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Forest Gap Size Alters the Functional Diversity of Soil Nematode Communities in Alpine Forest Ecosystems

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Abstract: Changes in the microenvironment driven by forest gaps have profound effects on soil nutrient cycling and litter decomposition processes in alpine forest ecosystems. However, it is unclear whether a similar forest gap effect occurs in the soil decomposer community. A field experiment was conducted in an alpine forest to investigate the composition and structure of the soil nematode community among four treatments, including under a closed canopy and in small (<10 m in diameter), medium (10–15 m in diameter), and large (15–20 m in diameter) gaps. A total of 92,787 individuals and 27 species (genera level) of soil nematode were extracted by elutriation and sugar centrifugation, respectively. *Filenchus* was the most abundant dominant taxa and represented 24.27–37.51% of the soil nematodes in the four treatments. Compared to the closed canopy, the forest gaps did not affect the composition, abundance, or species diversity of the soil nematode community but significantly affected the functional diversity of the soil nematode community. The maturity indices (MI, Σ MI, and MI2-5) of the soil nematode community in the closed canopy were significantly lower than those in the forest gaps. Moreover, the proportion of plant parasitic index and maturity index (PPI/MI) values of the closed canopy and small gaps were significantly higher than those of the medium and large gaps. Our results suggest that the forest gap size substantially alters the functional diversity of soil nematodes in the debris food web, and changes in soil nematode community structure due to gap formation may have profound effects on soil biogeochemical processes in alpine forests.

Keywords: gap size; nematodes; maturity indices; trophic structure; alpine forest

1. Introduction

A forest gap, which is caused by the death of one or more canopy trees, is the dominant form of disturbance in various forest ecosystems [1]. After gap formation, more irradiance and rainfall reach under the canopy, and the temperature and moisture conditions are generally improved compared to those under a closed canopy [2,3]. These changes driven by gap formation have profound effects on tree regeneration, plant nutrient uptake, and litter input under the canopy [4,5]. Moreover, the formation of forest gaps may alter the compositional and structural diversity of the soil decomposer food web on the forest floor through positive or negative effects to the microclimate and aboveground plant community [6,7].

Numerous studies have suggested that the composition and structure of the nematode community are sensitive ecological indicators that can be used to determine the integrated effects of disturbances

on small-scale spatial variations in the decomposer community in forest ecosystems [8–10]. The main reasons are that (1) soil nematodes are the Earth's most abundant metazoan and respond rapidly to environmental changes (e.g., warming, drought, and land-use change) and (2) their feeding specificity and high number of species play an indispensable role in the soil decomposer food web, such as by regulating the microbial community structure [11,12]. Furthermore, multitudinous studies have reported that nematode communities are greatly affected by the spatial and temporal patterns of soil moisture and temperature. For example, drought stress or warming was found to decrease the abundance of soil nematodes [13,14], whereas the trophic groups responded differently to soil moisture, with bacterivores decreasing and plant-parasitic nematodes increasing with an increase in moisture [15]. In alpine ecosystems, the microclimatic conditions (e.g., soil temperature and soil moisture) were found to be higher under an open canopy than under a closed canopy [16], and these changes accelerated litter decomposition, lignin loss, and nutrient cycling [17,18]. However, it is still unclear whether a similar gap effect occurs in the soil decomposer community (e.g., nematode) in alpine forests.

For this study, we conducted a field experiment to investigate the composition and structure of soil nematodes under a closed canopy and under different forest gaps in an alpine forest of southwestern China. We hypothesized that (1) the abundance and species diversity of soil nematodes were greater in the forest gaps than under a closed canopy due to increased soil temperature and moisture condition and that (2) the structure of the soil food web differed under a closed canopy and in the forest gaps due to variations in the functional diversity of soil nematodes. The aim of our study was to explore the feasibility of using soil nematode communities as indicator species for environmental changes and to gain a deeper understanding of the characteristics of soil biodiversity in alpine forests.

2. Materials and Methods

2.1. Site Description

This study was conducted at the Long-Term Research Station of Alpine Forest Ecosystems (31°14' N, 102°53' E, 3582 m a.s.l.), which is located on the eastern Tibetan Plateau, China. The study site is a primary fir (*Abies fargesii* var. *faxoniana*) forest with a tree age of approximately 140 years, and the forest canopy is dominated by fir (70–80%) and spruce (*Picea asperata*). The mean annual air temperature and the mean annual rainfall at the site are 2–4 °C and 850 mm, respectively. The understory shrubs are dominated by *Salix paraplesia*, *Sorbus rufopilosa*, *Rhododendron lapponicum*, and *Rosa sweginzowii*, and the coverage ratio of shrubs is approximately 0.4. The herbs consist of *Cacalia auriculata*, *Cystopteris montana*, *Carex* spp., *Cyperus* spp., and other species, and the coverage ratio of herbs is approximately 0.6 [19]. The coverage ratio of herbs is approximately 0.85 in the forest gaps [20]. The soil is classified as a Cambic Umbrisol according to the International Union of Soil Sciences (IUSS) Working Group, and the basic chemical soil properties (0–15 cm) can be found in Tan et al. [21].

