

Organic amendments increase the flow uniformity of energy across nematode food webs

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ABSTRACT

Energy dynamics within ecological communities are important in delivering ecosystem services. However, it remains elusive how the energy fluxes within soil food webs respond to agricultural fertilization regimes. Here, we studied the effects of long-term organic amendments and mineral fertilizers on the energetic structure of soil nematodes from a food-web perspective. We replicated our experiment in a rice paddy and in an upland maize cropping system. Results showed that the abundance of most trophic groups was higher in organically amended soils compared with mineral fertilizer treatments in both systems. Organic amendments, but not mineral fertilizers, increased the energy flux of total nematodes and most trophic groups compared with the no-fertilizer treatment. Furthermore, organic amendments increased the relative allocation of energy flux to microbivores but decreased the relative allocation to herbivores, supporting a higher flow uniformity than mineral fertilizers. We further found that organic amendments favored a higher total energy flux by supporting a greater nematode diversity, while sustained a higher flow uniformity by altering nematode community composition. Taken together, the result provides the evidence that a complex and species-rich community could transfer more energy to support ecosystem services. A broader perspective on linkages of biodiversity and energy dynamics spanning multitrophic groups is crucial for sustainable management, particularly in the light of non-random species loss under future environmental change.

1. Introduction

Management of agroecosystems modifies consumer-resource interactions and consequently influences the community structure and the energy fluxes through food webs (Banerjee et al., 2019; Cui et al., 2018; Richter et al., 2019). Emerging evidence suggests that an energetic food-web approach may be powerful in the assessment of ecosystem services, as energy dynamics across all trophic levels can be used to describe a range of key ecosystem processes (Barnes et al., 2018; Meehan, 2006; Moore and de Ruiter, 2012). For example, the energy flux through root herbivores is closely associated with carbon (C) transfer from living plants to the belowground food web (Gan and Wickings, 2020). Similarly, the energy flux through decomposers is typically

related to C sequestration, nutrient cycling and biological pest control (Pollierer et al., 2012; Trap et al., 2016). Despite the recent increase in research on energy dynamics across trophic networks, the focus has primarily been on soil macro- and meso-fauna in natural ecosystems (Buzhdygan et al., 2020; Potapov et al., 2019). The response of soil micro-food web energetics to agricultural management remains largely unknown.

Nematodes occupy various trophic positions in the soil micro-food web, and therefore provide an opportunity to examine the responses of community energetic patterns to agricultural managements (Wilschut and Geisen, 2021). Numerous studies have focused on nematode metabolic footprints as an energetic proxy, which has greatly improved our ability to predict ecosystem functions in agricultural and natural systems

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(Ewald et al., 2020; Zhang et al., 2017; Zhao et al., 2014). However, there are some key aspects that need to be integrated into food web energetics, such as trophic interactions, feeding preferences and metabolic efficiency (Fig. 1; Jochum et al., 2021). According to metabolic and food-web theories, the above-described aspects are tightly linked to the total energy flux and interaction strengths within soil communities, which allows for delivering more quantitative information on food-web energetics (Barnes et al., 2018; Jochum and Eisenhauer, 2021; Thakur and Geisen, 2019). Thus, quantifying energy fluxes between nematode trophic groups by incorporating the aforementioned aspects simultaneously can improve our ability to predict agroecosystem services.

Fertilization is indispensable in agricultural management to boost crop production. Previous studies have demonstrated that fertilization managements exert strong effects on soil community structure by providing C and nutrients (An et al., 2015; Cui et al., 2018; Lemanski and Scheu, 2014). For instance, incorporation of organic amendments can substantially increase the number of niche dimensions, favoring the coexistence of soil organisms (Katayama et al., 2019; van der Werf et al., 2020; Wall et al., 2015). Greater species richness and abundances are in turn expected to increase the utilization of C resources, with complementary effects on energy transfer within nematode food web (Finke and Snyder, 2008; Thorn et al., 2016). Additionally, soil nematodes are commonly characterized based on life history strategies using colonizer-persister (cp) classifications (Bongers, 1990). As taxon-specific life strategies are associated with phylogeny, feeding performance, and body size, patterns of nematode life history strategies can be used as a proxy for the energy flux and energy distribution (i.e., flow uniformity) among trophic channels (George and Lindo, 2015; Potapov et al., 2021). Opportunistic microbivores (bacterivores and fungivores) are mainly found in cp categories 1–2 which respond more quickly to the exogenous C supply than herbivores and omnivores in cp categories 3–5 (Turnbull et al., 2014; Zhang et al., 2017). It has, for example, been shown that organic fertilization results in a relatively larger increase in microbivores and a smaller increase in herbivores and omnivores (Liu et al., 2016b; Puissant et al., 2021). A disproportional increase in the abundance and biomass of microbivores could facilitate more energy flux across lower trophic levels, modifying the flow uniformity of energy through the soil food web (Malerba et al., 2018). Together, fertilization-induced shifts in soil biodiversity and community composition can steer the energetic structure (Schwarz et al., 2017) of nematode food webs simultaneously, but the relative strengths of these effects on the energy flux across trophic compartments remain uncertain.

