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The Short-Term Responses of Forest Soil Invertebrate Communities to Typhoon Disturbances

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Abstract: Knowledge regarding the response of soil invertebrate communities to typhoon disturbance is limited, although it is known that soil invertebrates are sensitive to forest disturbances and that tropical cyclones (typhoons/hurricanes) are the most destructive natural disasters affecting the structure and function of forest ecosystems. To fill this knowledge gap, soil invertebrates in both litter and topsoil layers were investigated in four representative subtropical coastal forests of eastern China one week before the first typhoon (Hinnamnor) (T1), one day after the first typhoon (Hinnamnor) (T2), one day after the second typhoon (Muifa) (T3), and one week after the second typhoon (Muifa) (T4) in September 2022. Typhoon disturbances decreased the density and taxa abundance of soil invertebrate communities in litter layer, but the first typhoon disturbance increased these values in the topsoil layer. One week after the second typhoon disturbance, soil invertebrate communities in the litter layer showed a gradual recovery trend. Meanwhile, the soil invertebrate communities in the litter layer were more sensitive to typhoon disturbances than those in the topsoil layer. Furthermore, the responses of the soil invertebrate communities to the typhoon disturbances varied greatly with the forest types. The invertebrate densities in the litter layer decreased by 62.1%, 63.53%, 47.01%, and 46.92% in Chinese fir, second broad-leaved, mixed, and bamboo forests, respectively. Particularly, these two non-catastrophic typhoons significantly altered the functional group composition of detrital food webs in the short term, and the proportion of phytophages in detrital food webs in the litter layer increased after the typhoon disturbances. In conclusion, the effects of typhoon disturbances on soil invertebrate communities vary greatly with forest type and soil layer, and soil invertebrate communities can gradually recover after typhoon disturbances. The legacy effects of typhoon disturbances on the functional group composition of detrital food webs may influence carbon and nutrient cycling in forest ecosystems.

Keywords: non-catastrophic tropical cyclones; soil biodiversity; detrital food web; forest disturbance; coastal mountain forest

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1. Introduction

Tropical cyclones (typhoons/hurricanes) are severe disturbances affecting the structure and function of forest ecosystems worldwide [1]. Tropical cyclones can bring rainfall, destroy canopy structures and even affect tree mortality [2,3], and alter the microenvironment of the forest floor (e.g., understory light, temperature, humidity, and moisture) [4–6]. Meanwhile, tropical cyclones can cause large amounts of abnormal litter, which might have a dramatic impact on the material cycle and energy flow of forest ecosystems [7,8]. Wu et al. [9] defined “abnormal litter” as the fresh plant residues produced under external forces such as extreme weather, fire, or geological disasters. According to IPCC (2021), the intensity and frequency of tropical cyclones will increase under global warming scenarios [10], implying that tropical cyclones might have a more profound impact on the structure and function of forests [11]. However, more attention has been paid to the short-term and long-term effects of catastrophic tropical cyclones on the belowground process. For example, Elise et al. (2007) observed that Hurricane Katrina caused a fourfold increase in tree mortality in the Pearl River Basin forest in Louisiana, USA [12]. Willig and Camilo (1991) found that Hurricane Hugo caused a 75% decline in soil invertebrate populations in the Luquillo Experimental Forest in Puerto Rico [13]. As yet, the short-term responses of forest soil faunal community to non-catastrophic tropical cyclones have not been reported.

Soil invertebrates are fundamental components of forest ecosystems and play an irreplaceable role in soil formation, carbon and nutrient cycling, and site fertility maintenance [14,15]. In particular, soil invertebrates are also sensitive indicators of forest disturbances. For example, Kataja et al. [16] and Kudrin et al. [17] have shown that forest harvesting has a dramatic effect on soil invertebrate populations. Peguero et al. [18] found that nitrogen addition resulted in a significant increase in the abundance of oribatid mites and a rapid decrease in populations of springtails, leading to changes in the soil invertebrate community in a Mediterranean forest. Meanwhile, soil invertebrate communities can recover after forest disturbance. For instance, Çakır et al. [19] reported that the density and taxa of soil invertebrate communities decreased significantly after a fire, but the soil invertebrates gradually recovered, with mites recovering more rapidly. However, the response and recovery mechanism of soil invertebrate communities following non-catastrophic typhoon disturbances is still unknown.

In theory, typhoons can affect the density and functional groups of soil invertebrate communities in the short term through the following pathways. To begin with, typhoon-induced changes in precipitation and temperature can directly increase soil moisture and reduce soil temperature, both of which can affect the activities and survival of soil invertebrate communities in the short term. Meanwhile, the large amount of abnormal litter inputs caused by typhoons provides abundant edible resources for soil invertebrates [20,21]. Undoubtedly, edible litter is beneficial for restoring and increasing soil invertebrate communities after typhoon disturbances. Additionally, typhoons might cause tree falls, which not only create canopy gaps but also increase the amount of coarse woody debris and litter on the ground, thus promoting microenvironment heterogeneity in forests. The terrains caused by uprooted trees provide a variety of substrates, such as exposed roots, bare mineral soil and rocks, and fallen trees themselves, offering diversified habitats to soil invertebrates [22]. Although typhoons can affect soil invertebrate communities by altering habitat and climate conditions, soil invertebrates with mobile and highly migratory abilities can seek shelter (such as soil, fallen trees, dead leaves, crevices in rocks, etc.) or escape to avoid adverse weather disturbances [23]. Furthermore, the strength of the impact of typhoon disturbances on forests varies with different forest types [24]. This means that the responses of soil invertebrate communities to typhoon disturbances may also vary with forest types. Meanwhile, the responses of soil invertebrate communities to typhoon disturbances may vary with soil layers due to differential exposure and moisture dynamics. Little information is available on whether the responses of soil invertebrate communities to typhoon disturbances vary with forest types and soil layers.

The coastal mountain forest ecosystems in southeastern Zhejiang Province suffer from frequent typhoon disturbances [25,26]. It is estimated that a total of 208 tropical cyclones made landfall in the southeastern coastal cities of China from 1984 to 2019, of which 88 were intense tropical storms [27]. Typhoons affecting the southeastern coastal region of Zhejiang Province mainly occur from July to October, and the average number of typhoons affecting the southeastern coastal region of Zhejiang is six per year, with the highest number recorded being 11 in a year, implying that, increasingly, typhoon disturbances will have a profound impact on the structure and function of coastal mountain forest ecosystems in southeastern Zhejiang Province. For instance, Wang et al. [28] observed that Typhoon

Hagupit disturbances had differential effects on carbon and nutrient concentrations and the ecological stoichiometric ratios in garden plant tissues of different life forms in Taizhou city. Wang et al. [29] also reported that the typhoon disturbances that occurred in 2004 significantly increased litter production in the Tiantong Mountain forest ecosystems in Zhejiang Province. These frequently disturbed montane forest ecosystems also provide an excellent natural experimental platform to investigate the response of soil invertebrate communities to typhoon disturbances. However, the response of soil invertebrate communities in these ecosystems is still unknown. To understand the response of soil invertebrate communities in the coastal mountain forests to non-catastrophic typhoon disturbances, we investigated the soil invertebrate communities in four representative mountain forests before and after typhoon disturbances, specifically one week before the first typhoon (Hinnamnor) (T1), one day after the first typhoon (Hinnamnor) (T2), one day after the second typhoon (Muifa) (T3), and one week after the second typhoon (Muifa) (T4). We hypothesized that (1) typhoon disturbances could alter the density, functional groups, and biodiversity of soil invertebrate communities and, in turn, alter the proportion of functional groups in detrital food webs but that these indicators would gradually recover after the typhoon disturbances; (2) the response of soil invertebrate communities in the litter layer to typhoon disturbances should be more sensitive than that of those in the topsoil layer, with greater changes in density, group number, diversity index, and functional groups; and (3) the impact of typhoon disturbances on soil invertebrate communities varies with forest types.

