Soil fauna show different degradation patterns of lignin and cellulose along an elevational gradient

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Highlights

- ✓ Warmer temperatures accelerated cellulose and lignin degradation independently of litter type
- ✓ Stimulating effects of fauna on cellulose and lignin degradation consistently occurred after 156–277 days of decomposition
- ✓ Soil faunal contributions to cellulose and lignin decomposition were 11.7–34.2 % and 14.2–32.7 %, respectively
- ✓ Temperature and fauna abundance positively affected the faunal effects on cellulose and lignin degradation

Abstract

The degradations of Cellulose and lignin from litter are crucial processes for carbon and nutrient cycling in forest ecosystems. However, the effects of soil fauna on these degradation processes are unclear despite their functional roles in litter fragmentation and microorganism regulation. Here we conducted a four-year field experiment using litterbags with two mesh sizes (3 and 0.04 mm) to assess the effects of soil fauna on cellulose and lignin degradation at four different elevations in southwestern China. Our results showed that the remaining masses of cellulose and lignin increased with elevation in the both meshed litterbags. Soil fauna decreased the remaining cellulose and lignin masses after 156–277 days of decomposition. At the end of the experiment, the stimulating effects of the soil fauna on the cellulose and lignin degradation were 11.7–34.2 % and 14.2–32.7 %, respectively, while soil fauna effects differed in magnitude on the degradations of lignin (higher) and cellulose (lower). The effects of soil fauna on lignin degradation significantly increased as the elevation decreased, regardless of the litter type; whereas soil fauna-derived cellulose degradation did not show the same pattern. The increases in temperature and/or fauna abundance promoted the effects of soil fauna on cellulose and lignin degradation, and these fauna effects were dependent to litter quality. These findings highlight that soil fauna promote cellulose and lignin degradation in different magnitude and these degradations are largely dependent on climate conditions and litter types.

Key words: elevational gradient; cellulose degradation; lignin degradation; soil fauna effects; litter quality

1. Introduction

Plant litter decomposition is critical for the cycling of soil organic matter in terrestrial ecosystems (Aerts, 1997; Berg, 2000). Climate, litter quality and the decomposer community (arranged according to decrease in importance) are thought to be the primary drivers of litter decomposition rates (Cornwell et al., 2008; Bradford et al., 2016; Yin et al., 2019). Lignin and cellulose are the most abundant components of plant litter and account for more than 50 % of the carbon sequestered in plant materials (Boerjan et al., 2003; Kalbitz et al., 2006; Rahman et al., 2013). Previous studies have suggested that the degradation of lignin and cellulose had important implications for litter decomposition rates (Fioretto et al., 2005; Kalbitz et al., 2006; Klotzbücher et al., 2011). Furthermore, the biodegradation of these recalcitrant components is tightly linked to soil fauna and microorganism interactions in detritus food chains (Pérez et al., 2002; Klotzbücher et al., 2011). The feeding activity, community biomass, population size, body size, species richness and functional composition of soil fauna have been considered to affect the patterns of litter lignin and cellulose decomposition (Bradford et al., 2002; Hättenschwiler and Gasser, 2005; Wall et al., 2008; Frouz, 2018).

Soil fauna can accelerate organic matter mineralization and nutrient cycling directly by digesting and fragmenting litter and indirectly by altering the soil structure, litter surfaces and the composition of microbial community (González and Seastedt, 2001; Bradford et al., 2002; Huhta et al., 2007; Yin et al., 2019). Numerous results have demonstrated that the effects of soil fauna on decomposition rates are dependent on the prevailing climatic conditions, and greater fauna effects generally occur at low elevation and latitude sites due to the higher abundance and diversity of soil fauna in warmer and wetter climatic conditions (García-Palacios et al., 2013; Liao et al., 2016;

Wang et al., 2018). Moreover, variations in litter lignin and cellulose concentrations during the early stage of decomposition can alter the later stage of decomposition and even the pattern of whole decomposition process (Fioretto et al., 2005; Rahman et al., 2013; Yue et al., 2016), and changes in the litter lignin concentration are also a predominant regulator of the decomposer community composition and decomposition rates (Pérez et al., 2002; Wang et al., 2018). Furthermore, the community composition of soil fauna is sensitive to the heterogeneity of litter quality across different climatic conditions (Makkonen et al., 2012; García-Palacios et al., 2013). High-quality litter (i.e., low ratios of C:N, lignin:N and lignin:cellulose) facilitates the consumption and colonization of soil invertebrate communities during litter decomposition (Makkonen et al., 2012; He et al., 2015, 2016; Wang et al., 2018). However, little information is available on how soil fauna control the processes of lignin and cellulose degradation during litter decomposition within and among ecosystems.

In general, it is thought that cellulose provides the dominant source of C in the early stages of decomposition (Fioretto et al., 2005; Berg and McClaugherty, 2014; He et al., 2015), and the decomposition of cellulose is relatively fast because its relatively simple structure (a long chain of glucose molecules) can be decomposed more easily by soil fauna and various microorganisms (Brown et al., 1967; Pérez et al., 2002; Wu, 2018). In contrast, lignin is thought to affect the mass loss in the late stages of decomposition (Fioretto et al., 2005; He et al., 2016), and lignin is more difficult for soil organisms to decompose since it has a stable and complex structure (a three-dimensional macromolecule). Only specialized fauna (termites) and microorganisms (mainly Basidiomycetes) are able to synthesize extracellular enzymes that are capable of metabolizing the recalcitrant lignin molecules into biologically accessible forms (Rahman et al., 2013; Yue et al., 2016; Frouz, 2018). Furthermore, cellulose is known to be protected by lignin in plant cell walls, which prevents the cellulose from enzymatic hydrolysis (Berg and McClaugherty, 2014; Keiser and Bradford, 2017). Thus, the differences in molecular structure between cellulose and lignin exert an important effect on the decomposition patterns (Fioretto et al., 2005). In addition, litter species have been regarded as a predominant factor affecting litter decomposition, and the rates of lignin and cellulose degradation can change significantly among different litter species (Cornwell et al., 2008; García-Palacios et al., 2013; Bradford et al., 2016). Therefore, the effects of soil fauna on lignin and cellulose degradation might differ significantly at different decomposition stages and in different forest ecosystems (Keiser and Bradford, 2017; Wang et al., 2018). Nevertheless, few studies have addressed the effects of soil fauna on lignin and cellulose degradation during litter decomposition along an elevational gradient.

The regions between the eastern Tibetan Plateau and Sichuan Basin have an obvious elevational gradient from 400 m to 4500 m a.s.l. (Liu et al., 2019; Tan et al., 2019), which leads to significant variations in climate, plant vegetation and the decomposer community (Tan et al., 2013a, 2013b; Tan et al., 2019). Therefore, a four-year field experiment was conducted using litterbags with two mesh sizes (3 and 0.04 mm) to assess the fauna effects on litter decomposition at 4 different elevations. The total difference in elevation between our forest study sites was 3100 m a.s.l.. We aimed to quantify the activities of the soil fauna on cellulose and lignin degradation in different subtropical forests. Specifically, we hypothesized that: (1) the fauna effects on cellulose and lignin degradation would decrease from the lower to higher elevations since the lower temperatures found at higher elevations would constrain the abundance of the soil fauna and their activity and (2) higher fauna effects on cellulose and lignin degradation would occur in litter species with low-quality (e.g., high lignin content and lignin/N) because the degradation of the recalcitrant component in these litter species is more associated with the fauna-microbe interaction.

2. Materials and methods

2.1. Study sites

The decomposition experiment was carried out at four forest sites along the Minjiang River Basin, Southwest China, covering an obvious elevational gradient with different the climatic conditions, canopy vegetation and soil types (Fig. S1). All the sites have similar slopes and aspects, but different canopy tree species (Table S1). Specifically, the dominant tree species in the canopy are pine (*Pinus massoniana*) and camphor (*Cinnamonum camphora*) at 453 m a.s.l., cedar (*Cryptomeria fortunei*) and oak (*Quercus acutissima*) at 945 m a.s.l., fir (*Abies faxoniana*) and birch (*Betula albosinensis*) at 3023 m a.s.l. and cypress (*Sabina saltuaria*) and dwarf willow (*Salix paraplesia*) at 3582 m a.s.l..

2.2. Experimental design and litterbag incubation

Freshly fallen leaf litter from the canopy was collected with 1 × 1 m litter traps at each site between September and October 2011. The leaf litter contained a coniferous species and a broadleaf species at each site. Specifically, coniferous leaf litter was collected from pine, cedar, fir and cypress at 453 m, 945 m, 3023 m and 3582 m a.s.l., respectively, and broadleaf species camphor was collected from oak, birch and willow at 453 m, 945 m, 3023 m and 3582 m a.s.l., respectively.

The collected samples were air-dried for 2 weeks at room temperature (25 ℃) and 10 ± 0.05 g was placed in 20 × 20 cm nylon litterbags. The weight of the samples in each litterbag was marked with a tag. Litterbags with two mesh sizes were used to exclude and permit the access of soil fauna into the litterbags to quantify the fauna effects on lignin and cellulose degradation during litter decomposition (Liao et al., 2016; Tan et al., 2019). Specifically, the bottom of each bag had a mesh size of 0.04 mm, but the tops of the bags were separated into two types: 0.04 mm to exclude the entry of soil fauna (fauna exclusion treatment) and 3.00 mm (the control) to permit the entry of macro, meso- and microfauna (Liao et al., 2016; Tan et al., 2019).