In this study, we tested the effects of fertilization on community

composition and energetic structure of nematode food webs in two long-term agricultural field experiments in rice paddy and upland maize fields in sub-tropical China. The fertilizer treatments included mineral fertilizers, organic amendments, and a combination of mineral fertilizers and organic amendments. We hypothesized that organic amendments would increase the energy flux through soil nematodes compared to mineral fertilizers. Specifically, we expected that the allocation of energy would be relatively higher in microbivores than in herbivores and omnivores, and that the disproportional energy allocation among trophic groups would increase the flow uniformity of energy through the nematode food webs. Given that trophic complementarity could facilitate the incorporation of C into food webs (Barnes et al., 2016; Buzhdygan et al., 2020), we further hypothesized that increased energy fluxes through nematode food webs upon fertilization would be positively correlated with nematode diversity across trophic groups.

2. Material and methods

2.1. Study sites and experimental design

The long-term fertilization experiments were established in 1981 at the Jiangxi Institute of Red Soil, China (116°20'24"E, 28°15'30"N). This region has a typical subtropical climate with a mean annual rainfall of 1727 mm, of which about 38% falls from March to early July and about 14% falls from late July to early November (Liu et al., 2009). The minimum monthly mean temperature is 5.5 °C in January and the maximum monthly mean temperature is 29.9 °C in July. The annual average temperature is 15.7 °C with an average of 262 frost-free days per year. The soil was derived from quaternary red clay and is classified as ultisol with a clay-loam texture (Dai et al., 2020). Initial soil properties of the paddy and upland maize fields were: pH, 6.9 and 6; organic C, 16.3 and 9.39 g kg⁻¹; total nitrogen (N), 1.49 and 0.98 g kg⁻¹; total phosphorous (P), 0.48 and 1.42 g kg⁻¹; available P, 5.3 and 12.9 g kg⁻¹, total potassium (K), 10.4 and 15.83 g kg⁻¹; and available K, 80.5 and 102 g kg⁻¹.

Identical fertilization regimes (treatments) and arrangements focusing on the interactions between organic and mineral fertilizers were conducted in a rice paddy and in an upland maize field. These two field experiments are more than 1 km away, with the roads and associated ditches being between them. Additional information of experiment design was also described in Wan et al. (2022). Briefly, both experiments had a randomized complete block design with five treatments. For each of the two field experiments, the fertilization treatments

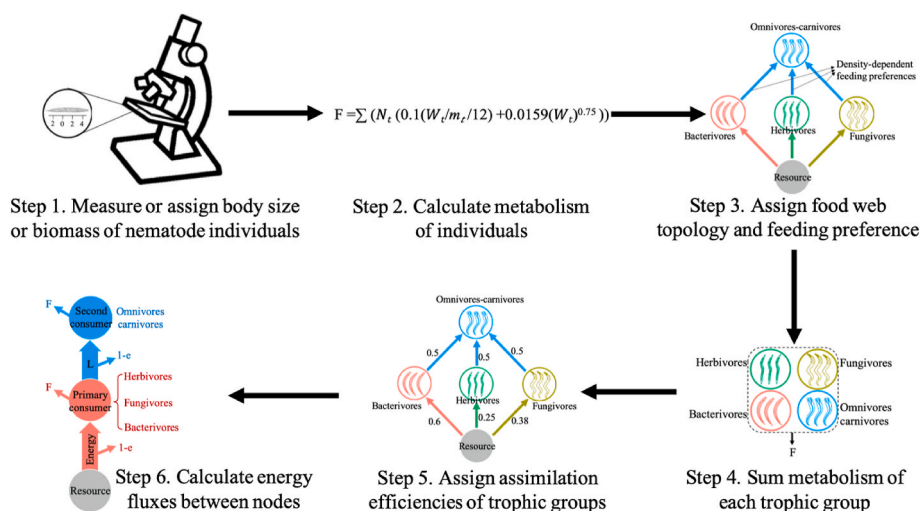


Fig. 1. Schematic diagram showing the main steps of the energy-based approach to assess the energetic structure of soil nematode communities. Step 1, the fresh biomass of each nematode individuals was calculated based on the measurement of body size or using publicly available data. Step 2, nematode metabolism (F) was then calculated according to Ferris (2010) and van den Hoogen et al. (2019), where N_t , W_t and m_t are the number of individuals, the fresh weight and the cp class of taxon t, respectively. Step 3, a five-node food web topology was constructed and the feeding preferences of omnivores-carnivores on other trophic groups was assumed according to community density. Step 4, the metabolism of each node was summed by all individual metabolism of the respective trophic group. Step 5, we used assimilation efficiencies (e_a) of 0.25 for herbivores, 0.60 for bacterivores, 0.38 for fungivores and 0.5 for omnivores-carnivores according to Barnes et al. (2014) and De Ruiter et al. (1993). Step 6, energy fluxes between nodes was calculated as follows: $F_i = (F + L)/e_a$, where L is the energy loss to higher trophic levels.

are: (1) control, no fertilizer; (2) 50% mineral fertilizers (50%NPK); (3) mineral fertilizers (NPK); (4) organic amendments (OM); (5) combined 50% mineral fertilizers and organic amendments (50%NPK + OM). Each treatment was replicated three times, i.e., three blocks, resulting in a total of 30 plots across both experiments. The area of each square plot was 22.22 m² and each plot was separated with cement barriers to avoid cross-contamination between plots. Detailed information of the doses and types of fertilizers are shown in the supporting materials (Table S1). The paddy field was planted with early rice (April to July) and late rice (July to November) cropping, and the upland field was planted with early maize (April to July) and late maize (July to November). Both cropping fields remained fallow from November until April of the next year. Crop straw residues were removed after harvest each year.

