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COMPARISON OF NEMATODE COMMUNITIES IN AGRICULTURAL SOILS OF NORTH CAROLINA AND NEBRASKA

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Abstract. Samples of agricultural soils were collected across North Carolina in 1992 and Nebraska in 1993 to determine which indices of nematode communities could be applied to distinguish ecological pattern at regional geographic scales. Sampling density was proportional to the area of agriculture in each region of each state. Maturity indices (based on life-history characteristics) were calculated to determine the successional status of nematode communities, and diversity indices were calculated to estimate relative abundance of nematode trophic groups. Population densities of nematode families were also compared between states and among regions within states. The range of maturity-index values for free-living and plant-parasitic nematodes was greater for soils in North Carolina than in Nebraska. The relative distribution of nematode trophic groups (bacterial feeders, fungal feeders, plant parasites, omnivores, and predators) was similar in the two states. Significant differences in maturity-index values for free-living and plant-parasitic nematodes were found between but not within states. We conclude that regional or national assessments of soil ecological condition based on measures of nematode community structure can be made at a geographic resolution of 125 000–200 000 km^2 of land area.

Key words: agricultural soils; bioindicators; diversity indices for nematodes; environmental monitoring; maturity index; Nebraska; nematode community structure; North Carolina; regional ecological assessment; soil ecological condition; survey methodology; trophic diversity.

INTRODUCTION

Nematodes (free-living and plant-parasitic) possess attributes that make them useful as ecological indicators (Freckman 1988, Neher and Campbell 1994) and, because of their ability to reflect change in soil structure and function, indices of nematode community structure show promise for monitoring soil ecological condition (Bongers 1990, de Goede 1993, Ettema and Bongers 1993, Freckman and Ettema 1993). For example, perturbations to soils, such as addition of mineral nitrogen fertilizers (Wasilewska 1989), cultivation (Hendrix et al. 1986), liming (Hyvonen and Persson 1990) and accumulation of heavy metals (Samoiloff 1987, Bongers et al. 1991) affect species richness and trophic structure (Wasilewska 1989) of nematode communities.

Previous studies have evaluated a variety of indices describing nematode community structure and diversity at spatial scales finer than land resource regions (LRRs). LRRs represent geographic areas with unique soil type, topography, climate and water resources (USDA-SCS 1981). Neher et al. (1995) quantified variance components of a multitude of indices including abundance of nematodes within trophic groups (plant-parasitic, bacterial-feeding, fungal-feeding, omnivores, predators), ratios of trophic groups, maturity indices (Bongers 1990) and diversity indices (Shannon and Weaver 1949). Maturity indices are based on life strategies to characterize the successional status of decomposer communities in soil. Trophic diversity describes the relative abundance and evenness of the occurrence of nematode trophic groups. Variance was estimated within samples (between subsamples), within field sites, and among field sites within major LRRs. Based on estimates of variance at contrasting spatial scales, power-curve analyses were performed to estimate appropriate sample sizes to detect 10% change between two time periods with a power $(1 - \beta)$ of 0.10 (Neher et al. 1995). A large amount of variability existed within samples and within fields. Because the goal was to make regional estimates, an index was preferred if its variability was relatively small, especially within samples. The best-performing indices were the maturity and diversity indices (Neher et al. 1995). Modifications of maturity indices improved reliability (signal : noise ratio) and, thus, performance on a regional scale (Neher and Campbell 1996). Enhancement modifications involved removing values for the early colonizing taxa (CP [colonizer–persister value] = 1; Popovici 1992) from the original index (Bongers 1990 [*c-p* values]) and combining plant-parasitic with free-living taxa of nematodes into a single index (Yeates 1994). Optimum sample sizes and sampling designs were identified

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TABLE 1. Percentage of fields in the total sample evaluated for nematodes that were planted to each type of crop within North Carolina (n = 164 fields) in 1992 and Nebraska (n = 154 fields) in 1993.

Crop†	North Carolina	Nebraska
Barley	1.2	0.0
Corn		
Field corn	20.1	51.3
Silage	4.9	1.3
Popcorn	1.2	0.6
Cotton	6.1	0.0
Cucumbers	0.6	0.0
Dry beans	0.0	3.2
Hay		
Alfalfa	0.0	6.5
Other	8.5	0.0
Millet	0.0	1.3
Oats	1.2	0.0
Peanuts	0.6	0.0
Rye	0.6	0.6
Sorghum	0.6	8.4
Soybeans	22.6	7.8
Sweet potatoes	1.2	0.0
Tobacco	9.8	0.0
Wheat	12.2	9.1
No annual crop		
Fallow	0.0	7.8
Idle	3.7	1.9
Pasture	2.4	0.0
Set-Aside	2.4	0.0

† Fields with annual row crops or annually harvested perennial crops, or fields that could be planted to these crops.

based on reliability ratios and additional power-curve analysis (Neher and Campbell 1996).

We had two priorities in the present study. First, indices of nematode communities were applied and evaluated on a regional scale to determine whether it was more appropriate to interpret indices on a whole-state basis or by LLRs within states. The study was designed to assess whether successional maturity or trophic diversity of nematode communities differed among or within North Carolina and Nebraska, two states with contrasting climate and soil types. Maturity and diversity indices were chosen because of their relatively low variance at fine spatial scales and independence of influence by annual crop species such as wheat, corn, and soybeans (Neher and Campbell 1994), the dominant crops in the geographic areas of concern in this study (Table 1). Second, relative abundance and frequency of occurrence of various nematode taxa in North Carolina and Nebraska were compared to determine whether regions with different climate and general soil types have inherently different nematode communities regardless of the relative ecological condition of soil. Similar index values could comprise varying compositions of nematode taxa. Therefore, composition of nematode communities for the two states was compared.

