

# Soil warming did not enhance leaf litter decomposition in two subtropical forests

Aogui Li<sup>a,b,1</sup>, Yuexin Fan<sup>a,b,1</sup>, Silu Chen<sup>b</sup>, Haowei Song<sup>b</sup>, Chengfang Lin<sup>a,b,c,\*</sup>, Yusheng Yang<sup>a,b,c</sup>

<sup>a</sup> State Key Laboratory for Subtropical Mountain Ecology of the Ministry of Science and Technology and Fujian Province, Fujian Normal University, Fuzhou, 350007, China

<sup>b</sup> School of Geographical Sciences, Fujian Normal University, Fuzhou, 350007, China

<sup>c</sup> Institute of Geography, Fujian Normal University, Fuzhou, 350007, China

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## ABSTRACT

Climate warming is expected to increase leaf litter decomposition rates. However, higher temperature may not uniformly affect the factors that influence decomposition, resulting in unexpected decomposition patterns. Over a period of two years, we studied litter decomposition in response to soil warming in a native *Castanopsis kawakamii* forest and a *Cunninghamia lanceolata* (Chinese fir) plantation. Our study aimed to determine how soil warming affects litter mass loss, extracellular enzymatic activities (EEAs), litter chemistry, and microbial biomass. In the *C. kawakamii* forest, soil warming caused variation in litter mass loss with time but had no net effect on the litter decomposition constant. In the Chinese fir forest, however, soil warming had a consistent negative effect on litter mass loss, leading to a significant decrease in the decomposition constant by the end of the study. Additionally, there was a significantly slower mass loss of the acid-insoluble C fraction in Chinese fir litter in response to warming. Soil warming did not affect the microbial biomass of either litter, and its effect on EEAs varied with time. Litter moisture was significantly reduced by soil warming, with a greater reduction in Chinese fir litter (−9.2%) than in *C. kawakamii* litter (−4.1%). Applying an ANCOVA model, we found a significant correlation between litter mass loss rate and litter moisture, but not with other litter characteristics. Our results suggest that litter drying in soil warming does not affect microbial activities or litter microbial decomposition, but may diminish the physical leaching of soluble compounds from the litter into the underlying soil horizons. This may be a mechanism that explains the soil warming effect on litter decomposition in subtropical forests.

## 1. Introduction

Litter decomposition is a fundamental biogeochemical process that returns more than half of the net primary production to soil (Wardle et al., 2004), and concurrently releases 60 Pg C per year to the atmosphere (Houghton, 2007). Multiple abiotic (i.e., temperature, moisture, and litter quality) and biotic (i.e., enzyme activities and microbes) factors are known to affect litter decomposition (Suseela and Tharayil, 2018; Prieto et al., 2019). Of these, temperature is the predominant control factor for its direct effects on microbial activity, and indirect effects on litter quality and quantity through changes in plant species

composition and abundance. Climate change scenarios predict that the Earth's surface temperature will increase between 2.6 °C and 4.8 °C by the end of this century (Field, 2014). Consequently, understanding litter decomposition in response to warming is critical for predicting soil chemistry, C storage, and fertility. While tropical and subtropical forests play a critical role in the global C cycle (Bonal et al., 2016), by accounting for approximately 33% of terrestrial net primary production, 25% of stored terrestrial C (Beer et al., 2010), the understanding of warming effect on forest litter decomposition in this region remains limited, which is one of the knowledge gap in modeling future global C cycling and climate.

\* Corresponding author. State Key Laboratory for Subtropical Mountain Ecology of the Ministry of Science and Technology and Fujian Province, Fujian Normal University, Fuzhou, 350007, China.

E-mail address: [tonylcf99@163.com](mailto:tonylcf99@163.com) (C. Lin).

<sup>1</sup> Both authors contributed equally to this manuscript.

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Litter decomposition rates mostly increase with temperature across latitudinal or altitudinal gradients and in laboratory incubations (e.g., Hobbie, 1996; Conant et al., 2011; Morrison et al., 2019), because warmer conditions generally increase the metabolic activity of microbes (Schindlbacher et al., 2011). However, in situ warming experiments on litter decomposition conducted so far have shown inconsistent results, with positive, neutral, and negative responses documented (Xu et al., 2012; Prieto et al., 2019; Chuckran et al., 2020). Unlike laboratory experiments, in situ warming manipulations are often accompanied by moisture decline in both soil and litter, which may potentially affect the litter decomposition. In arid ecosystems, warmer and drier conditions may select heat and drought resistant microbial communities, with less ability to decompose leaf litter (Prieto et al., 2019; Chuckran et al., 2020; Allison et al., 2013). For example, the decrease of litter mass loss rate by 23% in a semiarid shrubland was closely related to warming, which reduced the litter moisture content and microbial biomass (Prieto et al., 2019). In contrast, studies from temperate systems have reported overall positive effects of warming on litter decomposition (Lu et al., 2013), possibly because of increased microbial activity at higher temperatures (Melillo et al., 2002). However, a recent study in the Harvard Forest found that warming did not affect litter decomposition (Morrison et al., 2019). Similarly, litter mass loss in boreal ecosystems exposed to experimental warming was either unchanged (Christiansen et al., 2016) or decreased (Romero-Olivares et al., 2017), which was partly ascribed to a decline in litter moisture with warming. Lower litter moisture content may inhibit fungal decomposition activities (Christiansen et al., 2016; Romero-Olivares et al., 2017). These various results show that the temperature sensitivity of decomposition is dependent on climatic factors, as well as the specific site conditions (Aerts, 2006; Cornelissen et al., 2007). Furthermore, litter quality can alter the effects of warming on litter decomposition. For example, in the eastern Tibetan Plateau of China, experimental warming did not affect the mass loss of dragon spruce litter but significantly increased the mass loss of red birch litter by 19.0% (Xu et al., 2012). The authors argued that dragon spruce decreased litter moisture more readily than red birch, which could, to some extent, affect the different responses of litter mass loss to the elevated soil temperature (Xu et al., 2012). Along with climate warming, terrestrial ecosystems are also undergoing significant vegetation changes owing to factors such as land use, or forest conversion (Hansen et al., 2020). Changes in vegetation composition can influence decomposition rates by altering the quality and quantity of litter input to the soil (Ward et al., 2015), and generating different microclimates (Cornelissen et al., 2007).

Emerging evidence shows that litter decomposition is controlled by the activity of microbial communities (Moorhead and Sinsabaugh, 2006; Bradford et al., 2017; Glassman et al., 2018), which are sensitive to climate change (Lu et al., 2013; Almagro et al., 2017). However, it remains unclear how microbial communities affect decomposition in humid subtropical ecosystems in response to environmental changes (Allison et al., 2013). Furthermore, as proximate agents of organic matter decomposition (Burns et al., 2013), enzyme activities have been measured and to show a correlation with litter decomposition (Carreiro et al., 2000; Waring et al., 2014). These studies suggest that measurements of enzyme activities during litter decomposition could allow for a direct tracking of functional responses of the microbial community to environmental changes.

South China harbors more than 65% of the C sink in Chinese terrestrial ecosystem (Piao et al., 2009), where subtropical evergreen broad-leaved forests form the climax vegetation. The area is unique in that other areas in the same latitude consist mostly of desert or savanna ecosystems. Over the past decades, most native forests have been converted to plantations of more productive coniferous tree species, especially *Cunninghamia lanceolata* (Chinese fir), to meet the demand for timber and other forest products (Yang et al., 2009). Concurrently, this region is experiencing a significant increase in the Earth's surface temperature (Anderson, 2012), which raises concerns about how the major

forest ecosystems will respond to the climate warming. In 2015, we established warming experiments in a native forest, dominated by *Castanopsis kawakamii*, and a Chinese fir plantation by using buried heating cables.

Despite a number of studies dealing with warming effect on litter decomposition worldwide, little is known in subtropical forest, due largely to few warming experiments in the ecosystems of this region (Crowther et al., 2016). To fill this knowledge gap, we conducted the current study by making use of the established warming experiments to assess how soil warming affects litter decomposition. We measured litter mass loss, nutrient release, chemical components, litter moisture, microclimatic factors, microbial biomass, and extracellular enzyme activities (EEAs) during decomposition process to test following two hypotheses: (1) if warming enhances litter decomposition in wet ecosystems (Petraglia et al., 2019; Allison et al., 2013), then experimental warming will accelerate litter mass loss rates in the subtropical forests, because this area has a mean annual precipitation of 1670 mm (Li et al., 2018); (2) if warming generally increases the metabolic activity of microbes in litter decomposition (Schindlbacher et al., 2011), then experimental warming may increase microbial mass, stimulate EEAs and consequently increase litter decomposition in the subtropical forests, because EEAs are temperature dependent and well correlated with decomposition rates (Chen et al., 2020; Rejmankova and Sirova, 2007).

