculate incorrectly the other indices in the family. To obtain the correct index values, it is necessary to recalculate the proportions to be weighted with respect to the total number of nematodes in the sample which meet the specific criteria of each index.

Conceptual evolution underlying functional indices based on nematode faunae

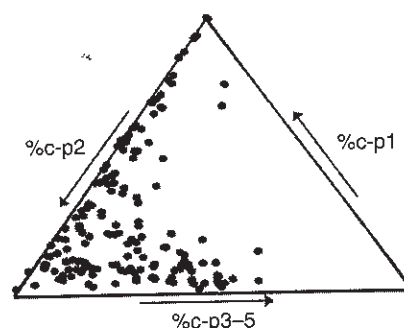
In their equilateral c-p triangles, (graphical representations of faunal composition), De Goede *et al.* (1993) and Ettema and Bongers (1993) accommodated two enrichment (%c-p1 and %c-p2) axes, and an ecosystem complexity (%c-p3-5) axis, based on unweighted proportions of the nematode fauna in each grouping (Fig. 5.1). The right-angled triangle representation of Bongers *et al.* (1995) depicted the proportional representation of c-p1 and c-p3-5 nematodes, further emphasizing the indicator distinction between the two groups. The graphical representations advanced the recognition that the c-p classes are indicators of ecosystem structure and function that are not necessarily aligned on a common trajectory. However, since each axis of the triangles indicates a proportion of the whole nematode fauna, an increase along one axis is accompanied by a decrease along another. The notion that enrichment

Table 5.2. Calculation of the MI, MI2-5, Σ MI, Σ MI2-5, PPI and PPI/MI for two nematode assemblages (Samples A and B) of the same number of taxa and the same number of individuals (cf. Table 5.1).

Nematode taxon	Sample A	Sample B	c-p	Feeding	A											
					MI			MI2-5			Σ MI			Σ MI2-5		
					MI	B	A	MI2-5	B	A	Σ MI	B	A	Σ MI2-5	B	A
					c-p wtd	propn	c-p wtd	propn	c-p wtd	propn	c-p wtd	propn	c-p wtd	propn	c-p wtd	propn
Hoplolaimidae	5	15	3	H							0.1	0.4	0.1	0.8	1.5	1.5
Pratylenchidae	5	15	3	H							0.1	0.4	0.1	0.8	1.5	1.5
Aphelenchidae	15	5	2	F	0.3	0.1	0.3	0.3	0.3	0.1	0.3	0.1	0.3	0.2		
Cephalobidae	15	2	2	B	0.3	0.1	0.3	0.1	0.3	0.0	0.3	0.0	0.3	0.1		
Plectidae	2	15	2	B	0.0	0.4	0.0	1.0	0.0	0.0	0.3	0.0	0.3	0.5		
Rhabditidae	2	50	1	B	0.0	0.6					0.0	0.5				
Dorylaimidae	50	5	4	O	2.0	0.3	2.1	0.7	1.8	0.2	1.9	0.2	1.9	0.3		
Discolaimidae	15	2	5	P	0.8	0.1	0.8	0.3	0.7	0.1	0.7	0.1	0.7	0.2		
Relevant total	109	109			99	79	97	29	109	109	109	107	59	10	30	
MI	3.4	1.6														
MI2-5	3.5	2.6														
Σ MI	3.4	2.0														
Σ MI2-5	3.4	2.8														
PPI	3.0	3.0														
PPI/MI	0.9	1.9														

H=plant feeders, F=fungal feeders, B=bacterial feeders, O=omnivores, P=predators. In the columns in which each index is calculated, the total number of nematodes meeting the criteria of the index is first determined (relevant total) and then the proportion of that total in taxa meeting the criteria is weighted by the c-p values of those taxa. The index value is the sum of the weighted proportions.

Fig. 5.1. C-p triangles, based on unweighted proportional representation of c-p1, c-p2, and c-p3-5 groupings of the nematode fauna, were a first step in distinguishing between basal fauna, enrichment indicators and structure indicators (modified from De Goede *et al.*, 1993).



should be independent of complexity led to development of separate trajectories of enrichment and structure to assess the magnitude of disparate services (Ferris *et al.*, 2001, 2004).

The nematode fauna provides information on two major characteristics of the soil environment and its resident communities. One characteristic is the flow of resources into the food web system as indicated by enrichment opportunist species; the other is the trophic connectance (*sensu* Cohen, 1989) of the system as indicated by prevalence and abundance of higher trophic level organisms. Ferris *et al.* (2001, 2004) considered general opportunist c-p2 nematodes to be representative of organisms that persist in most soil food webs, always present, and the survivors of the most adverse conditions. Two axes can be conceived as emerging from this basal state of the nematode fauna, one defined as an enrichment index, indicated by the weighted abundance of the proportion of all c-p1 and c-p2 nematodes that are c-p1 bacterivores and c-p2 fungivores, and the other as a structure index, derived from the proportional contribution of the weighted c-p3-5 nematodes to the c-p2-5 grouping. Also calculated in this system is a basal index, the relative proportion of the basal (c-p2) component of the fauna to all nematodes present (Berkelmans *et al.*, 2003). Further resolution to the enrichment component is provided by assessing the relative flow of resources into the food web through fungally- and bacterially-mediated decomposition channels (Ruess and Ferris, 2004).

