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Advancements in assessing soil health through functional traits and energy flow analysis of soil nematodes

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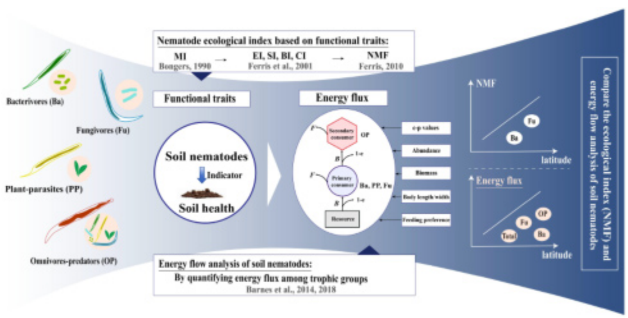
ABSTRACT

• We examined the development of soil nematodes ecological indices from the perspective of functional traits.

• We found that soil nematode energy flow analyses based on multiple functional traits quantify the dynamics of energy flow across multiple-trophic levels to provide a more comprehensive perspective.

• We conducted comparative analyses of the sensitivities of NMF and energy flow to verify that the energy flow analyses are more sensitive and have greater potential to reveal soil health and ecosystem function.

• Future in-depth studies of functional traits and energy flow analysis can help us achieve informed soil management practices, sustainable agriculture, and healthier soil ecosystems.



This paper examines the development of ecological indices for soil nematodes from the perspective of functional traits. It emphasizes the increasing significance of integrating multiple functional traits to achieve a more accurate assessment of soil health. Ecological indices based on life history strategies, feeding habits, and body size provide useful tools for assessing soil health. However, these indices do not fully capture the dynamics of energy flow across multiple-trophic levels in the soil food web, which is critical for a deeper understanding of the intrinsic properties of soil health. By combining functional traits such as functional group, body size, feeding preference and metabolic rate, nematode energy flow analyses provide a more comprehensive perspective. This approach establishes a direct correlation between changes in the morphology, physiology, and metabolism of soil organisms and alterations in their habitat environment. We conducted comparative analyses of the sensitivity of nematode metabolic footprints and energy flow to latitudinal variation using a nematode dataset from the northeastern black soil region in China. The findings suggest that energy flow analyses are more sensitive to latitude and have greater potential to reveal soil health and ecosystem function. Therefore, future research should prioritize the development of automated and efficient methods for analyzing nematode traits. This will enhance the application of energy flow analyses in nematode food webs and support the development of sustainable soil management and agricultural practices.

Keywords soil nematodes, soil health, nematode food web, functional traits, energy flux

1 Introduction

Soil health represents the capacity of soil to function as a vital living system, predominantly mediated by biological processes. Biological indicators, therefore, are of paramount importance in monitoring soil health (Dose et al., 2015; Lu et al., 2020). Among various biological indicators for soil health assessment, soil nematodes stand out due to their sensitivity to environmental changes and unique advantages

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in characterization (Mulder et al., 2005; Griffiths et al., 2016; Biswal, 2022; Martin et al., 2022). These advantages include their wide distribution across different soil ecosystems (Powers et al., 1995; Porazinska et al., 2012; Kerfahi et al., 2016); their transparent body structure which facilitates observation (Bongers and Ferris, 1999); and their occupation of various trophic levels within the soil food web, allowing for the provision of comprehensive and precise ecological information (Yeates and Bongers, 1999; van den Hoogen et al., 2019; Potapov et al., 2021).

When assessing soil health through soil nematodes, researchers initially extract nematodes from soil samples and then identify them using either morphological or molecular methods (Seesao et al., 2017). This identification is followed by a comprehensive analysis of nematodes, focusing on two primary aspects: diversity and functionality. Diversity analysis leverages indices such as the Shannon-Wiener index and Simpson's index (Li et al., 2020) to evaluate the taxa diversity, abundance and community composition. Additionally, researchers employ community ecological analysis methods like non-metric multidimensional scaling analysis (NMDS) and principal component analysis (PCA) (Wilschut et al., 2019; Martin and Sprunger, 2022), which are pivotal for comparing nematode community composition and elucidating their relationships with soil environmental factors.

