Drivers of leaf litter decomposition along a successional gradient in the upland Andes: linking environment, functional traits, biodiversity, and carbon cycling

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Chapter 1

General Introduction

General introduction

Carbon cycle and successional forests

Nowadays, climate change is one of the major threats to biodiversity (Cuervo-Robayo et al., 2020; IPCC, 2021; Shivanna et al., 2022). Temperature and rainfall have changed notably over the last 140 years and the frequency of extreme precipitation and drought events has increased in the last few decades (NOAA, 2020; Geng et al., 2023a). Altogether with habitat loss and fragmentation, climate change may cause irreversible impacts on biodiversity, which can alter ecosystem services that constitute the basis of human wellbeing (Sala et al., 2000; Loreau et al., 2001; Beer et al., 2010). The future impacts of climate change on biodiversity and its associated benefits will partly depend on the balance between greenhouse gas emissions released into the atmosphere and the carbon sequestration performed by ecosystems (IPCC, 2021; Castillo-Figueroa, 2021). Therefore, understanding the drivers that control carbon turnover in terrestrial ecosystems is fundamental to forecast the consequences of global environmental changes (Cao & Woodward, 1998; Vivanco & Austin, 2008).

Even though tropical forests only cover 14% of the earth's surface, they play a key role in carbon sequestration as they account for about 25% of the global carbon storage (Bonan et al., 2008) and 33% of the net primary production (Beer et al., 2010). Nonetheless, human-caused environmental changes have fostered the conversion of large extensions of natural forest into agricultural lands for most of the world's tropical biomes (Arroyo-Rodríguez et al., 2017; He et al., 2023). Human disturbance has also driven the expansion of secondary forests, which have been increasing significantly across different tropical regions (Brown & Lugo, 1990; Hansen et al., 2013; Chazdon 2014; Chazdon et al., 2016; 2020; Poorter et al., 2024). This coverage is likely to continue expanding with the rapid formation of human-modified landscapes (Arroyo-Rodríguez et al., 2017; Rubiano et al., 2017; Hurtado-M et al. 2022). However, ecological processes are understudied in secondary forests (Gilroy et al., 2014; Hurtado-M et al., 2022), and many questions about their functionality remain to be answered. Particularly, understanding the role of secondary forests in global biogeochemical processes, such as the carbon cycle, is essential to consider their importance for conservation and restoration plans.

Soils are central to the global carbon cycle, as they store most of the terrestrial carbon (Schmidt et al., 2011). In fact, soil carbon stocks contain two to three times more carbon than the atmosphere, holding approximately 2500 Pg C, according to the Harmonized World Soil Database (FAO, 2012). Consequently, soils play a crucial role in achieving many of the United Nations Sustainable Development Goals (Filser et al., 2016). Therefore, understanding the drivers of soil organic matter dynamics is fundamental to better predict potential shifts in global carbon cycling in future scenarios (Filser et al., 2016). Soils constitute one of the most complex ecological systems, and different aspects of their functioning are still understudied (Geisen et al., 2019). A deeper understanding of how biotic and abiotic components interact will help identify the mechanisms that govern soil carbon dynamics and develop a more comprehensive perspective.

To better understand carbon cycling in soils, it is essential to examine the fluxes of organic material, the decomposition of plant debris, and the amount of carbon that accumulates in soils. Nonetheless, carbon stock estimations in tropical regions have predominantly focused on the aboveground compartment (Figure 1), while soil carbon storage and its fluxes have been less studied due to the need for long-term research that include the measurement of multiple biotic and abiotic factors (Castillo-Figueroa, 2021). This is particularly relevant in ecosystems with low net primary productivity, such as upland ecosystems, where most of the carbon is stored in soils (Moser et al., 2011; Phillips et al., 2019; De la Cruz-Amo et al., 2020).

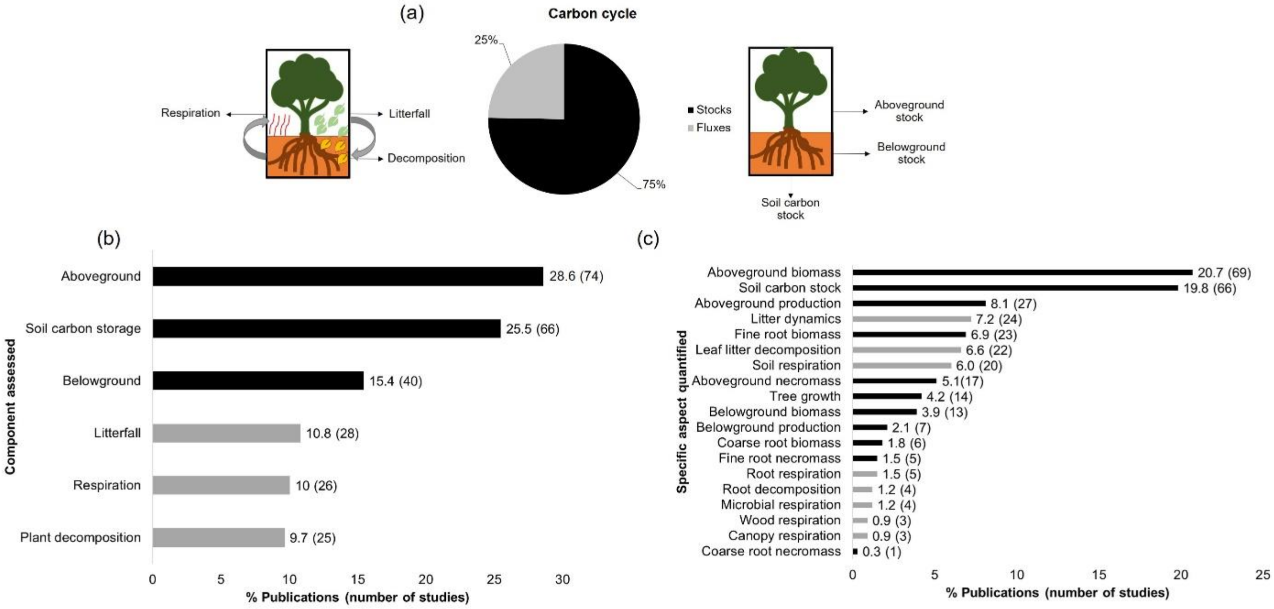

Figure 1. Information on the carbon cycle in tropical upland forests. (a) evaluated aspect of the carbon cycle (b) evaluated component. The colors correspond to the evaluated functions (carbon stocks in black, fluxes in grey). Graph from Castillo-Figueroa (2021).

Litter decomposition and its drivers

Decomposition of plant material represents the major flux of CO_2 to the atmosphere, but also contributes to nutrient mineralization, which is one of the most critical functions in the maintenance of productivity (Díaz et al., 2009; Berg & McClaugherty, 2020). Indeed, litter decomposition is responsible for the emission of about 68 Pg C yr $^{-1}$ which represents 70% of the total annual carbon release from soils (Raich & Schlesinger, 1992; Orgiazzi et al., 2016), and it is a major pathway of nutrient transfer between plants and soil (Cuevas & Lugo, 1998; Giweta, 2020). Studies conducted in temperate ecosystems and lowland tropical forests, have pointed out three specific drivers of decomposition: (1) abiotic conditions, (2) litter quality, and (3) decomposer community (Swift et al. 1979; Powers et al., 2009; Bradford et al., 2016; Berg & McClaugherty, 2020; Giweta, 2020). Nevertheless, these three factors have been commonly analyzed separately and a comprehensive framework, which also incorporates other aspects such as above- and belowground productivity, and successional stage, is generally lacking. Such approach is fundamental to unveil the principal mechanisms of decomposition in transformed ecosystems.

Abiotic conditions and litter quality play a central role in decomposition (Melillo et al., 1989; Coûteaux et al., 1995; Zhang et al., 2008), yet their relative contribution on decay rates is still unclear as their effects depend on decomposition stage, the environmental gradients considered, and species trait variation (Canessa et al., 2021). Although the interaction between abiotic conditions, litter traits, and decomposition has been analyzed across different ecosystems (Aerts, 1997; Cornwell et al., 2008; Makkonen et al., 2012), most of these studies have included a reduced number of species or a set of species with limited trait ranges in the functional space that can underestimate the effect of litter quality on decay rates (Canessa et al., 2021).

Trait-based approaches based on the leaf economics spectrum explain an important part of decomposition as leaf traits relate to litter quality (Wright et al., 2004; Bakker et al., 2011). It has been found, for example, that high concentrations of macronutrients in the leaf tissue such as nitrogen and phosphorus (Bakker et al., 2011; Esquivel et al., 2020), as well as low C:N ratios (Xuluc-Tolosa et al., 2003), correlate with high decomposition rates. Also, leaves with low specific leaf area, high toughness and high leaf density have been related to a slower processing of leaf material by soil fauna and microorganisms (Pérez-Harguindeguy et al., 2000; Bakker et al., 2011). Nonetheless, the fundamental basis that underlies the relationship between the leaf economics spectrum and leaf litter decomposition is far from being fully understood. Although some valuable progress has been made to understand the core anatomical and physiological trade-offs that underly the leaf economics spectrum (Shipley et al., 2006; He et al., 2018; Onoda et al., 2017; Harrison et al., 2021), the role of these key traits (e.g., thickness of epidermis, spongy, and palisade mesophyll) on litter decomposition are just starting to be explored (Pavlović et al., 2020).

In addition, multiple studies have revealed the significant contribution of soil communities to leaf litter decomposition in terrestrial ecosystems (Lavelle, 1996, 1997; García-Palacios et al., 2016a; Tresch et al., 2019). Decomposer communities, including soil fauna and fungi, play a role in carbon storage, fertilization, and plant growth (Brussaard, et al., 1997; Brussard, 1998; Briones, 2014; Li et al., 2022). Yet, the complex relationships between decomposition and soil food webs, as well as the underlying mechanisms, remain unclear, particularly in tropical upland regions such as the Andes mountains of South America, where leaf litter decomposition rates are low (Salinas et al., 2011; Pinos et al., 2017) and soil macrodecomposers tend to decline (Illig et al., 2010). Moreover, understanding these relationships is even more pressing considering that climate change in the tropics is occurring faster at higher elevations (Bradley et al., 2004; Bothwell et al., 2014), and the consequences of these environmental changes on soil communities and decomposition rates are largely unknown.

Tropical montane forests: a general context

Upper Andean Tropical Forests (UATF - 2600-3200 m *sensu* Cuatrecasas, 1989) are part of a global hotspot of biodiversity (Myers et al., 2000; Orme et al., 2005; Myster 2021), characterized by rapid-human transformation (Orme et al., 2005; Etter et al., 2008, 2021), extraordinary local endemism and high beta-diversity (Olson & Dinerstein, 2002; Anthelme et al., 2014; Barczyk et al., 2023). However, despite being one of the most threatened ecosystems in the Neotropics (Etter et al., 2021), our understanding about ecological processes in UATF is very limited. For instance, although recent studies have proposed that UATF are key ecosystems to counteract climate change by serving as global carbon sinks (Salinas et al., 2021; Duque et al., 2021; Vento et al., 2023), these have mostly focused on the aboveground compartment, while belowground fluxes are largely unknown (Malhi et al., 2011). In particular, few studies of leaf litter decomposition have been conducted in UATF (Pinos et al., 2017; Marian et al., 2017; 2018), and a multifaceted framework that analyze critical factors such as successional stage, abiotic conditions, decomposer communities, and functional traits as well as their relations to soil organic matter and ecosystem productivity is still lacking.

In Colombia, one of the most representative regions of UATF is found in the natural areas of the *Sabana de Bogotá* (Figure 2). Within this region, conservation priority ecosystems are found in peri-urban areas of the capital city of Bogotá (Forero-Medina & Joppa, 2010), the largest city of the Andean high tropical montane region (Calbi et al., 2021). Nevertheless, in the last century large-scale deforestation in the Andean region has caused a pervasive habitat transformation, and old-growth forests are now found into isolated forest remnants (Etter et al., 2008, 2021). In the case of Bogotá, natural forests around the capital have lost more than 80% of their natural cover, yet they still show high levels of irreplaceability and vulnerability (Bax & Francesconi, 2019; Hurtado-M et al., 2021; Etter et al., 2021). Furthermore, a gradual increase in natural forest area around Bogotá has been documented in the last decades (Rubiano et al., 2017; Calbi et al., 2020), which provides an opportunity to analyze carbon dynamics and recycling of organic material along regeneration gradients. Moreover, studying successional UATF can offer essential base information for major decision making in restoration and conservation plans for the *Sabana de Bogotá* region, but also elsewhere in Northern upper Andes. Based on this context, this study aims to understand the main biotic and abiotic drivers of leaf litter decomposition and their influence on soil organic matter along a successional gradient in a little studied biome like the tropical mountain Andes.

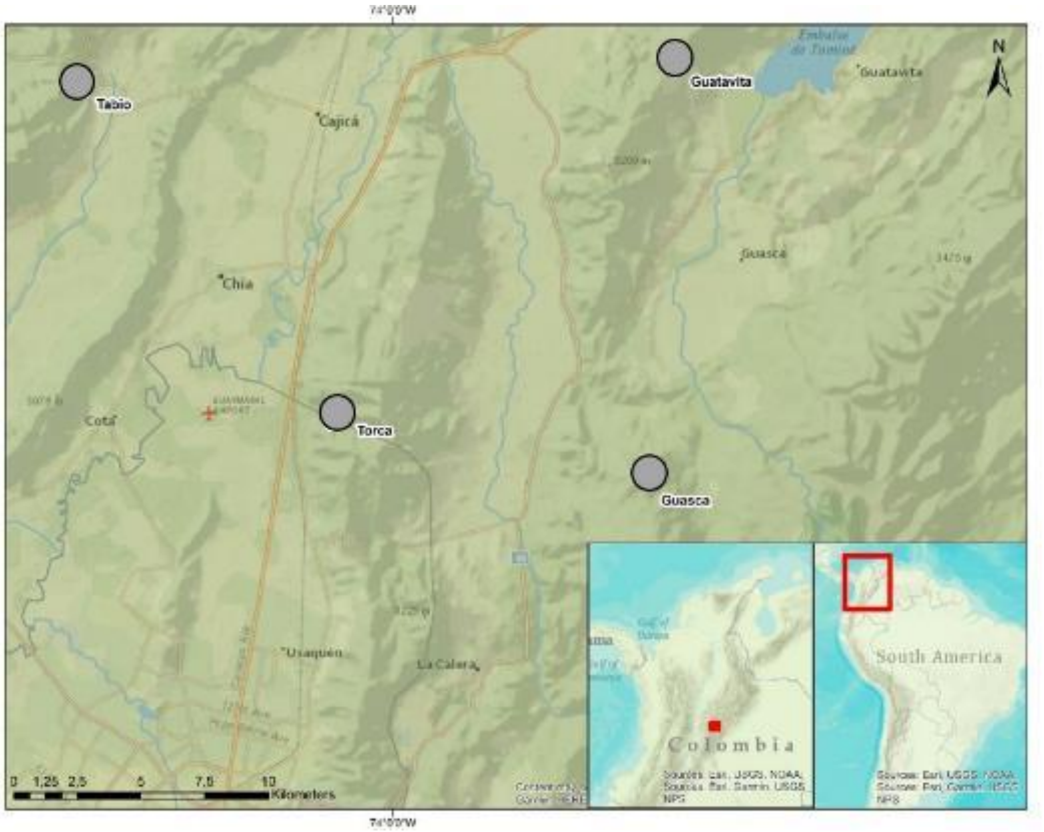

Figure 2. Upper Andean Tropical Forests in northern South America, located in the *Sabana de Bogotá* region of Colombia. The grey circles indicate the sites selected for this study.

General objective of the thesis:

Understand the main biotic and abiotic drivers involved in leaf litter decomposition and determine how decomposition influences the changes in soil organic matter along a successional gradient in UATF (Figure 3).

Specific objectives of the thesis:

Specific objective 1 (Chapter 2): Determine the relative contribution of leaf functional traits and soil microclimatic conditions on leaf litter decomposition along a successional gradient in UATF.

Specific objective 2 (Chapter 3): Establish the relationships between the anatomical leaf traits that are underlying leaf economics spectrum, and decomposition rates along a successional gradient in UATF.

Specific objective 3 (Chapter 4): Analyze the drivers of soil fauna communities along a successional gradient in UATF and their influence on decomposition rates.

Specific objective 4 (Chapter 5): Evaluate the factors shaping soil fungal communities along a successional gradient in UATF and their effect on decomposition rates.

Specific objective 5 (Chapter 6): Examine the changes in soil organic matter along a successional gradient in UATF and determine whether these changes are influenced by carbon inputs (aboveground and fine root productivity) and outputs (decomposition and its drivers).

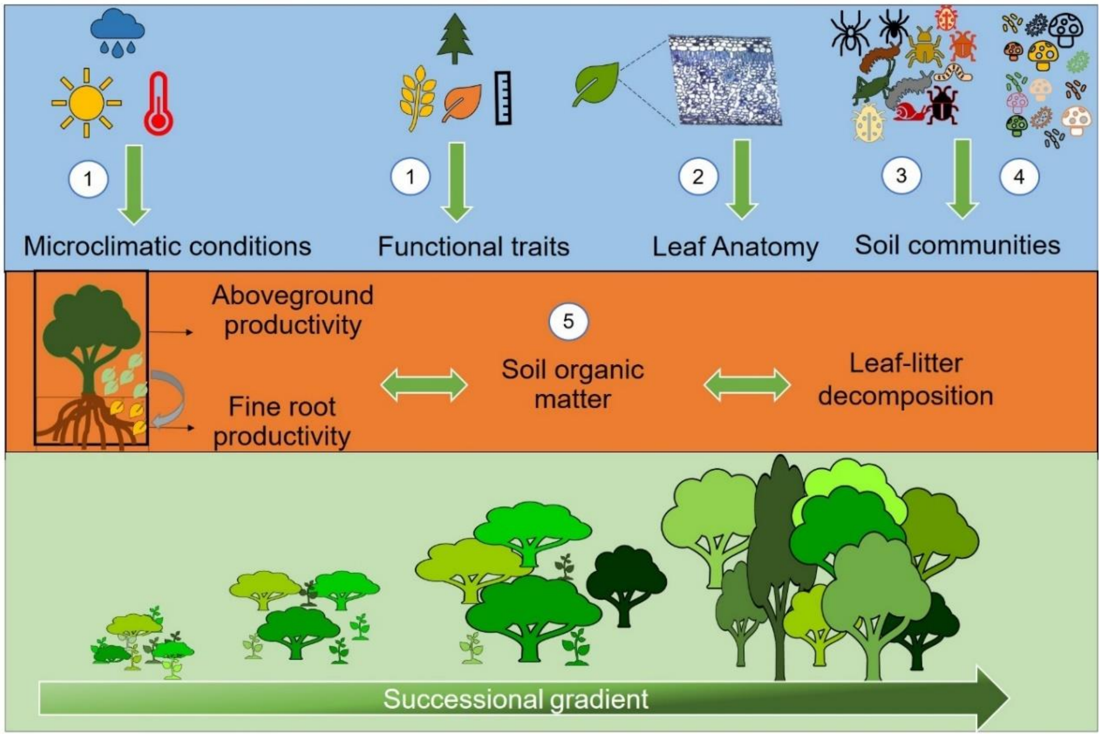

Figure 3. Conceptual framework delineating the principal aim and the four specific objectives of this doctoral project.

Thesis outline:

This doctoral project is organized into seven chapters: a general introduction (Chapter 1), five research chapters (Chapters 2-6), and a general discussion (Chapter 7), which synthesizes how microclimatic conditions, functional traits, leaf anatomy, and soil communities influence litter decomposition and its connections to changes in soil organic matter along a successional gradient in UATF.