Indicators of ecosystem function: enrichment, structure, basal and channel indices

The evolution of concepts, research and model validation associated with development of the Maturity Index family led to a functional guild classification of nematodes as a basis for studying and comparing ecosystem processes (Bongers and Bongers, 1998; Bongers and Ferris, 1999). The functional redundancy represented in the diversity of nematode faunae creates a high probability that the absence of a guild is a reliable indicator of disturbance and that the presence of a guild is a reliable indicator of lack of perturbation or of recovery from perturbation. In the case of organic enrichment of soil, opportunistic guilds (*r*-strategists) respond reliably (Sánchez-Moreno *et al.*, 2006). Considering soil nematode taxa as representatives of functional guilds generates an indicator

Basal condition

Fig. 5.2. A community resource-limited (Quadrat D group) and soil food web guilds along Enrichment

profile that is not constrained by population distribution patterns and micro-environment effects (Ferris and Bongers, 2006).

The Enrichment Index and the Structure Index, both based on the indicator importance of functional guilds of nematodes, are descriptors of food web condition. Functional guilds are defined as a matrix of nematode feeding habits with the biological, ecological and life history characteristics embodied in the c-p classification. Thus, the Ba3 functional guild comprises c-p3 bacterivores such as those in the Teratocephalidae or Prismatolaimidae. Nematodes of all feeding habits classified as c-p2 are considered basal (b) to both enrichment and structure trajectories. Bacterial-feeding c-p1 and fungivores in c-p2 are indicators of enrichment (e) while nematodes of all feeding habits in c-p3–5 are indicators of structure (s). Functional guild indicators are weighted according to growth and metabolic rates (resource utilization) on the enrichment axis (Figs 5.2 and 5.3), and according to estimates of the degree of connectance, as determined by numbers of nematodes in higher c-p classes, in food webs of increasing complexity (Figs 5.2 and 5.4). Greater detail on derivation of the structure and enrichment weightings (W_i) is provided in Ferris *et al.*, 2001.

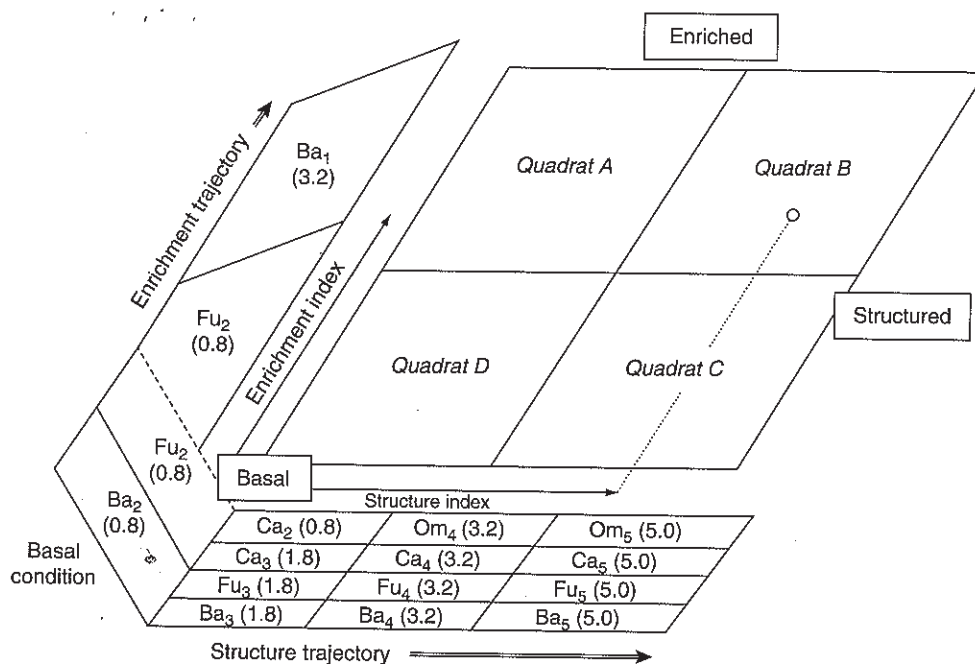


Fig. 5.2. A graphic representation of the nematode faunal profile indicates whether the soil community is enriched but unstructured (Quadrat A), enriched and structured (Quadrat B), resource-limited and structured (Quadrat C), or resource-depleted with minimal structure (Quadrat D). Functional guilds of soil nematodes are characterized by feeding habit (trophic group) and by life history characteristics, after Bongers and Bongers, 1998. Indicator guilds of soil food web condition (basal, structured, enriched) are designated and weightings of the guilds along the structure and enrichment trajectories are provided, for determination of the Enrichment Index and Structure Index of the food web. (Modified from Ferris *et al.*, 2001.)

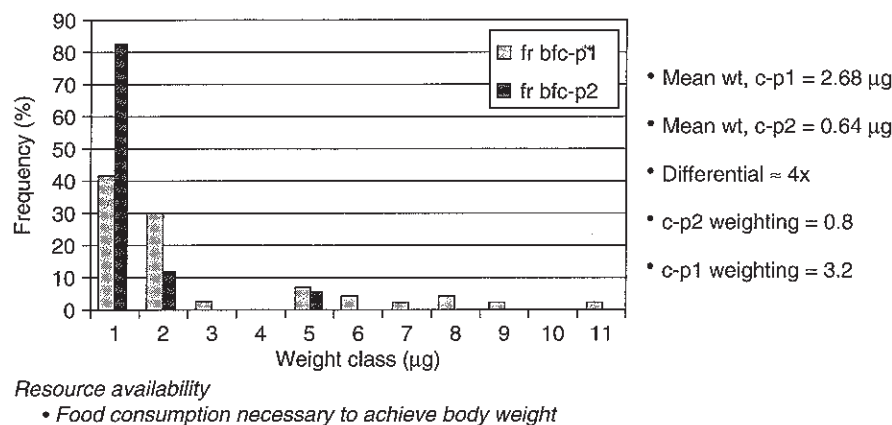


Fig. 5.3. Weighting system for enrichment and basal indicator soil nematodes as determined by mean weight of adults based on their frequency representation in different weight classes (adapted from Ferris *et al.*, 1996a,b).

