

An integrated fast–slow plant and nematode economics spectrum predicts soil organic carbon dynamics during natural restoration

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Summary

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- Aboveground and belowground attributes of terrestrial ecosystems interact to shape carbon (C) cycling. However, plants and soil organisms are usually studied separately, leading to a knowledge gap regarding their coordinated contributions to ecosystem C cycling.
- We explored whether integrated consideration of plant and nematode traits better explained soil organic C (SOC) dynamics than plant or nematode traits considered separately. Our study system was a space-for-time natural restoration chronosequence following agricultural abandonment in a subtropical region, with pioneer, early, mid and climax stages.
- We identified an integrated fast–slow trait spectrum encompassing plants and nematodes, demonstrating coordinated shifts from fast strategies in the pioneer stage to slow strategies in the climax stage, corresponding to enhanced SOC dynamics. Joint consideration of plant and nematode traits explained more variation in SOC than by either group alone. Structural equation modeling revealed that the integrated fast–slow trait spectrum influenced SOC through its regulation of microbial traits, including microbial C use efficiency and microbial biomass.
- Our findings confirm the pivotal role of plant–nematode trait coordination in modulating ecosystem C cycling and highlight the value of incorporating belowground traits into biogeochemical cycling under global change scenarios.

Introduction

Many ecosystems world-wide face exposure to ongoing climate change and human activities, resulting in catastrophic losses of carbon (C) and altered provisioning of critical ecosystem services (Vitousek *et al.*, 1997; Adla *et al.*, 2022). In this context, improving soil C content to recover multiple ecosystem services has become one of the central and longest-standing themes in ecology (Lal, 2015; Singh, 2018; Kopittke *et al.*, 2022). Soil organic C storage represents the largest terrestrial C pool and is derived from total C inputs to soils, including primary productivity, root exudates and organic matter ranging from living organisms to decomposing plant materials (Amundson, 2001; Jackson *et al.*, 2017). Natural restoration on abandoned land represents one of the most used restoration strategies implemented world-wide (Knops & Tilman, 2000; Morriën *et al.*, 2017), with the capacity not only to support biodiversity conservation but also to rebuild above- and belowground C pools

(Silver *et al.*, 2004; Hobbs & Cramer, 2008; Clewell & Aronson, 2013; Wu *et al.*, 2021; Fu *et al.*, 2023). However, the restoration of natural and well-functioning ecosystems is a long-term process (McLauchlan *et al.*, 2006; Lu *et al.*, 2018), dependent upon the interactions among different components of the community (Wardle *et al.*, 2004; Trivedi *et al.*, 2022).

Many restoration projects have aimed at increasing C pools using a taxonomic-centric perspective, for example based on community diversity or the abundance of target species (Yang *et al.*, 2019; Hua *et al.*, 2022; Tian & Zhang, 2023). However, there is evidence that achieving a target community composition and restoring self-sustaining populations of native species through restoration efforts can be a protracted process and may never be achieved (Lockwood & Pimm, 1999), owing to environmental filtering and biotic interactions under novel conditions. For example, restoring a target grassland community to its original species composition is almost impossible as global climate extremes continually induce shifts in the complex

plant–soil–biotic interactions (Matthews & Spyreas, 2010; Woodcock *et al.*, 2011; Perring *et al.*, 2015). Thus, the restoration of natural ecosystem functioning and properties requires complementary, theory-based frameworks, rather than solely focusing on reinstating functional groups that may fail to survive in a complex world (Seastedt *et al.*, 2008; Laughlin, 2014). Increasing emphasis has been placed on embracing a trait-based approach in restoration (Balachowski & Volaire, 2018; Carlucci *et al.*, 2020; Auclerc *et al.*, 2022; Coutinho *et al.*, 2023; Wong *et al.*, 2024), as the biological contribution to C cycling is more of a multivariate continuum than a situation where species are categorized into discrete groups (Funk *et al.*, 2017; Sobral *et al.*, 2023). However, there are still many uncertainties about how the coordination between aboveground and belowground organisms contribute to the sustainable enhancement of C dynamics.

Ecological strategy frameworks (Southwood, 1977; Westoby *et al.*, 2002; Reich *et al.*, 2003; Laughlin, 2023), for example those invoking ideas of resource ‘economics’ (Bloom *et al.*, 1985), provide a conceptual context for grounding trait-informed restoration (Laughlin, 2014; Carlucci *et al.*, 2020). Researchers increasingly recognize a plant economics spectrum (PES) which, incorporating ideas of trade-offs between growth and survival, underlies a spectrum of strategies ranging from ‘fast’ to ‘slow’ (Wright *et al.*, 2004; Reich, 2014; Bergmann *et al.*, 2020). Furthermore, the amount and composition of C that plants contribute to the soil is related to their traits and ecological strategies (De Deyn *et al.*, 2008; Sobral *et al.*, 2023). In ecosystems undergoing natural restoration, there is a shift in plant ecological strategies from fast to slow (Maharning *et al.*, 2009). The fast–slow spectrum of trait variation influences C dynamics: plant species at the fast end of the PES tend to allocate most of their C to resource acquisition and use structures with low-density and high-nutrient concentrations, leading to rapid growth and litter decomposition, which contribute to fast C fluxes and small C pools. By contrast, slow-growing and long-lived species produce low-quality plant materials that retard decomposition and thereby potentially increase soil C pools (De Deyn *et al.*, 2008; Faucon *et al.*, 2017; Ding *et al.*, 2021; Da *et al.*, 2023). However, the set of most commonly used plant traits alone are poor predictors of C cycling (van der Plas *et al.*, 2020). Furthermore, during the course of natural restoration, nutrients will become ‘locked-up’ within soil organisms, with consequences for the accumulation of soil organic matter (Odum, 1969). Belowground soil organisms, being extremely abundant and diverse, are major players in aboveground community dynamics and ecosystem C cycling (Briones, 2018; Griffiths *et al.*, 2021; Guerra *et al.*, 2021; Topalović & Geisen, 2023), thus holding the potential to utilize soil organism traits to improve our mechanistic understanding of SOC dynamics (Gebremikael *et al.*, 2016; Malik *et al.*, 2020). Consequently, restoration practitioners should integrate the ecological strategies and traits of plants and soil organisms to comprehensively understand C dynamics as natural restoration progresses, thereby providing a valuable tool to enhance the monitoring and assessment of restoration trajectories.

