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THE SPATIAL DISTRIBUTION OF NEMATODE TROPHIC GROUPS ACROSS A CULTIVATED ECOSYSTEM[1]

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Abstract. In order to better understand the spatial distributions of soil trophic groups and the potential significance of these distributions to ecosystem functioning we initiated a study to describe the within-site variability of nematode feeding groups in a row-crop ecosystem. Soil cores were removed from a 48-ha corn (*Zea mays*) field in the U.S. Midwest prior to spring planting, and nematodes were identified by phenotypic criteria to four groups: bacterivores, fungivores, omnivores/predators, and plant parasites. Within-site variability was high for all groups; population counts spanned two orders of magnitude, with coefficients of variation ranging from 40–130% (n = 115–138 soil samples). Probability distributions were strongly lognormal. Geostatistical analysis showed that a major part of this variability was spatially dependent; variograms suggest that 70–99% of sample population variance was related to spatial autocorrelation over our geographic range of 6–80 m, except for the parasitic group, for which we detected no autocorrelation to 1200 m. Maps of nonparasitic feeding groups across the field showed large multi-hectare areas of low to moderate population densities, with sub-hectare clusters of high-density populations towards one end of the site. Individual feeding groups were only weakly correlated with one another across the field (Kendall's $\tau \leq 0.363$, $P < 0.001$). Edaphic factors (bulk density, texture, pH, C availability, N availability) could collectively explain <30% of the variability in the nonparasitic groups across the area sampled.

Results suggest that important soil food web components are strongly patterned at sub-hectare scales in this site. That this patterning is maintained in an ecosystem subjected to the homogenizing influences of annual soil tillage and a monoculture plant population is remarkable, and suggests that such patterning may be even more common in less-disturbed sites. Inclusion of these patterns in studies of ecosystem processes and soil community dynamics may significantly improve soil trophic models and our understanding of the relationship between soil populations and ecosystem function.

Key words: agricultural ecosystems; autocorrelation; biodiversity; cultivation; food webs; geostatistics; nematodes; soil community structure; soil fauna; spatial variability.

INTRODUCTION

Nematodes are ubiquitous members of the soil faunal community that can have a significant impact on nutrient cycling and primary productivity in many ecosystems. As key members of soil food webs they affect the decomposition rate of plant litter and the turnover of nutrients from soil organic matter, and as important plant parasites they can directly affect plant growth and vigor (Coleman et al. 1984, Freckman and Caswell 1985, Ingham et al. 1985, Freckman 1988, Moore et al. 1988). Growing recognition that nematode populations can respond in predictable ways to ecosystem disturbance (e.g., Wasilewska 1989, Freckman and Ettema 1993) has led to suggestions that nematode community composition—or life history indices thereof—can be used as sensitive indicators of ecosystem change (Bongers 1990, Messer et al. 1991, Neher et al. 1995).

The usefulness of changes in nematode community structure for indicating ecosystem status or soil quality (sensu Doran and Parkin 1994) depends on the presumption that nematode populations can be adequately quantified in soils of targeted ecosystems. Plant feeding species are known to be highly aggregated in most soils (e.g., Goodell and Ferris 1981, Alby et al. 1983, McSorley et al. 1985, Noe and Campbell 1985, Ferris et al. 1990), with frequency distributions typically describing negative binomial functions (Taylor et al. 1979). This aggregation adds a substantial degree of uncertainty to most estimates of population size and adds significantly to the effort required for comprehensive measurement (see Cobb 1918, McSorley and Parrado 1982, Francl 1986, Schmitt et al. 1990). But perhaps more importantly, such aggregation also raises important issues related to the net effects of nematodes on ecosystem functioning: the spatial heterogeneity of

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trophic interactions in soil food webs, e.g., has been flagged as an important determinant of soil trophic dynamics (Parmelee and Alston 1986, Moore and de Ruiter 1991). Subsequent effects on ecosystem nutrient cycles and energy flow may be significant.