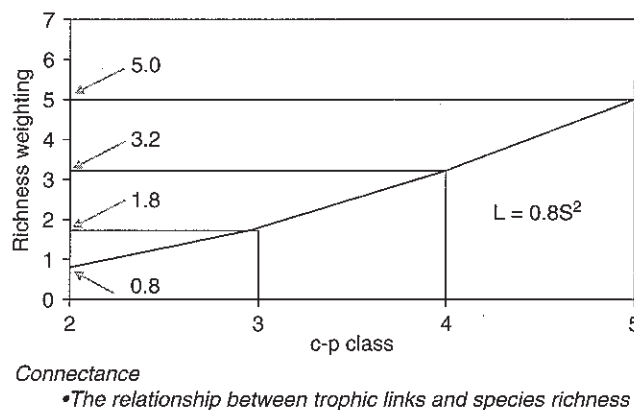


Fig. 5.4. Weighting system for structure and basal indicator soil nematodes as determined by taxonomic richness in food webs of different complexity (adapted from Ferris *et al.*, 2001).

The nematode fauna is comprised of basal, enrichment and structural components (b,e,s):

$$b = (Ba_2 + Fu_2) * W_2, \text{ where } W_2 = 0.8,$$

$$e = (Ba_1 * W_1) + (Fu_1 * W_1), \text{ where } W_1 = 3.2 \text{ and } W_2 = 0.8$$

$$s = (Ba_n * W_n + Ca_n * W_n + Fu_n * W_n + Om_n * W_n)$$

$$\text{where } n=3-5, W_3 = 1.8, W_4 = 3.2, W_5 = 5.0.$$

The Enrichment (EI), Structure (SI), Basal (BI), and Channel (CI) indices are calculated from the weighted faunal components (Ferris *et al.*, 2001; Berkelmans *et al.*, 2003):

$$EI = 100 * e / (e + b)$$

$$SI = 100 * s / (s + b)$$

$$BI = 100 * b / (e + s + b)$$

$$CI = 100 \text{ Fu}2 * W_2 / (Ba1 * W_1 + \text{Fu}2 * W_2).$$

The EI, SI and BI represent an evolution of the concepts embodied in the c-p triangles of De Goede *et al.* (1993) and provide higher resolution to the enrichment, disturbance and contamination effects on the ecosystem (Table 5.3). Clearly, Sample A represents an environment with an abundance of omnivore and predator nematodes, suggesting greater connectance in the soil food web and the probable top-down regulation of opportunistic species (Sánchez-Moreno *et al.*, 2006; Sánchez-Moreno and Ferris, 2007). Sample B represents a disturbed and enriched condition in which the disturbance has had detrimental effects on higher trophic levels. Faunal analyses based on these indices provide insights into food web enrichment and structure and allow derivation of testable hypotheses based on the relative enrichment and structure of the system (Table 5.4).

The CI provides a means to partition flow of resources through fungal and bacterial decomposition channels. Indices of fungal and bacterial activity based on the relative abundance of fungal- and bacterial-feeding nematodes have been proposed several times following the calculation of their relative proportions in grasslands, woodlands and cultivated fields by Twinn (1974). The indices have included a ratio of F/B (Sohlenius and Boström, 1984) which has been defined most recently as $NCR = B / (B + F)$ where NCR is the Nematode Channel Ratio, and B and F represent the abundance of bacterial- and fungal-feeding nematodes, respectively (Yeates, 2003). The CI differs in including weighting parameters for the size and metabolic rates of the nematode indicators.

When resources become available to soil organisms through external input, disturbance, organism mortality, turnover, or environment changes there is an enrichment pulse of opportunistic guilds. The pulse is followed by heterotrophic succession whereby the predominance of organisms changes through time depending on trophic roles, life course dynamics, and prevailing environmental conditions (Sudhaus, 1981; Ferris *et al.*, 1996b; Ferris and Matute, 2003). Substrates rich in labile carbon but deficient in nitrogen may favor the fungal rather than the bacterial decomposition channel (Ruess and Ferris, 2004).

Similar to the MI (Bongers and Bongers, 1998), the EI and CI are calculated excluding dauerlarvae to provide an index of the present state of the system. Rather than proliferate indices calculated with and without dauerlarvae, we consider that the ratio of dauerlarvae to active forms, as proposed by Sohlenius (1969, 1973), provides a clear metric of resource availability to functional guilds of bacterivores and fungivores. When the proportion of dauerlarvae is low, the resource supply is probably stable; when it is high, the system is probably in a state of resource-driven succession from bacterial to fungal domination of decomposition channels. However, considering the short lifespan of many enrichment opportunist nematodes (Ferris *et al.*, 1996a), frequent sampling will be necessary for using such calculations to model resource flow rates through the lower levels of the soil food web.

Further understanding of enrichment is determined by relative flow through and activity in fungal, bacterial and herbivore channels using total biomass of

Table 5.3. Calculation of the BI, EI and SI for two nematode assemblages (Samples A and B) of the same number of taxa and the same number of individuals (cf. Tables 5.1 and 5.2).

