

Long-term Disturbance Effects in the Nematode Communities of South Mississippi Woodlands

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Abstract: The effects of soil disturbance on the nematode community were assessed at 30 sites on the outer coastal plain of Mississippi, representing four ages since soil disturbance plus a control group of six undisturbed sites. Thirty-five taxa were encountered, dominated in abundance and taxonomic richness by plant and bacterial feeders. Nematodes were more abundant and more taxonomically rich in sites with a low slope and deep litter cover, distant from trees. Plant feeders were more numerous at sites with a dense herb cover, suggesting limitation by food availability. When sites were arranged as a chronosequence, herb cover, litter depth, soil organic matter, soil moisture, and tree canopy cover increased through time consistent with succession to forest. The abundance of most trophic groups decreased in the 10 to 20 years following disturbance and increased thereafter, a pattern repeated in taxonomic richness of plant and bacterial feeders. Fifty years after disturbance, nematode abundance had not returned to levels observed in control sites. These results suggest that nematode succession following soil disturbance is a gradual process regulated by establishment of aboveground vegetation. There was no evidence of dispersal limitation or facilitation by colonist nematode species.

Key words: *Cephalobus*, chronosequence, disturbance, ecology, forest, *Helicotylenchus*, nematode, Rhabditidae, soil, succession.

The spatial structure of ecological communities depends on the pattern, scale, and severity of disturbance (Pickett and White, 1985; Turner et al., 1997; Watt, 1947). Patchiness in plant communities may reflect physical gradients generated by disturbance (Moore and Vankat, 1986; Runkle and Yetter, 1987) or may be created by local eradication and limits on recolonization (Kupfer et al., 1997; Matlack, 1994; Wood and del Moral, 1987). Soil nematode communities show enormous patchiness at scales of 1 to 100 m (Boag et al., 1994; Campbell et al., 1996; Robertson and Freckman, 1995), but the role of disturbance in creating such pattern is unknown. Disturbed-soil sites in southern Mississippi are depauperate in nematode abundance and taxonomic richness (Matlack, 2001). Soil is naturally disturbed in this region by erosion and deposition of sediment, tree uprooting, and burrowing by animals, but these events are local in extent and never occupy more than a small fraction of the forest floor (Matlack, unpubl.). If soil disturbance has caused the observed heterogeneity in nematode distributions, the community response to disturbance (i.e., succession) must be long-lived relative to soil disturbance frequency. Our purpose here is to assess the role of soil disturbance in structuring nematode communities by examining the succession following severe soil disturbance, and to suggest mechanisms that control rate of succession.

Successional change following soil disturbance has been reported in a variety of nematode communities (Freckman and Ettema, 1993; Hodda et al., 1997; Wasilewska, 1970) and, occasionally, following above-

ground events such as tree harvesting (Armendariz et al., 1996; Sohlenius, 1982). In general, soil disturbance causes a sharp decrease in nematode diversity and may be accompanied by a shift to colonizing species (Bongers, 1990; Ettema and Bongers, 1993). Nematode abundance often declines significantly following disturbance in natural ecosystems (de Goede et al., 1993; Hodda et al., 1997; Wasilewska, 1970), whereas disturbance by cultivation in agroecosystems may cause an increase in abundance, probably due to resources provided by incorporation of crop wastes (Freckman and Ettema, 1993; Parmalee and Alston, 1986; Wardle et al., 1993).

Changes in distributions following disturbance have been linked to changes in physical and biotic properties of the soil (Beare et al., 1995; Freckman and Baldwin, 1990). Because nematodes are predators and parasites rather than primary producers, successional changes in the soil microenvironment may affect them indirectly by regulating prey populations, thereby creating resource limitation (“bottom-up limitation”) (Beare et al., 1995; Ingham et al., 1985). Resource limitation may be imposed by successional development of aboveground vegetation (Wasilewska, 1970, 1995) or growth of fungal and bacterial populations (Hendrix et al., 1986). Alternatively, nematodes may respond directly to soil properties at successional sites. Vegetation succession, for example, may act on nematode communities through physical changes created by shading or accumulation of organic matter (de Goede et al., 1993; Wasilewska, 1970). If physical changes influencing nematode succession are caused by other species, this process illustrates the concept of “facilitation” (Clements, 1916; Connell and Slatyer, 1977). Resource limitation implies regulation of succession by control of population growth rates, whereas facilitation involves physical alterations that influence the suitability of the site for colonization.

In plant communities, succession is often directed by availability of colonists, illustrated by dispersal limita-

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tion (Kupfer et al., 1997; Matlack, 1994). In nematodes, recovery in richness following disturbance is consistent with dispersal and colonization processes (de Goede et al., 1993; Wardle et al., 1995; Yeates et al., 1991). Dispersal by a variety of mechanisms has been reported in nematodes (Krnjaic and Krnjaic, 1970; Orr and Newton, 1971), but little information is available and (to our knowledge) availability of colonists has not been examined as a factor shaping nematode communities.