2.2. Soil sampling and measurements

We collected soil samples after the rice and maize harvest in November 2014. Nine soil cores (3.8 cm in diameter) were randomly collected from each plot at a depth of 0–20 cm, and then mixed together as one composite sample per plot. All samples were taken at least 1 m away from the cement barriers to avoid any ‘side’ effects. Each soil sample was divided into two subsamples for soil physicochemical and biological analyses. Total organic C and total N contents were determined by a modified Mebius method and the Kjeldahl digestion method, respectively (Lu, 2000). Soil pH was determined on air-dry soil samples using a ratio of 1:2.5 soil/water. Dissolved organic C (DOC) was extracted from 10.0 g fresh soil with 50 mL ultrapure water and determined using a total C analyzer (Elementar, Germany). Extractable N was calculated by the sum of NH₄⁺-N and NO₃⁻-N, which was extracted from 10 g fresh soil with 50 ml 2 M KCl and determined using a continuous flow analyzer (Skalar, Breda, the Netherlands).

2.3. Composition and diversity of nematode communities

Soil nematodes were extracted from 100 g fresh soils using modified Baermann trays following centrifugal flotation methods (Liu et al., 2008). The total number of nematodes in each sample was counted using a stereomicroscope. For each sample about 200 individuals were randomly selected and identified to genera based on morphological characteristics (Andrássy, 1983; Ahmad and Jairajpuri, 2010; Bongers, 1988; Yin, 1998). Based on feeding guilds and colonizer-persister values (*cp*), nematodes were classified into bacterivores, fungivores, herbivores and omnivores-carnivores (Yeates and Bongers, 1999). Nematode *cp* values were categorized from 1 to 5. Nematode individuals in the *cp*-1 category have a relatively short life course, while those in the *cp*-5 category have a relatively long life course. Nematode abundances were represented in numbers per 100 g dry soil. Nematode diversity (Shannon-Weiner diversity index, *H'*) was calculated using the formula: $H' = -\sum P_i \ln P_i$, where P_i is the proportion of individuals in the *i*th taxon (Shannon, 1948).

2.4. Energetic structure of nematode communities

We used network-wide metrics including total biomass and total energy flux of trophic groups in a micro-food web model to present the energetic structure of nematode communities (Fig. 1). The average fresh biomass for a given taxon was calculated using publicly available data (<http://nemaplex.ucdavis.edu/Ecology/EcophysiologyParms/EcoParameterMenu.htm>). Nematode *cp* values were used to normalize the amount of C partitioned into production per unit life course (Ferris, 2010). We first multiplied the average biomass of a specific taxon with the predicted number of individuals. The component of C partitioned into production (P_C) of individuals was calculated by assuming a dry weight of 20% of the fresh biomass and a C content of 52% of the dry weight (Mulder et al., 2005). We assumed that life-cycle duration of soil nematodes in days can be approximated as 12 times the *cp* scale (van den

Hoogen et al., 2019), and we calculated the total P_C values per day using the formula

$$P_C = \sum (N_i (0.1(W_i / m_i / 12))) \quad (1)$$

where N_i , W_i and m_i are, respectively, the number of individuals, the body weight, and the *cp* values of taxon *t*.

According to the allometric power dependence of metabolism and body size of soil organisms, respiration rate of nematode individual decreases with the increases of body weight (West et al., 1997). The total C used in respiration (R_C) of soil nematodes was calculated as follows:

$$R_C = \sum (N_i (a(W_i^b))) \quad (2)$$

where *b* is close to 0.75 according to Atkinson (1980), *a* is equal to the relative molecular weights of C and O in CO₂ (12/44 = 0.273). According to the literature, we used a coefficient of 0.058 to further convert the value of *a* to estimate C respiration in µg per day (Klekowski et al., 1972).

The energy flux of nematodes (F , µg C 100 g⁻¹ dry soil day⁻¹) is sum of the components of production and respiration (Ferris, 2010; van den Hoogen et al., 2019)

$$F = \sum (N_i (0.1(W_i / m_i / 12) + 0.0159(W_i^{0.75}))) \quad (3)$$

where N_i , W_i and m_i are, respectively, the number of individuals, the body weight, and the *cp* values of taxon *t*. We calculated the C flux to each node by taking into account the assimilation efficiency (e_a) and energy loss (L) to higher trophic levels (Barnes et al., 2014; Cui et al., 2018; Jochum et al., 2017). We assumed that,

$$F_i = (F + L) / e_a \quad (4)$$

Where F_i is the potential C flux calculated based on the biomass of nematode trophic group *i*, L is the energy loss to higher trophic levels, and e_a is the assimilation efficiency which defines the proportion of food uptake for respiration and production (Jochum et al., 2017). We used nematode assimilation efficiencies of 0.25 for herbivores, 0.60 for bacterivores, 0.38 for fungivores and 0.5 for omnivores-carnivores (Barnes et al., 2014; De Ruiter et al., 1993). We first calculated the energy flux through the omnivores-carnivores. This calculation of energy metabolism did not involve energetic losses to higher trophic levels but specifically aimed to assess nematode energetic demands (F_o). We assumed that omnivores-carnivores have the same feeding preference, and that their feeding preference for other trophic groups depended on community density (Cui et al., 2018). Subsequently, we calculated the energy loss of herbivores, bacterivores and fungivores to omnivores-carnivores as follows:

$$L = D_{io} \times F_o \quad (5)$$

where D_{io} is the density-dependent feeding preference of omnivores-carnivores for trophic group *i*, which was assigned according to their proportional abundance.