Nematode taxon	Sample A	Sample B	c-p	Feeding	b wt	e wt	s wt	A				B			
								b	e	s		b	e	s	
Hoplolaimidae	5	15	3	H				0.00	0.00	0.00		0.00	0.00	0.00	
Pratylenchidae	5	15	3	H				0.00	0.00	0.00		0.00	0.00	0.00	
Aphelenchidae	15	5	2	F	0.80	0.80		12.00	12.00	0.00		4.00	4.00	0.00	
Cephalobidae	15	2	2	B	0.80			12.00	0.00	0.00		1.60	0.00	0.00	
Plectidae	2	15	2	B	0.80			1.60	0.00	0.00		12.00	0.00	0.00	
Rhabditidae	2	50	1	B		3.20		0.00	6.40	0.00		0.00	160.00	0.00	
Dorylaimidae	50	5	4	O			3.20	0.00	0.00	160.00		0.00	0.00	16.00	
Discolaimidae	15	2	5	P			5.00	0.00	0.00	75.00		0.00	0.00	10.00	
Total	109	109						25.60	18.40	235.00		17.60	164.00	26.00	
Index															
Components															
BI	9.18	8.48													
EI	41.82	90.31													
SI	90.18	59.63													

H=plant feeders, F=fungal feeders, B=bacterial feeders, O=omnivores, P=predators. In the columns in which each index is calculated, the total number of nematodes in each taxon meeting the criteria of the index is weighted in terms of the basal, enrichment and structure characteristics of that taxon. The index values are calculated from the index components, that is the sum of the b, e and s values (see text).

Table 5.4. Inferred condition of the soil food web and its environment based on weighted nematode faunal analysis. Quadrats refer to faunal ordination in the faunal profile (Fig. 5.2) (from Ferris *et al.*, 2001).

General diagnosis	Quadrat A	Quadrat B	Quadrat C	Quadrat D
Disturbance	High	Low to mod.	Undisturbed	Stressed
Enrichment	N-enriched	N-enriched	Moderate	Depleted
Decomposition channels	Bacterial	Balanced	Fungal	Fungal
C-to-N ratio	Low	Low	Mod. to high	High
Food web condition	Disturbed	Maturing	Structured	Degraded

bacterivore (B), fungivore (F) and herbivore (H) nematodes. That provides the basis for developing the enrichment profile of the food web (Fig. 5.5). Changes through time in the abundance and type of organisms in the soil community may be considered structural succession; changes in food web function, not necessarily concurrent with community composition, are considered functional succession. The mass of available C diminishes with each trophic interchange, effectively dictating the abundance and biomass of organisms at each trophic level. Sustained organic enrichment may halt the succession and maintain a

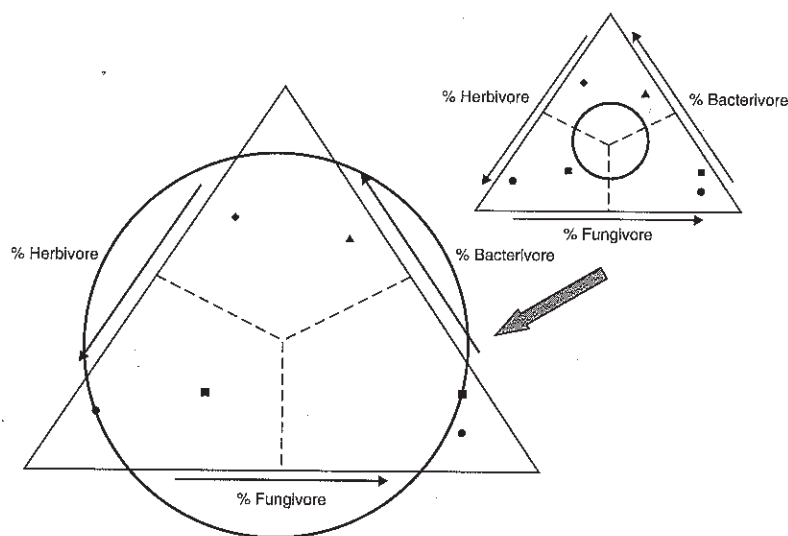


Fig. 5.5. Intake biomass of the soil food web partitioned into relative flows through herbivore-, fungivore- and bacterivore-mediated channels as indicated by the nematode fauna. The size of the triangle indicates the magnitude of resource flow. The circles indicate the biomass of generalist and specialist predators supported by the lower trophic levels.

consistent structure among functional guilds of soil organisms (Ferris and Bongers, 2006). Some of the organism responses to enrichment are ephemeral; others, including responses of certain guilds of nematodes, are more persistent and can be measured reliably (Ferris *et al.*, 1996b; Bongers and Ferris, 1999).

Abundance and biomass

The indices developed from nematode faunal analysis are all based on proportions of the faunae in various functional guilds. They provide an indication of the relative proportions of services and functions, but not of their magnitude. The biomass or abundance of organisms in various functional guilds must be important in determining the magnitude of services. Resource inflow into the soil food web can be represented as a subdivided triangle with the subdivisions indicating the proportion of inflow through separate channels. If the size of the triangle is based on the biomass of nematodes functioning in the inflow channels (Fig. 5.5), we are provided with a clearer understanding of the resources available to soil food web organisms and of the likely magnitude of services provided.

The constraints of resource inflow on higher trophic biomass are apparent when the biomass of higher trophic levels is represented as a circle superimposed on the intake triangle (Fig. 5.5). Also evident is the likelihood that the higher trophic level of the food web will provide the service of regulating populations of opportunistic organisms in the inflow channels. A low predator biomass relative to the intake (prey) biomass, as represented by a low MI, may indicate an environmental contamination or disturbance constraint on nematodes of higher c-p classes. A high predator biomass relative to the intake biomass, as represented by a high MI, indicates the possibility of top-down regulation of opportunistic species and, while there are sufficient intake resources to sustain the predator biomass, a relatively stable system.

