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Ecosystem type affects interpretation of soil nematode community measures

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Abstract

A better understanding of performance among major ecosystem types is necessary before nematode community indices can be applied at large geographic scales, ranging from regional to global. The objectives of this study were to: (1) determine the inherent variability in soil properties among and within wetland, forest and agricultural ecosystems; (2) compare nematode community composition among and within ecosystem types and report genera detected in wetland soils; (3) determine if community composition or composite indices are able to differentiate type and magnitude of disturbance; (4) identify seasonal responses of nematode communities and indices to disturbance; (5) quantify variance components of nematode community measures at the land resource region (LRR) and ecosystem scale. Nematode communities were extracted from soils in relatively undisturbed and disturbed wetland, forest and agricultural soils in three LRR (coastal plain, piedmont and mountain) in North Carolina (n = 18 sites), seven to eight times per year for 2 years, starting in March 1994 and ending in November 1995. Overall, 48, 44 and 45 nematode families were observed in wetland, forest and agricultural soils, respectively. This inventory totaling 110 genera represents the richest nematode fauna reported from wetlands. After adjusting for soil properties as covariables, nematode maturity index (MI) values were inconsistent among ecosystems in their ability to distinguish levels of disturbance. The magnitude of disturbance was greater between relatively undisturbed and disturbed wetland than forest or agricultural soil. Nematode family composition differentiated levels of disturbance and ecosystems better than community indices, and current efforts indicate that taxonomic resolution at the level of genus is necessary for interpretation of ecosystem function. Deviation between disturbance levels in all ecosystems was greatest in July. For use in large-scale environmental monitoring programs, it is more cost-effective and easier to calibrate and interpret indices if variance is greatest at larger rather than at smaller spatial scales, e.g., variance is progressively smaller from among regions, among ecosystems and disturbance within ecosystems. This preferred order of ranking of variance by spatial scale occurred for nematode community indices MI, MI25, ΣMI25, and SI and abundance of predaceous nematodes. Variance was greater at smaller than at larger spatial scales for nematode community

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indices PPI, FB, CI, EI, trophic and family diversity, and relative abundance of bacterivorous, fungivorous, plant-parasitic and omnivorous nematodes.

Keywords: Agriculture; Canonical correspondence analysis; Environmental monitoring; Forest; Maturity index; Principal response curves; Riparian; Wetlands

1. Introduction

Belowground communities are a critical natural resource with immense, but largely unexplored, biodiversity (Andre et al., 1994, 2001; Wheeler et al., 2004; Science Editors, 2004). The perceived value of soil communities as ecological indicators will be increased by establishing their functional links to ecosystem processes (Debruyn, 1997), determining a hierarchy of geographic scale (Neher et al., 1998) and measuring their utility across ecosystem boundaries. Soil nematodes have the potential to provide insights into soil processes and condition (Ritz and Tradgill, 1999). Nematodes are ubiquitous, diverse, abundant, in direct contact with dissolved compounds in the soil water through their permeable cuticle, and easily extracted and assigned to ecological groups. Nematodes can serve as a model subsystem that provides a holistic measure of the biotic and functional status of soils (Bongers and Ferris, 1999; Neher, 2001). The development of the maturity index (MI) (Bongers, 1990) represented a significant advance in interpreting the relationship between the ecology of nematode communities and soil function, and thus, facilitated bioassessment studies using nematodes as indicators. The maturity index is based on the principle that different taxa have contrasting sensitivities to stress or disruption of the sequence of ecological succession because of their life-history characteristics. Since the introduction of the index, several authors have proposed modifications of the original (Popovici, 1992; de Goede and Dekker, 1993; Yeates, 1994; Bongers et al., 1995; Neher and Campbell, 1996; Ferris et al., 2001; Neher, 2001). The evolution of these concepts led to a wider application of nematode communities as ecological bioindicators of various terrestrial ecosystems, including agroecosystems (Freckman and Ettema, 1993; Yeates and Bongers, 1999), grasslands (Ekschmitt et al., 2001; Verschoor et al., 2001), forests (de Goede and Dekker, 1993) and wetlands (Ettema et al., 1999). The family of maturity indices has been able to successfully detect changes in soil condition caused by contamination with heavy metals (Yeates, 1994; Korthals et al., 1996, 1998; Nagy, 1999), addition of animal waste (Ettema and Bongers, 1993; Neher, 1999; Neher and Olson, 1999), addition of inorganic nitrogen (de Goede and Dekker, 1993; Freckman and Ettema, 1993; Neher, 1999), sod-cutting (de Goede, 1996), cultivation (Freckman and Ettema, 1993; Neher and Campbell, 1994; Wasilewska, 1994; Yeates, 1994) and fumigation with non-specific biocides (Ettema and Bongers, 1993; Yeates and van der Meulen, 1996).

Environmental disturbances can be classified in many ways. First, disturbances may be classified by type, i.e., chemical, physical, or biological, which alter invertebrate communities in qualitatively and quantitatively different ways. Second, disturbance can be described by characteristics of the disturbance, e.g., intensity, frequency, regularity and magnitude (Dyer and Letourneau, 2003). Third, disturbances may be seasonal or otherwise cyclical. Fourth, disturbances may be large or small in scale of impact, e.g., tree-fall or clear-cut. Overall, a disturbance regime may be specific to an ecosystem, geographic location or local climate, e.g., nutrient and pest management in annual agricultural systems, grazing pressure (e.g., species, stocking rate) on pastures, and harvest method of forests. Community indices can integrate responses to 'disturbance' because nematodes represent between five and eight trophic groups (Yeates et al., 1998) and occupy positions at primary, secondary and/or tertiary consumer level in soil food webs (Moore and de Ruiter, 1991). Apparently, different functional groups and genera are more or less tolerant to different 'modes' of disturbance. Although maturity indices generally have the ability to respond to specific disturbances, responses have not been fully consistent across regions, ecosystems, seasons or other conditions.

A better understanding of maturity index performance among major ecosystem types is necessary before indices can be applied at large geographical scales, ranging from regional to global (Coleman et al., 1992). In the present study, nematode communities were extracted from soils in relatively undisturbed and disturbed wetland, forest and agricultural soils in three land resource regions (LRR) in North Carolina (Neher et al., 2003). The objectives of this study were to: (1) determine the inherent variability in soil properties among and within wetland, forest and agricultural ecosystems; (2) compare nematode community composition among and within ecosystem types and report genera detected in wetland soils; (3) determine if community composition or composite indices are able to differentiate type and magnitude of disturbance; (4) identify seasonal responses of nematode communities and indices to disturbance; (5) quantify variance components of nematode community measures at the LRR and ecosystem scale.

2. Methods

2.1. Site selection

North Carolina was chosen as the initial study site for testing a range of indicators of ecosystem condition that could be applied across terrestrial ecosystems. North Carolina has a wide range of soil types and a diversity of terrestrial ecosystems including wetlands, forests and agriculture. These terrestrial ecosystems are arranged spatially in a mosaic in three LRR within the state, i.e., coastal plain, piedmont, and mountains, which represent geographic areas with unique soil type, topography, climate and water resources (USDA-SCS, 1981). We sampled relatively undisturbed and disturbed systems sites paired with similar soil type in each of three ecosystems and three LRR (Table 1, Neher et al., 2003). This scale of resolution is recommended by Neher et al. (1998) as the finest necessary for establishment of reference comparisons.

2.2. Soil samples

Soil samples were collected at all 18 sites seven to eight times per year for 2 years, starting in March 1994 and ending in November 1995. Because many soil characteristics are aggregated spatially, soil samples were collected using a systematic design. Two sets of soil samples were taken along two independent diagonal transects within a 2 ha area, with a random starting point (Neher et al., 1995). Soil samples were collected using an Oakfield tube soil probe (2 cm diameter, 20 cm depth); litter layers in forest and wetland sites were excluded. Twenty soil cores were collected from transect 1 and 40 soil cores were collected from transect 2. The soil from each transect was pooled to form two composite samples which were separately homogenized by hand in a bucket. The composite sample from transect 2 was split into two subsamples so variance within site and within a sample could be quantified for each characteristic measured (Neher et al., 1995). All soil samples were stored at 14 °C until processed (Barker et al., 1969).

A small (50 cm^3) portion of each sample collected for nematodes was analyzed for soil properties: percentage soil organic matter (OM), pH, electrical conductivity (EC), total available N (nitrate and ammonium) and texture (Neher et al., 2003). Soil OM was determined by loss-on-ignition (Schulte et al., 1991). Soil pH and EC were measured according to Smith and Doran (1996). Available pools of N were measured as the colorimetric product of nitrogen mineralization. Nitrate was determined by the method of Cataldo et al. (1975). The indophenol blue method was used to determine ammonium concentration (Keeney and Nelson, 1982). EDTA was added to the soil filtrate to prevent interference by calcium and magnesium ions. Soil texture was determined by the hydrometer method (Gee and Bauder, 1986).