## 2. Materials and methods

### 2.1. Site description

This study was conducted at the Forest Ecosystem and Global Change Research Station in Sanming, Fujian, southeastern China (26° 09' N, 117° 28' E; 250–500 m a.s.l.). This area experiences a subtropical monsoonal climate, with evergreen, broad-leaved natural forest as the climax community. During the study period, the mean annual air temperature was 19.3 °C and annual precipitation was 1638 mm, with 78% occurring from March to August, according to the record of an automatic weather station (ELO105, LSI Lastem, Italy) installed 2 km away from the study site. The growing season is relatively long, with an annual frost-free period of approximately 300 days. The soils in the area are ultisols (lateritic red earths) formed from sandstone and are approximately 30–70 cm deep.

The experimental sites were chosen in an old-growth (>200 years) evergreen, broad-leaved natural forest dominated by *C. kawakamii* (82% of the basal area), and a neighboring Chinese fir plantation converted from natural forest in 1974. In addition to *C. kawakamii*, the natural forest included *Schima superba*, *Pinus massoniana*, *Lithocarpus glaber*, *Symplocos caudate*, and *Symplocos stellaris* in the overstory layer. The stand density was approximately 250 trees per hectare for the natural forest and 900 trees per hectare for the Chinese fir plantation. The other forest characteristics and soil physicochemical properties are listed in Table 1.

### 2.2. Experimental design

In each of the two forests, we established ten 6 m × 6 m plots and grouped them into five blocks in 2014. The spacing between the plots was greater than 6 m to avoid edge effects. Using a randomized block design, ambient control and warming treatments were randomly assigned to the two plots of each block. All ten plots were equipped with resistance heating cables (TXLP/1, Nexans, Norway), which were buried at a soil depth of 10 cm with a spacing of 20 cm. Six temperature sensors (T109, Campbell Scientific Inc., Logan, UT, USA) and four moisture sensors (CS616, Campbell Scientific Inc., Logan, UT, USA) were installed in each soil warming plot, whereas four temperature sensors and two moisture sensors were installed in each control plot. All sensors were buried at a soil depth of 10 cm. The warming system was controlled by a

**Table 1**Forest characteristics and soil physicochemical properties in the *Castanopsis kawakamii* and Chinese fir study sites.

Forest type	Forest characteristics				Soil physicochemical characteristics					
	Altitude (m)	Slope (°)	Tree height (m)	DBH (cm)	C (g·kg <sup>-1</sup> )	N (g·kg <sup>-1</sup> )	P (mg·kg <sup>-1</sup> )	C: N	N: P	pH
<i>C. kawakamii</i>	34	31	35.1	57.7	29.4 a	1.8 a	177 a	16.2 a	10.3 a	4.1 a
Chinese fir	300	29	20.4	24.0	23.7 b	1.8 a	185 a	13.2 b	9.7 b	4.0 b

DBH, diameter at breast height; C, carbon; N, nitrogen; P, phosphorus; C:N, carbon to nitrogen ratio; N:P, nitrogen to phosphorus ratio. Different letters indicate statistical significance at  $\alpha = 0.05$  between *C. kawakamii* and Chinese fir.

Campbell CR3000 data logger (Campbell Scientific Inc., North Logan, UT, USA) and was initiated in October 2015. The soil temperature of the warming plot was maintained at 4 °C above that of the control plot.

### 2.3. Litter preparation and decomposition measurement

Newly senesced leaf litter of *C. kawakamii* and Chinese fir was collected separately with litterfall traps in the two forests during the peak litterfall period. Litter samples were air-dried to a constant weight, and subsamples were oven-dried at 70 °C for 48 h to calculate the moisture correction factor. Litterbags (20 × 20 cm) made of polyester netting with a mesh size of 1 mm × 1 mm were used to determine litter decomposition, which may exclude all the macrofauna and part of mesofauna, such as millipede, termite, earthworm in the subtropical forests (Global Soil Biodiversity Atlas). In May 2018, litterbags filled with 10 g air dried leaf litter were placed on the soil surface of the experimental plots. After 30, 90, 180, 270, 360, 540, and 720 days, two litterbags in each plot were retrieved, transported to a nearby laboratory, and cleaned of adherent soil and other extraneous materials. The residual litter in one of the litterbags was weighed after oven-drying at 70 °C for 48 h to measure the remaining mass and then finely milled for subsequent chemical analyses. The residual litter in the other litterbag was stored at 4 °C in a refrigerator for the analysis of EEAs within one week.

### 2.4. Chemical analyses

The total C and N contents of the litter were assessed using an Elemental VARIO Micro Cube elemental analyzer (Elementar Vario MAX, Germany), and the total P content was measured applying the molybdenum blue method with an ultraviolet–visible spectrophotometer (UV-2550; Shimadzu, Kyoto, Japan). The chemical components of the litter were assessed using the forest product serial digestion technique (Hendricks et al., 2000; Ryan et al., 1990). Briefly, water-soluble extractives in the ground litter sample were removed after exposure to two-stage extraction in dichloromethane and boiling water, respectively. Acid-soluble structural components were removed after a two-stage digestion in 72% and 2.5% sulfuric acid, respectively. Acid-insoluble structural components were calculated by using the residual mass of the two-stage sulfuric acid digestion minus the ash mass. Concurrently, the residual litter was subsampled for ash determination (575 °C for 8 h, until no black residue remained) to express total mass, C fraction, and nutrient indices on an ash-free, dry mass basis.

### 2.5. Enzyme assays

The activities of  $\beta$ -glucosidase ( $\beta$ G), cellobiohydrolase (CBH), N-acetyl glucosaminidase (NAG), acid phosphatase (AP), phenol oxidase (PPO), and peroxidase (Px) were assessed in the residual litter samples from each plot according to a modified version of Sinsabaugh et al. (1993). Briefly, litter (0.5 g) was added to 125 mL of 50 mM acetate buffer (pH 5.0) and blended for 10 min. Then, 200  $\mu$ L aliquots were dispensed into 96-well microplates with 16 replicates per sample and per assay. Each replicate contained 200  $\mu$ L of sample suspension and 50  $\mu$ L of substrate. The hydrolytic enzyme activity was measured using 10  $\mu$ M methylumbelliferone (MUB)-linked substrates, including

4-MUB- $\beta$ -D-glucopyranoside, 4-MUB- $\beta$ -D-cellobioside, 4-MUB-N-acetyl  $\beta$ -D-glucosaminide, and 4-MUB-phosphate for the  $\beta$ G, CBH, NAG, and AP assays, respectively. The PPO and Px activities were measured using L-3,4-dihydroxyphenylalanine (L-DOPA) as the substrate. The microplates were incubated at 20 °C in the dark for 4 h for the hydrolytic enzyme analysis and for 18 h for the oxidative enzyme analysis. After incubation, 10  $\mu$ L 1 M NaOH were added to each well to terminate the reaction. A Synergy H4 Hybrid Reader (Biotek, Winooski, VT, USA) was used to quantify the absorbance of the oxidative enzyme samples at 450 nm and fluorescence of the hydrolytic enzyme samples at 365 nm excitation and 450 nm emission filters. Enzyme activity was calculated as the rate of substrate conversion in nmol·h<sup>-1</sup>·g<sup>-1</sup> for hydrolytic enzymes and  $\mu$ mol·h<sup>-1</sup>·g<sup>-1</sup> for oxidative enzymes (DeForest, 2009).

### 2.6. Statistical analysis

The model for constant potential mass loss is represented by the following equation:  $x/x_0 = \exp^{-kt}$ , where  $x$  is the mass at time  $t$ ,  $x_0$  is the initial mass,  $k$  is the decomposition coefficient, and  $t$  is the elapsed time. Because all five replicate plots was used in litter decomposition experiment, linear mixed models was applied to detect the effects of warming, litter, and time on soil temperature and moisture, enzyme activities (including AP,  $\beta$ G, CBH, NAG, PPO, and Px), litter moisture, litter N and P concentrations, and mass loss, with time as repeated measure factor and plot as a random factor. A Bonferroni test was used for pairwise comparisons.

To assess how the effects of W and T on mass loss could be mediated by changes in decomposition-related parameters, an analysis of covariance (ANCOVA) model was adopted, with mass loss as the dependent factor, warming and time as fixed factors, soil temperature and moisture, enzyme activities (including AP,  $\beta$ G, CBH, NAG, PPO, and Px), litter moisture, and litter N and P concentrations as covariates. The fixed effects included warming, time, and their interactions and the main effects of the 11 covariates. These 11 covariates were chosen based on a collinearity test, which showed no collinearity among them (i.e., variance inflation factors below 2). All statistical analyses were conducted using the SPSS software (version 21.0; SPSS Inc., Chicago, IL, USA).

