5 Indices Developed Specifically for Analysing Nematode Assemblages

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Abstract

Nematodes are well established as bioindicators of soil ecosystem status, exemplified by the development of nematode-based indices (NBIs). This chapter aims to: (i) detail the several NBIs derived from nematode assemblage data and based on nematode functional traits, ecophysiology and metabolic activity; (ii) highlight the advantages of NBIs over general community indices; and (iii) emphasize the power and versatility of newly described NBIs (second generation, since 2010) in inferring ecosystem status. A case study exemplifies the potential application of nematode metabolic footprints for indicating connections between soil food webs and ecosystem functioning. The discovery and validation of links between NBIs and agronomic, ecological and economic parameters will be an ongoing mission in soil ecology and may aid decision support tools for soil quality assessments and soil management practices.

5.1 Foundational Achievements that Established Nematodes as Bioindicators

The development of the 'De Man formulae' during the period between Bastian (1866) and De Man (1884–1893) simplified nematode taxonomy and introduced a period of discovery of terrestrial, freshwater and marine nematodes. Detail-rich taxonomic descriptions and advances made by nematologists in that period and thereafter (e.g. de Man, 1884) provided the scientific basis for the development of nematodes as bioindicators during the second half of the 20th century.

At the beginning of the 'green revolution' in the 1960s, studies on nematodes focused on plant-parasitic taxa in terrestrial ecosystems. However, research on nematode ecology exploded from 1970 onwards. The dominance of plant parasites (feeders) over other nematode functional groups was the first indication that management practices had the capacity to reduce functional diversity in the soil food web. Studies of anthropogenic impacts on soil nematode assemblages appeared around 1960, including the effects that liming and fertilization had on forest soils (Bassus, 1960, 1967). Other research demonstrated the restorative effects that woodlands

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and grasslands had on nematode assemblages after conversion from intensive agriculture (Pick-Hoong, 1966). Lastly, the identification of nematode assemblages in sand dunes, forests and grasslands (Yeates, 1968, 1972) demonstrated differences in community assemblages among contrasting ecosystems. For instance, Wasilewska (1979) and Johnson *et al.* (1972) studied nematode assemblages of forests and concluded that omnivorous dorylaimids were most sensitive to disturbances resulting from grazing (cattle, sheep) or cutting (human interference).

A few years later, the first studies appeared revealing that the incidence and prevalence of nematode species reflect the nature and quality of rivers (Zullini, 1976) and lakes (Prejs, 1977). As in terrestrial ecosystems, nematodes are omnipresent and more consistent than insects, molluscs and annelids in muddy, stony or sandy sediments of freshwater systems. Although some species were endemic to aquatic systems, most taxa found in Italian rivers were also terrestrial soil inhabitants (Zullini, 1976). Several authors made use of the work of Zullini to study the relationships between water quality and nematode assemblages (Cantelmo and Rao, 1978; Lambshead, 1986; Zullini and Peretti, 1986).

Based on these and many other fundamental studies (e.g. Freckman, 1982) in terrestrial and aquatic environments, Bongers *et al.* (1989) arranged nematode taxa into five categories along a colonizer–persister (*c-p*) scale that ultimately evolved into the Maturity Index (MI) for terrestrial and marine nematodes (Bongers, 1990; Bongers *et al.*, 1991). The index was developed as a measure of ecological succession. The MI and related indices (PPI, ΣMI) were the first set of nematode-based indices (NBIs) that served as indicators of disturbance intensity. Over the subsequent three decades, substantial advancements have been made in the development of NBIs for terrestrial nematodes (Du Preez *et al.*, 2022). With the development of nematode metabolic footprints (NMFs), Ferris (2010b) and Ferris and Tuomisto (2015) provided the first indices that evaluate the diversity-weighted magnitude of ecosystem functions fulfilled by soil biota.

NBIs represent a powerful ecological toolset that facilitate the study of ecological states, processes and functions. However, careful consideration should be given towards the correct time of investigation and selecting an appropriate subset of NBIs, which is dependent on the research question (Du Preez *et al.*, 2022). While this chapter focuses on terrestrial systems, the use and formalization of nematodes as bioindicators in aquatic systems are addressed in Chapters 6, 10 and 16 of this volume.