2.3. Nematodes

Nematodes were extracted from soil using a Cobb's sieving and gravity method (Thorne, 1961; Ayoub, 1980) modified by triplicate passes through 710 μm-, 250 μm-, 150 μm-, 75 μm- and 45 μm-mesh sieves. The final pass through the sieves was followed by centrifugal-flotation (Caveness and Jensen, 1955), modified by using a 1:1 (v:v) sugar solution and centrifuging for 1 min (Neher and Campbell, 1994). Numbers of nematodes in each taxonomic family and trophic group from 500 cm^3

Table 1
Descriptions of relatively disturbed and undisturbed study sites in North Carolina[a] (adapted from Neher et al., 2003)

Ecosystem	Land resource region	Relative condition	Soil type	Vegetation history	N ($\mu g\ g^{-1}$)	EC ($dS\ m^{-1}$)	%SOM	pH
Forest	Mountain	Disturbed	Clayey	Harvested in 1990; hilltop planted to white pine, *Pinus strobus*, in 1993	2.3 (0.33)	0.05 (0.006)	5.8 (0.25)	4.8 (0.09)
	Piedmont	Disturbed	Sandy clay loam	Loblolly pine, *Pinus taeda*, planted 1992	1.7 (0.11)	0.05 (0.004)	6.7 (0.13)	4.8 (0.05)
	Coastal plain	Disturbed	Fine sandy loam	Loblolly pine planted in 1992	1.9 (0.29)	0.06 (0.006)	2.2 (0.05)	4.7 (0.07)
	Mountain	Undisturbed	Clayey	>90 year old white pine (dominant) with holly, *Ilex vomitoria*	2.4 (0.27)	0.09 (0.007)	4.9 (0.15)	4.6 (0.04)
	Piedmont	Undisturbed	Sandy clay loam	Loblolly pine planted 1939	2.3 (0.16)	0.08 (0.008)	5.1 (0.07)	4.9 (0.22)
	Coastal plain	Undisturbed	Fine sand	>80 year old longleaf pine, *Pinus palustris* (dominant) with loblolly bay, *Gordonia lasianthus*	1.7 (0.12)	0.07 (0.002)	4.9 (0.22)	4.2 (0.06)
Wetland	Mountain	Disturbed	Loam	Cultivated > 45 years; corn, *Zea mays*, planted in 1993	7.7 (1.96)	0.18 (0.030)	5.0 (0.12)	5.4 (0.07)
	Piedmont	Disturbed	Fine sandy loam	Cultivated > 55 years; soybeans, *Glycine max*, planted in 1993	5.4 (0.47)	0.16 (0.010)	6.6 (0.19)	5.6 (0.08)
	Coastal plain	Disturbed	Fine sandy loam	Cultivation history unknown; corn planted in 1993	16.8 (2.62)	0.26 (0.020)	18.3 (0.93)	4.6 (0.07)
	Mountain	Undisturbed	Loam	Undisturbed since 1968	3.6 (0.38)	0.12 (0.020)	8.4 (0.15)	4.7 (0.06)
	Piedmont	Undisturbed	Fine sandy loam	Planted to pines in 1960	4.5 (0.19)	0.16 (0.010)	9.0 (0.13)	4.9 (0.05)
	Coastal plain	Undisturbed	Fine sandy loam	Closed canopy natural pond pine, *Pinus serotina*, woodland	3.6 (0.28)	0.14 (0.006)	41.6 (2.9)	3.3 (0.06)
Agriculture	Mountain	Disturbed	Coarse-loamy	Cultivated > 16 years; field corn planted in 1993	25.3 (6.37)	0.28 (0.040)	9.7 (0.20)	5.5 (0.11)
	Piedmont	Disturbed	Sandy clay loam	Cultivated > 55 years; wheat, *Triticum aestivum*, and soybean planted in 1993	6.4 (1.16)	0.16 (0.010)	3.7 (0.15)	6.2 (0.07)
	Coastal plain	Disturbed	Fine sand	Cultivated > 50 years	2.7 (0.76)	0.07 (0.010)	1.6 (0.28)	5.9 (0.07)
	Mountain	Undisturbed	Coarse-loamy	Planted in fescue, *Festuca ovina*, and ladino clover, *Trifolium repens*, >20 years	6.7 (2.18)	0.19 (0.020)	9.6 (0.19)	6.6 (0.09)
	Piedmont	Undisturbed	Sandy clay loam	Fescue pasture planted in 1959	3.7 (0.36)	0.17 (0.010)	4.8 (0.17)	5.68 (0.08)
	Coastal plain	Undisturbed	Fine sand	Pasture since 1956	4.3 (0.98)	0.09 (0.009)	2.8 (0.11)	4.97 (0.08)

EC, electrical conductivity; SOM, soil organic matter.
[a] Values represent means and standard errors (±S.E.) ($n = 30$).

soil extracted were not corrected for extraction efficiency. A list of nematode genera observed within each taxonomic family was prepared for descriptive purposes. Nematodes were identified and counted by Mae Noffsinger (N & A Nematode Identification Service, Davis, CA). Voucher specimens were preserved in 10% formalin and 1.0% glycerin, sealed with Parafilm®, and deposited in the Department of Plant and Soil Science, University of Vermont in Burlington, USA. Taxonomic families were assigned to a trophic group (plant-parasites, bacterivores, fungivores, omnivores and predators) according to Yeates et al. (1993).

Algal-feeding nematodes were classified as omnivores, because they often feed on a variety of food sources such as algae and fungi. Taxonomic families were also assigned a colonizer-persister (cp) value of 1–5 according to Bongers (1990) with Monhysteridae re-classified into cp group 2 (Bongers et al., 1995). Eleven community indices were computed. Diversity of trophic groups and families was estimated by the Shannon–Weaver diversity index, $H' = \exp[-\Sigma P_i(\ln P_i)]$, where P_i is the proportion of trophic group (or family) i in the total nematode community (Ludwig and Reynolds, 1988). Maturity indices were computed in five different ways, i.e., free-living nematodes with cp-1 through cp-5 (MI), free-living nematodes with cp-2 through cp-5 (MI25), plant-parasitic nematodes (PPI), combined free-living and plant-parasitic nematodes with cp-1 through cp-5 (ΣMI), and combined free-living and plant-parasitic nematodes with cp-2 through cp-5 (ΣMI25). All maturity indices are weighted means computed as Σ[cp − va-value $(i)\cdot f(i)$]/[total numbers of nematodes] where (i) is the individual taxon and $f(i)$ is the frequency of free-living taxa in a sample (Bongers, 1990). Four indices of trophic group ratios were computed, i.e., channel index (CI), enrichment index (EI), structural index (SI) and fungivore to bacterivore ratio (FB) (Ferris et al., 2001; Neher, 1999). Large values of CI, EI and SI represent a dominance of fungi in the decomposition pathway, reflect the relative abundance and activity of primary detritus consumers, and represent food webs where recovery from stress is occurring, respectively (Ferris et al., 2001). FB describes the decomposition pathway in detritus food webs (Söhlenius et al., 1988). Smaller ratios are associated with faster rates of decomposition and nutrient turnover.

2.4. Statistical analysis

Data were analyzed as a completely nested design (Type II sums of squares) with fixed, independent variables defined as ecosystem type and disturbance nested within ecosystem; LLR was a random variable. Repeated measures analysis of covariance was performed using the MIXED procedure in SAS Version 8 (Cary, NC). Separate analyses were performed for each nematode community index (trophic diversity, family diversity, MI, MI25, ΣMI, ΣMI25, PPI, CI, EI, SI, FB), family and trophic group with sequential sampling period as the subject variable. Covariates included soil organic matter, pH, electrical conductivity and total available nitrogen. To meet assumptions of normality, proportion of organic matter and electrical conductivity were transformed as $\ln(x + 0.01)$ and total nitrogen availability as $\ln(x + 0.1)$ prior to statistical analysis.

Canonical correspondence analysis (CCA) was performed to explore the distribution of nematode families in relation to ecosystem-disturbance combination. A direct gradient procedure was performed with 'CANOCO' software, Version 4.5 (ter Braak and Šmilauer, 2002). Site types (ecosystem, disturbance level) were treated as nominal (0, 1) environmental variables. Soil chemical properties thought to be most influential in structuring nematode populations were treated as covariates, i.e., pH, organic matter, electrical conductivity, total nitrogen (i.e., nitrate + ammonium). Scaling was focused on interspecies distances with Hill's scaling. Nematode abundances were transformed as $\ln(x + 0.1)$ to normalize data prior to application of CCA, as is typical for many analyses of nematode population counts that are skewed (Neher et al., 1995). Rare species were not down-weighted because they may represent taxa sensitive to disturbance or, otherwise, play key roles in soil function. A Monte Carlo permutation option was employed to determine the significance of first and second axes.

Differences in community composition between the relatively disturbed and undisturbed conditions for each ecosystem through time were analyzed and

illustrated using principal response curves (PRC). PRC is a multivariate method for the analysis of repeated measurement design. PRC is based on redundancy analysis (RDA); each experimental unit (3 ecosystems × 2 levels of disturbance), 13 sampling times and unit by time interactions were treated as dummy explanatory variables. Prior to analysis, abundances were log-transformed. The result is a diagram showing the sampling periods on the *x*-axis and the first Principal Component of the variance explained by treatment on the *y*-axis. For illustrative purposes, the undisturbed condition was treated as a 'control', representing a zero baseline, and the 'disturbed' condition of the same experimental unit as the 'treatment' to focus on the *differences* between the two states of condition through time. Monte Carlo permutation tests permuting whole time series were applied to compute statistical significance. Van den Brink et al. (2003) provide a review of the analytical procedure and detailed instruction is provided in the manual of Canoco Version 4.5 software (ter Braak and Šmilauer, 2002).

Variance components analysis was preformed with the VARCOMP procedure in SAS Version 8. Variance was estimated for each community index among LRR, among ecosystems and within ecosystems. Prior to analysis, values of each index were standardized (mean = 0, S.D. = 1) with the STANDARD procedure in SAS Version 8 for easier comparison.

3. Results

3.1. Soil properties

Ecosystems and the relative degree of disturbance within ecosystems were distinguished by contrasting soil properties (Fig. 1). For example, disturbed wetland ecosystems were characterized by relatively high total available N content and high EC values. Relatively undisturbed wetlands were typified by high soil OM content and low soil pH values. Forest soils were differentiated by low fertility, as indicated by low available N concentrations and low EC values. Organic matter levels and pH values in forests were intermediate between agricultural and undisturbed wetland soils. Agricultural sites showed no relative marked effect of disturbance.

