

Nematode Community Structure in Forest Woodlots. II. Ordination of Nematode Communities¹

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Abstract: Intersite relationships among nematode communities of 18 Indiana mixed hardwood stands of varying composition, soils, physiography and past management practices were determined by community ordination techniques. All sites were sampled in April, July and October of 1968 and 1969, and ordinations were based on the number of individuals of each nematode species at each site at each sampling period. The resulting groupings correlated well with groupings based on forest types and successional stages of the tree communities at the sites, and also with groupings based on well-defined soil types. Results were similar to those obtained previously with a resemblance equation which used qualitative data only; but the present study provided more information on species associations and relationships and ecological distance between sites. *Key Words:* Indiana hardwood stands.

Nematode community relationships among selected forest woodlots as determined by the "Resemblance Equation" of Preston (10) were discussed by Johnson et al. (6). Preston's technique is based on the presence or absence of a species and gives rare species importance equal to that of frequently found species. Sites very similar in species composition may still be quite distinct ecologically. The number of individuals of each species in a habitat provides an estimate of a species' importance in the community (1). Community ordination, a technique using quantitative data whereby

communities are arranged in a multi-dimensional order, was developed primarily by phytosociologists to help reduce the subjectivity inherent in classification of ecological association. Importance values derived from density, frequency and basal area (or dominance) measurements, form the basis for most plant ordinations. Beals (1) applied a modified version of ordination to animal populations in his study of the Apostle Island bird communities. A prominence value analogous to the importance value was calculated for each species as the product of its density (the total number of individuals) and the square root of its frequency (the number of samples in which it occurred).

Ferris et al. (4) used community ordination to classify plant parasitic nematode associations in cultivated fields in Indiana and Illinois. The present study, applying the ordination technique to the nematodes of forest communities, compares the results of an ordination of all nematode species present with results obtained previously using the qualitative resemblance equation technique (6).

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TABLE 1. Characteristics of 18 Tippecanoe County, Indiana, forest woodlot sites. All of the sites except C and G are as described by MacLean (8).

Site	Hectares	Management	Dominant Tree Species	Soil Type	Soil Drainage Rank ^a
A (Stewart Hillside)	16.30	Natural	Sugar Maple	Russell silt loam	2
B (Stewart Beech)	16.30	Natural	Beech-Sugar Maple	Miami silt loam	2
C (Stewart Stream)	16.30	Natural	Beech-Sugar Maple	Miami silt loam	2
D (Leitner South)	2.88	Cut-grazed	Mixed	Brookston silty clay loam	5
E (Leitner North)	2.88	Cut	Sugar Maple	Fincastle silt loam	3
F (McCormick West)	11.39	Cut	Mixed	Brookston silty clay loam	5
G (McCormick Ditch)	11.39	Cut	Mixed	Brookston silty clay loam	5
H (McCormick East)	11.39	Cut	Sugar Maple	Miami silt loam	2
I (Livestock)	4.27	Grazed ^b	Mixed	Brookston silt loam	5
J (Workman)	1.40	Grazed	Sugar Maple	Brookston silt loam	5
K (Cason)	2.57	Grazed	Beech-Sugar Maple	Cope silt loam	4
L (Higley)	3.04	Cut	Sugar Maple	Fincastle silt loam	3
M (Bramer 26)	3.20	Natural	Sugar Maple-Oak	Fincastle silt loam	3
N (Starrett)	1.57	Cut	Mixed	Cope silt loam	4
O (Bramer 550)	4.18	Cut-grazed	Mixed	Fincastle silt loam	3
P (Black Locust)	3.21	Cut	Black Locust	Russell silt loam	2
Q (Open Oaks)	3.42	Grazed ^{b,c}	White Oak	Fox loam	1
R (Wabash River)	1.67	Flooded ^b	Silver Maple-Cotton-wood	Genessee silty clay loam	2

^aBased on Indiana Soil Profile Ranking. Ranges from excessively drained (1) to very poorly drained (5).

^bRecent (within 1-4 years of this study).

^cData available for 1968 only.

MATERIALS AND METHODS

NEMATODE COUNTS: A detailed description of the study area of 18 Indiana mixed hardwood stands of varying plant composition, soils, physiography and past management practices has been given (6). Site characteristics are summarized in Table 1. All sites were sampled in April, July and October of 1968 and 1969. A sample for a given stand consisted of 50 cores of soil taken in a 0.2 ha subplot and mixed together. One liter of this soil was processed by sieving and Baermann funnels, and extracted nematodes were relaxed by gentle heat and fixed in 5% formalin. The nematode suspension was divided into two equal parts with one part used for counting and the other used for species identification. Two aliquots from one portion were counted, the mean recorded for each species and the total number of each species/500 cc of soil calculated. Nematodes were counted at $\times 35$ magnification on a compound microscope using a counting chamber designed so that small specimens could be examined at $\times 100$ magnification.

Juveniles of closely related species that could not be identified at $\times 100$ magnification were counted together and later assigned to

species based on the proportion of adults of each species found in the sample. Several of the tylenchid species could not be separated even in the adult stage at this magnification. *Tylenchus* sp. 1 and 3 were counted together as were the very small *Tylenchus* species 5, 6, 7, 8, 9 and 10. The total numbers of each species used in the analysis included the adults identified and the proportional number of juveniles assigned to that species.

The reproducibility of sampling techniques was tested for each species using counts from two samples from each of two sites. Two samples were collected from each of the two sites and the four samples processed separately as described. Counts were made for each species and a chi-square test for significance was made for each species between samples from the same site and, for certain species, between samples from the two different sites.

NEMATODE SPECIES RELATIONSHIPS BASED ON COMMUNITY ORDINATION: A prominence value was calculated for each species at each site by multiplying the species density by the square root of the species frequency in the six samplings (1). The prominence values were analyzed by a community ordination technique using a computer program titled ORDCOM written by

Dr. R. L. Giese of the Purdue Department of Entomology.

RESULTS AND DISCUSSION

NEMATODE COUNTS: The 175 species found in the 18 woodlot sites have been reported previously (6). All but eight of these species were counted in the present study. These eight were infrequently encountered species in only one or a few sites. Over the 2-year period the most species (ninety-five) were found in site C and the fewest species (fifty-eight) were found in site P. Site B, Stewart Beech, had the greatest number of nematodes and averaged 8384 individuals/500 cc soil or 2.5 million/m² calculated to depth of 15 cm. Site D, Leitner South, had the fewest nematodes and averaged 4017 individuals/500 cc soil or 1.2 million/m². The average for all 18 sites was 6005 individuals/500 cc soil or 1.8

million/m². These values are similar to those obtained by Overgaard-Nielson (9).

