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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

Table 1
List of studies included in the meta-analysis of soil nematode communities as influenced by fertilizer inputs in cropland, where N addition indicates application of inorganic fertilizer and C addition occurred when organic fertilizer was applied. The number of data points in each study is indicated. References for these meta-data citations are listed in the Supplemental Information.

Reference	Country	N addition	C addition	Data points
Akhtar and Mahmood (1996)	India	✓		1
Akhtar (1998)	India	✓		2
Arancon et al. (2003)	USA	✓	✓	1
Azpilicueta et al. (2014)	Spain	✓		2
Berkelmans et al. (2003)	USA		✓	5
Birkhofer et al. (2008)	Switzerland		✓	3
Briar et al. (2007)	USA		✓	3
Briar et al. (2011)	USA		✓	4
Bulluck et al. (2002)	USA		✓	6
Coll et al. (2012)	France		✓	3
Djigal et al. (2012)	France		✓	5
DuPont et al. (2009)	USA		✓	3
Ferris et al. (2004)	USA		✓	7
Garcıa-Alvarez et al. (2004)	Spain	✓	✓	8
Gu et al. (2015)	China		✓	4
Hu and Cao (2008)	China	✓	✓	1
Hu and Qi (2010a)	China		✓	4
Hu and Qi (2010b)	China	✓	✓	5
Hu and Qi (2011)	China	✓	✓	4
Hu and Qi (2013)	China	✓	✓	6
Ito et al. (2015)	Japan		✓	2
Jiang et al. (2013)	China		✓	6
Li et al. (2007)	China	✓		6
Li et al. (2010)	China	✓	✓	8
Li et al. (2014)	China		✓	1
Liang et al. (2005)	China	✓		10
Liang et al. (2009)	China	✓		4
Liu et al. (2015)	China	✓	✓	8
McSorley and Frederick (1999)	USA		✓	3
Nahar et al. (2006)	USA		✓	8
Nair and Ngouajio (2012)	USA		✓	6
Neher (1999)	USA		✓	2
Neher and Olson (1999)	USA		✓	1
Okada and Harada (2007)	Japan	✓	✓	2
Pan et al. (2010)	China	✓	✓	5
Pan et al. (2015a)	China	✓		4
Pan et al. (2015b)	China	✓		9
Porazinska et al. (1999)	USA		✓	2
Renčo and Kováčik (2012)	Slovak		✓	5
Roth et al. (2015)	Japan		✓	2
Ruan et al. (2013)	China	✓		2
Song et al. (2015)	China	✓		12
Tabarant et al. (2011)	France		✓	4
Treonis et al. (2010)	USA		✓	2
Van Diepeningen et al. (2006)	Netherlands		✓	2
Vestergård (2004)	Denmark	✓		2
Villenave et al. (2004)	Senegal		✓	5
Villenave et al. (2010)	Burkina Faso	✓	✓	2
Wang et al. (2004)	USA		✓	5
Wang et al. (2006)	USA	✓		6
Ye et al. (2013)	China	✓	✓	8
Zhang et al. (2009)	China	✓		1
Zhang et al. (2012)	China		✓	4
Zhang et al. (2013)	China		✓	3

fertilizer type (animal manure, animal compost, cover crop, straw compost, straw, sludge and waste) were determined as the difference between log-transformed mean value of the parameter in the fertilized treatment and the log-transformed mean value of the nematode parameter in the unfertilized control (CK) according to Hedges et al. (1999). The response is symmetric around 0. An effect value of 0 indicates no effect of fertilization on the nematode parameter, negative values indicate a decrease in the nematode parameter resulting from fertilization, whereas a positive effect values indicates an increase in the nematode parameter due to fertilization. All statistics were performed using the R version 3.1.2 (Team, 2014).

3. Results

Total nematode abundance and diversity (H′) were increased by all fertilization regimes, although species richness was greater in the MF fertilization regime and reduced in other regimes (i.e. NF, CF and MCF) (Fig. 1). Organic fertilizer regimes (i.e. MF and MCF) increased omnivore-predator nematode abundance, EI and SI, while these metrics of the nematode tended to be lower in ecosystems receiving the NF (by 9.4%) and CF (by 0.2%) treatments (Fig. 1).