2. Materials and Methods

2.1. Site Description

The Linhai Station of Zhejiang Provincial Forest Ecological Research is situated in Linhai City of southeastern Zhejiang Province (120°56′–121°04′ E, 28°44′–28°49′ N, altitude 300–900 m), China (Figure 1). The climate is a subtropical monsoon climate. The annual average temperature (MAT) is 14.9 °C, with a maximum temperature of 40 °C and a minimum temperature of −4 °C. The mean annual precipitation (MAP) is 1632 mm, ranging from 1185 to 2029 mm. The soil is classified as Ferralsol. The vegetation consists mainly of secondary broad-leaved forests (SFs), Chinese fir (*Cunninghamia lanceolata*) and Chinese sweetgum (*Liquidambar formosana*) mixed forests (MFs), Chinese fir forests (CFs), and bamboo (*Phyllostachys edulis*) forests (BFs). Information on these forests is given in Table 1. In addition, *Schima superba* evergreen broad-leaved forests, *Cryptomeria japonica* coniferous forests, and Masson pine forests, and *Camellia sinensis* plantations are widely distributed in the station. In particular, these forests are commonly affected by typhoons of varying intensity from July to October each year.

Table 1. Basic information on representative forests in Linhai Station of Zhejiang Provincial Forest Ecological Research.

Forest Type	Slope Aspect	Slope (°)	Plant Composition
MF	SE	15–20	*Cunninghamia lanceolata*, *Liquidambar formosana*, *Camellia sinensis*
BF	NW	20–25	*Phyllostachys pubescns*, *Camellia sinensis*, *Camellia cuspidate*, *Eurya japonica*, *Lilium speciosum*, *Dioscorea japonica*
CF	NW	20–25	*Cunninghami lanceolata*, *Schima superba*, *Lilium formosana*, *Symplocos setchuensis*, *Litsea rotundifolia*
SF	NW	15–20	*Bothrocaryum controversum*, *Lindera rubronervia*, *Camellia cuspidata*, *Pterocarya stenoptera*, *Cyclobalanopsis gracilis*

Notes: MF: mixed forest; BF: bamboo forest; CF: Chinese fir forest; SF: secondary broad-leaved forest; S: south, E: east, N: north, W: west.

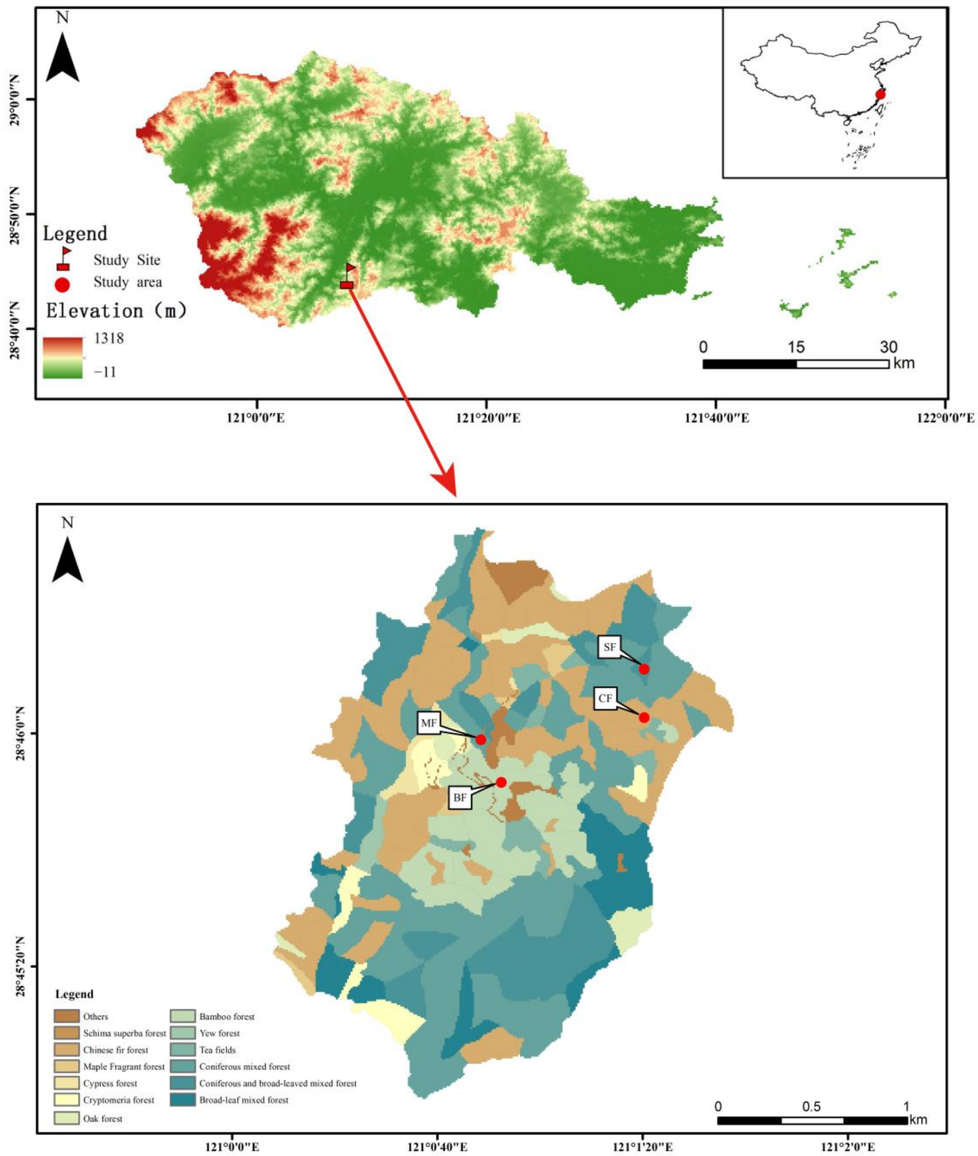

Figure 1. The Linhai Station of Zhejiang Provincial Forest Ecological Research is located in southeastern Zhejiang Province and China. MF: mixed forest; BF: bamboo forest; CF: Chinese fir forest; SF: secondary broad-leaved forest.

2.2. Experimental Design

The experiment was conducted during the typhoon-prone season, i.e., July to September 2022. Before the arrival of the typhoons, we had established long-term observation plots in mixed forests (MFs), Chinese fir forests (CFs), secondary broad-leaved forests (SFs), and bamboo forests (BFs) in July. Three replicate plots (10 m $\times$ 20 m) were established in each forest type, and five samples were collected in each sampling plot and mixed together based on the diagonal method. In early September 2022, two non-catastrophic typhoons successively affected forest ecosystems, namely Typhoon Hinnamnor (September 5) and Typhoon Muifa (September 14). Based on typhoon prediction information, we conducted the investigation and sampling one week before the first typhoon (Hinnamnor) (T1), one day after the first typhoon (Hinnamnor) (T2), one day after the second typhoon (Muifa) (T3), and one week after the second typhoon (Muifa) (T4), meaning that T1 began on August 30, and after 8 days, T2 began on September 6; 9 days after that, T3 began on September 15, and 6 days after that, T4 began on September 21. To begin with, macro-invertebrates in the litter and topsoil (0–5 cm) layers were collected by hand and placed in plastic bottles containing 75% ethanol. Meanwhile, meso- and micro-invertebrates in the topsoil layer were collected from a soil core using a 100 cm^3 ring knife (for calculation convenience, the units of soil density were converted to per square meter). Lastly, a circular stainless-steel collector with a diameter of 20 cm was used to collect samples in the litter layer. All samples were immediately placed in black cloth bags that were then sealed and transported to the laboratory for further processing. A total of 96 samples were obtained (3 replicate plots × 2 soil layers × 4 forest types × 4 sampling periods).

