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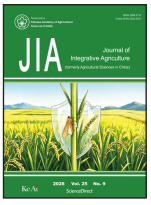

RESEARCH ARTICLE

Macroaggregates magnify the positive feedback of trophic cascades on soil organic carbon accrual

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Highlights

- Fungivorous nematodes enhanced fungal-derived carbon accrual *via* trophic cascade.
- Macroaggregates magnified trophic cascade effects on soil fungal carbon accrual.
- Manure amendments strengthened nematode-fungus interactions and soil organic carbon (SOC) accrual.

Abstract

The interactions between nematodes and fungi are important for soil carbon cycling. However, their cascading effects on soil organic carbon (SOC) accrual remain unclear, particularly the role of soil aggregates and manure amendments in mediating this trophic cascade. Using a 19-year fertilization experiment, we examined how nematode predation influences fungal necromass carbon (FNC) and glomalin-related soil proteins (GRSPs), and quantified their contributions to SOC across soil aggregates under different manure amendments. Our findings showed that nematode predation significantly enhanced fungal biomass and promoted deterministic assembly of fungal communities. These effects were strongly dependent on aggregate size, with the most pronounced responses observed in the large macroaggregate (LA) fraction. A complementary microcosm experiment confirmed that nematode predation increased fungal biomass by over 6%, particularly in the LA fraction. Manure amendments further stimulated fungal growth and reinforced deterministic community assembly, thereby enhancing trophic cascade-driven accrual of FNC and GRSPs. Of the two fungal-derived carbon sources, FNC contributed more substantially to SOC (40%) than GRSPs (17%), with the greatest contribution found in the LA fraction. Path analysis further revealed that nematode-induced changes in fungal communities mediated the positive effects of manure amendments on fungal-derived carbon accrual. Overall, these findings underscore the pivotal role of nematodes in driving positive trophic cascade impact on SOC accrual. Our study offers new insights into aggregate-scale carbon dynamics and biologically mediated strategies for soil carbon management.

Keywords: fungal communities, fungivorous nematodes, biomass, assembly process, fungal-derived products, SOC accrual

1. Introduction

Soil organic carbon (SOC) accrual is a fundamental mechanism underpinning the maintenance of soil fertility and the regulation of global carbon balance (Ling *et al.* 2025). In recent years, increasing evidence showed that fungi play a central role in mediating SOC accrual (Kennedy and Maillard 2023; Trejos-Espeleta *et al.* 2024). Fungi contribute to SOC not only by decomposing complex plant

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polymers into recalcitrant compounds, but also by forming microbial carbon fractions through necromass deposition and the secretion of glomalin-related soil proteins (GRSPs), thereby promoting long-term carbon stabilization (Liang *et al.* 2017; Irving *et al*. 2021; Camenzind *et al*. 2023). Fungal necromass — comprising dead fungal biomass — has emerged as a dominant source of stable microbial residues in soils, accounting for an estimated 23–87% of total SOC (Liang *et al.* 2019). Similarly, GRSPs, a complex mixture of proteins, lipids, and phenolic compounds, are increasingly recognized for enhancing carbon persistence through their role in aggregate stabilization (Holátko *et al.* 2021; Zhao *et al.* 2025). Despite these insights, a mechanistic understanding of fungal-derived carbon accrual across soil aggregate fractions remains limited, particularly neglecting the regulatory influence of higher trophic-level organisms (e.g., fungivorous nematodes) within soil food webs.

Nematodes are among the most abundant organisms in soils, occupying an intermediate trophic level and playing a crucial role in soil food webs (Gong *et al.* 2024; Liu *et al.* 2024). In particular, their predation on microbes can trigger cascading effects on microbial functions, including plant growth and productivity (Jiang *et al.* 2020). However, their influence on SOC accrual, especially through interactions with fungi, remain poorly understood. To elucidate the influence of trophic cascades on SOC dynamics, it is essential to investigate how nematode predation affects fungal communities. Nematode predation may regulate fungal communities through two main pathways: (1) top-down regulation of fungal biomass, and (2) modulation of fungal community assembly processes (Wang *et al.* 2024). Recent evidence indicates that under appropriate nematode predation pressure, fungi may exhibit compensatory growth, which may promote fungal carbon accrual (Crowther *et al.* 2012; Zhang *et al.* 2025). In addition, predation may modulate the fungal community assembly dynamics (Huang *et al*. 2021). In community ecology, species assembly is generally govern by the interplay between stochastic and deterministic processes (Stegen *et al.* 2013; Luan *et al.* 2020). Stochasticity reflects the random fluctuations in community composition, while determinism lead to structured, predictable community patterns driven by environmental filtering or biotic interactions (Hubbell 2005; Dini-Andreote *et al.* 2015). However, the application of community assembly theory to SOC cycling remains underdeveloped. Additionally, the relative importance of biomass regulation and community assembly modulation to nematode-driven fungal carbon accrual remains unclear.

Agricultural management practices and environmental factors can affect trophic interactions between nematodes and microbes, thereby modulating trophic cascade effect. Long-term manure application can enhance nutrient availability and restructure soil food web by promoting biomass of nematodes and microbes, increasing predation pressure, and strengthening trophic interactions *(*Jiang *et al.* 2020; Cao *et al.* 2024; Zhu *et al.* 2024). While such changes are likely to influence cascading effects in agricultural ecosystems, their impacts remain insufficiently evaluated, especially in the context of the spatial heterogeneity of soil aggregates (Jiang *et al.* 2023; Yao *et al.* 2024). Soil aggregates function as microhabitats with distinct spatial variability in properties such as pore architecture and oxygen availability (Yao *et al.* 2024; Zhang *et al.* 2025), which play a critical role in regulating trophic interactions (Rillig *et al.* 2017; Erktan *et al.* 2020). Macroaggregates, characterized by greater pore connectivity and higher oxygen concentrations, facilitate fungal hyphal extension and nematode migration, thereby creating favorable niches for fungi–nematode interactions (Liao *et al.* 2022; Yudina and Kuzyakov 2023). In contrast, microaggregates with smaller pore sizes constrain nematode mobility and reduce opportunities for nematode–fungi interactions (Jiang *et al.* 2017). However, how aggregate size influences the two trophic cascade pathways — and how these pathways respond to manure application and ultimately affect SOC accrual — remains poorly investigation.

Here, we aimed to elucidate the mechanisms by which nematode predation influences fungal communities and regulates SOC accrual through cascading effects under typical fertilization regimes, with a particular focus on aggregate-scale dynamics. We proposed two hypotheses: (i) fungivorous nematodes would enhance fungal biomass and promote deterministic community assembly, thereby facilitating the accrual of fungal necromass carbon and GRSPs, and (ii) manure amendments would magnify the trophic cascade effect on soil organic carbon accrual, with the strongest responses occurring in macroaggregates.

