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# Little influence of soil fauna on decomposition in successional upper Andean tropical forests

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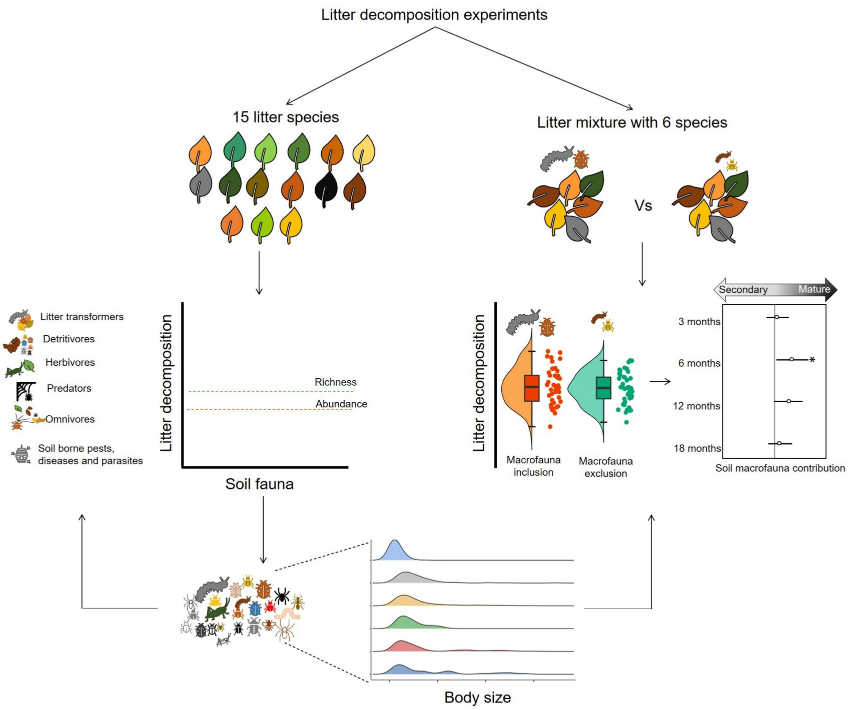
## ABSTRACT

- Soil fauna had little influence on decay rates, but the effect varied by species.
- Soil fauna richness and abundance did not influence decomposition environment.
- Body size traits of soil fauna were unrelated to decomposition environment.
- Limited macrofauna presence explained the lack of soil fauna’s effect on decay rates.
- Macrofauna contribution to decomposition had weak effects on succession.



Recent studies and global meta-analyses suggest that soil fauna is a key driver of litter decomposition. However, most research has focused on lowland ecosystems, leaving tropical mountain regions underexplored. Our study investigated the influence of the taxonomic and functional structure of soil fauna communities on litter decomposition in successional upper Andean tropical forests. We conducted two reciprocal translocation experiments: one examining 15 litter species (2525 litterbags) and another analyzing macrofauna exclusion (336 litterbags). We also performed extensive soil fauna sampling across four climatic seasons (6999 individuals) and measured body size traits for 93% of the morphospecies. We analyzed the role of soil fauna attributes (richness, abundance, body size) on litter decomposition at the species and ecosystem levels in four sites of successional upper Andean tropical forests in Colombia. Our findings indicated that soil fauna has little influence on decomposition, yet the effect varies by species, suggesting specific affinities between soil fauna and litter substrates. The lack of influence of soil fauna richness, abundance, and body size can be attributed to the dominance of small-sized fauna in upper Andean tropical forests. The contribution of soil macrofauna to decomposition was higher in mature forests, but this effect was weak over time. Further studies should explore indirect effects and microbial interactions to better understand soil fauna’s role in decomposition. Our study highlights that the influence of soil fauna on decay rates is context-dependent and should not be generalized across all ecosystems.

**Keywords** Andean forests, body size, forest succession, functional groups, soil invertebrates, litter decay

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## 1 Introduction

Litter decomposition plays a major role in both nutrient cycling and the formation of soil organic matter across terrestrial ecosystems (Swift et al., 1979; Krishna and Mohan, 2017; Giweta, 2020; Berg and McClaugherty, 2020), as over the half of aboveground productivity is returned into the soil detrital food web through leaf-litter (Cebrian, 1999; Wardle et al., 2004). Analyzing the factors that govern litter decomposition is therefore crucial not only for a deeper understanding of the process, but also for estimating and predicting global-scale carbon budgets and nutrient fluxes (Berg and McClaugherty, 2020; Castillo-Figueroa, 2021). Traditionally, climate, litter quality, and soil organisms have been considered as the main drivers of litter decomposition (Swift et al., 1979; Aerts, 1997; Prescott, 2010; Bradford et al., 2016). The two former factors have been extensively studied, with numerous investigations highlighting their relative importance in determining litter decomposition rates (Meentemeyer, 1984; Coûteaux et al., 1995; Cornwell et al., 2008; Makkonen et al., 2012; Canessa et al., 2021). Nevertheless, in the last few years, different studies have revealed that the influence of soil organisms on litter decomposition can be comparable to that of litter quality and climate, suggesting that biotic factors may account for as much or even more variability than abiotic factors at both local and regional scales (Bradford et al., 2016, 2017; Peng et al., 2022). Therefore, assessing the role of soil biota is becoming more important to disentangle the complex process of litter decomposition nowadays.

Within the soil biota, the influence of soil fauna on litter decomposition at a global scale can accelerate decay rates by more than one-third (García-Palacios et al., 2013; Peng et al., 2023; Cheng et al., 2023; Zeng et al., 2024). Different mechanisms of soil fauna activity can affect litter decomposition including: (1) the exchange of elements between mineral and organic soil layers, also enhancing water infiltration (Brown, 1995; Lavelle, 1996); (2) the alteration of the physico-chemical composition of soils (Lavelle, 1996; González et al., 2001); (3) the increase in the availability of substrates for microorganisms through litter fragmentation, which increases surface area (Joly et al., 2018; Peguero et al., 2019); (4) the increase of nutrients in soil by adding nitrogenous compounds from their excreta and dead tissue (González and Zou, 1999; Ristok et al., 2019); (5) the release of soil enzymes that aid to process root-derived carbon exudates, small organic matter, and fresh aboveground litter, providing an energy source for bacteria and fungi and thereby increasing microbial populations (Schinner, 1996; González and Zou, 1999; Patoine et al., 2020); and (6) microbial incubation during transit through animal guts that preconditions litter and ease decomposition (Filser et al., 2016; Grandy et al., 2016; Peguero et al., 2019). The interplay of these mechanisms indicates that the effect of soil fauna on litter decomposition is complex and, although important, may be more indirect in some cases. Moreover, studies have found that the influence of soil fauna on litter decomposition depend on the preference of the litter quality and its state of decomposition (Zimmer, 2002; De Oliveira et al., 2010; Marian et al., 2018; Edwards and Arancon, 2022), as well as the interactions with climatic conditions (Hättenschwiler et al., 2005; Sagi and Hawlena, 2024). This suggests that the effect of soil fauna on litter decay could be context-dependent.

