RESEARCH ARTICLE

Temporal shifts in the relative importance of climate and leaf litter traits in driving litter decomposition dynamics in a Chinese transitional mixed forest

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Abstract

Purpose To assess the direction and strength of climate and leaf litter trait effects on decomposition dynamics throughout the litter decomposition process.

Methods We performed a three-year-long litter-bag translocation experiment along an elevational gradient in a transitional mixed forest in China. We explored temporal shifts in the relative contribution of microclimate and litter traits of seven dominant species to mass loss throughout the decomposition process.

Results Air temperature and soil moisture imparted no significant effects on mass loss in the initial decomposition stage (0–6 months) but exerted positive effects after 6 months' incubation ($p < 0.05$). Initial specific leaf area (SLA) was positively associated with mass loss only during the early decomposition stages (0–12 months). Litter P concentration was positively while N concentration was negatively associated with mass loss for almost all decomposition stages. Both litter Mg and Ca concentrations were negatively associated with mass loss throughout the whole decomposition process ($p < 0.05$). The relative contribution of microclimate was weaker than that of litter traits during the early stages but increased in the late decomposition stage (after 36 months). SLA and Mg were the most important traits during the early stages (0-12 months), whereas N and Mg were relatively stronger during the later stages (30–36 months).

Conclusion Our results have highlighted that microclimate (particularly temperature) exerted dominant control over later-stage litter decomposition. Often-overlooked litter traits such as Mg, are key potential drivers of litter decomposition dynamics and should be more explicitly incorporated into current biogeochemical models to better understand litter-driven nutrient and carbon cycling.

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Introduction

Leaf litter decomposition represents a fundamental ecological process that influences nutrient cycling and soil organic carbon formation in ecosystems. This decomposition process is a key determinant of carbon fluxes between forests and the atmosphere, as it releases a large amount of CO_2 into the atmosphere along with nutrients such as nitrogen (N) and phosphorus (P) into the soils, which can be effectively utilized by plants for growth (Cotrufo et al. 2015; García-Palacios et al. 2016; Zanne et al. 2015). Therefore, there is a growing need to better understand the factors controlling the decomposition process to accurately predict how climate change may affect carbon and nutrient cycles via biotic feedback mechanisms. Numerous studies have demonstrated that prevailing climatic conditions along with leaf litter traits of species are among the main drivers of litter decomposition across diverse ecosystems (Berg 2014; Cornwell et al. 2008; García-Palacios et al. 2016; Suseela and Tharayil 2018). Still, our understanding of the drivers of litter decomposition remains relatively limited across decomposition stages and climates.

First, while leaf litter decomposition rate is tightly linked to the stage of decomposition, temporal dynamics of litter decomposition need to be further studied (Adair et al. 2010; Canessa et al. 2021; García-Palacios et al. 2016). The majority of past studies have explored leaf litter decomposition with a small number of harvests of litterbags (Berg and McClaugherty 2020; Cornwell and Weedon 2014). This approach strongly facilitates the robust evaluation of how this short-term decomposition might be influenced by various factors (García-Palacios et al. 2016; Moore et al. 2017). The problem with such an approach is that it provides a poor representation of the long-term dynamics of decomposition for various species in many ecosystems (Canessa et al. 2021; Moore et al. 2017). Therefore, this approach could yield inaccurate estimates across different decomposition stages (Cornwell and Weedon 2014; Manzoni et al. 2012). A more straightforward method is that litterbags are retrieved with several harvests over a longer duration.

Second, variation in the relative importance of climate versus leaf litter traits of tree species during the course of litter decomposition has not been fully elucidated (Canessa et al. 2021; Kou et al. 2020; Moore et al. 2017; Oberle et al. 2020). Though there is little reason to expect the shifting influence of climatic controls through the decomposition process, several empirical studies have suggested that the role of climate and litter traits could vary among different decomposition stages (Canessa et al. 2021; Currie et al. 2010; García-Palacios et al. 2016; Moore et al. 2017). Specifically, studies have highlighted a temporal shift in the control of decomposition by climatic factors between high- and low-quality litter (García-Palacios et al. 2016). However, these analyses only focused on the arbitrary classification of litters (rather than quantitative litter traits), which could lead to an inaccurate estimation of the role of litter traits of species (García-Palacios et al. 2013). Furthermore, a study conducted by Zanne et al. (2015) in temperate forests inferred that litter traits could be more relevant in the early stages of decomposition, while climate may be more important at later stages. However, other studies have indicated that litter decomposition was strongly regulated by the climate in early stages and by litter traits in late stages (Berg et al. 2015; Hobbie 2015; Waring 2012). These contradictory findings provide further justification for more empirical studies to accurately parse the relative roles of climate and leaf litter traits throughout the decomposition process (García-Palacios et al. 2016; Santonja et al. 2019).

