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Short Communication

Impacts of bacterivorous nematode identity and abundances on soil greenhouse gas emissions

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ABSTRACT

Soil organisms are essential drivers of greenhouse gas (GHG) emissions, with bacterivorous nematodes playing a crucial role in regulating soil carbon and nitrogen cycling processes. These nematodes influence microbial communities and nutrient dynamics, which in turn affect GHG fluxes. However, their species-specific contributions to GHG dynamics remain poorly understood. This study investigated the effects of two bacterivorous nematode species, *Protorhabditis* spp. and *Caenorhabditis elegans* on soil GHG emissions using a 20-day microcosm experiment. Seven treatments were established: a control (without nematodes) and inoculations of *Protorhabditis* spp. or *C. elegans* at densities of 1, 2, and 3 individuals per gram of dry soil. The results showed that *C. elegans* significantly increased the cumulative emissions of CO_2 and N_2O compared to the control. Random forest analysis identified *C. elegans* abundance was the most critical factor influencing cumulative GHG production. However, *Protorhabditis* spp. did not significantly affect CO_2 emissions compared to the control, despite its faster population growth rate and higher abundance over the experimental period. The contrasting effects of the two bacterivorous nematodes on GHG emissions highlight the distinct ecological roles of nematode species in regulating soil processes. These findings suggest that nematode species-specific traits exert a greater influence on soil GHG emissions than nematode abundance alone. In addition, the density-dependent effects observed for *C. elegans* demonstrate that abundance can also be an important determinant of GHG fluxes. This study provides novel insights into the differential roles of bacterivorous nematodes in soil biogeochemical processes and underscores the importance of species composition in regulating soil GHG emissions.

1. Introduction

Agriculture is both a significant source and a potential sink of greenhouse gas (GHG) emissions [1]. Recent studies have emphasized that shifts in soil biological communities can substantially influence GHG emissions [2–4]. Soil nematodes play an important role in organic matter decomposition, which has a direct impact on carbon release and nutrient cycling [5,6], ultimately contributing to greenhouse gas emissions. By breaking down soil organic matter, nematodes regulate soil biogeochemical cycles and potentially facilitate the release of CO_2 and other gases [7,8]. However, most relevant researches had focused on nematode communities or macrofauna, such as earthworms, leaving the specific roles of soil nematodes in regulating GHG emissions remain poorly understood [3,9–11].

Soil nematodes are the most abundant and diverse taxon of soil fauna, playing pivotal roles in the soil ecosystems [12,13]. There are five common trophic groups of soil nematodes - bacterivores, fungivores, herbivores, omnivores, and carnivores [14]. Among these, bacterivorous

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nematodes are often the dominate constituting 60–80 % of the total nematode population in karst agricultural soils [15]. Due to their feeding activities, bacterivorous nematodes regulate soil bacterial communities and nutrient cycling [16,17]. Their position within the soil food web enables them to mediate complex interactions with microbes, soil fauna, and plants, driving carbon and nitrogen cycling, altering microbial activity and community structure, and influencing GHG emissions. These effects are driven not only by the release of nutrients from microbial biomass consumption but also by the enhancement of microbial respiration and nutrient mineralization [18–20]. This feeding activity simultaneously sustains microbial communities and stimulates microbial processes, thereby nutrient mineralization and respiration [21,22]. Previous studies have shown that various soil fauna, such as earthworms, arthropods, and protozoa, significantly influence GHG emissions by modulating microbial-mediated processes. For instance, earthworms enhance organic matter decomposition and microbial activity, resulting in elevated CO_2 and N_2O emissions [23]. Similarly, protozoa facilitate nutrient mineralization through microbial predation [24,25] and affect carbon and nitrogen fluxes [26]. Bacterivorous nematodes contribute to soil organic carbon (SOC) stabilization and accumulation by regulating microbial decomposition pathways [27]. Experimental evidence suggests that bacterivorous nematodes can increase CO_2 emissions by stimulating microbial respiration [28]. However, the majority of studies have primarily examined the overall impact of nematode activity on GHG emissions, rather than the specific mechanisms driving these effects [2,9,11]. The specific roles of individual bacterivorous nematode species and the influence of their population densities on regulating soil GHG emissions remain underexplored. This knowledge gap limits our understanding of how nematode functional traits and population dynamics of nematodes drive GHG emissions.

