

Linking nematodes and ecosystem function: a trait-based framework

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Opinion

Linking nematodes and ecosystem function:
a trait-based frameworkChongzhe Zhang,^{1,2,6} Ian J. Wright,^{2,3,4} Uffe N. Nielsen,² Stefan Geisen,⁵ and Manqiang Liu ^{6,*}

Trait-based approaches are being increasingly adopted to understand species' ecological strategies and how organisms influence ecosystem function. Trait-based research on soil organisms, however, remains poorly developed compared with that for plants. The abundant and diverse soil nematodes are prime candidates to advance trait-based approaches belowground, but a unified trait framework to describe nematode ecological strategies and assess their linkages with ecosystem function is lacking. We categorized nematode traits as morphological, physiological, life history, and community clusters, and proposed the nematode economics spectrum (NES) to better understand nematode ecological strategies and their association with ecosystem function. We argue that bridging the NES and the plant economics spectrum will facilitate a more holistic understanding of ecosystem carbon and nutrient cycling under global change.

Why ecology needs trait-based approaches

Ecologists are increasingly recognizing the importance of **traits** (see [Glossary](#)) and adopting **trait-based approaches** to understand how organisms' ecological strategies vary along environmental gradients and their effects on ecosystem function [1,2]. Trait-based approaches provide general principles for explaining and predicting complex systems, which is essential in addressing macroecological questions and predicting ecosystem function [3]. A key question arises: what unique insights can be gained from trait-based approaches? One advantage is that traits introduce an additional dimension that reflects the function performed by the organism and cannot be attained through taxonomic approaches, thus providing valuable insights into organismal ecological strategies and their roles in ecosystems [4,5]. Moreover, the trait-based approach is an intuitive approach for delivering perspectives on the evolutionary dynamics of organisms, as evolution selects organisms on the basis of their function and not their taxonomy [6]. Trait-based approaches are most advanced in plant sciences, where they are used to understand adaptations across environmental gradients, potential responses to global change, and associated impacts on ecosystem function [3,6,7]. A notable achievement is the **plant economics spectrum (PES)**, which, by incorporating ideas such as tradeoffs between tissue construction costs and turnover rates, and between plant growth and survival, provides a useful framework for placing plant life history characteristics along a fast–slow continuum, as well as a means of explaining ecosystem assembly processes and function [8–11].

As ecology goes underground, evidence is mounting that the immense abundance and diversity of soil organisms contributes notably to the maintenance of ecosystem functions [12]. However, trait-based assessments of ecosystems predominantly rely on observations of plant attributes, despite the potential of utilizing proxies for soil functional attributes to increase our mechanistic understanding of ecosystem properties [13]. The past decade has witnessed an enormous research effort directed at adopting trait-based approaches for studying soil organisms, ranging from microbes to larger organisms such as collembola and ants [14–17]. This has substantially

Highlights

Emerging knowledge of plant–soil biotic interactions and the role of soil organisms in shaping the world aboveground is advancing our understanding of ecosystem function.

Nematodes are the most abundant animals on Earth. They are morphologically and functionally diverse, and play key roles in ecosystem function, making them ideal for developing a trait-based understanding of adaptation to the environment and for assessing their contributions to ecosystem function.

Trait-based approaches allow us to capture the functional attributes of organisms beyond their taxonomic identity, provide insights on evolutionary fitness, and make global comparisons possible.

We propose the nematode economics spectrum (NES), analogous to the plant economic spectrum, which describes the tradeoffs among growth, reproduction, and survival, potentially enabling us to predict the impacts of global change on nematode ecological strategies and the associated changes in ecosystem function.

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improved our understanding of soil organisms' adaptation and evolution to cope with environmental gradients and their role in ecosystem function. Still, there is much to gain from more targeted, trait-based approaches to assess soil-based biological communities, particularly where this can complement insights that can be gleaned from plant-centric trait-based research.

