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Body size is a sensitive trait-based indicator of soil nematode community response to fertilization in rice and wheat agroecosystems

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ABSTRACT

Nematode body size is a trait that could be responsive to environmental changes, such as agricultural management practices, and adopted as a standard trait-based indicator in soil community analysis. Our study investigated how body size in the nematode community responded to fertilization in a double-cropping system with paddy rice and upland wheat. Four fertilizer treatments were examined: an unfertilized control (CK), chemical fertilizer (CF), manure plus chemical fertilizer (MCF) and manure plus straw plus chemical fertilizer (MSCF). The community-weighted mean (CWM) of body size was the trait-based indicator used for nematode community analysis. A trend of increasing body size in fertilized plots was observed for most genera, with a relatively small increase in the size of small-bodied bacterivores and fungivores and a relatively large increase in the size of large-bodied omnivores. Fertilized plots had significantly greater CWM of body size than the CK treatment, although total nematode abundance increased significantly in the MSCF treatment only. Discriminant and multiple regression analyses showed that CWM of body size was positively correlated with the soil organic C, total N, available P and available K concentrations, which responded to fertilizer inputs. In contrast, soil fertility was weakly related to total body size in the wheat phase and the following abundance-based indicators: Margalef's richness index, Shannon's diversity index, summed maturity index ($\sum$MI) and enrichment index (EI) in both phases. Since fertilization resulted in larger body size but no other change in the nematode community (i.e. diversity and abundance were generally unaffected by fertilization), this implies that nematodes have a plastic growth habit that does not necessarily result in greater reproduction or fitness of offspring. We suggest that CWM of body size is a reliable trait-based indicator of the soil nematode community response to fertilization, but this requires further testing across a wider range of fertilized agroecosystems.

1. Introduction

The community structure of soil organisms provides insight into relationships between community composition, environmental change and ecosystem functions. Abundance-based indicators, e.g. total abundance, Margalef's richness index, Shannon's diversity index, Pielou's evenness index and nematode channel ratio, provide valuable information about community succession and are often used to predict and interpret the changes in soil community structure due to environmental change (Ferris et al., 1996; Li et al., 2007; Villenave et al., 2010; Zhang et al., 2012). Bongers (1990) ranked nematodes in five colonizer-persister (c-p) groups (c-p from 1 to 5) and developed the maturity index (MI) to better assess the free-living nematodes response to environmental disturbance. This approach is based on nematode reproductive strategies that correspond to their phylogeny, feeding habit and body size. The MI can be presented as the summed maturity index ($\sum$MI), which including both free-living and plant-parasitic nematodes (Yeates, 1994). Nematodes in agroecosystems are often described based on several feeding groups: bacterivores, fungivores, herbivores, omnivores and predators (Yeates et al., 1993). By integrating these feeding groups and c-p guilds, Ferris et al. (2001) developed the enrichment index (EI) as indicator for productive and relatively small-bodied nematodes, and the structure index (SI) based on the

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expected longevity of large-bodied nematodes. The EI and SI are suitable response metrics for nematode community change in response to environmental change (Ferris et al., 2004; Briar et al., 2007; Li et al., 2007; Liang et al., 2009).

Fertilization of agroecosystems constitutes an environmental change for nematodes, mainly because fertilizers increase trophic resources and alter habitat through their effect on soil structure. Total nematode abundance increases when organic fertilizers or inorganic nitrogen (N) fertilizers are applied (Li et al., 2007; Liang et al., 2009; Jiang et al., 2013). The EI value of the nematode community responds to the greater food supply and more favorable soil nutrient condition after fertilization because EI measures the number of opportunistic bacterial and fungal feeders that respond quickly to carbon (C) and N inputs (Ferris and Matute, 2003; Forge et al., 2008; DuPont et al., 2009). However, abundance-based indicators may not be sufficiently sensitive to detect environmental change due to fertilization. Multiple genera with similar functional traits are in the same c-p ranks, which can lead to similar results for EI and SI analyses (Ferris, 2010). Besides, the allocation of c-p scale to five rankings is too limited to indicate the variation in body size, and sometimes does not match well with body size, e.g. nematodes belonging to the c-p 1 class are larger than nematodes belonging to the intermediate classes (families with c-p 2, 3, or 4) (Vonk et al., 2013). These shortcomings of abundance-based indicators led Ferris (2010) to propose the use of trait-based indicators such as body mass and body size for soil nematode community analysis. It is not difficult to measure the body size of soil organisms (Wardle, 2002; Mulder et al., 2009; Mills and Adl, 2011; Lindo et al., 2012; Zhao et al., 2015) and it should be possible to use body size as a standard measurement of functional diversity in soil systems (Mulder et al., 2009; Turnbull et al., 2014; George and Lindo, 2015).

