



# Climate warming and nitrogen deposition had no significant interaction effect on litter decomposition of subtropical mountain forest in Southwest China

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## Abstract

**Background and aims** Litter decomposition is essential for the global carbon cycle, which is affected by environmental factors. In the context of global warming and increasing nitrogen deposition, the responses of litter decomposition are unclear in subtropical forests.

**Methods** Here, we carried out an interaction experiment of warming (3.3 °C) and nitrogen addition (50 kg ha<sup>-1</sup> yr<sup>-1</sup>) and a recovery experiment (remove warming and nitrogen addition treatments) in a subtropical evergreen broad-leaved forest for four years in total.

**Results** The results showed that during the treatment period, warming, nitrogen addition, and their combination significantly decreased litter decomposition according to the k values by 35.8%, 23.0%, and 42.2%, respectively. However, there was no

significant interaction effect between warming and nitrogen addition. Litter decomposition rates quickly returned to the same level during the two-year recovery period. Variance partitioning analysis (VPA) and covariance analysis (ANCOVA) simultaneously confirmed that warming and nitrogen addition significantly affected litter decomposition. VPA and ANCOVA also showed that soil temperature and water content significantly contributed to the decomposition rate during the treatment period.

**Conclusions** This study suggests that warming and nitrogen addition significantly inhibit litter decomposition, but this effect is not sustainable.

**Keywords** Leaf litter · Climate warming · Nitrogen addition · Soil physical properties · Initial decomposition degree

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## Introduction

Litter decomposition is essential in the global carbon cycle (Daan et al. 2018). Current studies suggest that litter decomposition mainly by microorganisms, being influenced by climate, litter quality, soil environmental factors, and the initial priming effect (Ge et al. 2013; Liu et al. 2023). Climate warming and increasing nitrogen deposition are important contributors to global climate change (De Frenne et al. 2021; Liu et al. 2011). Therefore, an increasing number of studies have focused on the effects

of warming and nitrogen addition on litter decomposition (Henry and Moise. 2015; Ma et al. 2011). However, the effects of warming, nitrogen deposition, and their interaction on litter decomposition in subtropical mountain forests are not clear (Gong et al. 2015).

Previous studies have shown that the effect of warming on the litter decomposition rate may be easily affected by water conditions in the environment (Butenschoen et al. 2011; Gorecki et al. 2021). A certain degree of warming can increase the activity of microorganisms, thereby promoting litter decomposition (Aerts 2006). However, the decrease in soil water content caused by warming inhibits microbial activity, which limits litter decomposition (Lee et al. 2014). Some studies have reported that warming tends to inhibit litter decomposition in grassland ecosystems (Chuckran et al. 2020; Penner and Frank 2018). Previous studies have confirmed that in some ecosystems with adequate water conditions, such as rivers and wetlands, warming usually promotes litter decomposition (Ferreira and Canhoto 2014; Gao et al. 2022; Migliorini and Romero 2020). In forest ecosystems, some studies have reported that warming promotes litter decomposition (Liu et al. 2015; Liu et al. 2017), while others have reported a negative effect (Li et al. 2022; Liu et al. 2022a). Therefore, the effects of warming might be closely linked to the intricate hydrological processes within mountain forest ecosystems (Brigham et al. 2018).

Similar to the effect of warming on decomposition, the response of litter decomposition to external nitrogen addition has not been fully elucidated (Zhang et al. 2018). Previous studies have shown that nitrogen addition may promote litter decomposition (Song et al. 2018; Zhang et al. 2019), inhibit litter decomposition (Peng et al. 2022; Zhang et al. 2022), or have no effect (Růžek et al. 2021). It is speculated that the different effects of nitrogen addition on litter decomposition may be closely related to the local atmospheric nitrogen deposition level, litter quality, and amount and form of added nitrogen (Knorr et al. 2005; Schulte-Uebbing and de Vries 2018). Besides, the nitrogen added may also lead to changes in soil water content by influencing the water absorption efficiency of dominant plant roots, thus indirectly influencing litter decomposition (Henriksson et al. 2021). Therefore, the effects of warming and nitrogen addition on the litter decomposition rate may be

affected by various factors and are highly uncertain (Zou et al. 2022). Current research on forest ecosystems has focused on the impact of individual factors on litter decomposition (Li et al. 2022; Wu et al. 2019; Xia and Wan, 2013). The interaction between warming and nitrogen addition on litter decomposition is rarely involved (Henry and Moise 2015; Moise and Henry 2014).

Subtropical forests play an essential role in the global terrestrial ecosystem carbon cycle and contain a wide range and a large amount of litter (Tan et al. 2011; Wu et al. 2014). Currently, subtropical forests in southwestern China suffer from climate warming and high nitrogen deposition (Huang et al. 2015; Li et al. 2018; Tian et al. 2018;). However, few studies have explored the response of litter decomposition to warming and nitrogen addition in similar regions (Zhang et al. 2017). Therefore, we hypothesized that 1) warming and nitrogen addition promote litter decomposition and that there is a significant positive interaction, and 2) warming and nitrogen addition have sustained effects on litter decomposition after warming and nitrogen addition treatments are stopped. Here, we conducted a comprehensive experiment that involved the application of warming and nitrogen addition treatments. Additionally, we performed a subsequent recovery experiment where all treatments were discontinued. The primary objective of these experiments was to test our hypotheses and gain a deeper understanding of the effects of these treatments on litter decomposition within the subtropical forest ecosystem.