A total of 240 litterbags (11 sampling times × 5 plots × 2 mesh sizes × 2 litterbags + 20 spare litterbags) of each litter type were carefully transferred to the corresponding sites in late November 2011. Each site had five 5 × 5 m plots ≥ 10 m apart. Within each plot, 96 litterbags (2 species × 2 mesh sizes × 2 litterbags × 11 sampling times + 8 spare litterbags) were placed on the forest floor. The litterbags with the same tree species and mesh size were strung together at distances of 2–4 cm. After litterbag placement, 5 bags of each foliar litter were randomly collected and returned to the laboratory to determine the mass losses, the initial water contents of the air-dried litter samples (8–10 %) and the initial chemical properties of foliar litter (Table S2) during sample establishment. The litterbag temperatures (n=3) were recorded every 2 h using an iButton DS1923-F5 instrument (Maxim-Dallas Semiconductor, Sunnyvale, CA, USA). Monthly precipitation data were obtained from the local weather bureaus. Snow thickness (n=9) at 3023 and 3582 m a.s.l. was manually measured 3 or 4 times with a steel ruler during winter (Yang et al., 2019).

2.3. Litterbag sampling and chemical analysis

The litterbags were harvested after 35, 156, 277, 398, 516, 628, 746, 896, 1079, 1261 and 1444 days of field incubation between December 2011 and October 2015. At each sampling event, eight litterbags (2 species × 2 mesh sizes × 2 replicates) were harvested from each plot. The sampled litterbags were stored in sealed soil fauna bags and transported to the laboratory within 12 h. Within each plot, the Tullgren funnel method was used to extract soil fauna from one control litterbag over a period of 48 h (Liao et al., 2016; Tan et al., 2019). The extracted soil fauna were counted and identified using a microscope (Leica MZ 125, Leica Microsystems GmbH, Wetzlar, Germany) to family level according to the keys of Yin et al (1998) and Moreira et al (2008).

Moreover, roots, mosses, soils and debris were removed from the remaining litterbags, and the foliar litter was oven-dried to constant weight at 65 ℃ for 48 h to measure the litter mass loss (Fig. S2). The oven-dried litter was milled and used to determine the concentrations of cellulose and lignin (lignin-like substrates) as previously described with some modifications (He et al., 2015, 2016). The litter is washed with different reagents and acid detergents, leaving the cellulose and lignin, or AUR (acid unhydrolyzable residue), and the remaining weight was used to determine the cellulose and lignin concentrations. Three replicates were taken from each litter sample.

2.4. Data calculation and statistical analysis

We calculated the cellulose and lignin masses remaining (R_m) and the contribution rate of the soil fauna to the cellulose and lignin mass loss (C_{fau}) during each specific period of the four-year study using the following equations:

$$R_{mt}\ (\%) = (M_0C_0 - M_tC_t)/\ M_0C_0 \times 100 \qquad (1)$$

$$C_{fau}\ (\%) = (R_{mft} - R_{umft})\ /\ R_{mft} \times 100 \qquad (2)$$

where M_0 represents the initial dry mass of the litter (g), M_t is the dry mass of the remaining litter after retrieval (g) at time t, C_0 is the initial concentrations of cellulose or lignin, C_t is the concentrations of cellulose or lignin at time t, R_{mft} is the cellulose or lignin mass remaining in the treated (fauna exclusion) litterbags at time t, R_{umft} is the cellulose or lignin mass remaining in the untreated (control) litterbags at time t, and t is the number of days the litterbags were incubated in the field (Seastedt, 1984; Wang et al., 2018).

One-way ANOVA (analysis of variance) and LSD (least significant difference) tests at a significance level of P=0.05 were used to evaluate the differences in the climate factors (i.e., temperature, precipitation and snow) and the initial substrate quality. A repeated-measure general linear model (GLM) was used to test the main effects of the soil fauna, elevation, litter type and sampling time on the concentration and remaining of cellulose or lignin. For the specific sampling times, Student's independent-sample t-test was used to compare the effects of the soil fauna. Levene's test for homogeneity of variance was performed before conducting the ANOVAs, and the data were log-transformed if required. Differences were considered significant at the $P < 0.05$ level for all analyses. Principal component analysis (PCA) was also performed to analyze the relationships between the contribution of soil fauna to cellulose and lignin mass loss and climate, litter quality and the community composition of soil fauna. The ANOVAs were performed using SPSS 20.0 (IBM SPP Statistics Inc., Chicago, IL, USA), and the data were presented as graphs in Origin Pro9.0 (OriginLab, Northampton, MA, USA), and the PCA was ran using R package ‘factoextra’ (http://www.r-project.org/).

3. Results

3.1 Microclimate

Both the temperature (Fig. S3) and precipitation (Fig. S4) showed a continuous decrease from 453 to 3582 m of elevation. Relative to the temperature and precipitation at elevations of 3582 and 3023 m, the litter at elevations of 945 and 453m had higher mean temperature and precipitation over the whole study period. The litter at elevations of 3582 and 3023 m experienced seasonal snow cover in the winter (Fig. S5). Although the litter water content obviously changed as litter decomposition proceeded (Fig. S6), it was not significantly (P=0.165, F=1.815) affected by elevation.

3.2 Cellulose concentration, mass remaining and soil fauna contribution

The fauna and elevation showed significant effects on the cellulose concentration and mass remaining, but the litter type did not affect the cellulose concentration (Table 1). Regardless of the litter type, the cellulose concentration in the four sites decreased during the first 516–628 days of decomposition (Fig. S7), resulting in a rapid decrease in the cellulose mass remaining (Fig. 1) during this stage. Subsequently, the cellulose concentration and overall mass remaining showed a convergence as decomposition proceeded. The cellulose mass remaining in the controls was significantly (all P<0.05) lower than that in the fauna exclusion treatments across the litter types (Fig. 1). The cellulose mass remaining in the coniferous litter decreased as the elevation decreased in both the control and fauna exclusion treatments (Fig. 1b, d, f and h).

The contributions of soil fauna to the cellulose mass remaining were significantly affected by the elevation and decomposition time (Table 2). The contributions of soil fauna to cellulose mass remaining varied between -8.8 % and 35.8 % among the litter types as decomposition proceeded (Fig. 2). At the end of the experiment, the contributions of soil fauna to the cellulose mass remaining for the coniferous litter were 11.7 %~24.8 % across the four elevations, and those for the broadleaf litter were 11.0 %~34.2 % among the four sites (Fig. 2). The maximum contributions of soil fauna to the cellulose mass remaining for the coniferous litter were higher than those for the broadleaf litter at 3582, 3023 and 945 m, whereas the opposite results were observed at 453 m (Fig. 2).

3.3 Lignin concentration, mass remaining and soil fauna contribution

The fauna and elevation showed significant effects on the remaining lignin mass, but the litter type did not affect the lignin concentration (Table 1). Irrespective of the litter type, the lignin concentration in the four sites showed a single-peak curve during the decomposition, which rose significantly at the beginning of the decomposition period and then decreased after reaching its maximum value between 398 and 628 days of decomposition (Fig. S8). With the exception of camphor, this resulted in a significant increase in lignin mass remaining (Fig. 3g) between 35 and 628 days of decomposition across the litter type. Subsequently, the lignin concentration and overall mass remaining showed a significant decrease in the proceeded decomposition. At the end of the experiment, the lignin mass remaining in the controls was significantly (all P<0.05) lower than that in the fauna exclusion treatments across the litter types (Fig. 3). The lignin mass remaining in the coniferous litter significantly decreased as the elevation decreased in both the control and fauna exclusion treatments (Fig. 3b, d, f and h).

The contributions of soil fauna to the remaining lignin mass were significantly affected by the elevation and decomposition time (Table 2). The contributions of soil fauna to the remaining lignin mass varied between -16.7 % and 41.2 % among the litter types and showed an increasing trend as decomposition proceeded (Fig. 4). At the end of the experiment, the contributions of soil fauna to the remaining lignin mass for the coniferous litter were 14.2 %~32.7 % across the four elevations, and those for the broadleaf litter were 16.9 %~27.1 % among the four sites (Fig. 4). Moreover, the contributions of soil fauna to the remaining lignin mass significantly increased as the elevation decreased, and their contributions for the conifer litter were higher than those for the broadleaf litter at elevations of 3023, 945 and 453 m.

3.4 The correlations between the fauna contribution and the climate, soil fauna community and litter quality

The principal component analysis showed that the contributions of soil fauna to the remaining cellulose and lignin masses were positively correlated with the density of soil fauna and litter temperature but negatively correlated with the lignin and C concentrations and litter moisture (Fig.5). Moreover, the contributions of soil fauna to the remaining cellulose mass were also positively correlated with the cellulose and N concentration. The contributions of soil fauna to the remaining lignin mass had a positive correlation with the ratios of lignin/N and C/N.