2. Materials and methods

2.1. Experimental design

The study was conducted at the Yingtan National Agroecosystem Field Experiment Station (Chinese Academy of Sciences), Jiangxi Province, China (28°15′20′′N, 116°55′30′′E), which is characterized by a subtropical climate (mean annual temperature: 17.6°C; precipitation: 1,795 mm). The soil, classified as Ferric Acrisol according to Food and Agriculture Organization System, was subjected to a long-term fertilization experiment spanning over 19 years. This field experiment included three manure treatments: (1) no manure (M0), (2) low manure (150 kg N ha^{-1} yr^{-1}; M1), and (3) high manure (600 kg N ha^{-1} yr^{-1}; M2). Each treatment was replicated three times in randomized concrete plots (2 m× 2 m). Pig manure (386.5 g kg^{-1} total C and 32.2 g kg^{-1} total N) was applied annually before maize sowing, with monoculture maize cultivated from April to July.

Soil samples were collected from the 0−20 cm layer after the maize harvest in July 2021. Five soil cores per plot were homogenized into a composite sample, transported on ice, and processed within 12 h. Visible debris was removed, and fresh soil was fractionated by dry-sieving into three aggregate sizes: large macroaggregates (>2,000 μm, LA), small macroaggregates (250−2,000 μm, SA), and microaggregates (<250 μm, MA) (Jiang *et al*. 2013). Soil moisture at the time of sampling was 13.2%, within the optimal range for aggregate stability (Mendes *et al.* 1999). The experimental design comprised 27 soil samples, representing 3 manure amendments, 3 aggregates fractions, and 3 biological replicates. Samples were systematically partitioned for chemical and biological analyses.

2.2. Soil fungal necromass and glomalin-related soil proteins

Amino sugars were extracted from soil samples following the protocol of Zhang and Amelung (1996) with a detailed description provided in the Appendix A. Four amino sugars were quantified: epichitosamine, muramic acid (MurA), galactosamine (GalN), and glucosamine (GluN). The carbon content of amino sugars was normalized to estimate fungal necromass (mg C kg^{-1} soil), using the equation provided by Appuhn and Joergensen (2006) and Wang *et al.* (2021):

$$\text{Fungal necromass C}=\left(\frac{\text{GluN}}{179.17}-2\times\frac{\text{MurA}}{251.23}\right)\times179.17\times9$$

where 179.17 represents the molecular weight of GluN, and 9 is the conversion factor used to derive fungal carbon form fungal GluN. Total extractable GRSP (T-GRSP) and easily extractable GRSP (EE-GRSP) were measured in each aggregate fraction using the method of Wright *et al.* (1998). Additional details on GRSP extraction and analysis were provided in the Appendix B.

2.3. MiSeq sequencing and processing

Total soil DNA was extracted from 0.5 g of soil using the PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA). The fungal internal transcribed spacer (ITS) region was amplified with primers ITS1F and ITS2R (Gardes and Bruns 1993) and sequenced on the Illumina MiSeq platform. Raw sequences data were processed using QIIME2 (Bolyen *et al.* 2019), and amplicon sequence variants (ASVs) were generated at 100% nucleotide similarity. Taxonomic classification was performed against the UNITE v. 8.0 database. ASV tables were rarefied to 32,293 reads per sample prior to fungal community analysis.

2.4. Determination of nematode types and abundance

Nematodes were extracted from 100 g of fresh soil using a modified Baermann funnel technique (Barker 1985) and quantified per 100 g of dry soil. Specimens were enumerated under 40× magnification, while community structure analysis was based on the taxonomic identification of at least 100 individuals per sample using 400–1,000× magnification. Fungivorous nematodes were identified through morphological characteristics of their feeding structures, including the stoma and esophagus. Predation pressure on fungal communities was determined as the ratio of fungivorous nematodes to fungal biomass, following Mathisen *et al.* (2016).

2.5. Microcosm experiment

A microcosm experiment was conducted to assess fungal biomass responses to predation by the fungivorous nematode *Aphelenchus*. Fresh soil samples were vortexed and suspended in sterile distilled water to prepare soil suspensions. These suspensions were centrifuged at 1,000×g for 10 min, and the resulting supernatants were filtered through 10 μm membranes to remove soil mesofauna. To suppress potential bacterial interference, bronopol was added, and the suspension was pre-incubated for 16 h (Pan *et al.* 2019). The dominant fungivorous nematode *Aphelenchus* was isolated from field soil at the experimental site and washed five times with sterile distilled water to minimize fungal contamination. Soil microcosms were established with four nematode inoculation densities (n=3 replicates per treatment): 0 (control), 20 (represent M0), 60 (represent M1), and 80 (represent M2) individuals per microcosm. Each 500-mL Mason jar contained 100 g of dry-weight-equivalent soil sterilized *via* γ-irradiation at 40 kGy. All microcosms received 10 mL of the prepared soil suspension and were incubated in darkness at 28°C for 30 days. After incubation, soil aggregates were fractionated for fungal biomass quantification and nematode enumeration.

2.6. Quantification of fungal abundance in soil aggregates and inside nematodes

Fungal biomass in soil aggregates was quantified using phospholipid fatty acid analysis, with 18:2ω6,9 serving as a fungal biomarker. Two dominant fungivorous nematode genera, *Aphelenchoides* and *Aphelenchus*, were isolated from field soils based on morphological identification. To eliminate surface microbial contaminants, nematodes were surface-sterilized in 2% sodium hypochlorite for 30 s and rinsed five times with sterile distilled water. Thirty individuals of each genus were transferred to sterile tubes for DNA extraction to assess fungal consumption. Fungal abundance within nematodes from each plot was determined by measuring ITS rRNA gene copy numbers per nematode using quantitative PCR on an ABI 7500 system (Applied Biosystems, CA, USA).

