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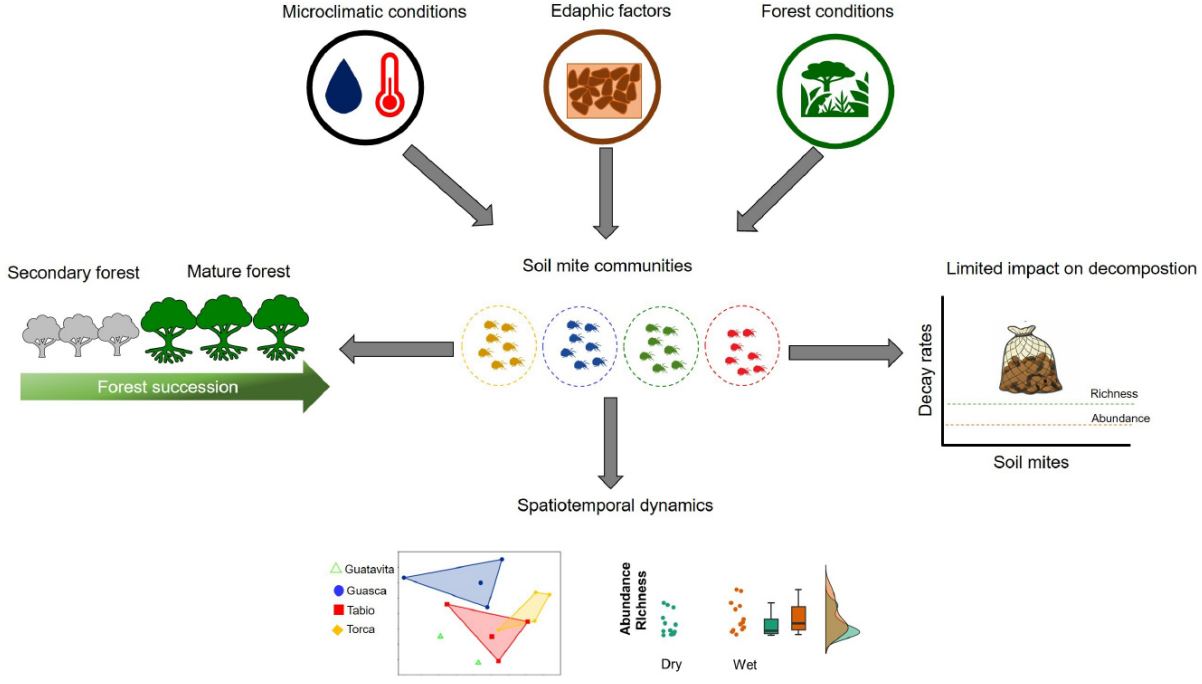
Environmental drivers shape soil mite communities along succession, with limited links to litter decomposition in upper Andean tropical forests

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ABSTRACT



- Mite composition varied among sites but was stable between wet and dry seasons.
- Succession altered mite composition but not abundance or richness.
- Microclimatic and edaphic factors drive mite communities, with group specific responses.
- Few associations between mites and litter decay rates were found.
- Mites exert a limited overall influence on decomposition in Andean montane forests.

Mites contribute directly and indirectly to several ecosystem functions such as nutrient cycling, soil formation, litter decomposition, and biological control. Despite their importance, the processes driving mite community assembly remain poorly understood in tropical montane ecosystems, where mite composition is unique and environmental gradients are steep. Here, we examined the structure of mite communities, their ecological drivers, successional patterns, and their associations with litter decomposition in upper Andean tropical forests (UATF). We collected 168 soil samples (30 cm × 30 cm × 5 cm) across four climatic seasons (two wet, two dry) from 14 permanent plots in four UATF sites. Microclimatic data were recorded using dataloggers, forest and soil data were collected through field sampling and soil analysis, and decay rates of 15 plant species were measured using reciprocal litter experiments. In total, 1387 mites were collected, belonging to 31 families and 42 morphospecies.

Mite communities varied markedly among sites but not between seasons, and were more abundant in the litter layer. While total Acari abundance and richness showed no significant differences along succession, Sarcoptiformes increased in abundance, reflecting their link to litter accumulation in old-growth forests. Community composition shifted strongly between mature and secondary forests. Total Acari were primarily associated with microclimatic conditions and soil nutrients, although responses varied among groups. Associations between mite attributes and decay rates were detected, but most litter species showed no link, suggesting a limited overall influence on decomposition. Our study provides a first step toward understanding the factors shaping mite communities and their associations with litter decay in UATF.

Keywords Acari, ecological succession, litter decomposition, Andean forests, microclimatic conditions, soil fauna

1 Introduction

Mites (Acari) are ubiquitous microarthropods present in nearly all terrestrial ecosystems, with ~55 000 species described (Krantz and Walter, 2009), representing less than 10% of the estimated global mite diversity (Walter and Proctor, 2013). They are particularly diverse in tropical ecosystems (Pachl et al., 2017), inhabiting both the litter and mineral soil layers (Zaitsev et al., 2002; Maraun et al., 2007; Walter and Proctor, 2013). Mites also exhibit remarkable trophic diversity, spanning three to four trophic levels, including algivores, primary decomposers, fungal feeders, scavengers, and predators (Schneider et al., 2004; Maraun et al., 2011; Potapov et al., 2022). Through these roles, they contribute to key ecosystem functions such as nutrient cycling, soil formation, litter decomposition, and biological regulation (Magilton et al., 2019; Zhang et al., 2023). Despite their ecological importance, mite diversity remains poorly understood and increasingly threatened (Sullivan and Ozman-Sullivan, 2022), underscoring the need for a deeper understanding of their ecology and responses to environmental change.

Within Acari, there are three ecologically distinct and well-recognized groups commonly found in soil and litter microhabitats: Mesostigmata, Sarcoptiformes (Oribatida), and Trombidiformes. These groups differ markedly in their trophic roles and ecological functions. Mesostigmata are mainly predators inhabiting the soil and litter layers, where they regulate soil fauna communities and indirectly influence decomposition dynamics through top-down control (Koehler, 1999; Walter and Proctor, 2013). Sarcoptiformes are typically detritivores and microbivores, playing a key role in decomposition and nutrient cycling through the processing of organic matter (Maraun and Scheu, 2000; Schneider et al., 2004; Erdmann et al., 2007). Trombidiformes comprise a functionally diverse group that includes saprophagous, predatory, and parasitic species, reflecting a wide range of ecological strategies within soil food webs (Krantz and Walter, 2009; Norton and Behan-Pelletier, 2009).

Studies in temperate and subtropical regions show that mite community composition and structure in soil and litter microhabitats is shaped by a complex interplay of abiotic, biotic, and spatiotemporal factors (Lindo and Winchester, 2008; Liu et al., 2018; Fei et al., 2024). Among the abiotic drivers, soil moisture plays a central role due to mites' sensitivity to desiccation, especially in mountain environments where microclimatic conditions can fluctuate drastically (Kamczyc et al., 2022; Sánchez-Galindo et al., 2025). Temperature and soil pH also influence community structure by affecting metabolic activity and microbial resource availability, particularly for detritivorous and microbivorous groups such as Oribatida (Walter and Proctor, 2013; Liu et al., 2018; Maraun and Scheu, 2000). Additionally, organic matter content and soil texture modulate microhabitat suitability and the vertical distribution of mites through their effects on soil porosity and water retention (Lindo et al., 2008). Biotic factors, including resource availability and diversity (e.g., litter quality, microbial biomass, and prey availability), further structure trophic guilds (Schneider et al., 2004; Potapov et al., 2022). Plant species composition and diversity indirectly influence mite communities by determining the quantity and heterogeneity of organic inputs (Lindo et al., 2008). Furthermore, spatial and temporal factors such as elevation (Scheu et al., 2008; Marian et al., 2020; Sánchez-Galindo et al., 2022), topography (Minor and Ermilov, 2015), successional stage (Zaitsev et al., 2002), and seasonality (Castillo-Figueroa and Castillo-Avila, 2025a) can cause strong shifts in mite diversity and composition, given that environmental filters and habitat structure vary across these gradients (Maraun et al., 2007; Illig et al., 2010). Despite these advances, the processes governing mite community assembly remain poorly understood in tropical montane ecosystems, where biodiversity is high and environmental gradients are steep (Walter and Proctor, 2013; Castillo-Figueroa et al., 2023). Because soil mites interact directly with their immediate environment, edaphic and microclimatic variables are expected to exert more direct effects on their communities, whereas forest structural attributes may influence mites indirectly through their effects on soil properties and microclimatic conditions, which also change across successional stages.

Soil mites are generally abundant in tropical Andean montane forests (Marian et al., 2020; Castillo-Avila et al., 2025), where soil fauna is often dominated by microarthropods and macrofauna is relatively scarce (Illig et al., 2010;

Maraun et al., 2008; Castillo-Figueroa and Castillo-Avila, 2025b). In these systems, increasing evidence from upper Andean tropical forests of Colombia and Ecuador suggests that litter decomposition is not directly mediated by soil microarthropods; instead, bacteria and fungi act as the dominant drivers of this process (Varela et al., 2007; Illig et al., 2008; Sánchez-Galindo et al., 2022; Castillo-Figueroa and Castillo-Avila, 2025b). Still, studies explicitly evaluating the relationship between mite groups and litter decomposition are scarce, as most research has treated soil mesofauna as a single group. Assessing how mite abundance and richness relate to litter decay may therefore provide new insights into their potential role in decomposition in these ecosystems.