To facilitate a more accurate prediction of C cycling, we recently proposed a new framework that combines the traits and ecological strategies of plants with those of nematodes (Zhang *et al.*, 2024). Nematodes, possessing a diverse array of traits, are the most abundant and functionally diverse animals on Earth, participating in biogeochemical cycling and making them prime candidates to advance trait-based approaches belowground (Bongers & Ferris, 1999; Bardgett & van der Putten, 2014; van den Hoogen *et al.*, 2019). Trade-offs between nematode traits have been proposed to explain their ecological strategies, encompassing a spectrum from fast-growing, higher-metabolism nematodes to slow-growing, but larger-bodied nematodes, described as the nematode economics spectrum (NES), parallel to the PES (Zhang *et al.*, 2024). Hence, bridging plants and nematodes across the fast–slow spectrum – PES–NES coordination – would provide an emergent perspective for enhancing the predictive power of SOC dynamics, compared to focusing solely on plant traits. Additionally, soil microbial traits of the belowground world, such as microbial C use efficiency (CUE; the ratio of C substrate retained in biomass to that respired) and microbial biomass, determine the C dynamics in soils (Sinsabaugh *et al.*, 2013; Geyer *et al.*, 2016; Tao *et al.*, 2023). Moreover, it is evident that variation in plant and nematode traits primarily affect microbial traits, thus shaping C cycling (Morriën *et al.*, 2017; Kardol & De Long, 2018; Nielsen, 2019; Schmitz & Leroux, 2020). For example, plants impact microbial biomass by altering the quantity and quality of resources entering the soil in the form of litter and root exudates, which are linked to SOC dynamics (Grigulis *et al.*, 2013; Borden *et al.*, 2021; Wan *et al.*, 2022). Similarly, nematode abundance shapes microbial activities responsible for the utilization of organic matter, thereby influencing C mineralization (Trap *et al.*, 2016; Kane *et al.*, 2023). Therefore, establishing the connections among PES–NES coordination, microbial traits and SOC dynamics would aid in monitoring and assessing C cycling during natural restoration (Kardol & Wardle, 2010), yet empirical evidence is still lacking.

The objectives of this study were to identify coordinated relationships between the fast–slow trait spectra of plants and nematodes; and, to evaluate whether and how this coordination is associated with SOC dynamics during the development of restored ecosystems. We sought to examine whether knowledge of these relationships could serve as a valuable tool for monitoring and assessing restoration trajectories within a highly diverse subtropical community, thus contributing to nature-based solutions (NbS) for restoration. Biodiversity-rich subtropical forests are a strong C sink, potentially contributing greatly to global C sequestration (Yu *et al.*, 2014; Zhang *et al.*, 2016). To achieve these aims, we synthesized evidence from a chronosequence spanning pioneer, early, mid, and climax stages of natural restoration on ex-arable lands that represent over 60 yr of restoration efforts. We determined plant, nematode and microbial traits and analyzed their linkages with SOC dynamics, aiming to inform trait-based assessment of restoration trajectories by integrating both above- and belowground traits. We then tested the following hypotheses: (1) plant and nematode traits would vary in a coordinated way. Plants and nematodes at the pioneer stage

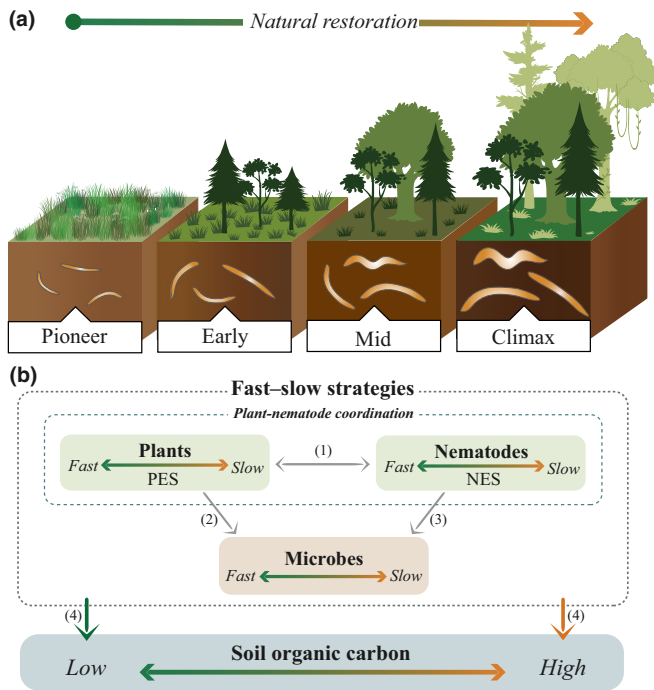


Fig. 1 (a) A conceptual diagram illustrating restoration trajectories in plant and soil nematode assemblages shows that ecological strategies of plants and nematodes progress from the pioneer stage characterized by fast strategies to the climax stage with slower strategies. The belowground icons represent nematodes, with the size of each icon indicating variations in body size. (b) The *a priori* models of expected linkages between plant-nematode coordination and soil organic carbon (SOC). Plant and nematode traits exhibit coordinated variation across the fast–slow economics spectrum (1) (Wardle *et al.*, 2004; Zhang *et al.*, 2024). The integrated fast–slow plant and nematode economics spectra indirectly affect SOC dynamics (2–4) by shaping microbial traits (Wan *et al.*, 2022; Kane *et al.*, 2023) and directly drive SOC dynamics (4) (Sobral *et al.*, 2023; Zhang *et al.*, 2024). Mid, middle; NES, nematode economics spectrum; PES, plant economics spectrum.

would exhibit more evident ‘fast’ strategies, whereas those at the climax stage would display more evident ‘slow’ strategies (Fig. 1a). (2) Joint consideration of plant and nematode traits – an integrated fast–slow plant and nematode trait spectrum – would explain more variation in SOC than the spectrum of either of the two groups alone. In addition, the integrated trait spectrum would predict SOC dynamics by mediating microbial traits, where plants and nematodes at the slow end of the spectrum correspond to high CUE and microbial biomass, as well as high-SOC contents, whereas those at the fast end of the spectrum would support lower CUE and microbial biomass, resulting in lower SOC contents (Fig. 1b).

Materials and Methods

Study site

The study site is located in the Daweishan National Natural Reserve (22°35′–23°07′N, 103°20′–104°03′E), Yunnan Province, China. This region features a subtropical monsoon climate

with a mean annual temperature of 22.6°C and a mean annual precipitation between 1700 and 1900 mm. The soils are derived from a limestone base classified as Calcaric Cambisols according to the FAO system (IUSS Working Group WRB, 2015). This area encompasses the majority of the rainforest habitat in the southeastern region. Notably, vegetation maps and documents provided by the local forestry department and the State Forestry Administration of China indicated that ecosystem degradation in this region has been exacerbated by agricultural expansion, excessive tillage, and ongoing cultivation. To effectively prevent further degradation, restoration projects have been initiated to abandon disturbed land and restore biodiversity along with associated ecosystem services. Here, we adopted the space-for-time substitution method (Walker *et al.*, 2010; Lovell *et al.*, 2023) to investigate natural restoration patterns using a chronosequence consisting of pioneer, early, mid, and climax stages (Supporting Information Fig. S1). The fields, historically used for decades to cultivate corn, were abandoned at various points in time. Following abandonment, the fields had been undergoing 5–60 yr of natural restoration with the aid of active management practices such as controlling competitive vegetation, thinning stands, and providing supplemental irrigation to assist recovery. The pioneer stage, characterized by herbaceous plant communities, has been restored for 5 yr since its abandonment. Subsequently, the early and mid-stages were dominated by trees with limited diversity and biomass, which had undergone recovery for 15 and 30 yr, respectively. Finally, the climax stage exhibited high diversity and biomass, achieved through over 60 yr of restoration.