Finally, while previous studies have demonstrated that the control of leaf litter decomposition by climate and leaf litter traits of species is forest-specific (Aerts 1997; Fujii et al. 2018; Hättenschwiler et al. 2011; Keller and Phillips 2019), field observations of litter decomposition are strongly biased toward tropical and temperate forests. Furthermore, our understanding of litter decomposition in transitional forests located between tropical and temperate regions is lacking, which seriously limits our understanding of litter decomposition across diverse forests. Litter decomposition in tropical regions with year-round high temperatures and seasonal precipitation is mostly moisture- and P-controlled, whereas the process is primarily temperature- and N-controlled in temperate regions with seasonally variable temperatures (Aerts

1997; Jiang et al. 2021; Marklein et al. 2016; Powers and Salute 2011). Since these ecosystems have different climate conditions and species composition compared to transitional forests, we expect that previously made generalizations and conclusions about decomposition drivers may not be correct and thus lead to uncertainty. More specifically, to develop the findings from temperate and tropical forests, new insights into the decomposition process in this under-represented forest are urgently needed.

To address these knowledge gaps, we have identified and quantified the relative contribution of specific microclimate and leaf litter traits for the decomposition process for different decomposition stages in a transitional mixed forest located between tropical and temperate forests. Specifically, we conducted a three-year-long leaf litter translocation decomposition experiment using the litterbag technique along an elevational climatic gradient in Central China. We measured leaf litter mass loss and initial traits of seven dominant tree species as well as local-scale microclimate (air temperature and soil moisture) during the decomposition trajectory. Based on the above-mentioned evidence from other studies, we predicted that (a) the relative importance of leaf litter traits and microclimate would vary temporally during the decomposition process, and (b) the decomposition dynamics of our targeted forest would show some common and unique features relative to tropical and temperate forests.

Materials and methods

Study site

The study site was located on the southern slope of Shennongjia Mountain in Central China. This region constitutes a geographical transition zone between the (sub-) tropical and temperate climates and is well known as an important biodiversity conservation hotspot both in China and globally (Xie and Shen 2021). The mean annual temperature is 10.6 °C and annual precipitation ranges between 1306–1722 mm. The dominant soil classes are mountain yellow–brown soil and mountain brown soil. Further details about the site have been previously reported (Ge et al. 2013) and are available in Appendix S1 and S2.

The mixed evergreen and deciduous broad-leaved forest, the zonal vegetation in this region, is unique among forests at similar latitudes (ca. 31°N) which are typically dominated by Fagaceae species in the Northern Hemisphere (Ge et al. 2013; Xie and Shen 2021). The mixed forest forms a critical climate and geographical transitional zone in Central China between year-round warm (sub-) tropical evergreen broad-leaved forest and seasonally temperate broad-leaved forest (See Appendix S1 for more details on this transitional forest). This forest harbors one of the highest levels of biodiversity in the world, and is particularly sensitive to climate change (Ge et al. 2019; Ge and Xie 2017; Wu 1980). Therefore, this kind of transitional forest provides a powerful model to comprehensively address how climate, along with the shift in litter traits of tree species will affect leaf litter decomposition dynamics.

Experimental design and setup

We performed a three-year-long (2011–2014) leaf litter translocation decomposition experiment along an elevational gradient using the litterbag method to measure litter mass loss over time. In November 2011, we established five experimental sites along an elevational gradient at 800, 1000, 1300, 1600, and 1800 m a.s.l. The selection of these sites allowed us to address a range of contrasting microclimates (in particular temperature), which could increase our current understanding of the effects of climate and leaf litter traits (Ge et al. 2013; Salinas et al. 2011; Sundqvist et al. 2013). We performed the same experimental layout for the seven tree species used. We collected leaf litter samples produced by seven dominant tree species of the transitional mixed forest in 2011, specifically *Cyclobalanopsis multinervis* (CM, the synonym of *Quercus hypargyrea*), *Cyclobalanopsis oxyodon* (CO, the synonym of *Quercus oxyodon*), *Quercus engleriana* (QE), *Fagus engleriana* (FE), *Fagus pashanica* (FP), *Quercus serrata* var. *brevipetiolata* (QS) and *Quercus aliena* var. *acuteserrata* (QA). The nomenclature of plant species here follows the Flora of China (The Editorial Board of Flora of China 2004). Samples from each species were collected independently and oven-dried at 65℃ for two days to reach a constant mass before being homogenized. For each species, 10.00 g of leaf litter was sealed in 15 cm×10 cm litterbags constructed from

1.5-mm mesh nylon netting. Eighteen bags (for 18 samplings across three years) for each species were placed in five clusters (replicates) at each site. Samples were harvested ca. every two months with one litterbag from each of the five replicated clusters at each one of five sites. Therefore, a total of 3150 litterbags (5 replicates × 18 sample litterbags × 5 sites × 7 species) were installed along this elevational gradient (See details in Appendix S2). After collection, litterbags were immediately transported to the laboratory where the remaining litter was cleaned and brushed carefully to remove roots, fauna, and soil particles adhered to the litterbags. Finally, the litterbags were oven-dried to a constant mass at 65℃ and weighed.

Leaf litters of these selected dominant tree species, constituting the major components of litterfall in this kind of forest (Ge et al. 2017; Gilliam 2016; Shen et al. 2019), are characterized by a wide range of initial litter traits which are expected to influence litter decomposition in this transitional forest (Canessa et al. 2021; Cornwell et al. 2008; Pérez-Harguindeguy et al. 2013). Here, we measured and calculated the initial mean specific leaf area (SLA) of leaf litter for each tree species using a leaf area meter (LI-3000, Li-Cor, USA). Furthermore, we determined initial concentrations of nitrogen (N), phosphorus (P), calcium (Ca), and magnesium (Mg) of leaf litter samples for each tree species. The laboratory analyses and corresponding results are available in Appendix S2.