Upper Andean tropical forests are among the most threatened ecosystems in the Neotropics due to extensive landscape transformation and urban expansion (Etter et al., 2020; Clerici, 2025). At the same time, secondary forests are increasingly dominating landscapes as land-use changes facilitate natural vegetation recovery (Hurtado-M et al., 2022). In this context, understanding how soil mite communities respond to forest succession is crucial, given their role in regulating key soil functions (Zhang et al., 2023). Recent studies on soil fauna have shown that energy availability—reflected in increasing forest productivity—tends to rise with succession (Castillo-Avila et al., 2025). Therefore, it is reasonable to expect that old-growth forests, with greater litter accumulation and more diverse litter types, will support higher mite abundance and richness, as well as shifts in community composition compared to younger secondary forests. Moreover, strong land-use legacies (Castillo-Figueroa and Posada, 2025a), high plant beta diversity (Hurtado-M et al., 2021), and pronounced seasonal variation in soil moisture in the Colombian Andes (Herzog et al., 2011) are likely to promote high species turnover across successional stages and climatic seasons. Understanding these patterns is essential to better characterize the ecology and community dynamics of mites in upper Andean tropical forests under different successional stages.

To better understand mite community dynamics in Andean montane ecosystems, we explore how microclimatic, forest, and soil variables influence mite communities in tropical upland forests. Specifically, we aimed to analyze mite community structure, evaluate successional patterns, identify the main ecological drivers, and assess their potential contribution to litter decomposition. We examined variation at both the community level and among the three major mite orders to capture differential ecological responses. Accordingly, we tested the following hypotheses:

(H1) mite communities exhibit pronounced beta diversity across spatial and seasonal contexts;

(H2) as forest succession progresses, increased litter inputs and aboveground biomass (as proxies of resource and energy availability), promote higher mite richness and abundance, along with changes in community composition for all mite groups;

(H3) edaphic and microclimatic factors are the primary drivers of mite abundance and richness, whereas forest structural attributes are expected to influence mite communities indirectly through their effects on soil properties and microclimatic conditions, with responses differing among groups;

(H4) litter decomposition rates are expected to show weak or context-dependent relationships with mite abundance and richness, given their indirect role in litter fragmentation, which may vary with litter substrate quality and mite groups.

2 Materials and methods

2.1 Study area

In Colombia, the Andean region covers 287 720 km^2 and is divided into the Eastern, Central, and Western cordilleras, which surround the Magdalena–Cauca valley, one of the country's main watersheds (Rodríguez Eraso et al., 2013). Despite its unique biological diversity, the Colombian Andes has a legacy of intense land-use and land-cover change, driven by diverse agricultural and industrial activities linked to its role as the country's economic center (Etter et al., 2020). Climatically, the Colombian Andes experience a bimodal precipitation pattern, with two wet seasons (April−June and October−December) and two dry seasons (January−March and July−September). Particularly, the climate around Bogotá is characterized by a mean annual temperature of 14.8 °C and an annual precipitation of 975 mm (Anselm et al., 2020).

In this region, we conducted our research in 14 permanent plots (20 m × 20 m) established in private properties and reserves the Eastern Cordillera, within peri-urban Andean montane forests of the Bogotá high plateau (Cundinamarca, Colombia) at elevations between 2685 and 3140 m. The plots in this study are distributed across four different sites (Fig. 1A): Guatavita, Guasca, Torca, and Tabio. A total of 63 species belonging to 50 genera and 35 families of shrubs and trees were recorded across the 14 plots. Five families—Ericaceae, Melastomataceae, Cunoniaceae, Primulaceae, and Asteraceae—dominated the community, comprising 56% of individuals with a basal diameter > 5 cm. At the genus level, *Miconia*, *Weinmannia*, *Cavendishia*, *Myrsine*, and *Myrcianthes* were the most abundant, together representing half of all individuals. Dominant species included *Weinmannia tomentosa*, *Cavendishia bracteata*, *Miconia ligustrina*, *Miconia squamulosa*, and *Myrcianthes leucoxyla* (Castillo-Figueroa et al., 2023; Castillo-Figueroa, 2024a,

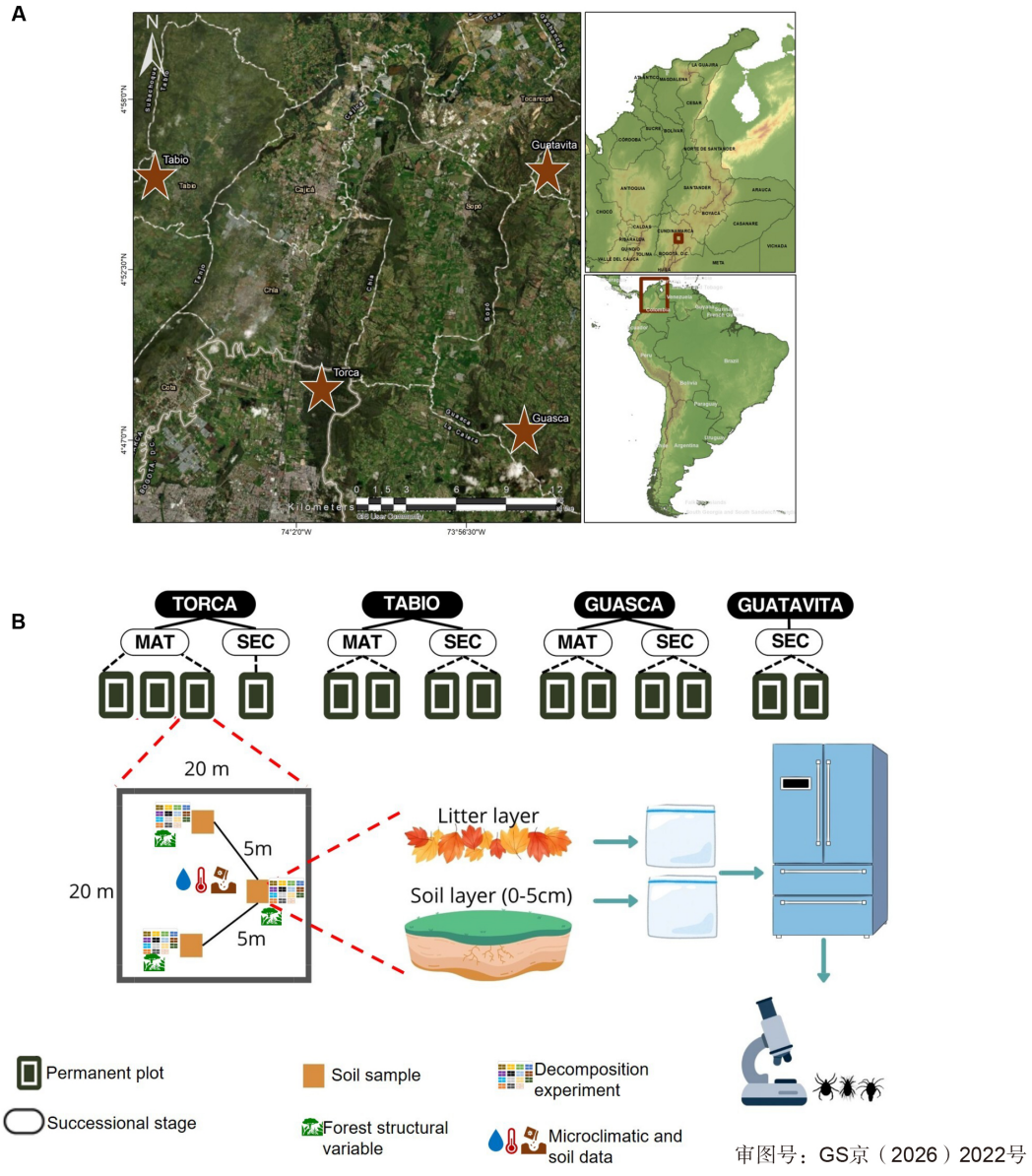


Fig. 1 Map of the study area in upper Andean tropical forests of Colombia where mites were collected, showing (A) the location of the study area, with the four sites indicated by brown stars, and (B) the experimental design and mite sampling scheme.

2024b). Detailed information on study sites and plot configuration (Rastrojos Project) is available in Castillo-Figueroa (2024a, 2024b) and Castillo-Figueroa and Posada (2025a).

2.2 Experimental design

Based on expert knowledge, interviews with local land owners, and structural attributes such as basal area, canopy height, stem density, and species composition, the 14 plots were classified as either secondary (7 plots) or mature (7 plots) (Table 1) (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023). Overall, mature forests are characterized by higher aboveground biomass and productivity, taller canopies, deeper soil organic horizons, elevated nitrogen concentrations, and greater soil fauna diversity compared to secondary forests (Castillo-Figueroa et al., 2023; Castillo-Figueroa and Posada, 2025a; Castillo-Avila et al., 2025).

Across the 14 plots, mites, forest structure, and litter decomposition were evaluated at three subsampling points within each plot, whereas soil and microclimatic measurements were obtained once per plot (Fig. 1B). Mites were sampled on four occasions at the same subsampling points, including two sampling campaigns during the dry season and two during the rainy season (see Mite sampling). For overall analyses, data from all sampling periods were combined, whereas seasonal analyses were conducted to evaluate differences between dry and rainy seasons. Values obtained from the three subsampling points were averaged to obtain a single value per plot for subsequent analyses (see Data analysis).