5.2 Indices of Ecosystem Status

NBIs are calculated using the *c-p* classification system based on the ecophysiological (life-history trait) characteristics of nematode communities (Du Preez *et al.*, 2022). The concept for the development and application of NBIs originated from the need to assess and monitor soil pollution in the 1980s. For this, nematodes proved to be sensitive indicators. Different taxa have varying sensitivities to biotic and abiotic stressors, leading to changes in index values in disturbed environments (Wasilewska, 1979; Bongers, 1990; Du Preez *et al.*, 2022). The advantage of using these indices over simple diversity indices (e.g. species richness, Simpson's diversity index) was statistically supported at scales that ranged from fields to regions (Freckman and Ettema, 1993; Neher *et al.*, 1995). Indices developed later expressed the potential of fungal- and bacterial-feeding nematodes to indicate prevalence of fungal or bacterial decomposition channels and nutrient turnover speed in soil. Omnivore and predatory nematodes, in turn, were seen as indicators of trophic connectance within the soil food web. Over time, a growing toolset of NBIs of diverse indicator functions crystallized and include the MI family (i.e. MI, Maturity Index 2-5 (MI2-5), Plant-Parasitic Index (PPI) and Sigma Maturity Index (ΣMI)), the food web diagnostic indices (i.e. Enrichment Index (EI), Structure Index (SI), Basal Index (BI) and Channel Index (CI)) and the NMFs. For a detailed description of the development (and evolution) of NBIs, please see Du Preez *et al.* (2022).

5.2.1 Basics of the *c-p* series and evolving taxon classifications

For the calculation of NBIs, soil nematodes are categorized into a *c-p* series (Fig. 5.1) ranging from r to K life-history strategists (Bongers *et al.*,

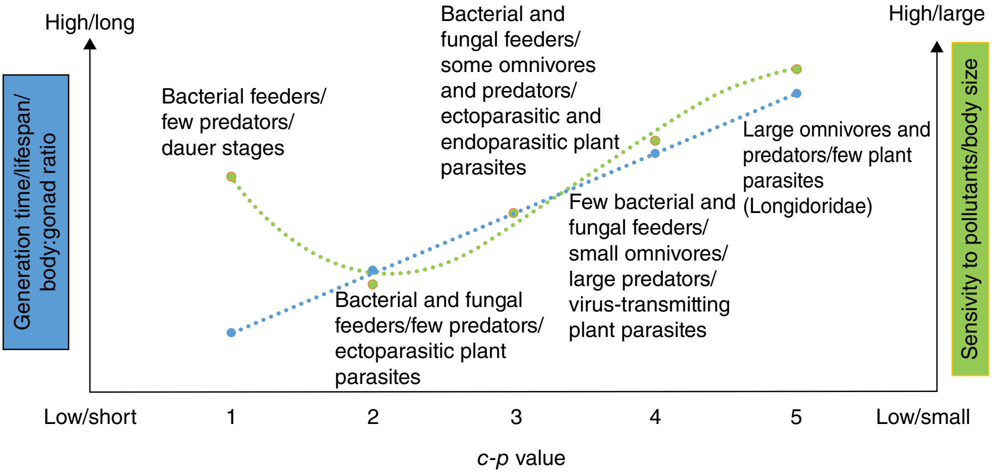

Fig. 5.1. Hypothetical concept of the colonizer–persister (c-p) values and their relation to nematode body characteristics, ecology and trophic group classification. (Author's own image.)

1989). 'Colonizer' (or early colonizer) nematodes are weighted 1 or 2 and indicate greater disturbance and/or resource availability; 'persister' (late successional) nematodes are weighted (3–5 and indicate increasing system stability, food web complexity and connectance among different trophic-level organisms therein.

As recognized early in the development of the *c-p* series (Bongers, 1990; Bongers *et al*., 1991), categorization at the genus or species level would be more informative than at the family level. 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). Empirical testing supported the *c-p* value assignments at the family level (e.g. Ettema and Bongers, 1993) with a few exceptions that became apparent as knowledge increased on the biology and sensitivity of individual genera and species (e.g. Fiscus and Neher, 2002). For example, bacterial feeders can be distinguished as enrichment opportunistic (*c-p*1) or general opportunists (*c-p*2-4) with the former having a non-feeding dauer stage. Because Monhysteridae species do not have a dauer stage and are tolerant of unfavourable conditions, the family was moved to the *c-p*2, a generalist bacterial-feeding category (Bongers *et al*., 1995). Another example is that of the genus *Filenchus*, which was originally classified as an epidermal-cell and root-hair feeder but later shown capable of reproducing when feeding on fungi (Okada *et al*., 2005). Some researchers also recategorized individual species. For example, Beier and Traunspurger (2001) changed *Tobrilus diversipapillatus* from *c-p*3 to *c-p*2 when the species was recorded at higher densities in polluted river sites. Over time, by the experimental generation of data on feeding and ecological preferences, morphologically inferred *c-p* values will be either confirmed or adjusted.