The impact of N and C addition on soil nematodes was moderated by the application amount. Species richness and total

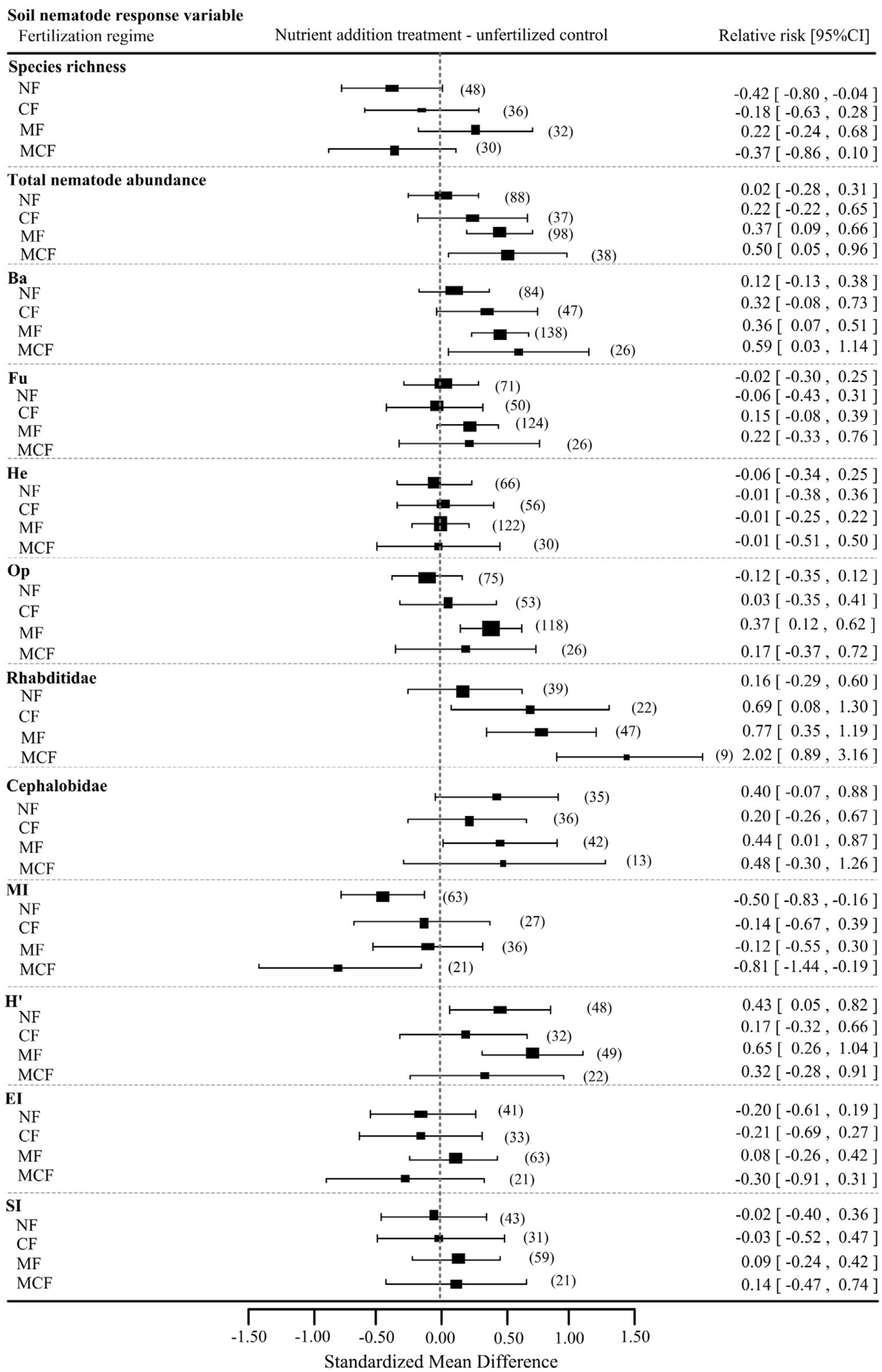


Fig. 1. Effect of fertilization regimes on soil nematode response variables: species richness, abundance of total nematodes, trophic groups, Rhabditidae family and Cephalobidae family, as well as ecological indices in cropland. Data points were the difference between the nutrient addition treatment minus the unfertilized control. Numbers of data points are given in brackets. Fertilization regimes were: N, inorganic nitrogen fertilizer only; CF, inorganic nitrogen, phosphorus and potassium fertilizers; M, organic fertilizers only; and MCF, organic fertilizers plus inorganic nitrogen, phosphorus and potassium fertilizers. Other abbreviations were: Ba, bacterial-feeding nematode; Fu, fungal-feeding nematode; He, plant-feeding nematode; Op, omnivore-predator nematode; MI, maturity index; H′, Shannon's diversity; EI, enrichment index; SI, structure index.

nematode abundance increased with greater organic C inputs (Fig. 2). In contrast, higher N inputs significantly reduced species richness, maturity index (MI), diversity (H′), structure index (SI) and omnivore-predator nemaotde abundance, but increased the abundance of plant-feeding nematode and Cephalobidae (Fig. 2, Fig. 3).

