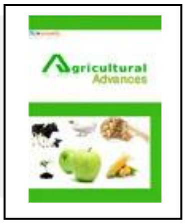
Agricultural Advances (2014) 3(3) 67-73
ISSN 2251-7820
doi: 10.14196/aa.v3i3.1185

Contents lists available at Sjournals

Agricultural Advances

Journal homepage: www.Sjournals.com



Review article

Nematode as a soil biodiversity indicator

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ARTICLE INFO

Article history,
Received 11 February 2014
Accepted 29 February 2014
Available online 20 March 2014

Keywords,
Biodiversity
Indicator
Nematode
Soil

ABSTRACT

Nematodes are one of the most abundant animals on earth. Their food specificity, the high number of species and high abundance in every habitat where decomposition takes place indicates that the structure of the nematode community has high information content. Since nematodes respond rapidly to new resources, and the nematode fauna can be efficiently analyzed, the structure of the nematode community offers an instrument to assess (changes in) the conditions of soils. Therefore, indicators based on nematode community composition are among the best developed metrics of soil health.

1. Introduction

Nematodes are the most abundant animals on earth, and bacteria are the most biologically and phylogenetically diverse (Curtis et al., 2002; Torsvik et al., 2002; Rappe and Giovannoni, 2003; Curtis and Sloan, 2004). Estimates of the number of species in the phylum range from 400,000– 10,000,000 (Hammond et al., 1995) to as high as 100,000,000 (Lambshead, 1993), on par with some of the higher insect estimates (Erwin, 1991). Cyanobacterial fossils date to 2.9 billion years ago (Noffke et al., 2003), whereas nematodes most likely arose slightly prior to or during the Cambrian explosion (Ayala and Rzhetsky, 1998; Rodriguez-Trelles et al., 2002). Free-living nematodes that feed on bacteria and fungi (as opposed to plants) contribute as much as 27% of the readily available nitrogen in the soil (Ekschmitt et al., 1999) and also promote rhizosphere colonization of beneficial rhizobacteria (Kimpinski and Sturz, 1996; Knox et al., 2003). The differences in the structure of nematode assemblages on large, horizontal scales are mainly related to differences in sediment composition, hydrodynamic conditions, salinity and food resource availability (Heip et al., 1985; Giere, 1993; Soetaert et al., 1994, 1995; Li et al., 1997; Steyaert et al., 1999; Tita et al., 2002; Somerfield et al., 2003; Steyaert et al., 2003).

Nematodes are an important component of the soil ecosystem with profound effects on organic matter decomposition, nutrient transformation and energy transfer (Neher, 2001; Coleman et al., 2004). Many reports suggest that nematodes are useful bioindicatorsin soil and aquatic ecosystems and their indicator value inrelation to soil functioning or soil properties have been well illustrated (Bongers and Ferris, 1999; Ekschmitt et al., 2001).

The traditional methods of nematode community analyses, deriving diversity and community structure from species abundance data, do not take account of the diverse biology and au ecological requirements of the taxa. Natural-history information on nematode species is scant, so studies which require information on nematode ecology have used a functional group approach (Thistle and Sherman, 1985). Species in functional groups share morphological traits that are thought or known to represent an important ecological function (Chalcraft and Resetarits, 2003). Agroecosystems are generally characterized by periodic disturbances such as tillage, use of pesticides, and fertilization that impede natural succession. Each of these disturbances has a specific effect but all of them can result in decrease of nematode diversity (Bongers and Bongers, 1998).

Phaeozem in Northeast China is characteristic for its high soil organic carbon content and is strongly influenced by human activities and climatic conditions. In this region, the mean annual temperature decreases from south to north, the decomposition intensity of soil microbes may decrease, and the growth periods of maize increase, which can increase the secretion of roots and result in the soil organic matter accumulation in phaeozem (Zhuang, 2007); and different geographic locations have different mean annual temperatures and precipitation, which can apparently influence the nematode diversity and distribution. At Hailun site, the total organic carbon and total nitrogen were higher than in the other sites (Zhuang, 2007), while the abundance of total nematodes and generic richness were significantly lower compared to other sampling sites. The relative low mean annual temperature may contribute to the lower abundance of nematodes and generic richness at Hailun site. In addition, the different reclamation history might be another important factor that affects soil nematode distribution in phaeozem agroecosystems. Since the soil had been cultivated for a longer period in the south (about 150 years in Gongzhuling) than in the north (about 100 years in Hailun), therefore, more soil organic carbon was lost in the south (Yang et al., 2004). Wang et al. (2002) found that soil organic matter decreased with increasing reclamation history in the phaeozem region, and this may influence nematode distribution indirectly.