## Materials and methods

### Study site description

This study was conducted at the Ailaoshan Station for Subtropical Forest Ecosystem Studies (24°32'N, 101°01'E; 2480 m above sea level), which is located in Jingdong County, Yunnan Province. It is an old-growth subtropical evergreen broad-leaved forest with a stand age > 300 years (Tan et al. 2011), and a tree density of 2728 ha<sup>-1</sup> (Lu et al. 2021). It is characterized by a subtropical mountain climate with an annual average temperature of 11.3 °C and annual precipitation of 1778 mm (Wu et al. 2014). There is a distinct annual rainy season from May to October. The soil

nitrogen content is  $6.53 \pm 0.83 \text{ g kg}^{-1}$  (Lu et al. 2017). The local background value of nitrogen deposition is  $10.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (Shi et al. 2017). The soils are Alfisols, which is acidic ( $\text{pH} < 5$ ) (Chan et al. 2006). The main tree species of the forest are *Machilus gambelii*, *Castanopsis wattii*, and *Hartia sinensis*. The forest litterfall is  $864 \text{ g m}^{-2} \text{ year}^{-1}$  (Wu et al. 2014).

### Experimental design and setup

In this study, we selected 12 subplots ( $1 \times 1 \text{ m}$ ) in a  $30 \times 40 \text{ m}$  experimental plot. We conducted two-factor experiments with two levels: control (CK), warming (W), nitrogen addition (N), and warming combined with nitrogen addition (WN). Each treatment had three replications and included treatment and recovery periods. For warming, we utilized three 90 cm lamps (with a lampshade length of 100 cm), each with a power of 200 W. These lamps were arranged in a triangle formation, positioned 1.2 m above the soil surface, and continuously powered for heating. The lamps were angled at  $30^\circ$  to the ground to optimize heat gathering. We added ammonium nitrate ( $\text{NH}_4\text{NO}_3$ ) solution at  $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  for the nitrogen treatments, which were divided into 12 months per year. Therefore, we weighed 1.19 g of  $\text{NH}_4\text{NO}_3$ , dissolved it in 500 ml of ultrapure water, and carried out monthly even spraying onto both litter and soil in the subplots. We also spread the same volume of ultrapure water on the subplots without nitrogen addition.

Fresh foliage litter samples were collected from several locations within the subtropical forest using  $1 \times 1 \text{ m}$  nylon nets hanging 1 m above the ground during the dry season from October to December 2017 (Wu et al. 2022). To avoid the impact of differences in the initial litter water content on the assessment of litter decomposition rates, we first air-dried and then oven-dried the leaf litter ( $60^\circ \text{C}$  for 72 hours). Twelve litter bags (2 mm mesh,  $10 \times 15 \text{ cm}$  in size) were prepared for each subplot. To facilitate optimal contact between the litter bag and the soil, we carefully removed the visible litter before the commencement of the experiment. Then, we placed the decomposition bags on the soil surface, with each bag 10 cm apart from each other. The decomposed litter samples were collected three times per year. The mass of each sample was measured before the decomposition experiment began, and the initial mass ( $M_i$ ) of litter

samples was approximately 4 g. Litter decomposition during the treatment period was terminated on December 31, 2019.

The recovery experiment started on March 31, 2021, and also lasted for two years. Fresh litter leaves were collected from early January to mid-March 2021 using the same method employed during the treatment period. Here, we prepared 6 litter bags (2 mm mesh, size  $15 \times 30 \text{ cm}$ ) for each subplot with an initial mass of approximately 14 g (to ensure consistent coverage of the designated area throughout the treatment period, Fig. 1) for the recovery period.

### Data collection and analysis

As mentioned above, we collected litter bags every four months for two years for a total of 12 times during the treatment and recovery periods. After each collection of litter collection, we cleaned, washed, air-dried, and subsequently dried them at  $60^\circ \text{C}$  for 72 hours (Liu et al. 2023; Wu et al. 2022). The litter dry weight ( $M_f$ ) was then weighed and recorded using an electronic analytical balance (accuracy 0.01 g).

We calculated the decomposition coefficient (k value) during the study period using the following decay model (Olson 1963):