In the test for reproducibility of sampling, significant differences ($P < .05$) between counts of individual species were found for only one species out of 43 at one site, and only three species out of 52 at the other site. These four species were found in small numbers and represented a very small percentage of the total numbers present at each site. Significant differences between sites were found for a number of species (*data not given*).

NEMATODE SPECIES RELATIONSHIPS BASED ON COMMUNITY ORDINATION: Results of the ordination based on species prominence values for 1968 and 1969 combined are presented in the X-Y plane in Fig. 1. Although the location of a site in the ordination is the result of all the species and their numbers found there, an attempt to

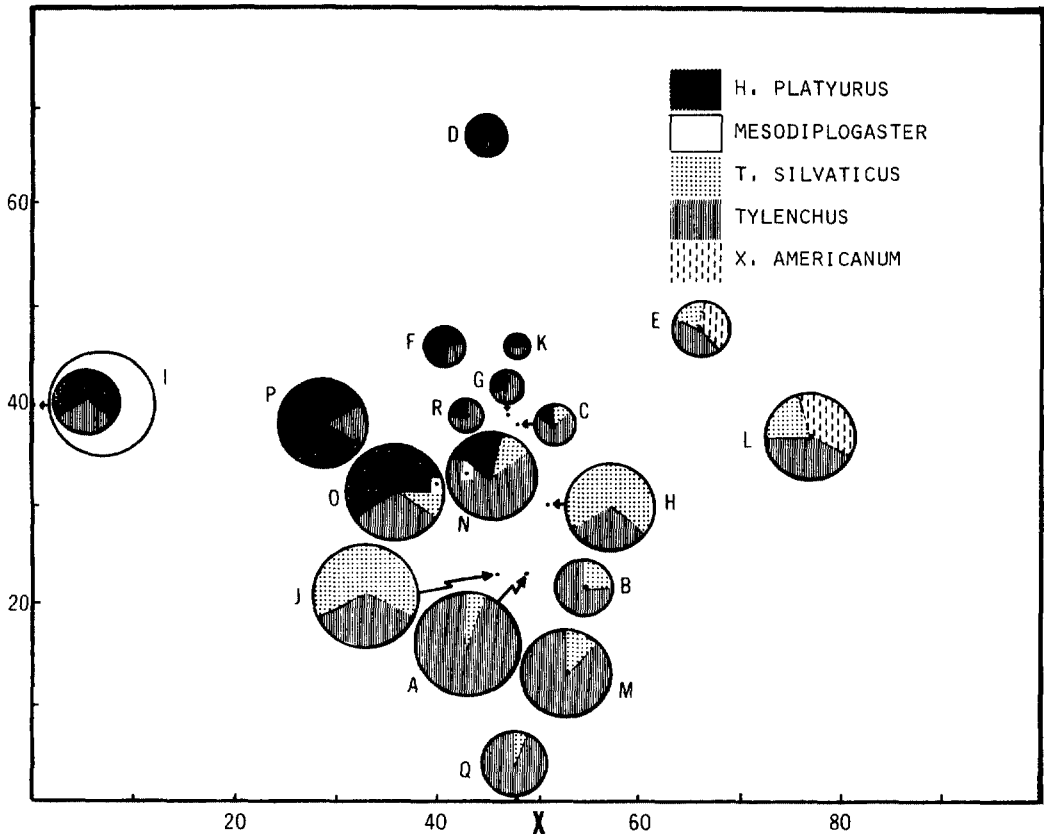


FIG. 1. Ordination of nematode communities at 18 forest sites (A through R) in Tippecanoe County, Indiana, for 1968-1969; X-Y plane. Circle size depicts relative numbers of *Helicotylenchus platyurus*, *Tylenchorhynchus silvaticus*, *Tylenchus* sp. 1 and 5, *Xiphinema americanum* and *Mesodiplogaster* sp. 1 which were dominant throughout the sites.

explain the ordination using all the species would be confusing. However, by using some of the more dominant species some relationships between the sites in the ordination cluster can be explained partially. The species chosen were well-distributed throughout the sites and occurred in fairly high numbers, accounting for 32% of the total number of nematodes. *Tylenchus* sp. 1 and 5 were found at every site as was *Xiphinema americanum* Cobb. *Tylenchorhynchus silvaticus* Ferris was found at every site except G and P, and *Helicotylenchus platyurus* Perry occurred at every site except site M.

Site I, Livestock, was the low reference site on the X-axis (Fig. 1) and thus the most dissimilar to all other sites. This was thought to be due to the large numbers of *Mesodiplogaster* sp. 1 found there in the spring of 1968. Cattle grazed there at that time and the large number

of *Mesodiplogaster* sp. 1 probably resulted from the abundant cattle manure. The numbers of *Mesodiplogaster* sp. 1 decreased following the addition of a drainage ditch and the removal of the cattle in the summer of 1968. Site L, Higley Woods, was the most dissimilar to site I and thus, the high X-axis reference site. At site L *Xiphinema americanum* attained its highest numbers and was the dominant species. Most sites cluster near the middle of the X-axis with site P, Black Locust, the most similar to site I, and site E, Leitner North, the most similar to site L.

Site Q, Open Oaks, was the low Y-axis reference site and characterized by having *Tylenchus* sp. 1 and 5 as the dominant species. Site D, Leitner South, was the most dissimilar to site Q and thus, the high reference site on the Y-axis. Site D was characterized by having the fewest number of nematodes of all the sites