We examined disturbance effects in the soil nematode community by comparison among a chronosequence of 30 sites spanning ca. 60 years since soil disturbance. Possible successional mechanisms were tested by comparing changes in the nematode community with aspects of the vegetation and soil microenvironment. If facilitation by non-nematode species influences the rate or direction of nematode succession, we expected increases in taxonomic richness to be correlated with changes in the soil and vegetation microenvironment. Among nematode species, facilitation would be consistent with changes in species composition through successional time. If the community response to disturbance is regulated by resource availability, we expected nematode abundance to recover more slowly than taxonomic richness, and to be correlated with relevant aspects of the edaphic or vegetational microenvironment. Conversely, if the rate or direction of succession is controlled by availability of colonists, we expected richness to increase more slowly than abundance and to decline with increasing distance to potential sources of colonists.

MATERIALS AND METHODS

Twenty-four sites were selected to represent four age classes since the last anthropogenic soil disturbance—<3 years, 10 to 20 years, 30 to 40 years, and >50 years—with six replicates in each age group, plus a control group of six undisturbed sites. Sites were situated on the outer coastal plain approximately 120 km north of the Gulf of Mexico near the city of Hattiesburg, Mississippi (31°17'N, 18°20'W). Natural soils in the study area are highly leached ultisols typical of the coastal plain, primarily consisting of well-drained sandy loams but also including expanding clays (Davis and Byers, 1975). Soils are relatively nutrient poor and considered of low-moderate agricultural value. Most of the area currently supports a mixed pine-hardwood forest.

Individual study sites (≥ 1 ha) were selected for within-site homogeneity of vegetation, landform, and management history. Disturbances were created by human earth-moving projects such as leveling of irregular land, grading of highways and building sites, and storage of unused soil. The time since disturbance was determined by comparing historical aerial photos. Control sites were naturally wooded tracts having large individual trees and showing no evidence of human soil

disturbance. By careful site selection we tried to minimize variation in topography and drainage among sites: All sites were at least 50 m away from continuously flowing streams. Floodplains and bottomlands were avoided. Sites that appeared to have received chemical amendments (i.e., fertilizers, pesticides, oil or gasoline runoff, etc.) were avoided.

Sampling: Soil samples were collected over a period of 6 days in early September 1999. At each site, five soil cores were collected (3.5-cm-diam. \times 15-cm-depth) at least 20 m from one another and >30 m from the site boundary to reduce the likelihood of edge effects. Before coring, all litter and humus were removed down to mineral soil. At each sampling point we recorded litter cover, litter depth, herbaceous cover, and slope in a centered 50 \times 50-cm quadrat, and circumference of the nearest woody stem >2 m in height. Distances were measured from each sampling point to the nearest woody stem >2 m and nearest undisturbed soil, and expressed as mean values for each site. Canopy openness was estimated using a Lemmon Spherical Densitometer (Forestry Suppliers, Jackson, MS) held at 1 m.

Soil cores were transported on ice to the laboratory in Hattiesburg, and nematode extraction was begun within 12 hours. Each core was weighed, passed through a coarse sieve (4-mm opening), and gently mixed. A 12-gm field-moist subsample was placed in a Baermann funnel for nematode extraction following Southey (1986) and Dropkin (1989). After 48 hours, equal draughts were taken from each funnel and combined to give a single extract for each site. Nematodes were fixed in sub-boiling formalin and shipped to Ever-Green Nematode Testing Labs, Inc. (Redmond, WA) for identification and counting.

Soil moisture was calculated from weight loss on drying (65 °C for 48 hours) and organic content estimated as weight loss on incineration of dry samples (Tiessen and Moir, 1993). Sample pH was recorded in aqueous solution (weight ratio 1:2; Hendershot et al., 1993). On aerial photos, we measured the narrowest width of the disturbed area, and distance from the site to nearby disturbed-soil sites.

Data analysis: Nematodes were classified and counted by family, genus, and occasionally species. It wasn't possible to identify all nematodes to species. To maximize information content of our data, all taxa were included in calculations at the level of finest discrimination, whether species, genus, or family. Taxa were grouped as bacterial feeders, plant feeders, predators, omnivores, or fungal feeders by reference to Yeates et al. (1993). Each feeding group was described in terms of abundance (total number of individuals at a site), taxonomic richness (number of taxa observed at a site), and evenness (similarity in abundance among taxa) (Magurran, 1988).

To determine if environmental variables influenced nematode abundance, richness, or evenness, backward-

stepwise multiple regression was applied (SYSTAT 7.0, SPSS Inc., Chicago, IL). Variables were removed until the model showed stable regression coefficients and low correlations among independent variables. Variables with low F values were eliminated to produce a final model significant overall ($P < 0.05$) and significant in all variables individually. Distance to the nearest tree and nearest undisturbed soil were log-transformed to emphasize variation at short distances. Due to ambiguity regarding the use of control (undisturbed) sites as a successional endpoint, controls were omitted from this phase of the analysis.

Differences among age classes were tested by the Kruskal Wallis procedure followed by pairwise Mann Whitney U tests (analysis of variance was not used due to widespread inequality of variance). Detrended Correspondence Analysis (PC-ORD 2.0; MjM Software Design, Gleneden Beach, OR) was applied to examine trends in nematode community composition.