Given the recent indication that local site conditions in which decomposition takes place may be poorly represented by macroclimatic parameters (Bradford et al. 2014; Bütikofer et al. 2020; Canessa et al. 2021), we used HOBO Onset microclimatic recorders (Onset Computer Corporation, USA) to measure actual microclimatic variables including air temperature (AT) and soil moisture (SM) at one-minute intervals for each site. See Figure S2 for temporal dynamics of AT and SM conditions for the five study sites along the elevational gradient during these incubation periods.

Calculations and statistical analysis

Because our studied forests experience strong climate seasonality (Ge et al. 2019), the initial decomposition rate will be influenced by the season in which the incubations were started. This issue could be partially remedied by reporting mass loss estimates across different decomposition stages. Thus, we chose mass loss as a proxy of decomposition and we analyzed these data using different litter harvests (6-month intervals). We calculated relative mass loss (%) for each sampling period by dividing the mass loss at any harvest by the initial mass (× 100) (Canessa et al. 2021; Santonja et al. 2019).

We analyzed these data by decomposition stage. First, we evaluated the effects of species identity and elevation on litter mass loss over time using a factorial ANOVA. Elevation, species, and incubation time were fixed effects in the model, while the cluster was a random effect. To interpret significant interaction terms, we used a simple main effects test. The Tukey's HSD test was used for post hoc comparisons of factors with more than two levels. Second, to further evaluate the underlying temporal drivers of mass loss across different tree species and multiple sites, we conducted commonly used multiple linear regression models and variation partition analysis for each decomposition stage. Here, grouped litterbag data were selected and defined at six decomposition stages, specifically 6, 12, 18, 24, 30, and 36 months after litterbag installation. We selected 6-month intervals since this time frame demonstrated a much greater ability to characterize the temporal patterns of different controls of litter decomposition as compared to 2- or 4-month intervals in our preliminary data exploration, although similar conclusions were achieved with the above-mentioned different time frames. See more details in Appendix S3.

Before performing multiple linear regression analysis, we checked all potential explanatory variables including microclimate (AT and SM) and the above-mentioned initial leaf litter traits (SLA, N, P, K, Ca, and Mg) for normality, and then log-transformed these variables when necessary. Microclimatic data were trimmed to the corresponding decomposition stages for statistical analyses following previous studies (Canessa et al. 2021; García-Palacios et al. 2016). Each explanatory variable was additionally standardized by subtracting the mean and dividing by the standard deviation before analysis to enable direct comparison of estimated regression coefficients for each decomposition stage (Bradford et al. 2016; García-Palacios et al. 2018; Ge et al.2022; Zuur et al. 2009). We also evaluated collinearity among the explanatory variables by evaluating the variance inflation factor (VIF) for each decomposition stage model

(Dormann et al. 2013). Separate models were run for each decomposition stage. Model selection was performed using both forward and backward selection. At each step, we quantified the variance inflation of the added explanatory variable to restrict multicollinearity in the model. In this study, no multicollinearity issues were found in the most parsimonious models for any decomposition stage. We then selected the best-fit models by calculating Akaike's information criterion (AIC) following the methods of similar studies (Canessa et al. 2021; García-Palacios et al. 2018). The model with the lowest AIC value within a given set of models for each decomposition stage was considered to have the greatest support (Ge et al. 2019; Zuur et al. 2009).

For the selected regression model for each decomposition stage, we further parsed the relative contribution of each explanatory predictor under consideration as drivers of mass loss. To do so, we calculated the relative effect of the parameter estimates for each of the predictors compared with the effect of all parameter estimates in the model (García-Palacios et al. 2018; Gross et al. 2017). This method is similar to variance decomposition analysis since we have standardized all explanatory predictors before

analysis. We also examined the overall relative contribution of climatic and leaf litter traits following the same method for each decomposition stage.

The statistical analyses carried out in this study were implemented in R 3.6.0 (R Core Team, 2013) using the basic statistical package, "car" package (Fox and Weisberg, 2019), and "MuMin" package (Bartoń, 2020). See Appendix S3 and S4 for additional information on data processing and statistical analyses.