In the publication year of the first edition of this book, Andrássy (2009) reassigned several families and subfamilies within the order Dorylaimida. This led to several changes of *c-p* classes among dorylaimid families. For example, the predatory Discolaimidae were reclassified as subfamilies Discolaiminae and Carcharolaiminae in the family Qudsianematidae and, consequently, were downgraded from *c-p*5 to *c-p*4. Similarly, *Ecumenicus*, formerly classified within the family Thornenematidae, was moved to the new subfamily Ecumenicinae of the Qudsianematidae. Furthermore, several genera of Thornenematidae (*Prodorylaimus*, *Prodorylaimium* and

Mesodorylaimus) were moved into the family Dorylaimidae. More recently, Peña-Santiago and Álvarez-Ortega (2014) transferred multiple genera from Qudsianematidae to the family of Dorylaimidae based on morphological features, embryonic development and 28 rDNA gene sequences. Although thit has not affected current *c-p* assignments, further changes based on gene sequences and developmental studies can be expected.

Therefore, as the original *c-p* classifications by Bongers and Bongers (1998) and Bongers *et al.* (1991) evolve, referral to the updated nematode ecophysiology data sets provided by the Nemaplex website of University of California, Davis (http://nemaplex.ucdavis.edu, accessed 9 August 2025) is recommended. For this reason, the preservation, evolution and accessibility of this web page should be a primary consideration for nematode ecologists.

5.2.2 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. The 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 *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* (Table 5.1).

Maturity Index (MI)

The MI is based on nematode taxa that are not parasitic on plants, insects or animals, and is considered a measure of environmental disturbance. Low MI values indicate a disturbed and/or enriched environment, while high MI values indicate 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. In the case of the nematode assemblage, the successional setback is reflected in a lower MI effected by an increase of r-strategists, characterized by shorter lifespans and smaller body sizes (Odum, 1985; Bongers *et al.*, 1997) (Fig. 5.1).

The dauer stages of enrichment opportunists (animal parasites and entomopathogenic nematodes are rare in soil samples) (Jaffuel *et al.*, 2018) may be included or excluded from the calculation of the MI (Bongers and Bongers, 1998). An abundance of dauer stages indicates a system that was enriched (increased microbial activity) previously, which shifted to a less enriched phase at the time of sampling. Such a phase may also be seasonal and caused by either temperature flux or drought and the corresponding change in microbial activity. The ratio of dauer stages to active stages of rhabditids, as an indicator of resource availability, was introduced and tested by Sohlenius (1969). Temporal assessments of this ratio may provide insights into the resource dynamics of a system. However, a difficulty with this approach is identifying dauer stages of different nematode taxa. For example, dauer stages of entomopathogenic nematodes may occur in soil in the absence of insect hosts but are not indicators of food web enrichment.

Plant-Parasitic Index (PPI)

The PPI is comparable to the MI but is computed using only plant-parasitic (feeding) nematodes. The rationale behind this is that their abundance is determined by the vigour of their host plants, which, in turn, is influenced by system enrichment and other management factors. Consequently, under nutrient-poor conditions of natural ecosystems, the PPI is often low (compared to fertilized or organically amended agricultural systems) and associated with a high proportion of Tylenchidae (*c-p*2) in the nematode assemblage. Furthermore, this index shows an inverse response compared to the MI when it comes to enrichment (Bongers, 1990; Bongers *et al.*, 1997). However, it should be noted that the PPI depends on the host suitability of plants and the type of (agro)ecosystem in which they occur. This may result in variance between studies. Any inference of the PPI should consider specific information on the taxa present in the plant-parasitic assemblage. Also, the reports that *Filenchus* spp. feed on fungi and were recovered from leaf litter (Brzeski, 1998; Okada *et al.*, 2005) underscore the need for further studies on the

Table 5.1. Calculation of the Maturity Index (MI), Maturity Index 2-5 (MI2-5), Sigma Maturity Index (ΣMI), Sigma Maturity Index 2-5 (ΣMI2-5), Plant-Parasitic Index (PPI), and general community indices (see Chapter 4, this volume), for two nematode assemblages (samples A and B). (Author's own table.)