Little detailed information is available on the spatial distributions of soil taxa in general in either agricultural or native plant communities. Almost all of our existing knowledge is based on studies of the soil mesofauna, in particular on studies of plant-parasitic nematodes, and these studies have largely focused on individual species. None to date have examined the distributions of functional groups, though knowledge of these distributions will be especially important for relating taxonomic distributions to ecosystem-level processes such as nutrient turnover and primary productivity.

In the present study we provide a comprehensive description of the spatial distributions of bacterivorous, fungivorous, omnivorous/predaceous, and plant-parasitic nematodes within a single row-crop ecosystem. We use geostatistical approaches to quantify spatial distributions and provide insight into the causes underlying the patterns detected. These tools offer substantial power for identifying the proportion of total population variance that is spatially related and for identifying the scale at which patterning, if detected, is expressed (Rossi et al. 1992, Robertson and Gross 1994).

Study Site

The study was conducted as part of a comprehensive analysis of soil chemical, physical, and biological properties of the W. K. Kellogg Biological Station's (KBS) Long-Term Ecological Research (LTER) site in agricultural ecology. KBS is located in southwest Michigan, USA (42°24′ N, 85°24′ W), on an outwash plain left by the last retreat of the Wisconsin glaciation ≈14 500 yr BP. Mean annual temperature at the site (30-yr mean) is 9°C; precipitation is 860 mm/yr, with about half falling as snow in winter months. Soils of the site are Typic Hapludalfs of moderate fertility, either Kalamazoo or the closely related Oshtemo series (Whiteside et al. 1959). Soils sampled at the time of this study averaged 1.3 g/cm^3 bulk density, 43% sand and 40% silt, 6.7 pH, 0.11% N, 10.6 μg NO_3-N/g soil, and had a mean laboratory respiration potential (soil C availability) of 487 ng CO_2-C·g^{-1}·d^{-1} (G. P. Robertson et al., *unpublished manuscript*).

Our 48-ha study site was chosen for its apparent homogeneity. With the exception of a 6-ha area on its northern end, the field had been managed as a single cropping system for decades prior to this study, in the previous 20 yr by the KBS farm staff who employed prevailing best management practices to produce grain and forage for a local dairy herd. These practices included conventional moldboard plowing in spring, followed by pre- and post-emergence herbicide treatment, and then post-emergence N fertilizer applications ranging from 100–200 kg/ha N. For >20 yr prior to this study the site had been cropped continuously to maize (*Zea mays*), with the exception of 2 yr in the late 1970s when the site was strip-cropped to wheat (*Triticum aestivum*) and maize and 4 yr in the 1980s when the northernmost 120 m (6 ha) was cropped to alfalfa (*Medicago sativa*).

Materials and Methods

Sampling design

In early spring after plowing and secondary tillage but prior to planting we removed two 8 cm diameter × 15 cm deep soil cores from each of 144 sample locations across the field. Sample locations were chosen randomly from a larger unaligned grid as described in G. P. Robertson et al. (*unpublished manuscript*), with locations defined to the nearest 10 cm using laser stratigraphy. Distances between pairs of sample locations ranged from 0.9 m to >1200 m. The two soil samples per location, taken within 30 cm of one another, were composited on site and immediately refrigerated prior to transport to the laboratory. In the laboratory, samples from each location were passed through a 4 mm sieve, mixed thoroughly, then subdivided for various analyses, including moisture. Samples for nematode analyses were then shipped by overnight courier to Riverside, California.