Results

Leaf litter mass loss across species along the elevational gradient

At the end of the experiment (after 36 months), mean leaf litter mass loss was 71.14% across all sites and tree species. The maximum leaf litter mass loss recorded for a sample was 95.7% for *Quercus aliena* var. *acuteserrata*. Mean mass loss for the seven individual tree species varied from 62.40% for *Fagus engleriana* to 78.76% for *Quercus serrata* var. *brevipetiolata,* which were significantly different from one another ($p < 0.05$) (Fig. 1). Mean mass loss across
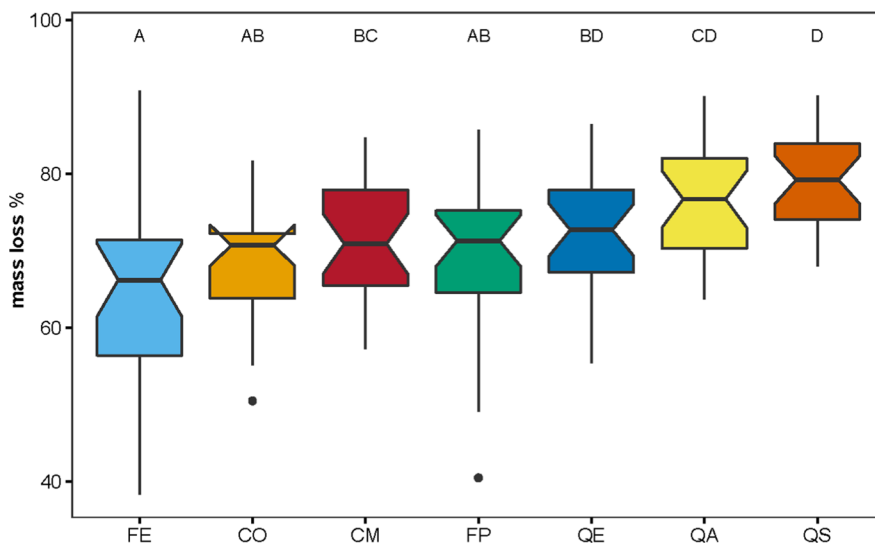

Fig. 1 Boxplot of leaf litter mass loss for seven tree species of the studied mixed evergreen and deciduous broad-leaved forest after three three-year of field incubation. Different capital letters at the top represent significant differences ($p < 0.05$) among the seven tree species (Tukey's post-hoc test). The abbreviations are used: FE = *Fagus engleriana*,

CO = *Cyclobalanopsis oxyodon*, CM = *Cyclobalanopsis multinervis*, FP = *Fagus pashanica*, QE = *Quercus engleriana*, QA = *Quercus aliena* var. *acuteserrata*, and QS = *Quercus serrata* var. *brevipetiolata*. The nomenclature of plant species here follows the Flora of China (The Editorial Board of Flora of China 2004)

all species among the sites ranged from 61.58% at 1800 m to 77.19% at 1000 m (Fig. 2). Leaf litter mass loss continuously increased with incubation time, and temporal patterns of leaf litter mass loss depended on the studied species and elevation, as indicated by the significant two-way interactions (Table 1 and Appendix S5).

Microclimate and leaf litter trait effects on mass loss at various decomposition stages

We found that different factors controlled litter mass loss across decomposition stages (Fig. 3 and Appendix S5). Microclimatic variables (AT and SM) did not display any significant effects on mass loss in the early decomposition stage (0–6 months). After 6 months, both AT and SM exerted consistent, significantly positive effects on mass loss ($p < 0.05$). The effects of individual leaf litter traits changed throughout the decomposition process Fig. 3). Initial

leaf litter SLA was positively associated with mass loss in the period from 0 to 12 months ($p < 0.05$), but this positive relationship disappeared after 12 months ($p > 0.05$). Leaf litter P concentration correlated positively with mass loss, while leaf litter N displayed a consistently negative association with mass loss at almost all decomposition stages ($p < 0.05$). Leaf litter Mg and Ca remained negatively associated with mass loss throughout the whole decomposition process ($p < 0.05$) (Fig. 3).

Temporal shifts in the relative contribution of microclimate and leaf litter traits

We found that the relative importance of microclimate and litter traits changed with the progression of litter decay (Fig.4). Overall, the relative contribution of microclimate was smaller than that of litter traits, but increased with advanced decomposition and exceeded the overall contribution of litter traits until

Fig. 2 Average mass loss for seven leaf litter species after three years' field incubation along an elevational gradient in Central China. Different capital letters at the top represent significant differences ($p < 0.05$) in mass loss among five sites (Tukey's post-hoc test)
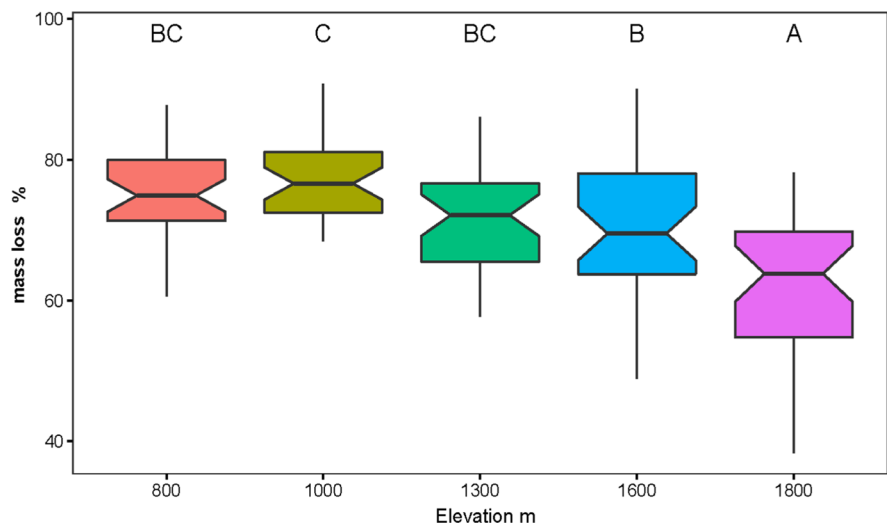
Table 1 Results of the two-way repeated measures ANOVA, which tested for the effects of elevation, species identity, harvest time, and their interactions on leaf litter mass loss. All interaction effects are specified below

