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Nematode diversity in agroecosystems

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Abstract

The diversity of nematode faunae in agroecosystems and their relationships to soil processes suggests that they are potential bioindicators. However, the effects of plants, soil types and nematode biogeography mean a ‘functional group’ may be a better indicator than particular nematodes. Traditionally plant-feeding nematodes (e.g., Heteroderidae, Longidoridae) have been used as indicators. Sampling strategies and methods for extracting, identifying, and indexing nematode assemblages are given. Permanent grassland may be regarded as providing a baseline for nematode diversity in a given soil. Current work suggests that the relative abundance of fungal-feeding and bacterial-feeding nematodes may be a sensitive indicator of management changes. Changes in nematode diversity shown by values of the Shannon–Wiener index (H') often reflect environmental differences. The nematode ‘maturity index’ can provide useful information on the direction of change within a particular soil, and there are prospects that the abundance or proportion of *c–p* Groups 1 and 2 may have value as a transferable index. Trends following disturbance events can be shown in *c–p* triangles. Morphologically distinct groups (e.g., Criconematidae, Longidoridae, Mononchoidea) may be useful within regions or soil types but fail to provide a universal indicator. ©1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Soil nematodes are very small (0.3–5.0 mm long as adults) worm-like animals which are very abundant (commonly millions m^{-2}) and diverse (commonly >30 taxa) in all soils (Yeates, 1979). As nematodes feed on a wide range of soil organisms and are dependent on the continuity of soil water films for movement, their activities are largely controlled by soil biological and physical conditions. Given the ease of recovering nematodes from soils and the ability to identify them to meaningful taxa or ‘functional groups’, soil nematodes offer great potential for use as indicators of biodiversity and for assessing the impact of changing land use on soil conditions.

Historically plant and soil nematodes have been related to land use. This is perhaps best reflected by the long-standing regulations in various countries that restrict the planting of crops such as potatoes (*Solanum tuberosum*) and sugarbeet (*Beta vulgaris*) if populations of potato cyst nematode (*Globodera rostochiensis*, *G. pallida*) or beet cyst nematode (*Heterodera schachtii*) in the particular parcel of land have been above locally determined thresholds (Nickle, 1991). The presence of such host-specific plant-pathogenic nematodes may indicate not only that the particular

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crops have been grown in the soil but also that their abundance is such that replanting would not give an economic crop return unless chemical control measures or a nematode-resistant plant variety is used.

When the sustainability of a particular land use is considered it is necessary to ensure that both the chemical and physical conditions of the soil remain suitable for plant growth (Wild, 1988). The major nutrients carbon, nitrogen, phosphorus, potassium, and sulphur (CNPKS) must not only remain in balance but they must be available for plant uptake. Nutrients removed in agricultural produce should be replaced. Soil physical conditions should not be allowed to deteriorate; the physical substrate should provide a suitable seedbed and adequate moisture for crop growth. Traditionally not only have some nematode species been associated with particular soil textures (Jones et al., 1969; Bongers, 1988) but also it is also known that populations of some of the larger nematodes are markedly reduced by soil cultivation (Oostenbrink, 1964; Jones et al., 1969). In the past decade soil nematodes have been found, through their roles in regulating soil bacterial and fungal populations, to be intimately associated with the cycling of major nutrients in soils (Ingham et al., 1985) and a more positive view of the role of nematodes in soil processes has been adopted (Yeates, 1987).

There are thus apparently significant possibilities for the use of nematode populations and diversity as indicators of overall soil condition. This chapter brings together published information on nematode diversity, ecology and feeding relations in agroecosystems, outlines methods for assessing nematode species and functional groups, and analyses the nematode populations associated with various management practices in a range of agroecosystems.

2. Sampling and handling nematodes

Nematodes found in a soil sample reflect not only the field population at the time and depth of sampling but also the effects of sampling and extraction procedures. As nematode populations change during the growth of a crop it is desirable, for a particular programme, to standardize sampling on a stage of crop growth; this is often the seedbed or immediately after harvest. In grasslands, sampling in spring or autumn when climatic extremes have been ameliorated gives a comparable effect.

While the litter or organic horizons normally contain the greatest concentrations of nematodes and a 10 or 15 cm deep sample including the organic horizon is appropriate, in some situations (e.g., woody horticultural crops) samples to 30 cm soil depth may be preferred. In some situations specific populations may be undetectable in superficial samples but may be present in significant numbers at depth (e.g., *Paratylenchus* only below 40 cm in an Italian field (Geraert, 1965). Use of a soil corer not only ensures that all depths of the profile are equally represented in a sample but also, from knowledge of its diameter, the sample size can be calculated as a proportion of 1 m^2 and nematode counts converted to a m^2 basis if desired.

Active migration, elutriation, decanting plus sieving, and centrifugation are the four main types of methods used to extract vermiform nematodes from the soil. Variation in nematode size, shape and activity is such that each method has a differential effect on the actual genera extracted. Further, some methods are more efficient for certain soil types. Some studies have demonstrated extraction efficiencies as high as 90% but typical recoveries are more likely to be 30–60%. While major laboratories may be equipped with mechanised elutriators, active migration techniques are the most easily used and the ‘tray method’ of Whitehead and Hemming (1965), which represents an extreme modification of the basic ‘Baermann funnel’ has optimised many of the variables. To reduce operator bias and therefore obtain more uniform results, several methods combine elutriation (removing the mineral fraction) with a tissue or filter stage (removing organic material). Elutriation may be used prior to centrifugation to isolate slow-moving or previously fixed nematodes from large samples. Overviews of extraction techniques are given by Ayoub (1980), s’Jacob and van Bezooijen (1984), Zuckerman et al. (1985), Southey (1986), and Evans et al. (1993).

The principles of sampling soil for phyto-sanitary regulations applied to particular nematode species are well-known (Southey, 1978), but for broad ecological studies concerned with all the nematode species present in a field no protocols have been established. We suggest that a biologically adequate and statistically robust assessment of the nematode populations in a field can be obtained as follows:

1. Within the field select 10 areas, each broadly representative of variation in vegetation, soil and topography in the field as a whole; crop rows generally have a significant effect on all variables in the soil. If an organic layer is present it is often useful to sample it separately.
2. From each of these 10 areas collect a sample made up of five cores (approximately 25 mm in diameter and from 0–10 cm soil depth, but exact size is determined by the capacity of extraction apparatus). Keep soil samples out of direct sun in the field and for samples from temperate areas store them at about 4°C as soon as practical; for warmer areas the optimum storage temperature may be greater; weigh the sample so that the results may be expressed per 100 g moist soil if desired.
3. Extract the total sample (with gentle breaking up of soil aggregates but without intensive mixing or subsampling).
4. Under a dissecting microscope at about 50× magnification, count all the nematodes present in the extract while still alive.
5. Fix the nematodes by adding an equal volume of boiling 8% formaldehyde to the suspension (N.B. this chemical is hazardous and should be used in a fume cupboard).
6. Transfer a sample of the nematodes from each replicate to a slide and, using up to a 60× objective, allocate at least 100 specimens to species, genus, feeding or functional group.

3. Diversity of nematodes and nematode faunae

While the body form of soil nematodes is basically worm-like in all stages, the length of adult nematodes ranges from under 0.3 (*Bunonema*) to over 5 mm (*Longidorus*). The greatest apparent morphological diversity of nematodes can be seen in their head structures, which are closely related to particular feeding habits.

The most recent review of nematode feeding groups (Yeates et al., 1993a) accepted the following groups:

1. Plant feeding;
2. Fungal (hyphal) feeding;
3. Bacterial feeding;
4. Substrate ingestion (especially the ingestion of the substrate on which bacteria are growing);
5. Predation on protozoa and soil animals (rotifers, enchytraeids, other nematodes);
6. Unicellular eucaryote feeding (diatoms and other algae);
7. Dispersal stages of animal parasites, of both invertebrates and vertebrates (some may actually have a bacterial or fungal feeding reproductive cycle in the soil);
8. Omnivores (a combination of 1–6 above, but generally used mainly for dorylaimid nematodes).

Given this range of feeding types, the soil nematode fauna interacts with many other groups of soil organisms. The pathogenic effects of plant root feeding have already been mentioned. Fig. 1(A) illustrates the relationship between a population of predacious nematodes and one of their bacterial-feeding prey. Fig. 1(B) shows the impact of bacterial and fungal grazing by nematodes on plant growth via the cycling of plant nutrients.

The abundance and diversity of nematodes in various agroecosystems on four soils are given in Table 1. Populations in some soils reach almost 10 million m^{-2} and there are differences between management regimes on individual soil types. The

Table 1
Comparison of nematode abundance (number m^{-2} in 0–7.5, 0–10 or 0–20 cm soil) and generic diversity under various land uses on five soils[a]

Soil and land use	Nematode abundance	Nematode genera
England		
Ungrazed grassland	3,311,000	21
Regenerating woodland	2,376,000	19
Sweden		
Mown grassland	8,708,000	30
Lucerne	9,844,000	31
Unfertilized barley	5,584,000	29
Fertilized barley	6,777,000	30
New Zealand		
Grazed pasture	2,902,000	32
Oats/maize rotation	1,156,000	17
Wales		
Grassland on sandy soil		
Conventionally managed	3,702,000	30
Organically managed	4,515,000	32

[a] After Yuen (1966), Sohlenius et al. (1987), Yeates and Hughes (1990) and Yeates et al. (1997).