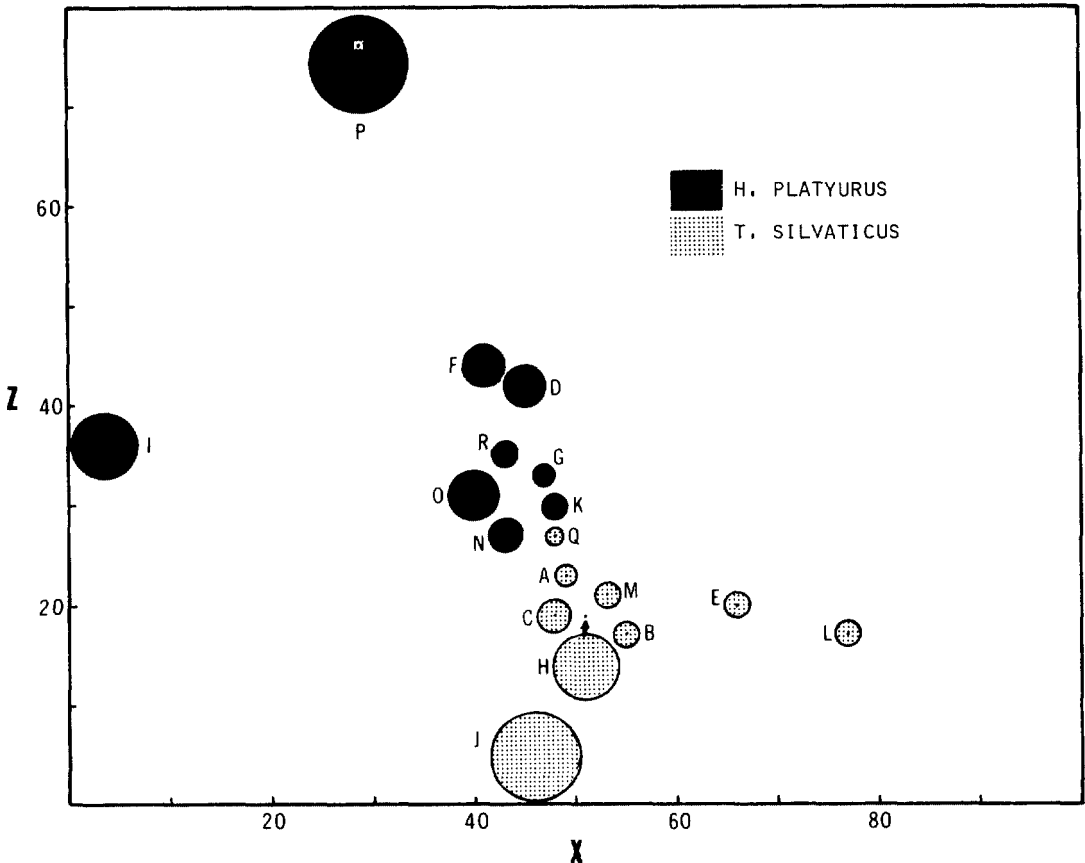


FIG. 2. Ordination of nematode communities at 18 forest sites (A through R) in Tippecanoe County, Indiana, for 1968-1969; X-Z plane. Circle size depicts relative numbers of *Helicotylenchus platyurus* and *Tylenchorhynchus silvaticus*.

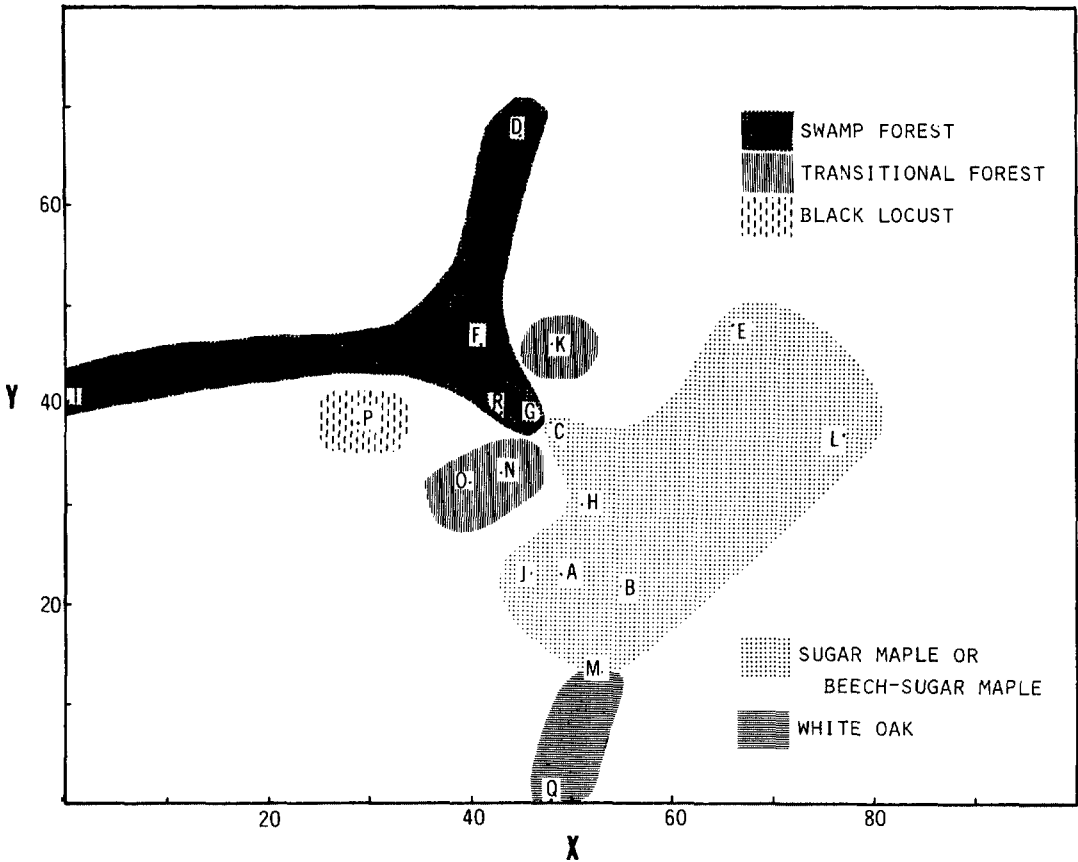


FIG. 3. Ordination of nematode communities for 1968-1969, X-Y plane, with tree communities superimposed.

studied and *H. platyurus* was the dominant species. In general, sites with *Tylenchus* sp. 1 and 5 as the dominant species are toward the low end of the Y-axis, and sites with *H. platyurus* as the dominant species are toward the high end. Although the large numbers of *Mesodiplogaster* sp. 1 at site I and the dominance of *X. americanum* at sites L and E were thought to distinguish these sites, the dominant species that they shared in common with other sites were thought to be more useful in interpreting their relationship to the other sites in the ordination.

Tylenchus sp. 1 and 5 are represented at all sites but together with *T. silvaticus* are more numerous and either dominants or co-dominants in the lower right quadrant of the X-Y plane. *H. platyurus* is the dominant species at those sites in the upper left quadrant. Sites N and O, almost centrally located, have large numbers of all four species. Site E appears more

similar to site D than would be expected based on the species used to interpret this ordination. Evidently, this relationship is due to other species common to both sites.

