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Leaf economics spectrum prevails over nutrient resorption in regulating the temperature sensitivity of litter decomposition in a subtropical forest ecosystem

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Abstract

The LES and nutrient resorption are thought to jointly modulate leaf litter traits, including the litter decomposition, but it is unknown how the two factors affect the temperature sensitivity of litter decomposition (Q_{10}). The Q_{10} of litter decomposition was evaluated for 15 co-occurring subtropical woody species under laboratory conditions. The LES of these species, as well as species-specific N (NRE) and P resorption efficiency (PRE) during leaf senescence, were also determined. Results showed that the Q_{10} values were significantly correlated to LES, with litters from resource-conservative species having higher Q_{10} values than those from resource-acquisitive species. Among the parameters characterizing LES, leaf N concentration, C:N ratio, and lignin:N ratio were correlated to Q_{10} , whereas leaf P and lignin concentrations, specific leaf area, and C:P ratio showed no relationships. The LES was correlated to litter C:N and lignin:N ratios, and, in turn, litter C:N and lignin:N ratios were correlated to Q_{10} . This result suggested that LES affects litter quality and thus the Q_{10} of litter decomposition did not depend on nutrient resorption, as indicated by the lack of correlation between LES and NRE or PRE. Our results reveal an association between plant functional features and forest C dynamics in a warmer future.

Keywords Global warming \cdot Vegetation strategy \cdot Litter respiration \cdot CO₂ efflux

Introduction

Litter decomposition can contribute 5-45% of total soil respiration and therefore plays a key role in influencing atmospheric CO₂ concentration (Aerts 2006; Gritsch et al. 2016; Sun et al. 2018). Litter decomposition is stimulated by temperature increase; hence, the ongoing global warming will substantially influence litter-derived CO₂ emission (Aerts 2006; Davidson and Janssens 2006). It is important

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to understand the underlying mechanisms for the response of soil C dynamics to climate change and related feedback processes. The temperature sensitivity of litter decomposition (Q_{10}) , the factor by which a 10 °C warming will increase the rate of decomposition) is mostly determined by litter quality (e.g., the lower the litter quality, the higher the Q_{10} values, Fierer et al. 2005; Li et al. 2021). Usually, litters inherit a significant portion of leaf functional properties like nutrient concentration and specific leaf area (SLA) that depend on plant resource use strategy (Freschet et al. 2010; Reich 2014; Jílková et al. 2020; Lin et al. 2020). However, it is unknown whether the functional features of vegetation exert a control on the Q_{10} of litter decomposition. Filling this knowledge gap is important to predict how functional features of various vegetation feedback to soil C turnover and thus to atmospheric chemistry (Freschet et al. 2012).

The leaf economics spectrum (LES) can affect plant strategies, shape their evolutionary history (Wright et al. 2004; Reich 2014), integrate a suite of leaf traits, and reveal a resource acquisition-conservation trade-off (Zhang et al. 2015; Guo et al. 2020). The plant species spectrum ranges from slow-growing, resource-conservative species with low SLA and low nutrient concentrations to fast-growing, resource-acquisitive species with high SLA and high nutrient concentrations (Díaz et al. 2016; de la Riva et al. 2019). Generally, resource-conservative species produce low-quality litter whereas, high-quality litter originates from resource-acquisitive species (Santiago 2007; Bakker et al. 2011;Jackson et al. 2013; Guo et al. 2020). Given these findings, LES is expected to affect the Q_{10} of litter decomposition, which still awaits experimental testing.

There is, however, also evidence that LES does not affect litter quality (Jackson et al. 2013; Zukswert and Prescott 2017). This controversy mainly stems from the fact that species often vary greatly in the efficiency of resorbing nutrients from senescing leaves. For instance, Zhang et al. (2015) reported that resource-acquisitive species resorb more nutrients from old leaves to meet the high nutrient demand caused by fast growth rate. This will offset the nutrient coupling between green leaf and litter across a large pool of species, and instead, nutrient resorption efficiency may be the predominant factor affecting litter quality (Deng et al. 2018; Xu et al. 2020). Therefore, it is important to assess the relative importance of LES and nutrient resorption in shaping litter traits and further the Q_{10} of decomposition. However, to which extent the Q_{10} of litter decomposition is determined by the two factors is still poorly understood.