2. Nematodes as bioindicators

As awareness of the diversity and ecological significance of nematodes has increased, they have increasingly been used as indicators in the areas of biodiversity and sustainability (Bongers and Ferris, 1999; Neher, 2001; Yeates, 2003; Liang et al., 2007; Li et al., 2008). Increasing interest in the biodiversity and the environment, concerns about maintaining the productive capacity of agricultural soils, and the interpretation of a growing knowledge of the contribution of nematodes to soil ecosystem process have resulted in a wider use of ecological indices, such as maturity index (Bongers, 1990), structural index, enrichment index (Ferris et al., 2001; Ferris and Matute, 2003), and so on. These indices facilitate conceptual interpretation and analysis of soil nematode community changes and thus promote bio assessment studies using nematodes as indicators of biodiversity.

The Enrichment indices (EI) indicate the response of primary decomposers to the available resources, while Structure indices (SI) suggest prevalence of trophic linkages (Ferris et al., 2001). The Channel indices (CI) measures dominance of fungal or bacterial decomposition channels (Ferris et al., 2001). Bongers (1990) developed the Maturity Index (MI) based on theweighted mean frequency of nematodes in five colonizer–persister(c–p) classes. The c–p scaling is based on functional responses ofsoil nematodes to resource and environmental change (Freckman and Ettema, 1993; Bongers and Ferris, 1999). Ferris et al. (2001) developed a graphic faunalanalysis system, which integrates the information of c–p scalingand trophic groups of nematodes and allows diagnosis of food webstructure and soil health condition.The nematode maturity index (MI) developed by Bongers (1990) incorporates quantitative and qualitative information of free-living nematode families. It assigns families to groups scoring 1e5 on a colonizerepersister (cep) scale according to their life history characteristics; colonizers (with lower scores on the cep scale) are fast reproducers and indicative of early stages of succession and persisters (with higher scores on the cep scale) are slow reproducers and are more abundant in later stages of succession. The MI has shown to be a useful means to differentiate nematode communities in soils collected from different management systems (Ettema and Bongers, 1993; Lundquist et al., 1999; Mulder et al., 2003). In general, in systems that have some type of nutrient enrichment resulting from additions of manure or mineral N fertilizer, MI values are low (Nahar et al., 2006), and the effect of organic N sources on MI reductions appear to be more extreme than that of mineral fertilizers (Forge et al., 2005; Nahar et al., 2006).

Studies on macro benthic invertebrates have shown that linking taxonomic and functionaldiversity, i.e. pooling species from different taxonomic entities into functionally similargroups, can reveal different relationships between assemblages (e.g. Bremner et al., 2003; Bostro¨m et al., 2006). This suggests that taxonomic and functional analyses shouldcomplement each other when deriving general descriptions of benthic diversity and thatusing only taxonomic analyses to infer the effects of environmental variables and humanactivities on biota may omit key functional attributes (Frid et al., 2000; Bremner et al., 2003).

The values of CI were higher at Hailun than at Gongzhuling, since the degree of fungal participation in the primary decomposition channels of soil food webs is suggested by the CI (Ferris et al., 2001); the higher values of CI indicated a higher proportion of fungal decomposition occurring at Hailun than at Gongzhuling. The differences in mean annual temperature, precipitation, and reclamation history may help to explain the differences in CI. Other possible reasons might be that when organic matter was degraded and more fibrous, the decomposition was fungal, whereas, it would be more bacterial when organic matter was being replenished by active root growth or new inputs.

