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Nematode communities as ecological indicators of ecosystem health

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Nematodes have attributes that make them useful as ecological indicators to reflect change in soil structure and function. Rigorous statistical analyses reveal that maturity and trophic diversity indices differentiate the ecological condition of soils on a regional scale better than do individual or ratios of trophic groups. Maturity and trophic diversity indices measure different aspects of soil communities and are complementary when used together. 'Maturity' is a measure of ecological successional status of a soil community and trophic diversity measures food web structure. Maturity indices are based on the principle that different taxa have different sensitivities to stress or disruption of the successional sequence because of differences in their life history characteristics. Because common agricultural practices interrupt succession at various stages, the successional status of a soil community reflects the history of disturbance. For example, addition of animal manure, cultivation and annual crops typically have smaller index values than without cultivation and perennial crops. In agricultural soils, greater diversity of trophic groups correlates with an increase in the frequency of generally less abundant trophic groups (i.e., fungivores, omnviores and predators) relative to the generally more abundant trophic groups (i.e., bacterivores, plantparasites). Disturbances such as cultivation and addition of manure decrease trophic diversity, and long-term perennial crops tend to increase trophic diversity. Measures of ecological succession and trophic diversity are single values that can be analyzed using traditional statistical tools such as regression and analysis of variance. The structural index is modification of the maturity indices.

Despite their useful attributes, maturity and diversity indices are subject to serious limitations. Notably, colonizer-persister (CP) values, representing life history characteristics, are inferred by morphology rather than confirmed by feeding preference experiments. Diversity indices are popular but do not preserve the identity of taxa within the community, adding ambiguity to interpretation. For example, soils with 100% exotic or



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100% native species could have identical diversity values. Alternatively, indices that incorporate and/or maintain taxon identity (e.g., similarity indices such as Jaccard and Sorensen) can be linked more convincingly to ecological process and function. Improvements to these indices will occur if identification of free-living nematodes improves from trophic groups to genera and species, life history characteristics of nematode species and genera are tested empirically, and indices are refined and calibrated. It is important for practitioners to use the latest CP-value assignments.

Ecological indices related to nematode communities do not provide absolute values of condition but require reference to some putatively undisturbed community for interpretation or comparison. Use of an undisturbed community for a reference point is unrealistic, because agroecosystems are disturbed intentionally for human purposes. The author recommends use of long-term (> 10 year old) forage and pasture agroecosystems as a reference point in monitoring the ecological condition of agricultural soils. Empirical research suggests that cultivation disrupted soil food webs more than synthetic chemicals such as fertilizers and pesticides.

The goal of contemporary environmental monitoring programs is to compare nematode communities in soils between geographic regions ranging in size from 375,000 to 600,000 km². Based on the results of regional surveys, it appears that regional studies require a minimum sampling of 50 to 100 fields, with three independent samples (transects) per field and two subsamples per sample. If cost is a major limiting factor, similar reliability can be achieved by increasing the number of fields with one subsample for each of two samples assayed per field. Maturity and trophic diversity indices need not be calibrated at a scale finer than major land resource regions. Two modifications of maturity indices increased reliability (signal to noise ratio) and thus improved performance on a regional scale: 1) Values for the early colonizing taxa (CP =1) were removed from the original MI index to give a new index, MI25, and 2) combining plant-parasites and free-living nematodes into a single index, Σ MI25.

Interpretation of biological indicators of soil quality depends on their ability to reflect ecological processes such as decomposition and nutrient mineralization. Maturity index values correlate negatively with available nitrogen in soil. At the family resolution, nematodes accounted for up to 12% of nitrogen mineralization in mature forest soils. The



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coupling of this relationship diminishes with increased disturbance, whether clear-cutting or cultivation. Interpretation varies with ecosystem type. Wetlands, agriculture, and forest differ in their community associations of nematodes.

Given the advances in computer technology, a variety of multivariate methods are accessible through commercial software packages. These allow you to look at the whole community assemblage. I typically use canonical correspondence analysis (CCA) or redundancy analysis (RDA) to examine how treatment or environmental variables overlay with nematode community composition. Biplots are a graphic display of CCA variables in two-dimensional space as a tool to discern patterns among genera and environment matrices. Axes are linear combinations of species/variables, with the first axis being most informative, followed progressively less with each additional axis. Vector length is proportional to loading, expressing the relative importance, and the angle between vectors proportional to correlation.

Many multivariate approaches capture a one-time "snapshot" of community composition. However, community composition often changes through time, requiring a repeated measures approach. Principal Response Curves is a multivariate method based on RDA that accommodates a repeated measurement design. Each experimental unit and sampling time and unit by time interactions are dummy explanatory variables. Practitioners should be aware of the many limitations, assumptions, and caveats of community assemblage and multivariate techniques by consulting with expert statisticians.

There are two major impediments to implement nematode communities in largescale environmental monitoring programs, i.e., ecological interpretation and accessibility to non-specialists capable of identifying a multitude of free-living nematode taxa. Molecular probes are one way to expedite identification and enumeration of nematodes within whole community samples. Although this approach is available to non-taxonomists, it does not address concerns about interpretation and potential errors in assignments. Alternatively, nematode community indices would be more cost-effective and interpretable if ambiguous genera were removed and indices reduced to include sentinel taxa with known sensitivity or response to specific types of disturbance. Sentinel taxa will represent a subset of nematode communities but require knowledge of species assemblage patterns under different



scenarios of management practices, which often represent a complicated mixture of abiotic and biotic factors. Once sentinel taxa are identified, subsequent studies are needed to verify their sentinel status to determine the geographic or ecological range of their utility.