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Effects of Soil Fauna on the Home-Field Advantage of Litter Total Phenol and Condensed Tannin Decomposition

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Abstract: Soil fauna play a vital role in contributing to the home-field advantage (HFA: litter decomposes faster in its natural habitat than elsewhere) during litter decomposition. Whether the presence of soil fauna affects the HFA of the decomposition of total phenols and condensed tannins, which are important components of litter, has rarely been investigated. In this study, litterbags with different mesh sizes were transplanted reciprocally, 0.04 mm (basically excluding soil fauna) and 3 mm (basically allowing all soil fauna to enter), in *Lindera megaphylla* and *Cryptomeria fortunei* forests. The results illustrated that the loss rates of total phenols and condensed tannins reached 64.07% to 84.49% and 69.67% to 88.37%, respectively, after 2 months of decomposition. Moreover, soil fauna positively contributed to the decomposition of condensed tannins in high-quality litter. After 2 months of decomposition, a significantly positive HFA (HFA index: 10.32) was found for total phenol decomposition in the coarse mesh, while a significantly negative HFA (HFA index: −1.81) was observed for condensed tannin decomposition in the fine mesh after 10 months of decomposition. Polyphenol oxidase (PPO) and peroxidase (POD) activities were significantly influenced by litter types. The loss rates of total phenols and condensed tannins were significantly negatively correlated with the initial N content, P content, N/P ratio, and POD activity and were positively related to the initial C content, total phenol content, condensed tannin content, C/P ratio, and C/N ratio. Only the loss of condensed tannins was negatively correlated with PPO activity (after 2 months' decomposition). However, none of these correlations were observed after 10 months of decomposition. Our study illustrated that (1) soil fauna contributed to the decomposition of total phenols and condensed tannins but were influenced by litter type for condensed tannins. (2) The soil fauna had inconsistent effects on the HFA of total phenols and condensed tannins, possibly due to the combined regulatory effects of environmental context, litter quality, and rapid decomposition rates. In sum, the results indicated that soil fauna played an important role in the decomposition of condensed tannins and total phenols in litter, and additional studies on the effects of soil faunal abundance and class on HFA of condensed tannins and total phenols are needed.

Keywords: home-field advantage; total phenols; condensed tannins; soil fauna; litter decomposition

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1. Introduction

Litter decomposition is the essential process through which nutrients are returned to the soil, and it plays a critical role in carbon storage as well as nutrient cycling in forest ecosystems [1]. Litter contains large amounts of lignin, cellulose, total phenols, condensed tannins, and other recalcitrant components [2,3]. In previous studies, total phenols and condensed tannins were suggested to be vital factors in controlling the litter quality and decomposition rate [4–8]. These components have been shown to precipitate proteins in litter [9,10], produce toxicological effects on soil fauna, and inhibit microbial activity involved in litter decomposition [11,12]. Hence, understanding the dynamics of total phenols and condensed tannins during litter decomposition could help reveal the mechanisms of litter decomposition and its influence on energy flow and the nutrient cycle in forest ecosystems [13].

Tannins are extensive and abundant polyphenols in plants that mainly include hydrolyzed tannins and condensed tannins; total phenols are composed of flavonoids, phenolic acids, and tannins and occur mainly as important secondary metabolites [14]. At the initial stage, litter decomposition is believed to be accompanied by rapid mass loss, as well as a decrease in soluble components, after which the decomposition of recalcitrant components such as condensed tannins and total phenols begins to occur [15]. During this period, it may be influenced by multiple factors such as freeze–thaw cycles, dry–wet alternations, and leaching (Table S1) [16–25]. Leaching from litter caused by the rainfall and snow melting promotes the loss of total phenols [22]. In addition, consistent with condensed tannins, total phenols can indirectly regulate litter decomposition by modifying the structure of decomposer communities [26,27].

As vital decomposers, soil fauna directly or indirectly affect litter decomposition by cracking, digging, feeding, and stimulating microbial activities [28]. Soil fauna may lead to different results in the decomposition of phenolic substances in litter [29,30]. Through the feeding and digestion by soil fauna, some phenolic substances that are abundant in litter are transformed into phenol-free feces [29], several soluble phenols are degraded by the gut microbes of soil fauna [29], and certain phenols are combined with proteins to form insoluble complexes [30,31]. Moreover, the enzymes secreted by microbes are crucial during decomposition [32,33]. Specifically, enzyme activity can quickly reflect litter decomposition conditions and indirectly reflect the decomposition rate [34]. Peroxidase (POD) and polyphenol oxidase (PPO) are commonly found in nature and promote the conversion and degradation of phenolic substances through catalytic oxidation [35,36], which is closely related to the degradation of total phenols and condensed tannins [37].

The decomposition rate of litter in native habitats is faster than that in other environments, a phenomenon that is referred to as the 'home field advantage' (HFA) [38,39]. Due to the competition for nutrients and adaptation to specific environments, soil organisms, such as soil fauna and microbes, exhibit greater specialization, and this specialization makes crucial contributions to the HFA for litter decomposition [38,40]. Utilizing interactive litter transplantation experiments, the effects of soil fauna on the HFA of litter decomposition have been experimental observations in multiple ecosystems with different litter types (Table 1). Most studies have shown that soil fauna significantly contribute to the HFA [41–45]. Some studies have shown no significant difference in the litter decomposition rate between 'home' and 'away' habitats in relation to the participation of soil fauna [42,43,46]; additionally, others have shown that soil fauna cause litter to decompose more slowly in 'home' habitats [47,48]. Many studies have shown that soil fauna influence the HFA of litter decomposition rate; however, an understanding of the impacts of soil fauna on the HFA of total phenol and condensed tannin decomposition is still lacking.

To explore the influences of soil fauna on the HFA of the decomposition of total phenols and condensed tannins, we studied litter from *Lindera megaphylla* and *Cryptomeria fortunei*, which are typical species of Mount Emei in the southwest Sichuan Basin. Field interactive transplantation tests were subsequently conducted, and the following questions were focused on: (1) How were the total phenols and condensed tannins degraded over time? Because the HFA is common during decomposition [43], we asked whether (2) the HFA effect also occurs during the decomposition of total phenols and condensed tannins. If so, (3) does the soil fauna influence the effect of the HFA on the decomposition of total phenols and condensed tannins?

Table 1. The effects of soil fauna on HFA in litter decomposition.