Distribution of the sites along the X-axis in the X-Y plane seems to result from an association between *Tylenchus* sp. 1 and 5 and *T. silvaticus* at one end and a similar association between *Tylenchus* sp. 1 and 5 and *H. platyurus* on the other. On the Z-axis in the X-Z plane (Fig. 2), however, the distribution results primarily from the relationship between *T. silvaticus* and *H. platyurus*. Site J, Workman Woods, as the low reference site on the Z-axis is where *T. silvaticus* attains its highest density and site P, Black Locust, as the high reference site is where *H. platyurus* attains its greatest density. Locations of the sites along the Z-axis can be explained easily by these two species. The presence of *T. silvaticus* in fairly high numbers at sites E and L are indicated here by

the location of these two sites at the low end of the axis. The actual clustering of most sites near the low center on the Z-axis indicates that species other than those discussed here are undoubtedly influencing the relationships.

NEMATODE ORDINATION AND TREE SPECIES: A comparison of the nematode ordination and the tree species at each site is presented in Fig. 3. Tippecanoe County is in the tension zone between the beech-maple forest region and the oak-hickory forest region of Braun (2) and thus characterized by diverse tree communities. Well-drained but moist areas are occupied by the beech-maple climax community whereas white oak (with some hickory) occupies drier areas. The more compact poorly aerated and poorly drained soils in areas of low depression support such swamp forest community tree species as swamp oak, red oak, white elm, red elm and silver maple (5, 7). Transitional forests contain most of the species found in the swamp forests but

with a larger percentage of sugar maple, beech and white ash. Where white oak occurs on moist soils, a trend toward the development of beech-sugar maple is sometimes evident. The succession here is from white oak to an increase in sugar maple, to beech-sugar maple (2).

Distribution of the sites in the nematode ordination is somewhat representative of a gradient from sites dominated by a mixture of hydro-mesophytic species in the upper left portion of the X-Y plane to sites representative of the climax communities in the lower right portion. Site I, the low X-axis site, is representative of the swamp forest since it is dominated by a mixture of hydro-mesophytic species (red elm, black ash, red oak, bur oak and silver maple). Site D, the high Y-axis site, resembles the transition forest, since besides a number of the hydro-mesophytic species, it also contains some sugar maple and basswood. Sites L and E, the high points on the X-axis, are where sugar maple attains its highest dominance

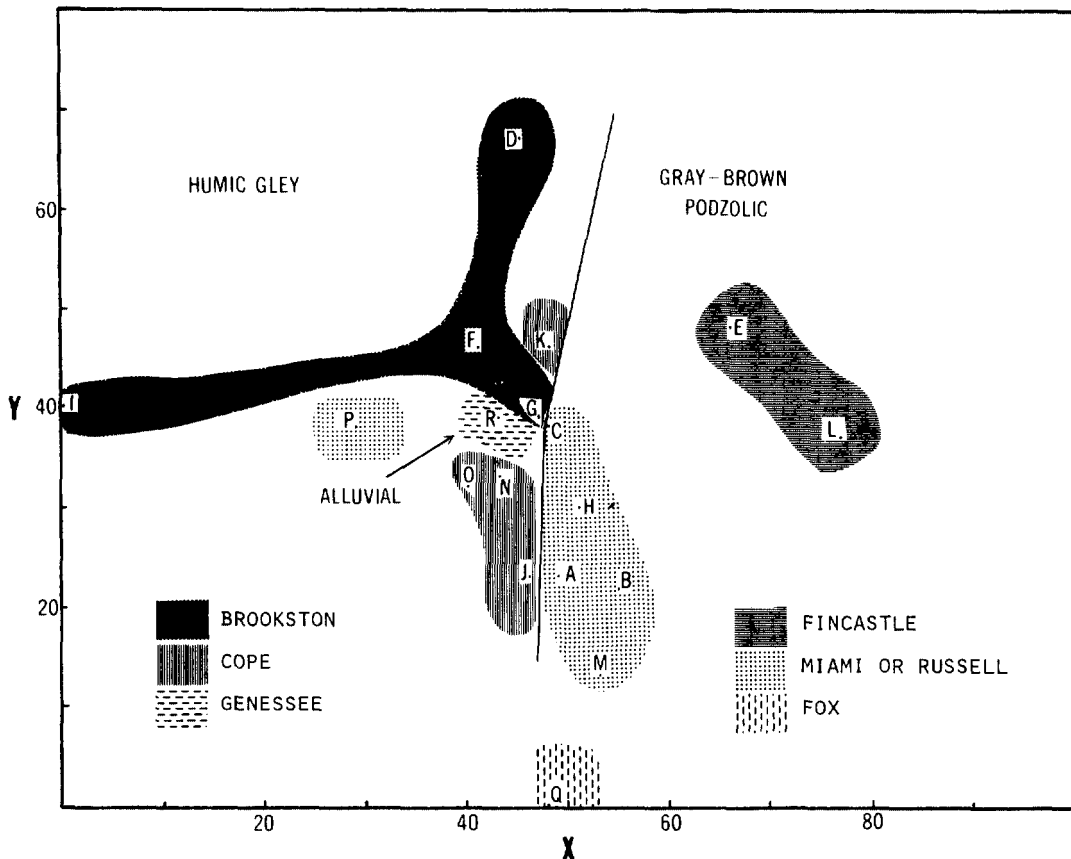


FIG. 4. Ordination of nematode communities for 1968-1969, X-Y plane, with soil types superimposed.