2.7. Statistical analysis

The relative change rate, defined as Δ(FNC/GRSPs)/ΔSOC, was calculated for each manure treatment (M1 or M2) relative to the control (M0) as: Δ(FNC/GRSPs)/ΔSOC=(FNC/GRSPs)_Mi-(FNC/GRSPs)_M0/SOC_Mi-SOC_M0. This index represents the contribution of fungal-derived carbon to SOC accrual acorss different manure levels. To evaluate the balance between stochastic and deterministic processes in community assembly, the normalized stochasticity ratio (NST) was calculated for all treatments using the "*NST*" R package (Ning *et al.* 2019), with a threshold of 50% used to distinguish between deterministic (<50%) and stochastic (>50%) processes. Two-way analysis of variance was employed to estimate the effects of manure amendments and aggregate fractions on soil properties, fungal and nematode communities, and fungal-derived products using SPSS 27.0 software (SPSS, Chicago, IL, USA). One-way analysis of variance was performed to test for significant differences in soil properties, the distribution and contribution of fungal-derived products to SOC, fungal community attributes (biomass, richness, and NST), and fungivorous nematode characteristics (density and predation pressure). Linear regression models were used to assess the relationships between the densities of total nematodes, *Aphelenchus*, and *Aphelenchoides*, fungal biomass, and NST. These models were also used to examine the associations between fungal biomass or NST, and the contributions of FNC, T-GRSP, and EE-GRSP to the SOC pool (expressed as FNC:SOC, T-GRSP:SOC, and EE-GRSP:SOC ratios). Random forest

modeling was conducted to identify the important predictors of these fungal-derived carbon contributions, based on soil properties, and fungal and fungivorous nematode community metrics. Partial least squares structural equation modeling was performed using SmartPLS 4.0 (Henseler *et al.* 2009) to evaluate the direct and indirect pathways through which soil properties, nematode density, fungal biomass, and NST influence the contributions of fungal-derived products to SOC pool.

3. Results

3.1. Soil nutrient content

Two-way analysis of variance indicated significant effects of both soil aggregates (P<0.01) and manure amendments (P<0.001) on soil nutrient content (Appendix C). Among the aggregate fractions, the MA fraction exhibited higher nutrient levels than the SA and LA fractions. Across all aggregate fractions, the high manure (M2) treatment significantly (P<0.05) increased soil pH, soil organic carbon (SOC), total nitrogen (TN), nitrate nitrogen (NO_3^--N), total phosphorus (TP), and available phosphorus (AP) compared to the no manure (M0) and low manure (M1) treatments (Table 1).

3.2. Contributions of fungal necromass carbon (FNC) and GRSPs to SOC

FNC and GRSPs significantly (P<0.05) differed across both aggregate fractions and manure amendments (Appendix C). The concentrations of FNC, T-GRSP, and EE-GRSP were the highest in the MA fraction, followed by the SA and LA fractions (Fig. 1-A–C). Compared to the M0 treatment, the M1 and M2 treatments significantly (P<0.05) increased FNC by 115 and 364%, respectively (Fig. 1-A). Similarly, T-GRSP increased by 42 and 209%, and EE-GRSP increased by 77 and 306% under the M1 and M2 treatments, respectively (Fig. 1-B and C).

The contributions of FNC and EE-GRSP to the SOC pool — expressed as FNC:SOC and EE-GRSP:SOC ratios — were significantly (P<0.05) higher in the MA and SA fractions than in the LA fraction (Fig. 1-D–F). With increasing manure application rates, the contributions of both FNC and EE-GRSP to the SOC pool exhibited a consistent upward trend. Compared to the M0 treatment, FNC contribution increased by an average of 25 and 75% under the M1 and M2 treatments, respectively, while EE-GRSP contributions increased by 112 and 252% (Fig. 1-D–F).

The relative changes in FNC and GRSPs to the SOC pool — expressed as ΔFNC:△SOC, ΔT-GRSP:ΔSOC, and ΔEE-GRSP:ΔSOC ratios. Manure application significantly (P<0.05) enhanced FNC accrual in soil, with its accrual rate considerably exceeding that of GRSPs (Fig. 1-G–I). On average, the relative change rate of FNC was approximately twice that of T-GRSP and 1.3 times greater than that of EE-GRSP (Fig. 1-G–I). Among aggregate fractions, the SA and LA fractions exhibited significantly (P<0.05) higher relative change rates of both FNC and GRSPs compared to the MA fraction. Furthermore, the relative change rates of FNC and GRSPs showed a clear, manure application rate-dependent pattern across all aggregate fractions (Fig. 1-G–I).

3.3. Fungal community properties

Fungal biomass, diversity (richness index), and community assembly processes, as indicated by NST, were significantly (P<0.05) influenced by aggregate fractions and manure amendments (Appendix C). Specifically, fungal biomass, diversity, and NST were significantly (P<0.05) higher in the MA and SA fractions than in the LA fraction (Fig. 2-A and B). Regardless of aggregate size, fungal biomass consistently increased with higher manure application rates, while fungal diversity and NST showed declining trends (Fig. 2-A–C). The fungal community was primarily composed of Ascomycota (87%), followed by Basidiomycota (8.3%) and Mucoromycota (3.0%) (Appendix D). Across soil aggregates, Ascomycota and Mucoromycota were significantly (P<0.05) more abundant in the LA fraction than in the MA fraction, whereas Basidiomycota exhibited the opposite pattern, being more abundant in the MA fraction (Appendix D). The M2 treatment significantly (P<0.05) increased the relative abundance of Ascomycota compared to the M0 treatment, while reducing the relative abundances of Basidiomycota and Mucoromycota (Appendix D).

3.4. Fungivorous nematode community structure

The densities of fungivorous nematodes and predation

Table 1 Soil properties across manure treatments and aggregate fractions[1)]

Aggregate fraction[2)]	Treatments[3)]	pH	SOC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})	NO_3^--N (mg kg^{-1})	NH_4^+-N (mg kg^{-1})	AP (mg kg^{-1})
MA	M0	4.46±0.03 b	5.70±0.16 c	0.55±0.03 c	0.29±0.01 c	7.19±1.11 c	2.98±0.08 ab	4.09±0.55 c
	M1	4.73±0.05 b	9.70±0.39 b	1.01±0.07 b	0.90±0.11 b	13.9±1.20 b	2.67±0.06 b	100±4.10 b
	M2	6.13±0.04 aA	15.0±0.86 aA	1.73±0.07 aA	2.05±0.06 aAB	51.4±0.75 aA	3.35±0.14 aA	500±15.7 aA
SA	M0	4.43±0.04 b	4.72±0.34 c	0.55±0.07 c	0.28±0.01 c	5.60±0.71 c	2.66±0.08 b	4.13±0.39 c
	M1	4.65±0.04 b	8.50±0.40 b	0.82±0.09 b	0.93±0.06 b	12.5±1.11 b	2.38±0.13 b	79.8±1.51 b
	M2	5.96±0.07 aB	13.0±1.56 aB	1.52±0.16 aAB	2.15±0.13 aA	49.1±1.94 aA	3.39±0.14 aAB	421±11.8 aB
LA	M0	4.47±0.04 b	4.92±0.39 c	0.55±0.04 c	0.29±0.03 c	5.01±0.82 c	2.72±0.12 a	4.82±1.77 c
	M1	4.68±0.07 b	7.83±0.69 b	0.84±0.02 b	0.80±0.04 b	10.8±1.13 b	2.53±0.15 a	83.0±6.71 b
	M2	5.98±0.06 aAB	12.9±0.82 aB	1.26±0.03 aB	1.79±0.08 aB	32.7±0.71 aB	2.48±0.09 aB	382±2.66 aB

[1)] SOC, soil organic carbon; TN, soil total nitrogen; TP, total phosphorus; AP, available phosphorus.
[2)] MA, microaggregates; SA, small macroaggregates; LA, large macroaggregates.
[3)] M0, no manure; M1, low manure; M2, high manure.
Values are presented as mean±standard error (n=3). Uppercase letters denote statistically significant differences among aggregate size fractions (P<0.05). Lowercase letters within the same aggregate fraction indicate significant differences among fertilization treatments (P<0.05).