Chapter 2 determines the relative contribution of leaf functional traits (8 green traits and 7 litter traits) and soil microclimatic conditions (soil temperature and moisture) on leaf litter decomposition for 15 common Andean species along a successional gradient in UATF. Additionally, this chapter evaluates the differences between traits from green and senescent leaves and their relationships with decomposition.

Chapter 3 establishes relationships between 38 anatomical traits underlying the leaf economics spectrum and decomposition rates along a successional gradient of UATF. First, this chapter analyzes the relationships between leaf anatomical traits and litter decomposability at the species level. Second, the chapter assesses how leaf anatomical traits influence community litter decomposability, using anatomical traits measured in 63 woody species that comprise the entire plant community of the studied plots. Third, it evaluates changes in functional diversity (functional richness and functional evenness) of anatomical traits that best predict decay rates along the successional gradient in UATF.

Chapter 4 analyzes the three classic hypotheses (i.e., energy, habitat heterogeneity, and physiological tolerance hypotheses) that have been proposed to explain the drivers of soil fauna communities (i.e., richness and abundance) along a successional gradient in UATF, as well as their role in decomposition rates. First, this chapter explores soil fauna biodiversity turnover between different UATF sites following a year-long sampling effort that encompasses all four climatic seasons. Second, it analyzes the changes in soil fauna richness, abundance and composition in mature and secondary forests. Third, the chapter identifies the primary microclimatic, forest, and soil conditions that drive changes in soil fauna richness and abundance, utilizing extensive data collected from both above- and belowground compartments in the permanent plots. Fourth, this chapter analyzes the effect of soil fauna richness, abundance, and body size traits on litter decomposition.

Chapter 5 evaluates key soil, forest, and microclimatic factors shaping soil fungal diversity indices ($q = 0$, $q = 1$, $q = 2$) and composition along a successional gradient in UATF, as well as their role in litter decomposition. The chapter begins by characterizing soil fungal diversity across UATF sites using Illumina sequencing. Next, it explores shifts in fungal diversity and composition between mature and secondary forests along the gradient. It then identifies the main environmental drivers for each fungal diversity index. Finally, it evaluates the influence of fungal communities, including all guilds, on litter decomposition.

Chapter 6 examines the changes in soil organic matter along a successional gradient in UATF and determines whether these changes are influenced by inputs (aboveground and fine root productivity) and outputs (decomposition and its drivers). This chapter developed a conceptual framework of the carbon balance in UATF by analyzing how soil organic horizon was related to its main causes and effects on soil physicochemical properties. First, as causes, it considered aboveground productivity, fine root productivity, decomposability (as an indicator of litter quality), and decomposition environment (i.e., standard decomposition). Second, as consequences, it included bulk density, soil carbon and nitrogen concentrations. To achieve this, the conceptual model integrated pre-existing data from the permanent plots and the decomposition experiment of this project.

Chapter 7 presents a general discussion and summary of this thesis, synthesizing the main contributions to the field, along with their implications for conservation and management.

List of abbreviations

%AbCT: Percentage of Abaxial cuticle thickness
%AbET: Percentage of Abaxial epidermis thickness
%AdCT: Percentage of Adaxial cuticle thickness
%AdET: Percentage of Adaxial epidermis thickness
%AdHT: Percentage of Adaxial hypodermis thickness
%AS: Percentage of Air space
%PMT: Percentage of Palisade mesophyll thickness
%SMT: Percentage of Spongy mesophyll thickness
AbCT: Abaxial cuticle thickness
AbEl: Abaxial epidermis cell long
AbET: Abaxial epidermis thickness
AbEw: Abaxial epidermis cell width
AdCT/AbCT: Adaxial cuticle thickness/ Abaxial cuticle thickness
AdCT: Adaxial cuticle thickness
AdEl: Adaxial epidermis cell long
AdET/AbET: Adaxial epidermis thickness/ Abaxial epidermis thickness
AdET/PMT: Adaxial epidermis thickness / Palisade mesophyll thickness
AdET/SMT: Adaxial epidermis thickness/ Spongy mesophyll thickness
AdET: Adaxial epidermis thickness
AdEw: Adaxial epidermis cell width
AdHT: Adaxial hypodermis thickness
AGB: Aboveground biomass
Amax: Photosynthetic capacity
As AbEc: Aspect ratio of Abaxial epidermis cells
As AdEc: Aspect ratio of Adaxial epidermis cells
As PMc: Aspect ratio of Palisade mesophyll cells
As SMc: Aspect ratio of Spongy mesophyll cells
AS: Air space
CWM: Community Weighed Mean
DAH: Diameter Ankle Height
DBH: Diameter Breast Height
K: Decomposition rates
LA: Leaf Area
LACT: Leaf area cell tissue
LCC: Leaf Carbon Content
LDMC: Leaf Dry Matter Content.
LES: Leaf Economic Spectrum
LMA: Leaf Mass per Area
LNC: Leaf Nitrogen Content
LT: Leaf thickness
LTA: Leaf total area
LWR: Leaf Water Retention
Mf: Mass final
Mi: Mass initial
ML: Mass loss
MRA: Multiple Regression Analysis
OTU: Operative Taxonomic Units
PCA: Principal Component Analysis

PMl: Palisade mesophyll cell long
PMT/SMT: Palisade mesophyll thickness/ Spongy mesophyll thickness
PMT: Palisade mesophyll thickness
PMw: Palisade mesophyll cell width
RDA: Redundancy Analysis
RMA: Reduced Major Axis Regressions
SD: Standard deviation
SLA: Specific Leaf Area
SMl: Spongy mesophyll cell long
SMT: Spongy mesophyll thickness
SMw: Spongy mesophyll cell width
SOH: Soil organic horizon
UATF: Upper Andean tropical forests
VBA: Vascular bundle area
VBD: Vascular bundle diameter
VIF: Variation Inflation Factor

Chapter 2

Effects of leaf functional traits, species identity and soil microclimatic conditions on decomposition along a forest successional gradient in the upland Andes.

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Functional traits and species identity drive decomposition across a successional gradient in upper Andean tropical forests

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Abstract

Leaf litter decomposition constitutes one of the most vital processes for maintaining productivity and carbon release in ecosystems. However, this remains one of the least understood processes in upper Andean tropical forests (UATF), a highly diverse ecoregion which has undergone extensive transformation over the centuries. In this study, we aimed to determine the relationships between decomposition rates of leaf litter, leaf functional traits and microclimatic conditions along a successional gradient of UATF. We also tested the "after-life effect" by analyzing changes between green and senescent leaves. We performed a fully reciprocal translocation experiment with 15 representative species of UATF in a set of 14 permanent plots by using 2520 litterbags distributed in 42 experimental units (three litterbeds per plot), for 1.5 years, with four harvesting times (3, 6, 12, 18 months). Chemical and physical traits were measured in green and senescent leaves to identify the best predictors of decomposition and to analyze "after-life effect". We found that functional traits and species identity drive litter decomposition in UATF rather than succession and microclimatic conditions of soil moisture and temperature. The relative importance of traits was prevalent in all stages of decay despite being stronger in the early phases. Although we found an "after-life effect" of green leaves in decomposition, changes in chemical composition from green to senescent leaves indicated substantial nitrogen resorption, which is a limiting resource in tropical montane forests. With the increasing landscape transformation in UATF, changes in plant species composition could have profound impacts by altering decomposition rates, nutrient cycling, and global carbon storage.

Key words: After-life effect, foliar traits, litter decay, reciprocal translocation experiment, tropical montane forests, carbon and nutrient cycling.

Introduction

Terrestrial ecosystems produce roughly 120 billion Mg of organic carbon per year, of which over 90% returns to soils as litter, thus constituting the major source of fresh dead organic matter (Beer et al., 2010; Orgiazzi et al., 2016). Leaf tissues comprise the bulk of that litter material, accounting for an average of ca. 70% of the aboveground litterfall (Zhang et al., 2014). In turn, litter decomposition plays a crucial role in carbon cycling, as the carbon released during this process is 10-fold more than that released by anthropogenic fossil fuel combustion (Prentice et al., 2001; Zhou et al., 2020). Simultaneously, litter decomposition serves as the central pathway for nutrient cycling, acting as the principal flux from the above- to the below-ground compartment, and is also critical in the provision of primary resources for soil food webs (Paudel et al., 2015; Berg & McClaugherty, 2020).

Leaf litter decomposition is a complex process determined by the interplay between litter quality and the community of decomposers, which are influenced by soil characteristics and climatic conditions (Makkonen et al., 2012; Bradford et al., 2016; Berg & McClaugherty, 2020). Over the last few decades, climate and litter quality have long been studied, showing a prime effect of the former at a global scale (Wall et al., 2008; Powers et al., 2009; Ostertag et al., 2022). Yet, the magnitude of the interactions between both factors on leaf litter decomposition can vary along space and time (Aerts, 1997; Melillo et al., 1989; Berg & McClaugherty, 2020; Canessa et al., 2021), and the relative importance of each one is still under debate (Bradford et al., 2016; Joly et al., 2023; Piper et al., 2024). That is especially the case in tropical mountain ecosystems where our understanding of the mechanisms of litter decomposition is still limited (Castillo-Figueroa, 2021).

Climatic conditions, such as temperature and soil moisture, are key for determining litter decomposition (Zhang et al., 2008; Berg & McClaugherty, 2020; Giweta, 2020). Low temperatures reduce enzymatic activity in decomposers, leading to decreased decay rates, particularly in mountain forests (Salinas et al., 2011; Marian et al., 2017; Esquivel et al., 2020). Soil moisture is another limiting factor affecting decomposition, as higher availability can exert a major positive effect on soil microbial biomass (Bradford et al., 2017). However, excessive soil water content can slow down decomposition by reducing in soil oxygen availability for decomposers (Schuur et al., 2001). The effect of climate on decomposition can also interact with litter quality and some studies have found that climatic conditions are more important at later stages of decay, when species converged in their litter quality (Preston et al., 2009; Parsons et al., 2014; Canessa et al., 2021). In contrast, other studies have shown that litter quality is a better predictor of decomposition over time than climate (Trofymow et al., 2002). These contradicting results suggest that the drivers of litter decomposition along time are highly context-dependent and may vary across ecosystems (Bradford et al., 2016) and among individual species' litter characteristics (Canessa et al., 2021).

Litter quality varies considerably between plant species (Pérez-Harguindeguy et al., 2000; Bakker et al., 2011; Poca et al., 2014), and numerous studies indicate that quality plays a central role in decomposition (Zhang et al., 2008; Cornwell et al., 2008; Makkonen et al., 2012; Zhou et al., 2020; Esquivel et al., 2020; Rosenfield et al., 2020). For example, leaf traits such as C:N ratio, total nutrient content, major cation concentrations, phenol concentration (Pérez-Harguindeguy et al., 2000; Coûteaux et al., 1995; Zhang et al., 2008; Ristok et al., 2019; Canessa et al., 2021), leaf thickness, and leaf dry matter content, are strong predictors of litter decomposition (Pérez-Harguindeguy et al., 2000; Ristok et al., 2019; Esquivel et al., 2020). Nevertheless, one limitation in our understanding of the role of litter quality is that different species, which encompass a broad variation of functional traits (Pérez-Harguindeguy et al., 2000; Canessa et al., 2021), are not always included. Only considering a few dominant species could lead to an underestimation of the functional contribution of other species to decomposition at the ecosystem scale, except in cases of monodominant forests (e.g. oaks forests, pine plantations). Moreover, these traits are usually measured on green leaves, assuming an “after-life effect” of green leaves on decomposition (Santiago, 2007; Bakker et al., 2011). Yet, green leaf traits may not fully capture the effect of trait variation on decomposition because their chemical and physical characteristics change with senescence, and shed leaves are the ones that really decompose (Zukswert & Prescott, 2017; Guo et al., 2025). Overall, few studies have analyzed these changes between green and senescent traits and their implications for decomposition.

Andean tropical mountain forests are a global hotspot of biodiversity, hosting approximately 10% of global vascular plant diversity and exhibiting the highest rates of endemism on the planet (Myers et al., 2000; Myster, 2021). They also play a significant role in global carbon cycling (Duque et al., 2021; Vento et al., 2023); nevertheless, our understanding of major carbon fluxes in these forests remains limited (Castillo-Figueroa, 2021). These mountain ecosystems are characterized by a thick organic layer (Wilcke, 2021), low soil nitrogen concentrations (Vitousek et al., 1988; Tanner et al., 1998; Wilcke et al., 2008), and slow organic matter decomposition rates (Salinas et al., 2011; Butenschoen et al., 2014; Marian et al., 2017). Nonetheless, Upper Andean Tropical Forests (henceforth UATF) in Northern South America, situated at elevations of 2600-3200 m, have undergone extensive centuries of landscape transformations since Spanish colonization (Etter & Wyngaarden, 2000; Etter et al., 2008; Etter et al., 2021), potentially affecting carbon release (Salinas et al., 2021; Vento et al., 2023). Notably, Bogotá, the capital of Colombia, located at an elevation of ca. 2600 m, is the largest city within the upper Andean tropical forest belt, with a metropolitan population over 11 million people (World Population Review, 2024). This large human presence has caused significant land-cover changes, including a mosaic of forests with diverse successional pathways, encompassing small and isolated old-growth forest fragments as well as early-secondary forests (Rubiano et al., 2017; Calbi et al., 2020, 2021; Hurtado-M. et al., 2021).

Natural ecological forest succession generally follows a gradient from high light and nutrient availability to lower resources states with reduced light and nutrients (Chua & Potts, 2018; Poorter et al., 2021a, 2023). Accordingly, acquisitive pioneer species, known for their fast-grow and rapid assimilation of resources, are common in early stages, but are then replaced by slow-growing and resource-conserving species later in succession (Odum, 1969; Bazzaz & Pickett, 1980; Garnier et al., 2004; Poorter et al., 2021a, 2023). Furthermore, the influence of environmental conditions can be more pronounced in early succession, when forest cover is low and cannot effectively moderate microclimatic conditions (e.g., high radiation and temperature) (Paudel et al., 2015). In contrast, later in succession, high canopy cover can increase soil humidity and decrease temperature (Paudel et al., 2015). These microclimatic changes can also influence soils conditions, resulting in changes in decomposer communities that can, in turn, affect litter decomposition (Seidelmann et al., 2016). However, only a limited number of studies have analyzed successional patterns in UATF (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023; Castillo-Figueroa, 2024a), where additional environmental filters, such as temperature variability and soil moisture, may exert different effects on succession and ecosystem processes.

Here, we assess the relative contribution of leaf functional traits and microclimatic conditions to leaf litter decomposition along a successional gradient in UATF through a fully reciprocal translocation experiment involving 2520 litterbags. We also analyze differences between traits from green and senescent leaves and their relationships with decomposition. We hypothesized that decomposition will be largely determined by differences in litter quality between species (H1); decomposition will be lower in mature than in secondary forests due to higher soil water content and lower temperatures in the former (H2); functional traits will predominantly determine decomposition in the early stages of decay, but as litter species converge in quality during later stages, microclimatic conditions will exert greater control over decomposition (H3); and leaf functional traits will be different in green and senescent leaves, particularly concerning leaf nitrogen, which is expected to be resorbed before being shed (H4).

Materials and methods

Study area

We conducted our study in the Eastern Colombian Andes along a successional gradient of UATF in the *Sabana de Bogotá* region. The Andean region covers 24.5% of the Colombian territory (Etter & Wyngaarden, 2000) and is catalogued as the economic center of country, with the highest population concentration (>70% of the total) (DANE, 2012). Within this region, dominant landscape transformations include agriculture, cattle pastures, urbanization, and mining (Montañez et al., 1994; Antonio-Fragala & Obregón-Neira, 2011; Etter et al., 2021). Around the capital city of Bogotá, average annual atmospheric temperature is 14ºC, and mean annual precipitation ranges from 600 mm in the center valleys to 1200 mm in the western part (Clerici et al., 2016). The study area experiences a bimodal precipitation regime with two rainy periods occurring from April to June and from October to December, and two dry seasons from January to March and July to September (IDEAM, 2024).

In this region, we studied 14 20x20 m pre-established permanent plots in both secondary (7 plots) and mature UATF (7 plots) across four study sites: Torca (three from mature forest and one from secondary forest), Tabio (two per successional stage), Guasca (two per successional stage), and Guatavita (two from secondary forest). These are part of a larger network consisting of 36 20x20 m and eight 50x50 m plots, established to monitor carbon cycling and biodiversity over the long term (Hurtado-Martilleti et al., 2021; Castillo-Figueroa et al., 2023, 2024). Torca is located in the Eastern hills of Bogotá and the other three sites are peri-urban municipalities in the countryside around Bogotá (Figure 1). We categorized forests as secondary or mature based on key structural attributes that vary with succession, such as aboveground biomass, tree height, tree density, and species composition (Poorter et al., 2021b, 2023), as outlined in previous studies (Hurtado-Martilleti et al., 2021; Castillo-Figueroa et al., 2023). More information about elevation, soil microclimate, common plants, and soil texture for all sites can be found in Figure 1.

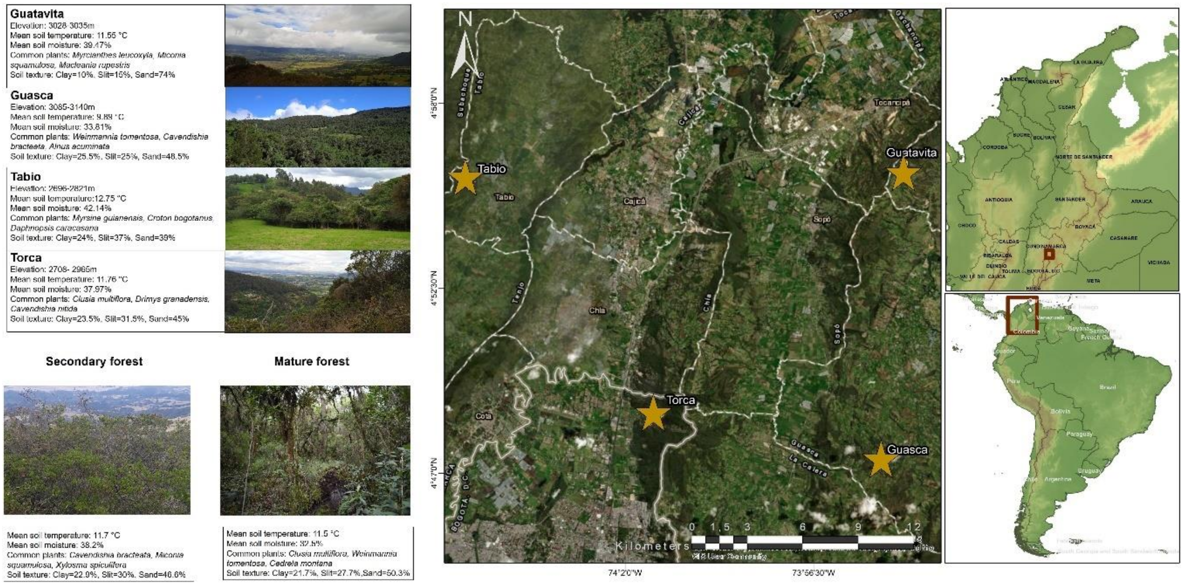

Figure 1. Experimental locations in Colombian Andes. Golden stars represent each of the four sites. Information on elevation, microclimatic data collected during the experiment, common plants, and soil texture is provided for each site and successional stage in the left panel. Mean soil temperature represents the average temperature at 0-8 cm depth, and mean soil moisture at 0-15 cm depth, both measured at 14 permanent plots (TMS4 loggers—TOMST).