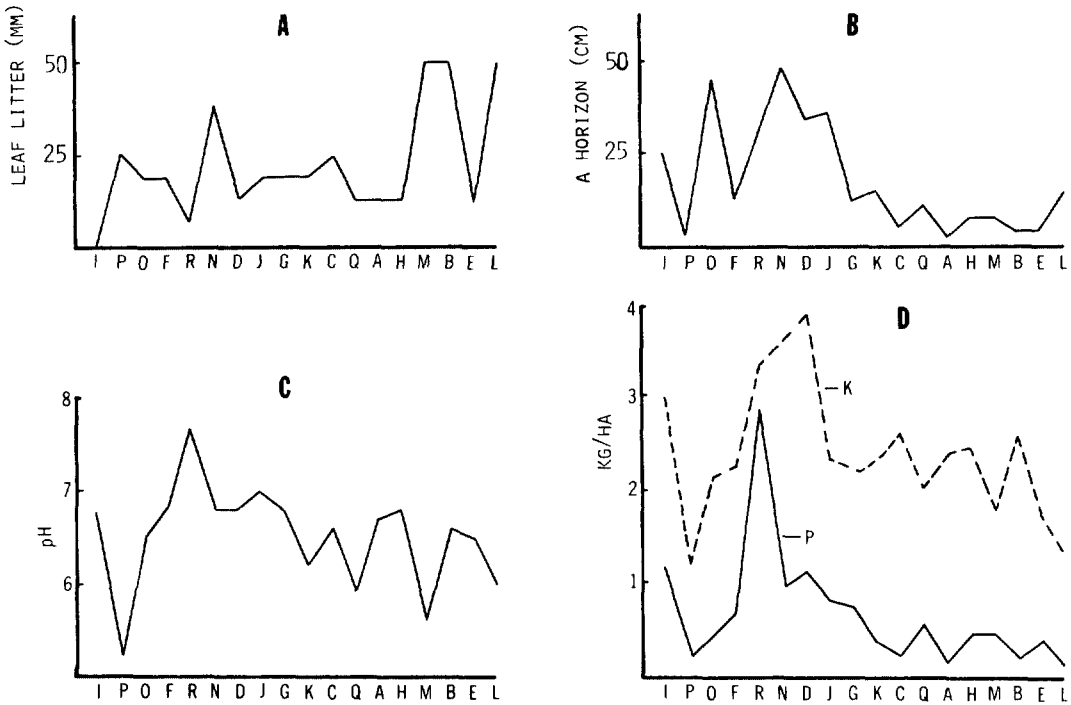


FIG. 5. Selected edaphic factors at 18 forest sites (A through R) in Tippecanoe County, Indiana, plotted against the sequential position of the forest sites along the X-axis of the 1968-1969 ordination (letters A-R on graphs refer to sites). A. Depth of leaf litter. B. Depth of "A" soil horizon. C. pH. D. Phosphorus and potassium levels.

at 63% and 58%, respectively. The fact that *X. americanum* attained its highest numbers at these two sites may not be unusual. Di Sanzo and Rohde (3) recently reported this species feeding on sugar maple roots and high numbers were found around the roots of moderately declining sugar maple trees. Site Q, the low Y-axis site, is predominantly white oak, whereas its most closely related site, site M, is 42% oak and 20% sugar maple. According to MacLean (8), oak is not reproducing well at site M, and an abundance of sugar maple seedlings is indicative of the trend here toward the beech-maple climax.

The positions of the other sites in the ordination are fairly consistent in demonstrating the transitional forest types at different stages of development along the gradients. In general, sites with higher percentages of hydro-mesophytic species are in the upper left portion of the ordination, whereas sites with higher percentages of sugar maple, beech, oak and hickory are in the lower right portion.

The main exception is the location of site P

at the hydromesophytic end of the X-Y plane. Site P is predominantly black locust (71%), but some red elm (18%) and white ash (7%) are also present (8). The location of site P on the low end of the X-axis can be explained only by the fact that a major disturbance (complete cutting over) has occurred there, resulting in the development of an almost homogeneous stand of even-aged black locust, which could best be characterized as a pioneer stand. Evidently, the disturbance has caused a change in the nematode populations making them more similar to those found in the poorly drained sites with hydro-mesophytic tree species. Site K falls closer to the hydro-mesophytic sites than would be expected by the composition of its tree species (sugar maple, beech, white ash), but the soil type at site K might offer a better explanation for this relationship.

NEMATODE ORDINATION AND SOIL TYPES: A comparison of the nematode ordination and the soil types found at the different sites is presented in Fig. 4. There are three basic soil groups represented among the 18 sites. The Gray-Brown Podzolic soils

developed on nearly level to sloping areas and are excessively drained, well drained, or imperfectly drained (11). The Fox soil type is the excessively drained member of this group whereas the Miami and Russell soils are well drained. The imperfectly drained member is the Fincastle soil type. The second group is comprised of the Humic Gley soils that are associated with Gray-Brown Podzolic soils but developed on nearly level areas or depressed flats where the natural drainage is poor to very poor. Cope soils are the poorly drained members of this group and represent the first level down toward the very poorly drained Brookston soils. The third soil group is comprised of the Alluvial soils found on the first bottoms near streams and rivers. These soils have been deposited by the floodwaters and new alluvium may be added during flooding. Genesee soil type found at site R on the Wabash River floodplain is the only representative of this soil group. In general, the

Gray-Brown Podzolic soils are located in the lower right portion of the X-Y plane, and the Humic Gley and Alluvial soils in the upper left portion. The reference sites I and D have very poorly drained Brookston silty clay loams whereas site L, the high X-axis site, is on an imperfectly drained Fincastle silt loam and site Q, the low Y-axis site, is on the excessively drained Fox loam. Site P, Black Locust, is the one site markedly out of position, but its location in the upper portion of the X-Y plane probably can be attributed to the dominance of black locust. However, MacLean (8) found that the Russell soil at site P had a silty clay loam texture. The fact that red elm and white ash are the other tree species found at site P is also somewhat indicative of a moist area.

NEMATODE ORDINATION AND OTHER EDAPHIC FACTORS: The location of the sites on the X-axis and some of the edaphic factors found at each site show some interesting

