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Soil fauna accelerated litter C and N release by improving litter quality across an elevational gradient

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Abstract

Background Soil fauna is an important driver of carbon (C) and nitrogen (N) release from decomposing litter in forest ecosystems. However, its role in C and N cycling concerning climate and litter traits remains less known. In a 4-year field experiment, we evaluated the effects of soil fauna on litter C and N release across an elevation gradient (453, 945, 3023, and 3582 m) and litter traits (coniferous vs. broadleaf) in southwestern China.

Results Our results showed that N was retained by –0.4% to 31.5%, but C was immediately released during the early stage (156–516 days) of decomposition for most litter species. Soil fauna significantly increased the peak N content and N retention across litter species, but reduced the C/N ratio for certain species (i.e., *Juniperus saltuaria*, *Betula albosinensis*, *Quercus acutissima*, and *Pinus massoniana* litter), leading to more C and N being released from decomposing litter across the elevation gradient. Contributions of soil fauna to C and N release were 3.87–9.90% and 1.10–8.71%, respectively, across litter species after 4 years of decomposition. Soil environment and initial litter quality factors caused by elevation directly affected litter C and N release. Changes in soil fauna resulting from elevation and fauna exclusion factors had a direct or indirect impact on C and N release during litter decomposition.

Conclusions Our findings suggest that soil fauna promote C and N release from decomposing litter in different magnitudes, mainly controlled by environmental conditions (i.e., temperature and moisture), litter quality (i.e., lignin and cellulose content, and lignin/cellulose), and its diversity across the elevation gradient.

Keywords Carbon remaining, Nitrogen remaining, Nitrogen retention, Soil fauna, Elevational gradient

Background

Carbon (C) and nutrients [i.e., nitrogen (N) and phosphorus (P)] released from decomposing litter are crucial for maintaining soil fertility and nutrient cycling in terrestrial ecosystems (Moore et al. 2006; Berg and McClaugherty 2014; Wang et al. 2021). Releasing of these elements is primarily regulated by interactions among climate, substrate quality, and decomposers (Aerts 1997; Bradford et al. 2016; García-Palacios et al. 2016). Although climate and substrate quality are the predominant regulators of decomposition globally (Cornwell et al. 2008; Wall et al. 2008; Zhang et al. 2008), several other factors, including the composition

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and diversity of decomposers, interactions among litter types and soil properties, may influence litter decomposition locally to a lesser degree (Makkonen et al. 2012; Fujii et al. 2018; Liu et al. 2021). In addition, studies have shown that decomposition generally occurs more rapidly in the presence of soil fauna (González and Seastedt 2001; Tan et al. 2021; Zhou et al. 2020). Soil fauna plays functional roles in improving organic matter decomposition and nutrient cycling, directly by litter fragmentation and indirectly by regulating the effects of abiotic factors and litter quality on decomposition processes via microorganism regulation (Hättenschwiler and Gasser 2005; García-Palacios et al. 2013, 2016; Frouz 2018; Tan et al. 2021). Therefore, the role of soil fauna in C and nutrient cycling is essential to better understand litter decomposition processes within and among ecosystems.

The functional roles of soil fauna in litter decomposition have been well-documented in a variety of climates (González and Seastedt 2001; Wall et al. 2008; García-Palacios et al. 2016; Tan et al. 2021). Moreover, the effects of simulated warming (Yin et al. 2019; 2020), N deposition (Liu et al. 2021), and biodiversity loss (Hättenschwiler and Gasser 2005; Handa et al. 2014) on soil fauna and litter decomposition have been tested in different ecosystems. The present consensus is that soil fauna generally accelerates litter mass loss and nutrient cycling, although soil fauna abundance, biomass, activity, and diversity vary significantly with climate conditions and litter quality (chemical and physical composition) (Powers et al. 2009; Makkonen et al. 2012; Handa et al. 2014; Mariana et al. 2018). Furthermore, increasing evidence emphasizes the role of decomposers (microbe and fauna) in explaining part of the residual variance in litter decomposition patterns beyond climate and litter quality (Wall et al. 2008; Powers et al. 2009; García-Palacios et al. 2013; Bradford et al. 2014; Zhou et al. 2020). For instance, the presence or absence of mesofauna has the largest impact on decomposition rates across a precipitation gradient in tropical forests compared to litter type, decomposition environment, and site treatments (Powers et al. 2009). Across forested sites in temperate regions, local-scale factors, including fauna and fungi, can explain 73% of the variation in wood decomposition rates when disaggregated data are instead considered (Bradford et al. 2014). To a certain extent, soil fauna is not always subordinate to climate and litter quality determining litter decomposition rates at regional and local scales (Meyer III et al. 2011; Bradford et al. 2014, 2016). However, despite the established importance of soil fauna, distinguishing their roles in organic matter decomposition and nutrient cycling in relation to climate and litter traits remains challenging in many ecosystems (Meyer III et al. 2011; Makkonen et al. 2012; Bradford et al. 2016; Zhou et al. 2020).

Increasing elevation can shift biotic and abiotic conditions across relatively small spatial scales due to variations in climate, vegetation, decomposition, and soil types along elevational gradients (Salinas et al. 2011; Marian et al. 2018; Cao et al. 2021). Furthermore, elevation studies can reflect the spatiotemporal pattern of large-scale environmental conditions along climatic gradients (Sang 2009), which is a useful method for assessing and quantifying the effects of the multiple drivers of litter decomposition at both regional and local scales, such as environmental factors, litter quality, and decomposers (Fujii et al. 2018; Tan et al. 2020; 2021). Elevation-related data have the potential to provide information on the response of soil ecological processes (i.e., N mineralization, enzyme biological degradation, and litter decomposition) to temperature (Tan et al. 2019; Cao et al. 2021), although the covariance of temperature with other elevation-dependent variables needs caution in interpretation (Salinas et al. 2011; Bothwell et al. 2014). Moreover, reciprocal transplant experiments conducted across latitudinal and altitudinal gradients have the potential to differentiate between direct environmental factors and other site-specific factors, such as litter quality and decomposer community diversity (Cornwell et al. 2008; Wall et al. 2008; Salinas et al. 2011; Makkonen et al. 2012). Nevertheless, it is still not well-understood whether the roles of soil fauna in C and nutrient cycling, in relation to climate and litter traits, vary across different climate zones or vegetation types.