Collection of litter material

We selected 15 plant species from the 14 permanent plots. The selection criteria was based on two main factors: (1) the dominance of the species considering that the most abundant ones will largely contribute to litter on the forest floor (Salinas et al., 2011; Esquivel et al., 2020); and (2) species representation in the functional trait space in the plots (Canessa et al., 2021) based on previous ordination analyses of litter traits (Figure S1). The selected species belonged to 15 families and 12 orders (Table S1).

We collected freshly fallen senescent leaves of the 15 species from the forest floor directly within and around the plots. We discarded young leaves that were bright green or red and with a soft lamina, but also leaves that were too old and with large necrotic area

(Cárdenas et al., 2017; Four et al., 2019). Leaves showing signs of pathogen infection, fungal damage, insect galls, or herbivory exceeding 30% were also excluded (visually estimated in the field) (Cárdenas et al., 2017; Four et al., 2019).

Litter decomposition experiment

Translocation field experiments with multiple species are a reliable method to understand the factors affecting decomposition rates (Powers et al., 2009; Esquivel et al., 2020; Ostertag et al., 2022). Thus, in this study, we set-up a reciprocal translocation decomposition experiment in the 14 permanent plots following methodological recommendations for the experimental design, storing, processing, and measuring (Bakker et al., 2011; Pérez-Harguindeguy et al., 2013; Berg & McClaugherty, 2020). For this purpose, we established three independent litterbeds per plot for a total of 42 litterbeds, which were installed in October 2021. These experimental units measured 1.70x1.70 m and were placed directly on the forest floor, trying to minimize disturbance to the soil and with a minimal distance of 5 m between them. Thus, we tried to capture the microenvironmental heterogeneity within each plot and ensure independence by spacing the experimental units adequately. During placement, we avoided forest gaps, topographic depressions, and highly irregular soil conditions. Each litterbed consisted of 60 litterbags, with four bags containing the same species arranged in a clockwise manner to account for consecutive harvesting times (3, 6, 12, 18 months). Final litterbag collection was made in April 2023. The distance between bags of different species (15 taxa) was 10 cm. Litterbags were made of a fiber glass flexible net (10x15 cm) with a mesh size of 2 mm that contained ca. 2 g of litter. For each of the four harvesting times, we collected one litterbag per species from each litterbed. In the lab, the content of the litterbags was sorted to separate litter from fine roots, forbs, mushrooms, mineral soil particles, and soil fauna. Litter material was gently cleaned with a brush to remove mineral soil particles. All remaining contents of the litterbags were discarded, except for the soil fauna, which were collected and preserved in 70% ethanol (Castillo-Figueroa et al., unpublished work).

The total number of litterbags was 2520, distributed in: 2 forest types x 7 permanent plots in each forest type x 3 decomposition beds in each plot x 15 litter types in each decomposition bed x 4 harvesting times. Thus, the experimental design included four factors: forest type (mature vs secondary), plant species (15 taxa), time (3, 6, 12, 18 months), and sites (Torca, Guatavita, Guasca, Tabio). Litter material was oven-dried at 60ºC for three days (72h) and weighted using a 0.0001 g precision scale (LX 220A scs) to determine both initial and final weights.

Functional traits

Green leaf traits were measured in three individuals per species for all the 15 studied species as part of another project of plant functional trait ecology (Posada et al., in preparation). All leaves were sun-exposed and collected with a branch pruner from the canopy in the studied plots. Here, we additionally measured traits from senescent leaves in five individuals per species for the 15 species selected in the decomposition experiment, following Bakker et al. (2011) and Pérez-Harguindeguy et al. (2013). The traits measured in green leaves were: photosynthetic capacity (Amax, nmol/g/s) using an infrared gas analyzer (LiCor, LI-6400XT); leaf thickness (LT, mm) measured with a micrometer, avoiding main veins; one-sided leaf area (LA, cm^2) measured with a scanner and analyzing the resulting pictures with ImageJ (Schneider et al., 2012, https://imagej.nih.gov/ij/); leaf fresh mass (g), measured after rehydrating terminal branches with their leaves attached at low temperature (4ºC) in the dark, following the method proposed by Garnier et al. (2001); leaf dry weight obtained after drying leaves in the oven at 60ºC for 72h. From these traits we calculated specific leaf area (SLA, cm^2/g) and its reciprocal leaf mass per area (LMA, g/m^2), leaf dry matter content (LDMC, mg/g), leaf water retention (LWR, %), and leaf density (LD, mg/mm^3). Chemical traits were leaf nitrogen content (LNC, mg/g) and leaf carbon content (LCC, mg/g) measured with an elemental gas analyzer (FlashSmart™ Thermo Fisher Scientific, USA). All the traits, except Amax, were also measured in senescent leaves.

Measurement of environmental variables

TMS-4 soil probes equipped with dataloggers (TOMST, Czech Republic) were installed in the center of each of the 14 plots to record temperature and volumetric soil water content every 15 minutes. This device bears temperature sensors at 15 cm above the soil surface, at the soil surface, and at 8 cm depth in the soil. Volumetric soil water content was registered at 15 cm depth (Wild et al., 2019). With these data we calculated mean soil temperature, mean surface temperature, mean atmospheric temperature, and mean volumetric soil water content for each stage of decay (0–3, 0–6, 0–12, and 0–18 months, from October 2021 to April 2023).

Data analysis

- Effect of litter identity and succession:

We determined the mass loss for each species during the incubation period as the percentage of initial dry mass loss at each of the harvesting times. That is, for each litterbag we calculated the percentage of biomass loss according to the following equation:

$$ML = \frac{(\mathrm{Mi}-\mathrm{Mf})}{\mathrm{Mi}} \mathrm{x}100$$

Where ML corresponds to the mass loss, Mi is the initial dry weight of the sample, and Mf is its final dry weight (Njoroge et al., 2023). To standardize mass loss for different sites we used relative mass loss (observed ML divided by mean ML of the 15 litter species in a given site) (Makkonen et al., 2012). We used a two-way ANOVA tests to evaluate whether decomposition rates based on both absolute and relative mass loss varied between species and successional stages, as well as their interaction (H1-H2). Effect size for each model was calculated through Eta-squared values (η^2). We also contrasted the effect of succession on decomposition for each species separately at every stage of decay through t-test (H2). In doing so, 95% confidence intervals for Cohen's d effect sizes were estimated.

Prior to doing multivariate analyses, we did Spearman correlation matrices between traits, decomposition and microclimatic variables (Figure S2). We excluded high correlated traits for principal component analyses (PCAs). To prevent multicollinearity between variables in the multiple regression analysis (MRA), we assessed the variance inflation factor (VIF) for each variable. We included in the model the variables with VIF values below 3.0, confirming the absence of collinearity among our variables (Chatterjee & Simonoff, 2013). To analyze how green and senescent traits of species were associated to decomposition we did two PCAs: one with eight traits for green leaves and another with seven traits for senescent leaves (H1). Species were used as data points (n = 15), and mass loss over 12 months was used as a standard measurement for decomposition. Data points and eigenvectors were scaled to the square roots of the corresponding eigenvalues to produce the correlation biplot (Legendre & Legendre, 1998).

- Effect of microclimatic variables and leaf traits over time

To test how microclimatic variables and leaf traits influenced mass loss and how their interaction changed with phases of decay and succession in UATF, we employed a MRA to explain mass loss for each decomposition stage separately (H3). In these models, we included green and senescent traits and microclimatic conditions to assess the individual effect of each independent variable on decomposition at each stage of decay (H4). Forest aboveground biomass and forest canopy height were also included in the models as independent variables, representing proxies for succession (Garnier et al., 2004; Poorter et al., 2021b; Castillo-Figueroa et al., 2023; Poorter et al., 2023). We employed a partition variance analysis and Venn diagrams to represent variation explained by functional traits and microclimate.

- Changes in green and senescent traits

Finally, to analyze changes between traits from green leaves and senescent leaves (H4), we utilized reduced major axis regressions (RMA, Pearson, 1901). Unlike ordinary least squares regression, this analysis can handle errors in both the x (senescent trait) and y (green leaf trait) axes (Warton et al., 2012). The RMA parameters were used to determine if the trait relationship varied between green and senesced leaves. When slopes were not different than 1.0, it signified that there was no change between green and senescent leaves for that particular trait. To do this, 95% bootstrapped confidence intervals of the slopes were calculated (n = 1999). Thus, if the confidence intervals of slopes were greater than 1, it indicated that green leaves exhibited higher values than senescent leaves. Conversely, if the confidence intervals of slopes were less than 1, it indicated that senescent leaves exhibited higher values than green leaves. All the analyses were conducted in PAST 4.14 (Hammer et al., 2001), JASP 0.14.1.0 (JASP Team, 2023), and JAMOVI 2.5 (Jamovi project, 2024).

Results

Decomposition rates in Andean montane forests

We found significant differences in mean litter decomposition rates between species at each of the stages of decay (Table 1). Across all sites, variation among the 15 species was also notably high and increased over time, from an average standard deviation (SD) of ± 14.09 at 3 months to ± 20.69 at 18 months (Table S2). Over the course of a year, the species with the highest mean mass loss were *Vallea stiupularis* (71%), *Piper bogotense* (68%), *Croton bogotanus* (61%), and *Daphnospsis caracasana* (49%), while the species with lowest mean decomposition were *Myrsine coryacea* (13%), *Cavendishia bracteata* (14%), *Prunus buxifolia* (17%), and *Drymis granadensis* (18%) (Figure 2; Table S2). Overall, this pattern remained similar in every stage of decay, and only small changes in the ranking of species by decomposition were observed within sites (Figure S3). After 18 months, Tabio exhibited the highest mean values of decomposition (45%), contrary to Guatavita that showed the lowest ones (37%), but no differences in the relative decomposition among sites were detected among sites overall (Figure 2, Figure S3, Table S3).

Table 1. Two-way ANOVA showing comparisons of absolute and relative decay rates among litter species and successional status as fixed factors and their interactions for each of the decomposition periods. Degrees of freedom (d.f.), F statistic (F), Type III sum of squares (SS), Mean squares (MS), Statistical significance (P), Eta-squared (η²). Numbers in bold represent significant differences.

Mass loss	**Factor**	**Time**	**d.f.**	**SS**	**MS**	**F**	**P**	**η²**
Absolute decay	Litter species	3 months	14	126595.972	9042.569	535.817	**< .001**	0.922
		6 months	14	165200.728	11800.052	539.648	**< .001**	0.924
		12 months	14	126.708	9.051	346.038	**< .001**	0.887
		18 months	14	247527.122	17680.509	232.972	**< .001**	0.836
	Succession	3 months	1	291.484	291.484	17.272	**< .001**	0.002
		6 months	1	87.739	87.739	4.013	**0.046**	4.908×10^{-4}
		12 months	1	0.145	0.145	5.526	**0.019**	0.001
		18 months	1	1770.766	1770.766	23.333	**< .001**	0.006
	Litter species x succession	3 months	14	271.810	19.415	1.150	0.310	0.002
		6 months	14	345.546	24.682	1.129	0.329	0.002
		12 months	14	0.239	0.017	0.652	0.821	0.002
		18 months	14	1287.456	91.961	1.212	0.262	0.004
	Residuals	3 months	600	10125.728	16.876			
		6 months	600	13119.728	21.866			
		12 months	600	15.693	0.026			
		18 months	600	1287.456	91.961			
Relative decay	Litter species	3 months	14	389.266	27.805	618.624	**< .001**	0.934
		6 months	14	290.454	20.747	573.455	**< .001**	0.929
		12 months	14	214.332	15.309	379.487	**< .001**	0.896
		18 months	14	163.057	11.647	267.616	**< .001**	0.856
	Succession	3 months	1	0.041	0.041	0.903	0.342	9.740×10^{-5}
		6 months	1	0.023	0.023	0.623	0.430	7.203×10^{-5}

	12 months	1	0.273	0.273	6.777	**0.009**	0.001
	18 months	1	0.650	0.650	14.927	**< .001**	0.003
Litter species x succession	3 months	14	0.573	0.041	0.910	0.547	0.001
	6 months	14	0.614	0.044	1.213	0.261	0.002
	12 months	14	0.413	0.030	0.732	0.743	0.002
	18 months	14	0.723	0.052	1.186	0.281	0.004
Residuals	3 months	600	26.968	0.045			
	6 months	600	21.707	0.036			
	12 months	600	24.205	0.040			
	18 months	600	26.113	0.044			

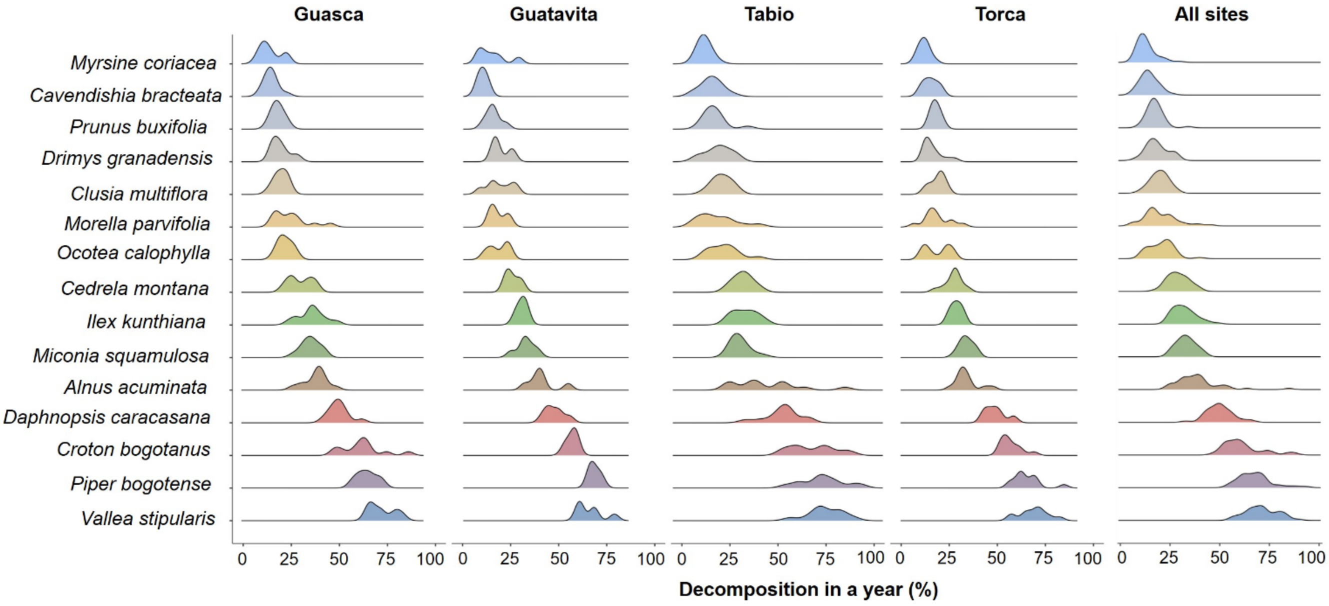

Figure 2. Density plots of decomposition in 15 common native Andean species in four different sites showing that species identity drives litter decomposition no matter the site.

Decomposition and successional stage

We detected a modest effect of forest successional status on litter decomposition (Table 1), with higher decay rates in mature than secondary forests for six out of the 15 individual species at different decomposition periods: *C. bracteada* (3 months, t = 2.24; P = 0.030, Cohen´s d = 0.69), *C. montana* (3 months, t = 2.51, P = 0.01, Cohen´s d = 0.33, 6 months, t = 3.06; P = 0.004, Cohen´s d = 0.94, 12 months, t = 2.56, P = 0.01, Cohen´s d= 0.79), *M. parvifolia* (3 months, t = 2.33, P = 0.02, Cohen´s d = 0.32, 18 months, t = 2.46; P = 0.018, Cohen´s d = 0.76), *P. bogotensis* (18 months, t = 2.29, P = 0.027, Cohen´s d = 0.71) and *A. acuminata* (3 months, t = 2.13, P = 0.039, Cohen´s d = 0.65) and *C. bogotanus* (18 months, t = 2.79, P = 0.008, Cohen´s d = 0.862) (Table S4, Figure 3). When decomposition was analyzed at site scale, only Tabio presented a higher mean in mature than in secondary forests at 18 months (t = 3.17, P = 0.002, Cohen´s d = 0.47), while no significant differences were found between successional stages for Torca or Guasca in any decomposition period (P > 0.05). Overall, succession was a weak predictor of decomposition, and it only had a small effect at later stages of decay (Table 2).

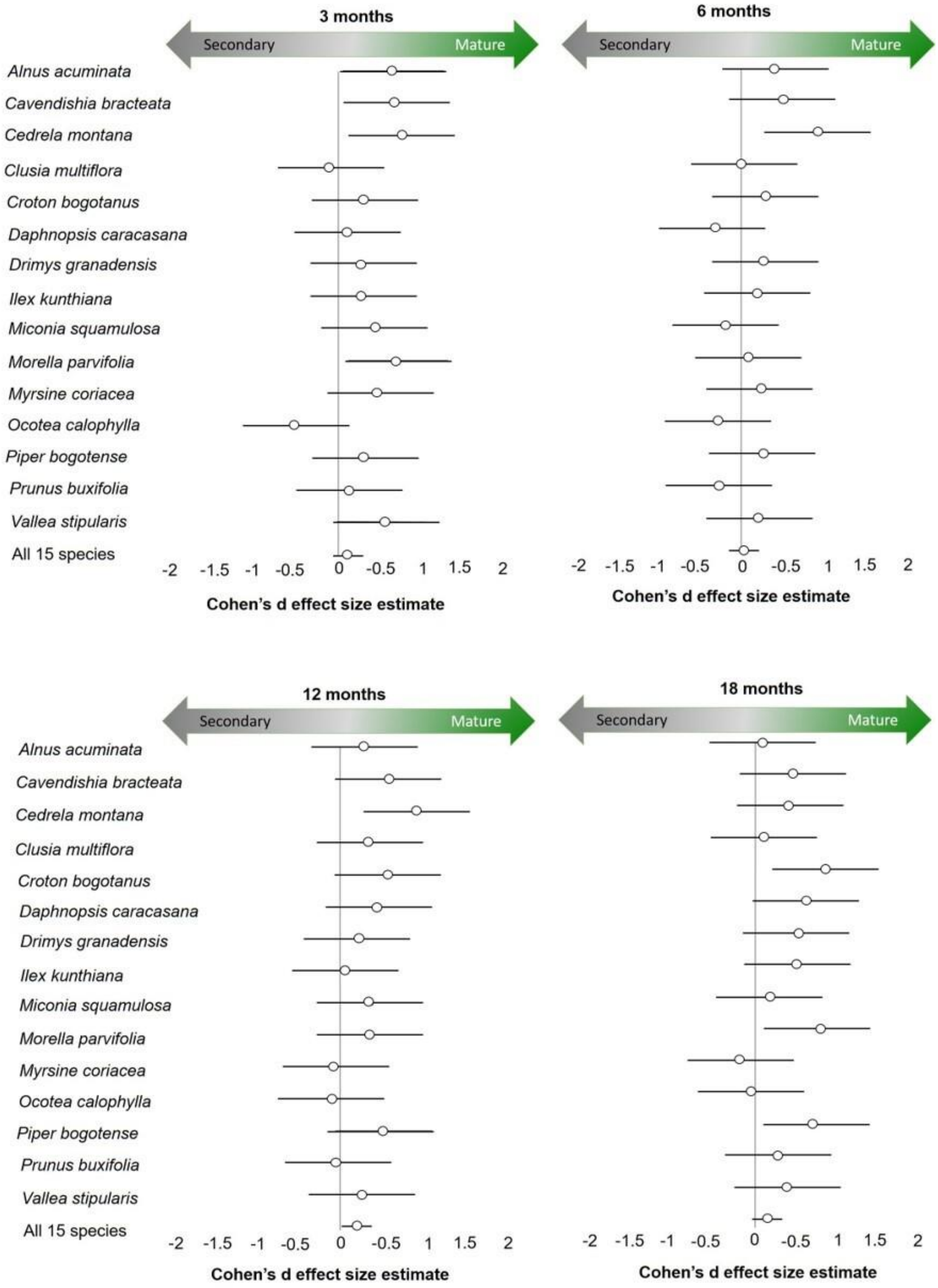

Figure 3. Effect of succession on decomposition in all the 15 common native Andean species at 3, 6, 12, and 18 months of decomposition. Each plot shows the 95% confidence intervals for Cohen's d effect size in the t-student tests comparing secondary forests vs mature forests. Values on the center line indicates no differences between successional stages. Positive values indicate greater decomposition rates in mature forests, while negative values denote higher decomposition rates in secondary forests.