Nematode analysis

A semi-automatic elutriator was used to extract nematodes from the soil samples (Byrd et al. 1976). Soil moistures were determined gravimetrically. Nematodes were identified to four trophic groups (bacterivores, fungivores, omnivores/predators, and plant parasites) based on known feeding habitats or stoma and esophageal morphology (Yeates et al. 1993). For taxonomic identifications see Freckman and Ettema (1993). Nematode counts, not corrected for extraction efficiency, were converted to an areal basis (number per square metre to 15 cm depth) using bulk density data available for every sampled point in the field (G. P. Robertson et al., *unpublished manuscript).*

Statistical analysis

Standard parametric analyses were performed with Systat (Wilkinson et al. 1992). Geostatistical analyses were performed using GS$^+$ (Gamma Design Software 1994), including variogram model fitting, which was performed via unweighted least-squares analysis (cf. Cressie 1985). For variograms, semivariance pairs were grouped into 16 separation distance classes (also called lag classes) between 0 and 200 m. The separation distance between each class was 12 m, with pairs of points in the first class separated by an average distance of 6.2 m. The number of pairs in the first through fifth distance classes were 6, 11, 30, 46, and 108 pairs, respectively. Data were lognormally transformed to

TABLE 1. Nematode functional groups across a 48-ha agricultural field in southwest Michigan, USA. Population size units are 10^3 individuals/m^2. Values presented are results of analyses on nontransformed data unless otherwise indicated. SD = standard deviation, CV = coefficient of variation (%).

Nematode feeding group	Population size (10^3 individuals/m^2)	Range		SD	CV	Nontransformed		Transformed [ln(z_i)]		n
		Minimum	Maximum			Skewness	Kurtosis	Skewness	Kurtosis	
Bacterivores	426.6	35.1	1406	256.5	59.9	1.23	1.73	−0.40	0.39	138
Fungivores	193.9	17.6	711	133.4	68.8	1.41	1.96	−0.30	0.21	136
Omnivores/predators	197.2	42.1	694	115.8	58.7	1.61	3.11	0.30	0.03	132
Plant parasites	135.9	7.5	1349	178.0	131.0	3.92	20.72	−0.08	−0.47	137
Total	944.3	175.6	2044	411.3	43.6	0.73	−0.07	−0.35	0.26	115

better normalize probability distributions; backtransformations followed Krige (1981).

For variogram models the semivariance data were fit to spherical functions (Webster 1985, Isaaks and Srivastava 1989). For comparative purposes all models were fit across a range of 200 m; although a range of up to 1400 m is possible for data from this field, in all cases variogram sills approached total sample variance s^2 within a separation distance of <200 m.

We use the proportion of model sample variance ($C + C_0$) explained by structural variance C (the inverse of the relative nugget effect sensu Isaaks and Srivastava 1989) as a normalized measure of spatial dependence for a given nematode population. Where the ratio of structural variance to sample variance (C:[$C + C_0$]) approaches 1, spatial dependence is high over the range of separation distances modeled; i.e., a large proportion of total sample variance s^2 is spatially dependent. Where the ratio of structural variance to sample variance (C:[$C + C_0$]) approaches 0, apparent spatial dependence is low. Because samples separated by a 0 m separation distance should be perfectly autocorrelated (a given sample is perfectly autocorrelated with itself), a low level of spatial dependence indicates either that sampling/analytical error is high or that dependence occurs at scales smaller than the average distance separating pairs in the first lag class, in our case 6 m. Where model sample variance ($C + C_0$) does not approach total sample variance s^2, spatial dependence may be occurring at ranges additional to and greater than the range modeled (Barnes 1991).

Population maps were also produced with GS$^+$, following ordinary block kriging with a block size of 2 m across the field and a 2 × 2 discretization grid within each block. Lognormally transformed data were backtransformed to original units prior to mapping as noted above.

The data used in this study are available electronically as part of the KBS LTER Site permanent data archives. These archives are available over World Wide Web at the address http://kbs.msu.edu/lter/home.html.

RESULTS

Nematode population sizes across the site ranged over two orders of magnitude for most groups. For example, populations of bacterivorous nematodes ranged from 35 × 10^3 to 1.4 × 10^6 individuals/m^2, and populations of plant parasitic nematodes ranged from 8 × 10^3 to 1.3 × 10^6 individuals/m^2 (Table 1). We found similar ranges for other groups, and coefficients of variation ranged concomitantly from 44 to 131% (Table 1).