In this study, we aim to quantify how soil fauna affects litter C and N release interactively with climate and litter traits along an elevational gradient. We conducted a 4-year field decomposition experiment using two dominant tree species (coniferous vs. broadleaf) per site across four elevations (453, 945, 3023, and 3582 m a.s.l.) in the transitional region between the eastern Tibetan Plateau and the Sichuan basin, southwestern China. Litterbags with different mesh sizes (3 mm vs. 0.04 mm) were used to include and exclude soil fauna. In addition, we focused on soil fauna, including macro-fauna (e.g., Coleoptera and Hymenoptera) and micro-fauna (e.g., Oribatida and Collembola), which are the predominant soil fauna along the elevational gradient (Tan et al. 2013). We test the following hypotheses: (1) due to the limitation of low temperature on the abundance and activity of soil fauna at high elevations, the impact of soil fauna on litter C and N release will decrease at high elevations, and (2) during the decomposition process, soil fauna may have a greater impact on C and N release from litter with low quality (e.g., high C/N and lignin/N) due to their feeding preferences.

Methods

Study sites

We selected four forest habitats in the Minjiang River Basin in southwest China with similar slopes and aspects but with different climates, vegetations, soil conditions, and elevations (Tan et al. 2020, 2021). The first forest habitat is in Gao County (453 m a.s.l.), which is a subtropical subhumid monsoon with an average annual precipitation of 1021 mm and an average annual temperature of 18.1 °C. The dominant tree species are pine (*Pinus massoniana*) and camphor (*Cinnamomum camphora*). The second forest habitat is in Dujiangyan (945 m a.s.l.), which is a subtropical humid monsoon with an average annual precipitation of 1243 mm and an average annual temperature of 15.2 °C. The dominant tree species are cedar (*Cryptomeria fortune*) and oak (*Quercus acutissima*). The third and fourth forest habitats (3023 m and 3582 m a.s.l.) are in the Long-Term Research Station of Alpine Forest Ecosystems, which are temperate mountain monsoon with an average annual precipitation of 850 mm and 820 mm, respectively, and an average temperature of 3 °C and 2.3 °C, respectively. Fir (*Abies faxoniana*) and birch (*Betula albosinensis*) are the dominant tree species at 3023 m a.s.l., and cypress (*Sabina saltuaria*) and dwarf willow (*Salix paraplesia*) are the dominant tree species at 3582 m a.s.l. (Tan et al. 2020, 2021).

Experimental design

This study investigated the effect of soil fauna on the release of C and N during litter decomposition using litterbags. The mesh of the lower part of the litterbag was 0.04 mm, and the upper part was divided into two categories. Using 3.00 mm as the control group, allowing macro-, meso- and micro-fauna to enter, and 0.04 mm as the treatment group that excludes soil fauna (Kampichler and Bruckner 2009; Tan et al. 2019, 2020).

Litter traps (1 m × 1 m) were used to collect freshly fallen leaves from dominant canopy trees at each elevation from September to October 2011, including one broad-leaved species and one coniferous species. To reduce the impact of home-field advantage, litter species with similar properties (i.e., C, N, and lignin content or C/N and lignin/N) were chosen for each litter type (broadleaf or coniferous) along the elevational gradient (Ayres et al. 2009; Tan et al. 2021). A total of 240 litterbags (11 sampling times × 5 plots × 2 mesh sizes × 2 litterbags + 20 spare litterbags) of each litter type were transferred to the corresponding sites in late November 2011. Within each plot, 96 litterbags (2 species × 2 mesh sizes × 2 litterbags × 11 sampling times + 8 spare litterbags) were placed on the forest floor (Tan et al. 2020; 2021).

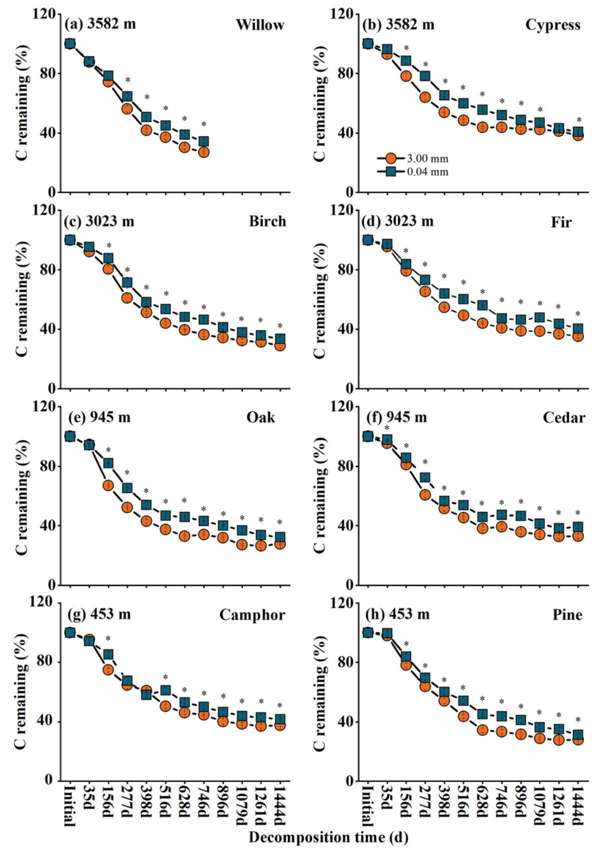

Fig. 1 Carbon (C) remaining (± SE, $n = 5$) in decomposing litters at different elevations and decomposition stages. **a** Willow, **b** Cypress, **c** Birch, **d** Fir, **e** Oak, **f** Cedar, **g** Camphor, **h** Pine. Asterisks denote significant ($P < 0.05$) differences between control (3 mm) and fauna exclusion treatments (0.04 mm) on each sampling date

Sampling and chemical analysis of litter

Litterbag sampling was carried out after 35, 156, 277, 398, 516, 628, 746, 896, 1079, 1261, and 1444 days of field incubation during the 4-year decomposition (December 2011 to October 2015). Eight litterbags were collected from each plot for each sampling time. The samples were placed in sealed soil fauna bags and sent to the laboratory in time. After removing roots, moss, fresh litter, soil, and tags adhering to the surface of the remaining litterbags, the wet weight of the remaining litter in each litterbag was first weighed, and then the soil fauna was extracted using the Tullgren funnel method (Macfadyen 1953; Tan et al. 2019; 2020; 2021). After collecting soil fauna, dry the litter in an oven at 65 °C for 48 h to measure the remaining dry mass. The oven-dried litter was ground and used to determine C and N concentrations. Dichromate oxidation–sulfate–ferrous titration and indophenol–blue colorimetry were used to measure C and N concentrations of litter samples, respectively, following the methods described by Lu (1999).