Table 2. Multiple regression analysis showing the coefficient of each trait at each stage of decay. Asterisks indicate statistical significance of each variable in the model at P < 0.001 (***), P < 0.01 (**) and P < 0.05 (*). VIF represents the Variance Inflation Factor, RMSE is the Root Mean Square Error, and R^2 is the Adjusted R^2 for each model.

Time	**Green traits**	**Standardized**	**Standard error**	**t**	**VIF**	**Senescent traits**	**Standardized**	**Standard error**	**t**	**VIF**
3 months	Green SLA (cm^2/g)***	0.256	0.023	4.729	2.506	Litter SLA (cm^2/g)***	0.782	0.016	14.480	2.657
	Green C (mg/g)***	-0.387	0.014	-8.817	1.645	Litter C (mg/g)***	-0.237	0.008	-6.559	1.193
	Green N (mg/g)***	0.274	0.072	6.401	1.561	Litter N (mg/g)***	0.162	0.158	3.895	1.581
	Green thickness (mm)***	-0.220	2.801	-5.514	1.354	Litter thickness (mm)***	0.216	3.807	4.664	1.949
	T soil	0.040	0.512	0.966	1.483	T soil	0.040	0.495	0.999	1.483
	Soil moisture	0.042	9.232	0.912	1.815	Soil moisture	0.042	8.926	0.944	1.815
	AGB (Mg C ha)	0.007	0.027	0.114	2.825	AGB (Mg C ha)	0.007	0.026	0.118	2.825
	Canopy height (m)	0.092	0.467	1.638	2.663	Canopy height (m)	0.092	0.451	1.694	2.663
	Model summary	**R^2 = 75.5**	**RMSE = 7.194**	**P < 0.001**		**Model summary**	**R^2 = 77.1**	**RMSE = 6.956**	**P < 0.001**	
6 months	Green SLA (cm^2/g)***	0.240	0.028	4.182	2.506	Litter SLA (cm^2/g)***	0.727	0.018	13.410	2.657
	Green C (mg/g)***	-0.397	0.017	-8.534	1.645	Litter C (mg/g)***	-0.283	0.009	-7.794	1.193
	Green N (mg/g)***	-0.281	0.087	-6.203	1.561	Litter N (mg/g)***	0.189	0.180	4.530	1.581
	Green thickness (mm)***	-0.202	3.379	-4.788	1.354	Litter thickness (mm)***	0.201	4.359	4.328	1.949
	T soil	-0.020	0.627	-0.441	1.577	T soil	-0.020	0.575	-0.480	1.577
	Soil moisture	0.032	11.455	0.659	1.749	Soil moisture	0.032	10.511	0.718	1.749
	AGB (Mg C ha)	-0.024	0.032	-0.400	2.741	AGB (Mg C ha)	-0.024	0.029	-0.435	2.741
	Canopy height (m)	0.083	0.561	1.404	2.645	Canopy height (m)	0.083	0.515	1.530	2.645
	Model summary	**R^2 = 72.6**	**RMSE = 8.679**	**P < 0.001**		**Model summary**	**R^2 = 76.9**	**RMSE = 7.964**	**P < 0.001**	
12 months	Green SLA (cm^2/g)***	0.265	0.036	4.328	2.506	Litter SLA (cm^2/g)***	0.684	0.022	12.362	2.657
	Green C (mg/g)***	-0.357	0.021	-7.186	1.645	Litter C (mg/g)***	-0.297	0.011	-8.007	1.193
	Green N (mg/g)***	0.283	0.111	5.862	1.561	Litter N (mg/g)***	0.214	0.220	5.012	1.581

	Green thickness (mm)***	-0.177	4.321	-3.925	1.354	Litter thickness (mm)***	0.187	5.326	3.946	1.949
	T soil	-0.057	0.810	-1.219	1.483	T soil	-0.057	0.710	-1.390	1.483
	Soil moisture	0.051	14.652	0.974	1.808	Soil moisture	0.051	12.846	1.111	1.808
	AGB (Mg C ha)	-0.055	0.041	-0.856	2.802	AGB (Mg C ha)	-0.055	0.036	-0.976	2.802
	Canopy height (m)	0.114	0.714	1.821	2.617	Canopy height (m)*	0.114	0.626	2.077	2.617
	Model summary	**R^2 = 68.7**	**RMSE = 11.09**	**P < 0.001**		**Model summary**	**R^2 = 75.9**	**RMSE = 9.730**	**P < 0.001**	
18 months	Green SLA (cm^2/g)***	0.241	0.039	3.759	2.506	Litter SLA (cm^2/g)***	0.652	0.024	11.708	2.657
	Green C (mg/g)***	-0.340	0.024	-6.551	1.645	Litter C (mg/g)***	-0.304	0.011	-8.137	1.193
	Green N (mg/g)***	0.306	0.122	6.059	1.561	Litter N (mg/g)***	0.234	0.235	5.459	1.581
	Green thickness (mm)***	-0.154	4.772	-3.265	1.354	Litter thickness (mm)***	0.206	5.671	4.324	1.949
	T soil	-0.006	0.876	-0.133	1.450	T soil	-0.007	0.741	-0.165	1.450
	Soil moisture	0.034	15.324	0.616	1.819	Soil moisture	0.033	12.951	0.718	1.819
	AGB (Mg C ha)*	-0.152	0.045	-2.273	2.736	AGB (Mg C ha) **	-0.152	0.038	-2.695	2.736
	Canopy height (m)***	0.268	0.813	3.974	2.781	Canopy height (m)***	0.268	0.687	4.703	2.781
	Model summary	**R^2 = 65.9**	**RMSE = 12.257**	**P < 0.001**		**Model summary**	**R^2 = 75.9**	**RMSE = 10.360**	**P < 0.001**	

Functional traits and environmental conditions

Associations between leaf functional traits and decomposition are depicted in PCAs, where the first axes explained 47.53% and 44.31% for green and senescent leaves, respectively (Figure 4). Mass loss related positively with green leaves SLA, Amax, LNC, and LA, and negatively with LCC; mass loss was orthogonal to LD, LT, and LDMC. Mass loss was positively related to LNC and SLA of senescent leaves, and negatively to LCC, and LD; mass loss was roughly orthogonal to LT, LA and LDMC of senescent leaves.

MRAs showed that functional traits from both green and senescent leaves strongly predicted litter decomposition in all stages of decay (Table 2). Specifically, SLA, LNC, LCC, and LT were the most important traits for litter decomposition and their effects remained consistent over time. Senescent traits showed higher predictive power (R^2) compared to green leaves (Figure 5, Table 2). Surprisingly, temperature and soil volumetric water content were poor predictors of decomposition in all stages of decay (Figure 5, Table 2). Similarly, forest aboveground biomass and forest canopy height—two structural measures of forest successional status—were not consistently related to decomposition in all models (Table 2).

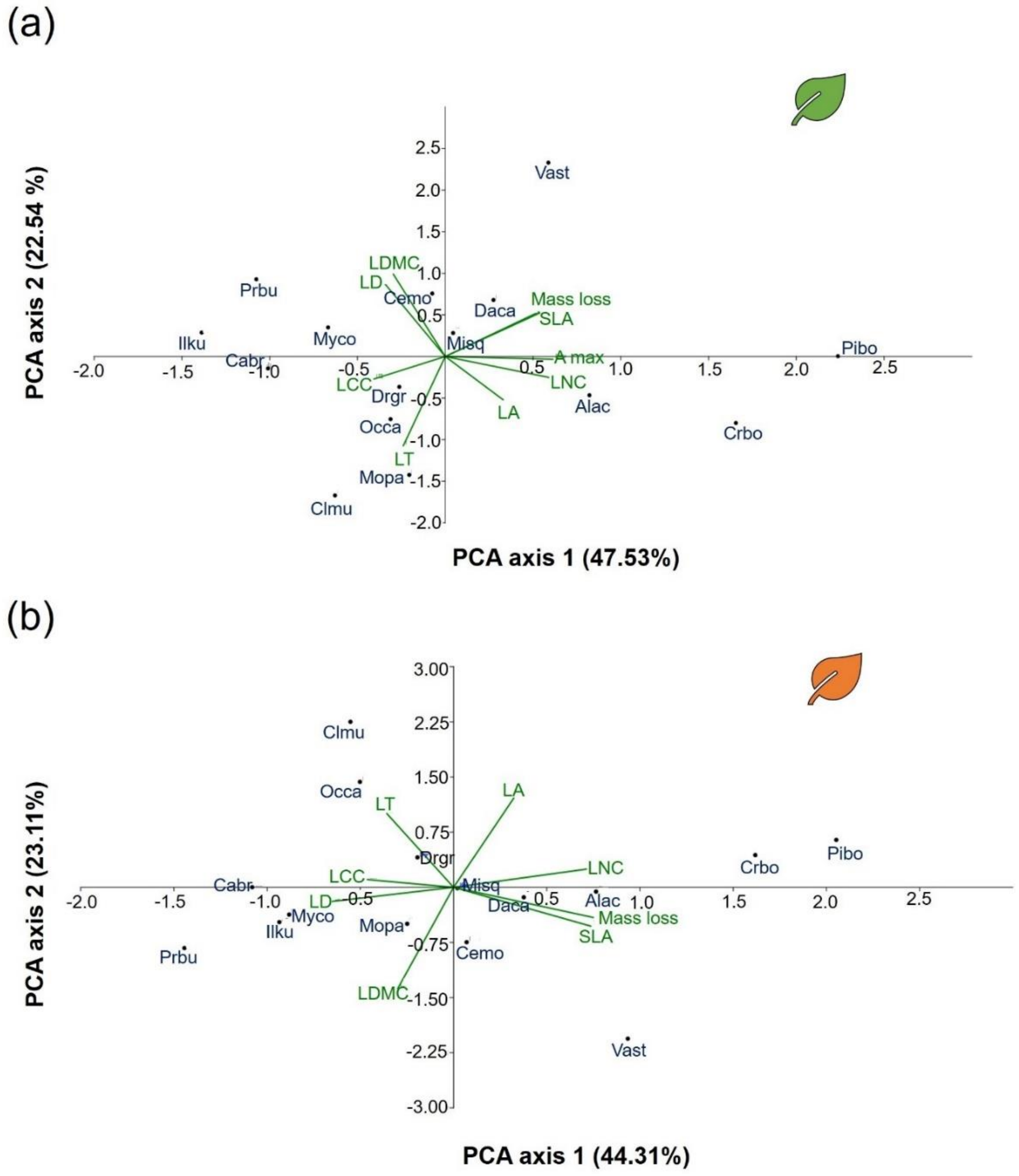

Figure 4. Principal component analysis of 8 green traits and 7 litter traits of 15 upper Andean tropical forests. (a) Loading plots of the green leaves and (b) senescent leaves. Acronyms and units of the traits (blue) are as follows: photosynthetic capacity (Amax, nmol/g/s), specific leaf area (SLA, cm/g^2) leaf nitrogen content (LNC, mg/g), leaf area (LA, cm^2), leaf carbon content (LCC, mg/g), leaf thickness (T, mm), leaf density (LD, mg/mm^3) and leaf dry matter content (LDMC, mg/g). In blue the species names: *Alnus acuminata* (Alac), *Cavendishia bracteata* (Cabr), *Cedrela montana* (Cemo), *Clusia multiflora* (Clmu), *Croton bogotanus* (Crbo), *Daphnopsis caracasana* (Daca), *Drimys granadensis* (Drgr) *Ilex kunthiana* (Ilku), *Miconia squamulosa* (Misq), *Morella parvifolia* (Mopa), *Myrsine coriacea* (Myco), *Ocotea calophylla* (Occa), *Piper bogotense* (Pibo), *Prunus buxifolia* (Prbu), *Vallea stipularis* (Vast).

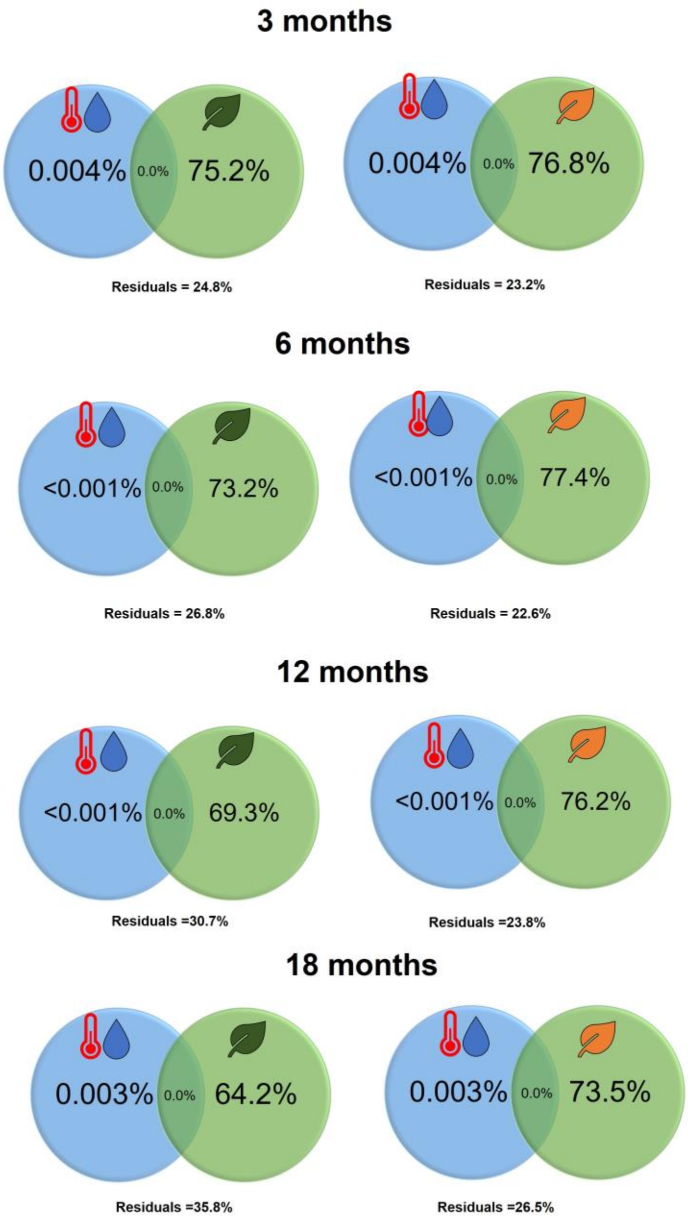

Figure 5. Venn diagrams showing the relative importance of green leaf traits and senescent traits in decomposition in each stage of decay thorough partition variance analysis. Note that microclimate had a poor explanatory power on predicting litter decomposition and did not interact with functional traits.

Changes between green and litter traits

Out of the 9 traits analyzed, RMA between three of the traits had slope confidence intervals different than 1.0 between green and senescent leaves (Figure 6). Overall, that resulted in higher SLA in senescent leaves than green leaves, while LNC and LCC were higher in green than in senescent leaves. Importantly, in species with a low SLA (<100 cm^2/g), green and senescent leaves exhibited similar values, whereas in species with a high SLA (>100 cm^2/g), green leaves were notably lower than senescent leaves.

Nitrogen resorption was particularly high (mean value of 62.26 ± 15.26) ranging from 46.83% in *I. kunthiana* to 92.09% in *P. buxifolia* (Table S5). In this set of species, despite the fact that the species ranking based on nitrogen concentration in green leaves displayed a similar pattern reflected in senescent leaves (Figure 6), nitrogen resorption was not correlated with these concentrations (P = 0.88, R^2 = 0.002). In other words, we did not observe any discernible pattern indicating higher nitrogen resorption in either acquisitive or conservative species.

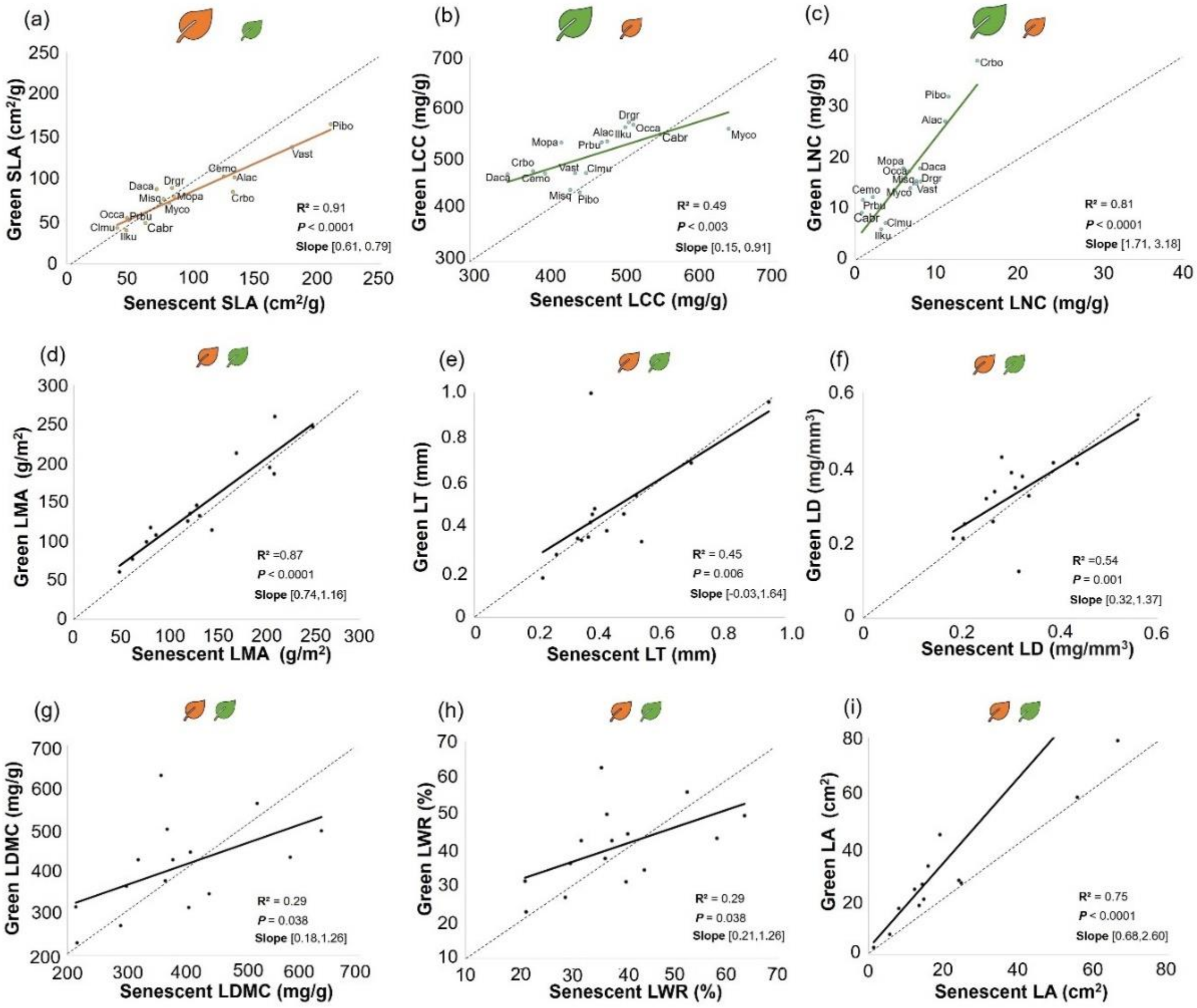

Figure 6. Reduced major axis regressions between green and senescent traits. Functional traits included (a) specific leaf area (SLA, cm/g^2), (b) leaf carbon content (LCC, mg/g), (c) leaf nitrogen content (LNC, mg/g), (d) leaf mass per area (LMA, g/m^2), (e) leaf thickness (LT, mm), (f) leaf density (LD, mg/mm^3), (g) leaf dry matter content (LDMC, mg/g), (h) leaf water retention (LWR, %), (i) leaf area (LA, cm^2). The size of the leaves in the top of the panel reflect significant changes between green and litter traits. Confidence intervals of the slopes, R^2, and P value are shown in the right bottom of each scatter plot. Figures a-c showed significant changes between green and senescent leaves, with the corresponding species names highlighted as follows: *Alnus acuminata* (Alac), *Cavendishia bracteata* (Cabr), *Cedrela montana* (Cemo), *Clusia multiflora* (Clmu), *Croton bogotanus* (Crbo), *Daphnopsis caracasana* (Daca*), Drimys granadensis* (Drgr) *Ilex kunthiana* (Ilku), *Miconia squamulosa* (Misq), *Morella parvifolia* (Mopa), *Myrsine coriacea* (Myco), *Ocotea calophylla* (Occa), *Piper bogotense* (Pibo), *Prunus buxifolia* (Prbu), *Vallea stipularis* (Vast).