$$RR = \frac{M_f}{M_i} \quad (1)$$

$$RR = e^{-kt} \quad (2)$$

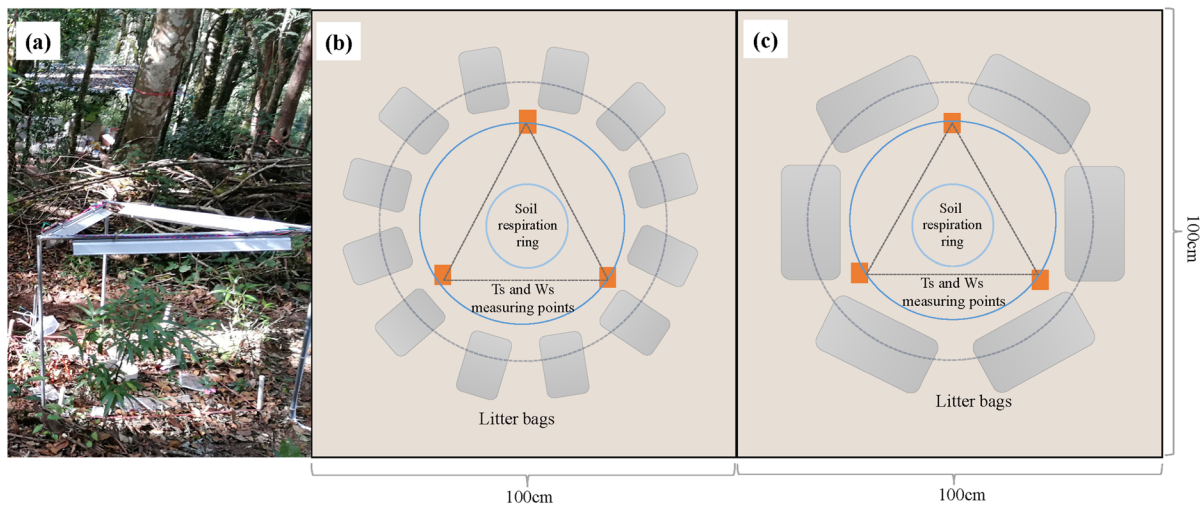
where RR is the residual rate and t (yr) is the corresponding decomposition time.

We used four months as a stage, so the 24 months divided the litter decomposition period into six stages and the decomposition rate (SDR, %/month) of each stage was calculated.

$$SDR_s = \frac{RR_{s-1} - RR_s}{RR_{s-1}} \div T_{stage} \div 12 \times 100\% \quad (3)$$

where s is the stage number from 1 to 6, and  $T_{stage}$  is the stage time (yr).

We utilized an automated digital thermometer (6310; Spectrum, Illinois, USA) and time domain reflectometry (MP-KIT; Beijing Channel, Beijing, China) to manually assess the soil temperature ( $T_s$ ) and water content (Ws) of each plot from January 2017 to March 2023. To minimize the impact of



**Fig. 1** Picture of the warming device (a), schematic diagram of litter bag positions, and soil temperature (Ts) and water content (Ws) measurement positions during the treatment period (b) and recovery period (c)

spatial heterogeneity on soil temperature and water content measurements, we randomly selected three points within the inner edge of the leaf litter bag for measurement. The measurements were conducted three times a month (every 10 days) at a 5-cm depth from the surface of the exposed soil (Fig. 1). We divided them into three periods: before treatment (2017.01–2017.12, background of each subplot), during the treatment period (2018.01–2019.12, treatment effect), and the recovery period (2021.04–2023.03). The averages of each period were used to test the treatment effect, taking the before-treatment period as the background value and calculating the ratio value of the treatment and recovery periods. We also divided the soil temperature and water content into six stages (SST and SSW) corresponding to the SDR in the treatment and recovery periods.

One-way ANOVA and Duncan's test were used to test the differences in each period's soil temperature, water content, ratio values, and k values among treatments. Two-way ANCOVA was used to test each period's k value and SDR difference. The warming and nitrogen addition treatments were the fixed factors, and soil water content was the covariate for k values. SST, SSW, and initial decomposition degree (IDD) were the covariates for the SDR. All the data passed the normality and homoscedasticity tests. The effects of warming, nitrogen addition, IDD, SST, and SSW on the SDR were analyzed by variance partitioning

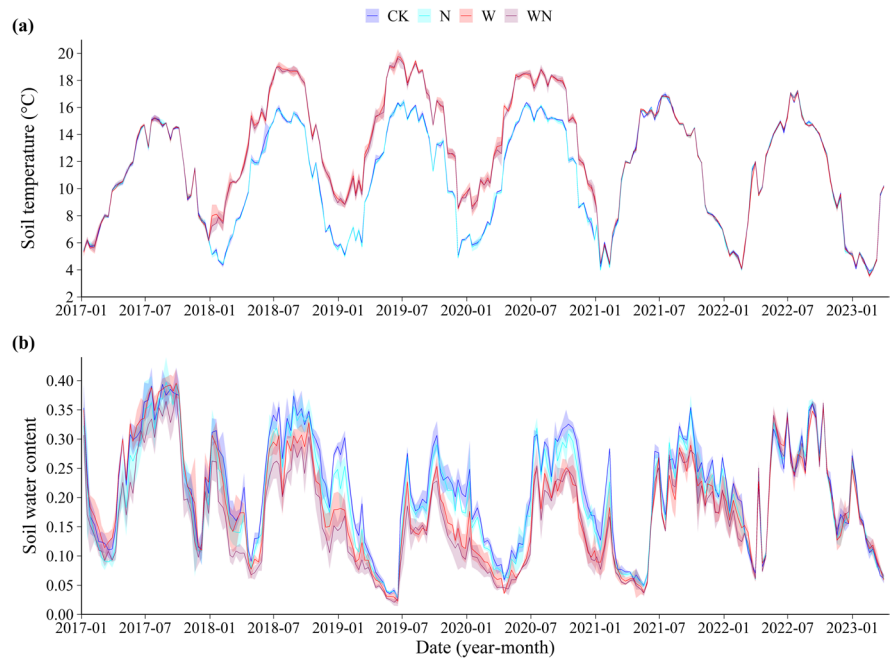
analysis (VPA). The variance inflation factor (VIF) test was conducted, and all VIF values were less than 4. All the statistical charts were generated using R software (version 4.3.0) and R Studio with the readxl, ggplot2, lubricate, ggpubr, car, gtsummary, agricolae, and ggbeeswarm packages.