To address this knowledge gap, we conducted a controlled microcosm experiment to investigate the effects of specific bacterivorous nematode species and their population densities on soil GHG emissions. The study focused on two nematode species with distinct ecological and biological characteristics: *Protorhabditis* spp., a prevalent bacterivorous nematode in agricultural soils known for its rapid growth, high abundance, and significant role in nutrient cycling [29]; and *Caenorhabditis elegans*, a widely studied model organism commonly used in laboratory research on soil biota interactions, nutrient turnover, and microbial regulation [30,31]. Recent studies have demonstrated that high nematode abundance can enhance soil CO_2 and N_2O emissions by stimulating microbial respiration and accelerating nitrogen cycling [2,11,32]. *Protorhabditis* spp., with its higher abundance and adaptability to agricultural soils, may exert a stronger influence on microbial-driven processes and GHG emissions compared to *C. elegans*, whose ecological relevance in natural and agricultural soils remains less well-documented [33]. Based on these considerations, we hypothesized that: (1) the addition of *Protorhabditis* spp. would result in higher CO_2 and N_2O emissions compared to *C. elegans* due to its greater abundance and ecological adaptability; and (2) increasing nematode abundance would amplify soil CO_2 and N_2O emissions by enhancing microbial activity and nitrogen transformation. This study aimed to elucidate the regulatory roles of bacterivorous nematode species and their population densities in soil GHG emissions, providing novel insights into nematode-driven processes relevant to agroecosystem management.

2. Materials and methods

2.1. Soil source and preparation

The soil used in this study was collected in September 2023 from a typical maize-soybean rotation cropland in Huanjiang County, Guangxi Province, China (107°57′-108°43′E, 24°55′-25°33′N). The region's climate is subtropical monsoon, with an average annual temperature of 18.5 °C and 1389 mm of precipitation. The soil is calcareous, formed from a dolostone basis [34]. Soil samples were sieved through a 5-mm screen to remove stones, plant roots, and visible soil fauna, then homogenized and separated into three subsamples. The first subsample was stored at 4 °C to preserve indigenous soil microorganisms. The second subsample was processed immediately for nematode extraction and culture. The third subsample was sterilized using γ-irradiation (dose: 25 kGy for 48 h) at Guangzhou FuRui High Energy Company to eliminate microorganisms and soil fauna. The 50g of fresh soil that had been kept at 4 °C was put into a 100 mL Erlenmeyer flask, combined with 100 mL of sterile distilled water, and agitated for 30 min to guarantee complete homogeneity in order to create the microbial suspension. A microbial suspension appropriate for reinoculation was then obtained by successively filtering the suspension through 300-μm, 65-μm, and 10-μm meshes to eliminate undesirable particles [35]. The 300-μm mesh was used to eliminate large soil aggregates, plant debris, and other coarse materials, followed by the 65-μm mesh, which further removed finer soil particles and nematodes while preventing excessive clogging of the final filter. Finally, the 10-μm mesh was used to ensure that only microorganisms within the desired size range were retained, and the filtrate collected from this step was used as the microbial suspension for subsequent experiments. This 50 mL microbial suspension was incubated with 15 kg of sterilized soil at 25 °C for one week to stabilize microbial activity. After homogenization, the soil moisture was adjusted to 60 % of the maximum field capacity.

2.2. Preparation of nematodes

The nematodes used in this study were *C. elegans* and *Protorhabditis* spp. *C. elegans* (wild type) was purchased from Hangzhou Hongsai Biotechnology Co. Ltd. (catalogue number: X2034C), and *Protorhabditis* spp. extracted from soil. Nematodes were extracted using a modified Baermann funnel method, purified by centrifugation and grown on nematode growth medium (NGM) plates with Escherichia coli OP50 as the food source.1 mL of cultured nematodes was first transferred from the culture dish into a 15 mL centrifuge tube. The nematodes were then washed with sterile water and centrifuged at 3000 rpm for 1 min. This washing and centrifugation step was repeated three times to remove bacteria. Adult nematodes were manually pipetted into equal 30g dry soil microcosms in 100 mL culture bottles to ensure precise density treatments. Culture bottles were randomly placed in a biochemical incubator set at 25 °C in the dark.