In the Neotropics, research on the role of soil fauna in litter decomposition–primarily conducted in lowland dry and rainforests–has consistently demonstrated a significant increase in decomposition rates, largely attributed to the activity of soil macrofauna (Cárdenas et al., 2017; Four et al., 2019; Peguero et al., 2019). However, in Neotropical upper mountain forests, soil fauna communities experience a decrease in species richness and exhibit a different composition compared to lowland forests (Illig et al., 2010; Sánchez-Galindo et al., 2022). These communities are predominantly composed of microarthropods, which, despite their importance in breaking down large litter fragments and dispersing microbial decomposers, are thought to have a lesser effect on litter decomposition than soil fauna communities from lowland ecosystems (Varela et al., 2007; Illig et al., 2008; Maraun et al., 2008; Castillo-Figueroa, 2024a). Nevertheless, in Neotropical mountain forests our understanding of the role of soil fauna in litter decomposition remains limited due to the few surveys and field experiments conducted in this region. Additionally, alternative approaches beyond assessing community structure and composition are needed to comprehensively understand the mechanisms underlying soil fauna communities and their effects on litter decomposition.

Upper Andean tropical forests are recognized as one of the most distinctive tropical mountain regions globally in terms of plant and animal biodiversity (Anthelme et al., 2014; Myster, 2021). Notably, these forests harbor high levels of endemism (Myers et al., 2000) and species turnover (Hurtado-M et al., 2021; Cedillo et al., 2023). In particular, soil fauna exhibits an exceptional diversity of oribatid mites, some groups of collembolans and millipedes, which are classified as primary and secondary decomposers (Schneider et al., 2004; Illig et al., 2005, 2010; Marian et al., 2020; Sánchez-Galindo et al., 2022). Additionally, other groups of arachnids and small predators can also be found in these forests (Guarderas et al., 2022; Castillo-Figueroa et al., 2024; Castillo-Avila et al., 2025). Despite this remarkable biodiversity of Andean mountain forests, extensive areas have been converted to agricultural and urban land (Etter and van Wyngaarden, 2000; Andrade et al., 2021).

Nonetheless, many disturbed forests have shown natural recovery following these land-use changes (Rubiano et al., 2017; Calbi et al., 2020). This has resulted in a landscape mosaic of mature forest patches and secondary forests (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023), which may influence the structural and functional attributes of soil fauna related to decomposition because of changes in energy resources, microhabitat heterogeneity, and microclimatic conditions (Castillo-Avila et al., 2025). Yet, there are currently no studies examining the effect of soil fauna on litter decomposition between successional stages of Andean mountain forests.

In recent years, there has been a notable increase in the adoption of the trait-based approach in soil fauna studies within litter decomposition research (Raymond-Léonard et al., 2018, 2019; Brousseau et al., 2019; McCary and Schmitz, 2021; Laigle et al., 2021). This approach offers deeper insights into the mechanistic underpinnings of the process compared to species-based methodologies (Moretti et al., 2017; Brousseau et al., 2018). Traits associated with body size, including total length, width, and biomass, have been found to correlate with the quantity and composition of resources consumed (Moretti et al., 2017). Experimental exclusion of macrofauna have been commonly employed in litter decomposition studies to compare the influence of micro-, meso-, and macrofauna on decay rates (Cárdenas et al., 2017; Peguero et al., 2019; Ristok et al., 2019; Meyer et al., 2020). However, this approach does not directly address the influence of body size on decomposition, instead, it examines the non-additive effects within size categories. That is, in mesofauna inclusion treatments, the observed effect results from the combined action of microfauna and mesofauna, while in macrofauna inclusion treatments, the actual effect stems from the collective actions of micro-, meso-, and macrofauna. Consequently, a more comprehensive analysis of body size is essential for gaining a deeper understanding of the role of soil fauna in decomposition processes.

In this study, our goal was to investigate the influence of both the taxonomic and functional structure of soil fauna communities on litter decomposition within successional upper Andean tropical forests. Specifically, we aimed to address the following research questions: (i) How does soil fauna influence decay rates across different litter species? (ii) Is there a relationship between soil fauna and decomposition environment? (iii) To what extent does Community Weighted Mean (CWM) of soil fauna body size traits (i.e, CWM width, CWM length, CWM biomass) affect decomposition environment? (iv) How do the contributions of soil macrofauna differ between mature and secondary forests? We hypothesized that: the effect of soil fauna richness and abundance on decay rates will vary depending on the litter species due to differences in litter quality, which influence the consumption preferences of soil fauna for conservative or acquisitive species (H1). However, at the ecosystem level (i.e., decomposition environment), we expect a positive effect of soil fauna richness and abundance on decay rates given its major role in litter transformation (H2). Additionally, we anticipate positive relationships between CWM of body size traits and decomposition environment due to greater litter ingestion by soil macrofauna (H3), which likely contributes more to decomposition in mature forests, where litter resources are diverse and more abundant and microclimatic conditions are more stable compared to secondary forests (H4).

## 2 Materials and methods

### 2.1 Study area

Our study was conducted in a set of permanent plots established in 2013 along a successional gradient of tropical montane forests in the eastern region of the Colombian Andes. This region covers approximately a quarter of the country, accounts for three-quarters of the total population, and generates over half of the national gross domestic product (DANE, 2018, 2024). The permanent plots are part of a larger network that comprise a set of 36 plots of 20 m×20 m and eight plots of 50 m×50 m, located at elevations ranging from 2685 to 3140 m (*Rastrojos* project, Hurtado-M et al., 2021, Castillo-Figueroa et al., 2023). For the purpose of this study, we focused our work in 14 20 m×20 m permanent plots located in four upper Andean tropical forest sites (i.e., Guatavita, Guasca, Tabio, Torca). Across these locations, half of the plots were classified as secondary forests, while the other half were categorized as mature forests (Table 1). This classification was based on key structural attributes, including basal area, tree height, tree density, and species composition, as outlined in previous studies (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023). Within these plots, the dominant plant families include Ericaceae, Melastomataceae, Cunoniaceae, Primulaceae, Clusiaceae, and Asteraceae, with dominant genera such as *Miconia*, *Weinmannia*, *Cavendishia*, *Myrsine*, and *Myrcianthes*. A total of 63 species of shrubs and trees were identified in the study area, with common species including *Cavendishia bracteata*, *Miconia squamulosa*, *Vallea stipularis*, *Piper bogotense*, and *Clusia multiflora.* More details of the study area can be found in Castillo-Figueroa (2024a, 2024b).

