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Elevation-Driven Divergence in Forest Litter Decomposition and Stabilization: Disentangling Thermal, Nutrient, and Topographic Controls

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Abstract
Litter decomposition in forests governs nutrient turnover and carbon sequestration, but litter decomposition and stabilization may not follow the same trends along an elevation gradient. This needs to be understood to predict forest carbon response to environmental change. This study examined elevation-driven variation in forest litter decomposition and stabilization and identified the relative influence of thermal, nutrient, and topographic controls. A quantitative cross-sectional analysis was conducted using 451 observations from multiple mountain systems. Decomposition rate (K) and stabilization factor (S) were analyzed as response variables using descriptive statistics, elevation-gradient regressions, multiple regression, and mixed-effects models, with mountain included as a random effect. Decomposition rate decreased significantly with elevation, whereas stabilization factor increased, indicating divergent responses along the gradient. Elevation explained 19.8% of the variation in K and 5.2% in S. Mean soil temperature emerged as the strongest predictor, exerting a positive effect on K but a negative effect on S. Soil total phosphorus significantly influenced both processes, while slope affected stabilization only. Limited mountain-level clustering indicated that environmental controls were consistent across sites. These findings demonstrate that decomposition and stabilization are governed by distinct mechanisms and should be evaluated separately to better understand carbon cycling in mountain forest ecosystems under changing environmental conditions.

Keywords: forest litter decomposition, stabilization factor, elevation gradient, soil temperature, carbon cycling

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1. Introduction

Litter decomposition in forests is a key process in the cycling of nutrients and carbon in terrestrial ecosystems. The decomposition of organic matter controls the recycling of nutrients into the soil, and can affect ecosystem productivity and soil carbon pools (Bärlocher et al., 2020). In forests, litter decomposition plays a key role in connecting the above-ground ecosystem with the below-ground biogeochemical cycles, ultimately determining long-term ecosystem processes (Körner, 2022). Litter decomposition and the stabilization of organic matter control the release of carbon back to the atmosphere and storage in soils, making decomposition processes important in global carbon cycling (Castillo-Figueroa, 2021). Litter decomposition is not a singular process but rather a combination of decomposition and stabilization processes regulated by environmental factors, substrate quality and biological activity. The interplay between these can be different across ecosystems, especially along environmental gradients. Litter production and decomposition in tropical forests interact to control nutrient availability and ecosystem processes, demonstrating the importance of these processes in ecosystems (Giweta, 2020). Elevation gradients are particularly valuable in this context, given that they encompass changes in temperature, moisture and energy availability over relatively short distances. Such gradients offer a natural laboratory for studying the variability of environmental conditions and their effects on ecological processes, such as decomposition (Verheyen et al., 2019). Along these gradients, changes in climatic and edaphic conditions affect microbial activity and enzymatic reactions, which in turn influence litter decomposition rates and pathways (JIA, 2019).

Temperature has long been recognised as a key factor in litter decay. It affects microbial activity and enzyme function, which in turn affect the decomposition of organic matter (Liu et al., 2019). Higher temperatures typically stimulate decomposition, whereas lower temperatures limit microbial activity and carbon cycling. But temperature is not the only factor influencing decomposition, with nutrients and substrate quality also important. One such nutrient, phosphorus, has been shown to play a key role in regulating decomposition, especially in forest ecosystems where nutrient availability can limit microbial processes. Researchers have demonstrated that the phosphorus level in litter can control decomposition rates in the short term, while the influence of soil enzymes is more significant over longer time scales (Liu et al., 2025). Likewise, soil chemical characteristics, such as carbon-to-nitrogen ratios, can affect decomposition and stabilization, with variable effects depending on the ecosystem (Blanco et al., 2023). Plant traits also play a role in decomposition by influencing litter quality and soil organisms. Plant composition and diversity affect the spatial distribution of organic matter and microbial habitat, impacting decomposition (Durán & Delgado-Baquerizo, 2020). However, biodiversity effects on decomposition are context-specific, with some studies showing strong effects, but others showing little to no effects.