Table 1 Abundance (N) and richness (S) of mites in 14 permanent plots of upper Andean tropical forests in Colombia. Total Acari, Mesostigmata, Sarcoptiformes and Trombidiformes are shown in the table.

Site	Plot	Succession	Total Acari attributes	Mesostigmata attributes	Sarcoptiformes attributes	Trombidiformes attributes
Guatavita	1	Secondary	N=121, S=19	N=54, S=5	N=52, S=13	N=15, S=1
Guatavita	2	Secondary	N=25, S=10	N=7, S=3	N=7, S=3	N=11, S=4
Guasca	3	Mature	N=60, S=11	N=17, S=5	N=40, S=4	N=3, S=2
Guasca	4	Secondary	N=116, S=11	N=73, S=5	N=43, S=6	N=0, S=0
Guasca	5	Mature	N=37, S=10	N=9, S=4	N=19, S=4	N=9, S=2
Guasca	6	Secondary	N=35, S=5	N=33, S=4	N=0, S=0	N=2, S=1
Tabio	7	Secondary	N=182, S=20	N=116, S=7	N=61, S=11	N=5, S=2
Tabio	8	Secondary	N=37, S=16	N=21, S=6	N=11, S=7	N=5, S=3
Tabio	9	Mature	N=121, S=24	N=47, S=8	N=57, S=13	N=17, S=3
Tabio	10	Mature	N=150, S=18	N=62, S=8	N=79, S=8	N=9, S=2
Torca	11	Mature	N=235, S=20	N=34, S=5	N=201, S=15	N=0, S=0
Torca	12	Mature	N=63, S=19	N=9, S=3	N=49, S=14	N=5, S=2
Torca	13	Secondary	N=100, S=17	N=49, S=6	N=43, S=8	N=8, S=3
Torca	14	Mature	N=105, S=19	N=14, S=5	N=88, S=12	N=3, S=2

2.3 Mite sampling

We sampled mites by collecting three soil samples (30 cm × 30 cm × 5 cm) with a shovel in each plot (Fig. 1B). In 2022, 168 samples were collected across four climatic seasons, with 42 samples taken in each: January–February and July–August (dry seasons, n = 84), and April–May and October–November (wet seasons, n = 84). We separated mites from the litter and soil layers in each sample by dividing the material into two sub-samples, which were stored in plastic bags for further analysis: (1) litter material and (2) soil depth at 0–5 cm (Fig. 1B). Mites were manually extracted using a Zeiss Stemi 305 stereomicroscope and preserved in 70% ethanol. With expert assistance (see acknowledgments), specimens were identified using original descriptions and regional identification guides to achieve the highest possible taxonomic resolution (Krantz, 1962; Smith Meyer and Ueckermann, 1987; Balogh and Balogh, 1988, 1989; Lindquist et al., 2009; Walter et al., 2009; Hernandes et al., 2016; Hrúzová and Fenďa, 2018; Ott and Ott, 2018; Subías and Shtanchaeva, 2023). Most specimens were identified to family or genus level, whereas only a small proportion (4.9%) could not be assigned to family level due to the lack of diagnostic characters. A complete list of morphospecies, their taxonomic resolution, and assignment to the three major groups considered in this study (i.e., Mesostigmata, Sarcoptiformes, and Trombidiformes) is provided in Table S1. All collections were carried out under the national collection permit (ANLA–Resolución 530, 27 May 2014).

2.4 Litter decomposition experiment

Between October 2021 and April 2023, we conducted a reciprocal translocation experiment to evaluate litter decomposition across multiple Andean species (Castillo-Figueroa et al., 2025b). This experiment was implemented across the 14 plots, each containing three distinct litter beds (microsites) separated by at least 5 meters, which correspond to the same locations used for mite sampling (Fig. 1B). We employed 15 litter species, exposed to four different decomposition durations—3, 6, 12, and 18 months—resulting in a total of 2520 litterbags deployed (14 plots × 3 beds × 15 species × 4 harvest periods). The litterbags sized 10 cm × 15 cm and were made from 2 mm mesh fiberglass, permitted access to micro- and meso-faunal decomposers. Upon retrieval, litterbags were carefully cleaned of mineral soil using brushing, then oven-dried at 60 °C for 72 hours before weighing on a precision analytical balance (0.0001 g accuracy; LX 220A scs). Decomposition rates (K, year^{-1} (y^{-1})) for each species were calculated following the methodology described by Olson (1963).

2.5 Microclimatic, forest and soil variables

Soil microclimatic variables were recorded throughout the year of mite sampling in 2022. To achieve this, TMS-4 soil probes (Temperature and Moisture Sensor; TOMST, Czech Republic) equipped with data loggers were installed at the center of each of the 14 plots to measure soil temperature and volumetric water content every 15 minutes (Castillo-Figueroa, 2024b, 2025). Each device comprised three temperature sensors positioned 15 cm above the soil surface, at the soil surface, and at an 8 cm soil depth. Additionally, a probe located at 14 cm depth measured volumetric soil moisture. For each of the four microclimatic variables recorded—air temperature, surface temperature, soil

temperature, and soil moisture—potential outliers caused by installation or retrieval errors were removed before calculating mean, minimum, maximum, range, standard deviation, and variance (Castillo-Avila et al., 2025).

Forest structural variables were measured at the microsite level within each plot, including slope, litter depth, canopy openness, and leaf area index, at the same locations used for the decomposition experiment and mite sampling (Fig. 1B). Slope was measured using a clinometer via the Angle Meter app, while litter depth was calculated as the average of five random measurements taken with an electronic digital caliper (accuracy: 0.1 mm). Canopy openness and leaf area index were assessed using hemispherical photography with a Canon fisheye lens (EW-77, EF 8–15 mm f/4, Japan). Four photographs per microsite were taken at 1 m above ground level and analyzed using Gap Light Analyzer software (GLA version 2.0; Frazer et al., 2000). Values were then averaged to represent each microsite (Castillo-Figueroa, 2024b, 2025).

Soil data for the study plots were sourced from previously published work (Hurtado-M and Norden, 2020). The dataset encompassed measurements of bulk density (g cm^{-3}), soil pH, particle size distribution (%silt, %sand, %clay), and concentrations of calcium (Ca), potassium (K), magnesium (Mg), sodium (Na), aluminium (Al), nitrogen (N), phosphorus (P), cation exchange capacity (CEC), and % organic carbon. These variables were derived from composite samples created by pooling five soil cores per plot, collected at a depth of 10–30 cm following removal of the surface litter layer (Hurtado-M et al., 2021). Laboratory analyses were performed at the Laboratorio de Aguas y Suelos of the National University of Colombia (Bogotá).

2.6 Data analysis

To avoid pseudoreplication, plots were treated as the unit of replication in all correlation and regression analyses (n = 14). Microsite-level measurements within each plot were averaged prior to analysis. Likewise, mite community attributes were first averaged across microsites within each plot and, depending on the objective of each analysis, were then either averaged across sampling periods to assess overall community patterns or analyzed separately by season to evaluate seasonal patterns. Litter decomposition and forest structural variables were averaged across microsites within each plot, whereas soil and microclimatic variables already measured at the plot level were incorporated directly. This aggregation approach allowed all response and explanatory variables to be analyzed at a common spatial scale and focused the analyses on broad plot-level ecological patterns. Although the relatively small number of plots may limit the statistical power to detect weak or complex interactions, the plot-level design supports robust inference at the ecosystem level.

To evaluate variation in mite communities across sites and climatic seasons (H1), we first assessed the completeness of species richness by constructing rarefaction curves based on samples collected across the four sites and the four climatic seasons. Mite community diversity was quantified through Hill numbers (q = 0, 1, 2) following Jost (2006), with 95% confidence intervals calculated for each mite group (Fig. S1). As a general measure of alpha diversity, we focused on species richness as a parsimonious and widely interpretable metric that captures the main patterns of alpha diversity without overcomplicating the analyses. Given the limited number of plots, focusing on richness (q = 0) as the primary response variable also helped reduce model complexity and minimize the risk of overfitting in the inferential analyses. Community composition analyses were performed using Non-metric Multidimensional Scaling (NMDS) to visualize compositional similarity across sites. Differences in community composition among sites and climatic seasons, as well as their interaction, were tested using a two-way Permutational Multivariate Analysis of Variance (PERMANOVA) with 9999 permutations (Anderson, 2001). Both NMDS and PERMANOVA were based on Bray–Curtis dissimilarity matrices and were performed for total Acari and for each mite group. For quantitative variables such as abundance and richness, we additionally used Mann–Whitney U tests to evaluate differences between dry and wet seasons for total Acari and for each mite group.

We assessed successional changes in mite abundance and richness by modelling its relationship with aboveground biomass (AGB), employed as a quantitative proxy for successional stage (H2). This gradient ranged from secondary forests characterized by low AGB to mature forests with high AGB values (Poorter et al., 2021; Matsuo et al., 2025). Plot-level AGB data were sourced from Castillo-Figueroa et al. (2023). We performed the same analysis separately for the three mite groups to determine whether their responses differed. In addition, a one-way PERMANOVA was used to test for differences in community composition between secondary and mature forests for total Acari and for each mite group, complemented by NMDS ordination to visualize patterns of compositional similarity.