Discussion

Our results show that functional traits and species identity drive litter decomposition in UATF, more than succession, soil moisture, or temperature. Foliar traits consistently influenced all stages of decay, with stronger effects in early phases. Senescent leaf traits were better predictors of decomposition because they reflect the characteristics of fallen leaves. Key changes between green and senescent leaves include lower nitrogen content in the latter, indicative of high nitrogen resorption. This strong resorption can slow down decomposition by reducing litter quality from the very beginning of decomposition.

Effects of litter identity and functional traits on decomposition

In support of our first hypothesis (H1), we found a strong effect of species identity and their traits on decomposition, similar to outcomes from reciprocal translocation experiments in other biomes (e.g., Makkonen et al., 2012; Esquivel et al., 2020; Canessa et al., 2021). This finding supports the fact that decomposer communities prefer high quality litter substrates regardless of the site. Decomposers showed little specialization to local litter, but responded strongly to litter quality, demonstrating that functional traits drive decomposition (Cornwell et al., 2008; Makkonen et al., 2012; Zhou et al., 2020; Castillo-Figueroa, 2024b).

Our findings suggest that changes in plant species composition are crucial for litter decomposition, especially under current anthropogenic pressures that largely influence plant communities in UATF, such as thermophilisation (Duque et al., 2015, 2021), land-use change (Hurtado-M et al., 2021), and invasive species (Saavedra-Ramírez et al., 2018). Overall, UATF is predominantly composed by conservative species distinguished by low litter quality (Homeier et al., 2021; Báez et al., 2022), leading to slow decay rates and increased soil carbon accumulation (Myster, 2021; Salinas et al., 2021). Therefore, shifts in plant community composition towards more acquisitive species with elevated nitrogen content have the potential to increase decomposition rates, resulting in higher carbon release into the atmosphere and reduced carbon accumulation in soils. However, more acquisitive species could also be related to higher litter production so the overall effect of changes in species composition on soil carbon will need more detailed studies.

Comparison of decomposition between successional stages

We found weak differences in decomposition with succession, contrary to our second hypothesis (H2). Small effects were only found at latter stages of decay when succession was treated as a continuous gradient of aboveground biomass and height (i.e., older forests being taller and with higher biomass than younger forests). Studies in the Neotropics highlight the variety of successional pathways, which can change between sites (Norden et al., 2015; Rozendaal et al., 2019; Poorter et al., 2021b; Jakovac et al., 2022). This variability may have dampened the influence of succession on decomposition rates. Moreover, despite clear differences in structural attributes between mature and secondary forests in our study (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023), we lacked the earliest successional covers with no canopy cover, where environmental conditions are more contrasting. Including these early phases could have led to more pronounced differences in decomposition.

However, when comparing mean decay rates between mature and secondary forests, we found significantly higher decomposition rates for some species in mature forests, particularly in the later stages of litter decay (12 and 18 months). This is consistent with studies showing increased in leaf litter decomposition in mature forests, although rates vary by species (Xuluc et al., 2003; Ostertag et al., 2008; Morffi-Mestre et al., 2023). Since mean soil microclimatic conditions did not significantly influence decomposition, other factors—such as greater soil organic layer thickness, higher nitrogen and carbon content, and increased litter production in mature forests—may explain the variation in decay rates between successional stages. These conditions could promote optimal environments for soil fauna and microbial communities specialized in litter breakdown. The variation in species-specific decomposition with succession may be linked to affinity effects between decomposer communities and these litter substrates during specific decomposition periods. For instance, studies have shown that soil fauna prefer specific plant species, particularly when their litter is partially decomposed or freshly fallen (Edwards & Bohlen, 1995; Zimmer, 2002; De Oliveira et al., 2010). Further research should examine how the role of decomposers changes across stages of decay and succession.

Microclimatic conditions and functional traits

Our third hypothesis (H3) was not supported, as functional traits predicted decomposition in all stages of decay, while soil water content and temperature showed no significant correlation with decomposition. At local scales, where environmental conditions remain relatively constant, litter quality strongly influences decomposition (Aerts, 1997; Poca et al., 2015). Furthermore, incorporating local-scale variation, as in our study, can significantly diminish the influence of climatic factors on decomposition (Bradford et al., 2014, 2016; García-Palacios et al., 2017), indicating that climate effects depend on the geographic scale of analysis.

Although other experiments have found a strong climate effect on decomposition (Wall et al., 2008; Canessa et al., 2021; Vaieretti et al., 2021), these studies were conducted across larger climatic gradients. In our experiment, the narrower elevational gradient (<600m) did not encompass distinct climatic zones. Considering that temperature and humidity are key drivers of decomposition (Zhang et al., 2008; Berg & McClaugherty, 2020; Giweta, 2020), the limited environmental range likely masked climate effects. Moreover, the narrow range of mean soil moisture (33.81%–42.14%) could be a consequence of the occurrence of La Niña event, which brought above-average rainfall (IDEAM, 2023), homogenizing soil moisture conditions during the decomposition experiment. While the site with the highest mean soil temperature (Tabio) exhibited the fastest decomposition, with some species fully decomposed after 18 months (e.g., *P. bogotense*, *C. bogotanus*, *V. stipularis*), other factors likely exerted more significant influence on decomposition rates.

Biotic factors may play a major role in litter decomposition at a local scale than environmental conditions. Our MRA indicated that SLA and LNC were the best predictors of decomposition, consistent with previous studies (Cornwell et al., 2008; Bakker et al., 2011; Poca et al., 2014; Esquivel et al., 2020). This is particularly relevant in Andean montane forests, where nitrogen is a limiting resource (Tanner et al., 1998; Soethe et al., 2008; Wilcke et al., 2008; Myster, 2021), leading decomposers to prefer nitrogen-rich leaves, a key nutrient for their metabolism. In nutrient-poor soils typical of these ecosystems (Wilcke et al., 2008), decomposers are likely more efficient at processing leaves, preferring to consume less leaf material per unit area (Bakker et al., 2011). This efficiency may explain the strong association between decomposition rates and SLA. Variation in decomposer communities, plant species composition, and their interactions may also influence decomposition in UATF, as suggested by other studies (Cárdenas et al., 2017; Four et al., 2019; Laigle et al., 2021).

After-life effect

Our fourth hypothesis (H4), which posited that green leaves have higher nitrogen than senescent leaves, was supported. We also found that senescent leaves had lower LCC and higher SLA than green leaves. Most studies have assumed the existence of an "after-life effect" in live leaves (Santiago, 2007; Bakker et al., 2011). While physical traits remain similar between green and senescent leaves, both of which influence decomposition, the leaf chemistry changes significantly, consistent with findings from other studies (Zukswert & Prescott, 2017; Guo et al., 2025). The higher nitrogen resorption suggests that this nutrient is a limiting resource in tropical montane forests, indicating high nitrogen use efficiency (Vitousek et al., 1988; Tanner et al., 1998). This implies the litter that drops into the soil is of poor quality, which, along with low temperatures (Pinos et al., 2017; Salinas et al., 2011), hypoxic soils (Schuur et al., 2001; Wilcke et al., 2002), and low microbial diversity (Nottingham et al., 2018), could slow down decomposition. However, despite the nitrogen change, the species' nitrogen ranking remained consistent, supporting the “after-life effect”. To our knowledge, only one study has quantified foliar nutrients in green and senescent leaves UATF, showing that nitrogen resorption is not controlled by green LNC (Vera et al., 1999), similar to our findings. This suggests that nitrogen use efficiency is not linked to a specific ecological strategy, acquisitive or conservative, and may result from habitat filtering driven by nutrient poor-soils in UATF. Further studies should explore nitrogen resorption across more Andean species to confirm this hypothesis.

The higher SLA of senescent leaves could be explained by a reduction in leaf biomass as senescent leaves are not photosynthetically active. This is consistent with the observed decreases in carbon and, to a lesser extent, nitrogen content due to cellular breakdown during senescence. The effect was more pronounced in high SLA leaves likely as a result of having less structural carbon than low SLA leaves. This aligns with global patterns in leaf construction traits (Xing et al., 2021), suggesting that high SLA leaves typically contain low concentrations of resource-demanding components, like lignin, in the cell wall, and high levels of 'cheap' constituents such as minerals and other nutrients (Villar et al., 2006; Xing et al., 2021).

Conclusions

Our results clearly demonstrate that species identity and functional traits are the primary drivers of litter decomposition in UATF. This implies that changes in species composition due to pressing human-induced changes such as thermophilisation, invasive species or landscape transformation, could have a strong impact on carbon and nutrient cycles in an ecosystem with substantial amounts of carbon stored in soils and limiting resources like nitrogen. Soil microclimatic conditions and succession were poor determinants of decomposition, but wider gradients need to be examined to validate these findings. Our results supported the "after-life effect", yet we also identified significant changes in traits (SLA, LNC, LCC), which can considerably reduce the quality of senescent leaves for decomposers, thus slowing down decay rates from the very beginning of the decomposition process. Under a scenario of global environmental change, our findings suggest that shifts in species composition in UATF may potentially impact greenhouse emissions from litter and alter soil carbon accumulation in one of the most important carbon sinks of the planet.

Acknowledgments

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Supplementary material

Figure S1. Functional spectrum of the 63 plant species in the 14 plots based on seven senescent traits (SLA = Specific Leaf area, g/cm^2, LA = Leaf Area, cm^2, LDMC = Leaf Dry Matter Content, mg/g, LCC = Leaf Carbon Content, mg/g, LNC = Leaf Nitrogen content, mg/g, LT = Litter thickness, mm, LD = Leaf Density, mg/mm^3). The first two axes explain the 64.83% of the variation. Species in red circles were selected for the litter decomposition experiment. Codes for species selected as follows: Alac =*Alnus acuminata,* Cabr = *Cavendishia bracteate*, Cemo = *Cedrela montana*, Clmu = *Clusia multiflora*, Crbo = *Croton bogotanus*, Daca = *Daphnopsis caracasana,* Drgr = *Drimys granadensis*, Ilku = *Ilex kunthiana*, Misq = *Miconia squamulose*, Mopa = *Morella parvifolia,* Myco = *Myrsine coriacea*, Occa = *Ocotea calophylla*, Pibo = *Piper bogotense*, Prbu = *Prunus buxifolia*, Vast = *Vallea stipularis.*

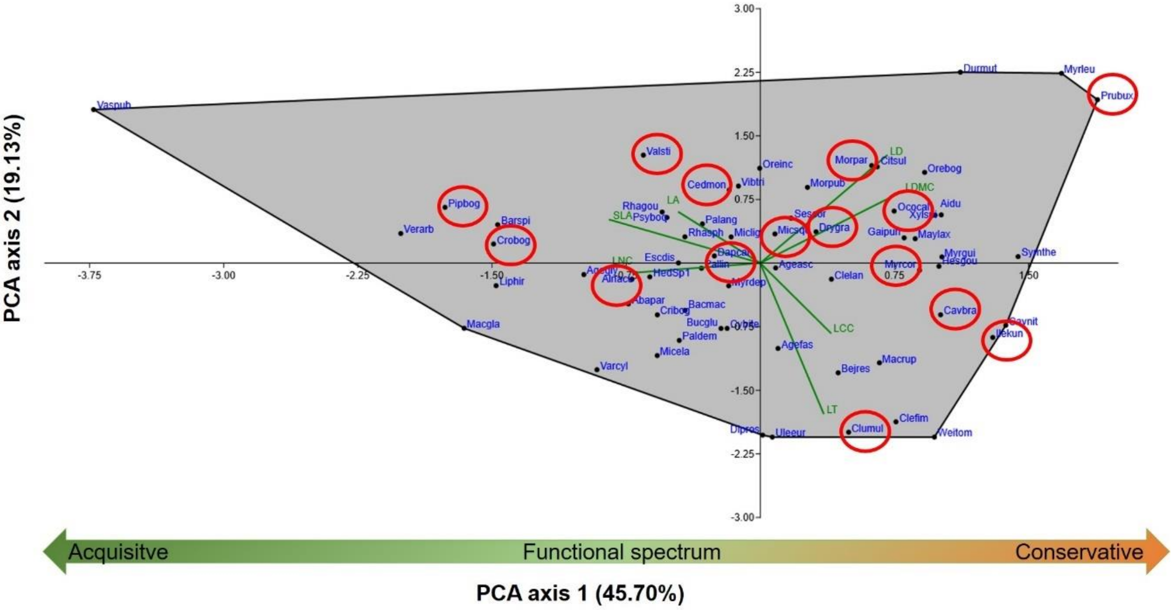


Figure S2. Heatmap showing spearman correlations between traits from green and senescent leaves with decomposition (i.e., mass loss, highlighted in red). Blue color depicts positive relationships red color represents negative relationships. Significant correlations (P < 0.001) are flagged with asterisk (*).

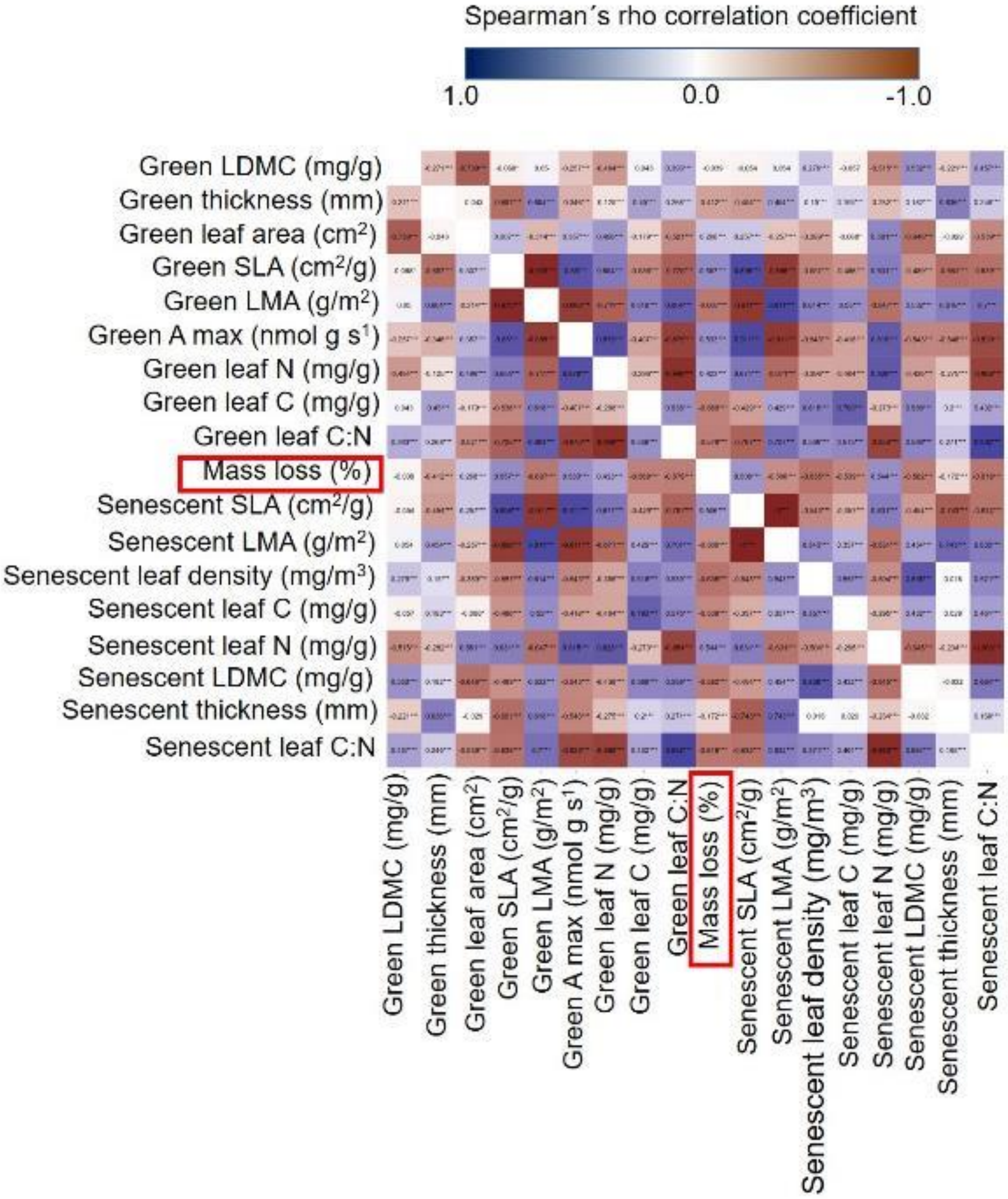


Figure S3. Boxplots among litter species in each site in every stage of decay (3,6,12,18 months), showing similar patterns of decomposition no matter the site or time. Species code is as follows: Alac=*Alnus acuminata,* Cabr = *Cavendishia bracteate*, Cemo = *Cedrela montana*, Clmu = *Clusia multiflora*, Crbo = *Croton bogotanus*, Daca = *Daphnopsis caracasana,* Drgr = *Drimys granadensis*, Ilku = *Ilex kunthiana*, Misq = *Miconia squamulose*, Mopa = *Morella parvifolia,* Myco = *Myrsine coriacea*, Occa = *Ocotea calophylla*, Pibo = *Piper bogotense*, Prbu = *Prunus buxifolia*, Vast = *Vallea stipularis.*

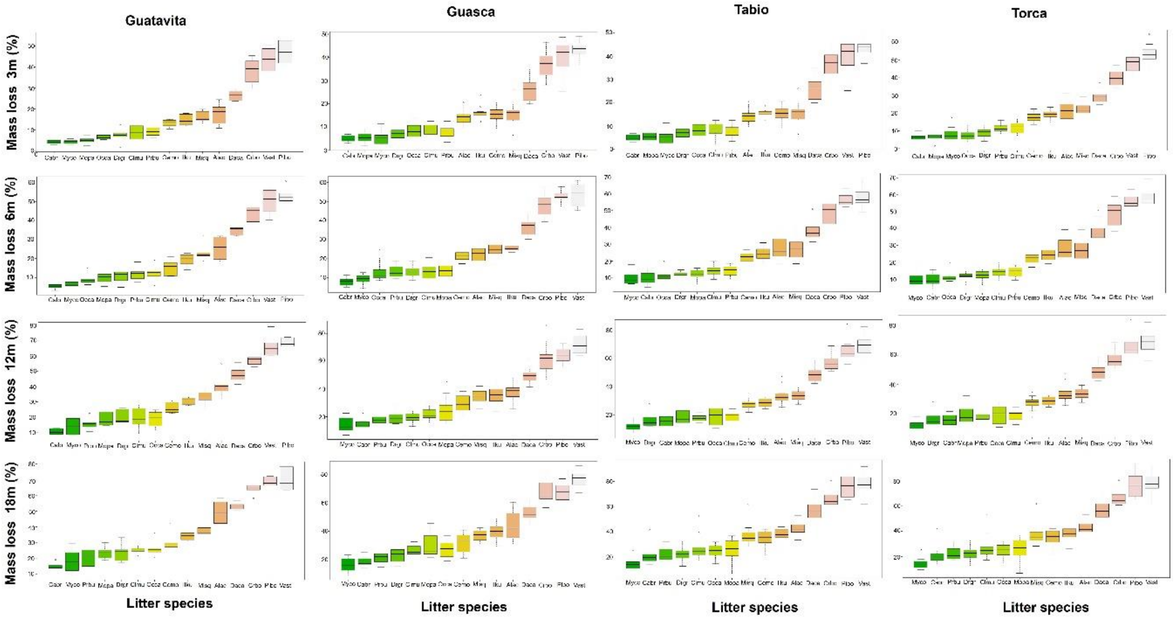


Table S1. Species selected for litter decomposition experiment. Names are based on Tropicos® Database from the Missouri Botanical Garden (https://www.tropicos.org/) and the World Flora Online Database (http://www.worldfloraonline.org).