2.2. Experimental Design and Soil Sampling

In this study, we defined the forest gaps according to the conception of an expanded forest gap, and the edges of the expanded gaps were defined by the trunk bases of the border trees [22,23]. Previous investigations have found that the shapes of the forest gaps in the study site were approximately elliptical [19]. Therefore, the distance between the two most distant trunks in the gap and the distance between the two trunks perpendicular to each other were used as the long and short axes of the ellipse, respectively, and the area of the gap was calculated by the ellipse area formula [22,24]. The gap age was calculated from the degree of decomposition of the gap maker [25]. Moreover, our previous studies suggested that treefalls account for 70% of the gap formation types and that the largest expanded forest gap at the experimental site was approximately 280 m² [19]. Thus, the treefall gap sizes selected in this experiment are 255–290 m² (large gap with a diameter 15–20 m), 153–176 m² (medium gap with a diameter 10–15 m), and 38–46 m² (small gap with a diameter <10 m).

The experimental plots were set up in a primary fir forest formed by natural vegetation succession. The average tree height and diameter at breast height (DBH) were 28 m and 30 cm, respectively [19]. Three plots showing homogeneous topography were established. Within each plot, treefall gaps were selected for soil sampling, including large, medium, and small gaps and a closed canopy area. The properties of the selected gaps are shown in Table 1. Soil samples (approximately 500 g each) were collected from the center of the forest gaps because the microclimates between the southern and northern edges of the gap often show significant differences [2]. In each plot, three intact soil cores (20 × 25 cm) were collected from the gaps and closed canopy at a depth of 15 cm for soil nematode extraction in August 2016. A total of 36 soil samples (4 treatments × 3 plots × 3 samples) were collected in the study. After screening out the rocks and coarse debris from the soil samples, the soil samples were stored in a cooler box with ice packs and transported to the laboratory within 24 h. The samples were stored in a laboratory refrigerator at 4 °C and the analysis was completed within one week.

Table 1. Characteristics of the four treatments (mean ± SE, $n = 3$).

Type of Gap	Gap Size (m ²)	Cause of Gap	Gap Age (Year)	Gap Makers	Soil Temperature (°C)	Soil Moisture (%)
Large gap	281.7 ± 4.4	Breakage at trunk	31.4 ± 2.7	Fir (78%) + spruce (22%)	9.23 ± 0.22 a	40.72 ± 2.33 ab
Medium gap	165.0 ± 5.8	Breakage at trunk	30.1 ± 2.8	Fir (71%) + spruce (29%)	7.81 ± 0.15 b	37.54 ± 2.69 ab
Small gap	43.3 ± 3.3	Standing death	26.7 ± 1.9	Fir	7.48 ± 0.14 c	36.67 ± 1.94 b
Closed canopy	-	-	-	-	7.42 ± 0.16 c	43.71 ± 1.72 a

Lowercase letters indicate differences within treatments at the $p < 0.05$ level.

2.3. Soil Nematode Extraction

The soil nematode community structure was determined by extracting the nematodes from each soil sample (100 g) using the elutriation and sugar centrifugation method [26]. The extracted nematodes were killed and fixed in hot formalin. After counting the total number of nematodes, 100 specimens per sample were randomly selected and identified to the genus level using an inverted compound microscope (Nikon Instruments, Melville, NY, USA) according to the reference of Yin [27]. The nematodes were assigned to the bacterivores (Ba), fungivores (Fu), omnivore-predators (OP) and plant parasites (PP) trophic groups according to their feeding habits [28,29].

2.4. Data Calculations and Statistical Analyses

The abundance (the number of individuals per 100 g of dry soil) and generic richness (mean number of genera per sample) were used to measure the response of the soil nematode community to changes in the microclimate from a large gap to a closed canopy. The dominant species, frequent species, and rare species were defined as those with abundances greater than 10% (+++), between 10% and 1% (++) , and less than 1% (+) of the total individual density, respectively [29]. Life strategy was assessed by the colonizer-persister (c-p) scale from 1 to 5, which was used to provide information on the functioning and condition of the nematode food web in the gaps and closed canopy [11].

