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Assessing nematode communities in agroecosystems of varying human intervention

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Abstract

The effect of disturbance on soil nematode communities was studied in eight treatments varying in intensity of human intervention at the Kellogg Biological Station Long Term Ecological Research site, Hickory Corners, MI. The agricultural treatments ranged from those manipulated with high chemical inputs and heavily impacted by human management to successional treatments that had no chemicals and little human impact. A canonical discriminant analysis of the nematode data separated the treatments into four systems: high chemical input (the conventional tillage and no tillage treatments, both corn/soybean rotations); organic (the low input and zero input treatments, both wheat/corn/soybean rotations); perennial (poplar and alfalfa treatments); successional (abandoned after tillage and never tilled treatments). Nematode abundance was highest in the high input and organic systems and lowest in the poplar treatment. Overall, bacterial feeding, plant parasitic and fungal feeding nematodes dominated the treatments. Species diversity was greatest in the successional treatments. The bacterial feeding trophic group and the modified Shannon index described differences at both the treatment and system levels, while the Shannon index demonstrated diversity at the system and annual and perennial crop level of analysis. Measures that detected differences ($P<0.05$) consistently across all treatments, systems, and annual vs. perennial crops were total abundance, the predator trophic group, the maturity index (MI) and the plant parasite index. The minimum analyses needed to detect disturbance reliably were a multivariate analysis and the MI. However, understanding and predicting the impact of the disturbance on the food web and ecosystem functioning would be increased with results from diversity indices and nematode functional groups.

Introduction

In agroecosystems, management practices, whether cultivation, pesticides, or organic mulch, are disturbances that impact the soil system (Elliott and Cole, 1989). Nematodes are ubiquitous soil fauna that interact in ecosystems directly as herbivores on plants and indirectly as consumers of microflora, thus regulating decomposition and the release of nutrients to plants (Cole-

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man et al., 1984). Any change to the soil habitat of nematodes that influences their food source or environment, such as agricultural management practices, should be reflected in the biodiversity of the nematode community (Ferris and Ferris, 1974; Wasilewska, 1989). In agroecosystems, the changes in the biodiversity of the plant parasitic nematode community have received the most attention because of the economic impact of these herbivores on crop plants (Thomas, 1978; Alby et al., 1983; Ferris et al., 1990). Fewer agricultural studies have investigated relationships of the plant feeders and the decomposition-based nematode community (Wasilewska, 1979; Freckman and Caswell, 1985; Niblack and Bernard, 1985; Parmelee and Alston, 1986; Sohlenius et al., 1987; Sohlenius and Sandor, 1989).

Analyses to determine the effect of management practices on nematode community structure and function are generally based on species, generic or trophic group abundance, biomass, diversity (Shannon index, Shannon and Weaver, 1949); Simpson's Diversity index (Pielou, 1977); and, frequently, associations between plant parasitic species (Topham et al., 1991). Additional ecological indices have been developed for consideration of the nematode community as an indicator of disturbance in aquatic and terrestrial ecosystems (Samoiloff et al., 1980; Warwick, 1981; Tietjen and Lee, 1984; Hodda and Nicholas, 1986; Bongers, 1990; Bongers et al., 1991). As pointed out by Heip et al. (1988) and Bongers (1990), these analyses offer slightly different information and when used in combination reveal more descriptive and quantitative information on the soil nematode community. However, there is no agreement as to which indices could best be used to detect differences in soil systems due to anthropogenic effects.

The soil nematode community was studied in ecosystems varying in intensity of human intervention, i.e. native successional systems and agroecosystems having different management practices, to: (1) describe the nematode community structure; (2) determine if the different treatments were reflected in the composition of the nematode community; (3) evaluate several ecological indices used to assess the nematode community.

Methods

The research was conducted at the Long Term Ecological Research (LTER) site established in autumn 1988 at the W.K. Kellogg Biological Station (KBS), Michigan State University, Hickory Corners, MI (Van Cleve and Martin, 1991). Soils at the site are of the Kalamazoo series, Typic Hapludalfs, fine loamy, mixed and mesic. The experiment included six agricultural treatments and two native successional treatments. The agricultural treatments varied in disturbance, from those manipulated with chemical inputs and impacted by human management of crops, to the successional treatments which had no chemicals and little human impact. The conventional tillage treatment (conv.

till) was a corn/soybean rotation which was moldboard ploughed. A corn/soybean rotation without ploughing was the no till treatment. Both treatments had been planted with soybeans the previous year and received chemical inputs such as fertilizers and herbicides at a level consistent with regional farming practices. Treatments 3 and 4 were corn/soybean/wheat rotations with a winter legume cover crop and low chemical inputs. Corn was the previous year's crop. Treatment 3 received chemicals only to control pest outbreaks and to provide an initial pulse of N at planting (low input). Treatment 4 received no chemical inputs at any time (zero input). Both treatments had disturbance from annual cultivation with a rotary hoe and annual ridge rebuilding (soil is moved from inter-row to row in the early growing season). Treatments 5 and 6 were perennial biomass plots. Treatment 5 was planted to woody biomass, *Populus euramericana* cultivar 'Eugenei' (poplar), while Treatment 6 was planted to alfalfa, a herbaceous biomass (alfalfa). The trees were a fast growing clone which offered little genetic diversity. In addition, poplar, which has little below-ground biomass in early stages of growth (P. Robertson, personal communication, 1992), had a ground cover of fescue which was mowed throughout the summer. Alfalfa had an insecticide applied annually and was mowed 3–4 times per year. The native successional treatments were Treatment 7, which was abandoned in 1988 after years of tillage (successional-A), and Treatment 8, which historically has never been tilled or planted, but is mowed annually (successional-N). The successional treatments have a diversity of annual and biennial plant species. There were six replicates of each treatment except for Treatment 8 which had four replicates. Plot size was 0.91 ha.

In April 1991, in Year 2 of the experiment, after a winter of minimal human impact in the fields and prior to tilling and planting the annual crop, cores (2.54 cm diameter) were taken to a depth of 10 cm, starting from the base of the plant and moving into the row at a distance of 0,10, 20, 30, 40, and 50 cm. Average soil temperature was 10.3°C. The six soil samples were bulked, mixed and subsamples shipped overnight in a refrigerated cooler to the University of California, Riverside, CA. Soil moistures were determined gravimetrically for each sample (w/w) (Page et al., 1982).

Nematodes were extracted with the Baermann funnel technique from two 50 g soil subsamples per sample (Flegg and Hooper, 1970). Nematodes were collected at 24 h intervals for 72 h and preserved in a 5% formalin solution. After counting the total number of nematodes in each subsample, 100 nematodes per subsample were randomly selected and identified to genus level if possible, using an inverted compound microscope. Nematode numbers were not corrected for extraction efficiency. Relative abundance of the taxa was calculated as the proportion of the 200 identified nematodes per sample. Total abundance (No. per kilogram of dry soil) was based on the product of the relative abundance of each taxa and total nematode density per sample.

