

# What controls forest litter decomposition? A coordinated, distributed teabag experiment across 10 mountains

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## Abstract

Forest litter decomposition is considered as an essential ecosystem process affecting carbon and nutrient cycling in mountains. However, there exists high uncertainty in accurately estimating the contribution of litter decomposition to terrestrial ecosystems, largely due to the incomparability of different studies and the data limitation in microclimate and non-climatic factors at spatially matched scales. Here we used the tea bag index (TBI) as a standardized protocol to evaluate spatial variations in forest litter decomposition rate ( $k$ ) and stabilization factor ( $S$ ) across 10 mountains spanning a wide range of subtropical and tropical forests. Based on the coordinated experiment of 6,864 teabags in 568 sampling sites along elevations, we evaluated the importance of 10 environmental factors covering soil microclimate, edaphic properties, plant diversity, and topography on  $k$  and  $S$  by using model averaging and linear-mixed effects models. Of the 10 mountains, we found a consistently decreasing pattern of  $k$  and an increasing pattern for  $S$  along elevations. And the significant effect of  $k$  with elevation was mainly found in the western and northmost mountains, while the effect of  $S$  occurred in the western and southernmost mountains. For microclimate, there was a general importance of soil temperature (coef. = 0.48) and temperature variation in the growing season (coef. = 0.36) in  $k$ , and soil temperature (coef. = -0.46) and moisture variation on  $S$  (coef. = -0.36). The dominant role of soil microclimate was mainly found in western mountains with relatively cold environments. For non-climatic drivers, a significant effect of tree diversity on  $k$  and a negative correlation of edaphic and topography with  $S$  in the western and southern mountains were detected. These findings provide a general understanding of spatial variations of driving factors in forest litter decomposition and highlight a dominant control of soil microclimate in cold forests in high elevations and latitudes.

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Keywords: altitudinal gradient; climate change; experimental macroecology; litter decay; microclimate

## Introduction

Mountainous forest ecosystems account for only 1.8% of the Earth's surface (Price et al. 2011), but they hold extremely high carbon storage globally (Cuni-Sanchez et al. 2021), and more than half of them are returned to soil through litter decomposition (Wardle et al. 2004). Forest litter decomposition is also considered as an essential ecosystem process affecting nutrient cycling and species diversity in an ecosystem (Mayer et al. 2021). However, there exists high uncertainty in accurately estimating the contribution of litter decomposition to terrestrial carbon cycle and its feedbacks to ecosystems, which largely hampers the development and prediction abilities of earth system models (Jones et al. 2005) and dynamic global vegetation models (Sitch et al. 2003). To enhance the estimates of the role of forest litter decomposition in global element cycling and multi-taxon biodiversity, the fundamental understanding of the dominant controls on decomposition across different mountains and forests is critically needed (Bradford et al. 2016).

The mass loss of litter components is mainly regulated by temperature, moisture availability, edaphic factors, and the quality of the plant litter (Tenney and Waksman 1929, Bradford et al. 2016). Air temperature and moisture at broad spatial scales are currently used as the predominant factor controlling decomposition rates due to their direct and indirect controls on decomposers and litter quality (Wall et al. 2008, Pablo García-Palacios et al. 2013, Steidinger et al. 2019, Ma et al. 2022). However, this climate-centred evidence relies heavily on air temperature and moisture at coarse spatiotemporal scales or in open areas that are not matched with the closely experienced microclimate within forest litter layers (Steidinger et al. 2019, Joly et al. 2023). For instance, soil temperature can differ from air temperature up to 10 owing to buffering effects by habitat terrain (Lembrechts et al. 2022). Despite a few recent studies assessing the role of microclimate on decomposition, its contrasting (little vs. significantly positive) effects on decomposition rates were reported,

with a substantial bias towards tundra ecosystems and temperate forests (Chen et al. 2018, 2023, von Oppen et al. 2024). This mismatch and data bias lead to knowledge gaps in the regulating effects of microclimate variation on litter decomposition, particularly the underrepresented subtropical and tropical forests where microclimate is perennially buffered by dominated evergreen tree species when compared to other terrestrial ecosystems.

Non-climatic biotic and abiotic factors (e.g., soil physiochemistry, microtopography and vegetation composition) can impact substantially litter degradation by adjusting directly and indirectly climate and the activity of soil microbes (Cornwell et al. 2008, Kaspary et al. 2008, Mori et al. 2020). But the extent and strength of these variables vary dramatically in different forests and mountains, causing discrepancies in the general importance of the same factor in decomposition processes. For instance, variations in soil pH change its association with decomposition processes via different extracellular enzyme activities under acidic or alkaline environments (Romani et al. 2006). Tree richness ranging from 1 to 4 had no effect on decomposition rates in a temperate forest (Fujii et al. 2017), while a gradient up to 24 in a subtropical forest explained 54.3% variation in decomposition (Seidelmann et al. 2016). Such discrepancy of inconsistent roles of these variables on decomposition among findings might associate with insufficient gradients due to sampling bias and the limitation in studied spatial scales (Keuskamp et al. 2013). Therefore, from a perspective of experimental macroecology, a distributed and coordinated study with wide environmental gradients across different mountains could shed insights into a general understanding of the underlying mechanisms that regulate forest litter decomposition.