METHODS

Survey design

An autumn sampling period was selected following cultivation of crops harvested in the fall to minimize within-field sampling variation (Francl 1986*a*, *b*). Free-living nematode populations are generally at their peak at this time (Boag 1977, Sohlenius 1982), because crop residues are incorporated into soil by cultivation (Kästner and Germershausen 1989) and temperatures are moderate (15–20°C) (Boag 1977, Stinner and Crossley 1982). Nematode surveys are best performed when maximum populations occur (Barker and Noe 1988).

Soil samples were collected from fields that were planted with annual row crops or an annually harvested perennial crop such as hay or alfalfa (Table 1), or could be planted to these crops in North Carolina (n = 164 fields) in 1992 and Nebraska (n = 154 fields) in 1993 (Campbell et al. 1994, Hellkamp et al. 1995) by non-specialists working in cooperation with the USDA National Agricultural Statistics Service (USDA-NASS). Land cover in both states was stratified based on percentage of land area in agricultural cultivation (Cotter and Nealon 1987). Most sample sites (93% in Nebraska and 16% in North Carolina) were located in areas with intensive agricultural production (>50% of land area cultivated). One to 14 field sites were located within each of 65 segments in North Carolina and 175 segments in Nebraska. A segment is a sample unit 0.5–11.3 km^2 in area used by the USDA-NASS in their area sampling frame (Cotter and Nealon 1987). The number and spatial distribution of segments were allocated in relation to degree of agricultural intensity. Sample distribution was such that statements could be made about the Piedmont (n = 149 samples) and Coastal Plains (n = 32) LRRs of North Carolina and the eastern (n = 46), northwestern (n = 24) and southern (n = 86) LRRs of Nebraska. LRRs were delineated in accordance with USDA-SCS (1981).

Within every field, soils were sampled by taking one core (2 cm diameter, 20 cm deep) at each of the 20 equally spaced sites along one 90-m linear transect across a random 2-ha area to obtain data to measure variation among fields (Neher et al. 1995). The transect traversed within and between crop-row areas equally to gain a representative estimate of population densities within fields. Cores for each transect were mixed thoroughly by hand to form a composite sample to reduce variance associated with the aggregated spatial pattern of nematodes in soil (Barker and Campbell 1981) and to obtain a realistic representation of the nematode community in the field. In every sixth field, a second transect was also sampled to quantify variability within fields. Variability within composite samples was quantified by splitting composite soil samples of double volume taken from a second independent transect in every twelfth field. All soil samples were stored at existing field moisture levels and 15°C to minimize changes in nematode populations prior to assay (Barker et al. 1969). Only data from the first transect are presented in this report. Data from the second transect were used to estimate variance components and provide

guidance for sample allocation (Neher et al. 1995, Neher and Campbell 1996).

Laboratory analyses

Nematodes were extracted using a Cobb's sifting 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 (volume : volume) sugar solution and centrifuging (4116 m/s^2) for 1 min (Neher and Campbell 1994). Given the magnitude and scale of the experiment, it was only feasible logistically and economically to identify and enumerate nematodes in each sample to taxonomic family. Thus, numbers of nematodes in each taxonomic family and trophic group were counted in 500-cm^3 soil and 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, California, USA). Taxonomic families (Table 2) were assigned to a trophic group (plant parasitic, bacterial feeding, fungal feeding, 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 value according to Bongers (1990) (Bongers denoted this ''*c-p*''; we use ''CP''). Voucher specimens were preserved in a 10% formalin and 1.0% glycerin solution, sealed with parafilm, and deposited at the University of California (Dr. James G. Baldwin, Department of Nematology, Riverside, California 92521 USA).

Statistical methods

Three indices were computed for the nematode community in each soil sample: (1) maturity index for free-living nematodes according to Bongers (1990) except taxa with a CP value of 1 were excluded (MINO or ''maturity index with no ones'' sensu Popovici 1992); (2) maturity index for all plant-parasitic nematodes (PPI) (Bongers 1990); and (3) diversity of trophic groups (H'; Shannon and Weaver 1949). Opportunistic taxa (CP = 1) were not included in MINO because they are considered enrichment opportunists and population densities increase rapidly in response to additions of nitrogen to soil and not necessarily to long-term changes in soil ecological condition (Bongers et al. 1995) and, thus, increase total variance and variance within composite soil samples, which may reduce reliability of detection of long-term trends in regional surveys (Neher and Campbell 1996). The maturity indices, MINO and PPI, were calculated as the weighted mean of the values assigned constituent nematode families (and the genera and species they contain). Weighted means were expressed mathematically as $(\Sigma\ v_i \times f_i)/n$, where v_i is the CP value assigned to family i, f_i is the frequency of family i in a sample, and n is the number of individuals in a sample. Diversity of trophic groups was estimated by using the Shannon-Wiener diversity index (H') or Hill's N1, i.e., $H' = \exp[-\Sigma\ P_i(\ln P_i)]$, where P_i is the proportion of trophic group i in the total nematode community (Ludwig and Reynolds 1988).

Cumulative distribution functions (CDFs) were constructed for MINO, PPI, and H' to illustrate the proportion of cropped land area that had an index of a certain value or less. CDFs were chosen because they illustrate the distribution of index values on a continous and cumulative scale. Ninety-percent confidence bands were estimated to quantify the precision of each CDF (Campbell et al. 1994). Differences between CDFs of North Carolina and Nebraska were calculated by subtracting cumulative proportion of land for each index value of North Carolina from Nebraska. If mean differences and 95% confidence intervals of the difference were either all above or all below zero, then the two CDFs were different statistically. Conversely, if the zero line occurred inside the 95% confidence intervals, then the CDFs were not considered to be different.