2.3. Sample Handling and Environmental Characterization

This study focused on dry soil invertebrates extracted based on the use of a Tullgren extractor. Meso- and micro-soil invertebrates were extracted from the samples of the litter and topsoil layers using a modified Tullgren extractor [30]. All extracted soil invertebrates were preserved in 75% ethanol and subsequently identified under a dissecting microscope [31]. We identified the collected invertebrates to family level according to the experimental methods of Yin [32,33].

Dried soil and litter samples were passed through a 1 mm sieve for chemical analysis. The concentration of organic carbon in soil was measured using the dichromate oxidation method [34]. The concentration of total nitrogen (TN) in the soil was measured using the Kjeldahl method [35]. The concentration of total phosphorus (TP) in the soil and litter was measured using the molybdenum antimony anti-colorimetric method [36]. The concentrations of C and N in the litter were determined using an element analyzer (Elementar Analysensysteme GmbH Hanau, Germany) [37]. The concentrations of lignin and cellulose in the litter were measured using the acid-detergent fiber–sulfuric lignin method [38].

Soil temperature and atmospheric temperature were determined at the sampling site using DS1923-F5 iButton loggers (Maxim Integrated Products, Inc., Sunnyvale, CA, USA). Soil bulk density and water content were determined using the ring knife method and the drying method in the soil testing criteria, respectively.

2.4. Data Analysis and Statistics

Based on the function of soil invertebrates in detrital food webs, we classified soil invertebrates into five functional groups, i.e., fungivores, omnivores, saprophages, phytophages, and predators [39]. Principal coordinate analysis (PCoA) and permutation multivariate analysis of variance (PERMANOVA) based on Bray–Curtis distance were used to evaluate the impact of typhoon disturbances on the functional group compositions of detrital food webs using the vegan package in R (v 4.1.1) [40]. The alpha diversity index was calculated for the soil invertebrates, as were the Shannon–Wiener diversity index, Simpson index, Pielou index, and Margalef index. Based on their proportion of the total number of individuals, each taxonomic unit was further classified into one of the following categories: dominant taxa with more than 10% of the total number of captured individuals, common taxa with 1–10%, and rare taxa with less than 1%. The differences in the individual density, functional groups, and alpha diversity indices of the invertebrate communities in the litter and topsoil layers and the differences the among different forest types were tested by Tukey's HSD test using IBM SPSS Statistics (v20). The results of our one-way ANOVA were significant at $p < 0.05$ [41]. Redundancy analysis (RDA) was used to screen the differential effects of environmental factors on the functional groups, alpha diversity index values, and individual densities of the soil invertebrate communities. This analysis was carried out using CANOCO 5.0 software. Graph production was carried out in Origin (2022).

3. Results

3.1. Compositions and Densities of Soil Invertebrate Communities

A total of 9011 invertebrates were collected, belonging to 123 families in 20 orders in 1 phylum and 8 orders (Figure S1), including 8411 individuals in the litter layer and 600 individuals in the topsoil layer. Regardless of forest type, Arachnoidea and Collembola have the highest number of invertebrates in both soil layers. Overall, 31 common taxa and 85 rare taxa with no dominant taxa were observed in the litter layer (Table S1). Correspondingly, 1 dominant taxon, 28 common taxa, and 50 rare taxa were observed in the topsoil layer (Table S2).

The compositions and densities of the soil invertebrate communities also varied significantly with the soil layers and forest types; therefore, they seemingly responded differently to the typhoon disturbances (Table 2). The typhoon disturbances significantly reduced the individual density and taxon richness of the soil invertebrate communities in the litter layer, and the individual density of invertebrates in the litter layer dropped to the lowest point after two successive typhoon disturbances. However, the values of these indices showed a gradual recovery trend after one week of the second typhoon disturbance. (Figure 2). In contrast to the litter layer, the first typhoon disturbance increased the individual density and taxa richness of the soil invertebrate communities in the topsoil, which were then maintained at a stable level in the following second typhoon disturbance and after the typhoon disturbances (Figure 2). Meanwhile, the effects of the typhoon disturbances on the soil invertebrate densities and taxa richness varied greatly with the forest types (Figure 2). The overall captures of soil invertebrates were in the order of MF > BF > CF > SF. Among them, the invertebrate density in the litter layer in both CF and SF decreased more significantly after the first typhoon, by 62.1% and 63.53%, respectively; invertebrate density in the litter layer in MF and BF decreased by 47.01% and 46.92%, respectively.