Source of variation	df	SS	MS	F	p
Elevation	4	30,071	7518	177.504	**< 0.001**
Species	6	162,261	27,043	638.527	**< 0.001**
Time	17	1,132,016	66,589	1572.246	**< 0.001**
Elevation × Species	24	3952	165	3.888	**< 0.001**
Elevation × Time	68	13,980	206	4.854	**< 0.001**
Species × Time	102	26,506	260	6.136	**< 0.001**
Elevation × Species × Time	408	16,477	40	0.954	0.729
Residuals	2520	106,729	42		

Fig. 3 Standardized coefficients for microclimate and individual initial leaf litter traits included in the final regression model for each decomposition stage. Coefficients represent relative percent change in mass loss for one standard deviation increase in the variable. Blue and red circles indicate negative and positive effects on mass loss, respectively. Circle size indicates the magnitude of effects. The number in the circles represents the effect size on mass loss. Note that the following microclimatic predictors were included with abbreviations: AT = air temperature, SM = soil moisture
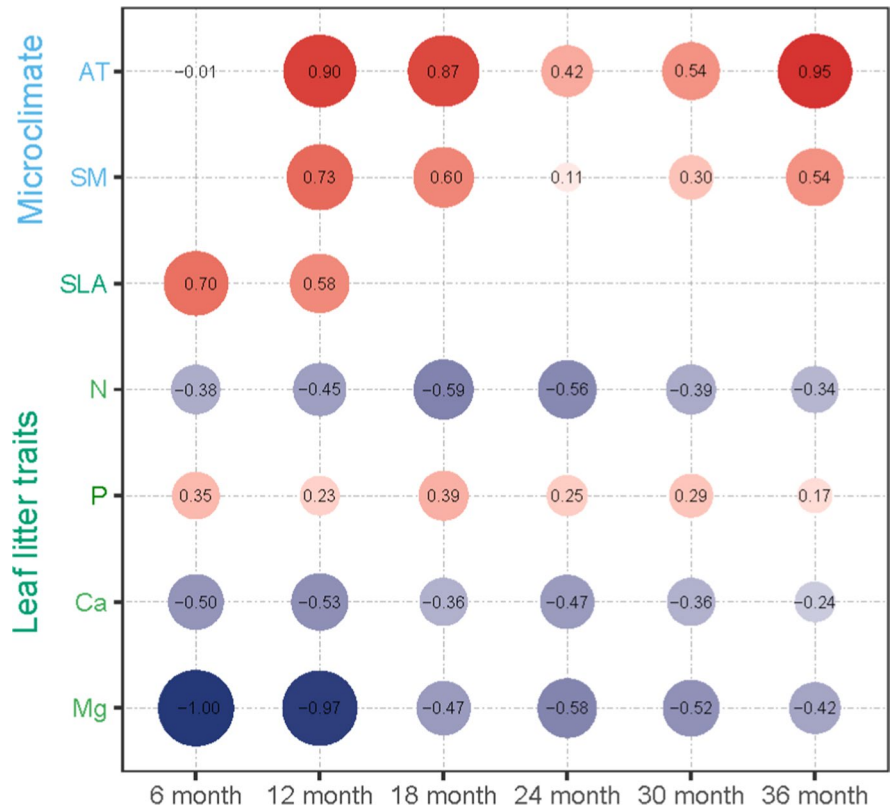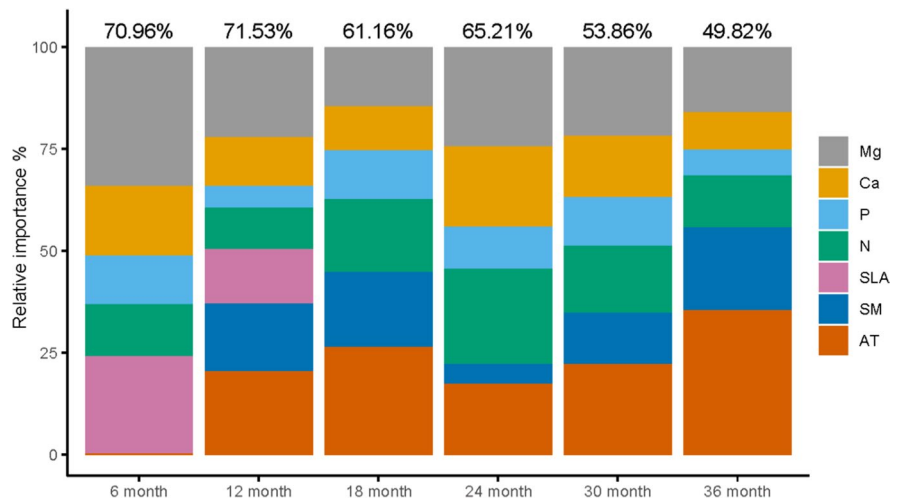

Fig. 4 The relative contribution of climate and individual initial leaf litter traits as drivers of litter mass loss for different decomposition stages. The numbers above the bars indicate the overall explanatory power of our selected most parsimonious models for different decomposition stages

36 months of field incubation (Appendix S6). Specifically, the relative role of air temperature (20.50% averaged across stages) was higher than soil moisture (14.54% averaged across stages) over the whole decomposition period. The relative contribution of single litter traits varied among the decomposition stages (Appendix S5). For instance, SLA and Mg ranked highest in importance among these litter traits in the period of 0 to 12 months, while N and Mg were relatively stronger at advanced stages (i.e. until 36 months) (Fig. 3 and 4). The roles of litter P and Ca were intermediate compared with other litter traits.