3. Soil properties and nematodes

In addition, different soil properties were also important limiting factors that affected nematode diversity and distribution. Clay percentage was found to positively influence nematode genera belonging to Ba2 group (such as Eucephalobus, Heterocephalobus) at Hailun site, whereas, EC and soil pH were negatively correlated with nematode genera at Gongzhuling site. In different study sites, the limiting factors that influence nematode genera were different. Freckman and Virginia (1997) studied nematode distribution and diversity in Antarctic soil and found that different nematode taxa were influenced by different factors, Scottnemalindsayae was best related to soil salinity factors (pH and EC), Plectusantarcticus to N and P, and Eudorylaimusantarcticus to moisture and organic C. In three Welsh soils pastures with conventional management, Yeates et al. (1997) found that the proportion of Cephalobidae increased with the clay percentage, where loam >silt >sand, and concluded that in a geographic region, the clay percentage and the proportion of Cephalobidae may be correlated.

Biodiversity, when viewed in relation to the condition of an ecosystem, is not only a matter of a high number of species, but is also concerned with the life strategy of the constituent species. Recently, there is a growing consensus that functional diversity is of crucial importance in determining ecosystem processes. However, there is still no consistent standard way to quantify functional groups, which is the key to the analyses of function diversity. The structure index and enrichment index based on integration of 'functional effect' (trophic group) and 'response types' (life strategy classification) may indicate the functional diversity of soil nematodes and accelerate progress in nematode diversity-functioning research (Wu et al., 2002; De Deyn et al., 2004; Liang et al., 2007). The inference of greater structure index at Hailun is that there are more links in the food web, more organism interactions, greater functional redundancy, and potentially, more stability of function.

Nematode faunal profile is a graphic representation of the effect of management practices or other perturbations on the structure and enrichment components of the food web, based on the relative weighted abundance of nematode guilds (Ferris et al., 2001). The effects of geographic location, climate change, and soil properties on the distribution of soil nematodes indicated that the integration of taxonomic diversity and functional diversity would probably prove to be a preferable method to indicate soil disturbance than particular nematode species or ecological indices.

4. Nematodes based on feeding groups

The allocation of nematodes to feeding groups is an effective method to condense information. Yeates et al. (1993) published a synthesis in which the following groups were distinguished:

1. Plant feeding

1a. Sedentary parasites
1b. Migratory endoparasites
1c. Semi-endoparasites
1d. Ectoparasites
1e. Epidermal cell and root hair feeders
1f. Algal and moss feeders
1g. Feeders on above-ground plant tissue
2. Fungal feeding
3. Bacterial feeding
4. Substrate ingestion
5. Animal predators
5a. Ingesters
5b. Piercers
6. Unicellular eucaryote feeding
7. Dispersal or infective stages of animal parasites
8. Omnivorous

Feeding group analyses offer opportunities to describe changes in decomposition pathways. There are numerous examples from which it appears that bacterial feeders increase in number as a result of increasing microbial activity caused by, for example, fertilization or other disturbances resulting in accelerated decomposition (Sachs, 1950; Huhta et al., 1979; Wasilewska et al., 1981; Sohlenius and BostroÈm, 1984; Dmowska and Kozlowska, 1988; Ettema and Bongers, 1993). Increase in the number of fungal feeders is an indirect effect and shows that toxicological effects observed in acute single species tests cannot simply be extrapolated to chronic conditions in the field.

Trends in the SI showed that there was also a shift from a relatively diverse community to one that was simpler in structure. Observed trends in EI values were in the opposite direction than trends in the CI and so were higher in systems with greater relative abundances of nematode families that are considered 'extreme colonizers' or 'enrichment opportunists' because these families are highly responsive to changes in resource availability (Bongers,1990).

Berkelmans et al. (2003) suggested that the CI and EI might not be robust indicators of system performance, arguing that high CI and low EI values can indicate situations where resources are chronically depleted or where low disturbance frequency promotes slower decomposition and nutrient immobilization (Ferris et al., 2001; Berkelmans et al., 2003). Where those authors see weakness, we see a nuance and an opportunity for interpretation as the biological implications of the CI and EI trends are clear.

5. Conclusions

By evaluating the relationship between the EI and CI with biochemical methods, management practices in these systems were not limiting crop productivity and were enhancing soil organic matter decomposition. However, those same conditions of soil management shifted the nematode community to a simplified foodweb structure revealed by low SI values that accounted for very low abundance of persisted nematodes. This carries the implication that high diversity is particularly important under changing conditions such as fluctuations in temperature, humidity, osmotic value of pore capillary water, CO2 and O2 concentrations, pH and seasonal inputs of organic material. We hypothesize that under fluctuating natural conditions in temperate zones nutrient leaching increases with decreasing nematode biodiversity.

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