4. Discussion

4.1 Decomposition characteristics of cellulose and lignin along an elevational gradient

The litter decomposition rate often decreases as temperature and precipitation decline with the increasing elevation (Wang et al., 2009; Makkonen et al., 2012). Overall, the remaining cellulose and lignin masses increased with increasing elevation, especially for the coniferous litter, this is consistent with the results of studies in subtropical forests and alpine forest-tundra ecotones (Wang et al., 2009; Wang et al., 2018). Furthermore, we also observed that the decomposition patterns of the cellulose were differ from those of the lignin, and the degradation rates of the cellulose were relatively faster than those of the lignin among the litter types, these findings are in agreement with Wang et al. (2018) and Ma et al. (2019). There are two possible mechanisms for these findings (Fioretto et al., 2005; Cornwell et al., 2008; Makkonen et al., 2012). First mechanism is associated with temporal dynamics. The rapid loss of soluble and low-molecular-weight compounds during the early decomposition stage contributes to the observed increase in lignin content (Pérez et al., 2002; Kalbitz et al., 2006; He et al., 2016). Furthermore, compared to cellulose, lignin is more resistant to degradation (Fioretto et al., 2005; Berg and McClaugherty, 2014). Temperature, soil organism activity and nutrient availability can more significantly moderate cellulose decomposition than lignin decomposition during the early stage of decomposition (Pérez et al., 2002; He et al., 2015; Wu, 2018). Second mechanism is associated with litter chemistries. McClaugherty and Berg (1987) suggested that the decrease in absolute lignin concentration during the early decomposition period occurs only in litter with a high initial lignin content (>30 %). The relative lignin concentration for litter species with a low initial lignin concentration often increases before an absolute decrease (Fioretto et al., 2005; He et al. 2016), which is caused by an increase in lignin-like compounds (microbial by-products) produced by soil microorganisms during decomposition (Brandt et al., 2010; He et al. 2016; Wu et al., 2018). These lignin-like compounds might obscure lignin degradation (Fioretto et al., 2005;

Wang et al., 2018).

4.2 Fauna effects on cellulose and lignin decomposition along altitudinal gradients

Generally, the contributions of soil fauna to litter decomposition decrease with increasing elevation and latitude (González and Seastedt, 2001; Wall et al., 2008; García-Palacios et al., 2013); this was also found in our study and in agreement with the findings of previous (Wang et al., 2009; Wang et al., 2018). Moreover, soil fauna consistently accelerated cellulose and lignin degradation across the litter types at the four elevations; this is in line with the results of studies in temperate forests (Ma et al., 2019) and alpine forest-tundra ecotones (Wang et al., 2018). Strikingly, the fauna effects on the overall lignin degradation increased as decomposition proceeded regardless of the litter type, whereas the contributions of soil fauna to cellulose degradation did not show the same trends as those to lignin degradation. Studies have indicated that litter chemistry influences a range of ecological processes, including the colonization of litter by soil fauna during the early phase of decomposition (Seastedt, 1984; Wang et al., 2018; Ma et al., 2019). Cellulose is typically thought to be easily broken down by soil fauna due to its relatively simple structure (Pérez et al., 2002; He et al., 2005; Wu, 2018). Lignin can enhance the mechanical strength of leaves and protect leaves from physical fragmentation, chemical digestion and biological decomposition by soil fauna (Hatfield and Vermerris, 2001). Thus, the differences in molecular structure, decomposability and litter chemistry between lignin and cellulose may cause variations in the effects of the soil fauna on the cellulose and lignin degradation as decomposition proceeded. These results support the statement that there is strong inertia among the different soil decomposer communities to attack the most recalcitrant biochemical fraction (i.e., lignin) only in the late decomposition stage (Fioretto et al., 2005; Perez et al., 2013). Additionally, our results indicated that the effects of soil fauna on lignin decomposition were higher than those on cellulose. A likely explanation is that cellulose is easily decomposed by soil fauna and microorganisms, whereas the decomposition of the recalcitrant lignin molecules is depended on the specialized fauna and microorganisms (Pérez et al., 2002; He et al., 2005; Rahman et al., 2013; Frouz, 2018).

Low litter quality (i.e., high lignin content and lignin/N) is thought to restrain the activities of the soil fauna (Wall et al., 2008; Makkonen et al., 2012; Sauvadet et al., 2017). Studies have suggested that a high lignin concentration can reduce litter decomposition rate, and a low initial lignin concentration can cause a high contribution of soil fauna to lignin degradation (Wall et al., 2008; Wang et al., 2018). This is also demonstrated in our experiment for elevations from 453 to 3023 m. Moreover, the relatively low lignin concentration seems to improve the availability of cellulose for decomposition by soil fauna, consequently leading to a higher contribution of soil fauna to cellulose decomposition for the litter species with low lignin contents at elevations of 945 and 3023 m. Furthermore, the relationship between litter quality and the effects of the soil fauna is further confirmed by the negative correlation between the contribution of the soil fauna to the remaining cellulose and lignin masses and the lignin concentration. In addition, many studies have indicated that the decomposition rate is positively correlated with the abundance of soil fauna (González and Seastedt, 2001; Liu et al., 2019; Ma et al., 2019). The more colonization by soil fauna in the litterbags can exert the greater direct and indirect effects of soil fauna on litter decomposition (Bradford et al., 2002; Hättenschwiler and Gasser, 2005; Frouz, 2018). In agreement with previous results (Bradford et al., 2002; Li et al., 2015; Wang et al., 2015), a significant positive correlation between the abundance soil fauna and contributions of soil fauna to cellulose and lignin decomposition was also observed in our study. However, it should be noted that overall the litter type shows a minor effect on the contributions of soil fauna to the remaining cellulose and lignin masses along the elevational gradient. A possible reason for this finding is that Collembola and Oribatida constitute the dominant taxa across the litter species in our four sites, and the abundance and richness of soil fauna are unaffected by the elevation over the four-year decomposition (unpublished data). This may conceal the variations in the fauna effects on cellulose and lignin decomposition among the litter types.

5. Conclusions

Our main findings suggest that soil fauna profoundly accelerate the degradation of cellulose and lignin during the litter decay process in subtropical forests of southwestern China. However, soil fauna show different contribution patterns in cellulose and lignin degradation, which are mainly due to the differences in climatic conditions (e.g. temperature and moisture), litter quality and composition, and the abundance of fauna themselves. Taken together, the fauna-driven litter decomposition is a series of complex processes, and further studies are needed to reveal those underlying mechanisms between fauna communities and the ecosystem functions they provide in this changing world.

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Table 1 Results of the repeated measures ANOVA for the effects of the fauna, elevation, litter type and decomposition time on the content and remaining mass of cellulose and lignin as well the ratios of cellulose/lignin and lignin/N.

Factors	Cellulose content			Cellulose remaining			Lignin content			Lignin remaining			Cellulose/lignin ratio			Lignin/N ratio		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Fauna	1	5.782	0.019^{*}	1	157.288	$<0.001^{**}$	1	0.298	0.587^{ns}	1	51.859	$<0.001^{**}$	1	2.379	0.128^{ns}	1	106.490	$<0.001^{**}$
Elevation	3	63.649	$<0.001^{**}$	3	51.268	$<0.001^{**}$	3	12.785	$<0.001^{**}$	3	15.077	$<0.001^{**}$	3	154.417	$<0.001^{**}$	3	66.693	$<0.001^{**}$
Litter type	1	2.699	0.105^{ns}	1	24.489	$<0.001^{**}$	1	0.347	0.558^{ns}	1	54.826	$<0.001^{**}$	1	7.116	0.010^{*}	1	78.234	$<0.001^{**}$

ns, $P>0.05$; *, $P<0.05$; ** $P<0.001$

The repeated measures ANOVA was conducted with decomposition time as the within-subject factor and fauna, elevation and litter type as the between-subject factors using the main effect model of a general linear model.

Note: the results of the effects of decomposition time are not shown in the table since all the variables were significantly affected at the level of $P<0.001$.

Table 2 Results of the repeated measures ANOVA for the effects of elevation, litter type and decomposition time on the fauna contribution to the remaining masses of cellulose and lignin in the control litterbags.

Factors	Faunal contribution to remaining cellulose			Faunal contribution to remaining lignin		
	df	*F*	*P*	*df*	*F*	*P*
Elevation	3	11.036	<0.001**	3	169.158	<0.001**
Litter type	1	3.782	0.061ns	1	1.131	0.296ns
Decomposition time	10	148.433	<0.001**	10	68.126	<0.001**

ns, P>0.05; *, P<0.05; ** P<0.001

The repeated measures ANOVA was conducted with decomposition time as the within-subject factors and elevation and litter type as the between subject factors using the main effect model of a general linear model.

Figure captions

Fig. 1. The remaining cellulose mass of the foliar litter (± SE, n = 5) at different elevations and decomposition stages. The * (asterisk) indicate the statistically significant (P<0.05) differences in the remaining cellulose mass between the controls (3 mm) and fauna exclusion treatments (0.04 mm) on each sampling date within each elevation.

Fig. 2. The contribution of soil fauna to the remaining cellulose mass of the foliar litter (n = 5) at different elevations and decomposition stages. The * (asterisk) indicate the statistically significant (P<0.05) differences in the contribution of soil fauna to the remaining cellulose mass between the litter types on each sampling date within each elevation.

Fig. 3. The remaining lignin mass of the foliar litter (± SE, n = 5) at different elevations and decomposition stages. The * (asterisk) indicate the statistically significant (P<0.05) differences in the remaining lignin between the controls (3 mm) and fauna exclusion treatments (0.04 mm) on each sampling date within each elevation.

Fig. 4. The contribution of soil fauna to the remaining lignin mass of the foliar litter (n = 5) at different elevations and decomposition stages. The * (asterisk) indicate the statistically significant (*P*<0.05) differences in the contribution of soil fauna to the remaining lignin mass between the litter types on each sampling date within each elevation.

Fig. 5. The principal component analysis of the correlation between the soil faunal contribution to cellulose and lignin degradation and the environment, soil faunal abundance and litter quality in the control litterbags (n=420).

Temperature, litter temperature; Moisture, litter moisture; C, carbon concentration; N, nitrogen concentration; Cellulose, cellulose concentration; Lignin, lignin concentration; Cellulose contribution, contribution of soil fauna to cellulose degradation; Lignin contribution, contribution of soil fauna to lignin degradation.

511 **Fig. 1** The remaining cellulose mass of the foliar litter (± SE, n = 5) at different

512 elevations and decomposition stages.