Another advantage of experimental macroecology in forest litter decomposition is to avoid the incomparability among a large number of studies in different ecosystems with diverse plant composition, which is a common issue in ecology (Spake et al. 2022). This top incomparability can be attributed to distinctive litter quality. The composition and quality of forest foliar litter are highly location-specific at both local and regional scales due to diverse species composition. The high plant diversity determines the diversity of litter, yielding an overriding influence of litter quality on decomposition processes across any type of ecosystem (Mori et al. 2020). Therefore, to tease environmental effects on decomposition apart from litter quality per se, standard litters, such as a full mix of all plant litters from a study site or uniform litter type that does not belong to any study sites (e.g., tea bags and wood stick), are a premium method to control the intrinsic effects by litter quality (Fanin et al. 2020, Joly et al. 2023). Except for the huge difference in litter quality, the incomparability also reflects on the absence or presence of the same environmental factors in different studies (Bradford et al. 2016). Hence, the use of standardized litter substrate and the inclusion of multiple environmental factors across multiple mountains are certainly helpful to reduce the biases induced by incomparability.

In this study, we conducted a macroecological litter decomposition experiment across 10 mountains spanning a wide range of Chinese subtropical and tropical forests. These mountains provide high divergence in abiotic and biotic environmental gradients. We buried 6,864 standardized teabags across 568 elevational sites in 10 mountains and quantitatively evaluated the influence of soil microclimate, tree diversity, soil physiochemistry, and topography on decomposition rate and litter stabilization factor within and among mountains. Specifically, we addressed three questions: 1) Are there general patterns of forest litter decomposition rates and stabilization along elevational gradients in these mountains? We predict that decomposition rates decrease along elevations and stabilization increase because of harsh environmental conditions and increased inhibition at high elevations. 2) Do soil microclimate (temperature, moisture, and their variations) play the predominant role in controlling decomposition rates and stabilization across mountains? We predict that temperature and its variation increase decomposition rates due to their direct and indirect controls on decomposers (Glassman et al. 2018), and the moisture and its variations affect stabilization because soil humidity conditions can modify the absorption and adhering of litter organic carbon on soil surface or aggregate (Morffi-Mestre et al. 2023, Feyissa et al. 2023). 3) To what degree do non-climatic factors (edaphic factors, tree diversity, and topography) contribute to explaining the variations in litter decomposition within and among mountains? We predict negative effects of high soil pH and slope on stabilization due to increased cation exchange capacity and water erosion (Zhu et al. 2019), and strong constraints of low tree diversity

on decomposition rates because of potentially lower microbial diversity (Joly et al. 2017).

## Material and Methods

### Study sites along elevations in 10 mountains

This study was conducted in 10 mountains of the BEST (Biodiversity along Elevational gradients: Shifts and Transitions research network (<https://BEST-mountains.org>). This network was designed to use standard field methods (e.g., plot design, plant survey, and sample collection) to demonstrate biogeographic patterns and ecological processes across regions. The 10 mountains belong to subtropical and tropical regions (Fig. 1a) where the climate is heavily buffered by dense canopies compared to temperate and boreal forests (De Frenne et al. 2019). The geographical distribution of the studied region spanned from 98°42' – 119°26' in longitude and 19°4' – 31°9' in latitude. Elevation ranges from 252 to 3835 m a.s.l. The mean soil temperature of the growth season (June to August) ranges from *ca.* 13 – 22, with the coolest climate in Jade Dragon Snow Mountain (YMT) and the warmest climate in the tropical mountain Bawangling (BWL). Along elevational gradients, species composition often shifts sequentially, i.e., evergreen-broadleaved species, mixed evergreen-broadleaved and deciduous species, deciduous and conifer species, and high mountain shrubs. In each mountain, 20 m × 20 m permanent sample plots were established from the mountain bottom to the top at a distance of *ca.* 100 m difference. In total, 142 plots were included in our study (Table S1). Within each plot, all tree individuals with stems > 1 cm were identified to species level. Tree species richness (using “Tree” when referred as environmental factor) was calculated and used as the biotic factor in decomposition processes.

### Standardized teabag experiment

We used the tea bag index (TBI) to investigate litter decomposition processes along the elevation of each mountain by following the protocol from Keuskamp et al. (2013). In this approach, two types of teabags (green tea: EAN8722700055525 and rooibos tea: EAN8722700188438) were used as standard leaf litter bags, which can be used globally and across biomes to generate comparable results (Keuskamp et al. 2013, Djukic et al. 2018). The material of the teabag is made of polypropylene and has a mesh size of 0.25 mm allowing the access of microfauna, microbes, and very fine roots (Fig 1c, d).