Further, the flow uniformity of energy in the nematode food web (unitless) was calculated as the ratio of the mean of summed energy fluxes through each energy channel to the standard deviation of these mean values (Buzhdygan et al., 2020). This metric indicates the energy distribution of different channels in nematode food webs.

2.5. Data analysis

All statistical analyses and figures were performed using R software, version 4.0.0 (R Core Team, 2020). All data were tested for normality using Kolmogorov-Smirnov tests and equality of error variances were tested using Levene's test. First, a Poisson generalized linear model (GLM) was used to analyze the fertilization effects on nematode

abundance. One-way analysis of variance (ANOVA) was used to test the fertilization effects on other response variables including the diversity, biomass and energy flux of nematode and trophic groups. For significant ($p < 0.05$) treatment effects, a post hoc least significant difference test was carried out to compare differences among fertilization treatments. Energetic structure of nematode food webs was visualized as a micro-food web model to present network-wide metrics (including biomass, energy flux and flow uniformity) using the *igraph* package (Gauzens et al., 2019). Edge width and node size in network-wide metrics were scaled by the mean of all fluxes to consumers and their biomasses, respectively. A partial least squares path model (PLS-PM) was conducted to further infer potential direct and indirect effects of fertilization, soil C and N (SOC, total N, DOC, and extractable N), soil environment (pH and moisture), root biomass, and nematode diversity and community composition on the flow uniformity and total energy flux using the *pls* package (Sanchez, 2013). Nematode composition was used as a latent variable, reflecting the relative abundance of each trophic group. The goodness of fit of the PLS-PM was evaluated by examining the Goodness-of-Fit index and the coefficient of determination (R^2) of the latent variables, an acceptable model should have a Goodness-of-Fit value > 0.7 (Sanchez, 2013). Further, to test the relationships between nematode diversity and energy flux or flow uniformity, we performed linear regression analyses using *vegan* package (Oksanen et al., 2020).

3. Results

3.1. Effects of fertilization on nematode abundance and diversity

Herbivores and bacterivores were most dominant trophic groups in terms of nematode abundance in both agroecosystems. Organically amended soils (OM and 50%NPK + OM) supported higher abundance of nematodes trophic groups (except herbivores) than no fertilizer treatment, while mineral fertilizer treatments (50%NPK and NPK) did not affect nematode abundance in both fields (Fig. 2, Table S2). Organic amendments increased the diversity of bacterivores and omnivores-carnivores compared with no fertilizer treatment in the upland field ($p < 0.05$; Fig. 2, Table S3).

3.2. Effects of fertilization on the energetic structure of nematode communities

Organic amendments increased the total energy flux through soil

nematodes compared with no fertilizer treatment ($p < 0.05$; Fig. 3a, Table S4), and the inconsistent effects on trophic groups clearly modified the energy distribution of nematode communities (Figs. 3b and 4). Compared with no fertilizer treatment, organic amendments increased the energy flux through bacterivores, fungivores and omnivores-carnivores in both fields, and increased the energy flux through herbivores in the paddy field. The energy flux through fungivores was higher under 50%NPK + OM than OM treatment in the paddy field. The energy flux of bacterivores was similar between OM and 50%NPK + OM treatments, but much higher in the treatments with OM than the other treatments. Organically amended soils supported a relatively lower energy of herbivores and a relatively higher energy of microbivores than mineral fertilizer treatment in both fields (Fig. 3c).

In both agroecosystems, omnivores-carnivores had the greatest biomass compared with other trophic groups (Fig. 4 and Fig. S1). Organic amendments increased the biomass of all trophic groups compared with no fertilizer treatment and mineral fertilizer treatments in the paddy field (Fig. 4). However, in the upland field, organic amendments only increased the biomass of bacterivores and omnivores-carnivores compared to no fertilizer treatment (Fig. 4). Organic amendments increased the energy flux from resources to bacterivores and fungivores, and from these lower trophic groups to higher trophic groups (i.e., omnivores-carnivores) compared with other treatments in both fields, but the energy flux from resources to herbivores only increased in the paddy field (Fig. 4). The flow uniformity of nematode energetic structure was highest in 50%NPK + OM treatment in the paddy field, and highest in OM treatment in the upland field (Fig. 4).