Table 1
Statistics used for analysis of the nematode community in eight treatments varying in intensity of human intervention at the Kellogg Biological Station LTER, Hickory Corners, MI

Index	Proposed use	Citation
Species/community measures		
1. Species richness	Number of taxa	(Magurran, 1988)
2. Abundance	Species/population density	
3. Trophic structure	Describes functional groups in nematode communities	(Yeates et al., 1992)
4. Fungivore/ bacterivore (f/b)	Decomposition pathway in detrital food webs	(Twinn, 1974)
Diversity measures		
1. Trophic diversity (T)	Describes diversity of functional groups within the nematode community	(Heip et al., 1988)
2. Shannon (H')	Species diversity index giving more weight to rare species; a higher index indicates greater diversity	(Pielou, 1977)
3. Transformed H' ($e \hat{} H'$)	Indicates equivalent number of equally common species, units are taxa	(Magurran, 1988)
4. Simpson's diversity (D)	Diversity index giving greater weight to common species; a lower index indicates dominance of a few species	(Pielou, 1977)
Maturity Indices		
1. Maturity index (MI)	Incorporates ecological characteristics of families based on a colonizers to persisters scale of 1–5; a lower index indicates disturbance	(Bongers, 1990)
2. Plant parasite index (PPI)	Plant parasite taxa based on a c–p scale of 2–5; a higher index reflects increased plant production	(Bongers, 1990)

The nematode community was analyzed by a multivariate analysis (Stepwise Discriminant Analysis, BMDP statistical package) and by the following approaches (Table 1): (1) species/community measures, (i) species richness, (ii) absolute abundance, (iii) trophic structure based on relative abundance, this procedure groups nematodes based on known feeding habits or stoma and esophageal morphology, (iv) fungal feeder/bacterial feeder ratio, (f/b); (2) diversity measures, (i) trophic diversity, (T), where $T = 1/\sum pi^2$, in which $p(i)$ is the proportion of trophic group i in the nematode community, (ii) Shannon index, (H'), a species diversity measure giving more weight to rare species, $H' = -\sum Pi(\log Pi)$, where Pi is the proportion of taxa in the total population, (iii) transformed Shannon index, ($e \hat{} H'$), (iv) Simpson Diversity index, (D), a species diversity measure giving more weight to common species, with $D = 1/\sum (n_i/N)^2$, where n_i is the number of individuals of species i, and N is the total number of individuals in the community; (3)

maturity indices, (i) maturity index, (MI), a measure based on the ecological characteristics of nematode taxa. Nematode taxa, except for plant feeders, are classified on a scale of 1–5, with colonizers (short life cycle, high reproductive rates, tolerant to disturbance) = 1, and persisters (long life cycles, low colonization ability, few offspring, sensitive to disturbance) = 5. The MI is calculated as the weighted mean of the constituent nematode taxa values:

$$\mathrm{MI} = \sum_{i=1}^{n} v(i) \cdot f(i)$$

where $v(i)$ is the colonizer–persister (c–p) value assigned to taxon i, and $f(i)$ is the frequency (dominance) of taxon i in the sample. The resulting index is a measure of disturbance, with lower values indicating a more disturbed environment and higher values characteristic of a less disturbed site, (ii) plant parasite index (PPI), which is similar to the MI formula based on a scale of 1–5, but excludes free-living taxa. Here, plant feeding taxa are assigned a c–p value from 2–5, because according to Bongers (1990) there are no plant feeding colonizers designated as 1. The PPI should increase with fertilization and increased primary, particularly root, production. Plant parasitic taxa were not included in the MI but were included in all diversity indices.

All analyses were based on relative abundance of nematode families unless otherwise stated. Univariate (ANOVA) analyses of variance were conducted on the data sets. Differences with $P < 0.05$ were considered significant.

Results

Over 40 genera in 31 families were identified in the eight treatments, but within treatments, the number of taxa ranged from 30 in conv. till to 36 in the succession–never tilled treatment (Table 2, Fig. 3d). Between three and five genera/families comprised more than 50% of the abundance on any one treatment. Families with the greatest mean abundance on all treatments were: Rhabditidae > Cephalobidae > Aphelenchidae > Tylenchidae > Pratylenchidae (Table 2). The Cephalobidae includes the genera *Acrobeles*, *Acrobeloides*, *Cervidellus*, *Chiloplacus*, and *Eucephalobus*. Tylenchidae and *Pratylenchus* were abundant plant feeders on all treatments, although there was a lower proportion of *Pratylenchus* in the successional-N, poplar and alfalfa treatments. Dominant bacterial feeding taxa were Rhabditidae, *Acrobeloides*, *Eucephalobus*, Monhysteridae, Neodiplogasteridae, and *Panagrolaimus*. *Aphelenchus* and *Aphlenchoides* were the most common fungivores, with *Aphelenchoides* more abundant on the succession–never tilled treatment. The predaceous nematodes *Clarkus* and *Mylonchulus* were common to all treatments. *Microdorylaimus* was the only omnivore found in all treatments.

The relative abundance of each taxon in a sample was analyzed by a mul-

Table 2
Mean relative abundance of nematodes in six agricultural treatments and two successional treatments. CT, conventional tillage; NT, no till; LI, low input; ZI, zero input; P, poplar; A, alfalfa; S–A, succession native; S–N, never tilled

Genus/family	Maturity Index c–p value	Treatment							
		CT	NT	LI	ZI	P	A	S–A	S–N
Plant feeders									
Criconematidae	*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13
Helicotylenchus	*	0.25	0.00	0.00	0.00	0.00	0.00	0.00	1.50
Paratylenchus	*	1.08	0.33	1.25	0.33	1.88	6.53	1.33	3.88
Pratylenchus	*	13.75	19.92	9.83	9.00	4.00	3.08	8.92	4.38
Psilenchus	*	0.00	0.00	0.00	0.08	0.30	0.00	0.17	0.13
Tylenchidae	*	10.67	10.92	11.25	11.75	20.03	23.48	19.75	10.13
Tylenchorhynchus	*	0.00	0.25	0.00	0.00	0.08	0.00	0.00	0.50
Xiphinema	*	0.00	0.00	0.00	0.00	0.33	0.00	0.17	0.25
Bacterial feeders									
Acrobeles	2	0.25	0.00	0.17	0.00	0.08	0.00	0.00	0.25
Acrobeloides	2	12.00	11.50	12.83	11.50	14.60	10.97	7.08	11.88
Alaimus	4	0.25	0.25	0.00	0.08	0.12	0.08	0.08	0.13
Bastianidae	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Cervidellus	2	0.00	0.42	0.42	0.00	0.00	0.00	0.00	0.75
Chiloplacus	2	0.42	0.67	0.25	0.42	0.62	1.45	2.50	0.13
Eucephalobus	2	2.50	2.17	1.42	2.42	2.52	3.87	6.42	2.13
Monhysteridae	1	1.25	3.92	1.25	2.00	4.05	2.95	1.75	1.88
Neodiplogasteridae	1	6.67	3.58	0.58	0.75	0.38	0.65	1.08	0.25
Panagrolaimus	1	0.58	0.33	6.25	8.00	0.57	2.15	1.83	1.25
Plectus	2	1.42	1.83	1.92	2.08	1.17	2.65	1.33	8.25
Prismatolaimus	3	0.00	0.08	0.17	0.08	1.60	0.43	0.17	3.75
Rhabditidae	1	17.67	14.58	23.33	25.00	17.53	14.22	12.67	10.63
Wilsonema	2	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.38