Maps of spatial distribution of categories of index values by regions within states were created using geographic information system (GIS) techniques with ArcInfo and ArcView software (Environmental Systems Research Institute 1992*a*, *b*). Average index values were aggregated by sampling segment and illustrated as categories defined separately for maturity (0–2, 2.0001–2.5, 2.5001–3, 3.0001–3.5, and 3.5–5) and trophic diversity (0–2.5, 2.5001–3, 3.0001–3.5, 3.5001–4, and 4–5) indices. Categories were defined to allow for ease of visualization on maps and to combine multiple observations within each category.

Complementary to the spatial maps of index values, a standardized frequency of each index category was calculated by dividing the number of total sample sites in each index category of a sub-state region by the total number of sample sites within that sub-state region. The quotient was multiplied by 100 to obtain a percentage.

Frequency ranks of nematode families were calculated for a comparison between North Carolina and Nebraska. Frequency was a measure of the number of sampling sites in which each specified family occurred. Ranks were assigned such that 1 = 75–100%, 2 = 50–74%, 3 = 25–49%, and 4 = 1–24% of soil samples containing the specified family. The most abundant nematode families within each CP group and their percentage of total abundance were quantified to reveal the predominant families within MINO and PPI indices within each state. Differences in population densities of taxonomic families between states were determined using a Wilcoxin rank-sum test (SAS Institute 1989).

TABLE 2. Families and respective genera of nematodes found in soil samples taken in North Carolina (NC; 1992) and Nebraska (NE; 1993) that were used in calculation of maturity and diversity indices.

Family	Frequency rank† NC	NE	Genera	Presence‡ NC	NE
Alaimidae§	2	4	*Alaimus*	x	x
			Amphidelus	x	x
Anatonchidae§	4	··‖	*Anatonchus*	x	o
			Miconchus	x	o
Anguinidae§	3	2	*Anguina*	o	x
			Ditylenchus	x	x
			Pseudhalenchus	x	x
Aphelenchidae§	2	1	*Aphelenchus*	x	x
Aphelenchoididae§	1	1	*Aphelenchoides*	x	x
Bastianidae§	4	··‖	*Bastiania*	x	o
Belondiridae§	4	4	*Axonchium*	x	x
			Belondira	x	x
Belonolaimidae¶	2	2	*Merlinius*	x	o
			Tylenchorhynchus	x	x
Bunonematidae	4	4	*Bunonema*	x	x
Carcharolaimidae§	4	4	*Carcharolaimus*	x	x
Cephalobidae§	1	1	*Acrobeles*	x	x
			Acrobeloides	x	x
			Cervidellus	x	x
			Cephalobus	o	x
			Chiloplacus	x	x
			Eucephalobus	x	x
			Zeldia	x	x
Chromadoridae§	4	4	*Chromadorita*	x	x
Criconematidae¶	3	4	*Criconemella*	x	x
			Hemicriconemoides	x	o
			Hemicycliophora	o	x
Cyatholaimidae§	4	4	*Achromadora*	x	x
Cylindrolaimidae§	4	4	*Cylindrolaimus*	x	x
Diphtherophoridae§	3	4	*Diphtherophora*	x	x
			Tylolaimophorus	x	x
Diplogasteridae	2	3	*Butlerius*	x	x
			Mononchoides	x	o
Diploscapteridae	3	4	*Diploscapter*	x	x
Dorylaimellidae§	4	4	*Dorylaimellus*	x	x
Dorylaimidae§	1	1	*Aporcelaimus*	x	x
			Discolaimus	x	x
			Dorylaimus	x	o
			Drepanodorus	x	x
			Eudorylaimus	x	x
			Labronema	x	x
			Longidorella	o	x
			Mesodorylaimus	x	x
			Prodorylaimus	o	x
			Pungentus	x	x
			Thornenema	x	o
Heteroderidae¶	1	4	*Heterodera*	x	x
			Meloidogyne	x	x
Hoplolaimidae¶	1	3	*Heliotylenchus*	x	x
			Hoplolaimus	x	x
			Rotylenchulus	x	x
			Rotylenchus	x	x
			Scutellonema	x	o
Iotonchulidae§	4	··‖	*Iotonchus*	x	o
Ironidae§	4	··‖	*Ironus*	x	o
Isolaimidae§	4	··‖	*Isolaimium*	x	o
Leptolaimidae§	4	··‖	*Aphanolaimus*	x	o
Leptonchidae§	4	4	*Dorylaimoides*	x	x
			Doryschota	o	x
			Leptonchus	x	x
			Proleptonchus	x	o
Longidoridae¶	3	3	*Paralongidorus*	o	x
			Xiphinema	x	x
Microlaimidae§	4	4	*Microlaimus*	x	x
			Prodesmodora	x	o
Monhysteridae	3	4	*Monhystera*	x	x
			Monhystrella	x	x
			Theristus	x	o
Mononchidae§	2	3	*Mononchus*	x	x
			Prionchulus	x	o
Mylonchulidae§	3	4	*Granonchulus*	x	x
			Mylonchulus	x	x
Nygolaimidae§	4	4	*Nygolaimus*	x	x
			Sectonema	x	x
Panagrolaimidae	4	4	*Panagrolaimus*	x	x
Paraphelenchidae§	4	4	*Paraphelenchus*	x	x
Plectidae§	2	3	*Anaplectus*	x	x
			Chronogaster	x	x
			Plectus	x	x
			Tylocephalus	o	x
			Wilsonema	x	x
			Wilsotylus	o	x
Pratylenchidae¶	2	2	*Nacobbus*	o	x
			Pratylenchus	x	x
Prismatolaimidae§	3	4	*Prismatolaimus*	x	x
Rhabditidae	1	1	*Bursilla*	x	x
			Cuticularia	o	x
			Cruznema	x	o
			Mesorhabditis	x	x
			Pelodera	o	x
			Poikilolaimus	x	x
			Rhabditis	x	x
			Rhitis	x	o
			Teratorhabditis	x	o
Rhabdolaimidae§	4	3	*Rhabdolaimus*	x	x
Seinuridae§	4	4	*Seinura*	x	x
Teratocephalidae§	4	4	*Euteratocephalus*	x	o
			Teratocephalus	x	x
Trichodoridae¶	3	4	*Paratrichodorus*	x	x
			Trichodorus	x	x
Tripylidae§	4	4	*Tobrilus*	x	x
			Tripyla	x	x
Tylenchidae¶	1	1	*Aglenchus*	x	x
			Atylenchus	x	x
			Basiria	x	x
			Boleodorus	x	x
			Coslenchus	x	x
			Ecphyadophora	x	o
			Filenchus	x	x
			Lelenchus	o	x
			Psilenchus	x	x
			Tylenchus	x	x
Tylencholaimellidae§	3	4	*Doryllium*	x	o
			Tylencholaimellus	x	x
Tylencholaimidae§	4	4	*Enchodelus*	x	x
			Tylencholaimus	x	x
Tylenchulidae¶	4	2	*Gracilacus*	o	x
			Paratylenchus	x	x

