

Article

Interactive Effects of Litter and Understory Removal on Soil Nematodes Community in a Climate Transitional Forest

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Abstract

Litter and understory are key components of forest ecosystems, playing vital roles in soil carbon inputs and microhabitat regulation. Their removal is a common forest management practice: litter removal (L) reduces fire and pest risks while promoting nutrient cycling, whereas understory removal (U) alleviates nutrient competition between understory plants and trees. However, the combined effects and underlying mechanisms of litter removal (L) and understory removal (U) on soil nematode communities remain unclear. This study investigated the individual and interactive effects of L and U on soil nematode communities in a coniferous–broadleaved mixed forest in a subtropical–warm temperate transition zone. The results showed that L significantly reduced soil nematode abundance by 18.1%, increased the relative abundance of bacterivores and omnivores–predators by 21.1% and 103.3%, respectively. U significantly elevated the relative abundance of fungivores by 30.8%, while both L and U reduced the relative abundance of plant-parasitic nematodes. Significant interactive effects between L and U were observed on soil nematode abundance, relative abundances of fungivores, plant-parasites, maturity index, and plant parasite index. Litter plus understory removal (LU) alleviated soil nematode resource limitation through synergistic regulation of resource pulses and microhabitat modification. Faunal analysis based on structure and enrichment indices indicated that LU enhanced food web structural complexity and resource-use efficiency. Redundancy analysis identified microbial biomass carbon, microbial biomass nitrogen, and soil total carbon as key drivers of nematode community differentiation. This study reveals the synergistic regulatory patterns of litter and understory vegetation on soil nematode communities, providing a theoretical reference for understanding the responses of soil nematodes to understory disturbance during the growing season in climate transitional forests, and offering basic data for long-term monitoring and forest soil management.



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Keywords: litter removal; understory removal; soil nematode community; trophic groups; ecological indices

1. Introduction

Forest soil carbon constitutes approximately 44% of the total forest carbon stock [1] and serves as a critical carbon sink for atmospheric CO₂ regulation [2]. Litter and understory vegetation, as key components maintaining forest soil carbon stability, jointly play fundamental roles in maintaining soil carbon dynamics and ecosystem stability. Litter

serves as the primary source of carbon input into forest soils, and changes in its input profoundly influence soil carbon dynamics [3]. The accumulation of litter on the forest floor is generally associated with increased soil carbon storage [4], while litter also fulfills dual functions of soil nutrient supply and microhabitat modification. On one hand, it acts as an intrinsic source of carbon-rich organic matter and nutrients, supporting soil organic matter accumulation and meeting the energy demands of soil communities [5]. On the other hand, it forms a protective layer that regulates microclimates and creates favorable conditions for the survival and activity of soil fauna [6]. Understory aids in the reduction of soil organic carbon loss and promotes carbon accumulation through continuous input of fresh organic matter [7]. It also performs multiple critical ecological functions: providing food and habitats for soil arthropods, large herbivores, and other organisms to sustain biodiversity and facilitate natural forest regeneration [8]; indirectly influencing greenhouse gas emissions by regulating aboveground biomass and carbon–nitrogen dynamics [8,9]; improving soil structure, enhancing nutrient availability, and regulating microbial activity to drive soil nutrient cycling [10]; and mitigating water loss and preventing soil erosion, thereby comprehensively safeguarding soil health through water and soil conservation [9]. The removal of litter and understory is regarded as an important forest management practice because it can reduce the frequency of forest fires [11], lower the risk of pest and disease outbreaks [12], facilitate nutrient cycling and plant growth by alleviating soil microbial nitrogen limitation and enhancing enzyme activity [13], and alleviate nutrient competition between understory vegetation and trees, thereby promoting tree growth [14].

As the most abundant animal group on Earth, soil nematodes not only constitute a major component of soil communities but also serve as a key foundation for maintaining the functional integrity of soil food webs across trophic levels [15–17]. Their community structure (e.g., diversity, functional group composition) and ecological indices (e.g., maturity index, structure index) are highly sensitive to environmental changes and respond rapidly to fluctuations in soil microhabitats and resource availability [18,19]. Consequently, soil nematodes are widely recognized as core bioindicators for assessing soil health and ecosystem functional stability [20]. Current global climate change (e.g., extreme precipitation, rising temperatures) and human activities (e.g., forest management, understory vegetation removal) frequently alter litter stocks and understory coverage [21,22]. Clarifying the impacts of these changes on soil nematode communities allows us to infer shifts in carbon cycling functions, nutrient supply capacity, and other key processes of forest soil ecosystems from nematode community structure [23], thereby providing a theoretical basis for the scientific management of forest ecosystems.

As a major carbon source and microhabitat provider in soil ecosystems, litter directly regulates soil nematode community structure [24,25]. Previous research has shown that litter removal may not significantly affect soil nematode abundance but can significantly reduce genus richness due to the loss of suitable microhabitats following the disappearance of the litter layer [26]. Litter reduction intensifies the surface temperature and moisture fluctuations, disrupts microenvironmental stability, leads to the loss of some sensitive genera, and consequently lowers genus richness [5]. Understory removal is a common forest management practice. After understory removal, the abundance of most nematode genera often shows a rapid initial increase followed by a gradual decline, a pattern associated with resource dynamics characterized by a short-term pulse of plant residue input followed by gradual depletion [27]. Some studies also reported that understory removal during the dry season significantly reduces the density of all nematodes, particularly plant-parasitic nematodes. In contrast, during the rainy season, only the density of plant-parasitic nematodes is significantly decreased [28].

Existing studies have primarily focused on the individual effects of either litter removal or understory removal on soil nematode communities, with limited attention given to their interactive effects. In forests, understory can reduce soil temperature fluctuations and maintain humidity by shading sunlight, thereby creating favorable conditions for litter decomposition [29]. In turn, nutrients such as nitrogen (N) and phosphorus (P) released during litter decomposition support understory growth [30], forming a close interdependent relationship between the two. However, it remains unclear how this relationship jointly alters soil resources and living environment, thereby collectively regulating soil nematode community structure and function. To address this gap, the present study examines a coniferous–broadleaved mixed forest, a common forest type in the transition zone between warm temperate and north subtropical regions, to investigate the effects of litter and understory removal on soil nematode community structure. The following hypotheses were formulated and tested: (1) as a key carbon source and microhabitat provider for soil nematodes, litter removal reduces available resources and consequently diminishes soil nematode abundance; (2) understory continuously supplies fresh organic matter and stabilizes the soil microhabitat, supporting the foraging and reproduction of plant-parasitic nematodes; thus its removal is expected to reduce the relative abundance of plant-parasitic nematodes; (3) the interactive effects between litter and understory removal alleviate the negative impacts of either litter or understory removal on soil nematode communities through synergistic regulation of resources and microhabitats.