2.3. Experimental design

The experiment was conducted using a randomized block design with seven treatments, each containing five replicates. A total of 35 culture bottles were sampled on the 5th, 10th, 15th, and 20th days of incubation for nematode abundance determination, resulting in 175 culture bottles in total. After 20 days, destructive sampling was conducted to analyze soil physicochemical properties. The treatments included a control (without nematodes) and inoculations of *Protorhabditis* spp. (P1, P2, P3) or *C. elegans* (C1, C2, C3) at densities of 1, 2, or 3 individuals per gram of dry soil.

2.4. Greenhouse gas sampling and analysis

Soil samples, equivalent to 30 g of dry weight, were placed into 100 mL culture bottles sealed with lids featuring rubber septa for gas sampling. An airtight seal was ensured using a vacuum-greased rubber gasket. Before sealing, bacterivores were introduced into the bottles, and the soil moisture content was adjusted to 60 % of the maximum field capacity. The microcosms were covered with sterile membranes that permitted air exchange while preventing microbial contamination and incubated in darkness at 25 °C. CO_2 and N_2O emission rates were measured on days 1, 2, 3, 5, 10, and 20 using a gas chromatograph

(Agilent 8890A; Agilent Technologies, Waldbronn, Germany).

N_2O and CO_2 fluxes were calculated using the following equation [29]:

$$F = \rho \times V \times \Delta C/\Delta V \times 273/(273+T)/m \quad (1)$$

where F represents the flux of N_2O (μg N kg^{-1} day^{-1}) or CO_2 (mg C kg^{-1} day^{-1}), ρ is the gas density under standard conditions (kg m^{-3}), V is the headspace volume (m^3), $\Delta C/\Delta t$ is the change in gas concentration (c) per unit of time (t) (ppb N_2O-N day^{-1}, ppm CO_2-C day^{-1}), T is the ambient temperature (°C) and m is the soil dry weight (kg).

Cumulative N_2O and CO_2 production was calculated as:

$$\text{Cumulative GHG production} = \sum_{i=1}^{n}(F_i + F_{i+1}) / 2 \times (t_{i+1} - t_i) \quad (2)$$

where F represents the GHG flux, at the i^{th} is the measurement, the term $t_{i+1}-t_i$ is the time interval between two measurements, and n is the total number of the measurement [35].

2.5. Soil analyses

After the final gas sampling, fresh soil samples were collected from each microcosm, for analysis of soil water content (SWC) the microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), nitrate-nitrogen (NO_3^-), ammonium-nitrogen (NH_4^+), dissolved organic carbon (DOC), and dissolved organic nitrogen (DON). The soil water content (SWC, g of water per 100g dry soil) was determined by oven-drying the soil at 105 °C for 48h. Total nitrogen (TN) and dissolved organic carbon (DOC) were extracted using 0.5 mol L^{-1} K_2SO_4 (soil:solution ratio = 1:5). The mixture was shaken for 60 min and filtered through a 0.42-μm filter. DOC in the filtrate was measured using a TOC analyzer (Elementar Analyzer System Vario TOC Cube, Germany), while TN was quantified via continuous flow auto-analysis (AA3, Germany) [36]. NH_4^+ and NO_3^- were extracted from 10 g soil by using 2 M KCl solution (1:5 w/v), shaken for 30 min, and analyzed using continuous flow auto-analysis (AA3, Germany). The microbial biomass carbon (MBC) was determined by the chloroform fumigation-direct extraction method [37].

2.6. Statistical analysis

The impact of nematode species and population density on soil CO_2 and N_2O emissions was examined through a two-way ANOVA approach. Temporal variations and treatment effects during the 20-day incubation period were analyzed using repeated measures ANOVA. For detecting significant variations in cumulative CO_2 and N_2O release, a one-way ANOVA coupled with the LSD post-hoc test was implemented. All statistical computations were executed on IBM SPSS 22.0 (IBM Corp., USA). To assess the relative contribution of soil characteristics (e.g., MBC, MBN, DOC, DON, NH_4^+, NO_3^-, SWC, TN) and biological elements to greenhouse gas emissions, random forest regression modeling was conducted utilizing the randomForest package in R software [38].