In order to fill this knowledge gap, the Q_{10} of litter decomposition of 15 species that are commonly distributed in subtropical China was examined using a laboratory incubation experiment. These species differed for LES depending on the functional traits of green leaves. The efficiency of N (NRE) and P resorption (PRE) from senescing leaves was also determined. We hypothesized that (i) litter from resource-conservative species has higher Q_{10} for decomposition, because of the lower quality; and (ii) nutrient resorption efficiency is positively related to the Q_{10} of litter decomposition, due to its negative effect on litter quality.

Materials and methods

Collection of leaf litter and fresh leaf

Leaf litter and their fresh leaf counterparts were collected in a mixed broadleaf-conifer forest located in the Huitong National Research Station of Forest Ecosystem (26°50'N, 109°36'E) in Hunan Province, Southern China. This region has a subtropical monsoon climate, with an annual temperature of 16.5 °C and an annual precipitation of 1200 mm on average (Li et al. 2021). The clay loam (sand, 32%; silt, 22%; and clay, 46%) soil is classified as an oxisol based on US soil taxonomy (Zhang et al. 2016) and has a pH value of 4.72, an organic C of 19.38 g/kg soil, and a total N of 1.44 g/kg soil (Li et al. 2021).

Fresh leaves of 15 woody species that are commonly distributed in this mixed forest ecosystem were collected in July 2020. The Latin name and corresponding abbreviation of each species are listed in Table 1. Leaf litters freshly fallen from these species were collected in November 2020, excluding leaves with evident signs of herbivory, galls, fungal attacks, or atypical coloration (Zhang et al. 2016). Afterwards, plant samples were taken back to the laboratory, oven-dried to a constant

Table 1 Name, growth form, and corresponding abbreviation of the species reported in this study	A.Species name	Growth form	Abbreviation
	Liquidambar formosana Hance	Deciduous broadleaf	LF
	Cinnamomum camphora (L.) Presl.	Evergreen broadleaf	CC
	Cunninghamia lanceolata (Lamb.) Hook.	Conifer	CL
	Schima superba Gardn. et Champ.	Evergreen broadleaf	SS1
	Michelia macclurei Dandy	Evergreen broadleaf	MM
	Castanea mollissima Bl.	Deciduous broadleaf	СМ
	Diospyros kaki var. sylvestris Makino	Deciduous broadleaf	DK
	Kalopanax septemlobus (Thunb.) Koidz.	Deciduous broadleaf	KS
	Castanopsis fargesii Franch.	Evergreen broadleaf	CF
	Quercus fabri Hance	Evergreen broadleaf	QF
	Betula luminifera H. Winkl.	Deciduous broadleaf	BL
	Sapium sebiferum (L.) Roxb.	Deciduous broadleaf	SS2
	Vernicia fordii (Hemsl.) Airy Shaw	Deciduous broadleaf	VF
	Ouercus delavavi Franch.	Evergreen broadleaf	OD
	\sim Hovenia acerba Lindl	Deciduous broadleaf	НА

weight at 60 °C, and powdered using a ball mill to pass through a 0.25-mm mesh sieve (Chao et al. 2019).

Litter incubation

The surface soil (0-20 cm) of this forest was sieved (< 2mm) after removing stones and plant debris by hand and then moistened to 60% of water holding capacity by adding distilled water and incubated at 20 °C for 10 days to stabilize microbial activity. Then, the equivalent of 20 g dry soil was weighed into an 840-mL Mason jar, which has two small holes in the lids to enable gas exchange but minimize soil drying, and mixed with powders of each litter species equivalent to 0.2 g C. The powdered litter was incubated; thus, our conclusion might involve the risk of deviating from the field scenario. However, the bias associated with this factor should be small because we focused mainly on the chemical traits of the litter, which will not change after litter powdering. Mason jars that contained only soil served as the controls. The mean annual temperature (MAT, 16.5 °C, T1) and MAT plus 5 °C (21.5 °C, T2) were set as the incubation temperatures for Q_{10} analysis (Li et al. 2021). Six jars were set for each species and control (three jars per temperature value), resulting in 96 jars being incubated. The litters were incubated for 22 days, during which the moisture content was maintained at 60% of water holding capacity by replenishing water loss with distilled water at regular intervals.