Fungal feeders									
Aphelenchoides	2	9.67	6.25	4.17	3.38	8.63	3.40	6.92	23.75
Aphelenchus	2	16.58	16.92	18.33	17.08	13.53	13.87	16.33	4.75
Diphtherophora	3	0.33	0.75	0.33	0.33	0.50	0.63	0.50	0.00
Tylencholaimellus	4	0.00	0.00	0.8	0.17	0.20	0.25	0.33	0.13
Algal feeders									
Achromadora	3	0.83	1.83	1.75	0.83	2.90	1.47	2.58	3.13
Predators									
Clarkus	4	1.42	0.42	0.67	0.67	0.52	0.95	1.33	0.88
Discolaimidae	5	0.33	0.00	0.17	0.00	0.08	0.18	0.00	0.00
Miconchus	4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13
Mylonchulus	4	0.25	0.25	0.25	0.33	0.65	0.77	1.17	0.25
Nygolaimus	5	0.00	0.00	0.00	0.08	0.00	0.00	0.08	0.00
Paravulus	5	0.00	0.00	0.33	0.17	1.08	1.62	1.17	0.00
Omnivores									
Aporcelaimellus	5	0.08	0.33	0.17	0.08	0.00	0.08	0.00	0.00
Belondiridae	5	0.00	0.08	0.00	0.25	0.00	0.18	0.67	1.38
Dorylaimid juv	4	0.58	1.17	0.83	0.50	0.30	0.73	0.83	1.50
Ecumenicus	5	0.17	0.00	0.08	0.08	0.10	0.27	0.17	0.00
Epidorylaimus	4	0.00	0.00	0.08	0.08	0.08	0.00	0.08	0.38
Eudorylaimus	4	0.08	0.08	0.00	0.00	0.00	0.00	0.17	0.13
Laimydorus	5	0.17	0.08	0.08	0.00	0.00	0.08	0.33	0.13
Mesodorylaimus	5	0.33	0.33	0.92	1.00	0.80	2.48	0.58	0.00
Microdorylaimus	4	0.17	0.17	0.50	0.58	0.55	0.35	0.75	0.63
Paraxonchium	5	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00
Prodorylaimus	5	0.08	0.08	0.00	0.00	0.00	0.08	0.00	0.00
Qudsianematidae	4	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00
Thonus	4	0.00	0.33	0.08	0.08	0.20	0.00	0.75	0.00
Thornia	4	0.17	0.08	0.17	0.17	0.00	0.08	0.00	0.13
Insect parasite		0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00
Total nematodes per kg dry soil·10^4 (±S.E.)		1.19(0.11)	1.22(0.13)	0.96(0.14)	1.06(0.07)	0.41(0.06)	0.51(0.09)	0.93(0.06)	0.52(0.07)

*, Plant feeding nematodes are not considered in the calculations of the MI (see Bongers, 1990), but for the PPI, the scaling for c–p was: *Paratylenchus, Psilenchus, Tylenchidae*=2; *Criconematidae, Helicotylenchus, Pratylenchus, Tylenchorhynchus*=3; *Xiphinema*=5 (see Bongers, 1990).

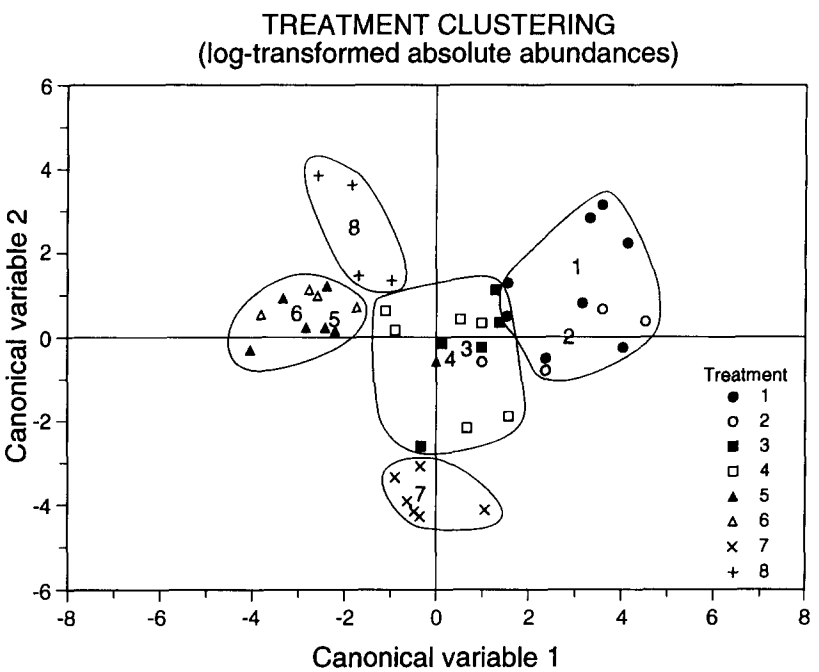

Fig. 1. Scatter plot of the first and second canonical variables for the eight treatments at the Kellogg LTER. Treatments are: 1, conventional tillage; 2, no tillage; 3, low input; 4, zero input; 5, poplar; 6, alfalfa; 7, succession-A, abandoned after years of historical tillage; 8, succession-N, never tilled. Data are Log (nematode abundance + 1).

tivariate analysis on the eight treatments. This separated the succession–never tilled treatment from all other treatments (data not shown). After transforming the absolute abundances to Log (nematodes + 1) (Fig. 1), conv. till and no till treatments (high input systems), low input and zero input (organic systems), and poplar and alfalfa (perennial systems), were grouped in similarity. This latter result would indicate that within these systems the nematode communities were not differentiated. Even following transformation, the successional–abandoned and succession–never till treatments were not grouped in similarity, indicating that these treatments were different from each other. The canonical variables one and two of the ordination were driven by abundances of the genera *Panagrolaimus*, *Pratylenchus* and *Aphelenchoides*, which cumulatively explained 86% of the dispersion. Based on this analysis, all indices were tested by ANOVA procedures on the eight treatments, four systems (high input = conv. till and no till treatments; organic = low input and zero input treatments; perennial = poplar and alfalfa treatments; and although not grouped in similarity, successional = abandoned and never tilled treatments). A further analysis was at the cropping level for