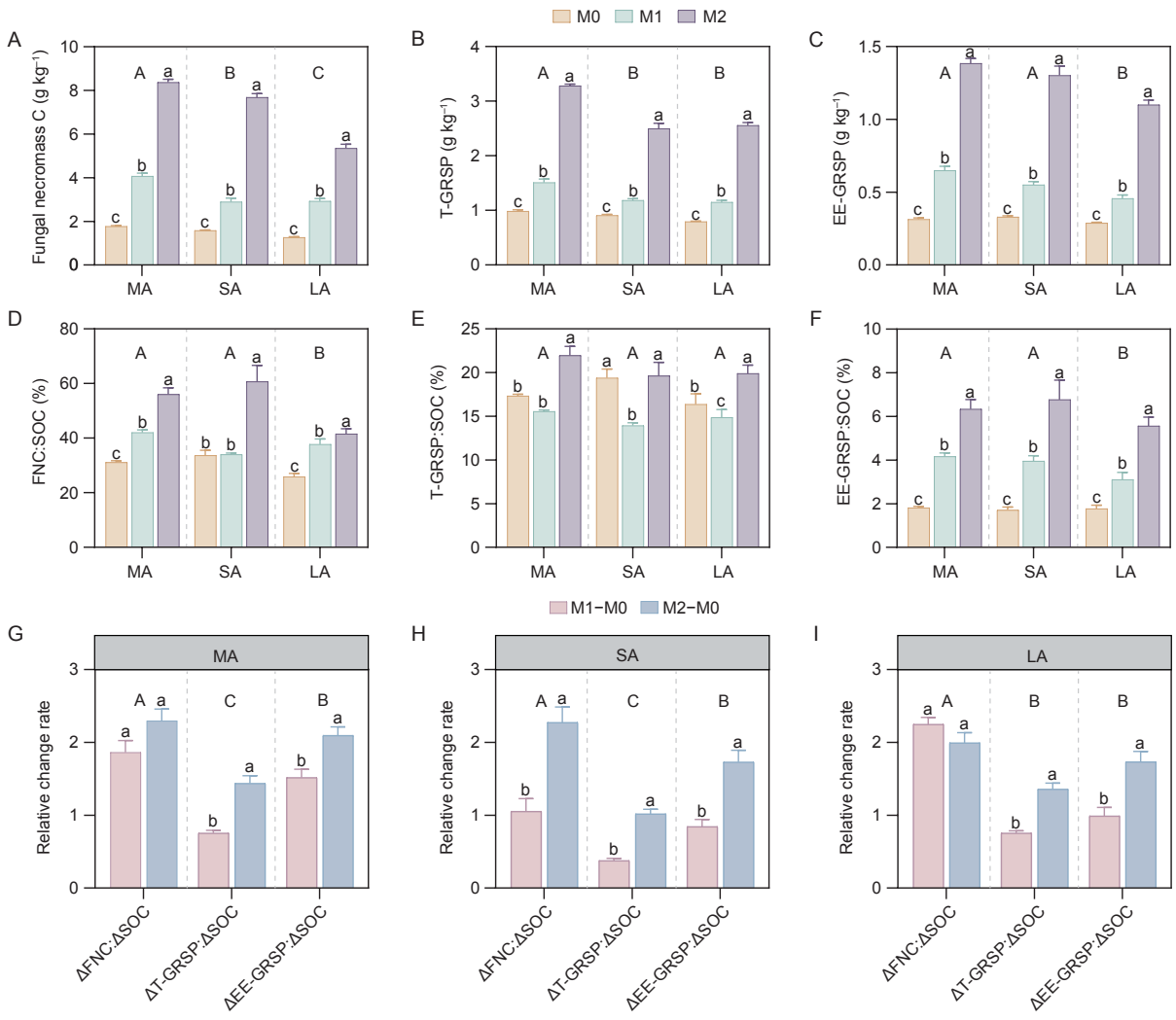

Fig. 1 Fungal-derived products distribution and contribution to soil organic carbon (SOC) across manure treatments and aggregate fractions. MA, microaggregates; SA, small macroaggregates; LA, large macroaggregates. M0, no manure; M1, low manure; M2, high manure. T-GRSP, total extractable glomalin-related soil proteins; EE-GRSP, easily extractable glomalin-related soil proteins; FNC, fungal necromass carbon. Different letters (uppercase for aggregate fractions, lowercase for manure treatments) represent significant differences at P<0.05. Error bars represent the standard errors from triplicate measurements.

pressure — expressed as the predator-to-fungi ratio — were significantly (P<0.05) higher in the LA fraction than in the MA and SA fractions (Fig. 3-A and B). Manure amendments (M1 and M2) significantly (P<0.05) increased fungivorous nematode densities across all aggregate fractions compared to the M0 treatment, although their effect on predation pressure was significant only in the LA fraction (Fig. 3-A and B). The fungivorous nematode community comprised five genera, with *Aphelenchus* (59.3%) and *Aphelenchoides* (25.5%) being the dominant taxa (Fig. 3-C). Their densities followed the same trend as the overall fungivorous nematode community, decreasing in the order of LA>SA>MA and M2>M1>M0 (Appendix E). Linear regression analysis revealed significantly positive correlations between fungal biomass and the densities of total fungivorous nematodes, *Aphelenchoides*, and *Aphelenchus* (R^2=0.32–0.96; P<0.01) (Fig. 3-D–F). In contrast, these densities were negatively correlated with NST (R^2=0.43–0.97; P<0.05) (Fig. 3-G–I).