RESULTS

A mean of 134 nematodes (± 85 sd) was extracted at each site (corresponding to a density of $2.8 \times 10^4 \pm 1.8 \times 10^4$ individuals/m²), predominantly plant and bacterial feeders (Table 1). Thirty-five taxa were encountered including 22 plant feeders and 10 bacterial feeders (see Appendix). Bacterial-feeding Rhabditidae were the most numerous taxon by a wide margin, occurring in relatively large numbers (34.9 individuals/site) and encountered in many sites (26/30). The bacterial-feeding genus *Cephalobus* spp. (11.6 individuals/site) and plant-feeding *Helicotylenchus* spp. (10.3 individuals/site) were also abundant and frequently observed (26 and 19 sites, respectively). Plant feeders *Heterodera* spp. and *Dolichodoros heterocephalus* were encountered only occasionally (7 and 3 sites, respectively) but were very abundant where present (31.1 and 21.7 individuals/site, respectively). Predators, omnivores, and fungal feeders were less frequently encountered.

Nematodes were most abundant in relatively level sites with an accumulation of litter, at a distance from individual trees (Table 2). A comparison of standardized coefficients suggests that distance from trees was

TABLE 1. Nematode community structure measured as overall abundance, taxonomic richness, and evenness of distribution in samples from 30 sites near Hattiesburg, Mississippi.

	Abundance	Richness	Evenness
Plant feeders	57.4 \pm 49.2	5.4 \pm 3.1	0.7 \pm 0.2
Bacterial feeders	59.8 \pm 44.7	3.8 \pm 1.2	0.7 \pm 0.2
Fungal feeders	7.8 \pm 13.6	0.6 \pm 0.5	—
Predators	2.5 \pm 5.2	0.4 \pm 0.5	—
Omnivores	6.3 \pm 8.5	0.8 \pm 0.4	—
Total	133.9 \pm 85.4	10.7 \pm 3.7	0.8 \pm 0.1

Figures are mean values per site and standard deviations. Evenness is not calculated for groups with mean richness < 1.0 . "Abundance" indicates total number of nematodes counted at each site.

most influential among these variables. Plant-feeding nematodes were most abundant in sites with a well-developed herbaceous layer. Numbers of predatory nematodes, distance from streams, slope, and nearest tree circumference were of secondary importance. Abundances of fungal and bacterial feeders were dependent on each other and (in the case of fungal feeders) absence of predators. Abundances of omnivores and predators were unrelated to the environmental variables considered here. Rather, their abundance appears to be dominated by stochastic effects at low densities.

Taxonomic richness was greatest in sites with a relatively narrow disturbed area, and in microsites that were relatively level and situated far from individual trees, and having a great litter depth (Table 3). Considered by trophic group, however, richness was unrelated (or weakly related in the case of plant feeders) to measures of the environment. Evenness of distribution was tested only in the two most abundant groups. Bacterial feeders were most evenly distributed at sites close to individual trees but far from undisturbed natural vegetation. Plant feeder evenness did not show a significant response to the environment.

Variation among age classes: Tree distance and canopy cover differed significantly among age classes (KW test statistic_{tree} = 19.3, $P = 0.001$; KW_{canopy} = 16.0, $P = 0.003$). In subsequent pairwise comparisons (Table 4), trees were significantly closer to sample points at undisturbed sites than to points in the < 3 , 10 to 20, and > 50 year age classes ($P < 0.05$), and points in the < 3 year age class were significantly farther from trees than points in the 10 to 20 year age class. These differences reflect the higher density of trees in successional older sites (Fig. 1A). Canopy cover increased with time (Fig. 1B), showing significant differences between the control and < 3 year age class and between the < 3 and 10 to 20 and 30 to 40 year age classes (Table 4), again consistent with a successional increase in vegetation density. Inspection shows depressed soil moisture, soil organic matter, litter depth, and herbaceous cover in recently disturbed sites relative to the control and oldest disturbed sites (Fig. 1C–F), although none of these differences were significant in pairwise comparisons ($P > 0.05$). Canopy cover increased most strongly between the < 3 and 10 to 20 year age classes, whereas all other variables increased most strongly between the 10 to 20 and 30 to 40 year classes. The pH did not differ significantly among age classes ($P > 0.05$).

Abundance of nematodes was depressed in the 10 to 20 year age class relative to the control but returned to control levels in the 30 to 40 year age class (Fig. 2A), largely due to trends in the numerically dominant plant and bacterial feeders. Numbers of predators, fungal feeders, and omnivores increased above the control following disturbance and remained high through the

TABLE 2. Regression models of abundance of soil nematodes on relevant environmental factors in 24 disturbed-soil sites near Hattiesburg, Mississippi.

	Coef.	Std. coef.	
Total = constant	51.7	0.00	F = 5.574 df = 3 reg, 20 res $p = 0.0006$, $r^2 = 0.455$
litter depth	10.2	0.37	
slope	-317.3	-0.38	
log tree dist	221.3	0.58	
Plant feeders = constant	-38.4	0.00	F = 11.968 df = 5 reg, 18 res $p < 0.001$, $r^2 = 0.769$
herb cover	1.7	0.58	
slope	-123.5	-0.27	
circum	0.8	0.28	
log stream dist	31.7	0.30	
predators	2.9	0.33	
Fungal feeders = constant	-1.41	0.00	F = 8.596 df = 2 reg, 21 res $p = 0.0002$, $r^2 = 0.450$
predators	-0.90	-0.35	
bacterial feeders	0.21	0.67	
Bacterial feeders = constant	20.45	0.00	F = 8.808 df = 2 reg, 21 res $p = 0.002$, $r^2 = 0.456$
herb cover	0.99	0.35	
	1.74	0.53	
Omnivores NS			
Predators NS			

“Std. coef” are regression coefficients standardized to a y-intercept = 0. “NS” = nonsignificance, ($p > 0.05$).

chronosequence. However, the large standard errors in predators, fungal feeders, and omnivores probably reflect stochastic effects at low densities. Larger samples would be required to comment with certainty on these groups.