## Results

### Effects on soil microenvironmental factors

Warming and nitrogen addition did not change the seasonal variation in soil temperature and water content in this study (Fig. 2). There was no significant difference in temperature between all plots before and after treatment (Fig. 3a). Soil temperature had no significant difference among each plot before treatment, only in the treatment period, was the temperature of the warming group and the warming and nitrogen addition group significantly higher than that of the non-warming group, with a temperature increase of 3.3 °C (Fig. 3a, b). In contrast to soil temperature, the soil water content had high heterogeneity before treatment (Fig. 3a, c). Considering the heterogeneity of the initial water content, the soil water content in the treatment stage and recovery stage of the sample plot was compared with soil water content before treatment to show its change (Fig. 3d). The results showed

**Fig. 2** Mean soil temperature (Ts) and water content (Ws) at 5 cm depth in the environmental plots of the control (CK), nitrogen addition (N), warming (W) and warming and nitrogen (WN) treatments from January 2017 to January 2023



that during treatment period, the soil water content in the W and WN plots was significantly lower than that in the CK and N addition plots (Fig. 3d). In general, the soil temperature returned to the same level in all plots after removal of warming and nitrogen addition treatments (recovery period). Meanwhile, the soil water content in the other plots also recovered to similar levels except for that in the warming treatment plots.

#### Effects of warming and nitrogen addition on litter decomposition

In the treatment period, the differences in the litter residual rate increased with decomposition time (Fig. 4a). One-way ANOVA showed that all treatments (N, W, WN) significantly affected the litter decomposition rate in terms of  $k$  value and SDR in the treatment period, and the  $k$  values of CK, N, W, and WN were  $0.422 \pm 0.008$ ,  $0.325 \pm 0.046$ ,  $0.271 \pm 0.032$  and  $0.244 \pm 0.039$  (mean  $\pm$  SD), and the mean values of SDR were  $3.20 \pm 0.12$ ,  $2.33 \pm 0.28$ ,  $2.16 \pm 0.45$ , and  $1.85 \pm 0.30\%/month$  (mean  $\pm$  SD), respectively. The N, W, and WN treatments reduced the  $k$  values by 23.0%, 35.8%, and 42.2%, and reduced the SDR by 27.2%, 32.5%, and 42.2%, respectively (Fig. 4b, d). In the recovery period, there was no significant

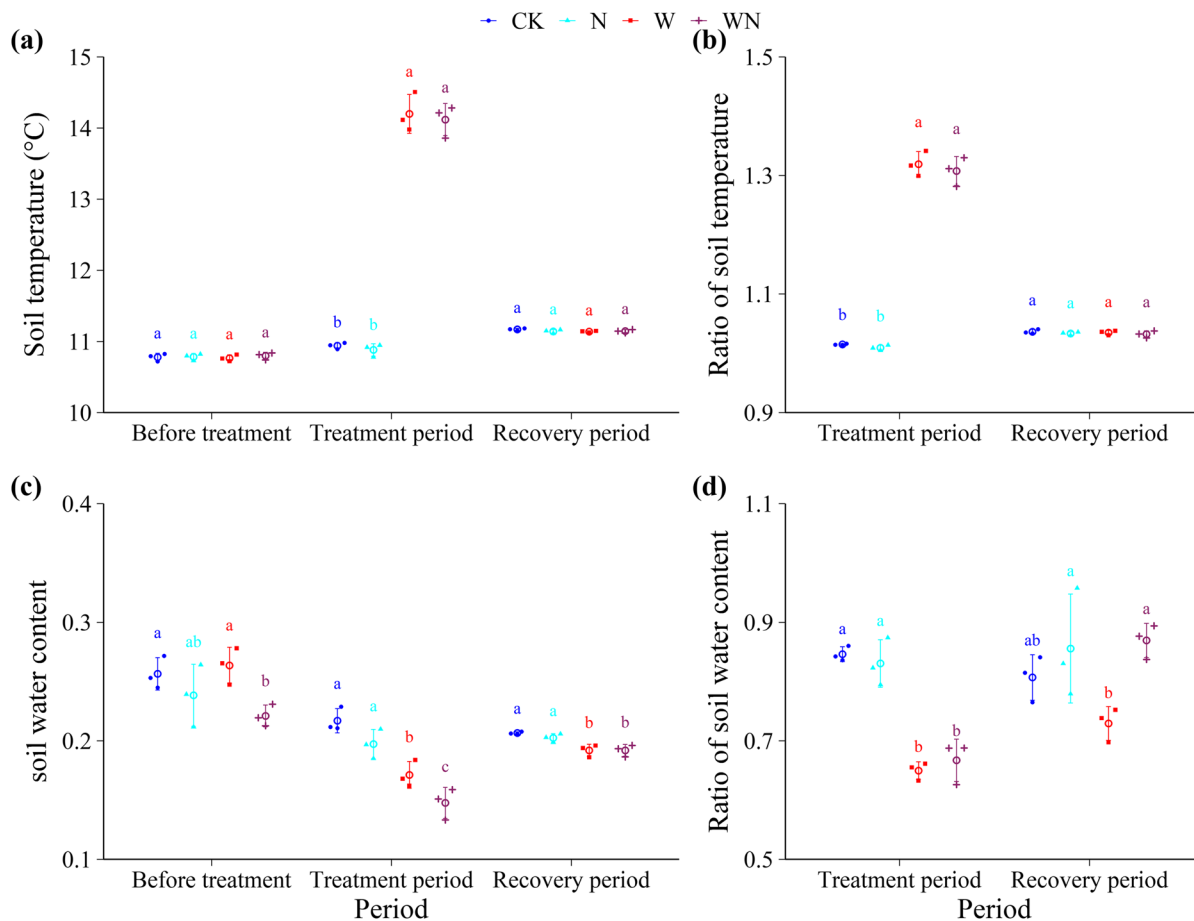
difference in  $k$  values and SDR between treatments (Fig. 4b, d). Two-way ANCOVA showed that warming and nitrogen addition had significant effects on the  $k$  values and mean SDR without considerable interactions, and the covariate had no significant effect (Table 1). Further analysis also showed no difference after the warming and nitrogen addition treatments were terminated (Table 1), suggesting that the effects of warming and nitrogen addition on litter decomposition were not persistent.