Field sampling

The field survey was conducted in August 2020. Four experimental plots were designated for each stage, selected with elevations ranging from 1600 to 1683 m to mitigate climatic and topographic variations. In forests (early, mid, and climax stages), we established 30 m × 40 m plots and recorded the height and diameter at breast height (DBH) of each tree taller than 1.5 m. To avoid neighboring effects and spatial autocorrelation, the horizontal interval between any two plots was maintained at 50 m. In grasslands (pioneer stage), 1 m × 1 m plots were designated, with a 20 m horizontal interval between each plot, to measure species coverage, number, average height, and maximum height. The information reflecting the conditions at various stages of restoration is presented in Table S1. In each plot, importance values were calculated to confirm the dominant species based on three descriptors of abundance: frequency, quantity (number of individuals) and coverage (Avolio *et al.*, 2019). The dominant plant species in each plot were selected as target species for sampling. A total of 105 species from 49 families were collected across four restoration stages, representing 41 species in grassland (pioneer stage) and 64 species in forests (33 species in the early stage, 30 species in the mid-stage, and 40 species in the climax stage) (Table S2). Soil samples were collected from the 0–15 cm layers using a 5-cm diameter auger at 20–30 random points in each forest plot and at five points in each grassland plot. These samples were then mixed to get one composite sample per plot.

Functional trait analysis

Plant traits We focused on nine plant traits reflecting the PES (Wright *et al.*, 2004; Reich, 2014; Bergmann *et al.*, 2020). We randomly selected five to ten individuals per woody species and 15 to 20 individuals per herbaceous species within the experimental plots to measure these traits. Plant leaf and root samples were collected following the standardized protocols by Cornelissen *et al.* (2003) and Freschet *et al.* (2021). For each species, 20–50 fully expanded and undamaged leaves were selected. These samples were then placed in labeled bags. Leaves were scanned using a scanner (EPSON V19; Epson, Suwa, Japan) to estimate leaf area, then oven-dried at 70°C for a minimum of 72 h and weighed to determine leaf dry weight. Leaf mass per area (LMA, g m^{-2}) was calculated as the ratio of leaf dry weight to leaf area. Leaf N concentration (N_{leaf} , %) were gathered using the Sercon Integra 2 elemental analyzer (Sercon Ltd., Crewe, UK). Leaf lignin concentration ($\text{Lignin}_{\text{leaf}}$, %) were measured using the Van Soest method (Van Soest & Wine, 1967). Root samples were obtained from each woody plant by tracing roots from the plant basal stem, while root systems of 30–50 well-developed individuals were carefully dug out for each herbaceous plant. All root samples were transported to the laboratory within a few hours for further processing. In the laboratory, the root samples were carefully washed to remove adhering soil particles, scanned to images using an EPSON LA2400 scanner (Epson), and then oven-dried at 70°C for at least 72 h to determine root dry weight. Subsequently, root images were analyzed using WINRHIZO 2004a software (Regent Instruments, Quebec, QC, Canada) to obtain root length, volume, area, and diameter (RD, mm). Specific root length (SRL, m g^{-1}) was the ratio of the total root length and root dry weight, and specific root area (SRA, $\text{cm}^2 \text{g}^{-1}$) was the total root area per unit root dry weight. Root C (C_{root} , %) and N concentration (N_{root} , %), as well as P concentration (P_{root} , %), were determined using the Sercon Integra 2 elemental analyzer (Sercon Ltd.) and inductively coupled plasma spectroscopy (ICP-OES, Agilent 710; Agilent Technologies, Palo Alto, CA, USA), respectively.

Nematode traits From the composite soil sample collected at each site, nematodes were extracted from 100 g of fresh soil using a sequential extraction procedure (Liu *et al.*, 2008). Nematode counting was conducted utilizing a stereomicroscope (SMZ-168; Motic, Xiamen, China), with the first 200 nematodes in each sample identified to the genus level under a light microscope (magnification range: 400–1000 \times ; Olympus BX50, Tokyo, Japan) according to Bongers (1988) and Yin (1998). If the sample contained < 200 nematodes, all nematodes were identified. For trait measurements, we selected 10–30 individuals from each genus and focused on traits that reflect the NES (Zhang *et al.*, 2024), including length (μm), diameter (μm), and specific nematode biomass (SNB, μg per ind). Body length (distance from mouth to tail) and diameter (widest part of the body) were measured with the image processing software MOTIC IMAGES PLUS 3.0. Biomass (μg) was estimated using the Andrassy formula ($\text{length} \times \text{diameter}^2 \times 1.6 \times 10^{-6}$) (Ferris, 2010a,b). SNB

(biomass per individual) was calculated as the ratio of total biomass of each nematode genus to its abundance.

Soil microbial traits Soil microbial CUE was determined using the ^{18}O - H_2O tracer method (Spohn *et al.*, 2016). Initially, 8 g of fresh soil was placed in a respiration bottle, sealed with plastic wrap, and incubated for 7 d. Moisture content was monitored and adjusted to maintain consistency with natural field conditions. Subsequently, two replicates, each comprising 0.5 g of cultured soil, were preincubated in 2 ml vials. One replicate was enriched with ^{18}O - H_2O to reach 20% ^{18}O enrichment, while the other received the same volume of ^{16}O - H_2O . All soil samples were then transferred into 20 ml incubation containers and incubated for 24 h. Additionally, three soil-free bottles serve as controls for CO_2 determination. After the 24-h incubation period, 10 ml gas samples were collected with a syringe, and the CO_2 concentration was analyzed using a gas chromatography (Agilent 7890A; Agilent Technologies). The vials were subsequently closed, frozen using a lyophilizer, and stored at -80°C until DNA extraction. DNA extraction was performed using a DNA extraction kit (DNeasy PowerSoil Pro Kit) following the manufacturer's instructions, with DNA concentration quantified using a NanoDrop ND-1000 spectrophotometer (Thermo Scientific, Waltham, MA, USA). Furthermore, the ^{18}O abundance was assessed using a MAT253 isotope-ratio mass spectrometer coupled with an elemental analyzer (FLASH 2000; Thermo Fisher Scientific, Waltham, MA, USA). CUE was calculated using equations presented by Zheng *et al.* (2019).

