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Applications of Nematode Community Structure Research to Agricultural Production and Habitat Disturbance¹

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Abstract: Nematode communities in agricultural habitats are diverse, usually comprising tens of species and a large number of individuals. The study of nematode community structure can be approached in a number of ways which can be categorized under a synecological approach. Although the plant-parasitic species are of most obvious interest to plant nematologists, these are only a part of the nematode fauna that affects agroecosystems. The application of community structure research to investigation of those effects can help elucidate their importance. This information is not only intrinsically valuable, but it is necessary in the development of sustainable agricultural production systems.

Key words: agroecosystem, ecology, trophic group.

Pondering an introduction to this review brought two nematological clichés to mind: 1) "nematodes are ubiquitous in terrestrial ecosystems," and 2) "nematode communities are polyspecific." Clichés may not help explain the need for a study, but they may obviate the necessity for elaborate justification of studies of these ubiquitous, polyspecific nematode communities. The terrestrial ecosystems of most obvious (but certainly not exclusive) interest to plant nematologists are agroecosystems, and the polyspecific nature of their nematode communities can be investigated by application of the techniques and theories of community and population ecology to nematode community structure. It is not my intent to review all the approaches that have been, or could be, taken, but to suggest where they apply to agricultural production.

COMMUNITY STRUCTURE AND CLASSIFICATION

"Community structure" is one of those phrases that conjures images for everyone but has no precise meaning. Structure, or patterns of occurrence, can be investigated within or among communities. It is difficult, and fortunately unnecessary, to restrict the definition of "community." As Pielou (40) states, community studies would have to be suspended indefinitely if that were the case; delimitations are nearly always a matter of common sense and convenience. Techniques, old and new, abound for dealing with the multivariate data characteristic of community studies (26,40,41). Studies of vertical and horizontal distributions of soil nematodes, relative sizes of taxonomic or trophic groups, and patterns of taxonomic group prominence are three very different examples of what has been referred to as "community structure."

Community structure studies begin with some form of classification of the nematode fauna and are occasionally limited to the qualitative level, but usually also involve enumeration and investigation of the numbers. The purpose of the study dic-

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tates the type of classification used. Taxonomic classification generally is to the species level, which is difficult and time consuming because the number of species in a single cultivated field can be as high as 74 (2) and the number of plant-parasitic species alone can range up to 16 (31). Historically, this kind of study has been valuable to plant nematologists in suggesting possible economic associations between nematode taxa and hosts. Sasser et al. (46) identified peanut and soybean fields with 5–9 plant-parasitic nematode species and attempted to sort out host and nematode interrelationships with correlation analyses. Such studies typically include only the plant-parasitic species and lead to more controlled autecological investigation with, at most, three nematode species (8).

Different levels of resolution give different pictures of the community (9,22,23,59). Some investigators have used trophic groups to classify and enumerate a complete nematode community (9,12,30,39,57,59,61). Several schemes have been used, but most reflect that of Wasilewska (57), comprising five trophic groups: 1) bacterivores, 2) fungivores, 3) plant parasites, 4) predators, and 5) omnivores. Freckman and Caswell (13) provide succinct descriptions of these categories, in which nematodes can be classified on the basis of known feeding habits or esophageal morphology. However, feeding habits are poorly known for many taxa and esophageal morphology can be misleading, thus trophic group classification should be supported by corresponding lists of genera (12). Insect-parasitic species in soils are rarely taken into account (14).

COMPLETE NEMATODE FAUNAE

The abundance and diversity of nematodes are mostly dependent on the type and distribution of vegetation, regardless of the trophisms of individual taxa, and are affected by various abiotic factors (24,33,34,59). Total abundance of nematodes is lower in agricultural than in non-agricultural systems (9), and although total nematode numbers may be higher or lower

in no-till than in conventionally tilled land (29,39,51), tillage clearly affects community structure (2,39). The responses of individual taxa and trophic groups to site disturbance may be different from the response of the community as a whole (21–23,30,31,59). One might speculate about whether nematode communities fall under the category of “interactive,” in which the members regularly interact, or “isolationist,” in which a community is no more than a fortuitous combination (42). For the time being this will remain speculation, as so little is known about the nature of nematode communities. The significance of looking into such questions for plant-parasitic species in agroecosystems is obvious, but is there a need to address the rest of the nematode community in agroecosystems?

Considerable interest has been shown recently in the roles of nematodes in nutrient cycling. Increases in plant-parasitic nematodes are known to cause yield reductions, but several workers have shown a positive correlation between total nematode abundance and primary production (19,58,61). This probably represents a general situation (60); thus plant nematologists should take a closer look at the agroecosystem effects of nematodes other than plant parasites.