† 1 = 75–100%, 2 = 50–74%, 3 = 25–49%, and 4 = 1–24% of soil samples that contained this nematode family.

‡ x = present; o = absent.

§ Families used in calculating the maturity index with no ones (MINO; CP [colonizer–persister value] = 25) for free-living nematodes; also used in calculating H', the Shannon-Wiener trophic diversity index.

‖ No samples contained this family.

¶ Families used in calculating the maturity index for all plant-parasitic nematodes (PPI; CP = 2–5); also used in calculating H'.

Population abundances were transformed as $\ln(x + 1)$ prior to analysis.

Results

At each percentile of the cumulative distribution function (CDF), values of MINO the maturity index for free-living nematodes (excluding those with a colonizer–persister value [CP] = 1, were larger consistently for North Carolina than Nebraska soil samples (Fig. 1A) and the 95% confidence interval about the mean difference between the two CDFs did not include zero at any percentile. Values of PPI, the maturity index for all plant-parasitic nematodes, in the CDF were larger for North Carolina than Nebraska soil samples for values <2.9. For PPI values >2.9, however, the 95% confidence interval about the mean difference between the CDFs did include zero and the two CDFs were, thus, not different significantly (Fig. 1B). For H' (Shannon-Wiener trophic diversity index), CDFs for North Carolina and Nebraska were not different (Fig. 1C). Differences in MINO and PPI observed between states were attributed to most sample sites within North Carolina occurring in category 3 (MINO or PPI = 2.5001–3.0) and most sites within Nebraska occurring in category 2 (MINO or PPI = 2.0001–2.5) (Fig. 2). For the Shannon-Wiener trophic diversity index, the greatest abundance of sample sites in North Carolina had index values within category 4 (H' = 3.5001–4) and sites in Nebraska had index values within category 3 (H' = 3.0001–3.5) (Fig. 2). Overall, the category of each index represented most frequently among sites sampled was greater numerically in North Carolina than Nebraska.

Maturity, but not trophic diversity, indices of nematode community structure varied among LRRs (land resource regions; USDA-SCS 1981) within states; however, differences observed within states were less than between states (Table 3). Larger values of MINO were observed in the Piedmont than Coastal Plain and Mountain regions of North Carolina (Fig. 3A) and in northwestern than southern or eastern regions of Nebraska (Fig. 4A). Values of PPI were larger in Coastal Plain and Piedmont than Mountain regions in North Carolina (Fig. 3B), whereas index values were similar among regions in Nebraska (Fig. 4B).

Richness of nematode taxa was slightly greater in agricultural soils of North Carolina (50 families, 107 genera) than Nebraska (43 families, 98 genera) (Table 2). Families of free-living nematodes encountered frequently for both North Carolina and Nebraska were Aphelenchoididae (CP = 2), Cephalobidae (CP = 2), Dorylaimidae (CP = 4), Rhabditidae (CP = 1) and Tylenchidae (CP = 2) (Table 2). Aphelenchidae (CP = 2) was also encountered frequently but more often in North Carolina than Nebraska (P = 0.0001; Table 2). Perhaps larger MINO values in North Carolina are due to the relative frequency of Alaimidae (CP = 4) in North Carolina compared to Nebraska (Table 2). Also, populations of free-living nematode families assigned CP values of 3–5 were most abundant in North Carolina and populations assigned a CP value of 2 were most abundant in Nebraska (Fig. 2A and D). Frequently encountered families representing different CP value categories used for calculation of MINO were similar between states except for the most abundant CP = 5 family (Table 4).

Differences in plant-parasitic nematode families observed between states were greater than for free-living nematode families (Table 2). For example, Heterodoridae (CP = 3) and Hoplolaimidae (CP = 3) populations were more abundant in North Carolina than Nebraska (P = 0.0001). Tylenchulidae (CP = 2) populations were more abundant in Nebraska than North Carolina (P = 0.0001; Table 2). Families with greatest population densities for each CP group used in calculation of PPI were similar for each state (Table 4).