Microbial biomass was determined using phospholipid fatty acids (PLFAs) analysis, as described by Frostegård *et al.* (1991). Briefly, fatty acids were extracted from 8 g freeze-dried soil samples with a chloroform/methanol/citrate buffer (1/2/0.8 v/v/v). Lipid classes and phospholipids were separated by solid-phase extraction tubes (ANPEL Laboratory Technologies Inc., Shanghai, China), and the fatty acid methyl esters were quantified by gas chromatography (6850; Agilent Technologies). The sum of i-15 : 0, a-15 : 0, 16 : 0, i-16 : 0, 16:1 ω 7c, cy-17 : 0 ω 7c, 18:1 ω 7c, 16:1 ω 5, 18:1 ω 9c, 18:2 ω 6c, 14 : 0, 16 : 0, 17 : 0, 18 : 0, and 20 : 0 was used to represent microbial biomass (Joergensen, 2022).

Soil organic carbon

Soil organic carbon content was analyzed using the Sercon Integra 2 elemental analyzer (Sercon Ltd.). Before analysis, the soil samples were pretreated with 1 M hydrochloric acid to remove inorganic C (Paul *et al.*, 2006).

Statistical analysis

Data analyses were conducted using R software 4.3.3 (R Core Team, 2023). First, all plant and nematode traits were log-transformed to meet standard assumptions of homoscedasticity and normality. One-way ANOVA with Fisher's least significant difference (LSD) tests were adopted to assess the variation of plant traits, nematode traits, microbial traits and SOC contents among different restoration stages.

Second, the fast–slow axes of plant and nematode community-level traits across restoration stages were identified by performing principal component analyses (PCA) on the covariance matrix using the *VEGAN* package (Oksanen *et al.*, 2019). Generally, plants with ‘fast’ strategies exhibit high SRL and SRA, and high concentrations of leaf and root N, as well as root P, while ‘slow’ plants have high LMA, high diameter roots, and concentrations of root C and leaf lignin (Wright *et al.*, 2004; Reich, 2014). Similarly, ‘fast’ nematodes tend to have smaller length and width with low SNB, whereas ‘slow’ nematodes display the opposite traits (Zhang *et al.*, 2024). The community-weighted mean (CWM) values for plant and nematode traits were calculated as follows: plant CWM was determined based on the importance values ((relative frequency + relative quantity + relative coverage)/3) derived from plant communities, while nematode CWM relied on relative abundance within their communities. PCAs were then performed to identify the fast–slow axis at the community level using CWM trait values for: (1) only plant traits, (2) only nematode traits, and (3) plant and nematode traits, together.

Third, the scores of the first axis were extracted from the PCAs because they captured 75.6–96.8% of the variation, making them suitable proxies for the fast–slow spectra. Furthermore, to evaluate which fast–slow spectrum was the most important and credible predictors of SOC, we performed a classification random forest analysis (RFs) employing the *rffPermute* function within the *RFPERMUTE* package. In the RFs, the plant fast–slow trait spectrum, the nematode fast–slow trait spectrum, and the integrated plant and nematode fast–slow trait spectrum were included as predictors of CUE, microbial biomass, and SOC. The significance of each predictor was evaluated through 5000 permutations of response variables using the *rffPermute* function. Moreover, we assessed the significance values of the overall model using the *a3* function within the *A3* package. Furthermore, we used variation partitioning analysis and Venn diagrams (Borcard *et al.*, 1992) to partition the unique and joint contributions of the plant fast–slow trait spectrum and the nematode fast–slow trait spectrum to CUE, microbial biomass, and SOC. The analyses were conducted utilizing the *varpart* function within the *VEGAN* package.

Finally, structural equation modeling (SEM) using the *LAVAN* package (Rosseel, 2012) was conducted to analyze direct and indirect effects of the integrated plant and nematode fast–slow trait spectrum on SOC. In the model, a direct effect is indicated by a single-headed arrow pointing from the integrated fast–slow trait spectrum to SOC, whereas the indirect effects of the integrated fast–slow trait spectrum on SOC are mediated by soil microbial traits (microbial CUE and microbial biomass). Initially, *a priori* models were constructed (Fig. 1b). Furthermore, we used PC1 of the PCA of plant–nematode traits, which explained 78.4% of the total variation, to represent the integrated plant and nematode fast–slow trait spectrum. The quality of the SEM model was evaluated using degrees of freedom (df), the chi-square goodness-of-fit statistic ($P > 0.05$ indicate statistically significant model fit), the comparative fit index (CFI), and the standardized root mean square residual (SRMR), and the root mean square error of approximation (RMSEA).

Results

Variation of individual-level traits during natural restoration

Most plant and nematode traits differed significantly across the pioneer, early, mid and climax stages of restoration ($P < 0.05$, Fig. 2). Traits linked with a fast strategy at the pioneer stage, such as high N_{leaf} , SRL, SRA, N_{root} , and P_{root} (Fig. 2a), displayed negative loadings on PC1 (Fig. S2a). Conversely, traits associated with a slow strategy at the climax stage, including high C_{root} , RD, $\text{Lignin}_{\text{leaf}}$, and LMA for plants (Fig. 2a), as well as high diameter, length, and SNB for nematodes (Fig. 2b), exhibited positive loadings on PC1 (Fig. S2).

Covariation in community-level plant and nematode traits

Trait variation along the first axis of the PCAs identified the fast–slow spectra of plants (PC1: 75.6% variance, Fig. 3a), nematodes (PC1: 96.8% variance, Fig. 3b), and plant and nematode together (PC1: 78.4% variance, Fig. 3c). Plant communities were arrayed along an axis representing variation from ‘fast’ to ‘slow’ traits (and thus ecological strategies), with fast communities characterized by species associated with high N, P concentration, SRL, and SRA, and slow communities comprised of species with higher C and lignin concentration, as well as larger RD and LMA (Figs 3a, S3a). This corresponded neatly to stage in the restoration chronosequence. Similarly, there was an axis from Climax sites with slow nematode communities dominated by larger length and diameter, as well as higher SNB, to Pioneer sites with fast communities consisting of smaller-bodied nematodes with lower SNB (Figs 3b, S3b). Moreover, the covariation of plants and nematodes showed a slow-fast axis, where distinct trait syndromes characterized fast to slow communities (Fig. 3c).