CO₂ emission and Q₁₀ calculation

The CO_2 emission was measured on days 1, 5, 14, and 22. When measuring, the small holes in the lid of the Mason jars were sealed, and the released CO₂ inside was absorbed by 10 mL 0.4 M NaOH contained in a small beaker. Then the CO₂ amount was determined via titrating the NaOH solution with 0.1 M HCl solution after precipitating the carbonates with excessive BaCl₂ (Wang et al. 2019). Litter-derived CO₂ emission (LE) was calculated by the differential CO₂ efflux between the treated Mason jars and the controls. Although this experiment simulates fieldlike edaphic conditions for litter decomposition, it might involve the risk of triggering a "priming effect" because of the input of labile substrates (Kuzyakov et al. 2000). Thus, the amount of soil added to each jar was as little as possible to minimize the influences of the "priming effect" (Li et al. 2021). The Q_{10} values of LE were calculated using the following equation (Wang et al. 2018),

$$Q_{10} = \left(\frac{LE_{T2}}{LE_{T1}}\right)^{\left(\frac{10}{T_2 - T_1}\right)}$$

where LE_{T2} and LE_{T1} are the LE values at T2 and T1, respectively.

Nutrient stoichiometry and resorption

The concentrations of C, N, P, and lignin were determined for green leaf and litter. C and N concentrations were assessed using a C/N analyzer (Elementar, Germany). Subsamples were digested with H_2SO_4 and $HClO_4$ solutions (5:1 in volume ratio), and the total P concentration was analyzed using a continuous flow injection analyzer (AA3, Seal, Germany) (Li et al. 2022a). Lignin was determined as described by Sluiter et al. (2008). Briefly, subsamples were first fractionated into easily quantified forms by a two-step acid hydrolysis. Then, the lignin contents of both acid-insoluble and acid-soluble forms were colorimetrically measured by UV-Vis spectroscopy (Lambda 25; PerkinElmer, Singapore).

The NRE and PRE were calculated by the concentrationbased difference of N or P between green leaves and litters (Deng et al. 2018). In addition, the mass loss correction factor (MLCF) was used for determining NRE or PRE, because the loss of leaf quality as a result of the loss of soluble C during senescence may lead to the underestimation of the actual nutrient resorption efficiency (Xu et al. 2021). The equation is as follows:

NRE or PRE (%) =
$$\left(1 - \frac{C_{litter}}{C_{green}} \times MLCF\right) \times 100$$

where C_{green} and C_{litter} are the concentrations of N or P measured in green leaves and litters, respectively. The MLCF values are 0.780 for evergreen broad-leaved species, 0.784 for deciduous broad-leaved species, and 0.745 for conifers.

Statistical analysis

Principal component analysis (PCA) was conducted to visualize LES based on a suite of green leaf traits, including N, P, and lignin concentrations, C:N, C:P, and lignin:N ratios, and SLA. In the PCA, variables with communality values < 0.5 were excluded, and only the main components with latent root > 1 were considered. Kaiser-Meyer-Olkin measure and Bartlett's test of sphericity were also carried out to judge the fitness of the PCA. Linear regression was used to assess the relationship between Q_{10} values and the scores of the PCA axes or the traits of green leaf and litter. The effect of N or P resorption on litter C:N, C:P, and lignin:N ratios, as well as the correlation between green leaf and litter traits, was also tested by linear regression. Statistical analysis was implemented in SPSS 19.0, and an alpha level of 0.05 was used if necessary.

Results

Q₁₀ of litter decomposition

In the present study, the 15 target species, with different growth forms, are representative of the overall plant functional feature in the study area (Table 1). On average, 18.1% (12.4–23.9%) and 24.7% (19.8–30.4%) of the initial litter C were respired as CO₂ at 16.5 °C and 21.5 °C, respectively, after 22 days of incubation (Fig. 1a). The 5 °C temperature increase enhanced litter decomposition rates by 21.7–60.2%, indicating the positive response of litter decomposition ranged from 1.63 \pm 0.14 for *Hovenia acerba* Lindl. to 2.57 \pm 0.07