Differences among age classes were significant in total abundance and plant feeder abundance ($KW_{total} = 10.6$, $P = 0.031$; $KW_{plant} = 10.6$, $P = 0.031$). Pairwise comparisons distinguished the <3 and 10 to 20 year age classes from the 30 to 40 year age class among plant feeders, and the 10 to 20 year age class from the control (Table 4). This pattern of depression and rebound was also evident in total abundance and present (although not significant) in abundance of bacterial and fungal feeders and predators (Fig. 2C–E). Taxonomic richness showed a pattern similar to abundance ($KW_{total} = 12.9$,

$P = 0.012$; $KW_{plant} = 10.6$, $P = 0.031$; Fig. 3). Indeed, total richness and abundance were strongly correlated (Pearson $r = 0.758$; $P < 0.000$). Pairwise comparisons of both total and plant feeder richness distinguished the <3 year age class from the control and the 30 to 40 and >50 year age classes (Table 4). Other trophic groups were too poorly represented to make meaningful comparisons. Evenness differed significantly among age classes in bacterial feeders ($KW = 9.6$, $P = 0.048$). Greatest mean values were observed in the undisturbed controls and lowest in the <3 year age class, but pairwise comparisons were not significant.

In Detrended Correspondence Analysis, the first three ordination axes accounted for only 4.6% of total variation in community composition indicating an absence of strong trends among sites and age classes.

TABLE 3. Taxonomic richness and evenness of soil nematodes in relation to environmental factors in 26 disturbed soil sites near Hattiesburg, Mississippi.

Richness	Coef.	Std. coef.	
Total = constant	19.32	0.00	F = 4.150 df = 5 reg, 18 res $p = 0.0011$, $r^2 = 0.535$
width	-0.01	-0.44	
bulk density	-0.03	-0.37	
litter depth	0.46	0.41	
slope	-20.51	-0.61	
log tress dist	6.78	0.44	
Plant feeders = constant	0.35	0.00	F = 4.852 df = 1 reg, 22 res $p = 0.038$, $r^2 = 0.181$
log stream dist	2.83	0.43	
Bacteriovores, fungivores, predators, and omnivores NS			
Evenness			
Total = constant	0.89	0.00	F = 6.885 df = 1 reg, 22 res $p = 0.015$, $r^2 = 0.238$
log tree dist	-0.16	-0.49	
Bacterial feeders = constant	0.88	0.0	
log natural dist	0.07	0.36	F = 12.338 df = 2 reg, 21 res $p = 0.000$, $r^2 = 0.540$
log tress dist	-0.46	-0.72	
Plant feeders NS			
Predators, omnivores, and fungivores were not tested.			

“Std. coef.” are regression coefficients standardized to a y intercept of 0. “NS” = non-significance ($p < 0.05$).

TABLE 4. Mann Whitney pairwise comparisons between age classes.

Environment									
Tree distance					Canopy				
age class									
	<3	10-20	30-40	>50		<3	10-20	30-40	>50
undist	0.004	0.004	0.015	0.004	undist	0.006	ns	ns	0.025
<3		0.004	ns	ns	<3		0.007	0.007	ns
10-20			ns	0.025	10-20		ns	ns	
30-40				ns	30-40				ns
Nematode abundance									
Total					Plant feeders				
	<3	10-20	30-40	>50		<3	10-20	30-40	>50
undist	ns	ns	0.037	ns	undist	ns	0.030	ns	ns
<3		ns	ns	ns	<3		ns	0.030	ns
10-20			0.010	0.025	10-20			0.025	ns
30-40				ns	30-40				ns
Taxonomic richness									
Total					Plant feeders				
	<3	10-20	30-40	>50		<3	10-20	30-40	>50
undist	0.020	0.010	ns	ns	undist	ns	0.007	ns	ns
<3		ns	0.037	ns	<3		ns	ns	ns
10-20			0.015	0.034	10-20			0.018	0.050
30-40				ns	30-40				ns

Comparisons are calculated for variables judged significantly different among age classes in previous Kruskal Wallis tests. Levels of significance are presented. "ns" = nonsignificance.

DISCUSSION

Soil disturbance resulted in sites with low soil moisture, little organic matter, a shallow litter layer, and low canopy coverage, with no nearby trees. Through the chronosequence, these parameters changed consistent with vegetational succession to forest. However, values in the oldest age class often were not comparable to the undisturbed controls, indicating that 50 years of succession has not entirely erased the impact of disturbance.

Soil disturbance also affected the nematode community. Plant feeders were less abundant in disturbed soil than controls for up to 20 years; other trophic groups were more abundant in disturbed soil, suggesting that disturbance had improved substrate quality or resource availability. Taxonomic richness was lower in recently disturbed soil than controls, implying eradication of species in the disturbance event (or reduction to undetectable levels) (Beare et al., 1995; Freckman and Ettema, 1993; Hodda et al., 1997). Richness in all trophic groups was within ranges reported for forest sites on the southeastern coastal plain (Matlack, 2001; McSorley, 1993). According to general observation (Bloemers et al., 1997; Freckman and Ettema, 1993; McSorley, 1993), fewer predator and omnivore taxa were encountered than herbivores and bacteriovores. In the present study sieving may have removed or damaged some of the largest predators, which would have contributed to their scarcity. However, most of the

predators observed were far smaller than the size of the sieve openings, so sieving has probably not strongly influenced the results. Relatively few fungivore taxa were observed, contrary to the observation of McSorley (1993) in nearby Florida, but consistent with their low abundance.