Topographic factors also influence microclimate. Aspect and slope can modify soil moisture and temperature, while position can influence organic matter inputs (Leuthold et al., 2021). These relationships demonstrate the interacting effects of the environment on decomposition, where multiple factors are operating at multiple scales. Elevation gradients offer a way to incorporate these drivers, as they reflect simultaneous changes in climate, energy and water. The controls of biodiversity along elevation gradients are frequently driven by water-energy interactions that also affect ecosystem functioning, like decomposition (Vetaas et al., 2019). But although many studies have focused on individual factors, fewer have studied the combined effects of environmental factors on decomposition and stabilization processes.

While the effects of environmental factors on litter decomposition have been extensively studied, most studies have only examined decomposition rates without explicitly separating decomposition and stabilization. This has hindered the understanding of how carbon is allocated between fast and slow turnover pools. Moreover, while temperature, nutrients, and topography are frequently studied, they are often isolated from each other and their interactions. There is also little understanding of how these processes operate across elevation gradients, especially regarding whether decomposition and stabilization processes are similar or differ as environmental conditions change. Finally, there is little evidence of the comparative significance of environmental factors relative to spatial variation among mountain systems. This limits our capacity to make projections of ecosystem responses to changing environments, particularly in mountains with steep climatic gradients.

This research seeks to understand the elevation-based variability in forest litter decomposition and stabilization, and determine the involved environmental controls. Through the combination of elevation gradient analysis and multivariate statistical modeling, this study aims to separate the effects of temperature, nutrients and topographic features. This enables it to analyze that decomposition and stabilization responses to environmental gradients are convergent or divergent and that these responses are consistent across mountain systems.

2. Methodology

2.1 Research design

This research uses an observational, quantitative approach to investigate the effects of environmental factors on forest litter decomposition and stabilization with elevation. We employed a cross-sectional design to examine observations across several mountain systems and detect patterns. This involved moving from descriptive statistics to elevation models, multiple regression to determine the most important factors, and mixed-effects models to account for clustering at the mountain scale and increase the statistical power.

2.2 Data source

This study used data from a multi-site field experiment on forest litter decomposition in mountains (Ma et al., 2024). The data comprise standardized measurements of litter decomposition rate and stabilization factor, and associated environmental variables including elevation, soil characteristics, microclimate, vegetation structure and topography.

2.3 Variables and measurements

The response variables were the decomposition rate (K) and the stabilization factor (S), which represent different aspects of the litter degradation and carbon stabilization. The explanatory variables were chosen to represent important environmental dimensions at topographic, soil, microclimatic and vegetation levels. Elevation was used to represent topographic conditions, with slope. Soil pH and soil total phosphorus were used to represent soil conditions. Microclimate was represented by soil temperature, soil temperature seasonality, soil moisture, and soil moisture seasonality. The vegetation variables were species richness, canopy cover and litter thickness. All explanatory and response variables were continuous, except for the grouping factors (mountain and plot), which were retained in the mixed-effects models.

2.4 Data processing

The data were checked for integrity before analysis. Cases with missing data in critical variables were removed to allow for model comparisons. Names of variables were standardized to facilitate analysis, and labels for categorical variables were appropriately coded for model fitting. No transformations were made to response variables, which were deemed appropriate for regression analysis. A total of 451 observations were used for the analysis.

2.5 Statistical analysis

Analyses were performed in a statistical software package with well-developed packages for linear regression and mixed-effects modeling. Measures of central tendency and variability were computed.

Correlation analysis (Pearson correlation coefficient) was applied to explore relationships between variables and detect multicollinearity. Univariate linear regression models were initially used to test the association between each response variable and elevation. Subsequently, multiple linear regression models were fitted to assess the relative influence of environmental variables, omitting highly collinear variables for model stability. Linear mixed-effects models were also fitted to allow for potential spatial autocorrelation, with mountain as a random effect. This enabled us to distinguish between within- and between-mountain variability, thus facilitating more accurate estimation of fixed environmental effects. Models were assessed using traditional indicators such as coefficients, probability of significance and confidence intervals. We interpreted the findings in terms of statistical significance and ecological relevance.