HFA	Influence Factor	Direction	Come From	Reference
Litter mass loss	Soil mesofauna	Positive	*Pinus massoniana*	[49]
Nitrogen, sulfur release Litter mass loss Carbon release	Soil mesofauna	Negative Positive	*P. Koraiensis*, *Larix olgensis*	[50]
Litter mass loss	Soil fauna	Negative	*Quercus variabilis*, *P. massoniana*	[48]
Litter mass loss	Macro- and meso-invertebrates	None	Atlantic Rainforest of Brazil 3 successional stages	[46]
Litter mass loss	Meso- and micro-fauna	Positive/Negative	*P. taiwanensis*	[51]
Litter mass loss	All size classes of soil fauna	Positive	*Raphanus raphanistrum-Dactylis glomerata-Q. rubra* late successional stage	[41]
Litter mass loss	Mesofauna	Positive	*R. raphanistrum-D. glomerata-Q. rubra* mid successional stage	
Carbon release	Soil fauna	Positive	*Acer pseudosieboldianum*, *Juglans mandshurica*	[42]
Nitrogen release	Soil fauna	Positive	*Q. mongolica*, *J. mandshurica*	
Nitrogen release	Soil fauna	Positive	*A. pseudosieboldianum*	
Sulfur release	Soil fauna	Positive	*Q. mongolica*, *A. pseudosieboldianum*	
Sulfur release	Soil fauna	Negative	*A. Pseudosieboldianum*, *Q. mongolica*	
Litter mass loss	Soil fauna	None	*Q. mongolica*, *A. pseudosieboldianum*, *J. mandshurica*	
Litter mass loss	Mite	Negative	*Ursinia laciniata* tree (kanuka) litter	[47]
Dry matter and nitrogen disappearance	Mesofauna Macrofauna Microfauna	Positive	Solid cattle manure	[44]
Wood mass loss	Soil fauna	Positive	*Platy carya strobilacea* wood *Cryptomeria japonica* wood	[45]
Phosphorus release	Soil fauna Soil mesofauna	None	Broadleaf litter, Coniferous litter	[43]
Litter mass loss	Soil fauna Soil mesofauna	Positive	Broadleaf litter	
Nitrogen release	Soil fauna Soil mesofauna	Positive	Coniferous litter	
Litter mass loss	Soil mesofauna	Positive	*P. sylvestris*	[52]
Litter mass loss	Soil mesofauna	Positive	*Q. cerris*	

2. Materials and Methods

2.1. Site Description

The research area was situated in the southwest region of the Sichuan Basin on Mount Emei (29.60° N, 103.36° E). This area features special topography and geomorphology, a complex vertical climatic zone, a rich species composition, and evergreen broad-leaved forests. In the altitudinal range of 660–1500 m, species of Lauraceae, Magnoliaceae, and Conchoaceae, such as *Lindera megaphylla*, *Machilus pingii*, *Phoebe zhennan*, and *Michelia martinii*, are distributed, and occasionally other species, such as *Symplocaceae*, are distributed. In addition, secondary forests, such as those composed of *Castanopsis hystrix*, *Pinus massoniana*, *Cunninghamia lanceolata*, or *Cryptomeria fortunei*, are distributed. The climate in the research area is a subtropical humid monsoon climate, with a mean annual temperature of 17.2 °C, 7 °C in the coldest month (January) and 26.3 °C in the hottest month (July). The average annual precipitation is 1555.3 mm, with the precipitation from May to September accounting for 70%–80% of the annual total precipitation. The soil type is yellow soil, with scattered yellow lime soil and black lime soil in some areas.

2.2. Experimental Design

The experimental plot was established in Xueya village, approximately 900 m a.s.l., on Mount Emei. Three 20 m × 20 m sample plots were randomly established in *L. megaphylla* and *C. fortunei* forests, which are widely distributed on Mount Emei (Figure 1). In April 2021, during the spring litter peak in the evergreen deciduous forest, litter was collected from the *L. megaphylla* and *C. fortunei* forests and returned to the laboratory for natural air drying for 2 weeks. The air-dried litter was put into two kinds of litterbags: one with a diameter of 0.04 mm (basically excluding soil fauna; fine mesh) at the bottom (in contact with the fresh litter layers) and at the surface (in contact with the atmosphere) and the other with a diameter of 0.04 mm at the bottom and 3 mm (basically allowing all soil fauna to enter; coarse mesh) at the surface.

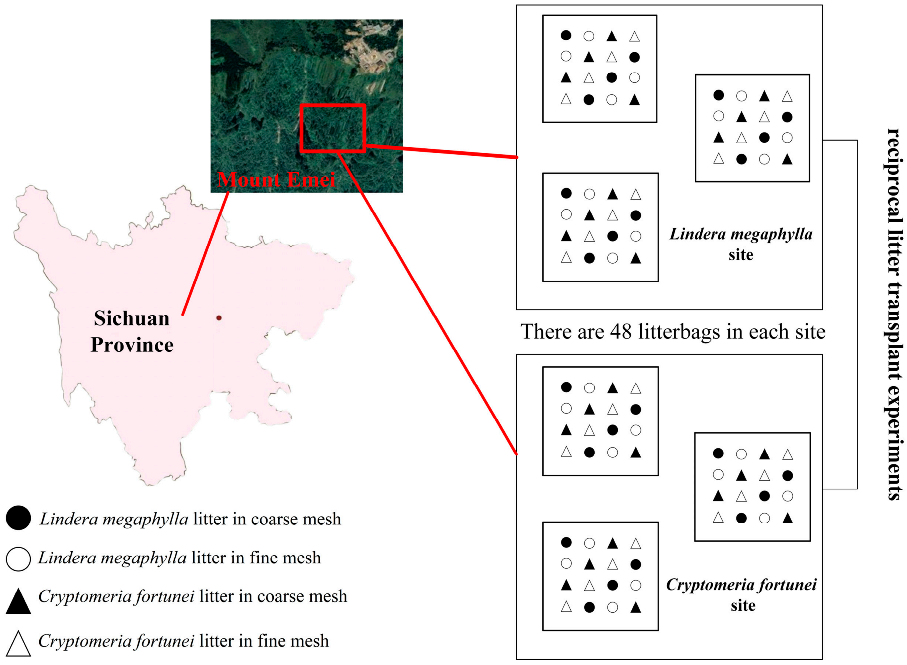

Figure 1. Diagram of plot setting of the reciprocal transplant experiments.

The size of the litterbags was 20 cm × 20 cm, and air-dried foliar litter with 7 ± 0.05 g was accurately weighed by a percentile (0.01) electronic scale. Another three parts (7 g) of each type of foliar litter were taken, oven-dried at 65 °C, and ground and sieved through a 0.3 mm mesh for the determination of the initial carbon (C), nitrogen (N), phosphorus (P), and total phenol and condensed tannin contents.

In May 2021, reciprocal litter transplant experiments were conducted; specifically, foliar litter from species A (*L. megaphylla*) and species B (*C. fortunei*) decomposed at sites a (dominated by *L. megaphylla*) and b (dominated by *C. fortunei*). A total of 96 litterbags were laid flat on the surface of the sample plots with a spacing of at least 5 cm between each litterbag. Considering potential seasonal variations in litter decomposition, dynamic sampling was conducted in July 2021, September 2021, December 2021, and March 2022, and 24 litterbags were collected at each sampling point (2 sites × 2 species × 2 mesh sizes × 3 replicates). After the soil and foreign matter were carefully removed during collection, the litter was immediately packaged in a sealed pocket and put into a crisper box accompanied by an ice pack. Approximately one-third of the subsamples were used for the determination of POD and PPO activities. The remaining subsamples were oven-dried at 65 °C to a constant weight for determination of the moisture content and mass loss rate of the foliar litter. Then, the samples were ground with a mill and passed through a 0.3 mm mesh for the determination of total phenol and condensed tannin contents.