2. Materials and Methods

2.1. Site Description

The experiment was conducted at the Henan Dabieshan National Forest Ecosystem Observation and Research Station (32°06′ N, 114°01′ E, 200 m a.s.l.). Located south of the Huaihe River, the study area lies within a continental monsoon climate transitional between north subtropical and warm temperate zones, featuring four distinct seasons with marked climatic variation and winter frost. The mean annual temperature is 15.3 °C, with a mean annual precipitation of 1100 mm concentrated predominantly between May and October. The research object is an approximately 40-year-old coniferous–broadleaved mixed forest, with canopy, shrub, and herb layer coverages of 83%, 23%, and 10%, respectively. The canopy layer is dominated by *Pinus massoniana* and *Quercus acutissima* [31]; understory shrubs mainly include *Vitex negundo*, *Symplocos chinensis*, *Lindera glauca*, and *Smilax china*; and the herbaceous layer is primarily composed of *Lygodium japonicum* and *Carex duriuscula*. The understory vegetation includes tree saplings, shrubs, and herbs. The mass ratio of coniferous to broadleaved litter is 53.5:46.5, with a litter layer thickness of 1.2 cm [32,33]. The soil is classified as yellow-brown soil with a pH of 4.5 [34].

2.2. Experimental Design

The experiment was established in 2016, with monthly maintenance of litter and understory vegetation treatments, and had been continuously running for eight years by the time of soil sampling in August 2024. The experimental site was located on a south facing slope with a total area of approximately 5 ha. A relatively flat area within the coniferous–broadleaved mixed forest was selected as the experimental zone, with no obvious depressions, mounds, or undulating topography. The experimental area was divided into four blocks (55 m × 10 m each), separated by 5 m intervals. Within each block, four plots (10 m × 10 m each, separated by 5 m) were established and assigned to four treatments: control (C), litter removal (L), understory removal (U), and combined litter and understory removal (LU). Each treatment had four replicates, resulting in a total of 16 plots. In the C plots, natural litter accumulation and the original understory community were

left undisturbed. In the L and LU plots, all visible litter on the soil surface was manually removed at the beginning of each month using brooms and rakes. In the U and LU plots, understory vegetation was cut at ground level and removed from the plots with sickles and rakes at the start of each month.

2.3. Soil Sampling and Processing

Soil was collected in August 2024 using a soil auger with a diameter of 5 cm. Following the principles of random sampling and the five-point sampling method (four corners and the center of each plot), five soil cores were collected from the 0–10 cm soil layer in each plot. The five soil cores from the same plot were pooled as sub-samples and thoroughly mixed to form one composite sample per plot, in order to minimize within-plot micro-scale spatial heterogeneity and to ensure the representativeness of the samples [35]. In this study, each treatment consisted of four independent plots ($n = 4$), totaling 16 independent plots and 16 composite samples. The mixed soil samples were then passed through a 2 mm sieve to remove plant roots and debris. The sieved soil was then labeled and divided into two portions. One portion was stored at 4 °C for nematode extraction and identification. The other portion was sealed and stored at −20 °C for subsequent analysis of soil physicochemical properties.

Soil nematodes were extracted from 100 g of fresh soil using the modified Baermann funnel method [36]. After extraction, soil nematodes were heat killed and fixed in 5 mL of TAF solution (composition: 91 mL distilled water, 7 mL 40% formaldehyde, 2 mL triethanolamine, diluted to 100 mL). The fixed samples were stored at 4 °C for subsequent analysis. Soil nematodes were counted under an optical microscope. For each sample, the first 100 individuals encountered were identified to genus level (or all if fewer than 100 were present). Based on feeding habits and morphological characteristics of the head and tail, soil nematodes were assigned to four trophic groups: bacterivores, fungivores, plant-parasites, and omnivores-predators [37].

Soil pH was measured potentiometrically at a soil-to-water ratio of 2.5:1. Soil water content (SWC) was determined using the gravimetric method via oven-drying. Soil total carbon (TC) and total nitrogen (TN) were analyzed with a semi-micro elemental analyzer (Elementar vario MACRO CUBE, Elementar Co., Hanau, Germany) following the combustion method. Microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were measured using the chloroform fumigation-extraction method with potassium sulfate as the extractant. Soil ammonium nitrogen ($\text{NH}_4^+\text{-N}$), soil nitrate nitrogen ($\text{NO}_3^-\text{-N}$), and available phosphorus (AP) were measured with an automated chemical analyzer (AMS Smartchem200, Les Allues, France). Soil temperature (ST) was recorded using a soil temperature and moisture monitor (SWM5000, STEPS Co., Nuremberg, Germany).

2.4. Data Processing and Statistical Analysis

All soil nematode ecological indices were calculated based on the taxonomic identification results of nematodes:

$$\text{Shannon–Weiner diversity index } (H') : H' = -\sum p_i \times \ln(p_i) \quad (1)$$

$$\text{Simpson index } (\lambda) : \lambda = 1 - \sum p_i^2 \quad (2)$$

$$\text{Maturity index (MI)} : \text{MI} = \sum (v_i \times f_i) \quad (3)$$

$$\text{Plant parasite index (PPI)} : \text{PPI} = \sum (v_i \times f_i) \quad (4)$$

$$\text{Basal index (BI)} : \text{BI} = 100 \times \left(\frac{b}{s + e + b} \right) \quad (5)$$

$$\text{Enrichment index (EI) : EI} = 100 \times \left(\frac{e}{e+b} \right) \quad (6)$$

$$\text{Structure index (SI) : SI} = 100 \times \left(\frac{s}{s+b} \right) \quad (7)$$

$$\text{Channel index (CI) : CI} = 0.8 \times \left(\frac{Fu_2}{3.2 \times Ba_1 + 0.8 \times Fu_2} \right) \quad (8)$$

In the formulas, p_i denotes the frequency of each genus in a soil sample. v_i denotes the cp value of the genus. f_i denotes the proportion of free-living nematode guilds relative to the total number of nematodes in a soil sample. The enrichment component e consists of bacterivores with cp 1 and fungivores with cp 2. The basal component b includes bacterivores with cp 2 and fungivores with cp 2. The structural component s comprises bacterivores, fungivores, and omnivores-predators with cp values of 3–5. In the channel index calculation, Ba_1 denotes bacterivores with cp 1, and Fu_2 denotes fungivores with cp 2.