Within each plot, we selected four sampling sites according to the criteria below: 1) understory species composition at each site is representative and similar to neighbor sites; 2) homogeneous in microhabitat between sites, e.g., slope and canopy cover; 3) no clear rocks, big tree roots, anthropogenic disturbances; 4) four sites were as evenly distributed as possible within a plot. Each site was labeled with a PVC tube (Fig. 1b). Before the start of the field experiment, all teabags were oven-dried at 70 °C for 24 h. Each teabag was identified and buried in the upper 8 cm of the top soil layer for three months. At each site, we buried 12 teabags (6 red vs. 6 green). In total, 6,864 teabags were buried (6 replications × 2 tea types × 4 sites × 142 plots), and 87% (5,996) of the bags were retrieved. With intensive cooperation from each region, this field experiment was conducted nearly simultaneously across all mountains, buried between late May and early June 2021 and retrieved between late August and early September 2021. This decomposing period was designed to capture energy flow in peak growing season in subtropical and tropical forests.

At the end of the decomposition period, we retrieved all tea bags and transported them immediately in ice-isolated boxes to the Lab at East China Normal University, Shanghai. During the process of retrieval and transportation, sterilized gloves and sampling bags were used to avoid any contamination. Soil particles adhered on the surface of the litter bag were removed once received and dried at 70 °C for 48 h. Dried litter bags were again cleaned by hand carefully to avoid ash falls. Then we recorded the extent of damage to each tea bag according to the number and size of holes. Undamaged bags with one or several minor holes (< 1 mm) were used for weighing the remaining materials. According to the decomposition protocol, we calculated

TBI, which includes the decomposition rate constant ( $k$ ) and stabilization factor ( $S$ ). In short, mass loss ( $W$ ) at time  $t$  is a double-exponential function of decomposed fraction ( $a$ ) with the constant  $k$  (eqn. 1). The  $k$  represents how fast the labile carbon is about to be decomposed under a certain environment, reflecting the velocity of carbon loss.  $S$  indicates the fraction of the recalcitrant which stabilized from a theoretically hydrolysable fraction ( $H$ ) due to environmental constraints (eqn. 2):

$$W(t) = ae^{-kt} + (1 - a) \quad \text{eqn. 1}$$

$$S = 1 - \frac{a}{H} \quad \text{eqn. 2}$$

Meanwhile, we measured three microhabitat factors (Cover: canopy cover, Thick: ground litter thickness, and slope) which can potentially affect decomposition directly and indirectly. Canopy cover was measured at 50 cm above the soil surface during the sunny day (avoid solar radiation at noon) at each site three times by using a fish-lance (238@, wide-angle view). Canopy pictures were analyzed using the software Gap Light Analyzer (Frazer et al. 1999). Ground litter thickness was the layer of dead leaves and debris that covered the soil surface. The slope of each site was measured with consistent orientation, i.e., standing the downhill side and facing the mountain slope.

## Microclimatic and edaphic variables

Soil microclimate (temperature and humidity) was recorded at the centre of each plot at a depth of 8 cm relative to the soil surface at 15-minute intervals using temperature and moisture loggers (TMS4, TOMST Ltd.). Due to the high risk of monkey disturbance in EMS, the microclimate in this mountain was recorded using iButton (Maxim Integrated DS1925), which can fully be buried under the soil. Soil microclimate indices of the three months included 8 temperature indices and 7 moisture indices referring to the bioclimatic variables in WorldClim or CHELSA. Eventually, four microclimatic indices were retained after controlling the collinearity. These four indices reflect both the mean and variation of soil microclimate matching with decomposing period (growing season), including the monthly mean soil temperature (Temp<sub>m</sub>), standard deviation of soil temperature (TempV), the monthly mean soil moisture (Mois), and standard deviation of soil moisture (MoisV).

Soil samples were collected at 0 – 10 cm using 5-cm augers. In each plot, five soil cores were taken randomly and mixed homogeneously, after the removal of visible roots, debris, and stones. Soil samples were air-dried and sieved through a 1-mm mesh. We measured soil pH and total phosphorus (P) following the standard protocol of Ma et al. (2019). We focused on the two soil factors because: 1) soil pH plays a major role in the structure of microbial community composition globally locally (Hendershot et al. 2017, Ma et al. 2022); 2) the large variation of soil total P across the studied regions implies its potential constraints on ecosystem processes (He et al. 2016).