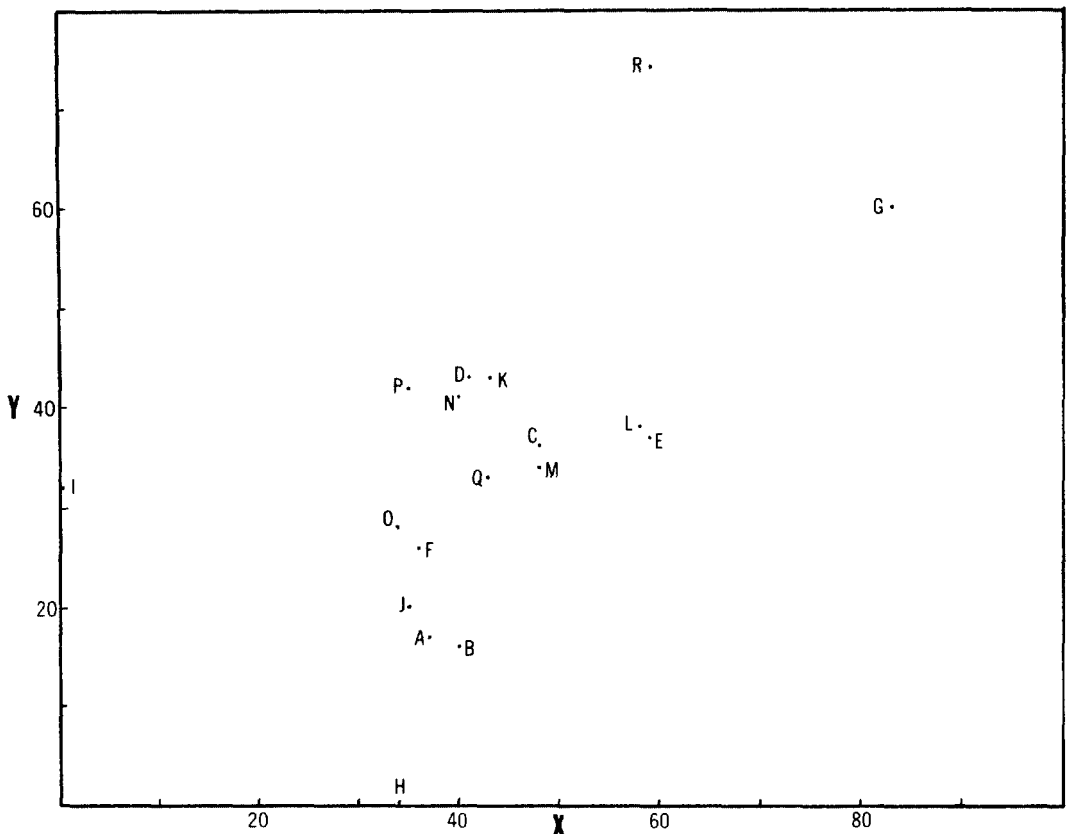


FIG. 6. Ordination of nematode communities at 18 forest sites (A through R) in Tippecanoe County, Indiana, for 1968.

correlations. Figure 5 depicts the sequential but not relative position of the sites along the X-axis, and the leaf litter, "A" horizon depth, pH and kg of phosphorus and potassium/ha at each site. Leaf litter is less well developed (Fig. 5A) and the "A" soil horizon better developed (Fig. 5B) at sites on Humic Gley soils than at sites on Gray-Brown Podzolic soils. The pH is generally more basic at the more poorly drained sites in this study and is the most alkaline at site R on the Wabash River (Fig. 5C). The poorly drained sites also contain larger amounts of phosphorus and potassium than are found at the better-drained sites (Fig. 5D). The most phosphorus and potassium was found at the often-flooded site R on the Wabash River.

Site P is the outstanding exception to the general trend on almost every graph. Site P is located on a well-drained Gray-Brown Podzolic soil, and its edaphic factors are characteristic of this soil group. The peculiarities associated with site P have been discussed.

NEMATODE ORDINATIONS FOR 1968 AND 1969: Separate ordinations for 1968 and for 1969 were constructed. In 1968 site I, Livestock, was the low reference site on the X-axis (Fig. 6), as was expected, because of the large numbers of *Mesodiplogaster* sp. 1 found there in the spring. Site G, located on a ditch in McCormick Woods, was the high X-axis site and was probably so because it had fewer numbers of nematodes than any other site during 1968. Sites I and G were both quite dissimilar to all other sites resulting in a rather tight grouping of the sites near the center of the X axis. The positions of the different sites in this group cannot be explained readily except that they share about equally between sites I and G with respect to nematode species and numbers. By the addition of the Y-axis, relationships between the sites become more apparent. The better-drained sites with *Tylenchorhynchus silvaticus* and *Tylenchus* sp. 1 and 5 move down in the lower portion of the X-Y plane while the

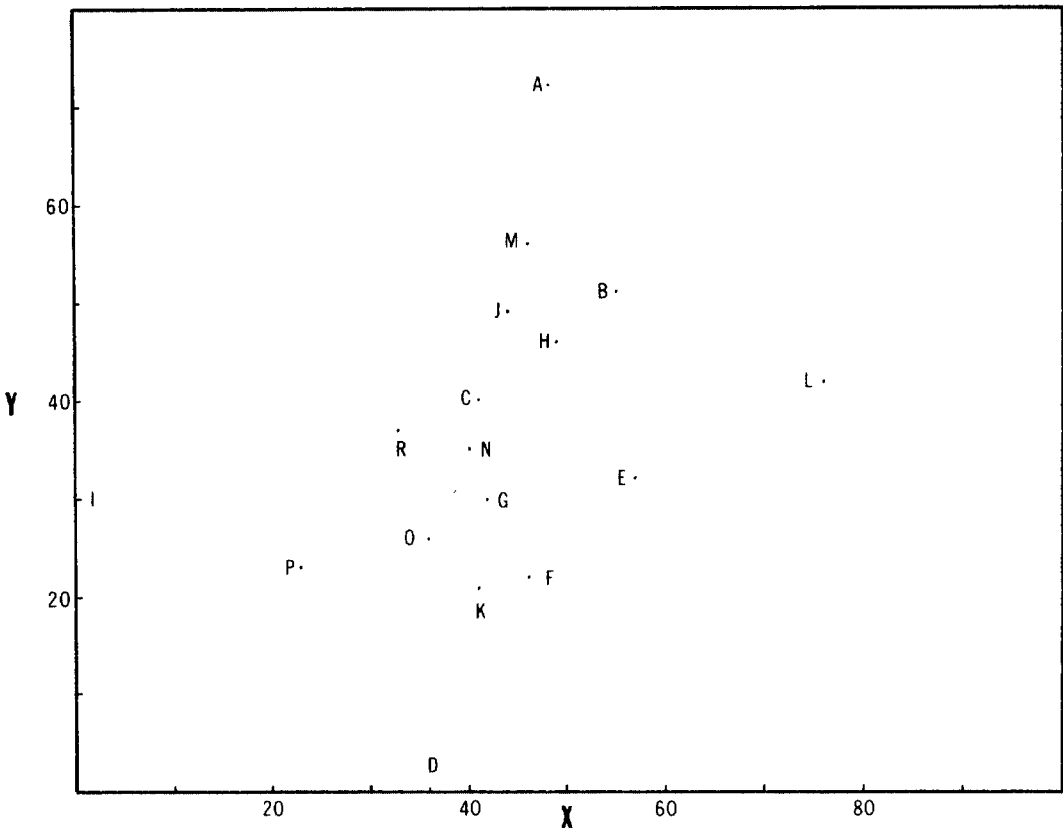


FIG. 7. Ordination of nematode communities for 18 forest sites (A through R) in Tippecanoe County, Indiana, for 1969.