3. Results

3.1 Descriptive statistics of environmental and response variables

The study involved 451 observations spanning a wide range of elevation (252-3835 m), including high variability in environmental predictor and response variables. The average decomposition rate (K) was 0.0180 (SD = 0.0064), while the average stabilization factor (S) was 0.1314 (SD = 0.0611), suggesting higher variability in S than in K. Environmental predictors such as soil temperature, soil phosphorus and slope showed high variability, capturing high spatial diversity in mountain ecosystems. As shown in Table 1, elevation and soil temperature seasonality were particularly variable, whereas soil moisture variables displayed relatively lower dispersion.

Table 1. Descriptive statistics of key variables (N = 451)

Variable	Mean	SD	Minimum	Q1	Median	Q3	Maximum
Elevation (m)	1848.19	978.09	252.00	1084.20	1586.55	2709.00	3835.00
Decomposition rate (K)	0.0180	0.0064	0.0025	0.0138	0.0166	0.0206	0.0494
Stabilization factor (S)	0.1314	0.0611	0.0064	0.0867	0.1289	0.1680	0.3449
Species richness	29.92	15.43	4.00	19.00	28.00	37.50	93.00
Soil pH	4.41	0.58	3.07	4.07	4.35	4.64	7.16
Soil total phosphorus	0.77	0.39	0.06	0.46	0.70	1.04	1.97
Slope (°)	23.54	9.94	0.25	14.50	24.75	31.00	42.50
Litter thickness	2.74	1.39	0.57	1.88	2.42	3.25	7.50
Canopy cover (%)	74.82	8.51	45.41	70.66	77.39	80.42	93.83
Soil temperature (mean)	17.38	3.61	10.84	14.58	17.95	20.05	25.52
Soil temperature seasonality	88.91	67.11	9.18	36.56	55.97	132.68	251.84
Soil moisture (mean)	0.34	0.11	0.04	0.29	0.35	0.42	0.60
Soil moisture seasonality	0.09	0.12	0.01	0.02	0.05	0.11	1.03

3.2 Elevation gradients in decomposition and stabilization

Both decomposition rate and stabilization factor were significantly affected by elevation. Both decomposition rate (K) and stabilization factor (S) changed along the elevation gradient, with a negative trend for K and a positive trend for S. The results of the linear regressions (Table 2) reveal that elevation accounted for 19.8% of the variation in K and 5.2% of the variation in S, respectively, with both relationships being statistically significant ($p < 0.001$). These relationships are shown in Figure 1, with Figure 1A depicting the decrease in decomposition rate with elevation, and Figure 1B the non-linear pattern of the stabilization factor with elevation, with more pronounced effects at higher altitudes. The fitted lines in each case show a steady decrease in K and an non-linear increase in S at elevations over 3000 m.

Table 2. Elevation-gradient regression models

Response	Variable	Estimate	Standard Error	t value	p value	CI lower	CI upper	R²
K	Intercept	0.02336	0.00058	40.60	<0.001	0.02223	0.02449	0.198
K	Elevation	-0.00000	0.00000	-10.52	<0.001	-0.00000	-0.00000	
S	Intercept	0.10522	0.00600	17.54	<0.001	0.09342	0.11701	0.052
S	Elevation	0.00001	0.00000	4.94	<0.001	0.00001	0.00002	