Nematode traits: an opportunity to advance belowground ecology

Nematodes are ubiquitous, highly diverse and the most abundant animal group on Earth, making them ideal for the application of trait-based approaches belowground [18,19]. Nematodes occupy multiple trophic positions within the **soil food web**, rendering them indispensable in soil ecosystems [20], where they play pivotal roles in almost all ecosystem functions including **carbon (C) cycling** and **nutrient cycling** [21]. Classic taxonomic-based approaches, which involve identifying individual nematodes and categorizing them into trophic and **colonizer–persister ('cp') groups** primarily on the basis of morphological attributes, have made enormous contributions to soil health assessment and monitoring [22,23]. Moreover, well-established indices based on life history strategies, such as the maturity index and enrichment index, contribute to the comprehensive assessment of soil health but face challenges regarding cross-ecosystem comparability [24]. Although nematodes representing specific trophic or cp groups may appear to be structurally similar at first glance, closer examination reveals substantial trait variation among species within groups. For example, feeding preferences or cp values may remain static while the patterns of intra- and interspecific trait variation, including body size, egg size, or lifespan, may exhibit adaptive responses to altered environmental conditions or to the increasing frequency and severity of global change [25]. Therefore, by comprehensively quantifying trait variations, we can better understand nematode ecological strategies and predict their effects on ecosystem function under current and future global change scenarios.

Nematodes exhibit substantial variation in their morphology, physiology, and life history strategies that influence their growth, reproduction, and survival in response to environmental change [26,27]. Indeed, recent studies have embraced trait-based approaches to study the role of nematodes in changing environments. For example, N fertilization was shown to affect nematode morphological traits, resulting in increased body width but decreased stylet and esophageal length at the community level [28]. In another study, nematode biomass increased in response to elevated monthly precipitation and soil water content [29] and decreased in response to water stress [30]. Xue *et al.* [31] revealed that the bacterial-feeding nematode *Plectus murrayi* has higher somatic phosphorus (P) content when it occurred in P-rich soils, and the bacterial-feeding nematodes *P. murrayi* and *Caenorhabditis elegans* showed delayed egg laying and prolonged reproductive periods when the P content was insufficient. In addition, such changes have implications for ecosystems because nematodes fundamentally influence C and nutrient cycling through regulating the decomposition of organic matter, nutrient mineralization, and soil microorganisms [32]. Studies have shown that a high abundance of nematode increases microbial activity, thereby enhancing C and N mineralization [33,34]. Furthermore, recent advances have demonstrated increases in energy flux within the nematode food web in response to organic amendments, thereby strengthening ecosystem multifunctionality [35]. Similarly, variations in body size, mouth width, and egg size have considerable potential to influence the roles of nematodes in regulating C and nutrient cycling [36,37]. These examples illustrate the potential value of utilizing traits of the nematodes to advance belowground ecology, but a conceptual framework to achieve this is lacking. Here, we propose a new conceptual framework to advance our understanding of the complex roles of nematodes in ecosystems, based on the traits of the nematodes involved.

A brief overview of nematode traits

We define **nematode traits** as the morphological, physiological and life history attributes related to fitness through their impact on nematode performance, including growth, reproduction, and

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survival, which evolved in response to environmental pressures and determine effects of nematodes on ecosystem functions (Figure 1). Morphological traits encompass quantifiable physical and structural characteristics which are commonly used in the identification and classification of nematodes, such as body size, the stylet's length and shape (where a stylet is present), length of the esophagus and intestine, and the thickness, length and shape of the tail [28]. Physiological traits are related to the ways in which nematodes cope with their surroundings and carry out essential physiological processes. These traits include the ability to enter a state of suspended animation (anhydrobiosis) in response to extreme environmental conditions [38]; the respiration rate, which quantifies C utilization in metabolic activity [39]; and C:N:P stoichiometry, reflecting the diet, nutritional status, and energy allocation strategies [40]. Life history traits represent adaptations that dictate nematode growth, reproduction, and survival strategies. For example, lifespan and egg size provide information for assessing population dynamics [41] as well as on fundamental life history tradeoffs (e.g., the size versus number of offspring), while the sex ratio reflects reproductive capacity [42]. In addition, we recognize community traits that describe community-level attributes and biotic interactions, with the aim of generating a more nuanced understanding of the contributions of nematodes to ecosystem function what would be than possible with traits of individual species alone. For example, the predator to prey ratio serves as an indicator of trophic connection [43], and abundance provides a context for assessing other parameters such as total biomass or community-weighted traits [44]. A summary of nematode traits, along with their potential ecological interpretations and functional relevance, is presented in Table 1.