The differences in soil nematode diversity between the gaps and the closed canopy were described by using the species diversity indices, such as the Shannon–Wiener index (H'), Pielou index (J'), dominance index (λ), and Margalef index (SR). Moreover, the life history diversity indices based on different life history characteristics were also calculated to determine the differences in the soil nematode community between the gaps and closed canopy, including the free-living nematodes with c-p1 through c-p5 (MI), free-living nematodes with c-p2 through c-p5 (MI2-5), the plant parasite index (PPI), the sum maturity index ($\sum MI$), and the proportion of PPI and MI (PPI/MI). The structure index (SI), enrichment index (EI), and channel index (CI) are functional diversity indices that were used to assess the soil quality in the gaps and closed canopy. Life history diversity indices and functional diversity indices were collectively referred to as functional group indices, which were used to characterize the functional

structure of soil nematodes in the different treatments (Supplementary Materials). All indices were calculated using the following equations:

$$H' = - \sum_{i=1}^S P_i (\ln P_i), \quad (1)$$

$$J' = \frac{H'}{\ln(S)}, \quad (2)$$

$$SR = \frac{S-1}{\ln N}, \quad (3)$$

$$\lambda = \sum P_i^2, \quad (4)$$

where N is the number of individuals identified, S is the number of taxa identified, and P_i is the proportion of individuals in the i th taxon (a given taxon is regarded as the i th taxon) [30–32];

$$MI(\sum MI, MI2-5, \text{ and PPI}) = \sum_{i=1}^n cp_i \cdot p_i, \quad (5)$$

where n is the number of taxa in the sample, cp_i is the c-p value of soil nematodes to the i th taxon, and P_i is the proportion of individuals in the i th taxon [31,33–35];

$$SI = 100 \times (s / (s + b)), \quad (6)$$

$$EI = 100 \times (e / (e + b)), \quad (7)$$

$$CI = 100 \times (0.8Fu_2 / (0.8Fu_2 + 3.2Ba_1)). \quad (8)$$

The b component is calculated as $\sum k_b n_b$, where the k_b values are the weightings assigned to the guilds that indicate the basal characteristics of the food web (0.8Ba₂, 0.8Fu₂) and the n_b values are the abundances of nematodes in those guilds. The e and s components are calculated similarly, and the k_b values are calculating using the guilds indicating enrichment (3.2Ba₁, 0.8Fu₂) and structure (1.8Fu₃, 1.8Ba₃, 3.2Fu₄, 3.2Ba₄, and 3.2OP) [36].

One-way ANOVA was conducted to test for significant differences in the nematode community among the four gap treatments, and if significant differences were identified by ANOVA, multiple comparisons were performed using Tukey's honestly significant difference (HSD) post-hoc test. Levene's test for homogeneity of variance was performed before conducting the ANOVAs, and the data were logarithmic transformed if required. ANOVAs were performed using SPSS version 20.0 (IBM SPSS Inc., Chicago, IL, USA), and figures were prepared using Origin 9.1 (OriginLab, Northampton, MA, USA). Principal component analysis (PCA) was performed using Canoco 5.0 (Microcomputer Power, Ithaca, NY, USA) to assess the effects of the gap treatment on the composition of the soil nematode community. The PCA was run separately for each treatment to reduce the number of variables and the figure complexity. The PCA analyses were performed with the abundance data (ind.·100 g⁻¹ dry soil) at the family level.

3. Results

3.1. Soil Nematode Composition

In the four treatments, a total of 92,787 individuals and 27 species (genera level) of soil nematodes were trapped. Compared to the closed canopy, the three gap treatments did not significantly ($F = 2.40$, $p = 0.09$) affect the abundance of soil nematodes. The abundance of soil nematodes varied from 774.3 to 1288.5 ind.·100 g⁻¹ with the rank of the medium gap > closed canopy > large gap > small gap (Table 2).

Table 2. Composition and abundance (ind.·100 g⁻¹ dry soil) of soil nematodes in the closed canopy and three types of forest gaps.