3. Results

The abundance of *Protorhabditis* spp. increased steadily over the 20-day incubation period (Fig. 1A). Among the treatments, P3 exhibited the highest abundance, significantly surpassing P1 and P2. Similarly, the abundance of *C. elegans* increased during the first 15 days, followed by a decline by day 20 (Fig. 1B).

For *Protorhabditis* spp., CO_2 production rates in P2 and P3 treatments were higher than that in the control (CK) (Fig. 2A). In P2, CO_2 production rates initially decreased from days 1–2, then increased from days 2–3, before decreasing again from days 3–20 (Fig. 2A). The N_2O production rate in P2 decreased from days 1–2, increased from days 2–3, and decreased from days 3–5, increased again by day 20 (Fig. 2. C). The incubation time had significant effects on CO_2 production rate, and the treatment had significant effects on N_2O production rate (Table S2).

For *C. elegans*, CO_2 and N_2O production rates in C2 and C3 treatments were significantly higher than in the control (Fig. 2B–D). In C3, CO_2 production rates decreased on day 2, peaked on day 3, and gradually declined over the incubation period. In C2, CO_2 production rates initially increased from days 1–2, then decreased from days 2–3, then increased again from days 3–5, and decreased (Fig. 2B). For N_2O production rates, C2 and C3 showed a decrease with incubation time (Fig. 2D). Incubation time had a significant effect on CO_2 production rate, while both incubation time and treatment had significant effects on N_2O production rate (Table S2).

The cumulative CO_2 and N_2O production were significantly higher in the *C. elegans* addition treatments (C2, C3) compared to both the control and the *Protorhabditis* spp. addition treatments (Fig. 2E and F). Among the *Protorhabditis* spp. treatments, the cumulative N_2O production was higher in P2 than in the control.

The random forest model identified the abundance of *C. elegans* as the most critical factor associated with cumulative CO_2 and N_2O production (Fig. 3C and D, Fig. S1). In *C. elegans* treatments, dissolved organic carbon (DOC) was the primary contributor to cumulative CO_2 production, while soil water content (SWC) was the primary driver of N_2O production (Fig. 3C and D). For *Protorhabditis* spp., total nitrogen (TN) was identified

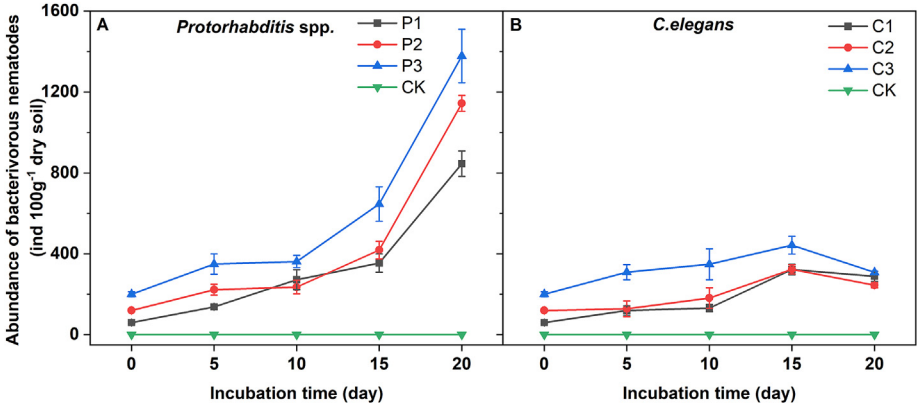

Fig. 1. Temporal changes in the abundance of *Protorhabditis* spp. (A) and *C. elegans* (B) during the incubation period. P1: *Protorhabditis* spp. addition at 1 individual g^{-1} dry soil; P2: *Protorhabditis* spp. addition at 2 individuals g^{-1} dry soil; P3: *Protorhabditis* spp. addition at 3 individuals g^{-1} dry soil; C1: *C. elegans* addition at 1 individual g^{-1} dry soil; C2: *C. elegans* addition at 2 individuals g^{-1} dry soil; C3: *C. elegans* addition at 3 individuals g^{-1} dry soil. Values represent means ± SE (n = 5).