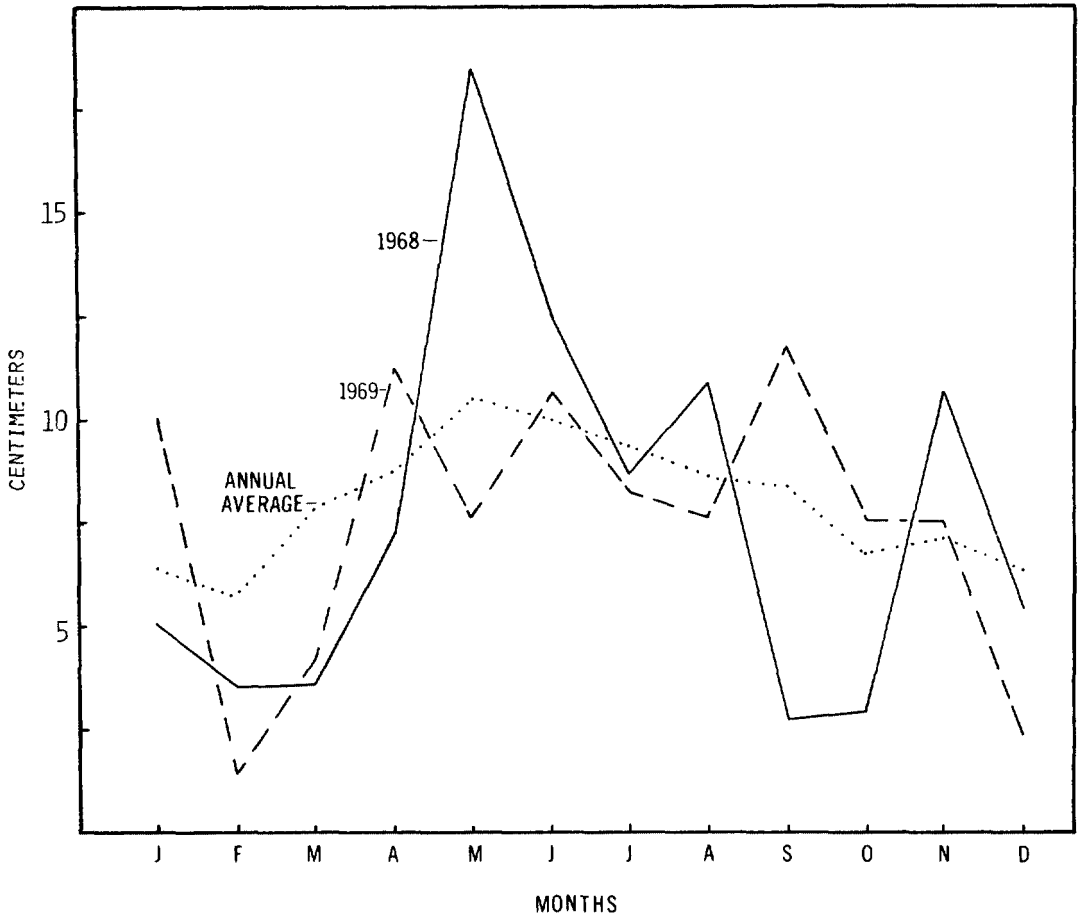


FIG. 8. Rainfall data for Tippecanoe County, Indiana, for 1968 and 1969.

poorly-drained sites with *Helicotylenchus platyurus* as one of the major dominants are about centrally located. Sites F and O move toward the low end of the Y-axis, and this might be due to the fact that these sites shared some of the more dominant rhabditid species with site H during 1968.

In 1969, Site I, the low X-axis reference site for 1968, was also the low X-axis stand for 1969, and site L replaced site G as the high X-axis site (Fig. 7). *Mesodiplogaster* sp. 1 occurred in very low numbers at site I during 1969, and thus, could not account for its selection as the low X-axis reference site for both years.

Site D, Leitner South, was the low Y-axis site and site A, Stewart Hillside, the high for 1969. The distribution of sites in the X-Y plane is scattered evenly, and there appear to be no highly dissimilar sites as the distances between

the reference sites and the other members of the ordination are nearly equal. This even distribution of sites in the X-Y plane and the absence of any highly dissimilar sites is in contrast to the 1968 ordination. Since there appears to be a relationship between moisture and the nematode populations at the different sites, rainfall data (Fig. 8) were examined. The total rainfall for the 2 years was almost identical, but quite different in time of occurrence. During 1968 the July sampling was after 2 months of above normal rainfall and the October sampling after 2 months of below normal rainfall. The distribution of the rainfall throughout 1969 was close to normal, and sampling periods were preceded by near normal amounts. The abnormal distribution of rainfall in 1968 could have affected the nematode populations and masked the relationships between the sites.

NEMATODE ORDINATION WITHOUT SITES I, P AND Q: In community ordination techniques the selection of the reference sites is critical, since once selected, all other sites are ordered on the axis according to the degree of dissimilarity to the reference sites. Site I is the most dissimilar site to all others in this study, as evidenced by its selection as the low X-axis reference site in the 1968, 1969 and combined ordinations. Site P was also quite dissimilar as evidenced by its close association with site I. The recent grazing of cattle at site I and the almost complete dominance of black locust trees at site P were two features thought to contribute to their dissimilarity. An ordination was calculated omitting these most dissimilar sites to determine existing relationships between the other less disturbed and undisturbed sites. Site Q was also omitted since it also was recently grazed and only 1 year's data was available.

Results of the ordination without sites I, P

and Q are presented in Fig. 9. Site K, a poorly drained, disturbed site, (Table 1) was the low X-axis reference site. Site A, a well-drained, natural site was the high X-axis site. Site G, located on a ditch in McCormick Woods, was the low Y-axis reference site and site L, an imperfectly drained, slightly disturbed site was the high.