Taxa	**Code**	**Site collected**
AQUIFOLIALES Aquifoliaceae *Ilex kunthiana* Triana	Ilku	Torca, Tabio
ERICALES Ericaceae *Cavendishia bracteata* (Ruiz & Pav. ex J. St.-Hil.) Hoerold	Cabr	Guasca
Primulaceae *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult	Myco	Guasca, Torca, Tabio
MALPIGHIALES Clusiaceae *Clusia multiflora* Kunth.	Clmu	Torca
Euphorbiaceae *Croton bogotanus* Cuatrec.	Crbo	Tabio
LAURALES Lauraceae *Ocotea calophylla* Mez	Occa	Torca
ROSALES Rosaceae *Prunus buxifolia* Koehne	Prbu	Torca
OXALIDALES Elaeocarpaceae *Vallea stipularis* L. f.	Vast	Guatavita, Torca, Tabio
MYRTALES Melastomataceae *Miconia squamulosa* (Sm.) Triana	Misq	Tabio, Guatavita, Torca
FAGALES Betulaceae *Alnus acuminata* Kunth	Alac	Guasca
Myricaceae *Morella parvifolia* (Benth.) Parra-Os.	Mopa	Guatavita, Tabio, Torca
SAPINDALES Meliaceae *Cedrela montana* Moritz ex Turcz.	Cemo	Tabio
MALVALES Thymelaeaceae *Daphnopsis caracasana* Meisn.	Daca	Tabio
PIPERALES Piperaceae *Piper bogotense* C. DC.	Pibo	Tabio, Guasca, Torca

CANELLALES Winteraceae *Drimys granadensis* L.f.	Drgr	Torca, Guasca

Table S2. Mean ± SD and range of litter decomposition in 15 litter species from upper Andean tropical forests.

Stage of decay	**Litter species**	**All sites**
3 months	*Alnus acuminata*	19.07 ± 5.35 (9.55-31.34)
	Cavendishia bracteata	5.51 ± 1.83 (2.45-9.90)
	Cedrela montana	16.49 ± 3.39 (9.18-25.83)
	Clusia multiflora	9.44 ± 3.48 (1.96-17.86)
	Croton bogotanus	39.24 ± 5.22 (27.96-46.92)
	Daphnopsis caracasana	27.84 ± 4.59 (16.15-37.00)
	Drimys granadensis	7.99 ± 2.83 (1.72-16.34)
	Ilex kunthiana	17.11 ± 3.08 (11.21-23.69)
	Miconia squamulosa	18.58 ± 5.26 (6.61-32.39)
	Morella parvifolia	5.72 ± 1.84 (1.51-9.71)
	Myrsine coriacea	6.11 ± 2.92 (2.06-17.52)
	Ocotea calophylla	7.37 ± 2.61 (2.03-14.02)
	Piper bogotense	49.23 ± 6.34 (36.86-64.95)
	Prunus buxifolia	9.57 ± 2.65 (3.30-15.97)
	Vallea stipularis	44. 33 ± 6.74 (25.21-58.93)
6 months	*Alnus acuminata*	26.67 ± 7.36 (12.47-40.43)
	Cavendishia bracteata	8.18 ± 3.00 (2.78-15.59)
	Cedrela montana	21.66 ± 4.51 (10.79-34.74)
	Clusia multiflora	13.54 ± 3.76 (5.83-23.49)
	Croton bogotanus	48.88 ± 6.81 (38.27-62.90)
	Daphnopsis caracasana	36.83 ± 4.81 (28.34-50.74)
	Drimys granadensis	11.71 ± 3.09 (4.86-18.76)
	Ilex kunthiana	23.94 ± 3.69 (14.08-30.77)
	Miconia squamulosa	24.97 ± 5.29 (15.15-39.43)

	Morella parvifolia	11.72 ± 3.46 (5.38-20.58)
	Myrsine coriacea	8.83 ± 2.63 (4.40-17.88)
	Ocotea calophylla	11.36 ± 4.04 (6.27-24.26)
	Piper bogotense	55.85 ± 4.71 (47.49-66.38)
	Prunus buxifolia	13.05 ± 2.93 (7.50-18.55)
	Vallea stipularis	54.99 ± 6.77 (40.38-70.47)
12 months	*Alnus acuminata*	38.97 ± 11.37 (23.26-84.84)
	Cavendishia bracteata	14.39 ± 4.38 (6.31-26.2)
	Cedrela montana	29.03 ± 5.33 (17.41-40.00)
	Clusia multiflora	19.66 ± 4.47 (9.12-28.50)
	Croton bogotanus	61.53 ± 9.93 (46.85-87.99)
	Daphnopsis caracasana	49.93 ± 6.57 (33.06-66.20)
	Drimys granadensis	18.47 ± 5.44 (7.72-28,67)
	Ilex kunthiana	32.14 ± 5.88 (23.65-48.82)
	Miconia squamulosa	33.03 ± 4.75 (24.32-42.11)
	Morella parvifolia	20.29 ± 8.56 (6.48-45.31)
	Myrsine coriacea	12.94 ± 4.68 (6.89-29.15)
	Ocotea calophylla	20.60 ± 6.19 (10.56-39.87)
	Piper bogotense	67.83 ± 8.52 (53.79-93.47)
	Prunus buxifolia	17.36 ± 4.08 (9.63-34.23)
	Vallea stipularis	71.14 ± 8.07 (56.18-89.47)
18 months	*Alnus acuminata*	47.02 ± 12.82 (23.92-84-92)
	Cavendishia bracteata	20.25 ± 8.18 (6.45-50.80)
	Cedrela montana	34.60 ± 7.22 (20.98-56.83)
	Clusia multiflora	26.72 ± 7.28 (16.14-52.60)
	Croton bogotanus	70.16 ± 11.45 (51.79-100)
	Daphnopsis caracasana	57.12 ± 10.79 (38-35-92.12)
	Drimys granadensis	24.35 ± 7.51 (8.81-51.25)
	Ilex kunthiana	38.23 ± 7.15 (24.61-61.76)

Miconia squamulosa	37.94 ± 10.03 (24.10-85.19)
Morella parvifolia	26.44 ± 9.46 (6.50-46.61)
Myrsine coriacea	16.20 ± 5.24 (8.87-29.34)
Ocotea calophylla	27.92 ± 7.96 (14.27-53.49)
Piper bogotense	75.55 ± 10.78 (53.84-100)
Prunus buxifolia	21.87 ± 5.17 (9.97-34.33)
Vallea stipularis	77.99 ± 8.30 (61.77-100)

Table S3. Mean ± SD and ranges of litter decomposition in sites from upper Andean tropical forests. Same letters indicate no significant differences between sites in terms of relative decay rates ($P > 0.1$).

Site	**3 months**	**6 months**	**12 months**	**18 months**
Guatavita	17.50 ± 14.57^a (1.72-54.42)	22.24 ± 16.30^a (3.16-60.92)	32.58 ± 19.24^a (7.71-78.99)	37.29 ± 18.92^a (9.04-78.81)
Guasca	16.96 ± 13.42^a (1.77-49.12)	24.53 ± 15.77^a (4.40-61.01)	34.50 ±19.42^a (6.89-85.93)	38.66 ± 19.74^a (8.87-85.39)
Tabio	19.67 ±15.26^a (2.45-64.95)	25.49 ± 18.03^a (2.78-70.47)	35.46 ± 22.81^a (6.31-93.47)	45.50 ± 24.87^a (6.45-100)
Torca	20.8 ± 15.27^a (1.15-64.42)	25.69 ± 16.96^a (4.39-63.30)	32.13 ± 19.57^a (6.65-84-65)	39.28 ± 21.20^a (6.86-93.59)

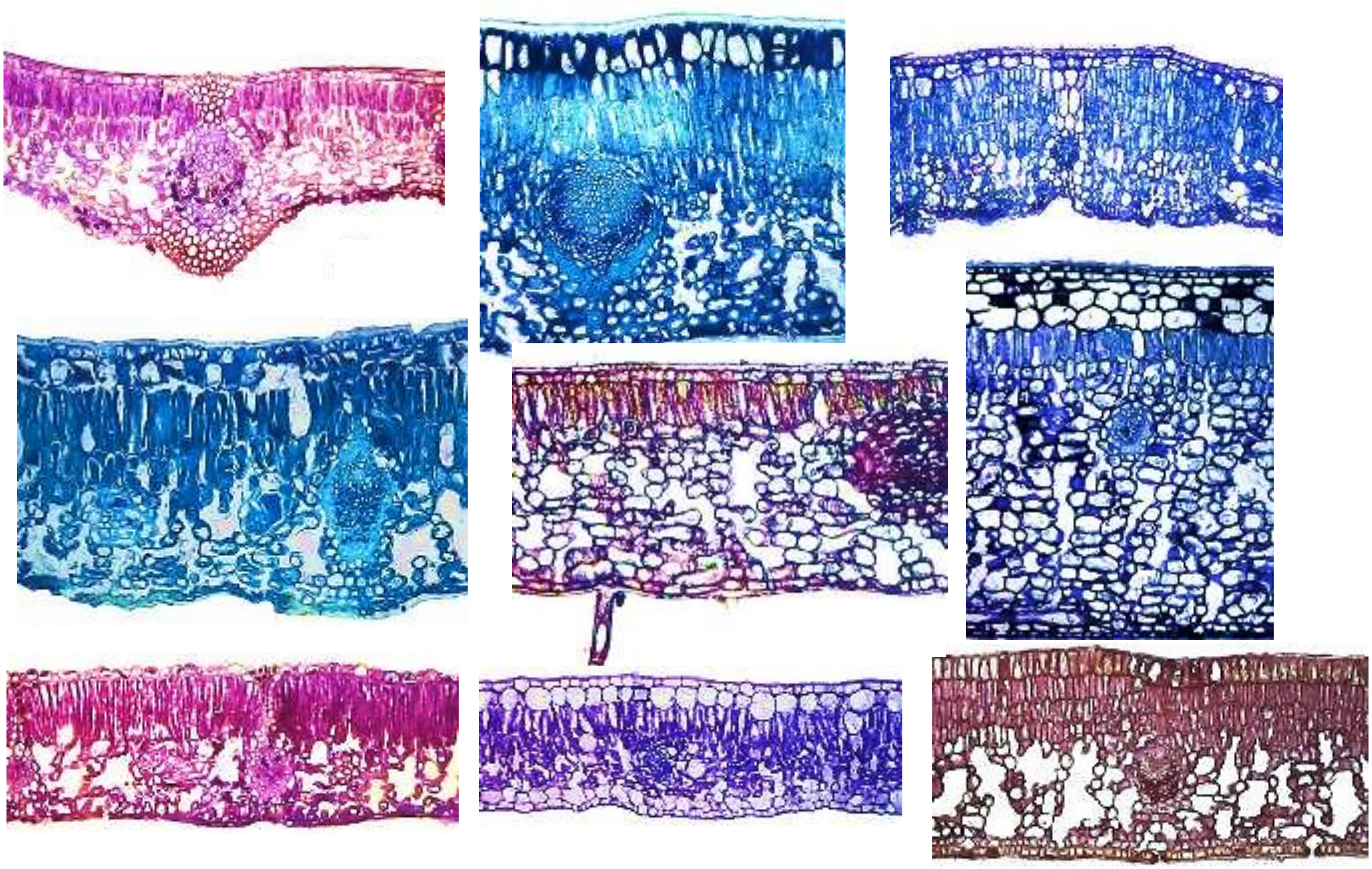
Table S4. T-test tests showing comparisons between successional stages for all the species and for each one of them. The total number of litterbags in each decomposition period was 630 (315 for each successional stage) and was 42 per period for each species (21 for each successional stage). Different letters indicate significant differences between successional stages (P < 0.05).

Litter species	**Successional stage**	**3 months**	**6 months**	**12 months**	**18 months**
All species	Mature	19.591^{a} ±15.119	25.188^{a} ± 16.958	34.467^{a} ± 20.714	41.704^{a} ± 22.584
	Secondary	18.231^{a} ±14.412	24.442^{a} ± 16.776	33.183^{a} ± 20.003	38.351^{a} ± 20.673
Alnus acuminata	Mature	20.764^{a} ± 6.035	28.187^{a} ± 7.578	39.825^{a} ± 8.787	47.505^{a} ± 11.225
	Secondary	17.381^{b} ± 4.031	25.163^{a} ± 6.991	38.119^{a} ± 13.662	46.534^{a} ± 14.509
Cavendishia bracteata	Mature	6.120^{a} ± 2.029	8.911^{a} ± 2.326	15.385^{a} ± 3.479	22.093^{a} ± 9.151
	Secondary	4.905^{b} ± 1.424	7.455^{a} ± 3.454	13.397^{a} ± 5.019	18.419^{a} ± 6.812
Cedrela montana	Mature	17.729^{a} ± 3.222	23.603^{a} ± 3.914	31.019^{a} ± 4.905	36.076^{a} ± 6.082
	Secondary	15.252^{b} ± 3.168	19.720^{b} ± 4.298	27.054^{b} ± 5.102	33.135^{a} ± 8.097
Clusia multiflora	Mature	9.268^{a} ± 3.722	13.561^{a} ± 3.901	20.170^{a} ± 4.229	27.159^{a} ± 6.836
	Secondary	9.625^{a} ± 3.304	13.523^{a} ± 3.720	19.161^{a} ± 4.754	26.281^{a} ± 7.853
Croton bogotanus	Mature	40.073^{a} ± 5.445	49.88^{a} ± 6.846	63.738^{a} ± 10.863	74.737^{a} ± 12.980
	Secondary	38.411^{a} ± 4.987	47.880^{a} ± 6.795	59.338^{a} ± 8.611	65.594^{b} ± 7.519
Daphnopsis caracasana	Mature	28.100^{a} ± 3.832	36.036^{a} ± 4.428	51.001^{a} ± 5.378	60.370^{a} ± 12.218
	Secondary	27.598^{a} ± 5.335	37.639^{a} ± 5.153	48.876^{a} ± 7.569	53.877^{a} ±8.213
Drimys granadensis	Mature	8.395^{a} ± 2.976	12.146^{a} ± 3.148	18.674^{a} ± 5.533	26.219^{a} ± 8.709
	Secondary	7.588^{a} ± 2.686	11.284^{a} ± 3.052	18.268^{a} ± 5.475	22.495^{a} ± 5.707
Ilex kunthiana	Mature	17.552^{a} ± 2.715	24.312^{a} ± 3.062	31.925^{a} ± 5.682	39.995^{a} ± 8.025
	Secondary	16.678^{a} ± 3.420	23.586^{a} ± 4.286	32.358^{a} ± 6.213	36.467^{a} ± 5.828
Miconia squamulosa	Mature	19.736^{a} ± 5.654	24.511^{a} ± 3.656	33.606^{a} ± 4.926	38.848^{a} ± 11.974
	Secondary	17.435^{a} ± 4.691	25.432^{a} ± 6.600	32.469^{a} ± 4.619	37.045^{a} ± 7.820
Morella parvifolia	Mature	6.360^{a} ± 1.792	11.888^{a} ± 3.029	21.230^{a} ± 8.577	29.841^{a} ± 9.111
	Secondary	5.096^{b} ± 1.715	11.554^{a} ± 3.927	19.361^{a} ± 8.650	23.045^{b} ± 8.735
Myrsine coriacea	Mature	6.815^{a} ± 3.547	9.158^{a} ± 2.956	12.454^{a} ± 3.286	15.695^{a} ± 3.742
	Secondary	5.414^{a} ± 1.977	8.512^{a} ± 2.306	13.434^{a} ± 5.800	16.709^{a} ± 6.466
Ocotea calophylla	Mature	6.815^{a} ± 3.547	9.158^{a} ± 2.956	12.454^{a} ± 3.286	15.695^{a} ± 3.742
	Secondary	5.414^{a} ± 1.977	8.512^{a} ± 2.306	13.434^{a} ± 5.800	16.709^{a} ± 6.466

Piper bogotense	Mature	50.241^{a} ± 6.474	56.502^{a} ± 4.755	69.447^{a} ± 9.386	77.194^{a} ± 10.382
	Secondary	48.218^{a} ± 6.194	55.198^{a} ± 4.687	66.212^{a} ± 7.432	69.917^{b} ± 10.150
Prunus buxifolia	Mature	9.747^{a} ± 2.770	12.656^{a} ± 2.627	17.020^{a} ± 2.648	22.612^{a} ± 4.254
	Secondary	9.403^{a} ± 2.582	13.446^{a} ± 3.229	17.704^{a} ± 5.194	21.145^{a} ± 5.979
Vallea stipularis	Mature	46.276^{a} ± 5.856	55.700^{a} ± 6.457	71.628^{a} ± 8.403	79.534^{a} ± 8.231
	Secondary	42.392^{a} ± 7.139	54.289^{a} ± 7.170	70.663^{a} ± 7.900	76.449^{a} ± 8.290

Table S5. Averages of leaf nitrogen concentration (%) in green and senescent leaves and nitrogen resorption for 15 Andean species. Nitrogen resorption was calculated as (Green leaf N% – Senescent leaf N% /Green leaf N%) according to Vera et al. (1999) (see references).

Litter species	Green leaf N (%)	Senescent leaf N (%)	N resorption (%)
Alnus acuminata	2.70	1.09	59.61
Cavendishia bracteata	0.91	0.08	91.70
Cedrela montana	1.21	0.21	82.52
Clusia multiflora	0.71	0.37	48.00
Croton bogotanus	3.88	1.48	61.87
Daphnopsis caracasana	1.78	0.78	55.84
Drimys granadensis	1.52	0.79	48.02
Ilex kunthiana	0.59	0.31	46.84
Miconia squamulosa	1.53	0.74	51.62
Morella parvifolia	1.78	0.54	67.26
Myrsine coriacea	1.39	0.67	51.98
Ocotea calophylla	1.72	0.65	62.24
Piper bogotense	3.18	1.13	64.41
Prunus buxifolia	1.16	0.09	92.09
Vallea stipularis	1.48	0.74	49.93
All species	1.70 ± 0.72	0.65 ± 0.38	62.26 ± 15.26



Chapter 3

Linkages between leaf anatomical traits and decomposition rates of woody Andean species along a forest successional gradient in the upland Andes.