## 3. Results

### 3.1. Initial litter properties

The initial litter concentrations of C, N, and P were significantly lower in *C. kawakamii* than those in Chinese fir (Table 2). For the initial litter C fractions, the water-soluble C-fraction content of *C. kawakamii* was significantly higher than that of Chinese fir, while an opposite pattern was detected for the acid-insoluble C-fraction content. In addition, *C. kawakamii* litter had higher ratios of C:N, C:P, and lignin:P than Chinese fir litter (Table 2).

### 3.2. Warming effect on soil temperature and moisture, and litter moisture

There was a significant warming effect on soil temperature at 10 cm depth in both forests throughout the experimental period (Fig. 1), with an average increase of 4 °C in the warming treatments (Fig. 1).

During the two-year experimental period, warming resulted in

**Table 2**  
Initial leaf litter chemical properties of *Castanopsis kawakamii* and Chinese fir.

Litter type	<i>C. kawakamii</i>	Chinese fir
C (g·kg <sup>-1</sup> )	476 ± 1 b	508 ± 4 a
N (g·kg <sup>-1</sup> )	11.1 ± 0.8 b	18.7 ± 2.0 a
P (g·kg <sup>-1</sup> )	0.34 ± 0.00 b	1.09 ± 0.02 a
WSE (%)	56.7 ± 1.7 a	47.6 ± 1.3 b
ASF (%)	19.8 ± 0.6 a	19.0 ± 0.6 a
AIF (%)	23.4 ± 1.1 b	33.4 ± 1.3 a
C: N	43.2 ± 3.1 a	27.4 ± 3.2 b
C: P	1388 ± 16 a	466 ± 6 b
N: P	32.3 ± 2.5 a	17.2 ± 1.9 b
AIF: N	21.2 ± 1.2 a	18.1 ± 2.7 a
AIF: P	68.3 ± 4.0 a	30.7 ± 0.9 b

Values are presented as mean ± SE ( $n = 5$ ). C, carbon; N, nitrogen; P, phosphorus; WSE, water-soluble extractive; AIF, acid-insoluble fraction; ASF, acid-soluble fraction; C:N, carbon to nitrogen ratio; C:P, carbon to phosphorus ratio; N:P, nitrogen to phosphorus ratio; AIF:N, acid-insoluble fraction to nitrogen ratio; AIF:P, acid-insoluble fraction to phosphorus ratio. Different letters indicate statistical significance at  $\alpha = 0.05$  between *C. kawakamii* and Chinese fir.

substantial soil moisture decrease, mainly from October 2018 to January 2019, for both *C. kawakamii* natural forest and Chinese fir plantations. In addition, we also documented a period of warming-induced soil moisture decrease in Chinese fir plantation during September 2018 (Fig. 1).

There was no significant effect of warming × time on the litter moisture (Fig. 2,  $P = 0.095$ ), but there was a significant warming effect (Fig. 2,  $P = 0.033$ ) on litter moisture, indicating that the warming effect on litter moisture did not vary with time. Specifically, warming reduced the litter moisture of *C. kawakamii*, but only significantly on the 360th day. Warming also reduced the litter moisture of Chinese fir, but only significantly on day 180 and day 360. Notably, the litter moisture content of Chinese fir was higher than that of *C. kawakamii* before the 180th sampling day, but was on the contrary afterwards.

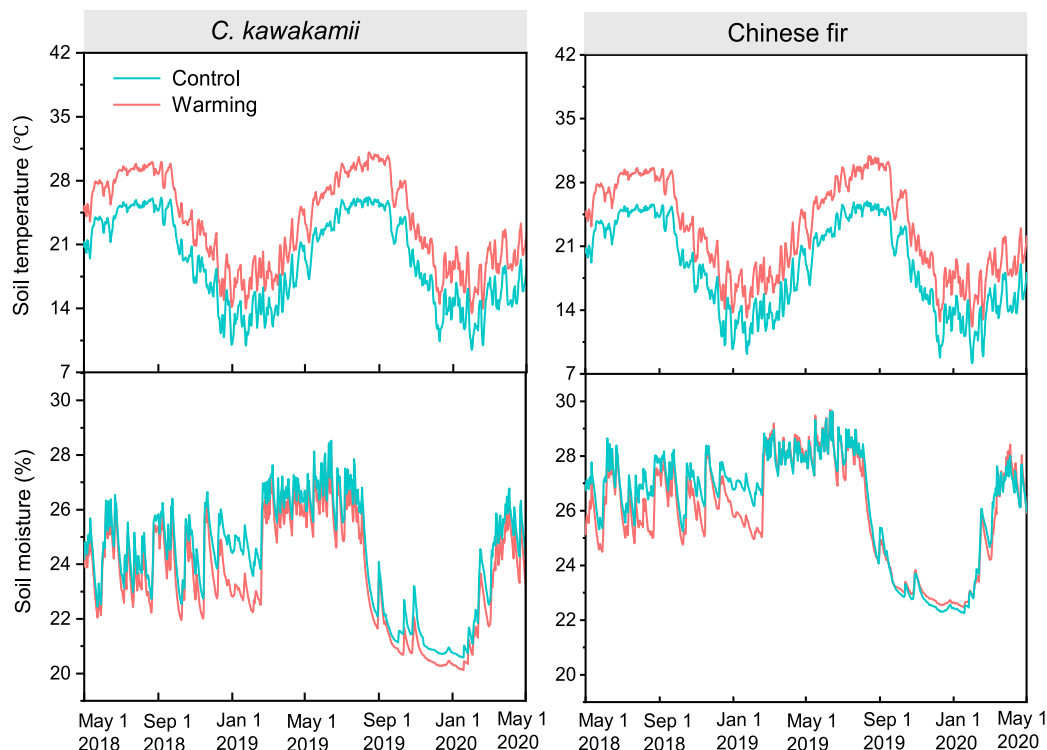
### 3.3. Warming effect on litter enzyme activities and microbial biomass

For the two forests, the interaction of warming × time had a significant effect on extracellular enzyme activities, including AP,  $\beta$ G, CBH, NAG, PPO, and Px, with Px an exception in *C. kawakamii* litter (Fig. 3,  $P < 0.01$ ), which indicates that the warming effect varied with time. Pairwise comparisons demonstrated that, for *C. kawakamii* litter, warming significantly reduced enzyme activities of AP only on the 360th day,  $\beta$ G on the 270th and 360th day, CBH on the 360th day, NAG on the 180th day and 360th day, and PPO on the 270th day (Fig. 3). For Chinese fir litter, warming significantly increased the enzyme activities of CBH only on the 90th and 180th day, PPO on the 270th day, and Px on the 270–720th day, while it significantly reduced the activities of NAG on the 30th and 270th day, respectively (Fig. 3). Notably, variation in oxidase activities, including PPO and Px, showed a rising trend with the decomposition time for both *C. kawakamii* and Chinese fir litter (Fig. 3). Variations in hydrolase activities, including AP,  $\beta$ G, CBH, and NAG, peaked on the 360th day of decomposition for *C. kawakamii* litter, and on the 90th or 180th day for Chinese fir litter (Fig. 3).

There was no significant warming effect on the microbial biomass C in either the *C. kawakamii* or Chinese fir litter on the 720th decomposition day (Fig. 4). However, there was a significant litter quality effect on the microbial biomass, with higher microbial biomass in *C. kawakamii* than in Chinese fir litter (Fig. 4).

### 3.4. Warming effect on litter decomposition rates, C, N, P, and C fractions mass remaining

There was an effect of warming × time on the litter decomposition of *C. kawakamii* (Fig. 5, Table 3,  $P = 0.027$ ). In contrast, there was no effect of warming × time, but a significant warming effect on the litter decomposition of Chinese fir (Fig. 5, Table 3,  $P = 0.001$ ), indicating that warming consistently decreased Chinese fir litter decomposition during the experiment. After the 2-year decomposition, the mass loss varied



**Fig. 1.** Soil temperature and moisture at 10 cm depth during the control and warming treatment in the *Castanopsis kawakamii* natural forest and Chinese fir plantation.