2.3. Analyses and Calculations

The initial C, N, and P contents of the foliar litter were determined by an elemental analyzer (Elementar Vario MACRO Cube, Elementar Company, Hanau, Germany). The condensed tannins were analyzed by the conventional vanillin–HCl assay method [11]. The total phenol content was determined using the Folin–Ciocalteu method [53]. The POD and PPO activities were determined according to the improved microplate reader method of the Allison Laboratory [54,55]. The enzyme activity unit was defined as μmol g^{-1} h^{-1}.

The loss rates of total phenols, the loss rates of condensed tannins, the fauna effect, and the HFA indices of total phenols and condensed tannins were calculated.

The loss of total phenols and condensed tannins over time was calculated as follows:

$$Loss(\%) = (M_0C_0 - M_tC_t)/M_0C_0 \times 100 \quad (1)$$

where M_t represents the remaining litter dry mass at the current (t) sampling date; C_t represents the condensed tannin or total phenol content (%) at the current sampling date; and M_0 and C_0 represent the initial litter dry mass and the initial condensed tannin content or total phenol content, respectively.

The effects of the fauna on the total phenol and condensed tannin loss rates were calculated as follows:

$$Fauna\ effect(\%) = \frac{L_{fauna}}{L_{total}} \times 100 \quad (2)$$

L_{fauna} represents the difference in condensed tannin or total phenol loss between the 3 mm and 0.04 mm litterbags. L_{total} represents the condensed tannin or total phenol loss rate in the 3 mm litterbags.

The HFA indices of the loss rates of total phenols and condensed tannins were calculated as follows [38]:

$$A_{RMLa} = \frac{A_a}{A_a + B_a} \times 100 \quad (3)$$

where A_{RMLa} represents the relative mass loss of litter from species A at site a and A_a and B_a represent the percentage mass loss of leaf litter from two plant species decomposing at site a. The measures of relative mass loss were used to calculate HFA.

HFA index (*HFAI*):

$$HFAI = \frac{A_{RMLa} + B_{RMLb}}{A_{RMLb} + B_{RMLa}} \times 100 - 100 \quad (4)$$

where *HFAI* represents the litter mass loss rates when it decomposes at home versus away, and represents the net value of the two litter types (A and B) involved in the reciprocal transplant.

2.4. Statistical Analyses

A repeated-measure ANOVA in general linear models was used to examine the effects of decomposition site, species, mesh size, and decomposition time on the condensed tannin and total phenol contents and loss rates. Independent-sample t-tests were used to test for significant differences in initial litter quality and soil fauna effects, which vary with species. One-way ANOVA was used to analyze the contents of total phenols and condensed tannins, the loss rates of total phenols and condensed tannins, and PPO and POD activities among treatments within the same species at the 0.05 level. A single-sample t-test (compared with the 0 value) was used to analyze the significance of the differences in the soil fauna effect and HFA index at the 0.05 level. Pearson correlation analysis was used to test the correlation between initial litter quality, PPO and POD activities, and the contents and loss rates of condensed tannins and total phenols after two and ten months of decomposition (without distinguishing species and mesh size of litterbags). All of the statistical analyses were performed and graphics were generated using IBM SPSS statistics program (v 25.0, Chicago, IL, USA) and SigmaPlot 15 (v 15.0, Systat Software).

3. Results

3.1. Initial Foliar Litter Quality

The initial C, condensed tannin, and total phenol contents in the foliar litter of *C. fortunei* were significantly higher than those in the foliar litter of *L. megaphylla*. Additionally, the C/N and C/P ratios were significantly greater in the foliar litter of *C. fortunei* than in the foliar litter of *L. megaphylla*. However, the N and P contents and N/P ratio in the foliar litter of *L. megaphylla* were significantly higher than in the foliar litter of *C. fortunei* (Table 2).

Table 2. Initial foliar litter quality of *Lindera megaphylla* and *Cryptomeria fortunei* (mean ± SE, n = 3).

Species	C (g/kg)	N (g/kg)	P(g/kg)	CT (g/kg)	TP (g/kg)	C/N	C/P	N/P
Lindera megaphylla	464.47 ± 0.89	23.47 ± 0.29	1.66 ± 0.01	6.00 ± 0.16	10.05 ± 0.51	19.80 ± 0.22	279.93 ± 1.12	14.14 ± 0.15
Cryptomeria fortunei	495.3 ± 1.59	12.83 ± 0.38	1.45 ± 0.03	17.57 ± 1.35	17.61 ± 0.58	38.65 ± 1.01	343.04 ± 8.73	8.89 ± 0.36
***F** value*	0.743 ***	0.124 ***	8.500 *	12.047 *	0.014 ***	2.328 ***	5.932 **	4.296 ***

CT: Condensed tannins; TP: Total phenols. (independent-sample *t*-test, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

3.2. Losses of Total Phenols and Condensed Tannins in Foliar Litter

Overall, the decomposition time, species, and mesh size rather than whether the decomposition site was a home or away site had significant effects on the loss of total phenols and condensed tannins (Table 3). The total phenol and condensed tannin loss rates reached 64.07% to 84.49% and 69.67% to 88.37%, respectively, after 2 months of decomposition and 86.48% to 95.53% and 89.86% to 96.51%, respectively, after 10 months of decomposition (Figure 2).

Table 3. Results of repeated-measure ANOVA for testing the effects of home vs. away (HA), species (SP), mesh size (MS), and decomposition time (DT) on the content and loss of condensed tannins and total phenols and peroxidase (POD) and polyphenol oxidase (PPO) activities (n = 3).

Source	Condensed Tannin Content		Total Phenol Content		Condensed Tannin Loss		Total Phenol Loss		POD		PPO	
	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
Decomposition time (DT)	37.37	<0.001	26.25	<0.001	233.61	<0.001	121.60	<0.001	94.14	<0.001	24.28	<0.001
Home vs. away (HA)	1.30	0.27	0.02	0.903	0.01	0.932	0.07	0.795	10.51	0.005	7.72	0.013
Species (SP)	14.93	0.001	8.60	0.01	47.55	<0.001	11.81	0.003	183.43	<0.001	83.09	<0.001
Mesh size (MS)	6.75	0.019	1.70	0.211	21.50	<0.001	8.58	0.01	32.58	<0.001	1.11	0.308
DT × HA	0.18	0.679	0.37	0.554	3.90	0.066	1.63	0.22	2.27	0.092	1.91	0.174
DT × SP	0.85	0.37	0.04	0.837	40.13	<0.001	9.82	0.006	34.26	<0.001	5.19	0.013
DT × MS	3.60	0.076	0.29	0.595	6.52	0.021	0.80	0.384	6.71	0.001	3.82	0.034
HA × SP	12.42	0.003	86.06	<0.001	0.20	0.657	0.94	0.346	6.71	0.001	9.91	0.006
HA × MS	0.94	0.348	2.18	0.16	0.18	0.677	2.83	0.112	5.69	0.03	17.73	0.001
SP × MS	0.27	0.609	3.11	0.097	7.58	0.014	0.15	0.701	0.33	0.576	5.99	0.026
DT × HA × SP	0.20	0.661	0.36	0.558	10.26	0.006	3.06	0.099	13.62	<0.001	0.80	0.513
DT × HA × MS	0.06	0.817	0.65	0.432	0.10	0.755	2.58	0.128	5.76	0.002	8.90	0.001
DT × SP × MS	1.04	0.323	1.88	0.19	3.02	0.102	0.01	0.913	2.00	0.127	7.64	0.003
HA × SP × MS	0.14	0.713	0.00	0.99	0.75	0.399	2.20	0.157	1.28	0.274	2.33	0.146