Table 1 Results of univariate ANOVA for the effects of elevation and litter type on the fauna effects of the C and N release of litters after 4 years of decomposition

Factors	C release			N release		
	d.f.	*F*	*P*	*d.f.*	*F*	*P*
Elevation	3	4.721	0.008**	3	2.846	0.053 ns
Litter type	1	1.096	0.303 ns	1	0.160	0.692 ns
Elevation × Litter type	3	17.933	< 0.001**	3	3.268	0.034*

ns $P > 0.05$, *$P < 0.05$, **$P < 0.01$

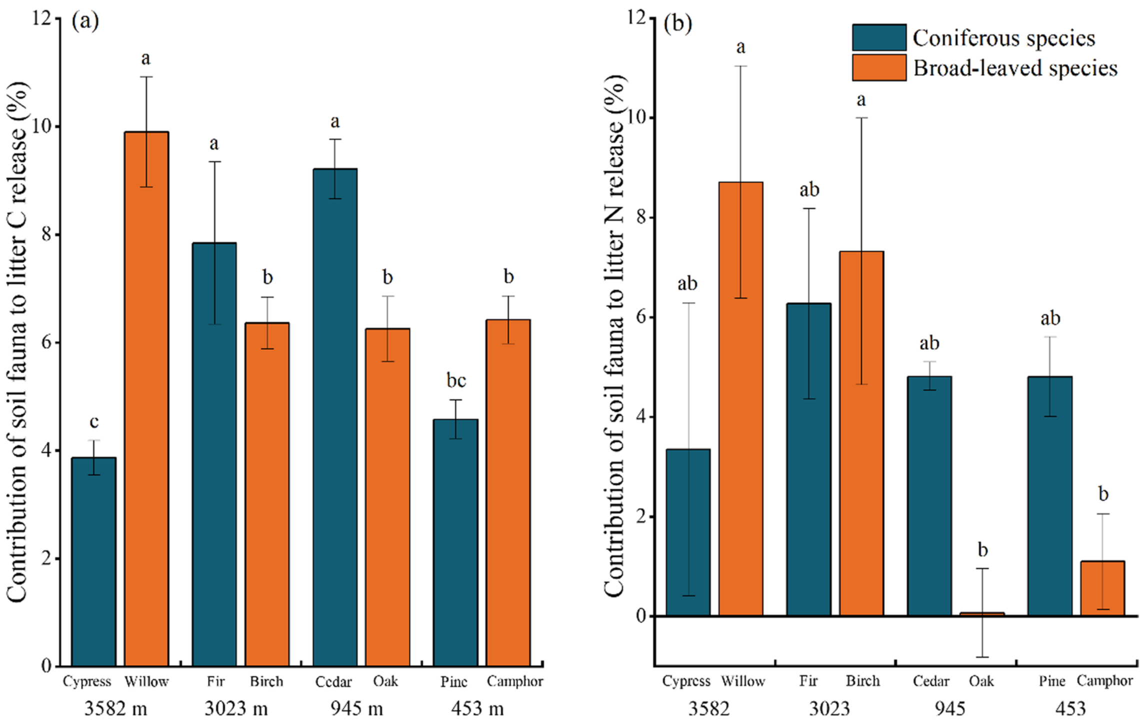

Fig. 2 Contribution of soil fauna to litter C (**a**) and N (**b**) release at different elevations after 4 years of decomposition (± SE, $n = 5$). Different lowercase letters denote statistically significant ($P < 0.05$) differences between different species

Data calculation and statistical analysis

Peak N content and critical C/N ratio were calculated at the time when litter net N loss started (Moore et al. 2006). N retention refers to the amount of N remaining at the peak N content relative to the original level (100%) (Ni et al. 2018). The mass remaining (R_m) of C and N during each specific period of the 4-year study, and the contribution of soil fauna to C and N release of litters after 4 years of decomposition (C_{fau}) were calculated as follows:

$$R_{mt}(\%) = M_t C_t / M_0 C_0 \times 100\%$$

$$C_{fau}(\%) = (100 - R_{mt3.00}) - (100 - R_{mt0.04})/100 - R_{mt3.00}$$

M_0 in the formula represents the initial dry mass (g) of litter; M_t represents the dry mass of the remaining litter (g) after retrieval at time t; C_0 represents the initial C and N concentrations; C_t represents the concentrations of C and N at time t; t is the incubation days of litterbags in the field.

Structural equation models (SEMs) were run using the 'piecewiseSEM' package (Lefcheck 2016) with the inclusion of the elevation gradient to disentangle the potential pathways by which elevation influences the soil fauna-driven litter C and N releases. Fisher's $C > 0.05$ indicates that the model under test is adequately fitted. Based on the explanatory power of independent variables to the