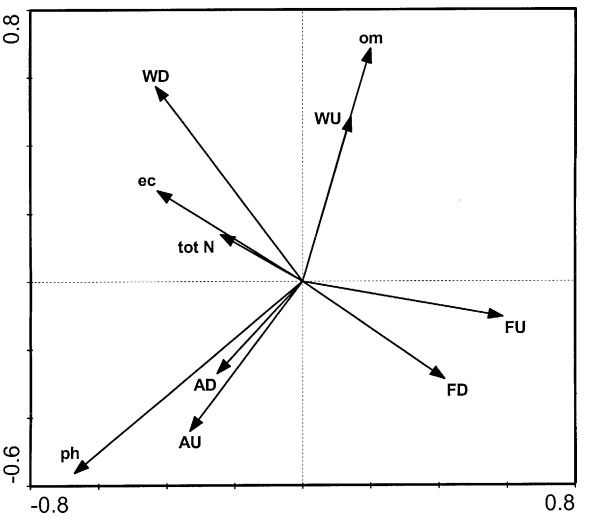

Fig. 1. Canonical correspondence analysis bi-plot of association of soil properties (om, % organic matter; ec, electrical conductivity; ph, pH; totN, sum of mg nitrate and ammonium per g dry soil) and ecosystem-disturbance variables (FD—forest, disturbed; FU—forest, undisturbed; AD—agriculture, disturbed; AU—agriculture, undisturbed; WD—wetlands, disturbed; WU—wetlands, undisturbed). Data represent two independent samples from all 18 sites sampled 13 times in 1994 and 1995 combined ($n = 540$). Eigenvalues (lambda) are 0.094 ($F = 35.3$, $p = 0.0020$), 0.058, 0.036 and 0.021 for first (horizontal), second (vertical), third and fourth axes, respectively. The first two axes explained 58% of the variation.

3.2. Nematode communities

The total abundance of nematodes was greater in wetland and agricultural than in forest soils (Table 2). Overall, we detected 48, 44 and 45 nematode families in wetland, forest and agricultural soils, respectively (Table 2). Within an ecosystem, disturbance tended to reduce family richness. Although detectable only in very low numbers in undisturbed soils, five of the nematode families were undetectable in any disturbed soils: Bunonematidae, Chromadoridae, Iotonchulidae, Isolaimidae and Microlaimidae.

Among ecosystems, the percentages of the community represented by omnivores and predators were not different significantly (Table 2). The percentage of bacterivores was greatest in forest, intermediate in wetland, and least in agricultural soils. The percentages of fungivores were greatest in forest, intermediate in agricultural, and least in wetland soils. The percentages of plant-parasites

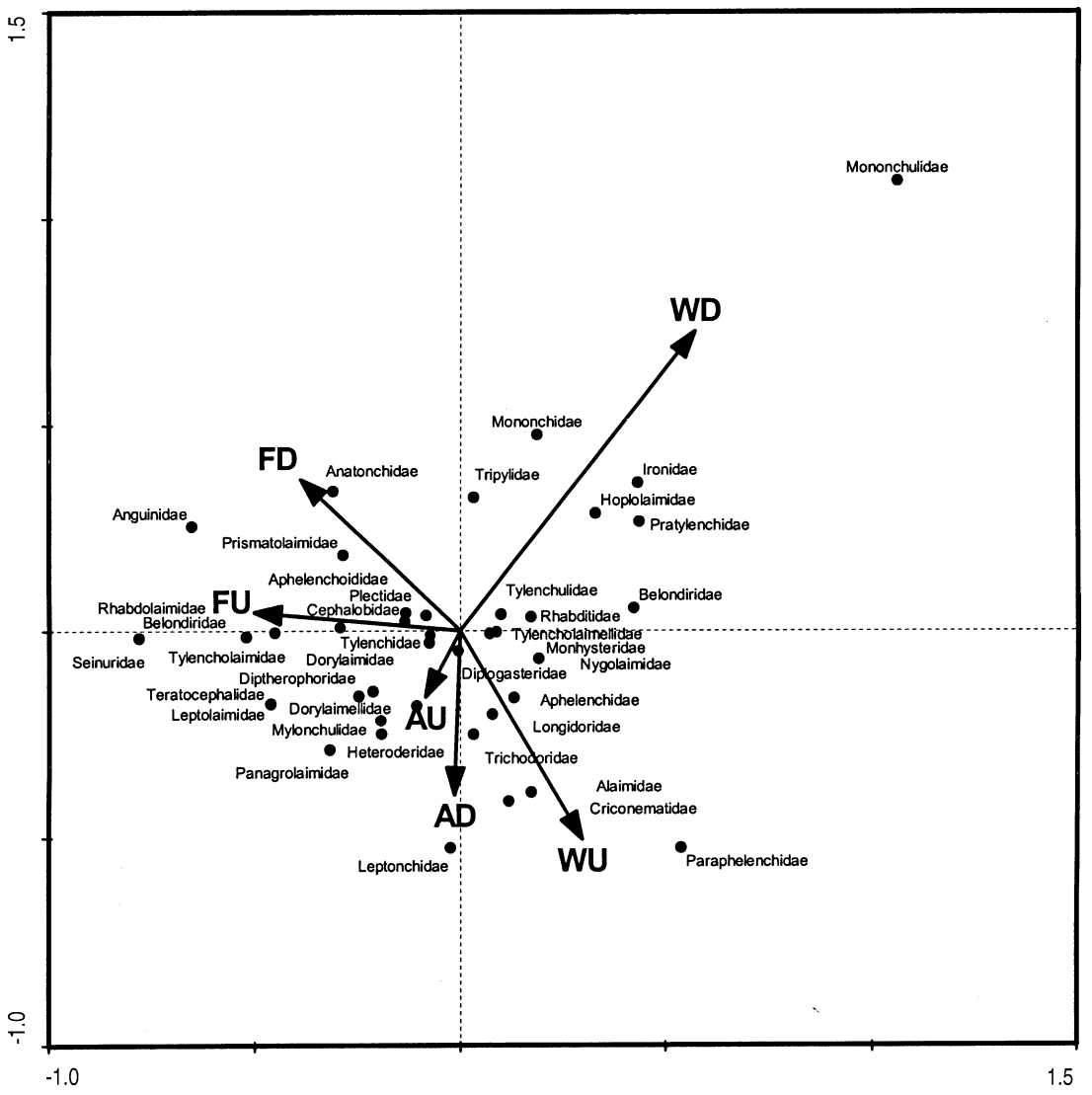

Fig. 2. Canonical correspondence analysis bi-plot of soil nematode families and ecosystem-disturbance variables (FD—forest, disturbed; FU—forest, undisturbed; AD—agriculture, disturbed; AU—agriculture, undisturbed; WD—wetlands, disturbed; WU—wetlands, undisturbed). Soil properties (organic matter, electrical conductivity, pH and total nitrogen, see Fig. 1) were treated as covariables. Points represent numbers of nematodes enumerated to family; abundances decrease with increasing distance from each point in a unimodal fashion (ter Braak and Šmilauer, 2002). Data represent two independent samples from all 18 sites sampled during 13 sampling times in 1994 and 1995 ($n = 540$). Eigenvalues (lambda) are 0.051 ($F = 20.4$, $p = 0.002$), 0.034, 0.022 and 0.016 for first (horizontal), second (vertical), third and fourth axes, respectively. The first two axes explain 62.7% of the variation.

were greatest in wetland, intermediate in agricultural, and least in forest soils.

Nematode community composition varied more among ecosystem types than between levels of disturbance within ecosystem type (Fig. 2). Two taxa were unique to wetlands: Microlaimidae and Oxydiridae (Tables 2 and 3). Within wetlands, nematodes in the families Cephalobidae, Hoplolaimidae, Rhabditi-

Table 2
Mean ± S.E. abundance of nematode families per 100 g dry soil in relatively disturbed (D) and undisturbed (U) wetland, forest and agricultural ecosystems