Selection of the natural site, site A, as the high reference site on the X-axis is an interesting feature of this ordination and results in the grouping of the three natural sites, A, B and M at the high end of the axis. Site C, on the stream in Stewart Woods, is also a natural site but because of the way it was sampled, it probably represents two fairly distinct habitats (6). On this ordination, it falls near the center of the X-axis and shows a closer similarity to the ditch at site G on the X-axis. Site R, also somewhat of a natural site, is in the lower portion of the ordination and shows a high degree of similarity to the disturbed sites,

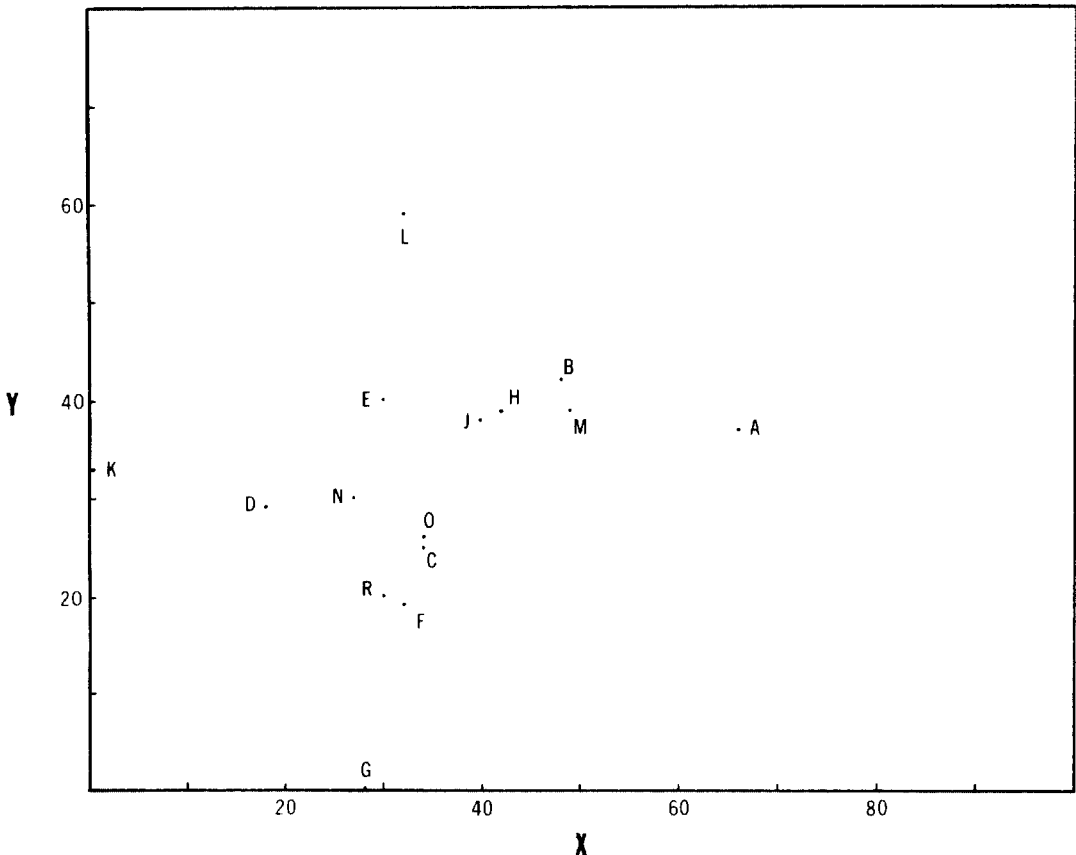


FIG. 9. Ordination of forest nematode communities for 1968-1969 excluding sites I, P and Q.

indicating the disturbances of the flood waters. All other sites have been disturbed to some degree (Table 1). The distribution of the sites in the X-Y plane was remarkably similar to the ordination including sites I, P and Q, in that the poorly drained sites with mixed tree species are closely associated in one portion whereas the better drained sites with sugar maple or white oak as the dominant tree species occur in the other portion. Of interest is the shorter length of the axes and the fairly even distribution throughout this ordination, indicating the closer relationship among the sites without the presence of the sites that are known to have definite features (disturbances) to make them more dissimilar.

CONCLUSIONS

Ordinations of the nematodes at the 18 sites, representing a continuum of forest types and successional stages, show relationships between the nematode communities and the tree communities and soil types. Those sites with poorly drained Humic Gley soils, dominated by hydro-mesophytic tree species and designated swamp forest communities, were the sites where *Helicotylenchus platyurus* was a dominant nematode species. These sites cluster in the upper left quadrant of the X-Y and X-Z planes of the ordinations. Sites on well-drained Gray-Brown Podzolic soils and supporting beech-sugar maple climax or oak climax tree communities were those sites dominated by the two *Tylenchus* species and *Tylenchorhynchus silvaticus*. These sites tend to occupy the lower right quadrant of the X-Y and X-Z planes of the ordinations. Other sites considered to be transitional in forest type or successional stage occupy intermediate positions in the ordinations. The two sites where *Xiphinema americanum* reached highest densities were characterized by an imperfectly drained Fincastle soil and sugar maple as the dominant tree species. These two sites also shared the *Tylenchus* species and *T. silvaticus* as co-dominants with the beech-sugar maple climax sites and ordinate to the right of the climax sites in both planes. Site P, the black locust site best characterized as a pioneer stand, ordines closely with the sites dominated by hydro-mesophytic tree species.

No single edaphic factor could adequately explain the relationships, but leaf litter, depth of the "A" soil horizon, pH and kg of

phosphorus and potassium/ha show a general relationship when compared to the sequential position of each site on the X-axis. Since these factors are directly related to the topography, soil type and tree community it seems unlikely that any one factor would have a dominating influence over the whole community. Probably the community responds to the many factors that together characterize the habitat. Single features that are by themselves major characteristics of a habitat may show closer relationships, as evidenced by the relationships between the nematode ordination and the tree communities and soil types.

Disturbances within a habitat may have a marked influence on the nematode community depending on the degree of the disturbance. Known disturbances at sites I and P appear to have resulted in striking changes in their nematode community structure, as evidenced by the dissimilarity between these two sites and all other sites. An ordination omitting these two highly dissimilar sites results in a more even distribution of the remaining sites in the X-Y plane and shorter axes.

Results of the ordinations reported here and the resemblance equation technique utilized previously (6) are somewhat similar in that both studies indicate that nematode communities can be related to dominant tree species and major soil characteristics. But ordination shows relationships among the communities not evident in the resemblance equation dendrogram (6) and considerably more information is obtained regarding correlations with well-defined tree communities and soil types. The distribution of the sites along several axes has the advantage of separating sites that appear similar on a single axis.

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