Fig. 1 Percentage litter C respired at different incubation temperatures during the experimental period (a); and Q10 values of the decomposition of litters from these species (b). Error bars indicate standard error (SE, n = 3). LF, Liquidambar formosana Hance; CC, Cinnamomum camphora (L.) Presl.; CL, Cunninghamia lanceolata (Lamb.) Hook .; SS1, Schima superba Gardn. et Champ.; MM, Michelia macclurei Dandy; CM, Castanea mollissima B1.; DK, Diospyros kaki var. sylvestris Makino; KS, Kalopanax septemlobus (Thunb.) Koidz.; CF, Castanopsis fargesii Franch.; QF, Quercus fabri Hance; BL, Betula luminifera H. Winkl.; SS2, Sapium sebiferum (L.) Roxb.; VF, Vernicia fordii (Hemsl.) Airy Shaw; QD, Quercus delavayi Franch.; HA, Hovenia acerba Lindl

for *Liquidambar formosana* with a mean value of 1.93 (Fig. 1b).

Litter quality and Q₁₀ values as affected by LES and nutrient resorption

A suite of green leaf traits was integrated into a framework using PCA to describe LES across species (Fig. 2). The consensual criteria for PCA were also met (Table S1). The first and second PCA axes explained 55.4% and 22.0% of the variation, respectively (Fig. 2). Most of the variation in green leaf traits could be interpreted by the first PCA axis, which was correlated positively to the ratios of C: N, lignin: N, and C:P and lignin concentration but was correlated negatively to leaf SLA and N and P concentrations (Fig. 2). Therefore, the first PCA axis represented LES, with resource-acquisitive species to the left, and resource-conservative species to the right. Species scores of the first PCA axis showed significant positive correlations with Q₁₀ values ($R^2 = 0.38$, P =





Fig. 2 Biplot showing the results of principal component analysis (PCA) based on seven leaf functional traits for the 15 species. Species position in the plot was determined from their mean scores on the two axis (n = 3). Litter trait abbreviations: N, N concentration; P, P concentration; SLA, specific leaf area

0.014), litter C:N ($R^2 = 0.39$, P = 0.013), and lignin:N ratio ($R^2 = 0.27$, P = 0.048) but not C:P ratio (P > 0.05) (Fig. 3a, and Fig 4a, c, and e). The Q₁₀ values were correlated positively to the C:N and lignin:N ratios of green leaf and litter and negatively correlated to leaf and litter N concentrations (Table 2). The P and lignin concentrations, SLAs, and C:P ratios of green leaf and litter showed no correlation with Q₁₀ values (Table 2).

The species exhibited a wide variation in nutrient resorption rates, with NRE and PRE values varying by 2.7 (27.1–75.4%) and 2.1 folds (41.9–86.3%), respectively. Neither showed a relationship with the Q_{10} of litter decomposition (Fig. 3b and c). In comparison, significantly positive correlations were found between NRE and litter C:N ratio ($R^2 = 0.52$, P = 0.003), as well as between PRE and litter

C:P ratio ($R^2 = 0.61$, P = 0.001) (Fig. 4b and f). Conversely, no correlation was found between NRE and litter lignin:N ratio (Fig. 4d). Litters had co-varied C concentration ($R^2 =$ 0.75, P < 0.001), N concentration ($R^2 = 0.57$, P = 0.001), C:N ratio ($R^2 = 0.44$, P = 0.007), lignin:N ratio ($R^2 = 0.38$, P = 0.015), and SLA ($R^2 = 0.78$, P < 0.001) with those of green leaves (Fig. 5a, c, e, f, and h). However, the lignin concentration, P concentration, and C:P ratio of litters were not correlated with those of green leaves (Fig. 5b, d, and g). Moreover, LES had no correlation with NRE and PRE (Fig. 6).

Discussion

The species of our study formed a LES (Fig. 2), which was in line with many previous case studies (Bakker et al. 2011; Lin et al. 2019). The decomposition of litters from resource-conservative species was more temperature-sensitive than those from resource-acquisitive species supporting our first hypothesis (Fig. 3). Our second hypothesis was not supported by data because NRE and PRE were not responsible for the Q_{10} variance (Fig. 3). Although the estimation of litter decomposition rate might involve a bias caused by the priming effect of litter-derived labile C on soil organic C (SOC) mineralization (Kuzyakov et al. 2000), this bias should be negligible. In the studied region, Chao et al. (2019) reported a priming effect of < 24% after input to soil of leaf litter. If so, the primed CO_2 in the present study only accounts for less than 3% of the litterrespired CO₂, because the litter-respired CO₂ was nine times as that respired by SOC (3.57 mmol vs. 0.39 mmol in mean value), due to the high litter-to-soil ratio. Although this is a local scale study, we may generalize the observed data at a greater scale, because within-site difference in plant features is likely equal to or greater than mean variation across sites (Reich et al. 1999).