Most of the organic materials applied to soils were animal manure/compost and straw/straw compost, and these tended to

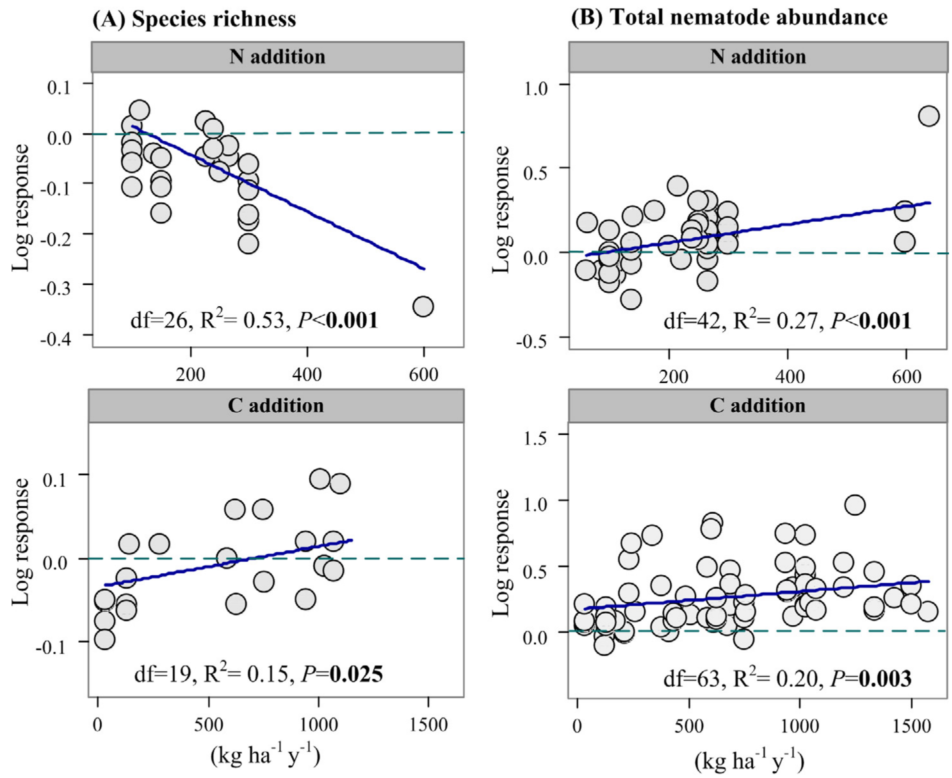


Fig. 2. Effect of N addition and C addition (kg ha^{-1} y^{-1}) on species richness (A) and total nematode abundance (B) in cropland. Data points were the difference between the nutrient addition treatment minus the unfertilized control treatment. Values in **bold** indicate a significant relationship ($P < 0.05$) between N or C addition and species richness or total nematode abundance. df, degree of freedom.