#### Factors affecting litter decomposition

To explore the factors affecting litter decomposition, we used the litter mean SDR, IDD, and corresponding soil environmental factors for further analysis (Figs. 4c and 5). Two-way ANCOVA showed that the SDR significantly differed due to warming and nitrogen addition, and was affected by SST and SSW (Table 2). Nevertheless, only SST, SSW, and IDD in the recovery period greatly influenced the SDR (Table 2), suggesting that the effect of the treatments disappeared.

VPA showed that SST, warming, and SSW significantly contributed to the SDR by 36.7%, 25.3%, and 24.5%, respectively, during the treatment period, IDD





**Fig. 3** Average soil temperature and water content in different treatment plots at different periods (before treatment, treatment period, recovery period) (a, c), and ratio of soil temperature and water content (soil temperature and water content data

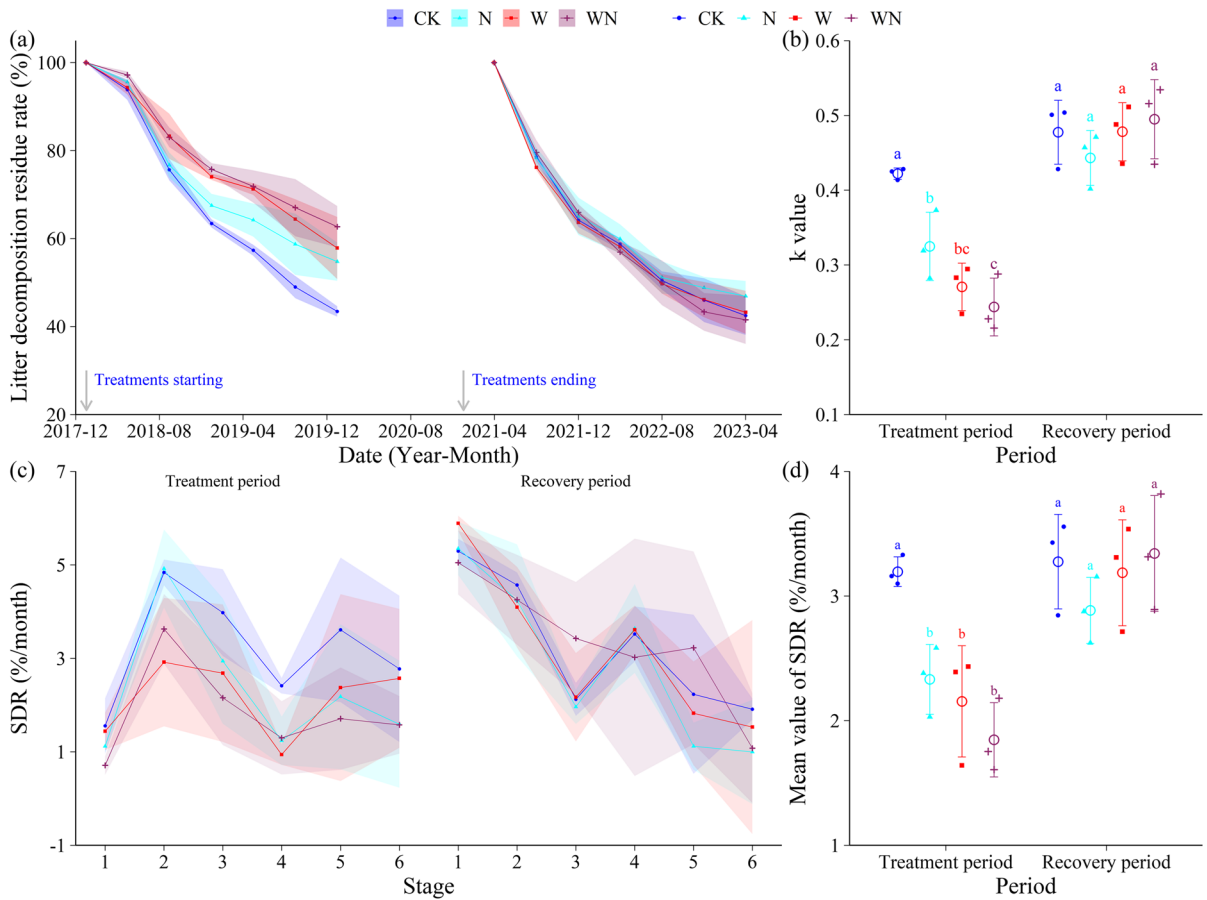
from the treatment and recovery periods were compared with those in the same plots before treatment to indicate the change in soil environmental factors) (b, d)