					MI		MI2-5		ΣMI		ΣMI2-5		PPI	
	Abundance				A	B	A	B	A	B	A	B	A	B
Nematode taxon	Sample A	Sample B	*c-p*	Feeding group	*c-p* wtd propn	*c-p* wtd propn	*c-p* wtd propn	*c-p* wtd propn	*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	0.2		
Cephalobidae	**15**	**2**	2	B	0.3	0.1	0.3	0.1	0.3	0.0	0.3	0.1		
Plectidae	**2**	**15**	2	B	0.0	0.4	0.0	1.0	0.0	0.3	0.0	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	0.3		
Aporcelaimidae	**15**	**2**	5	P	0.8	0.1	0.8	0.3	0.7	0.1	0.7	0.2		
Relevant total	**109**	**109**			**99**	**79**	**97**	**29**	**109**	**109**	**107**	**59**	**10**	**30**
MI	**3.4**	**1.6**												
MI2-5	**3.5**	**2.6**												
ΣMI	**3.4**	**2.0**												
ΣMI2-5	**3.4**	**2.8**												
PPI	**3.0**	**3.0**												
Simpson	**0.27**	**0.27**												
Shannon	**1.61**	**1.61**												
Hill N1	**1.31**	**1.31**												
Pielou J´	**0.77**	**0.77**												

Feeding group: H = plant parasites (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). Next, the proportion (propn) of that total represented by taxa that meet the criteria is calculated and weighted (wtd) by the *c-p* values of those taxa. The index value is the sum of these weighted proportions.

feeding habits of the many genera and species in the ubiquitous Tylenchidae group (Qing and Bert, 2019). Such nematodes, able to feed on both root hairs and hyphal fungi, can be considered as root associates. There is an ongoing debate about whether to include (Bongers, 1990) or exclude (Neher and Campbell, 1996) Tylenchidae in the PPI. The controversy stems from the classification of Tylenchidae members as fungal, root, algal or lichen feeders. To date, this issue has been resolved for only a minority of the 44 genera in this highly diverse family (Qing and Bert, 2019).

Maturity Index 2-5 (MI2-5)

This index is identical to the MI but excludes the *c-p*1 enrichment opportunists. The index was first proposed by Popovici (1992) and was empirically tested and confirmed during studies of the relationship between MI and copper concentration under agricultural conditions (Korthals *et al*., 1996a,b). In those studies, it was apparent that there was a strong relationship between decreased abundance in higher *c-p* value nematodes and pollution-induced stress while the *c-p*1 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-p*1 nematodes. The use of this index (instead of or supplementary to MI) should thus be considered in studies evaluating the effect of heavy metals, and potentially other pollutants, or when the effects of ephemeral nutrient resources on similarly ephemeral *c-p*1 nematodes can be ignored.

Sigma Maturity Index (ΣMI)

This index was proposed by Yeates (1994) and is equivalent to the Total MI of Wasilewska (1994). It represents the MI for all nematodes in the system, including plant parasites, based on the assertion that the complete assemblage provides integral information. This includes the assumption of a congruent relationship between MI and PPI, offering insight into disturbance and environmental conditions. However, sampling of more than 150 agricultural sites in North Carolina and Nebraska (Neher and Campbell, 1996) revealed that the use of either the MI or ΣMI may be plant-host-dependent. When crops that are good hosts for *c-p*3 plant parasites are grown, the relationship between MI and PPI may be incongruent. In contrast, in (agro)ecosystems with high plant diversity (e.g. extensive crop rotations, natural ecosystems), an inverse relationship of MI and PPI does not occur (Neher and Campbell, 1996).

Sigma Maturity Index 2-5 (ΣMI2-5)

This index computes the MI for all nematodes within the *c-p*2-5 range (Neher and Campbell, 1996). It acknowledges that higher *c-p* values of plant-parasitic species also provide valuable information on environmental stress. However, the index may be influenced by the presence of large numbers of *c-p*3 plant parasites, which can affect its overall interpretation, like the ΣMI.

For ease of calculating NBIs, and to ensure accuracy, the use of the Nematode Indicator Joint Analysis (NINJA) online tool is recommended (Sieriebriennikov *et al*., 2014) (https://shiny.wur.nl/ninja/, accessed 9 August 2025). This tool processes, calculates and displays the NBIs by making use of the large, updated repository of nematode ecophysiological data included in Nemaplex (http://nemaplex.ucdavis.edu, accessed 9 August 2025). A thorough interpretation support for each NBI is provided by Du Preez *et al*. (2022).