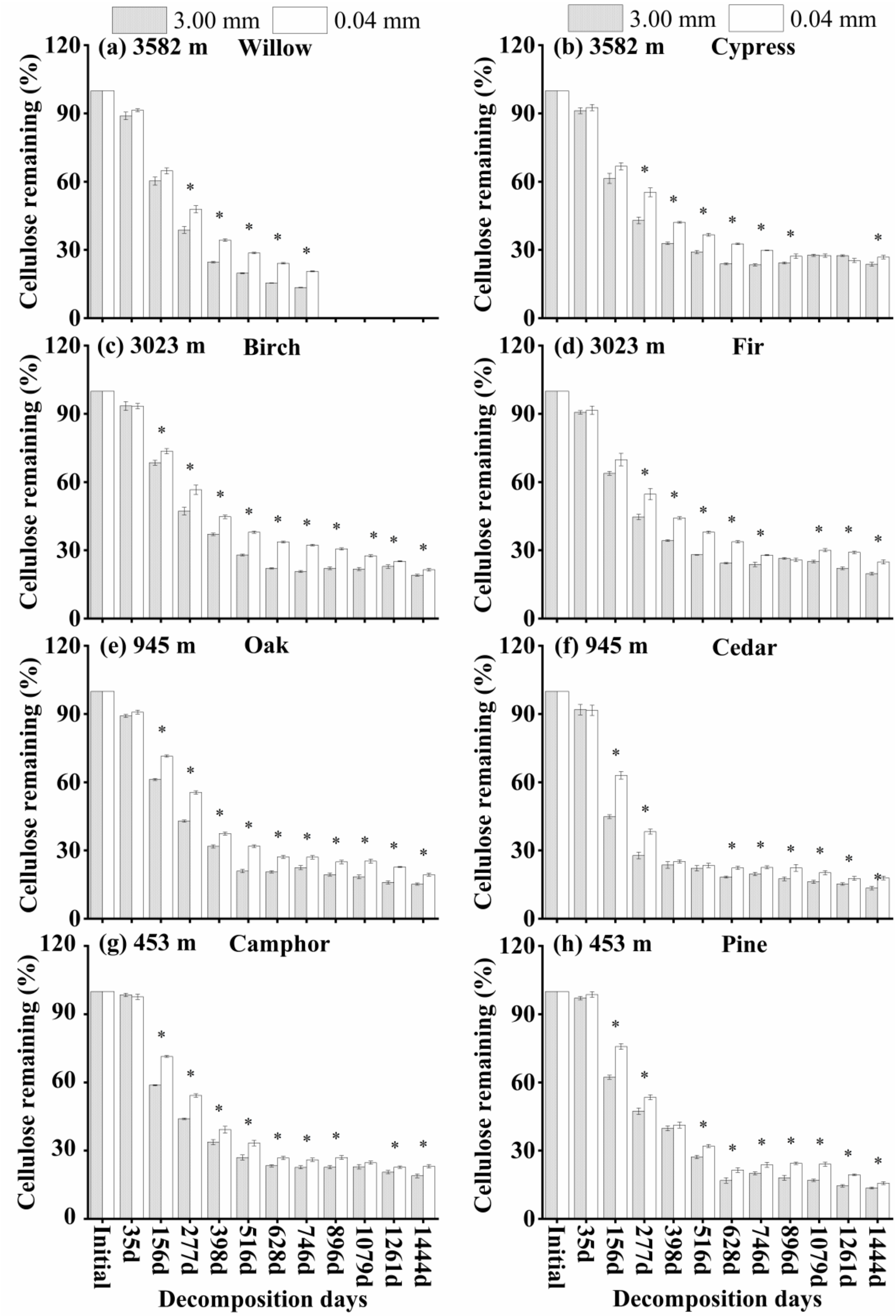
513 

Fig. 2 The contribution of soil fauna to the remaining cellulose mass of the foliar litter (n = 5) at different elevations and decomposition stages.

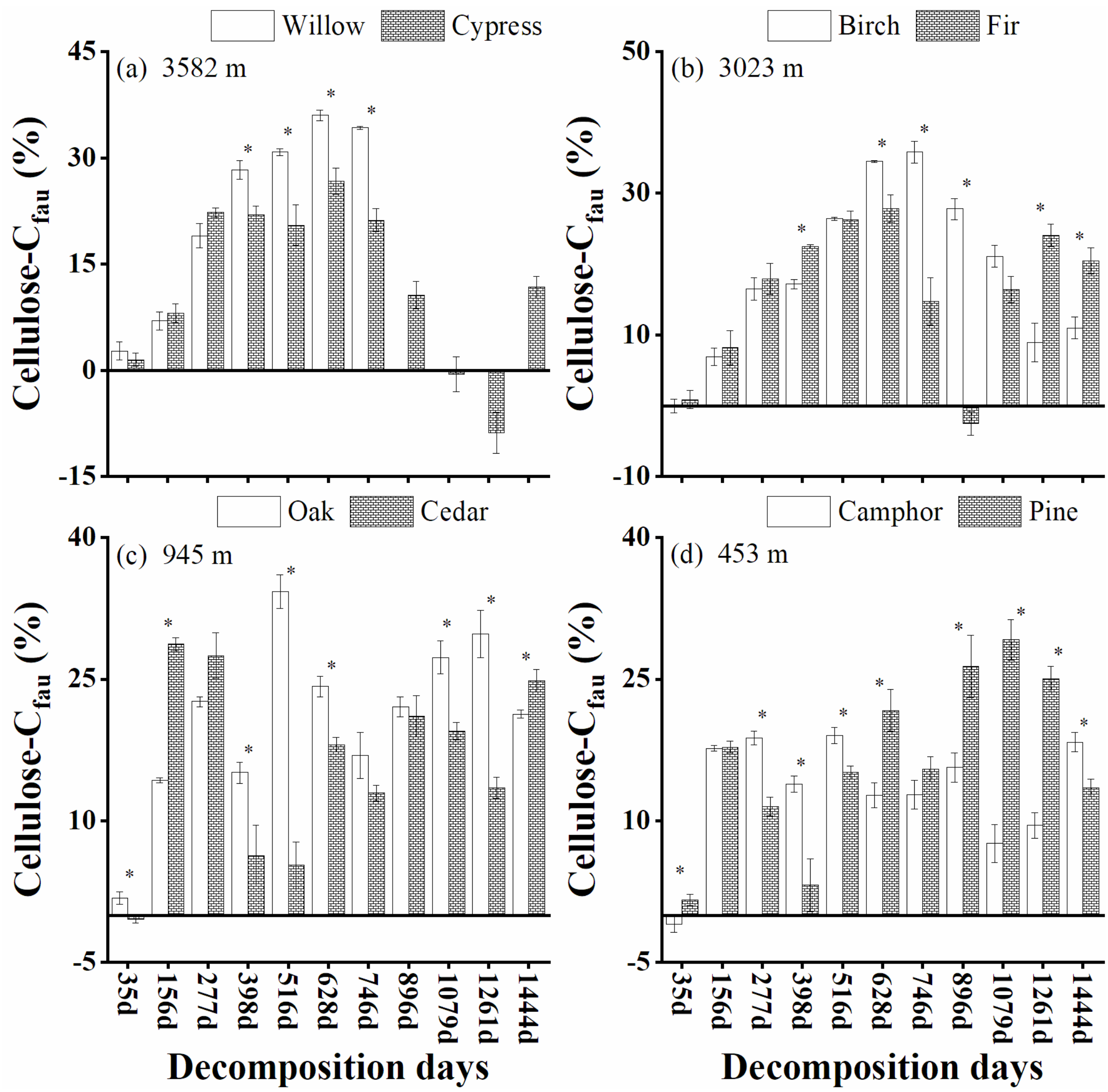


Fig. 3 The remaining lignin mass of the foliar litter (± SE, n = 5) at different elevations and decomposition stages.