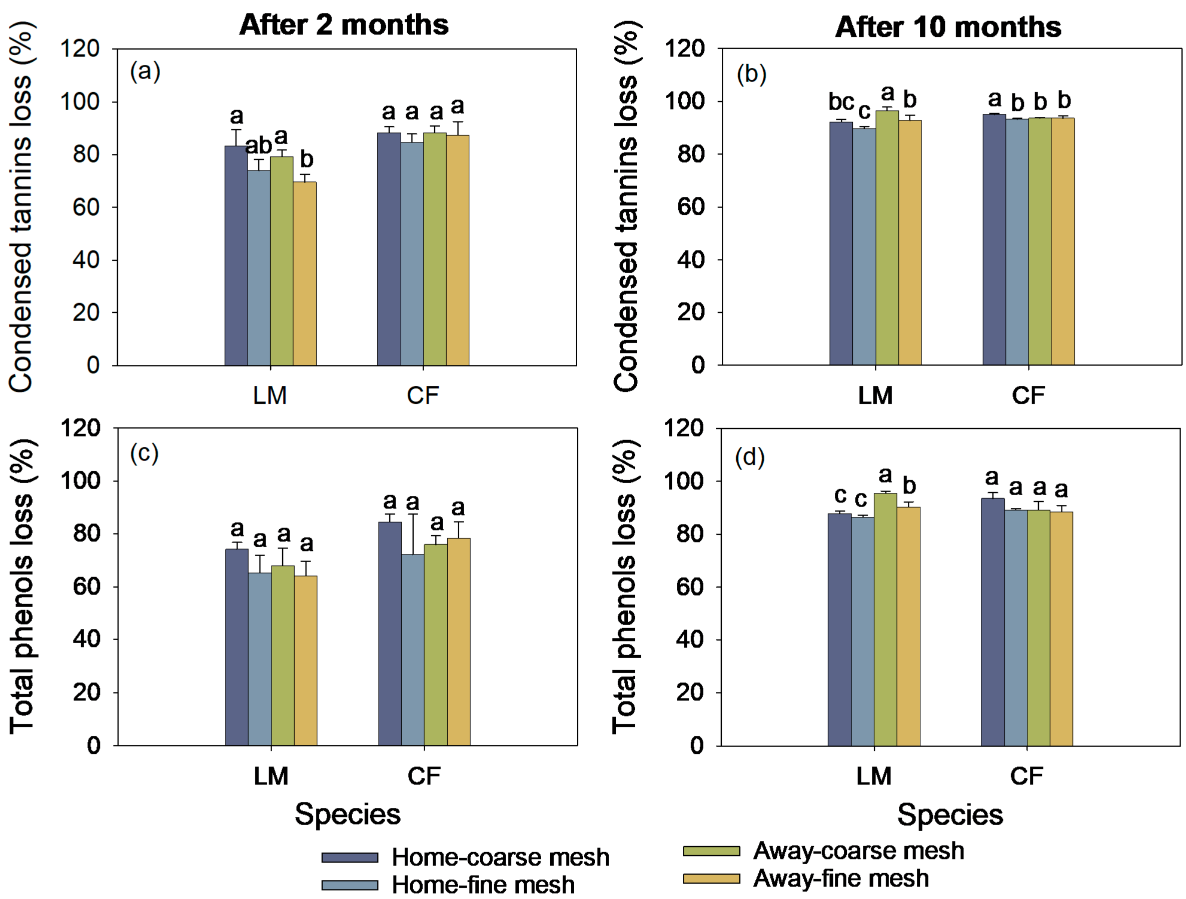

Figure 2. Condensed tannin (**a**,**b**) and total phenol (**c**,**d**) losses (%) in foliar litter from *Lindera megaphylla* (LM) and *Cryptomeria fortunei* (CF) at decomposition sites in *L. megaphylla* and *C. fortunei* forests. Different lowercase letters represent significant differences among treatments within the same species (One-way ANOVA, $p < 0.05$, $n = 3$).

For *C. fortunei*, the loss of condensed tannins in coarse mesh litterbags at the home site was significantly higher than that in other mesh litterbags and at home or away sites after 10 months of decomposition (Figure 2b), while no significant difference was observed in total phenol and condensed tannin losses among home or away sites and coarse or fine mesh sizes (Figure 2a,c,d). For *L. megaphylla*, after 2 months of decomposition, the condensed tannin losses in the coarse mesh litterbags were higher than those in the fine mesh litterbags, regardless of whether the sites were home or away, and no significant differences were observed in the total phenol loss among the home or away sites and coarse or fine mesh sizes (Figure 2a,c). After 10 months of decomposition, the total phenol and condensed tannin losses at the away site were significantly higher than those at the home site, and they were significantly higher in the coarse mesh litterbags than in the fine mesh litterbags at the away site (Figure 2b,d).

3.3. Total Phenol and Condensed Tannin Content in Foliar Litter

Overall, decomposition time and species rather than decomposition site (home or away) had significant effects on the total phenol and condensed tannin contents. Mesh size significantly affected the condensed tannins content but not the total phenols content (Table 3). The contents of total phenols and condensed tannins were 3.05% to 6.22% and 1.60% to 2.97%, respectively, after 2 months of decomposition and 1.86% to 4.55% and 1.02% to 2.08%, respectively, after 10 months of decomposition (Figure 3).