5.2.3 Indicators of soil food web condition: Enrichment, Structure, Basal and Channel indices

The evolution of concepts, research and model validation associated with the development of the MI family led to a functional guild classification of nematodes, i.e. 'groups of nematodes that have similar effects on ecosystem processes', as a basis for studying and comparing ecosystem services (Bongers and Bongers, 1998; Bongers and Ferris, 1999). This functional redundancy 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. Hence, the nematode fauna indicates 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 opportunists; the other is the trophic connectance of the system as indicated by the prevalence and abundance of higher-trophic-level organisms with multichannel (omnivory) feeding characteristics (Wolkovich, 2016). Considering soil nematode taxa as representatives of functional guilds generates an indicator profile that is not constrained by population distribution patterns and microenvironment effects (Ferris and Bongers, 2006).

The Enrichment, Structure and Basal indices rely on the relative abundance of functional guilds of nematodes and are descriptors of food web condition (Table 5.2, Fig. 5.2). Nematodes of all feeding habits classified as *c-p*2 are considered basal (b) to both enrichment and structure trajectories, i.e. they exist in most soil food webs, are almost always present and survive the most adverse conditions. Ferris *et al.* (2001) hypothesized that bacterial-feeding *c-p*1 and fungal feeders in *c-p*2 are indicators of enrichment (e), while nematodes of all feeding habits in *c-p*3-5 are indicators of structure (s). Functional guild indicators are weighted according to growth and metabolic rates (resource utilization) on the enrichment axis. On the structure axis, they are weighted by the number of nematodes in higher *c-p* classes, reflecting the degree of connectance in food webs of increasing complexity (Fig. 5.2). Greater detail on derivation of the structure and enrichment weightings (W_i) is provided in Ferris *et al.* (2001).

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

$$b = (\mathrm{Ba}_2 + \mathrm{Fu}_2) \times W_2,\ \text{where } W_2 = 0.8$$

$$e = (\mathrm{Ba}_1 \times W_1) + (\mathrm{Fu}_2 \times W_2),\ \text{where } W_1 = 3.2 \text{ and } W_2 = 0.8$$

$$s = (\mathrm{Ba}_n \times W_n + \mathrm{Ca}_n \times W_n + \mathrm{Fu}_n \times W_n + \mathrm{Om}_n \times W_n),\ \text{where } n = 3-5,\ W_3 = 1.8,\ W_4 = 3.2 \text{ and } W_5 = 5.0$$

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):

$$\mathrm{EI} = 100 \times \left[e / (e + b)\right]$$

$$\mathrm{SI} = 100 \times \left[s / (s + b)\right]$$

$$\mathrm{BI} = 100 \times \left[b / (e + s + b)\right]$$

$$\mathrm{CI} = 100 \times \left[(\mathrm{Fu}_2 \times W_2) / (\mathrm{Ba}_1 \times W_1 + \mathrm{Fu}_2 \times W_2)\right]$$

We used the nematode assemblages of Table 5.1 to calculate the above-described indices (Table 5.3). Accordingly, 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 (Quadrat C in Fig. 5.2). Sample B represents a disturbed and enriched condition in which the disturbance has had detrimental effects on higher trophic levels but fostered quickly developing *c-p*1 bacterial feeders (Quadrat B in Fig. 5.2). Faunal analyses based on these indices provide insights into food web enrichment and structure and allow derivation of testable hypotheses (e.g. Table 5.2) based on the relative enrichment and structure of the system.

The CI represents a partitioning of resource flow 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). These approaches included a ratio of F/B (Sohlenius and Bostrom, 1984), which has been defined most recently as the Nematode Channel Ratio (NCR) = B/(B + F), where B and F represent the abundance of bacterial- and fungal-feeding nematodes, respectively (Yeates, 2003). The CI differs

Table 5.2. 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). (Modified 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:N ratio	Low	Low	Mod. to high	High
Food web condition	Disturbed	Maturing	Structured	Degraded