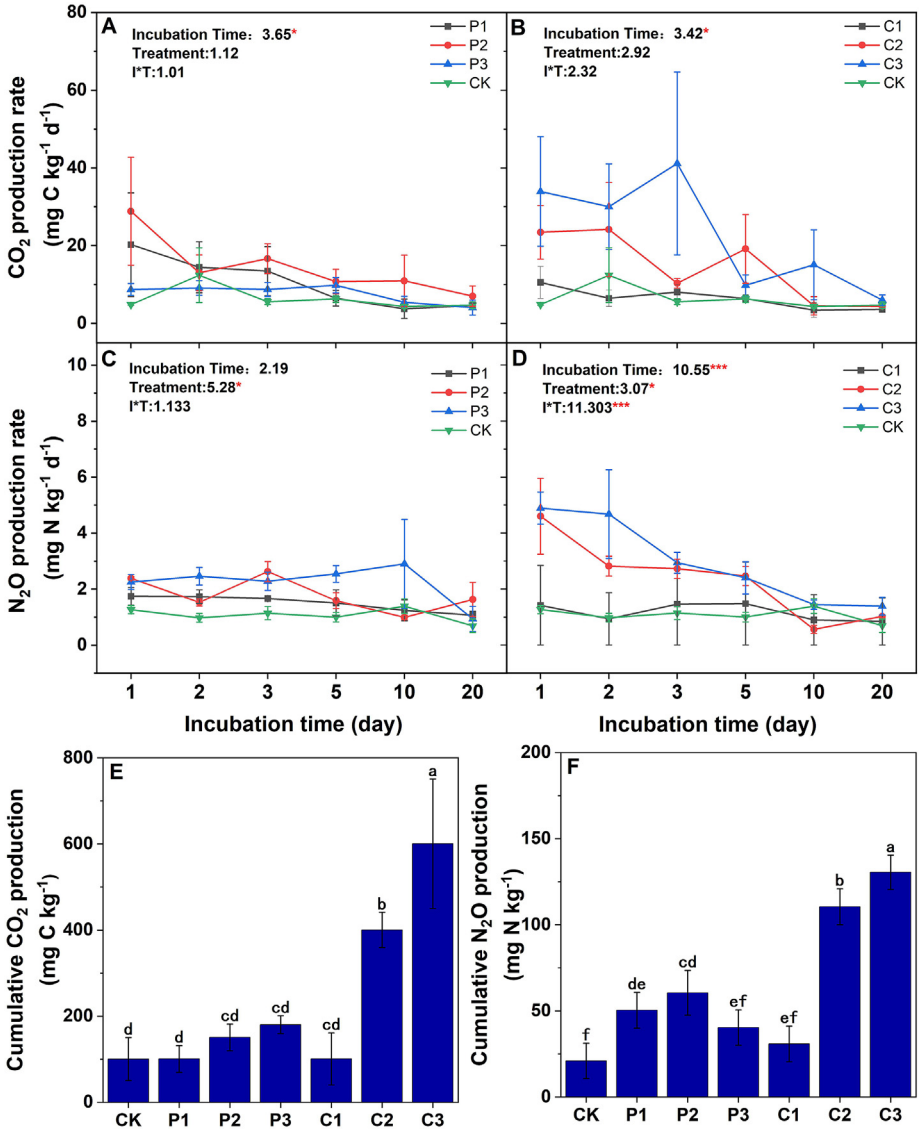

Fig. 2. Soil CO_2 and N_2O production rates (A, B, C, D) and cumulative emissions (E, F) under *Protorhabditis* spp. and *C. elegans* nematode addition treatments. F values are derived from repeated-measures ANOVA. I, T, and I × T represent the effects of incubation time, treatment, and their interactions, respectively. Significance levels are denoted as $^{*}p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$. CK: control (no nematode addition); P1: *Protorhabditis* spp. addition at 1 individual g^{-1} dry soil; P2: *Protorhabditis* spp. addition at 2 individuals g^{-1} dry soil; P3: *Protorhabditis* spp. addtion at 3 individuals g^{-1} dry soil; C1: *C. elegans* addition at 1 individual g^{-1} dry soil; C2: *C. elegans* addition at 2 individuals g^{-1} dry soil; C3: *C. elegans* addition at 3 individuals g^{-1} dry soil.

as the key factor influencing cumulative CO_2 production (Fig. 3A), there is no significant correlation was found between soil characteristics and N_2O production (Fig. 3B).