To elucidate the principal ecological determinants of mite community attributes (H3), we initially performed reduced major axis (RMA) regressions examining relationships between mite abundance and richness and individual microclimatic, forest, and soil variables. RMA was selected because both response and explanatory variables are subject to measurement error and no clear a priori causal direction was assumed, as is common in ecological studies. For each regression, 95% confidence intervals of slope estimates were obtained via bootstrapping with 1999 iterations. Subsequently, variables demonstrating significant associa-

tions in the RMA analyses were incorporated into a stepwise multiple linear regression (MLR) framework, treating microclimatic, forest, and soil factors as independent predictors and mite abundance and richness as the response variables. To mitigate multicollinearity, only predictors with a Variance Inflation Factor (VIF) less than 3.0 were retained (Neter et al., 1990). Model selection criteria included adjusted R^2, which accounts for model complexity by penalizing superfluous predictors to reduce overfitting (James et al., 2013), and root mean square error (RMSE), which quantifies predictive accuracy as the average deviation between observed and predicted values in the units of the dependent variable (Chatterjee and Hadi, 2015).

Lastly, to evaluate the relation between mite communities and litter decomposition (H4), we performed RMA regressions relating abundance and richness to the decomposition environment, defined as the mean decomposition rate per plot across the 15 litter species included in the experiment. Additionally, we assessed associations between abundance and richness of each of the three mite groups and decomposition rates using a Spearman correlation matrix to examine relationships between group-specific mite metrics and species-specific litter decay rates. All diversity analyses were conducted using the online version of iNEXT (available at the website of chao.shinyapps.io/iNEXTOnline/ Hsieh et al., 2016). Species composition, correlation, and linear regression analyses were performed in PAST v.5.0, while multiple linear regression analyses were conducted in JASP v.0.18.1.0.

3 Results

3.1 Mite community

We collected a total of 1387 mites belonging to 31 families and 42 morphospecies (Table 1), with Mesostigmata comprising 545 individuals and 11 morphospecies, Sarcoptiformes 750 individuals and 25 morphospecies, and Trombidiformes 92 individuals and 6 morphospecies. Mean total Acari abundance and richness (± SD) were 99.07 ± 61.62 individuals and 15.64 ± 5.33 morphospecies, respectively. Mean abundance and richness were 38.93 ± 30.79 individuals and 5.29 ± 1.59 morphospecies for Mesostigmata, 53.57 ± 49.70 individuals and 8.43 ± 4.67 morphospecies for Sarcoptiformes, and 6.57 ± 5.21 individuals and 1.93 ± 1.14 morphospecies for Trombidiformes, respectively.

Based on the two-way PERMANOVAs, mite composition varied significantly among sites when considering all Acari together (p = 0.0041, pseudo-F = 2.1849, Table S2, Fig. 2A). When analyzed by group, both Mesostigmata (p = 0.0242, pseudo-F = 1.9293, Table S3, Fig. 2B) and Sarcop-

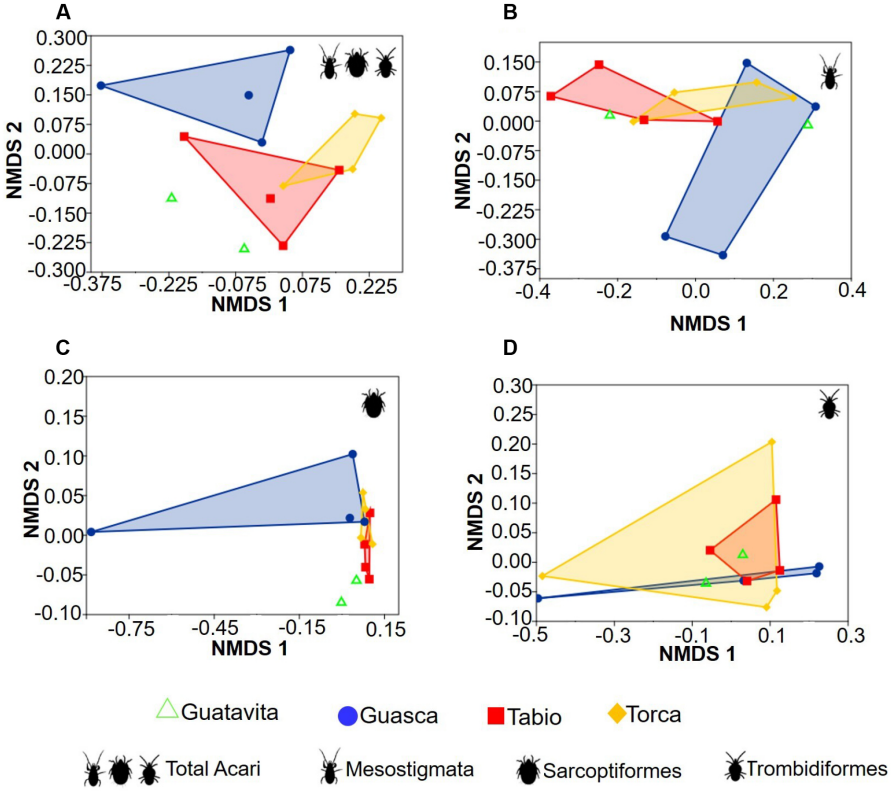


Fig. 2 Non-metric multidimensional scaling (NMDS) showing variation in mite community composition among sites for (A) total Acari, (B) Mesostigmata, (C) Sarcoptiformes, and (D) Trombidiformes. Sites are represented by different colours and symbols: Guatavita (green triangles), Guasca (blue circles), Tabio (red squares), and Torca (yellow diamonds).

tiformes showed significant variation in composition (p = 0.0006, pseudo-F = 2.3676, Table S4, Fig. 2C), whereas Trombidiformes (p = 0.064, pseudo-F = 1.7354, Table S5, Fig. 2D) did not differ significantly among sites.

Overall, although mean abundance and richness were higher during the wet season, especially during the first rainy season (April–May) (Fig. S2), no significant seasonal differences were detected in total Acari abundance or individual mite groups, except for a marginal effect on Sarcoptiformes abundance (p = 0.045; Table S6). The two-way PERMANOVA revealed no seasonal effect and no interaction with sites for any of the groups (p > 0.05, Tables S2−S5), consistent with the NMDS ordination, which showed no clear seasonal separation (high overlap) in mite composition (Fig. 3). Most mites were more abundant in the litter microhabitat than in the soil layer, with all groups exceeding 60% of their abundance in the former (Fig. S3).

3.2 Mite community along succession

Total Acari abundance and richness did not vary along succession, nor did those of Mesostigmata and Trombidiformes (p > 0.05, Fig. 4). In contrast, Sarcoptiformes showed a significant increase in abundance with succession (p = 0.013, r = 0.64, R^2 = 0.41, Fig. 4H). Community composition also differed between mature and secondary forests according to the one-way PERMANOVA, with significant effects detected for total Acari (p = 0.0004, pseudo-F = 4.557), Mesostigmata (p = 0.0047, pseudo-F = 3.612), and Sarcoptiformes (p = 0.0018, pseudo-F = 3.233). Conversely,