The NES: describing nematode ecological strategies

Natural selection operates upon each individual nematode's interactions with its surroundings [20]. Consequently, nematode traits and trait–trait relationships reflect fundamental eco-evolutionary tradeoffs that can be recognized as constraints among diverse functions with conflicting benefits and costs. For example, there are tradeoffs related to morphology: investing more energy in body size leads to a reduction in motility [23]. There is a life history tradeoff between reproduction and survival: long-lived nematodes produce fewer but larger eggs than short-lived species [45]. These tradeoffs shape the response of nematodes to environmental stresses. Therefore, a trait-based scheme underpinned by these and other key evolutionary tradeoffs holds great promise for building a new understanding of nematode ecological strategies as shaped by the environmental conditions and by their evolutionary history [3,46].

Here, we propose a '**nematode economics spectrum**' (NES), with a focus on five key attributes related to nematode growth, survival, and reproduction (Figure 2). Body size relates to resource acquisition and energy requirements [39]. Here, body size refers to body length, width, or both. Egg size describes the mass of eggs, with large eggs corresponding to a greater investment in offspring quality (as opposed to quantity). Reproductive rate reflects the number of eggs [41] (i.e., quantity). Lifespan reflects the time from the egg to eventual demise and is generally positively correlated with body size [44]. Metabolic rate reflects the pace at which C is released through respiration; metabolic activity is influenced by body size [23]. Both a low reproductive rate and a long lifespan are correlated with a low metabolic rate [47].

The NES runs from species with potential for fast growth and fast returns on investment into resource acquisition and metabolism, to species that have the potential to invest in reproduction with slow returns (Figure 2). At the fast end are species with a small body size, high rates of metabolism and reproduction, and short lifespans that produce small eggs. Species at the slow end have large body and egg sizes, long lifespans, and low rates of metabolism and reproduction. Categorizing nematodes along this continuum would describe nematode variations

Glossary

Carbon (C) cycling: processes by which carbon is used, transformed, and recycled among organisms (plants, microbes and animals) and the environment, including the soil, water, rock and atmosphere.

Colonizer–persister ('cp') groups: five groups, ranging from 'colonizers' (r-strategists) to 'persisters' (K-strategists) on a scale of 1 to 5, encompassing the entire range of ecological adaptations across all trophic guilds of nematodes.

Nematode economics spectrum (NES): a multivariate axis of nematode trait variations encompassing diverse adaptive strategies. Species with similar strategies tend to converge along this axis.

Nematode traits: morphological, physiological, and life history attributes related to fitness through their impact on nematode performance, including growth, reproduction, and survival, which evolved in response to environmental pressures and determine the effects of nematodes on ecosystem function.