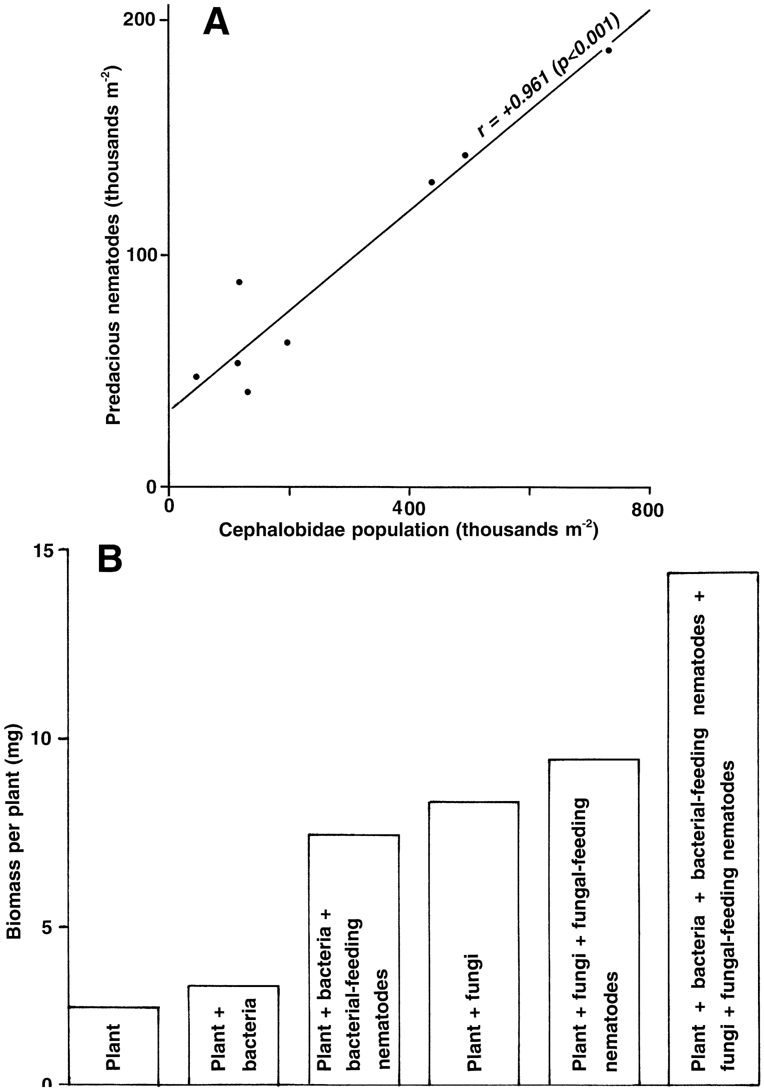

Fig. 1. (A) Relationship between predacious nematode populations in an asparagus agroecosystem on eight sampling occasions and populations of bacterial-feeding Cephalobidae at the previous sampling time (adapted from Wardle et al., 1995); (B) Effect of increasing food web diversity on shoot growth (over 40 days) of a plant (*Bouteloua gracilis*) in pots of a previously sterilized soil (adapted from Ingham et al., 1985).

greatest number of nematode species recorded from a terrestrial ecosystem is 154 from a chalk grassland in southern England (Hodda and Wanless, 1994). The specialised input required to compile such species lists means that most work is done at a less detailed level; for this reason practical identification is typically limited to genera with some distinctive species being separated.

4. Identification of nematodes

Traditionally only presumed plant-pathogenic nematodes in soil samples have been identified to species, and attempted identification of total nematode faunae is relatively recent. The classic work of Goodey (1963) is still the best for an overview of plant and soil nematodes. Maggenti (1981, 1991) gives a systematic coverage of all Nematoda, including animal parasitic and marine forms.

For tylenchids, keys to genus level are given by Siddiqi (1986), and in a series of papers concluding with Maggenti et al. (1988), the systematics of the Tylenchina are revised. Nickle (1991) provides more recent keys for the identification of plant-feeding tylenchids. Keys for plant-feeding dorylaimids (longidorids and trichodorids) and aphelenchids, a group resembling tylenchids, are given by Hunt (1993). Keys to genera of free-living, predacious and plant-feeding dorylaimids are given by Jairajpuri and Ahmad (1992). Andrássy (1984) provides keys to most species of terrestrial and freshwater nematodes which do not have a spear. Bongers (1988) gives keys to all soil and freshwater nematodes from The Netherlands. An introduction to nematodes from brackish and marine waters is given by Platt and Warwick (1983).

5. Measurement of nematode diversity

Nematodes are aquatic animals and must be able to move freely though water to feed and complete their life cycles. Thus in agroecosystems soil texture, soil moisture and the availability of suitable food are critical in determining the diversity of the nematode fauna. The nematode fauna comprises native species which have survived agricultural management, species which may have been introduced by human activity and species which have arrived by natural dispersion. Not only the climate-driven annual cycles of agriculture but also longer term cycles of land use influence the proportion of various nematode taxa which make up the nematode fauna at a particular time. As a sample from an agroecosystem may contain in excess of 50 nematode taxa in varying proportions, it is often necessary to summarise the complexity of the fauna in a single value or index.

5.1. General indices

Overviews of the application of general indices to nematodes have been given by Norton and Niblack (1991) and Bernard (1992). While the use of $\log_e$ is suggested below some workers prefer the use of $\log_2$. The basic information on identified specimens can be summarised as:

N, the number of individuals identified;
S, the number of taxa identified; a given taxon is regarded as the ith taxon;
p, the proportion of individuals in the ith taxon.

Basic indices which can be calculated are:

$$\text{diversity } H' = -\sum_{I=1}^{S} p_i \log_e p_i$$

$$\text{evenness } J' = \frac{H'}{H'_{\max}} \quad \text{where } H'_{\max} \text{ is } \log_e S$$

$$\text{richness SR} = \frac{S-1}{\log_e N}$$

$$\text{dominance } \lambda = \sum p_i^2$$

$$\text{diversity } H_2 = -\log_e \lambda$$

The Shannon–Wiener index H' is commonly used to assess *diversity* but as it may be dominated by abundant taxa or the overall number of taxa, both *evenness* and *richness* (Margalef index) are often calculated. The Simpson index (D) or its reciprocal ($\lambda = 1/D$)) can be used to assess *dominance* and its $\log_e$ transformation offers an alternative measure of *diversity* (H_2).

Great care must be taken when comparing values of indices between studies. In addition to differences in calculation, factors which affect index values include texture, seasonal patterns (e.g., migratory infective juveniles of Heteroderidae), vegetation type and rotation (via host specificity and litter quality), predator : prey interactions (e.g., reduction of prey by predators) and microsites (e.g., row and inter-row samples).

5.2. Nematode maturity indices

The nematode maturity index (MI) of Bongers (1990) was proposed as a gauge of the condition of the soil ecosystem. It is the weighted mean of the colonizer−persister (*c–p*) values for the non plant-feeding nematode taxa in a sample; the (*c–p*) values reflect the perceived position of taxa on an $r-K$ spectrum, based on their reproduction rate and correlated characteristics. For nematodes feeding on higher plants, the PPI (plant parasite index) was proposed. Based on effects of the geographic distribution of nematodes, nematode feeding types, soils and succession, Yeates (1994) argued that all nema-

Table 2
Nematode families with the *c–p* values which are used in calculating the maturity index (MI) and related values (PPI, ΣMI). Includes changes proposed by Bongers et al. (1995)

Family	*c–p* value
Alaimidae	4
Aphelenchidae	2
Aphelenchoididae	2
Anguinidae	2[a]
Aporcelaimidae	5
Bastianiidae	3
Belondiridae	5
Bunonematidae	1
Cephalobidae	2
Chromadoridae	3
Criconematidae	3[a]
Diphtherophoridae	3
Diplogasteridae	1
Dolichodoridae	3[a]
Hemicycliophoridae	3[a]
Hoplolaimidae	3[a]
Leptonchidae	4
Longidoridae	5[a]
Monhysteridae	2
Mononchidae	4
Nordiidae	4
Panagrolaimidae	1
Paratylenchidae	2[a]
Plectidae	2
Pratylenchidae	3[a]
Prismatolaimidae	3
Qudsianematidae	4
Rhabditidae	1
Teratocephalidae	3
Thornenematidae	5
Tobrilidae	3
Trichodoridae	4[a]
Tripylidae	3
Tylenchidae	2[a]

[a] Values for families which should be included in the PPI rather than the MI.

todes should be included in a summed maturity index (ΣMI). Bongers et al. (1995) demonstrated that under certain conditions the PPI and MI behave in opposite manners and suggested that an increase in the PPI/MI ratio might reflect ecosystem enrichment. Table 2 lists nematode families with the presently accepted $c\text{–}p$ values and indicates those which should be included in the PPI rather than the MI.