### 2.2 Litter decomposition field experiments

We conducted two reciprocal translocation field decomposition experiments within the 14 permanent plots during the period from October 2021 to April 2023. In the first experi-

**Table 1** General characteristics of the soil fauna communities in each plot sampled within the upper Andean tropical forests of Colombia.

| Plot ID | Coordinates | Elevation (m) | Site | Succession | Shannon | Simpson | Pielou |
|---|---|---|---|---|---|---|---|
| 1 | 4°56′9.716″N,<br>73°53′54.237″W | 3036 | Guatavita | Secondary | 3.75 | 0.96 | 0.87 |
| 2 | 4°56′12.618″N,<br>73°53′51.825″W | 3028 | Guatavita | Secondary | 3.82 | 0.97 | 0.91 |
| 3 | 4°47′28.667″N,<br>73°54′25.886″W | 3140 | Guasca | Mature | 2.97 | 0.87 | 0.68 |
| 4 | 4°47′24.124″N,<br>73°54′31.332″W | 3086 | Guasca | Secondary | 3.36 | 0.93 | 0.80 |
| 5 | 4°47′26.609″N,<br>73°54′25.904″W | 3107 | Guasca | Mature | 3.47 | 0.93 | 0.81 |
| 6 | 4°55′40.858″N,<br>74°6′29.194″W | 3095 | Guasca | Secondary | 3.04 | 0.87 | 0.74 |
| 7 | 4°55′47.149″N,<br>74°6′31.021″W | 2696 | Tabio | Secondary | 3.62 | 0.95 | 0.82 |
| 8 | 4°55′33.961″N,<br>74°6′47.225″W | 2708 | Tabio | Secondary | 3.11 | 0.93 | 0.76 |
| 9 | 4°55′31.683″N,<br>74°6′31.579″W | 2821 | Tabio | Mature | 3.99 | 0.97 | 0.85 |
| 10 | 4°48′48.674″N,<br>74°0′58.527″W | 2685 | Tabio | Mature | 3.61 | 0.95 | 0.79 |
| 11 | 4°48′47.937″N,<br>74°0′56.997″W | 2946 | Torca | Mature | 3.56 | 0.94 | 0.78 |
| 12 | 4°48′31.216″N,<br>74°1′19.178″W | 2966 | Torca | Mature | 3.24 | 0.90 | 0.72 |
| 13 | 4°48′45.912″N,<br>74°0′58.852″W | 2709 | Torca | Secondary | 3.17 | 0.89 | 0.70 |
| 14 | 4°47′28.667″N,<br>73°54′25.886″W | 2954 | Torca | Mature | 3.69 | 0.95 | 0.82 |

ment, a set of 15 representative Andean species were selected based on their biomass and litter functional traits. This is because higher biomass implies a greater contribution of litter to the soil (Salinas et al., 2011), and a wide range of the litter functional traits encompass the functional spectrum of the plant community (Castillo-Figueroa et al., 2025). Thus, three independent litterbeds were established per plot ($n = 42$), each containing 60 litterbags. Four litterbags of the same species were arranged in a clockwise manner within each litterbed to facilitate consecutive harvesting times (3, 6, 12, 18 months). The litterbags were constructed from flexible fiberglass netting (10 cm×15 cm) with a mesh size of 2 mm, each containing approximately 2 g of dry litter. Importantly, these experimental units were strategically positioned directly on the forest floor, with meticulous attention given to minimizing soil disturbance. A minimum distance of 5 m was ensured between each unit. Moreover, during placement, areas with forest gaps, topographic depressions, and highly irregular soil conditions were avoided (Castillo-Figueroa et al., 2025).

In the second decomposition experiment, we performed a litter mixture translocation using litterbags of the same material and size as those from the first experiment, filled with 1 g of dry weight from each of the six dominant upper Andean species (i.e., *Alnus acuminata*, *C. bracteata*, *C. multiflora*, *Cedrela montana*, *M. squamulosa*, and *Myrsine coriacea*). The experiment included two soil fauna treatments: the first excluded macrofauna, allowing only micro- and mesofauna access through the 2 mm mesh size (i.e., macrofauna exclusion), while the second allowed access to all soil fauna by opening 6 mm diameter holes in the bag to facilitate macrofaunal entry (i.e., macrofauna inclusion) (Salinas et al., 2011; Castillo-Figueroa, 2024a).

Once litterbags were collected for each of the four harvesting times, the litter material was processed in the laboratory of Natural Sciences at Universidad del Rosario. The contents of the litterbags were meticulously sorted to separate litter from fine roots, forbs, mushrooms, mineral soil particles, and soil fauna. The litter material underwent a gentle cleaning process using a brush to eliminate mineral soil particles. All remaining contents of the litterbags were discarded, except for the soil fauna, which were carefully collected and preserved in 70% ethanol for other studies (Castillo-Figueroa et al., unpublished work). The total number of litterbags was 2520 in the first experiment (i.e., 14 permanent plots × 3 decomposition beds per plot × 15 litter species in each decomposition bed × 4 harvesting times), and 336 in the second experiment (i.e., 14 permanent plots × 3 decomposition beds per plot × 2 soil fauna treatments × 4 harvesting times). After cleaning, all litter material was oven-dried at 60 °C for 72 h and weighed using a precision scale accurate to 0.1 mg (LX 220A scs) to determine both initial and final weights (Castillo-Figueroa et al., 2025).

### 2.3 Soil fauna sampling

We conducted soil fauna samplings associated with leaf-litter decomposition by collecting three soil samples (30 cm×30 cm×5 cm in depth) near to each litterbed (*n* = 42) from each plot (*n* = 14). These collections were performed in the four climatic seasons of 2022 (*n* = 168): January–February (dry season), April–May (rainy season), July–August (dry season), and October–November (rainy season). All the soil fauna samplings were conducted under the legal national collection permit (ANLA-Resolution 530 of May 27, 2014). From each soil sample, two sub-samples were stored in plastic bags to differentiate fauna from leaf-litter and soil depth at 0–5 cm (Anderson and Ingram, 1994; Camara et al., 2021). In the laboratory, soil fauna was manually extracted under a stereoscopic microscope and preserved in 70% ethanol. Annelids were fixed in 5% formaldehyde for 72 h, followed by preservation in 70% alcohol. Samples were examined under a Zeiss Stemi 305 stereoscope (Germany) at 4× to 80× magnification, then counted and identified taxonomically with the assistance of experts, using original descriptions and region-specific identification guides to ensure the highest possible taxonomic resolution (Castillo-Avila et al., 2025). When a morphospecies was recognized for the first time, dorsal, ventral, and lateral reference images were taken using a Hayear 4K UHD digital camera. These images were used for comparison with all similar specimens that appeared later.