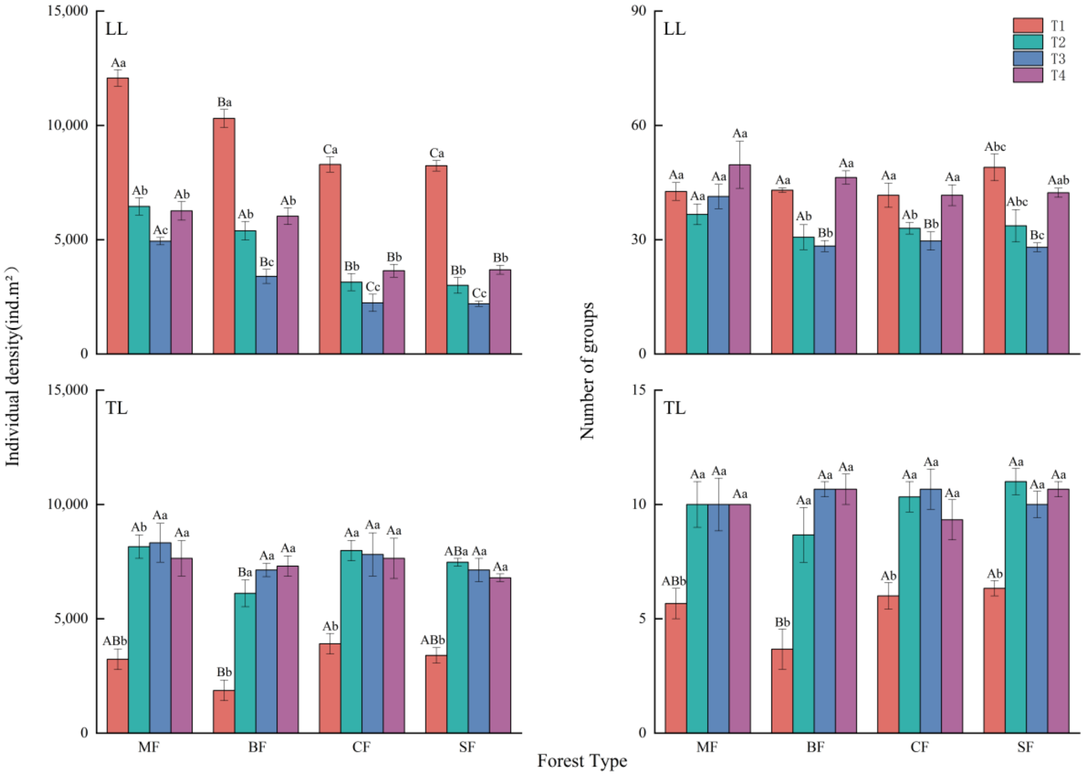

Figure 2. Changes in soil invertebrate communities before and after the typhoon disturbances. Here, LL and TL represent the litter layer and topsoil layer, respectively. T1: one week before the first typhoon (Hinnamnor). T2: one day after the first typhoon (Hinnamnor). T3: one day after the second typhoon (Muifa). T4: one week after the second typhoon (Muifa). MF: mixed forest; BF: bamboo forest; CF: Chinese fir forest; SF: secondary broad-leaved forest. The individual density in the figure refers to the number of soil invertebrates per square meter. The number of groups in the figure refers to the number of classifications at family level. Different capital letters indicate significant differences between different forest types at the same time, and different lowercase letters indicate significant differences between different periods ($p < 0.05$).

Table 2. Two-way ANOVA for individual density, group number, and alpha diversity index of soil invertebrate communities.

Site	Factor	Shannon–WIENER Index	Pielou Index	Simpson Index	Margalef Index	Density	Group
Litter layer	Forest type	3.964 *	4.183 *	3.535	2.378	89.497 ***	3.552 *
	Typhoon/Period	24.562 ***	6.839 **	8.21 ***	14.822 ***	305.944 ***	22.349 ***
	Forest type ∗ Typhoon/Period	3.085 **	1.182	1.667	1.53	1.344	1.622
Topsoil layer	Forest type	2.363	7.107 ***	7.108 ***	1.684	4.36 *	1.464
	Typhoon/Period	34.976 ***	6.697 **	3.573 *	15.732 ***	59.356 ***	41.262 ***
	Forest type ∗ Typhoon/Period	2.032	1.138	1.688	1.112	0.734	1.307

Notes: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. The values in the table represent the F-value.

3.2. Soil Invertebrate Functional Groups and Detrital Food Webs

The detrital food web on the forest floor was composed of predators, omnivores, saprophages, fungivores, and phytophages of the soil invertebrate communities. Overall, the typhoon disturbances had a significant effect on the functional group compositions of detrital food webs (Figure 3). The typhoon disturbances, forest types, soil layers, and their interactions also had a significant effect on the functional group compositions of detrital food webs (Table 3). However, the impact of the typhoon disturbances on the functional group compositions of the detrital food web in the litter layer was more significant than that in the topsoil layer (Figure 4). In addition, there were significant differences in the functional group compositions of detrital food webs between the litter and topsoil layers (Figure 4), with a higher proportion of phytophages and saprophages in the litter layer than in the topsoil layer (Figure 3). Notably, there were significant changes in the proportion of soil invertebrate functional groups in all forest types and soil layers before and after the typhoon. Specifically, compared to other functional groups, the proportion of saprophages fluctuated more significantly (Figure 3). Meanwhile, the proportion of phytophages in the litter layer were more stable than in the topsoil layer under the typhoon disturbances, and the proportion of phytophages in the litter layer significantly increased one week after the typhoon disturbances (Figure 3).

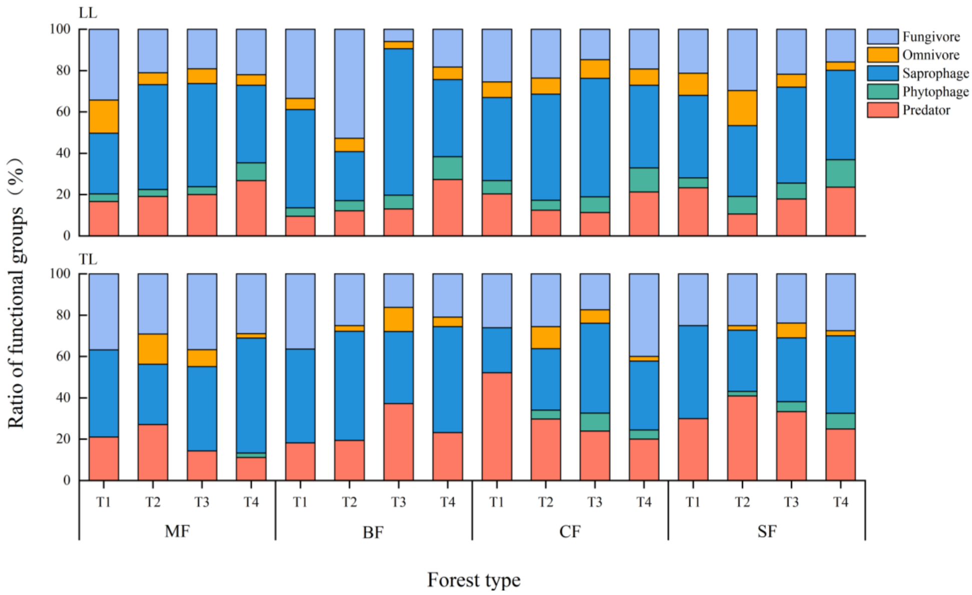

Figure 3. Changes in the proportions of functional groups of detrital food webs before and after the typhoon disturbances (based on the numbers in each functional group). Here, LL and TL represent the litter layer and topsoil layer, respectively. T1: one week before the first typhoon (Hinnamnor). T2: one day after the first typhoon (Hinnamnor). T3: one day after the second typhoon (Muifa). T4: one week after the second typhoon (Muifa). MF: mixed forest; BF: bamboo forest; CF: Chinese fir forest; SF: secondary broad-leaved forest.

Table 3. Permutation multivariate analysis of variance on impact of typhoon disturbances on functional groups of detrital food webs.

Factor	Fungivores		Omnivores		Saprophages		Phytophages		Predators	
	r^2	p	r^2	p	r^2	p	r^2	p	r^2	p
Typhoon/Time	0.07	***	0.11	***	0.05	***	0.23	***	0.05	***
Forests type	0.04	*	0.04	ns	0.05	***	0.11	***	0.05	***
Layer	0.19	***	0.12	***	0.20	***	0.11	***	0.17	***
Typhoon ∗ Forests type	0.10	**	0.12	ns	0.08	*	0.09	ns	0.09	**
Typhoon ∗ Layer	0.06	***	0.04	*	0.05	***	0.05	***	0.04	***
Forests type ∗ Layer	0.03	*	0.05	*	0.04	**	0.02	ns	0.05	**
Typhoon ∗ Forests type ∗ Layer	0.09	**	0.12	***	0.09	*	0.03	ns	0.10	***

Notes: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. ns: not significant, $p > 0.05$.