Data normality and homogeneity of variance were first verified. Two-way analysis of variance (ANOVA) was then performed using SPSS (Version 27.0, SPSS Inc., Chicago, IL, USA) to examine the effects of litter removal, understory removal, and their interactive effects on soil nematode community characteristics. Significant differences were determined by the least significant difference (LSD) test at $p < 0.05$. Correlation analyses between soil nematode communities and soil physicochemical properties were also conducted with SPSS. To assess the differentiation of soil nematode community composition among treatments and to quantify the explanatory power of soil physicochemical factors, redundancy analysis (RDA) was performed using Canoco 5 software. Furthermore, faunal analysis based on SI and EI was conducted using the dplyr and ggplot2 packages in R (version 4.2.2) to quantify resource allocation and stability characteristics of the soil food web.

3. Results

3.1. Soil Physicochemical Properties

The two-way ANOVA results showed that L significantly reduced SWC, AP, and MBC by 22.7%, 31.6%, and 73.9%, respectively ($p < 0.05$, Table 1). U significantly decreased $\text{NH}_4^+\text{-N}$ and MBC by 17.7% and 52.7%, while it significantly increased TC by 27.7%, ($p < 0.05$, Table 1). In addition, significant interactive effects between L and U were detected on $\text{NO}_3^-\text{-N}$, MBC, MBN, TC, and TC:TN (all $p < 0.05$, Table 1). When understory was present, L decreased $\text{NO}_3^-\text{-N}$, MBC, MBN, TC, and TC:TN by 46.9%, 82.9%, 61.5%, 38.3%, and 14.7%, respectively. In contrast, when understory was removed, L increased $\text{NO}_3^-\text{-N}$, MBN, TC, and TC:TN by 10.1%, 88.9%, 18.2%, and 4.1%, respectively, it decreased MBC by 49.7%. When litter was present, U reduced $\text{NO}_3^-\text{-N}$, MBC, MBN, TC, and TC:TN by 47.5%, 63.1%, 58.7%, 5.3%, and 5.6%, respectively. Conversely, when litter was removed, U increased these parameters by 9.0%, 8.2%, 102.4%, 81.2%, and 15.2%, respectively.

Table 1. Results (Mean $\pm$ SE) of soil properties under different treatments and p values from two-way ANOVA indicate the effects of litter removal (L), understory removal (U), and their interactions on soil properties.

Response Variables	Treatments (Mean $\pm$ SE)				Two-Way ANOVA		
	C	L	U	LU	L	U	LU
Soil pH	4.37 $\pm$ 0.08	4.21 $\pm$ 0.23	4.37 $\pm$ 0.09	4.57 $\pm$ 0.06	0.874	0.198	0.210
SWC (%)	13.62 $\pm$ 0.60	9.20 $\pm$ 0.88	11.07 $\pm$ 0.97	9.87 $\pm$ 1.48	0.019	0.381	0.144
$\text{NH}_4^+\text{-N}$ (mg/kg)	21.94 $\pm$ 1.24	17.33 $\pm$ 0.31	16.50 $\pm$ 1.61	15.83 $\pm$ 1.95	0.087	0.031	0.189
$\text{NO}_3^-\text{-N}$ (mg/kg)	11.16 $\pm$ 1.62	5.92 $\pm$ 1.05	5.87 $\pm$ 1.20	6.46 $\pm$ 1.09	0.090	0.083	0.030

Table 1. Cont.

Response Variables	Treatments (Mean $\pm$ SE)				Two-Way ANOVA		
	C	L	U	LU	L	U	LU
AP (mg/kg)	0.42 $\pm$ 0.04	0.31 $\pm$ 0.02	0.38 $\pm$ 0.08	0.24 $\pm$ 0.05	0.033	0.326	0.798
ST ($^{\circ}$ C)	34.03 $\pm$ 0.21	33.75 $\pm$ 0.93	33.90 $\pm$ 0.38	34.88 $\pm$ 0.28	0.522	0.365	0.262
MBC (mg/kg)	254.14 $\pm$ 31.16	43.57 $\pm$ 7.56	93.78 $\pm$ 7.21	47.15 $\pm$ 7.37	<0.001	0.001	<0.001
MBN (mg/kg)	17.43 $\pm$ 4.21	6.72 $\pm$ 1.12	7.20 $\pm$ 0.86	13.59 $\pm$ 0.83	0.358	0.471	0.003
TC (g/kg)	26.04 $\pm$ 2.45	16.07 $\pm$ 1.05	24.66 $\pm$ 4.18	29.13 $\pm$ 1.97	0.324	0.049	0.019
TN (g/kg)	1.70 $\pm$ 0.12	1.25 $\pm$ 0.13	1.72 $\pm$ 0.31	1.94 $\pm$ 0.15	0.570	0.090	0.105
TC:TN	15.30 $\pm$ 0.55	14.45 $\pm$ 0.22	13.06 $\pm$ 0.56	15.05 $\pm$ 0.26	0.077	0.206	0.006

Abbreviations: SWC, soil water content; NH_4^+ -N, soil ammonium nitrogen; NO_3^- -N, soil nitrate nitrogen; AP, soil available phosphorus; ST, soil temperature; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; TC, soil total carbon; TN, soil total nitrogen; TC:TN, total-carbon-to-total-nitrogen ratio. The bold numerals highlight the significance at $p < 0.05$.

3.2. Nematode Abundance and Relative Abundances of Trophic Groups

Two-way ANOVA results indicated that L significantly decreased soil nematode abundance by 18.1% ($p < 0.05$, Table 2, Figure 1), whereas U had no significant effect on it ($p > 0.05$, Table 2, Figure 1). A significant interactive effect between L and U on soil nematode abundance was observed ($p < 0.05$, Table 2, Figure 1). When understory was present, L reduced soil nematode abundance by 37.1%. In contrast, when understory was removed, L only caused a slight reduction of 1.2%. When litter was present, U decreased soil nematode abundance by 19.9%. However, when litter was removed, U resulted in a 15.9% increase in soil nematode abundance.

Table 2. Results (p values) of two-way ANOVA on the effects of litter removal (L), understory removal (U), and their interactions on soil nematode abundance, trophic group relative abundances, and functional indices.