## Statistical analyses

We first tested the elevational pattern of decomposition rate ( $k$ ) and stabilization ( $S$ ) within each mountain using least square regression followed by model diagnostics of residuals normality and homoscedasticity using the function *autoplot* from the R package *ggfortify* (Tang et al. 2016). Before the test, we scaled the elevation of each mountain to 0 – 1 to avoid scale differences in elevation ranges between mountains. The regression was also used to examine the correlation between  $k$  and  $S$  within each mountain. The same correlation method was used for testing the correlation significance of environmental drivers (Fig. S1). Spearman correlation coefficients ( $< |0.7|$ ) were used as a threshold to identify multicollinearity (Dormann et al. 2013) when multiple regression analyses were applied.

To quantify the dominant role ( $w$ ) of soil microclimate in decomposition processes, we applied all possible combinations of the ten environmental variables and fitted these component models with the least square regression for  $k$  and  $S$  in each mountain separately, and calculated the relative importance value ( $w$ ) as the weight of Akaike's Information Criterion (AIC) based on model averaging. For each mountain and the

response variable, we extracted the best model which contained the lowest AIC and was used to indicate the significant drivers in each mountain. To avoid multicollinearity, we calculated VIF values and refit the best model by excluding variables that had a VIF value  $> 4$ . This operation only occurred in the three best models (Temp in BWL when predicting  $k$ , Temp and TempV in TMS when predicting  $S$ , and TempV and Cover in EMS when predicting  $S$ ). As the extent of the significance matched well with the value of the weight (Table S2), we used the latter to represent the relative importance because full model averaging optimizes the uncertainties and biases from threshold-selected models (Burnham and Anderson 2002). Since the data of Tree, edaphic factors, Mois, and MoisV were unavailable in EMS, we removed EMS and focused on 9 mountains when comparing the relative importance of each factor in decomposition.

Finally, we assessed the specific effect of the four soil microclimatic factors and three non-climatic factors on  $k$  and  $S$  within each mountain and across all mountains. The three factors were tree diversity, soil pH, and slope, which were representative in terms of its profound direct and indirect influences on decomposition via litter quality, decomposers, and microhabitat, respectively. We used least square regression models and a linear mixed-effects models (mountain as a random effect) to test each factor's influence on  $k$  and  $S$  within each mountain and across all mountains. The mixed-effects model was estimated using the *lme4* package (Bates et al. 2015), and the values of explained variance ( $R^2$ ) of the models were calculated using the function *r.squaredGLMM* in R package *MuMin* (Bartoń 2023).

All statistical analyses were conducted in R 4.3.1 (R Core Team 2014).

## Results

### Decomposition rates and stabilization in 10 mountains

Across the 10 mountains, the decomposition rate ( $k$ ) ranged from 0.002 to 0.05 (0.02 on average), and the stabilization factor ( $S$ ) ranged from 0.006 to 0.35 (0.13 on average). JFS experienced the fastest mass loss ( $k = 0.02$ ), which was significantly higher than that in six mountains on its east side (Fig. S2). The highest mean  $S$  occurred in EMS and YMT (0.18), which was significantly higher than  $S$  in GMT and the five eastern mountains (Fig. S3). There were no significant correlations between  $k$  and  $S$  (except DBS) (Fig. S4).

Although both significant and non-significant correlation existed, there was a consistent pattern in each mountain that  $k$  decreased along elevations (but see a slight hump-shape in YMT), and an opposite trend for  $S$  (Fig. 2). For  $k$ , the significant elevational pattern was mainly found for four western mountains (GMT, YMT, EMS, and JFS) and the northmost mountain (DBS). For  $S$ , the statistically significant trend occurred in three western mountains (GMT, YMT, and JFS), and the southernmost mountain (BWL).

### The importance of microclimate in decomposition

Among 10 climatic and non-climatic variables, soil microclimate related variables, mainly Temp, TempV, and MoisV, emerged as the most important factors in controlling litter decomposition in the western mountains (Figs 3-4, Table S2). Across all mountains,  $k$  was mainly impacted by soil temperature (*coef.* = 0.48,  $P < 0.001$ ) and its variation (*coef.* = 0.36,  $P < 0.001$ ), while  $S$  was subjected to significant effects from all microclimatic factors, with particularly strong relation with soil temperature (*coef.* = -0.46,  $P < 0.001$ ) and the variation of soil moisture (*coef.* = -0.36,  $P < 0.001$ ) (Fig. 5).

### The effects of non-climatic drivers in decomposition

Non-climatic factors, i.e., tree diversity, soil (pH and P), and microhabitat (litter thickness, canopy cover, and slope) emerged as important as soil microclimate in western mountains and the northmost mountain (DBS) (Figs 3-4, Table S2). Among mountains, three representative factors (tree diversity, soil pH, and slope) showed substantially spatial variations in its relations with  $k$  and  $S$  (Fig. 6). Across all mountains,

tree diversity ranged from 4 to 93 and increased  $k$  significantly ( $coef. = 0.25, P < 0.001$ ). Soil pH (ranged from 3.06 – 7.16) and slope (0.25 – 42.5) had no significant effect in this respect. For  $S$ , we found no significant effects of tree diversity but a significantly negative association with soil pH ( $coef. = -0.17, P < 0.001$ ) and slope ( $coef. = -0.14, P < 0.001$ ).