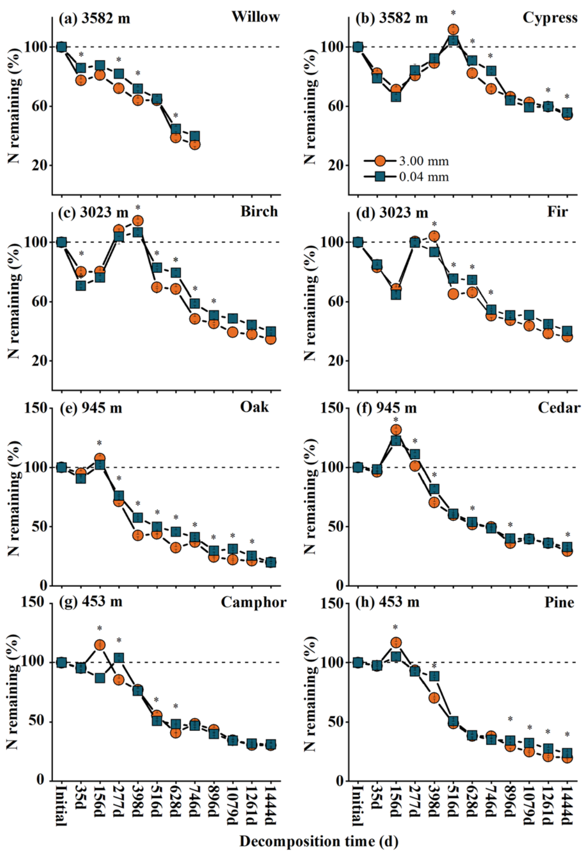

Fig. 3 Nitrogen (N) remaining (± SE, $n = 5$) in decomposing litters at different elevations and decomposition stages. **a** Willow, **b** Cypress, **c** Birch, **d** Fir, **e** Oak, **f** Cedar, **g** Camphor, **h** Pine. Asterisks denote significant ($P < 0.05$) differences between control (3 mm) and fauna exclusion treatments (0.04 mm) on each sampling date

dependent variables, the best model was determined by highly fitting by deleting the nonsignificant relationships in the model. Among them, initial litter quality included C/N, C/P, N/P, and lignin/N. Environmental factors included temperature and moisture across the elevational gradient. The soil fauna community represented the diversity of soil fauna colonizing litter during decomposition. In addition, based on the significant changes in litter chemistry during decomposition (Wickings et al. 2012), we divided it into litter structural C and nutrients, including cellulose, lignin contents, and lignin/cellulose, as well as N, P, and N/P contents, respectively.

A general linear model (GLM) with repeated measures was used to test the individual effect of soil fauna treatment, elevation, litter type, and decomposition time on C and N release. Univariate analysis of variance (ANOVA) was used to test the impact of elevation and litter type on the contribution of soil fauna to litter C and N release after 4 years of decomposition. For each sampling time, a Student's independent sample *t* test was used for comparison of the effects of soil fauna treatment. All the differences analyzed were significant at the level of $P < 0.05$. ANOVAs were performed using SPSS 20.0 (IBM SPP Statistics Inc., Chicago, IL, USA).

Results

C remaining

The C content and C remaining varied significantly among litter types and elevations (Additional file 1: Table S1). Regardless of litter species and elevation, the C content remained relatively stable around the initial C content over the 4-year decomposition period, with soil fauna occasionally increasing or decreasing the C content across litter species at specific sampling times (Additional file 1: Fig. S1). At the end of the experiment, the C remaining in the control and fauna exclusion treatment decreased over time, ranging from 27.15% to 38.38% and 31.29% to 41.71%, respectively (Fig. 1). Soil fauna significantly decreased the C remaining in the control treatments across elevations after a rapid decrease during the first 35–398 days for all litter species. In both treatments, C remaining in coniferous litter increased with elevation (Fig. 1b, d, f and h). Furthermore, after decomposition for 4 years, soil fauna contributions to C release were significantly influenced by elevation and its interaction with litter type at the end of the experiment (Table 1), with its contribution ranging from 3.87% to 9.90% among litter species (Fig. 2a). Soil fauna contributions to C release of litter at different elevations were different, with higher contribution to coniferous litter at 3023 and 945 m, and higher contribution to broadleaf litter at 3582 m and 453 m (Fig. 2a).

N remaining

The N content and N remaining as decomposition proceeded were significantly affected by the fauna treatment, litter type, and elevation (Additional file 1: Table S1). After a rapid leaching stage at 35–277 days of decomposition, the N content in the control and fauna exclusion treatments increased by 3.8–73.6% and 1.5–49.8%, respectively (Additional file 1: Fig. S2), resulting in remaining N increase at elevations 453 m, 945 m, and 3023 m (Fig. 3). However, the remaining N at these elevations consistently decreased after 398 days of decomposition (Fig. 3c–h). At elevation 3582 m, the remaining N in the two treatments continued to decrease for the broadleaf litter (willow) at the beginning of the litterbag incubation, but it showed a steady increase for the coniferous litter (cypress) after the leaching stage (Fig. 3a, b). At the end of the decomposition, the remaining N in both treatments ranged from 19.8% to 54.0% (control) and 19.8% to 55.6% (fauna exclusion) across the litter types and elevations,