Response Variables	p		
	L	U	LU
Soil nematode abundance (individual/100 g dry soil)	0.004	0.342	0.005
Relative abundance of bacterivores nematodes (%)	0.028	0.420	0.054
Relative abundance of fungivorous nematodes (%)	0.625	0.001	0.001
Relative abundance of omnivores-predators nematodes (%)	<0.001	0.098	0.560
Relative abundance of plant-parasitic nematodes (%)	<0.001	0.001	<0.001
Shannon–Weiner diversity index (H')	0.493	0.168	0.633
Simpson index (λ)	0.998	0.251	0.813
Maturity Index (MI)	0.002	0.006	0.031
Plant parasite index (PPI)	<0.001	<0.001	<0.001
Basal index (BI)	<0.001	0.214	0.502
Enrichment index (EI)	0.059	0.494	0.281
Structure index (SI)	0.003	0.489	0.490
Channel index (CI)	0.064	0.592	0.541

The bold numerals highlight the significance at $p < 0.05$.

L and U significantly affected the relative abundances of different nematode trophic groups (both $p < 0.05$, Table 2, Figure 2). Additionally, a significant interactive effect between L and U was observed for the relative abundances of fungivores and plant-parasitic nematodes (both $p < 0.05$, Table 2, Figure 2b,d). L significantly increased the relative abundances of bacterivores and omnivores-predators by 21.1% and 103.3%, respectively, while it significantly reduced the relative abundance of plant-parasitic nematodes by 52.2% (all $p < 0.05$, Table 2, Figure 2a,c,d). U significantly elevated the relative abundance of fungivores by 30.8% and lowered that of plant-parasitic nematodes by 50.7% ($p < 0.05$, Table 2, Figure 2b,d). When understory was present, L increased the relative abundance

of fungivores by 31.7% and decreased that of plant-parasitic nematodes by 69.8%. In contrast, when understory was removed, L reduced the relative abundance of fungivores by 23.1% but increased that of plant-parasitic nematodes by 4.0%. When litter was present, U raised the relative abundance of fungivores by 71.3% and decreased that of plant-parasitic nematodes by 68.6%. However, when litter was removed, U had no significant effect on the relative abundance of fungivores but increased that of plant-parasitic nematodes by 8.3%.

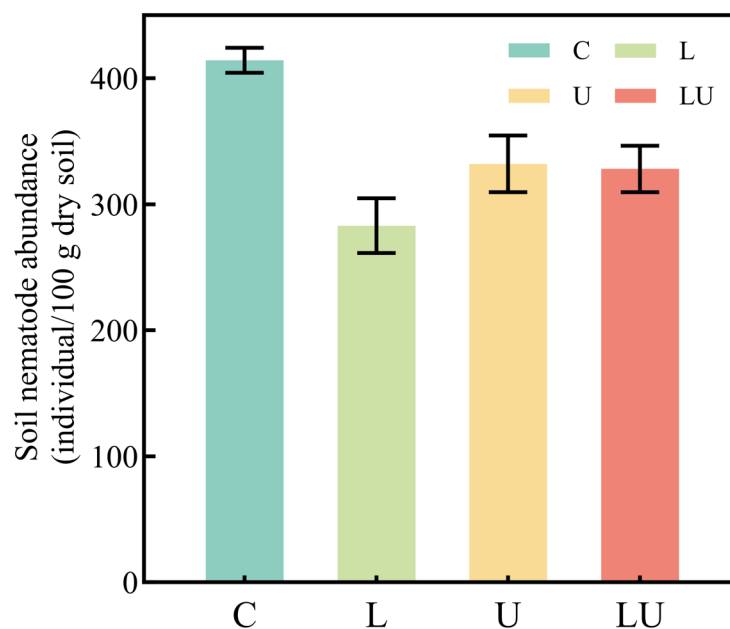


Figure 1. Soil nematode abundance under different treatments (Mean $\pm$ SE). C, control; L, litter removal; U, understory removal; LU, litter plus understory removal.

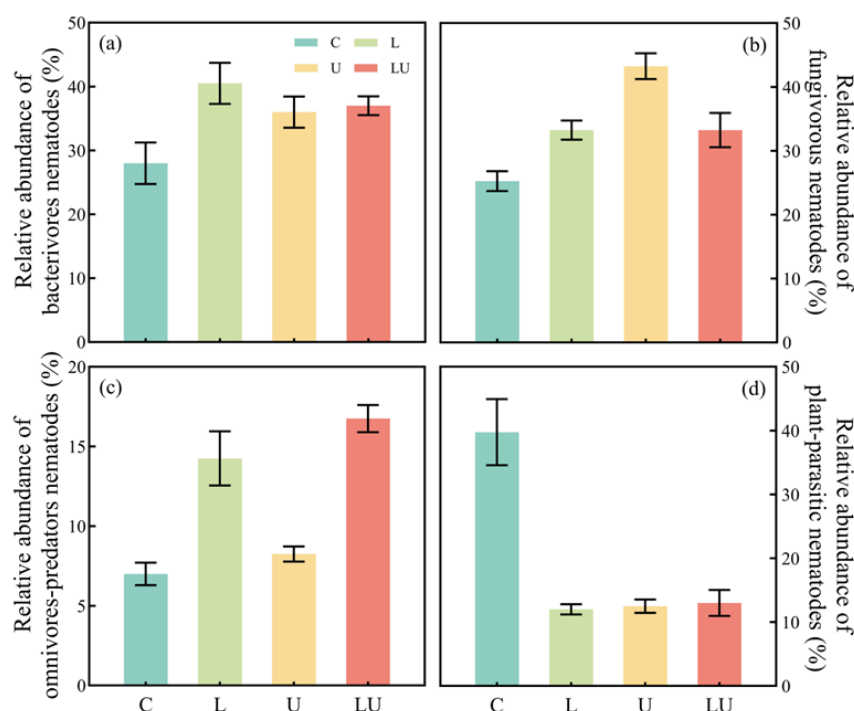


Figure 2. Relative abundance of four trophic groups of nematodes under different treatments (Mean $\pm$ SE). (a) Relative abundance of bacterivores nematodes; (b) Relative abundance of fungivorous nematodes; (c) Relative abundance of omnivores-predators nematodes; (d) Relative abundance of plant-parasitic nematodes. See Figure 1 for abbreviations.

3.3. Soil Nematode Ecological Indices

According to the two-way ANOVA, neither L nor U had significant effects on H' , λ , EI, or CI (all $p > 0.05$, Table 2, Figure 3a,b,f,h). L significantly increased the MI and SI by 23.4% and 24.2%, respectively ($p < 0.05$), while it significantly reduced the PPI and BI by 27.5% and 29.7%, respectively ($p < 0.05$). U significantly elevated the MI by 19.4% and significantly decreased the PPI by 47.2% (both $p < 0.05$). Significant interactive effects between L and U were observed for the MI and PPI (both $p < 0.05$, Table 2, Figure 3f,g). When understory was present, L increased the MI by 45.8% and decreased the PPI by 66.3%. In contrast, when understory was removed, L raised the MI by 7.5% and increased the PPI by 7.7%. When litter was present, U increased the MI by 41.4% and reduced the PPI by 66.0%. However, when litter was removed, U only caused slight increases in the MI and PPI, by 4.3% and 8.6%, respectively.