TG/Genera	FG	Closed Canopy		Small Gaps		Medium Gaps		Large Gaps		Total	
		Ind.	Dominance	Ind.	Dominance	Ind.	Dominance	Ind.	Dominance	Ind.	Dominance
Ba		386.5		250.2		423.7		370.1		1430.4	
<i>Rhabditis</i>	Ba1	92.1	++	45.4	++	61.4	++	40.6	++	239.5	++
<i>Bunonema</i>	Ba1	7.1	+	6.7	+	5.0	+	0.9	+	19.7	+
<i>Eucephalobus</i>	Ba2	35.3	++	21.2	++	26.6	++	17.8	++	100.9	++
<i>Heterocephalobus</i>	Ba2	6.5	+	0.9	+	1.3	+	2.0	+	10.6	+
<i>Acrobeloides</i>	Ba2	62.4	++	17.6	++	35.1	++	29.9	++	145.0	++
<i>Plectus</i>	Ba2	36.4	++	27.8	++	75.1	++	82.4	++	221.6	++
<i>Wilsonema</i>	Ba2	31.9	++	22.9	++	26.4	++	23.5	++	104.7	++
<i>Microloaimus</i>	Ba2	1.7	+	0.9	+	10.7	+	5.2	+	18.5	+
<i>Teratocephalus</i>	Ba3	43.9	++	55.8	++	70.4	++	66.3	++	236.4	++
<i>Metateratocephalus</i>	Ba3	10.2	+	5.2	+	0	-	0.7	+	16.1	+
<i>Rhabdolaimus</i>	Ba3	3.8	+	0	-	4.2	+	1.9	+	9.9	+
<i>Prismatolaimus</i>	Ba3	30.5	++	17.2	++	53.7	++	25.9	++	127.4	++
<i>Alaimus</i>	Ba4	11.3	++	16.1	++	38.6	++	63.2	++	129.2	++
<i>Paramphidelus</i>	Ba4	13.4	++	12.4	++	15.2	++	9.8	+	50.9	++
Fu		537.3		354.2		416.7		320.5		1628.8	
<i>Filenchus</i>	Fu2	421.3	+++	278.7	+++	312.8	+++	261.6	+++	1274.4	+++
<i>Aphelenchoides</i>	Fu2	89.3	++	48.1	++	23.8	++	10.4	++	171.6	++
<i>Diphtherophora</i>	Fu3	17.1	++	14.6	++	36.5	++	27.0	++	95.2	++
<i>Tylencholaimus</i>	Fu4	9.5	+	12.9	++	43.6	++	21.5	++	87.5	++
OP		46.5		40.7		113.7		68.8		269.7	
<i>Epidorylaimus</i>	OP4	5.9	+	9.9	++	47.0	++	20.3	++	83.0	++
<i>Dorydorella</i>	OP4	40.6	++	30.8	++	66.7	++	48.6	++	186.6	++
PP		153.1		129.1		334.5		271.2		887.8	
<i>Coslenchus</i>	PP2	2.1	+	0	-	0	-	0	-	2.1	+
<i>Basiria</i>	PP2	24.7	++	4.1	+	26.2	++	6.7	+	61.6	++
<i>Paratylenchus</i>	PP2	10.9	+	8.7	++	10.1	+	14.4	++	44.1	++
<i>Nagelus</i>	PP3	15.4	++	6.9	+	33.8	++	4.5	+	60.6	++
<i>Pararotylenchus</i>	PP3	90.1	++	102.0	+++	259.8	+++	237.5	+++	689.3	+++
<i>Pratylenchus</i>	PP3	3.4	+	3.4	+	1.1	+	0.7	+	8.6	+
<i>Macroposthonia</i>	PP3	6.5	+	3.9	+	3.6	+	7.5	+	21.5	+
Total individuals		1123.3		774.3		1288.5		1030.6		4216.7	
Total genera		27		25		25		26		27	

TG, trophic group; FG, functional guild; trophic group with c-p value (Ba, bacterivores; Fu, fungivores; OP, omnivore-predators; PP, plant parasites). +++, dominant genera; ++, common genera; +, rare genera; -, none observed.

According to species proportions (Table 2), *Filenchus* was the most abundant dominant taxa and represented 24.27–37.51% of the soil nematodes in the four treatments. *Pararotylenchus* was the dominant genera that existed in only the forest gaps, whereas *Coslenchus* was a rare genus that occurred in only the closed canopy. The PCA showed that the composition of the soil nematode community was similar in the four treatments (Figure 1), but the spatial variations in nematode community composition were relatively large in the closed canopy and medium gap. Tylenchidae and Hoplolaimidae were the main taxonomic families associated with the separation of PC1 and PC2, respectively.