Variation among sites: Nematode distributions corresponded to gradients of moisture retention and (in the case of plant feeders) food availability. Total abundance and richness were greatest in level areas with a thick litter mat—features that would improve water retention in a drought. Disturbed soil was dry relative to controls, and moisture has often been linked to nematode abundance (Armendariz et al., 1996; Matlack, 2001; McSorley, 1997; Sohlenius, 1982), implying that drought protection is critical in the sites surveyed here. However, the absence of a direct soil moisture effect indicates that moisture is not limiting under normal conditions.

Correlation of abundance with herb cover suggests resource limitation among plant feeders. In a study of undisturbed sites nearby (Matlack, 2001) other trophic groups also appeared to be limited by food availability, but resource limitation was not evident among them in the present study. Numbers of omnivores and predators were not predicted by abundance of potential prey, nor were fungivores associated with potential fungal substrates. It seems likely that the occasional appear-

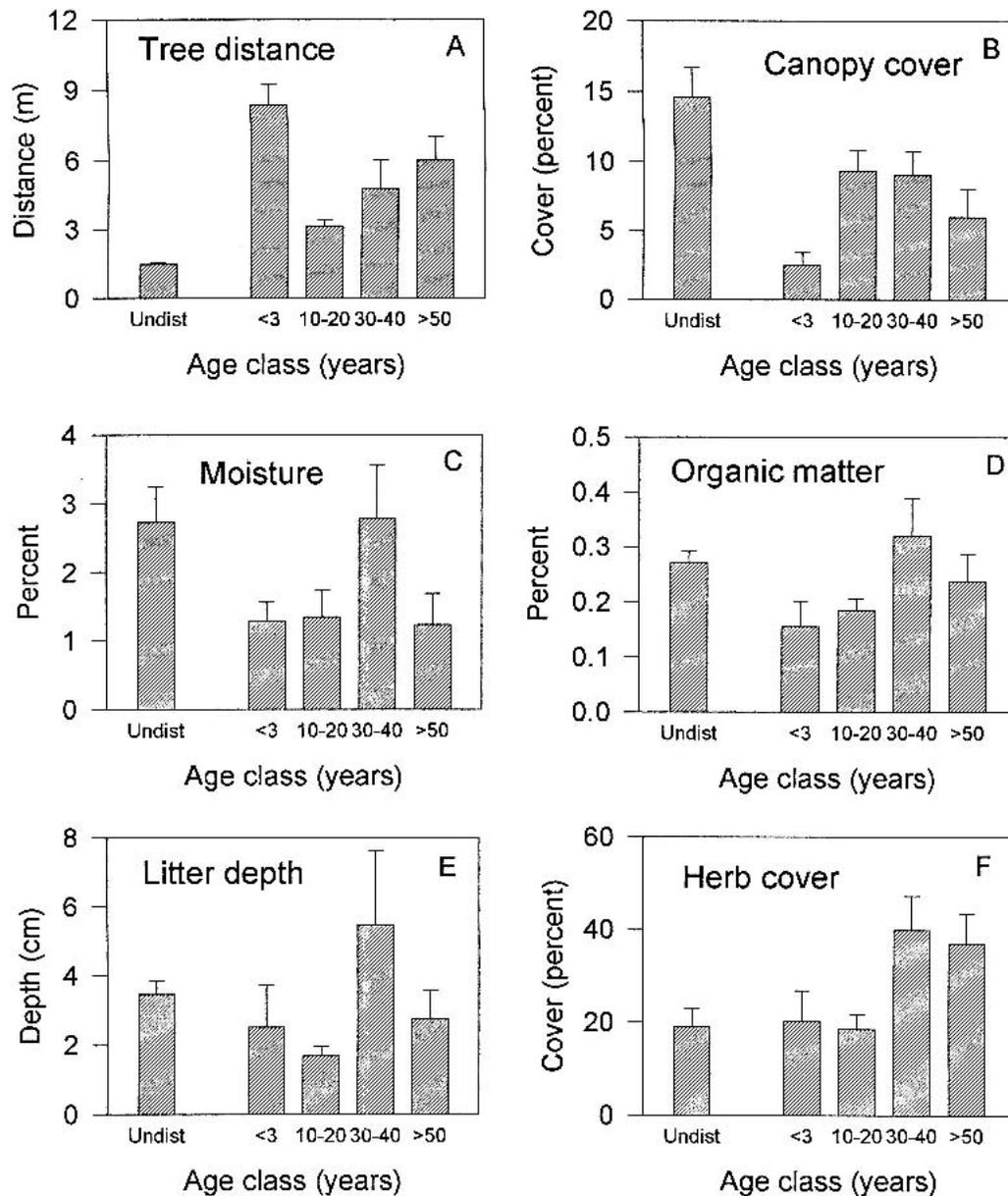


FIG. 1. Soil and vegetational variables in a chronosequence representing >50 years following soil disturbance in southern Mississippi. "Undist" indicates undisturbed (control) sites. Bars are one standard error.

ance of predators, bacteriovores, and fungivores as predictive variables in abundance regressions reflects a common response to an unmeasured environmental variable rather than a direct predator-prey relationship.