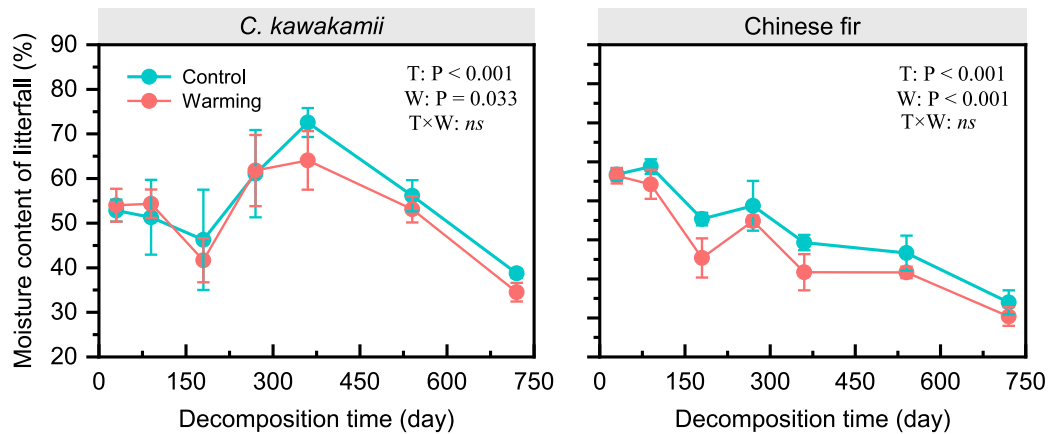


Fig. 2. Influences of warming on the litter moisture of *Castanopsis kawakamii* and Chinese fir with decomposition time. The values are means  $\pm$  SD ( $n = 5$ ). W, warming; T, time; W  $\times$  T, interaction between warming and time;  $ns$ , no significant difference ( $P > 0.05$ ).

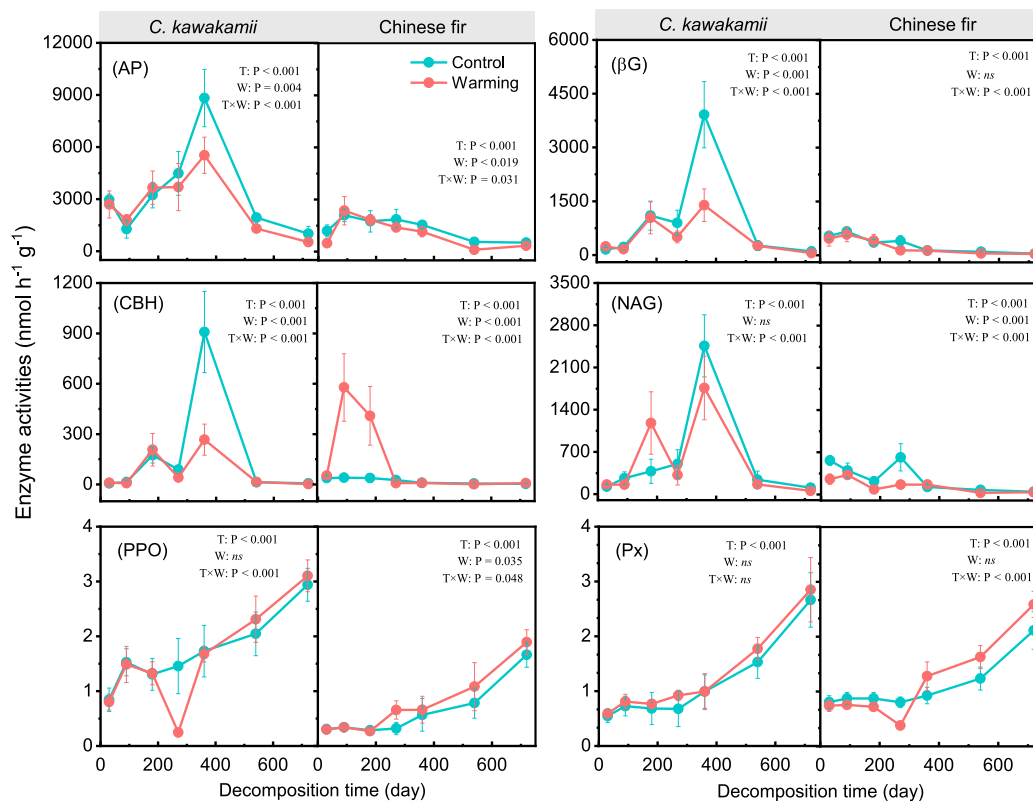


Fig. 3. Influences of warming on the enzyme activities of *Castanopsis kawakamii* and Chinese fir with decomposition time. The values are means  $\pm$  SD ( $n = 5$ ). AP, acid phosphatase;  $\beta$ G,  $\beta$ -glucosidase; CBH, cellobiohydrolase; NAG, N-acetyl glucosaminidase; PPO, phenol oxidase; Px, peroxidase; W, warming; T, time; W  $\times$  T, interaction between warming and time;  $ns$ , no significant difference ( $P > 0.05$ ).

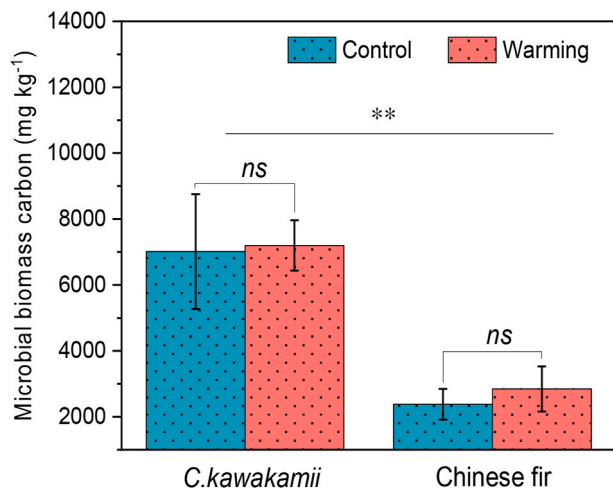
significantly among the measured litters. The largest dry mass loss (70.1% of the original mass) was observed for *C. kawakamii* litter in the warming treatment, whereas the lowest loss (61.6%) was observed for Chinese fir litter in the warming treatment (Fig. 5). The mass loss pattern for each litter sample was characterized by a negative exponential equation ( $R^2 > 0.89$ ,  $P < 0.05$ ).

For *C. kawakamii* litter, there were no significant warming effects on litter C, N, and P mass remaining, and C fraction mass remaining, including water-soluble, acid-soluble, and acid-insoluble fractions, at

the end of the 2-year decomposition (Fig. 6).

For Chinese fir litter, warming did not affect litter C, N, and P mass remaining (Fig. 6). It also did not affect the water-soluble and acid-soluble C fraction mass remaining, but significantly increased the litter acid-insoluble C fraction mass remaining at the end of the decomposition period (Fig. 6).





**Fig. 4.** Influences of warming on the microbial biomass carbon of *Castanopsis kawakamii* and Chinese fir. The values are means  $\pm$  SD ( $n = 5$ ). Different capital letters indicate statistical significance at  $\alpha = 0.05$  between *C. kawakamii* and Chinese fir litter. *ns* and *\*\** indicate statistical significance at  $\alpha > 0.05$  and  $\alpha < 0.01$ , respectively.

### 3.5. Effect of warming, decomposition time, soil temperature, soil moisture, enzyme activity, litter moisture, and N and P concentration on mass loss rate

For *C. kawakamii* litter, the ANCOVA models showed that, among the covariates tested, only litter moisture had a positive effect on the litter decomposition rate ( $P = 0.001$ , Table 4; Table S1). By accounting for the effects of these covariates, the effects of warming disappeared, whereas the effect of time remained significant. This shows that the effects of warming on litter decomposition rate were mediated by these covariates, especially litter moisture.

For Chinese fir litter, the ANCOVA models showed that among the covariates tested, soil temperature and litter moisture had a positive effect on the litter decomposition rate ( $P = 0.001$ , Table 4; Table S1). The effects of warming and time remained significant after accounting for the effects of these covariates. These results show that the warming effects on litter decomposition rate were mediated by factors other than these covariates.