Larvae of holometabolous insects that could not be linked to any adult species were categorized as distinct morphospecies. Regarding nymphs of hemimetabolous insects that displayed morphological differences, albeit not in color, from any adult morphospecies, they were designated as new morphospecies (Castillo-Avila et al., 2025). This taxonomic resolution has been deemed adequate for identifying significant community composition patterns in both temperate and tropical systems (Timms et al., 2013; Lamarre et al., 2016; Cárdenas et al., 2017). Moreover, identification at the family level has been proven useful in providing ecologically suitable substitutes for species in functional diversity studies (Cardoso et al., 2011; Cárdenas et al., 2017). Morphospecies (i.e., richness) and abundance were the variables employed for soil fauna communities. Soil fauna was classified into traditional functional groups according to Cárdenas et al. (2017). That is, litter transformers, detritivores, herbivores, omnivores, predators, and soil-borne pests and parasites.

### 2.4 Body size estimation

To analyze body size of soil fauna, we took measurements of width, length, and biomass of 93% of the morphospecies found in our samplings (Fig. S1, Table S1). Depending on the availability of the specimens collected, we included between three to five individuals per morphospecies, and one in the case of rare morphospecies. All individuals measured corresponded to adults, excepting for dipteran larvae that were included due to their importance in litter decomposition (Frouz et al., 2015). We took photos of each individual using a Zeiss Stemi 305 stereoscope, Germany, accompanied with a digital camera Hayear 4K UHD. Then, length and width of each individual were measured by using Hayear HY-1 070 software. Given the availability of numerous allometric equations proposed for estimating the biomass of different soil fauna groups, we selected equations based on three main criteria: (1) most of the equations we used incorporate both length and width, as numerous studies have shown that biomass estimation significantly improves when both measurements are considered, rather than using length alone (Sample et al., 1993; Sohlström et al., 2018); (2) we prioritized using the most specific equations available for each group, preferring equations developed for orders over those for the entire class when possible; and (3) we preferred equations constructed from tropical species rather than those from temperate regions, as tropical regions exhibit distinct species composition, leading to more accurate biomass predictions (Sohlström et al., 2018). However, in a few cases, the only equations for specific groups were developed in temperate regions (e.g., nematoda, gastropoda), so we applied them. The details of the references used for estimating the biomass of each group are provided in Table S2.

### 2.5 Data analysis

To determine decomposition for each litter species, K rates $y^{-1}$ were calculated as a standard measure of decomposition (Olson, 1963; Njoroge et al., 2023). Reduced Major Axis (RMA) regressions were conducted between both soil fauna richness and abundance and decay rates for each litter species with 95% bootstrapped confidence intervals (H1) (N = 1 999). We also did a more general analysis by analyzing the relationship between standard decomposition (i.e., decomposition environment) and both soil fauna richness and abundance (H2). Decomposition environment was determined by the average decomposition rates of the 15 litter species in each plot during the first experiment. Homoscedasticity was confirmed in all the RMA regressions using Breusch-Pagan statistic test ($p$>0.05).

To analyze the soil fauna functional groups that best explain decay rates, we conducted two stepwise Multiple

Linear Regression (MLR) models, using the decomposition of each litter species as the dependent variable. In one MLR, soil fauna richness of each functional group was used as an independent variable, while in the other MLR, soil fauna abundance of each functional group was used as an independent variable (H1). To prevent multicollinearity between variables, we computed the Variance Inflation Factor (VIF) for each variable. We included in the MLR only the variables with VIF values below 3.0, confirming the absence of collinearity among variables (Chatterjee and Simonoff, 2012). To select the best model for each litter species, Root Mean Squared Error (RMSE) and the adjusted $R^2$ were estimated. RMSE measures the accuracy of the model's predictions in absolute terms, providing a direct measure of the average deviation of the predicted values from the actual values, in the same units as the dependent variable (Montgomery et al., 2012; Chatterjee and Hadi, 2015). Adjusted $R^2$ offers a relative measure of the model's fit, taking into account the number of predictors and penalizing the inclusion of irrelevant variables, which helps to avoid overfitting (Kutner et al., 2004; James et al., 2021).

To analyze the effect of body size on litter decomposition, we estimated CWM of length, width, and biomass weighted by the abundance recorded in each plot. Thus, we did RMA regressions between these three measurements of body size and decomposition environment (H3). Lastly, to analyze the contribution of soil macrofauna to decomposition we subtracted the %mass loss of both soil fauna treatments (%mass loss macrofauna inclusion – %mass loss macrofauna exclusion). We calculated 95% confidence intervals for Cohen's *d* from *t*-tests to assess the effect size of soil macrofauna's contribution to decomposition in mature versus secondary forests for each decomposition period (H4). Significant differences were considered using an α level of 0.05 for all statistical analyses. All analyses were conducted in JASP 0.17.2.1 (JASP Team, 2024) and PAST 4.0 (Hammer et al., 2001).

## 3 Results

### 3.1 Taxonomic and functional structure of soil fauna communities

We collected a total of 6999 individuals, with counts ranging from 176 to 788 per plot, and identified 351 morphospecies, ranging from 61 to 111 across the 14 permanent plots. The groups that contributed over the half of the soil fauna community were millipedes (25.58%), mites (19.82%), and beetles (11.60%). Torca exhibited the highest average in soil fauna richness (*S*) and abundance (*N*) ($S$ = 93.75±3.59, $N$ = 636.5±134.04) followed by Tabio ($S$ = 89.25±20.69, $N$ = 567.5±184.02), Guasca ($S$ = 72±8.46, $N$ = 423.5±132.55), and Guatavita ($S$ = 72±7.07, $N$ = 244.5±96.87).

Regarding the abundance of soil fauna functional groups, litter transformers ($N$ = 3354, 47.92%) and detritivores ($N$ = 1694, 24.22%) were the most dominant, followed by predators ($N$ = 733, 10.47%), herbivores ($N$ = 593, 8.46%), omnivores ($N$ = 319, 4.56%), and soil-borne pests, diseases, and parasites ($N$ = 306, 4.37%). In terms of species richness, litter transformers ($S$ = 121, 34.47%) were also the most diverse, followed by herbivores ($S$ = 81, 23.08%), detritivores ($S$ = 60, 17.09%), predators ($S$ = 49, 13.96%), omnivores ($S$ = 20, 5.70%), and soil-borne pests, diseases, and parasites ($S$ = 20, 5.70%).