For all nematode groups the frequency distributions of population sizes across the site were highly skewed. In all cases a lognormal transformation of the data prior to analysis effectively removed both skew and kurtosis (Table 1).

All nematode groups except the plant parasites were spatially autocorrelated at scales of 0–80 m. Variograms (Fig. 1) suggest that 70–99% of sample population variance is spatially dependent at these scales (Table 2). That sill ($C + C_0$) values coincide almost exactly with the overall sample variance s^2 for each group suggests that there is little further structure beyond this range.

The distributions of groups across the site (Figs. 2–4) show similar general trends for each of the three mappable groups (plant parasitic nematodes were not spatially dependent at the scales measured and thus could not be reliably mapped). Distributions of the bacterivorous, the fungivorous, and the omnivorous/predaceous groups all show relatively large patches of low population densities in the southern half of the field, with a more heterogeneous distribution of high-density patches in the northern half. As is apparent from visual comparison of the three distributions (Figs. 2–4), the distributions of these populations were somewhat correlated with one another. Results of pairwise rank-correlation analysis (Kendall's τ, $n > 125$) show that the distribution of bacterivorous nematodes was significantly correlated with both fungivores ($t = 0.363$, $P < 0.001$) and, to a lesser extent, omnivores/predators ($t = 0.229$, $P < 0.001$); the distributions of fungivores and omnivores/predators were more weakly correlated

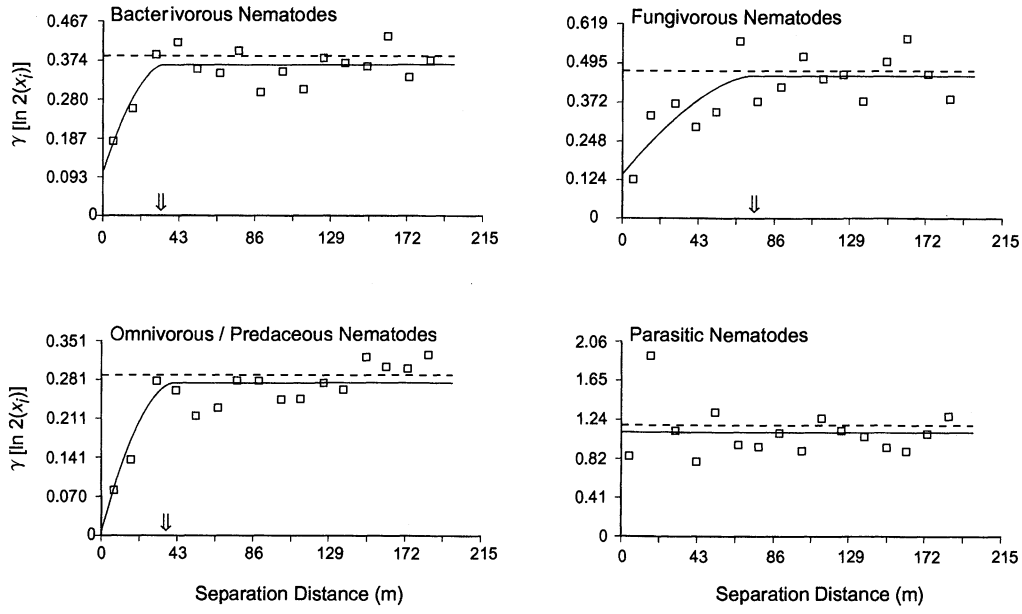

FIG. 1. Variograms for nematode groups across the site. Arrows in each diagram indicate the variogram range (the distance over which spatial dependence is expressed) for each group except the parasitic. Dotted lines indicate overall sample variance. Model parameters appear in Table 2.