## Discussion

Lacking a general understanding of dominant factors driving forest litter decomposition leads to high uncertainties in the estimation of carbon dynamics at both regional and global scales and its feedback to climate changes (Davidson and Janssens 2006, Krishna and Mohan 2017). From the perspective of experimental macroecology, this study took advantage of highly diversified environmental gradients along elevations of multiple mountain ecosystems, and analysed the effects and relative importance of 10 abiotic and biotic factors in decomposition processes both within and among mountains by using standardized litter materials. The results demonstrate a high variation of decomposition rates (0.002 – 0.05) and stabilization (0.006 – 0.35) across study sites. Within mountains, soil microclimate played a dominant role in decomposition processes mainly in the western high-altitude mountains with colder environments, a similar magnitude of importance for non-climatic factors emerged in the western and the northernmost mountain, indicating the spatial variation of driving factors in decomposition processes. Across mountains, although tree richness impacted decomposition rates, and moisture, soil pH, and slope affected stabilization significantly, soil temperature possessed the strongest association with both decomposition rates (0.48) and stabilization (-0.46), supporting the importance of microclimate and environmental range or gradient in controlling decomposition processes (Bradford et al. 2014, Gallois et al. 2023). Our study provides a general understanding of microclimate and non-climatic factors' effects on decomposition across mountains, shedding light on the underlying mechanisms for forest carbon dynamics under global change.

### Decomposition rates and stabilization along elevations

Among mountains, the velocity of litter mass loss is generally higher in the east than in the west due to the premium hydrothermal conditions. The highest decomposition rate reached 0.24, with no significant difference between the southeastern mountains. This result is comparable to a study in Kilimanjaro Mountain which used the same standardized litter. Their maximum mean decomposition rate is nearly the same as our observations. The difference is that the stabilization in Kilimanjaro is generally higher possibly caused by the obvious transition between warm-dry and warm-wet weather during the decomposition period (Becker and Kuzyakov 2018). For both studies, high elevations are projected to promote carbon stocks due to slow decomposition rates and/or higher capacity in stabilization possibly contributed by large macroaggregates (Feyissa et al. 2023).

### The dominant role of microclimate in decomposition

Of the 10 mountains, the significant changes in decomposition rates and stabilization with elevation are nearly in line with mountains that experienced significant correlations between decomposition (stabilization) and microclimatic factors. Although non-linear and linear correlations emerged for the same factor among mountains, there is a potential convergence of significant effects of microclimate in mountains located in the west. The western mountains generally possess higher elevations and cooler environments because of the expanded monsoon that was caused by the fast uplift of the Tibetan Plateau at  $\sim 41$  million years ago (Wu et al. 2022). Colder environments are often associated with a higher thermal sensitivity of microbes or soil animals, resulting in increased decomposition rates with temperatures (Koven et al. 2017). In contrast, the expected positive effects from the evident temperature gradient on decomposition rates in warmer tropical environments can be neutralized by thermal-adapted microbes (Koven et al. 2017).

Across mountains, we found a significant change in the slope of the decomposition rate as a function of soil mean temperature across all mountains (the best breakpoint at 19.79 ,  $N = 998$ ,  $P < 0.001$ ). Below the breakpoint, decomposition rates increased with soil temperatures significantly, and the mean soil temperatures of these western mountains fell into this range. Beyond the breakpoint, the increase in soil temperature no longer accelerates decomposition rates. Of the 10 mountains, this ecotone mountain is the only one with an east-west orientation and acts as a barrier to the southward flow of the cold air (Wang et al. 2016), which also experienced a mean soil temperature lower than the breakpoint. Taken together, these observations stress the key role of microclimate in decomposition processes and imply that there might be a threshold of temperature effects on decomposition rates.

## Inconsistent effects of non-climatic drivers on decomposition

Non-climatic environmental drivers (e.g., tree species richness, soil biochemistry, and topography) emerge as significant factors constraining litter decay across mountains. For instance, litter decomposition rates increased with tree species diversity, echoing the facilitation of high plant species diversity on decomposition rates via complementary effects caused by multiple functional traits (Handa et al. 2014). Given temperature and species diversity co-vary at the global scale, i.e., tropical forests often possess higher species diversity than boreal forests, it is essential to consider their interaction to increase the predicting accuracy of carbon stocks in forest ecosystems (Spohn et al. 2023). In complex terrain, topography emerges as a significant driver regulating decomposition through the effect on stabilization of litter-derived organic carbon (Fig. 6). Across the globe, complex terrain accounts for more than 50% of the land surface (Rotach et al. 2014), and the explanatory power of slope on the variance of soil CO<sub>2</sub> flux exceeds 50% in such complexed ecosystems (Reyes et al. 2017). Our results thus advocate that the prediction of ecosystem functions at large spatial scales should take the assumption of microhabitat (e.g., topography and canopy cover) into account, which has been currently underrepresented in multiple earth system models (Bonan et al. 2013, Phillips et al. 2019, Ren et al. 2024).