## 4. Discussion

### 4.1. Warming effect on soil temperature, soil and litter moisture

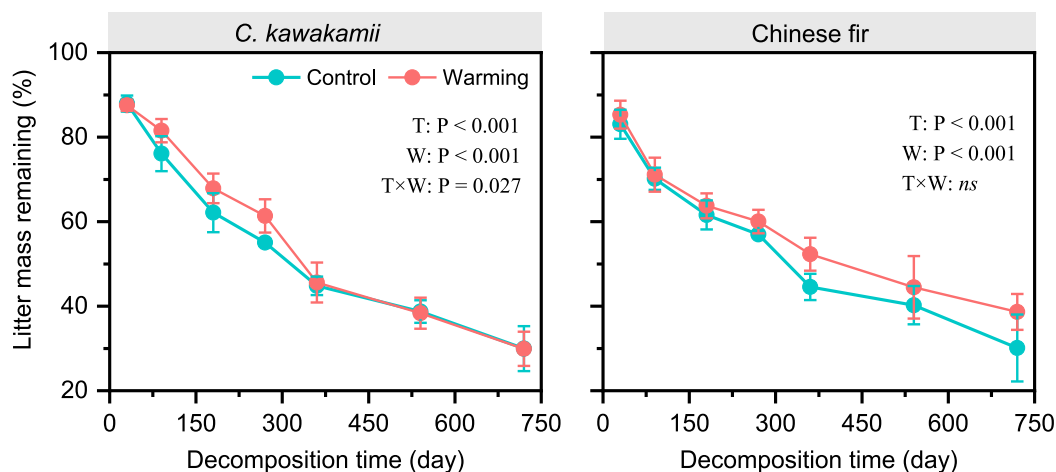
Buried heating cable is widely used to conduct manipulative warming experiments in forest ecosystem, which was also adopted in the Harvard forest (Melillo et al., 2002), and in the present study as well. Our results indicated that heating cables increased the soil temperature at 10 cm depth by 4 °C on average (Fig. 1). Additionally, the surface soil temperature was elevated up to about 2 °C higher than the control, which can be inferred by the photos shot by infrared thermometer (see S1), and suggests the treatment is suitable to test the warming effect on litter decomposition. The temperature increase in our study is comparable to the average soil temperature increase (3.6 °C,  $n = 5$ ) in other experiments that induced soil warming via heating cables (Carey et al., 2016). Manipulative warming often affects the soil moisture (Carey et al., 2016). A meta-analysis by Xu et al. (2013) showed that experimental warming decreased soil moisture across studies, with the largest reduction (11.7%) observed in forests. Our results indicated that warming reduced soil moisture in the natural forest and Chinese fir plantation by 2.4% and 3.3%, respectively, during the litter decomposition period. This was less than the 6.4% reduction in a tallgrass prairie (Luo et al., 2001) and 5.2% reduction in dragon spruce forests in the Tibetan Plateau of China (Xu et al., 2012). In addition, soil moisture in both the natural forest and Chinese fir plantation exceeded 23%. The small warming effect on soil moisture in this study may be ascribed to the high yearly rainfall in the study region, which makes it unlikely to be a limiting factor for soil microbial activities. Compared to soil moisture, litter moisture is more directly linked to microbial activity and plays a role in litter decomposition (Prieto et al., 2019). Over the 2-year

**Table 3**

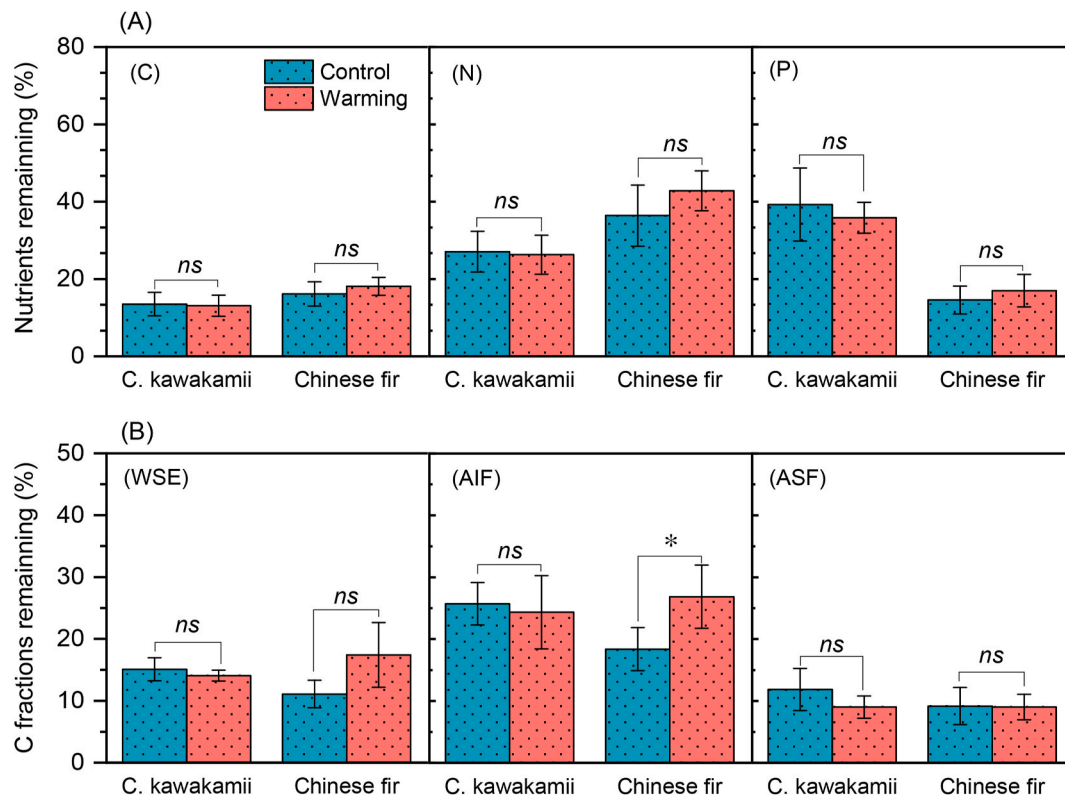
Estimated initial mass, decomposition constant ( $k$ ;  $y^{-1}$ ), half-life time ( $T_{1/2}$ ) and time required for 95% loss ( $T_{95}$ ) of different litter types.

Litters	Treatments	$M_0$ (%)	$R^2$	Decay constant/ $k$	$T_{1/2}$ (y)	$T_{95}$ (y)
<i>C. kawakamii</i>	CT	94.4	0.94	0.70 a	0.9	4.18
	W	95.8	0.97	0.63 a	1.03	4.67
Chinese fir	CT	90.6	0.92	0.68 a	0.88	4.27
	W	90.6	0.89	0.50 b	1.19	5.79

$M_0$  is the estimated initial mass,  $k$  is calculated from a single-exponential model,  $T_{1/2} = 0.693/k$ , and  $T_{95} = 3/k$ . Different letters indicate statistical significance at  $\alpha = 0.05$  in the same litter type.



**Fig. 5.** Influences of warming on the litter mass remaining of *Castanopsis kawakamii* and Chinese fir. The values are means  $\pm$  SD ( $n = 5$ ). W, warming; T, time;  $W \times T$ , interaction between warming and time; *ns*, no significant difference ( $P > 0.05$ ).



**Fig. 6.** Influences of warming on the litter carbon, nitrogen, and phosphorus mass remaining (A) and carbon fractions mass remaining (B) at the end of the 2-year decomposition experiment. The values are means  $\pm$  SD ( $n = 5$ ). C, carbon; N, nitrogen; P, phosphorus; WSE, water-soluble carbon; AIF, acid-insoluble carbon; ASF, acid-soluble carbon. ns, \*, \*\*, and \*\*\* indicate statistical significance at  $\alpha > 0.05$ ,  $\alpha < 0.05$ ,  $\alpha < 0.01$ , and  $\alpha < 0.001$ , respectively.

**Table 4**

Analysis of covariance model on the litter mass loss rate (%) for *Castanopsis kawakamii* and Chinese fir in the warming and control treatments across the 2-year decomposition period.

Sources of variances	<i>C. kawakamii</i>				Chinese fir			
	Df	Mean square	F	P-value	df	Mean square	F	P-value
Intercept	1	31.1	1.92	0.16	1	44.4	6.48	0.01
W	1	30.5	0.94	0.34	1	44.5	5.38	0.03
T	6	35.7	18.7	0.00	6	36.6	3.11	0.01
W $\times$ T	6	32.4	4.24	0.30	6	33.3	1.18	0.34
Soil temperature	1	30.3	0.95	0.34	1	38.7	4.31	0.05
Soil moisture	1	23.4	0.01	0.92	1	9.00	3.15	0.11
AP	1	37.0	1.23	0.28	1	36.5	0.21	0.65
BG	1	41.2	0.44	0.51	1	44.2	0.70	0.41
CBH	1	43.8	0.02	0.88	1	36.3	1.24	0.27
NAG	1	35.0	0.49	0.49	1	44.1	2.47	0.12
PPO	1	30.1	0.00	0.97	1	13.6	1.30	0.27
Px	1	39.9	0.05	0.83	1	23.9	0.00	1.00
Litter moisture	1	37.4	17.6	0.00	1	42.7	16.0	0.00
N	1	39.0	0.55	0.46	1	43.0	0.20	0.66
P	1	41.1	0.52	0.48	1	44.9	2.95	0.09

W, soil warming; T, time; N, leaf litter nitrogen concentration; W  $\times$  T, interaction between warming and time; P, leaf litter phosphorus concentration.

experimental period, significant warming effects on litter moisture occurred for both Chinese fir litter and *C. kawakamii* litter, which may be due to the substantial increase in evaporation in subtropical forests in response to warming, consistent with previous studies (Prieto et al., 2019; Morrison et al., 2019).