Conclusions

The evolution of functional indices based on nematode faunal analysis provides insights into functioning and services of ecosystems. It has been greatly advanced by inference and observation of nematode feeding habits in relation to stomal architecture and by knowledge of the life history traits of nematode functional guilds. Undoubtedly, refinement and finetuning of the system is warranted and will occur as further information is developed on feeding habits and life history traits and the assignment of taxa to functional guilds. There are other examples of the use of the community structure of various organism groups for environmental monitoring. The advantage of those based on nematode functional guilds derives from the abundance and ubiquity of nematodes, the relationships between form and function, the differences among families in sensitivity to environmental disturbance, and the ease with which nematodes can be separated from substrate and categorized into taxonomic groups or functional guilds.

Referenc

- Baird, W. (1981) *The British Nematode Fauna* (the British Nematode Fauna of the British Isles). Part 1. The British Nematode Fauna of the British Isles (Ticino).
- Bassus, W. (1981) *Kalkdün*.
- Bassus, W. (1981) *Nematode*.
- Bastian, H. C. (1981) *water; v*.
- Bazzanti, M. (1981) *land riv*.
- Beier, S. and (1981) *as indic*.
- Beier, S. and (1981) *Kraeher*.
- (1981) *Nematode*.
- Berkelmans, (1981) *manage*.
- (1981) *of disru*.
- Bongers, T. (1981) *Bongers, T. (*.
- Bongers, T. (1981) *based on*.
- Bongers, T. (1981) *radiation*.
- Bongers, T. a (1981) *239-251*.
- Bongers, T. a (1981) *mental r*.
- Bongers, T. a (1981) *the nem*.
- (1981) *Protection*.
- Bongers, T. a (1981) *Nematode*.
- Bongers, T., C (1981) *de Nede*.
- (1981) *71860200*.
- Bongers, T., A (1981) *rity decr*.
- (1981) *Ecology F*.
- Bongers, T., C (1981) *classifica*.
- Bongers, T., V (1981) *tode mal*.
- (1981) *Soil Ecolo*.
- Boucher, G. (1981) *Marine P*.
- Brzeski, M. (1981) *Institute*.

References

- Baird, W. (1853) *Catalogue of the species of Entozoa or intestinal worms contained in the collection of the British Museum*, Woodfall and Kinder, London, pp. 132.
- Barbuta, M. and Zullini, A. (2005) The nematode community of two Italian rivers (Taro and Ticino). *Nematology* 34 (2), 667–675.
- Bassus, W. (1960) Die Nematodenfauna des Fichtenrohhumus unter der Einfluss der Kalkdüngung. *Nematologica* 5, 86–91.
- Bassus, W. (1967) Der Einfluss von Meliorations- und Düngungsmassnahmen auf die Nematodenfauna verschiedener Waldböden. *Pedobiologia* 7, 280–295.
- Bastian, H. Ch. (1865) Monograph on the Anguillulidae or free Nematoids, marine, land and fresh-water; with descriptions of 100 new species. *Transactions Linnaean Society London* 25, 73–184.
- Bazzanti, M. (2000) Macrobenthic nematodes as biological indicators in a Mediterranean low-land river in Central Italy: a case study. *Archiv für Hydrobiologie* 148, 59–70.
- Beier, S. and Traunspurger, W. (2001) The meiofauna community of two small German streams as indicator of pollution. *Journal of Aquatic Ecosystem Stress and Recovery* 8, 387–405.
- Beier, S. and Traunspurger, W. (2003) Seasonal distribution of free-living nematodes in the Kraehenbach, a fine-grained submountain carbonate stream in southwest Germany. *Nematology* 5, 113–136.
- Berkelmans, R., Ferris, H., Tenuta M., and Van Bruggen, A.H.C. (2003) Effect of long-term crop management on nematode trophic levels other than plant feeders disappear after one year of disruptive soil management. *Applied Soil Ecology* 23, 223–235.
- Bongers, T. (1988) *De Nematoden van Nederland*. Pirola, Schoorl.
- Bongers, T. (1990) The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83, 14–19.
- Bongers, T. (1999) The Maturity Index, the evolution of nematode life history traits, adaptive radiation and cp-scaling. *Plant and Soil* 212, 13–22.
- Bongers, T. and Bongers, M. (1998) Functional diversity of nematodes. *Applied Soil Ecology* 10, 239–251.
- Bongers, T. and Ferris, H. (1999) Nematode community structure as a biomonitor in environmental monitoring. *Trends in Ecology and Evolution* 14, 224–228.
- Bongers, T. and Korthals, G. (1993) The Maturity Index, an instrument to monitor changes in the nematode community structure. *Summaries of the 45th International Symposium on Crop Protection, May 4, 1993, Ghent, Belgium*. 80.
- Bongers, T. and Korthals, G. (1995) The behavior of MI and PPI under enriched conditions. *Nematologica* 41 (3), 286.
- Bongers, T., Goede, R.G.M. de, Kappers, F.I. and Manger, R. (1989) Ecologische typologie van de Nederlandse bodem op basis van de vrijlevende nematodenfauna. *RIVM-rapport* 718602002.
- Bongers, T., Alkemade, R. and Yeates, G.W. (1991) Interpretation of disturbance-induced maturity decrease in marine nematode assemblages by means of the Maturity Index. *Marine Ecology Progress Series* 76, 135–142.
- Bongers, T., Goede, R.G.M. de, Korthals, G. and Yeates, G.W. (1995) Proposed changes of c-p classification for nematodes. *Russian Journal of Nematology* 3, 61–62.
- Bongers, T., Van der Meulen, H. and Korthals, G. (1997) Inverse relationship between the nematode maturity index and plant parasite index under enriched nutrient conditions *Applied Soil Ecology* 6, 195–199.
- Boucher, G. (1980) Impact of Amoco Cadiz oil spill on intertidal and sublittoral meiofauna. *Marine Pollution Bulletin* 11, 95–101.
- Brzeski, M. (1998) Nematodes of Tylenchina in Poland and temperate Europe. Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, pp. 396.