## Forest litter decomposition towards experimental macroecology

With massively accumulated evidence of different factors controlling decomposition (Cornwell et al. 2008, Becker and Kuzyakov 2018, Forrester et al. 2023), the incomparability between findings impeded our general understanding of drivers in this critical process because of differentiations in approaches, designs, and methodologies (Spake et al. 2022, Catford et al. 2022). This extent of incomparability can be partially addressed by statistical methods in meta-analyses, while a straightforward and efficient solution is conducting a standardized experimental design at multiple locations at once (“coordinated distributed experiments”) (Vellend 2016). For instance, a meta-analysis focusing on surface litterbags at a global scale (a wide vegetation type) uncovers that 70.2% variation in decomposition rates has been attributed to litter quality but not climate (Zhang et al. 2008). A macroecological experiment spanning from Mediterranean forests to boreal forests in Europe verifies the dominant control of macroclimate in decomposition (Joly et al. 2023). These contrasting results expand our view of decomposition but also indicate that there are intrinsic differences in terms of system characteristics that cause divergent results, such as surface vs. buried decomposition, and forest vs. non-forested ecosystem. Our coordinated distributed experiment controls this difference one step forward to the microenvironment in mountainous forests where the microclimate has been intensively buffered by dense canopies and tree diversity is generally high. As tea bags have been used as standardized litter in many ecosystems (e.g., grassland, alpine and boreal forests) (Althuizen et al. 2018, Chen et al. 2018; von Oppen et al. 2024), future macroecological experiments may consider the transferability of these standardized results to realistic mass loss of local litters, contributing profoundly to current and future dynamics of terrestrial carbon and nutrient cycling.

In conclusion, our macroecological experiment across 10 mountains provides empirical evidence that there is a large spatial variation of soil microclimate and non-climatic factors controlling decomposition processes, with a dominant role of microclimate in the western mountains with colder environments. Across all mountains,

drivers differ between decomposition rates and stabilization, with a positive effect of temperature-related variables and tree diversity on decomposition rates and mainly negative effects of microclimate, pH, and slope on stabilization. This coordinated distributed experiment generates a general understanding of abiotic and biotic influences in decomposition, laying underlying mechanisms for carbon dynamics in complex terrain.

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## Figure Legends

**Fig. 1** The geographic location of the 10 mountains and experimental setup. a: the distribution of the studied mountains spanning subtropical and tropical regions in China. From the West to East: GMT: Gao-ligong Mountain; YMT: Jade Dragon Snow Mountain; EMS: E'mei Mountain; JFS: Jinfo Mountain; DMS: Daming Mountain; BWL: Bawangling; GS: Guan Mountain; DBS: Dabie Mountain; DYS: Daiyun mountain; TMS: Tianmu mountain. Different elevations are shown in colours. b: An example of decomposing design. c: standard tea bags before burying. d: retrieved tea bags after 90-day decomposition.

**Fig. 2** Elevational patterns of decomposition rate (a) and stabilization (b) in each mountain. Colours represent different mountains. Dashed and solid least squares regression lines represent non-significant and significant relationships between elevation and decomposition rates or stabilization, respectively. The elevation of each mountain has been scaled between 0 to 1.

**Fig. 3** The relative importance of environmental drivers for explaining the elevational variations of decomposition rate ( $k$ ) in each mountain. The importance value of each driver is extracted from AIC weight based on model averaging. Colours indicate the four groups (navy blue-Microclimate; gray-plant; yellow-Soil physiochemistry; red-microhabitat) of environmental drivers. Temp: mean temperature of the growth season; TempV: temperature variation of the growing season; Mois: mean moisture of the growth season; MoisV: moisture variation of the growth season, Tree: tree species richness; Soil P: soil total phosphorus, Cover: Canopy cover; Thick: ground litter thickness.

**Fig. 4** The relative importance of environmental drivers for explaining the elevational variations of stabilization ( $S$ ) in each mountain. Other explanations can be found in Figure 3.

**Fig. 5** Scatter plots showing the effect of four microclimatic drivers on decomposition rates (a, b, c, d) and stabilization (e, f, g, h) in each mountain. The black regression line in each panel represents the relationship across all mountains. The shaded area shows the confidence interval at the 95% level. Solid and dashed lines indicate significant and non-significant effects, respectively.

**Fig. 6** Scatter plots showing the effect of three selected non-climatic drivers on decomposition rates (a, b, c) and stabilization (d, e, f) in each mountain. Other explanations can be found in Figure 5.