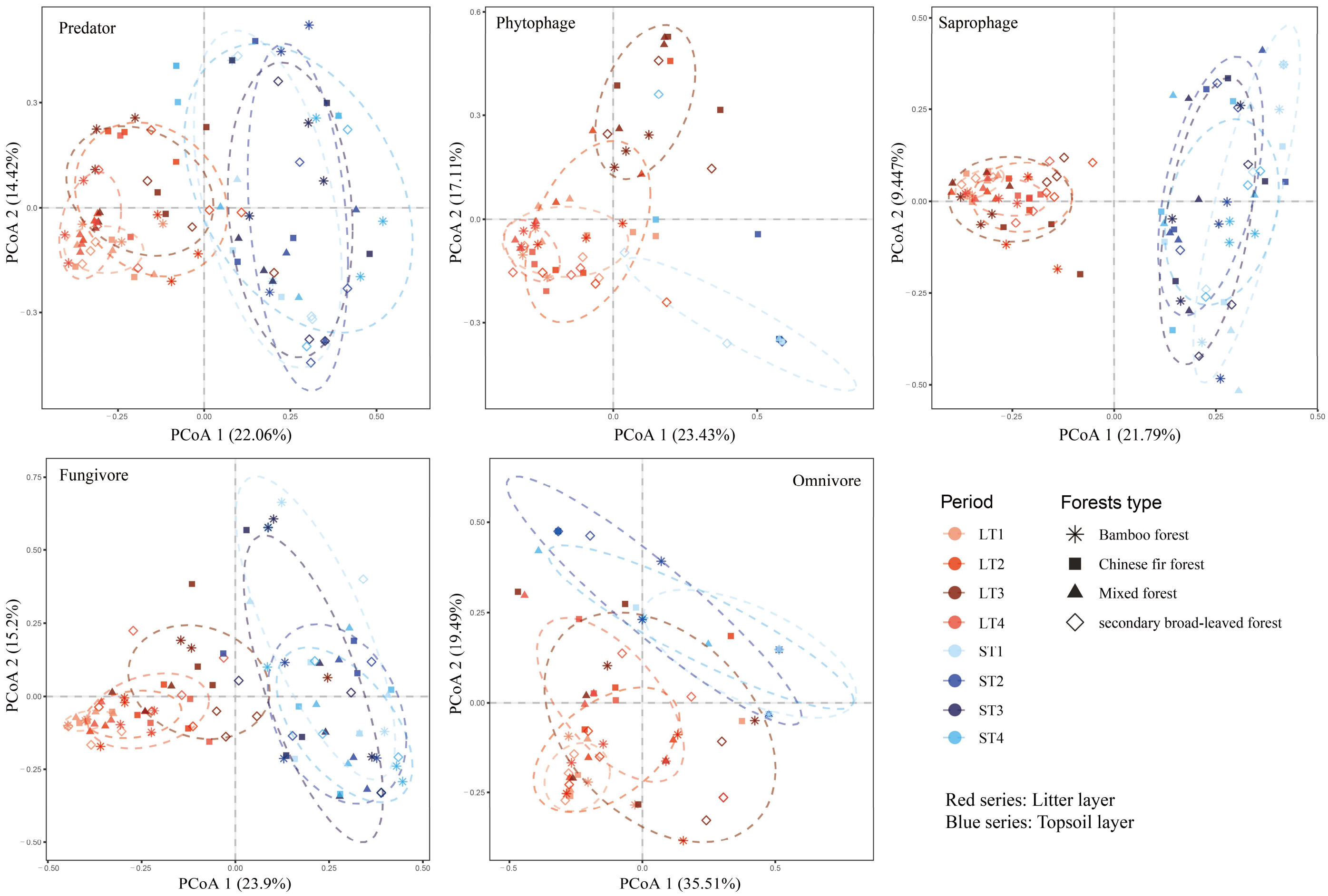

Figure 4. Principal coordinate analysis (PCoA) of functional groups of invertebrates in forest litter layer and topsoil layer before and after typhoon disturbances. LT1: litter layer (one week before the first typhoon, Hinnamnor). LT2: litter layer (one day after the first typhoon, Hinnamnor). LT3: litter layer (one day after the second typhoon, Muifa). LT4: litter layer (one week after the second typhoon, Muifa). ST1: topsoil layer (one week before the first typhoon, Hinnamnor). ST2: topsoil layer (one day after the first typhoon, Hinnamnor). ST3: topsoil layer (one day after the second typhoon, Muifa). ST4: topsoil layer (one week after the second typhoon, Muifa).

3.3. Soil Invertebrate Diversity

The effects of the typhoon disturbances on soil invertebrate diversity depended considerably on the soil layers and forest types (Figure 5). The typhoon disturbances significantly decreased the Shannon–Wiener index and Margalef index of the soil invertebrate communities in the litter layer but increased the Simpson index. However, the Pielou index changed slightly, and all these indices gradually recovered one week after the typhoon disturbances. Correspondingly, the first typhoon disturbance increased the Shannon–Wiener index and Margalef index of the invertebrate communities in topsoil layer, but these indices were slightly affected by the second typhoon disturbance. Moreover, Typhoons Hinnamnor and Muifa slightly affected the Pielou index and Simpson index for the invertebrates in the topsoil layer. Additionally, the responses of the soil invertebrate alpha biodiversity indices to the typhoon disturbances also varied widely with the forest types. The most sensitive alpha diversity index response to the typhoon disturbances was observed in the BF, and the responses for the other three forest types varied extremely with the index.