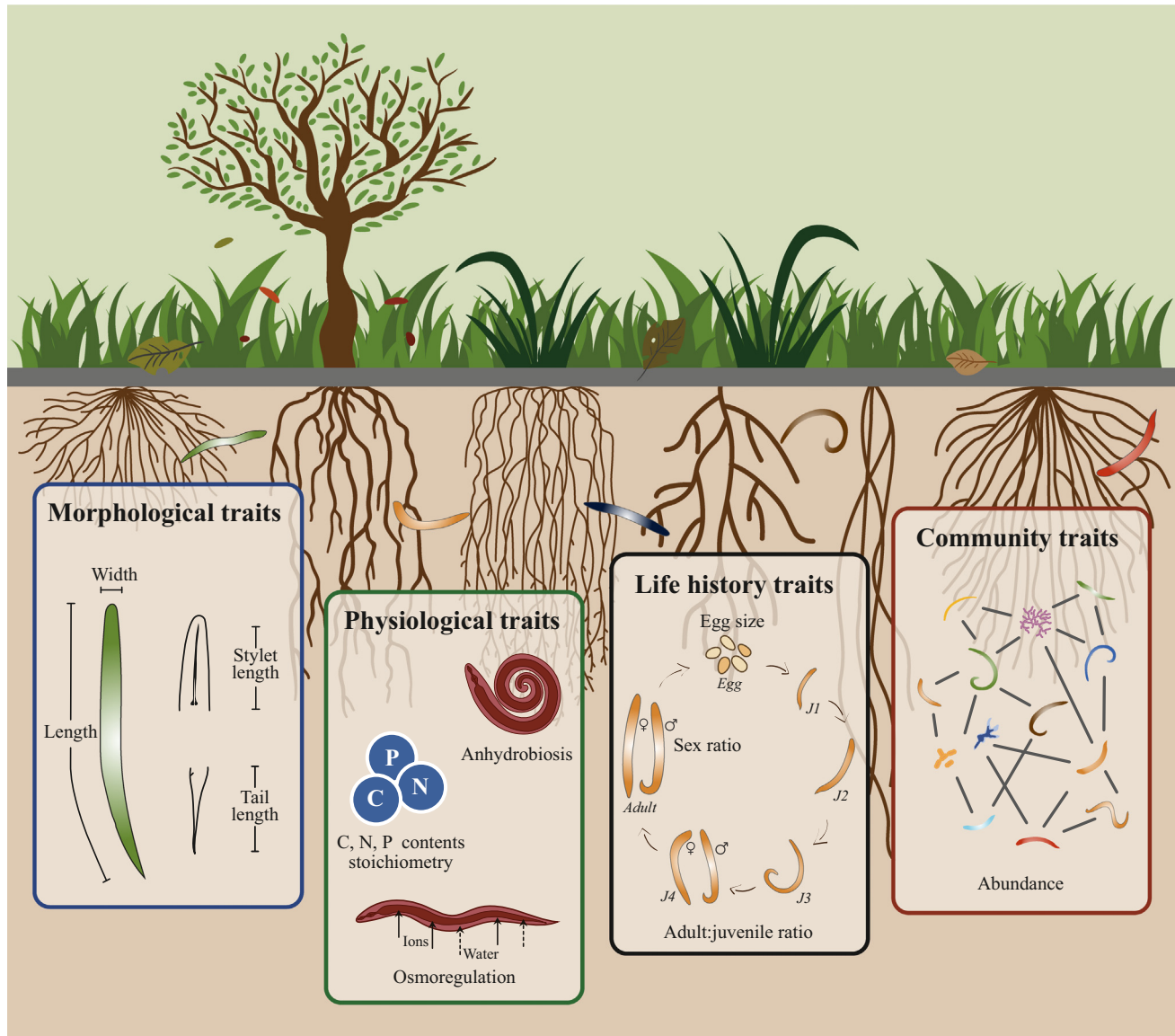
Nutrient cycling: the movement and transformation of essential elements or nutrients, such as nitrogen, phosphorus, sulfur, and other elements that are essential for the growth and functioning of organisms, through various biotic and abiotic components of ecosystems.

Plant economics spectrum (PES): an axis of plant trait variations, representing a gradient of ecological strategies, which determine the species' growth rates and their ecological roles along resource gradients.

Soil food web: a complex living system in the soil, comprising a community of organisms that interact with the environment, plants, and animals.

Trait: the morphological, physiological, phenological, and behavioral attributes of organisms that influence their response to environmental conditions and their effect on ecosystem processes and functioning.

Trait-based approaches: any method that focuses on the functional attributes of organisms rather than their taxonomic identity.