#### 4.2. Warming effect on litter EEAs and microbial biomass

No significant warming effects on the microbial biomass C of either *C. kawakamii* or Chinese fir litter may reflect little warming effect on litter microbial C use efficiency, which rejected our hypothesis (2) that

warming may increase microbial biomass. Microbial biomass responses to manipulative warming are highly variable, with higher (Belay-Tedla et al., 2009), lower (Frey et al., 2008) or unvarying (Biasi et al., 2008) microbial biomass documented. Unvarying microbial biomass in this study may be ascribed either to direct soil heating by cable or high warming magnitude (+4 °C), which inhibit the microbial growth (Lu et al., 2013).

It is well known that enzyme kinetics are temperature sensitive (Davidson and Janssens, 2006), so we expected that warming to stimulate EEAs. However, this study showed an interactive effect of warming  $\times$  time on six EEAs, including AP, BG, CBH, NAG, PPO, and Px

(Fig. 3,  $P < 0.01$ ). This indicates that the warming effect varied with season, which partly rejected our hypothesis (2). Specifically, warming significantly reduced EEAs of AP,  $\beta$ G, CBH, NAG, and PPO in *C. kawakamii* litter. Similar patterns were detected in the study in a post-harvest forest (McDaniel et al., 2013) and a handful of other studies (Allison and Treseder, 2008; Cusack et al., 2010; Kardol et al., 2010). The underlying mechanisms remain unclear and could be due to interactive effects or concomitant decreases in soil moisture with warming (Carlyle et al., 2011). No significant warming effects on AP and  $\beta$ G in Chinese fir litter, and on Px in *C. kawakamii* litter in this study, was in line with a study in alpine grassland on Tibetan plateau (Jing et al., 2014), which could be ascribed to little warming effects on microbial biomass in both studies. In addition, the positive warming effect on the EEAs of PPO, and Px in Chinese fir litter, particularly at the later decomposition stage, was consistent with a recent global meta-analysis (Meng et al., 2019), which indicated that warming led to decreases in soil labile C and increases in recalcitrant C compounds, consequently stimulated oxidative EEAs. Theoretically, EEAs increase with temperature, and thus, climate warming will at least increase the rate of enzymatically catalyzed reactions (Wallenstein and Weintraub, 2008). However, microbes may decrease enzyme synthesis and secretion in response to warming (Burns et al., 2013; Wallenstein et al., 2012). Thus, owing to the counteracting effects of enzyme production and degradation, it is still difficult to generalize the effects of warming on EEAs.

#### 4.3. Warming effect on litter decomposition

The litter decomposition rate, driven mainly by microbial activity, is largely temperature dependent (Davidson and Janssens, 2006; Kirschbaum, 2006). In terrestrial ecosystems, warming generally leads to reduced soil and litter moisture content, which together affect litter decomposition via their direct influence on reaction kinetics and microbial physiology (Suseela and Tharayil, 2018). Thus, we anticipated that warming may increase litter decomposition in subtropical forests, where the mean annual precipitation is high (1638 mm between 1961 and 2016). In the present study, however, the warming effect on litter decomposition of *C. kawakamii* varied with time, and both positive and negative results were obtained, while the warming effect on Chinese fir litter was consistently negative during the 2-year decomposition period, which rejected our hypothesis (1). Because litter decomposition is a process of litter mass loss accumulation, the net effect of warming on *C. kawakamii* was insignificant, but that on Chinese fir was negative after the 2-year decomposition period. The lack of warming effects on *C. kawakamii* litter decomposition was in agreement with a study in the Harvard Forest, which considered that litter decomposition was retarded mainly by a warming-induced alteration of the fungal community, with mycorrhizal fungi increased and saprophytic fungi reduced (Morrison et al., 2019). In contrast, the negative warming effect on litter decomposition of Chinese fir was consistent with the results obtained in the study done in an Arctic tundra ecosystem, where warming-induced litter moisture decline inhibited fungal decomposition activities (Christiansen et al., 2016). Another study in an arid ecosystem found that a decline in litter moisture reduced litter microbial biomass (Prieto et al., 2019), thus decreasing litter decomposition.

Our analysis using the ANCOVA model indicated that litter mass losses in both forests were significantly correlated with litter moisture content but not with litter EEAs (Table 4; Table S1). Additionally, warming did not affect the litter microbial biomass of either Chinese fir or *C. kawakamii* at the end of the 2-year decomposition, although warming decreased the litter moisture in both cases (i.e., on average,  $-4.1\%$  for *C. kawakamii* and  $-9.2\%$  for Chinese fir). Thus, microbial activity may not be significantly influenced by the warming-induced decline in litter moisture and the primary driver of litter decay dynamics in the current experiment. This result is in accordance with findings in the Harvard Forest, where warming decreased litter moisture by  $6.9\%$  on average, and the authors argued that the litter moisture

content in both warming treatment and control was still within the optimal range for microbial activities (Morrison et al., 2019; Strickland et al., 2015). However, low litter moisture content, in other word, drier litter, can also restrict solute diffusion (Schimel et al., 2007), consequently affecting the litter leaching process. In subtropical areas, where annual rainfall is abundant, leaching loss plays a significant role in litter decomposition (Cleveland et al., 2006). The warming-induced litter moisture decline in this experiment may dampen leaching and reduce litter mass loss during the decomposition process. Furthermore, the Chinese fir is a conifer with a litter of thick hydrophobic cuticles, which dries out more rapidly than litter of broadleaf species (Xu et al., 2012; Zheng et al., 2014). The greater litter moisture decline in Chinese fir ( $-9.2\%$ ) than that in *C. kawakamii* ( $-4.1\%$ ) may more strongly affect the physical leaching of the litter, contributing to the greater retardation of litter decomposition under warming. Thus, litter moisture reduction under warming conditions may play a role in decreasing litter decomposition in subtropical forests. The present study recorded higher microbial biomass in natural forest (Fig. 4), which is consistent with previous studies showing that higher abundance and diversity of soil biota were observed in subtropical natural forests as compared to Chinese fir plantation (Islam et al., 2022; Meng et al., 2019). According to stabilization effects of biodiversity on ecosystem function (Loreau et al., 2001; Tilman et al., 2014), high diversity can buffer fluctuations in environmental conditions such as temperature (Luan et al., 2018), which could be another explanation for the insignificant warming effect on *C. kawakamii* litter decomposition in natural forest.

The ANCOVA model also indicated that after accounting for the effect of litter moisture, EEAs, N and P concentration, soil temperature, and soil moisture, the warming  $\times$  time or warming effect (Table 4) on the litter decomposition did not disappear for *C. kawakamii* and/or Chinese fir litter, which indicates that other factors may have affected litter decomposition. In addition to microbes, animals living in the soil also play an important role in litter decomposition because of their feeding and fragmentation effects (Bokhorst and Wardle, 2013). The litterbags of  $1\text{ mm} \times 1\text{ mm}$  mesh size used in this study may not fully prevent the entry of soil animals and the removal of microbial undecomposed litter. In response to warming, the soil nematode density decreased by  $34\%$  and  $54\%$  at  $0\text{--}10\text{ cm}$  soil depth (unpublished data) in the *C. kawakamii* forest and Chinese fir plantation, respectively. Although soil nematodes may not feed directly on litter, the decline in nematode abundance responding to warming may also influence litter decomposition via trophic cascading effect (García-Palacios et al., 2016). Future studies should include soil animals to explain the warming effect on litter decomposition.

Notably, the litters used in the current study were not collected in the warming plots. In fact, climate warming can alter plant metabolism and shape the final chemical composition of plant litter, thus indirectly influence decomposition. This indirect effect of warming on litter decomposition, however, remains largely unknown (Suseela and Tharayil, 2018), which necessitates additional study.

#### 4.4. Warming effect on litter C, N, P, and C fractions mass remaining

The release of nutrients and the C fraction were closely related to mass loss. Previous studies have indicated that warming increases litter decomposition, thereby accelerating the release of nutrients and C fraction (Xu et al., 2012). As there was no net warming effect on the mass loss of *C. kawakamii* litter, no warming effect on the C, N, P, and C fractions was released by the end of the 2-year decomposition experiment. In contrast, warming decreased the litter mass loss in Chinese fir. This decrease was mainly due to the higher mass remaining in the acid-insoluble fraction compared to that in the control, which may indicate that warming does not favor the decomposition of the litter recalcitrant C fraction. The change in the chemistry of litter residue is in agreement with a litter decomposition study in the Harvard Forest (Morrison et al., 2019), and it likely impacts the soil C stocks under



future climate change scenarios.