- Bütschli, O. (1873) Beiträge zur Kenntnis der Freilebenden Nematoden. *Nova Acta Academiae Naturae Curiosorum* 36 (5), 1–124.
- Callahan, C.A., Ferris, V.R. and Ferris, J.M. (1979) The ordination of aquatic nematode communities as affected by stream water quality. In: Cairns, J., Patil, G.P. and Waters, W.E. (eds) *Environmental Biomonitoring, Assessment, Prediction and Management*. International Cooperative Publishing House, Baltimore, Maryland, pp. 101–106.
- Cantelmo, F.R. and Rao, K.R. (1978) Effect of pentachlorophenol (PCP) on meiobenthic communities in an experimental system. *Marine Biology* 46, 17–22.
- Christie, J.R. (1959) *Plant Nematodes, their Bionomics and Control*. Agricultural Experiment Stations, University of Florida, Gainesville, Florida.
- Cobb, N.A. (1914) North American free-living fresh-water nematodes. Reprinted from *Transactions of the American Microscopical Society* 33 in Cobb, N.A. *Contributions to a Science of Nematology*.
- Cobb, N.A. (1915) Nematodes and their relationships. *USDA Yearbook of Agriculture* 1914, 457–490.
- Cohen, J.E., (1989) Food webs and community structure. In: Roughgarden, J., May, R.M. and Levin, S.E. (eds), *Perspectives in Ecological Theory*. Princeton University Press, Princeton, New Jersey, pp. 181–202.
- Daday, E. (1897) Die freilebenden Süßwasser-Nematoden Ungarns. *Zoologisches Jahrbuch. (Systematik)* 10, 91–134.
- Dujardin, F. (1845) *Histoire naturelle des Helminthes ou vers intestinaux*. Librairie encyclopédique de Roret (Suites a Buffon). Paris.
- Eberth, C.I. (1863) *Untersuchungen über Nematoden*. W. Engelmann, Leipzig.
- Ettema, C. H. and Bongers, T. (1993) Characterization of nematode colonization and succession in disturbed soil using the Maturity Index. *Biology and Fertility of Soils* 16, 79–85.
- Ferris, H. and Bongers, T. (2006) Nematode indicators of organic enrichment. *Journal of Nematology* 38, 3–12.
- Ferris, H., and Matute, M.M. (2003) Structural and functional succession in the nematode fauna of a soil food web. *Applied Soil Ecology* 23, 93–110.
- Ferris, H., Eyre, M., Venette, R.C., and Lau, S.S. (1996a) Population energetics of bacterial-feeding nematodes: Stage-specific development and fecundity rates. *Soil Biology and Biochemistry* 28, 271–280.
- Ferris, H., Venette, R.C. and Lau, S.S. (1996b) Dynamics of nematode communities in tomatoes grown in conventional and organic farming systems and their impact on soil fertility. *Applied Soil Ecology* 3, 161–175.
- Ferris, H., Bongers, T. and Goede, R.G.M. de (2001) A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. *Applied Soil Ecology* 18, 13–29.
- Ferris, H., Bongers, T. and Goede, R. de (2004) Nematode faunal analyses to assess food web enrichment and connectance, pp. 503–510. In Cook R.C., and Hunt D.J., (eds) *Proceedings of the Fourth International Congress of Nematology*. Nematology Monographs and Perspectives 2. Brill, The Netherlands, 866p.
- Filipjev, I.N. (1918) Free-living marine nematodes of the Sevastopol area. *Transactions of the Zoological Laboratory and Sevastopol Biological Station, Russian Academy of Sciences, Series II, No. 4.* (translated from Russian, 1968).
- Filipjev, I.N. and Schuurmans Stekhoven, J.H. (1941) *A Manual of Agricultural Helminthology*. E.J. Brill, Leiden.
- Goede, R.G.M. de, Bongers, T. and Ettema, C. (1993) Graphical presentation and interpretation of nematode community structure: C-P triangles. *Mededelingen Faculteit Landbouwwetenschappen Universiteit Gent*, 58/2b, 743–750.
- Hill, M.O. (1973) Diversity and evenness: A unifying notation and its consequences. *Ecology* 54, 427–432.

Hodda, M.
Hunt
Ingham, R.
fungi
Monog
Jairajpuri,
Nemat
Johnson, S.
wood
Nemat
Johnson, S.
wood
Johnson, S.
wood
118–12
Kappers, I.
Procee
11–15
Karssen, G.
Korthals, G.
(1996a
differe
Korthals, G.
term e
Enviro
Korthals, G.
as an
Krivol
Lambshead
reveale
Leuckart, I.
Naturg
Linstow, O.
Micoletzky,
de l'Acc
10 (2),
Ncher, D.A.
muniti
Nicholas, W.
Odum, E.P.
Okada, H.,
1958) L
pholog
Okada, H.,
the gen
Overgaard
Natura
Paramonov,
of Scier
Pielou, E.C.
Journal