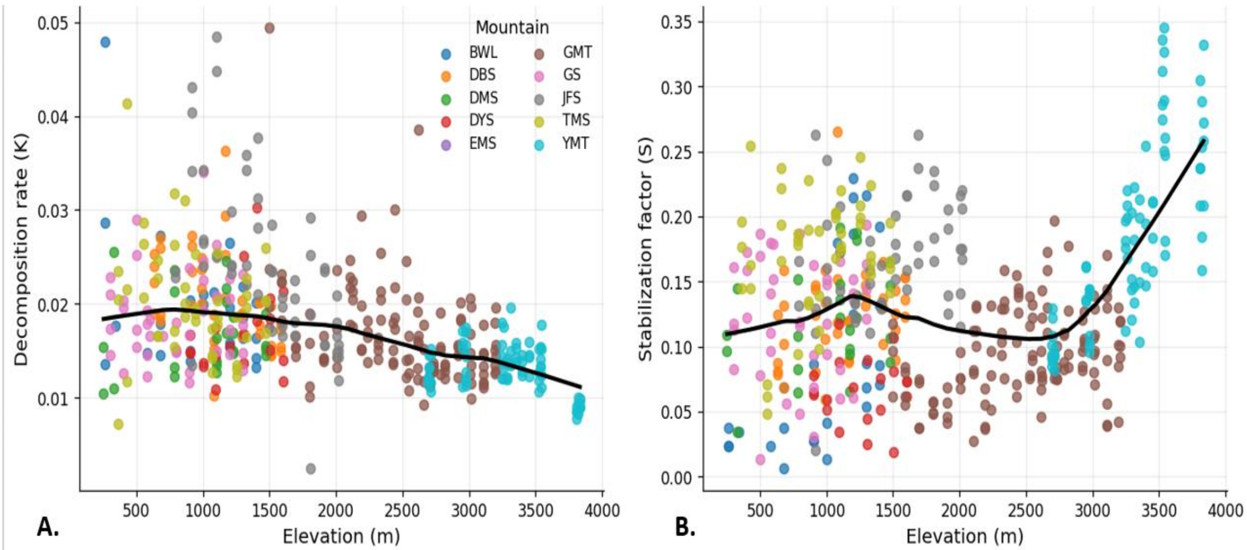

Figure 1. Elevation gradient in decomposition rate (A) and stabilization factor (B)

3.3 Environmental controls on decomposition rate (K)

We found that environmental predictors of decomposition rate displayed uniform relationships. Decomposition rates were positively related to mean soil temperature, soil temperature seasonality and moderately related to soil total phosphorus. This is illustrated in Figure 2, where Figure 2A shows a unimodal response of K to mean soil temperature, Figure 2B shows a linear increase in K with soil temperature seasonality, and Figure 2C shows a slight increase in K with soil phosphorus. The fitted lines indicate that temperature variables are more influential than soil phosphorus.

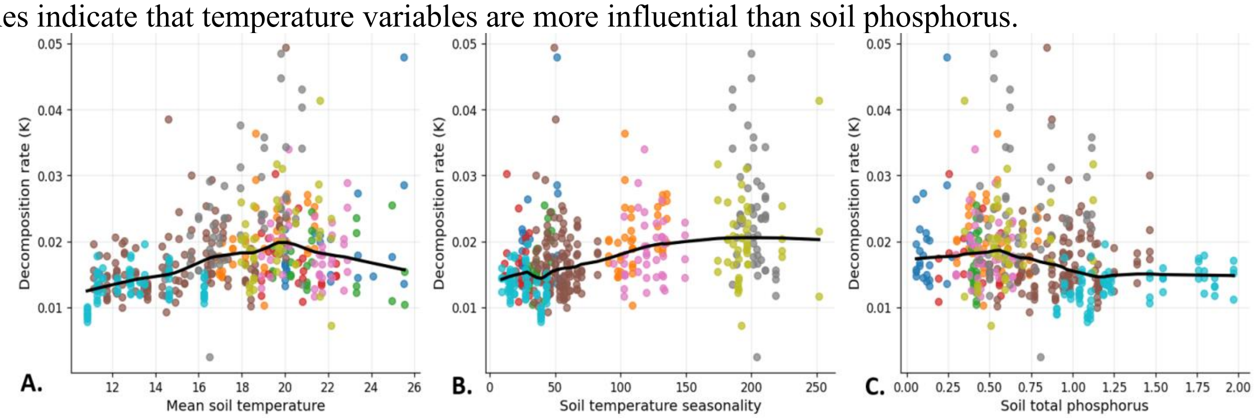

Figure 2. Effects of soil temperature (A), soil temperature seasonality (B), and soil total phosphorus (C) on decomposition rate (K)

3.4 Environmental controls on stabilization factor (S)

Patterns of stabilization factor with environmental factors differ from decomposition. Stabilization was lower at higher mean soil temperatures and slopes, but showed a weak non-linear relationship with soil total phosphorus. As depicted in Figure 3, Figure 3A exhibits a negative association between S and mean soil temperature, Figure 3B reveals a weak non-linear relationship with soil phosphorus, and Figure 3C reveals a decrease in S with increasing slope. These relationships suggest that stabilization is more constrained by environmental factors than by nutrients.