Discussion

Our work is the first to compare nematode communities in soils between statewide regions of a country. Our results suggest that it is unnecessary to calibrate indices of nematode community structure at a scale finer than major land resource regions (LRRs) for regional-scale studies. Differences in successional maturity and trophic structure of nematode communities (free living and plant parasitic) between two states of contrasting climate and soil type—North Carolina than Nebraska—exceeded those among LRRs within states (Table 3, Figs. 3 and 4). Based upon these relatively large differences, we recommend calibrating maturity and diversity indices of soil for geographic areas no smaller than the land area of North Carolina (126 180 km^2) and Nebraska (199 120 km^2). It has yet to be determined how large a region or state must be before subdivision is necessary for index calibration. Perhaps nematode community descriptions could be added to the list of attributes describing LRRs.

This study represents a significant advance in demonstrating the applicability of maturity indices as ecological measures of soil biological condition on a regional geographic scale. The survey's unique design and large sample size illustrate the possibility for using maturity indices to suggest strategies for managing agricultural ecosystems for sustainability on a regional basis. Soil quality, particularly the biological and ecological components, is managed knowingly or unknowingly through the use of specific agricultural practices (e.g., cultivation, crop rotation) and the availability of a metric of regional applicability, such as the maturity indices, will facilitate the evaluation and alteration of management practices in agroecosystems.

The range of maturity-index (MINO for free-living nematodes and PPI for plant-parasitic nematodes) values that we found was greater than values reported earlier for annual crops (Freckman and Ettema 1993, Yeates and Bird 1994) because we did not include nem-

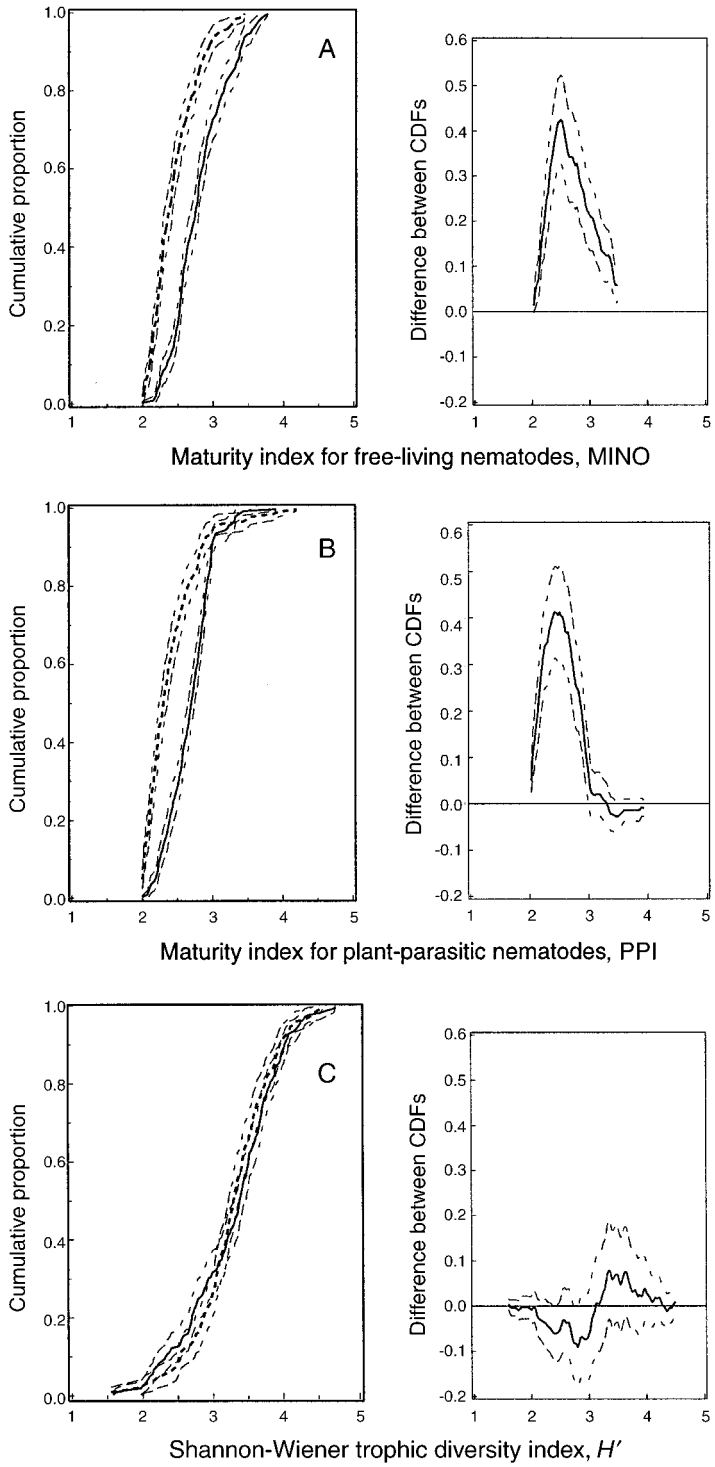

FIG. 1. Cumulative distribution functions (CDF) for (A) maturity index for free-living nematodes, (B) maturity index for plant-parasitic nematodes, and (C) Shannon-Wiener trophic diversity index in North Carolina (———) and Nebraska (— —). Cumulative proportion refers to land area cropped with annually harvested, herbaceous crops. Outer dashed lines represent 90% confidence bands around the CDF. If difference means and standard error lines were either all above or all below zero, then the two CDFs were different statistically; otherwise, they are not different. For each respective index, the adjacent plot to the right represents the difference between the cumulative distribution functions (mean and 95% confidence intervals) for Nebraska and North Carolina.