3.3. Quantitative examination of the effects of fertilization on the energy flux and flow uniformity of nematode communities

In the paddy field, the PLS-PM model explained 93% of the variation in flow uniformity and 24% of the variation in total energy flux, respectively (Fig. 5a). Similarly, in the upland field, the PLS-PM model explained 85% of the variation in flow uniformity and 21% of the variation in total energy flux, respectively (Fig. 5c). Fertilization-induced changes in soil carbon and nitrogen (SOC, total N, DOC and extractable N) were positively correlated with nematode diversity and trophic group composition. The flow uniformity was strongly related to trophic group composition, which exerted a highest positive effect among all variables in the paddy and upland fields (Fig. 5a–d). Furthermore, nematode diversity was positively related to total energy flux, and the standardized total effects on total energy flux were

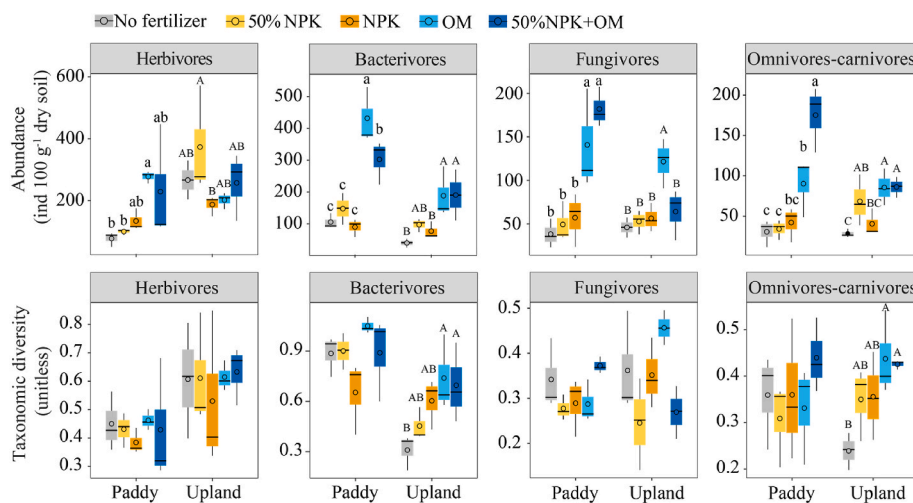


Fig. 2. Effects of long-term fertilization on the abundance (a) and taxonomic diversity (b) of soil nematodes in the rice paddy and upland maize field. Box plots represent the lower quartile, median and upper quartile values. Black lines and circles in the boxes represent median and mean values of all variables. Different letters above the boxes indicate values that differ significantly among treatments at $p < 0.05$ (LSD's test) in paddy (a, b, c) and upland (A, B, C) fields.

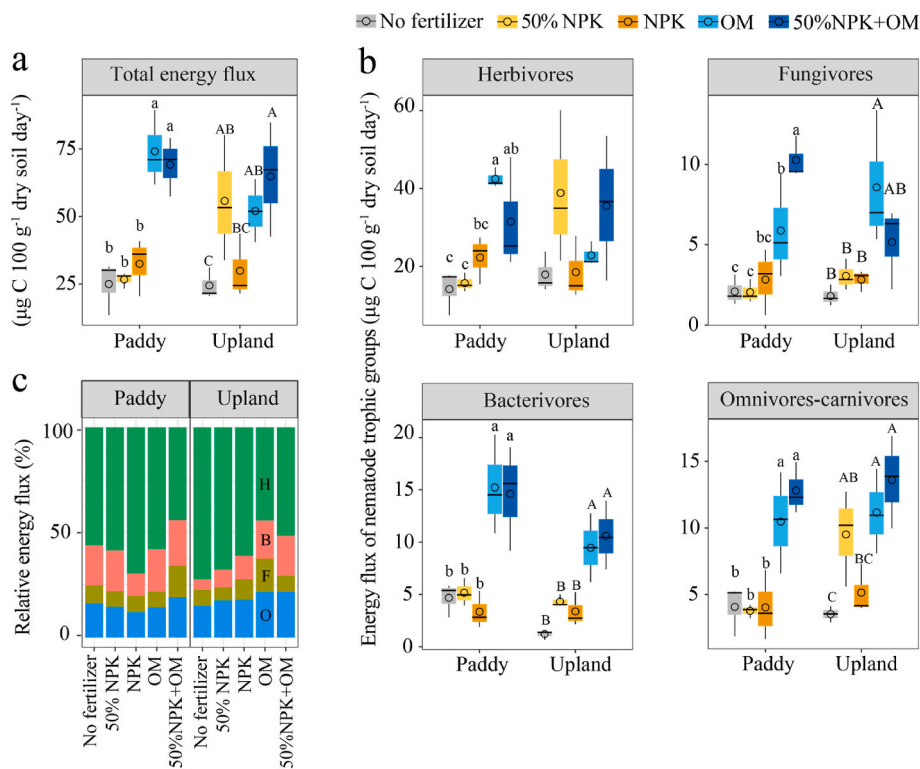


Fig. 3. Effects of long-term fertilization on the energy flux through soil nematodes (a) and through each trophic group (b) and the relative contributions of trophic groups (H, herbivores; B, bacterivores; F, fungivores; O, omnivores-carnivores) to the whole-community energy flux (c) in the rice paddy and upland maize field. Box plots represent the lower quartile, median and upper quartile values. Black lines and circles in the boxes represent median and mean values of all variables. Different letters above the boxes indicate values that differ significantly among treatments at $p < 0.05$ (LSD's test) in paddy (a, b, c) and upland (A, B, C) fields.