and nitrogen addition contributed 8.3% and 5.2%, respectively (Fig. 6a). During the recovery period, IDD significantly contributed to 60.4% of the SDR; SST and SSW contributed 20.9% and 7.1%, respectively, but these differences were not significant (Fig. 6b).

## Discussion

Temperature is a critical factor affecting litter decomposition (Liu et al. 2023; Wu et al. 2022). In general, modest warming promotes the activity of microorganisms to some extent, thereby promoting litter decomposition (Liu et al. 2015). Previous research reported

that an increase in soil temperature by 1.84 °C significantly promoted litter decomposition by 10.3% (Gao et al. 2022). Other studies also found similar results (Ferreira and Canhoto 2014; Migliorini and Romero 2020). However, the results of this study showed that the litter decomposition rate decreased significantly when the temperature increased by 3.3 °C (Fig. 3c, d), similar to previous studies (Li et al. 2022; Liu et al., 2022a; Penner and Frank 2018). We speculate that this difference may be related to the decrease in soil water content caused by warming. In this study, the soil water content under warming treatment decreased by 18.2%, which was consistent with earlier studies in forest ecosystems (Li et al. 2022; Liu et al. 2015, 2017). The decreasing soil water content may



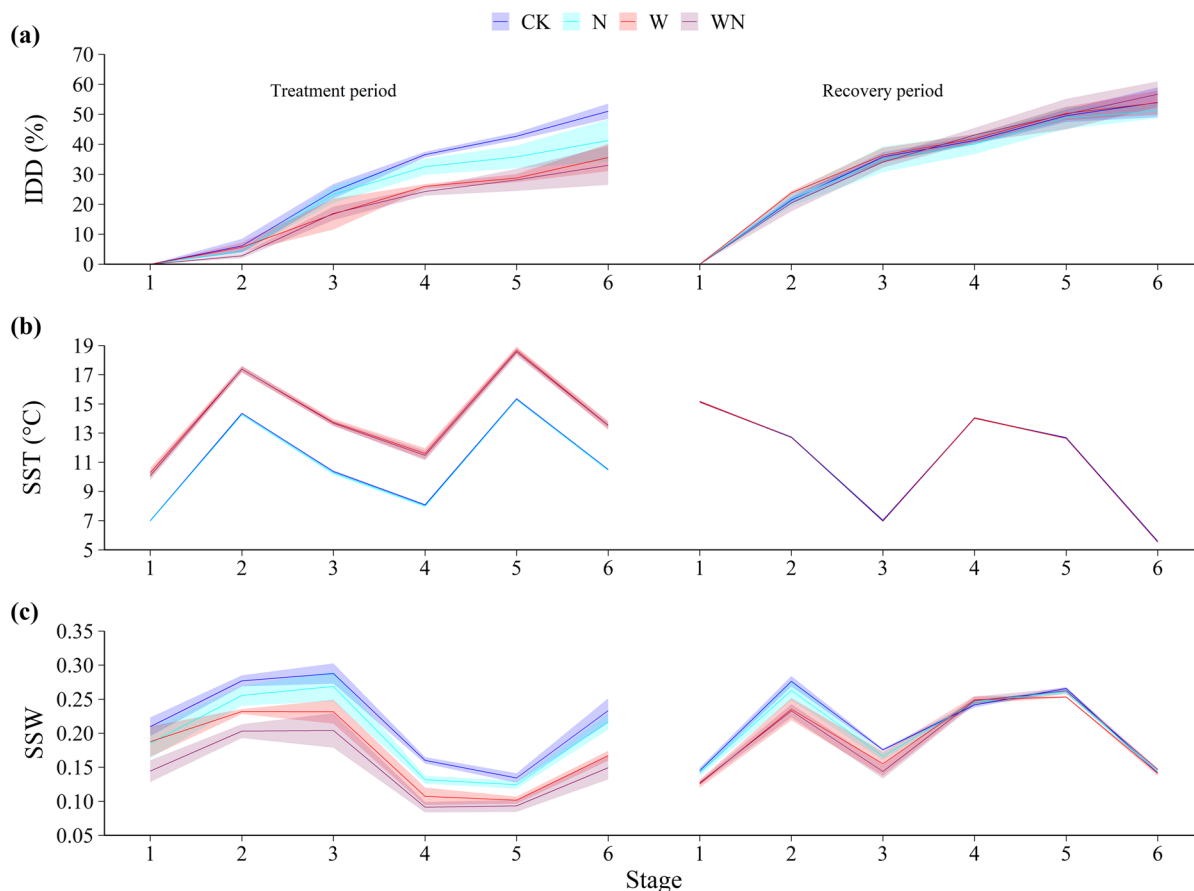
**Fig. 4** Litter residue rate (a), and K value (b) in the treatment and recovery periods. Stage decomposition rate (SDR) (c) and mean SDR in the treatment and recovery periods (d)