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Are leaf anatomical traits strong predictors of litter decomposability? Evidence from upper Andean tropical species along a forest successional gradient

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Abstract

Litter decomposability has been linked to "soft" traits of green leaves, but relationships with "hard" traits associated with leaf anatomy remain unexplored. Examining anatomical traits within the leaf economic spectrum may enhance our understanding of litter decomposability. In this study, we analyzed the relationships between leaf anatomical traits and decomposability at both species and community levels along a successional gradient of upper Andean tropical forests in Colombia. We conducted a reciprocal translocation field experiment with 15 upper Andean species in 14 permanent plots around Bogotá, collecting 2520 litterbags at four times (3, 6, 12, 18 months). Using a multiple regression model based on foliar traits, we estimated decomposability for the remaining 48 species that compose the plant community (63 species in total) in the studied successional gradient. We measured several leaf anatomical traits in all 63 species and calculated community-weighted means and functional diversity indices with the most effective anatomical predictors of decomposability. We found that thicker cuticles, larger vascular bundles, higher spongy mesophyll proportion, and lower palisade mesophyll proportion are related to low decomposability. Plant communities with thicker protective structures slow down decay rates, while large palisade tissues with cylindrical cells increase litter breakdown. Decomposability did not change along succession due to the balance between high functional evenness in secondary forests and high functional richness in mature forests. Despite potential circularity and interdependence between functional diversity metrics, our study provides novel insights into the anatomical basis of decomposability and community dynamics in successional gradients of upper Andean tropical forests.

Key-words: Andean forests, functional traits, leaf anatomy, leaf economic spectrum, litter decay.

Introduction

Leaves are the main organs for photosynthesis and play a crucial role in the functioning of terrestrial ecosystems (Wright et al., 2004; He et al., 2018; Ni et al., 2022). They contribute directly not only to key physiological functions such as carbon fixation, but also to respiration, transpiration, resource use, and plant growth (e.g., Kröber et al., 2015; Kuster et al., 2016; Rey-Sanchez & Posada, 2019). Leaves have multiple functional traits, whose relationships have been extensively examined within the conceptual framework provided by the Leaf Economic Spectrum (LES) (Wright et al., 2004; Reich, 2014; de la Riva et al., 2017). This framework accounts for approximately 75% of interspecific variation in traits related to carbon gain, water regulation, and nutrient use (Wright et al., 2004; Díaz et al., 2016; Esquivel et al., 2020), and explores selective pressures that give rise to trade-offs between the acquisition and conservation of resources (Reich, 2014). Consequently, the LES has been extended to encompass significant ecosystem processes, such as water use efficiency and productivity (He et al., 2018), as well as nutrient cycling and litter decomposability (Bakker et al., 2011; de la Riva et al., 2019; Esquivel et al., 2020).

Previous investigations of litter decomposability have focused on “soft” leaf functional traits, which are more readily measurable, including Leaf Mass per Area (LMA), Leaf Nitrogen Content (LNC), and Leaf Dry Matter Content (LDMC) (Santiago, 2007; Bakker et al., 2011; Pérez-Harguindeguy et al., 2015; Garnier et al., 2016; Li et al., 2023). However, the LES is expected to be the result of fundamental trade-offs in form and function that are closely related to the anatomy of leaves. Specifically, it has been suggested that the LES is governed by trade-offs between allocation to structural tissues and to metabolic (‘liquid phase’) processes (Shipley et al., 2006; Onoda et al., 2017). Thus, measuring the anatomical traits that underpin the LES could improve our understanding of litter decomposability.

Trade-offs between traits are partially expressed in the relationships between epidermis, cuticle, vascular bundles, and mesophyll tissues (Onoda et al., 2012; Somavilla et al., 2014; Harrison et al., 2021). Within leaf anatomical structures, thicker cuticles and epidermis serve as the initial physical barrier for plants, representing crucial defenses that enhance leaf protection and longevity (Onoda et al., 2012; Harrison et al., 2021). The epidermis also plays a key role in light transmission, and it holds the stomata that control CO2 diffusion (Verboven et al., 2015; He et al., 2018), transpiration, and heat balance (Liu et al., 2021). Thus, given their function as a barrier, the epidermis and cuticle should also influence decay rates by reducing the entry of decomposers (Zukswert & Prescott, 2017; Onoda et al., 2012). In addition, larger spongy mesophyll thickness has been related to lower water use efficiency because of higher water loss by evaporation (He et al., 2018). Nevertheless, the spongy mesophyll is positively related to gross primary production at the community level, as it enhances gas transportation and maximizes carbon assimilation (Somavilla et al., 2014; He et al., 2018). Thicker palisade mesophyll is associated with higher photosynthetic capacity and greater pigment content, which improves light capture and overall plant growth (Terashima et al., 2011; Chen et al., 2015; Kröber et al., 2015; Harrison et al., 2021). Therefore, the ratio of palisade tissue thickness to spongy tissue thickness serves as a good proxy for leaf gas exchange and photosynthetic efficiency (Somavilla et al., 2014; He et al., 2018; Harrison et al. 2021; Liu et al., 2021). Lastly, vascular bundles are conductive tissues responsible for the transport of critical resources such as water, nutrients, sugars, and amino acids, but also, they play a fundamental role in the provision of mechanical support to the leaves (Lucas et al., 2013; Ni et al., 2022).

Although the LES has been mainly investigated from the perspective of the economics of carbon gain (Wright et al., 2004; Harrison et al., 2021; Onoda et al., 2017), the same leaf traits can also predict decomposability due to 'after life effects' (Santiago, 2007; Bakker et al., 2011; de la Riva et al., 2019; Esquivel et al., 2020). This relationship should be reflected in the connection between anatomy and litter decomposability. For instance, some evidence suggests that mesophyll cells decompose faster than upper and lower epidermis tissues due to their chemical composition (Pavlović et al., 2020). Specifically, mesophyll contains higher nitrogen in the form of proteins, while epidermis and cuticles consist of waxes, fats, and cutins that shield leaves from degradation (Pavlović et al., 2020). Other anatomical structures in leaves, such as vascular bundles, hypodermis, and air spaces, may also play a significant role in decomposability but they require further investigation (Harrison et al., 2021).

Leaf traits can change along environmental gradients, influenced by state factors such as light, soil nutrients, temperature, and water availability (Siefert et al., 2015; An et al., 2021; Xu et al., 2021; Galviz & Valerio, 2021; Ni et al., 2022). These environmental factors can vary widely with forest succession, resulting in changes in leaf traits within the community (Poorter et al., 2021a). This is particularly relevant given that secondary forests are becoming one of the most common cover in the tropics due to the pervasive landscape transformation (Chazdon et al., 2014). Nonetheless, research on changes in leaf anatomical traits at the plant community level across successional gradients in tropical regions is scarce, and their potential implications for litter decomposability remain largely unexplored.

One of the tropical regions undergoing significant transformation is located in the Andean montane forests surrounding the Colombian capital city, Bogotá, situated in Northern South America. Despite this place is the highest tropical Andean forest belt and represents a region with an extraordinary beta-diversity (Calbi et al., 2021; Hurtado-M et al., 2021; Cedillo et al., 2023), and endemism (Myers et al., 2000; Myster, 2021; Castillo-Figueroa et al., 2024), less than the 20% of the original cover remains because of the expansion of agricultural activities since the Spanish colonization and subsequent urbanization (Etter & Wyngaarden, 2000; Etter et al., 2021). Recent studies, however, have shown an increase in forest regeneration resulting from land use changes over the last few decades (Rubiano et al., 2017; Calbi et al., 2020), leading to a mosaic of forests with diverse successional pathways. Although some efforts have been made to study the functional recovery of upper Andean tropical forests (Castillo-Figueroa et al., 2023, 2025; Castillo-Figueroa & Posada, 2025), our understanding about how leaf functional traits relate to different components of the carbon cycle along successional gradients remains limited

(Castillo-Figueroa, 2021). Analyzing leaf anatomical traits along these Andean successional forests can be useful to better understand how plant communities respond to forest regeneration and whether these traits are good predictors of litter decomposability.

Successional theory suggests that leaf functional traits become more conservative as succession progresses (e.g., high LDMC, LMA, and C:N ratio; Pinho et al., 2018; Poorter et al., 2021a). This pattern arises because the successional gradient reflects a shift from environments with high nutrient and light availability to conditions of lower resources, with reduced light and nutrients (Chua & Potts, 2018; Poorter et al., 2023). Such changes drive species turnover, potentially shifting the community's strategy from acquisitive (high decomposability) to conservative (low decomposability) (Poorter et al., 2021a). Therefore, the decline in community-level decomposability along the gradient should correspond to the dynamics of community structure influencing decay rates. Based on this, one would expect a decrease in the functional diversity of leaf anatomical traits that most strongly influence decomposability as succession advances, leading to lower decay rates in old-growth forests.

In this study, we investigate the relationships between leaf anatomy and litter decomposability along a successional gradient in tropical Andean montane forests of Colombia. Based on functional traits from different leaf tissue types, our objectives were to: (1) analyze the relationships between leaf anatomical traits and litter decomposability at species level, (2) assess how leaf anatomical traits influence community litter decomposability and, (3) evaluate changes in community litter decomposability and the functional diversity of anatomical traits that best predict decay rates along the successional gradient in tropical Andean montane forests. We hypothesized that the size (thickness and area) and fractions (percentages) of tissue types such as mesophylls, epidermis, vascular bundles, and cuticles will exhibit strong associations with decomposability due to their links to physiological processes related to resource acquisition and leaf defenses that “carry over” once leaves die (H1). We also predicted that forests with higher community weighted thickness or area in protective and conductive tissues, such as cuticles, epidermis, and vascular bundles, but with lower thickness of photosynthetic tissues, including spongy and palisade mesophylls, will display lower decay rates (H2). Finally, we predicted that community litter decomposability will decrease with advancing succession because plant communities will converge towards more conservative strategies. This will result in mature forests exhibiting lower functional richness, evenness, divergence, and dispersion in anatomical traits related to decomposability (H3).

Materials and methods

Study area

The Andean region encompasses 24.5% of Colombia's territory (Etter & Wyngaarden, 2000). This region stands as the economic epicenter of the country and is home to approximately 70% of its population (DANE, 2018). This study was conducted within the Eastern Colombian Andes, specifically in the Cundiboyacense high plains, a highly transformed region situated within the tropical Andean montane forests (Etter et al., 2021).

In this region, dominant human activities include agriculture, cattle ranching, urban development, and mining (Montañez et al., 1994; Etter & Wyngaarden, 2000; Mendoza & Etter, 2002). The area surrounding the capital city of Bogotá experiences an average annual atmospheric temperature of 14°C, with mean annual precipitation ranging from 600 mm in central valleys to 1200 mm in the western regions (Clerici et al., 2016). The high plains display a bimodal precipitation pattern, characterized by two rainy periods from April to June and from October to December, separated by two drier seasons from January to March and July to September (IDEAM, 2024).

Our research took place on 14 permanent plots (20x20 m) established as part of the "Rastrojos" project (a larger network consisting of 36 20x20 m plots and eight 50x50 m plots, see acknowledgments). These 14 plots were originally set up in 2013 within private properties/reserves in upper Andean tropical forests at four distinct sites, at elevations ranging from 2685 to 3140 m (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023; Castillo-Figueroa & Posada, 2025). The four study sites were: Torca (4° 48' 48.674" N, 74° 0' 58.527" W, 2708-2965m), Tabio (4° 55' 33.961" N, 74° 6' 47.225" W, 2685-2821m), Guasca (4° 47' 20.318" N, 73° 54' 31.812" W, 3085-3140m), and Guatavita (4° 56' 9.716" N, 73° 53' 54.237" W, 3028-3035 m) (Figure S1).

At these sites, the 14 permanent plots were evenly distributed between secondary (seven plots) and mature forests (seven plots) across the study locations of Tabio (two per successional stage), Guasca (two per successional stage), Torca (three in mature forest and one in secondary forest), and Guatavita (two in secondary forest). Mature and secondary forests were categorized based on structural attributes such as tree height, tree density, basal area, and species composition, according to previous studies (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023). Among the plant families found in these plots, Ericaceae, Melastomataceae, Cunoniaceae, Primulaceae, and Asteraceae collectively constitute 56% of all individuals with a basal diameter exceeding 5 cm. The most dominant genera include *Miconia*, *Weinmannia*, *Cavendishia*, *Myrsine*, and *Myrcianthes*, which together account for 51% of all individuals. In the study area, we identified a total of 63 species of shrubs and trees, with the dominant species being *Weinmannia tomentosa* Linnaeus filius 1782, *Cavendishia bracteata* Hoerold 1909, *Miconia ligustrina* Triana 1872, *Miconia squamulosa* Triana 1872, and *Myrcianthes leucoxyla* McVaugh 1963 (Clerici et al., 2016; Castillo-Figueroa et al., 2023).

Litter decomposition set-up

We set-up a reciprocal translocation field decomposition experiment with 15 upper Andean tropical species in the 14 permanent plots between October 2021 and April 2023 (Castillo-Figueroa et al., 2025). These species belonged to 15 families and 12 orders and were selected based on two criteria: (1) the dominance of the species (Table S1), considering that the most abundant ones would contribute more significantly to litter on the forest floor (Salinas et al., 2011; Esquivel et al., 2020); and (2) the representation of species in the functional trait space within the plots (Canessa et al., 2021), based on previous analyses (Table S2; Castillo-Figueroa et al., 2025).

We prepared three independent litterbeds per plot for a total of 42 litterbeds. Each litterbed was placed directly on the forest floor, trying to minimize disturbance to the soil and with a minimal distance of 5 m between them. We avoided forest gaps, topographic depressions, and very irregular soil conditions. Each litterbed was made of 60 litterbags with four litterbags per species arranged clockwise according to consecutive harvesting times (3, 6, 12, and 18 months). The distance between litterbags of different species (15 taxa) was 10 cm. Litterbags were made of fiber glass (10x15 cm) with a mesh size of 2 mm that contained ca. 2 g of oven dried litter (60 ºC). This resulted in a total of 2520 litterbags in the decomposition experiment (15 species x 4 times x 42 litterbags).

We collected one litterbag per species from each litterbed at each of the four harvesting times. In the laboratory, the contents of the litterbags were sorted to separate litter from fine roots, forbs, mushrooms, mineral soil particles, and soil fauna. The litter material was gently cleaned with a brush to remove mineral soil particles and then was oven-dried at 60°C for 72 hours and weighed using a precision scale with a sensitivity of 0.1 mg (LX 220A scs) to determine both initial and final weights.

Foliar functional traits

We measured green leaf traits for all 63 species present in the 14 permanent plots, collecting three leaves from three individuals per species (Posada et al., unpublished). Leaves were collected from the sunny canopy using a branch cutter, within the permanent plots, following standardized protocols (Pérez-Harguindeguy et al., 2013). We measured one-sided leaf area by scanning the leaves and analyzing the resulting images using ImageJ (Schneider et al., 2012, https://imagej.nih.gov/ij/). To determine maximum fresh mass (g), we rehydrated leaves in plastic bags filled with moist paper for 24-48 hours at a low temperature (4°C) in the dark, following the complete rehydration method proposed by Garnier et al. (2001). Each leaf sample was then dried in the oven at 60°C for 72 hours to determine its dry mass (g). From these measurements we obtained Leaf Mass per Area (LMA, g m^{-2}), its reciprocal Specific Leaf Area (SLA, cm2 g^{-1}), and Leaf Dry Matter Content (LDMC, mg g^{-1}). We also measured Leaf Nitrogen Content (LNC, mg g^{-1}), Leaf Carbon Content (LCC, mg g^{-1}) and Carbon-to-Nitrogen content ratio (C:N) using an Elemental Analyzer (FlashSmart™ Thermo Fisher Scientific, USA). Finally, we measured leaf photosynthetic capacity (Amax, nmol g^{-1} s^{-1}) by exposing leaves to a saturating photosynthetic photon flux density (PPFD, µmol m^{-2} s^{-1}) using an infrared gas analyzer (LiCor, LI-6400XT) equipped with a red-blue light source (LiCor, 6400-02B).

Leaf anatomical traits

For leaf anatomical traits, we measured the cuticle, epidermis, hypodermis, palisade mesophylls, spongy mesophylls, vascular bundles, and air space from the 63 species present in the 14 permanent plots (Figure S2, Table 1). To do this, we collected three sun leaves from three individuals for each species directly in the permanent plots. Then, we cut rectangular sections (1.0x0.5 cm) of the leaf lamina, including the midrib, which were then fixed in Formalin-Acetic acid-Alcohol (FAA, 50 ml 38% formalin, 50 ml glacial acetic acid, 70% ethanol 900 ml) (He et al., 2018). Leaf tissues were gradually dehydrated in an ethanol series (50%, 70%, 85%, 95%, 100%) and were infiltrated with hot paraffin (He et al., 2018; Harrison et al., 2021).

Transverse sections of the leaf were cut with a Leica RM2255 microtome to obtain a flat surface for the subsequent estimation of cell fractions. The anatomical cuts of the leaves had a thickness between 5 and 7 µm. Lignified tissues were red-stained using Safranin and non-lignified tissues were stained with Toluidine blue, and then mounted in slides (Bancroft and Cook 1984; He et al., 2018). Then, we took photographs using a reflected (episcopic) light illumination microscope (Leica DM 750) equipped with a digital camera (Leica MC170 HD) with a 10X objective lenses. Calibration was done with a Nikon micrometer (MBM 11100 stage micrometer type A) with a 1 mm ruler with 0.01 mm graduations (i.e., 10 µm). For each individual, we took 10 focused images of different leaf segments for a total of 30 images per species.

Measurements of anatomical traits were conducted in the software ImageJ (Schneider et al., 2012, https://imagej.nih.gov/ij/). From each anatomical image, the thickness of the cuticles, epidermis, hypodermis (if any), palisade and spongy mesophylls, and vascular bundles were measured (Figure S2, Table 1), resulting in a total of 10 measurements per leaf and 30 per species for each trait. In the case of epidermis and cuticles, both adaxial and abaxial thickness were measured. Based on these thickness measurements, we also calculated percentages (%) of each anatomical trait relative to the total leaf thickness. To measure % air spaces, we selected 10 rectangles that were 100 µm wide by the total leaf thickness and calculated the area with and without leaf tissue (Figure S2, Table 1; Harrison et al., 2021). We enhanced these sections for color and contrast, and then transformed them into black (cell tissues) and white (air space) in the software ImageJ (Harrison et al., 2021).

Ratios of adaxial epidermis/palisade mesophyll thickness, adaxial epidermis/spongy mesophyll thickness, palisade/spongy mesophyll thickness, adaxial/abaxial epidermis thickness, and adaxial/abaxial cuticle thickness were obtained per image (Table 1). We also measured the length and width of 10 random cells from both the adaxial and abaxial epidermis, palisade and spongy mesophylls to compute cell aspect ratios (i.e., width/length) (Table 1, Figure S2). Higher values correspond to cells with more circular or squared shapes, while lower values correspond to more cylindrical or rectangular shapes. Given that this study focused on interspecific variations, we did not account for intraspecific variability. Therefore, all measurements of anatomical traits were averaged at the species level.