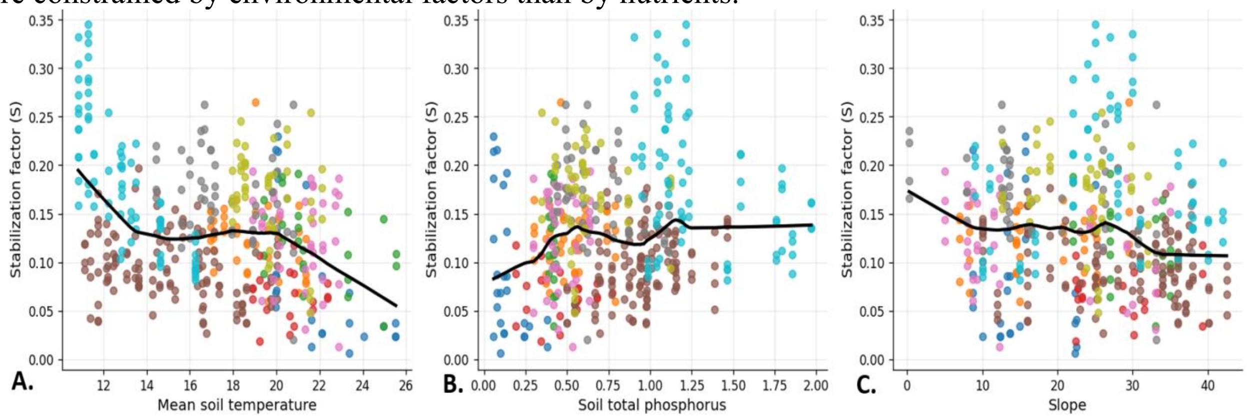

Figure 3. Effects of soil temperature (A), soil total phosphorus (B), and slope (C) on stabilization factor (S)

3.5 Mixed-effects model results

The mixed-effects models provided additional insight into the relative roles of environmental factors, once mountain-level differences were removed. As shown in Table 3, the decomposition rate (K) was explained by soil temperature (mean), soil temperature seasonality and soil total phosphorus. Stabilization factor (S), on the other hand, was significantly influenced by soil temperature (mean), soil total phosphorus, and slope. This is consistent with Figure 4, in which Figure 4A shows the coefficient estimates for the K model and Figure 4B for the S model. Here, positive influences of soil temperature on decomposition and negative influences on stabilization, as well as the consistent effects of soil phosphorus and slope, are clearly visible.

Table 3. Mixed-effects model results

Response	Variable	Estimate	Standard Error	z value	p value	CI lower	CI upper
K	Soil temperature (mean)	0.00086	0.00015	5.78	<0.001	0.00057	0.00116
K	Soil temperature seasonality	0.00003	0.00001	2.50	0.012	0.00001	0.00005
K	Soil total phosphorus	0.00330	0.00112	2.93	0.003	0.00110	0.00550
S	Soil temperature (mean)	-0.00828	0.00126	-6.57	<0.001	-0.01075	-0.00581
S	Soil total phosphorus	-0.02086	0.00969	-2.15	0.031	-0.03985	-0.00188
S	Slope	-0.00050	0.00025	-2.02	0.043	-0.00098	-0.00001