Family	Trophic group[a]	cp Value	Wetland		Forest		Agriculture	
			U (n = 70)	D (n = 70)	U (n = 75)	D (n = 74)	U (n = 75)	D (n = 72)
Alaimidae	B	4	116.9 ± 26.8	7.8 ± 2.1	8.9 ± 1.5	3.4 ± 1.1	9.1 ± 2.0	6.2 ± 1.4
Anatonchidae	P	4	0.3 ± 0.2	1.2 ± 0.4	0.8 ± 0.3	1.3 ± 0.4	2.1 ± 1.2	0.7 ± 2.5
Anguinidae	F	2	3.6 ± 1.4	3.8 ± 1.0	33.6 ± 7.9	56.6 ± 12.2	24.3 ± 6.4	19.9 ± 9.2
Aphelenchidae	F	2	42.7 ± 7.5	28.1 ± 4.9	0.6 ± 0.2	13.3 ± 2.7	96.1 ± 16.5	48.6 ± 7.2
Aphelenchoididae	F	2	28.0 ± 5.1	22.4 ± 4.0	23.5 ± 3.2	24.8 ± 3.1	27.9 ± 3.5	24.9 ± 4.1
Bastianidae	B	3	2.7 ± 2.0	0.07 ± 0.07	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0
Belondiridae	O	5	0.5 ± 0.2	0.3 ± 0.2	0.09 ± 0.09	1.6 ± 0.4	5.8 ± 1.3	1.2 ± 0.5
Belonolaimidae	PP	2	11.5 ± 3.1	48.4 ± 7.9	1.0 ± 0.4	1.1 ± 0.3	24.7 ± 5.1	35.6 ± 5.4
Bunonematidae	B	1	1.5 ± 1.5	0	0	0	0.07 ± 0.07	0
Carcharolaimidae	P	4	1.6 ± 1.6	0	1.5 ± 1.5	0	1.2 ± 1.2	1.2 ± 0.5
Cephalobidae	B	2	191.8 ± 21.3	145.0 ± 16.8	163.6 ± 14.7	109.9 ± 13.7	253.5 ± 23.9	151.9 ± 18.0
Chromadoridae	P	3	13.0 ± 11.1	0	0.7 ± 0.4	0	0	0
Criconematidae	PP	3	160.9 ± 26.0	20.4 ± 5.8	14.1 ± 2.2	19.1 ± 3.4	59.9 ± 8.9	102.9 ± 12.6
Cyatholaimidae	O	3	2.9 ± 2.1	0.6 ± 0.3	0.8 ± 0.3	1.7 ± 1.2	0	0.9 ± 0.3
Cylindrolaimidae	B	3	6.4 ± 4.4	0.06 ± 0.06	0	0	0.06 ± 0.06	0.05 ± 0.05
Diphtherophoridae	F	3	11.8 ± 3.5	2.2 ± 0.9	14.9 ± 3.9	12.1 ± 3.1	24.0 ± 5.9	7.8 ± 1.5
Diplogasteridae	O	1	4.7 ± 1.8	7.1 ± 1.8	2.4 ± 0.7	0.4 ± 0.2	27.8 ± 8.6	6.1 ± 1.9
Diploscapteridae	B	1	10.9 ± 10.9	0	0.2 ± 0.2	0	0	0.2 ± 0.1
Dorylaimellidae	O	5	7.7 ± 5.0	2.7 ± 2.5	0.08 ± 0.04	2.0 ± 0.6	4.8 ± 1.8	1.2 ± 0.5
Dorylaimidae	O	4	60.4 ± 13.2	43.0 ± 5.4	38.6 ± 5.2	39.4 ± 4.6	69.2 ± 7.4	63.4 ± 5.4
Heteroderidae	PP	3	7.8 ± 5.1	3.1 ± 2.5	0.7 ± 0.4	2.5 ± 1.4	4.9 ± 1.6	2.5 ± 0.9
Hoplolaimidae	PP	3	113.3 ± 16.4	187.9 ± 17.9	8.1 ± 1.7	33.5 ± 7.1	33.6 ± 4.4	22.1 ± 4.1
Iotonchulidae	P	4	0	0	0.2 ± 0.1	0	0	0
Ironidae	P	4	1.6 ± 1.6	0.7 ± 0.3	0	0.06 ± 0.06	0	0.5 ± 0.3
Isolaimidae	B	4	0	0	0	0	0.07 ± 0.07	0
Leptolaimidae	B	3	3.6 ± 2.5	0	0.3 ± 0.2	0.6 ± 0.4	0.4 ± 0.3	0.4 ± 0.4
Leptonchidae	O	4	4.7 ± 2.7	0.1 ± 0.1	1.6 ± 0.6	0.2 ± 0.2	2.1 ± 1.2	2.9 ± 1.1
Longidoridae	PP	5	0.3 ± 0.2	2.4 ± 0.6	0.7 ± 0.3	1.3 ± 0.4	8.5 ± 1.6	9.9 ± 2.0
Microlaimidae	B	3	0.08 ± 0.08	0	0	0	0	0
Monhysteridae	B	2[b]	1.2 ± 1.0	0.8 ± 0.3	0.6 ± 0.3	0.07 ± 0.07	0.3 ± 0.2	0.9 ± 0.3
Mononchidae	P	4	4.2 ± 1.2	11.2 ± 2.2	1.5 ± 0.4	6.2 ± 1.3	3.3 ± 1.5	3.5 ± 0.7
Mononchulidae	P	4	0.09 ± 0.09	3.1 ± 2.4	0.1 ± 0.1	0.06 ± 0.06	0.06 ± 0.06	0
Mylonchulidae	P	4	6.4 ± 3.9	1.3 ± 0.4	1.8 ± 0.5	0.8 ± 0.3	1.4 ± 0.4	4.1 ± 0.7
Nygolaimidae	P	5	974.6 ± 759.2	4.3 ± 1.8	0.3 ± 0.1	0.1 ± 0.09	3.0 ± 1.4	6.7 ± 1.6
Oxydiridae	PP	4	448.6 ± 257.7	452.9 ± 320.1	0	0	0	0
Panagrolaimidae	B	1	0.2 ± 0.1	0.6 ± 0.4	0.07 ± 0.07	0	0	0
Paraphelenchidae	F	2	0	0.8 ± 0.4	0	0	0.3 ± 0.2	0.6 ± 0.3
Plectidae	B	2	21.1 ± 4.1	17.1 ± 2.9	17.5 ± 2.9	11.0 ± 2.5	11.5 ± 1.9	26.5 ± 5.5
Pratylenchidae	PP	3	42.2 ± 12.0	60.5 ± 16.3	18.6 ± 6.1	4.8 ± 1.6	14.1 ± 2.4	20.0 ± 4.5
Prismatolaimidae	B	3	45.8 ± 15.3	35.4 ± 11.2	18.4 ± 4.6	10.8 ± 3.0	6.7 ± 1.4	10.0 ± 4.8

Table 2 (*Continued*)

Family	Trophic group[a]	cp Value	Wetland		Forest		Agriculture	
			U ($n = 70$)	D ($n = 70$)	U ($n = 75$)	D ($n = 74$)	U ($n = 75$)	D ($n = 72$)
Rhabditidae	B	1	126.9 ± 23.0	129.9 ± 23.6	56.0 ± 15.8	33.2 ± 9.3	66.5 ± 15.3	122.0 ± 22.6
Rhabdolaimidae		3	1.4 ± 1.4	1.8 ± 1.8	0.5 ± 0.3	1.4 ± 0.9	0.08 ± 0.08	0.3 ± 0.3
Seinuridae	P	2	0	0.07 ± 0.07	0.8 ± 0.4	0	0.5 ± 0.4	0.1 ± 0.1
Teratocephalidae	B	3	0.08 ± 0.08	0.7 ± 0.6	0.09 ± 0.09	0.2 ± 0.2	0.2 ± 0.1	0.6 ± 0.6
Trichodoridae	PP	4	2.5 ± 1.1	1.3 ± 0.4	2.2 ± 0.8	1.1 ± 0.3	5.0 ± 2.1	2.3 ± 0.6
Tripylidae	O	3	4.9 ± 2.5	7.0 ± 3.4	1.9 ± 0.6	0.5 ± 0.2	11.7 ± 10.6	2.5 ± 1.7
Tylenchidae	F	2	192.1 ± 25.2	156.7 ± 20.7	79.6 ± 9.0	102.3 ± 14.6	129.8 ± 14.5	188.1 ± 22.3
Tylencholaimellidae	F	4	1.5 ± 1.0	1.2 ± 0.5	1.0 ± 0.5	1.3 ± 0.4	1.3 ± 0.5	1.6 ± 0.6
Tylencholaimidae	F	4	1.7 ± 0.9	7.8 ± 5.4	5.1 ± 0.9	5.5 ± 1.3	2.0 ± 1.2	1.5 ± 0.6
Tylenchulidae	PP	2	16.2 ± 4.2	7.4 ± 2.4	10.0 ± 2.4	8.9 ± 2.3	30.6 ± 7.6	17.1 ± 4.2
Trophic structure (%)								
Bacterivores			41.7 ± 1.8 Aa[c]	31.8 ± 1.8 a	48.2 ± 1.8 Ba	33.0 ± 1.9 b	34.6 ± 1.7 Ba	29.2 ± 1.6 a
Fungivores			25.8 ± 1.2 Aa	18.4 ± 1.2 b	31.7 ± 1.5 Ba	39.6 ± 2.0 b	30.5 ± 1.3 Ca	30.4 ± 2.0 a
Plant-parasites			24.5 ± 1.8 Aa	40.2 ± 2.1 b	8.6 ± 1.1 Ba	13.8 ± 1.7 b	21.8 ± 1.4 Ca	27.2 ± 2.3 a
Omnivores			7.0 ± 0.8 Aa	6.5 ± 0.6 a	10.1 ± 1.0 Aa	11.3 ± 1.5 a	12.0 ± 1.2 Aa	10.9 ± 1.0 a
Predators			0.9 ± 0.2 Aa	3.1 ± 0.6 b	1.4 ± 0.3 Aa	2.3 ± 0.4 a	1.0 ± 0.3 Aa	2.3 ± 0.5 b
Total abundance			1618 ± 203 Aa	1053 ± 95 a	469 ± 30 Ba	494 ± 39 a	1084 ± 88 Aa	814 ± 59 a

Values are pooled across 13 sampling times from March 1994 to November 1995.

[a] B, bacterivores; F, fungivores; O, omnivores; P, predators; PP, plant-parasites.

[b] cp changed from 1 to 2 (Bongers et al., 1995).

[c] Statistical significance is designed by contrasting letters, with upper case (A, B) comparing ecosystems ($p < 0.05$) and lower case (a, b) comparing D and U within an ecosystem ($p < 0.05$).