The general equation for calculating these indices is

$$\text{maturity index} = \sum_{i=1}^{n} c\text{–}p\, i \cdot p\, i$$

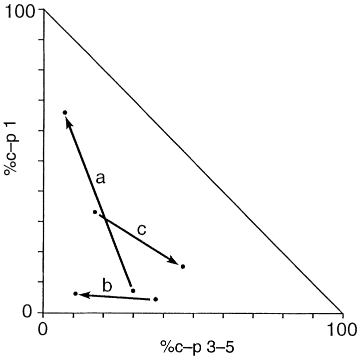

Fig. 2. $c\text{–}p$ triangle showing shifts during (a) eutrophication, initial situation and 2 weeks after adding powdered cow-dung (Ettema and Bongers, 1993); (b) artificial acidification of coniferous forest soil (Hyvönen and Persson, 1990) and c) recovery, 33 and 44 weeks after organic manuring (Ettema and Bongers, 1993). (After Bongers et al., 1995).

where *c–p* is the *c–p* value (Table 2), *p* is the proportion of individuals in the *i*th taxon and *n* is the number of taxa in the sample.

For graphical presentation of changes in the nematode fauna, de Goede et al. (1993) proposed combining $c\text{–}p$ groups 3–5 and plotting $c\text{–}p = 1$, $c\text{–}p = 2$ and $c\text{–}p = (3\text{–}5)$ as a triangle. The alternative plot given in Fig. 2 omits $c\text{–}p = 2$ and enrichment is expressed by a shift to the upper left, stress to the lower left and natural succession or recovery to the right. Analysis of data for a given series of treatment or succession sites may allow interpretation of patterns in the nematode fauna due to change over time or recovery following ecosystem disturbance.

To measure heavy metal-induced stress, where microbial activity differs between samples, it may be advantageous to omit the enrichment opportunists (scaled $c\text{–}p = 1$) and to present the MI as MI(2–5). In Fig. 3 the effect of copper and pH on the MI(2–5) of the nematode fauna of a Dutch arable agroecosystem is presented.

5.3. Functional groups

As the soil biota play critical roles in controlling the mineralization of nutrients for plant growth, studies are made of various ‘functional groups’ of soil organisms in an effort to understand soil processes and perhaps identify key stages. This can be contrasted to the historic interest in essentially only one functional group

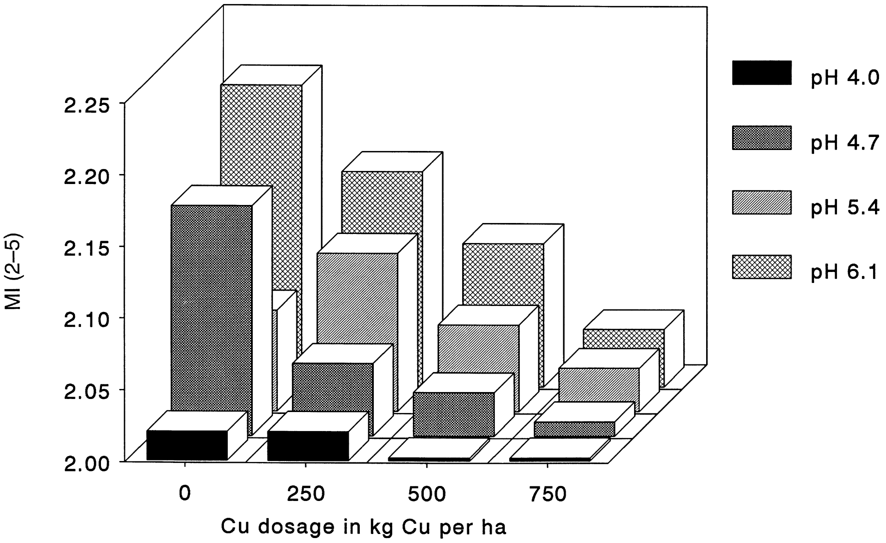

Fig. 3. Influence of copper and pH on the nematode maturity index (MI) for *c–p* groups 2–5 in a maize agroecosystem, 10 years after application of copper and adjustment of pH; each column represents eight replicates (after Korthals et al., 1993).

(i.e., plant pathogens). The accepted feeding groups of plant and soil nematodes have been given above (Section 3). However, many nematodes are allocated to these groups on the basis of inadequate evidence, and as many species have various food sources, ideally the feeding activity of each species in each particular soil: crop: management: climate combination should be quantified.

Various workers have calculated ratios of nematode feeding groups in diverse agroecosystems and some of their results are discussed below. The use of 'indicator species', of whatever feeding group, reflects the functional group approach.

6. Grassland nematodes

Grasslands of various types are found in agricultural regions and, given (a) their relative uniformity of sward cover and (b) soil exploitation by roots, (c) their vegetative cover throughout the year and (d) their lack of cultivation, grasslands at least 3 years old are probably the best bench-mark vegetation or land use for each soil type in a given region. As with any multi-species plant community, grasslands are patchy. Despite the difficulty in observing nematode damage, significant loss of productivity due to nematode activity has been recorded (Cook and Yeates, 1993). Hodda and Wanless (1994) have recently reported 154 nematode species, belonging to a range of feeding groups, from a natural English chalk grassland. Such diversity means that simple effects of soil and management can often be demonstrated in long-term grasslands. In young pastures nematodes will not be in equilibrium with local conditions (e.g., Wasilewska, 1994). In long-term grasslands the seasonal changes in nematode populations are such that averages over several sampling times are of more value than results from single sampling events.

An intensive New Zealand study showed the greater importance of the soil rather than month, year or management practices in determining the composition of the nematode fauna (Fig. 4). Diversity (H'), evenness (J'), and richness (SR) of the nematode fauna were all greatest in Rotoiti soil, the youngest, most texturally heterogeneous soil (Table 3). Texture itself is important in affecting the movement, feeding and reproduction of all nematodes; however, at present we are uncertain whether the mineralogy of the soil, in addition to its effect on plant growth and microbial activity, has a direct effect on the nematode fauna.

A textural effect is apparent in nematode populations from a series of moist soils in Wales (Table 4). Species richness (SR), the maturity index (MI), and

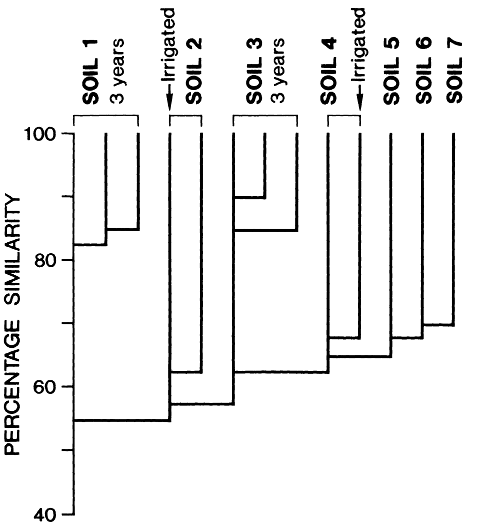

Fig. 4. Similarity dendrogram for nematode faunae in 0–10 cm soil below grazed pastures on seven New Zealand soil types. Each line represents monthly samples for a year; soils 1 and 3 were each sampled for 3 years; soils 2 and 4 were taken from both dryland and irrigated sites (adapted from Yeates, 1984).

Table 3
Indices of diversity (H'), evenness (J') and richness (SR) for nematode genera in New Zealand permanent pastures on seven soil types; each value is an annual one computed from 12 monthly samples (adapted from Yeates, 1984)

Soil	Diversity	Evenness	Richness
Judgeford	2.57	0.76	3.90
Pomare	2.51	0.74	4.01
Kaitoke			
Year 1	2.14	0.64	3.89
Year 2	2.37	0.69	3.92
Year 3	2.20	0.65	3.86
Otiake			
Dryland	2.04	0.62	3.62
Irrigated	1.95	0.60	3.48
Rotoiti	2.74	0.78	4.69
Tokomaru			
Dryland	2.48	0.73	3.61
Effluent irrigated	2.67	0.76	3.93
Kokotau			
Year 1	2.22	0.67	3.52
Year 2	2.22	0.68	3.47
Year 3	2.24	0.73	2.60

summed maturity index (ΣMI) were all greatest in the coarsest soil. The changes in MI and ΣMI reflect the increasing contribution to the nematode fauna by larger, omnivorous nematodes which have greater *c–p* values (Table 4). In addition to the effect of texture on the nematode fauna there was also a marked effect of pasture management at each texture. In each of the three soils there was a greater abundance of the fungal-feeding nematodes under organically managed grassland than under conventionally managed grassland (Table 4). A comparison of the nematode faunae under pasture on two soils in South Australia showed the maturity index to be similar in both soils despite differences in texture (Table 5). That the maturity index did not show the same trend as in the moist Welsh soils may reflect the lower proportion of omnivorous Dorylaimida and higher proportion of plant-feeding taxa in the drier South Australian soil. Thus it seems that in these agroecosystems the soil moisture regime affects the impact of texture on the nematode fauna.