3.5. Verifying the nematodes–fungi interactions by microcosm experiments

A notable increase in fungal biomass was associated with fungivorous nematode predation, particularly in the LA fraction. To validate this observation, a microcosm experiment was conducted with and without the addition of *Aphelenchus*. After a 30-day incubation, fungal biomass significantly (P<0.05) increased under the M2 treatment. The addition of *Aphelenchus* further enhanced fungal biomass, with increases of 11, 11, and 19% in the MA, SA, and LA fractions, respectively (Fig. 4-A). To confirm active predation of fungivorous nematode in the field experiment, we quantified fungal gene copy numbers within the two dominant genera, *Aphelenchus* and *Aphelenchoides*. We found that the copy numbers of the fungal ITS gene within both genera were significantly (P<0.05) higher in the LA fraction than in the MA and SA fractions. Moreover, the M2 treatment led to a more pronounced increase in fungal ITS gene copy numbers

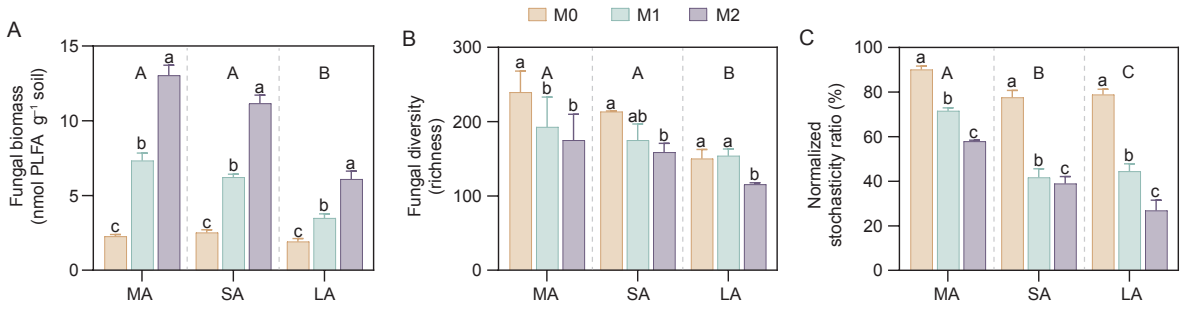

Fig. 2 The fungal community across manure treatments and aggregate fractions. MA, microaggregates; SA, small macroaggregates; LA, large macroaggregates. M0, no manure; M1, low manure; M2, high manure. Different letters (uppercase for aggregate fractions, lowercase for manure treatments) represent significant differences at $P<0.05$. Error bars represent the standard errors from triplicate measurements.

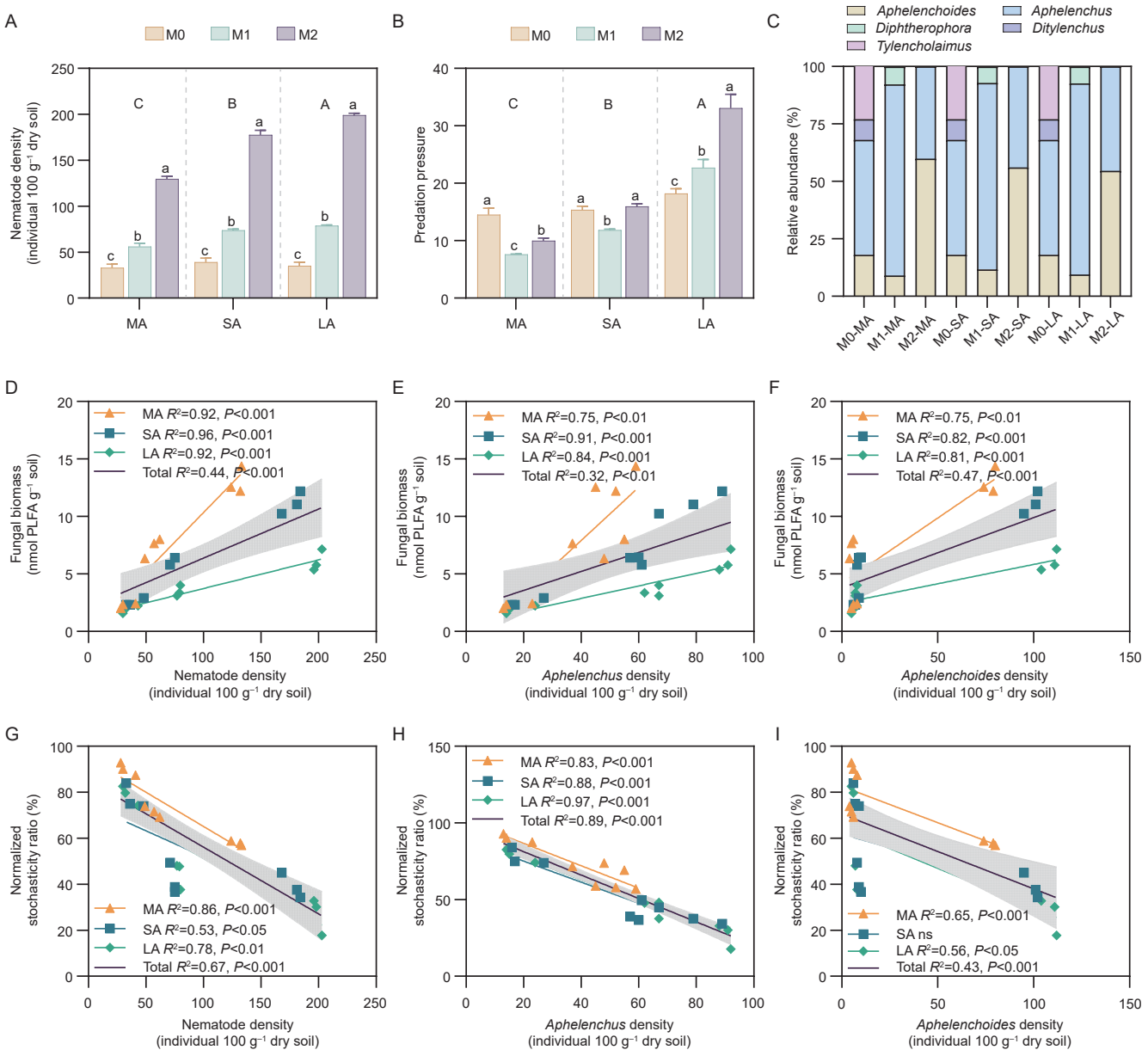

Fig. 3 Dynamics of fungivorous nematode community and their ecological relationships with fungal community across manure treatments and soil aggregate fractions. MA, microaggregates; SA, small macroaggregates; LA, large macroaggregates. M0, no manure; M1, low manure; M2, high manure. PLFA, phospholipid fatty acid analysis. Different letters (uppercase for aggregate fractions, lowercase for manure treatments) represent significant differences at $P<0.05$; ns indicates no significance at $P<0.05$. Error bars represent the standard errors from triplicate measurements.

within nematodes in the LA fraction compared to the M1 and M0 treatments (Fig. 4-B).