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Figure 1. A trait-based categorization encompasses various nematode traits, including morphological, physiological, life history, and community traits. Nematode traits are morphological, physiological, and life history attributes related to fitness through their impact on nematode performance, including growth, reproduction, and survival, which evolved in response to environmental pressures and determine effects of nematodes on ecosystem functions. In addition, community traits describe community-level attributes and biotic interactions, with the aim of generating a more nuanced understanding of the contributions of nematodes to ecosystem function than what would be possible with traits of individual species alone.

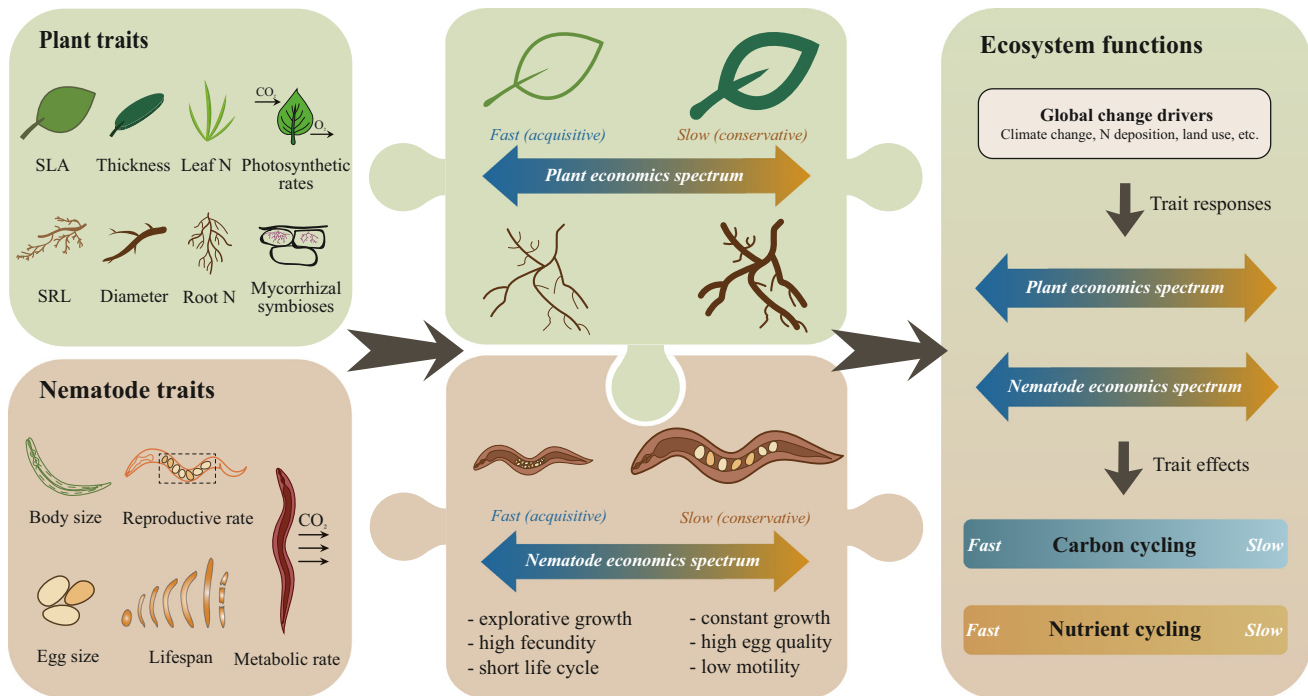
better than their functional guilds (trophic or cp groups), as functional guilds substantially overlap in the traits. This, in turn, can serve as a powerful predictive tool for assessing the function of ecosystems. Potential advancements from positioning nematodes along the NES include the following:

- The NES quantitatively mirrors the fundamental ecological strategies of nematodes, aiding in the identification of key trait assemblages and trait combinations within the NES that are sensitive to environmental changes.