Table 3
Abundance ± S.E. of nematodes per 100 g dry soil in relatively disturbed (D) and undisturbed (U) wetland ecosystems

Family	Genus	U ($n = 72$)	D ($n = 70$)
Alaimidae	*Alaimus*, *Amphidelus*	113.7 ± 26.1	7.8 ± 2.1
Anatonchidae	*Anatonchus*, *Miconchus*	0.3 ± 0.1	1.2 ± 0.4
Anguinidae	*Anguina*, *Ditylenchus*, *Pseudhalenchus*	3.5 ± 1.4	3.8 ± 1.0
Aphelenchidae	*Aphelenchus*	41.5 ± 7.3	28.1 ± 4.9
Aphelenchoididae	*Aphelenchoides*	27.9 ± 4.9	22.4 ± 4.0
Belondiridae	*Axonchium*, *Belondira*	0.5 ± 0.2	0.3 ± 0.2
Belonolaimidae	*Belonolaimus*, *Merlinius*, *Tylenchorhynchus*	11.2 ± 3.0	48.4 ± 7.9
Cephalobidae	*Acrobeles*, *Acrobeloides*, *Cervidellus*, *Eucephalobus*, *Chiloplacus*, *Placodira*, *Zeldia*	285.6 ± 55.7	160.6 ± 21.5
Criconematidae	*Hemicriconemoides*, *Hemicycliophora*, *Criconemella*, *Ogma*	196.0 ± 34.7	20.4 ± 5.8
Diphtherophoridae	*Diphtherophora*, *Tylolaimophorus*	18.8 ± 5.4	2.3 ± 0.9
Diplogasteridae	*Butlerius*, *Mononchoides*, *Paroigolaimella*, *Pristionchus*	4.6 ± 1.7	7.1 ± 1.8
Dorylaimellidae	*Dorylaimellus*	2.5 ± 2.0	0.2 ± 0.2
Dorylaimidae	*Aporcelaimus*, *Discolaimus*, *Dorylaimus*, *Drepanodorus*, *Eudorylaimus*, *Labronema*, *Longidorella*, *Mesodorylaimus*, *Prodorylaimus*, *Pungentus*, *Thornenema*	63.6 ± 11.6	45.6 ± 5.7
Heteroderidae	*Meloidogyne*, *Heterodera*, *Meloidodera*	2.6 ± 0.8	0.7 ± 0.4
Hoplolaimidae	*Helicotylenchus*, *Hoplolaimus*, *Rotylenchulus*, *Scutellonema*	188.1 ± 54.9	244.8 ± 54.6
Ironidae	*Cryptonchus*, *Ironus*	1.5 ± 1.5	0.8 ± 0.3
Leptolaimidae	*Aphanolaimus*	1.9 ± 1.8	0
Leptonchidae	*Leptonchus*, *Dorylaimoides*, *Doryschota*, *Paraphanolaimus*, *Proleptonchus*, *Doryllium*	8.7 ± 3.9	0.1 ± 0.1
Longidoridae	*Xiphinema*	0.3 ± 0.2	2.4 ± 0.6
Monhysteridae	*Monhystera*, *Monhystrella*, *Theristus*	1.1 ± 1.0	0.8 ± 0.3
Mononchidae		4.0 ± 1.2	11.2 ± 2.2
Mononchulidae	*Dionchus*	0.09 ± 0.09	3.1 ± 2.4
Mylonchulidae	*Mylonchulus*, *Granonchulus*, *Sporonchulus*	6.8 ± 3.8	1.3 ± 0.4
Nygolaimidae	*Nygolaimus*, *Sectonema*	0.3 ± 0.2	4.3 ± 1.8
Panagrolaimidae	*Panagrolaimus*	0.5 ± 0.4	0.07 ± 0.07
Paraphelenchidae	*Paraphelenchus*	1.4 ± 0.6	0.3 ± 0.2
Plectidae	*Anaplectus*, *Chronogaster*, *Plectus*, *Tylocephalus*, *Wilsonema*	44.0 ± 8.5	16.8 ± 2.7
Pratylenchidae	*Pratylenchus*	12.7 ± 3.0	95.1 ± 17.9
Prismatolaimidae	*Prismatolaimus*	69.1 ± 16.0	16.8 ± 5.4
Rhabditidae	*Bursilla*, *Cruznema*, *Mesorhabditis*, *Poikilolaimus*, *Rhabdititis*, *Rhitis*, *Teratorhabditis*	150.7 ± 25.0	156.0 ± 26.1
Rhabdolaimidae	*Rhabdolaimus*	3.1 ± 2.2	0.09 ± 0.09
Seinuridae	*Seinura*	3.5 ± 3.5	0
Teratocephalidae	*Euteratocephalus*, *Teratocephalus*	0.7 ± 0.6	0.09 ± 0.09
Trichodoridae	*Trichodorus*, *Paratrichodorus*	3.7 ± 1.2	1.0 ± 0.7
Tripylidae	*Tripyla*, *Tobrilus*	3.1 ± 2.5	3.1 ± 1.4
Tylenchidae	*Aglenchus*, *Atylenchus*, *Basiria*, *Boleodorus*, *Coslenchus*, *Ecphyadophora*, *Filenchus*, *Miculenchus*, *Psilenchus*, *Tylenchus*	317.5 ± 39.5	125.7 ± 14.7
Tylencholaimellidae	*Tylencholaimellus*	1.3 ± 0.5	1.5 ± 0.6
Tylencholaimidae	*Enchodelus*, *Tylencholaimus*, *Longidorella*	3.3 ± 1.7	1.9 ± 0.7
Tylenchulidae	*Paratylenchus*, *Gracilacus*, *Trophotylenchulus*	15.4 ± 5.6	17.6 ± 4.2

Values are pooled across 13 sampling times from March 1994 to November 1995.

dae, Pratylenchidae, and Tylenchidae were most abundant. We measured greater differences between disturbance level in wetland than in forest or agricultural soil. Generally, Nygolaimidae, Monhysteridae, Tylencholaimellidae, Rhabditidae, and Belondiridae were more abundant in wetland than in forest or agricultural soils, regardless of relative level of disturbance. Paraphelenchidae were more abundant in

relatively undisturbed than disturbed wetland soils. Even though both were planted to agricultural crops, Pratylenchidae, Hoplolaimidae, Ironidae, Mononchulidae, Mononchidae, and Tripylidae were more numerous in disturbed wetlands than in agricultural ecosystems.

The effect of disturbance on the trophic structure of nematode communities varied among ecosystems (Table 2). The trophic structure associated with disturbance was altered more in wetland and forest than in agricultural soils. The percentages of plant-parasites and predators increased, and fungivores decreased with disturbance in wetland soils. In forests, percentages of fungivores and plant-parasites increased, and bacterivores decreased, with disturbance. In agricultural soils, the percentages of predators increased significantly with disturbance; no other trophic group changed.

After adjusting for soil properties as covariables, maturity index values were inconsistent among ecosystems in their ability to distinguish levels of disturbance (Table 4). The only index that distinguished levels of disturbance in wetland soils was the CI; values were greater in undisturbed than disturbed soils. The EI and diversity based on nematode family distinguished levels of disturbance in forests; both were greater in disturbed compared with undisturbed soils. MI and ΣMI25 were greater in disturbed than in undisturbed agricultural soils. MI25, PPI, SI, FB and diversity based on trophic groups were not able to distinguish level of disturbance in any of the ecosystems.

3.3. Seasonal fluctuation

Community composition fluctuated seasonally in all ecosystems. Deviation of community composition relative to the undisturbed condition was greatest in July 1994 for all ecosystems (Fig. 3). The pattern of change was similar in direction in July 1995, but the magnitude of difference in community composition was inconsistent. The nematode community that was associated with disturbed wetland soils differed in composition from the community associated with disturbance in forest and agricultural soils (Figs. 2 and 3).

3.4. Components of variance

Relatively greater variance was observed among LRRs than among ecosystems for the MI, MI25, ΣMI25, and SI indices and proportion of predaceous nematodes (Table 5). More variance was observed among and/or within ecosystems than for LRR for PPI, FB, CI, EI and trophic and family diversity and

Table 4
Mean index value ± S.E. by ecosystem disturbance level

Index	Wetlands		Forest		Agriculture	
	U (n = 72)	D (n = 70)	U (n = 75)	D (n = 74)	U (n = 75)	D(n = 71)
MI	2.24 ± 0.04 Aa[a]	2.16 ± 0.04 a	2.36 ± 0.04 Aa	2.39 ± 0.04 a	2.19 ± 0.04 Aa	2.32 ± 0.05b
MI25	2.48 ± 0.03 Aa	2.47 ± 0.04 a	2.44 ± 0.03 Ba	2.45 ± 0.04 a	2.39 ± 0.03 Ba	2.49 ± 0.04a
PPI	2.96 ± 0.01 Aa	2.84 ± 0.02 a	3.07 ± 0.07 Aa	2.96 ± 0.07 a	2.73 ± 0.04 Aab	2.90 ± 0.03b
ΣMI25	2.61 ± 0.02 Aa	2.65 ± 0.03 a	2.48 ± 0.03 Ba	2.51 ± 0.04 a	2.48 ± 0.03 Ba	2.60 ± 0.04b
CI[b]	59.3 ± 4.3 Aa	38.2 ± 3.4 b	71.6 ± 3.5 Ba	80.6 ± 2.8 a	65.6 ± 3.9 Ba	56.8 ± 3.6a
EI	70.4 ± 2.6 Aa	76.1 ± 1.8 a	51.1 ± 2.1 Ba	64.5 ± 2.0 b	65.1 ± 2.4 Ba	69.8 ± 2.3a
SI	44.5 ± 2.2 Aa	50.0 ± 2.4 a	48.4 ± 2.4 Aa	47.5 ± 2.7 a	43.6 ± 2.3 Ba	49.6 ± 2.6a
FB[c]	0.39 ± 0.02 Aa	0.37 ± 0.02 a	0.40 ± 0.02 Aa	0.54 ± 0.02 b	0.48 ± 0.02 Aa	0.50 ± 0.02a
Trophic diversity[d]	3.24 ± 0.06 Aa	3.33 ± 0.07 a	3.03 ± 0.06 Ba	3.22 ± 0.08 a	3.49 ± 0.05 ABa	3.44 ± 0.06a
Family diversity[d]	8.73 ± 0.29 Aa	9.24 ± 0.32 a	10.46 ± 0.45 Aa	14.82 ± 3.62 b	9.94 ± 0.38 Aa	10.02 ± 0.30a

Values are pooled across 13 sampling times from March 1994 to November 1995.

[a] Statistical significance is designed by contrasting letters, with upper case (A, B) comparing ecosystems ($p < 0.05$) and lower case (a, b) comparing D and U within an ecosystem ($p < 0.05$).

[b] CI, channel index; EI, enrichment index; SI, structural index (Ferris et al., 2001).

[c] FB = fungivores/(fungivores + bacterivores) (Neher, 1999).

[d] Computed as Hill's N1, i.e., $H' = \exp[-\Sigma P_i(\ln P_i)]$, where P_i is the proportion of group i in the total nematode community (Ludwig and Reynolds, 1988).