Table 3
Univariate analysis of variance (ANOVA) for soil nematodes in eight treatments, four systems and two crops at Kellogg Biological Station LTER. All analyses are based on relative abundance except for absolute abundance

Index	Treatment		Systems		Crops	
	F-test	*P* value	*F*-test	*P* value	*F*-test	*P* value
1. Abundance	10.61	1.0000E-4	15.78	1.0000E-4	27.75	1.0000E-4
2. Trophic Structure						
PF	2.670	NS	2.157	NS	2.694	NS
BF	2.850	0.0172	5.204	0.0038	2.152	NS
FF	1.707	NS	2.247	NS	2.912	NS
AF	1.946	NS	2.868	0.0477	2.449	NS
PR	3.057	0.0118	3.280	0.0301	8.924	0.0052
OM	2.206	NS	2.353	NS	0.878	NS
3. f/b	1.683	NS	3.709	0.0187	1.482	NS
4. *T*	2.027	NS	4.338	0.0095	2.591	NS
5. *H'*	2.214	NS	4.676	0.0066	6.490	0.0140
6. *e^H'*	2.567	0.0287	5.491	0.0028	1.151	NS
7. *D*	1.145	NS	2.405	NS	0.283	NS
8. MI	6.210	1.0000E-4	9.611	1.0000E-4	7.615	0.0093
9. PPI	7.725	1.0000E-4	17.566	1.0000E-4	42.107	1.0000E-4

Indices are: (1) Absolute abundance·kg^{-1} dry soil. (2) Trophic structure: PF, plant feeders; BF, bacterial feeder; FF, fungal feeder; AF, algal feeder; OM, omnivore; PR, predator. (3) f/b, fungivore/bacterivore ratio. (4) *T*, trophic diversity. (5) *H'*, Shannon Index. (6) *e^H'*, modified Shannon index. (7) *D*, Simpson's diversity. (8) MI, maturity index. (9) PPI, plant parasite index. Values with $P<0.05$ were considered significant, NS, non significant.

two crops (annual = high input and organic treatments; perennial = poplar and alfalfa treatments).

Table 3 shows results of the ANOVA procedures for treatments, systems and crops. Measures that detected significant differences consistently across all treatments (Table 3, 4a), systems (Table 3, 4b) and crops (Table 3, 5) were: total abundance, the trophic group predators, the MI and PPI. Two indices, bacterial feeders and *e^H'*, showed differences at both the treatment (Table 4a) and system levels (Table 4b), while the Shannon index demonstrated diversity at the system (Table 3, 4b) and crop (Table 5) level of analysis and was close at the treatment level ($P=0.0546$) (Table 3). Algal feeders, f/b ratio, and trophic diversity (*T*) indices displayed differences only at the systems grouping (Table 3,4b). Differences between annual and perennial crops were shown by total abundance, predators, *H'*, and MI, all of which were greater in perennial cropping systems (Tables 3 and 5). The PPI also separated the two crops, with a higher PPI on the annual crops. Simpson's Diversity index (*D*) did not discriminate among treatments, systems or crops (Table 3).

Total nematode abundance was highest in the corn/soybean no till treat-

Table 4

(A) Matrix indicating which indices within treatments showed differences based on a univariate ANOVA at $P<0.05$. Significant indices are: t, total abundance; (all other indices are based on relative abundance); p, predators; B, bacterial feeders; H, Shannon index (H'); e, modified Shannon index ($e^{H'}$); M, maturity index; P, plant parasite index

	Conv. till 1	No till 2	Low input 3	Zero input 4	Poplar 5	Alfalfa 6	Succession abandoned 7	Succession-never tilled 8
1								
2	–[1]							
3	–	–						
4	–	B,P	–					
5	t,P	t,P	t,P	t,P				
6	t,M,P	t,p,M,P	t,p,M,P	t,p,M,P	M			
7	M,P	t,p,M,P	B,p,e,M	B,p,H,e,M	B,t,M	t,P		
8	t,H,e,M	t,H,e,M,P	t,H,e,M	t,H,e,M	H,e,M	p,H,e,P	t	

[1]Indicates no significant differences.

(B) Matrix indicating which indices within the four systems showed differences based on a univariate ANOVA at $P<0.05$. Significant indices were: t, total abundance; (other indices based on relative abundance); B, bacterial feeder; G, algal feeder; p, predator; T, trophic diversity index; f, fungal feeder/bacterial feeder ratio; H, Shannon index (H'); e, modified Shannon index ($e^{H'}$); M, maturity index; P, plant parasite index

	Systems			
	High input	Organic	Perennial	Successional
High input				
Organic	B,T,P			
Perennial	t,p,P	t,B,p,f,T,M,P		
Successional	t,G,H,e,M,P	t,B,G,f,T,H,e,M	t,f,H,e,P	

ment and lowest in poplar (Fig. 2a), and did not appear to be related to soil moisture (Fig. 2b). The high input and organic treatments (conv. till, no till, low input, zero input) had greater densities than the perennial and the successional-N treatments (Fig. 2a), results that were also apparent at the systems level (Table 4b, Fig. 4a). Total abundance also separated the two successional treatments (Fig. 2a).

Trophic structure (Fig. 3a) in all treatments was dominated by bacterial feeders, fungal feeders and plant feeders. Proportions of plant parasites were highest in alfalfa, successional-A and no till, but plant parasites were never greater than 33% of the community. Bacterial feeders were 52% of the community in the zero input treatment and more than 40% of all treatments except in the alfalfa and successional-A (Fig. 3a). Fungivores ranged from 18%

Table 5
Indices used to analyze the nematode community in two cropping systems at the Kellogg Biological Station LTER. Data shown are means and standard error and are based on relative abundance except for abundance, which is total abundance. Annual cropping systems were based on combined data from conventional tillage, no tillage, low input and zero input treatments. Perennial cropping systems were based on data from poplar and alfalfa treatments

Crops		
Indices	Annual	Perennial
Abundance (No./kg dry soil)	10475 (644)	5747 (607)
Trophic groups (proportion)		
Plant parasites	0.25 (0.02)	0.23 (0.02)
Bacterial feeders	0.46 (0.02)	0.41 (0.02)
Fungal feeders	0.24 (0.01)	0.21 (0.02)
Algal feeders	0.01 (0.00)	0.02 (0.01)
Predators	0.01 (0.00)	0.03 (0.01)
Omnivores	0.03 (0.00)	0.03 (0.01)
Fungivore/bacterivore ratio	0.54 (0.04)	0.65 (0.08)
Trophic diversity index	2.94 (0.08)	3.14 (0.09)
Shannon index	2.10 (0.02)	2.15 (0.02)
Modified Shannon index	8.25 (0.19)	8.64 (0.35)
Simpson's diversity index	6.54 (0.20)	6.73 (0.27)
Maturity index	1.78 (0.03)	1.94 (0.07)
Plant parasite index	2.51 (0.03)	2.16 (0.04)

(alfalfa) to 29% (successional-N). Algal feeders, predators and omnivores collectively were less than 10% of the population in all treatments. The relative abundance of predators was significantly higher on the alfalfa and successional-A treatments compared with no till, low input, and zero input treatments (Fig. 3a). The alfalfa treatment also had more predators than the successional-N treatment. Significant differences between the four systems occurred only with bacterial feeders, algal feeders and predators (Table 4b, Fig. 4b). Bacterial feeders were more abundant in the organic system and predators were more numerous in the perennial system (Table 4b, Fig. 4b). At the cropping level, predators were the only trophic group to have significantly higher densities in the perennial cropping system (Tables 2 and 5).

