Nematology Monographs & Perspectives, 2004, Vol. 2, 503-510

Nematode faunal analyses to assess food web enrichment and connectance

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Summary – The cp classification recognises that nematode taxa with anatomical and physiological commonalities are probably similarly adapted to specific environmental conditions. Functional guild analysis, which integrates cp-scaling with food sources, reveals that some guilds respond opportunistically to enrichment while others represent the presence of higher trophic connectance in the food web. This dichotomy was portrayed graphically in cp triangles as the proportional representation of enrichment opportunists (cp-1), general opportunists (cp-2) and taxa indicating higher connectance (cp-3-5). Confounded in the calculation of cp triangles is interdependence of the axes; proportionality of the three groupings to the whole nematode fauna requires that increase in food web structure (cp-3-5 taxa) concomitantly decreases the enrichment indicator (cp-1 taxa). The categorical separation of nematode taxa into five cp classes does not imply unit increments in r or K characteristics. We use body size and growth rates to weight the importance of enrichment indicators and estimates of corresponding food web connectance to weight the importance of structure indicators. We consider cp-2 taxa basal to both trajectories and calculate position along the enrichment and structure axes of a faunal diagram independently as the weighted ratios of the indicator and basal taxa.

The classification of soil nematodes into five coloniser-persister (cp) categories, based on a progression from r to K characteristics (Bongers, 1990), recognises that nematode taxa with anatomical and physiological commonality are probably similarly adapted to specific

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environmental conditions. The subsequent evolution of that scheme into a functional guild classification (Bongers & Bongers, 1998), which integrates cp-scaling with food sources, reveals that some guilds respond opportunistically to enrichment while others represent greater diversity and greater trophic connectance in the food web. This dichotomy was portrayed graphically in cp triangles as the proportional representation of enrichment opportunists (cp-1), general opportunists (cp-2) and taxa indicating higher connectance (cp-3-5) (De Goede *et al.*, 1993). The response of nematodes in cp 2-5 classes to contaminants and disturbance is recognised in their application as an indicator of environmental pollution (Korthals *et al.*, 1996).

Confounded in the calculation of cp triangles is interdependence of the axes. The calculation of the three groupings as proportions of the whole nematode fauna determines that an increase in food web structure (proportion of cp-3-5 taxa) concomitantly forces a decrease in the enrichment indicator (proportion of cp-1 taxa). Since that outcome seems artefactual, we calculated two trajectories for the soil food web based on guilds that indicate enrichment and guilds that indicate structure. We used nematodes in the cp-2 class, which appear to be universally present in soils, as basal to both trajectories (Ferris *et al.*, 2001). Positions along the enrichment and structure axes of a faunal diagram are calculated independently as the weighted ratios of the indicator (enrichment or structure) and basal taxa. The numerical value applied to cp classes in calculation of a Maturity Index (Bongers, 1990) does not infer that the r or K characteristics of the nematode taxa assigned to those classes are separated by equal unit increments. Consequently, we developed separate weighting schemes for taxa representing the enrichment and structure trajectories of the soil food web.

For the structure trajectory, we conjectured that the degree of trophic connectance in the food web is an indicator of its diversity and complexity. We reasoned that the abundance of nematode taxa in a web could be used as an estimator of the total biodiversity of that web. We calculated relative taxonomic richness up to each cp-class for data from several sources (*e.g.*, Yeates & van der Meulen, 1996; McSorley, 1997; Bongers & Bongers, 1998; De Goede & Bongers, 1998; and our unpublished data) and used the relationship between connectance and species richness ($L = \alpha S^2$) (Martinez, 1992) to estimate the degree of connectance if only cp-2 nematodes were present, cp-2 and cp-3, cp-2-4,

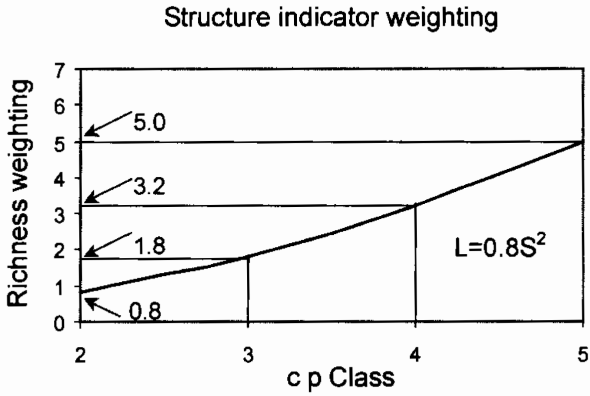

Fig. 1. *Determination of weights applied to functional guilds of soil nematodes that represent diversity, connectance and complexity in the food web.*

Table 1. *Weightings assigned to functional guilds of bacterivore* (Ba)*, fungivore* (Fu)*, predator* (Ca)*, and omnivore* (Om) *nematodes as indicators of food web enrichment* (k_e)*, structure* (k_s) *and basal attributes* (k_b)*.*