Nematode functional analysis focuses on the assessment of functional traits, which include morphological, physiological and life history attributes that influence fitness through their impact on growth, reproduction and survival (Violle et al., 2007; Sechi et al., 2018; Zhang et al., 2024). This approach is increasingly recognised for its sensitivity in detecting changes in soil health beyond what nematode diversity analyses can reveal (Violle et al., 2007; Sechi et al., 2018; Zhang et al., 2024). Hou et al. (2023) observed notable changes in nematode functional traits, such as body width, stylet length, and oesophagus length, with no substantial shifts in nematode taxonomic diversity indices following eight years of nitrogen (N) fertilizer application in grassland ecosystems. These changes indicate an enhanced impact of plant-parasitic nematodes on these ecosystems and underscore the vital role of free-living nematodes in soil N cycling. The superior accuracy of functional trait analysis over conventional diversity analysis is evident in reflecting the nuanced structural or functional alterations within soil ecosystems due to environmental changes (Cesarz et al., 2015).

Nematode functional traits include colonizer-persistor (c-p) values, feeding habits, body size, and the lengths of stylet, oesophagus and intestine (Hou et al., 2023). Body size, in particular, has emerged as a key functional trait and successfully applied to study various ecological factors like fertilization, precipitation, grazing and land use management (Liu et al., 2015; Mulder and Maas, 2017; Andriuzzi et al., 2020; Ma et al., 2024). Moreover, studies that combine multiple functional traits of nematodes can yield more comprehensive insights. Xue et al. (2023) revealed that nematode functional traits, including body length, body weight, and life history strategies, vary with phosphorus levels in the environment which affect gene expression. Knowledge of these traits offer a better understanding of nematode ecological strategies and their implications for soil health.

In order to more accurately assess soil health in the context of global change, Zhang et al. (2024) recently introduced the concept of nematode economics spectrum by integrating multiple functional traits. However, a broader collection of functional traits may pose challenges in identifying core functional traits and accurately reflect nematode ecological strategies at the individual and community levels. Indeed, nematode ecological indices, which are commonly used to evaluate soil health, have been developed based on these functional traits (Vonk et al., 2013; Du Preez et al., 2022). These indices can assist in explaining the response of key functional traits to environmental changes. The maturity index (MI), for example, is based on the development of life history traits (Bongers, 1990). Furthermore, a new trend involves combining various functional traits of individual nematodes with the food web energy approach. This offers a novel method for assessing soil health in terms of energy fluxes within the food web (Barnes et al., 2018; Potapov et al., 2019; Wan et al., 2022a,b; Zheng et al., 2023). This innovative perspective on energy fluxes not only merges key functional traits of nematode at the individual level with those at the community level, but also provides new insights into the structure and service functions of soil food webs.

To better illustrate the contribution of soil nematodes in indicating soil health status and their potential for further assessment, this paper summarizes current research on soil nematodes on the assessment of soil health highlighting functional trait-based ecological indices and energy flow analysis methods. Our objective is to assess the potential and future directions of energy flow analysis in nematode food webs, which will contribute to a better understanding of the vital role of soil nematodes in soil health.

2 Development of soil nematode ecological indices based on functional traits

Many studies describe nematode ecological indices in chronological order, but rarely examine the evolution of nematode ecological indices from the perspective of nematode functional traits. The evolution of nematode ecological indices is closely related to the ecologists' deepening understanding of nematode functional traits (see Fig. 1). Firstly, Bongers proposed MI in 1990, followed by Ferris et al. in 2001, who proposed the structure and enrichment index based on life history strategies and functional guilds with feeding habits. Over the last decade, the nematode metabolic footprint, proposed by Ferris in 2010, has become the most widely used. This index integrates life history strategies, feeding habits, and body size. Clearly, the main trend in the development of nematode ecological indices is to incorporate more functional traits to achieve a comprehensive assessment of soil health. In order to gain a better understanding of these ecological indices and their link to soil health assessment, the development, strengths, and weaknesses of each ecological index were discussed in detail below.