Distance to the nearest tree was a strong predictor of nematode abundance, richness, and evenness, with significantly more individuals, more taxa, and lower evenness found at greater distances. This result contradicts observations of dry savanna sites in Kenya (Coleman et al., 1991) in which greater numbers were encountered under trees than in openings, presumably because N and water were more available under trees. Intuitively we might expect trees to moderate environmental extremes by shading and adding organic matter to the soil, allowing larger and richer nematode communities

than unshaded areas (Matlack, 1993). This may not have occurred in the present study because "trees" were often recently established saplings, and cast little shade. Alternatively, soil near trees may have been unacceptably dry due to water removal by transpiration. Although the mechanisms remain unclear, the tree distance response in another example of pattern in above-ground vegetation shaping nematode distributions.

Trends in time: Comparisons among age classes are complicated by variation among replicate sites. Clearly, succession has not produced similar nematode communities in all sites of similar age. In vegetation, multiple successional pathways have been demonstrated in cases of primary succession following severe disturbance (Baker and Walford, 1995; Fastie, 1995; Myster and

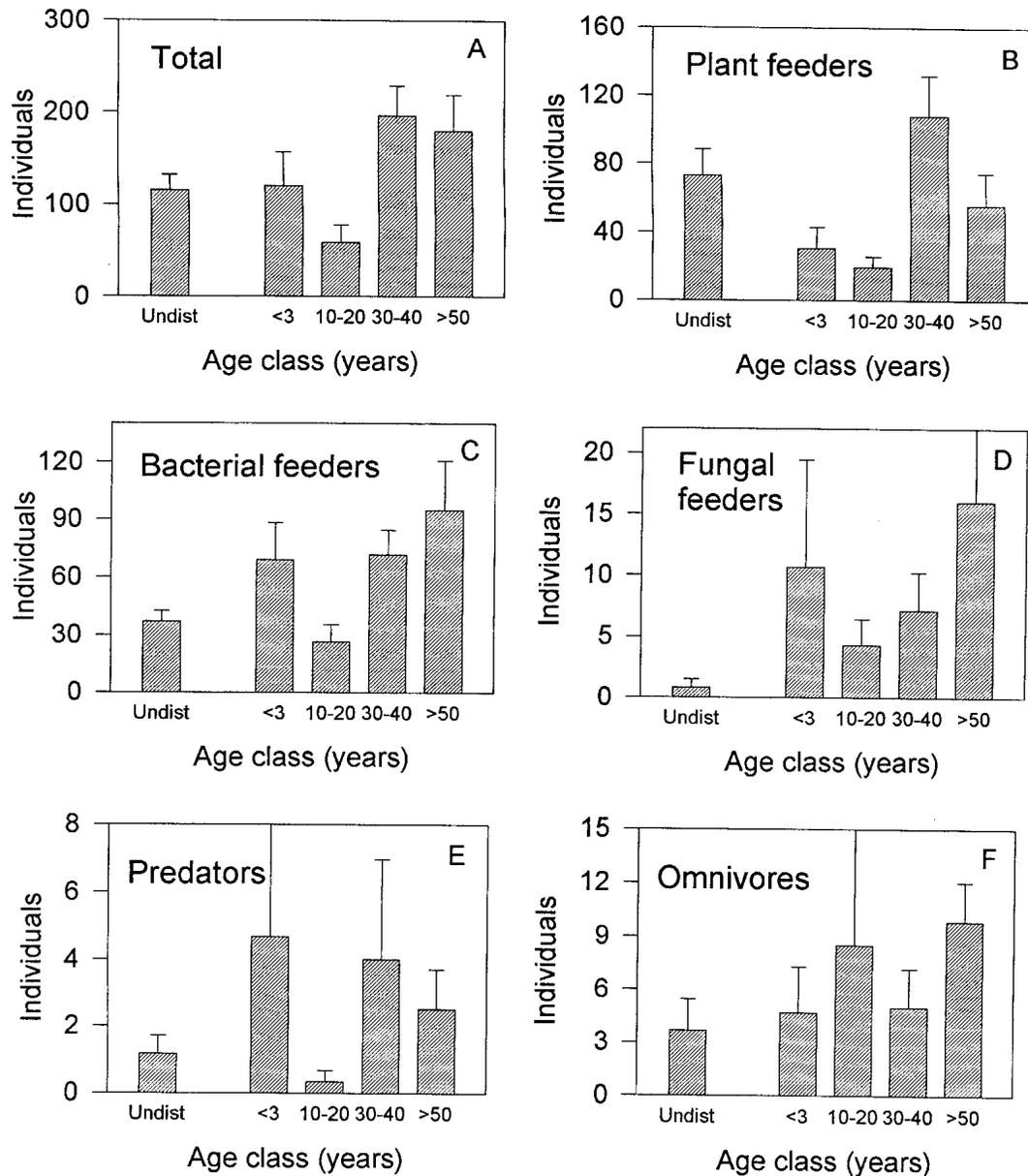


FIG. 2. Soil nematode abundance in a chronosequence representing >50 years following soil disturbance in southern Mississippi. "Undist" indicated undisturbed (control) sites. Bars are one standard error.