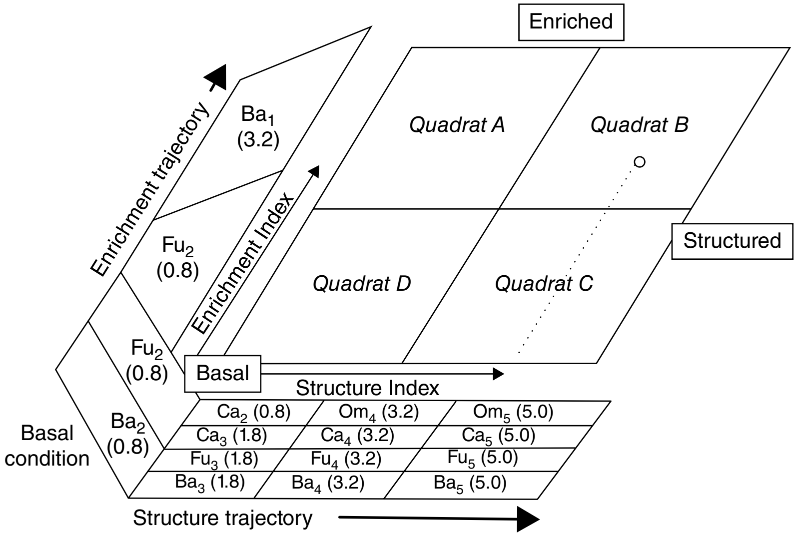

Fig. 5.2. A graphical representation of the nematode faunal profile indicates whether the soil community is enriched but unstructured (Quadrat A), enriched and structured (Quadrat B), resource-limited and structured (Quadrat C), or resource-depleted with minimal structure (Quadrat D): functional guilds of soil nematodes are characterized by diet (trophic group) and 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.)

in including weighting parameters for the size and *c-p* values (for detailed information, see Ferris *et al.*, 2001) of the nematode functional guilds. As such, values above 50 indicate predominantly fungal-mediated (sample A) and values below 50 indicate predominantly bacterial-mediated (sample B) decomposition pathways (Table 5.2).

When resources become available to soil organisms through external input, disturbance, organism mortality, turnover or environment changes, there is an enrichment pulse of early successional taxa (opportunists). 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 (Ferris, 2010a). Substrates with high C:N ratios may favour the fungal rather than the bacterial decomposition channel (Ruess and Ferris, 2004).

Further understanding of enrichment is determined by the carbon flow through active fungal and bacterial channels using their biomass and respiration rates. These concepts led to the development of metabolic footprints which measure the magnitude of ecosystem functions fulfilled by soil biota (Ferris, 2010b). It is also the first NBI that increases proportionally to the abundance (and biomass) of nematode taxa.

5.2.4 Abundance, biomass and functional diversity – the metabolic footprint concept

To study ecosystem functions of nematodes, and their roles in contributing to ecosystem services, it is important to consider their biomass and biomass-dependent activity. Since previous NBIs are based on relative abundances or proportions, communities with different abundances may present the same index values. Consequently, correlating the relative abundances of nematode feeding guilds and/or indices to microbial activity and biomass, and magnitudes of their functions (e.g. nutrient mineralization), is problematic. Even within bacterial-feeding nematode families, size and biomass may vary greatly between genera. For example, the biomass for

Table 5.3. Calculation of the Basal Index (BI), Enrichment Index (EI), Structure Index (SI) and Channel Index (CI) for two nematode assemblages (samples A and B) of the same number of taxa and the same number of individuals (cf. Table 5.1). (Author's own table.)

								A			B		
Nematode taxon	Sample A	Sample B	*c-p*	Feeding group	b wtd	e wtd	s wtd	b	e	s	b	e	s
Hoplolaimidae	**5**	**15**	3	H				0.0	0.0	0.0	0.0	0.0	0.0
Pratylenchidae	**5**	**15**	3	H				0.0	0.0	0.0	0.0	0.0	0.0
Aphelenchidae	**15**	**5**	2	F	0.8	0.8		12.0	12.0	0.0	4.0	4.0	0.0
Cephalobidae	**15**	**2**	2	B	0.8			12.0	0.0	0.0	1.6	0.0	0.0
Plectidae	**2**	**15**	2	B	0.8			1.6	0.0	0.0	12.0	0.0	0.0
Rhabditidae	**2**	**50**	1	B		3.2		0.0	6.4	0.0	0.0	160.0	0.0
Dorylaimidae	**50**	**5**	4	O			3.2	0.0	0.0	160.0	0.0	0.0	16.0
Aporcelaimidae	**15**	**2**	5	P			5.0	0.0	0.0	75.0	0.0	0.0	10.0
Total	**109**	**109**											
								25.6	18.4	235.0	17.6	164.0	26.0
Index components													
BI	**9.2**	**8.5**											
EI	**41.8**	**90.3**											
SI	**90.2**	**59.6**											
CI	**65.2**	**2.4**											

Feeding group: H = plant parasites (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 (wtd) in terms of the basal (b), enrichment (e) and structure (s) characteristics of that taxon. The index values are calculated from the index components, i.e. the sum of the b, e and s values (see text).