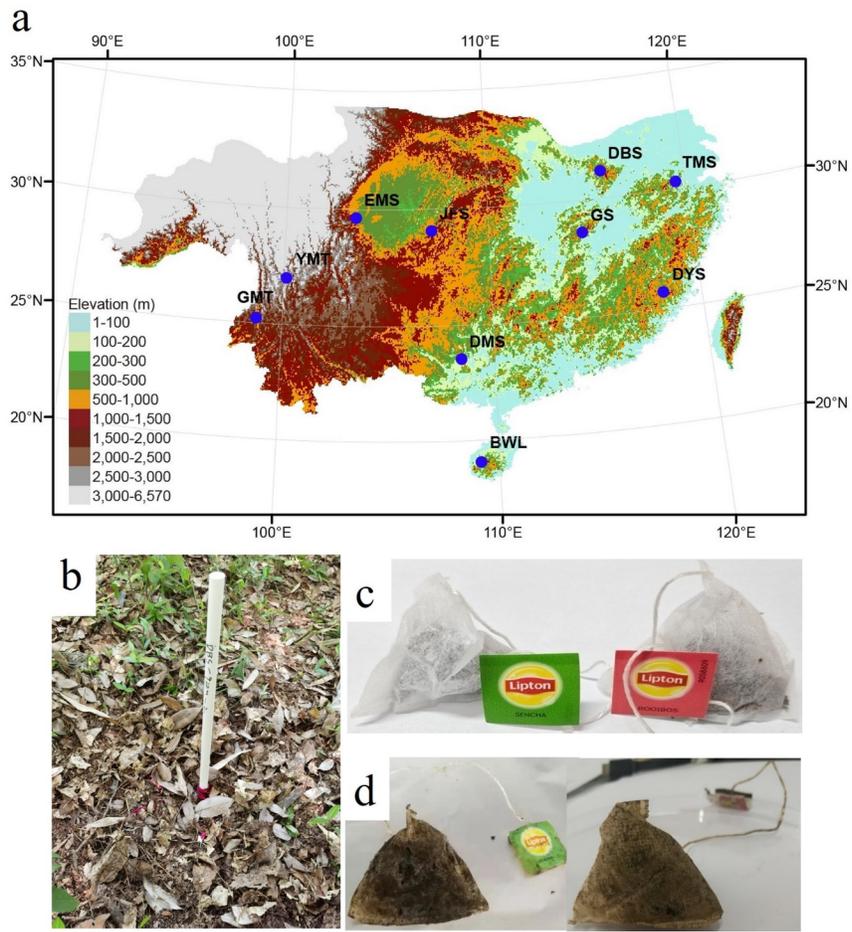


Figure 1

Figure 2

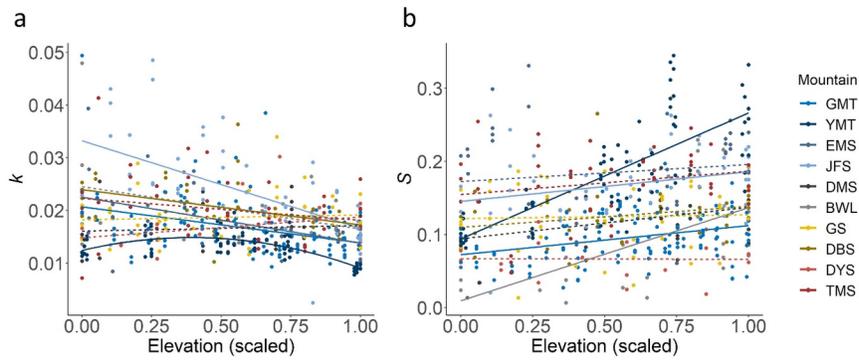


Figure 3

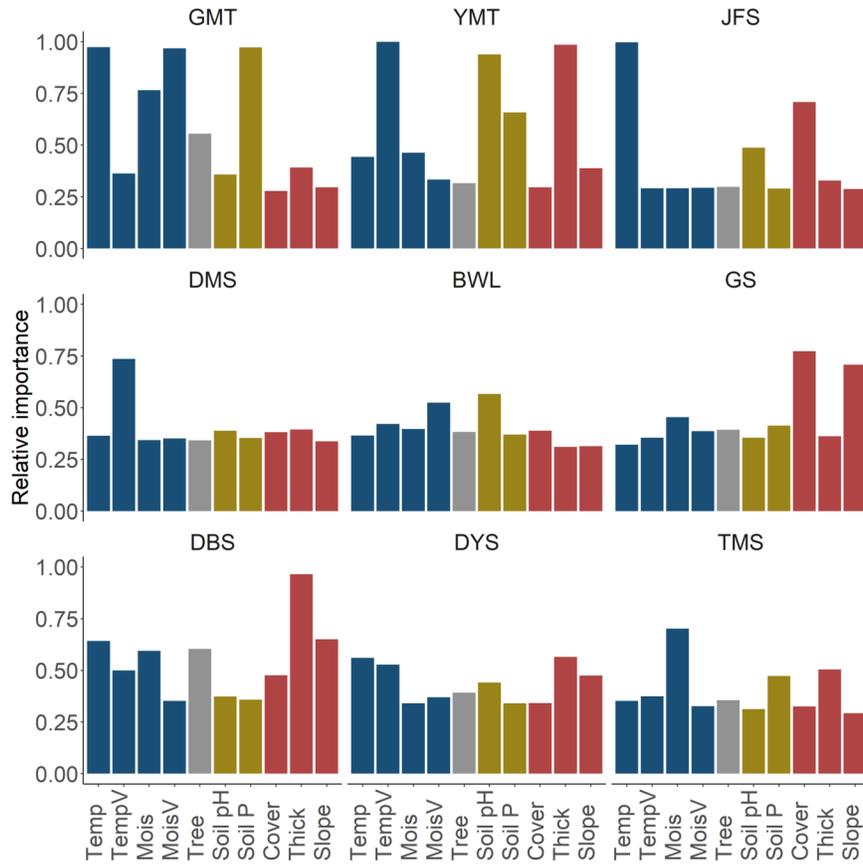