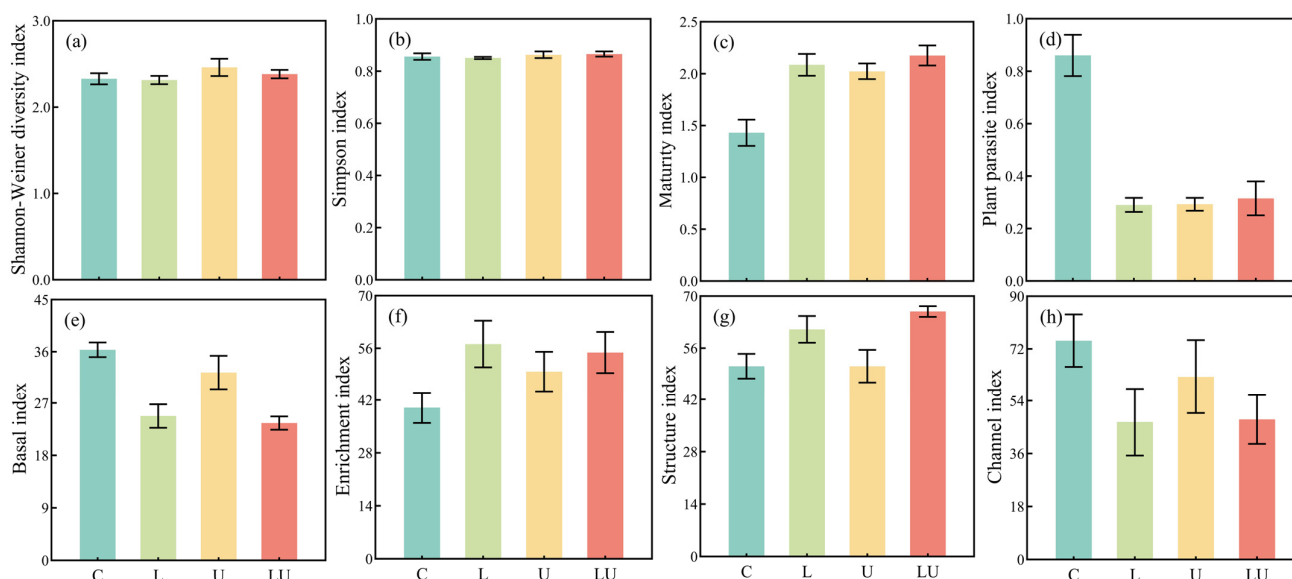


Figure 3. Nematode ecological indices under different treatments (Mean ± SE). (a) Shannon–Weiner diversity index; (b) Simpson index; (c) Maturity index; (d) Plant parasite index; (e) Basal index; (f) Enrichment index; (g) Structure index; (h) Channel index. See Figure 1 for abbreviations.

The two-dimensional faunal analysis based on SI and EI showed distinct separations among treatments (Figure 4). The C treatment was primarily located in quadrants C and D, indicating a relatively low level of resource enrichment and a structurally simple soil food web. In contrast, the L treatment and U treatment showed a more dispersed distribution. Both L and U treatments exhibited higher values in either the SI, EI, or both indices compared to the control. Samples from the LU treatment were mainly concentrated in quadrant B and its vicinity. This distribution reflects a more complex food web structure and a greater capacity for resource enrichment.

3.4. Correlations Between Soil Nematode Communities and Soil Physicochemical Properties

The first two axes of the RDA explained 54.1% of the total variation in the relationship between soil nematode genera and soil physicochemical factors (RDA1: 43.4%; RDA2: 10.7%). MBC and MBN were identified as the primary driving factors along the first axis, while TC was the main factor along the second axis. Collectively, these results indicate that MBC, MBN, and TC significantly influenced soil nematode community composition (Figure 5).

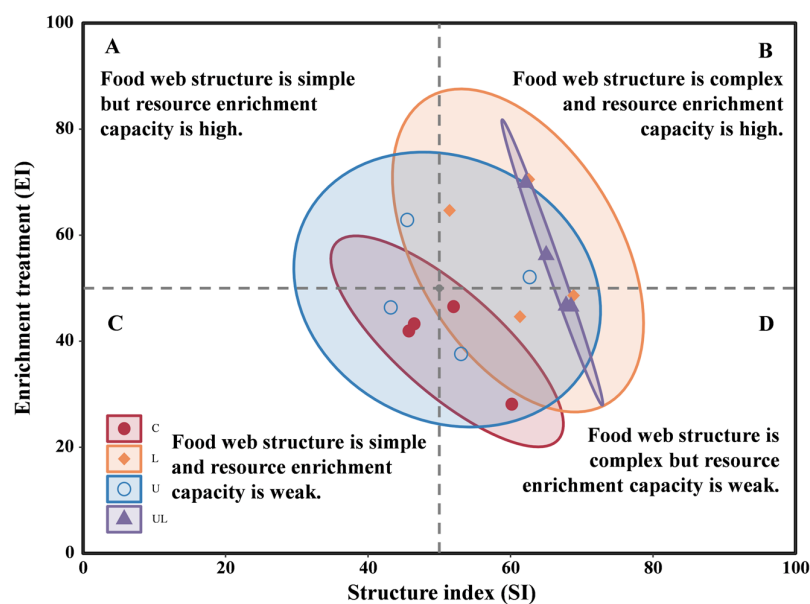


Figure 4. Analysis of soil nematode fauna under different treatments (based on SI and EI). See Figure 1 for abbreviations.