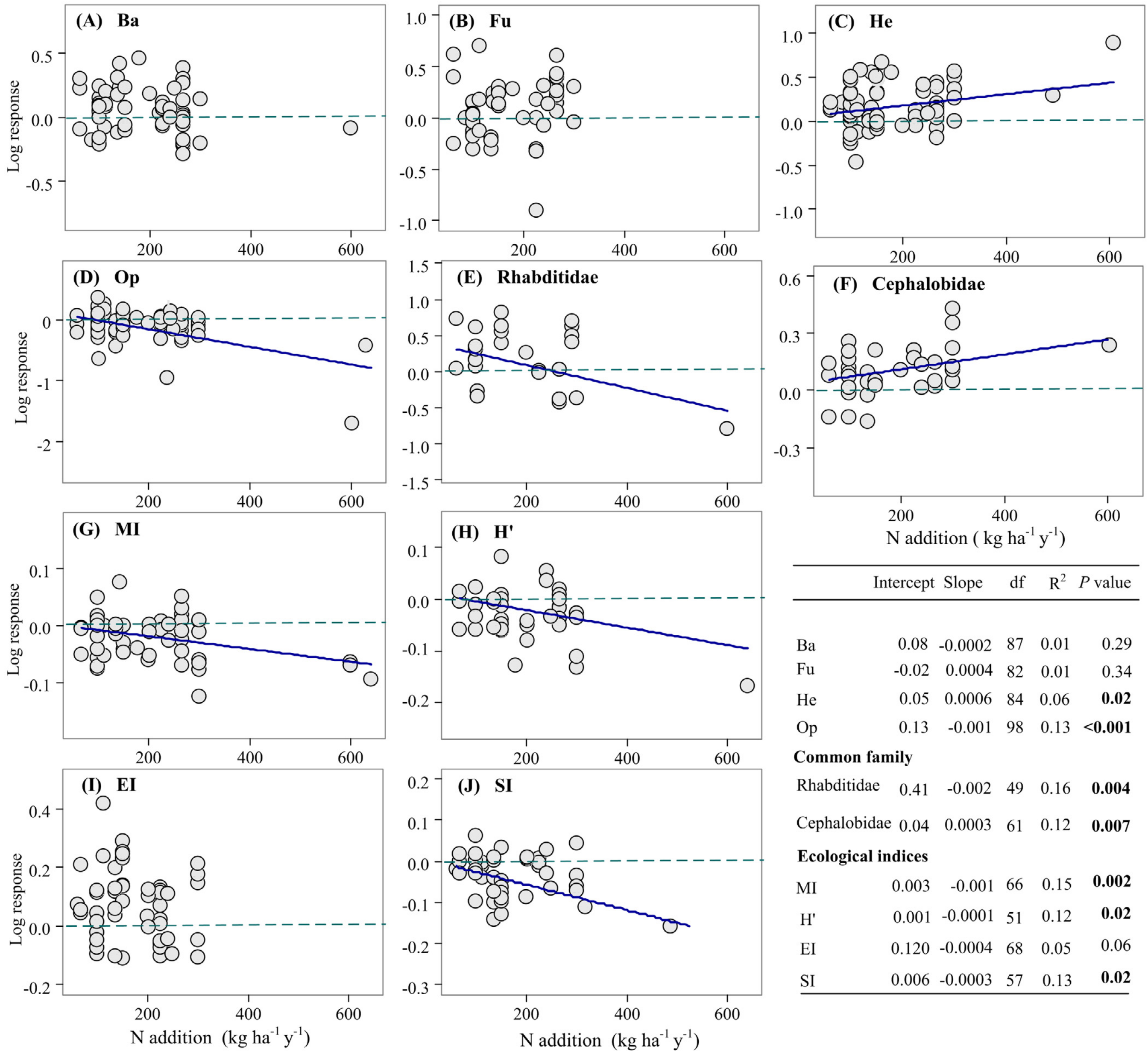
increase the total nematode abundance, diversity (H′) and EI, but decreased the MI and SI (Fig. 4). The nature of the organic fertilizer also impacted the nematode community. The N-rich organic fertilizers like animal manure, compost and sludge were associated with a smaller number of plant-feeding nematodes, with the greatest decline (15–225%) occurring after sludge application (Fig. 4). The C-rich straw and straw compost was better than other organic materials to increase the population of free-living nematodes and reduce the MI, whereas incorporating cover crop residues tended to increase nematode indices including H′, MI, EI and SI (Fig. 4).