Table 1. Categorization of nematode traits and their ecological interpretations and functional relevance

	Trait	Ecological interpretations	Functional relevance	Refs
Morphological traits	Body size	Size of the body, including length and width	Mobility, energy requirements, and resource use	[50]
	Body length	Distance from mouth to tail	Mobility, energy requirements, and resource use	[36]
	Body width	The widest part of the body	Mobility, energy requirements, and resource use	[28]
	Length–width ratio	Ratio of maximum length to width	Mobility and resource use	[36]
	Biomass	Total mass of the nematode	Decomposition and nutrient flow	[30]
	Stylet length	Distance from the tip to the base of a specialized feeding structure in the mouth	Niche differentiation	[64]
	Esophagus length	Length of the muscular tube that connects the mouth to the intestine	Feeding efficiency	[28]
	Intestinal length	Length of the intestinal tract	Digestion and absorption efficiency	[28]
	Cuticle thickness	Thickness of the flexible and chemically inert exoskeleton	Defense capacity and mobility	[65]
	Buccal cavity size	The form and size of the feeding organ	Feeding habits	[22]
Physiological traits	Tail types	The thickness, length, and shape of the tail	Mobility and feeding capacity	[66]
	Anhydrobiosis	Ratio of coiled nematodes to total nematodes	Habitat quality and environmental tolerance	[38]
	Osmoregulation	Cuticular permeability to the surroundings	Tolerance to the ionic composition of the habitat	[67]
	Metabolic rate	The amount of C released through respiration	Growth rate and C cycling	[68]
	C contents	The carbon contents of the nematode	Carbon allocation strategy	[39]
	N contents	The nitrogen contents of the nematode	Metabolic activity	[39]
	P contents	The phosphorus contents of the nematode	Gene expression and protein synthesis	[31]
	$\delta^{13}\text{C}$; $\delta^{12}\text{C}$; $\delta^{15}\text{N}$; $\delta^{14}\text{N}$	The stable isotope C and N contents of the nematode	Feeding habits and trophic positions in the soil food web	[69]
	Fatty acid composition	Components of the cell membranes	Feeding habits and trophic niches	[70]
	Sex ratio	Ratio of female to male nematodes	Genetic diversity and reproductive capacity	[42]
Life history traits	Adult–juvenile ratio	Ratio of adult to juvenile nematodes	Reproductive potential and nutrient fluxes	[44]
	Egg size	Mass or volume of an egg	Habitat quality and food availability	[41]
	Reproductive rate	The number of eggs	Habitat quality and population density	[41]
	Lifespan	The amount of time an individual lives, encompassing the egg, four juvenile stages, and adult	Population dynamics	[41]
	Male–parthenogenetic ratio	The proportion of different reproductive models	Population dynamics and the system's stability	[42]
Community traits	Abundance	The number of nematodes per unit of mass of soil	The soil's biological activity and ecosystem net productivity	[44]
	Predator–prey ratio	Ratio of predatory nematodes to other nematodes	Trophic connection	[43]
	Energy flux	Expressed in C per unit area over time	Energy consumption and energetic structure	[35]

- Well-studied ‘model species’, such as *C. elegans*, can be strategically placed relative to other species, providing insights into the extent to which their findings can be extrapolated.
- Strengthening our understanding of the tradeoffs among growth, survival, and reproduction across resource gradients sheds light on the question of how species’ distribution and community assembly occur across diverse environmental conditions.
- Providing insight into the outcomes of evolution by natural selection by better understanding the patterns of trait variation and trait–trait correlations within and among habitats in relation to specific environmental gradients.



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Figure 2. A conceptual framework based on a trait-based approach that integrates plants and nematodes. Left: key traits related to growth, survival, and reproduction are of fundamental importance in reflecting the ecological strategies of plants and nematodes. Centre: the plant economics spectrum (PES) and nematode economics spectrum (NES) serve as conceptual frameworks to understand plants' and nematodes' adaptations to their environments, as well as their effect on ecosystem function. Right: the combined NES-PES framework, based on a trait-centered view that spans from plants to nematodes, enhances the predictive power of organismal trait responses triggered by drivers of global change, such as climate change, N deposition, and changes in land use, and their effects on ecosystem-scale carbon and nutrient cycling. Abbreviations: SLA, specific leaf area; SRL, specific root length.

- Offering valuable extensions to modeling the shift in C and nutrient cycling and the associated (coupled) aboveground–belowground ecosystem functions under global change.