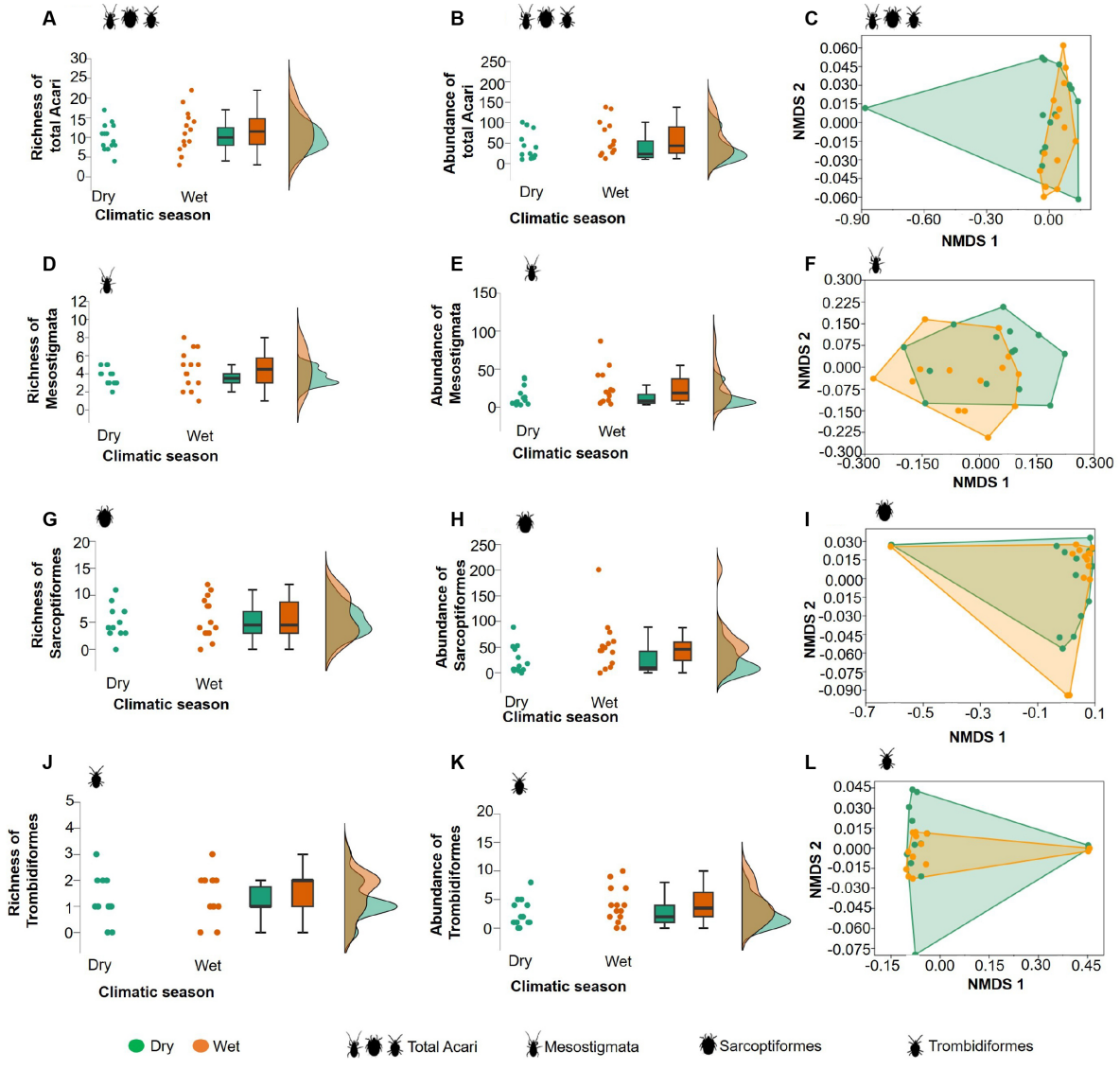


Fig. 3 Pairwise comparisons of richness, abundance, and community composition between dry and wet seasons for (A–C) total Acari, (D–F) Mesostigmata, (G–I) Sarcoptiformes, and (J–L) Trombidiformes. Dry seasons are shown in green and wet seasons in orange. Richness and abundance are presented as jittered raw data points with boxplots and one-sided violin plot, whereas community composition is visualized using NMDS ordination.

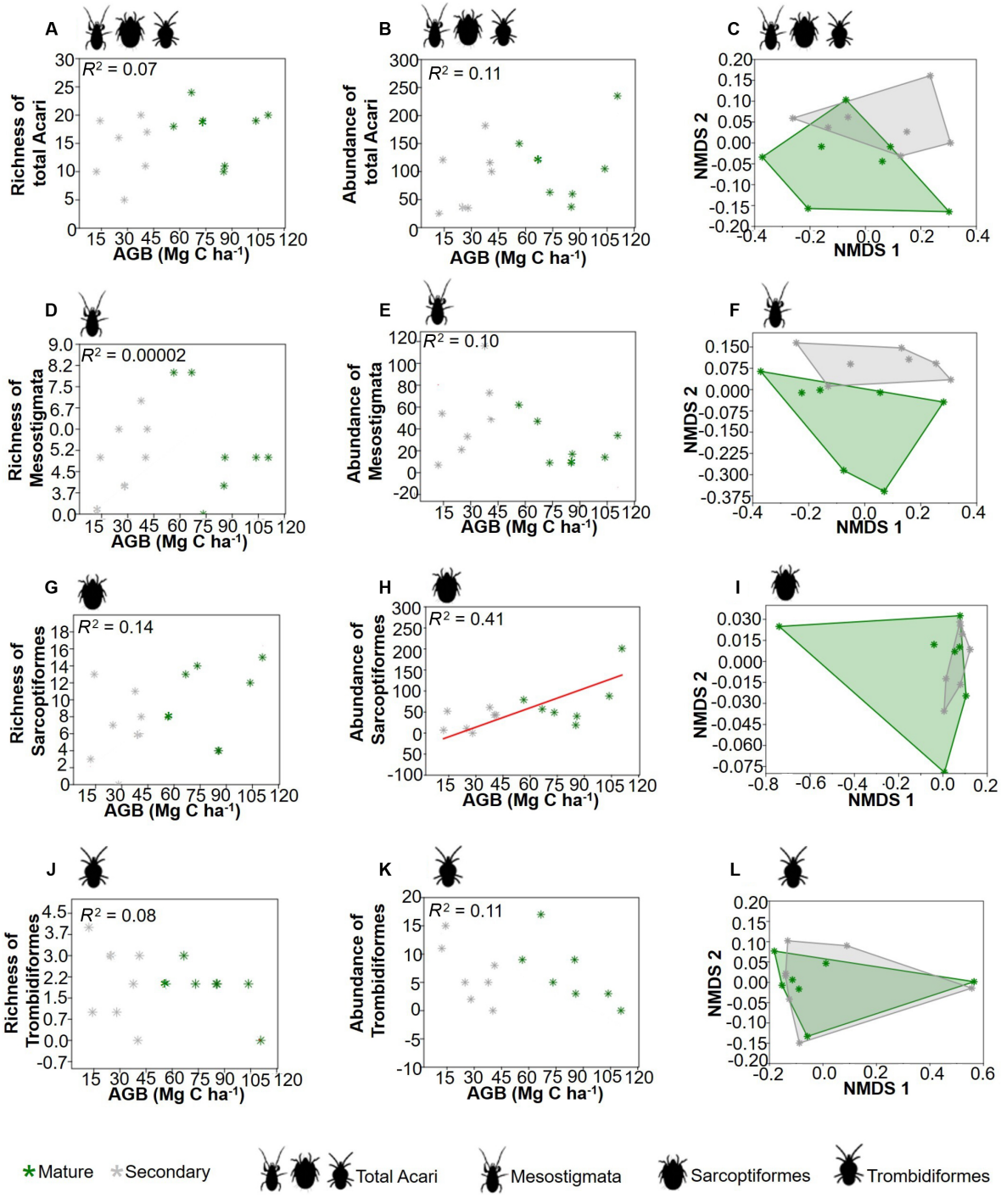


Fig. 4 Variation in richness, abundance, and composition along the successional gradient for (A–C) total Acari, (D–F) Mesostigmata, (G–I) Sarcoptiformes, and (J–L) Trombidiformes. Green asterisks represent mature forest plots, while grey asterisks indicate secondary forest plots. The R^2 value is shown in the upper left corner. The red line represents a significant relationship in the RMA regression ($p < 0.05$). Community composition is visualized using NMDS ordination.

Trombidiformes did not show compositional differences (p = 0.6993, pseudo-F = 0.5959).

3.3 Environmental factors influencing mite communities

RMA regressions revealed significant relationships between environmental variables and mite community attributes (Fig. 5). Total Acari abundance was not related to any variable ($p > 0.05$), whereas richness showed positive associations with mean (p = 0.0045, r = 0.71, R^2 = 0.50, Fig. S4a), minimum (p = 0.003, r = 0.73, R^2 = 0.53, Fig. S4b), and maximum soil temperature (p = 0.007, r = 0.68, R^2 = 0.47, Fig. S4c), mean (p = 0.0038, r = 0.72, R^2 = 0.52, Fig. S4d) and minimum surface temperature (p = 0.0195, r = 0.61, R^2 = 0.38, Fig.