The f/b was highest in the succession-A treatment (Fig. 3b). There was a higher f/b in the successional system than in the organic systems (Table 4b, Fig. 4c), but f/b did not differentiate annual and perennial cropping systems (Table 3, 5).

Diversity indices

There was a significantly greater trophic diversity (T) in the perennial and successional systems than in the organic system (Table 4b, Fig. 4c), but there

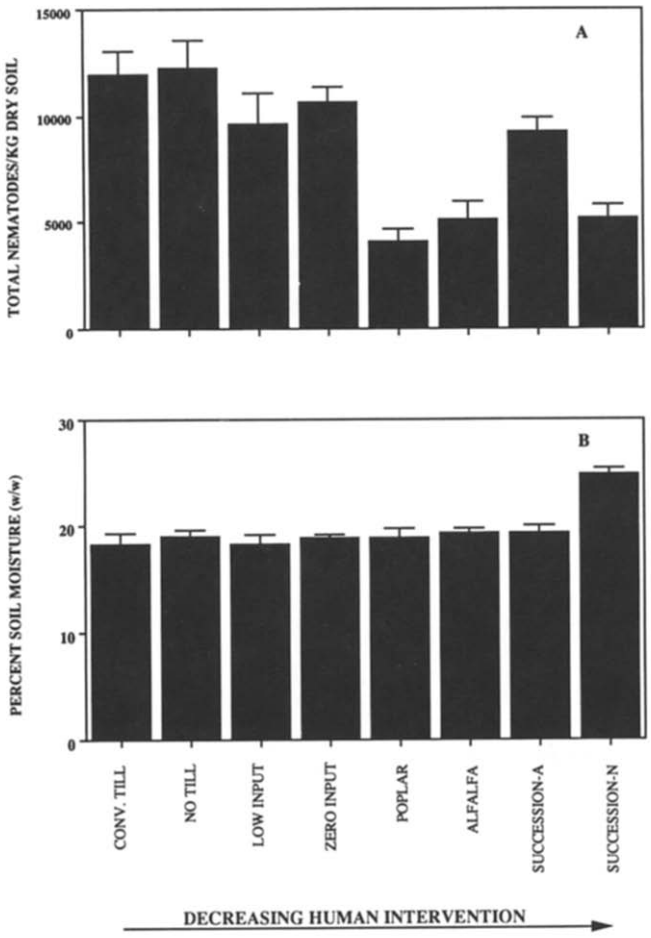

Fig. 2. (a) Mean abundance of nematodes·kg^{-1} dry soil in eight treatments at the Kellogg LTER ranked according to potential human impact. (b) Percent soil moisture (gravimetric) determined for each replicate sample for the eight treatments. Data are means of six replicates for the first seven treatments and of four replicates for succession-N. Treatments are: conv. till, corn/soybean, conventional tillage; no till, corn/soybean, no tillage; low input, wheat/corn/soybean, low input chemicals; zero input, wheat/corn/soybean, no chemical input; poplar, poplar trees; alfalfa, succession-A, historically tilled, then abandoned in 1988; succession-N, never tilled, ploughed, or planted.

were no differences at the treatment or crop level of analysis (Tables 3 and 5). Trophic diversity was higher in successional-A and lower in zero input treatments (Fig. 3b).

The H' (Fig. 3c) and $e \hat{} H'$ (Fig. 3e) indices indicated a greater nematode diversity in successional-N than in Treatments 1–6, and in successional-A than in zero input (Table 4a). The only difference between $e \hat{} H'$ and H' at

the treatment level of analysis was that $e^{H'}$ showed more diversity in the successional-A than in the low input (Fig. 3c,e). The successional system was more diverse than the other three systems by both Shannon and the $e^{H'}$ indices (Table 4b, Fig. 4d, e), but only the H' distinguished annual from perennial crops (Table 3).

Simpson's Diversity index, although showing no significant differences in treatments, systems and crops, had lowest values in the zero input treatment

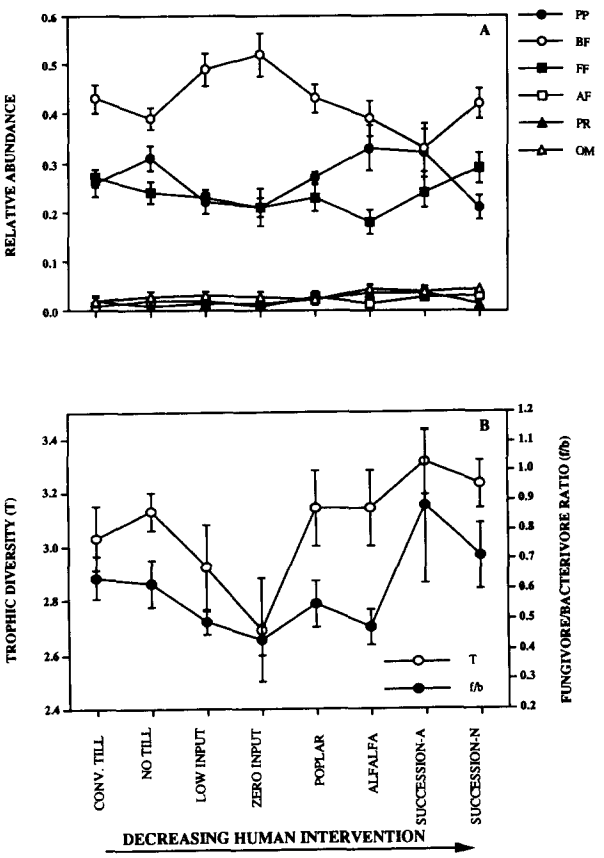

Fig. 3. Soil nematodes in eight treatments ranked according to potential human impact at the Kellogg LTER. Data are based on relative abundance of nematodes. See Fig. 2 legend for treatments. (a) Relative abundance of trophic groups in the nematode community of the eight treatments. PP, plant parasites; BF, bacterial feeders; FF, fungal feeders; AF, algal feeders; PR, predators; OM, omnivores. (b) Fungivore/bacterivore ratio (f/b) and trophic diversity (T). (c) Shannon index (H'). (d) Species richness. (e) Modified Shannon index ($e^{H'}$), and Simpson's diversity index (D). (f) Maturity indices: PPI, plant parasite index; MI, maturity index.