- Hodda, M. and Nicholas, W.M. (1986) Nematode diversity and industrial pollution in the Hunter river estuary, NSW, Australia. *Marine Pollution Bulletin* 17, 251-255.
- Ingham, R.E., Trofymow, J.A., Ingham, E.R. and Coleman D.C. (1985) Interactions of bacteria, fungi, and their nematode grazers: Effects on nutrient cycling and plant growth. *Ecological Monographs* 55, 119-140.
- Jairajpuri, M.S. and Ahmad, W. (1992) *Dorylaimida, Free-living, Predaceous and Plant-Parasitic Nematodes*. Oxford and IBH Publishing, New Delhi, Bombay, Calcutta.
- Johnson, S.R., Ferris, V.R. and Ferris, J.M. (1972) Nematode community structure of forest woodlots: I. Relationships based on similarity coefficients of nematode species. *Journal of Nematology* 4, 175-183.
- Johnson, S.R., Ferris, J.M. and Ferris, V.R. (1973) Nematode community structure of forest woodlots: II. Ordination of nematode communities. *Journal of Nematology* 5, 95-107.
- Johnson, S.R., Ferris, J.M. and Ferris, V.R. (1974) Nematode community structure of forest woodlots: III. Ordinations of taxonomic groups and biomass. *Journal of Nematology* 6, 118-126.
- Kappers, F.I. and van Esbroek, M.L.P. (1988) Ecological recovery of decontaminated soil. *Proceedings of the Second International TNO/BFTM/Conference on Contaminated Soil*. Hamburg, 11-15 April 1988.
- Karssen, G. (2006) *Life and work of Dr. Johannes Govertus de Man (1850-1930)*. Brill, Leiden.
- Korthals, G.W., Ende, A. Van der, Megen, H. Van, Lexmond, T.M., Kammenga, J.E. and Bongers, T. (1996a) Short-term effects of cadmium, copper, nickel and zinc on soil nematodes from different feeding and life-history strategy groups. *Applied Soil Ecology* 4, 107-117.
- Korthals, G.W., Alexiev, A.D., Lexmond, T.M., Kammenga, J.E. and Bongers, T. (1996b) Long-term effects of copper and pH on the nematode community in an agroecosystem. *Environmental Toxicology and Chemistry* 15 (6), 979-985.
- Korthals, G.W., Goede, R.G.M. de, Kammenga, J.E. and Bongers, T. (1996c) The Maturity Index as an instrument for risk assessment of soil pollution. In: Straalen, N.M. Van, and Krivolutsky, D.A. (eds) *Bioindicator systems for Soil Pollutions*, pp. 85-93.
- Lambhead, P.J.D. (1986) Sub-catastrophic sewage and industrial waste contamination as revealed by marine nematode faunal analysis. *Marine Ecology Progress Series* 29, 247-260.
- Leuckart, R. (1849) Zur Kenntnis der Fauna von Island. Erster Beitrag (Würmer). *Archiv Naturgeschichte* 15, 148-206.
- Linstow, O. von (1876) Helminthologische Beobachtungen. *Archiv Naturgeschichte* 42, 1-18.
- Micoletzky, H. (1925) Die freilebenden Süßwasser- und Moornematoden Dänemarks. *Mémoires de l'Académie Royale des Sciences et des Lettres de Danemark, Copenhagen, Section de Sciences* (8) 10 (2), 55-310.
- Neher, D.A. and Campbell, C.L. (1996) Sampling for regional monitoring of nematode communities in agricultural soils. *Journal of Nematology* 28, 196-208.
- Nicholas, W.L. (1975) *The Biology of Free-living Nematodes*. Clarendon Press, Oxford.
- Odum, E.P. (1985) Trends expected in stressed ecosystems. *BioScience* 35, 419-422.
- Okada, H., Tsukiboshi, T. and Kadota, I. (2002) Mycetophagy in *Filenchus misellus* (Andrassy, 1958) Lownsbery and Lownsbery, 1985 (Nematoda: Tylenchidae), with notes on its morphology. *Nematology* 4, 795-801.
- Okada, H., Harada, H. and Kadota, I. (2005) Fungal-feeding habits of six nematode isolates in the genus *Filenchus*. *Soil Biology and Biochemistry* 37, 1113-1120.
- Overgaard Nielsen, C. (1949) Studies on the soil microfauna II. The soil inhabiting nematodes. *Natura Jutlandica* 2, 1-131.
- Paramonov, A.A. (1962) *Plant-parasitic Nematodes Vol. 1*. Laboratory of Helminthology, Academy of Sciences of the USSR (translated from Russian, 1968).
- Pielou, E.C. (1966) The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* 13, 131-144.