4. Discussion

4.1. Nematode community affected by inorganic vs. organic fertilizers

As we predicted in hypothesis (i), nematode abundance and species richness were greater in organically fertilized soils than inorganically fertilized soils. Because cropland with annual crops have relatively low inputs of organic C from plant residues, microbial residues and their associated exudates, the nematode assemblage in the cropland should benefit from organic fertilizer applications. This assertion is consistent with Bengtsson et al. (2005), who reported that organically fertilized soils usually had about 30% higher species richness than inorganic farming systems. They further concluded that positive effects of organic farming on species richness and diversity are expected in intensively managed agricultural landscapes, meaning that we can re-establish a diverse nematode assemblage by adopting some of the practices employed on organic farms. Organic C inputs should be of particular importance for the population growth and activity of soil organisms including nematodes, since nematode tissues are approximately 50% C in dry weight and have a C:N ratio of 8–12 (Coleman et al., 1977; Wang et al., 2002). We acknowledge that organic C is first metabolized by primary decomposers (bacteria, fungi) before it is transferred to higher trophic groups in the food web, including nematodes. Thus, the abundance of bacterivores (e.g. families of Rhabditidae and Cephalobidae), fungivores and omnivores nematodes as well as the SI show the greatest positive responses to organic fertilizer regimes (i.e. MF and MCF) (Fig. 1). Besides, a slightly increase of total nematode abundance associated with greater organic C inputs indicates that extra sources of organic C, beyond what is contributed by rhizodeposition and the recycling of unharvested crop residues, is essential to sustain the belowground communities and ecological functions of cropland.

As predicted, nematode species richness was reduced significantly by high inorganic N inputs. Similar results could be found in other studies of below- and above-ground communities. For example, inorganic N addition decreased the species richness of ectomycorrhizal fungal (Parrent et al., 2006; Parrent and Morris, 2006; Cox et al., 2010), while experimental addition of inorganic N to grasslands resulted in a loss of 3–4% of species richness in the plant community for each 100 kg N ha^{-1} added over the course of the experiment (Wedin and Tilman, 1996; Stevens et al., 2004). Higher N inputs appear to favor a few highly competitive species, which become dominant and suppress the growth and reproduction of other species, a process of competitive exclusion that causes a loss of biodiversity (Pausas and Austin, 2001). In their study of soil nematodes, Wei et al. (2012) found the relative abundance of *Acrobeloides* (bacterivores of cp 2) and *Helicotylenchus* (herbivores of cp 3) was 0.8% and 6.7% in soils receiving low N inputs, but rapidly increased to 12.9% and 15.6% of the community in the high N treatment. Meanwhile, *Aporcelaimellus* (omnivores of cp 5) and *Mylonchulus* (predators of cp 3) disappeared from soils with the high N treatment. The disappearance of some nematode species in N-rich soil conditions may be due to their poor competitive



	Intercept	Slope	df	R^2	*P* value
Ba	0.08	-0.0002	87	0.01	0.29
Fu	-0.02	0.0004	82	0.01	0.34
He	0.05	0.0006	84	0.06	**0.02**
Op	0.13	-0.001	98	0.13	**<0.001**
Common family					
Rhabditidae	0.41	-0.002	49	0.16	**0.004**
Cephalobidae	0.04	0.0003	61	0.12	**0.007**
Ecological indices					
MI	0.003	-0.001	66	0.15	**0.002**
H'	0.001	-0.0001	51	0.12	**0.02**
EI	0.120	-0.0004	68	0.05	0.06
SI	0.006	-0.0003	57	0.13	**0.02**

Fig. 3. Effect of N addition (kg ha^{-1} y^{-1}) on soil nematode response variables: trophic groups, Rhabditidae family and Cephalobidae family, as well as ecological indices in cropland. Data points were the difference between the nutrient addition treatment minus the unfertilized control. Values in **bold** indicate a significant relationship ($P < 0.05$) between N addition and response variables. Ba, bacterial-feeding nematode; Fu, fungal-feeding nematode; He, plant-feeding nematode; Op, omnivore-predator nematode; MI, maturity index; H′, Shannon's diversity; EI, enrichment index; SI, structure index; df, degree of freedom.

advantage, or it could be a function of changes to soil abiotic factors such as pH. Stevens et al. (2010) reported that the decline in soil pH with greater atmospheric N deposition was responsible for the loss of nematode species richness.

Although greater abundance of bacterial-feeding and omnivores-predators nematodes was found in soils receiving low inorganic N fertilizer inputs, the total nematode abundance increased with greater inputs of inorganic N fertilizer, which was contrary to our hypothesis (i). This occurred because plant-feeding nematodes were significantly more abundant in soils that had high inorganic N fertilizers. Still, a nematode assemblage dominated by plant-feeding nematodes were significantly less diverse (indicated by H′) and suggested an unbalanced food web (indicated by MI). Since bacterial-feeding and omnivores-predators nematodes were affected more strongly by abiotic factors (e.g. pH) than by food resources (Chen et al., 2013), this may imply that soil acidification and lower soil pH that accompanies higher inputs of inorganic N fertilizers is responsible for the decline in these trophic groups.