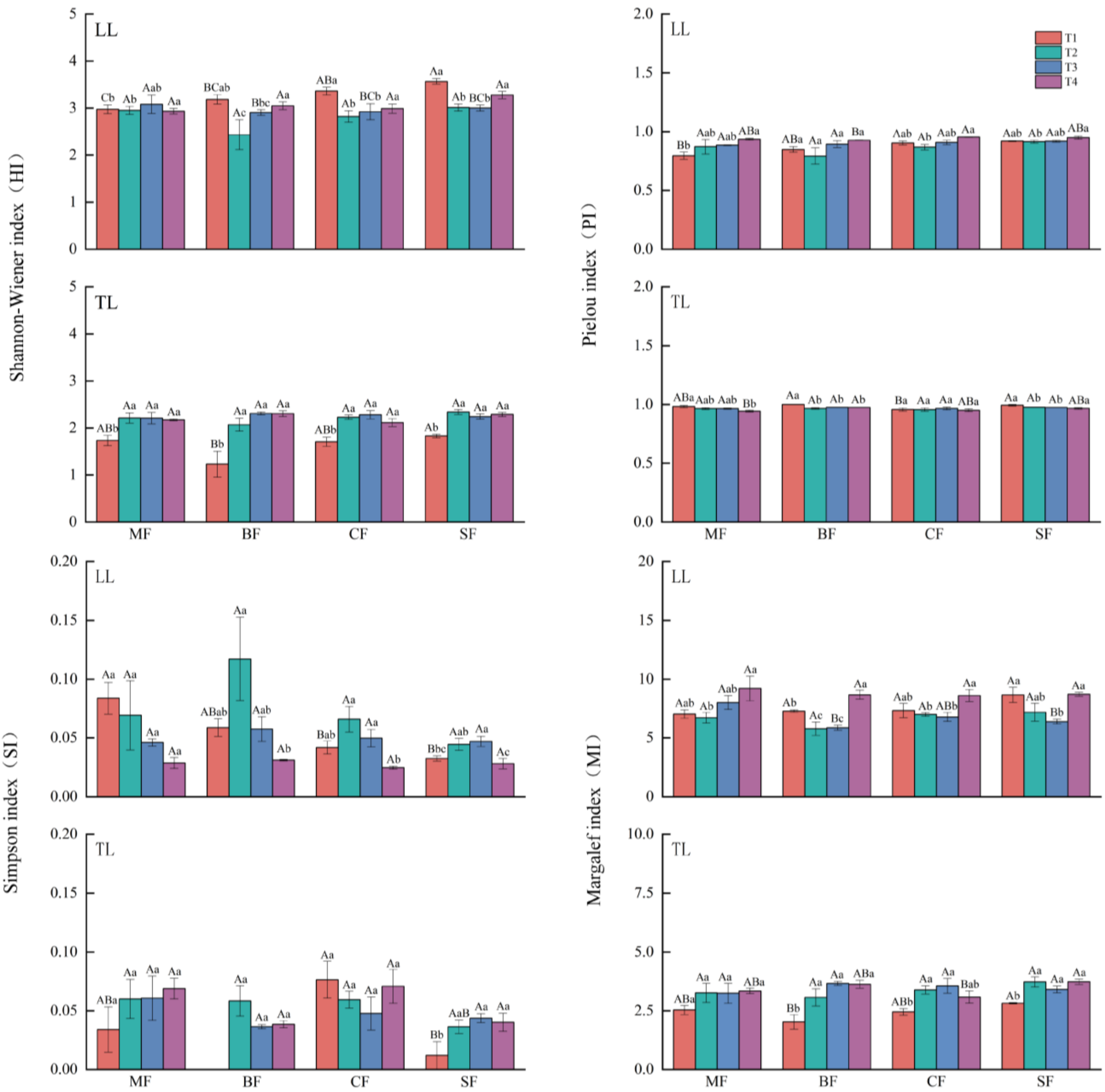

Figure 5. The changes in soil invertebrate diversity before and after the typhoon disturbances. The missing values are due to the absence of groups in this functional group. Here, LL and TL represent the litter layer and topsoil layer, respectively. The numbers in the figure represent the values of the soil invertebrate diversity index. T1: one week before the first typhoon (Hinnamnor). T2: one day after the first typhoon (Hinnamnor). T3: one day after the second typhoon (Muifa). T4: one week after the second typhoon (Muifa). MF: mixed forest; BF: bamboo forest; CF: Chinese fir forest; SF: secondary broad-leaved forest. Different capital letters indicate significant differences between different forest types at the same period, and different lowercase letters indicate significant differences between different periods ($p < 0.05$).

3.4. Relationships between Soil Invertebrate Communities and Soil Environmental Factors

The changes in the soil invertebrate communities before and after the typhoon disturbances were closely related to the forest environmental factors (Figure 6). Axes 1 and 2 explain 60.4% and 34.44% of the changes in soil invertebrate communities in the litter layer and 80.55% and 11.98% of the changes in soil invertebrate community in the topsoil layer (Figure 6). Among all the environmental factors, atmospheric temperature (AT), TC, and TP had significant effects on the soil invertebrate communities in the litter layer ($p < 0.01$; Table 4), while the invertebrate communities in the topsoil layer were significantly affected by soil temperature (ST), AT, and TP ($p < 0.01$; Table 4). AT was significantly and positively correlated with individual density, the number of taxa, the Shannon–Wiener index, the Pielou index, the Margalef index, and the functional taxa of species in the litter layer and only significantly and negatively correlated with the Simpson index (Figure 6). In addition, TN and litter water content (LWC) were significantly and positively correlated with the Shannon–Wiener index, Pielou index, and Margalef index, and cellulose (Ce) was significantly and positively correlated with individual density, functional group number, the Simpson index, and five functional taxa. In the topsoil samples, TC, TN, and TP were significantly and positively correlated with individual density, functional group number, predators, the Shannon–Wiener index, the Pielou index, the Margalef index, and soil pH (Figure 6). In contrast, AT was significantly positively correlated with omnivores, fungivores, saprophages, and the Simpson index. Importantly, ST was significantly and positively correlated with the Pielou index only and significantly and negatively correlated with all other terms. In contrast, soil water content (SWC) exhibited behavior opposite to ST, which was only negatively correlated with the Pielou index and positively correlated with all other terms (Figure 6).

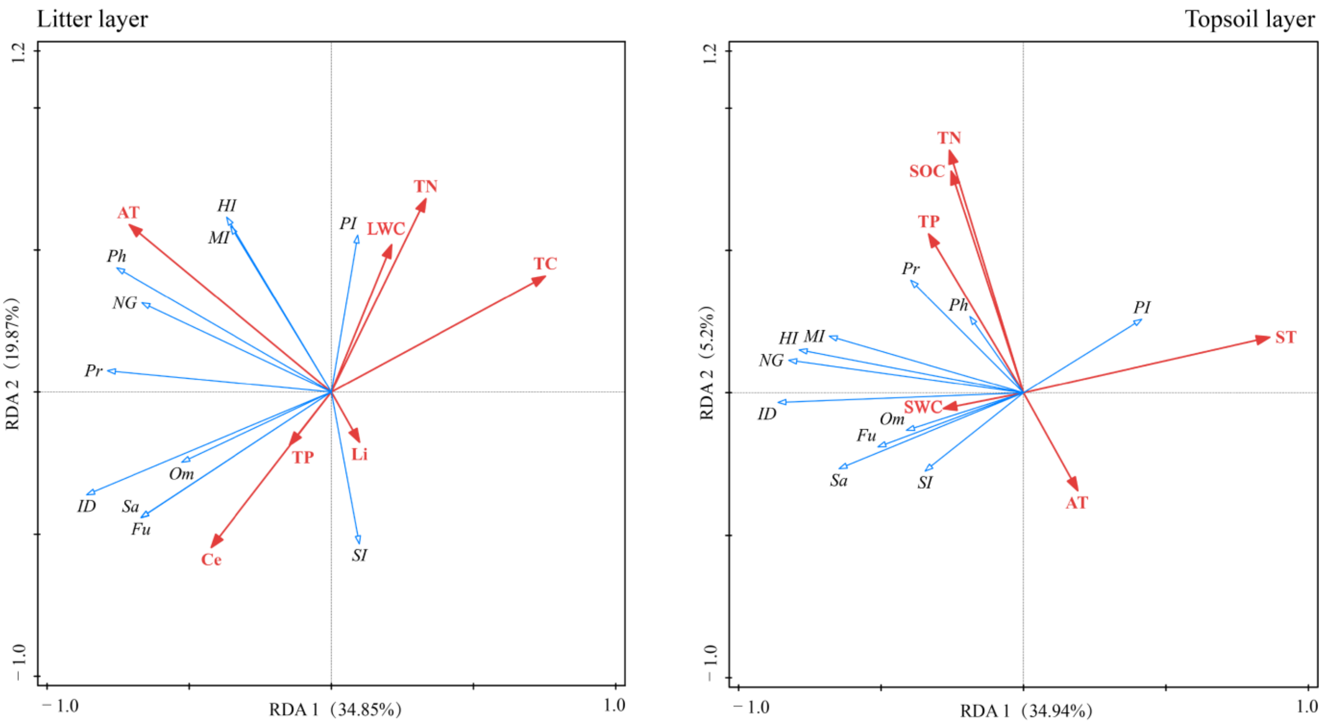

Figure 6. RDA analysis of soil invertebrate communities in litter and topsoil layers with forest environment factors before and after typhoon disturbances. ID: individual density; NG: number of functional groups; HI: Shannon–Wiener index; PI: Pielou index; SI: Simpson index; MI: Margalef index; Fu: fungivore; Om: omnivore; Sa: saprophage; Ph: phytophage; Pr: predator; TC: total carbon; TN: total nitrogen; TP: total phosphorus; SOC: soil organic carbon; LWC: litter water content; SWC: soil water content; ST: soil temperature; AT: atmospheric temperature; Li: lignin; Ce: cellulose.

Table 4. Relationships of soil invertebrate communities in litter and topsoil layers with environmental variables.