- Platt, H. M. (1994) Foreword. In: *The Phylogenetic Systematics of Free-living Nematodes*, Lorenzen, S. (ed.), pp. i-ii, The Ray Society, London.
- Prejs, K. (1970) Some problems of the ecology of benthic nematodes (Nematoda) of Mikolajskie Lake. *Ekologia Polska* 25 (9), 225-242.
- Prejs, K. (1977) The littoral and profundal benthic nematodes of lakes with different trophy. *Ekologia Polska* 25 (1), 21-30.
- Ruess, L. and Ferris, H. (2004) Decomposition pathways and successional changes, pp. 547-566. In Cook, R.C. and Hunt, D.J. (eds) *Proceedings of the Fourth International Congress of Nematology. Nematology Monographs and Perspectives 2*. Brill, Netherlands, 866p.
- Samoiloff, M.R. (1987) Nematodes as Indicators of Toxic Environmental Contaminants. In: Veech, J.A. and Dickson, D.W. (eds) *Vistas on Nematology*. E.O. Painter, DeLeon Springs, Florida, pp. 433-438.
- Sánchez-Moreno, S. and Ferris, H. (2007) Suppressive service of the soil food web: Effects of environmental management. *Agriculture, Ecosystem and Environment* 119, 75-87.
- Sánchez-Moreno, S., Minoshima, H., Ferris, H. and Jackson, L.E. (2006) Linking soil properties and nematode community composition: effects of soil management on soil food webs. *Nematology* 8, 703-715.
- Shannon, C.E. and Weaver, W. (1949) *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- Simpson, E.H. (1951) The interpretation of interaction in contingency tables. *Journal of the Royal Statistical Society, Series B* 13, 238-241.
- Sohlenius, B. (1969) The monoxenic cultivation of some rhabditid nematodes. *Oikos* 20, 287-293.
- Sohlenius, B. (1973) Structure and dynamics of populations of Rhabditis (Nematodes: Rhabditidae) from forest soil. *Pedobiologia* 13, 368-375.
- Sohlenius, B. and Boström, S. (1984) Colonization, population development and metabolic activity of nematodes in buried barley straw. *Pedobiologia* 27, 67-78.
- Spenneman, D.H.R. (2003) *Nathan Augustus Cobb Plant Pathologist. A Bibliography of his Work. Retrospect*, Letao Publishing, Albury, Australia.
- Stinner, B.R. and Crossley, D.A., Jr. (1982) Nematodes in no-tillage agroecosystems. In: Freckman, D.W. (ed.) *Nematodes in Soil Ecosystems*. University of Texas Press, Austin, pp. 14-28.
- Sudhaus, W. (1981) Über die Sukzession von Nematoden in Kuhfladen. *Pedobiologia* 21, 271-297.
- Sudhaus, W., Rehfeld, K., Schlüter, D. and Schweiger, J. (1988) Beziehungen zwischen Nematoden, Coleopteren und Dipteren in der Sukzession beim Abbau von Kuhfladen. *Pedobiologia* 31, 305-322.
- Tietjen, J.H. (1980) Population structure and species composition of the free-living nematodes inhabiting sands of the New York Bight Apex. *Estuarine and Coastal Marine Science* 10, 61-73.
- Tsalolikhin, S.J. (1976) Free-living nematodes as indicators of polluted freshwaters. In: Skarlato, O.A. (ed.) *Methods of Biological Analysis of Freshwaters*. Akademia Nauk, Leningrad, pp. 118-122.
- Twinn, D.C. (1974) Nematodes. In: Dickinson, C.H. and Pugh, G.J.F. (eds) *Biology of Plant Litter Decomposition II*. Academic Press, London, pp. 421-465.
- Villot, A. (1875) Recherches sur les Helminthes libres ou parasites des côtes de la Bretagne. *Archives de Zoologie Expérimental et Générale* (1) 4, 451-482.
- Vranken, G., Herman, P.M.J. and Heip, C. (1988) Studies of the life-history and energetics of marine and brackish-water nematodes. I. Demography of *Monhystera disjuncta* at different temperature and feeding conditions. *Oecologia* 77, 296-301.
- Wasilewska, L. (1970) Nematodes of the sand dunes in the Kampinos Forest. I. Species structure. *Ekologia Polska* 18, 429-443.

Wasilewska,
Ekologicz
Wasilewska,
commur
Yeates, G.W.
Himanta
Yeates, G.W.
23, 178-
Yeates, G.W.
New Zea
Yeates, G.W.
Yeates, G.W.
38, 97-10
Yeates, G.W.
and Ferti
Yeates, G.W.
D.W. (ed
Yeates, G.W.,
habits in
Nematolo
Yeow, H.S.,
assembl
Russian
Yuen, P.H. (19
wildern
Zullini, A. (19
Zullini, A. an
area. Wa

- Wasilewska, L. (1974) Rola wskaźnikowa wszytkozernej grupy nicieni glebowych. *Wiadomości Ekologiczne* 20, 385–390.
- Wasilewska, L. (1994) The effect of age of meadows on succession and diversity in soil nematode communities. *Pedobiologia* 38, 1–11.
- Yeates, G.W. (1968) An analysis of annual variation of the nematode fauna in dune sand, at Himantangi beach, New Zealand. *Pedobiologia* 8, 173–207.
- Yeates, G.W. (1972) Nematoda of a Danish beech forest. I. Methods and general analysis. *Oikos* 23, 178–189.
- Yeates, G.W. (1974) Studies on a climosequence of soils in Tussock grasslands. 2. Nematodes. *New Zealand Journal of Zoology* 1, 171–177.
- Yeates, G.W. (1979) Soil nematodes in terrestrial ecosystems. *Journal of Nematology* 11, 213–229.
- Yeates, G.W. (1994) Modification and qualification of the Nematode Maturity Index. *Pedobiologia* 38, 97–101.
- Yeates, G.W. (2003) Nematodes as soil indicators: functional and biodiversity aspects. *Biology and Fertility of Soils* 37, 199–210.
- Yeates, G.W. and Coleman, D.C. (1982) Role of nematodes in decomposition. In: Freckman, D.W. (ed.) *Nematodes in Soil Ecosystems*. University of Texas Press, Austin, pp. 55–81.
- Yeates, G.W., Bongers, T., Goede, R.G.M. de, Freckman, D.W. and Georgieva, S.S. (1993) Feeding habits in soil nematode families and genera – an outline for soil ecologists. *Journal of Nematology* 25, 315–331.
- Yeow, H.S., Finney-Crawley, J.R., Lawlor, J. and King, I.W. (1999) Free-living nematode assemblages downstream from a pulp and paper mill in Humber Arm, Newfoundland. *Russian Journal of Nematology* 7 (2), 95–103.
- Yuen, P.H. (1966) The nematode fauna of the regenerated woodland and grassland of broadbalk wilderness. *Nematologica* 12, 195–214.
- Zullini, A. (1976) Nematodes as indicators of river pollution. *Nematologia Mediterranea* 4, 13–22.
- Zullini, A. and Peretti, E. (1986) Lead pollution and moss-inhabiting nematodes of an industrial area. *Water, Air and Soil Pollution* 27, 403–410.