### 3.2 Soil fauna communities and decomposition

We found a positive relation between soil fauna richness and decay rates of *C. bracteata* ($P$ = 0.03, $n$ = 14, $R^2$ = 0.32, $\mathrm{CI}_{\mathrm{slope}}$ = [0.001, 0.003]), *Daphnopsis caracasana* ($P$ = 0.04, $n$ = 14, $R^2$ = 0.31, $\mathrm{CI}_{\mathrm{slope}}$ = [0.004, 0.009]), and *P. bogotense* ($P$ = 0.005, $n$ = 14, $R^2$ = 0.49, $\mathrm{CI}_{\mathrm{slope}}$ = [0.01, 0.03], Table 2). However, no relation was found between soil fauna abundance and any of the litter species assessed (Table 2).

Based on the MLR analyses, we found that the richness of detritivores and herbivores influenced the decomposition of eight litter species, while the abundance of predators, detritivores, litter transformers, omnivores, and soil-borne pests

**Table 2** Reduced Major Axis regressions between soil fauna attributes (richness and abundance) and decay rates (K rates $y^{-1}$) of each of the 15 litter species.

| Litter species | Soil fauna richness | | | Soil fauna abundance | | |
|---|---|---|---|---|---|---|
| | $R^2$ | Slope | Intercept | $R^2$ | Slope | Intercept |
| *Alnus acuminata* | 0.09 | 0.01 | –0.51 | 0.02 | 0.0009 | 0.02 |
| *Cavendishia bracteata* | **0.32*** | 0.002 | –0.04 | 0.22 | 0.0001 | 0.06 |
| *Cedrela montana* | 0.09 | 0.004 | 0.04 | 0.03 | 0.0002 | 0.20 |
| *Clusia multiflora* | 0.12 | 0.003 | –0.02 | 0.08 | 0.0002 | 0.11 |
| *Croton bogotanus* | 0.21 | 0.02 | –0.59 | 0.24 | 0.002 | 0.24 |
| *Daphnopsis caracasana* | **0.31*** | 0.006 | 0.16 | 0.22 | 0.0005 | 0.44 |
| *Drimys granadensis* | 0.008 | 0.002 | –0.01 | 0.04 | –0.0002 | 0.31 |
| *Ilex kunthiana* | 0.004 | –0.004 | 0.78 | 0.004 | –0.0003 | 0.58 |
| *Miconia squamulosa* | 0.005 | 0.003 | 0.12 | 0.04 | 0.0003 | 0.27 |
| *Morella parvifolia* | 0.0001 | –0.005 | 0.71 | 0.001 | 0.0004 | 0.003 |
| *Myrsine coriacea* | 0.08 | –0.002 | 0.38 | 0.08 | –0.0002 | 0.25 |
| *Ocotea calophylla* | 0.003 | –0.002 | 0.47 | 0.03 | 0.0002 | 0.11 |
| *Piper bogotense* | **0.49**** | 0.019 | –0.39 | 0.23 | 0.001 | 0.42 |
| *Prunus buxifolia* | 0.03 | 0.002 | 0.01 | 0.005 | 0.0001 | 0.11 |
| *Vallea stipularis* | 0.11 | 0.01 | 0.21 | 0.21 | 0.001 | 0.78 |

Size effect ($R^2$), slope, and intercepts are shown in the table. Statistical significance is displayed in bold and *$P$<0.05,**$P$<0.01.

and parasites affected the decay rates of 12 litter species. Only *Drimys granadiensis*, *M. squamulosa*, and *M. coriacea* were not influenced by either richness or abundance of any functional group (Fig. 1, Table S3, Table S4).

When analyzing the influence of soil fauna on decomposition environment, we found no significant relationship with richness ($P = 0.06$, $n = 14$, $R^2 = 0.26$, $\mathrm{CI}_{\mathrm{slope}} = [0.003, 0.01]$, Fig. 2A) or abundance ($P = 0.13$, $n = 14$, $R^2 = 0.18$, $\mathrm{CI}_{\mathrm{slope}} = [0.0002, 0.009]$, Fig. 2B).

### 3.3 Body size traits and decomposition

Overall, 863 individuals were measured from 327 morphospecies, representing 93% of the total morphospecies richness (Table S1). Body size of soil fauna exhibited low mean values in width (1.18±1.07 mm), length (4.86±5.33 mm) and biomass (2.77±18.92 mg) (Fig. 3, Table S5). The smaller animals were nematodes (1.49e-7 mg) and the larger ones were gastropods (481 mg) (Fig. S2, Table S5). We did not find any relationship between decomposition environment and CWM width ($P = 0.48$; $n = 14$; $R^2 = 0.04$; $\mathrm{CI}_{\mathrm{slope}} = [-1.704, -0.251]$, Fig. 4A), CWM length ($P = 0.23$; $n = 14$; $R^2 = 0.12$; $\mathrm{CI}_{\mathrm{slope}} = [-0.154, -0.001]$, Fig. 4B), or CWM biomass ($P = 0.305$; $n = 14$; $R^2 = 0.09$; $\mathrm{CI}_{\mathrm{slope}} = [0.086, 0.549]$, Fig. 4C).