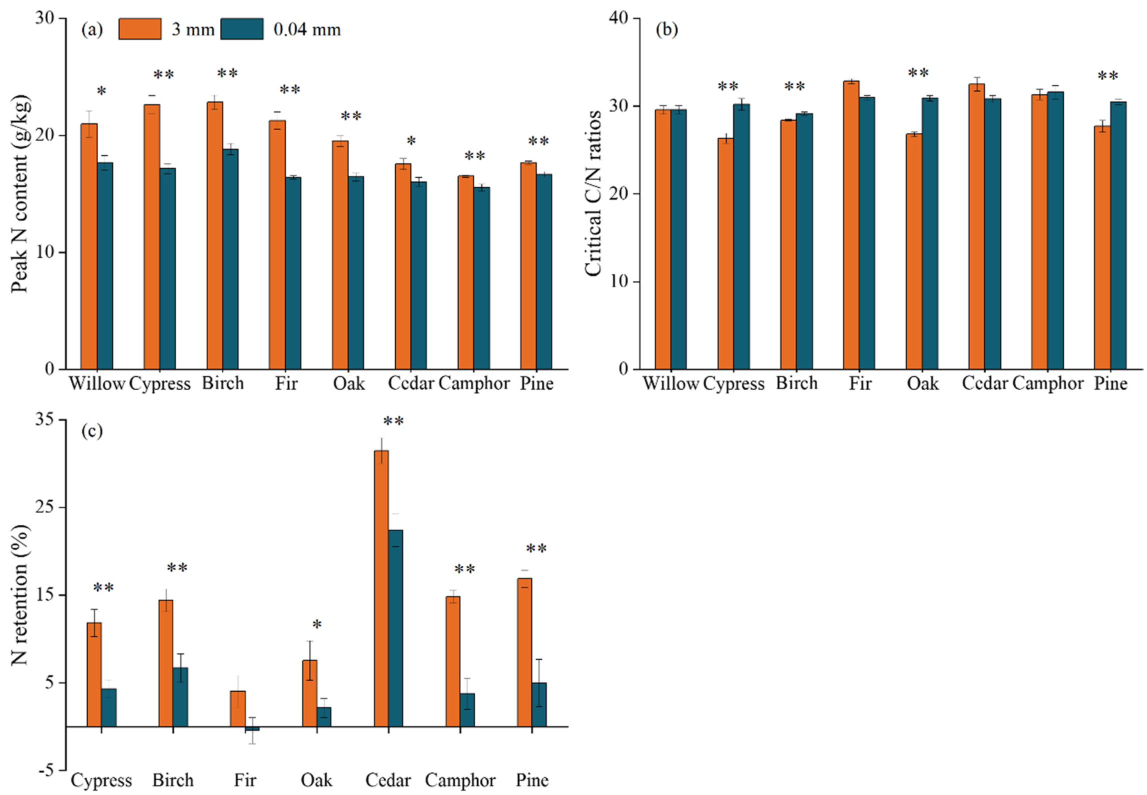

Fig. 4 Critical nitrogen (N) thresholds. **a** Peak N content, **b** Critical C/N ratio, **c** N retention. Values are means (± SE) of the 5 replicates for the eight foliar litters in control (3 mm) and fauna exclusion treatments (0.04 mm). Asterisks denote significant ($P < 0.05$) differences between control (3 mm) and fauna exclusion treatments (0.04 mm). $^{*}P < 0.05$, $^{**}P < 0.01$

respectively. In addition, after 4 years of decomposition, the remaining N in cypress, cedar, and pine litter was significantly lower in the controls than in the fauna exclusion treatments. However, the elevation and litter type did not affect the contributions of soil fauna to the N release at the end of the experiment (Table 1). Soil fauna contributions to N release varied between 1.10% and 8.71% among litter species after 4 years of decomposition (Fig. 2b). Soil fauna contributions to the N release for coniferous litter were higher at 945 and 453 m, whereas the contributions to the N release for broadleaf litter were higher at 3582 m and 3023 m (Fig. 2b).

The peak N content in the control and fauna exclusion treatments ranged from 16.5 to 22.8 g/kg and 15.5 to 22.6 g/kg across litter species, respectively (Fig. 4a). The critical C/N ratios in the two treatments were 26.3 to 32.8 and 29.2 to 31.6, respectively (Fig. 4b). Compared to the controls, the fauna exclusion treatment significantly reduced the peak N content for all litter species, and the N retention except willow and fir litter (Fig. 4a, c). In addition, fauna exclusion treatment significantly increased the critical C/N ratios of cypress, birch, oak, and pine (Fig. 4b). After 4 years of decomposition, N release was correlated with the peak N content and initial N content, but not with the critical C/N ratio in both the controls and fauna exclusion treatments (Fig. 5a–c). However, N release was related to the initial C/N ratio in only the controls ($P = 0.040$), but not in the fauna exclusion treatments ($P = 0.204$; Fig. 5d). Regardless of the peak N content, the relationship between remaining N and remaining C was negative across litter species in both treatments (Additional file 1: Fig. S3).

C/N ratios

The C/N ratio of litter species was significantly affected by the fauna treatment, litter type, elevation, and decomposition time (Additional file 1: Table S1, Fig. 6). The C/N ratios of litter species were decreased by soil fauna during most of the decomposition time (Fig. 6). The litter C/N ratio at different elevations showed differences with decomposition time (Fig. 6). At elevations of 3582 m and 3023 m, the C/N ratio increased during the first 156 days of decomposition, followed by a significant decrease, and then gradually increased again after 398–516 days of decomposition (Fig. 6a–d). The trend was opposite at elevations of 945 m and 453 m,