Feeding habit	cp-class	k_e	k_s	k_b
Ba	1	3.2	0.0	0.0
Fu	2	0.8	0.0	0.8
Ba, Fu, Ca	2	–	0.0	0.8
Ba, Fu, Ca, Om	3	–	1.8	0.0
Ba, Fu, Ca, Om	4	–	3.2	0.0
Ba, Fu, Ca, Om	5	–	5.0	0.0

or cp-2-5 were present. The estimates were normalised to a maximum value of five for the latter grouping by setting $\alpha = 0.8$ (Fig. 1). These calculations rely on the validity of the assumption that, in the instance of environmental perturbance, nematode taxa in the various cp-classes will be eliminated sequentially, with those in the cp-5 category being most sensitive. From that, the weights applied to cp-classes 2-5 are 0.8, 1.8, 3.2 and 5, respectively (Fig. 1, Table 1).

For the enrichment trajectory, we reasoned that cp-1 nematodes increase in size and abundance to an extent commensurate with the availability of resources. Therefore, we used the body length and diameter measurements for all cp-1 nematodes described in Bongers (1994) and calculated the fresh weight biomass according to Andrássy (1956). The same calculation was made for all cp-2 nematodes. The average biomass of cp-1 taxa (2.68 μg) was approximately four times that of cp-2 taxa (0.64 μg). Since the weight assigned to cp-2 taxa for the structure trajectory was 0.8, we used this basis to establish a weight four times that magnitude (3.2) for the cp-1 nematodes of the enrichment trajectory (Table 1).

In a faunal analysis, distance along the enrichment trajectory is calculated as the enrichment index (EI). The EI is a measure of resources available to the soil food web based on the relative weighted abundance of nematodes in guilds representing enrichment (e) and basal (b) characteristics. For example, the e component is determined as $\sum k_e n_e$, where k_e are the weightings (Table 1) assigned to guilds that indicate enrichment characteristics of the food web and n_e are the abundances of nematodes in those guilds. The b component is determined similarly, using cp-2 guilds, which indicate basal characteristics. The EI is calculated as $100(e/(e+b))$. Distance along the structure trajectory, the structure index (SI) is calculated as $100(s/(s+b))$, where the s component is based on the weighted abundance of taxa in cp-3-5 and the b component as taxa in cp-2.

Besides the EI and SI, we use the weighting system to calculate a Channel Index (CI) as a measure of the relative prevalence of fungi and bacteria in the soil food web and consequently the importance of fungal and bacterial decomposition pathways. The CI is based on opportunistic guilds of cp-1 bacterivores (Ba_1) and cp-2 fungivores (Fu_2) and, with applicable weights, is calculated as $100(k_e Fu_2/(k_e Ba_1 + k_e Fu_2))$.

Based on the position of the faunal analysis on the diagram, we infer characteristics of the environment and condition of the food web, which provide a framework for testing, validation, recalibration and implementation (Fig. 2). We hypothesise that a food web with a high EI and low SI has active bacterial decomposition channels, is enriched with low C/N organic materials, may be recently disturbed and, because of the lack of connectance in the web, is probably conducive to opportunistic organisms that include pest species. A food web with high EI and high SI is probably also enriched with high-N, readily decomposed organic material but is relatively undisturbed. Due to the high connectance, opportunistic species may be regulated. Where the SI is high and EI low, the system is probably undisturbed and not enriched by organic input from external sources. Decomposing organic material may be of high C/N ratio and decomposition pathways tend to be dominated by fungi. When both EI and SI are low, resources are depleted and the system

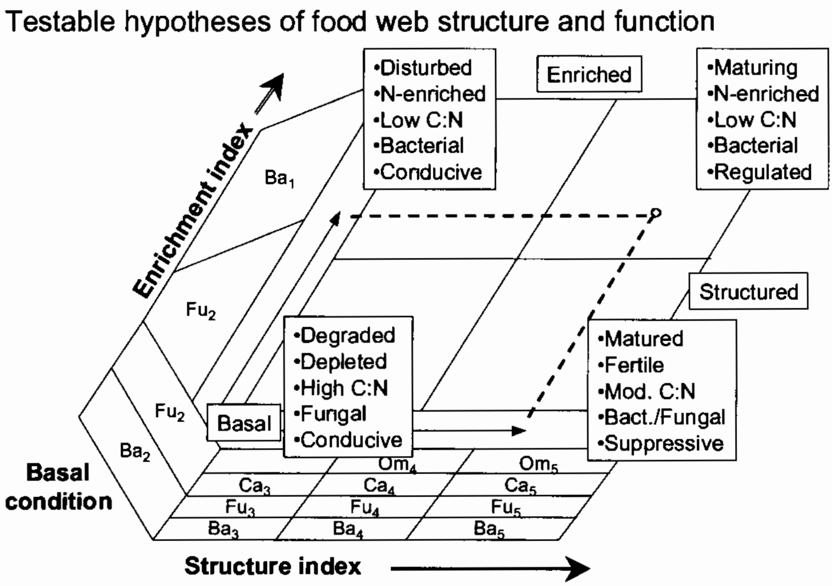

Fig. 2. *Functional guilds of soil nematodes characterised by feeding habit (trophic group) and by life history characteristics expressed along a coloniser-persister (cp) scale (after Bongers & Bongers, 1998). Indicator guilds of soil food web condition (basal, structured, enriched) are designated and 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.*

may be under stress due to adverse environmental conditions, extreme disturbance or contamination.