2.1 Based on life history strategies: c-p values and the maturity index

Near the end of 1980s, Bongers (1990) proposed a nematode maturity index (MI) based on reproductive rates and resource availability. He classified soil nematodes into five groups, ranging from colonizers (c-p 1), which reproduce quickly in nutrient-rich environments, to persisters (c-p 5), which are larger, longer-lived and slower to respond to food availability. This classification from life history strategies led to the creation of MI, which is useful for assessing the evolution and recovery of soil ecosystems in response to external disturbances (Bongers, 1990,1999; Bongers et al., 1997). However, the predictive capability of MI varies across wetland, forest, and agricultural soil ecosystems, as shown by Neher et al. (2005). A notable limitation of MI is that it overlooks differences in nematodes' feeding habits within the same c-p categories and the body size variation. For example, *Cephalobidae* which feed on bacteria, and *Aphelenchiods* which feed on fungi, have the identical c-p values but different feeding habits. Furthermore, nematodes classified in the higher c-p classes (c-p 4 and 5) may have a larger body size than those in the intermediate c-p classes (c-p 2 and 3) (Vonk et al., 2013).

2.2 Based on life history strategies and feeding habits: Functional guilds and related ecological index

Further developing the field, Ferris et al. in 2001 categorized nematodes into functional guilds based on their life history strategies and feeding habits. This categorization grouped nematodes that exhibit similar responses to nutrient enrichment and environmental disturbances within the soil food web. Subsequently, the nematode community was divided into enrichment (e), structural (s) and basic (b) components, leading to the creation of ecological indices such as enrichment index (EI), structure index (SI), basic index (BI) and channel index (CI). These indices were designed to provide a more nuanced depiction of the structure and functionality of the soil food web (Ferris et al., 2001). DuPont et al. (2009) used the changes in these indices to assess the distribution of soil resources and energy channels, and successfully explained the effects of cover crop quality and quantity on nematode-based soil food webs and nutrient cycling. However, these indices primarily focus on the relative proportion of nematodes and do not reflect the absolute proportion in a sample. Meanwhile, multiple nematode genera with similar functional traits will be attributed to the same c-p values and thereby generate similar EI and SI values (Ferris, 2010).

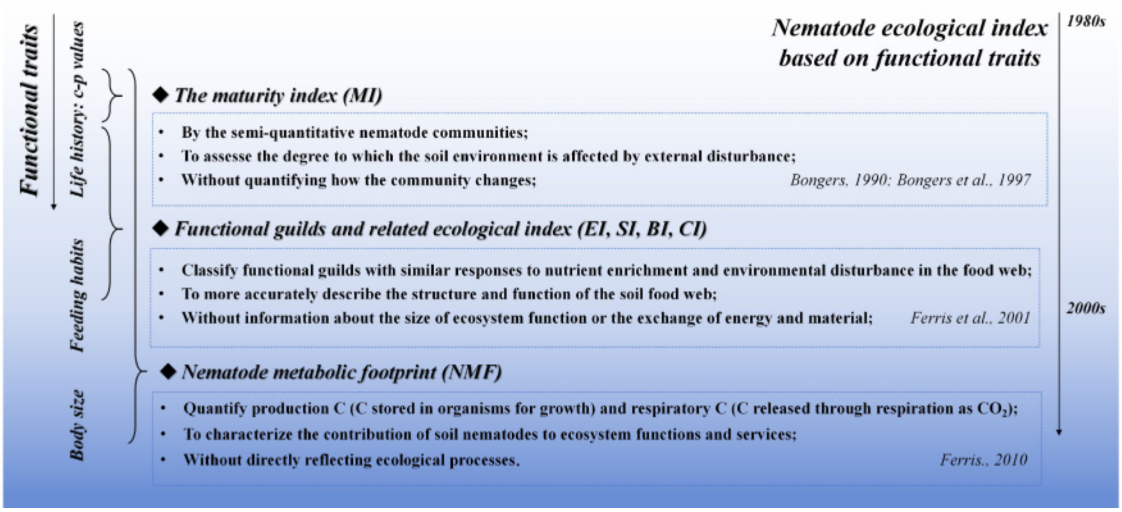

Fig. 1 A simplified history and diversification of soil nematode ecological indices based on functional traits. The left parenthesis indicates the functional traits on which each ecological index is based. The direction of the arrows on the right corresponds to the temporal sequence of the index.