Fig. 3 Relationship of Q_{10} values with LES (**a**), N resorption efficiency (**b**), and P resorption efficiency (**c**). Error bars indicate SE (n = 3). Abbreviations: LES, leaf economics spectrum (measured as species scores of the first PCA axis); NRE, N resorption efficiency; PRE, P resorption efficiency



Fig. 4 Subplots showing the correlations of LES with litter C:N ratio (a), lignin:N ratio (c), and C:P ratio (e), respectively; subplot (b) and (d) showing the correlations of NRE with litter C:N and lignin:N ratio, respectively; subplot (\mathbf{f}) showing the correlation between PRE and litter C:P ratio. Error bars indicate SE (n = 3). Abbreviations: LES, leaf economics spectrum (measured as species scores of the first PCA axis); NRE, N resorption efficiency; PRE, P resorption efficiency



Table 2 Correlation coefficients (*r*) between green leaf or litter traits and the Q_{10} of litter decomposition (N = 15). The significance (*P* values) is also given. Litter trait abbreviation: SLA, specific leaf area

	r	Ρ
Green leaf		
Ν	-0.680	0.005
Р	-0.025	0.929
Lignin	0.491	0.063
SLA	-0.457	0.087
C:N ratio	0.713	0.003
Lignin:N ratio	0.723	0.002
C:P ratio	0.040	0.89
Litter		
Ν	-0.617	0.014
Р	-0.422	0.118
Lignin	-0.101	0.720
SLA	-0.439	0.102
C:N ratio	0.662	0.007
Lignin:N ratio	0.696	0.004
C:P ratio	0.194	0.49
C:P ratio	0.194	0.49

LES and nutrient resorption as controllers of litter quality

Our results demonstrated the tight controls of LES over litter quality in terms of the C:N and lignin:N ratios (Fig. 4). Traits of green leaf are not always parallel with those of litter, owing to the nutrient resorption process (Zhang et al. 2015; Zhao et al. 2017). In our study, substantial N resorption took place during leaf senescence (Fig. 5), but it did not change the rankings among species for litter N concentration and thus for the C:N and lignin:N ratios (Fig. 5), as already reported (Aerts 1996; Santiago 2007; Bakker et al. 2011). Surprisingly, the litter C:P ratio, as another indicator of litter quality, was decoupled from LES, which mainly resulted from the uncoupled P concentrations of green leaf and litter (Fig. 5). One possible explanation is that P is deficient relative to N for trees grown in the subtropical ecosystem (Bakker et al. 2011), and this may cause P resorption to ensure an optimal P use efficiency (Reed et al. 2012). Moreover,



Fig. 5 Comparison of C concentration (**a**), lignin concentration (**b**), N concentration (**c**), P concentration (**d**), C:N ratio (**e**), lignin:N ratio (**f**), C:P ratio (**g**), and specific leaf area (**h**) between green leaf and litter. Error bars indicate SE (n = 3)



Fig. 6 Relationship between leaf economics spectrum and N or P resorption efficiency. LES, leaf economics spectrum (measured as species scores of the first PCA axis); NRE, N resorption efficiency; PRE, P resorption efficiency

P in plants is stored in more labile forms than N, which will favor a greater resorption of leaf P by plants (Bieleski 1973). These interpretations were underpinned by

the higher values for PRE than NRE (64% vs. 54% in mean value). The litter C:N and C:P ratios increased with NRE and PRE, respectively, indicating that litter quality

decreased as leaf nutrient resorption increased (Fig. 4), as already reported (Deng et al. 2018; Xu et al. 2020). However, such a relationship was not observed between NRE and litter lignin:N ratio (Fig. 4), likely because litter lignin concentration had a greater variation across species than litter C concentration.