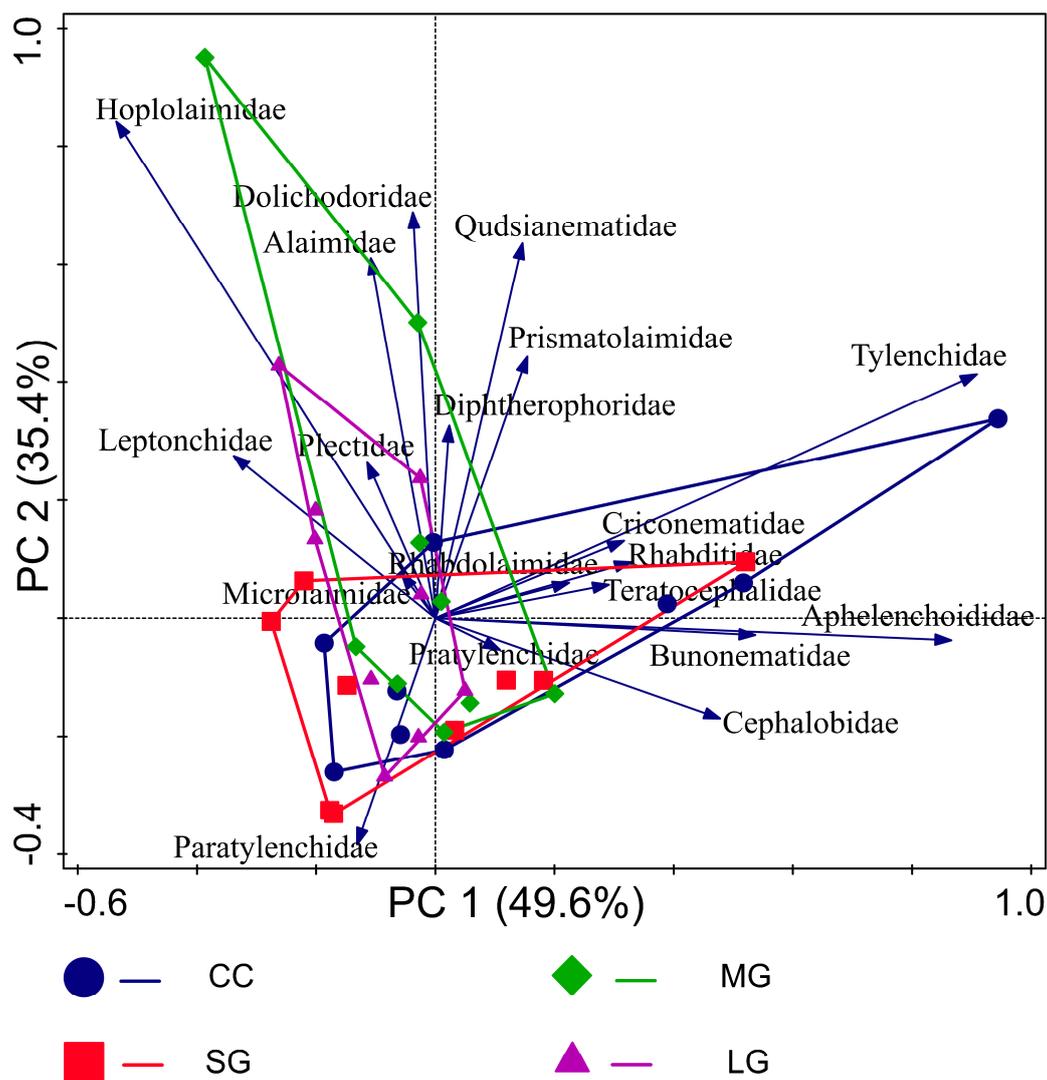


Figure 1. Variations in community structure of the soil nematodes in four treatments. CC, closed canopy; SG, small gaps; MG, medium gaps; LG, large gaps.

3.2. Soil Nematode Functional (Trophic, c-p) Groups

According to the proportions in the soil nematode trophic structure (Figure 2), fungivores and bacterivores were the two main trophic taxa and represented 31.10–47.83% and 32.31–35.91% of the soil nematodes in all treatments, respectively. Moreover, the trophic structure of the nematode community varied among the four treatments. The fungivores were the most numerous trophic taxa in the closed canopy and small gaps, whereas the bacterivores were the most numerous trophic taxa in the medium and large gaps. The nematode community trophic structure was unaffected (all $p > 0.5$) by the gap treatment.

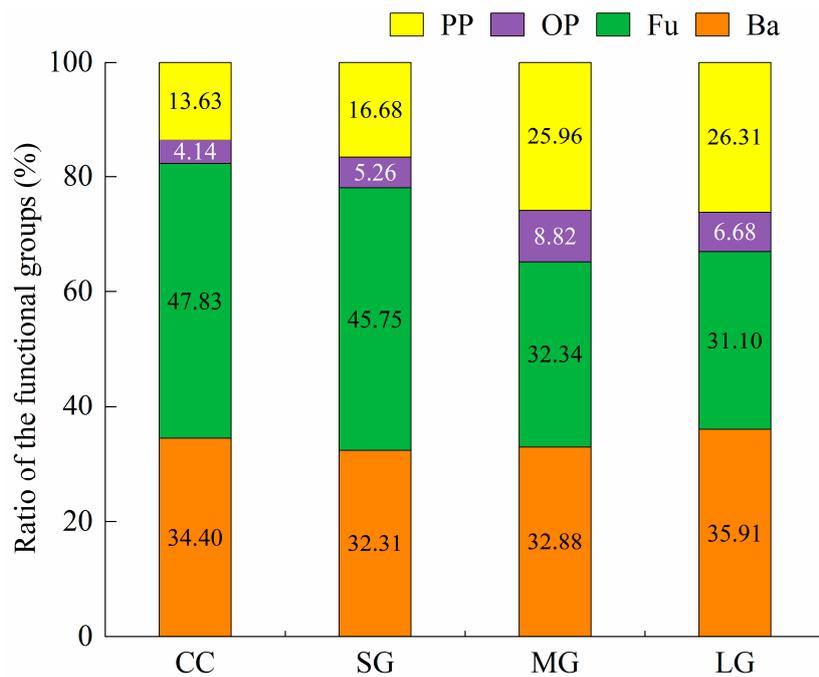


Figure 2. Ratio of the functional groups of the soil nematode community in the closed canopy and three types of forest gaps (small, medium, and large gaps). Ba, bacterivores; Fu, fungivores; OP, omnivore-predators; PP, plant parasites. CC, closed canopy; SG, small gaps; MG, medium gaps; LG, large gaps.