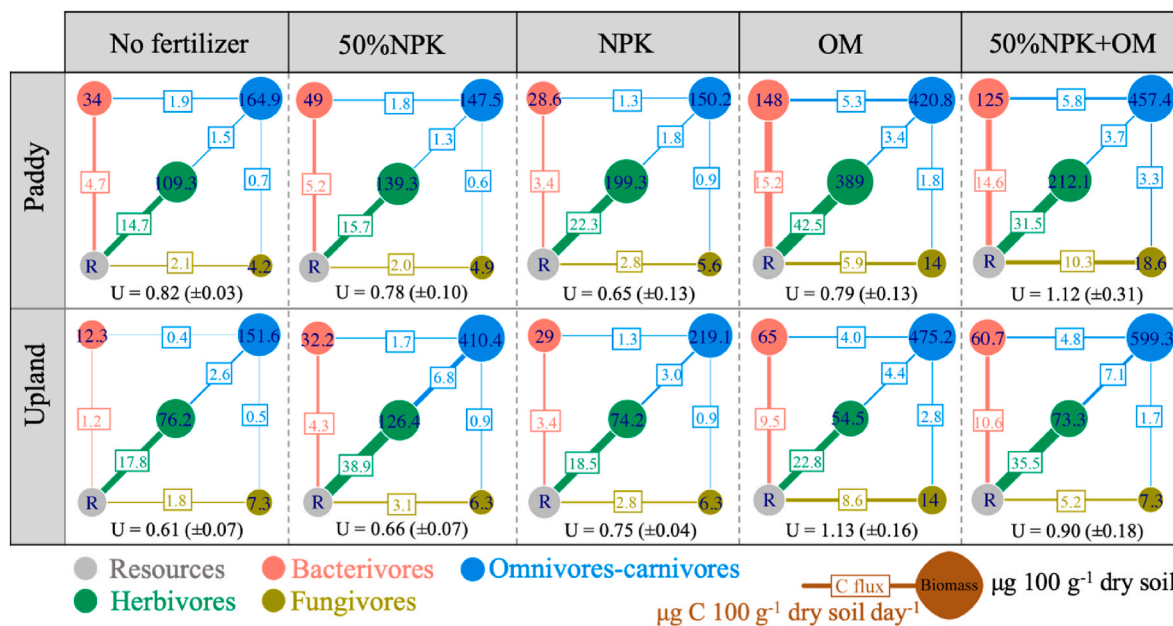


Fig. 4. Effects of long-term fertilization on the energetic structure of nematode communities in the rice paddy and upland maize field. For each fertilization treatment, a five-node food web was constructed with bacterivores (red), fungivores (yellow) and herbivores (green) receiving energy from basal resources (R), omnivores-carnivores (blue) receiving energy from other nodes. Numbers along the lines represented energy flux ($\mu\text{g C } 100 \text{ g}^{-1} \text{ dry soil day}^{-1}$). The size of nodes corresponds to the fresh biomass ($\mu\text{g } 100 \text{ g}^{-1} \text{ dry soil}$). Uniformity (U) of soil nematode energetic structure (unitless, mean \pm standard error) was calculated as the ratio of the mean of summed energy flux through each energy channel to the standard deviation of these mean values. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

primarily resulted from soil carbon and nitrogen, and nematode diversity in both fields (Fig. 5a–d).

The regression analyses showed that nematode diversity was positively related to total energy flux and flow uniformity, and these positive relationships were also found in each nematode trophic group

(Fig. 6a–c). The slopes between the diversity of herbivores, bacterivores or fungivores and energy flux were steeper in the paddy (53.7, 19.2 and 31.8, respectively) than in the upland (50.4, 15.7 and 14.8, respectively) fields, while the slope between diversity of omnivores-carnivores and energy flux was steeper in the upland (38.1) than in the paddy (24.6)