**Table 1** Covariance analysis of nitrogen, warming, their interactions, and soil water content on litter decomposition rate (K values) and litter stage decomposition rate (SDR) during treatment and recovery periods

Factor	K values				SDR			
	Treatment period		Recovery period		Treatment period		Recovery period	
	F value	P	F value	P	F value	P	F value	P
N	8.9475	0.0202	0.1198	0.7394	10.5322	0.0141	0.2468	0.6345
Warming	31.3716	0.0008	1.0645	0.3365	17.8359	0.0039	0.6014	0.4634
N × Warming	2.9987	0.1269	0.4867	0.5079	2.6315	0.1488	0.8996	0.3745
Ws	0.0621	0.8103	1.2334	0.3034	0.5012	0.5018	0.6553	0.4449

significantly inhibit the activity of microorganisms and soil fauna, thus inhibiting decomposition (Butenschoten et al. 2011; González and Seastedt 2001; Liu et al. 2022b). Meanwhile, the dry heat stress caused by warming may also indirectly inhibit litter decomposition by inhibiting the quantity and activity of soil

fauna (Barajas-Guzmán and Alvarez-Sánchez 2003; Collison et al. 2013). VPA showed that soil temperature and water content were positively correlated with the litter decomposition rate. In contrast, the warming treatment was significantly negatively correlated with the litter decomposition rate (Fig. 6a).



**Fig. 5** Initial decomposition degree (IDD, %), soil temperature (SST, °C) and soil water content (SSW) at each stage (4 months) of the treatment and recovery periods

**Table 2** Covariance analysis of nitrogen, warming, their interactions, SST, SSW and IDD on litter stage decomposition rate (SDR, %) during treatment and recovery periods

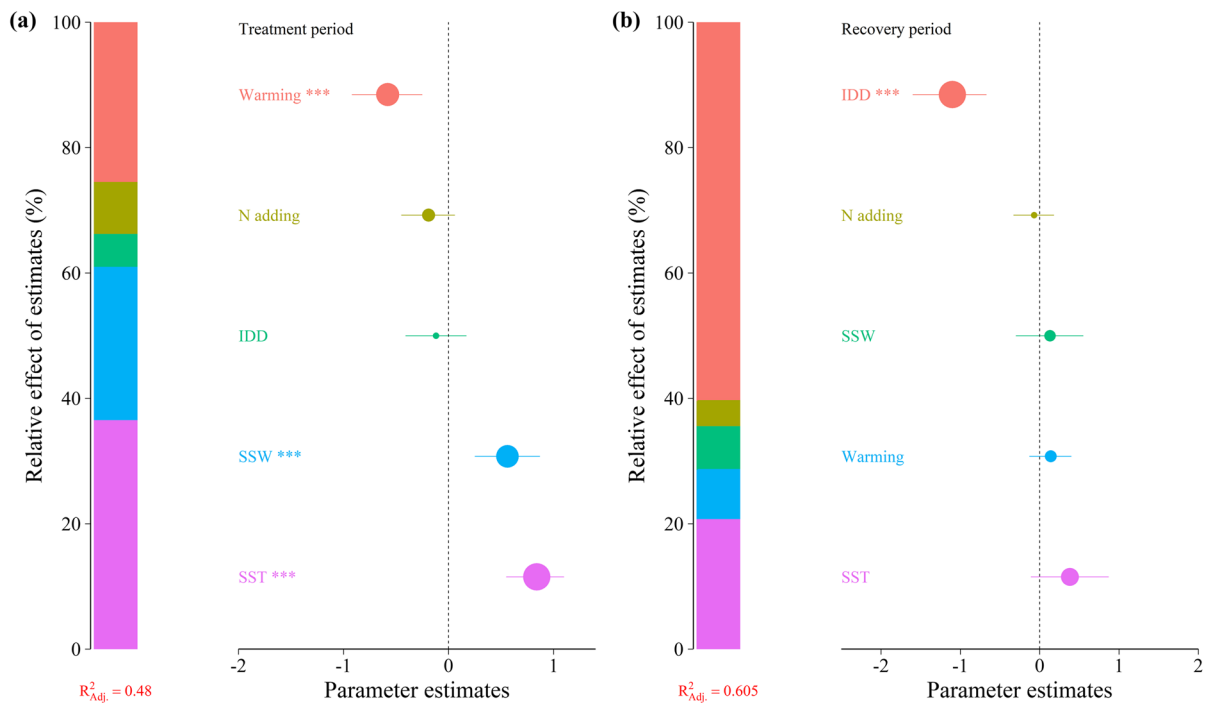
Effect	Treatment period		Recovery period	
	<i>F</i> value	<i>P</i>	<i>F</i> value	<i>P</i>
N	5.62	0.02	0.21	0.65
Warming	9.51	0.01	0.51	0.48
N × Warming	1.63	0.21	1.22	0.27
SST	34.93	<0.001	56.91	<0.001
SSW	15.77	<0.001	25.50	<0.001
IDD	2.64	0.11	28.24	<0.001