Work in the previous decade showed that nematodes account for little direct mineralization of organic matter in soils and probably contribute less than 1% to total soil respiration (49); however, the evidence suggests nematodes have considerable impact on nutrient cycling in their role as regulators of the soil microflora (19,25,49,50,60). Ingham et al. (19) reviewed the evidence and summarized the common responses to microfloral grazers, including nematodes, such as increased plant growth, increased N uptake by plants, decreased or increased bacterial populations, increased CO₂ evolution, increased N and P mineralization, and increased substrate utilization. Their evidence shows that the increase in N mineralization is short term but may occur during critical times

in the growth of plants (19), such as the spring and fall increases in bacterivores and fungivores frequently observed (9,30,58). Norton et al. (35) found positive correlations between microbivorous nematodes and percentage of soil organic matter in soybeans under conventional tillage. Parmelee and Alston (39) found that such increases occurred after plowing conventionally tilled plots. They speculated that changes in nematode trophic structure were indicators of changes in decomposer populations following soil disturbance and of essential differences in the nature of nutrient cycling in no-till vs. conventional tillage systems. Baird and Bernard (2) compared nematode trophic structure in conventional and no-till soybeans but concluded that nematode community structure was more affected by host than by tillage systems. Both studies just mentioned, but not only these, suffer from a difficulty pointed out by Yeates (59): they report data from only 1 year. Investigations of this nature deserve long-term attention, as their results have bearing on the development of sustainable agricultural production systems (37,44). As Crawley (5) has noted for plant communities, the short-term dynamics following perturbation can be very different from the long-term effects of the same manipulation.

Agroecosystems retain the functional properties of natural ecosystems (4,6,37), so it is reasonable to look at data gathered in natural or lightly managed ecosystems in order to comprehend processes in agroecosystems (1,44,58). Johnson et al. (21–23), in a study of nematode communities in forest wood lots, observed that disturbed sites, those which had been subject to some manipulation in the past, were the most dissimilar among 18 sites in their nematode communities. Most sensitive to site disturbance was the dorylaimid component of the nematode communities, a relationship supported by observations in tree nurseries in which numbers of dorylaimids that were not plant parasitic increased with tree age (30) and by other studies (13). In three single-year studies of

various tillage regimes of annual crops, the relationships between disturbance and dorylaimid numbers were positive, negative, and neutral (2,39,51). Wasilewska (56), however, found an inverse relationship between omnivores and plant succession in forested sand dunes. Some of this disparity can be attributed to assigning dorylaimids to trophic groups; in some communities, they may be represented in all trophic groups. Dorylaimid microbivores may be responsible for more P mineralization than their biomass indicates (61), and their role should be investigated.

The preceding paragraph suggests another level of complexity in community structure studies, one that is just as applicable to any other part of the nematode community, or to the whole, as to dorylaimids. The fundamental question is, are they a community at all? One assumes that among groups exploiting different resources, competitive interactions are minimal; however, Wasilewska (55) suggested that reciprocal interactions occurred among nematode trophic groups. Freckman and Caswell (13) provided a diagrammatic illustration of the possibilities. Branch, in Holmes (18), showed that competition among marine organisms for space, an absolute requirement that cannot be shared or renewed, may result in exclusion of species more frequently than competition for food. Such competition could have a profound effect on community structure. Elliott et al. (7) demonstrated that microbial trophic structure was related to habitable pore space in a microcosm study. On the other hand, Yeates (59) eschewed use of trophic groups because of a lack of evidence about feeding habits and concluded from his study of supraspecific diversity in pastures in a variety of soil types, that nematode faunae represent “the sum of numerous specific populations . . . neither a community of interacting species nor a guild of species exploiting a resource. The nematode fauna represents populations at a level of animal organization which influence, and are influenced by, energy and nutrient flows as well as biological inter-

actions and other factors at a range of trophic levels.”

Clearly, the importance of the complete nematode community as an entity in agricultural production is unresolved. Whether the community is an artificial assemblage, an historical accident, or a meaningful biological unit, studying the comparative structure of nematode communities can provide information on the patterns of similarity among other components of agroecosystems (9,40,41).

PLANT-PARASITIC NEMATODES

The trophic level or guild of greatest interest to plant nematologists is, of course, the plant parasitic. Plant parasites often constitute a large percentage of the nematode communities in agroecosystems (9,13) and can comprise a large number of species in a single site, as stated earlier. In fact, most nematode community structure studies have included only the plant-parasitic species. The studies span a range from no more than lists of species associated with a particular crop or locality (20,28,47) to various quantitative analyses of interrelationships among nematodes, plants, and habitat (9,33,34) to infracommunities of a single site or taxonomic group (15,17,32,36). The subject of plant nematode communities has been reviewed recently, from another viewpoint, by Norton (34).

Community structure can be thought of in terms of the distribution of species within sites (33,34). This approach has obvious application, especially to those who provide diagnostic services and design and interpret data from field experiments (15,32). We have a fair literature documenting within-field aggregation, as well as the effects of soil characteristics both within and between fields.