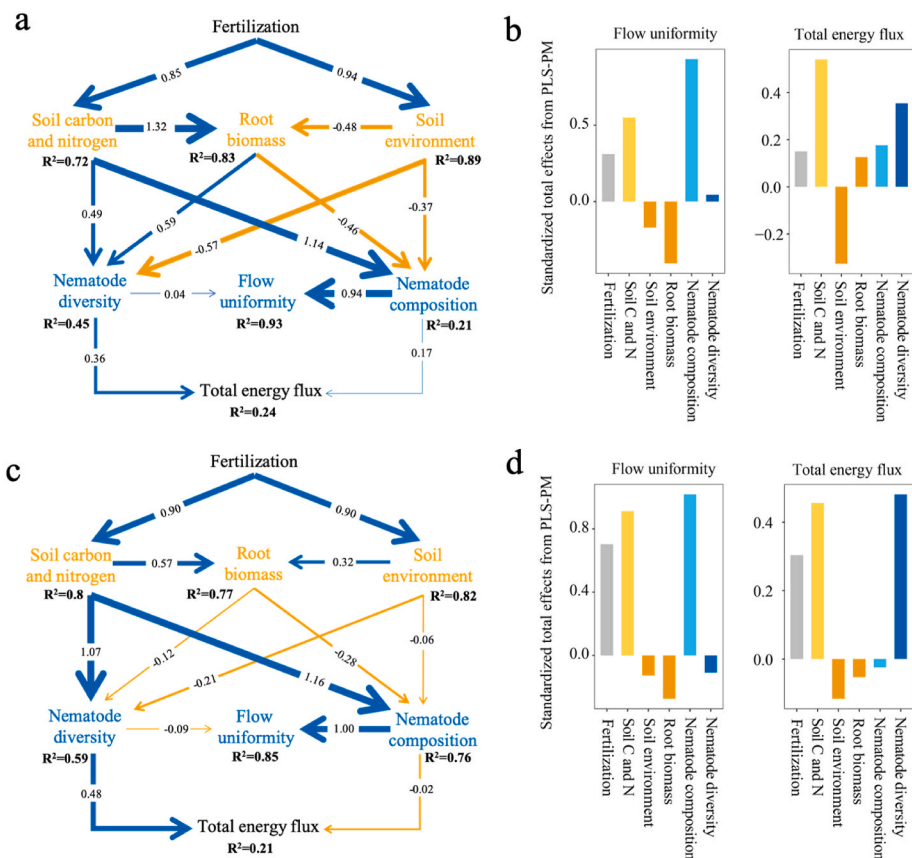


Fig. 5. Partial least squares path models (PLS-PM) depicting the direct and indirect effects of long-term fertilization, soil carbon and nitrogen, soil environment (pH, moisture), root biomass, nematode diversity, and nematode composition on the flow uniformity and the total energy flux and standardized total effects in the rice paddy (a, b; Goodness-of-Fit = 0.75) and upland maize (c, d; Goodness-of-Fit = 0.73) field. Nematode composition was used as a latent variable, reflecting the relative abundance of each trophic group. The R^2 values indicate the proportion of variance explained. Arrow thickness were scaled proportionally to the standardized path coefficients (numbers on arrows). Solid blue and yellow arrows indicate positive and negative relationships respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

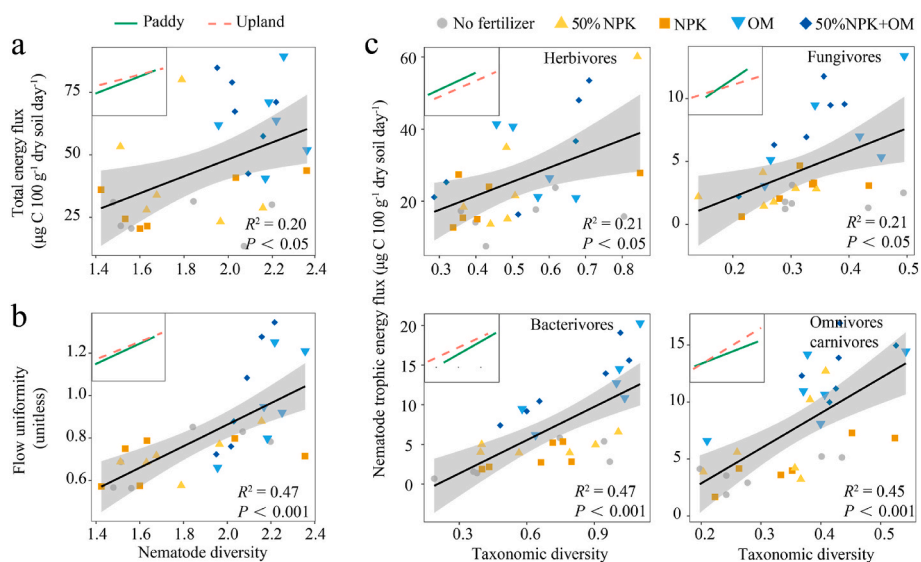


Fig. 6. Relationships between nematode diversity and total energy flux (a) or energy uniformity (b) of nematode communities. Relationships between the diversity and the corresponding energy flux of nematode trophic groups (c). Black lines denote overall model fits and colored lines indicate different land-use systems (rice paddy, upland maize field).

field (Fig. 6a and c).

4. Discussion

Organic amendments boosted nematode abundance and supported a higher diversity of multiple trophic groups than mineral fertilizer treatments, suggesting that soil nematodes particularly free-living

bacterivores and omnivore-carnivores benefit from exogenous organic amendments (Puissant et al., 2021). We propose several mechanisms to explain the positive effects of organic fertilizers on soil nematode abundance and diversity. First, organic matter may provide broader resource niches (Börjesson et al., 2012; Vazquez et al., 2019) as well as better soil habitats (e.g., well-developed aggregation and porosity network) for the soil biota (Erktan et al., 2020; Wall et al., 2012;

Yazdanpanah et al., 2016). Besides, organic fertilization can increase the top-down forces, which could further enhance species diversity via regulating the competitively superior prey species (Conti et al., 2020; Karakoç et al., 2020; Thakur and Geisen, 2019), and favor certain nematodes from competitive interactions (Schmidt et al., 2019; Zhou and Ning, 2017). For example, the larger-bodied predators (e.g., predatory nematodes and mites) could induce greater diversification rates and promote the coexistence of prey species (Schwarz Müller et al., 2015), as they could feed on a wide size range of prey and thus encourage the number of interactions (Brose, 2010; Brose et al., 2019). Furthermore, biodiversity change is non-randomly driven by environmental filtering but associated with species traits, another plausible explanation might come from the divergent traits of species such as trophic level and body size, and interaction partners (Hines et al., 2015; Mulder and Maas, 2017; Quist et al., 2019). For instance, bacterivores and omnivores-carnivores would be facilitated by increasing soil pH and adequate aeration (Quist et al., 2019; Vestergård et al., 2018). Overall, our results support current opinions that soil food web structure is simultaneously regulated by both bottom-up and top-down forces mediated by agriculture management and climate change (Thakur and Geisen, 2019). However, the direction and strength of biotic interactions are likely to change under different environmental conditions. Future research needs to consider joint species distribution models to untangle these complex processes at broad spatial scales (Pollock et al., 2014).