Indicator values of the EI and SI are demonstrated by data from biointegrative orchards (Fig. 3A), natural vegetation in a desert (Fig. 3B) and from pasture and forest soils (Fig. 3C). The orchards have been maintained without the use of pesticides and mineral fertilisers for varying numbers of years. Fertility is supplied through cover crops and applications of composted manure. The desert system receives little external input, rainfall is rare and sporadic, and net primary productivity is low. The amount of C flowing into the soil system may be too low to support an abundance of organisms at higher trophic layers and the environmental extremes may not be conducive to survival of cp-3-5 predators and omnivores. Food webs of the pasture and forest soils decompose detritus from the plant system but have little external input. The decomposing plant material is usually of high C/N ratio and

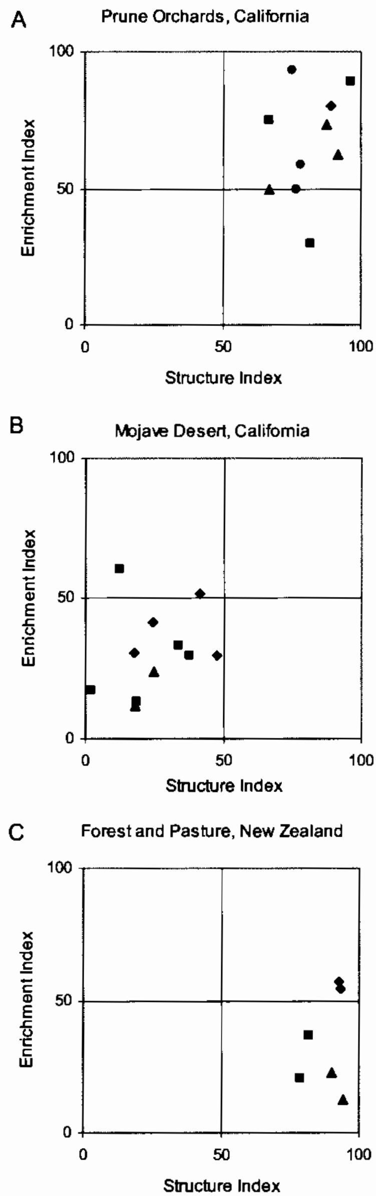

Fig. 3. *Application of nematode faunal analyses in diagramming the condition of soil food webs. A: Biointegrative orchards in California; B: Natural vegetation in the Mojave desert, California; C: Forest and pasture soils in New Zealand. A, B: Data from Ferris (unpubl.); C: Data from Yeates and van der Meulen (1996).*

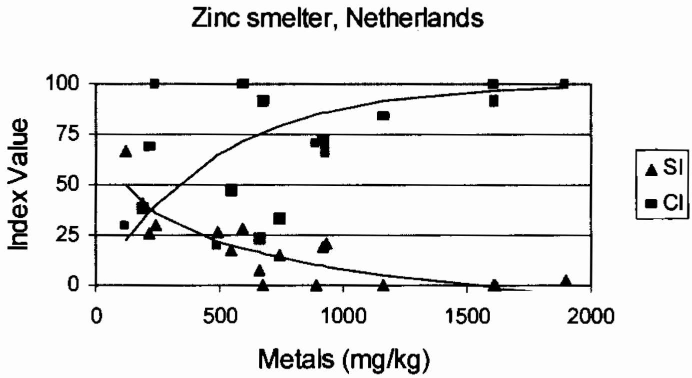

Fig. 4. *Structure Index (SI) and Channel Index (CI) for soil samples from heathland at different distances from a zinc smelter near Budel, The Netherlands. Data from Korthals* et al. *(1998).*

probably conducive to fungal decomposition. Although fertility is low, the systems are undisturbed and structure of the food web is high.

At a higher level or resolution, the effects of soil pollution on the sensitive species that constitute the SI is demonstrated by data from soils around a zinc smelter (Fig. 4). The same data also suggest sensitivity of bacterial decomposition pathways to heavy metal pollution and the increasing predominance of fungal decomposition at higher levels of contamination.

In each of the application examples provided (Figs 3, 4), the nematode faunal analyses support the hypotheses implicit in Figure 2. Extensive studies are now required to validate that the inferred enrichment and disturbance conditions actually prevail at such sites and that nematode faunal analyses provide acceptable and efficient measures of their magnitude.

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