The cp1, cp2, cp3, and cp4 groups of soil nematodes accounted for 6.26%, 51.05%, 29.96%, and 12.73% of the total number of soil nematodes, respectively. The result of one-way ANOVA indicated that only the values of cp4 exhibited significant differences ($p < 0.05$) between the closed canopy and the forest gaps. The proportions of soil nematodes in the cp1 and cp2 groups in the closed canopy were higher than those in the forest gaps. In contrast, the proportions of soil nematodes in the cp3 and cp4 groups in the closed canopy and small gaps were lower than those in the medium and large gaps (Figure 3).

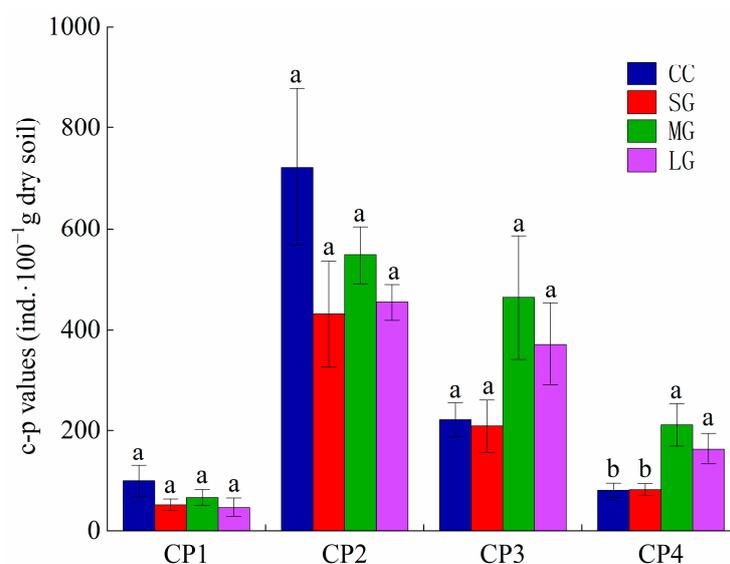


Figure 3. The colonizer-persister (c-p) values of the four habitats (mean \pm SE, $n = 9$). Lowercase letters indicate differences within treatments at the $p < 0.05$ level. CC, closed canopy; SG, small gaps; MG, medium gaps; LG, large gaps. CP1, CP2, CP3, and CP4 are the colonizer-persister scales from 1 to 4.

3.3. Soil Nematode Community Indices

The species diversity indices (H' , J' , λ , and SR) of soil nematodes were not significantly different among the four treatments. The highest H' , J' , and SR values were in the medium gaps, whereas the lowest λ values were also in the medium gaps. The maturity indices of MI, Σ MI, and MI2-5 were significantly lower in the closed canopy than in the gaps. Moreover, the PPI/MI values of the closed canopy and small gaps were significantly higher than those of the medium and large gaps (Table 3). The enrichment index (EI) and channel index (CI) exhibited no significant differences among the four treatments, but the structure index (SI) in the closed canopy was significantly ($p < 0.05$) lower than that in the three gaps (Table 3 and Figure 4).

Table 3. Soil nematode community indices of the four treatments.

Indices	Closed Canopy	Small Gaps	Medium Gaps	Large Gaps
H'	2.09 ± 0.24a	2.09 ± 0.26a	2.31 ± 0.24a	2.17 ± 0.19a
J'	0.78 ± 0.08a	0.76 ± 0.07a	0.82 ± 0.06a	0.80 ± 0.05a
λ	0.19 ± 0.07a	0.21 ± 0.08a	0.16 ± 0.05a	0.17 ± 0.04a
SR	2.01 ± 0.32a	2.22 ± 0.38a	2.23 ± 0.41a	2.08 ± 0.47a
MI	2.19 ± 0.13c	2.38 ± 0.18b	2.53 ± 0.14a	2.52 ± 0.14ab
Σ MI	2.29 ± 0.19b	2.47 ± 0.20a	2.59 ± 0.17a	2.60 ± 0.16a
MI2-5	2.32 ± 0.10b	2.52 ± 0.21a	2.65 ± 0.17a	2.61 ± 0.12a
PPI	2.68 ± 0.29a	2.88 ± 0.12a	2.73 ± 0.33a	2.80 ± 0.28a
PPI/MI	1.22 ± 0.10a	1.22 ± 0.10a	1.08 ± 0.11b	1.11 ± 0.10b
EI	54.92 ± 8.50a	57.53 ± 8.13a	53.74 ± 7.60a	49.31 ± 10.45a
SI	44.07 ± 8.84b	59.21 ± 13.48a	67.01 ± 8.47a	64.99 ± 6.88a
CI	59.42 ± 24.57a	57.59 ± 17.12a	58.90 ± 18.25a	69.02 ± 24.18a

Values are mean ± SE ($n = 9$). Different lowercase letters indicate significant differences among the four habitats ($p < 0.05$). H' , Shannon–Weaver index; J' , Pielou index; λ , Simpson index; SR , Margalef index; MI, maturity index; Σ MI, sum MI; MI2-5, MI without c-p1; PPI, plant parasitic index; PPI/MI, proportion of PPI and MI; EI, enrichment index; SI, structure index; CI, channel index.