Effects of the integrated fast–slow plant and nematode economics spectrum on microbial traits and SOC

Microbial CUE and biomass generally increased from pioneer to climax stages, ranging from 0.25 to 0.85 and from 50.4 to 168.4 nmol g^{-1} soil, respectively ($P < 0.05$, Fig. 4a,b). Similarly, SOC content generally increased across the pioneer, early, mid and climax stages, ranging from 39.4 to 118.2 g C kg^{-1} soil ($P < 0.05$, Fig. 4c). Soil physiochemical properties also significantly varied across restoration stages (Table S3). Ranking the importance of the spectra of plants, nematodes, and plant and nematode together according to the Random Forest models, the results identified that the integrated economics spectrum was generally the most important predictors of CUE ($r^2 = 0.80$, $P < 0.001$; Fig. 5a), microbial biomass ($r^2 = 0.73$, $P < 0.001$; Fig. 5b) and SOC ($r^2 = 0.72$, $P < 0.001$; Fig. 5c). Variation partitioning analysis revealed that the PES and the NES together accounted for 91%, 87% and 84% of the total variation in CUE, microbial biomass and SOC, respectively (Fig. 6). The common patterns of variation in the fast–slow spectra of plants and nematodes (the joint effects) explained 88% (Fig. 6a), 83% (Fig. 6b), and 76% (Fig. 6c) of the total variation.

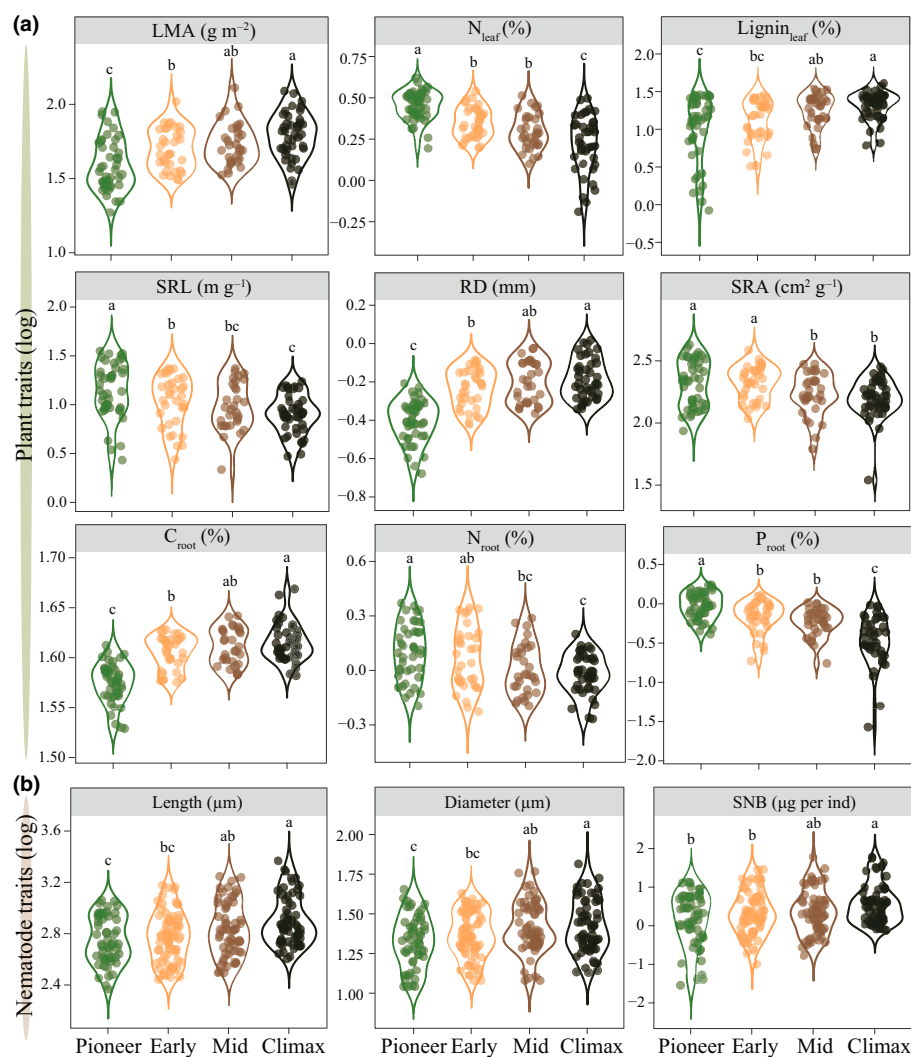


Fig. 2 Violin plots illustrating distributions of plant traits (a) and nematode traits (b) across the pioneer, early, mid, and climax stages of restoration. Each data point represents a plant species or nematode genus. Different letters indicate significant differences (LSD test, $P < 0.05$; note the logarithmic scale on the y-axis of plant and nematode traits). Whiskers in violin plots indicate the range of the data and points beyond the whiskers are outliers. Abbreviations for traits are as follows: C_{root} , root carbon concentration; $\text{Lignin}_{\text{leaf}}$, leaf lignin concentration; LMA, leaf mass per area; N_{leaf} , leaf nitrogen concentration; N_{root} , root nitrogen concentration; P_{root} , root phosphorus concentration; RD, root diameter; SNB, specific nematode biomass; SRA, specific root area; SRL, specific root length.

SEM demonstrated the initially conceptualized *a priori* model was a good fit for our data (degrees of freedom = 1, P -value = 0.403, SRMR = 0.006, CFI = 1.000, RMSEA < 0.001; Fig. 7). Specifically, our SEM revealed that the integrated plant and nematode fast–slow trait spectrum directly and/or indirectly regulated SOC. This spectrum exhibited a strongly positive association with CUE (covariance coefficient = 0.96) and microbial biomass (covariance coefficient = 0.34, Fig. 7). By increasing CUE and microbial biomass, the fast–slow trait spectrum indirectly promoted high-SOC dynamics (covariance coefficient = 0.57, Fig. 7). In addition to this indirect regulation of SOC via microbial traits, plant and nematode fast–slow trait spectrum directly controlled the SOC dynamics (covariance coefficient = 0.37, Fig. 7).

Discussion

Coordination between plant and nematode traits?

This study is the first empirical attempt to investigate the coordination between plant and nematode traits, as well as their

connections with microbial traits and SOC dynamics. Specifically, it highlights the existence of an integrated fast–slow axis of plants and nematodes, aligning with previously identified fast–slow trade-offs in the PES and NES (Wright *et al.*, 2004; Reich, 2014; Zhang *et al.*, 2024). This extends the knowledge of prior studies that investigated the coordinated responses of nematode trophic groups and ecological indices to plant traits (Dietrich *et al.*, 2020; Otfinowski & Coffey, 2020; Zhang *et al.*, 2020, 2022a,b), thereby demonstrating the tight functional linkages between aboveground and belowground moieties or attributes of the ecosystem (Wardle *et al.*, 2004; Neyret *et al.*, 2024).