The total explanatory power of both microclimate and leaf litter traits decreased from 70.96% to 49.82% as decomposition advanced (Appendix S6).

Discussion

Our current work has identified whether and how the relative importance of microclimate and leaf litter traits on litter decomposition shifted across different decomposition stages by tracking a longer incubation period than that of previous studies (Moore et al. 2017; Oberle et al. 2020; Waring 2012; Zhang et al. 2008). We found that microclimate displayed a relatively smaller influence than initial litter traits at early stages of decomposition, but had a larger influence at later stages. The overall effect of initial litter traits faded with the progression of decomposition, and the relative contribution of specific litter traits depended not only on the decomposition stage but also on the trait studied. These findings provide complementary evidence for reconciling the seemingly debated paradigms regarding the relative contributions of climate vs. litter traits for decomposition (Bradford et al. 2016; Cornwell et al. 2008; Hoeber et al. 2020) and emphasize the urgent need to capture a more complete picture of temporal-dependent key drivers of litter decomposition dynamics.

Microclimate predominantly drove later-stage litter decomposition

Several previous studies have indicated that climate has a negligible influence at the initial but is stronger at later stages of decomposition (Canessa et al. 2021; García-Palacios et al. 2016), while the opposite trend was detected in others (Berg et al. 2015; Hobbie 2015; Waring 2012). Here, we have simultaneously taken temporal dynamics of local concurrent microclimate and mass loss into account and minimized any error that may arise from a temporal-scale mismatch between mass loss data and long-term climate averages (Bradford et al. 2017; Currie et al. 2010; García-Palacios et al. 2016). Our results indicate that microclimate, and in particular air temperature, took precedence over leaf litter traits as the main predictor of later-stage decomposition (after 36 months of field incubation) in our transitional mixed forest (Figs. 3

and 4), a contrasting pattern compared to previous findings (Berg et al. 2015; Waring 2012).

Here, we assumed that this delay in the appearance of microclimatic effects on decomposition may be linked to the relative availability of labile versus recalcitrant compounds of leaf litters. During the early stages of decomposition, microbes preferentially target labile compounds such as cellulose and hemicellulose (Berg 2014; Suseela et al. 2013). As the majority of labile compounds could be utilized by a wide range of microbial communities, representing various climatic tolerances, the potential of climate to influence the utilization of these labile compounds by microbes could be largely restricted (Berg 2014; Suseela et al. 2013; Zanne et al. 2015). Therefore, the decomposition process at the early stage is insensitive to climate. As litter decomposition progresses into later phases, most of these labile substrates have been metabolized and exhausted by the microbial decomposers and recalcitrant complexes of leaf litters have been resided and formed (Averill and Waring 2018; Berg and McClaugherty 2020; Hobbie 2015). At this advanced stage, the ability of microbes to degrade more recalcitrant compounds requires favorable climatic conditions and therefore a higher activation energy (García-Palacios et al. 2016; Keiser and Bradford 2017).

Distinct litter traits related to distinct stages of decomposition

Although initial litter traits are known to be key drivers of litter decomposition across tropical and temperate forests, their specific temporal role throughout the decomposition process is not well documented (Li et al. 2020; Parsons et al. 2014; Suseela and Tharayil 2018; Zanne et al. 2015). Here, we have selected commonly used litter traits including SLA, leaf litter N, and P, along with non-conventional litter traits such as Ca and Mg (Berg et al. 2021; Cornwell et al. 2008), to identify their specific roles during the course of decomposition. We found that these litter traits were adequate predictors of litter decomposition in this transitional forest, but their effects varied among different decomposition stages. Specifically, initial litter traits prevailed over microclimatic drivers of litter decomposition during the first 30 months of field incubation (Appendix S6). This result is in contradiction with the findings of Trofymow et al. (2002)

and Santonja et al. (2019), who observed that leaf litter traits increased in predictive importance throughout the course of decomposition but were in qualitative agreement with some studies which stated that litter traits were relatively more important than the climate in controlling initial decomposition, and their relative importance declined in subsequent decomposition stages (Canessa et al. 2021; Currie et al. 2010; García-Palacios et al. 2016). The results among various studies may be related to the study duration of field decomposition incubation and the definition of decomposition stage (mass loss classes vs. specific period) (Canessa et al. 2021; García-Palacios et al. 2016) along with different targeted ecosystem types (forests vs. shrubland) that may respond differently to changes in climatic conditions (Cusack et al. 2009; Moore et al. 2017; Santonja et al. 2019).

Leaf litter SLA emerged as the main driver of initial-stage decomposition

Interestingly, SLA has played a positive role in the initial decomposition stage, but this stimulatory effect disappeared after 12 months of incubation. The vast majority of litter decomposition studies have also reported that SLA was positively correlated with litter decomposition in various forests globally (Cornwell et al. 2008; Santiago 2007; Sun et al. 2018). For example, Cornwell and others (2008) found that global-scale litter decomposition increased significantly with leaf litter SLA. However, these studies have considered relatively short experimental duration, mainly encompassing the early stages of decomposition alone (Cornwell and Weedon 2014; Currie et al. 2010; Moore et al. 2017), which may not hold for later decomposition stages (Coûteaux et al. 1995; Moore et al. 2017; Oberle et al. 2020).