Table 5
Components of variance

Index[a]	Among LRR[b]	Among ecosystems	Within ecosystems
MI	0.0211	0.0117	0.0089
MI25	0.0963	0.0784	0.0209
PPI	0	0.0797	0.0612
ΣMI25	0.0106	0.0098	0.0044
FB	0	0.1461	0.1489
%CI	94.20	175.78	198.58
%EI	68.16	76.68	62.65
%SI	72.10	24.13	18.35
Trophic diversity[c]	0	0.2480	0.0385
Family diversity[c]	0	0.0332	0.0077
Prop. bacterivores	0	0.0026	0.0058
Prop. fungivores	0	0.0050	0.0035
Prop. plant-parasites	0.0001	0.0119	0.0062
Prop. omnivores	0	0.0009	0.0003
Prop. predators	0.0001	0	0.0001

Values are pooled across 13 sampling times from March 1994 to November 1995. Valid comparisons are among columns within a row.
[a] CI, channel index; EI, enrichment index; SI, structural index (Ferris et al., 2001).
[b] LRR, land resource regions.
[c] Computed as Hill's N1, i.e., $H' = \exp[-\Sigma P_i(\ln P_i)]$, where P_i is the proportion of group i in the total nematode community (Ludwig and Reynolds, 1988).

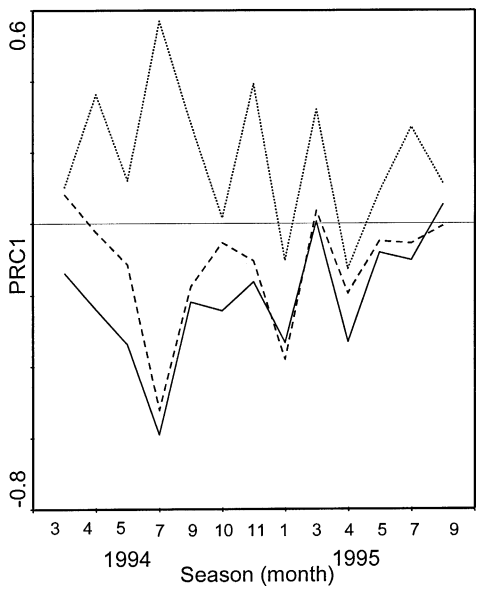

Fig. 3. Principal response curves, illustrating changes of nematode community composition through 13 sampling times in 1994 and 1995. The horizontal line at 0 represents undisturbed condition and fluctuating lines represent the deviation from the undisturbed condition that disturbance caused in wetlands (dotted line), forest (solid line) and agriculture (dashed line) ecosystems. The numbers on the x-axis represent months (1 = January to 11 = November).

relative abundance of bacterivorous, fungivorous, plant-parasitic and omnivorous nematodes.

4. Discussion

Implementation of the use of nematode community indices for large-scale environmental monitoring faces two major impediments: the lack of empirical tests of their universality across regions and ecosystems, and inaccessibility to taxonomic expertise needed before indices can be calculated (Bloemers et al., 1997; Neher, 2001). It is more cost-effective to use community indices calculated on the basis of coarse taxonomic resolution because of their statistical reliability with relatively few samples (Neher et al., 1995; Neher and Campbell, 1996). Nematode communities and indices have been evaluated for their ability to detect changes in response to environmental characteristics in many types of ecosystems (de Goede and Dekker, 1993; Freckman and Ettema, 1993; Ettema et al., 1999; Yeates and Bongers, 1999; Ekschmitt et al., 2001; Verschoor et al., 2001). Here, we evaluated the ability of several measures of soil nematode communities to

detect the relative level of disturbance across LRR and ecosystems.

4.1. Ecosystems

We included wetlands in our study because of their high productivity and role as an environmental buffer. Despite the importance of wetlands, we are aware of only a few reports on wetland nematodes. We detected a total of 110 nematode genera. To our knowledge, this inventory represents the richest nematode fauna among wetland nematode studies. Murialdo et al. (2002) observed relatively low diversity at the La Tapera creek wetland, and reported *Boleodorus*, *Clarkus*, *Discolaimium*, *Discolaimoides*, *Hoplolaimus*, *Ibipora*, *Macroposthonia*, *Mesorhabditis*, *Mylonchulus,* and *Rhabditis*. Ettema et al. (1998) recorded the spatio-temporal distribution of bacterivorous nematodes in a riparian wetland and reported *Acrobeloides*, *Prismatolaimus*, *Rhabdolaimus*, *Chronogaster*, *Monhystrella*, *Heterocephalobus*, *Eumonhystera* and Rhabditinae. We detected all of these bacterivorous genera except for *Heterocephalobus* and *Eumonhystera*.

Unique suites of soil properties characterize wetland, forest and agricultural soils. Land management, through its effects on plant species and diversity, fertility inputs and other characteristics, affects nematode communities (e.g., de Goede and Bongers, 1994; Yeates et al., 1999). Shayestehfar et al. (1998) note positive correlations among nematode abundance, soil moisture, pH and organic matter in soils adjacent to a lake. We did not detect a direct relationship between nematode abundance and diversity with soil OM. This may have been due to interactions with other factors, e.g., soil pH. In our study, the accumulation of litter to 1 m depth (which we did not sample) in an undisturbed wetland in the coastal plains was accompanied by a soil pH of 4.3, which correlated with negligible decomposition (Neher et al., 2003). Root and fungivorous nematodes are probably more tolerant of soil acidification than bacterivorous nematodes. Our results agree with Hyvönen and Persson (1990) who found that abundance of the fungivore, *Aphelenchoides*, remained unchanged in acidified soil in Norwegian coniferous forests. In contrast, abundance of bacterivores *Acrobeloides*, *Protorhabditis* and *Eumonhystera* increased and *Wilsonema* decreased with additions of lime, with a net result of decreasing MI index values (de Goede and Dekker, 1993). Values of maturity indices correlate negatively with inorganic N fertilization in agricultural soils (Neher, unpublished) and positively with inorganic and organic N in grassland soils (Ekschmitt et al., 2001). In undisturbed wetlands and agricultural systems, pH and OM, and in forests and disturbed wetlands, total available N and EC, should be used as covariables when interpreting nematode communities (Neher et al., 2003).

4.2. Effects of ecosystem/disturbance level

The composition and structure of nematode communities reflect disturbance within an ecosystem. The impact of disturbance was ecosystem specific. In our study, the magnitude of difference in nematode community composition due to disturbance was greater in wetland than in forest or agricultural soils.

4.2.1. Wetlands

Wetlands experience periods of water saturation and anoxia that forest and agricultural soils may not. At our sites, disturbed wetlands were converted from forest vegetation to annual agriculture. Once wetlands are converted to agricultural use, they are drained, which changes both the hydrological and oxygen profiles; typically, moisture and temperature are related inversely. This conversion not only changes the vegetation, but also introduces an intense physical disturbance through cultivation. Our results suggest that this disturbance to wetland ecosystems reduces abundance, richness, and proportions of bacterivores and fungivores. The relative abundance of Chromadoridae and Bunonematidae in undisturbed wetlands agrees with their adaptation to moist soils and accumulation of litter, respectively (Nicholas, 1975; Dindal, 1990). Our observations of the reduction in numbers of *Eudorylaimus* in wetland soils disturbed by cultivation agree with de Goede (1996), who noted a similar pattern in forest soils subjected to sod-cutting.

In contrast, Wasilewska (2002) found that, except for omnivorous taxa, abundance of nematodes increased initially after drainage of fens in Poland, and declined through time. During a period from 2 to 117 years after drainage and conversion to pastures,

indices of diversity and maturity correlated positively with years after drainage. In our study, the only nematode community index that reflected disturbance in wetland soils was the CI. Values of CI were smaller in relatively disturbed than undisturbed wetlands, indicating a shift from decomposition pathways dominated by fungi to one dominated more by bacteria (Ferris et al., 2001). With comparable absolute numbers, a decline in proportion of fungivores was accompanied by an increase in proportion of plant-parasites rather than bacterivores.

4.2.2. Forests

In our study, relatively undisturbed forests had not been harvested for at least 75 years, whereas relatively disturbed forests had been harvested within the previous 3 years. The vegetation in undisturbed forests was dominated by trees, whereas the disturbed forests were a mix of young trees, shrubs, broad-leaved annuals and grasses. Total nematode abundance was similar in disturbed and undisturbed forests. However, diversity of nematode families and the proportions of plant-parasites increased with disturbance. FB values also increased with disturbance, opposite of our expectation that forest soils would represent a later stage of succession in the decomposer community, and thus, have relatively more numerous fungivores than bacterivores (López-Fando and Bello, 1995; Yeates, 1999; Thornton and Matlack, 2002; Ruess, 2003). Perhaps undisturbed forests in our study had reached a 'climax' stage in succession; the undisturbed pine forests were 75–100 years old (Neher et al., 2003). The intermediate disturbance hypothesis suggests that a shift from a climax to an intermediate position increases diversity (Connell, 1978). Others have observed no change in trophic composition in harvested forests (Panesar et al., 2000; Wright and Coleman, 2002). Háněl (1995) notes that the proportions of bacterivores and fungivores are relatively balanced in early succession forest soils of Bohemia.

4.2.3. Agriculture

Two of the key characteristics of disturbed agricultural soils were the presence of regular disturbance (tillage) and lack of permanent vegetative cover. The abundance of Mylonchulidae was greater in agricultural than forest soils, supporting the suggestion that these nematodes are tolerant to cultivation (Fiscus and Neher, 2002). Anatonchidae were more abundant in non-cultivated than cultivated ecosystems but were considered tolerant to cultivation by Fiscus and Neher (2002). This indicates that taxonomic resolution can affect interpretation of nematode community indices. In this study, we identified nematodes to family. Fiscus and Neher (2002) identified nematodes to genus and found genera within the same family, e.g., Cephalobidae, Plectidae, to respond differently to disturbances.