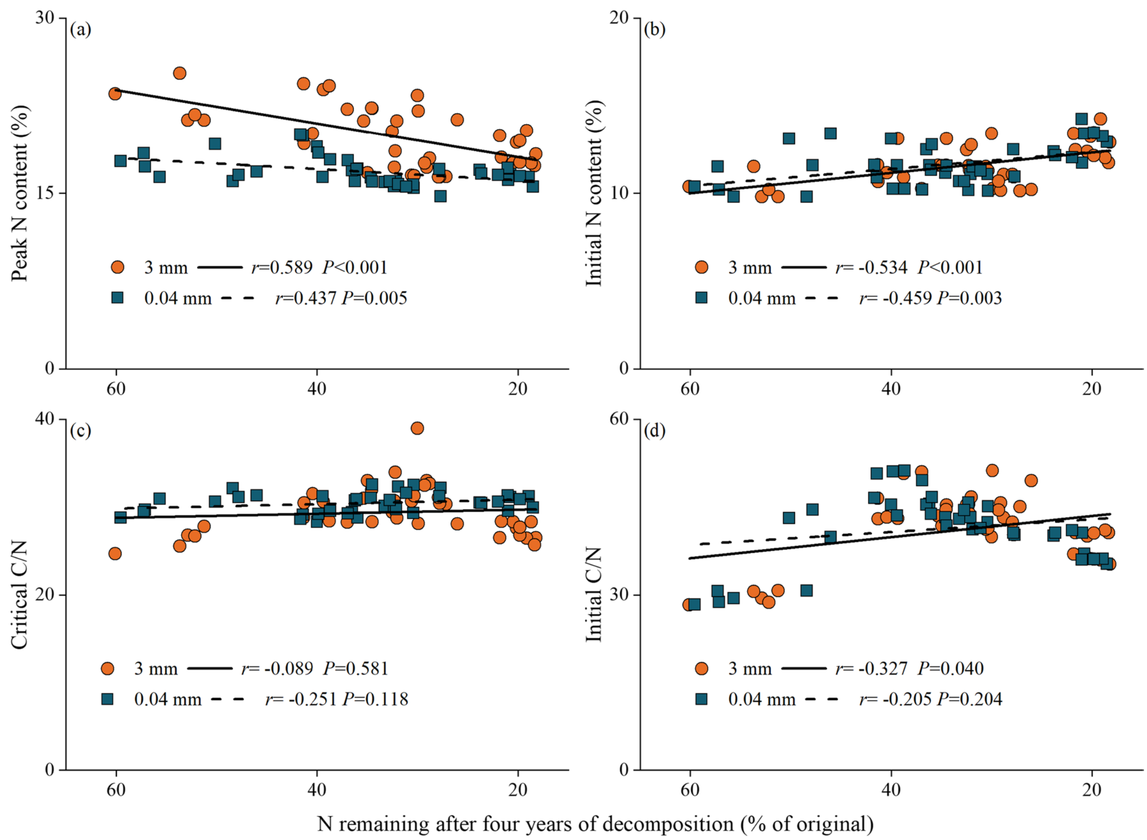

Fig. 5 Remaining nitrogen (N) vs. **a** peak N content ($n=40$), **b** initial N content ($n=40$), **c** critical C/N ratio ($n=40$), and **d** initial C/N ratio ($n=40$). Values are means (± SE, $n=5$) for the eight foliar litters in control (3 mm) and fauna exclusion treatments (0.04 mm). Pearson's r and P values from linear regressions are shown in each panel

where the C/N ratio reached its lowest point during the first 156 days of decomposition and then gradually increased (Fig. 6e–h). At the end of the experiment, the C/N ratios in the controls and fauna exclusion treatments ranged from 23.4 to 57.5 and 25.4 to 59.0, respectively (Fig. 6).

Factors influencing C and N remaining

The structural equation models indicated that environmental factors, litter chemical composition changes, and soil fauna diversity were the most significant drivers of litter C and N remaining during decomposition (Fig. 7). The decrease in soil temperature and moisture with increasing elevation may weaken the release of soil C and N, leading to an increase in soil C and N remaining. In addition, there is a direct positive correlation between the litter's initial quality change caused by elevation and C and N remaining (Fig. 7a, b). Litter structural C quality (lignin and cellulose content, and lignin/cellulose) and litter nutrients (N, P, and N/P) showed direct negative correlations with litter C and N remaining (Fig. 7), while soil fauna had significant negative effects on litter C remaining (Fig. 7a). Moreover, soil fauna may indirectly affect N remaining by affecting the litter structural C (Fig. 7b).

Discussion

Litter is the primary source of soil organic matter, and the C and N released in its decomposition is essential for soil fertility and nutrient cycling in forest ecosystems (Bradford et al. 2016; Wang et al. 2021). Decomposition in most ecosystems largely results from the activities of microorganisms and fauna, which break down non-living organic matter to obtain energy and matter (Bradford et al. 2002; Handa et al. 2014). Soil fauna strongly regulates the effects of abiotic factors and litter traits on decomposition processes (Frouz 2018). Many studies have widely demonstrated that soil fauna accelerates litter mass loss and nutrient cycling globally and regionally (Wall et al. 2008; Yang and Chen 2009; García-Palacios et al. 2013; Yin et al. 2023). In our study, different leaf litter types and elevations resulted in the immediate release of C but retention of N during the

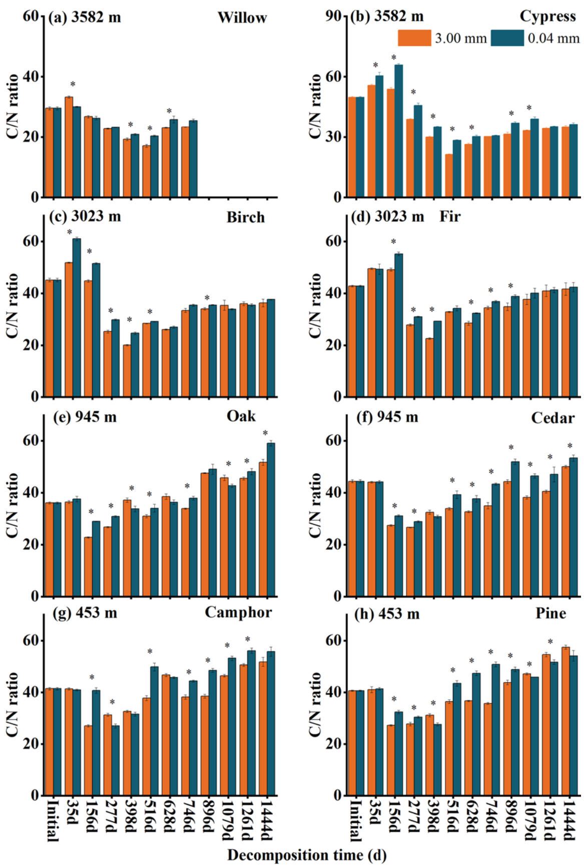

Fig. 6 C/N ratio (± SE, $n = 5$) in decomposing litters at different elevations and decomposition stages. **a** Willow, **b** Cypress, **c** Birch, **d** Fir, **e** Oak, **f** Cedar, **g** Camphor, **h** Pine. Asterisks denote significant ($P < 0.05$) differences between control (3 mm) and fauna exclusion treatments (0.04 mm) on each sampling date

early stage of decomposition. This is consistent with the results of existing decomposition study (Ni et al. 2018). As soil organisms use C in the litter as an energy source (González and Seastedt 2001), this results in the direct release of C. In addition, soil fauna participates in feeding, producing feces, and directly assimilating C sources, which optimizes the enzymatic degradation environment of microorganisms (Joly et al. 2020; Liu et al. 2023). Ultimately, these soil biological factors collectively accelerate the litter C release. However, soil organisms typically prefer high-quality litter with a low C/N ratio or litter with an initial quality close to their own C/N ratio. In this study, the initial C/N ratio of all litter was greater than the critical C/N ratio for N retention and release (25:1) (Chapin et al. 2002), which requires microorganisms to obtain N from the environment to meet their metabolic activities (Berg and McClaugherty 2014). Therefore, litter often undergoes an N-enrichment process in the early decomposition stages before gradually degrading.