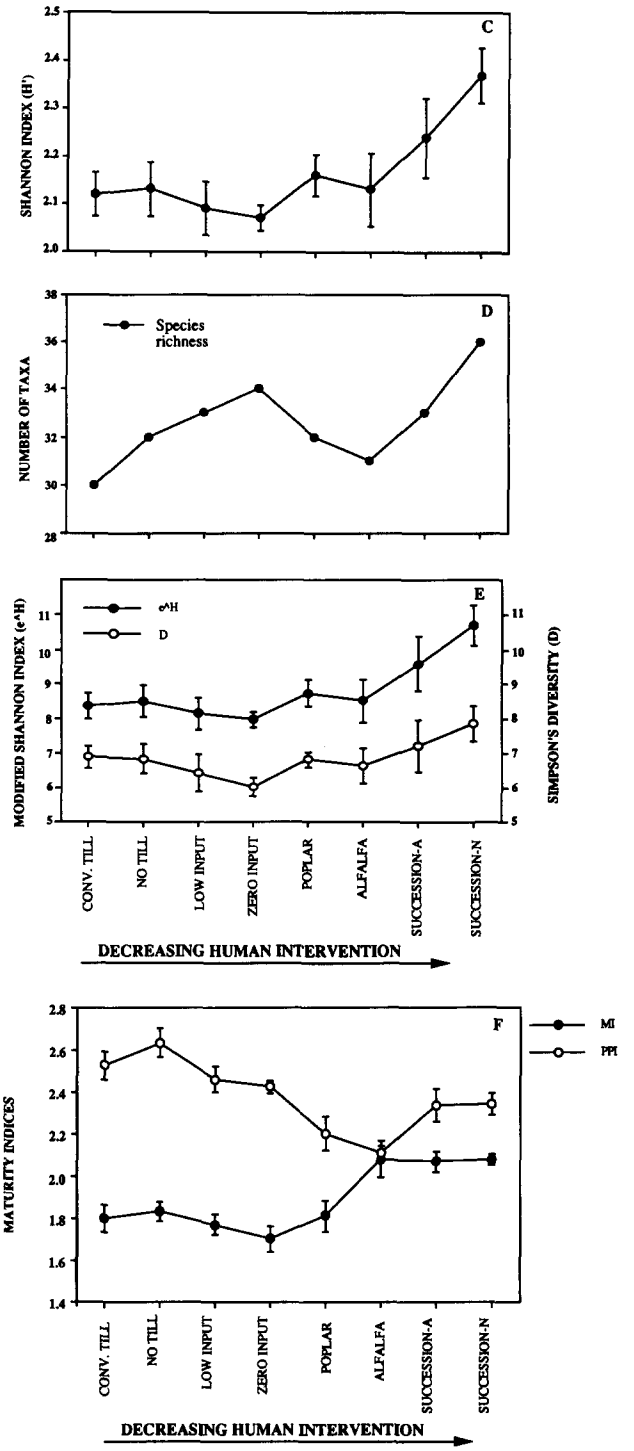

Fig. 3. (continued).

and highest values at the succession-N (Fig. 3e). This was also reflected in the systems level of analysis, where there appeared to be a higher species diversity in the successional system than in the organic system (Fig. 4e). Perennial crops had a higher index than annual crops (Table 5).

Maturity indices

The MI differentiated the high input, organic and poplar (Treatments 1–5) as having a lower index than the alfalfa and successional treatments (Table

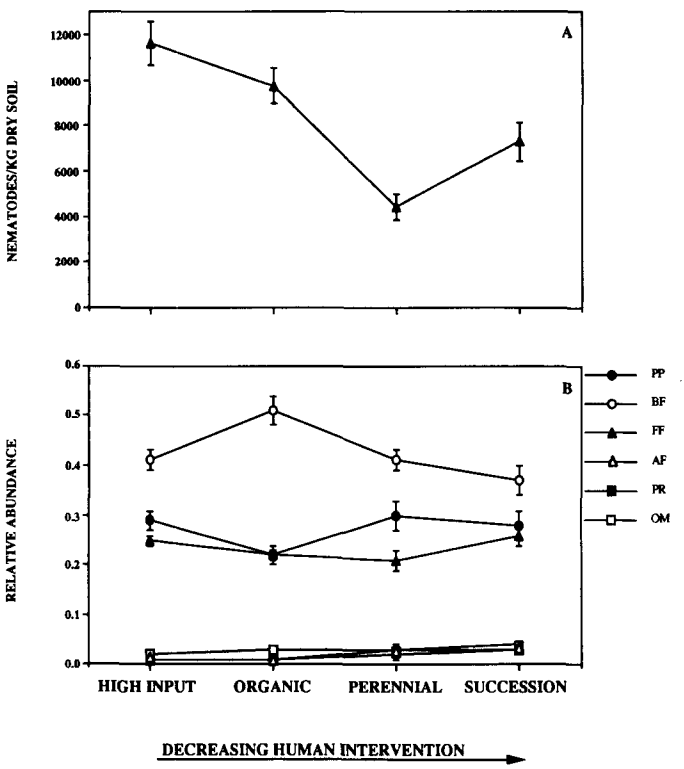

Fig. 4. Soil nematodes in four systems ranked according to potential human impact at the Kellogg LTER. Systems are: high input, conventional tillage and no tillage treatments; organic, low input and zero input treatments; perennial, poplar and alfalfa treatments; succession, succession-abandoned after years of historical tillage, and the succession-N, never tilled, ploughed, or planted. (a) Mean absolute abundance of nematodes·kg^{-1} dry soil. (b) Relative abundance of trophic groups in the nematode community. PP, plant parasites; BF, bacterial feeders; FF, fungal feeders; AF, algal feeders; PR, predators; OM, omnivores. (c) fungivore/bacterivore ratio (f/b) and trophic diversity (T). (d) The Shannon index (H'). (e) Modified Shannon index ($e\hat{}H'$), and Simpson's Diversity index (D). (f) Maturity indices: PPI, plant parasite index; MI, maturity index.