### 3.4 Effect of soil macrofauna on decomposition between successional stages

We found that soil macrofauna increased mean decomposi-

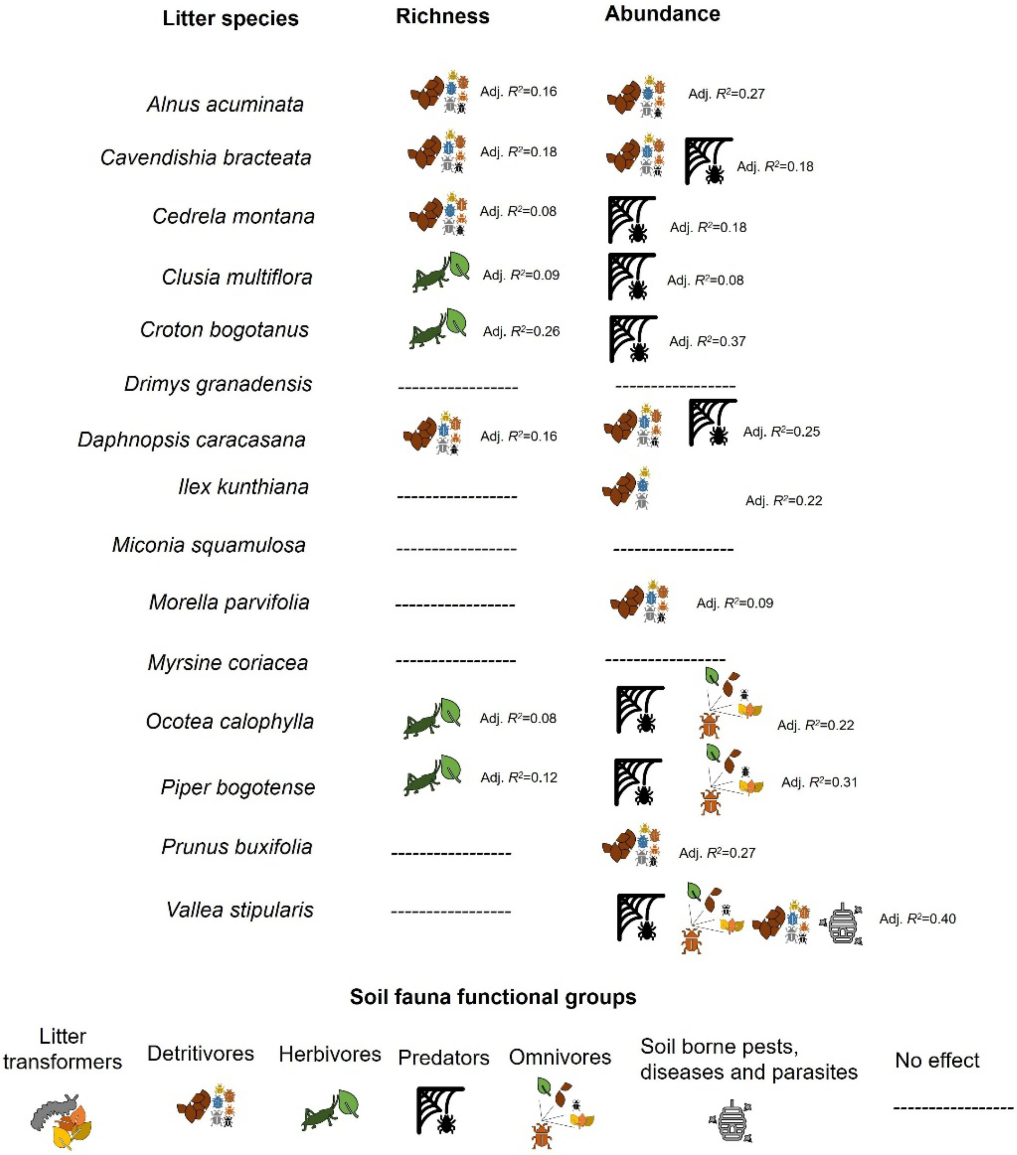

**Fig. 1** Effect of richness and abundance of the soil fauna functional groups on decay rates (K rates $y^{-1}$) of each of the 15 litter species. Soil fauna functional groups are represented in the bottom of the figure and Adjusted $R^2$ is depicted for each litter species.

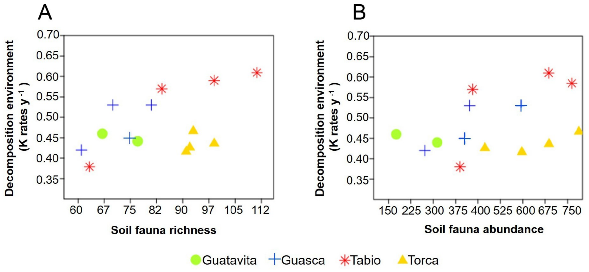

**Fig. 2** Reduced Major Axis regressions between decomposition environment and both (A) soil fauna richness and (B) abundance. Guatavita is depicted with green dots, Guasca with blue plus, Tabio with red stars, and Torca with yellow triangles.

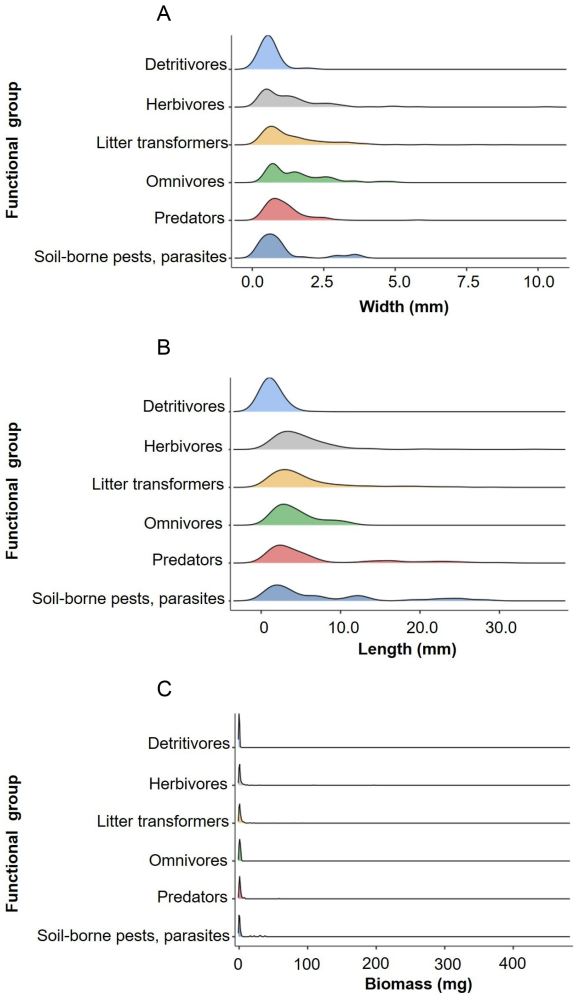

**Fig. 3** Density plots of each functional group in terms of (A) Width (mm), (B) Length (mm), and (C) Biomass (mg).

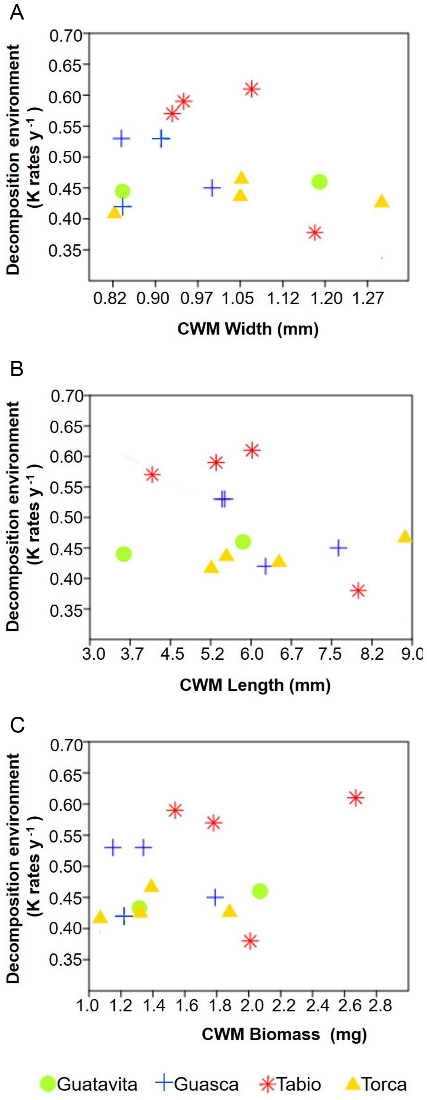

**Fig. 4** Reduced Major Axis regressions between decomposition environment and Community Weighted Mean (CWM) of (A) Width (mm), (B) CWM Length (mm), and (C) CWM Biomass (mg). Guatavita is depicted with green dots, Guasca with blue plus, Tabio with red stars, and Torca with yellow triangles.