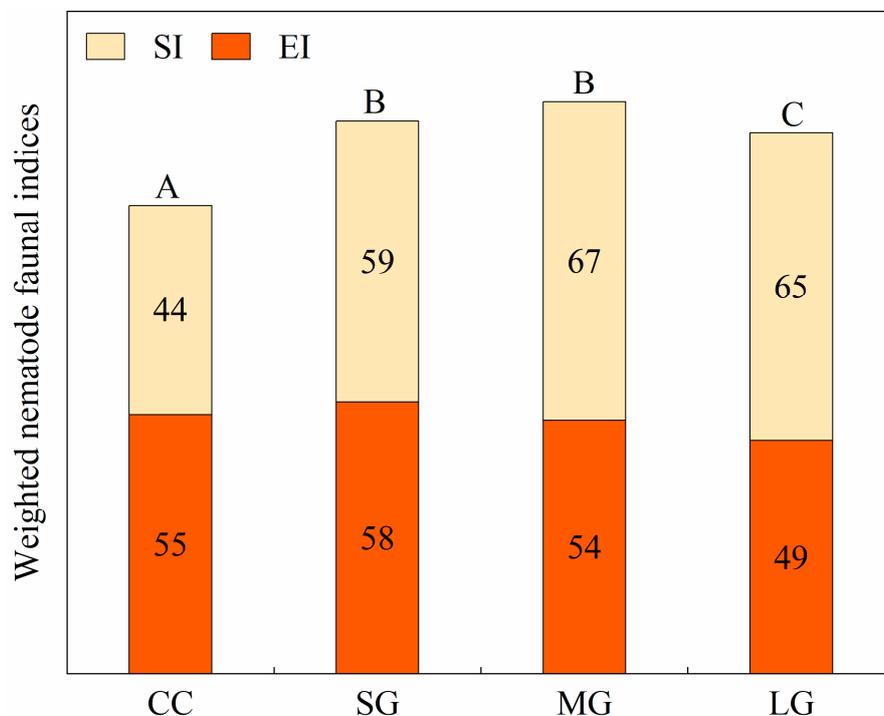


Figure 4. Enrichment index (EI) and structure index (SI) values for the four treatments. CC, closed canopy; SG, small gaps; MG, medium gaps; LG, large gaps. Food web diagnostic quadrants are indicated above each bar, and the means are from Ferris et al. [36].

4. Discussion

In high-elevation ecosystems, the formation of forest gaps alters the soil temperature and moisture conditions compared with those under a closed canopy [16], which has positive, negative, or neutral effects on litter decomposition and soil nutrient mineralization [17,37,38]. Previous studies have shown that the individual density and genera of the soil nematodes in a forest gap are significantly higher than those under a closed canopy, although the soil physical and chemical properties show slight differences between the gaps and the closed canopy [39,40]. Contrary to our first hypothesis and previous results, forest gap formation did not affect the abundance of the soil nematode community in this study. Moreover, the composition of the soil nematode community was similar in the closed canopy and the forest gaps, and the species diversity indices (H' , J' , λ , and SR) of the soil nematodes were not significantly different among the four treatments. One possible explanation for this finding is that the vegetation types on the forest floor were the same among treatments, and the ratio of herb coverage was similar in the closed canopy (0.6) and the forest gaps (0.85) during the growing season at the study sites [19,20], as plant species diversity affects nematode diversity. Another possible explanation is that the ecological niches of the soil nematodes in the four treatments were completely differentiated through long-term adaptation (Table 1, gap age), so there were no significant differences in soil nematode diversity among the different treatments [41]. *Coslenchus* (plant parasites) existed in only the closed canopy, which was consistent with our previous findings in the same alpine and subalpine forests [42], indicating that the roots of the primary fir (*Abies fargesii* var. *faxoniana*) forest may be highly suitable for *Coslenchus*. In addition, Walker proposed that the loss of certain species can be compensated for by the transformation of the abundance of other species to maintain the stability of the entire soil ecosystem [43]. Interestingly, the medium gap had the lowest number of genera but the highest abundance among the four treatments, which is consistent with Walker's hypothesis. Therefore, a medium gap (153–176 m²) may be a critical gap size for the change in the soil decomposer community in an alpine forest.

The changes in forest gap size have been suggested to affect the activities of the soil decomposer community and nutrient cycle under the canopy [4,6,44]. In our study, soil nematodes under the closed canopy and in the small gaps (38–46 m²) were dominated by fungivores, whereas those in the medium (153–176 m²) and large (255–290 m²) gaps were dominated by bacterivores. This finding is similar to the results in the alpine forests of southeastern Tibet [40]. However, the CI of the soil nematode community in the four treatments was greater than 50, illustrating that the soil organic matter in the four treatments is mainly decomposed by fungal channels in the debris food web. This result is different from the finding that the decomposition channel of soil organic matter in the debris food web changes from fungi to bacteria from a closed canopy to a large gap. The disparate results can be mainly explained as follows: (1) the recalcitrant substrates (e.g., lignin, cellulose, and hemicellulose) and C/N ratios in the soil organic layer of the studied forest are relatively high [45–47], and the decomposition of recalcitrant substrates is highly dependent on fungal involvement [48–50] and (2) the soil temperature and moisture often increase with the increase in forest gap sizes in the growing season (Table 1). The high temperature and moisture conditions are suitable for the growth of the bacterial community [2,51], leading to the bacteria being the main trophic group in the medium and large gaps.