Mesorhabditis (= *Bursilla*) *labiata* and *Cruznema tripartitum* adult females, both belonging to the family Rhabditidae, is 0.48 µg and 7.7 µg, respectively (Ferris *et al.*, 1995). Consequently, the magnitude of certain functions (e.g. regulation of microbial populations) might vary with the absolute abundance or biomass of a given species population in a given soil sample (16 *M. labiata* = 1 *C. tripartitum*).

To overcome this limitation, Ferris (2010b) developed NMFs as an assessment of the metabolic activity of nematode functional guilds. These footprints rely on the assessment of the carbon utilization of nematodes on growth and egg production (production component) and respiration (respiration component). The production component is based on the calculation of nematode carbon biomass according to the individual taxon body volume calculated with the Andrássy formula (Andrássy, 1956) and weighted by the taxon lifespan inferred from its *c-p* value (Fig. 5.1). The respiration component is estimated through the allometric power dependence of basal metabolism and body weight. Therefore, NMFs are calculated as the sum of both components and as an index of carbon utilization of each taxon. Applied to nematode functional guilds, the Enrichment Footprint is the estimation of carbon utilization by enrichment-opportunistic nematodes, and the Structure Footprint the estimation of carbon utilization by higher trophic links which are indicators of regulatory (and/or disease-suppressive) functions. Such footprints can be graphically depicted as a rhomboid shape around the (EI, SI) point in a biplot, and the Functional NMF calculated as the area of the rhombus (Ferris, 2010b).

Another option is to link NMFs directly with their expected function (Sánchez-Moreno and Ferris, 2018), exemplified here with radar charts with data from Tables 5.1 and 5.3 (Fig. 5.3) as well as from Schmidt *et al.* (2020, 2022) (Fig. 5.4). These graphs provide additional information on individual trophic-group footprints: the Herbivore, Bacterivore, Fungivore, Omnivore and Predator NMFs refer to the estimation of carbon and energy flow through the soil food web by different functional groups. The Composite Footprint represents the metabolic footprint of the entire nematode community.

This resource inflow into and within the soil food web can be visualized using a radar chart. The underlying data for this representation may include metabolic footprints (Figs 5.3 and 5.4). An alternative is the use of single components of the metabolic footprint, namely nematode body mass, respired carbon and incorporated carbon (all obtainable from http://nemaplex.ucdavis.edu/,

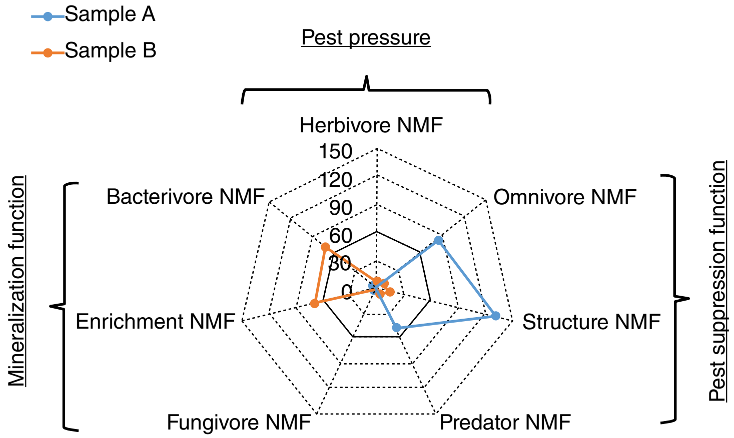

Fig. 5.3. Nematode metabolic footprint (NMF) family comprising Herbivore, Omnivore, Structure, Predator, Fungivore, Enrichment and Bacterivore NMFs. NMFs (µg carbon per functional group respired and incorporated in biomass) were calculated for the nematode assemblages of samples A and B (Tables 5.1 and 5.3). Individual nematode family characteristics were extracted from http://nemaplex.ucdavis.edu/ (accessed 9 August 2025) (note that the Predator and Omnivore NMFs are not separated on this web page and need manual reassignments according to the feeding codes of Yeates *et al.*, 1993). Ecosystem functions (underlined) are from Sánchez-Moreno and Ferris (2018).