Soil fauna influences the dynamics of litter decomposition and element release, including C and N (García-Palacios et al. 2013; Yang et al. 2022; Yin et al. 2023). Studies have shown that the effects of soil fauna on element release can vary in different environments (Frouz 2018; Long et al. 2019) and may be influenced by temperature, moisture, and elevation (Xu et al. 2020). Previous research has indicated that natural environmental gradients exist at different elevations in our study area (Tan et al. 2021). As elevation increases, soil temperature and biological activity gradually decrease (Zhang et al. 2018), which can weaken C and N release during litter decomposition (Peng et al. 2019). However, our study found that the influence of soil fauna on litter C and N release did not decrease with increasing elevation. The release of C and N from different types of litter also varies, which contradicts our initial hypothesis. The highest contributions of soil fauna to C and N release for broad-leaved litter were both observed at an elevation of 3582 m, while their highest contributions to coniferous litter C and N releases were observed at elevations of 945 m and 3023 m, respectively. Several possible explanations for this inconsistency are presented below. First, the abundance and diversity of soil fauna and their effects on litter decomposition rates did not decrease significantly along the elevation gradient (Tan et al. 2021). In addition, the C concentrations of all litters fluctuated minimally throughout the decomposition process (Additional file 1: Fig. S1). This may have resulted in a consistent litter mass loss and C release pattern. Moreover, differences in the initial substrate quality characteristics of different tree species (Peng et al. 2019; Tan et al. 2020) and the increase of N concentration in the early stages of litter decomposition (Fig. 3) may weaken the effect of elevation to some extent. Second, litter quality plays a crucial role in mediating the fauna's role in litter decomposition at the regional scale (Yang et al. 2022). High-quality broad-leaved litter is more easily consumed by soil fauna and degraded (Peng et al. 2019; Xu et al. 2020). Willow has a low initial C/N ratio and high N content (Tan et al. 2021), which can cause soil fauna to contribute more to litter. In addition, the lower initial lignin and lignin/N of cedar are more conducive to soil fauna contribution. Third, thicker litter accumulation and richer soil organic matter in high-elevation areas can provide ample habitat and food resources for soil fauna, which may increase the impact of fauna on litter decomposition. Finally, soil fauna contribution to mass loss in the decomposition process may also be affected by the interaction between litter quality and climate at different sites (Table 1).

Studies have found that initial litter quality determines the extent of the impact of soil fauna on C and N release

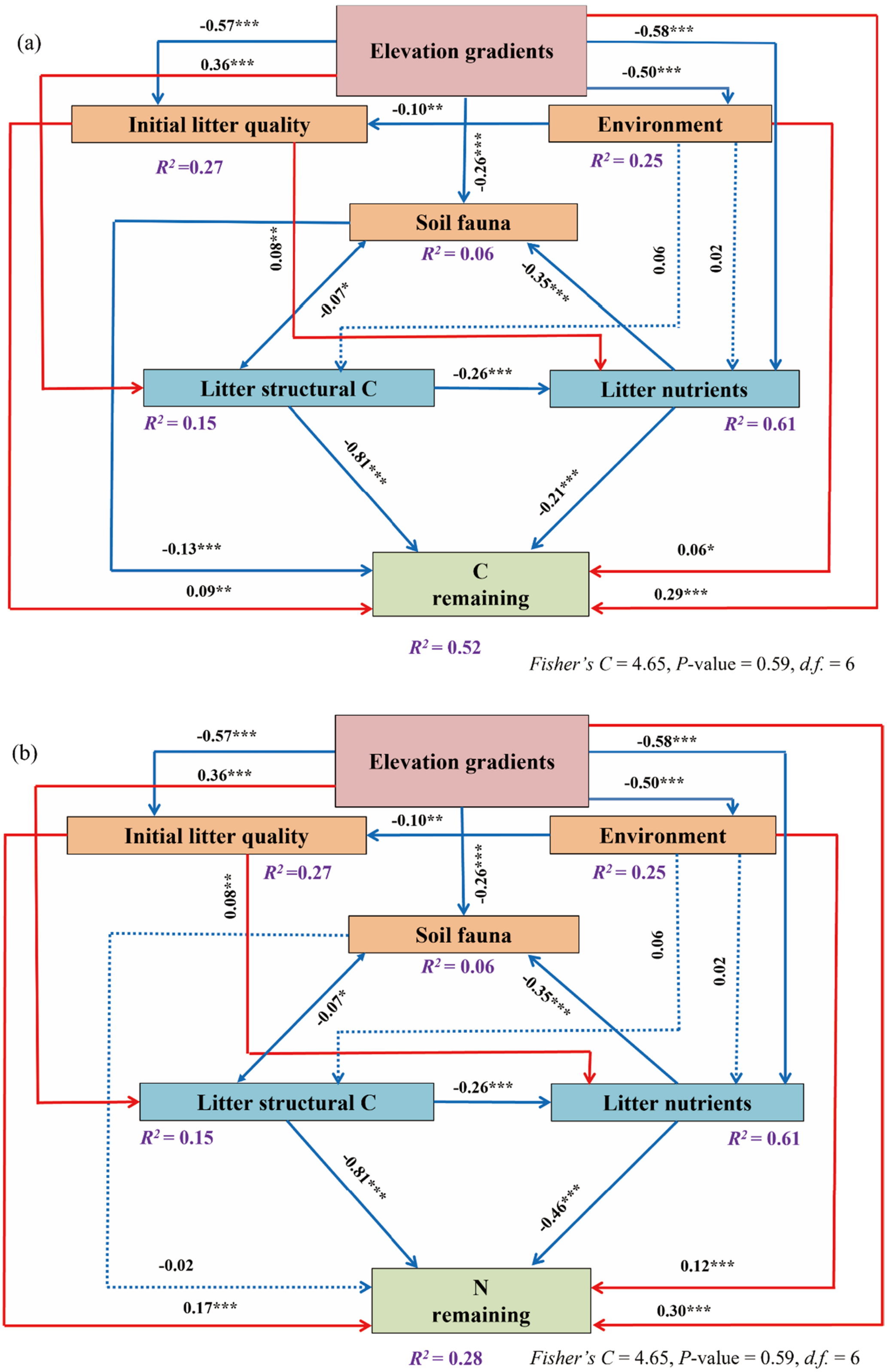

Fig. 7 Structural equation models (SEMs) show the potential pathways by which elevation changes may affect the soil fauna-driven litter remaining C (**a**) and N (**b**). The C and N remaining model (AIC 62.65) with Fisher's C = 4.65, P value = 0.59, $d.f.$ = 6. Numbers along the arrows are standardized path coefficients. The variance explained (R^2) is shown in each panel. Solid red arrows represent significant positive relationships and blue arrows represent significant negative relationships. $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Dashed arrows represent non-significant relationships