Nematode life history diversity indices (MI, $\sum MI$, MI2-5, PPI, and PPI/MI) can sensitively respond to the changes in the soil environment and the situation of the soil food web structure [52]. The values of MI and PPI between 1 and 4 are used to indicate the succession status of the soil nematode community and the stability of the soil environment. Generally, a small value suggests a weak soil environment, and the soil nematode community can be considered to be in the early succession stage [34,41]. Additionally, cp1-2 nematodes have a competitive strategy (r-strategy) with a short life cycle, reproduce well, and can tolerate external disturbance. In contrast, cp 3-5 nematodes have a competitive strategy (k-strategy) with a long life cycle, reproduce weakly, and are sensitive to external disturbance [11]. The abundances of cp4 groups in the medium and large gaps were significantly higher than those in the closed canopy and small gaps, indicating that the competitive strategy changed with gap size in the

present study. Consistent with our second hypothesis, forest gaps significantly affected the functional diversity of the soil nematode communities in our experimental sites. The maturity indices (MI, Σ MI, and MI2-5) were significantly lower in the closed canopy than in the forest gaps, indicating that the soil microenvironment and soil nematode community structure in the closed canopy differed from those in the forest gaps. Moreover, the MI values gradually increased from the closed canopy to the large gaps, which suggested that a continuous change in the functional diversity of the soil nematode community may occur between the closed canopy and forest gaps.

Bongers et al. considered that disturbance would increase the PPI/MI value of a soil nematode community, whereas the PPI/MI value of an undisturbed natural environment would be lower than that of a disturbed environment [33]. Plants optimally use nutrient resources when the PPI/MI values are close to 0.9, whereas the PPI/MI values near 1.2 indicate slight nutrient disturbances [12]. As shown in this study, the PPI/MI values of the closed canopy and small gaps were significantly higher than those of the medium and large gaps (Table 3), which indicated that the environment of the medium and large gaps was relatively stable or less disturbed. The reason for this finding may be that the characteristics of the medium and large gaps are similar, such as the gap size, cause of the gap, gap year, gap makers, and soil moisture (Table 1). Furthermore, according to the calculated EI and SI, the nematode fauna can be divided into four quadrants, A, B, C, and D, where the values of EI and SI vary from 0 to 100. When EI is greater than 50 but SI is less than 50 (A quadrant), the soil nutrient status is good but the degree of disturbance is high, and the food web is subject to a certain degree of disturbance. When both EI and SI are greater than 50 (B quadrant), the soil nutrient condition is improved, the degree of disturbance is small, and the food web is stable and mature. When EI is less than 50 but SI is greater than 50 (C quadrant), the soil nutrient condition is poor but the degree of disturbance is small, and the food web is in a structured state. When both EI and SI are less than 50 (D quadrant), the soil nutrient condition is poor and the degree of disturbance is highest, which causes stress to the environment and degrades the food web [36]. Nematode faunal analysis suggested that the closed canopy belonged to quadrant A, the small and medium gaps belonged to quadrant B, and the large gaps belonged to quadrant C (Figure 4). The results indicated that the degree of disturbance ($SI < 50$) in the closed canopy was high, whereas it was low in the gaps. Moreover, soil nutrient enrichment (EI) was close to 50 in all four treatments. Thus, the food web structure was more stable and mature in the gaps than under the closed canopy.

5. Conclusions

In summary, this experiment investigated the effects of forest gap formation on the composition and functional structure of the soil nematode community in an alpine forest. Our results suggested that the changes in gap size caused slight changes in the composition, abundance, and diversity of the soil nematode community. However, forest gaps showed significant effects on the functional diversity of the soil nematode community. The maturity indices (MI, Σ MI, and MI2-5) significantly increased from the closed canopy to the large gap, whereas the PPI/MI values of the closed canopy and small gaps were significantly higher than those of the medium and large gaps. Our results highlight the conclusion that forest gap sizes have non-negligible effects on the soil nematode community in the debris food web in alpine forests. Changes in the functional structure of the soil nematode community due to gap formation may have profound effects for soil biogeochemical processes in alpine forests.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/10/9/806/s1>, Supplementary files S1: Detailed description of the soil nematode community indices.

Author Contributions: W.Y., J.Z., and B.T. conceived and designed the experiments. Y.S. and B.T. analyzed the data and wrote the paper. Y.L., C.Y., and H.L. participated in field investigations. B.T., W.Y., Z.X., and L.Z. contributed resources.

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