As we hypothesized, organic amendments increased the total energy flux through soil nematodes than mineral fertilizer treatments. Long-term mineral fertilizer treatments resulted in carbon limitation and decreased substrate use efficiency of soil microbial community, which may switch active soil microbes to a dormant state (Fontaine et al., 2003; Xiao et al., 2021). These changes may lead to less carbon transferring from soil microbes to nematodes, resulting in a decrease in the energy flux of nematodes under mineral fertilizer scenarios. Given plant root biomass was higher under organically amended soils than mineral fertilizer treatments in the present study, the dual supply of carbon resources from organic amendments and plant roots are expected to foster energy (C) utilization of soil communities via both the detrital-based and primary producer-based energy channels (Scharroba et al., 2012). Our results were consistent with the outcome of carbon stable isotope signature of Cui et al. (2018), who observed that manure increased the utilization of exogenous carbon resource by soil micro-food web as well as increased the biomass of soil microbes and nematodes compared with mineral fertilizer treatments. The present work suggests that organic amendments have a higher potential for carbon sequestration than the soils receiving mineral fertilizers due to high net flux of microbial biomass formation.

Fertilization effects on energy flux were largely driven by the diversity of nematode trophic groups, supporting our second hypothesis. This is because a greater richness of soil invertebrates generally has a higher energetic demand (Barnes et al., 2016), which facilitates higher energy flux and a more even energy distribution across the entire food webs via increasing trophic complementarity (Barnes et al., 2018; Buzhdygan et al., 2020). Additionally, as same as the previous analysis of nature system, the positive linkages between species diversity and energy fluxes within food webs depend on land-use systems and trophic groups (Barnes et al., 2014; Potapov et al., 2019). Our results also revealed that species loss proportionately resulted in higher energy losses of soil nematodes in the paddy field, compared with equal species losses in the upland field. The result suggests that biodiversity conservation in relatively nutrient-rich systems (e.g., paddy field) may be more urgent for ecosystem processes than in nutrient-poor systems (e.g., upland field) due to the lower functional redundancy. Furthermore, different effects of diversity on energy flux between microbivores and omnivores-carnivores indicated that trophic levels jointly increased the performance of the community, highlighting the importance of multi-trophic complementarity on ecosystem functioning.

Organic amendments increased the relative energy of microbivores

and decreased the relative energy of herbivores in both fields, leading to an increase in the flow uniformity of energy flux through soil nematodes. One possible reason is that the rapid growth of gram-negative bacteria in N-rich (such as animal manures) treatments produces inhibitory substances that are more effective in controlling herbivores (Liu et al., 2016a; Oka, 2010). Divergent energy distribution among nematode trophic groups also suggested that the energetic food webs were susceptible to fertilization practices (Lemanski and Scheu, 2014). Compared with the upland soil, the paddy habitats supported a greater total energy flux through microbivores (bacterivores and fungivores) under organically amended soil than mineral fertilizer treatments, possibly because a greater organic subsidy in the paddy soil transformed more food resources from microbes to microbivores (Chen et al., 2021). Although total energy flux through microbivores was similar between organic amendment (OM) and incorporation with mineral fertilizers (50%NPK + OM), the energy allometric scaling of bacterivores and fungivores was found in both fields. A carbon dynamic balance between bacterivores and fungivores is accompanied with large inputs of labile carbon from organic amendments (Cui et al., 2018; Ruess and Ferris, 2004), suggesting that the energy distribution within food webs had been optimized via avoiding competition over resources (Moore et al., 2005; Poisot et al., 2013). In light of the energy distributions (which also represent interaction strengths) determine the stability of food webs (Rip and Mccann, 2011; Schwarz et al., 2017), our evidence further reinforces the critical roles of considering multitrophic energy dynamics in contributing to ecosystem stability (Buzhdygan et al., 2020; Potapov et al., 2021; Wan et al., 2022).

5. Conclusions

By taking a food-web energetics approach, our study demonstrates that organic amendments support higher energy flux and flow uniformity within nematode food webs. The increased energy flux within species-rich food webs proves that more exogenous carbon is accumulated by soil community, highlighting potential feedbacks of the ongoing decline in global biodiversity on soil carbon sequestration. Given the importance of the energy fluxes within ecological networks being increasingly acknowledged worldwide, our results raise new concerns about whether the observed changes in energy fluxes across soil food webs might explain the variation in multiple ecosystem services, and their relative contributions (Wan et al., 2022). Future work of the holistic analysis in food web energy structure is needed, synthesizing other dimensions of biodiversity in complex systems, to disentangle potential mechanisms in driving ecosystem multifunctionality.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2022.108695>.

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