Here, two possible but not mutually exclusive explanations could account for the positive role of SLA observed only during the early stages of litter decomposition. First, initial litter SLA is tightly linked to leaf palatability and concentration of soluble substances, which is likely due to the relative differences in carbon investments in protective compounds (Chomel et al. 2016; Hättenschwiler and Jørgensen, 2010). Higher SLA renders leaf litter more immediately available and accessible to microbes and macro-decomposers such as soil animals during the initial physical transformation process of litter

materials (Fujii et al. 2018; Li et al. 2020; Manzoni et al. 2012). Second, the positive effect of SLA on leaf litter decomposition may be indirect, as this trait is tightly associated with other structural characteristics such as leaf litter physical toughness and litter water saturation, both of which improve micro-environmental conditions (Makkonen et al. 2012; Santonja et al. 2019). Following initial transformations on litter decomposition by soil fauna, initial species differences of litter SLA become less distinct. Thus the strong positive effect of SLA disappeared and was progressively replaced by other traits as decomposition progressed (Fig. 4). This finding further emphasizes the need to take caution when applying SLA as an adequate descriptor of litter physical traits to explore the effects of litter traits in the late-stage decomposition.

Leaf litter N slowed while P stimulated decomposition throughout the decomposition process

While both initial leaf litter N and P generally affect decomposition, their specific influences on decomposition are rather complex (Berg 2014; Canessa et al. 2021; Hobbie 2015). We found that initial litter N showed a strong, consistently negative effect while initial litter P was positively correlated with mass loss and the overall contribution of litter N was much more important than that of P across the stages of decomposition. This finding contrasts the widely held notion that litter N typically stimulates decomposition in temperate short-term studies and global-scale analyses (Berg et al. 2015; Cornwell et al. 2008; Cusack et al. 2009), but broadly agrees with previous findings in tropical forests (Hättenschwiler et al. 2011; Waring 2012; Wieder et al. 2009).

The contrasting roles of litter N and P in driving litter decomposition may be related to the nature and relative availability of these nutrients for microbes over time (Berg and McClaugherty 2020; Marklein et al. 2016). The negative influence of N on decomposition is related to the different forms and localizations of organic N in leaf litters (Berg 2014; Hobbie 2015; Suseela et al. 2013). For instance, high N concentrations in initial litters could also reflect high concentrations of N-based defense secondary compounds such as alkaloids, or the formation of compounds via covalent bonding to macromolecules that resist microbial attack and in turn inhibit decomposition

(Berg and McClaugherty 2020; Hobbie 2015; Zanne et al. 2015). Another possibility is that N is preferentially immobilized into litter while P is preferentially released from the litter during decomposition, leading to a potential mismatch between nutrient availability of decomposing litters and decomposer nutrient demand (Keiser and Bradford 2017; Marklein et al. 2016). We caution, however, that our inferences regarding both litter N and P effects are based on the rather limited size of observational samples. Therefore, we suggest that site-based multi-species field studies that focus on nutrient dynamics of decomposing litters across decomposition stages are urgently needed to further clarify the specific role of these elements during the litter decomposition process.

The suppressed roles of litter Mg and Ca with progressive decomposition

Whereas initial litter micronutrients such as Ca and Mg may be key predictors of litter decomposition, the nature, and extent of their specific effects throughout the decomposition process have been often overlooked in comparison with those of litter N and P, especially for transitional forests such as ours (Makkonen et al. 2012; Waring 2012; Zhou et al. 2020). Here, our findings expand on previous studies in underscoring the key inhibitory roles of Mg and Ca during the decomposition process (García-Palacios et al. 2016; Moore et al. 2017; Zanne et al. 2015). We found that litter Ca and Mg explained a larger amount of variation in the decomposition process compared to the role of N or P litter traits. The strength of the negative effect of Mg was overwhelmingly greater in the early stage of decomposition. These results contrast with some findings in temperate and tropical forests which concluded that both litter Ca and Mg were positively correlated with mass loss (Makkonen et al. 2012) but supported other observations for leaf and root litter decomposition in temperate forests (Goebel et al. 2011; Jiang et al. 2021).

How do we reconcile our results with those of previous studies that observe different litter Mg- and Ca- decomposition relationships? While both litter Mg and Ca favor decomposition since they are vital for the general function and are also components of decomposition enzymes in decomposers (Makkonen et al. 2012; Zhou et al. 2020), prior laboratory and field studies have demonstrated a suppressing role

for Mg and Ca via chelation or cross-linking with decomposers (e.g. cation bridges) (Jiang et al. 2021; Powers and Salute 2011). Magnesium and calcium oxalate are common stable components of fungal cell walls (Powers and Salute 2011), where they provide a hydrophobic coating that in turn prevents hyphae from becoming hydrated and thus reduces microbial attachment. Fungal populations can therefore easily colonize Mg- and Ca-rich leaf litters and impede their decomposition by forming the Mg- and Ca-rich fungal hyphae (Powers and Salute 2011; Wiesmeier et al. 2019). Alternatively, it may be the case that Mg- and Ca-rich decomposing litters easily form secondary compounds, such as antibiotics and antifungals, which may inhibit the activity of microbes and in turn impede litter decomposition (Jiang et al. 2021; Powers and Salute 2011; Rowley et al. 2018). While it is not possible to distinguish among these specific mechanisms with our current analyses, our results indeed highlight that future work should consider both stimulatory and inhibitory effects of a wider range of elements that are traditionally studied in driving leaf litter decomposition and biogeochemical cycling across various forests.