This further indicated that the inhibitory effect of a decrease in soil water content on litter decomposition may be much greater than the promoting effect of soil warming. Therefore, the impact of warming on litter

decomposition in forest ecosystems depends on the combined effects of warming and the adverse effects of changes in soil water conditions caused by warming (Canessa et al. 2020; Ferreira and Canhoto 2014).

Previous studies suggested that nitrogen addition could improve litter quality (with a lower C/N ratio), thereby promoting litter decomposition to a certain extent (Jiang et al. 2014; Tian et al. 2018). However, similar conclusions were not reached in our study. In agreement with other authors, this difference may be closely related to the concentration of nitrogen added (Tu et al. 2014; Zhang et al. 2016). Previous studies have shown that a low concentration of nitrogen addition promotes litter decomposition, while a high concentration inhibits litter decomposition (Knorr et al. 2005). In this study, the nitrogen concentration was 50 kg ha<sup>-1</sup> yr<sup>-1</sup>, which is approximately 3 to 4 times the local atmospheric nitrogen deposition (Liu et al.





**Fig. 6** The proportion of influencing factors (warming, N adding, IDD, SSW and SST) on litter decomposition rate in treatment and recovery stages (P values are expressed as an asterisk: \*\*\*  $P \leq 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ , #  $P < 0.1$ )

2002). Previous studies have shown that continuous high concentrations of nitrogen addition might alter microbial community composition and function (Wu et al. 2019), inhibit the activity of catabolic enzymes (Jiang et al. 2014), and reduce N dependence from litter, thereby inhibiting litter decomposition. Furthermore, the addition of high nitrogen concentrations may also result in a decline in soil arthropod group richness and individual abundance, thereby inhibiting litter decomposition (Tie et al. 2021).

In this study, warming and nitrogen addition significantly inhibited litter decomposition (Fig. 4b, d). However, there was no significant interaction effect between warming and nitrogen addition (Table 1), which differs from previous research conclusions in grassland ecosystems and wetlands (Ma et al. 2011; Tao et al. 2019). It is suggested that this may be related to the decreased soil water content caused by the warming treatment (Chuckran et al. 2020). Under low soil water content, the litter decomposition rate was significantly inhibited and the inhibitory effect of nitrogen addition was weakened (Fig. 3c, d), agreeing with the previous study's result (Yan et al.

2018). Therefore, the inhibition effect of WN on litter decomposition did not show a noticeable amplification effect compared to warming and nitrogen addition alone. In addition, it was observed that the soil water content of the initial WN plot was also relatively lower than that of the other treatment groups (Fig. 3c), which may further weaken the interaction. Therefore, soil water content variation may influence the interaction effect of warming and nitrogen addition on litter decomposition.

The experimental results during the recovery period of this study showed that the decomposition rate of the litter rapidly recovered to the level of the control. Meanwhile, soil environmental factors recovered well after the warming and nitrogen addition treatments were removed (Fig. 4a, c), suggesting no lasting effect of warming and nitrogen addition. The IDD determined the decomposition dynamics of litter during the recovery period, which masked the contribution of SST and SSW to litter decomposition, which may be related to the regulation of the litter decomposition rate by initial soil environmental factors (Liu et al. 2023). In this study, the beginning of the treatment period was

January, while the beginning of the recovery period was April (Fig. 4a), and the decomposition rate of the first decomposition stage was significantly higher in the recovery period than in the treatment period, similar to our previous study (Liu et al. 2023), which also changed the earlier IDD and thus the whole decomposition stage. Most importantly, the recovery period results confirmed the treatment effects of warming and nitrogen addition during the treatment period.

## Conclusions

In summary, warming and nitrogen addition inhibited litter decomposition rate in the subtropical forests, without a significant negative interaction. Variance partitioning analysis (VPA) showed that soil temperature (SST) and soil water content (SSW) had positive effects on the decomposition rate (SDR), and the contribution rate of SST was greater than that of SSW. The recovery experiment showed the effect of all treatments disappeared, confirming the effects of the treatments during the treatment period. This study is a further step toward better understanding the role of high N deposition levels on litter decomposition under climate warming scenarios.

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**Author contributions** Chuansheng Wu performed the material preparation and data collection. Shuai Liu and Chuansheng Wu presented the main idea and performed the data analysis. Yue Li, Simeng Wang, Ying Wang, and Menglong Bu finished the initial draft. Yue Li, Shuai Liu, and Chuansheng Wu modified the whole manuscript. All the authors have read and approved the final manuscript.

**Data availability** Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

## Declarations

**Competing interests** 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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