2.3 Based on life history strategies, feeding habits and body size: Nematode metabolic footprint

Expanding on these indices, Ferris developed the nematode metabolic footprint (NMF) in 2010, using carbon (C) as a metric for assessing the response of nematodes to resource distribution (Ferris, 2010; the formula is shown below in Section 3). This approach takes into account the nematode life history strategies, feeding habits and body size (body length and width used to calculate biomass). NMF can effectively measure two key aspects: the C stored for growth (production C) and the C emitted via respiration (respiratory C). Thereby it can offer a valuable tool for tracking resource availability and gauging nematodes' contributions to ecosystem services and functionalities (Ferris et al., 2012; van den Hoogen et al., 2019; Zhang et al., 2019; Ewald et al., 2020). Zhang et al. (2015) used NMF to analyze of the C dynamics of soil nematode community in differently-aged temperate forests. They found that NMF indicated not only the response of the nematode assemblage to resources, but also the functions and services provided by nematodes. However, the NMF does not take into account the foraging behaviour of predatory and/or omnivorous nematodes at the highest trophic level towards other nematodes at the lower trophic levels (e.g., feeding preferences), and therefore fails to capture the dynamics of energy and C flows across multiple trophic levels within the soil food web. This limitation is crucial, as these dynamics are key to assessing the intrinsic "sustainability" of soil health (Barnes et al., 2018).

3 Food web energy flow analysis: links ecosystem traits with soil food web energy flow

Simply describing the energy state does not meet the need for a dynamic description of soil health. A comprehensive approach is needed that is capable of analyzing the full spectrum of energy flow throughout the food web. In this context, the importance of food web energy flow analysis becomes particularly apparent. Energy flow analysis relies on the energy transfer mechanisms of food webs by quantifying energy flux across various trophic levels (Barnes et al., 2018; Jochum et al., 2021; Jochum and Eisenhauer, 2022). This process involves the construction of a food web energy flow model to estimate the exchange of matter and energy between nodes in the food web. Therefore, the development of accurate food web energy flow models is essential for understanding the functioning of soil ecosystems and maintaining their health.

Notable works were conducted by Hunt (1987) and De Ruiter et al. (1993). They used soil food web energy model to estimate C and N mineralization rates for each trophic group and to simulate population dynamics and trophic interactions (predation relationships). Their efforts were aimed at elucidating the relationship between energy and/or nutrient flux in food webs and their service function (Hunt et al., 1987; De Ruite et al., 1993). The soil food web energy model operates on the steady-state assumption that the energy input to the food web is equal to the energy output over a given period of time. The method calculates energy fluxes between the trophic groups by estimating biomass stocks, production and predation efficiencies, and natural mortality rates.

The soil food web energy model relies on tracking population dynamics over time for accurate calculations, focusing primarily on biomass stocks. However, it does not account for the significant variation in metabolic activity, and hence energy conversion rates, within these biomass pools (Barnes et al., 2014). To overcome these shortcomings, Barnes et al. (2014) refined the methodology by incorporating individual metabolic requirements, taking into account body size, phylogeny differences, and the influences of temperature on metabolic rate, into the assessment of energy flow through network nodes (Gillooly et al., 2001; Lang et al., 2017). The refined approach to measuring community-wide energy flux captures not only biomass but also key ecosystem attributes, providing a richer, more holistic view of community dynamics based on functional traits (e.g., feeding habits, body size and metabolism) and temperature effects (Barnes et al., 2018). This enhancement aids in a deeper understanding of food web energy flow and illustrates the links between functional traits and environmental changes (Jochum and Eisenhauer, 2022). For example, Schwarz et al. (2017) investigated how warming, alongside canopy disturbance and drought, influences energy fluxes, thereby facilitating assessment of the resilience of soil food webs in boreal-temperate ecotones.

Analyzing energy flow throughout the entire soil food web is a large and time-consuming task, although it can provide a more precise picture of soil health. Soil nematodes are a key node connecting energy transfer between soil microbes and soil other fauna. Energy flow studies in soil nematode food webs provide a means of gaining insight into the energy flow throughout the entire soil food web. This approach goes beyond traditional assessment methods based on estimates of biomass and metabolic activity, such as the nematode metabolic footprint (NMF) (Zhao et al., 2021; Wan et al., 2022a, 2022b). Energy flow analyses that consider multiple functional traits, allow us not only to pay close attention to the soil organisms themselves, but also to link the changing characteristics of these organisms, such as morphology, physiology, and metabolism, directly to changes in their environment. This further reinforces the ability to use soil nematodes as a bio-indicator for assessing soil health.