Table 6 summarises nematode faunae in a climosequence of soils with increasing altitude from uniform parent material under tussock grassland and supporting appropriate management. Total nematode populations declined significantly ($p < 0.05$); this trend was present at all three depths sampled. As both soil pH and plant-available phosphorus declined with altitude ($p < 0.05$, $p < 0.05$, respectively) there were positive correlations ($p < 0.01$, $p < 0.01$) between total nematodes and pH and phosphorus. In this situation both of these soil chemical parameters parallelled plant growth. Nematode taxa increased with altitude but the increase was significant only for 8–12 cm soil depth. The proportion of fungal-feeding nematodes declined with both altitude and precipitation ($p < 0.1$, $p < 0.1$) (Table 6). Plant-associated nematodes had the opposite trend ($p < 0.1$, $p < 0.05$). Bacterial feeders decreased ($p < 0.01$) and omnivores increased ($p < 0.01$) with precipitation. Table 6 refers to semi-natural grasslands but most grasslands under agricultural management represent marked changes from natural vegetation. Changes in the nematodes of Polish fens 100 years after their clearance, drainage and development into meadows are given in Table 7. In no case was there a decrease in the number of genera present following development, and in every case a substantial increase (1.4–41 ×) in total nematode abundance was noted.

Table 4
Mean values of selected indices and populations for three Welsh grasslands with differing soil textures; based on nematode genera; texture values are means for two management regimes; management regime values are averaged over soil textures[a]

	Soil texture			Management regime	
	Fine silty	Coarse loamy	Sand	Conventional	Organic
Species richness (SR)	5.00	5.40	5.78^{**}	5.32	5.47ns
Diversity (H’)	0.65	0.69	0.68ns	0.63	0.72^{b}
Maturity indices					
ΣMI	2.40	2.43	2.61^{***}	2.45	2.52ns
MI	2.30	2.27	2.77^{***}	2.38	2.51^{b}
PPI	2.46	2.58	2.46^{*}	2.49	2.52ns
Omnivorous nematodes (thousands m^{-2})	89	149	266^{***}	147	189ns
Fungal-feeding nematodes (thousands m^{-2})	429	297	516^{**}	259	570***

[a] Significance of effects (^{b} $p<0.1$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$) is based on analysis of variance of arithmetic data (Yeates et al., 1997).

Table 5
Mean diversity (H') (based on nematode genera) and maturity (MI) under three cultivation regimes on silty loam (Kapunda) and sandy loam (Avon) soils in South Australia (adapted from Yeates and Bird, 1994)

	Diversity index (H')		Maturity index (MI)	
	Silty soil	Sandy soil	Silty soil	Sandy soil
Pasture	1.97	2.36	2.34	2.33
Direct drilled wheat	1.86	1.85	2.09	2.20
Conventionally cultivated wheat	1.51	1.94	1.87	2.05

Table 6
Site characteristics and nematode faunae in six soils under grassland (*Festuca* or *Chionochloa* dominated) soils forming a climosequence in New Zealand; soil textures were sandy loam to fine sandy loam (adapted from Molloy and Blakemore, 1974; Yeates, 1974)

Soil	Altitude (m asl)	Precipitation (mm per year)	Soil phosphate (0.5 M H_2SO_4)	Soil pH	Nematode species (No.)	Total nematodes (/50 g soil)	Nematode feeding groups (%)					
							Fungal-feeding	Bacterial-feeding	Preda-cious	Plant-feeding	Plant associated	Omni-vorous
Conroy	300	350	66	6.4	18	4195	13	26	0	30	20	10
Cluden	450	600	45	6.0	27	3105	8	49	1	17	13	12
Tawhiti	900	850	19	4.9	27	1107	13	47	2	12	16	10
Carrick	1300	1300	17	5.0	35	781	7	37	4	6	30	15
McKerrow	1300	5000	5	4.4	32	412	1	16	3	18	40	21
Obelisk	1500	1600	19	5.0	24	120	1	20	22	24	28	5

Table 7
Comparison of the composition of the nematode faunae in 0–25 cm soil under natural vegetation and managed grassland on three soils in Poland (adapted from Wasilewska, 1991)

Vegetation	Nematode genera	Total nematodes (thousands m^{-2})	Nematodes in feeding groups (%)				
			Bacterial-feeding	Fungal-feeding	Plant-pathogenic	Plant associated	Predacious + omnivorous
Sedge/moss fen	35	3939	62	14	2	17	5
Meadow	39	6208	49	13	11	22	5
Sedge fen	47	1064	59	6	14	15	6
Meadow	47	6676	42	9	25	17	7
Alder fen	22	251	80	6	7	1	6
Meadow	35	10400	78	1	15	5	1

Table 8
Vertical distribution of total nematodes (thousands m^{-2}) and genera in the upper 90 cm of soil under three grassland swards on Horotiu sandy loam (adapted from Yeates et al., 1983a)

Soil depth (cm)	*Dactylis glomerata*		*Lolium perenne* cv. Nui		*L. perenne* cv. Nui + *Trifolium repens*	
	Abundance	Genera	Abundance	Genera	Abundance	Genera
0–10	4750	14	1306	9	6400	20
10–20	331	6	34	8	77	5
20–30	212	4	37	5	160	4
30–40	44	5	44	5	40	4
40–50	10	4	100	3	308	1
50–60	9	3	74	4	244	3
60–70	2	2	12	4	4	2
70–80	6	5	2	3	n.d.	n.d.
80–90	1	1	1	1	n.d.	n.d.
Total	5365	14	1610	14	7133	23

In every case there was a substantial (1.8–5.5 ×) increase in the proportion of plant-feeding nematodes found in the meadows. While the proportion of bacterial-feeding nematodes declined, albeit slightly at the third site, there were still more bacterial-feeding nematodes under meadows than under fens. Comparisons of nematodes under forests and grasslands in England and New Zealand have shown a greater proportion of plant-feeding species in grasslands, and in contrast, a greater proportion of bacterial-feeding taxa under forest (Yuen, 1966; Egunjobi, 1971).

As plant-feeding nematodes dominate nematode faunae under grasslands, changing the composition of the grassland sward will have direct effects on host-specific plant-feeding nematodes and indirect effects on members of other feeding groups. Taxonomic diversity may differ at depth (Table 8), reflecting fertility, moisture, texture, and rooting resistance of successive soil layers which are integrated in the rooting pattern of the plant species. In Table 8 it can be seen that more nematode genera were found under the mixed sward than in either of the single-species swards. Similarly, Wasilewska (1995) found values for both diversity (H') and maturity (MI) indices to be higher under a mixed species grass sward than under a cocksfoot (*Dactylis glomerata*) monoculture. Root lesion nematode, *Pratylenchus*, was markedly more abundant in the monoculture. The diversity of nematode faunae is not solely governed by the type of grass. Management plays an important role. Sohlenius and Sandor (1987) found that whereas under a 3-year old perennial grass (*Festuca pratensis*) ley there were 7,600,000 nematodes m^{-2} dominated by bacterial-feeding forms, under a different member of the Gramineae (annual barley, *Hordeum distichum*) there were only 5,000,000 m^{-2} dominated by plant-feeding forms.

While soil texture has a major impact on nematode diversity under grasslands, there are also management effects on a given soil via plant species, irrigation, pesticide, and fertilizer application. The dominant taxa under various plant species on a sandy loam varied markedly (Table 9). Of the nine genera contributing $\geq$10% under the seven grass species, four lacked spears and none were known plant pathogens. In the two irrigation studies there was an increase in the proportion of omnivorous or bacterial-feeding nematodes (Table 9). After pesticide application on two soils there was an increase in the proportion of bacterial-feeding nematodes (Table 9).

Increasing the intensity of grassland management is usually intended to increase plant production. This implies not only a greater plant resource for plant-feeding nematodes but also larger populations of bacterial-feeding nematodes, which contribute to nutrient cycling and larger populations of predacious nematodes to feed on them. In one case on a silt loam it was found that increasing superphosphate (containing approximately 10% phosphorus) application from 12.5 to 50 kg ha^{-1} was associated with an increase in root lesion nematodes (*Pratylenchus*) from 27,800 to 106,000 m^{-2} ($p < 0.001$) and in predacious Mononchidae from 11,300 to 16,000 m^{-2} ($p < 0.001$) (Yeates, 1976); for *Pratylenchus* this represented an increase from 1.75 to 5.9% of the nematode fauna.