As expected, diversity at trophic and family levels was reduced by disturbance in agriculture. Cultivation, litter accumulation, and soil pH are all important factors for shaping nematode assemblages in agricultural soils (Mishra and Dash, 1987; López-Fando and Bello, 1995; Lenz and Eisenbeis, 1998). Abundance and diversity of bacterivorous, fungivorous, omnivorous and predatory nematodes are greater in no-till than in tilled soil (López-Fando and Bello, 1995). Neher and Campbell (1994) observed greater values of PPI and FB in arable soil without annual cultivation and perennial crops than with annual cultivation and crops. In our study, several maturity and diversity indices did not behave as expected. Specifically, MI and ΣMI25 were greater in disturbed than undisturbed soil. We did not measure bulk density or pore size distribution in this study, but we hypothesize that compaction due to grazing may have contributed to greater bulk densities. In other studies, nematode abundance was reduced, and soil bulk densities were greater in pastures than in cultivated soils (Barbercheck, unpublished data). Bulk density or pore size distribution may be an additional characteristic to measure as a covariate for interpreting nematode community indicators (Rosolem et al., 2002; Jordan et al., 2003).

4.3. Geographical scale

Nematode fauna may differ by virtue of biogeographic, climatic or edaphic factors (Yeates, 1994; Háněl, 2003a, 2003b). Coastal plain, piedmont and mountain LRRs varied by topography, soil type, and climate. Therefore, it is not surprising that nematode communities varied among regions, and it may be necessary to base interpretation of index values according to region or ecosystem type. Ruess (2003) noted that FB and CI indices were affected more by soil

and climate factors than differences among grassland, agricultural and forest ecosystems. In our study, FB values were similar among ecosystems and CI values were greater in forest and agricultural than wetland ecosystems, although CI values were greater in undisturbed than disturbed wetlands. Some indicators may have local rather than national application (Yeates and van der Meulen, 1996).

Neher et al. (1995) determined variance components at finer scales of resolution (among sites, within sites, within samples) for these indices in agricultural ecosystems. This research expands the spatial scale to LRR and includes forests and wetlands in addition to agricultural ecosystems. For use in large-scale environmental monitoring programs, it is more cost-effective and easier to calibrate and interpret indices if variance is greatest at larger rather than at smaller spatial scales, e.g., variance is progressively small from among regions, among ecosystems and disturbance within ecosystems. This preferred order of ranking of variance by spatial scale occurred for nematode community indices MI, MI25, ΣMI25, and SI and abundance of predaceous nematodes. We found that variance was greater at small than at larger spatial scales for nematode community indices PPI, FB, CI, EI and trophic and family diversity and relative abundance of bacterivorous, fungivorous, plant-parasitic and omnivorous nematodes.

In addition to differences among geographic regions, there are also seasonal patterns within sites. In our study, we observed seasonal patterns of the *difference* between levels of disturbance, illustrated with principal response curves. This approach can provide insight to the appropriate time of year to sample to detect differences in soil condition. Our research suggests that July (mid-summer) is an optimal month to detect the effects of disturbance. However, this differs from previous research, which indicated that autumn or spring is optimal (Neher, 1999; Neher et al., 2003). It is likely that different times of year are appropriate for different groups of bioindicators.

5. Conclusion

A hierarchy of scale exists in the differentiation of nematode communities, but it varies by the taxonomic resolution and/or index applied. MI, MI25, ΣM125 and SI followed the expected hierarchical ranking of spatial scale in this study. However, family composition differentiated among levels of disturbance and ecosystems better than did community indices. Current efforts suggest that taxonomic resolution at genus is necessary for interpretation of ecosystem function. Because it is often impractical and expensive to perform an ecological census, it will be necessary to identify a suite of key taxa representing critical functional groups and trophic positions, identified specifically for each ecosystem and region combination to account for inherent contrasts in soil properties and climate.

The relatively coarse resolution of identification of this study represents the 'early' phase of indicator testing and development that existed when this study was initiated in 1993. We required indicators to integrate many kinds of disturbance. We suggest that interpretations of disturbance should be tailored to the type of ecosystem because 'disturbance' is both qualitatively and quantitatively different in each type. Perhaps we need to refine our idea of 'disturbance' for better interpretation (Fiscus and Neher, 2002). Choice of bioindicators needs to be based on sound knowledge of soil ecology and on the effects of various kinds of disturbances on individual indicator taxa or groups of taxa.

To achieve a greater level of precision in the use of nematodes as bioindicators, we may need efforts to create a genetic fingerprint database, as has occurred with other groups, e.g., *Caenorhabditis elegans* (Floyd et al., 2002; Hebert et al., 2003a, 2003b; Blaxter, 2003; Waite et al., 2003). Certainly, we have increased our understanding of nematode bioindicators during the past 15 years. Activities such as database building and data mining, identification of the environmental sensitivities and tolerances of specific taxa, and research on effects of various disturbances on genetic damage measures will move this discipline forward.

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References

Andre, H.M., Noti, M.I., Lebrun, P., 1994. The soil fauna: the other last biotic frontier. Biodivers. Conserv. 3, 45–56.

Andre, H., Xavier, D., Anderson, J., Crossley Jr., D.A., Koehler, H., Paoletti, M., Lebrun, P., 2001. Skilled eyes are needed to go on studying the richness for the soil. Nature 409, 761.

Ayoub, S.M., 1980. Plant Nematology, An Agricultural Training Aid. California Department of Food and Agriculture, NemaAid Publications, Sacramento, California, USA, 195 pp.

Barker, K.R., Nusbaum, C.J., Nelson, L.A., 1969. Effects of storage temperature and extraction procedure on recovery of plant-parasitic nematodes from field soils. J. Nematol. 1, 240–247.

Blaxter, M., 2003. Counting angels with DNA. Nature 421, 122–124.

Bloemers, G.F., Hodda, M., Lambshead, P.J.D., Lawton, J.H., Wanless, F.R., 1997. The effects of forest disturbance on diversity of tropical soil nematodes. Oecologia 111, 575–582.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19.

Bongers, T., Ferris, H., 1999. Nematode community structure as a biomonitor in environmental monitoring. TREE 14, 224–228.

Bongers, T., de Goede, R.G.M., Korthals, G.W., Yeates, G.W., 1995. Proposed changes of c-p classification for nematodes. Russ. J. Nematol. 3, 61–62.

Cataldo, D.A., Haroon, M., Schrader, L.E., Youngs, V.L., 1975. Rapid colorimetric determination of nitrate in plant tissue by nitration of salicylic acid. Comm. Soil Sci. Plant Anal. 6, 71–80.

Caveness, F.E., Jensen, H.J., 1955. Modification of the centrifugal-flotation technique for the isolation and concentration of nematodes and their eggs from soil and plant tissue. Proc. Helminth. Soc. Wash. 22, 87–89.

Coleman, D.C., Odum, E.P., Crossley, D.A., 1992. Soil biology, soil ecology and global change. Biol. Fertil. Soils 14, 104–111.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

Debruyn, L.A.L., 1997. The status of soil macrofauna as indicators of soil health to monitor the sustainability of Australian agricultural soils. Ecol. Econ. 23, 167–178.

de Goede, R.G.M., 1996. Effects of sod-cutting on the nematode community of a secondary forest of *Pinus sylvestris* L. Biol. Fertil. Soils 22, 227–236.

de Goede, R.G.M., Dekker, H.H., 1993. Effects of liming and fertilization on nematode communities in coniferous forest soils. Pedobiologia 37, 193–209.

de Goede, R.G.M., Bongers, T., 1994. Nematode community structure in relation to soil and vegetation characteristics. Appl. Soil Ecol. 1, 29–44.

Dindal, D.L., 1990. Soil Biology Guide. John Wiley, New York, USA, 1349 pp.

Dyer, L.A., Letourneau, D., 2003. Top-down and bottom-up diversity cascades in detrital vs. living food webs. Ecol. Lett. 6, 60–68.

Ekschmitt, K., Bakonyi, G., Bongers, M., Bongers, T., Bostrom, S., Dogan, H., Harrison, A., Nagy, P., O'Donnell, A.G., Papatheodorou, E.M., Sohlenius, B., Stamou, G.P., Wolters, V., 2001. Nematode community structure as indicator of soil functioning in European grassland soils. Eur. J. Soil Biol. 37, 263–268.

Ettema, C.H., Bongers, T., 1993. Characterization of nematode colonization and succession in disturbed soil using the maturity index. Biol. Fertil. Soils 16, 79–85.

Ettema, C.H., Lowrance, R., Coleman, D.C., 1999. Riparian soil response to surface nitrogen input: temporal changes in denitrification, labile and microbial C and N pools, and bacterial and fungal respiration. Soil Biol. Biochem. 31, 1625–1638.

Ettema, C.H., Coleman, D.C., Vellidis, G., Lowrance, R., Rathbun, S.L., 1998. Spatiotemporal distributions of bacterivorous nematodes and soil resources in a restored riparian wetland. Ecology 79, 2721–2734.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil foodweb diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13–29.

Fiscus, D.A., Neher, D.A., 2002. Distinguishing nematode genera based on relative sensitivity to physical and chemical disturbances. Ecol. Appl. 12, 565–575.

Floyd, R., Abebe, E., Papert, A., Blaxter, M., 2002. Molecular barcodes for soil nematodes identification. Mol. Ecol. 11, 839–850.

Freckman, D.W., Ettema, C.H., 1993. Assessing nematode communities in agroecosystems of varying human intervention. Agric. Ecosyst. Environ. 45, 239–261.

Gee, G.W., Bauder, J.W., 1986. Particle-size analysis. In: Klute, A. (Ed.), Methods of Soil Analysis. Part 1. Physical and Mineralogical Methods, A. Agronomy Monograph 9. American Society of Agronomy, Madison, WI, pp. 383–412.

Háněl, L., 1995. Secondary successional stages of soil nematodes in Cambisols of south Bohemia. Nematologica 41, 197–218.

Háněl, L., 2003a. Comparison of soil nematode communities in three forest types on sand and clay coal-mining dumps in Germany and Czech Republic. Helminthologia 40, 237–243.