Litter decomposition, as a complex set of processes interwoven with chemical, physical and biological actions, is influenced by an ensemble of factors, including climate, litter chemistry, and decomposer activity. Thus, under warming scenario, using litter collected from warming plot is requested to accurately predict the litter decomposition. In the future, we still need to characterize the dynamics of soil fauna, which were excluded in this study. Bioturbation and litter fragmentation by soil fauna are likely important mechanisms affecting the litter decomposition in the subtropical forests, and need further consideration.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2022.108716>.

## References

- Aerts, R., 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. *Journal of Ecology* 94, 713–724.
- Allison, S.D., Lu, Y., Weihe, C., Goulden, M.L., Martiny, A.C., Treseder, K.K., Martiny, J. B.H., 2013. Microbial abundance and composition influence litter decomposition response to environmental change. *Ecology* 94, 714–725.
- Allison, S.D., Treseder, K.K., 2008. Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. *Global Change Biology* 14, 2898–2909.
- Almagro, M., Martínez-López, J., Maestre, F.T., Rey, A., 2017. The contribution of photodegradation to litter decomposition in semiarid Mediterranean grasslands depends on its interaction with local humidity conditions, litter quality and position. *Ecosystems* 20, 527–542.
- Anderson, B.T., 2012. Intensification of seasonal extremes given a 2°C global warming target. *Climatic Change* 112 (2), 325–337.
- Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Papale, D., 2010. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* 329, 834–838.
- Belay-Tedla, A., Zhou, X., Su, B., Wan, S., Luo, Y., 2009. Labile, recalcitrant, and microbial carbon and nitrogen pools of a tallgrass prairie soil in the US Great Plains subjected to experimental warming and clipping. *Soil Biology and Biochemistry* 41, 110–116.
- Biasi, C., Meyer, H., Rusalimova, O., Hämmerle, R., Kaiser, C., Baranyi, C., Daims, H., Lashchinsky, N., Barsukov, P., Richter, A., 2008. Initial effects of experimental warming on carbon exchange rates, plant growth and microbial dynamics of a lichen-rich dwarf shrub tundra in Siberia. *Plant and Soil* 307, 191–205.
- Bokhorst, S., Wardle, D.A., 2013. Microclimate within litter bags of different mesh size: implications for the 'arthropod effect' on litter decomposition. *Soil Biology and Biochemistry* 58, 147–152.
- Bonal, D., Burban, B., Stahl, C., Wagner, F., Herault, B., 2016. The response of tropical rainforests to drought—lessons from recent research and future prospects. *Annals of Forest Science* 73, 27–44.
- Bradford, M.A., Veen, G.F. (Ciska), Bonis, A., Bradford, E.M., Classen, A.T., Cornelissen, J.H.C., Crowther, T.W., De Long, J.R., Freschet, G.T., Kardol, P., Manrubia-Freixa, M., Maynard, D.S., Newman, G.S., Logtestijn, R.S.P., Viketof, M., Wardle, D.A., Wieder, W.R., Wood, S.A., van der Putten, W.H., 2017. A test of the hierarchical model of litter decomposition. *Nature Ecology and Evolution* 1, 1836–1845.
- Burns, R.G., DeForest, J.L., Marxsen, J., Sinsabaugh, R.L., Stromberger, M.E., Wallenstein, M.D., Weintraub, M.N., Zoppini, A., 2013. Soil enzymes in a changing environment: current knowledge and future directions. *Soil Biology and Biochemistry* 58, 216–234.
- Carey, J.C., Tang, J.W., Templer, P.H., Kroeger, K.D., Crowther, T.W., Burton, A.J., Dukes, J.S., Emmett, B., Frey, S.D., Heskell, M.A., Jiang, L., Machmuller, M.B., Mohan, J., Panetta, A.M., Reich, P.B., Reinsch, S., Wang, X., Allison, S.D., Bamminger, C., Bridgman, S., Collins, S.L., de Dato, G., Eddy, W.C., Enquist, B.J., Estiarte, M., Harte, J., Henderson, A., Johnson, B.R., Larsen, K.S., Luo, Y., Marhan, S., Melillo, J.M., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Rastetter, E., Reinmann, A.B., Reynolds, L.L., Schmidt, I.K., Shaver, G.R., Strong, A.L., Suseela, V., Tietema, A., 2016. Temperature response of soil respiration largely unaltered with experimental warming. *Proceedings of the National Academy of Sciences* 113, 13797–13802.
- Carlyle, C.N., Fraser, L.H., Turkington, R., 2011. Tracking soil temperature and moisture in a multi-factor climate experiment in temperate grassland: do climate manipulation methods produce their intended effects? *Ecosystems* 14, 489–502.
- Carreiro, M.M., Sinsabaugh, R.L., Repert, D.A., Parkhurst, D.F., 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. *Ecology* 81 (9), 2359–2359.
- Chen, J., Elsgaard, L., Groenigen, K., Olesen, J.E., Liang, Z., Jiang, Y., Lærke, P.E., Zhang, Y., Luo, Y., Hungate, B.A., Sinsabaugh, R.L., Jørgensen, U., 2020. Soil carbon loss with warming: new evidence from carbon degrading enzymes. *Global Change Biology* 26 (4), 1944–1952.
- Christiansen, C.T., Haugwitz, M.S., Priemé, A., Nielsen, C.S., Elberling, B., Michelsen, A., Grogan, P., Blok, D., 2016. Enhanced summer warming reduces fungal decomposer diversity and litter mass loss more strongly in dry than in wet tundra. *Global Change Biology*. <https://doi.org/10.1111/gcb.13362>.
- Chuckran, P.F., Reibold, R., Throop, H.L., Reed, S.C., 2020. Multiple mechanisms determine the effect of warming on plant litter decomposition in a dryland. *Soil Biology and Biochemistry* 145, 107799.
- Cleveland, C.C., Reed, S.C., Townsend, A.R., 2006. Nutrient regulation of organic matter decomposition in a tropical rain forest. *Ecology* 87 (2), 492–503.
- Conant, R.T., Ryan, M.G., Ågren, G.I., Birge, H.E., Davidson, E.A., Eliasson, P.E., Evans, S.E., Frey, S.D., Giardina, C.P., Hopkins, F.M., 2011. Temperature and soil organic matter decomposition rates—synthesis of current knowledge and a way forward. *Global Change Biology* 17, 3392–3404.
- Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A. E., et al., 2007. Global change and arctic ecosystems, is lichen decline a function of increase in vascular plant biomass? *Journal of Ecology* 89, 984–994.
- Crowther, T.W., Todd-Brown, K.E.O., Rowe, C.W., Wieder, W.R., Carey, J.C., Machmuller, M.B., Snoek, B.L., Fang, S., Zhou, G., Allison, S.D., Blair, J.M., Bridgman, S.D., Burton, A.J., Carrillo, Y., Reich, P.B., Clark, J.S., Classen, A.T., Dijkstra, F.A., Elberling, B., Emmett, B.A., Estiarte, M., Frey, S.D., Guo, J., Harte, J., Jiang, L., Johnson, B.R., Kröel-Dulay, G., Larsen, K.S., Laudon, H., Lavelle, J.M., Luo, Y., Lupascu, M., Ma, L.N., Marhan, S., Michelsen, A., Mohan, J., Niu, S., Pendall, E., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Reinsch, S., Reynolds, L.L., Schmidt, I.K., Sistla, S., Sokol, N.W., Templer, P.H., Treseder, K.K., Welker, J.M., Bradford, M.A., 2016. Quantifying global soil carbon losses in response to warming. *Nature* 540, 104–108.
- Cusack, D.F., Torn, M.S., McDowell, W.H., Silver, W.L., 2010. The response of heterotrophic activity and carbon cycling to nitrogen additions and warming in two tropical soils. *Global Change Biology* 16, 2555–2572.
- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440, 165–173.
- DeForest, J.L., 2009. The influence of time, storage temperature, and substrate age on potential soil enzyme activity in acidic forest soils using mub-linked substrates and l-dopa. *Soil Biology and Biochemistry* 41, 1180–1186.
- Field, et al., 2014. IPCC, 2014: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Frey, S.D., Drijber, R., Smith, H., Melillo, J., 2008. Microbial biomass, functional capacity, and community structure after 12 years of soil warming. *Soil Biology and Biochemistry* 40, 2904–2907.
- García-Palacios, P., Shaw, E.A., Wall, D.H., Hättenschwiler, S., 2016. Temporal dynamics of biotic and abiotic drivers of litter decomposition. *Ecology Letters* 19, 554–563.
- Glassman, S.I., Weihe, C., Li, J., Albright, M.B.N., Looby, C.I., Martiny, A.C., Treseder, K. K., Allison, S.D., Martiny, J.B.H., 2018. Decomposition responses to climate depend on microbial community composition. *Proceedings of the National Academy of Sciences* 115, 11994–11999.
- Hansen, W.D., Fitzsimmons, R., Olnes, J., Williams, A.P., 2020. An alternate vegetation type proves resilient and persists for decades following forest conversion in the north american boreal biome. *Journal of Ecology* 109, 85–98.
- Hendricks, J.J., Aber, J.D., Nadelhoffer, K.J., Hallett, R.D., 2000. Nitrogen controls on fine root substrate quality in temperate forest ecosystems. *Ecosystems* 3, 57–69.
- Hobbie, S.E., 1996. Temperature and plant species control over litter decomposition in alaskan tundra. *Ecological Monographs* 66, 503–522.
- Houghton, R.A., 2007. Balancing the global carbon budget. *Annual Review of Earth and Planetary Sciences* 35, 313–347.
- Islam, W., Saqib, H.S.A., Adnan, M., Tayyab, M., Wang, Z., Ding, X., Su, X., Huang, Z., Chen, H.Y.H., 2022. Natural forest chronosequence maintains better soil fertility indicators and assemblage of total belowground soil biota than Chinese fir monoculture in subtropical ecosystem. *Journal of Cleaner Production* 334, 130228.
- Jing, X., Wang, Y., Chung, H., Mi, Z., Wang, S., Zeng, H., He, J.S., 2014. No temperature acclimation of soil extracellular enzymes to experimental warming in an alpine grassland ecosystem on the Tibetan plateau. *Biogeochemistry* 117, 39–54.
- Kardol, P., Cregger, M.A., Campy, C.E., Classen, A.T., 2010. Soil ecosystem functioning under climate change: plant species and community effects. *Ecology* 91, 767–781.
- Kirschbaum, M.U.F., 2006. The temperature dependence of organic-matter decomposition—still a topic of debate. *Soil Biology and Biochemistry* 38, 2510–2518.