Table 9
Dominant nematode genera (≥10% in 0–10 cm soil) under pastures with differing management regimes on four New Zealand soils[a]

Variable	Soil	Treatment	Dominant nematode taxa (%)
Plant species	Horotiu sandy loam	*Lolium x hybridum*	*Pungentus* 15, *Dorylaimellus* 14, *Aporcelaimus* 13
		Agrostis tenuis	Rhabditidae 36, *Pungentus* 12, *Eudorylaimus* 11
		Bromus willdenowii	Rhabditidae 19, *Tylenchus* 14, *Panagrolaimus* 11, *Cephalobus* 10
		Dactylis glomerata	*Pungentus* 17, *Dorylaimellus* 10
		Paspalum dilatatum	*Tylenchus* 19, *Prismatolaimus* 11
		Phalaris aquatica	Rhabditidae 40, *Aporcelaimus* 16
		Festuca arundinacea	Rhabditidae 37, *Tylenchus* 11
Irrigation	Otiake silt loam	Dryland pasture	*Tylenchus* 26, *Paratylenchus* 26
		Irrigated pasture	*Paratylenchus* 35, Rhabditidae 16, *Pratylenchus* 11
	Tokomaru silt loam	Dryland pasture	*Cephalobus* 14, *Pungentus* 13, *Tylenchus* 12
		Effluent irrigated pasture	*Tylenchus* 15, *Heterocephalobus* 10, *Aporcelaimus* 10
Pesticide	Horotiu gravelly loam	*Lolium perenne* cv. Nui control sward	*Paratylenchus* 16, Rhabditidae 8
		cv. Nui + oxamyl	Rhabditidae 20, *Paratylenchus* 10
	Atiamuri gravelly sand	*Lolium perenne* control sward	*Paratylenchus* 61
		L. perenne + oxamyl	*Paratylenchus* 66, *Aporcelaimus* 14, *Panagrolaimus* 11, *Cephalobus* 11

[a] Adapted from Yeates et al., 1983b; Yeates and Barker, 1986; Yeates and Prestidge, 1986.

In grasslands there are clear relationships between the diversity of nematodes and soil texture, climate, plant species, pesticides, and management practices.

7. Nematodes in managed forest ecosystems

Forest agroecosystems, even more than grasslands, provide long-term freedom from human interference. While many studies have concerned possible economic loss through pathogenic response to nematodes, particularly in forest nurseries (Sutherland and Webster, 1993), there also have been general ecological investigations, and more recent, studies of developmental sequences in managed forests. Estimates of species diversity include 79 for a Danish *Fagus sylvatica* forest (Yeates, 1972), 92 for a Slovakian oak-hornbeam forest (Šály, 1975) and 106 from a *Picea abies* stand in south-west Germany (Ruess, 1995a).

Forest soils have differing quantities and qualities of organic material above the mineral soil; the various organic mineral horizons have distinct physical, chemical and biological properties. From the composition of the nematode faunae in Table 10, which have been calculated as far as possible for the organic layers plus the upper 10 cm of mineral soil, it is clear that bacterial-feeding nematodes were the numerically dominant group. The difficulty in allocating many spear-bearing nematodes to feeding groups probably explains why the contribution of fungal-feeding and plant-associated forms varied between these managed forests. The contribution of predacious and plant-feeding nematodes was consistently low (Table 10).

The nature and amount of organic material strongly affect nematodes and usually influence the overall composition of the nematode fauna. Detailed studies consider the properties and populations of the various depths separately and should be consulted for details (Yeates, 1973; Arpin and Ponge, 1986; de Goede and Dekker, 1993; Ruess, 1995b). For the upper 8 cm of forest floor material under *Picea abies*, Ruess (1995b) found 92% of nematodes to be in the upper 4 cm. Furthermore, Arpin et al. (1988) demonstrated that in forest litter dimensions of adults of *Clarkus papillatus* not only varied seasonally but also different humus types contained populations with distinct dimensions.

Forest management practices impact on nematodes. Clear-felling of Scots pine in Sweden was followed by an increase in both nematode and microbial populations (Sohlenius, 1982). If litter was removed there was no increase in populations. Although nematode groups were not identified in this study, it is clear that the populations were important in nitrogen dynamics in the agroecosystem.

Table 10
The contribution of feeding groups to the nematode faunae of various forest soils; as far as possible the figures represent the organic layers plus the upper 10 cm of mineral soil

Country and reference	Denmark (Yeates, 1973)	France (Arpin and Ponge, 1986)			The Netherlands (de Goede and Dekker, 1993)		New Zealand (Yeates, 1995)
Forest type	*Fagus sylvatica* org + 6 cm	*Quercus petraea* 10 cm	*Pinus sylvestris* 10 cm	*Q. petraea* + *P. sylvestris* 10 cm	*Pinus sylvestris* organic	10 cm	*Pinus radiata* org + 10 cm
Nematode group							
% bacterial feeders	36	42	42	41	57	43	43
% fungal feeders	26	10	10	14	32	42	23
% predators	4	3	2	<1	0	0	1
% plant feeding	5	4	5	<1	0	<1	2
% plant associated	23	32	35	39	9	13	8
% omnivores	6	9	2	<1	2	<1	23
Total nematodes	$1.4 \times 10^6\ \mathrm{m}^{-2}$	$1.5 \times 10^6\ \mathrm{m}^{-2}$	$1.7 \times 10^6\ \mathrm{m}^{-2}$	$1.2 \times 10^6\ \mathrm{m}^{-2}$	$10.5 \times 10^3\ 100\ \mathrm{g}^{-1}$	$1.3 \times 10^3\ 100\ \mathrm{g}^{-1}$	$1.89 \times 10^6\ \mathrm{m}^{-2}$

Table 11
Nematode populations 4 years after lime application to a *Pinus sylvestris* plantation in The Netherlands[a]

	Organic layers		Mineral soil	
	Control	+ Lime	Control	+ Lime
Total nematode ($100\ \mathrm{g}^{-1}$soil)	18480	13520*	1290	1530
Feeding groups				
% bacterial-feeding	55.7	58.8	43.0	55.2**
% fungal-feeding	32.2	30.1	41.4	35.2
% plant-feeding	9.3	7.2	12.9	6.9
% omnivores	2.2	2.6	0.5	1.2*
Maturity Index (MI)	2.06	2.01	2.13	2.09
% Class Secernentea	66.4	72.2**	80.9	76.6
% Order Rhabditida	25.9	36.3**	30.9	42.5*

[a] Significance of effect of lime application is denoted by * $p < 0.05$, ** $p < 0.01$ (after de Goede and Dekker, 1993).

In a 20–25-year old Scots pine (*Pinus sylvestris*) forest in central Sweden, application of fertilizers with or without irrigation depressed the abundance of fungal-feeding and omnivorous nematodes (Sohlenius and Wasilewska, 1984). The bacterial-feeding functional group, on the other hand, seemed to be favoured when fertilization and irrigation were combined. Similar results were also reported by Bassus (1967) and Hyvönen and Huhta (1989). Nematode population responses to liming of a *Pinus sylvestris* plantation in The Netherlands are summarised in Table 11. The contribution of Secernentea, in particular bacterial-feeding Rhabditida, was significantly greater in the organic layer following liming, despite a decrease in total nematodes. In the mineral soil, both bacterial-feeding nematodes and Rhabditida were significantly increased after liming. While there were no marked changes in the Maturity Index (Table 11) *c–p* triangles can be used to demonstrate changes over time in the composition of the nematode fauna in this and other forest management situations (de Goede and Dekker, 1993).

Bacterial-feeding nematodes are generally dominant in forests. Their populations, concentrated in the surface organic horizons, are very responsive to impacts of forest management activities.

8. Impact of other agroecosystems and management practices

Under cropping and horticultural regimes there is regular disturbance of soil, soil fauna and plant cover. No equilibrium is established between the various components. The study of Freckman and Ettema (1993) addressed the impact of differing de-

Table 12
Nematode populations found in April (pre-cultivation) sampling of eight ecosystems on a fine loamy soil in Michigan with varying degrees of human intervention (adapted from Freckman and Ettema, 1993)

Treatment	Total nematodes (thousands kg^{-1} in 0–10 cm soil)	% in feeding groups					
		Plant-feeding	Bacterial-feeding	Fungal-feeding	Algal-feeding	Predacious	Omnivorous
Ploughed corn/soybean rotation	11.9	25.8	43.0	26.6	0.8	2.0	2.0
No till corn/soybean rotation	12.2	31.4	39.4	23.9	1.8	0.7	2.7
Low input corn/soybean rotation	9.6	22.2	48.4	23.5	1.7	1.4	3.0
Zero input corn/soybean rotation	10.6	21.1	52.3	21.0	0.8	1.2	2.9
Woody biomass, trees, *Populus*	4.1	26.6	43.2	22.9	2.9	2.3	2.0
Herbaceous biomass, *Medicago*	5.1	33.1	39.4	18.2	1.5	3.5	4.3
Previously tilled but abandoned for 3 years	9.3	30.3	34.9	24.1	2.6	3.8	4.3
Never tilled but mown annually	5.2	20.9	41.9	28.6	3.1	1.3	4.3

grees of human intervention on the nematode fauna in a single soil in Michigan (Table 12). While the greatest nematode populations were found in the four annual rotations, bacterial-feeding nematodes represented the predominant feeding group of nematodes in every ecosystem. In four of the agroecosystems plant-feeding nematodes were the second most important group and in the never-tilled treatment fungal-feeders ranked second. The sum of the relatively large predacious and omnivorous nematodes was $\geq$5.6% in the three least disturbed, perennial systems. It does appear that sampling in spring, before cultivation, resulted in relatively high populations of bacterial-feeding nematodes, and that the full impact of the differing regimes had been obscured. At the end of the growing season much larger populations of plant-feeding nematodes would probably have been found. This strong seasonal trend of plant-feeding nematodes in cropped systems is acknowledged in basing nematode control strategies on pre-sowing populations and basing population dynamics in the changes in specific populations over the growing season (P_f/P_i) (e.g., McSorley and Phillips, 1993). We have already summarised a study of variation in diversity (H') and maturity (MI) in Table 5; it should be noted that many of the results we have adapted from Yeates and Bird (1994) are means of three dates during the growing season. Changes over time must be considered in any study of nematodes in agroecosystems; the use of *c–p* triangles (de Goede et al., 1993) may be a useful tool for demonstrating this (Fig. 2).