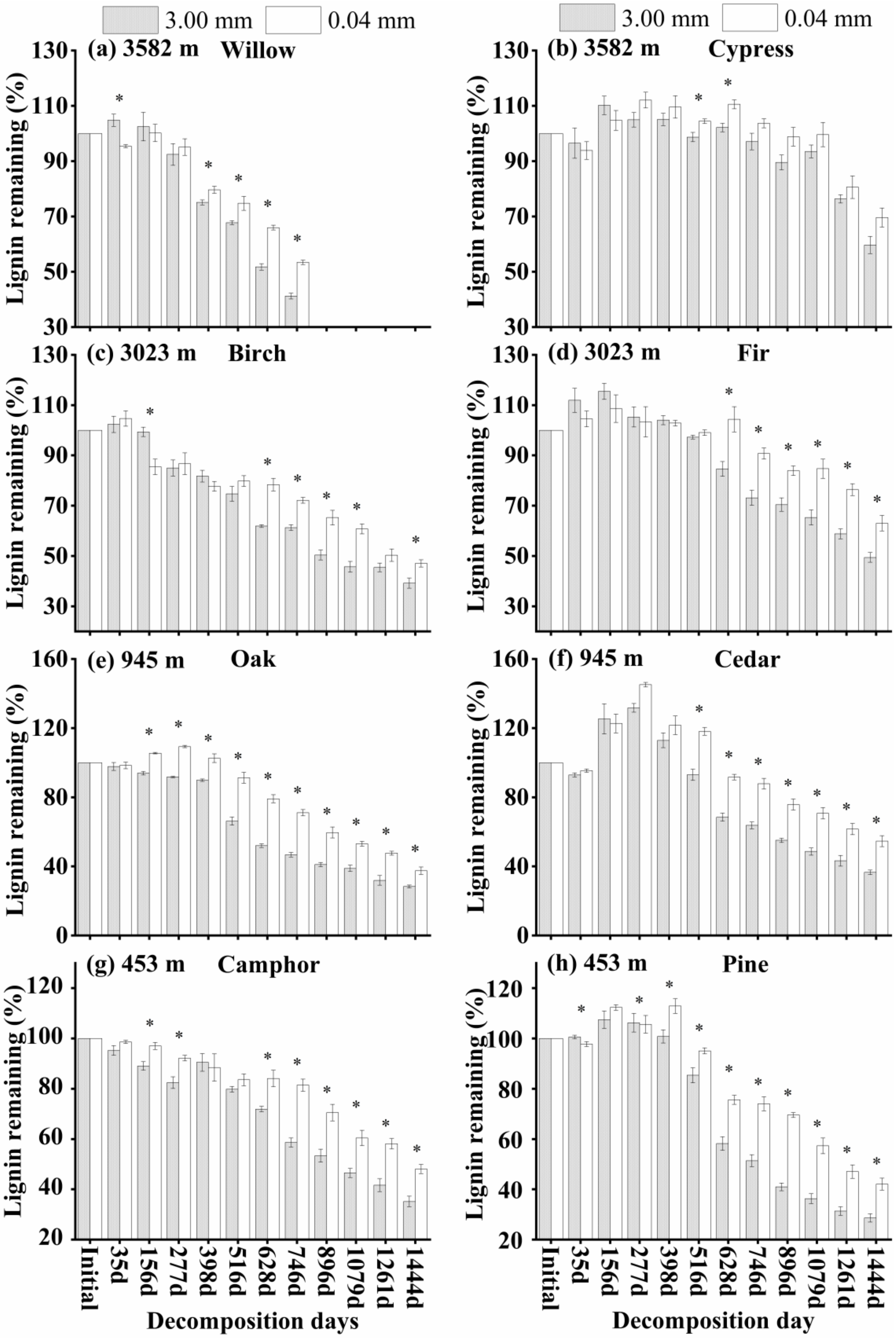


Fig. 4 The contribution of soil fauna to the remaining lignin mass of the foliar litter (n = 5) at different elevations and decomposition stages.

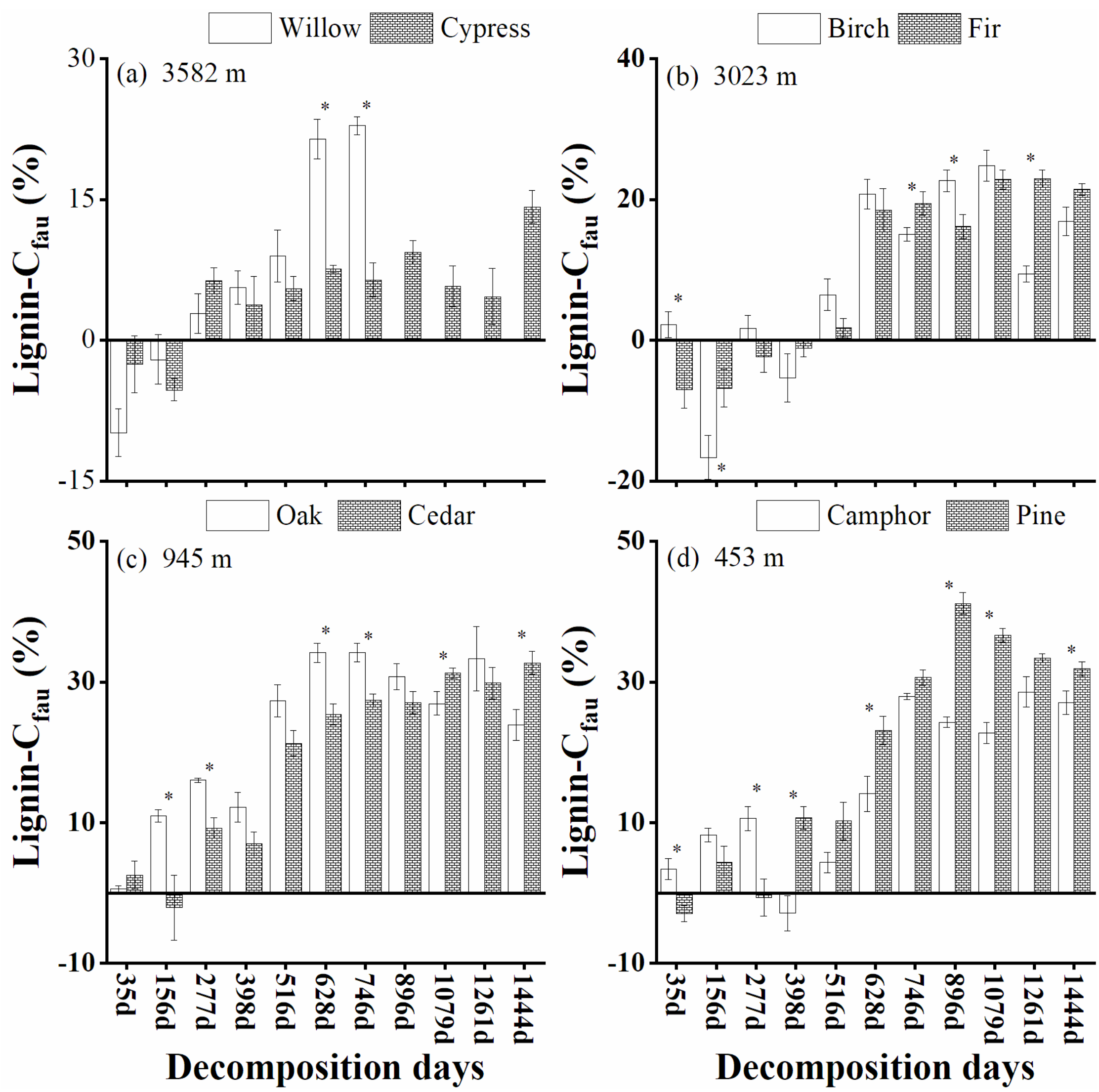
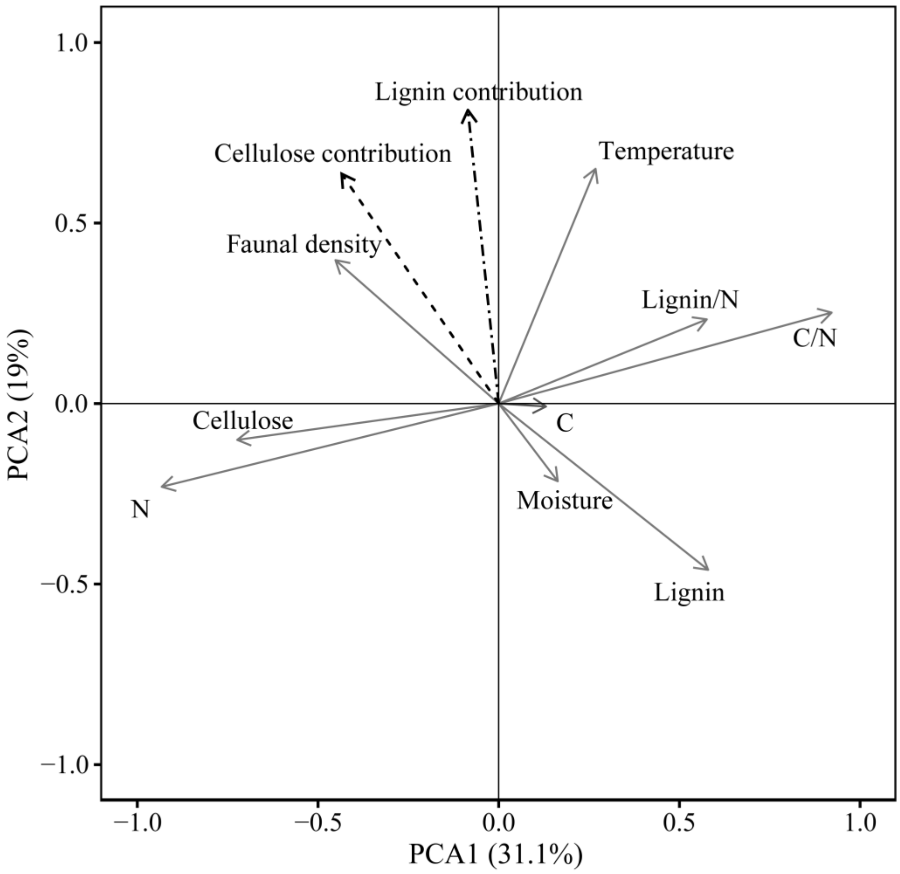


Fig. 5 The principal component analysis of the correlation between the soil faunal contribution to cellulose and lignin degradation and the environment, soil faunal abundance and litter quality in the control litterbags (n=420).



Supplementary Information

Table S1 Characteristics of the four study sites along the altitudinal gradient

Site	453m	945m	3023	3582m
Coordinates	28°34’N, 104°32’E	31°01’N, 103°34’E	31°18’N, 102°56’E	31°14’N, 102°53’E
Slope (°)	14	15	15	16
Annual air temperature (℃)	18.1 ±1.4^{a}	15.2 ±1.6^{b}	3.8 ±1.8^{c}	2.1 ±1.6^{c}
Annual precipitation (mm)	1021 ±42^{b}	1243 ±33^{a}	832 ±16^{c}	856 ±18^{c}
Soil type	Leptic Cambisols	Dystric Luvisols	Cambic Umbrisol	Cambic Umbrisol
Soil pH	4.3 ±0.4^{c}	5.3 ±0.3^{b}	6.5 ±0.3^{a}	6.2 ±0.3^{a}
Soil TOC (g kg^{-1})	16.3 ±1.5^{c}	19.8 ±1.2^{b}	161.9 ±31.1^{a}	161.4 ±20.3^{a}
Soil N (g kg^{-1})	2.0 ±0.3^{b}	1.8 ±0.2^{b}	8.1 ±1.6^{a}	9.5 ±1.9^{a}
Soil Olsen P (mg kg^{-1})	0.7 ±0.1^{c}	0.6 ±0.1^{c}	0.9 ±0.1^{b}	1.2 ±0.2^{a}

Different lowercase letters in the same line indicate statistically significant (P<0.05) differences among the four study sites.