Hence, the NES is one piece of a larger puzzle for nematode ecology that provides a first step for addressing broader ecological and evolutionary questions.

Linking nematode traits to plants, global change, and ecosystem functions

There is a wealth of evidence that nematodes exhibit high plasticity in response to plant attributes and drivers of global change such as climate change, N deposition, and land use changes, and that the scale of these responses potentially impacts ecosystem function. For example, plant traits play a key role, either through direct interactions or indirectly by mediating microbial activities, in structuring nematode traits both during the life and afterlife of plant organs [48,49]. Furthermore, Lu *et al.* [50] observed that drought shifts the nematode community composition towards species with smaller body sizes, leading to the prediction that an increased frequency of drought events will lead to the loss of larger taxa, potentially causing slower C fluxes. Likewise, morphological and life history traits along the NES are able to respond rapidly to various climate factors including precipitation and temperature, and thus increased precipitation leads to a shift in nematodes towards larger community-weighted body mass [51], while warming decreases individual reproductive rates [52]. Moreover, a recent meta-analysis across global grassland ecosystems revealed the negative responses of community traits such as abundance to N deposition, consequently impacting C mineralization and cycling [53]. Similarly, morphological traits respond to

long-term N enrichment, resulting in greater body width but shorter stylet and esophagus length [28]. The reorganization of nematode communities also results from land use changes, as larger-bodied and less fecund nematodes are more sensitive to the increased intensity of land use [54,55].

Given their considerable variation and high plasticity, it is not surprising that nematode traits play crucial roles in driving ecosystem function. Regarding C cycling, a spectrum of traits that determine metabolic demands, including body size and lifespan, contribute significantly to C fluxes [56], with larger nematodes with conservative resource use and long lifespans retaining more C. Nematode life history traits, such as a short lifespan, and community traits, such as high abundance, indirectly influence C cycling by altering plant C allocation and facilitating the release of root exudates [57]. Similar evidence is emerging that nematode traits influence nutrient cycling. For example, soil N dynamics can be explained by variations in nematode community and life history traits, with rates of N mineralization and nitrification being negatively related to plant-parasitic nematode abundance [58], and a shift toward a higher number of males per female, due to the low resource availability caused by climate change, may affect nutrient cycles [42]. Additionally, the abundance and structure of microbial assemblages, which serve as key drivers involved in N cycling, were related to the metabolic rate and abundance of microbivorous and predatory nematodes, implying a strong influence on nutrient cycling [43]. These links between nematode traits and ecosystem function show that the NES has potential to reveal variations in ecosystem-scale biogeochemical cycles. Specifically, ‘fast’ nematodes with high metabolic and reproductive rates are associated with fast C and nutrient cycling, whereas ‘slow’ nematodes with a large body size and a long lifespan are associated with slow C and nutrient cycling.

Digging deeper: integrating plant and nematode traits to improve predictions of ecosystem responses to global change

Developing general frameworks to understand ecosystem responses to intensifying global change remains a grand challenge in ecology [1]. Here, we contribute to addressing this challenge by focusing on a global proxy of biodiversity: soil nematodes. Our idea parallels those developed for plants, where habitats dominated by species at the fast end of the PES exhibit fast C and nutrient cycling, while habitats dominated by slow species are associated with slow rates of C and nutrient cycling [59]. Given the fundamental role played by above-ground–belowground interactions in regulating ecosystem properties [60], bridging plant and nematode trait-based approaches will help us predict ecosystem function better under future conditions. This agenda can be guided by recent research that combined the traits and ecological strategies of plants with those of nematodes. A long-term field experiment showed that a fast–slow continuum of ecosystem function (plant productivity) in grasslands was explained by the combined influence of nematode traits and plant economic traits [61]. Likewise, Zhang *et al.* [62] leveraged cover crops with distinct ecological strategies and discovered that leaf and root traits, along with various nematode traits, explained soil resource availability and microbial activities that sustain C and nutrient cycling. This illustrates that plant and nematode traits collectively explain more of the variation in ecosystem function across the fast–slow continuum than either of the two groups alone. Therefore, we also propose an NES–PES framework in which plant and nematode species at the fast end of the continuum contribute to fast C and nutrient cycling, while ecosystems with slow C and nutrient cycling are dominated by species at the slow end (Figure 2). This framework aids in providing deeper insights into ecosystem function and advancing predictive science in the era of global change.