We predicted that plant-feeding nematodes would respond to the availability of resources and habitat within plant roots, rather than soil abiotic factors (Chen et al., 2013; Liu et al., 2016a). Our findings imply that higher rates of inorganic N fertilizer that favor crop development, including production of root biomass and rhizodeposition, create a conducive environment for the plant-feeding nematodes. Since many plant-feeding nematodes are pests that damage crops and reduce marketable yields, the practice of applying high rates of inorganic N fertilizer that stimulate the growth of plant-feeding nematode populations is not advised. There must be a trade-off between applying inorganic N fertilizer rates to meet yield targets while still maintaining a balanced nematode community assemblage where omnivores-predators

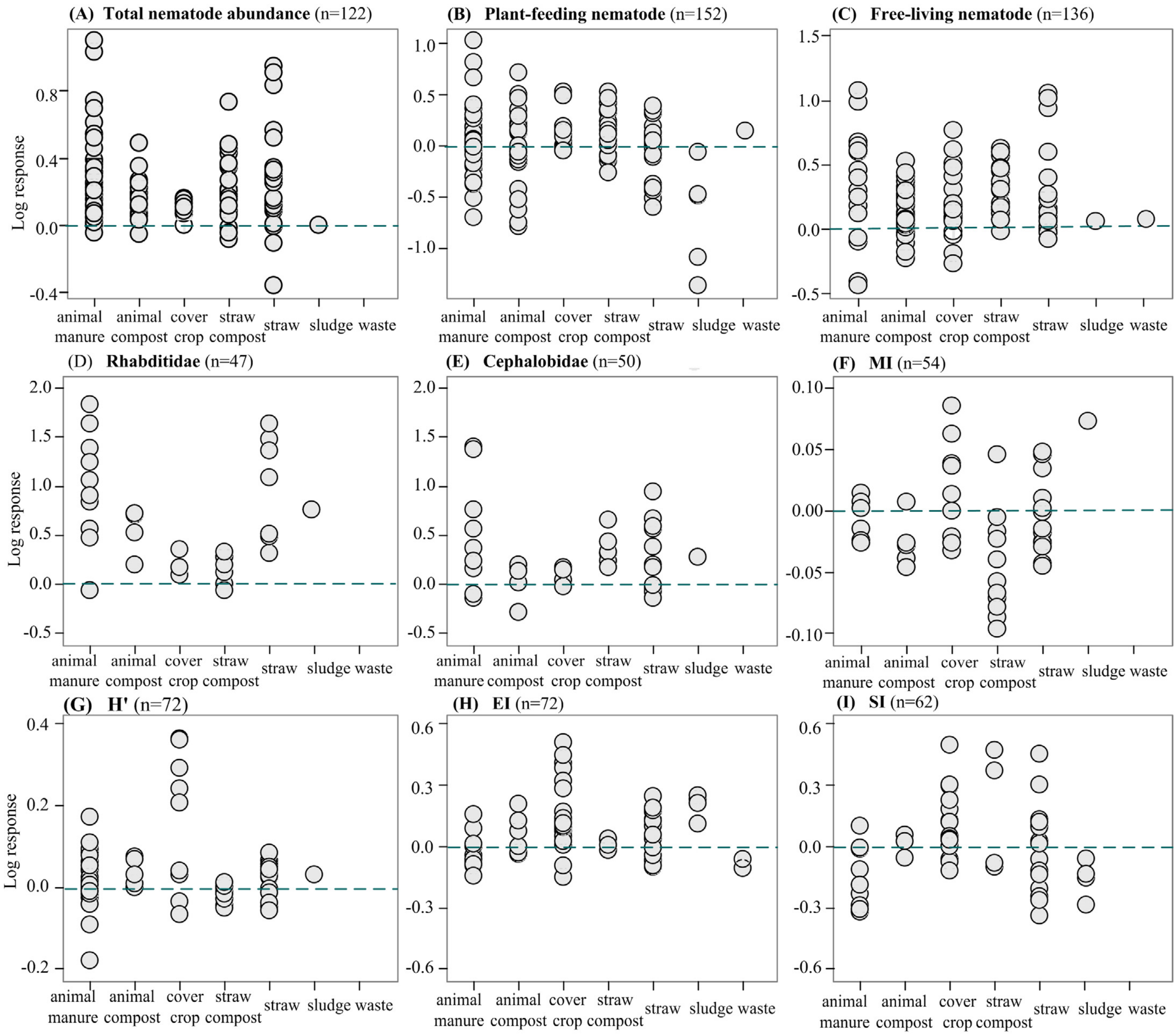


Fig. 4. Effect of organic fertilizers on soil nematode response variables: abundance of total nematodes, plant-feeding and free-living nematodes, Rhabditidae family and Cephalobidae family, as well as ecological indices in cropland. Data points were the difference between the nutrient addition treatment minus the unfertilized control. Numbers of data points are given in brackets. Free-living nematodes includes bacterial-feeding, fungal-feeding and omnivores-predators. MI, maturity index; H′, Shannon's diversity;. EI, enrichment index; SI, structure index.

can provide some biological control of plant-feeding nematodes, thus helping to prevent crop infestation and damage by these pests. It appears that regulating the inorganic N fertilizer input to cropland might help to control the plant-feeding nematode populations by encouraging more ecological interactions in the soil food web. Our findings have important implications for researchers considering ecological methods of crop protection against plant-feeding nematodes.

4.2. Nematode community affected by N-rich vs. C-rich organic fertilizers

Straw-based organic fertilizers had the greatest benefits for the soil nematode community because they resulted in greater nematode abundance and species richness, and created a well-structured and complex nematode community, as demonstrated by several indicators like MI, H′, EI and SI (Fig. 3). These results were consistent with our hypothesis (ii), and suggested that straw-based organic materials are more effective than animal manure in building a resilient nematode community. Straw-based crop residues are always C-rich (organic matter ranges from 44 to 83%), the result being that soils receiving straw amendment have higher soil respiration, greater soil water retention, more soil porosity and lower bulk density than soils fertilized with farmyard manure (Zhao et al., 2009). Improvement of these soil physical properties are well known to create an optimal habitat for nematodes and facilitate their movement through soil pore water (Nielsen et al., 2014), while higher soil respiration implies an active community of bacteria and fungi, which are preferred food resources for bacterivores and fungivores.