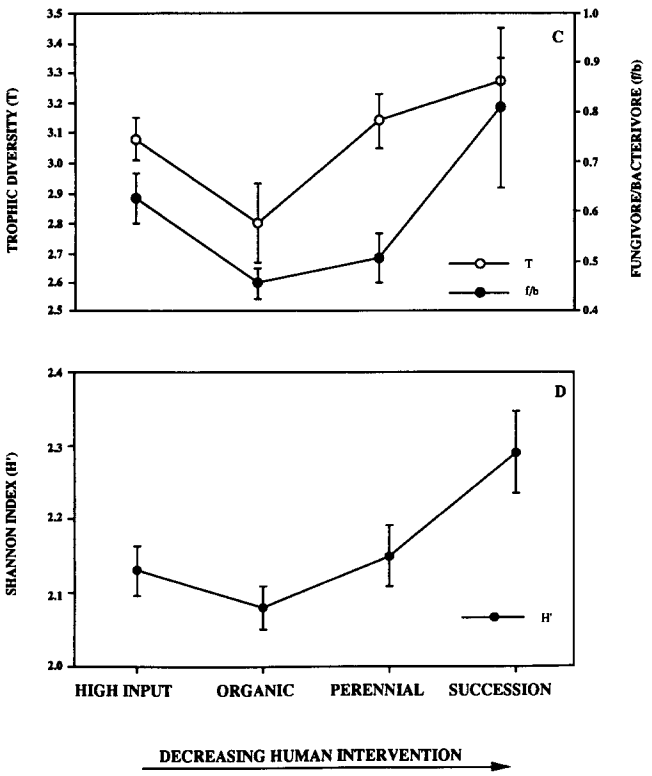

Fig. 4. (continued).

4a, Fig. 3f). At the systems level, the high input system had a significantly lower MI than the successional system (Table 4b, Fig. 4f). Both MI of the high input and organic systems were lower than the perennial and successional system. The annual crops had a lower MI than the perennial cropping system.

The plant parasitic taxa in the PPI were represented in only three of the four c–p groups, 2, 3, and 5. The high input treatments and systems had the highest PPI, and the perennial treatments the lowest indices (Table 4a, Fig. 3f, 4f). The high input treatments were dominated by an endoparasite (c–p rating=3), *Pratylenchus*, and the perennial systems by the Tylenchidae and the ectoparasite, *Paratylenchus* (both with c–p rating=2) (Table 2). The PPI was higher on conv. till than on alfalfa, poplar, and successional-A treatments; and, higher on no till than on the zero input, perennial and successional treatments (Table 4a, Fig. 3f). The successional treatments had a higher

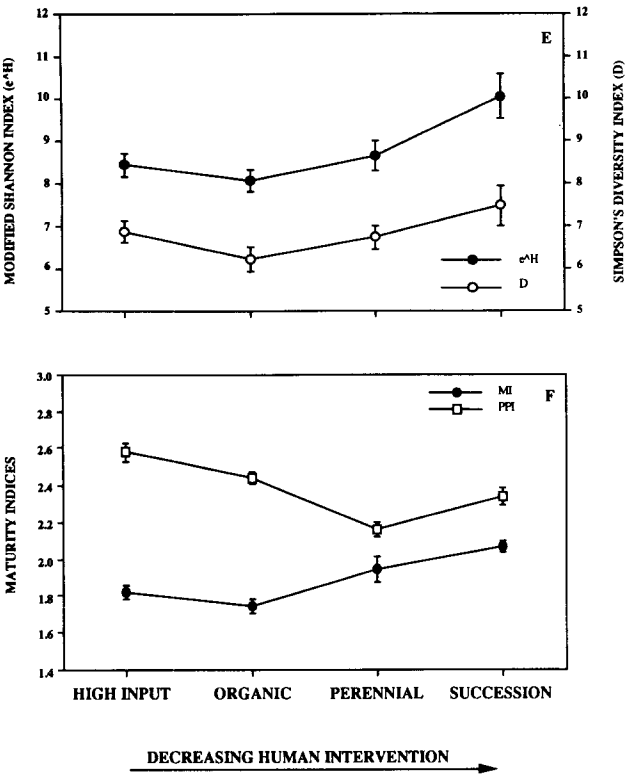

Fig. 4. (continued).

PPI than the alfalfa treatment. All the systems except the organic vs. successional systems were significantly different using the PPI (Table 4b, Fig. 4f).

Discussion

The treatments in this study represented a range of management practices and crops that should affect the heterogeneity of the below-ground soil food web and be reflected in the nematode community. There were four annual crops, a perennial clone, poplar, all with high above-ground biomass, a perennial herbaceous crop that should produce greater below-ground root productivity (Juma and Mishra, 1988), and two successional treatments, one recently abandoned, one never tilled.

The number of nematode taxa in this study, about 30, was less than in a Swedish arable cropping system (Sohlenius et al., 1987), and similar to that found in soybean-wheat fields (Baird and Bernard, 1984) and conventionally

tilled and no tilled systems of Georgia (Hendrix et al., 1986) (Table 2). Although the study was limited to one sampling date and six cores per sample, taxonomic composition was similar to other studies of arable crops in tillage and no tillage systems (Baird and Bernard, 1984; Hendrix et al., 1986; Parmelee and Alston, 1986; Sohlenius et al., 1987; Juma and Mishra, 1988). The increased species richness (36 taxa) of the succession-N treatment compared with the first six treatments (Fig. 3d) was reflected in the modified Shannon and Shannon Diversity indices (Figs. 3c,e and 4d,e), corroborating the results of Ferris and Ferris (1974) and Wasilewska (1989). The organic-based zero input treatment, which had no chemical additions, also had a high number of taxa (35), but an uneven distribution of species, and thus a lower H' (Figs. 3c,d and 4d). Species richness alone was not useful in distinguishing differences among treatments. Similarly, Simpson's Diversity index did not discriminate differences in this study, possibly because only a few taxa were dominant (Table 2).

Nematode abundance was highest in the annual treatments compared with perennial or succession-N treatments (Fig. 2), reflecting differences that could be attributed to more intensive agriculture. The difference between the two successional treatments was noted by total abundance and the canonical discriminant analysis (Fig. 1). Although total abundance was sufficient to differentiate treatments, other studies have shown variation or no differences in nematode abundance in conventional vs. no tillage and annual vs. perennial cropping systems (Baird and Bernard, 1984; Hendrix et al., 1986; Sohlenius et al., 1987; Gallaher et al., 1991; Niles, 1991). The variation in these and other results indicate that total abundance would not be a reliable measure when used alone.

Multivariate analyses such as canonical discriminant analysis are powerful tools that are being used more frequently in community ecology to allow assessment of environmental patterns on a wide array of organisms (Hodda, 1986; Heip et al., 1988; Moore et al., 1988; Moore and de Ruiter, 1991; Kremen, 1992). Kremen (1992) noted that these techniques are particularly useful for testing the indicator properties of a group of organisms in poorly known systems. In this study, the canonical discriminant analysis clustered treatments into systems of similar agricultural management based on nematode taxa. This type of analysis, combined with another index of the nematode community, could be an effective assay for assessing disturbance in soil systems.