($t = 0.148$, $P < 0.01$). Parasitic nematodes were weakly correlated with omnivores/predators ($t = 0.145$, $P < 0.01$), but not significantly ($P > 0.05$) correlated with the other two groups.

Comparisons of interpolated values for nematode populations across the site vs. interpolated values for a number of edaphic characteristics sampled on the same date as nematodes (G. P. Robertson et al., *unpublished manuscript*) show that feeding groups were only weakly correlated with subsets of edaphic factors including bulk density, soil texture (in particular percentage sand and percentage silt), soil pH, soil C availability, total soil N, and levels of inorganic N (Table 3). In a stepwise multiple regression analysis these factors together could explain only 13–27% of the variation in bacterivorous, fungivorous, and omnivorous/predaceous nematodes ($n = 1197$ interpolated points). Neither bulk density nor total soil N was a significant contributor to regression models for bacterivores and fungivores, and neither percentage sand nor percentage silt was a significant contributor to regression models for omnivores/predators. Other soil measures (including % clay, N mineralization potentials, moisture, total % C, and soil C:N ratio) did not contribute additional significant power to any models.

DISCUSSION

Distributions of nematode groups across the site were highly variable, spanning 1–3 orders of magnitude. Plant parasitic nematodes were the most variable, with a coefficient of variation of 130%; bacterivores, fungivores, and omnivores/predators were about equally variable, with coefficients of variation around 60–70%. All groups had a lognormally skewed frequency distribution that appears to be typical of at least plant-parasitic nematode populations in other systems (e.g., Ferris et al. 1990).

Although highly variable, populations across the site

TABLE 2. Variogram model parameters for nematode groups (lognormally transformed) across the site. C_0 = nugget variance, $C/(C_0 + C)$ = relative structural variance; range = distance (m) over which structural variance is expressed, $C + C_0$ = sill or asymptote, s^2 = sample variance for transformed variates. In all cases models describe a spherical function*; variograms appear in Fig. 1.

Nematode feeding group	C_0 (nugget)	$C/(C + C_0)$ (relative structure)	a_0 (m) (range)	r^2	$C + C_0$ (sill)	s^2
Bacterivores	0.107	0.708	35.0	0.664	0.366	0.386
Fungivores	0.142	0.688	77.3	0.582	0.455	0.483
Omnivores/predators	0.001	0.996	40.8	0.748	0.273	0.299
Plant parasites	1.100	0.0	···	0.021	1.100	1.214

* For $h < a_0$, $\gamma(h) = C_0 + (C - C_0)\cdot(1.5\cdot h/\text{range}) - [0.5\cdot(h/\text{range})^3]$; for $h \geq a_0$, $\gamma(h) = C$; where $\gamma(h)$ = semivariance for lag class (separation distance) h.

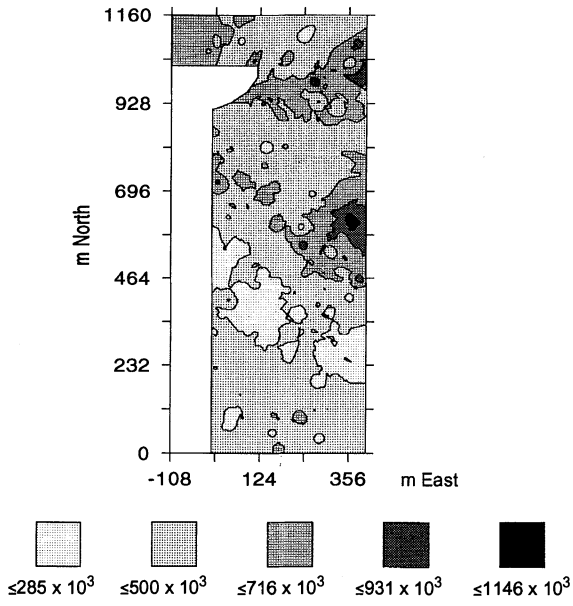

FIG. 2. Population isopleth for bacterivorous nematodes across the site. Units are individuals/m².