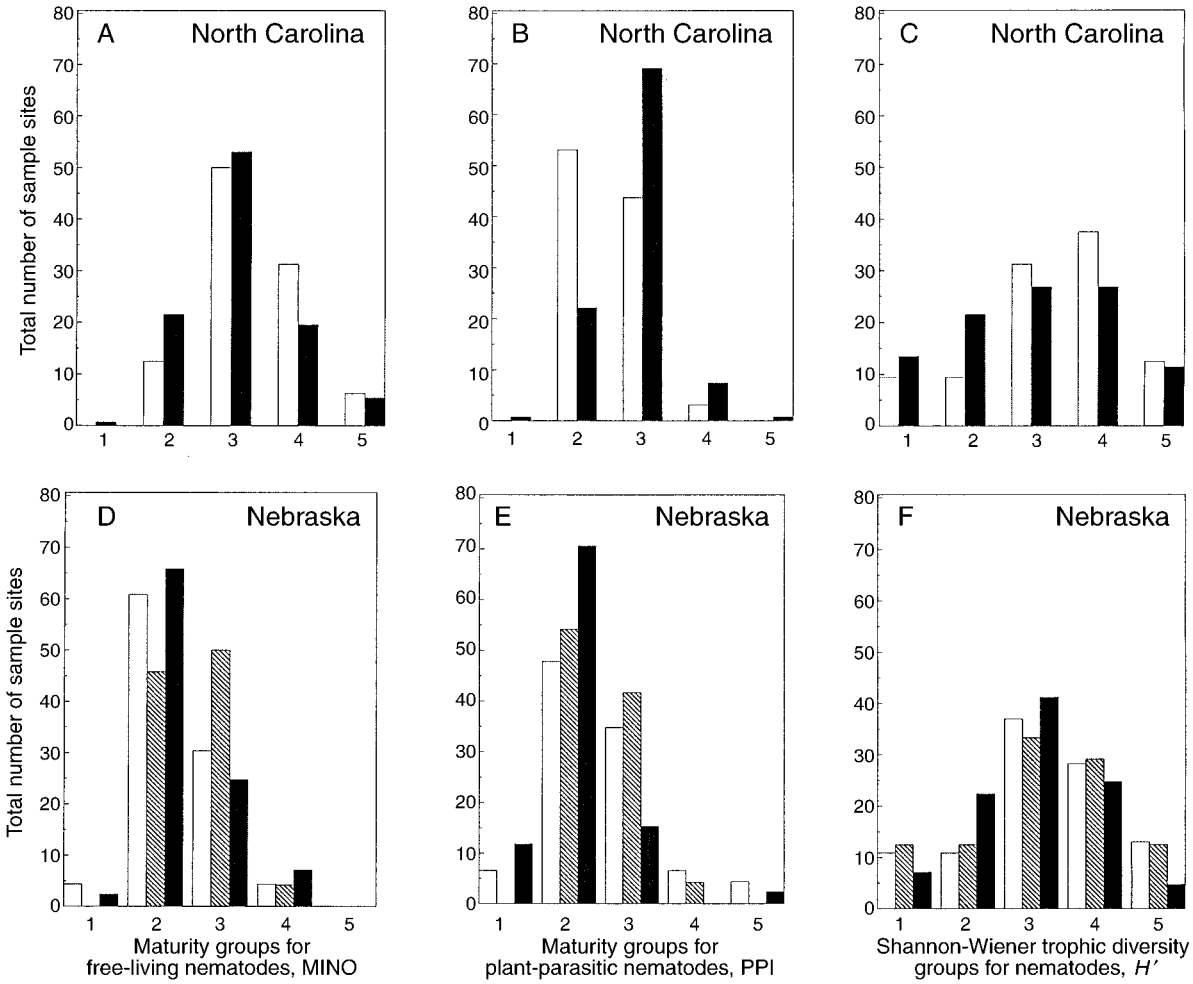

FIG. 2. Standardized frequency of index values, for (A and D) maturity index for free-living nematodes, MINO; (B and E) maturity index for plant-parasitic nematodes, PPI; and (C and F) Shannon-Wiener trophic diversity index in Piedmont (n = 149 fields, solid bars) and Coastal Plain (n = 32 fields, open bars) regions of North Carolina (1992; A–C) and from eastern (n = 46 fields, open bars), northwestern (n = 24 fields, hatched bars), and southern (n = 86 fields, solid bars) regions of Nebraska (1993; D–F). The Mountain region of North Carolina was not illustrated because of its small sample size (n = 4 fields). Standardized frequency was calculated by dividing the total number of sample sites in each index category of a sub-state region by the total number of sample sites within that sub-state region. The quotient was multiplied by 100 to obtain a percentage. Categories 1–5 of maturity indices of free-living and plant-parasitic nematodes represent index values of 0–2, 2.0001–2.5, 2.5001–3, 3.0001–3.5, and 3–5, respectively. Categories 1–5 of Shannon-Wiener trophic diversity represent index values of 0–2.5, 2.5001–3, 3.0001–3.5, 3.5001–4, and 4–5, respectively.

TABLE 3. Values of maturity and diversity indices among land resource regions of North Carolina (1992) and Nebraska (1993). Data are means ± 1 SE.

State	Land resource region	Sample size	MINO†	PPI‡	Trophic diversity, H'
North Carolina	Mountains	4	2.55 ± 0.11	2.42 ± 0.10	3.38 ± 0.30
	Piedmont	149	2.79 ± 0.03	2.71 ± 0.03	3.25 ± 0.05
	Coastal plains	32	2.92 ± 0.06	2.56 ± 0.05	3.40 ± 0.10
Nebraska	Northwestern	24	2.61 ± 0.06	2.51 ± 0.07	3.32 ± 0.13
	Southern	85	2.44 ± 0.04	2.31 ± 0.03	3.26 ± 0.05
	Eastern	46	2.40 ± 0.05	2.52 ± 0.07	3.33 ± 0.09

† Maturity index for free-living nematodes (Bongers 1990), excluding those with a colonizer–persister value of 1.
‡ Maturity index for all plant-parasitic nematodes.