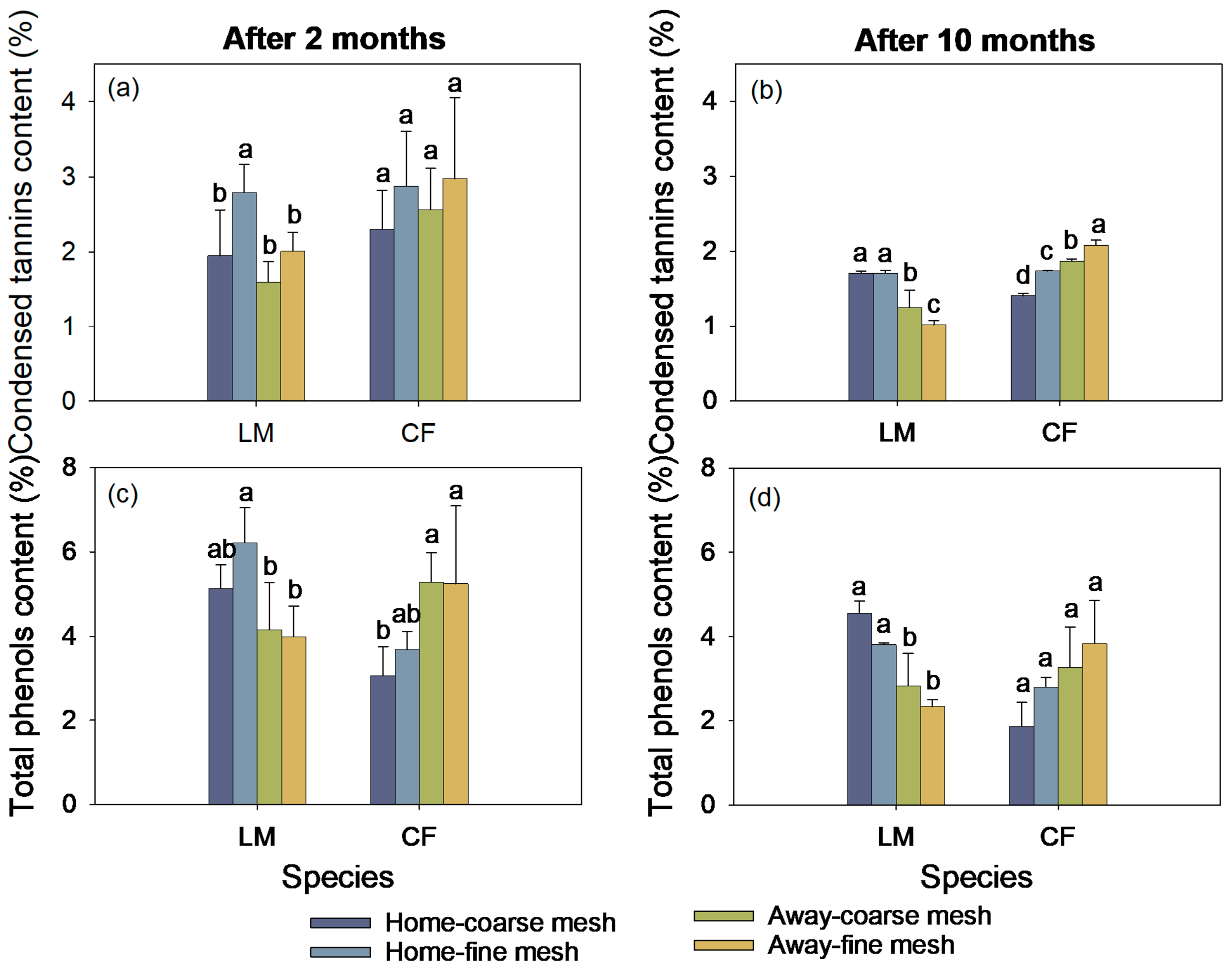

Figure 3. Condensed tannin (**a**,**b**) and total phenol (**c**,**d**) contents in the foliar litter of *Lindera megaphylla* (LM) and *Cryptomeria fortunei* (CF) at decomposition sites in *L. megaphylla* and *C. fortunei* forests. Different lowercase letters represent significant differences among treatments within the same species. (One-way ANOVA, $p < 0.05$, $n = 3$).

Specifically, for the species *L. megaphylla*, the total phenol and condensed tannin contents in the fine mesh litterbags at the home site were significantly higher than those in the other litterbags and sites after 2 months of decomposition (Figure 3a,c). However, no significant difference was detected in the total phenol or condensed tannin contents of *C. fortunei* between the home or away sites or between coarse or fine mesh sizes after 2 months and 10 months of decomposition (Figure 3a,d). After 10 months of decomposition, the total phenol and condensed tannin contents of *L. megaphylla* at the home site were significantly higher than those at the away site (Figure 3b,d).

3.4. POD and PPO Activities in Foliar Litter

The decomposition time, species, and decomposition site (home or away) had significant effects on the activities of POD and PPO (Table 3). The activities of POD and PPO reached 0.99 μmol g^{-1} h^{-1} to 16.62 μmol g^{-1} h^{-1} and 3.68 μmol g^{-1} h^{-1} to 19.94 μmol g^{-1} h^{-1} after 2 months of decomposition and 1.69 μmol g^{-1} h^{-1} to 22.54 μmol g^{-1} h^{-1} and 0.39 μmol g^{-1} h^{-1} to 11.96 μmol g^{-1} h^{-1} after 10 months of decomposition, respectively (Figure 4).