Litter Layer			Topsoil Layer		
Environmental Factor	**Pseudo-F**	***p***	**Environmental Factor**	**Pseudo-F**	***p***
AT	0.24	**	ST	0.26	**
TC	0.18	**	AT	0.10	**
TP	0.06	**	TN	0.04	**
TN	0.03	ns	TP	0.01	ns
Li	0.03	*	TC	0.01	ns
Ce	0.02	ns	SWC	0.04	ns
LWC	0.01	ns			

Notes: AT: atmospheric temperature; TC: total carbon; TP: total phosphorus; TN: total nitrogen; Li: lignin; Ce: cellulose; LWC: litter water content; ST: soil temperature; SOC: soil organic carbon; SWC: soil water content; *, $p < 0.05$; **, $p < 0.01$; ns: not significant, $p < 0.05$.

4. Discussion

Our results showed that the two typhoon disturbances significantly reduced the individual density and taxa abundance of the soil invertebrate communities in the litter layer, but these indices gradually recovered after a week of typhoon disturbances. These results partially support the first hypothesis, i.e., our hypothesis that the typhoon disturbances would decrease the density and biodiversity of the soil invertebrate communities and alter the composition of the soil invertebrate communities but that these indices would gradually recover after the typhoon disturbances. Unlike in the litter layer, invertebrate density and the number of groups in the topsoil layer increased after the first typhoon disturbance but did not show significant changes after the second typhoon disturbance. This fully supports our second hypothesis, i.e., the response of soil invertebrate communities in the litter layer to typhoon disturbances is more sensitive than that of invertebrates in the topsoil layer. In agreement with the third hypothesis, the effects of the typhoon disturbances on the soil invertebrates varied significantly with the forest types, and the strongest and weakest effects were observed in CF and SF, respectively. Moreover, these two non-catastrophic typhoons significantly altered the functional group compositions of detrital food webs in the short term, and the proportion of phytophages in detrital food webs in the litter layer increased after the typhoon disturbances. These findings demonstrate the importance of the short-term response of soil invertebrate communities to typhoon disturbances in maintaining soil invertebrate biodiversity and the functional structure of forest ecosystems in climate change scenarios.

4.1. The Short-Term Response and Restoration of Soil Invertebrate Communities to Typhoon Disturbances

The short-term responses of soil invertebrate communities to typhoon disturbances varied greatly with the soil layers, forest types and typhoon frequencies, and the composition of soil invertebrate communities can be gradually recovered. Typhoons Hinnamnor and Muifa significantly decreased the individual density and taxa abundance of the soil invertebrates in the litter layer, but the values of these indices showed a recovery trend one week after the typhoon disturbances. This result is similar to the results reported by Schowalter et al. [42], who found that walkingstick density on the forest floor in the Luquillo Experimental Forest of Puerto Rico decreased immediately after a hurricane disturbance and then rapidly increased. One possible reason for this is that some soil invertebrates might deform, escape, or hide in shelter such as deeper soil or microhabitats under stones and coarse woody debris when they face the dangerous environment perturbation and become active when the dangers are relieved. Of course, some small soil invertebrates may be blown off the ground by strong winds, washed away, or even drowned by heavy rainfall [20]. In addition, the changes in and/or destruction of microhabitats and the associated changes in the microclimate may also affect the activities of soil invertebrates [13]. The possible reasons for why soil invertebrate communities in the litter layer can be restored after typhoon disturbances are as follows. Firstly, after typhoon disturbances, some soil invertebrates hide in shelters or dive in the soil to migrate back to the litter layer. Secondly, a lot of the abnormal litter created by tropical cyclone (typhoon/hurricane) disturbances provides edible food sources for detritovores for the longer term after a hurricane disturbance [43,44]. Moreover, the microhabitats and microclimates of soil invertebrates can be gradually restored after non-catastrophic typhoon disturbances and enable many species to recover rapidly in the short term [43,45]. Meanwhile, our analysis also showed that AT, TC, and TP had a large effect on the soil invertebrate communities in the litter layer based on RDA, indicating that microclimate changes also play a crucial role in the reduction in and recovery of soil invertebrate density in the litter layer before and after typhoons. It is likely that the addition of P can increase the abundance of soil invertebrate communities, while the green leaves (abnormal foliar litter) caused by typhoon disturbances have higher P concentrations, and the P in green leaves can also be easily leached into soil. As a result, the soil invertebrate communities in the litter layer were significantly affected by TC and TP.

Different from the litter layer, the first typhoon disturbance significantly increased the individual density and taxa abundance of the soil invertebrates in the topsoil layer, but subsequently, the second typhoon slightly affected the density and taxa abundance of the soil invertebrate communities. It is likely that the active invertebrates, such as Formicidae and Oribatida, in the litter layer move into the topsoil layer rapidly when the typhoon arrives. For instance, Cours et al. [23] reported that disturbances can eliminate exposed insect populations or insect populations with poor adaptability, but insects with strong tolerance can survive or settle in altered ecosystems, and some habitats can protect insects from disturbances. Meanwhile, our results also showed that the soil invertebrate communities in the litter layer were more sensitive to typhoon disturbances. This result is similar to the results reported by Ding et al. [46], who indicated that soil animals in the litter layer are more susceptible to environmental factors at different altitude scales. Fekete et al. [47] also found that the presence of litter can buffer the impact of temperature changes on the soil layer, creating a more balanced microclimate for soil layer organisms. In addition, the effect of AT on the soil invertebrates in the litter layer was higher than that of the soil invertebrates in topsoil layer, implying that soil invertebrates exposed to the soil surface are more susceptible to typhoon disturbances.

The effects of typhoons on soil invertebrate individual density and functional group composition in the litter layer beneath CF and SF were more significant than those beneath MF and BF. These results can be explained by the differential sensitivity of the environmental factors in the different forest types and the differential sensitivity of litter-dwelling invertebrates to environmental factor change. For instance, Alejandro et al. [48] showed that microhabitat destruction and large reductions in lower trophic level species caused by rainfall can make it difficult for predatory functional taxa and soil invertebrates with poor dispersal abilities (e.g., ants and spiders) to survive. In contrast, soil invertebrates with a high dispersal capacity (e.g., beetles) are slightly affected by rainfall [49], and these mobile populations are able to expand their ranges [50] and travel to additional areas to access food resources [51]. We also found that the population density of predators, i.e., Coleoptera and Lepidoptera insects, in CF and SF was higher than that in MF and BF and significantly decreased during the typhoon disturbances (Table S1), which undoubtedly confirms our idea. These findings suggest that soil invertebrate populations in different forest types have different response strategies to typhoon disturbances to maintain their stability.

4.2. The Effects of Typhoon Disturbances on Detrital Food Webs

Soil arthropod communities are mainly composed of fungivores, saprophages, phytophages, omnivores, and predators [32], and their composition are regulated by a complex mix of biotic and abiotic factors [52]. For example, phytophages chew leaf tissue, sap feeders siphon fluids from the phloem or xylem, and saprophages feed on detrital material collected on leaf surfaces or branches [53]. Our results showed that Typhoons Hinnamnor and Muifa significantly affected the proportion of soil invertebrate functional groups, especially the saprophagous functional groups, regardless of the forest types and soil layers. When a typhoon strikes, the saprophagous functional groups, mainly composed of mites, may be more susceptible to the impact of the rainfall generated by the typhoon. These results can be attributed to the food preferences of different functional groups and sharp changes in temperature and humidity. For instance, Debnath et al. [54] and Amin et al. [55] have found a linear relationship between mites and climatic factors, and the correlation is positive in the case of temperature and radiation and negative in the case of rainfall and humidity. Our analysis also showed that saprophage abundance was negatively correlated with litter water content based on RDA, indicating that rainfall is an important factor affecting the functional group compositions of detrital food webs.

