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Carbon-rich organic fertilizers to increase soil biodiversity: Evidence from a meta-analysis of nematode communities

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ABSTRACT

Organic fertilizer applications that boost soil fertility and crop production are expected to enhance soil biodiversity, making ecosystems more resilient to stress. Numerous studies have compared biodiversity in soil receiving organic fertilizer to soil under other fertilizer regimes (inorganic fertilizers, unfertilized), yet the data were not analyzed systematically across studies. We evaluated fertilizer effects on soil nematode communities with a meta-analysis of more than 229 data points from 54 studies around the world that were published between 1996 and 2015. Data were from cropland and considered five fertilizer regimes. These regimes include unfertilized soils and those receiving inorganic fertilizers (2 regimes), as well as organic fertilizers (2 regimes). Species richness and total nematode abundance increased with increasing carbon (C) inputs from fertilizers, whereas greater nitrogen (N) application rates from fertilizers significantly reduced the species richness, Shannon's diversity (H′), maturity index (MI) and omnivore-predator nematode abundance. This could indicate that high fertilizer N inputs simplifies the nematode community structure and functions. Species richness, omnivore-predator nematode abundance and structural index (SI) increased with the organically-fertilized regime and declined in inorganically-fertilized regimes, suggesting that organic fertilizers can buffer stresses and sustain soil food web functions. Furthermore, organic fertilizers differed in their impact on soil nematodes, as those with C-rich crop residues supported larger free-living nematode populations and greatly promoted H′, SI and enrichment index (EI), whereas N-rich animal manure was more effective in controlling plant-feeding nematodes. Our review suggests that the application of C-rich crop residues is the most effective practice to enhance soil biodiversity in intensively managed agroecosystems, highlighting the importance of regular applications of straw and other C-rich residues to preserve the ecological resilience of cropland.

1. Introduction

Nematode community structure, a measure of the abundance and diversity of soil nematode assemblages, provides insight into ecosystem resilience where larger, more diverse assemblages reflect a capacity to perform numerous ecological functions and therefore sustain soil productivity and health (Yeates, 2007). Nematodes are appropriate indicators of soil ecosystem resilience due to the presence of multiple feeding groups – bacterivores, fungivores, herbivores, omnivores and predators – participating in soil food webs. Their diverse life history strategies may indicate whether the ecosystem has experienced a recent disturbance (e.g. large-bodied omnivores and predators are persistent K-strategists, whereas bacterivores and fungivores are smaller, more numerous and respond to environmental perturbations as r-strategists) (Bongers and Bongers, 1998). Bacterivores in the families Rhabditidae and Cephalobidae reflect changes in soil ecological functions due to the tendency of the Rhabditidae to increase following nutrient inputs, while the ubiquitous Cephalobidae increase in abundance during primary and secondary succession (Yeates, 2003). Other indices of nematode assemblages used to describe changes in soil ecological functions are: (1) maturity index (MI) to assess the free-living nematodes response to stress, where higher values represent a more stable community (Neher,

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2010), (2) enrichment index (EI) to indicate the availability of food resources and measure the increase in small-bodied opportunistic bacterial and fungal feeders that respond quickly to C and N inputs, and (3) structure index (SI), where higher values suggest more linkages in the food web and greater soil resilience (Ferris et al., 2001).

Annually cropped agroecosystems, referred to hereafter as cropland, are the most important terrestrial ecosystems for human survival and are highly disturbed due to land use change, modification and fragmentation of habitats, degradation of soil and water, and loss of diverse food resources to support the biodiversity in soil food webs (Foley et al., 2005). Intensive management of cropland typically reduces nematode abundance and species richness, especially of the K-strategists that are sensitive to environmental stress. Cropland that provides ample food resources for nematode-feeding groups can support diverse and abundant nematode communities, but are generally impoverished in K-strategists compared to undisturbed grasslands and forests (Neher, 2010). Thus, cropland should be the target of interventions, such as organic fertilizer applications, to sustain nematode communities and therefore improve the resilience of soil ecological functions.

Nitrogen (N) fertilizers are applied to cropland to enhance aboveground net primary productivity, but can significantly alter both plant and soil biotic communities, reducing their diversity and ultimately changing the food web structure and ecological functions (Bai et al., 2010). N inputs to cropland generally reduce the belowground species richness and diversity by favoring a few opportunistic species that are well adapted to high nutrient levels (Stevens et al., 2004). The same pattern was noted in pasture soils, where Rhabditidae nematode abundance increased by 72% with high inorganic N fertilizer rate (400 kg N ha^{-1} y^{-1}) compared to a lower inorganic N input of 200 kg N ha^{-1} y^{-1} (Sarathchandra et al., 2001). When organic fertilizers are the source of N applied to terrestrial ecosystems, the impact of fertilizer application on nematode communities must consider the combined effect of organic C and N inputs from the fertilizer source.