To validate the effectiveness of the energy flow analysis method in assessing changes in soil food webs and facilitating the assessment of soil health, we used the specific nematode data to calculate the energy flow within nematode food webs using the energy flow analysis method. In addition, we used nematode metabolic footprints (NMF) as a reference against the traditional assessment method. This approach aims to scientifically evaluate the practical value of the method and provide a basis for future research.

4 An example: Response to the latitudinal change of soil nematodes from the black soil region of northeast China−evidence from energy flux

In the black soil region of northeastern China, where the latitude ranges from 42°50′ to 49°08′ N, 75 soil samples were collected from the plough layer in the long-term maize cultivation. By morphologically identifying and counting the nematodes in these samples and measuring their body lengths and widths, the sensitivity of nematode metabolic footprints (NMF) and nematode energy flow analysis methods across the latitudinal gradient was comparatively analyzed.

The NMF was calculated according to the method outlined by Ferris (2010), which quantified the total amount of C utilized daily by the nematode for growth and respiration.

The NMF (μg C 100g^{-1} dry soil d^{-1}) was calculated by Eq. (1):

$$\mathrm{NMF} = \sum (N_t(0.1(W_t/m_t/12) + 0.0159(W_t^{0.75}))) \quad (1)$$

where N_t, W_t and m_t are the abundance, biomass, and c-p values of nematode taxon t, respectively. The average biomass of all individuals within a nematode taxon (W_t) is calculated using Andrássy's formula: $W = LD^2/(1.6\times 10^6)$, where L and D are individual body length and body width (μm) (Andrássy, 1956).

For energy flux calculation, we constructed a nematode food web topology (Fig. 2), following the formulae provided by Barnes et al. (2018) and Zhang et al. (2021):

$$F_i = (F + B)/e_\alpha \quad (2)$$

$$B = D_{io} \times F_o \quad (3)$$

Equation (2) describes the total energy flux of each trophic group (μg C 100g^{-1} dry soil d^{-1}) as the sum of the C flux released by respiration (F) and the energy loss by predation (B), divided by the assimilation efficiency (e_a). The metabolic rate of various genera within the corresponding trophic group is used to calculate F. The values of e_a are assigned as 0.6 for bacterivores, 0.38 for fungivores, 0.25 for plant-parasites and 0.5 for omnivores-predators (Schwarz et al., 2017). In Eq. (3), D_{io} represents the feeding preference of predators, and is calculated based on the density-independent feeding preference of omnivores-predators to other trophic groups, i, as described by Zhang et al. (2021).

Since the top predators were assumed to have no loss of energy from being preyed upon, omnivorous-predatory nematodes energy flux was calculated first. Then, the calculation was proceeded downwards to the lower trophic groups of nematodes. The energy loss to predation of lower trophic groups was equal to the energy flux to omnivorous-predatory nematodes (Barnes et al., 2018; Wan et al., 2022a).

We employed ordinary least square regression analysis to fit general linear models and compared the response of NMF and energy flux of nematodes to latitudinal change (Fig. 3). As observed in Fig. 3, except for plant-parasites, the energy flux of the total nematode community and specific trophic groups showed a significant positive correlation with latitude. This trend was not mirrored in the NMF data, where only bacterivores and fungivores demonstrated a positive correlation with latitude. These findings suggest that NMF, which primarily quantifies the metabolism rate of C in nematode communities, may not fully encapsulate the nuances of how soil nematodes respond to changes in latitude. In contrast, the energy flux metric, which represents the energy flow of C within the nematode food web, offers a more comprehensive reflection of the response of soil nematodes