Pickett, 1990; Turner et al., 1997; Wood and del Moral, 1987), where differences among pathways reflect contrasting starting conditions, different locations relative to potential sources of colonists, and variation on broad physical gradients. If sufficient samples have been collected in each time class, within-class variation will represent the range of possible pathways, and mean values will show the general successional trend. Our chronosequence is well replicated relative to most similar studies, so we feel safe in presenting these data as a pattern of nematode response typical of the study area.

The nematode community conformed to the general model of depletion and recovery, dominated by plant feeders in which abundance declined and increased in parallel with successional development of herb cover.

Bacterial feeders were also correlated with herb cover, possibly because root exudates promote bacterial growth (Coleman et al., 1991). In contrast to plant feeders, bacterial and fungal feeders increased in numbers following disturbance, and mean values remained above controls through most of the chronosequence. Disturbance appears to have created long-term opportunities for population growth, presumably by fostering growth of bacterial and fungal prey populations.

Richness of plant feeders declined substantially following disturbance, only returning to background levels in 30 to 40 years. The return to stability following disturbance varies considerably among nematode communities depending on substrate, ecosystem, and character of disturbance (Armendraz et al., 1996; Hodda et

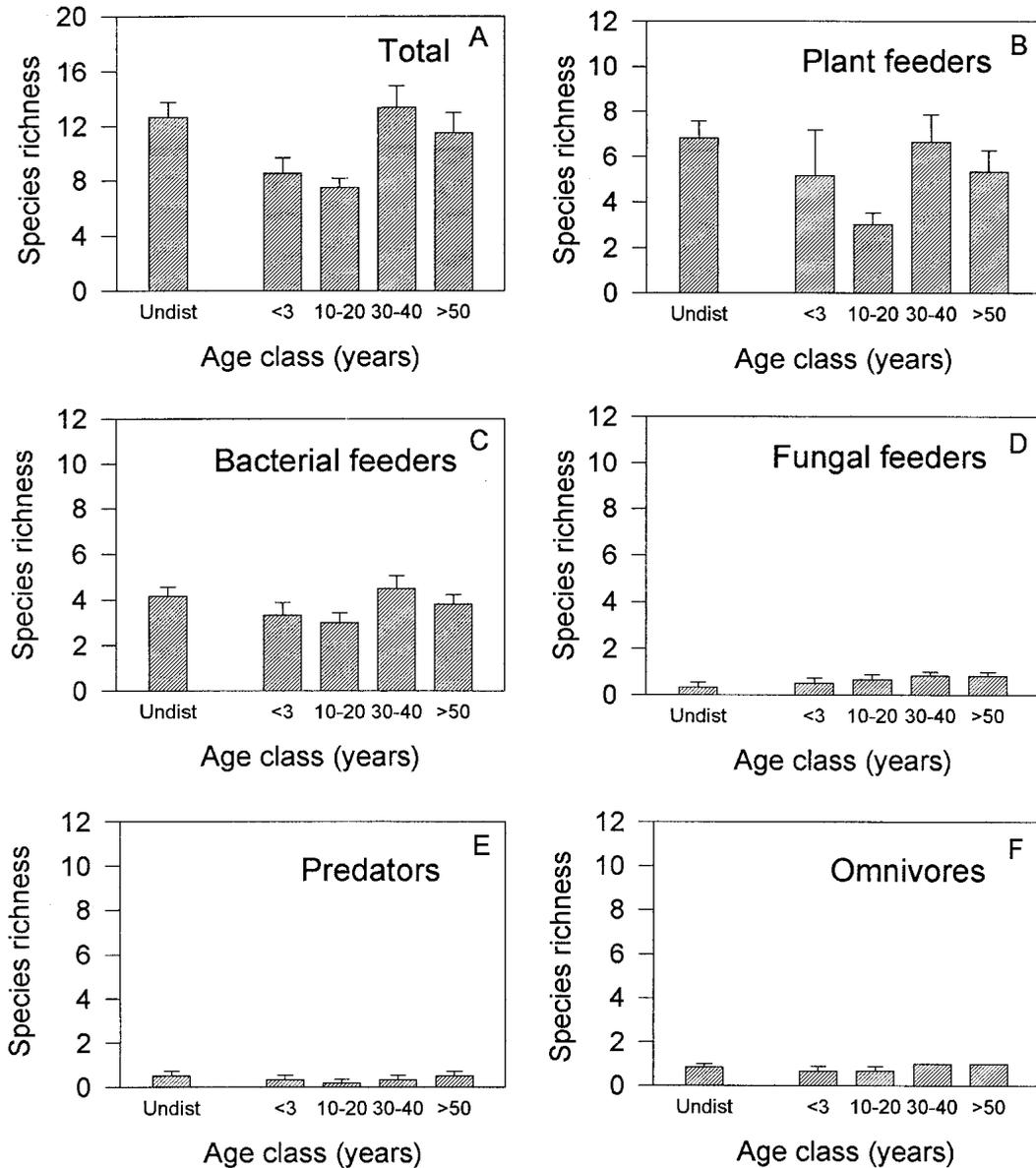


FIG. 3. Taxonomic richness soil nematode in a chronosequence representing >50 years following soil disturbance in southern Mississippi. "Undist" indicates undisturbed (control) sites. Bars are one standard error.

al., 1997; Sohlenius, 1982). Plant feeders described here showed a pattern of recovery comparable to communities on unstable, temperate-zone dune systems succeeding to forest (de Goede et al., 1993; Wasilewska, 1970), although the great length of recovery is unique to the present study. The appearance of low richness may have been exaggerated at low abundance because individual species dropped below the level of detection. More extensive sampling would be required to definitively separate richness from abundance in cases of low nematode density.