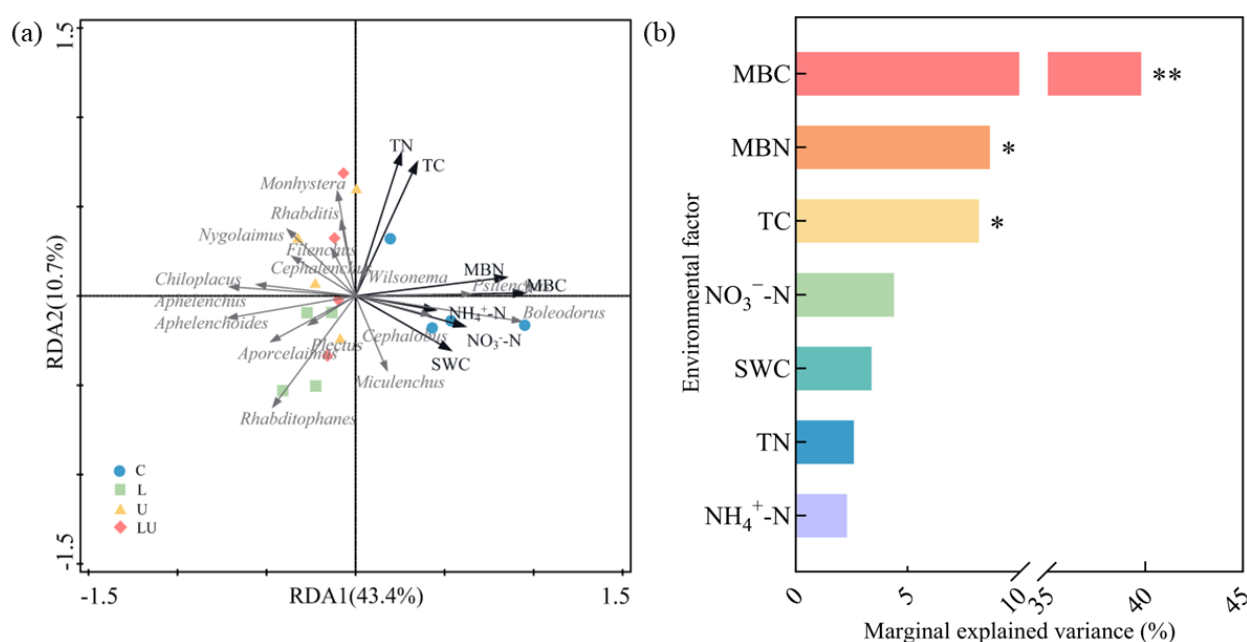


Figure 5. Redundancy analysis (RDA) of soil nematode community composition and environmental factors. (a) Ordination biplot showing relationships between nematode genera and soil environmental variables. Arrows represent both environmental factors and nematode genera; the length and direction of each arrow indicate its relative contribution and correlation with the RDA axes; (b) Marginal explained variance (%) of each environmental factor from forward selection. *, $p < 0.05$; **, $p < 0.01$. See Table 1 for abbreviations.

The correlation analysis revealed significant relationships between soil nematode community characteristics and soil physicochemical properties (Figure 6). Soil nematode abundance and the relative abundance of plant-parasitic nematodes showed significant positive correlations with SWC, while the relative abundance of omnivores-predators and MI were significantly negatively correlated with SWC. Negative correlations were observed between relative abundance of fungivores, MI, and $\text{NH}_4^+\text{-N}$. In contrast, the relative abundance of plant-parasitic nematodes, PPI, and BI were positively correlated with

NH₄⁺-N. Similarly, soil nematode abundance, the relative abundance of plant-parasitic nematodes, and PPI were positively correlated with NO₃⁻-N, while MI was negatively correlated with NO₃⁻-N. The relative abundance of omnivore-predators was negatively correlated with AP, while BI and CI were positively correlated with AP. Positive correlation was found between soil nematode abundance, the relative abundance of plant-parasitic nematodes, PPI, BI and MBC. Conversely, the relative abundances of bacterivores, fungivores, and omnivores-predators, as well as the MI, EI, and SI, were negatively correlated with MBC. Soil nematode abundance, the relative abundance of plant-parasitic nematodes, and PPI were positively correlated with MBN. The relative abundances of bacterivores and fungivores, as well as MI, were negatively correlated with MBN. Additionally, both *H'* and λ showed significant positive correlations with TN.

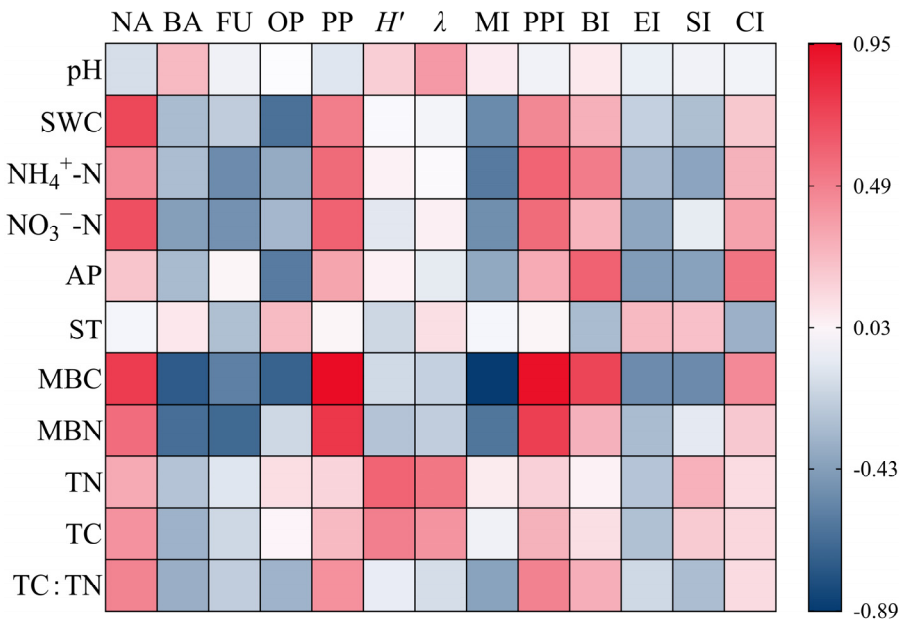


Figure 6. Correlation analysis of soil nematode community composition, ecological indices, and soil physicochemical properties. NA, soil nematode abundance; BA, relative abundance of bacterivores nematodes; Fu, relative abundance of fungivorous nematodes; OP, relative abundance of omnivores-predators nematodes; PP, relative abundance of plant-parasitic nematodes. See Tables 1 and 2 for other abbreviations.

4. Discussion

4.1. Effects of Litter Removal on Soil Nematode Communities

In this study, litter removal (L) reduced soil nematode abundance. Litter acts as a core source of energy and nutrients for soil food webs; a decline in its input restricts the availability of organic matter accessible to nematodes, in turn lowering their population abundance [24]. Furthermore, the litter layer physically buffers external disturbances and stabilizes soil temperature and moisture. Its removal disrupts the microenvironmental buffering effect, amplifies soil environmental fluctuations, and consequently inhibits nematode growth and reproduction [38]. These results support our first hypothesis that L reduces soil nematode abundance by decreasing resource availability and weakening microenvironmental stability.