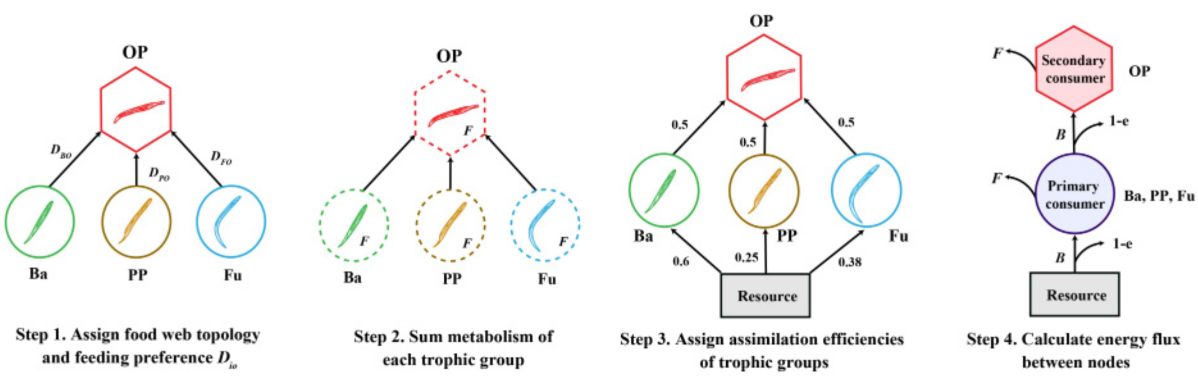

Fig. 2 A simplified flow chart illustrating the calculation of energy flux. The border color distinguishes among trophic groups, and the arrows indicate the direction of energy flow.