Litter quality mediated LES- and resorption-Q₁₀ relationship

Litter quality negatively affected Q_{10} , as indicated by the positive relationship between Q₁₀ values and litter C:N and lignin:N ratios (Table 2). This finding confirmed what was observed in our previous study (Li et al. 2021). Likely decomposing recalcitrant substrates requires higher activation energy, and thus, it is more sensitive to warming than the decomposition of labile substrates ("C quality temperature" hypothesis, Davidson and Janssens 2006). These results contradict what was reported by Gershenson et al. (2009), Thiessen et al. (2013), and Pang et al. (2015). Likely, the low quality of litter in these studies is due to low substrate availability, which is not enough to stimulate microbial decomposition by warming (Thiessen et al. 2013). In this case, our results were not against this substrate availability-related Q₁₀ model, for the following reasons. Microbial metabolism in natural soil is typically C-limited, and thus, substrate availability is the predominant factor that regulates the Q₁₀ of microbial decomposition (Gershenson et al. 2009). In this study, however, the C input with litter addition should have alleviated microbial C limitation, with substrate recalcitrance becoming the main factor limiting microbial decomposition (Karhu et al. 2010; Thiessen et al. 2013).

We found that leaf C:N and lignin:N ratios predicted the Q_{10} of litter decomposition (Table 2), stronger than LES, likely because some other components unrelated to litter quality were included in the LES framework. Determining green leaf traits that can accurately predict the Q_{10} of litter decomposition can be useful for modeling purposes, because green leaf trait databases are extensive in the literature, while this is not the case for litter traits (Kattge et al. 2011; Rosenfield et al. 2020). Therefore, we support using individual green leaf traits rather than the more comprehensive LES to predict the temperature dependency of litter decomposition in future modeling study.

Unlike LES, NRE and PRE had no effects on Q_{10} , although they had some influences on litter quality (measured as C:N and C:P ratios). This result demonstrated that LES played a predominant role over nutrient resorption in shaping the response of litter decomposition to warming. Indeed, the litter C:P ratio did not affect the Q_{10} of decomposition (Table 2), contradicting what was reported by Mao et al. (2018), who found the positive correlation between litter C:P ratio and the Q_{10} of decomposition due to the warming induced shift from N limitation towards N and P co-limitation for microbial decomposition. It is difficult to explain the lack of Q_{10} response to litter C:P ratio variation, considering that P is often more limited in the studied subtropical region than in their temperate region (Bakker et al. 2011; Li et al. 2022b). We speculated this discrepancy as partly due to the fact that the P concentration of our litters showed a narrower range compared with that of Mao et al. (2018).

Nutrient resorption had a consistent effect on the control of LES over litter quality and the Q_{10} of decomposition for the following reasons. The resorption process prevents nutrients from saving in the litter, contributing to the difference between foliar and litter traits. In this study, the nutrient resorption efficiency did not vary with LES (Fig. 6), indicating that nutrient resorption has caused an equal inhibition of the potential for resource-conservative and resource-acquisitive species to leave their nutrients to the litter. However, there was evidence that higher resorption occurred for resource-acquisitive species to meet high nutrient demand (Zhang et al. 2015), or for resource-conservative species to compensate for the limited nutrient uptake from soil (Lamaze et al. 2003). The most likely explanation for this discrepancy is that nutrient resorption can also be affected by factors other than LES, such as climate, nutrient supply, and leaf morphology, which have confounded the "LES-nutrient resorption" relationship (Freschet et al. 2010; Zhang et al. 2015; Zhao et al. 2017; Deng et al. 2018).

Conclusion

In this study, we separated the impacts between LES and nutrient resorption on the Q_{10} of litter decomposition. The LES, rather than NRE and PRE, controlled the Q₁₀ of litter decomposition by affecting litter quality. The LES had no interactive effect with NRE or PRE on the Q₁₀ values. Therefore, LES prevailed over nutrient resorption in modulating the Q₁₀ of litter decomposition. We emphasized that forest ecosystems dominated by resource-conservative species might have a greater feedback to atmospheric CO₂ rise and global warming than those dominated by resource-acquisitive species. This study shows the afterlife effect of plant strategy on terrestrial C dynamic. However, there were some limitations in this study. First, our experiment lasted for a short period to reduce the bias associated with unparallel substrate availability decrease over time between temperature regimes (Fierer et al. 2006). Second, we calculated nutrient resorption efficiency without considering the influence of leaf leaching, although it is a minor contributor to nutrient depletion during senescence (Freschet et al. 2010).

Further investigation is needed regarding whether these limitations affect our conclusions.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00374-023-01758-w.

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Declarations

Conflict of interest The authors declare no competing interests.

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