tion along time by 0.36±1.91% (3 months), 0.73±2.56% (6 months), 1.06±3.91% (12 months), and 1.10±2.56% (18 months). In some cases, soil macrofauna contributed negatively to decomposition, with effects ranging from –0.17% to –7.62%. However, the average contribution of soil macrofauna was higher in mature forests (3 months = 0.35±2.06%; 6 months = 2.13±2.79%; 12 months = 2.79±4.14%; 18 months = 1.36±2.78%) compared to secondary forests (3 months = 0.38±1.96%; 6 months = –0.67±2.72%; 12 months = –0.68±4.01%; 18 months = 0.84±2.62%). This difference was marginally significant only at 6 months of decomposition (*t* = 2.271, *P* = 0.042, df=12, Cohen's *d* = 1.214±0.625) (Fig. 5). There were no significant differences between mature and secondary forests at other decomposition periods: 3 months (*t* = –0.031, *P* = 0.976, df = 12, Cohen's *d* = –0.017±0.535), 12 months (*t* = 1.796, *P* = 0.098, df = 12, Cohen's *d* = 0.960±0.593), and 18 months (*t* = 0.363, *P* = 0.723, df = 12, Cohen's *d* = 0.194±0.537) (Fig. 5).

## 4 Discussion

Our results showed that soil fauna had only a modest effect

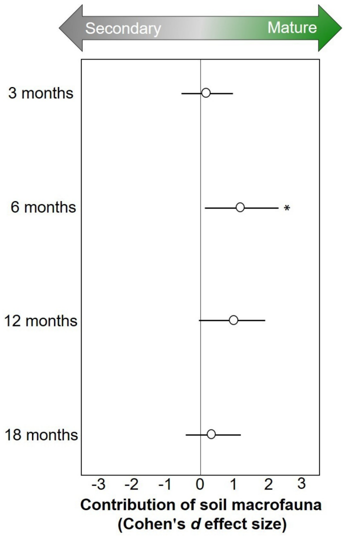

**Fig. 5** Confidence intervals (95%) of Cohen's *d* showing the contribution of soil macrofauna to decomposition in secondary (negative values) and mature forests (positive values). Asterisks (*) show significant effects ($P$<0.05).

on litter decomposition in upper Andean tropical forests. However, this influence varied by litter species and soil fauna functional groups, indicating that the interplay between litter species and soil fauna groups can affect decomposition, albeit to a lesser extent. The relatively low presence of large-sized soil fauna may contribute to this limited effect on decomposition. Despite this, soil macrofauna contributed more to average decomposition rates in mature forests than in secondary forests, although this effect was small and inconsistent over time. The following sections will delve into each of these findings in detail.

## 4.1 Variation across litter species

In line with our first hypothesis (H1), we found that the effect of soil fauna varied across litter species (Fig. 1,Table 2). This is consistent with previous studies that have shown the role of litter identity on the contribution of soil fauna to decomposition (Cárdenas et al., 2017; Njoroge et al., 2022; Peng et al., 2022). This variation could be attributed to the affinity of soil fauna to the quality of different substrates (De Oliveira et al., 2010; Makkonen et al., 2012). Indeed, the litter species with the highest affinity with soil fauna richness was the *P. bogotense* which is also the species with the highest nitrogen content (Castillo-Figueroa et al., 2025). This may also explain the positive relationship with other high-quality species such as *D. caracasana*. Surprisingly, a more conservative species like *C. bracteata*, characterized by its toxic or recalcitrant compounds (Castrillón-Cardona et al., 2015), also showed a positive relationship with soil fauna richness (Table 2). Likely, the fact that this litter species is difficult to decompose results in providing shelter to a greater diversity of soil fauna.

When analyzing the effect of specific soil fauna functional groups, we found that only the richness of detritivores and herbivores significantly affected decomposition (Fig. 1, Table S3). However, this effect was minimal (Adjusted $R^2$ < 30%), and seven species showed no influence associated with the richness of any soil fauna group. Since the diversity of herbivores and detritivores is directly related to litter consumption (Srivastava et al., 2009; Cárdenas et al., 2017; Lavelle et al., 2022), higher richness in these groups may enhance litter decay rates through niche partitioning, which improves the energy efficiency from litter (Hättenschwiler et al., 2005; Peng et al., 2022), albeit to a limited extent.

In terms of abundance, predators affected decay rates in half of the litter species (Fig. 1, Table S4). This influence likely arises from top-down effects, either through direct predation on small litter consumers (Kajak, 1995; Liu et al., 2020) or by indirectly reducing competition and resource overexploitation (Melguizo-Ruiz et al., 2020). Notably, *V. stipularis* was the species most influenced by the abundance of multiple soil fauna groups. As a common and labile species in upper Andean forests (Hurtado-M et al., 2021), it represents a frequently encountered and preferred litter type for soil fauna. Different trophic groups likely influence litter decay in this species. All in all, while soil fauna did influence various litter species, the effect was relatively minor.

## 4.2 Influence of soil fauna on decomposition environment

Contrary to our second hypothesis (H2), we found that soil fauna had no significant influence on decomposition environment (Fig. 2). Even though soil fauna has been posed as a major driver of litter decomposition in many studies (Hättenschwiler et al., 2005; García-Palacios et al., 2016a, 2016b; Peng et al., 2023; Zeng et al., 2024), most of these investigations have focused on macrofaunal exclusion experiments in tropical lowland forests. These ecosystems differ significantly from upper mountain regions in their soil fauna communities (Maraun et al., 2008; Sánchez-Galindo et al., 2022). Notably, species richness and density decline along the elevational gradient (Scheu et al., 2008; Maraun et al., 2008; Marian et al., 2018). Furthermore, some key decomposers, such as termites and social ants–critical for litter decomposition globally (Zanne et al., 2022; Zeng et al., 2024)–are absent from these highland forests (Guarderas et al., 2022).