Another obvious application of research on plant-parasitic nematode community structure is in assessing the impact of conservation tillage on the community. This subject was recently reviewed by Minton (29), who illustrated the need for information in this area. A related area that

needs attention is the mechanism involved in plant-parasitic nematode control in soils following addition of organic amendments (11,61).

As with the study of complete nematode communities, the question arises for plant parasites: are they a true community whose members can be predicted, or is their assemblage simply fortuitous? Many phytophagous nematodes are widespread, present in natural communities in low densities but becoming established and increasing in numbers as land is cleared and cultivated (38). These species should then reflect their widespread occurrence in natural communities. Ferris et al. (10) commented on the “remarkable similarity” among plant-parasitic nematode populations in soybean fields distributed throughout Indiana and Illinois. Niblack and Bernard (31) noted that, among tree nursery sites of diverse soil types distributed throughout five counties in Tennessee, 38% of the total species of plant-parasitic nematodes occurred in more than 10% of the sites, and nematode communities did not cluster by host in an ordination analysis. The core-satellite species concept of Hanski (16), current in animal parasitology, is worth pursuing for plant nematodes to help explain the polyspecific nature of phytonematode communities.

The multispecies characteristic was attributed by Oostenbrink (38) to four factors: 1) the effect of humans dispersing nematodes in soil and plant parts, 2) the polyphagy of many plant-parasitic nematode species, 3) their long persistence, and 4) the low incidence of interspecific competition among them. The latter factor is controversial; as Norton pointed out (34), many interactions between nematode species are attributed to competition with little or no actual proof. Furthermore, not all interactions among parasites are competitive (18). As mentioned earlier in this paper, competition for space in soil may be a more limiting mechanism than competition for food. An interesting twist, reported for bird communities (similar to

nematodes perhaps only in that their communities exist in three dimensions) is that predation patterns result in population levels and stratification that exactly correspond with what would be expected from competition for food (27). As Holmes (18) and Boughey (3) point out, some areas of analysis commonly used in population studies are rarely used in community level studies, but they are applicable. Holmes (18) outlines the potential of such studies to distinguish among types of competition in parasite communities. The existence, the nature, and the effects of interspecific competition among plant-parasitic nematodes deserves more and better attention (34,54). Some of the caveats expressed by Sikora and Carter (48) about nematode interactions with other pathogens apply to studies of nematode-nematode interactions.

Oostenbrink's first factor, the human factor, has been approached in a study by Niblack and Bernard (31). In looking for patterns of occurrence among plant-parasitic nematode species in nurseries by ordination, they discovered no clustering of sites due to any of the floristic or edaphic variables they measured; however, they did observe clustering according to the individual nursery to which a site belonged, even though sites were often separated by considerable geographical distances. No great imaginative stretch is required to attribute this to movement of nematodes on machinery from one field to another, resulting in a general regional similarity among nematode communities. Indeed, agricultural systems cannot be considered apart from the human factor (13,37,44).

Two other factors cited by Oostenbrink, polyphagy and persistence, have not been directly addressed in community structure studies, but the former suggests two other levels of complexity that may be superimposed on the study of plant-parasitic nematodes. First is the consideration of "facultative plant parasites." Granted, their exact roles should be investigated in autecological studies, but their inclusion or exclusion from the plant-parasite group would have

an obvious impact on community studies. Second, it is almost reflexive to think of plant parasites as plant pathogens, although plant stimulation is a commonly reported response (60). This phenomenon is also appropriate for autecological investigation, but with conceptual consequences at the community level.

CONCLUSIONS

Nematode communities may or may not be "true" communities in any rigid sense; the distribution of species may follow a gradient established by some other factor(s), and the intersection points of tens or hundreds of continua may be mere coincidence. Nonetheless, classifying the community and analyzing the classes in various ways can give us valuable insights into a number of questions addressed here. I echo Freckman (12) in pleading for, and Yeates (60) in applauding, greater communication between soil ecologists and plant nematologists. Plant-parasitic species are the usual focus of community studies in agroecosystems by nematologists, but clearly the nematode community has effects other than those caused by pathogenicity. Information on other effects is needed in order to develop sustainable agricultural systems. Even if our emphasis remains on chemical control of plant-parasitic species, we need to know how these compounds affect the nontarget components of the nematode community (43,52,53).

As I began this paper with a cliché, so I will end it with a whole paragraph of them. Not only is there intrinsic value in the study of nematode communities, but a number of concerns involved in the development of sustainable agricultural systems and the evolution of the integrated pest management concept also require a holistic view. Of course, the need for autecological investigations of nematode populations continues, but the area of community structure needs more attention. To quote Price (42): "Among those who debate the relative importance of ecological factors affecting the organization of communities,

the sobering realization is, usually, that we do not have the critical information at hand."

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