Table S2 The initial contents and ratios of carbon (C), nitrogen (N), lignin (L) and cellulose (CL) in the foliar litter used for this study.

Altitudes	Litter Species	C/g kg^{-1}	N/g kg^{-1}	L/%	CL/%	C/N	L/N	L/CL
3582 m	Cypress	517.69^{d} (20.31)	10.20^{a} (0.71)	20.75^{c} (1.32)	12.17^{ab} (0.66)	50.86^{f} (2.22)	2.04^{b} (0.08)	1.70^{d} (0.03)
	Willow	379.81^{a} (23.28)	12.35^{d} (0.87)	25.43^{f} (1.70)	13.52$_{b}$ (0.68)	30.81^{a} (1.34)	2.06^{b} (0.07)	1.88^{f} (0.05)
3023 m	Fir	505.85^{cd} (30.64)	11.43^{c} (1.11)	22.58^{b} (1.15)	12.59^{a} (0.65)	44.39^{d} (2.18)	1.98^{b} (0.11)	1.79^{e} (0.02)
	Birch	484.27^{bc} (17.00)	10.41^{ab} (0.79)	26.87^{e} (1.11)	12.90^{c} (0.71)	46.64^{e} (2.39)	2.59^{d} (0.11)	2.08^{g} (0.04)
945 m	Cedar	480.73^{bc} (20.34)	10.66^{ab} (0.48)	19.58^{a} (0.60)	19.32^{f} (0.31)	45.10^{d} (0.39)	1.84^{a} (0.04)	1.01^{a} (0.01)
	Oak	490.49^{bc} (24.13)	13.23^{e} (0.70)	24.05^{d} (0.09)	14.90^{d} (0.61)	37.07^{b} (0.66)	1.82^{a} (0.09)	1.62^{c} (0.05)
453 m	Pine	496.99^{c} (14.64)	12.18^{d} (0.37)	24.80^{de} (0.72)	16.78^{e} (0.57)	40.80^{c} (0.46)	2.04^{b} (0.03)	1.48^{b} (0.01)
	Camphor	461.22^{b} (17.70)	11.03^{bc} (0.56)	27.02^{f} (0.55)	16.92^{e} (0.49)	41.86^{c} (1.19)	2.45^{c} (0.10)	1.60^{c} (0.03)

Different lowercase letters within a column indicate statistically significant (P<0.05) differences of the litter qualities among litter species

Fig. S1 The study region and the experimental sites along the Minjiang River Basin, Southwest China.

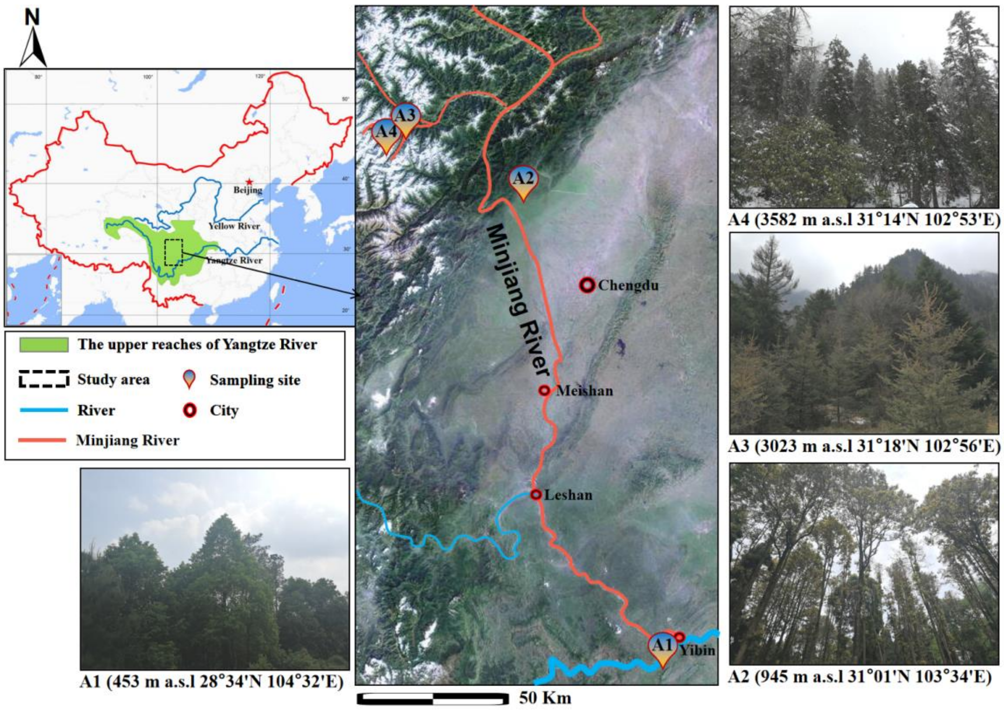


Fig. S2 The mass remaining of the foliar litter (± SE, n = 5) at different elevations and decomposition stages. The * (asterisk) indicate the statistically significant (P<0.05) differences in the remaining litter mass between the controls (3 mm) and fauna exclusion treatments (0.04 mm) on each sampling date.

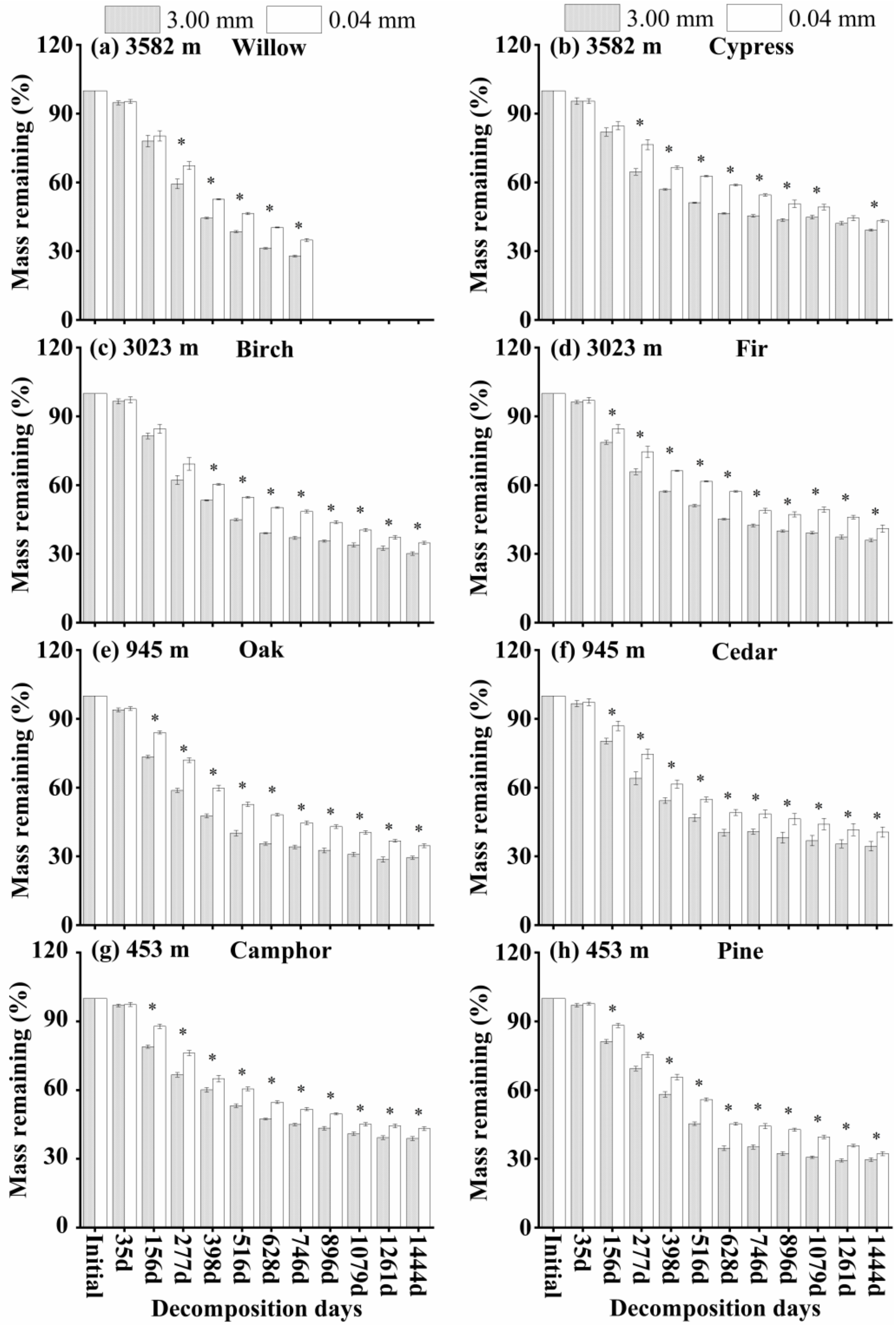


Fig. S3 The mean temperature (± SE, n = 3) of litterbag on the surface of soil at different elevations and decomposing stages. Different lowercase letters indicate statistically significant (P<0.05) differences in the mean temperature among different elevations during each decomposing stages.