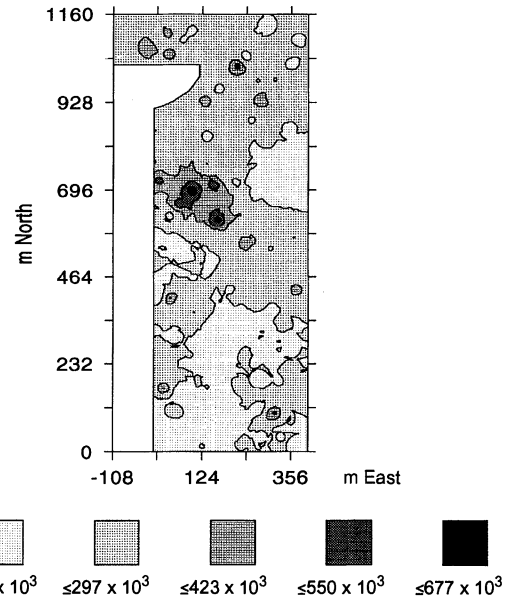

FIG. 4. Population isopleth for omnivorous/predaceous nematodes across the site. Units are individuals/m².

were not randomly distributed. Variograms show that up to 99% of sample variance in the nonparasitic populations was spatially dependent at scales of <80 m. Isarithms of these groups across the site show large multi-hectare patches of low to moderate population densities across most of the site, with smaller, subhectare patches of higher densities clustered towards the north. None of these patches of higher densities, however, were exclusively associated with the northernmost 120 m of the site that was earlier planted to alfalfa.

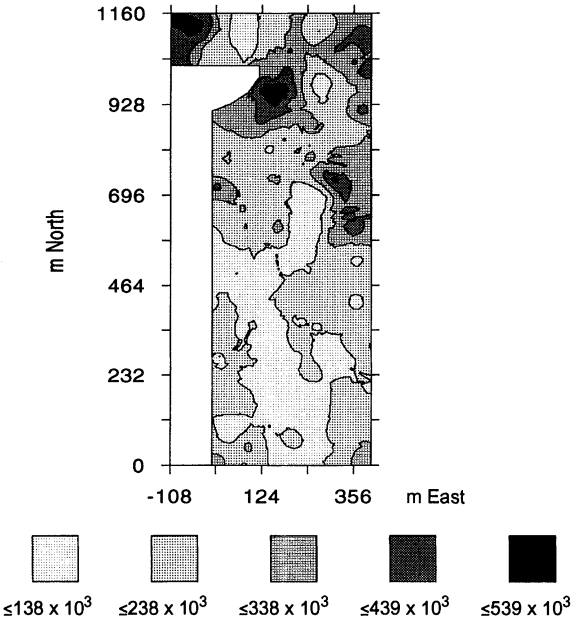

FIG. 3. Population isopleth for fungivorous nematodes across the site. Units are individuals/m².

The variance not explained by spatial autocorrelation in these groups, including all of the variance in the parasitic populations, is either random or expressed at scales below the minimum average separation distance used in this analysis (6.2 m). That we detected no autocorrelation in the parasitic populations at the 6–1200 m scale may be primarily a temporal effect, i.e., due to the dispersed nature of these nematodes prior to planting. Parasitic nematodes appear to be temporally variable in most annual crops, with maximum populations expressed during times of peak plant growth (Barker and Campbell 1981, Barker et al. 1984). The average population size of parasitic nematodes in our sampling was about four times lower than for other groups (Table 1), which further suggests that our in-

TABLE 3. Standardized regression coefficients and (last row) r^2 values for multiple stepwise regression analyses of nematode groups vs. significant ($P < 0.001$) sources of variation. Missing coefficients were not significant and thus not included in the respective regression equations.