The functional group compositions of detrital food webs were also affected by soil layer and typhoon frequency. In this study, the typhoon disturbances had stronger effects on the functional group composition of the soil invertebrate communities in the litter layer than on that of the invertebrates in the topsoil layer. As discussed above, soil invertebrates exposed to the soil surface are more susceptible to environmental disturbances. Moreover, our study also showed that the proportion of phytophages in the litter layer was more stable under the typhoon disturbances than that in the topsoil layer, and the proportion of phytophages in the litter layer significantly increased one week after the typhoon disturbances. This may be due to the abundant resources of fresh leaves and plant residues in the litter layer, which is more conducive to the lives of phytophages and saprophages [39]. Meanwhile, strong winds increase the edible resources of phytophages, such as fallen trees, broken stems, and fallen branches, thereby increasing the number of phytophages in the litter layer [22,56–58]. These results suggest that different functional groups of soil invertebrates in litter and soil layers have their own survival modes under non-catastrophic typhoon disturbances. For example, the responses of spiders to typhoon disturbances are extremely dependent on the location of spider webs, with webs close to the ground and anchored to dead leaves or fallen logs experiencing increases in density, while webs on living foliage experience a decrease in density [59]. Some species may become extinct locally due to disturbances [60], while some species may erupt due to an increase in edible resources [61]. In addition, the recovery of detrital food webs followed the patterns of phytophages, fungivores, saprophages, omnivores, and predators. It is likely that the phytophages will firstly break out when larger amounts of abnormal litter with lower ratios of lignin/N and C/N fall on the forest floor. Next, the proportion of fungivores will increase in the middle stage of abnormal litter decomposition, while the proportion of saprophages will increase in the later stage of decomposition. Last, omnivores may require a longer recovery cycle [62], and their increase will drive the increase in predators.

4.3. The Effects of Non-Disastrous Typhoon Disturbances on Soil Invertebrate Biodiversity

Biodiversity indices can provide integrative information for understanding the similarities and differences in the taxa abundance and diversity of soil invertebrate communities. Our results indicated that the typhoons significantly affected the Shannon–Wiener and Margalef indices of the soil invertebrate communities in the litter layer, but these indices gradually also recovered after one week of typhoon transit. Compared with the litter layer, the first typhoon disturbance increased the Shannon–Wiener and Margalef indices of the topsoil layer but only slightly changed after the second typhoon disturbance. Due to the Shannon–Wiener index being able to reveal the response mechanism of soil animal communities to environmental changes, the Margalef index is a parameter reflecting the habitats of soil animals. Together, these two indices indicate the complexity of soil animals' community compositions and habitat conditions. Our findings suggest that typhoon disturbances can deteriorate the microhabitat conditions for litter-dwelling invertebrates immediately, leading to a decrease in the diversity of their community composition, whereas the microhabitat conditions of invertebrate communities in the topsoil layer are less affected. As mentioned above, the abundance and diversity of invertebrate communities can be gradually restored due to the input of a large amount of abnormal litter and the restoration of abiotic factors such as light, temperature, and moisture in the litter layer. So, the same is true of soil biodiversity.

Our results also indicated that the typhoon disturbances increased the Simpson index of the invertebrates in the litter layer and that it gradually recovered one week after the typhoon disturbance, but slight changes in the Simpson index of the invertebrate communities in the topsoil layer were observed. This means that the typhoon disturbances greatly affected the dominance of litter-dwelling invertebrates but had no significant effect on the dominance of the soil invertebrate communities in the topsoil layer, since the Simpson index is used to evaluate the dominance of a biological community. It is likely that only a few litter-dwelling species are still active, and the vast majority of soil invertebrates are still in the soil or other shelters, making the dominant organisms more prominent. However, the dominance of a litter-dwelling invertebrate community can be gradually restored due to community restoration, as mentioned above. Moreover, the typhoon disturbances led to slight changes in invertebrate community diversity, also owing to the weaker effect of non-catastrophic typhoons on the microhabitats for the invertebrates in the topsoil layer. Interestingly, the Pielou index of the invertebrate communities in both the litter and topsoil layers was slightly affected by the typhoon disturbances, implying that the stability of the soil invertebrate communities was not significantly affected by the observed non-catastrophic typhoon disturbances in this study regardless of forest type, since the Pielou index is used to evaluate the stability of a community. This also means that soil invertebrate communities have different strategies to cope with typhoon disturbances and gradually recover.

Our results also demonstrated that the effects of typhoon disturbances on the soil invertebrate alpha diversity index varied with forest type and typhoon frequency to some extent. In this study, the soil invertebrate alpha diversity index in the BF was the most sensitive to the typhoon disturbances. It is likely that the bamboo trees have shallow roots, small diameters, and hollow trunks, which make bamboo forests more vulnerable to uprooting and stem breakage and make the microhabitats of soil invertebrates more likely to be destroyed. As a result, the density and diversity of soil invertebrate communities in bamboo forests are more susceptible to typhoon disturbances.

5. Conclusions

The responses of the composition of taxa and functional groups and diversity of soil invertebrate communities to typhoon disturbances varied greatly with the soil layers and forest types. Typhoons Hinnamnor and Muifa significantly decreased the individual densities and taxa abundance of the soil invertebrate communities in the litter layer and showed a gradual recovery trend one week after the typhoon disturbances. However, the first typhoon disturbance significantly increased the density and taxa abundance of the soil invertebrate communities in the topsoil, and the second typhoon only affected these slightly. Meanwhile the effects of the typhoon disturbances on the soil invertebrate communities in Chinese fir forests and secondary broad-leaved forests were more significant than those in the mixed forests and bamboo forests. In addition, the typhoon disturbances also significantly altered the functional group compositions of detrital food webs in the litter and topsoil layers and varied greatly with the forest types and soil layers. Additionally, the effects of the first typhoon disturbance on the soil invertebrate communities was more significant than that of the second typhoon disturbance. These results imply that non-catastrophic typhoon disturbances can alter the composition of taxa and functional groups of forest soil invertebrates in the short term and that some soil- and litter-dwelling invertebrates can also respond to non-catastrophic typhoon disturbances via the behaviors of escaping, hiding, and deformation. The legacy effects of typhoon disturbances on the functional group compositions of detrital food webs may influence carbon and nutrient cycling in forest ecosystems.

With regret, we only demonstrated the short-term responses of soil invertebrate communities to two consecutive non-catastrophic typhoon events. Meanwhile, we only investigated the response of dry soil invertebrate communities extracted using a modified Tullgren extractor to typhoon disturbances. Although dry soil invertebrates may be more sensitive to heavy rainfall caused by typhoons, wet soil invertebrates extracted based on the use of Baermann extractors, such as nematodes, planarian worms, bear worms, etc., may also be quite sensitive to changes in soil moisture before and after typhoon disturbances. Therefore, invertebrate responses to catastrophic and non-catastrophic typhoon events should be studied more comprehensively in the future.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15040583/s1, Figure S1: Soil invertebrate community composition and number distribution.; Table S1: Composition of soil invertebrate community in the litter layer; Table S2: Composition of soil invertebrate community in topsoil layer.

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