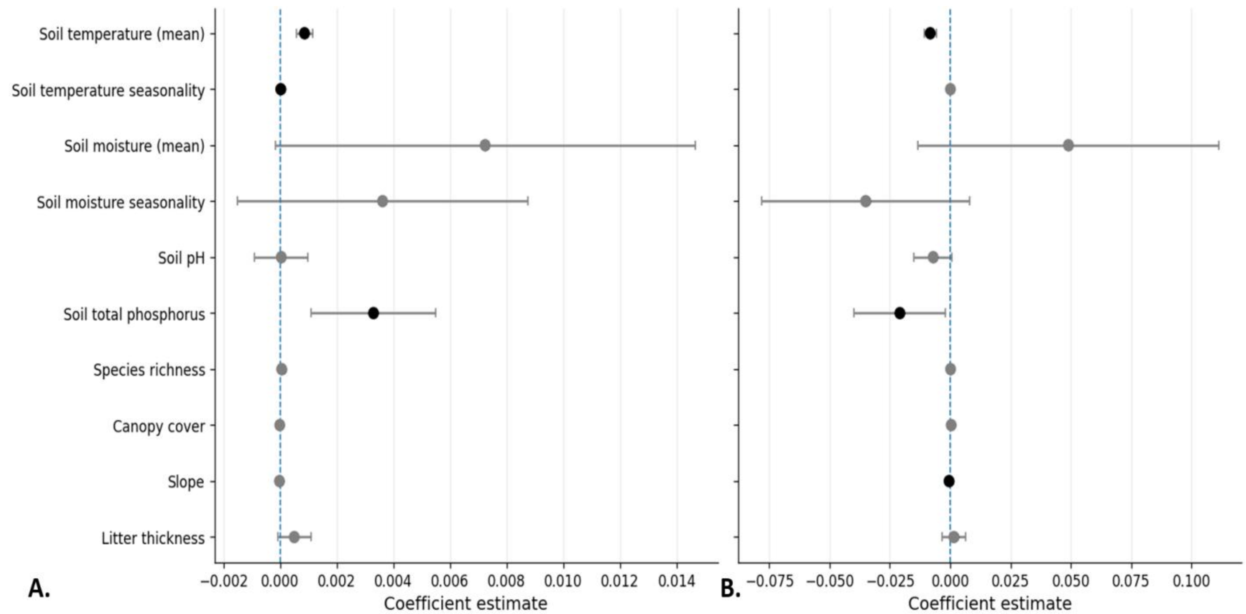

Figure 4. Mixed-effects model coefficients for decomposition rate (A) and stabilization factor (B)

4. Discussion

Our findings reveal a clear separation between forest litter decomposition and stabilization along the elevation gradient. Decomposition rate was negatively related to elevation, while the stabilization factor was positively related to elevation. This suggests that carbon turnover and stabilization are not equally responsive to increasing environmental constraints. Rather, decomposition is likely limited by more elevated conditions, while stabilization factor is likely facilitated by these conditions. The contrasting responses are key to understanding the mechanisms that control carbon turnover in mountain forest ecosystems along environmental gradients. The most important and consistent predictor for both response variables was mean soil temperature, but it had opposite effects. Decomposition rate was positively related to soil temperature, which implies that warmer soils stimulate microbial and biogeochemical processes that decompose organic matter. By contrast, stabilization factor decreased with soil temperature, suggesting that warmer soil conditions may decrease the stability of decomposed organic matter. This suggests that increasing temperature could enhance mass loss from litter, but reduce the amount of organic matter stored in more stable forms in the soil.

Soil total phosphorus had contrasting effects on decomposition and stabilization. Its positive effect on decomposition suggests that phosphorus may enhance biological activities involved in litter decomposition. But its negative association with stabilization suggests that the availability of nutrients may lead to rapid turnover and decomposition. Slope was significant only for stabilization, suggesting that topographic factors may play a more important role in carbon retention than in decomposition. Slope steepness may decrease organic matter retention or change water and substrate retention, and hence stabilization. Vegetation-related factors (e.g., species richness, canopy cover) were less consistent when mountain variation was accounted for. This implies that within the current analytical context, vegetation structure was less important than temperature, nutrients and topography. The low random effects also suggest the relationships were not mainly the result of variation between mountain ranges, but rather generalised controls across the elevation gradient.

The overriding influence of temperature is consistent with previous findings that temperature and moisture control decomposition through different ecological mechanisms, including the effects on soil fauna and microorganisms (Tan et al., 2021). The observed reduction in decomposition rate at higher elevations also accords with studies showing temperature impacts on litter decomposition are frequently mediated by soil moisture and vegetation effects, particularly in environmentally diverse regions (Petraglia et al., 2019). The beneficial effects of soil temperature on decomposition are also in line with large-scale syntheses, which found that soil organic carbon decomposition is sensitive to temperature, but that the extent of this sensitivity may differ between climatic zones and mechanisms (Wang et al., 2019). Our study builds on this knowledge by demonstrating that temperature can stimulate decomposition while hindering stabilization, highlighting that decomposition and stabilization are not equivalent.