Source of variation	Regression coefficients		
	Bacterivores	Fungivores	Omnivores/predators
Bulk density	···	···	0.269
Sand	0.612	0.558	···
Silt	0.883	0.792	···
pH	0.203	0.329	···
C availability	0.213	−0.089	−0.093
Inorganic N	0.256	0.226	0.257
Total N	···	···	−0.187
r^2	0.273	0.263	0.129

ability to detect spatial structure in the parasitic group at these scales may be due to sample timing.

Other studies that have examined the spatial distributions of nematodes, although almost exclusively focused on plant parasitic groups, have noted associations of individual species with edaphic characteristics that have explained a significant proportion of within-field variance. Noe and Barker (1985), e.g., used discriminant analysis of three plant parasite densities and 26 edaphic variables to show that 3–8 soil parameters could together explain up to 50% of the spatial variability of these species. Although different parameters tended to predict different populations, they found that texture, sodium, and copper concentrations were especially useful predictors. Goodell and Ferris (1981) also found correlations of individual parasitic species with soil texture, although they found that regression coefficients varied substantially by species.

In the present study we found that edaphic characteristics (including measures of bulk density, texture, pH, moisture, total and available carbon and nitrogen) could collectively account for only 13–27% of variance among bacterivores, fungivores, and omnivores/predators. Of the 15 edaphic factors measured, the subset that best fit individual regression models included bulk density, percentage sand, percentage silt, pH, available C, total N, and inorganic N pools. Of these, soil pH and texture were best correlated with population counts for the three nonparasitic groups (Table 3). We could not examine regression models for parasitic nematodes because we could not reliably interpolate population isopleths as noted above.

Levels of spatial dependence in this study are similar to those published for a wide range of soil properties. While detailed spatial studies of soil taxa and biological activities are relatively rare compared to spatial studies of soil physical and chemical properties (see, e.g., Webster and Oliver 1990), available studies of biological activities have also found spatial dependence expressed primarily at scales of <100 m. These include studies of soil respiration in Kansas, USA wheat fields (Aiken et al. 1991) and of nitrogen availability and nitrogen gas loss in California cropland (Folorunso and Rolston 1985), Michigan cropland (Robertson et al. 1993), Michigan old fields (Robertson et al. 1988), and UK pastures (Ambus and Christensen 1995).

We find it encouraging that the soil taxa evaluated in this study vary at geographic scales that are similar to scales for nontaxonomic properties here and elsewhere. This suggests promise for using physical and chemical properties as predictors in spatially explicit models of soil population dynamics, although we could not identify a very satisfactory suite of predictors for our site. Our enumeration of patches at scales of metres to hectares does not preclude the occurrence of patches at substantially smaller scales in other sites. It is likely, in fact, that long-term cultivation has increased average patch sizes on our site (Robertson et al. 1993). Moreover, even within our site, populations may be patchy at substantially smaller scales than our minimum 1-m sampling intervals. One might well imagine that patches of nematodes could also occur at the scales of individual plant rhizospheres and organic matter particles, similar to the sub-centimetre scales identified by Hodda (1990) and Hogue and Miller (1981) for marine nematodes.

Nevertheless, patch sizes of the sort encountered in this field can have important consequences for our understanding of field-scale trophic relationships. If the spatial arrangement of food-web components is an important determinant of community-level properties such as trophic efficiencies and dispersal rates, then an accurate picture of these properties—whether measured or simulated—can only emerge from a sampling or simulation analysis that takes this arrangement into account. That functional group sizes in our study varied by 2–3 orders of magnitude across the field suggests that this spatial arrangement may well have a substantial impact on community dynamics. A modeling exercise that incorporates this level of variability and its spatial arrangement could be useful for elucidating more exactly its importance at field and larger geographic scales. It might also suggest more appropriate subunits than habitat or crop management boundaries for making large-scale assessments of soil community health. From this study it appears that there may be as much or even more variability associated with subtle edaphic boundaries within fields or habitats than with historical boundaries imposed by land managers or farmers.

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