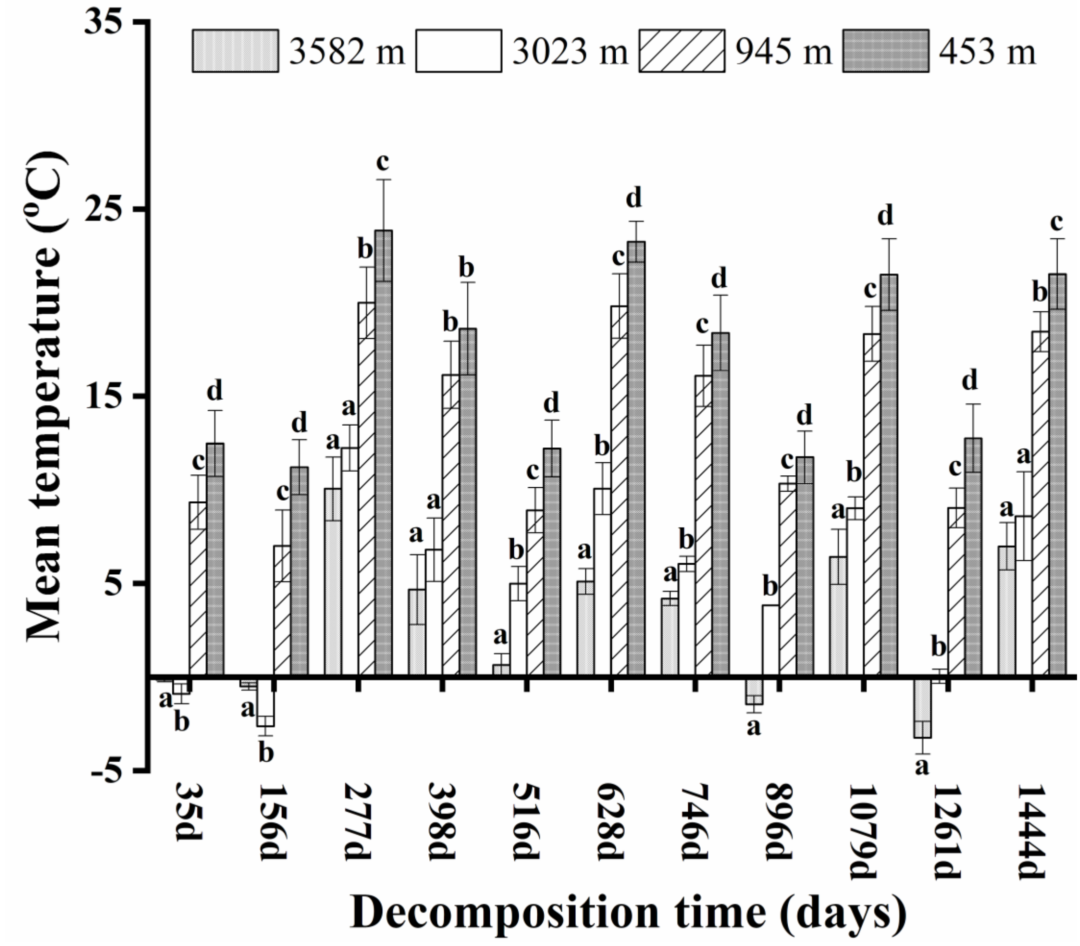


Fig. S4 The dynamics of monthly and annual precipitation in the experimental sites at different elevations during the study period. Different lowercase letters indicate statistically significant (P<0.05) differences of monthly precipitation between elevations.

Note: mean monthly precipitation was calculated according to the precipitation data between 2012 and 2015. The precipitation data of 2013 at elevation of 945 m was not calculated since extreme rainfall event occurring in July and August.

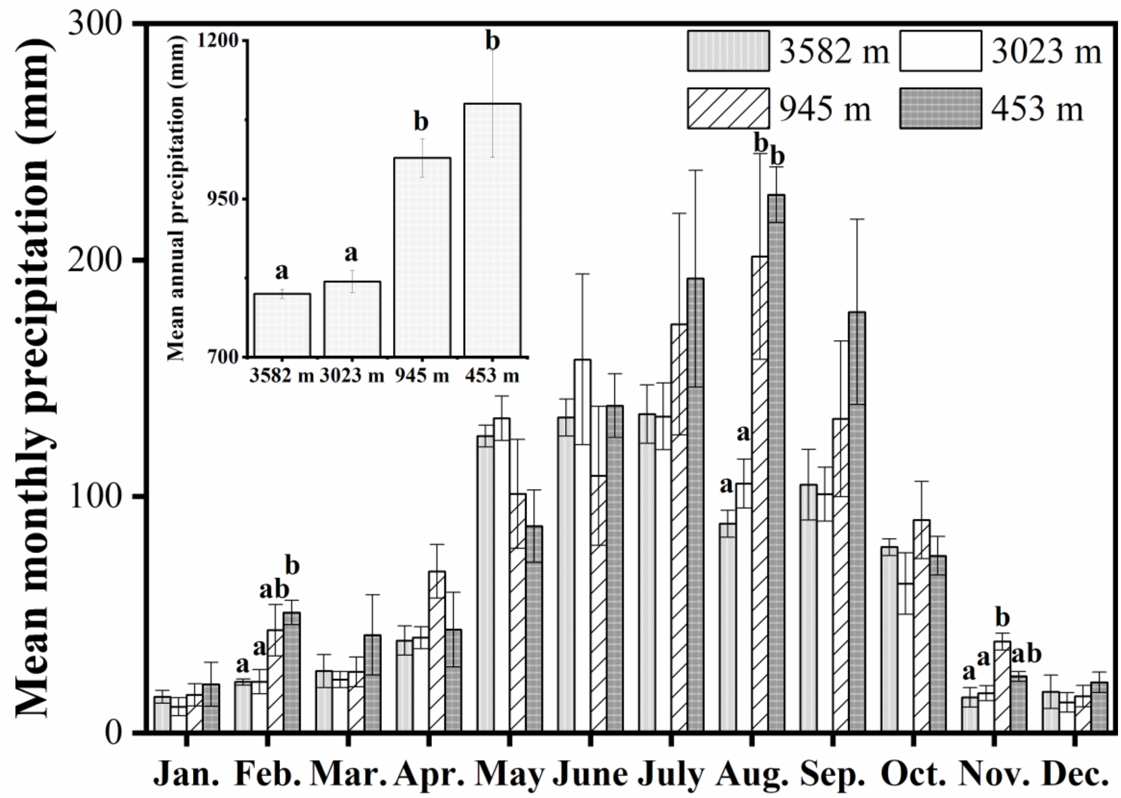


Fig. S5 The dynamics of snow depth (± SE, n = 9) at elevations of 3582 and 3023 m in the winter during the study period. The * (asterisk) indicate the statistically significant (*P*<0.05) differences in the snow depth between the 3582m and 3023m on each measurement date.