Trophic structure is a functional classification that contributes to understanding the structure of the nematode community, and how each grouping of taxa affects the transfer of matter or energy in the ecosystem (Freckman and Caswell, 1985; Hendrix et al., 1986; Parmelee and Alston, 1986; Juma and Mishra, 1988). However, designation of nematode taxa into trophic groups is frequently based on buccal structures rather than known feeding

habits, possibly leading to the wrong classification in trophic groups (Freckman and Caswell, 1985). In addition, for many nematodes the feeding habits are unknown and have to be assumed based on available data (Yeates et al., 1992), making publication of taxonomic and trophic groups a criteria for nematode ecology studies. Moore et al. (1988) expanded the trophic grouping and formalized the functional links of soil food webs to ecosystem level processes by proposing that the species be assigned to functional groups based on similar food sources, feeding modes, life histories and habitats. Moore and de Ruiter (1991) found this functional grouping useful in quantifying the flow of nitrogen through two similar systems, a shortgrass steppe of North America and agricultural soils of reclaimed marine sediments in the Netherlands. In this study, analysis of trophic structure found only a few groups displaying significant differences at the treatments, systems and crops levels of analysis (Table 3, Figs. 3a, 4b).

The f/b ratio reflected the dominance of bacterial feeders (Fig. 3b) and may indicate abundant populations of bacteria (Baath et al., 1981), a bacterial decomposition pathway, and higher rates of mineralization in these treatments (Wasilewska, 1979; Hendrix et al., 1986). Fungivores were a greater proportion of the community in the successional treatments, particularly in the successional-N as compared with the successional-A treatment (Fig. 3a).

Plant feeders had the lowest relative abundance in the organic-based low input treatments. One endoparasitic genus, *Pratylenchus*, that dominated the plant parasites in the corn/soybean conv. till and no till treatments, was less abundant in all other treatments. This herbivore is frequently found associated with an economic loss of corn and soybeans under conventional and no till management in the midwestern USA (Bergeson and Ferris, 1986). Alfalfa had the highest proportion of plant parasites, because of abundances of Tylenchidae and *Paratylenchus*. In the successional-N treatment, plant parasites were less abundant than bacterial and fungal feeding groups, perhaps indicating more food resources for the decomposition-based nematodes than for the herbivorous nematodes.

Algal feeders, omnivores and predators represented a small proportion of the community in all treatments. Omnivores can be sensitive to management practices that disturb the soil (Ferris and Ferris, 1974; Wasilewska, 1979), but in this study differences were not apparent, similar to the results of Juma and Mishra (1988). Predators were one of the more consistent measures in discriminating treatments, systems and crops. However, their low abundance and frequent absence in some arid systems would make their use as an indicator of disturbance questionable.

The MI has proved useful in assessing disturbance of terrestrial, freshwater (Bongers, 1988, 1990) and marine (Bongers et al., 1991) ecosystems, but has not been assessed in agricultural systems. This index was developed to monitor colonization and succession based on the characteristics of the constituent

species, such as length of life cycle (Bongers, 1990). In habitats with inputs of organic matter and/or pollutants, the increased bacterial activity would favour colonizer nematodes that feed on bacteria and respond quickly and persisters would decrease. In this study, the MI was based on analysis at the family level because some groups were difficult to identify to genus, and further, family level identification is a suggested level of taxonomic resolution for MI analysis (Bongers, 1990; Bongers et al., 1991). Family level of analysis assumes that related species in a family all have similar life histories and c–p characteristics (Bongers, 1990). The MI consistently showed differences at treatment, systems and cropping levels, which indicated that the alfalfa (perennial) and successional treatments and systems were less disturbed.

The PPI, which is not considered an index of disturbance (Bongers, 1990), includes plant feeding species whose feeding habits and ecological life histories are more well known than other nematode groups (Table 1). This measure could potentially be a more useful index of disturbance than the MI, because most nematologists and soil ecologists are familiar with the ecology and taxa of plant parasites. The PPI, when combined with estimated impacts of these herbivores on plant productivity (Ferris, 1982; Freckman and Virginia, 1989), could also be useful in assessing herbivore function in natural systems. Bongers (1990) has suggested that the PPI, in heavily fertilized agronomic crops with greater root production than in natural systems, would increase and the MI decrease. In the present study, whereas a depressed MI was detected with increased human intervention, the PPI was lower in alfalfa than in, as would be expected, the 'natural' successional treatments. With alfalfa, the lower PPI was driven by more taxa at a c–p scale of 2 (Tylenchidae and *Paratylenchus*) (Table 2).

Several measures of the nematode community consistently distinguished variation in treatments which can not be attributed to site differences or plant species. The successional treatments were the least disturbed and the annual crops the most disturbed. The conv. till and no till treatments with the same plant species were not differentiated by any indices although trophic structure contrasted as in other studies (Table 4a, Fig. 3a) (Hendrix et al., 1986; Parmelee and Alston, 1986). Treatments with different plant species, i.e. alfalfa and the successional treatments, were grouped by the MI, which contrasted sharply with other indices that grouped the perennials, alfalfa and poplar. The perennials appear to differ in root architecture, energy inputs to the soil system, allocation of plant production and management regimes. Alfalfa might be more similar to successional-N in below-ground biomass and the minimal disturbance mowing regime. Poplars send 40% of their fixed carbon below-ground, but only 16% ends up in the roots and 1–2% in the soil microflora, further indicating that the two perennials may be quite different as suggested by the MI (Horwath et al., 1992). A recent analysis of anthropogenic effects at the KBS LTER suggested the Poplar treatment was the least perturbed of

all treatments (K. Gross, personal communication, 1992), although this was not reflected by analyses of the soil nematodes.

The soil nematode community was sensitive to a gradient of changes in the soil environment. Several indices tested could be used singly or in combination to detect habitats affected by human intervention. The MI, the PPI, total abundance and the predator trophic group displayed differences across treatments, systems and crops. Total abundance and the canonical discriminant analysis distinguished successional-A from the successional-N. Other indices, nematode species richness, species diversity (H', $e^{\wedge}H'$, D), trophic diversity (T), f/b, and trophic structure were less reliable in showing differences among treatments, systems and crops, and would not be good predictors of human disturbance. However, these latter measures contribute to an understanding of the food web and ecosystem processes, i.e., how these systems are functioning.

With the increasing interest in the ecology of nematodes and their use as indicators of pollution, sensitive and reliable methods of analyzing nematode communities are necessary. All methods except total nematode abundance require taxonomic knowledge. Of these indices based on taxa, the results indicate that the MI and the multivariate analysis were excellent predictors of the range of anthropogenic effects in these agricultural and successional systems. The MI, combined with multivariate techniques, would maximize information for assessing human intervention in soil systems. Additional testing of these indices, particularly the PPI, is necessary to determine the realistic use of nematodes as indicators of soil disturbance.

Acknowledgments

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