Another key finding of our meta-analysis was that N-rich organic fertilizers such as animal manures and sludge were more effective in controlling plant-feeding nematodes than straw-based crop residues (Fig. 3). The effect of animal manure/compost on nematodes must be complex, since high rates of inorganic N fertilizer are counter-indicated in soils prone to infestations of plant-feeding nematodes. One possible mechanism for plant-feeding nematode suppression is a feedback induced by a rapid increase in size and activity of microbial populations that are antagonistic to nematodes. For example, nematode infection was lower on tomato planted in soil with non-sterilized chicken manure than on tomato grown in soil amended with sterilized chicken manure, leading the researchers to propose that the endogenous microorganisms in the chicken manure are important for nematode suppression (Kaplan and Noe, 1993). This is hard to understand, since endogenous microorganisms adapted to the animal digestive tract are not expected to grow well in soil. An alternative explanation is that the exponential growth of gram negative bacteria in soil on N-rich organic fertilizer produces inhibitory substances that affect the plant-feeding nematode populations. However, the relationship between animal manures/compost, antagonistic microorganisms and nematode suppression was never demonstrated clearly (Oka, 2010), and warrants systematic investigation in the future.

5. Conclusions

Our meta-analysis suggests that nematode species richness was reduced significantly by high inputs of inorganic N fertilizers but increased with the application of C-rich organic fertilizers. Organic fertilizers were favored over inorganic fertilizers because they create more diversity in the nematode community assemblage. Interestingly, C-rich organic fertilizers supported a more structured nematode community and preserved the ecological resilience, whereas N-rich animal manure was effective in protecting crops against plant-feeding nematodes. However, the underlying mechanisms that explain how C-rich and N-rich organic fertilizers control the species richness and composition of nematode assemblage are still not well understood – not only due to the diversity of organic amendments, but also due to the variety of soil environments included in this meta-analysis. We do not have a good explanation about why N-rich animal manure seems to control plant-feeding nematode populations, but encourage other researchers to consider that N-rich animal manure has potential as a cultural control against root nematodes that cause damage and reduce yields of many economically important crops. Our meta-analysis also offer insights into how fertilization management influences soil productivity and health. We recommend that agricultural producers consider a fertilizer regime that includes regular applications of C-rich organic fertilizers to increase nematode diversity and build ecological resilience in their cropland.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.07.015.

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