Research conducted in Andean mountain forests from Ecuador has indicated that decomposer microarthropods have a minimal effect on decay rates (Illig et al., 2008; Marian et al., 2018; Sánchez-Galindo et al., 2022). In Colombia, similar results have been found in the Cundiboyacense high plain using exclusion macrofaunal experiments (Varela et al., 2007; Castillo-Figueroa et al., 2024a). All these findings suggest that in upper mountain regions soil fauna exert a lesser influence on litter decomposition than that from lowland ecosystems. In this sense, the role of soil fauna should not be generalized across all ecosystems as suggested by global meta-analyses, since it is highly dependent on the specific ecological context.

### 4.3 Relationship between body size and decomposition rate in Andean mountain forests

Our third hypothesis (H3) was rejected, as soil macrofauna was nearly absent from our samples, with mesofauna, including mites and small millipedes, dominating the community (Fig. 3, Fig. S2). Larger body size is typically associated with higher metabolic rates (Fielding and Defoliart, 2008; Grula et al., 2021) and greater litter consumption (Cárdenas et al., 2017; Hedĕnec et al., 2022; Mamabolo et al., 2024). Thus, the predominance of smaller body sizes in our samples likely explains the lack of influence of body size traits on litter decomposition (Fig. 4, Fig. S2). Several factors can filter out large sizes of soil fauna in Andean mountain forests: (1) lower soil fertility and primary productivity provide less food resources for growth; (2) reduced availability of oxygen can limit the growth and body size; (3) lower temperatures slow down metabolic rates, which in turn affect growth rates and body size; (4) increased environmental stresses, such as strong wind and UV radiation, favor smaller fauna that are less exposed to physical stress; and (5) selective pressures of predation and competition for resources, given that smaller animals may have advantages in escaping from predators and maximizing niche use (Mani, 1968; Shelomi, 2012; Myster, 2021).

However, our study only examined the direct effects of soil fauna on litter decomposition and did not address the indirect effects through interactions with the microenvironment and microbial decomposers. Some research suggests that at these elevations, soil fauna is crucial for dispersing fungal and bacterial decomposers that colonize litter fragments, potentially accelerating decay rates (Illig et al., 2010; Sánchez-Galindo et al., 2022). Furthermore, there is evidence that soil fauna may influence the effects of litter mixtures on decomposition (Castillo-Figueroa et al., 2024). Thus, other unmeasured factors and interactions could provide additional mechanisms by which soil fauna affect decomposition. Future studies should explore the relationships between soil fauna attributes, soil microorganisms, and the soil microenvironment to unveil other potential roles of soil fauna in decomposition processes in tropical mountain regions.

### 4.4 Contribution of soil macrofauna to decomposition and its effects between successional stages

Consistent with the previous results, our study revealed that soil macrofauna had a minimal contribution to decomposition. Global meta-analyses have reported that soil macrofauna can increase decomposition by 30% to 40% (García-Palacios et al., 2013; Peng et al., 2023; Cheng et al., 2023; Sagi and Hawlena, 2024; Zeng et al., 2024), which is nearly fourteen times the effect we observed in our experiment after a year (1.06±3.91%). Surprisingly, we even found negative effects of soil macrofauna on decomposition. Similar studies have shown that soil macrofauna can exert top-down effects on litter decomposition by preying on small decomposers, thus reducing decomposition and synergistic effects on litter mixtures (Liu et al., 2020; Castillo-Figueroa, 2024a). Additionally, the litter composition of the experiment, dominated by conservative species, may amplify the negative influence of soil macrofauna by increasing antagonistic effects on decomposition, as recently demonstrated (Castillo-Figueroa, 2024a). Another potential explanation is that the difference between soil fauna treatments in the experiment may not reflect decomposition per se, but rather the transformation into smaller litter particles, such as soil animal feces, collected during litterbag harvest (David, 2014; Joly et al., 2018; Tan et al., 2021). The effect of these smaller particles is largely unknown because may attract or repel microbial decomposers (Ristok et al., 2019; Prescott and Vesterdal, 2021). These limitations could obscure the effects of soil fauna on litter decomposition (Tan et al., 2021).

However, we observed a modest effect of soil macrofauna's contribution to decomposition between successional stages, with higher contributions in mature forests compared to secondary forests only at 6 months of decay, which partially support our fourth hypothesis (H4) (Fig. 5). A previous study in the same plots found that mean decomposition was greater in mature forests for some litter species (Castillo-Figueroa et al., 2025). Mature forests are characterized by higher litter productivity (Souza et al., 2019; Poorter et al., 2023; Castillo-Figueroa and Posada, in press), elevated soil nitrogen concentrations, a more developed soil organic horizon, and taller tree canopies (Poorter et al., 2021; Castillo-Figueroa et al., 2023; Castillo-Figueroa et al., in preparation). These factors collectively enhance resource availability, microhabitat heterogeneity, and favorable microclimatic conditions for soil fauna (Barberena-Arias and Aide, 2003; Castillo-Avila et al., 2025), likely promoting soil macrofauna and its role in litter ingestion.

## 5 Conclusion

Our study reveals that soil fauna exerts minimal influence on litter decomposition in upper Andean tropical forests. Even though recent research has highlighted an increasingly significant role of soil fauna in decomposition, this statement should not be generalized to all biomes or ecosystems. Through extensive soil sampling, litter decomposition experiments, and a trait-based approach, we demonstrate that soil fauna plays a limited role in decomposition, with these effects being largely dependent on the litter substrate. The main potential explanation for this pattern is the limited presence of soil macrofauna and the dominance of small-sized fauna with minimal litter consumption. Indeed, the contribution of soil macrofauna to decomposition was generally low but was more pronounced in mature forests, although this effect weakened over time. Future research should investigate the indirect effects of soil fauna on decomposition in Andean mountain forests. Our study highlights that the effect of soil fauna on decay rates is context-dependent and is less relevant in upper Andean tropical forests than in tropical lowland forests.

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## CRediT authorship contribution statement

DC-F: Conceptualization, Formal analysis, Investigation, Methodology, Data curation, Resources, Supervision, Software, Visualization, Writing–original draft, Writing–review & editing. CC-A: Conceptualization, Data curation, Investigation, Methodology, Writing–review&editing.

## Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Electronic supplementary material

Supplementary material is available in the online version of this article at https://doi.org/10.1007/s42832-024-0277-8 and openly available in the Open Science Framework at: osf.io/wvzbr.

## Open Access

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