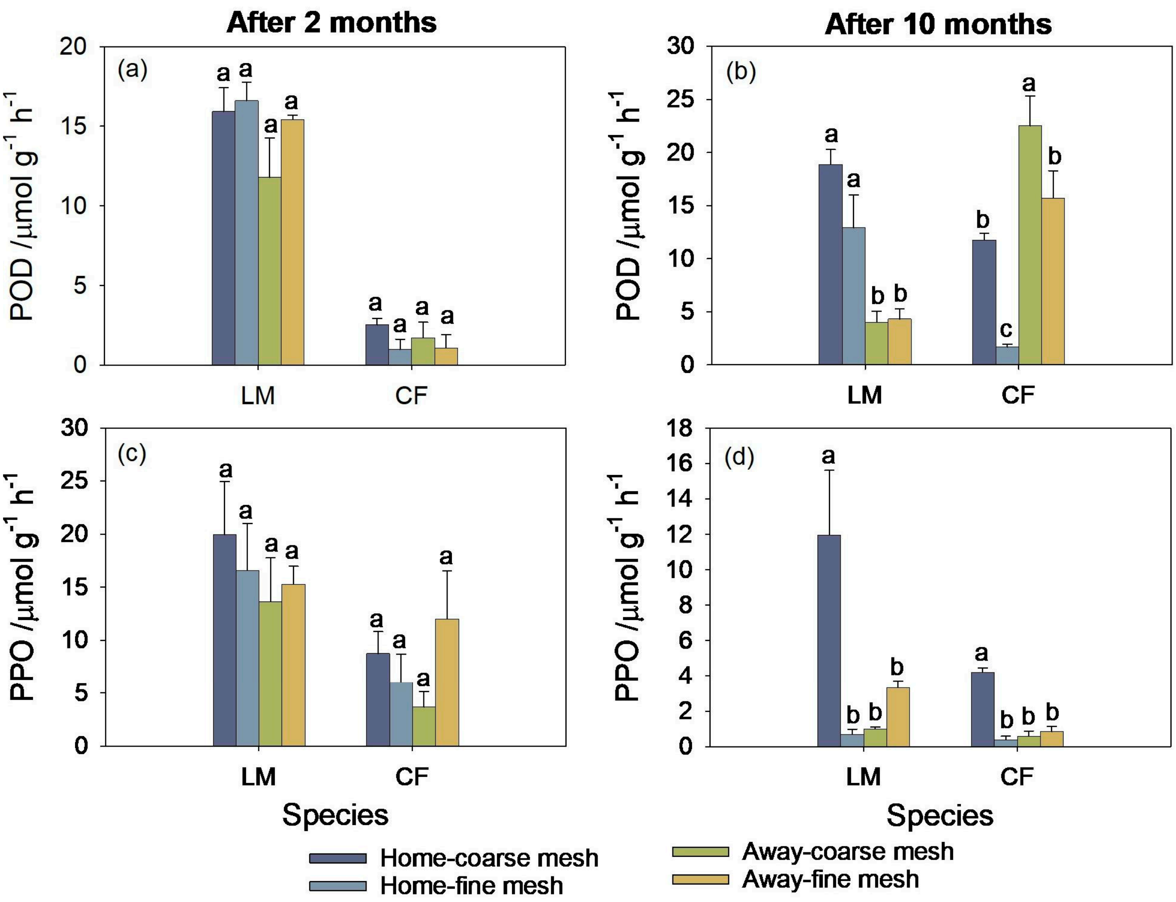

Figure 4. POD (**a**,**b**) and PPO (**c**,**d**) (μmol g^{-1} h^{-1}) activities of the foliar litter of *Lindera megaphylla* (LM) and *Cryptomeria fortunei* (CF) at decomposition sites in *L. megaphylla* and *C. fortunei* forests. Different lowercase letters represent significant differences among treatments within the same species. (One-way ANOVA, $p < 0.05$, $n = 3$).

For *L. megaphylla*, the activities of POD and PPO in the coarse mesh litterbags at the home site were significantly greater than those in the other litterbags and sites after 10 months of decomposition (Figure 4b,d). For *C. fortunei*, after 10 months of decomposition, the activity of POD at the away site was greater than that at the home site (Figure 4b). However, no significant differences were detected in the POD or PPO activities of *L. megaphylla* or *C. fortunei* among the home or away sites or the coarse or fine mesh sizes after 2 months of decomposition (Figure 4a,c).

3.5. Fauna Effect and HFA Indices of Condensed Tannin and Total Phenol Loss

Soil fauna contributed more to the decomposition of condensed tannins in the litter of *L. megaphylla* than in that of *C. fortunei* (Figure 5a,b). After 2 months of decomposition, the effect of the soil fauna on condensed tannin loss in *L. megaphylla* was significantly positively different from zero (12.14%) at the away site Figure 5a). However, after 10 months of decomposition, the soil fauna effect on condensed tannin loss in *L. megaphylla* and *C. fortunei* was significantly positively different from zero (2.63%, 1.97%) at the site home site rather than at the away site (Figure 5a). The effect of soil fauna on the total phenol content was significantly positively different from zero (5.49%) at the away site for *L. megaphylla* after 10 months of decomposition and was positively different from zero (4.72%, 4.63%) at the home site for *C. fortunei* after 2 months and 10 months of decomposition, respectively (Figure 5c,d).

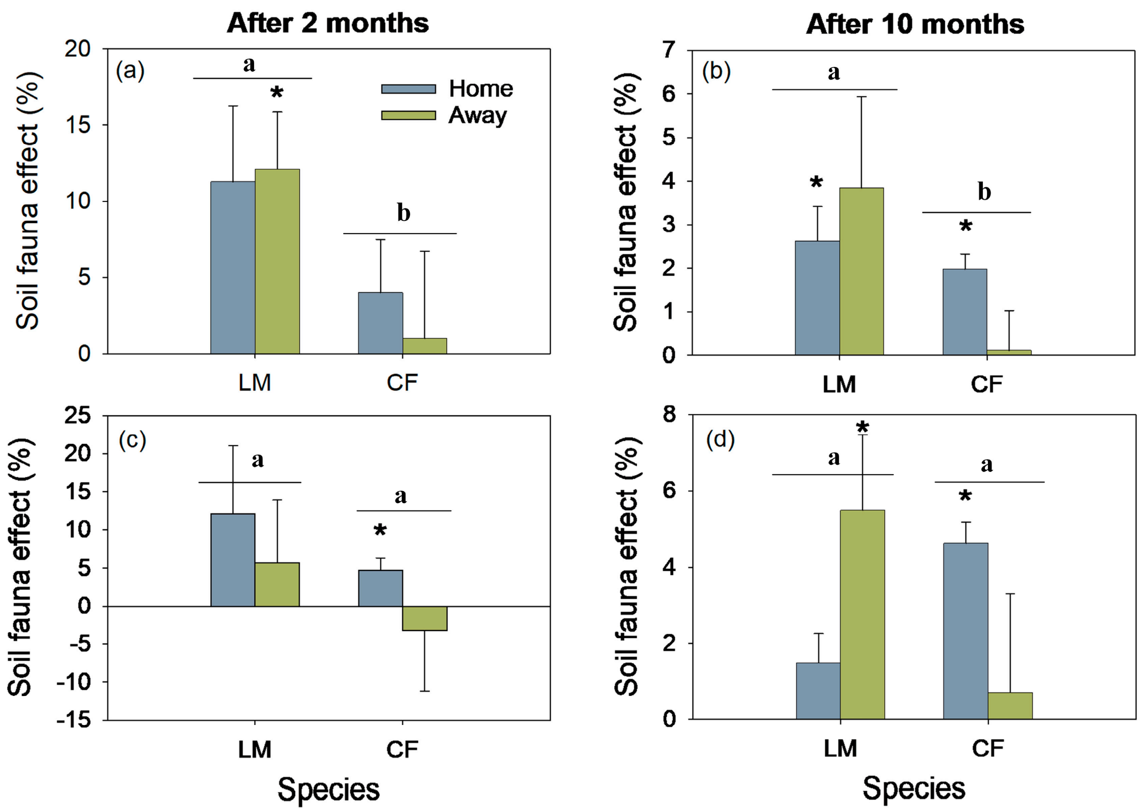

Figure 5. Faunal effect (%) on condensed tannin loss (**a**,**b**) and total phenol loss (**c**,**d**). The asterisk represents a significant difference from the zero value (single-sample *t*-test, $p < 0.05$). Horizontal lines with different lowercase letters represent significant differences between species within the same variable (independent-samples *t*-test, $p < 0.05$). LM: *Lindera megaphylla*; CF: *Cryptomeria fortunei* ($n = 3$).

After 10 months of decomposition, the HFA index (−1.81) of condensed tannins in fine mesh litterbags was significantly negatively different from zero (Figure 6a). Moreover, the HFA index (10.32) of total phenol loss was significantly positively different from zero after 2 months of decomposition (Figure 6b).