The observed covariation in plant and nematode traits provided compelling evidence for synchronous changes in plants and nematodes during natural restoration (Figs 2, 3), ranging from small-bodied organisms characterized by fast resource acquisition and metabolic activities in the pioneer stage to large and slow-growing organisms in the climax stage, consistent with our first hypothesis. The theoretical framework of the fast–slow strategies and traits is well-established in plants (Wright *et al.*, 2004; Reich, 2014; Díaz *et al.*, 2016; Salguero-Gómez *et al.*, 2016),

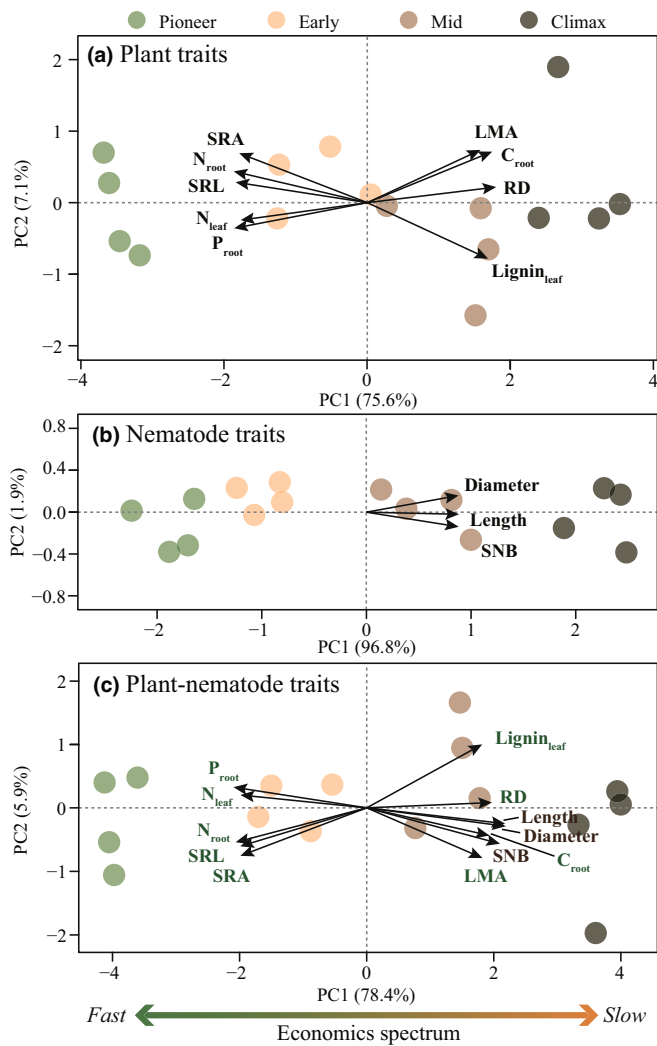


Fig. 3 Principal components analyses (PCA) of community-level plant traits (a), nematode traits (b), and integrated plant and nematode traits (c) across the pioneer, early, mid, and climax stages of restoration. In (c), each trait was weighted as $1/n$, with n representing the number of traits available for plants and nematodes, so that they are weighted equally. Each data point represents a plot. Abbreviations for traits are as follows: C_{root} , root carbon concentration; $\text{Lignin}_{\text{leaf}}$, leaf lignin concentration; LMA, leaf mass per area; N_{leaf} , leaf nitrogen concentration; N_{root} , root nitrogen concentration; P_{root} , root phosphorus concentration; RD, root diameter; SNB, specific nematode biomass; SRA, specific root area; SRL, specific root length.

and has shown potential linkages with ecosystem C cycling (Roumet *et al.*, 2016; De Long *et al.*, 2019; Xu *et al.*, 2021; Ridgeway *et al.*, 2022). However, such theories are still in their infancy for soil nematodes, and it is crucial to utilize diverse trait indices to fully elucidate nematode ecological strategies and to establish links with C cycling (Du Preez *et al.*, 2022).

Here, we leveraged two functional attributes – abundance and biomass – to quantify the nematode biomass per individual (specific nematode biomass, SNB). Our findings revealed significant relationships among SNB, nematode economic traits, and SOC (Fig. S4), indicating that nematodes with low SNB favor fast

growth and rapid returns on investment in resource acquisition and metabolism, while those with high SNB exhibit the contrasting performance. Similarly, SNB emerges as a significant predictor of microbial traits (Fig. S5), implying its potential role in top-down forces regulating microbial metabolism and production. This is likely due to variations in abundance and biomass reflecting nematode activities and performance and being tightly linked to plants, microbes, and C cycling (Ritz & Trudgill, 1999; Ferris, 2010a,b; van den Hoogen *et al.*, 2019). Our finding allows us to utilize SNB for mirroring nematode growth, reproduction, and survival strategies, while also generating insights into its role as predictors of C cycling. This highlights the need to develop informative nematode traits that effectively capture the cost–benefit principles and comprehensively understand C cycling, which are both theoretically and practically essential for advancing in belowground trait ecology.

Disentangling trait drivers of SOC dynamics

Consistent with our second hypothesis, joint consideration of plant and nematode traits, that is the integrated fast–slow trait spectrum, explained more variation in SOC than considering either plants or nematodes alone, which emphasizes the potential value of extending the trait-centric view that spans from plants to soil organisms to fully understanding C cycling. We provide evidence that the integrated fast–slow trait spectrum is a good predictor of SOC, and the joint effect of the PES and NES explains the majority of the total variation in SOC (Figs 5, 6). This is presumably because of the close linkages between plant and nematode attributes, resulting in a tight alignment between the NES and PES (Zhang *et al.*, 2024). Consequently, it is reasonable to expect a higher joint contribution to SOC dynamics from the PES and NES than their unique contributions. Furthermore, plant–nematode coordination corresponded to SOC through steering microbial traits, as indicated in SEM (Fig. 7). Coordination at the slow end of the fast–slow spectrum is known to be related to reduced metabolic activities, lower tissue resource contents, and slower turnover rates (Wardle *et al.*, 2004; Yvon-Durocher & Allen, 2012; Neyret *et al.*, 2024), cascading to microbes that allocate more C to biomass formation and less to respiration, resulting in higher C use efficiency and biomass (Wan *et al.*, 2021; C. Wang *et al.*, 2021). Subsequently, the combined effects of slow plants, nematodes, and microbes are associated with increased SOC contents in the climax stage. Conversely, coordination characterized by fast strategies mirrors low-SOC formation in the pioneer stage. Finally, our findings revealed that two plant and nematode traits, N_{leaf} and body diameter, serve as key predictors of both microbial traits and SOC (Fig. S5), highlighting that restoration practitioners in this region with such highly diverse biodiversity could utilize variations in plant leaf N concentration and nematode diameter as indicators to monitor and assess restoration trajectories.