Organic fertilizers containing animal manure and crop residues increase soil nematode abundance. Nematode populations were 30–140% larger and species richness was 9–11% higher in agroecosystems receiving organic fertilizers plus inorganic N, compared to inorganic N fertilizer alone (Liang et al., 2009; Liu et al., 2016b). Moreover, the response of nematode communities was related to the organic C input and the quality of organic materials, such that chemically-complex plant residues (e.g. straw and cover crop residues) supported more nematodes and greater species richness than animal manures (e.g. pig manure and pig compost) (Villenave et al., 2010; Liu et al., 2016b). Still, high manure applications that supplied 600 kg N ha^{-1} supported a significantly higher species richness and nematode abundance than low manure application that added 150 kg N ha^{-1} to cropland (Jiang et al., 2013). The patterns emerging from disparate experimental studies published in the literature can be helpful in predicting how soil nematode communities respond to organic fertilizer applications, based on the organic C and N input to cropland from these materials. The central position of nematodes in soil food webs implies that a meta-analysis could enhance our understanding of how organic fertilizers may be used to sustain soil ecological functions.

Our study provides the first systematic and quantitative review of fertilization effects on soil nematode communities in cropland using a meta-analysis approach. Data points were collected from 12 countries reporting the effect of fertilization regimes (unfertilized, inorganic fertilizers and organic fertilizers) on nematode abundance, species richness and characteristics of nematode assemblages. We hypothesized that (i) soils receiving organic fertilizer or lower rates of inorganic N fertilizer will support greater abundance and species richness of nematodes than soils that receive higher rates of inorganic N fertilizer, and (ii) greater nematode abundance, species richness and ecological stability of the nematode assemblage will be favored with the application of organic fertilizers containing complex organic substrates (e.g. crop residues) that constitute a C-rich input.

2. Materials and methods

2.1. Data collection

To assess the effect of fertilization on soil nematode communities, studies included in the meta-analysis should meet the following criteria:

(1) Study should be carried out in cropland (cereal crop, economic crop).
(2) Soil sampling should be conducted within the soil layer of 0–20 cm depth.
(3) Besides a control experiment with no fertilization (CK), the analytical data should be obtained from one of the four following fertilization regimes: inorganic nitrogen fertilizer only (NF, including the amount applied in kg N ha^{-1} y^{-1}); inorganic nitrogen, phosphorus and potassium fertilizers (CF); organic fertilizer only (MF, including the amount applied in kg organic C ha^{-1} y^{-1}); and organic fertilizer plus inorganic nitrogen, phosphorus and potassium fertilizers (MCF).
(4) Six kinds of organic fertilizer were considered and categorized as follows: animal manure (pig, cattle, chicken, horse), animal compost (pig, cattle, chicken, horse), cover crop (mulch, clover, legume, grain, grass, rye, vetch, oats), straw compost, straw, sludge (sewage, sugarcane) and waste (food, paper, biosolids).

Based on these criteria, the meta-analysis of soil nematode communities in response to fertilization was based on 229 data points from 54 references in the peer-reviewed literature from 1996 to 2015 (detailed in Table 1, which summarizes the studies included in the meta-analysis as influenced by fertilizer inputs).

Nematode genera were assigned to four trophic groups: bacterial-feeding, fungal-feeding, plant-feeding and omnivore-predator nematodes. Total nematode abundance, the abundance of the four trophic groups and common family (i.e. Rhabditidae and Cephalobidae) were expressed as individuals per 100 g soil. Ecological indices including maturity index (MI), enrichment index (EI), structure index (SI), and Shannon's diversity index (H′) which takes into account both species number and relative abundance, were included in the database.

2.2. Data analysis

Publication bias was assessed *a priori* using funnel plot asymmetry (Sterne and Egger, 2001; Song et al., 2013) under the R package *metafor* (Viechtbauer, 2010), and revealed no publication bias because the data fell within the expected 95% confidence interval (as an example, funnel plots of species richness and total nematode abundance in the dataset are shown in Fig. S1).

The effect of fertilizer regime on nematode abundance (in total, in trophic groups and in common families), species richness and ecological indices (MI, H′, EI and SI) was determined as the difference between the mean value of the nematode parameter in the fertilized treatment (NF, CF, MF, or MCF) and the mean value of the nematode parameter in the unfertilized control (CK) using the function *cumul* of the R package *metafor* (Viechtbauer, 2010). The effect on nematode abundance, species richness and ecological indices of N application rate, C application rate and organic