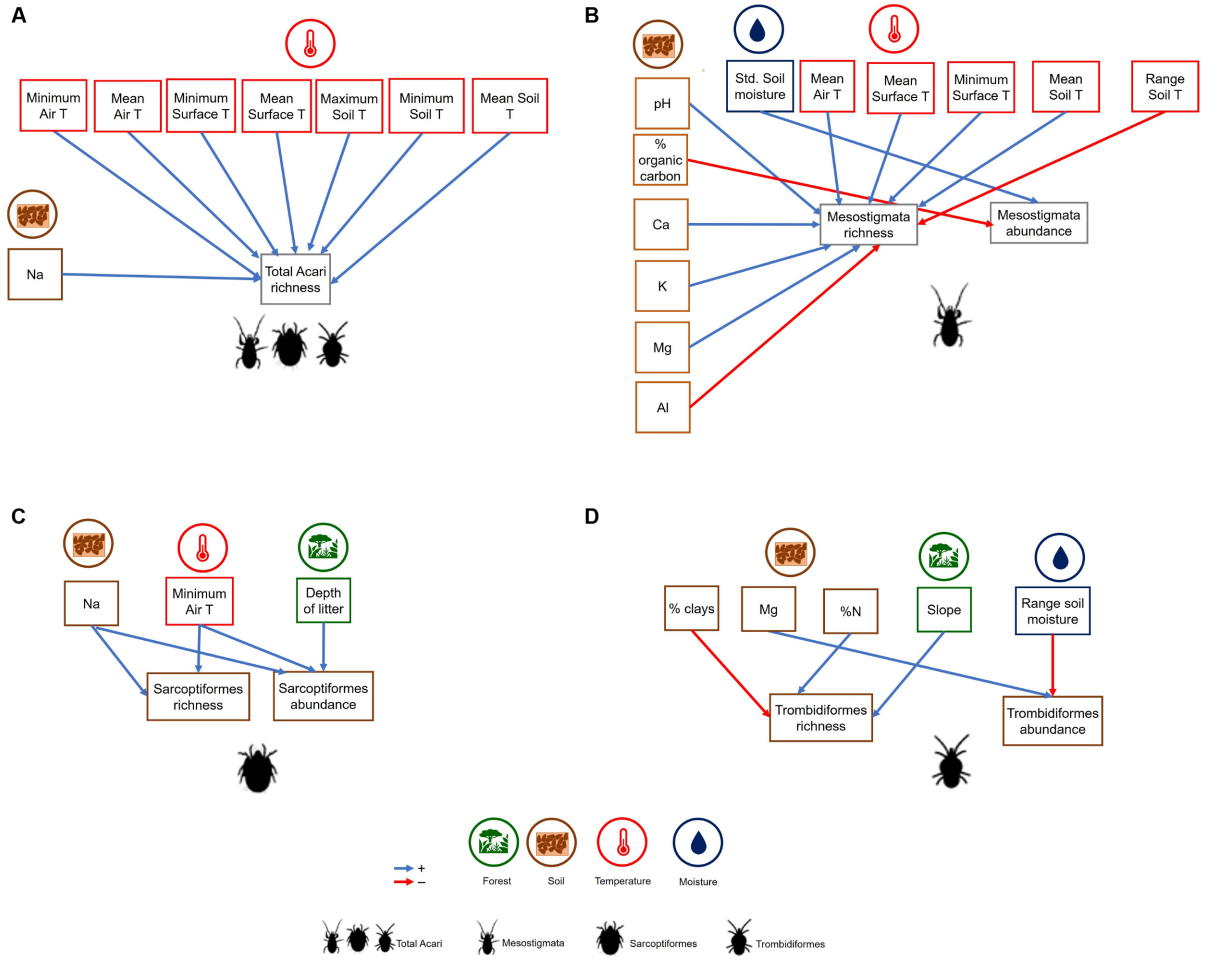


Fig. 5 Significant relationships between microclimatic, forest, and soil variables and the richness and/or abundance of (A) total Acari, (B) Mesostigmata, (C) Sarcoptiformes, and (D) Trombidiformes. Blue arrows indicate significant positive relationships, while red arrows represent negative relationships based on RMA regression results shown in Figs. S4–S7.

S4e), mean (p = 0.0027, r = 0.73, R^2 = 0.54, Fig. S4f) and minimum air temperature (p < 0.0001, r = 0.79, R^2 = 0.62, Fig. S4g), as well as with soil Na (p = 0.0095, r = 0.66, R^2 = 0.44, Fig. S4h). MLR identified minimum air temperature and minimum soil temperature as the variables most strongly associated with total Acari richness (p = 0.026, r = 0.872, R^2 = 0.76, adjusted R^2 = 0.71, Table S7).

For Mesostigmata (Fig. 5B), abundance was positively related to the standard deviation of soil moisture (p = 0.007, r = 0.68, R^2 = 0.46, Fig. S5a) and negatively to % organic carbon (p = 0.046, r = –0.54, R^2 = 0.29, Fig. S5b). Richness was positively associated with minimum (p < 0.0001, r = 0.82, R^2 = 0.67, Fig. S5c) and mean surface temperature (p = 0.0134, r = 0.64, R^2 = 0.41, Fig. S5d), mean soil temperature (p = 0.0467, r = 0.54, R^2 = 0.29, Fig. S5e), mean air temperature (p = 0.012, r = 0.65, R^2 = 0.42, Fig. S5f), soil pH (p = 0.0097, r = 0.66, R^2 = 0.44, Fig. S5g), base cations including soil Ca (p = 0.002, r = 0.74, R^2 = 0.55, Fig. S5h), K (p = 0.002, r = 0.74, R^2 = 0.55, Fig. S5i), and Mg (p = 0.0019, r = 0.75, R^2 = 0.56, Fig. S5j). In contrast, richness was negatively related to the range of soil temperature (p = 0.043, r = –0.55, R^2 = 0.30, Fig. S5k), and Al (p = 0.0004, r = –0.81, R^2 = 0.66, Fig. S5l). MLR indicated that standard deviation of soil moisture was the variable most closely related to abundance (p = 0.007, r = 0.68, R^2 = 0.46, adjusted R^2 = 0.42, Table S8), whereas minimum surface temperature and Ca were the variables most strongly associated with richness (p = 0.003, r = 0.93, R^2 = 0.86, adjusted R^2 = 0.83, Table S9).

For Sarcoptiformes (Fig. 5C), abundance was positively related with Na (p = 0.045, r = 0.54, R^2 = 0.29, Fig. S6a), litter depth (p = 0.0085, r = 0.67, R^2 = 0.45, Fig. S6b), and minimum air temperature (p = 0.03, r = 0.58, R^2 = 0.33, Fig. S6c), whereas richness was positively associated with Na (p = 0.0081, r = 0.68, R^2 = 0.46, Fig. S6d) and minimum air temperature (p = 0.0036, r = 0.72, R^2 = 0.52, Fig. S6e). MLR showed that abundance was mainly associated with litter depth (p = 0.009, r = 0.67, R^2 = 0.45, adjusted R^2 = 0.41, Table S10), while richness was primarily related to minimum air temperature (p = 0.004, r = 0.72, R^2 = 0.52, adjusted

R^2 = 0.48, Table S11).

For Trombidiformes (Fig. 5D), abundance was positively associated with Mg (p = 0.025, r = 0.59, R^2 = 0.35, Fig. S7a) and negatively related to the range of volumetric soil moisture (p = 0.037, r = –0.56, R^2 = 0.31, Fig. S7b), whereas richness was positively related to %N (p = 0.0179, r = 0.62, R^2 = 0.39, Fig. S7c) and slope (p = 0.03, r = 0.58, R^2 = 0.33, Fig. S7d), and negatively to % clays (p = 0.01, r = –0.63, R^2 = 0.40, Fig. S7e). MLR indicated that Mg was the variable most closely associated with abundance (p = 0.025, r = 0.59, R^2 = 0.35, Adjusted R^2 = 0.30, Table S12), while % clays and slope were the variables most strongly related to richness (p = 0.016, r = 0.81, R^2 = 0.65, Adjusted R^2 = 0.59, Table S13).

3.4 Relations between mites and litter decay

We identified specific associations between soil mite community attributes and the decomposition of some of the 15 litter species (Fig. 6A). However, half of the litter species showed no significant association with either total Acari community attributes or any individual mite group, and total Acari abundance and richness were not significantly related to the decomposition environment (Fig. 6B, 6C). Among the significant associations between soil mite community attributes and litter decomposition rates, most were positive, whereas only two species (*Prunus buxifolia* and *Ocotea calophylla*) exhibited negative relationships. Overall, of the 120 possible associations between abundance or richness of total Acari or individual mite groups with litter-specific decomposition rates, only 16 were significant (13.33%).

4 Discussion

Soil mite communities remain largely understudied in tropical

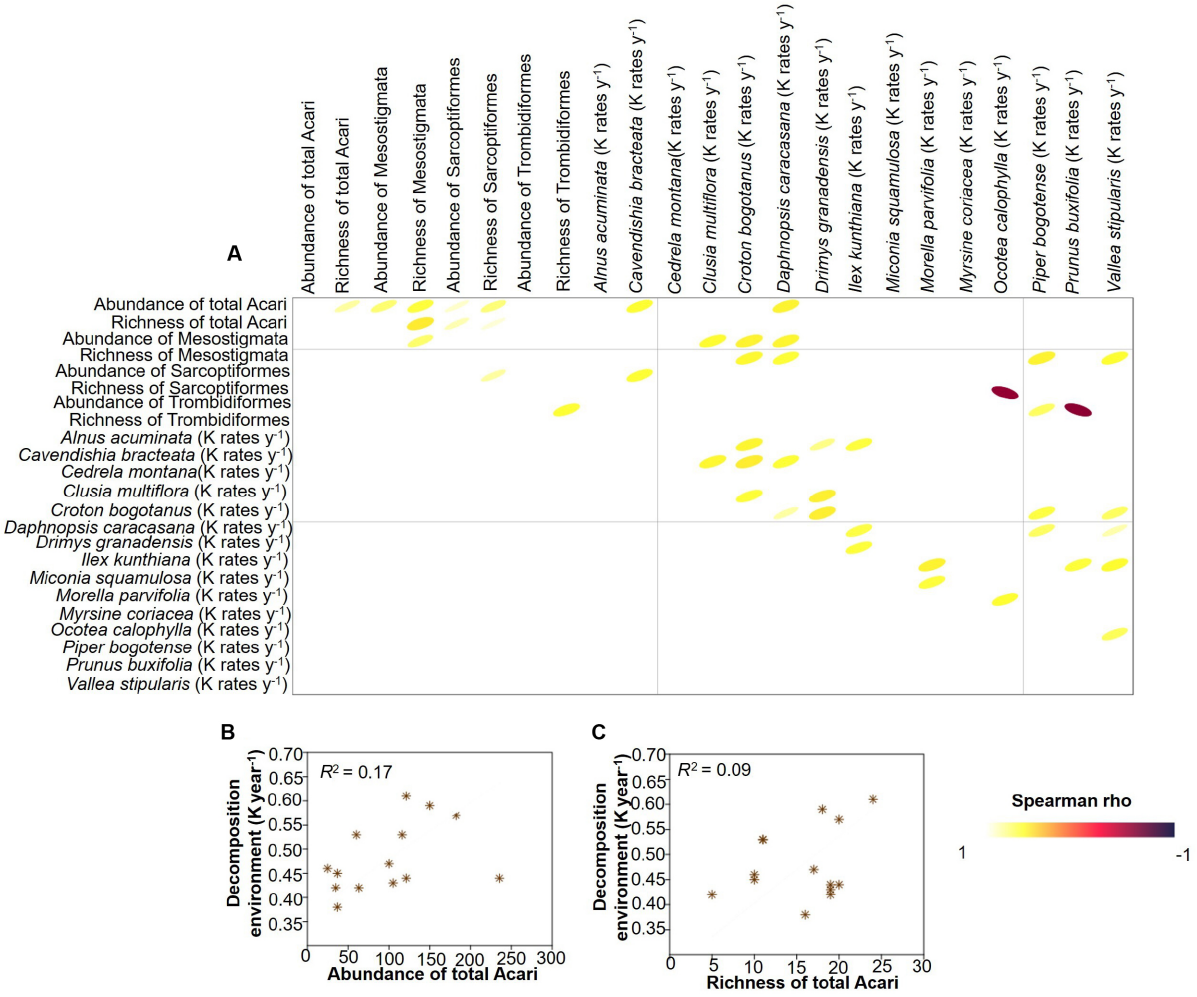


Fig. 6 Spearman correlations showing (A) the relationships between mite abundance and richness, and each group's association with litter decay rates (K year^{-1}) of 15 litter species. Blank cells indicate non-significant relationships (p > 0.05). Yellow cells represent significant positive relationships, while burgundy cells indicate significant negative ones. RMA regressions between the decomposition environment and (B) total Acari abundance and (C) total Acari richness showed no significant relationships (p > 0.05). The R^2 value is shown in the upper left corner.