The variations in microbial traits corresponded to a transition in microbial communities from a fast, metabolically wasteful strategy in the pioneer stage to a slower, oligotrophic strategy in the climax stage (Fig. 4). This sheds light on how plant,

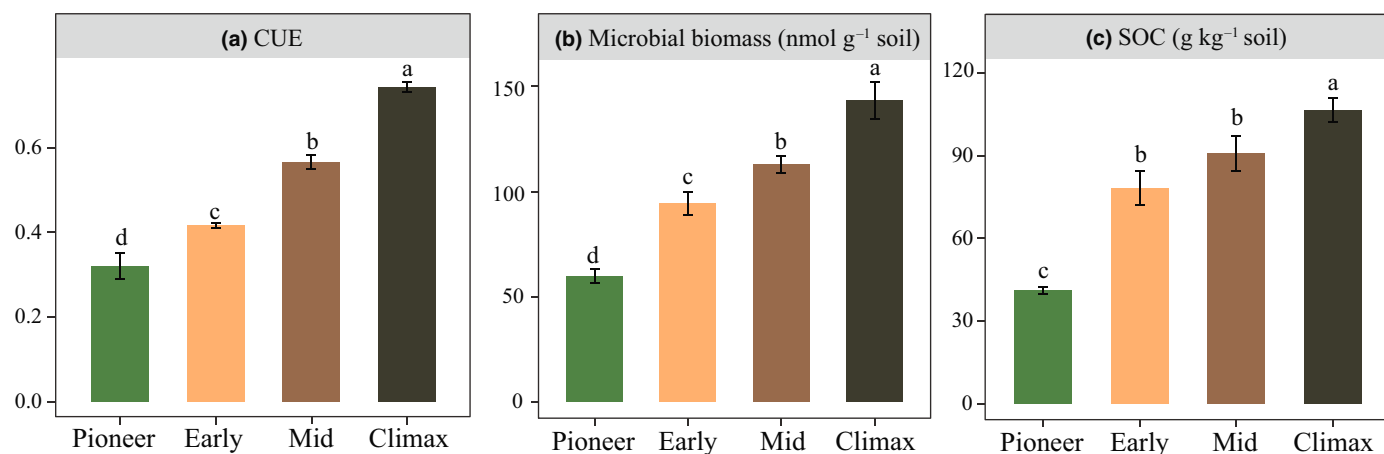


Fig. 4 Microbial C use efficiency (CUE, a), microbial biomass (b), and soil organic carbon (SOC, c) across the pioneer, early, mid, and climax stages of restoration. Bars (means \pm SE, $n = 4$) with different letters indicating significant differences (LSD test, $P < 0.05$).

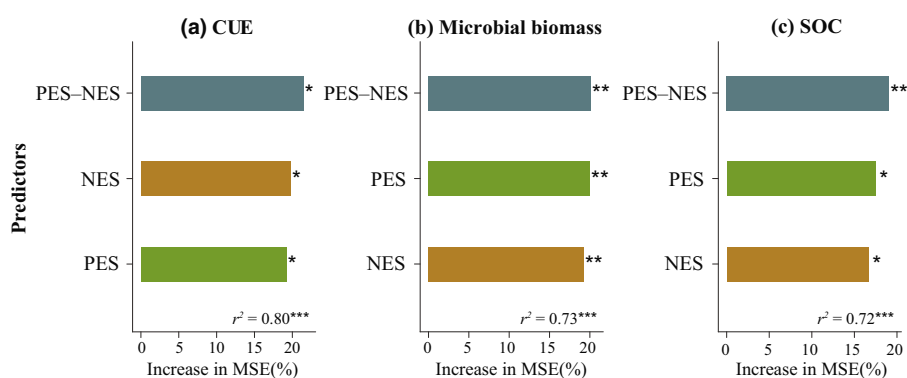


Fig. 5 The relative importance of predictors in the random forest model predicting microbial C use efficiency (CUE, a), microbial biomass (b), and soil organic carbon (SOC, c). Percentage increases in the MSE (mean squared error) of the three spectra were used to estimate the importance of these predictors, and higher MSE% values implied more important predictors. In all panels, the P -values are indicated by asterisks: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. NES, nematode economics spectrum; PES, plant economics spectrum; PES-NES, integrated plant and nematode economics spectrum.

nematode and microbial traits interact to mechanistically influence SOC during restoration efforts (Fry *et al.*, 2019; Schmitz & Leroux, 2020). Evidence suggests that microbial traits exhibit high plasticity in response to plant and nematode attributes through bottom-up and top-down regulations (Leff *et al.*, 2018; Thakur & Geisen, 2019; Defrenne *et al.*, 2021; Spitzer *et al.*, 2021; Wang *et al.*, 2022; Jiang *et al.*, 2023). First, slow plants prioritize C allocation toward dense structures, producing recalcitrant litter such as lignin, which enhances microbial biomass retention (De Deyn *et al.*, 2008). Second, plant diversity and biomass peak at the climax stage boost plant-derived C input into the soil, improving microbial C use efficiency and biomass (Duan *et al.*, 2023), thereby contributing to SOC dynamics (Manzoni *et al.*, 2012; Guo *et al.*, 2021; Xiao *et al.*, 2024). Third, larger nematodes with high SNB released excess nutrients, such as mineral N, influencing microbial resource acquisition strategies and regulating microbial communities to preserve more C substrate within their biomass (Jiang *et al.*, 2017; Zhu *et al.*, 2018; S. Wang *et al.*, 2021). Overall, our findings suggest that the coordination of plant and nematode traits, as

demonstrated in our SEM (Fig. 7), can meaningfully associate with microbial traits and SOC dynamics as natural restoration progresses. Further research deserves attention to a broader collection of microbial traits, such as maximum growth rate, genome size and C and N stable isotope, which are tightly linked to plant and nematode resource-use strategies (Ruess & Chamberlain, 2010; Westoby *et al.*, 2021; Yang, 2021), to better understand the trophic interactions across taxa and how these interactions cascade to ecosystem C cycling, complementing insights gleaned from plant- and nematode-centric trait-based research.

Implications for trait-informed restoration

Traditional restoration projects often consider aboveground and belowground components of ecosystems in isolation (Crouzeilles *et al.*, 2016; Guan *et al.*, 2018; Wang *et al.*, 2022). However, there is increasing recognition of the primary role played by aboveground–belowground linkages in controlling ecosystem functioning (Bardgett & Wardle, 2010; Kardol & Wardle, 2010;

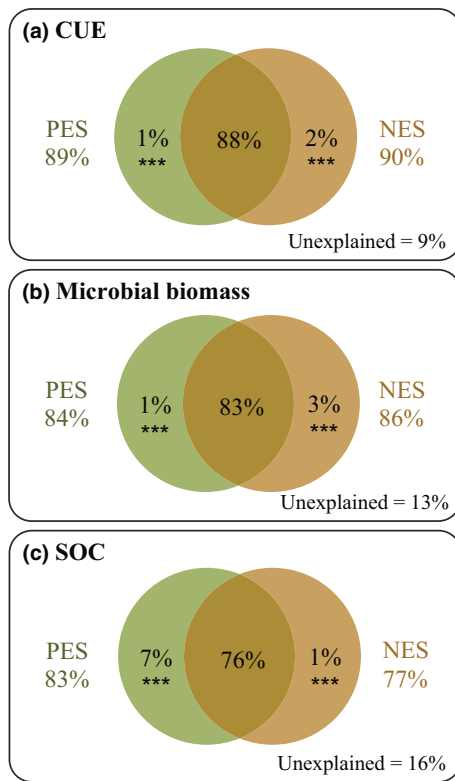


Fig. 6 Variance partitioning used to reveal explained variation of the plant economics spectrum (PES), the nematode economics spectrum (NES), and their joint effect with microbial C use efficiency (CUE, a), microbial biomass (b), and soil organic carbon (SOC, c). The total percentage of the explained variation of each factor is shown. Significant values were tested by 999 permutations with repetitions. The *P*-values are indicated by asterisks: ***, *P* < 0.001.