4. Discussion

Our study revealed that the addition of high-density *C. elegans* significantly increased the cumulative emissions of both CO_2 and N_2O, whereas the addition of *Protorhabditis* spp. had no discernible effect on CO_2 cumulative emissions but did increase N_2O emissions. These findings are inconsistent with our initial hypothesis. The contrasting effects can be attributed to the biological and ecological differences between the two bacterivorous nematode species. The active feeding behavior and higher metabolic traits of *C. elegans* appear to enhance microbial biomass turnover, stimulating respiration and accelerating SOC decomposition and nitrogen cycling-key processes associated with N_2O release [39–41]. Previous studies have reported that *C. elegans* preys on diverse bacterial communities, *potentially driving* heightened microbial respiration and nutrient turnover [42]. Additionally, *C. elegans* exhibited high metabolic activity per unit of biomass (Table S1), which may further amplify CO_2 and N_2O emissions [43].

In contrast, the negligible impact of *Protorhabditis* spp. on CO_2 emissions, despite its increase in N_2O emissions, indicated a distinct metabolic and ecological role compared to *C. elegans*. *Protorhabditis* spp. may exhibit a more selective feeding behavior, targeting specific bacterial populations that contribute to microbial community stability, rather than promoting rapid microbial turnover [18]. This aligns with previous research indicating that selective predation by nematodes can stabilize microbial activity and nutrient mineralization, ultimately reducing GHG [16,31]. Furthermore, the slower metabolic rate of *Protorhabditis* spp. likely results in weaker stimulation of microbial respiration and nitrogen transformations, which may explain its minimal impact on CO_2 and N_2O emissions.

Contrary to our second hypothesis, the abundance of *Protorhabditis* spp.—despite its rapid growth during the incubation period—did not correlate with enhanced microbial turnover or increased GHG emissions. This result challenges the assumption that nematode abundance alone directly drives GHG emissions [3,4,44]. One possible explanation is that *Protorhabditis* spp. selectively preys on microbial populations in a way that supports microbial biomass stability rather than triggering accelerated decomposition or nitrogen transformation processes [9,45,46]. Another possibility is that relatively short duration of the incubation period, which may have been insufficient for *Protorhabditis* spp. to exert a measurable effect on microbial-mediated CO_2 and N_2O production.

Overall, these findings highlight the critical importance of species-specific traits, such as metabolic activity, feeding behavior, and