How to link nematode traits and ecological strategies to ecosystem function

This trait-based framework leverages knowledge from existing trait-based studies and identifies critical data gaps in nematode ecology. Analyses of nematode traits have focused on how

morphological traits cope with changing environmental conditions and serve as valuable proxies for ecosystem function. However, a more extensive collection of trait data, including physiological or life history traits spanning a broader range of species, would strengthen the understanding of nematode ecological strategies and the trait-based assessment of ecosystem function. Here, we propose a roadmap detailing, in brief, the key steps toward developing and implementing the framework to better understand nematode ecological strategies and assess their associations with ecosystem function:

- (i) Conduct a strategic assessment of nematode traits, encompassing the key traits proposed herein and potentially informative traits. Verify the coordination of these traits and validate the utility of specific traits as indicators of the NES framework.
- (ii) Quantify the variation in traits and trait-based spectra across environmental gradients, ideally developing a cost–benefit understanding of nematode ecological strategies, specifically in terms of their growth, reproduction, and survival.
- (iii) Determine the link between the traits and ecological strategies of nematodes and ecosystem function, such as C and nutrient cycling.

Concluding remarks

Our trait-based framework for nematodes proposes a unified language for understanding trait variations and their influence on ecosystem function, with clear potential for facilitating the next generation of advances in belowground ecology. Further studies are needed to strengthen and implement this framework (see [Outstanding questions](#)). First, comprehending nematode ecology and evolution through the lens of trait variation requires sufficient trait data. Thus it is essential to establish a trait database that defines the global spectrum of nematode forms and functions and establishes links between the traits of nematodes and plants. Second, future research should focus on developing community-level attributes that offer a valuable perspective into the evolution and ecological strategies of complex nematode communities to better predict ecosystem function. Ongoing advancements in molecular tools [63], such as quantitative PCR and metabarcoding, have made it possible to obtain community-level attributes such as abundance and community composition more quickly and cost-effectively. Third, the advancement of nematode traits requires a well-defined protocol for standardized measurements of nematode traits worldwide. Developing such a protocol with comprehensive, step-by-step directions applicable to any biome would be a fruitful avenue for ecology based on nematode traits. The conceptual and functional connections between nematode traits and ecosystem function presented here may provide more robust predictions of complex ecosystem dynamics under global changes.

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Declaration of interests

The authors declare no competing interests.

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Outstanding questions

Do plant and nematode traits exhibit similar or diverging trajectories under global change?

How can soil nematode traits be incorporated into biogeochemical models to improve the accuracy of their predictive power?

How can we integrate other soil organisms (e.g., microbes, protists) that play important roles in supporting ecosystem services and functions into the nematode-centric framework, potentially expanding this to the whole soil food web?

Do additional dimensions exist within nematode ecological strategies; if so, what tradeoffs form the underlying basis for each of these strategies' dimensions?

What other kinds of trait data could be included in the proposed framework? Traits that can effectively capture the major dimensions of the economic principles of nematodes are necessary to reveal the interactions among traits within nematode communities and between soil nematodes and plants.

How can we fully understand nematode growth, reproduction, and survival (the three components of nematode performance) by expanding trait diversity? A promising approach would be to extract the core functional parameters from the ecological indices to develop new trait indices at both the individual and community level that can indicate nematode ecological strategies.

How can molecular methods aid in studying nematode traits? Molecular methods could facilitate the rapid and cost-effective acquisition of data on the identification, abundance, and community attributes of nematodes. Integrating molecular methods with microscopic techniques could supplement important quantitative data on nematode communities, making it easier to apply the NES at a higher resolution.

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