Háněl, L., 2003b. Structure and dynamics of soil nematode community in wheat and potato fields. Biol. Bratislava 49, 153–159.

Hebert, P.D.N., Cywinska, A., Ball, S.L., deWaard, J.R., 2003a. Biological identifications through DNA barcodes. Proc. R. Soc. Lond. B Biol. Sci. 270, 313–321.

Hebert, P.D.N., Ratnasingham, S., deWaard, J.R., 2003b. Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. Proc. R. Soc. Lond. B Biol. Sci. 270 (Suppl. 1), S96–S99.

Hyvönen, R., Persson, T., 1990. Effects of acidification and liming on feeding groups of nematodes in coniferous forest soils. Biol. Fertil. Soils 9, 205–210.

Jordan, D., Ponder Jr., F., Hubbard, V.C., 2003. Effects of soil compaction, forest leaf litter and nitrogen fertilizer on two oak species and microbial activity. Appl. Soil Ecol. 23, 33–41.

Keeney, D.R., Nelson, D.W., 1982. Nitrogen—inorganic forms. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil

Analysis. Part 2. Chemical and Microbiological Properties. Agronomy Monograph 9. second ed. American Society of Agronomy, Madison, WI, pp. 643–698.

Korthals, G.W., van der Ende, A., van Megen, H., Lexmond, T.M., Kammenga, J.E., Bongers, A.M.T., 1996. Short-term effects of cadmium, copper, nickel and zinc on soil nematodes form different feeding and life-history strategy groups. Appl. Soil Ecol. 4, 107–117.

Korthals, G.W., Popovici, I., Iliev, I., Lexmond, T.M., 1998. Influence of perennial ryegrass on a copper and zinc affected terrestrial nematode community. Appl. Soil Ecol. 10, 73–85.

Lenz, R., Eisenbeis, G., 1998. The vertical distribution of decomposition activity and of litter-colonizing nematodes in soils under different tillage. Pedobiologia 42, 193–204.

López-Fando, C., Bello, A., 1995. Variability in soil nematode populations due to tillage and crop rotation in semi-arid Mediterranean agroecosystems. Soil Tillage Res. 36, 59–72.

Ludwig, J.A., Reynolds, J.F., 1988. Statistical Ecology: A Primer on Methods and Computing. John Wiley, New York, USA, 337 pp.

Mishra, C.C., Dash, M.C., 1987. Effects of soil amendments on soil moisture, pH, microbial population, soil respiration and nematodes. Ann. Biol. 3, 17–27.

Moore, J.C., de Ruiter, P.C., 1991. Temporal and spatial heterogeneity of trophic interactions within below-ground food webs. Agric. Ecosyst. Environ. 34, 371–397.

Murialdo, S.E., Fuertes, M.G., Gonzalez, J.F., Chavez, E., 2002. Nematodes as indicators of wetland pollution. J. Environ. Biol. 23, 423–428.

Nagy, P., 1999. Effect of an artificial metal pollution on nematode assemblage of a calcareous loamy Chernozem soil. Plant Soil 212, 35–43.

Neher, D.A., 1999. Nematode communities in organically and conventionally managed agricultural soils. J. Nematol. 31, 142–154.

Neher, D.A., 2001. Role of nematodes in soil health and their use as indicators. J. Nematol. 33, 161–168.

Neher, D.A., Campbell, C.L., 1994. Nematode communities and microbial biomass in soils with annual and perennial crops. Appl. Soil Ecol. 1, 17–28.

Neher, D.A., Campbell, C.L., 1996. Sampling for regional monitoring of nematode communities in agricultural soils. J. Nematol. 28, 196–208.

Neher, D.A., Olson, R.K., 1999. Nematode communities in soils of four farming cropping management systems. Pedobiologia 43, 430–438.

Neher, D.A., Easterling, K.N., Fiscus, D., Campbell, C.L., 1998. Comparison of nematode communities in agricultural soils of North Carolina and Nebraska. Ecol. Appl. 8, 213–223.

Neher, D.A., Peck, S.L., Rawlings, J.O., Campbell, C.L., 1995. Measures of nematode community structure and sources of variability among and within fields. Plant Soil 170, 167–181.

Neher, D.A., Barbercheck, M.E., El-Allaf, S.M., Anas, O., 2003. Effects of disturbance and ecosystem on decomposition. Appl. Soil Ecol. 23, 165–179.

Nicholas, W.L., 1975. The Biology of Free-living Nematodes, first ed. Clarendon Press, Oxford, UK, 219 pp.

Panesar, T.S., Marshall, V.G., Barclay, H.J., 2000. The impacts of clearcutting and partial harvesting systems on population dynamics of soil nematodes in coastal Douglas-fir forests. Pedobiologia 44, 641–665.

Popovici, I., 1992. Nematodes as indicators of ecosystem disturbance due to pollution. Stud. Univ. Babes-Bolyai Ser. Biol. 37, 15–27.

Ritz, K., Tradgill, D.L., 1999. Utility of nematode community analysis as an integrated measure of the functional state of soils: perspectives and challenges—discussion paper. Plant Soil 212, 1–11.

Rosolem, C.A., Foloni, J.S.S., Tiritan, C.S., 2002. Root growth and nutrient accumulation in cover crops as affected by soil compaction. Soil Tillage Res. 65, 109–115.

Ruess, L., 2003. Nematode soil faunal analysis of decomposition pathways in different ecosystems. Nematology 5, 179–181.

Schulte, E.E., Kaufman, C., Peter, J.B., 1991. The influence of sample size and heating time on soil weight loss-on-ignition. Commun. Soil Sci. Plant Anal. 22, 159–166.

Science Editors, 2004. Areas to watch in 2004. Science 302, 2040.

Shayestehfar, A., Mayel, M., Rezaie, B., Dehghani, L., Karami, A., Saadzadeh, E., Rasekhi, M.H., Sami, S., Gashmardi, N., Dezhkam, L., Motamedi, F., 1998. Biological observations of soil nematodes around Parishan (Fammur) Lake, Kazeroun, Fars-Iran. J. Environ. Biol. 19, 357–361.

Smith, J.L., Doran, J.W., 1996. Measurement and use of pH and electrical conductivity for soil quality analysis. In: Doran, J.W., Jones, A.J. (Eds.), Methods for Assessing Soil Quality. SSSA Special Publication 49, Madison, WI, pp. 169–185.

Söhlenius, B., Böström, S., Sandor, A., 1988. Carbon and nitrogen budgets of nematodes in arable soil. Biol. Fertil. Soils 6, 1–8.

ter Braak C.J.F., Šmilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide, Software for Canonical Community Ordination (Version 4.5), Biometris, Wageningen and Česke Budějovice, Netherlands, 500 pp.

Thorne, G., 1961. Principles of Nematology. McGraw-Hill, New York, NY, USA, 553 pp.

Thornton, C.W., Matlack, G.R., 2002. Long-term disturbance effects in the nematode communities of south Mississippi woodlands. J. Nematol. 34, 88–97.

USDA-SCS, 1981. Land Resource Regions and Major Resource Areas of the United States. USDA-SCS Agriculture Handbook 296. U.S. Government Printing Office, Washington, DC, USA, 156 pp.

Van den Brink, P.J., Van den Brink, N.W., ter Braak, C.J.F., 2003. Multivariate analysis of ecotoxicological data using ordination: demonstrations of utility on the basis of various examples. Aust. J. Ecotoxicol. 9, 141–156.

Verschoor, B.C., de Goede, R.G.M., de Hoop, J.-W., de Vries, F.W., 2001. Seasonal dynamics and vertical distribution of plant-feeding nematode communities in grasslands. Pedobiologia 45, 213–233.

Waite, I.S., O'Donnell, A.G., Harrison, A., Davies, J.T., Colvan, S.R., Ekschmitt, K., Dogan, H., Wolters, V., Bongers, T., Bongers, M., Bakonyi, G., Nagy, P., Papatheodorou, E.M., Stamou, G.P., Bostrom, S., 2003. Design and evaluation of nematode 18S rDNA primers for PCR and denaturing gradient gel electrophoresis (DGGE) of soil community DNA. Soil Biol. Biochem. 35, 1165–1173.

Wasilewska, L., 1994. The effect of age of meadows on succession and diversity in soil nematode communities. Pedobiologia 38, 1–11.

Wasilewska, L., 2002. Post-drainage secondary succession of soil nematodes on fen peat meadows in Biebrza, Poland. Pol. J. Ecol. 50, 269–300.

Wheeler, Q.D., Raven, P.H., Wilson, E.O., 2004. Taxonomy: impediment or expedient? Science 303, 285.

Wright, C.J., Coleman, D.C., 2002. Responses of soil microbial biomass, nematode trophic groups, N-mineralization, and litter decomposition to disturbance events in the southern Appalachians. Soil Biol. Biochem. 34, 13–25.

Yeates, G.W., 1994. Modification and qualification of the nematode maturity index. Pedobiologia 38, 97–101.

Yeates, G.W., 1999. Effects of plants on nematode community structure. Annu. Rev. Phytopathol. 37, 127–149.

Yeates, G.W., van der Meulen, H., 1996. Recolonization of methylbromide sterilized soils by plant and soil nematodes over 52 months. Biol. Fertil. Soils 21, 1–6.

Yeates, G.W., Bongers, T., 1999. Nematode diversity in agroecosystems. Agric. Ecosyst. Environ. 74, 113–135.

Yeates, G.W., Bongers, T., de Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera—an outline for soil ecologists. J. Nematol. 25, 315–331.

Yeates, G.W., Shepherd, T.G., Francis, G.S., 1998. Contrasting response to cropping of populations of earthworms and predacious nematodes in four soils. Soil Tillage Res. 48, 255–264.

Yeates, G.W., Wardle, D.A., Watson, R.N., 1999. Responses of soil nematode populations, community structure, diversity and temporal variability to agricultural intensification over a seven-year period. Soil Biol. Biochem. 31, 1721–1733.