In trophic groups other than plant feeders, taxonomic richness varied little among age classes. It is unlikely that richness was unaffected by soil disturbance, considering the impact of disturbance on abundance and the findings of similar studies (noted above). As-

suming a disturbance effect, richness must have recovered so quickly as to escape detection in this chronosequence. Rapid stabilization in richness implies a regional pool of relatively few species, homogeneously distributed, all with effective dispersal. Although dispersal properties of the observed species are unknown, homogeneous distribution is supported by similarity among sites in the Detrended Correspondence Analysis (Matlack, 2001) and the unvarying evenness in abundance.

Models of succession: Soil mixing is the most severe form of disturbance observed in the outer coastal plain ecosystem and, therefore, the most likely to demonstrate ecological facilitation (Turner et al., 1997; Wood and del Moral, 1987). In the present study, richness of plant feeders paralleled development of aboveground

vegetation, perhaps because a progressively more dense or diverse plant community provided additional niches for plant parasites—a form of facilitation. Other trophic groups showed little change in richness or evenness through time, and overall composition did not vary systematically, implying that sites of all ages were equally congenial for most species. Plant feeders aside, the concept of succession as a progression of changing species composition (Connell and Slatyer, 1977) does not apply and facilitation cannot be invoked.

Resource limitation, noted above in plant feeders, appears to have regulated nematode succession by linking population growth to establishment of host plants in the aboveground community. Thus, the rate and character of nematode succession can be viewed as a consequence of the successional dynamics of higher plants. Plant density also appears to have determined successional development in bacterial and fungal feeders, an indirect effect in which vegetation presumably fostered bacterial and fungal prey populations.

Dispersal limitation, which directs primary succession in many plant communities (Fastie, 1995; Kupfer et al., 1997; Wood and del Moral, 1987), does not appear to be important in the nematode community described here. Most trophic groups were well represented in even the youngest disturbed sites, implying no limitation on dispersal or colonization. Richness does not lag behind abundance as predicted. Greater total richness was observed in narrow sites, as one might expect if isolation limited colonization, but measures of distance to potential sources of colonists had no predictive power. It is possible to understand the observed responses to stream- and tree-distance in terms of physical gradients rather than colonization events.

Conclusion: Disturbance of the soil has long-term impacts on nematode abundance that appear to be controlled by successional development of vegetation. The longevity of such effects supports the idea that local disturbance processes maintain heterogeneity in soil communities, but soil disturbance is infrequent in natural forest and validation will require data on disturbance intensity and frequency. In commercial timber operations, however, soil disturbance is quite common and widespread. Present findings are consistent with observations in sites prepared for tree planting by deep plowing (Matlack, 2001). Our results suggest that such intensive site preparation may have effects in the soil community lasting at least 50 years. Implications for the larger forest community have yet to be explored but, considering the vital role of nematodes in nutrient cycling and plant parasitism, prudent management requires that such long-lived disturbance effects be understood. Further research is needed to understand successional interactions of nematodes with other soil organisms, and to examine the complex interactions between soil communities and aboveground vegetation.

APPENDIX: Nematode taxa encountered in disturbed and control sites near Hattiesburg, Mississippi, USA. Taxa are assigned to feeding groups following Yeates et al. (1993). Forty nematodes occurring at four sites (<1% of the total) were not identified and were entered into the analysis as a dummy taxon "Other."

Bacterial feeders	Plant feeders
<i>Acrobeles</i> spp.	<i>Atylenchus</i> spp.
<i>Acrobeloides</i> spp.	<i>Cephalenchus emarginatus</i>
Cephalobidae	<i>Criconemella</i> spp.
<i>Cephalobus</i> spp.	<i>Dolichorus heterocephalus</i>
Diplogasteridae	<i>Filenchus</i> spp.
<i>Pelodera</i> spp.	<i>Gracilacus</i> spp.
Plectidae	<i>Helicotylenchus</i> spp.
Rhabditidae	<i>Hemicycliophora</i> spp.
Strongyloidea	<i>Heterodera</i> spp.
	<i>Meloidodera</i> spp. (juveniles)
Omnivores	<i>Meloidogyne</i> sp.
	<i>Paratylenchus</i> spp.
<i>Dorylaimus</i> spp.	<i>Pratylenchus</i> sp.
	<i>Psilenchus</i> spp.
Predators	<i>Rotylenchus</i> spp.
	<i>Rotylenchulus</i> spp.
<i>Mononchus</i> spp.	<i>Scutellonema</i> spp.
	<i>Trichodorus</i> spp.
Fungal feeders	Tylenchidae
	<i>Tylenchorhynchus</i> sp.
<i>Aphelenchus</i> spp.	<i>Tylenchus</i> spp.
	<i>Xiphinema</i> sp.

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