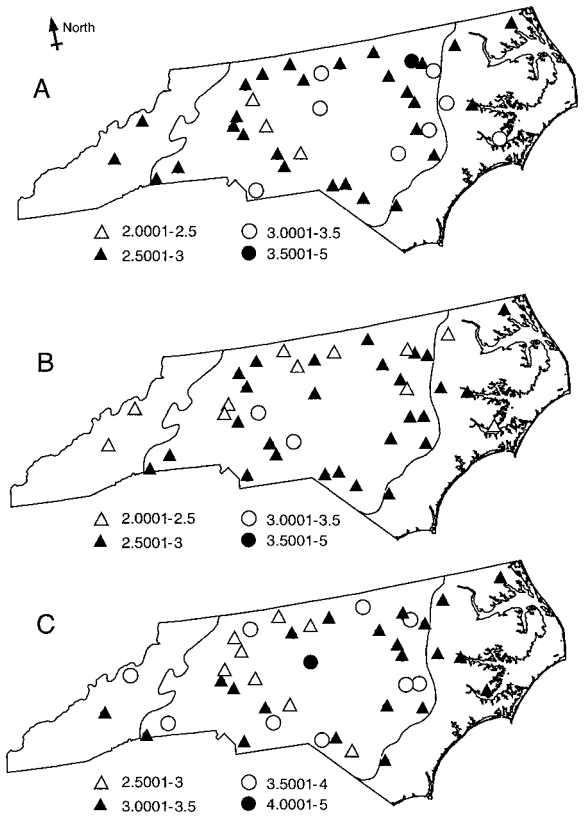

FIG. 3. Maps of the spatial distribution of index categories in North Carolina: maturity indices of (A) free-living nematodes and (B) plant-parasitic nematodes; and (C) the Shannon-Wiener trophic diversity index, H'. Sub-state regions were delineated as Mountains (west), Piedmont (central), and Coastal Plains (east). The maps were created using ArcInfo and ArcView (ESRI 1992*a*, *b*). Each symbol point represents an average of all sample sites (n = 1–14) within one segment (a segment = a sampling unit 0.5–3.2 km^2 in area). Most segments contained >1 agricultural field.

atode taxa with colonizer–persister (CP; Bongers 1990) values of 1 in the calculations. Larger values of successional maturity in North Carolina corresponded with greater abundances of free-living and plant-parasitic nematodes in categories of larger CP values in North Carolina than in Nebraska. A maturity index for free-living taxa, MI, may be viewed as a measure of disturbance, with smaller values being indicative of a more disturbed environment and larger values characteristic of a less disturbed environment. A lower value for the maturity index for plant-parasitic nematodes, PPI, may (Neher and Campbell 1994, Yeates 1994) or may not (Bongers 1990, Freckman and Ettema 1993) indicate more disturbance. Maturity indices are based on frequency of taxa assigned particular CP values or weightings. Greater CP values are assigned to nematode taxa believed to be more sensitive to disturbance (Bongers 1990). Progressive increases in abundances of large CP values through time have been documented following a disturbance such as additions of animal manure to soil (Ettema and Bongers 1993). Similarly, soil communities in uncultivated or no-till agricultural systems have been considered successionally more mature than in frequently cultivated agricultural soil (Hendrix et al. 1986, Freckman and Ettema 1993). Consequently, soils with perennial crops are successionally more mature than soils with annual crops (Freckman and Ettema 1993, Neher and Campbell 1994). Time scales for measurable change in successional maturity of soils may range from one (Ettema and Bongers 1993) to many years without cultivation (Freckman and Ettema 1993, Wasilewska 1994). Generally, disturbances such as fertilization and cultivation are frequent in agricultural systems. Therefore, fewer taxa with CP values of 4 and 5 would be expected to occur in an annually cultivated field than in a system disturbed less frequently such as a meadow (Freckman and Ettema 1993, Wasilewska 1994) or permanent pasture (Neher and Campbell 1994). By comparison, these results im-

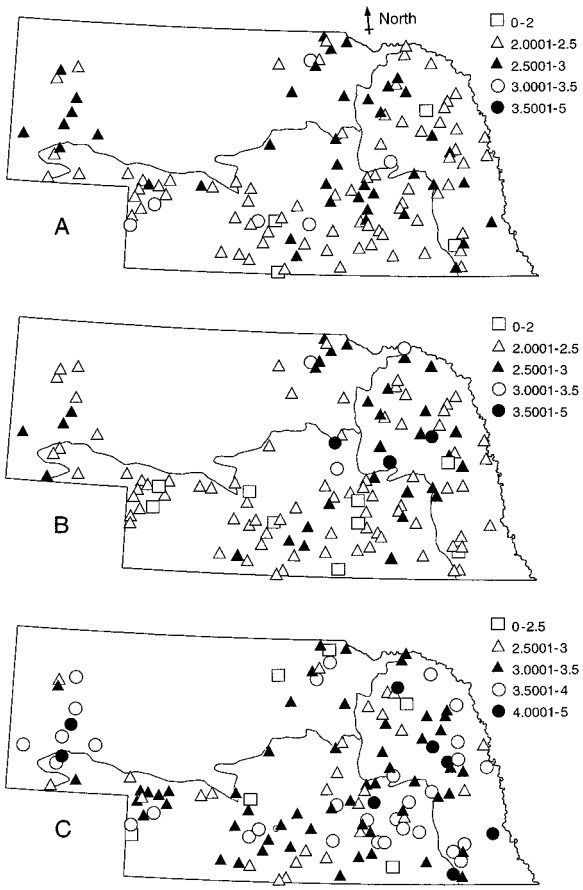

FIG. 4. Maps of spatial distribution of index categories in Nebraska: maturity indices of (A) free-living nematodes and (B) plant-parasitic nematodes; and (C) the Shannon-Wiener trophic diversity index. Sub-state regions were delineated as northwestern, southern, and eastern. The maps were created using ArcInfo and ArcView (ESRI 1992*a*, *b*). Each symbol point represents an average of all sample sites (n = 1–2) within one segment (segment range: 0.7–11.3 km^2). Most segments contained >1 agricultural field.