(Peng et al. 2019). The difference in initial litter quality often leads to variations in the contribution of soil fauna to litter decomposition across different litter species (Xu et al. 2020; Yin et al. 2022). Inconsistent with the second hypothesis, although soil fauna has a higher impact on the release of C and N from low-quality litter in general, the results are opposite at the elevation of 3582 m. Moreover, the interaction effects of elevation and litter type significantly affected litter C and N release, although the litter type had a minor effect on these processes. This is consistent with previous studies that the contribution of soil fauna to litter nutrient release is influenced by species, but this effect varies across different ecosystems (Yang and Chen 2009; Peng et al. 2019). On one hand, high-quality litter contains more dissolved nutrients, leading to direct fixation and utilization by microorganisms (Zhang et al. 2021), weakening the role of soil fauna in decomposition. Conversely, low-quality litter tends to contain more recalcitrant components and requires more physical fragmentation by soil fauna before being settled by microorganisms (González and Seastedt 2001; Perez et al. 2013), which may lead to its higher contribution. At the same time, the feeding and intestinal degradation of soil fauna can often reduce the substrate quality of litter (e.g., reduce the C/N ratio and lignin/N ratio), making it easier to be degraded by microorganisms (Aerts 1997; Yang and Chen 2009; Tan et al. 2020), which will increase the contribution of soil fauna. This was also verified in this study. In most sampling periods, soil fauna decreased the litter C/N ratio. The opposite result obtained at 3582 m may be because low-quality litter in alpine areas can delay the development and reproduction of soil fauna (Steinwandter et al. 2019), while high-quality litter has a higher fauna density (Tan et al. 2021), thus increasing the decomposition of litter (Mueller et al. 2016).

Soil fauna effects on C and N release were controlled by environmental conditions, litter qualities, and biodiversity across elevation gradients (Peng et al. 2019). The initial N content of litter largely determines whether N is released or retained during decomposition (Manzoni et al. 2010). Soil fauna can affect nutrient release by changing the litter N and C/N ratio with different substrate qualities. Interestingly, our research also confirmed this effect. The presence of soil fauna increased peak N content and N retention across litter species (Fig. 4). Presumably, the decomposable components in the early stage of litter decomposition are more easily colonized by different soil fauna communities (Fujii et al. 2018). As soil fauna reproduce, more energy is obtained from the soil, which increases the peak N content and N retention of litter. However, as decomposition progresses and the content of refractory substances in litter increases the impact of soil fauna on mass loss may be reduced (Marian et al. 2018). Nevertheless, the increased soil fauna can also lead to soil N mineralization and nitrification (Bardgett and Chan 1999; David 2014; Wang et al. 2019), producing more ammonium and nitrate leaching (Zhang et al. 2016; Wang et al. 2019). The critical C/N ratio of litter is an essential indicator of the beginning of net nutrient release (Manzoni et al. 2010). Our research found that soil fauna reduced the critical C/N ratio of some species (Fig. 4), which may lead to releasing more N during decomposition from the litter (Zechmeister-Boltenstern et al. 2015). In addition, the structural equation model shows that the chemical characteristics of litter (e.g., lignin, cellulose, and N content) can affect the C and N release of litter by affecting the diversity of soil fauna (Fig. 7). This may be because of the relatively simple structure of cellulose can be more easily decomposed by soil fauna (He et al. 2015; Xu et al. 2020). After decomposition, the microbial community and extracellular enzyme activity in the litter residue can also change, which may affect the release of C and N in the later stage of decomposition.

Conclusion

This study tested the effects of soil fauna on C and N release during litter decomposition in southwestern China. Our results suggested that during the initial stage of decomposition, C was rapidly released from litter species, while N was retained. The net N release began when the critical C/N ratio of litters reached 26.3 to 32.8. The presence of soil fauna increased the peak N content and N retention across litter species, but reduced the C/N ratio for certain species, resulting in greater release of litter C and N across the elevation gradient. Moreover, after 4 years of decomposition, soil fauna showed a trend of stimulating the C and N release of plant litter. The differences in the soil environment, initial litter quality, and soil fauna caused by elevation had a direct or indirect impact on C and N release during litter decomposition. These findings suggest that soil fauna can accelerate the release of C and N during litter decomposition in different magnitudes, through the synergistic regulation of environmental conditions, litter quality, and soil fauna diversity across the elevation gradient.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-023-00459-4.

Additional file 1: Table S1. Results of the repeated measures ANOVA for the effects of the fauna treatment (F), elevation (E), litter type (L), and decomposition time (DT) on the content and remaining carbon (C) and nitrogen (N) as well as the ratio of C to N. **Fig. S1.** Carbon (C) content of the foliar litter (±SE, $n = 5$) at different elevations and decomposition stages. The asterisk (*) denotes the statistically significant ($P < 0.05$) differences in the C content between the controls (3 mm) and fauna exclusion treatments (0.04 mm) on each sampling date within each elevation. **Fig.**

S2. Nitrogen (N) content of the foliar litter (±SE, $n = 5$) at different elevations and decomposition stages. The asterisk (*) denotes the statistically significant ($P < 0.05$) differences in the N content between the controls (3 mm) and fauna exclusion treatments (0.04 mm) on each sampling date within each elevation. **Fig. S3.** Remaining carbon (C) vs. remaining nitrogen (N). **a** Before the peak N content ($n = 225$). **b** At the peak N content ($n = 40$). **c** After the peak N content ($n = 205$). **d** After 4 years of decomposition ($n = 35$). Values are means (± SE, $n = 5$) for the eight foliar litters in control (3 mm) and fauna exclusion treatments (0.04 mm). Pearson's r and P values from linear regressions are shown in each panel.

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Author contributions
LZ and JL contributed equally. BT and ZX conceived the study. LZ, LW, SL, HL, ZX, and BT provided project support. CY, HX, LX, YL, YW, and SL performed the research and analyzed the data. LZ, JL, and BT wrote the manuscript. RY, LW, and ZX contributed to the editing. All authors contributed to the work and gave final approval for publication.

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Availability of data and materials
The data sets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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