The influence of phosphorus on decomposition is also in line with recent studies that show that microbial function and soil organic matter decomposition are influenced by nutrient conditions across elevational gradients (Hu et al., 2023). Yet, the inverse relationship between phosphorus and stabilization would be consistent with the idea that nutrient additions may accelerate organic matter turnover. This finding is consistent with evidence that soil degradation and enzymatic stoichiometry can influence microbial nutrient limitation during litter decomposition (Li et al., 2023). The lack of vegetation effects is in contrast to findings that plant litter can enhance biodiversity-ecosystem functioning relationships over time (Zhang et al., 2023a). This may reflect that vegetation effects may take longer to manifest, while the current analysis focused on more short-term processes. Likewise, soil fauna has been found to accelerate the release of litter carbon and nitrogen with increasing elevation by enhancing litter quality, implying that biological processes may play a role that vegetation structure alone cannot explain (Zhang et al., 2023b). Our findings that terrain affects stabilization agree with evidence that microclimate and surface residues regulated by local terrain can regulate decomposition (Leuthold et al., 2021). Thus, the negative effect of slope may reflect the loss of moisture and organic matter, or increased downslope movement of decomposed organic matter. Finally, the overall association between nutrient conditions and ecosystem function is consistent with evidence that nutrient-induced acidification may affect soil biodiversity-ecosystem function relationships, highlighting the importance of understanding the effects of nutrients in broad soil ecological contexts (Hu et al., 2024).

The results have potentially significant consequences for carbon dynamics in mountain forests. The lack of a consistent response in decomposition and stabilization implies that environmental change may impact not only the rate of litter decomposition, but also the post-decomposition fate of organic matter. With warming, increased decomposition may enhance short-term carbon release, whilst decreased stabilization may decrease the potential for long-term carbon storage. This is relevant for ecosystem models, which generally focus on decomposition but may underestimate the importance of stabilization. The study further suggests that disentangling the effects of temperature, nutrients, and slope is useful for understanding forest carbon processes. Climate was the strongest control, but phosphorus and slope also contributed, particularly to stabilization. This suggests that models of carbon cycling under environmental change should consider microclimate, nutrients and topography, rather than elevation. The results suggest that for forest management, high-elevation systems may serve as key areas of reduced decomposition and increased carbon stabilization, and are, as such, vulnerable but potentially valuable carbon stocks.

There are limitations. Our analysis used secondary, cross-sectional data, which precludes direct inference about temporal trends and mechanisms. While mixed-effects models adjusted for mountain-level clustering, several unmeasured site-level characteristics (such as aspect, soil texture, microbial community structure, and more specific aspects of hydrology) were not considered. There may also have been some residual multicollinearity among the environmental predictors, despite our careful treatment of highly correlated variables.

It would be valuable for future studies to investigate seasonal and long-term dynamics of decomposition along elevation gradients to test whether the observed trend is sustained. Manipulation experiments with temperature, moisture, and nutrients would help to tease apart causal links. Inclusion of microbial and soil fauna data would also enhance understanding of biological mediation. Finally, incorporating terrain derivatives, remote sensing and spatial analyses would improve predictions of decomposition and stabilization in mountain ecosystems.

5. Conclusion

Litter decomposition and stabilization responses to elevation exhibited different patterns, confirming that they are regulated by different factors. Decomposition rate decreased, and stabilization factor increased with elevation, suggesting that forest ecosystems at higher elevations may exhibit decreased decomposition but increased carbon retention. Average soil temperature was the strongest driver, having a positive impact on decomposition but a negative impact on stabilization. Soil total phosphorus also influenced both processes, while slope primarily influenced stabilization. These results show that decomposition and stabilization cannot be used interchangeably as indicators of litter turnover. Rather, their contrasting responses suggest it is important to consider carbon turnover and carbon retention separately, especially in mountainous regions facing climatic change. The weak effect of mountain-level clustering also indicates that temperature, nutrients and topography have a uniform influence on the gradient. In conclusion, this study highlights the need to consider microclimate, soil nutrients and topography when forecasting forest carbon dynamics in a changing environment.

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