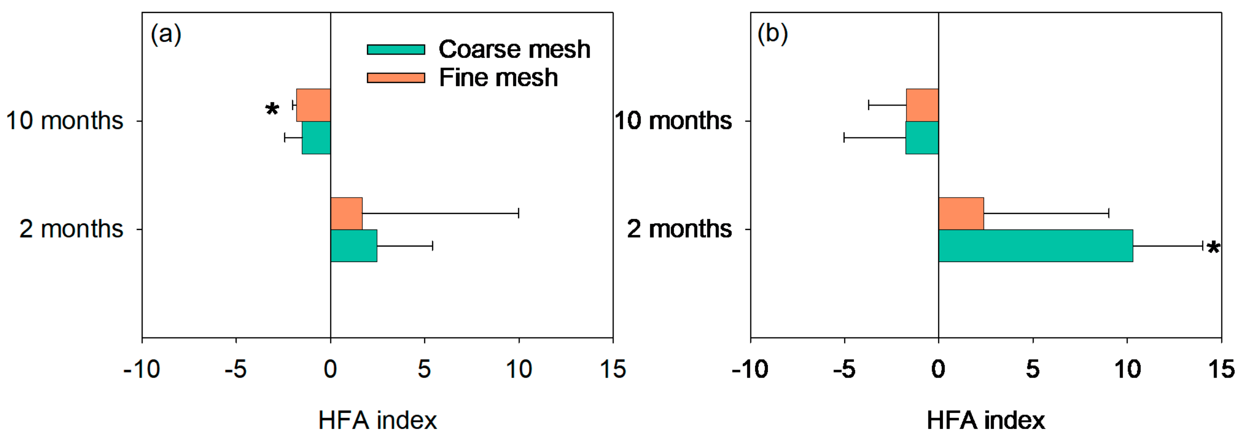

Figure 6. HFA indices for condensed tannin loss (**a**) and total phenol loss (**b**) in litterbags with coarse and fine mesh sizes. The asterisk represents a significant difference from the zero value (single-sample *t*-test, $p < 0.05$, $n = 3$).

3.6. Correlations

After 2 months of decomposition, the loss rates of condensed tannins and total phenols were significantly negatively related to the initial N content, initial P content, POD activity, and N/P ratio and significantly positively related to the initial C content, total phenol content, condensed tannin content, and C/P and C/N ratios. In addition, the loss rates of condensed tannins were significantly negatively correlated with the PPO activity. However, these correlations were not observed after 10 months of decomposition (Figure 7a,b).

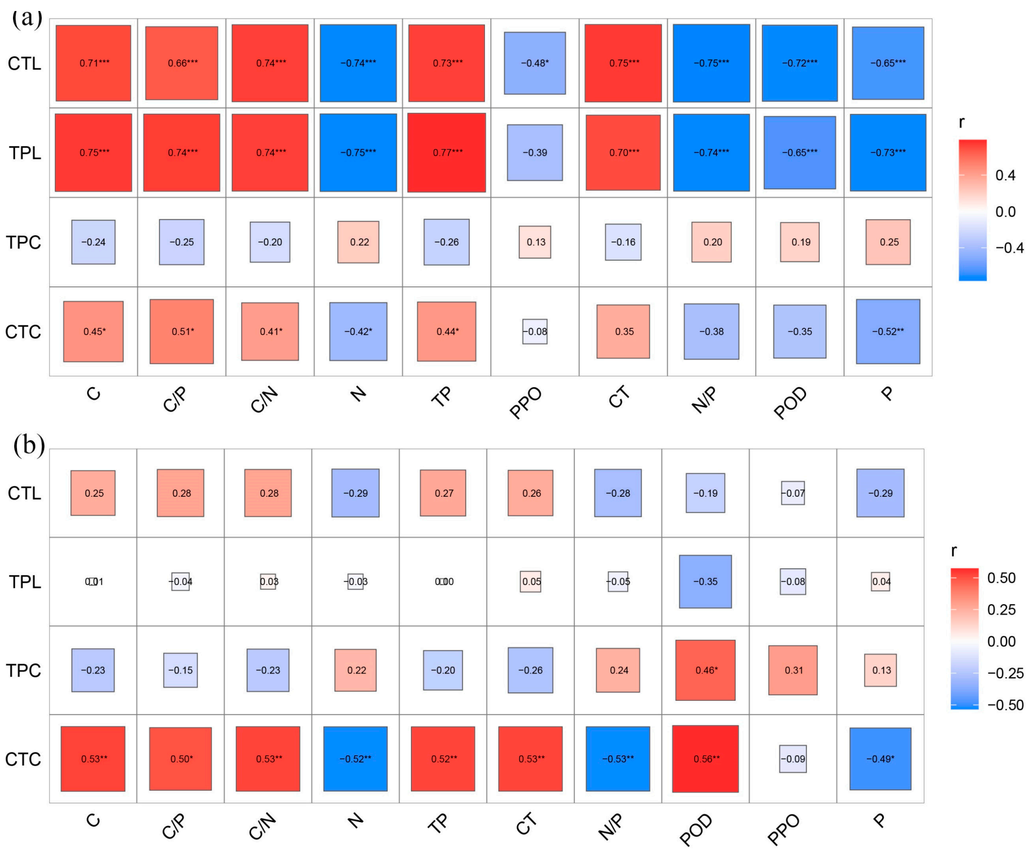

Figure 7. Correlations between initial foliar litter quality and content and loss rate of condensed tannins and total phenols after 2 months of decomposition (**a**) and 10 months of decomposition (**b**). CTL: condensed tannin loss rate; TPL: total phenol loss rate; CTC: condensed tannin content; TPL: total phenol content; LM: *Lindera megaphylla*; CF: *Cryptomeria fortunei*; POD: peroxidase; PPO: polyphenol oxidase (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

After 10 months of decomposition, the condensed tannin content was significantly negatively related to the initial N content, initial P content, and N/P ratio and positively correlated with the initial C content, total phenol content, condensed tannin content, POD activity, and C/P and C/N ratios. Moreover, there was no obvious correlation with PPO activity (Figure 7b).

4. Discussion

4.1. Decomposition Characteristics of Total Phenols and Condensed Tannins in Foliar Litter and Soil Faunal Contributions

In the present study, total phenols and condensed tannins degraded substantially after two months of decomposition, and the loss rates reached 64.07% to 84.49% and 69.67% to 88.37%, respectively. And a slow rate of loss occurred from decomposition of two months to decomposition of ten months (Figure 2, Figures S1 and S2). This is in line with early findings which illustrated that total phenols and condensed tannins can degrade rapidly during litter decomposition [25,56]. This phenomenon might occur because decomposition took place in the rainy area of Western China, and the experimental period was characterized by rain and heat synchrony, creating conditions that were conducive to litter decomposition [57,58]. Specifically, in the rainy area of Western China, abundant rainfall provides better soil moisture conditions for a longer period [59,60] and increases the leaching of total phenols and condensed tannins from fresh litter to soil [61]. In addition, the forest surface litter layer has a strong water-holding capacity [62] and increases the reproduction, growth, and activity of soil fauna, which in turn promotes litter decomposition [63–65].