3.6. Predictors of FNC and GRSPs contributions to SOC

Linear regression analysis revealed significant associations between the FNC:SOC ratio, T-GRSP:SOC ratio, EE-GRSP:SOC ratio, fungal biomass, and NST (Fig. 5-A–F). The FNC:SOC and EE-GRSP:SOC ratios were positively correlated with fungal biomass (R^2=0.25–0.98, P<0.05), but negatively correlated with NST (R^2=0.25–0.96, P<0.05) (Fig. 5-A, C, D and F). In contrast, the T-GRSP:SOC ratio showed a positive correlation with fungal biomass (R^2=0.25–0.57, P<0.05), but no correlation with NST (Fig. 5-B and E). Random forest modeling was employed to evaluate the relative importance of variables influencing the incorporation of FNC and GRSPs into the SOC pool (Fig. 5-G–I). Among edaphic factors, AP, SOC, and NO_3^-−N were the most important predictors for the contributions of FNC (10.9, 6.8, and 8.9%), T-GRSP (10.9, 6.8, and 8.9%), and EE-GRSP (9.2, 9.8, and 11.4%), respectively. Furthermore, fungal biomass (16.6, 11.5, and 17.8%), NST (10.4, 10.6, and 12.9%), and fungivorous nematode density (14.6, 16.0, and 16.8%) made significant (P=0.01) contributions to FNC and GRSPs accumulation in the SOC pool (Fig. 5-G–I).

We employed linear regression, random forest modeling, and partial least squares structural equation modeling to evaluate the direct and indirect effects of edaphic factors (AP and SOC), fungal community (biomass and NST), and fungivorous nematode density on the contributions of FNC and GRSPs to the SOC pool (Fig. 6). Overall, both AP and SOC were positively correlated with fungivorous nematode density across all three aggregate fractions (path coefficient=0.19~0.94, P<0.05). Increases in fungivorous nematode density induced by manure application subsequently affected fungal biomass and community assembly in divergent ways. Specifically, fungivorous nematode density was positively correlated with fungal biomass (path coefficient=0.94–0.96, P<0.001), but negatively correlated with NST (path coefficient=–0.55–(–0.89), P<0.01). These predation effects were more pronounced in the LA fraction compared to the SA and MA fractions. Our analysis reveals that fungivorous nematodes enhance the SOC pool in the LA fraction by simultaneously promoting fungal biomass and increasing deterministic assembly processes. In contrast, fungivorous nematodes primarily promoted fungal biomass with minimal effects on community assembly in the SA and MA fractions. Moreover, FNC contributed more substantially to SOC accrual than GRSPs.

4. Discussion

4.1. Nematode predation promoted SOC accrual by regulating fungal community

Consistent with our first hypothesis, nematode predation regulated fungal community *via* both fungal biomass and community assembling processes, thereby cascading into the formation of fungal-derived C. Field and microcosm experiments verified that fungivorous nematode grazing stimulated fungal biomass, as evidenced by the positive association between fungivores and fungi (Figs. 3 and 4). Although some studies have reported reductions in microbial biomass due to nematode predation, a growing body of evidence suggests the opposite trend — the stimulation of microbial biomass, particularly in nutrient-rich ecosystems (Tamang *et al.* 2024). This increase in fungal biomass is attributed to nematode-induced trophic interactions, which trigger compensatory growth responses (Fu *et al.* 2005). By feeding on fungal cells, fungivores accelerate nutrient cycling, enhance nutrient availability, and promote the growth and reproduction of acting fungal populations (Table 1 and Fig. 4). These processes resulted in the accumulation of fungal necromass and products such as GRSPs (See *et al.* 2022). Compared to bacterial necromass, fungal necromass and GRSPs are more recalcitrant and contribute more substantially to the SOC pool as fungal derived carbon (Camenzind *et al*. 2023). Moreover, fungal necromass and GRSPs act as key binding agents in the formation of soil aggregates, thereby enhancing SOC stabilization and promoting long-term carbon accrual. Notably, our findings indicated that FNC contributes significantly more to SOC

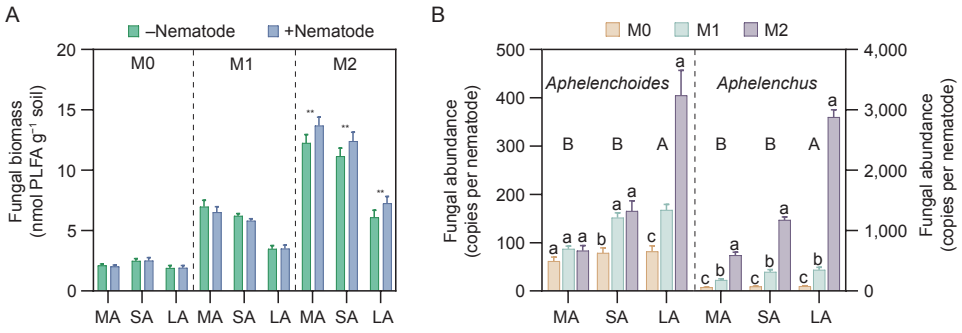

Fig. 4 Microcosm experiment on predation by fungivorous nematodes. A, effect of inoculation (+nematodes) and non-inoculation (–nematodes) of *Aphelenchus* on fungal biomass over 30 days. B, fungal abundance inside the body of the two dominant fungivorous nematodes *Aphelenchoides* and *Aphelenchus*. MA, microaggregates; SA, small macroaggregates; LA, large macroaggregates. M0, no manure; M1, low manure; M2, high manure. PLFA, phospholipid fatty acid analysis. **, P<0.01. Different letters (uppercase for aggregate fractions, lowercase for manure treatments) represent significant differences at P<0.05. Error bars represent the standard errors from triplicate measurements.