The body size of five nematode functional groups ranges from 23×10^3 to 5120×10^3 μm^3, with more than 200-fold difference in the biovolume of the largest and smallest soil nematodes (Yeates, 1988). Smaller individuals (e.g. bacterivores and fungivores) are important for decomposition and nutrient recycling from microbial biomass, whereas larger individuals (e.g. omnivores and predators) function as top-down controllers of the nematode community by suppressing herbivores and modifying the abundance of intermediate nematode, both of which affect nutrient dynamics (Norkko et al., 2013). According to the conventional “size-advantage” hypothesis (Ghiselin, 1969; Berglund, 1990), individual nematodes or nematode functional groups that grow to a larger body size are expected to gain an advantage in competition for limited resources; as well, they may have the potential to become more influential in soil nutrient cycling.

An increase in body size of most nematode families is expected when agroecosystems receive nutrient inputs, such as from dung or urine patches (Mills and Adl, 2011). However, the response of nematode body size to fertilizer nutrients is not well described. Organic fertilizers supply C for microbial growth, while the N, phosphorus (P) and potassium (K) contained in organic and inorganic fertilizers enhance microbial growth directly and indirectly, by promoting crop growth. Fertilization should promote nematode growth and body size increase because greater microbial and crop biomass in fertilized agroecosystems provides more trophic resources for nematode communities. The organic C obtained from organic fertilizer, microbial biomass and crop tissues should be of particular importance for determining gains in nematode body size since nematode tissues are approximately 50% C (dry weight basis) and have a C: N ratio of 8–12 (Coleman et al., 1977; Wang et al., 2002). Resources containing organic C are a growth factor for the model organism *Caenorhabditis elegans* (Lu et al., 1979; Scotti et al., 2001), which is further evidence of the relationship between C nutrition and body size. Thus, we expect that nematode body size will be more strongly correlated with soil organic C than with other soil nutrients (total N, available P and available K) that increase as a result of fertilizer application. Still, how nematode body size responds to nutrient inputs from fertilizer could depend on the growing season and timing of fertilizer applications.

Finally, we must consider how to describe body size in nematode communities due to the wide disparity in size across diverse genera. The total body size of the community is readily measured, but a few large omnivores and predators will influence the value more than many small bacterivores and fungivores. Thus, we introduce the community-weighted mean (CWM) of body size as a new and unbiased trait-based indicator. This is due to the fact that it normalizes the mean body size according to the abundance of nematodes in a particular genus. This weighting method is common in plant community analysis (Garnier et al., 2004; Díaz et al., 2007; Lavorel et al., 2008; Suding et al., 2008; Niu et al., 2014) but has not yet been applied to soil communities.

The objective of this study was to compare the trait-based indicator CWM of body size with total body size and abundance-based indicators, the total nematode abundance, Margalef's richness index, Shannon's diversity index, $\sum$MI and EI, for their ability to detect changes in the nematode community due to fertilization. We hypothesize the CWM of body size will be more sensitive than abundance-based indicators to changes in soil nutrient concentrations following fertilization. A secondary objective was to determine whether the trait-based and abundance-based indicators responded consistently to fertilization in a double-cropping system of paddy rice and upland wheat, which have distinctive soil moisture regimes that could provoke shifts in the nematode community structure.

2. Materials and methods

2.1. Site and experimental design

The study was conducted in Jintan city, Jiangsu Province, China (31°39′N, 119°28′E, 3 m a.s.l). This region has a subtropical monsoon climate, with a mean annual temperature of 15.3 °C and a mean annual precipitation of 1063.6 mm. The experimental site was an agricultural field that supported double-cropping of winter wheat (*Triticum aestivum* L.) and summer rice (*Oryza sativa* L.) for the past 65 years. The soil is classified as Fe-leachic-gleyic-stagnic Anthrosol with a clay loam texture (250 g clay kg^{-1} and 300 g sand kg^{-1}). Before initiating the experiment, soil analyses found 13.5 g organic C kg^{-1}, 1.6 g total N kg^{-1}, 18.0 mg available P kg^{-1}, 56.4 mg available K kg^{-1} with pH of 7.3.

The fertilization experiment was established in November 2010. Sixteen plots were randomly allocated four fertilizer treatments into four blocks (=four replicates per treatment). Every plot was 5 m × 8 m and separated by 0.15 m concrete buffers on both sides and a 1.5 m lane between blocks. The four fertilizer treatments were: an unfertilized control (CK), chemical fertilizer (CF), manure + 50% chemical fertilizer (MCF) and manure + straw + 50% chemical fertilizer (MSCF). Each year, the CF treatment received 240 kg N ha^{-1}, 120 kg P_2O_5 ha^{-1} and 100 kg K_2O ha^{-1}, while the MCF and MSCF treatments received 120 kg N ha^{-1}, 60 kg P_2O_5 ha^{-1} and 50 kg K_2O ha^{-1}, respectively. In the MSCF treatment, pig manure containing 2.3% N, 1.3% P, 1.0% K and 45.4% organic matter with moisture content of 29.1% was applied at 400 kg pig manure ha^{-1} (wet weight basis). Straw in the MSCF treatment contained 0.63% N, 0.11% P, 0.85% K, 78.6% organic matter and 33.1% moisture when applied as 18 t rice straw ha^{-1} (wet weight basis) in the wheat phase, while wheat straw with 0.52% N,