- Li, Y., Q. Y., L. M., Chen, S., Yang, Z., Lin, C., Yang, Y., 2018. Effects of artificial warming on different soil organic carbon and nitrogen pools in a subtropical plantation. *Soil Biology and Biochemistry* 124, 161–167.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294, 804–808.
- Lu, M., Zhou, X., Yang, Q., Li, H., Luo, Y., Fang, C., Chen, J., Yang, X., Li, B., 2013. Responses of ecosystem carbon cycle to experimental warming: a meta-analysis. *Ecology* 94, 726–738.
- Luan, J., Liu, S., Wang, J., Chang, S.X., Liu, X., Lu, H., Wang, Y., 2018. Tree species diversity promotes soil carbon stability by depressing the temperature sensitivity of soil respiration in temperate forests. *The Science of the Total Environment* 645, 623–629.
- Luo, Y., Wan, S., Hui, D., Wallace, L.L., 2001. Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413, 622–625.
- McDaniel, M.D., Kaye, J.P., Kaye, M.W., 2013. Increased temperature and precipitation had limited effects on soil extracellular enzyme activities in a post-harvest forest. *Soil Biology and Biochemistry* 56, 90–98.
- Meng, M., Lin, J., Guo, X., Liu, X., Wu, J., Zhao, Y., Zhang, J., 2019. Impacts of forest conversion on soil bacterial community composition and diversity in subtropical forests. *Catena* 175, 167–173.
- Meng, C., Tian, D., Zeng, H., Li, Z., Niu, S., 2019. Global meta-analysis on the responses of soil extracellular enzyme activities to warming. *The Science of the Total Environment* 705, 135992.
- Morrison, E.W., Pringle, A., Van Diepen, L.T.A., Grandy, A.S., Melillo, J.M., Frey, S.D., 2019. Warming alters fungal communities and litter chemistry with implications for soil carbon stocks. *Soil Biology and Biochemistry* 132, 120–130.
- Moorhead, D.L., Sinsabaugh, R.L., 2006. A theoretical model of litter decay and microbial interaction. *Ecological Monographs* 76, 151–174.
- Petraglia, A., Cacciatori, C., Chelli, S., Fenu, G., Carbognani, M., 2019. Litter decomposition: effects of temperature driven by soil moisture and vegetation type. *Plant and Soil* 435, 187–200.
- Piao, S., Fang, J., Ciais, P., Peylin, P., Huang, Y., Sitch, S., Wang, T., 2009. The carbon balance of terrestrial ecosystems in China. *Nature* 458, 1009–1013.
- Prieto, I., Almagro, M., Bastida, F., Querejeta, J.I., 2019. Altered leaf litter quality exacerbates the negative impact of climate change on decomposition. *Journal of Ecology* 107, 2364–2382.
- Rejmankova, E., Sirova, D., 2007. Wetland macrophyte decomposition under different nutrient conditions: relationships between decomposition rate, enzyme activities and microbial biomass. *Soil Biology and Biochemistry* 39, 526–538.
- Romero-Olivares, A.L., Allison, S.D., Treseder, K.K., 2017. Decomposition of recalcitrant carbon under experimental warming in boreal forest. *PLoS One* 12, e0179674.
- Ryan, M.G., Melillo, J.M., Ricca, A., 1990. A comparison of methods for determining proximate carbon fractions of forest litter. *Canadian Journal of Forest Research* 20, 166–171.
- Schimel, J., Balser, T.C., Wallenstein, M., 2007. Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88, 1386–1394.
- Schindlbacher, A., Rodler, A., Kuffner, M., Kitzler, B., Sessitsch, A., Zechmeister-Boltenstern, S., 2011. Experimental warming effects on the microbial community of a temperate mountain forest soil. *Soil Biology and Biochemistry* 43 (7), 1417–1425.
- Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., McClaugherty, C.A., Rayburn, L., Repert, D., Weiland, T., 1993. Wood decomposition: nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. *Ecology* 74, 1586–1593.
- Strickland, M.S., Keiser, A.D., Bradford, M.A., 2015. Climate history shapes contemporary leaf litter decomposition. *Biogeochemistry* 122, 165–174.
- Suseela, V., Tharayil, N., 2018. Decoupling the direct and indirect effects of climate on plant litter decomposition: accounting for stress-induced modifications in plant chemistry. *Global Change Biology* 24, 1428–1451.
- Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. *Annual Review of Ecology Evolution and Systematics* 45, 471–493.
- Wallenstein, M.D., Haddix, M.L., Lee, D.D., Conant, R.T., Paul, E.A., 2012. A litter slurry technique elucidates the key role of enzyme production and microbial dynamics in temperature sensitivity of organic matter decomposition. *Soil Biology and Biochemistry* 47, 18–26.
- Wallenstein, M.D., Weintraub, M.N., 2008. Emerging tools for measuring and modeling the in situ activity of soil extracellular enzymes. *Soil Biology and Biochemistry* 40, 2098–2106.
- Ward, S.E., Orwin, K.H., Ostle, N.J., Brionse, M.J.I., Thomson, B.C., Griffiths, R.I., Oakley, S., Quirk, H., Bardgett, R.D., 2015. Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. *Ecology* 96 (1), 113–123.
- Wardle, D.A., Walker, L.R., Bardgett, R.D., 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305, 5683.
- Waring, B.G., Weintraub, S.R., Sinsabaugh, R.L., 2014. Ecoenzymatic stoichiometry of microbial nutrient acquisition in tropical soils. *Biogeochemistry* 117 (1), 101–113.
- Xu, W., Yuan, W., Dong, W., Xia, J., Liu, D., Chen, Y., 2013. A meta-analysis of the response of soil moisture to experimental warming. *Environmental Research Letters* 8, 731–735.
- Xu, Z.F., Pu, X.Z., Yin, H.J., Zhao, C.Z., Liu, Q., Wu, F.Z., 2012. Warming effects on the early decomposition of three litter types, Eastern Tibetan Plateau, China. *European Journal of Soil Science* 63, 360–367.
- Yang, Y.S., Guo, J.F., Chen, G.S., Yin, Y.F., Gao, R., Lin, C.F., 2009. Effects of forest conversion on soil labile organic carbon fractions and aggregate stability in subtropical China. *Plant and Soil* 323, 153–162.
- Zheng, W., Lin, K., X. B., Zhao, C., K. C., Guo, Y., 2014. Comparative study of water holding capacity of litter in seven different trees' species. *Journal of water and soil conservation* 28, 88–91 (In Chinese with English abstract).