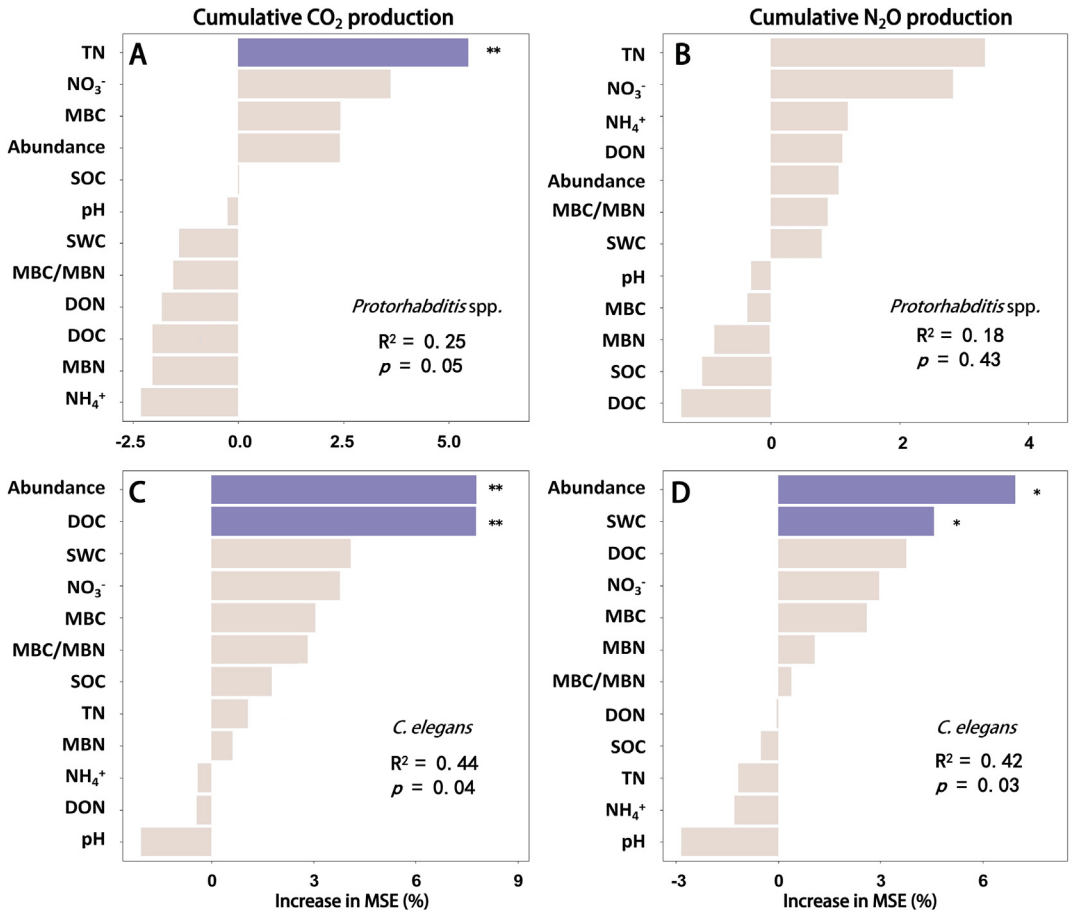

Fig. 3. Importance of soil biological and abiotic factors in explaining cumulative CO_2 production (A, C) and cumulative N_2O production (B, D) based on random forest regression analysis. Panels A and B refer to *Protorhabditis* spp., while panels C and D to *C. elegans*. Abbreviations: TN, total nitrogen; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; SOC, soil organic carbon; SWC, soil water content; DON, dissolved organic nitrogen; DOC, dissolved organic carbon; NH_4^+, ammonium nitrogen; NO_3^-, nitrate nitrogen. Significance levels are indicated as $^*p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$.

ecological roles, in determining the contributions of bacterivorous nematodes to soil carbon and nitrogen cycling. Our results suggest that the effects of nematode species on GHG emissions are not solely driven by their abundance or growth rate but are strongly mediated by their interactions with soil microbial communities. *C. elegans*, by enhancing microbial biomass turnover, leads to increased CO_2 and N_2O emissions, whereas *Protorhabditis* spp. appears to stabilize microbial biomass without accelerating respiration or decomposition processes. These insights contribute to a deeper understanding of how nematode-driven processes influence soil GHG dynamics and have important implications for agricultural management. By strategically balancing nematode species composition, it may be possible to optimize soil GHG emissions while maintaining soil health and productivity. Such approaches could contribute to more sustainable agricultural practices in the context of global climate change.

CRediT authorship contribution statement

Yao Yu: Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Data curation. **Xianwen Long:** Writing – review & editing. **Yaping Lin:** Resources. **Tibor Magura:** Writing – review & editing. **Siqi Wang:** Resources. **Xionghui Liao:** Writing – review & editing. **Jiangnan Li:** Writing – review & editing. **Jie Zhao:** Writing – review & editing, Funding acquisition.

Data availability statement

The data will be made available upon request.

Declaration of competing interest

The co-authors Jie Zhao and Xionghui Liao are affiliated with Climate Smart Agriculture, with Jie Zhao serving as the Editorial Board Member and Xionghui Liao as the Youth Editor. They were not involved in the editorial review process or the decision to publish this article. All other authors declare that they have no competing interests related to this work.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.csag.2025.100049.

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