L increased the relative abundances of bacterivores and omnivores-predators, while decreasing that of plant-parasitic nematodes. L can reduce inputs of recalcitrant substrates, increase the proportion of labile organic carbon, and lower TC:TN. A decrease in TC:TN further drives the shift of microbial communities toward bacterial dominance [39]. As obligate consumers of bacteria, the elevated relative abundance of bacterivores reflects a direct

response to the increased availability of bacterial resources. The increase in omnivores-predators is directly attributed to the elevated relative abundance of bacterivores, which serve as their primary prey, providing an adequate food supply [40]. A negative correlation was observed between AP and the relative abundance of omnivores-predators. This finding aligns with results from a long-term nitrogen and phosphorus fertilization experiment in the black soil region of Northeast China [41]. The study demonstrated that AP modifies the soil physicochemical environment, suppresses omnivores-predators (K-strategists) which are sensitive to disturbance, and promotes the proliferation of low-trophic-level bacterivores, ultimately simplifying the food web and intensifying survival pressure on higher-trophic-level nematodes.

L reduced the relative abundance of plant-parasitic nematodes. This finding supports the view proposed by Pulavarty et al. [42] that the survival and reproduction of plant-parasitic nematodes are highly dependent on root-derived resources and suitable microenvironments. On one hand, sufficient N supply promotes root growth and improves soil nutrient conditions [43]. L decreases soil $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$, thereby inhibiting plant growth, reducing root biomass, and limiting foraging sites for plant-parasitic nematodes. On the other hand, adequate soil water supply creates favorable conditions for the movement and infection by plant-parasitic nematodes [43]. By lowering soil moisture, L directly degrades this critical microhabitat, thereby hindering the migration and foraging activities of these nematodes [44]. Increases in the PPI are often associated with improved availability of root-derived resources, where enhanced nutritional quality or biomass of plant roots supplies more foraging sites for plant-parasitic nematodes and elevates the PPI [45,46]. In our study, L reduced root biomass of host plants, leading to a shortage of foraging sites for plant-parasitic nematodes. Consequently, the PPI declined under this resource limitation.

L increased the MI, which reflects ecosystem stability via soil nematode community structure. A rise in MI correlates with enrichment of nematode groups with higher cp values (3–5, e.g., omnivores-predators), indicating a shift toward greater community stability [47]. Litter can impede gas diffusion between the soil and the atmosphere and its removal improves soil aeration, enhances gas exchange efficiency, and optimizes soil physical structure [48]. Nematodes with higher cp values are sensitive to low-oxygen conditions [49]. Thus, the improved soil aeration following L favors the growth and reproduction of high-cp-value nematodes in the short term. Furthermore, L elevated the relative abundance of bacterivores. This increase provides abundant resources for omnivores-predators [40], ultimately promoting the enrichment of nematodes with high cp values. This leads to an elevated MI, presenting a short-term appearance of community stability.

4.2. Effects of Understory Removal on Soil Nematode Communities

In this study, understory removal (U) did not produce a significant effect on soil nematode abundance. This result can be attributed to the functional substitution effect of litter. As demonstrated by Feng et al. [50], the continuous input of organic matter from litter can partially compensate for the carbon and nutrient supply typically supplied by root exudates and the decomposition of understory residues. This compensatory mechanism helps buffer the direct impact of U on the soil nematode community.

U increased the relative abundance of fungivorous nematodes. This effect is closely linked to the enrichment of fungal resources. Research in a subtropical Moso bamboo plantation showed that U reduces soil pH and SWC, creating a favorable habitat for moderately acidophilic fungi [51]. Additionally, He et al. [52] reported that U simplifies litter composition to less decomposable tree litter, which further promotes the growth of saprophytic fungi. The substantial proliferation of the fungal community provides ample

food resources for fungivores, thereby increasing their relative abundance. A negative correlation was observed between the relative abundance of fungivores and $\text{NH}_4^+\text{-N}$, as higher $\text{NH}_4^+\text{-N}$ concentrations can exert salt toxicity on fungi, suppressing fungal growth and consequently reducing food sources for fungivores [51]. Although total microbial biomass declined after U, the availability of fungal resources increased, leading to a higher proportion of fungi within the microbial community [53]. This shift further enhances the food supply for fungivorous nematodes. In contrast, the growth and reproduction of plant-parasitic nematodes depend on sufficient root-derived resources and suitable microenvironments [42]. U directly reduces the population size and root biomass of host plants, thereby limiting foraging and infection sites for plant-parasitic nematodes, resulting in a decrease in both the relative abundance of plant-parasitic nematodes and PPI.

U also increased the MI through the restructuring of cp value groups within the soil nematode community. On one hand, U directly reduces fine root density, decreasing the relative abundance of low-cp-value plant-parasitic nematodes that depend on root resources [42]. On the other hand, following U, the dominant input of recalcitrant tree litter promotes the fungal proliferation [52], which elevates the relative abundance of fungivorous nematodes. This increase, in turn, supplies more prey for omnivores-predators with high cp values. Through these synergistic effects, the proportion of high-cp-value nematodes increases, ultimately raising the MI and shifting the community toward a more stable condition [47].

4.3. Interactive Effects Between Litter and Understory Removal on Soil Nematode Communities

Significant interactive effects between L and U on soil nematode community were identified. The reduction in soil nematode abundance caused by L was amplified when understory was present, but this suppressive effect was notably alleviated after U. While U decreased soil nematode abundance in the presence of litter, it led to an increase in following L. The 0–10 cm surface soil layer is the primary recipient of litter decomposition products and root exudates, and its microenvironment is highly sensitive to changes in surface cover conditions [54,55]. After L, understory continues to regulate soil water and nutrient distribution through its root system, indirectly shaping resource acquisition conditions for soil organisms [28,29]. This root-mediated regulation, coupled with the cessation of litter-derived resource input, creates a dual limitation that severely restricts resource availability for microbes and nematodes, resulting in a substantial decrease in soil nematode abundance. When understory vegetation is also removed, root competition is eliminated. The decomposition of remaining plant residues generates a short-term resource pulse, boosting microbial biomass and replenishing food resources for bacterivores and fungivores, thereby alleviating food limitation [28]. Furthermore, after U, the soil surface loses its protective shading and moisture-retaining layer. The remaining litter tends to form a compact layer that impedes soil aeration and disrupts the thin water-film microhabitat essential for nematodes [56]. A similar phenomenon was reported by Lee et al. [57] in a temperate deciduous broadleaved forest, where litter accumulation under reduced vegetation cover alters soil aeration and moisture stability, impacting soil faunas. L alleviates this physical constraint, optimizes soil water and aeration conditions, and creates a more suitable environment for nematode activity.