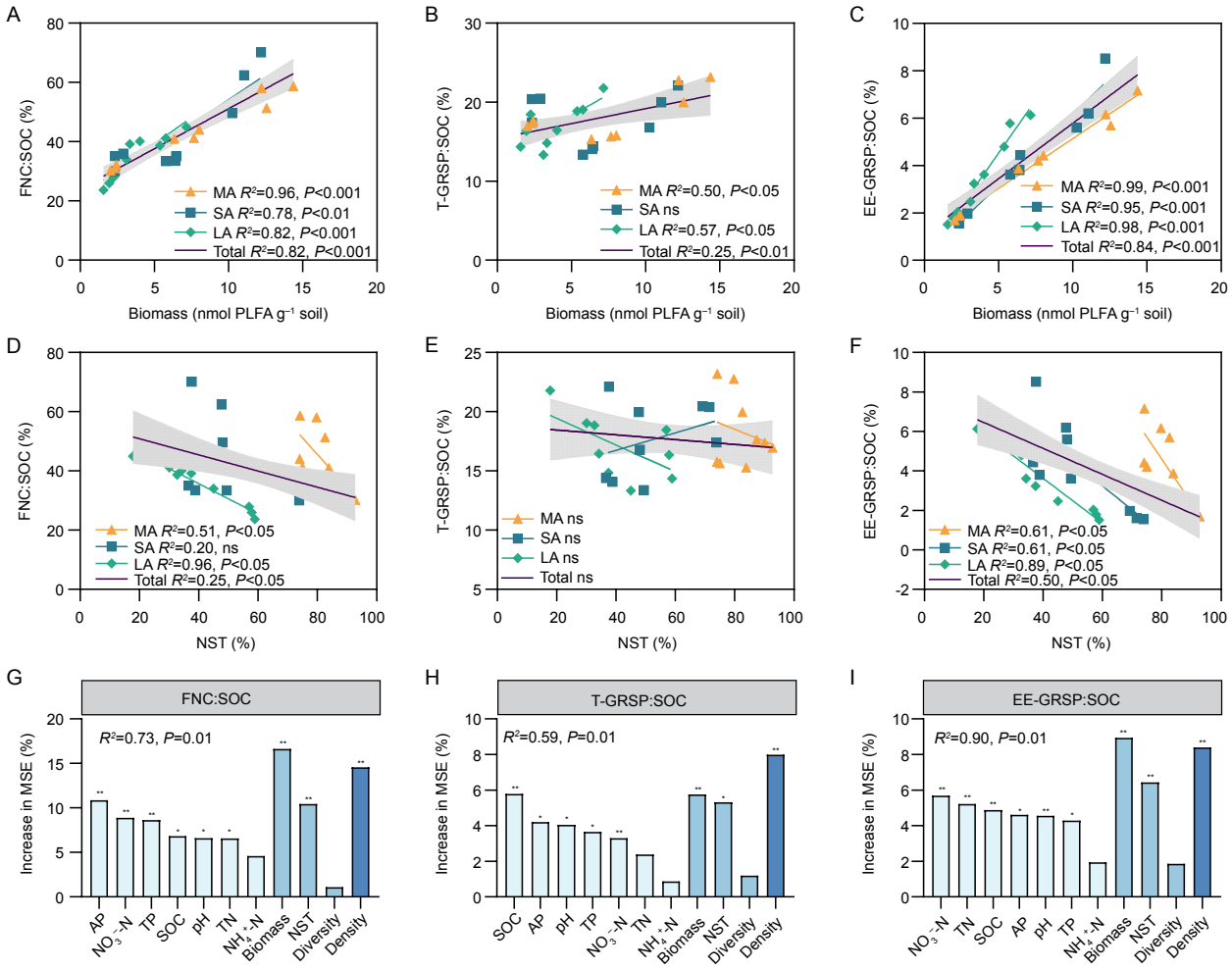

Fig. 5 Fungal biomass and normalized stochasticity ratio relationships with fungal-derived products and their predictive determinants. FNC, fungal necromass carbon; SOC, soil organic carbon; T-GRSP, total extractable glomalin-related soil proteins; EE-GRSP, easily extractable glomalin-related soil proteins; PLFA, phospholipid fatty acid analysis; NST, normalized stochasticity ratio; AP, available phosphorus; TP, total phosphorus; TN, total nitrogen. MA, microaggregates; SA, small macroaggregates; LA, large macroaggregates. ns indicates no significance at $P<0.05$. **, $P<0.01$; *, $P<0.05$.

accrual than GRSPs. This difference primarily arises because arbuscular mycorrhizal fungi, which serve as the main source of GRSPs, accounted for only about 0.03% of the total fungal community in our soil samples, thereby limiting the potential pool of GRSPs. In contrast, FNC includes necromass inputs derived from a wide range of fungal functional groups, and its complex chemical composition (e.g., melanin and chitin) enhances resistance to decomposition and promotes long-term soil stability (Yolima *et al.* 2025). This differential contribution highlights the crucial role of conventional fungal necromass in SOC accrual.

Secondly, selective predation by fungivorous nematodes is expected to reinforce deterministic assembly processes (Zhu *et al.* 2024). Consistent with this expectation, we observed a negative correlation between the NST and nematode predation pressure (Appendix F). Selective predation resulted in more deterministic assembly, which coincided with a significant increase in the relative abundance of Ascomycota (Appendix D). Particularly, the dominant nematode genera *Aphelenchoides* and *Aphelenchus* selectively preyed on fungal genera *Ascobolus* and *Pseudaleuria*, both dominant members of the Ascomycota phylum, and fostered their proliferation, as evidenced by positive correlations among these genera (Appendix G). Ascomycota are considered Y-strategists, characterized by high growth efficiency (Malik *et al.* 2020; Shao *et al.* 2021), enabling them to rapidly assimilate labile carbon into biomass. This in turn promotes fungal necromass formation and GRSP production, contributing to SOC accrual (Wang *et al.* 2024). Moreover, deterministic assembly processes were associated with reduced fungal diversity (Fig. 2). The directional enrichment of dominant functional taxa under deterministic filtering may compensate for diversity loss by enhancing carbon transformation efficiency through functional redundancy, ultimately facilitating necromass production (Xun *et al.* 2019). Overall, selective predation-mediated deterministic assembly promotes the accrual of fungal-derived carbon and the stabilization of SOC. Importantly, our study focused primarily on nematodes, which may limit the