The diversity values (H') for genera under grazed pasture in Table 3 can be compared with values of 4.0–4.9 for genera in grasslands, 3.2–4.3 for forests and 3.1–4.2 in crop-field systems in Poland (Wasilewska, 1979). The values of 0.7–1.3 reported for four seral stages (meadow, *Populus*, *Abies*, *Picea*) in Utah by Bennett and Vetter (1980) apparently represent a quite different approach. Ten years of double-cropping an old pasture with oats and maize reduced the number of genera found from 18 to 14 (Yeates and Hughes, 1990); similar trends can be seen in values for diversity and maturity indices in two South Australian soils (Table 5).

The decrease in diversity of nematode faunae with increasing level of management reflects not only physical disturbance and change in the quantity and quality of organic matter being returned to the soil, but also possible increases in specific plant-feeding nematodes associated with crops. This is dramatically illustrated by results from Utah, in which 89–94% of the nematodes in a sample from a sugar-beet field consisted of the various developmental stages of the beet cyst nematode *Heterodera schachtii* (Thorne, 1927). Similar trends can be seen in results of Yeates and Bird (1994) in which the transition from semi-natural shrubland through introduced grassland to wheat was reflected in the contribution of plant feeding nematodes being 3, 47, 49% and 3, 45, 51% of the nematode fauna in soils of two different textures. Generally, soils with annual arable crops contain fewer nematode species than do grasslands, where up to 154 species have been recorded (Hodda and Wanless, 1994).

Burial of plant material during cultivation provides resources for microbial-feeding nematodes, whose populations may exceed 3000 g^{-1} dry matter (Sohle-

Table 13
Average biomass (kg C ha^{-1}, 0–25 cm soil) of nematode feeding groups and total nematodes during three growing seasons (winter wheat, sugar beet, winter wheat) in Dutch arable fields[a]

	Conventional management			Integrated management		
	1986	1987	1990	1986	1987	1990
Bacterivores	0.613	0.121	0.218	0.587	0.362	0.336
Fungivores	0.035	0.025	0.078	0.033	0.030	0.012
Herbivores	0.042	0.009	0.179	0.209	0.153	0.334
Omnivores/predators	0.201	0.111	0.053	0.383	0.368	0.056
Total nematodes	0.891	0.266	0.528	1.212	0.913	0.738

[a] Fields received either conventional management and inputs or integrated management with higher organic returns and lower agrochemical and tillage inputs (adapted from Bouwman and Zwart, 1994).

nius and Boström, 1984). Initially the populations tend to be dominated by bacterial-feeding genera of the Rhabditidae, Cephalobidae, and Panagrolaimidae, with fungal-feeding Aphelenchidae contributing during later stages of decomposition. Such pockets of plant and animal residues occur in the field but, unless they are specifically sampled their effect is diluted during 'whole soil' sampling. Similarly, the concentration of biological activity on the rhizosphere of plant roots (e.g., Hofman and s'Jacob, 1989; Griffiths, 1990) is usually diluted during sampling. Studies of the rhizosphere of peas, barley, grass and turnips showed that the biomass of microbial-feeding nematodes exceeded that of protozoa (Griffiths, 1990) and led to the conclusion that nematodes were more important than protozoa in terms of nutrient cycling. Given differences found between the plants, it is apparent that plant species affects not only specific plant-feeding nematodes but also the contribution of the microbial-feeding nematodes to the nematode fauna.

Application of farm management philosophy affects soil processes. In a Dutch study, arable fields receiving lower agrochemical and tillage inputs ('integrated management') consistently had increased total nematode biomass (Table 13). The greatest increase was in herbivores, but omnivore/predators were also always greater under integrated management. The proportion of, and generally the number of, fungivores was lower under this regime. However, at 40–69% bacterivores comprised the dominant feeding group. A similar dominance of bacterivores was reported in Swedish arable cropping studies by Hansson et al. (1990) and can be related to bacterial populations under the two management regimes. The increase in omnivores/predators probably reflects the reduced tillage under integrated management.

Table 14
Diversity (H') and maturity (MI) for nematode genera found in rows and between rows of soybean (*Gylcine max*) at different times after sowing (adapted from McSorley and Frederick, 1996)[a]

Index Position	Diversity (H')		Maturity (MI)	
	Row	Inter-row	Row	Inter-row
5 June (planting)	2.28	2.37	2.00	2.00
14 July	2.52	2.31	2.11	2.05[b]
20 August	2.13	2.52*	2.07	2.14
1 October	2.25	2.45	1.97	2.04

[a] Significance of differences between positions at a given sampling time are denoted by [b] $p < 0.1$, * $p < 0.05$.

Under maize, Norton and Oard (1981) found diversity to vary significantly with position on the slope. Values for H' were generally greatest on the backslope and lowest on the shoulder; this variation partly reflected soil properties in the toposequence. In a study of a soybean field in Florida significant differences in diversity (H'), evenness (J'), and richness (SR) indicated changes in the composition of the nematode fauna during the second part of the growing season (Table 14). Norton and Edwards (1988) have plotted changes in H' and J' for the six plant-pathogenic nematodes affecting maize in the 140 days after planting in Iowa. Yeates and Bird (1994) found marked changes in total diversity and maturity index values under conventionally cultivated wheat in a silty loam in South Australia in 3 successive months (1.59, 1.25, 1.70 and 1.90, 1.67, 2.04, respectively); the indices varied to a similar degree under pasture. Clearly, temporal and spatial factors must be taken into account when considering nematode diversity in agroecosystems.

In Section 7 it was found that, for a given soil, nematode faunae of forests typically have more bacterial-feeding nematodes than plant feeders (Table 10); in perennial grasslands the two groups are often similar in abundance (Tables 6 and 7). Under cropping in some situations plant-feeding nematodes may predominate (Thorne, 1927; Sohlenius and Sandor, 1987; Yeates and Bird, 1994) but in other situations microbial feeders may predominate (Tables 12 and 13). Although buildup of plant pathogens may contribute to these differences, seasonal changes are such that the single sampling times on which such data are often based do not reflect average annual populations or, perhaps more importantly, average annual contributions to soil processes.

Most of the work discussed so far has been based on superficial soil samples. On woody plants nematodes probably extend as far into the soil as do roots. *Tylenchulus semipenetrans* may occur on citrus roots to 2.44 m, *Radopholus similis* on citrus may occur down to 3.66 m (Wallace, 1963). In experiments carried out using an underground observation chamber, *Trichodorus viruliferus* has been observed migrating through soil with extending apple roots (Pitcher, 1967). In arable and ley situations where populations of *Longidorus leptocephalus* above a soil depth of 30 cm did not exceed 15 l^{-1} soil, Evans (1978) found populations in 30–60 cm soil as great as 250 l^{-1} associated with significant yield depression. Populations of *Paratrichodorus teres* around roots of unhealthy sugar beet were 3520 l^{-1} soil at 5–10 cm soil depth and were 760 l^{-1} at 45–50 cm depth (Kuiper and Loof, 1962). *Meloidogyne* may occur as deep as 1.5 m in soils (Koen, 1966) and there is debate as to the relative contributions of migration and differential reproduction to changes in this nematode's vertical distribution during the year.

Indices show clear changes in the composition of the nematode fauna of agroecosystems according to management practices. While cultivation, plant species and agrochemicals can all be shown to have effects most such effects are indirect, arising from changes in the quantity and quality of plant inputs to the soil. An in vitro suppression of egg hatching in *Heterodera glycines* has been found with one of eight herbicides tested (Wong et al., 1993) and direct-applied agrochemicals.

Šály (1989) suggested that soil nematodes could serve as bioindicators of soil condition following long-term, routine application of five herbicides to a vineyard. However, the results again show seasonal differences in the response of the nematode fauna (Table 15), and without information on the effectiveness of the control (i.e., was there growth of weeds that then affected soil processes in some treatments?) it is difficult to interpret such results. A comparison of physical and chemical weed control measures on fallow ground showed that, in comparison with 0–10 cm of adjacent pasture with 1,174,000 nematodes m^{-2} of 24 taxa, nematode diversity in the weed control plots declined to 5–8 species and the population to 14,000–225,000 m^{-2} (Yeates et al., 1976). Recent work has utilized the impacts of weed control measures on agroecosystems to investigate the interactions between nematode and microbial populations and a range of ecosystem processes (Yeates et al., 1993b; Wardle et al., 1995).