montane ecosystems, particularly in upper Andean tropical forests, where research integrating abiotic, forest, and soil variables—and their links to litter decay across different substrates—remains scarce (Marian et al., 2020; Sánchez-Galindo et al., 2025). In our study, mite communities varied markedly across sites but showed no seasonal differences and were consistently more abundant in the litter layer. While abundance and richness remained largely unchanged along succession, except for an increase in Sarcoptiformes, community composition differed markedly between mature and secondary forests. Overall, mite assemblages were primarily associated with microclimatic conditions and soil nutrients, although responses varied among groups and reflected specific relationships with soil physicochemical properties, forest structure, temperature and moisture conditions. Associations between mite attributes and litter-specific decomposition rates were limited, with most litter species showing no significant relationships. These findings suggest a limited direct role of mites on decomposition in Andean montane forests, with associations restricted to specific litter types and mite groups.

4.1 Andean mite community across space and time

We found that mite composition differed markedly among sites but remained stable between wet and dry seasons, partially supporting our first hypothesis (H1). Spatial differences were driven primarily by Mesostigmata and Sarcoptiformes, whereas Trombidiformes showed relatively similar composition across sites. This pattern is consistent with the limited dispersal ability of mite communities, which tend to respond more strongly to local environmental factors, leading to pronounced site-specific community composition (Erdmann et al., 2012; Corral-Hernández et al., 2016). In line with this, several studies have demonstrated that mite communities often develop close associations with plants and the litter traits they generate (St. John et al., 2006; Skoracka and Kuczyński, 2012; Thakur and Eisenhauer, 2015; de Lillo et al., 2018; Zhou et al., 2022), suggesting that shifts in plant composition may drive mite biodiversity turnover across sites. Still, in these same plots, other soil biota such as centipedes (Castillo-Figueroa et al., 2025a), microarthropods (Castillo-Avila et al., 2025), and fungi (Castillo-Figueroa et al., 2026) also change in composition, and their roles as prey or predators may further contribute to structuring mite communities. Abiotic factors such as temperature, soil pH, nutrient availability, and forest structure also shape mite communities (Erdmann et al., 2012; Wehner et al., 2018; Chi et al., 2025), particularly in tropical Andean mountains, where these variables change markedly over short spatial scales (Wilcke et al., 2008; Pierick et al., 2021; Castillo-Figueroa, 2025).

In the case of Mesostigmata, compositional differences among sites are more likely related to changes in prey availability and trophic structure within the litter layer, reflecting their predominantly predatory habits and indirect responses to litter quantity and quality through bottom-up effects in the soil food web (Urbanowski et al., 2018; Manu et al., 2021).

For Sarcoptiformes, which are closely associated with litter and plant-derived detritus (Maraun and Scheu, 2000), their variation among sites may be linked to differences in floristic composition. Although temporal changes in litter quality during decomposition may influence resource availability for Sarcoptiformes, particularly through changes in soil nutrient availability (Franklin et al., 2004), previous studies in this system indicate that relative decomposition patterns across litter species are consistent among sites, despite differences in absolute decomposition rates (Castillo-Figueroa, 2025; Castillo-Figueroa et al., 2025b). This suggests that temporal shifts in litter quality are unlikely to drive the observed spatial variation in Sarcoptiformes communities, which is more plausibly associated with differences in vegetation composition and litter inputs among sites.

The lack of significant site-level differences in Trombidiformes is potentially linked to their wide ecological range and low relative abundance compared to other soil mite groups. Trombidiformes include taxa with varied habitat associations that are not tightly linked to broad environmental gradients, unlike Mesostigmata and Sarcoptiformes, which often show clearer responses to environmental variation in soil studies (Minor and Ermilov, 2015; Manu et al., 2019, 2021, 2022). However, Trombidiformes often comprise a small proportion of the total soil mite community (Table 1), which can limit statistical power to detect differences among sites (Seniczak et al., 2022).

Contrary to our expectations, we found no significant seasonal differences in richness or abundance for any mite group, despite slightly higher mean values in the wet season. This suggests limited seasonal turnover, in agreement with reports from temperate regions (Pacek et al., 2020), although local fluctuations may still occur depending on microhabitat conditions (Wehner et al., 2018). While the Andean mountain region typically exhibits pronounced seasonality, particularly in precipitation (Herzog et al., 2011), increased soil moisture did not result in differences in mite communities, contrasting with patterns reported for other soil fauna groups from the same region (Castillo-Figueroa and Castillo-Avila, 2025a; Castillo-Figueroa et al., 2025a; Castillo-Avila and Castillo-Figueroa, 2026). One possible explanation is that the sampling year coincided with an ENSO event characterized by above-average rainfall (IDEAM – Instituto de Hidrología Meteorología y Estudios Ambientales, 2023), meaning mites may not have experienced water limitation even though soil moisture differed significantly between seasons. In fact, volumetric water content remained relatively high even during the driest

period (28 ± 2.85%; Castillo-Figueroa and Castillo-Avila, 2025a), a level unlikely to constrain mites, which are generally sensitive to extreme drought (Xu et al., 2012). In addition, temperature remained stable across seasons, showing no significant variation (Castillo-Figueroa and Castillo-Avila, 2025a). This limited temporal fluctuation likely contributed to the weak seasonal patterns observed, as relatively constant thermal conditions reduce environmental constraints on mite activity and distribution.

4.2 Mites along successional gradients

Successional changes were not reflected in abundance or richness of total Acari or any group, except for Sarcoptiformes. In contrast, species composition differed markedly between mature and secondary forests across all groups except Trombidiformes, partially supporting our second hypothesis (H2). These compositional shifts could be linked to changes in plant community composition between successional stages, as reported in the same plots (Hurtado-M et al., 2021), potentially influencing detrital food webs where mites are embedded.

Mesostigmata, which are primarily predators of micro- and meso-fauna (Walter and Proctor, 2013), may be influenced by shifts in soil fauna composition between mature and secondary forests, as these changes likely alter the pool of available prey. This interpretation is supported by evidence from the same system showing that increased energy inputs associated with forest productivity alter soil fauna composition during succession (Castillo-Avila et al., 2025).

In contrast, Sarcoptiformes may respond more strongly in older forests due to higher litterfall productivity, which enhances microhabitat availability and detrital resources. Supporting this view, studies in Andean tropical montane forests have documented increased litterfall productivity, stem productivity, and net primary productivity with succession (Murcia, 2019; Castillo-Figueroa et al., 2023; Castillo-Figueroa and Posada, 2025a), which may, in turn, influence Sarcoptiformes abundance. These responses may also reflect shifts in microbial communities or the colonization of soil macrofauna (Erdmann et al., 2012). Together, this suggests that Sarcoptiformes may serve as indicators of forest succession due to their dependence on litter-derived resources.

Trombidiformes showed consistently low abundances and no significant changes in richness, abundance, or composition along the successional gradient. This outcome may reflect a combination of factors, including low detectability due to limited sample size, the predominance of generalist trophic strategies among the captured taxa, and methodological constraints in sampling this group. Alternatively, Trombidiformes may be more influenced by factors that do not vary substantially across successional stages in Andean forests, such as litter decomposability (Castillo-Figueroa and Posada, 2025b), or soil fungal communities (Castillo-Figueroa et al., 2026).

4.3 Ecological factors linked to soil mite communities

Supporting our third hypothesis (H3), microclimatic and edaphic factors were the primary drivers of mite community attributes, although responses differed among groups. Total Acari richness was strongly associated with temperature, a well-known regulator of mite diversity (Xu et al., 2012; Wehner et al., 2018; Thakur et al., 2023). In Andean tropical montane ecosystems, where mean air and soil temperatures are low (10.68–11.57 °C) and frost events can occur (Castillo-Figueroa and Castillo-Avila, 2025a), higher minimum temperatures were positively related to soil fauna richness (Castillo-Avila et al., 2025). A similar pattern was observed for total Acari richness, particularly in relation to minimum air and soil temperatures. We also found that soil nutrients, particularly sodium, were associated with richness, likely due to its role as a soil modulator influencing microbial activity and litter decomposition (Morrissey et al., 2014; Canhoto et al., 2017), thereby altering soil organic matter dynamics and the availability of trophic resources for mites.