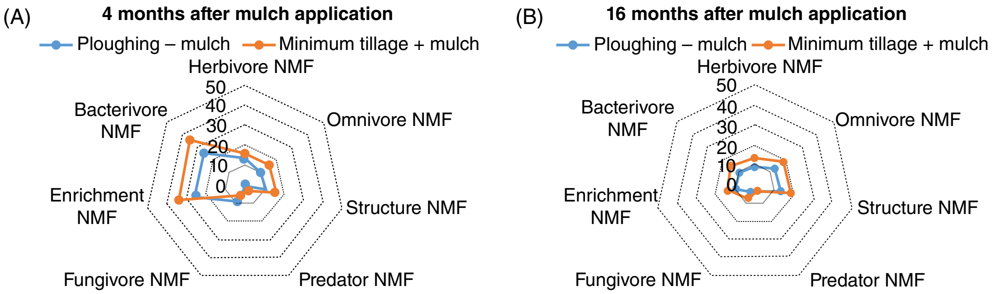

Fig. 5.4. Long-term field experiments conducted by the University of Kassel compared a plough system, where potatoes were frequently hilled in rotation, with a minimum tillage system that applied cover crop mulch (10–15 t ha^{-1}, C:N = 20–25) on top of the potato hills before tiller emergence. Square-root-transformed nematode metabolic footprints (NMFs) are presented for better visualization (µg C 100 ml soil^{-1}) at 4 months (A) and 16 months (B) after the last mulch application. (Data from Schmidt *et al.*, 2020, 2022.)

accessed 9 August 2025). The arrangement of the radar chart allows the inference of two specific ecosystem functions assessed by the nematode assemblage: the left side (Bacterivore, Enrichment and Fungivore NMFs) represents the nutrient turnover function that is more pronounced in sample B than in sample A (Fig. 5.3). In contrast, the right side of the radar chart reflects the degree of disease suppressiveness (regulatory function) indicated by the Omnivore, Structure and Predator NMFs. According to Fig. 5.3, the disease-suppressive ability is greater in sample A than in sample B. In contrast, the Herbivore NMF is interpreted as the disservice that indicates whether plant-parasitic nematodes interfere with plant growth and/or yield production.

Furthermore, we used nematode community data from two long-term German field experiments to demonstrate how NMF analyses can be applied to natural (agro)ecosystems (Fig. 5.4). Four months after application, the mulch in the potato cropping system with minimum tillage increased the NMFs of bacterial feeders substantially compared to the plough system without mulch (Fig. 5.4A). The Bacterivore NMF collapsed 16 months after mulch application (Fig. 5.4B). However, the slight increase of the Omnivore and Fungivore NMFs and the maintained Herbivore NMF indicate a growing food web connectance in the minimum tillage system. This may explain the greater resilience to fungal-mediated pea root rots in this particular system (Schmidt *et al.*, 2022). The low Predator NMF relative to the food resource (prey) indicates the effect of environmental perturbations on nematodes of higher *c-p* classes (here, intensive soil tillage).

In an attempt to improve the correlations of NMFs, biomass and abundance with ecosystem functions, Ferris and Tuomisto (2015) proposed weighting these indices by nematode diversity:

$$\theta = \left({}^{q}\mathrm{D}\right)^{b} \times \sum_{i=1}^{R} \left(A_i\right),$$

where θ is the diversity-weighted abundance (or biomass or NMF), $\left({}^{q}\mathrm{D}\right)^{b}$ is the true diversity and A_i is the value for biomass, abundance or NMF of species *i* of the *R* (R = species richness) species in that sample that fulfil a specific functional trait. In the simplest case, $\left({}^{q}\mathrm{D}\right)^{b}$ reflects the Shannon diversity index of all species that are, for example, responsible for mineralization of nutrients. According to Fig. 5.3, A_i may be then either Fungivore, Bacterivore and Enrichment NMFs, or their corresponding biomass or abundance. The rationale behind this is based on the concept of functional redundancy, as discussed earlier. For a given function, higher nematode diversity allows for the occupation of more niches (e.g. soil pores of different sizes). In our example, as nematode diversity increases, the potential for available prey (bacteria and fungi) also increases, which in turn enhances the nutrient mineralization potential.

Although diversity-weighted indicators have been used in several studies (Landi *et al.*, 2018; Mejía-Madrid and Sánchez-Moreno, 2022), more evidence is necessary to ascertain their relationships to soil functioning.

5.3 Conclusions

The evolution of functional indices based on nematode faunal analysis provides insights into the 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, calibration of indices by quantitative levels of disturbance, ecosystem type and major land-resource regions guided by new information on feeding habits, life-history traits and the assignment of taxa to functional guilds is necessary for improving the interpretative value of NBIs. 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 taxa in sensitivity to environmental disturbance, and the ease with which nematodes can be separated from substrate and categorized into taxonomic groups or functional guilds. The NMFs and diversity-weighted abundances represent potentially useful tools for ecologists, agronomists and (soil) biologists in that they contribute to further understanding of nematode biodiversity and links to ecosystem functions in soils shaped by natural events and anthropogenic activities.

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