Table 15
Relative nematode population densities, on two sampling dates, in 0–20 cm soil in a Slovak vineyard after treatment with herbicides for 4–8 years (adapted from Šály, 1989)

Herbicide treatment	Month of sampling	
	April	September
Control	100	100
Semperol	62.2	64.5
Prefix G	224.3	22.5
Herbex	50.0	29.0
Caragard Combi	33.7	27.4
Ustinex Spezial	71.6	4.8

9. Nematodes in polluted ecosystems

9.1. Air-borne pollutants

The following examples show the effects of various air-borne pollutants in ecosystems of increasing diversity

In mosses collected in the Po River plain (Italy), Zullini and Peretti (1986) found significant declines in the number of nematode species and in the diversity of the nematode fauna inhabiting mosses with increasing Pb pollution (Fig. 5). Although the absolute number of nematodes did not decrease, there was a decline in the proportion of the relatively large Dorylaimida, thus reducing nematode biomass.

Tamis (1986) studied the effect of the deposition of ammonia discharged from a poultry farm on the

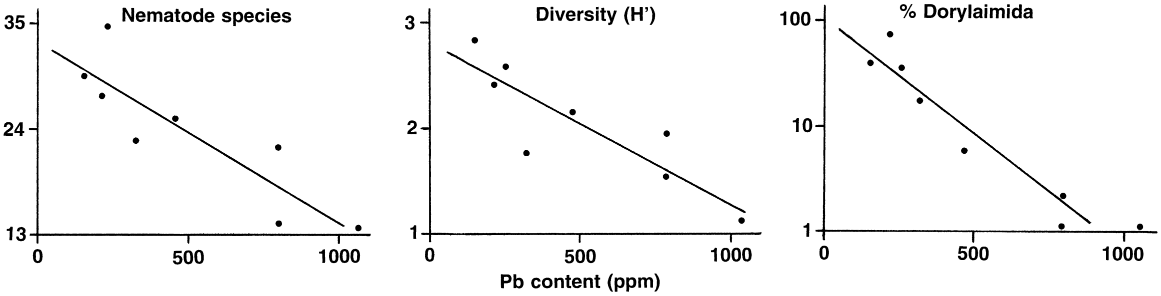

Fig. 5. Effect of increasing aerial pollution with lead on nematode species, diversity (H', calculated using $\log_2$) and proportion of Dorylaimida in the nematode fauna of clumps of moss with the indicated lead contents (adapted from Zullini and Peretti, 1986).

Table 16
Relation between ammonia deposition gradient in a *Pinus sylvestris* plantation and composition of the nematode fauna (after Tamis, 1986)

	Distance from source (m)		
	75	150	400
Total nitrogen deposition (kg N ha^{-1} per year)	68.0	52.5	47.9
Soil nitrogen (μg g^{-1})	27	15	3
Stem flow (mg NH_4^+ l^{-1})	45	30	15
Soil pH	4.9	5.2	5.3
Total nematodes (thousands m^{-2} in litter and 0–20 cm soil)	1302	1023	916
% bacterial-feeding	26.9	23.4	47.0
% fungal-feeding	11.5	18.8	21.9
% plant-feeding	54.2	53.9	22.2
% omnivores	0.3	0.4	7.1
% insect associates	7.1	3.5	1.8
Maturity index (MI)	2.03	2.37	2.46
Plant parasite index (PPI)	2.96	2.80	2.27
Simpson diversity	0.87	0.88	0.93

nematode fauna of a pine forest (*Pinus sylvestris*); values for selected parameters are given in Table 16. Ammonia deposition seems to be correlated with an increasing proportion of both plant-feeding nematodes (mainly *Rotylenchus*) and insect-associated dauer-larvae. There were decreasing proportions of bacterial-feeding nematodes (but a shift towards rhabditids), fungal-feeding and omnivorous nematodes. The increased population of *Rotylenchus* led to an increase in the plant parasite index, although values for the maturity index and diversity were lower at the more contaminated sites.

Popovici (1994) studied the effect of exhaust fumes and fine powder discharged from a metallurgical plant on the soil nematode communities in forest agroecosystems. As lead and copper pollution increased, nematode abundance decreased; diversity (H') and maturity index (MI) also decreased. The percentage of *r*-strategists (bacterivores) increased from 50 to 72%, while plant-feeding nematodes were reduced and both omnivores and predators disappeared. Similarly, in the vicinity of a zinc smelter in The Netherlands, Popovici and Korthals (1995) found pollution-associated decreases in total nematodes, plant-feeding nematodes and the maturity index (Table 17); bacterial-feeders again increased.

In 60–80-year old Bavarian spruce (*Picea abies*) plantations Ruess and Funke (1995) consistently found a higher proportion of bacterial-feeding nematodes in stands with severe decline (‘acid rain’) than in slightly damaged sites (45.5 and 38.8%, respectively) and the opposite trend in root/fungal-feeding nematodes (39.5 and 55.6%, respectively). There were, however, no marked changes in either the number of species present (40.5 and 44%, respectively) or the maturity index. The trends in the two feeding or functional groups

Table 17
Comparison of 12 sites near a zinc smelter in The Netherlands with five control sites (after Popovici and Korthals, 1995)

	Control	Polluted
Vegetation	*Calluna, Betula*	*Calluna, Agrostis*
Nematodes		
Total m^{-2} in 0–10 cm soil	2,520,000	1,970,000
% plant-feeding	30	17
% bacterial-feeding	42	58
% fungal-feeding	26	24
Maturity Index	2.14–2.45	1.86–2.07

were considered to reflect pH-induced changes in the soil microflora.

9.2. *Water-borne pollutants*

Irrigation water may contain not only populations of plant-feeding nematodes (Faulkner and Bolander, 1966) but also traces of heavy metals, salts and organic compounds. As the effects of these pollutants cannot be distinguished from other applications, they are treated in Section 9.3. Impacts of pollutants on the nematodes of rivers have been discussed by Zullini (1988).

9.3. *Applied pollutants*

In addition to the direct (intended) and indirect (ecosystem) effects of agrochemicals which may be applied to agroecosystems, some of which are discussed above (Section 8), various land-uses result in intentional or unintentional application of pollutants. The most common of these pollutants are organic or heavy metal contaminants of organic-rich material applied to soil. Sewage sludge containing heavy metals is probably the greatest single source.

In cases where nematodes have been studied for the effects of applying effluent to agroecosystems the key factor to emerge is that of the marked change in soil moisture content, which affects most aspects of soil biological activity. This is especially obvious in the activity of earthworms. In general terms the rate of decomposition of organic matter increases following effluent application and can be related to an increase in the abundance of bacterial-feeding nematodes and a decrease in fungal-feeding nematodes (Table 18).

Table 18
Percentage contribution of feeding groups to the nematode faunae of two New Zealand agroecosystems with and without application of effluent (from Yeates, 1978, 1995)

Ecosystem Soil texture	Pasture Silt loam		*Pinus* forest Sand	
	Control	Effluent	Control	Effluent
Bacterial feeders	29.7	37.2	43.2	65.6
Fungal feeders	8.8	4.2	23.2	4.8
Predators	1.2	0.8	1.1	6.2
Plant-feeding	14.0	14.5	2.0	8.3
Plant associated	32.0	29.1	8.0	2.1
Omnivores	14.3	14.2	22.5	12.9

Contamination with small amounts of heavy metals (e.g., As, Cd, Cu, Cr, Ni, Pb, Zn) may have minimal effects on nematodes and other soil biological activity, and plant growth may continue. However, with gross contamination, plant growth may cease and organic matter present may decompose. These trends will be shown in the relative abundance of the different nematode functional groups. In a German cropping soil, addition of slightly contaminated sludge led to a decrease in the proportion of plant-feeding nematodes (Table 19). When additional heavy metals were added the principal change was a five-fold increase in the proportion of what Weiss and Larink (1991) termed predacious nematodes (we would regard the Diplogasteridae identified to be bacterial-feeding); the omnivores (mainly Dorylaimida) became undetectable. A New Zealand pasture showed broadly similar trends, with increases in bacterial-feeders and predators and a decrease in omnivores (Table 19).

In a Dutch arable field, plots were treated with copper at up to 750 kg ha^{-1} and the soil pH was adjusted. Some 10 years later nematode populations were sampled. Copper strongly decreased the total abundance of nematodes, especially at lower pHs, where it is more available. At pH 4, plots treated with 750 kg ha^{-1} Cu had relatively fewer plant-feeding nematodes than untreated plots (12% vs. 35%) and there was a corresponding increase in bacterial and fungal-feeding nematodes. Copper reduced nematode diversity and increased the proportion of *r*-strategists, resulting in a lower Maturity Index (Fig. 3). At higher pH levels the effect of Cu on the Maturity Index was much more pronounced than the effect on numbers.