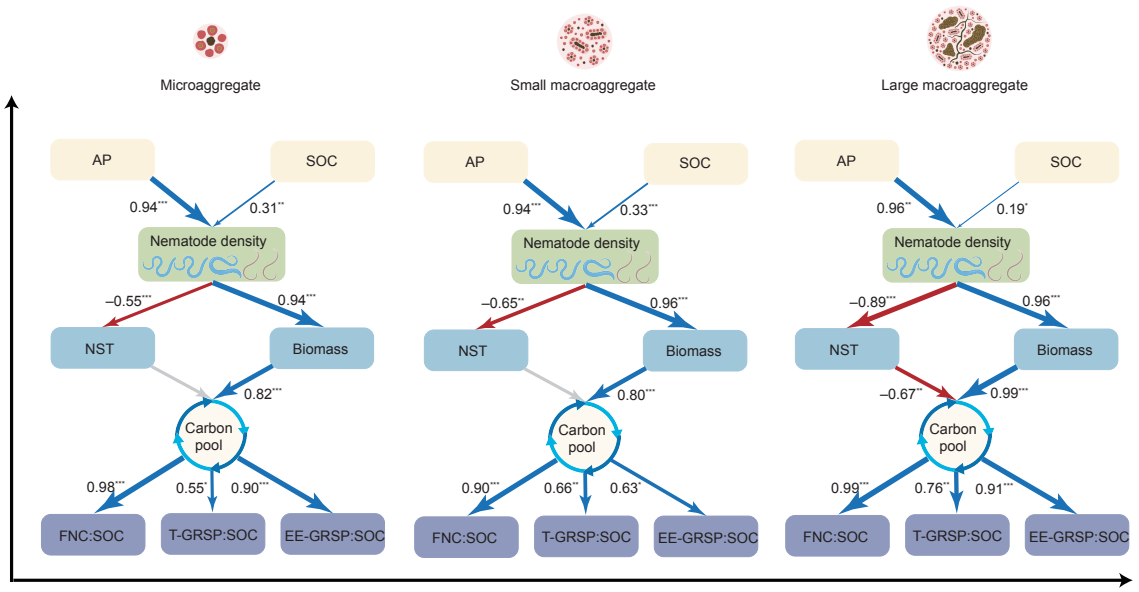

Fig. 6 A conceptual diagram depicting the influence of nematode predation on soil organic carbon (SOC) accrual within soil aggregates. The models elucidate the direct and indirect pathways through which soil properties, nematode density, and normalized stochasticity ratio (NST) and biomass of fungal community influence the contribution of fungal-derived products to SOC. Blue and red arrows denote positive and negative relationships, respectively. Line weights scaled to coefficient strength (gray indicates $P>0.05$). AP, available phosphorus; T-GRSP, total extractable glomalin-related soil proteins; EE-GRSP, easily extractable glomalin-related soil proteins; FNC, fungal necromass carbon. ***, $P<0.001$; **, $P<0.01$; *, $P<0.05$.

generalizability of our findings to broader soil fauna (e.g., higher-level predators) that differentially impose distance pressures on microbial communities. Future research should encompass more diverse faunal communities to evaluate the generality and magnitude of these cascading effects across trophic levels. Additionally, this study was based on a long-term field experiment and the number of observations was limited, more studies should be conducted to evaluate whether this conclusion can be applied to other environmental conditions. Thus, while the patterns observed here are robust, extrapolation to other soil types (e.g., sandy soils) or climatic zones should explicitly account for these environmental constraints.

4.2. Trophic cascade effect on SOC accrual mediated by manure amendments and soil aggregates

A stable trophic cascade is driven not only by top-down control (trophic predation) but also by bottom-up forces (particularly nutrient availability), which play a fundamental role in triggering and shaping the trophic dynamics (Thakur and Geisen 2019; Wu *et al*. 2024). Consistent with our second hypothesis, long-term manure application significantly enhanced trophic interactions between fungivorous nematodes and the fungal community, thereby promoting the accrual of fungal-derived carbon, most notably in macroaggregates (Fig. 6). This finding aligns with previous studies showing that organic amendments stimulate micro-food web activity and restructure soil trophic cascades (Kou *et al*. 2023). Manure application enhanced the availability of key nutrients such as AP and SOC (Table 1), which in turn improved fungal biomass and increased nematode density. These changes intensified trophic interactions and consequently facilitated the formation of fungal-derived carbon (Fig. 5). This trophic cascade effect on fungal-derived carbon formation and its contribution to SOC accrual was the most pronounced in LA. This pattern is likely attributable to the smaller pore sizes in microaggregates, which restrict nematode access and activity, as evidenced by the lower predation pressure observed in microaggregates compared with macroaggregates (Fig. 3-B). This finding supports the notion that soil physical structure fundamentally shapes trophic interactions by constraining the ability of soil organisms to locate and access food resources, ultimately amplifying the contribution of fungal-derived carbon to SOC pools (Erktan *et al.* 2020).

Soil macroaggregates not only amplified the top-down regulation of fungal biomass, but also enhanced the deterministic assembly of fungal communities. This is probably due to greater nematode mobility and increased contact with fungal hyphae in macroaggregates, which imposes stronger selection pressure (Martin and Sprunger 2023). Particularly, manure application and nematode predation tended to deterministic nourish the growth of the Y-strategists, particularly Ascomycota. However, lower oxygen concentration and reduced pore connectivity in microaggregates limited the growth, reproduction, and hyphal extension of Y-strategists. These unfavorable conditions favored the dominance of Basidiomycota, an A-strategist group (Li *et al.* 2021; Shao *et al.* 2021). Additionally, under predation pressure, different fungi may escape and persist in microaggregates, resulting in higher alpha diversity (Erktan *et al.* 2020; Zhong *et al.* 2025). These factors minimized the strength of deterministic assembly process of fungal communities in microaggregates. Collectively, our findings

indicate that manure amendments not only directly increase microbial carbon inputs but also indirectly regulate carbon accrual through trophic cascades within the soil micro-food web. Importantly, these results suggested that integrating organic manure management with the targeted promotion of soil biotic interactions (e.g., nematode-fungi) could serve as a biologically mediated strategy for enhancing soil carbon accrual. In the future, multitrophic food webs incorporating both soil meso- and micro-fauna can be designed based on known trophic interactions, by leveraging positive trophic cascade effects between species to enhance soil carbon accrual efficiency (Luan *et al.* 2025).

5. Conclusion

This study reveals a previously underappreciated mechanism through which the soil micro-food web regulates SOC dynamics at the soil aggregate scale. Specifically, predation by fungivorous nematodes enhanced fungal biomass and shifted fungal community assembly toward more deterministic processes. These changes collectively promoted the accrual of fungal necromass and GRSPs, thereby increasing their contributions to SOC, particularly within macroaggregates. This represented a trophic cascade in which top-down control by fungivorous nematodes indirectly stimulated fungal-mediated carbon accrual. Notably, these trophic cascades were magnified by manure amendments, particularly in macroaggregates. However, we acknowledge that single-site field experiments may not fully capture the spatiotemporal heterogeneity of trophic-cascade dynamics across diverse soil types and climatic regions. Furthermore, this study specifically focused on the interactions between fungivorous nematodes and fungi, delineating the scope of our analysis. Other trophic groups (e.g., higher-level predators) were not explicitly considered, which renders our estimates of soil food web complexity conservative. Despite these limitations, our findings underscore the central role of soil aggregate architecture and manure amendments in modulating nematode-fungus interactions and propagating cascading effects on SOC accrual.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

Data availability

All sequencing reads of the fungal community have been deposited in the National Center for Biotechnology Information (NCBI) with the accession number PRJNA1066972.

Appendices associated with this paper are available at https://doi.org/10.1016/j.jia.2026.01.005

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