Litter type significantly influenced the loss of total phenol and condensed tannin contents (Table 3), consistent with the findings of previous studies showing that litter quality is a fundamental driver of decomposition [66,67]. Correlation analysis indicated that the loss rates of total phenols and condensed tannins were significantly positively related to the initial C content, C/N ratio, and C/P ratio and significantly negatively related to the initial N and P contents and N/P ratio; however, these correlations disappeared after 10 months of decomposition (Figure 7). These findings indicated that the initial C, N, and P contents and C/N, C/P, and N/P ratios can be regarded as good predictors of the early stage or middle stage of total phenol and condensed tannin decomposition. In practical applications, by transforming a single coniferous artificial forest into a mixed coniferous and broad-leaved forest, the changes in C, N, P, and the stoichiometric ratio of litter caused by conversion will affect the degradation rates of recalcitrant components (e.g., total phenols and condensed tannins), potentially affecting the entire decomposition process and carbon and nutrient cycling [68,69]. The interactions between soil fauna and litter characteristics substantially influence the degradation process [70,71]. Previous studies have shown that soil fauna contributes more to relatively high-quality (low C/N ratio) litter decomposition rates than to relatively low-quality (high C/N ratio) litter decomposition rates [72,73]. In the present study, according to their C/N ratios, the *C. fortunei* litter was considered low quality, and the *L. megaphylla* litter was considered high quality. This would explain why the soil fauna contributed more to the condensed tannin loss of *L. megaphylla* than to that of *C. fortunei*. In addition, *L. megaphylla* is a common dominant broad-leaved tree species; broad and soft litter can be easily crushed by soil fauna, thus strengthening leaching [28]. In addition, the effect of the soil fauna on the decomposition of total phenols did not vary with litter species; however, the opposite result was found for condensed tannins. This might be because condensed tannins require additional biological degradation [27].

In addition, after 2 months of decomposition, the loss rates of total phenols and condensed tannins were negatively correlated with POD and PPO activity. And no correlation was found between the total phenol content, condensed tannin content, and POD and PPO activity (Figure 7). This is possibly because they are not the only substrates for the POD and PPO enzymes; other substances such as lignin can also serve as substrates [74]. Moreover, due to the uniqueness of the research area, in addition to enzymatic degradation, the degradation of total phenols and condensed tannins in this study may have been more affected by leaching and soil fauna. The loss rates of total phenols and condensed tannins were significantly negatively related to the initial N and P contents. N and P are essential elements for the growth and reproduction of microorganisms [75,76]; thus, lower N and P contents affect microbial growth, which in turn affects enzyme production.

During 10 months of decomposition, the condensed tannin content was significantly positively correlated with the POD activity (Figure 7), and the POD enzyme level increased to some extent (Figure 4). Several studies suggest that the combination of tannins with proteins may lead to a decrease in N utilization efficiency [77,78]. There was a significant positive correlation between the total phenol content, condensed tannin content, and POD activity, possibly because when the total phenol content and condensed tannin content are high and N utilization is low, microorganisms alleviate N restriction by increasing POD enzymes [79]. After 10 months of decomposition, there was no correlation between POD and PPO, so PPO did not show a similar correlation to POD and increased enzyme activity (Figure S3).

4.2. Home-Field Advantage and Soil Faunal Contributions of Total Phenol and Condensed Tannin Decomposition

In this study, there was a significant positive HFA for total phenol decomposition in the presence of soil fauna (HFA index: 10.32), after two months of decomposition (Figure 6). This suggested that soil faunal specialization had a positive effect on the HFA for total phenol decomposition. Consistent with previous research, the specialization of soil fauna played a key role in the HFA [38,42,70]. Additionally, as the temperature increases (from May to July), the environmental conditions may become more suitable for the soil fauna, which may cause an increase in the relative importance of the soil fauna [46,80]. This also indicated that specialization dynamics are correlated with environmental context [47,50].

Moreover, after 10 months of decomposition (Figure 6), the condensed tannins had a significantly negative correlation with the HFA without the involvement of soil fauna (HFA index: −1.81). One explanation for this phenomenon may be that soil fauna have a more positive effect on litter with a lower C/N ratio [81]; thus, they can feed and excrete nutrients and indirectly or directly influence soil microbes, after which 'away' microbial communities adapt to decompose condensed tannins. Some studies have indicated that decomposer communities may alter the chemical composition of litter during decomposition [82–84]. Hence, due to changes in litter quality, the microbial communities may accelerate the degradation of condensed tannins at away sites after 10 months. Additionally, the functional breadth hypothesis states that the functional breadth of decomposers may be affected by litter quality [85]. Decomposer communities have a wider functional ability from recalcitrant litter, meaning that they decompose litter types that vary widely in their litter traits [86]. Thus, compared to *L. megaphylla*, *C. fortunei*, a recalcitrant coniferous tree species, may have a high functional breadth that reduces the specialization of microbial communities in the 'home' litter [87,88], indirectly causing a negative HFA. Overall, the soil fauna had inconsistent effects on the HFA of total phenol and condensed tannin decomposition, possibly due to the combined effects of environmental factors, litter quality, and rapid decomposition rates.

5. Conclusions

This study describes the effects of soil fauna on the HFA of condensed tannin and total phenol decomposition in litter. A positive effect of the soil fauna was observed on the decomposition of condensed tannins in high-quality litter. After 2 months of decomposition, total phenols and condensed tannins rapidly degraded. The initial C, N, and P contents and C/N, C/P, and N/P ratios can be regarded as good predictors of the early stage or middle stage of total phenol and condensed tannin decomposition. After 2 months of decomposition, in the presence of soil fauna, a significantly positive HFA was found for total phenol decomposition, while a significantly negative HFA was observed for condensed tannin decomposition without soil fauna after 10 months of decomposition. Future research should focus on the effect of soil faunal abundance and class on the HFA for total phenol and condensed tannin decomposition.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f15020389/s1, Table S1: The effect of influence factors on the decomposition of phenolic substances in litter, Figure S1: Condensed tannin (a,b) and total phenol (c,d) losses (%) in foliar litter from *Lindera megaphylla* (LM) and *Cryptomeria fortunei* (CF) at decomposition sites in *L. megaphylla* and *C. fortunei* forest after 4 months and 7 months of decomposition, Figure S2: Condensed tannin (a,b) and total phenol (c,d) contents in the foliar litter of *Lindera megaphylla* (LM) and *Cryptomeria fortunei* (CF) at decomposition sites in *L. megaphylla* and *C. fortunei* forests after 4 months and 7 months of decomposition, Figure S3: Correlations between PPO and POD after 2 months (T1) and 10 months (T4) of decomposition.

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Data Availability Statement: The data used are primarily reflected in the article. Other relevant data are available from the corresponding author upon request.

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