Table 19
Percentage contribution of feeding groups to the nematode faunae of two agroecosystems with addition of sludge and heavy metals, and contaminated to differing degrees with copper, chromium, arsenic (CCA) timber preservative (from Weiss and Larink, 1991; Yeates et al., 1994)

Agroecosystem Soil texture	Cropping (Germany) Loamy sand			Pasture (New Zealand) Silt loam (stony)			
	Control	Sludge	Sludge + heavy metals	Control	Low CCA	Medium CCA	High CCA
Bacterial feeders	18	40	42	18.1	29.4	62.3	48.3
Fungal feeders	33	30	31	1.5	3.0	2.4	0.5
Predators	0	2	10	0.9	1.3	7.6	10.6
Plant-feeding	43	27	18	36.8	27.4	11.2	28.4
Plant associated	in above	in above	in above	13.6	20.4	8.8	10.2
Omnivores	5	1	0	29.0	18.4	7.7	2.0

10. General patterns — the search for indicators

Most current work on nematodes as indicators involves the use of indices or perhaps feeding or functional groups. So far no generally applicable, simple indicators have been found among nematodes of agroecosystems. Perhaps the best approach to date involves studies of the plant-feeding nematodes (Heteroderidae, Longidoridae, Trichodoridae), for which there are various threshold soil populations above which particular crops or varieties of crops should not be planted. All such definitive assessments require methodologies of specialised agricultural laboratories.

There are some relatively distinctive forms among nematodes (e.g., criconematids or ‘ring nematodes’ with their stubby bodies and superficial annules, mononchids with their prominent mouth cavities). Studies in various parts of the world are attempting to relate the abundance of such distinctive forms to various land uses and management practices in the hope that their abundance in particular areas may be used to indicate the general biological conditions in the soil. If a suitable ‘guild’ of readily identified nematodes can be found they may fulfill this purpose.

10.1. Predacious mononchid nematodes as potential indicators

These relatively large nematodes with their characteristic barrel-shaped mouth cavity have been of interest since the beginnings of nematology for their potential as biological control agents for plant-feeding nematodes. However, recent work suggests that in addition to being able to multiply using bacterial food sources, they predominantly prey on bacterial-feeding nematodes rather than plant-feeders (Yeates and Wardle, 1996). Being relatively large nematodes, they are thought to be more common in soils of more open texture, particularly forest litter. They are also considered to be susceptible to cultivation-induced mortality. In forest litter, Arpin et al. (1988) demonstrated that dimensions of adults of *Clarkus papillatus* not only varied seasonally but also different humus types contained populations with distinct dimensions.

To assess the sensitivity of mononchids to tillage, four New Zealand soils, each of which had been cropped annually for 11–29 years, were sampled. It was found that in two soils mononchids remained high (11,600–34,200 m^{-2}) while in the other two their abundance was much lower (300–2500 m^{-2}) after long-term cultivation (Yeates, Shepherd and Francis, unpubl.). Different responses in populations of topsoil-mixing earthworms (Lumbricidae) were also noted in this study; earthworms remained abundant (117–228 m^{-2}) in those soils in which mononchid numbers were low but they lacked viable populations in the other two soils. The soils in which earthworm numbers remained high with cultivation were found to have greater ‘soil aggregate stability’, and it appears that better ‘soil aggregate stability’ improved earthworm survival at cultivation. That mononchid nematodes increased in those soils in which earthworms declined is an illustration of the close relationship between populations of soil organisms and the consequent difficulty in using a single population or functional group as an indicator of soil quality in agroecosystems.

10.2. ‘Pin nematodes’ as indicators of disturbance

Extremely large populations of ‘pin nematodes’ (Tylenchida: *Paratylenchus*, *Gracilacus*) are often found but generally have not been associated with significant crop loss. They often occur in variable environments, where their resistant, sub-adult stage provides an adaptive advantage (Loof, 1975). Their distribution is often highly aggregated, probably due to both the distribution of roots of host plants (Brzeski, 1977) and the dispersal/colonizing ability of the nematodes (Yeates and van der Meulen, 1995). Historically, high-country farmers in New Zealand have burned snow-tussock (*Chionochloa rigida*) to improve stock access and induce nutritious plant regrowth. In the search for an indicator of the sustainability of this management practice it was found that the population of *Paratylenchus* in the upper 2 cm of litter and soil increased markedly following burning. This was apparently not only a response to root growth but also a reflection of the competitive advantage of *Paratylenchus* under the variable temperature and moisture regimes in the more exposed surface conditions (Yeates and Lee, 1997). Both 18 and 30 months after burning there were significantly ($p < 0.001$) more *Paratylenchus* at the burned site than at the unburned site (30,100 versus 340 m^{-2} at 18 months and 17,444 versus 620 m^{-2} at 30 months, respectively). Further sampling would be necessary to determine how soon the two populations became equivalent in number.

11. Process-based integration

Following the development of nematocides in the 1950s much nematode ecology concerned the biology and chemical control of plant-feeding nematodes. In the late 1960s ecological studies examined relationships between nematodes and abiotic factors, total soil respiration and finally the whole of the nematode fauna in relation to ecosystem function (Yeates, 1987). Studies of nematodes in agroecosystems have now moved on to include nematodes as part of food webs. Integrated studies include arable cropping with conventional and integrated management (Bouwman and Zwart, 1994), conventional and no-till cropping (Beare et al., 1992) and weed management strategies under various crops (Yeates et al., 1993b; Wardle et al., 1995). Such studies contribute to understanding the fundamental processes which underlie production in agroecosystems and it has already been found that:

1. The biomass of bacterial-feeding nematodes in an arable soil under integrated management is substantially greater over winter than in a conventional field;
2. The biomass of both bacterial- and fungal-feeding nematodes is consistently greater in litter buried in conventionally tilled soil than in that exposed on no-tillage agroecosystems; and
3. Over 3 years’ primary succession in sawdust the population of predacious Mononchidae closely mirrored that of bacterial-feeding Cephalobidae.

Such studies show that functional groups or species composition may be sensitive indicators for assessing the response of nematodes to disturbance. However, it is clear from the studies of Yeates (1994) and Neher et al. (1995) that regional differences are such that nematodes are unlikely to provide universal indices of ecosystem condition. Regional differences include the differing relationship between soil texture and omnivorous Dorylaimida under differing moisture regimes (Wales cf. South Australia) (Section 6) and the apparent greater abundance of Dorylaimida in New Zealand than Europe (Yeates, 1994).

Identification of all nematode taxa in samples is suitable only as a research tool. Therefore, nematode species richness cannot be widely used as a regulatory or management guide. Selected, morphologically distinct forms such as Mononchidae, *Paratylenchus*, *Pratylenchus* or cysts of Heteroderidae may reflect key parts of the web of soil processes and may be useful indicators.

The distribution of nematode populations between active root tips of various plant species and senescent roots, between rhizosphere and pockets of decaying organic material, between bacterial and fungal food sources and the effect of time, temperature and moisture on specific activity provide diverse niches for the nematode fauna. Nematode species diversity matches this. There is similar diversity in most groups of soil biota. The structural heterogeneity of the soil and the complementary biodiversity of nematodes are inseparable from essential soil processes in agroecosystems. However, as described by Lee (1994), with present knowledge it is not possible to state whether less diverse ecosystems are intrinsically less sustainable. Further understanding of functional interactions between groups of soil biota, and between the biota and soil particles and aggregates, are necessary to understand the links between soil fertility, soil resilience and sustainability.

12. Conclusions

1. The diversity of nematode faunae in agroecosystems offers excellent prospects for finding bioindicators. However, the effects of crop plant, nematode biogeography and soil characteristics on the distribution of particular nematode species means some ‘functional group’ will probably prove to be a better indicator of soil condition than particular nematode species.
2. The traditional nematode ‘functional group’ which has been applied as indicators in agroecosystems is formed by the specific plant-feeding nematodes such as cyst nematode (Heteroderidae), virus vectors (Longidoridae, Trichodoridae) and root lesion nematodes (*Pratylenchus*).
3. If a technique using DNA technology would become available it would need to reflect the relative abundance of particular species or functional group. Classical biological techniques need to be used to define an appropriate target group, perhaps ‘keystone’ organisms, for such development.
4. If permanent grassland is regarded as sustainable, then it may be regarded as providing a baseline for the composition/diversity of the nematode fauna in a given soil. The similarity of the sum of bacterial-feeding and fungal-feeding nematodes to plant-feeding nematodes may be a useful guide. Current work suggests that the relative abundance of fungal-feeding and bacterial-feeding nematodes is sensitive to management changes and may be a good indicator of underlying change in the composition of the nematode fauna.
5. The ‘maturity index’ can provide useful information on the direction of change within a particular soil. There are prospects that the abundance or proportion of *c–p* Groups 1 and 2 may have value as a transferable index. Trends following disturbance events can be shown in *c–p* triangles.
6. While some distinctive groups (e.g., criconematids, longidorids, mononchids) have been tested, results to date suggest that while they too will fail to provide a universal indicator species or group, they may be of value within regions or soil types.

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