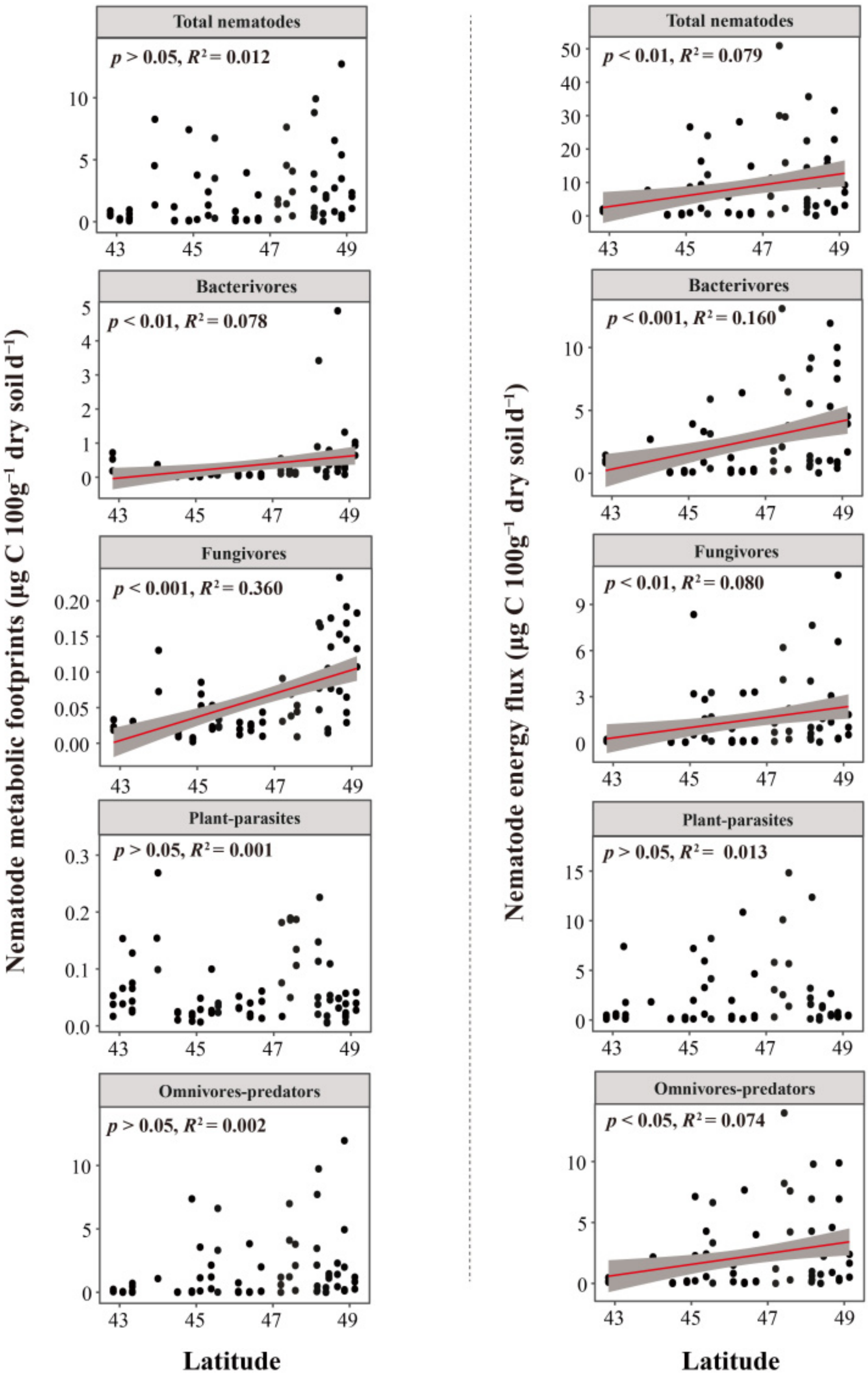

Fig. 3 Responses of soil nematode metabolic footprint (NMF, left hand panels) and energy flux (right hand panels) to the latitudinal change. The red fitted lines represent the ordinary least square regressions obtained by fitting general linear models. The shaded area shows the 95 % confidence interval of the fit.

and various trophic groups to latitudinal variations. At the same time, the apparent mechanism of the nematode's geographical distribution pattern needs to be further explored by researchers, perhaps due to environmental factors such as climate and soil factors, or from biological factors, that also change with latitude (Liu et al., 2023).

5 The effectiveness of nematode food web energy flow analysis as a soil health indicator

Nematode food web energy flow analysis stands out as an indicator of soil health because of its unique ability to trace energy flow through different trophic levels, linking biodiversity with ecosystem functionality. This approach highlights the importance of energy or nutrient flows from primary decomposers, such as bacteria and fungi, to top consumers. This process is critical to capturing the nuances of C sequestration, nutrient cycling and the broader implications for plant, animal and human health (Trap et al., 2016).

Despite its insightful contributions to ecological understanding, nematode food web energy flow analysis faces challenges that limit its more comprehensive application. The method's accuracy depends on precisely identifying nematode functional traits, including c-p values, body size, and feeding habits, with morphological traits playing a crucial role. The difficulty in accurately identifying soil nematodes and the time-consuming process of measuring their body size are significant hurdles. Advancements in research methods, such as the adoption of molecular approaches for studying nematode traits and the development of automated species identification through microscopy and imaging, are vital for overcoming these obstacles (Lu et al., 2020; Hou et al., 2023). Furthermore, a deep understanding of predator-prey interactions, essential for accurate energy flow analysis, often eludes direct verification methods like stomach content analysis or isotopic tracking (Heidemann et al., 2014; Eitzinger et al., 2019). Thus, implementing complementary sensitivity analyses and validation procedures is imperative to ensure the reliability of the findings.

To maximize nematode food web energy flow analysis as a tool for soil health, research needs to be broadened and deepened. Studies across large spatial and temporal scales will shed light on how ecosystems respond to change and disturbance, improving our understanding of soil health and ecosystem resilience (Hou et al., 2023; Liao et al., 2023). In addition, it is critical to closely examine factors that influence the flow of energy in food webs − both biotic, such as interactions and cascading effects between multi-trophic groups, and abiotic, such as climate and soil types (Zheng et al., 2023). This will improve our understanding of the role of soil biodiversity in ecosystem function, leading to breakthroughs in ecological research and the application of nematode food web analysis in soil health assessments.

6 Conclusions

The incorporation of nematode functional traits into soil health assessments represents a significant advancement. Notably, the energy flow analysis of nematode food web establishes a direct link between multifunctional traits (such as morphology, physiology, and metabolism) and environmental changes, offering insights beyond what nematode metabolic footprint analysis can provide. Although identifying nematode functional traits presents challenges, advancements in molecular biology and automated species identification techniques offer the potential for broader application. Developing powerful indices that include key functional trait assemblies is essential to improve the use of nematodes in diagnosing soil health.

Conflict of 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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