TABLE 4. Most abundant nematode families within each colonizer–persister (CP) group and their total abundance within North Carolina (1992) and Nebraska (1993).†

		North Carolina			Nebraska		
			Total abundance			Total abundance	
Nematode group	CP	Family	No.‡	%	Family	No.‡	%
Free living	5	Belondiridae	1960	0.31	Dorylaimellidae	920	0.19
	4	Dorylaimidae	37 120	5.92	Dorylaimidae	30 440	6.17
	3	Prismatolaimidae	7220	1.15	Prismatolaimidae	1600	0.32
	2	Cephalobidae	74 320	11.85	Cephalobidae	112 720	22.84
Plant parasitic	5	Longidoridae	8500	1.36	Longidoridae	7440	1.51
	4	Trichodoridae	5840	0.93	Trichodoridae	460	0.09
	3	Hoplolaimidae	85 500	13.63	Hoplolaimidae	26 520	5.37
	2	Tylenchidae	65 080	10.37	Tylenchidae	86 780	17.58

† North Carolina: 627 380 nematodes/500 cm^3 fresh soil; Nebraska: 493 600 nematodes/500 cm^3 fresh soil.
‡ No. = cumulative total of nematodes per 500 cm^3 of fresh soil.

ply that, on a regional basis, nematode communities appear successionally more mature in North Carolina than Nebraska.

Richness of nematode genera and families was greater in North Carolina than Nebraska (Table 2). In both states, richness of nematode taxa (98–107 genera) was greater than earlier reports for rye and potatoes (19–33 genera) in Poland (Wasilewska 1979). However, some of the difference may be due to use of different taxonomic keys (i.e., different levels of taxonomic differentiation).

Diversity indices combine measures of taxa richness and evenness (Ludwig and Reynolds 1988). In agricultural soils, greater diversity of trophic groups is correlated with an increase in the frequency of occurrence of less abundant trophic groups, i.e., fungal-feeding, omnivores, and predators, relative to that of the more generally abundant trophic groups, i.e., bacterial-feeding and plant-parasitic nematodes (Wasilewska 1979). The range of trophic diversity measured in North Carolina and Nebraska for continual production of annual crops (1.55–4.75) was comparable with an average trophic diversity of 2.94 measured for corn, soybean, and wheat in Michigan (Freckman and Ettema 1993) and 2.44–3.05 for wheat cultivated continuously in South Australia (Yeates and Bird 1994). Because values of the trophic diversity index were similar between states (Figs. 1 and 2, Table 3), we concluded that trophic structure of nematode communities was similar in North Carolina and Nebraska. However, we take caution in making this conclusion because recent ecological studies have revealed that feeding-habit groupings may be ambiguous in some cases. For example, abundant populations of *Aphelenchoides, Tylenchus, Tylencholaimus,* and *Ditylenchus* can be classified as ''plant/fungal-feeding'' nematodes (Sohlenius et al. 1977) or some ''predacious'' mononchids can grow and reproduce by feeding on bacteria (Yeates 1987). Assignment of traditional nematode feeding groups may have been inferred rather than confirmed by maintenance of nematodes over many generations under biologically defined conditions (Yeates et al. 1993). This problem may contribute to the perceived lack of trophic diversity between the two states. The problem could be minimized if supplementary studies were conducted to examine critically the feeding preferences of nematode taxa in defined environments.

Another disadvantage of relying on trophic groups for a program that seeks to make regional or interstate comparisons is that the method of extraction may affect the relative efficiency of removal of nematodes from soil and, thus, the proportion of each trophic group obtained. For example, the modified Cobb's sifting and gravity method used in this survey was more time consuming but retained a higher proportion of total nematodes and a greater representation of the trophic groups present than would be obtained with a semi-automatic elutriation (Neher et al. 1995). Thus, similar extraction methods would need to be used in each area for results to be comparable among states or other geographic regions.

Contrary to conclusions based on greater successional maturity of soils in North Carolina than Nebraska, one could conclude that the agronomic potential for production of agricultural crops was better in Nebraska than North Carolina based upon relative abundances of plant-parasitic nematodes in the two states (Table 4). Or, stated alternatively, crop plants would be expected to be less at risk from nematode parasitism in Nebraska than in North Carolina. Plant-parasitic nematodes in the families Heteroderidae and Hoplolaimidae (Yeates et al. 1993) that are capable of reducing crop productivity were more abundant in North Carolina than Nebraska and their host specificity is well documented (Maggenti 1981). Heteroderidae include known major pathogens such as cyst, *Heterodera* spp., and root-knot, *Meloidogyne* spp., nematodes. Soybeans are a host of cyst nematodes and are prevelant in North Carolina. In addition, root-knot nematodes have a wide range of hosts present in North Carolina (Christie 1959). In contrast, members of the Tylenchulidae, and more specifically the plant-parasite *Paratylenchus* (pin nematodes), which feed on a variety of crops including

wheat, oats, and numerous vegetables, were more abundant in Nebraska than North Carolina.

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