L and U had a significant interactive effect on the relative abundance of fungivorous nematodes: either L or U alone increased their relative abundance, but the promoting effect was markedly reduced under the simultaneous removal of both. This study was conducted in a climatic transition zone between the north subtropical and warm temperate regions, where summers are hot and rainy, and surface litter decomposition rates reach their annual peak during this period [55]. In the control (C) treatment, where both litter

and understory vegetation were retained, the soil fungal community was subject to dual chemical and physical constraints. On the one hand, *Pinus massoniana* litter is rich in antifungal secondary metabolites such as condensed tannins and phenolics, which are continuously released during decomposition and directly inhibit the colonization and metabolism of saprotrophic fungi [58–60]. On the other hand, the dense understory canopy, together with the accumulated litter layer, formed a physical barrier that suppressed fungal biomass and metabolic activity through microclimatic regulation and physical interception [29,61], thereby limiting the food resources and population development of fungivorous nematodes. U improved aeration and light conditions in the litter layer, optimized the microbial environment, and the mixed coniferous–broadleaf litter continued to supply organic substrates, thereby substantially alleviating the constraints on fungal growth. L interrupted the input of allelopathic compounds from pine needles, alleviating the chemical stress on fungal metabolic activity. Both L and U partially alleviated the constraints, while each retained a carbon supply pathway to sustain the fungal community, resulting in a significantly higher relative abundance of fungivorous nematodes compared to the C. Although LU eliminated the dual constraints, it simultaneously interrupted carbon inputs from both aboveground litter and belowground roots, leaving the soil in a long-term carbon-limited state. Carbon limitation directly impedes saprotrophic fungal biomass accumulation. Under low-carbon conditions, bacteria assimilate labile organic carbon 1.4–5 times more efficiently than fungi, sharpening microbial resource competition and further suppressing fungal proliferation [62,63]. The negative effects of resource limitation on fungi offset the benefits of environmental improvement, resulting in a weaker rise in the relative abundance of fungivorous nematodes under LU than under L or U.

When litter or understory was removed individually, the relative abundance of plant-parasitic nematodes decreased. However, their relative abundance increased when both of them were simultaneously removed. In this study, LU elevated soil NO_3^- -N and MBN relative to individual treatment. As a key plant nutrient, nitrogen enrichment can enhance the growth vigor of tree roots [64], providing more foraging and infection sites for plant-parasitic nematodes [43], and leading to increases in their relative abundance and the PPI. The observed positive correlations between the relative abundance of plant-parasitic nematodes (as well as the PPI) and NO_3^- -N and MBN support this nitrogen-mediated regulatory pathway.

The interactive effect between L and U attenuated the increase in the MI. RDA identified MBC as the primary driver of the soil nematode community. LU substantially reduced MBC, which suppressed the nematodes with high cp values, thereby lowering the MI. This aligns with report that declines in carbon storage can suppress high-cp-value nematodes through food web constraints [65]. However, faunal analysis revealed that LU was concentrated in the region of high SI and high EI. This indicates that despite reduced stability, LU enhances food web structural complexity and resource enrichment through resource restructuring. This outcome corresponds with the core perspective of faunal analysis: shifts in resource allocation can regulate food web structure independently of total biomass [66].

4.4. Limitations and Future Research

Several limitations should be considered when interpreting the results of this study. First, soil sampling was conducted only once, in August 2024 during the peak growing season. The observed results therefore represent a snapshot of the community at a specific time point following eight years of long-term treatment, and cannot fully capture the interannual or seasonal dynamics of the nematode community. Soil nematode communities exhibit pronounced seasonal fluctuations driven by temperature and precipitation, and a single sampling event cannot disentangle the relative contributions of interannual climatic

variability versus treatment effects. However, it should be noted that the treatments have been maintained monthly since 2016, with eight years of differential management leading to consistent divergence in organic matter and microbial backgrounds among treatments. The differences observed between treatments are thus genuine responses shaped by long-term cumulative disturbance, rather than short-term stochastic fluctuations.

Second, our experiment was conducted at a single site, a mixed coniferous–broadleaved forest of *Pinus massoniana* and *Quercus acutissima* in the Dabie Mountains, and the observed regulatory patterns may not be directly extrapolated to other forest types or climatic zones. Litter composition, understory plant communities and soil physicochemical properties vary considerably among forest types, which could alter both the direction and magnitude of the effects of litter or understory removal on soil nematodes. Nevertheless, our study site lies in the climatic transition zone between subtropical and warm temperate zones, an area particularly sensitive to climate change, so our findings can serve as a reference for managing similar transitional mixed forests, both planted and naturally regenerated.

To address these limitations, future research can be strengthened from two directions. First, repeated sampling at the same site in August 2025 and 2026, combined with multi phenological monitoring, would help distinguish the relative contributions of interannual climatic variability and long-term treatment effects, and verify the temporal consistency of nematode community response patterns. Second, comparative experiments across a broader range of forest types and climatic transition zones would test the generality of the regulatory patterns observed in this study, thereby providing a broader theoretical basis for the sustainable management of forests in climate transitional regions.

5. Conclusions

This study investigated the effects and regulatory mechanisms of litter removal (L) and understory removal (U) on soil nematode communities in a coniferous–broadleaved mixed forest located in a subtropical–warm temperate transition zone. Although both L and U influence nematode communities through resource provision and microhabitat modulation, their primary pathways of influence differ. L reduces overall carbon input and disrupts the buffering capacity of the surface microenvironment. This leads to changes in soil nematode abundance and the relative abundances of bacterivores, omnivores–predators, and plant-parasites, reflecting its integrated regulation of basal resource consumers and higher trophic levels in the soil food web. In contrast, U primarily affects the relative abundances of fungivores and plant-parasites through altering the supply of fresh root-derived organic matter and modifying soil nutrient conditions, demonstrating a more targeted effect on specific trophic groups. Significant interactive effects between L and U were observed on soil nematodes. Their interaction not only mitigates the decline in nematode abundance, but also enhances the structural complexity and resource-use efficiency of the soil web. Integration with soil physicochemical analysis identified MBC, MBN, and TN as key factors mediating this regulatory process, thereby clarifying the linkage pathways among litter, understory, and soil nematode communities. This study clarifies the relationships between litter and understory removal treatments and soil nematode communities in a transitional coniferous–broadleaved mixed forest. The results provide a theoretical basis for local forest floor management based on short-term observations, and supply empirical data for exploring the responses of forest belowground biota to environmental change.

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