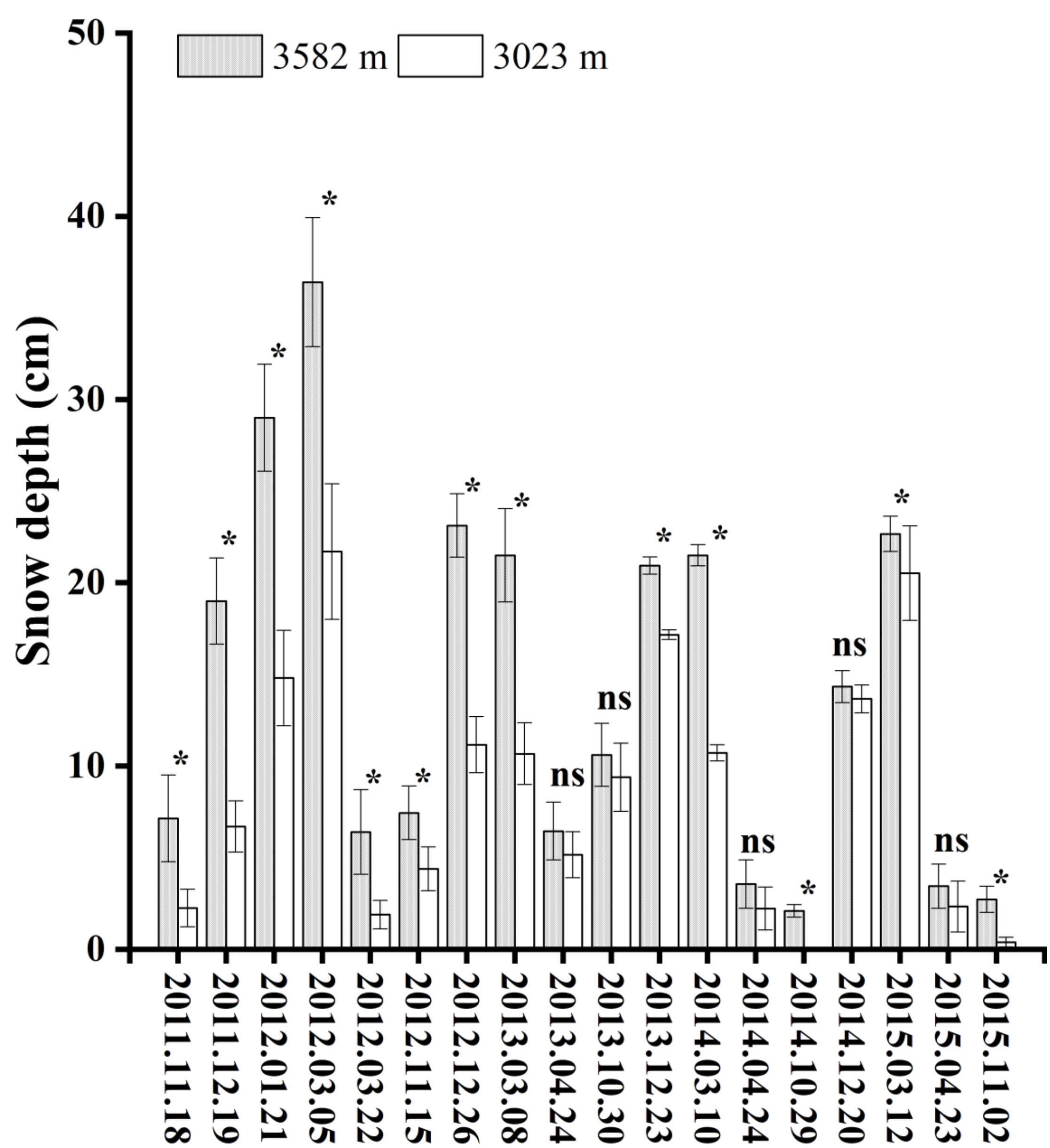


Fig. S6 The water content of the foliar litter (± SE, n = 5) at different elevations and decomposition stages. Water content of foliar litter at the same elevation were graphed together since the water content of each litter between the controls (3 mm) and fauna exclusion treatments (0.04 mm) showed minor difference during litter decomposition. The * (asterisk) indicate the statistically significant (*P*<0.05) differences in the water content between the litter types on each sampling date within each elevation.

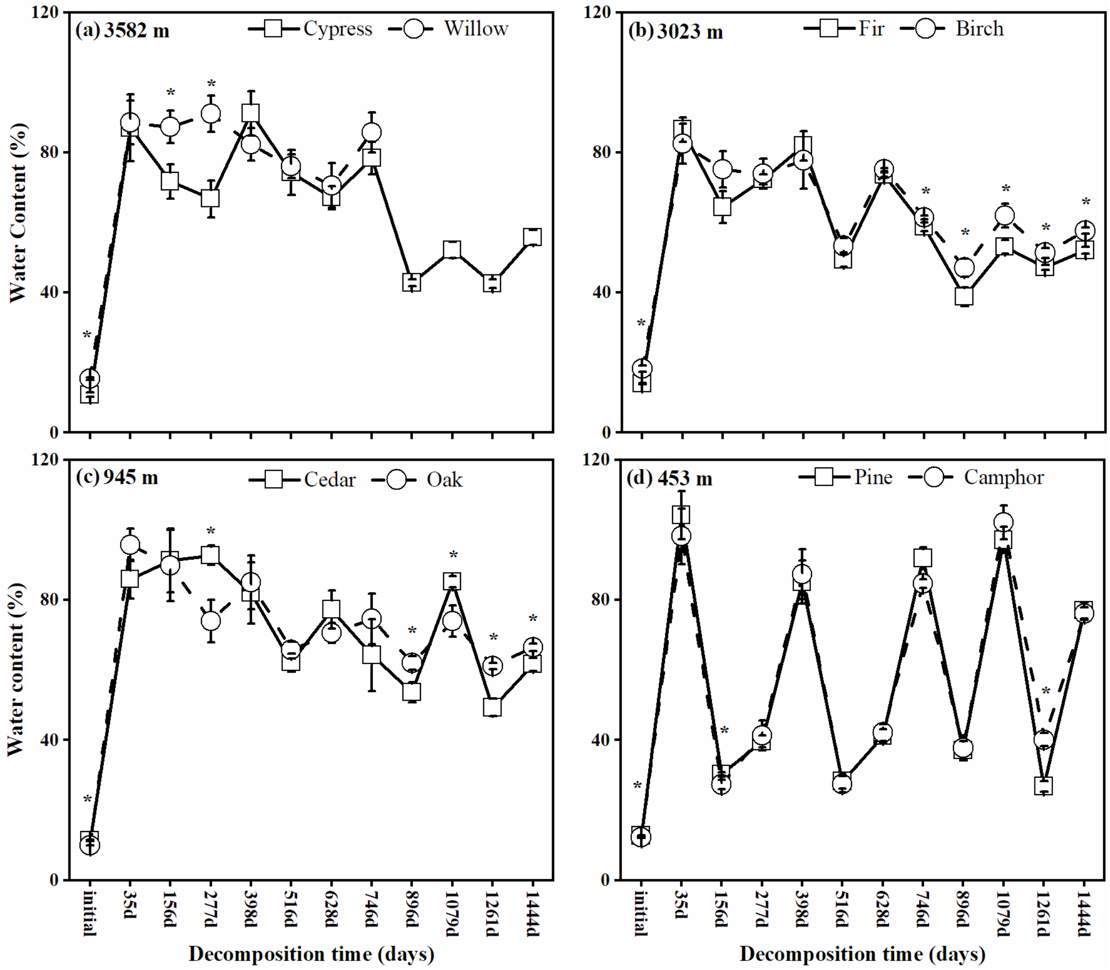


Fig. S7 The cellulose concentration of the foliar litter (± SE, n = 5) at different elevations and decomposition stages. The * (asterisk) indicate the statistically significant (*P*<0.05) differences in the cellulose concentration between the controls (3 mm) and fauna exclusion treatments (0.04 mm) on each sampling date.

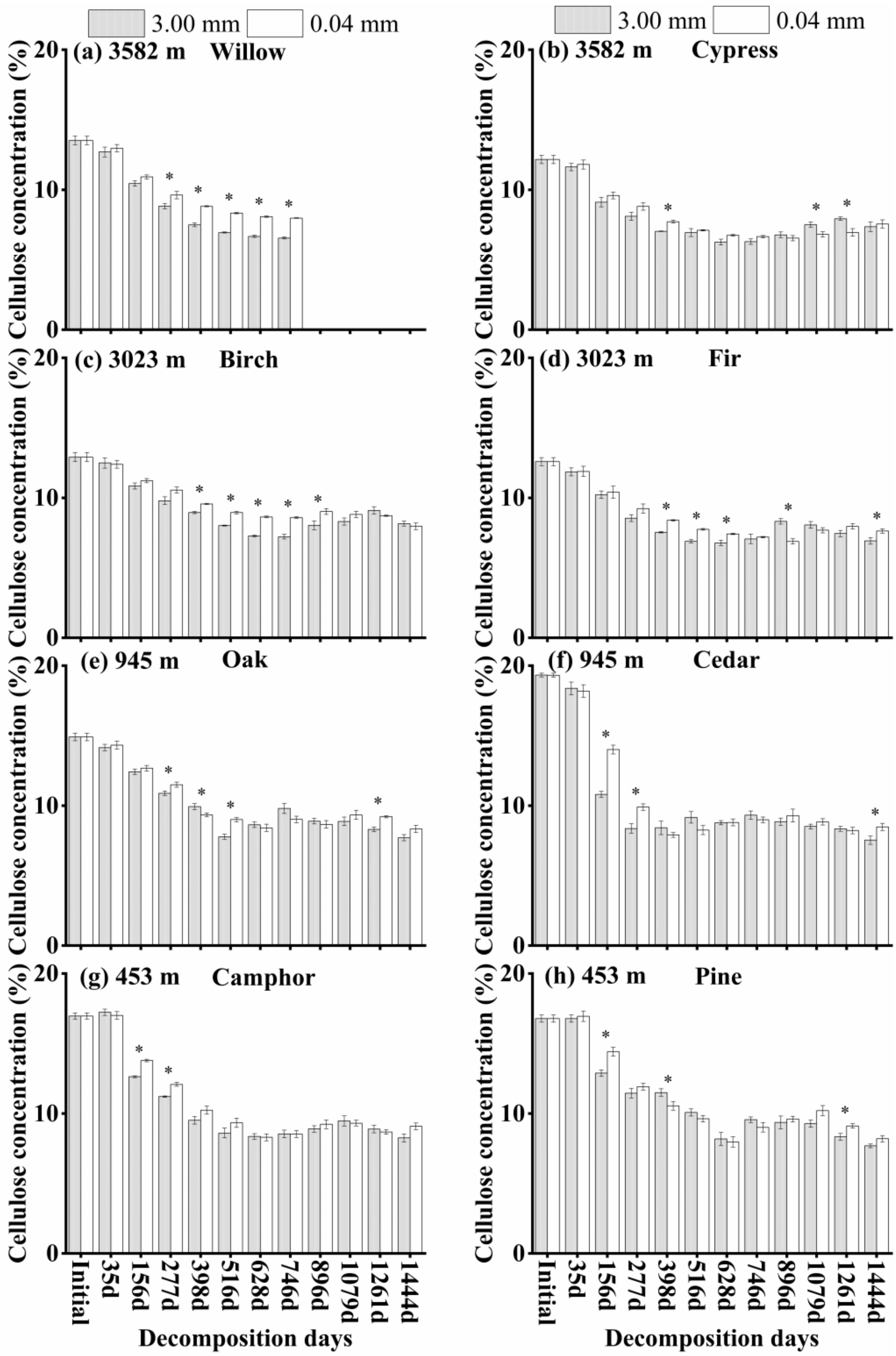


Fig. S8 The lignin concentrations of the foliar litter (± SE, n = 5) at different elevations and decomposition stages. The * (asterisk) indicate the statistically significant (P<0.05) differences in the lignin concentration between the controls (3 mm) and fauna exclusion treatments (0.04 mm) on each sampling date