Figure 4

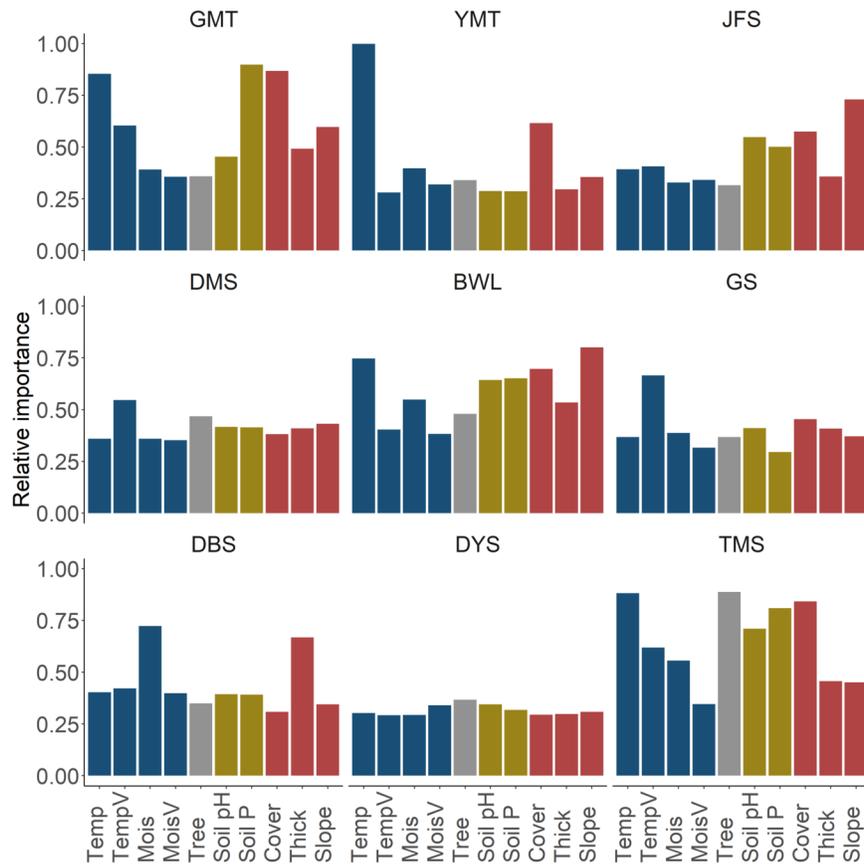


Figure 5

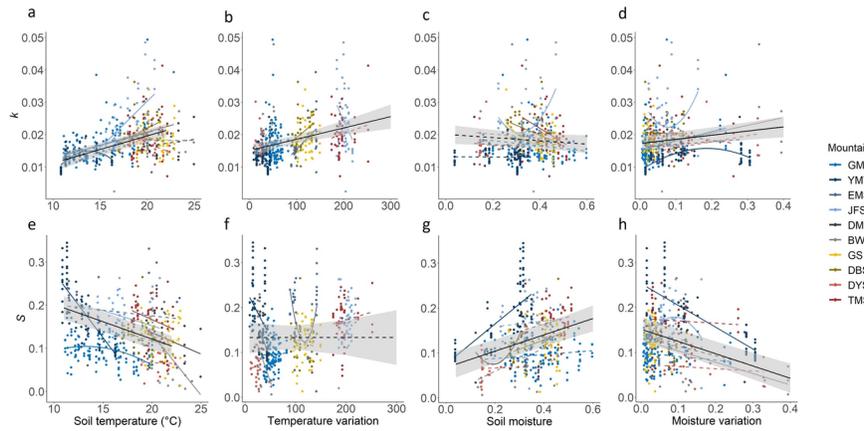


Figure 6