When analyzed by group, we found differential responses. In Mesostigmata, abundance was primarily associated with soil moisture variability, likely reflecting sensitivity to fluctuations in humidity (Manu et al., 2022), whereas richness was related to minimum surface temperature and soil calcium. This suggests that Mesostigmata are influenced not only by soil moisture but also by temperature, likely through its effects on the availability of micro- and mesofaunal prey, which are themselves temperature-sensitive (Castillo-Avila et al., 2025). Additionally, calcium concentrations in soil and litter can alter soil fauna community composition (Ohta et al., 2014; Mamabolo et al., 2024; Castillo-Avila et al., 2025). The positive association between soil calcium and Mesostigmata richness may therefore be linked to calcium's role as a key element for exoskeleton development, both in mesostigmatid mites and in their microarthropod prey (Mamabolo et al., 2024).

For Sarcoptiformes, abundance was primarily associated with litter depth, and richness with minimum air temperature. This finding aligns with previous studies highlighting the importance of the litter layer in sustaining Sarcoptiformes populations (Erdmann et al., 2012; Marian et al., 2020). Litter depth reflects the accumulation of material on the forest floor, resulting from the balance between litter production and decomposition (Kaspari and Yanoviak, 2008), and was measured in this study as the thickness of the surface litter layer, composed mainly of undecomposed and partially decomposed leaf material. Mature forests typically exhibit

higher litterfall rate with more soil organic layer that increase the microhabitat for detritivore organisms such as sarcoptiform mites (Castillo-Figueroa and Posada, 2025a). Although belowground inputs, including fine roots, may also contribute to soil organic matter dynamics (Soethe et al., 2007; de la Cruz-Amo et al., 2020), the observed relationship between litter depth and Sarcoptiformes abundance is more likely driven by increased habitat complexity and the greater availability of litter-derived organic resources associated with deeper leaf litter. We also found that minimum air temperature was positively associated with Sarcoptiformes richness, whereas no relationship was detected with soil moisture ($p > 0.05$). The effect of minimum temperature is consistent with previous studies showing that higher minimum temperature thresholds may promote more favorable environmental conditions for soil microarthropods in cold environments (Castillo-Figueroa et al., 2024; Castillo-Avila et al., 2025). However, the lack of a relationship with soil moisture contrasts with recent findings from Andean mountains in Ecuador, where oribatid abundance and richness were reported to be more strongly driven by humidity than by temperature (Sánchez-Galindo et al., 2025).

For Trombidiformes, abundance was mainly associated with magnesium, and richness with a combination of clays and slope, suggesting that soil chemistry, texture, and topography all shape their distribution. The association with magnesium may be explained by its role in enhancing microbial productivity (Yang et al., 2021), as microbes represent a key prey base for many trombidiform mites, as well as by its contribution to soil aggregate stability (Lima et al., 2024), which provides more stable microhabitats for mites and their potential prey. Similarly, higher clay content can increase water and nutrient retention and promote microhabitat heterogeneity, while slope influences drainage and organic matter accumulation, jointly shaping habitat conditions for trombidiform richness (Lee et al., 2025; Zheng et al., 2025).

4.4 Association between mites and litter decay

We found only a few positive associations between mites and litter decay rates, and in some cases, they were negative. Overall, these results provide partial support for our fourth hypothesis (H4), indicating that mite–decomposition relationships are generally weak and highly context-dependent. This finding is consistent with previous studies highlighting the limited and substrate-specific role of mites in decomposition (Franklin et al., 2004; Varela et al., 2007; Sánchez-Galindo et al., 2022; Castillo-Figueroa and Castillo-Avila, 2025b). In particular, mesostigmatid mites showed the highest number of associations, mostly positive with litter from acquisitive species characterized by labile compounds and higher nitrogen content (e.g., *Croton bogotanus*, *Piper bogotense*, *Vallea stipularis*, *Daphnopsis caracasana*), based on previously reported trait data from the same system (Castillo-Figueroa et al., 2025b). This pattern likely reflects the role of these predators in decomposition through coupled top-down and bottom-up processes within the soil food web. On the one hand, mesostigmatid mites may control soil fauna that feed on bacteria and fungi, potentially accelerating litter decay. On the other hand, in nitrogen-poor Andean soils (Wilcke et al., 2008), decomposers may preferentially colonize higher-quality litter that decomposes faster, which in turn may also attract their predators, including mesostigmatid mites and other soil mesofauna groups (Bakker et al., 2011; Castillo-Figueroa et al., 2025b).

Sarcoptiform mites were associated with only two conservative species, showing contrasting responses: a positive relationship between abundance and *C. bracteata* and a negative one between richness and *O. calophylla*. The thick leaves and smaller leaf area of *C. bracteata* may create microclimatic refuges favorable to mites, modifying litter structure and enhancing decomposition. By contrast, *O. calophylla*, with thinner leaves and larger leaf area, may host a greater number of soil fauna species, which could accelerate decomposition but also intensify competition and predation, reducing sarcoptiform richness. This aligns with previous experiments showing that physical litter traits strongly influence soil fauna interactions and decomposition rates (Hättenschwiler et al., 2005; Makkonen et al., 2013).

Finally, trombidiform mites showed similar contrasting associations, being positively related to the acquisitive species *P. bogotense* and negatively to the conservative species *P. buxifolia.* In our experiment, *P. bogotense* was the most labile species (Castillo-Figueroa et al., 2025b), with the highest nitrogen content, attracting more decomposers and soil fauna, including trombidiforms, thereby enhancing decomposition. In contrast, for *P. buxifolia*, trombidiforms may prey on primary decomposers that facilitate decay, exerting a top-down effect that indirectly reduces decomposition. Such dynamics illustrate how soil fauna could indirectly regulate litter breakdown in mountain ecosystems, as suggested by other studies (Tan et al., 2021; Castillo-Figueroa, 2024a). Nevertheless, these correlations should be interpreted in light of the spatial scale of our analyses, as mite communities were not measured at the level of individual litterbags and therefore reflect broader microsite-level associations rather than direct interactions with specific litter substrates.

4.5 Limitations of the study

We present contributive and compelling findings on poorly known soil fauna groups within a little-studied ecosystem such as the tropical Andean mountains. Although species

representation was well supported by species accumulation curves for all mites and individual groups (Fig. S1), manual extraction under a stereomicroscope may underestimate abundance due to the lack of specific extraction stimuli (Barberena-Arias et al., 2012; Bruckner, 2024). Nevertheless, hand sorting has been shown to provide reliable species representation and can serve as an alternative sampling method (Castillo-Figueroa and Castillo-Avila, 2025b; Castillo-Avila et al., 2025), while also avoiding damage to soft-bodied mites often caused by Berlese–Tullgren funnels (Dritsoulas and Duncan, 2020). Gentler approaches, such as those developed for eriophyoid mites, enable the collection of live individuals and the preservation of behavioral and physiological traits—advantages often lost with harsher methods like excessive heat or prolonged exposure in Berlese funnels (Monfreda et al., 2007).

Despite these limitations, our approach represents a valuable complement to traditional methods (Barberena-Arias et al., 2012; González et al., 2021; Bruckner, 2024; Castillo-Avila et al., 2025) and is particularly useful for detecting organisms in complex microhabitats such as Andean montane forests (Castillo-Figueroa, 2025). However, manual processing is time-intensive and may limit large-scale applications. Complementary methods such as moisture gradients or flotation could improve recovery (Walter et al., 1987). Therefore, integrating manual and conventional techniques may provide a more comprehensive characterization of mite communities. In addition, linking mite communities directly to individual litter substrates would help refine species-specific interpretations of mite–decomposition relationships.

5 Conclusion

We found that mite communities were concentrated primarily in the litter layer rather than in the soil, and they varied strongly across spatial scales but not across temporal ones. Along succession, total Acari abundance and richness remained stable, whereas community composition shifted markedly between mature and secondary forests. Notably, Sarcoptiformes abundance increased with succession, reflecting its association with litter accumulation in old-growth forests, suggesting its potential as an indicator of forest succession in Andean montane ecosystems.

Overall, mite communities were mainly associated with microclimatic conditions and soil nutrients, underscoring the importance of environmental characteristics in shaping their communities in Andean tropical mountains. Interestingly, responses varied among mite groups, reflecting distinct relationships with soil physicochemical properties, forest structure, temperature and moisture conditions. These patterns suggest that environmental changes driven by human activities may alter mite community structure, with potential implications for soil functioning through their roles as both prey and predators within soil food webs.

Although we detected some associations between mite attributes and litter decay rates, most litter species showed no such link, indicating a generally limited and context-dependent role of mites in decomposition. Nonetheless, both positive and negative relationships suggest that mites may influence decomposition through specific and potentially indirect pathways. Further research on trophic interactions is needed to better understand their role in litter decay dynamics.

Electronic supplementary material

Supplementary material is available in the online version of this article at https://doi.org/10.1007/s42832-026-0489-1 and is accessible for authorized users.

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Author contributions

Castillo-Figueroa Dennis: Writing – original draft, Writing – review & editing, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. Castillo-Avila Camilo: Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Conflicts of interest

The authors declare no conflict of interest.

Data availability

All data associated to this study can be found in the open

science framework repository at the website of osf.io/vwf4c/overview.

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