Main implications of current findings

In comparison to previous decomposition studies that focus on tropical and temperate forests, our transitional forest study has some potential implications. Here, we found that litter decomposition in our targeted forest displayed unique features compared to tropical and temperate forests (Fig. 5). For example, air temperature rather than soil moisture strongly controls leaf litter decomposition in this transitional forest, similar to temperate but not tropical forests. Additionally, litter decomposition seems to be controlled both by N and P, a transitional feature between temperate and tropical forests (Cusack et al. 2016; Marklein et al. 2016; Waring 2012). The observed negative effect of litter Mg concentration on leaf litter decomposition, in contrast to that of temperate and tropical regions (Makkonen et al. 2012; Zhou et al. 2020), has highlighted the urgent necessity to incorporate these decomposition drivers into our current understanding of broad-leaved forest latitudinal transitions. We also highlight the need for more direct evidence with additional manipulative experiments and observational studies to provide more powerful
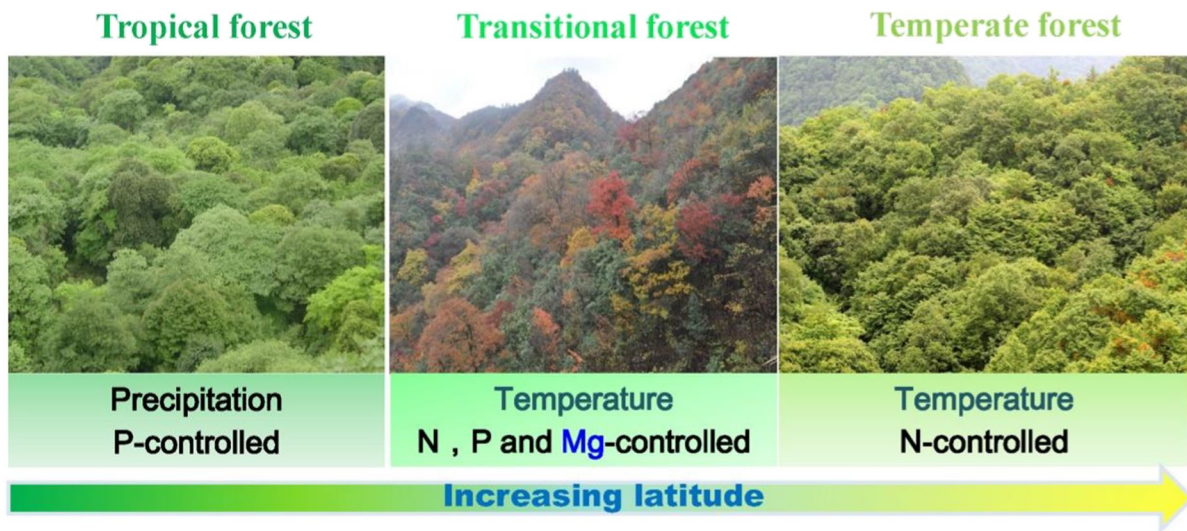
Fig. 5 Comparisons on climate and leaf litter trait controls of litter decomposition among tropical, transitional and temperate forests, based on our current understanding of litter decomposition

information that can generalize their temporal roles of climate and particularly traits over the decomposition process throughout diverse forests, but particularly in under-studied ecosystems. Additionally, future studies should incorporate these potential dynamic shifts in the major drivers of decomposition to better predict temporal dynamics of carbon and nutrient cycling via leaf litter decomposition pathways (Cornwell and Weedon 2014; Ge et al. 2017; Oberle et al. 2020).

Concluding remarks

Collectively, this study has quantified temporal shifts in local microclimate and leaf litter traits control of litter decomposition at varying decomposition stages in a transitional forest between temperate and tropical regions over a longer decomposition period than the average of earlier studies (Dale et al. 2015; Moore et al. 2017; See et al. 2019; Waring 2012). This expands our current knowledge of litter decomposition beyond these relatively well-studied tropical and temperate forests (García-Palacios et al. 2016; Wieder et al. 2009; Zanne et al. 2015). We have underscored that microclimate and in particular, temperature exerts a relatively smaller influence than initial litter traits at early but larger at

later stages of litter decomposition. We have further provided observational evidence that the decomposition process in our targeted forest displays some unique characteristics. Specifically, often overlooked litter traits such as Mg, as key potential drivers of temporal dynamics of litter decomposition found here, should be more explicitly incorporated into a coherent framework with which to better understand and predict litter-driven nutrient and carbon cycling in current biogeochemical models (García-Palacios et al. 2016; Jiang et al. 2021; Makkonen et al. 2012).

Author's contribution J.G. and Z.X. conceived of and designed study, performed research, and wrote the manuscript. J.G., B.M., B.B., W.X., and C.Z analyzed data and revised this manuscript. All the authors approved the manuscript.

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