van der Putten *et al.*, 2016). In the current context of highly diverse forests facing intense anthropogenic disturbance, our study highlights that the interplay between the aboveground and belowground organisms could help to establish a trait-based criterion for assessing restoration trajectories based on the fast–slow strategies and their trait proxies of plants and nematodes. Notably, plant–nematode coordination closer to the slow end of the fast–slow spectrum signifies better restoration performance that has the capability to retain more C and mitigate climate change. These insights offer valuable information for restoration practitioners, enabling them to monitor whether restoration trajectories are progressing in the right direction. Subsequently, they can make trait-informed choices in forest management, tailored to effectively address local needs. However, caution must be exercised when generalizing the results of our case study. The mounting evidence of a multidimensional root trait space influenced by multiple environmental constraints (Weemstra *et al.*, 2016) was first empirically demonstrated by Kramer–Walter *et al.* (2016). Subsequent studies have further confirmed another dimension of root traits (Bergmann *et al.*, 2020; Carmona *et al.*, 2021; Weigelt *et al.*, 2021; Klimešová & Herben, 2023). Similarly, nematodes are subjected to multiple constraints in the soil (Yeates, 2003), implying the existence of additional dimensions

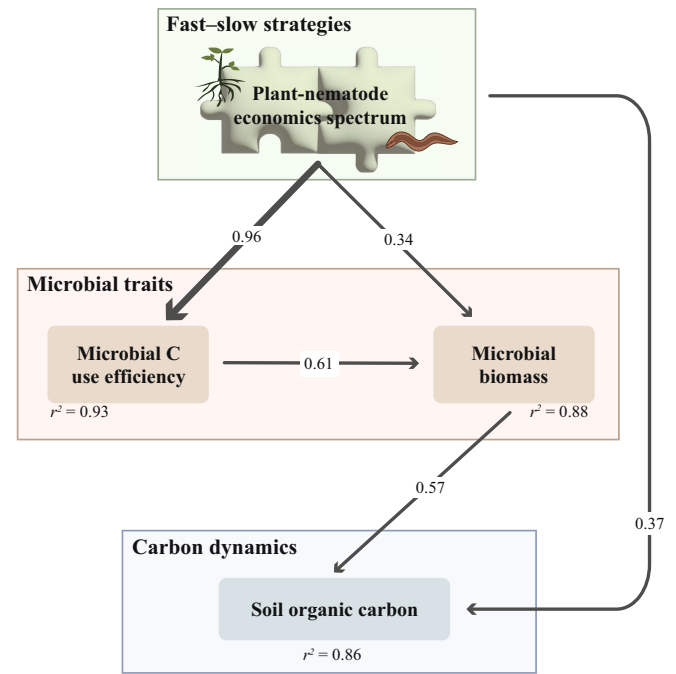


Fig. 7 Structural equation model (SEM) used to evaluate the direct and indirect effects of the integrated plant and nematode fast–slow spectrum on soil organic carbon (SOC) as mediated by effects on microbial C use efficiency (CUE) and microbial biomass. The scores of PC1 in Fig. 3(c) were used to represent the plant–nematode fast–slow spectrum. Results of a goodness-of-fit analysis of the model: degrees of freedom = 1, *P*-value = 0.403, standardized root mean square residual = 0.006, comparative fit index (CFI) = 1.00, and root square mean error of approximation (RMSEA) < 0.001. The width of arrows is proportional to the strength of path coefficients (standardized coefficients). Numbers next to the arrows represent the path coefficients. *r*² values denote the amount of variance explained by the model for the response variables.

within nematode ecological strategies, thus suggesting a multidimensional plant–nematode trait framework. Therefore, we encourage future studies to thoroughly embrace a multidimensional aboveground–belowground framework that integrates other soil organisms for a more nuanced evaluation of restoration trajectories. This could be achieved by actively incorporating larger sample sizes across multiple sites and climatic conditions, covering various trait variations, temporal and spatial scales, and ecosystem types.

Conclusion

Our results establish an empirical coordination between the ecological strategies of plants and nematodes by connecting different puzzle pieces of plant and nematode traits. The analyses further revealed that plant and nematode traits jointly explain more of the variation in SOC dynamics than the traits of either of the two groups alone. The integrated fast–slow trait spectrum plays a crucial role in predicting C cycling by regulating microbial traits, highlighting the significance of functional linkages between aboveground and belowground communities as a monitoring tool for providing trait-informed predictions of restoration trajectories and enhancing our understanding of incorporating

belowground traits into biogeochemical cycle models. Moreover, the current study provides insights into integrating the traits and ecological strategies of plants and soil organisms to develop NbS that could aid in meeting the global targets of the United Nations Decade on ecosystem restoration (2021–2030).

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Competing interests

None declared.

Author contributions

TZ, CZ and ML conceived the idea of this study. CZ, TZ, NL and XC performed the experiments. CZ and NL analyzed the data and prepared the original manuscript with the help of UNN, IJW, XC and ML. All authors significantly revised the manuscript and approved it for submission.

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Data availability

The data that support the findings of this study can be accessed on Figshare at doi: [10.6084/m9.figshare.27015031](https://doi.org/10.6084/m9.figshare.27015031).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Schematic illustration to demonstrate the four restoration stages and their dependencies in this study.

Fig. S2 Principal components analyses (PCA) of individual-level plant traits (a) and nematode traits (b) across the pioneer, early, mid, and climax stages of restoration.

Fig. S3 Community-level plant traits (a) and nematode traits (b) across the pioneer, early, mid, and climax stages of restoration.

Fig. S4 The heatmap shows relationships between plant traits, nematode traits, microbial traits, and soil organic carbon.

Fig. S5 Variable importance ranking of plant and nematode traits in the random forest model predicting microbial C use efficiency (CUE, a), microbial biomass (b), and soil organic carbon (SOC, c).

Table S1 The number of species, average height and average diameter at breast height (DBH) across the pioneer, early, mid, and climax stages of restoration.

Table S2 List of sampled plant species across the pioneer, early, mid, and climax stages of restoration.

Table S3 Soil physiochemical properties across the pioneer, early, mid, and climax stages of restoration.

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