Table 1. Description of leaf anatomical traits based on thickness measurements, percentage of tissues (relative to leaf thickness), tissue ratios, and cell shapes**.**

Leaf anatomical trait	**Acronym**	**Unit**
Thickness measurements		
Adaxial cuticle thickness	AdCT	µm
Abaxial cuticle thickness	AbCT	µm
Adaxial epidermis thickness	AdET	µm
Abaxial epidermis thickness	AbET	µm
Adaxial hypodermis thickness	AdHT	µm
Palisade mesophyll thickness	PMT	µm
Spongy mesophyll thickness	SMT	µm
Vascular bundle diameter	VBD	µm
Leaf thickness	LT	µm
Air space	AS	μm^2
Vascular bundle area	VBA	μm^2
Leaf total area	LTA	μm^2
Leaf area cell tissue	LACT	μm^2
Percentage of tissues (relative to LT)		
Percentage of Adaxial cuticle thickness	%AdCT	%
Percentage of Abaxial cuticle thickness	%AbCT	%
Percentage of Adaxial epidermis thickness	%AdET	%
Percentage of Abaxial epidermis thickness	%AbET	%
Percentage of Adaxial hypodermis thickness	%AdHT	%
Percentage of Palisade mesophyll thickness	%PMT	%
Percentage of Spongy mesophyll thickness	%SMT	%
Percentage of Air space	%AS	%
Tissue ratios		
Adaxial epidermis thickness / Palisade mesophyll thickness	AdET/PMT	Adimensional
Adaxial epidermis thickness/ Spongy mesophyll thickness	AdET/SMT	Adimensional
Palisade mesophyll thickness/ Spongy mesophyll thickness	PMT/SMT	Adimensional
Adaxial epidermis thickness/ Abaxial epidermis thickness	AdET/AbET	Adimensional
Adaxial cuticle thickness/ Abaxial cuticle thickness	AdCT/AbCT	Adimensional
Cell shapes		
Adaxial epidermis cell width	AdEw	µm
Adaxial epidermis cell long	AdEl	µm
Palisade mesophyll cell width	PMw	µm
Palisade mesophyll cell long	PMl	µm
Spongy mesophyll cell width	SMw	µm
Spongy mesophyll cell long	SMl	µm
Abaxial epidermis cell width	AbEw	µm
Abaxial epidermis cell long	AbEl	µm
Aspect ratio of Adaxial epidermis cells	As AdEc	Adimensional
Aspect ratio of Palisade mesophyll cells	As PMc	Adimensional
Aspect ratio of Spongy mesophyll cells	As SMc	Adimensional
Aspect ratio of Abaxial epidermis cells	As AbEc	Adimensional

Statistical analysis

To estimate decay rates coefficients per year (K rate y^{-1}), we followed the negative exponential model (Jenny et al., 1949; Olson, 1963), using the mass loss obtained for each species at the harvesting time of 12 months:

$$Y_t = Y_o * \exp^{(-kx)}$$

where Yt represents the remaining dry weight of leaf litter after time t, Yo indicates the initial dry weight of leaf litter (maximum Y value), k depicts the decomposition constant that determines the steepness of the curve, and x is the time for decomposition (years) (Berg & McClaugherty, 2020). With this equation, we obtained mean decomposition constants for each species (K rate y^{-1}, species = 15) as follows:

$$\frac{\ln(Yt/Y0)}{x} = -k$$

We obtained Spearman correlations (rho coefficients) between anatomical traits and decay rates (H1), as Shapiro-Wilk test for multivariate normality indicated a deviation from normality ($P < 0.01$). Correlations were divided in four separate plots: thickness measurements, percentage of tissues (relative to the leaf thickness), tissue ratios, and cell shapes (Table 1). To evaluate the association between leaf anatomical traits, foliar traits, and decomposability, we conducted a Principal Component Analysis (PCA) using functional traits and decay rates as variables, with species as data points (n = 15), following the approach outlined by Bakker et al. (2011). Given the limited number of species, we ran a PCA using the variables that were significantly correlated with decay rates in the Spearman correlation plots, excluding those with high intercorrelation (rho > 0.85). Additionally, we included the LMA, LDMC, and C:N ratio measured for these species.

To analyze the community-level response (H2), we did a multiple linear regression model between decay rates and the four foliar traits (i.e., SLA, LNC, LCC, Amax) measured in the 15 species that were part of the decomposition experiment ($R^2 = 0.71$, see Results). We selected these traits as they are the baseline of the LES (Wright et al., 2004; Reich, 2014), which is strongly related to decomposition (Santiago, 2007; Bakker et al., 2011; de la Riva et al., 2019). Then, we used the parameters of this multiple regression model to estimate decay rates for the remaining 48 species in our plots with their foliar traits measured (Table S3). Following, we calculated Community-Weighted Mean (CWM) of decomposability per plot (CWM K rate y^{-1}) by weighting each estimated decay rate value by the biomass of each individual species in the plot (Castillo-Figueroa et al., 2023). This assumption was grounded on the premise that plot decay rates are primarily influenced by the species with the highest biomass, rather than the overall number of species in the community (i.e., mass ratio effect; Garnier et al., 2004; de la Riva et al., 2019). We then estimated biomass weighted CWM of each anatomical trait and performed reduced major axis regressions analyses with 95% bootstrapped confidence intervals of the slopes (n = 1999) between each one of these traits and CWM K rate y^{-1}. Aboveground Biomass (AGB) in each plot was calculated by using allometric equations developed for tropical Andean montane forests (Sierra et al., 2007; Pérez & Díaz, 2010).

Lastly, to analyze changes in community litter decomposability and the functional diversity of anatomical traits that best predict decay rates along the successional gradient (H3), we did a stepwise multiple linear regression model with the traits that exhibited significant relations with CWM K rate y^{-1}. We used AGB as a proxy for succession, as it is a widely accepted indicator of forest recovery (Garnier et al., 2004, 2016; Lohbeck et al., 2015; Poorter et al., 2021b). To prevent multicollinearity between anatomical traits, we assessed the Variance Inflation Factor (VIF) for each trait. We included traits with VIF values below 1.1, to prevent collinearity between our variables (Neter et al., 1990). We assessed the best model based on the Adjusted R^2 and Root Mean Squared Error (RMSE). Adjusted R^2 offers a relative measure of model fit, considering the number of predictors and penalizing the inclusion of irrelevant variables to prevent overfitting (James et al., 2013), while RMSE provides a direct measure of prediction accuracy by quantifying the average deviation of predicted values from actual values in the same units as the dependent variable (Chatterjee & Hadi, 2015). This enabled us to identify the anatomical traits that best predicted CWM K rate y^{-1} to compute functional richness (i.e., volume of the functional trait space occupied by the community), evenness (i.e., species abundances distribution across the functional trait space), divergence (i.e., deviance of abundance from the center of gravity of the functional space), and dispersion (i.e., abundance-weighted distance of species from the trait space centroid) (Mason et al., 2005; Villéger et al., 2008; Schmera et al., 2023). To standardize functional traits, we transformed the trait values into a common scale using Z-scores, with a mean of 0 and a standard deviation of 1 (Zar, 1999). We regressed AGB on CWM K rate y^{-1} as well as on each of the functional diversity indices to analyze the dynamics of community structure underlying decomposability along the successional gradient. Bar plots showing mean values with 95% confidence intervals for each variable in mature and secondary forests were included to provide complementary information. All the analyses were conducted in PAST 4.14 (Hammer, 2001) and JASP 0.14.1.0 (JASP Team, 2023) and Fdiversity (Casanoves et al., 2011).

Results

Anatomical traits

Leaf anatomy from the 15 plant species of the experiment exhibited high variation in all the tissues measured. Average values and standard deviations of leaf tissues across these plant species are presented in Table S4. AdCT varied ca eight folds (2.68 to 22.52 µm); AdET ca five folds (8.70 to 44.11 µm); AdHT, when present, ca six fold (17.54 to 111.73 µm); PMT ca two folds (53.79 to 144.04 µm); SMT ca ten folds (56.90 to 567.48 µm); AbET ca three folds (7.38 to 22.58 µm); AbCT ca four folds (2.30 to 10.44 µm); AS ca 11-folds (702.88 to 8202.49 μm^2); VBA ca 46-folds (1287 to 59821.36 μm^2); VBD ca seven folds (41.99 to 331.40 µm), and LT ca five folds (157.62 to 832.06 µm) (Table S4).

Anatomical leaf traits were positively correlated between them in 52 of the 78 possible correlations (66.7%), while they were not correlated in the remaining 26 cases (33.3%) (Figure 1a). AdHT was the only trait that was not correlated to any mainly because it was only present in a few species. Lastly, PMT thickness was not correlated to the other traits, except for LT, LTA y LACT (Figure 1a).

Correlations between leaf anatomy and species decay rates

We found significant negative correlations between decay rate and the size of the AdCT ($P = 0.002$, rho = -0.75, $n = 15$), AbCT ($P = 0.011$, rho = -0.65, $n = 15$), VBA ($P = 0.010$, rho = -0.65, $n = 15$), and VBD ($P = 0.007$, rho = -0.68, $n = 15$) (Figure 1a). We also found negative correlations between K rate y^{-1} and %AdCT ($P = 0.013$, rho = -0.64, $n = 15$), %SMT ($P = 0.008$, rho = -0.67, $n = 15$), % AbCT ($P = 0.036$, rho = -0.55, $n = 15$), and %AS ($P = 0.021$, rho = -0.60, $n = 15$), while K rate y^{-1} was positively related to %PMT ($P = 0.012$, rho = 0.64, $n = 15$) (Figure 1b). Only the ratio PMT/SMT was related to K rate y^{-1} ($P = 0.005$, rho = 0.70, $n = 15$) and the relationship was positive (Figure 1c). Regarding cell size and shape, we only found a negative relationship between PMw ($P = 0.035$, rho = -0.55, $n = 15$) and K rate y^{-1} (Figure 1d).

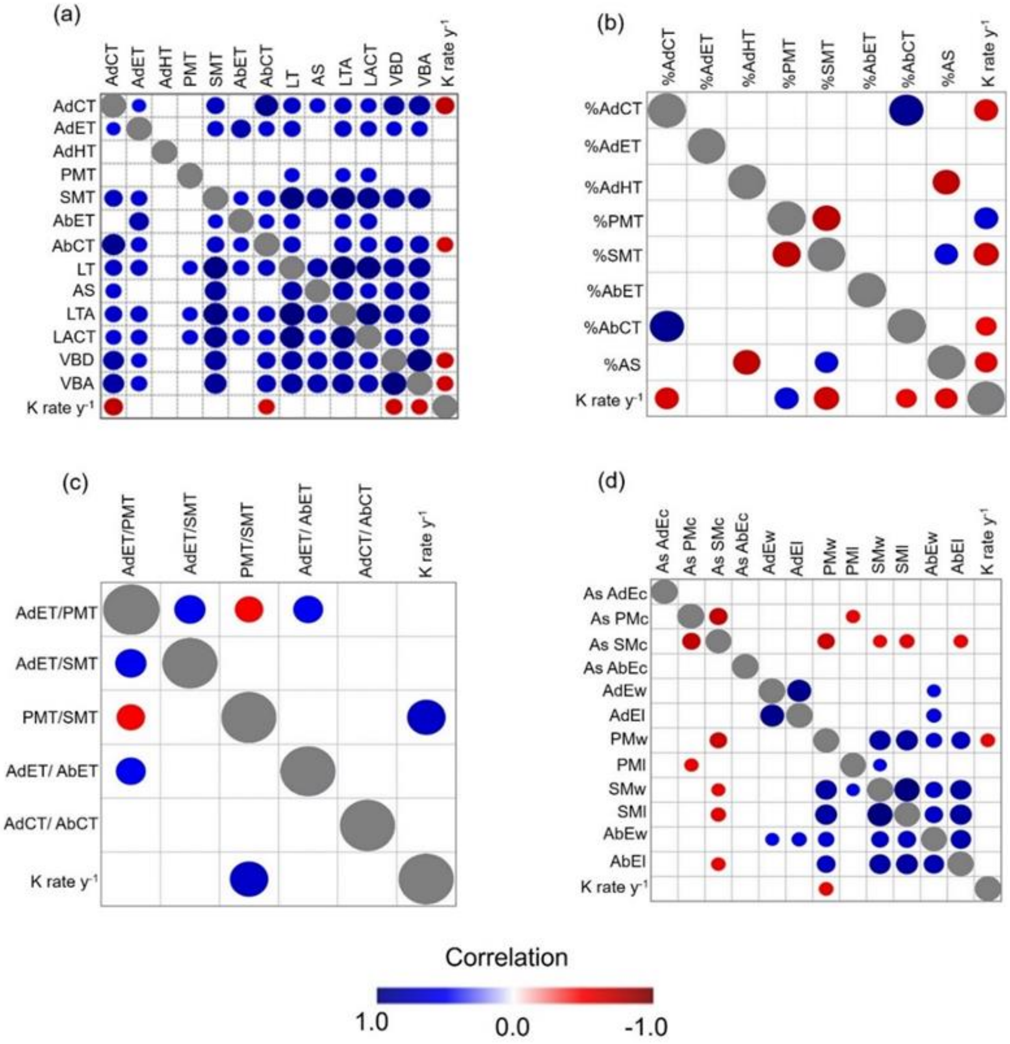

Figure 1. Spearman correlations between anatomical traits and (a) decomposition considering absolute thickness measurements (b) percentage of the tissues (c) ratios between tissues (d) and cell shapes. Positive correlations are indicated in blue, while negative correlations are represented in red. The legend color corresponds to the correlation coefficient and its gradient. The color intensity varies proportionally with the correlation coefficients from -1 to 1. In cases where the indicator is not statistically significant ($P > 0.05$), it is symbolized with blank. Acronyms can be found in Table 1.

Multidimensional relationships between anatomical and foliar traits, with decay rates were analyzed with the PCA (Figure 2). The first axis explained 53.76% of the variation, and was positively related to LMA, C:N, VBD, AdCT, PMw, %SMT and %AS, but it was negatively related to %PMT, PMT/SMT and decay rates. The second axis explained 15.14% of the variation and was positively related to %AbCT and LDMC (Figure 2). Species are clustered in this multivariate foliar and anatomical space according to their decomposability. Species with high decay rates, such as *Piper bogotense* (Pibo) and *Croton bogotanus* (Crbo), were positioned at the left extreme of the first axis, while species that exhibit low decay rates, such as *Cavendishia bracteata* (Cabr) and *Clusia multiflora* (Clmu), were positioned on the right side of the first axis. Nevertheless, litter species occupied different positions in the multivariate functional space, indicating a diversity of combinations between anatomical traits.

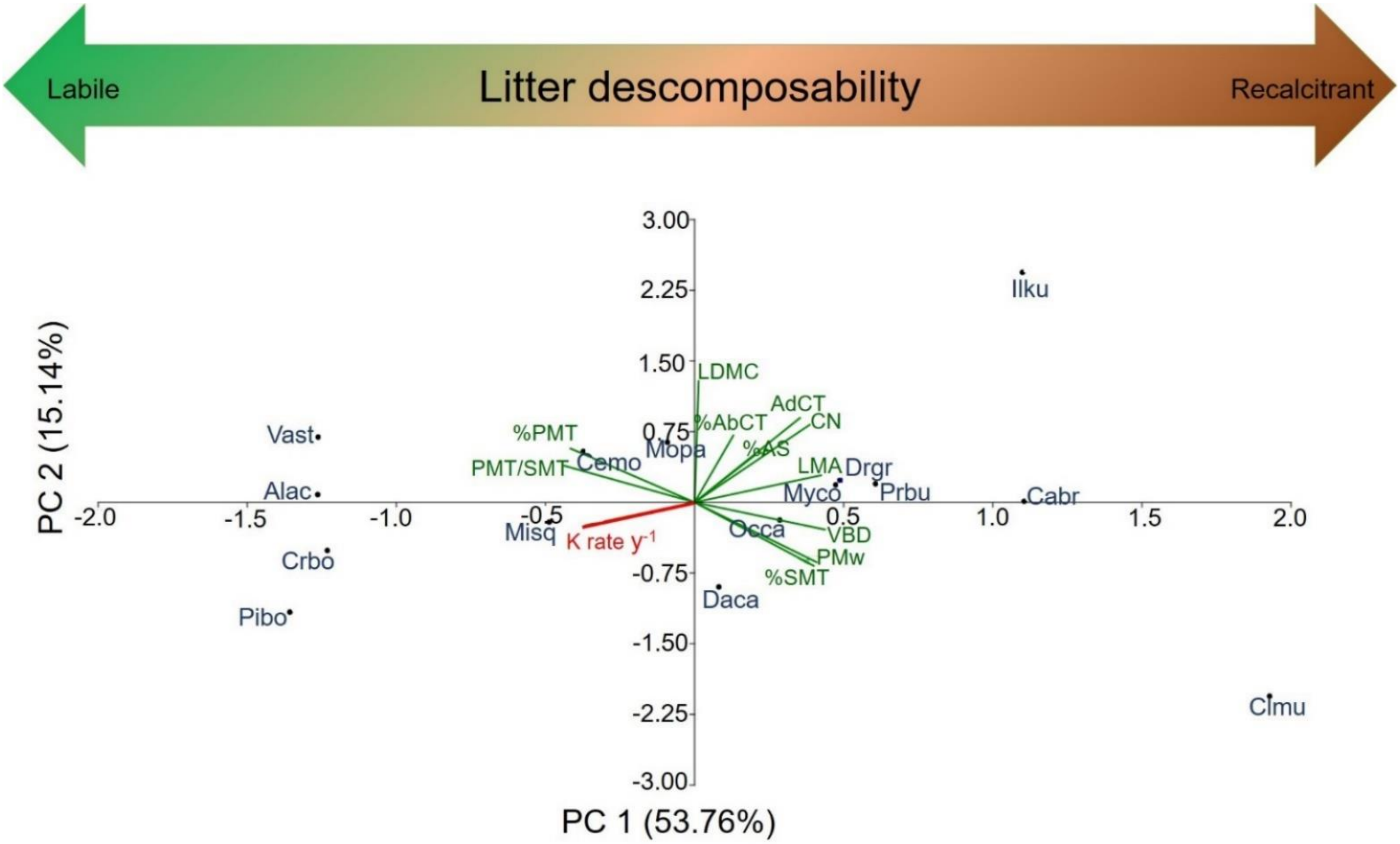

Figure 2. Principal component analysis between anatomical traits and decay rates (K rate y^{-1}, in red). The leaf functional traits are shown in green: %Abaxial cuticle thickness (%AbCT), Adaxial cuticle thickness (AdCT, µm), Pallisade mesophyll cell width (PMl, µm), %Pallisade mesophyll thickness (%PMT), %Spongy mesophyll thickness (%SMT), %Air space (%AS), Vascular bundle diameter (VBD, µm), Pallisade/Spongy ratio(PMT/SMT), Leaf mass per area (LMA, g m^{-2}), Leaf carbon: nitrogen ratio (C:N), and Leaf dry matter content (LDMC, mg g^{-1}). The 15 litter species are shown in blue: *Alnus acuminata* (Alac), *Cavendishia bracteata* (Cabr), *Cedrela montana* (Cemo), *Clusia multiflora* (Clmu), *Croton bogotanus* (Crbo), *Daphnopsis caracasana* (Daca), *Drimys granadensis* (Drgr), *Ilex kunthiana* (Ilku), *Miconia squamulosa* (Misq), *Morella parvifolia* (Mopa), *Myrsine coriacea* (Myco), *Ocotea calophylla* (Occa), *Piper bogotense* (Pibo), *Prunus buxifolia* (Prbu), *Vallea stipularis* (Vast).

Leaf anatomy and decomposability at community level

We estimated decay rates for each of the 63 species through a multiple regression analysis based on SLA (cm^2/g), LNC (mg/g), LCC (mg/g), and Amax (nmol g s^{-1}). These four traits predicted 71% of the variation in decay rates of the 15 species from the decomposition experiment (P = 0.009, r = 0.84, R^2 = 0.71, n = 15, Table S3). Following, we calculated community-level decomposability per plot to estimate the relationships between CWM K rate y^{-1} and CWM of each leaf anatomical trait. This modelled CWM K rate y^{-1} showed and average of 0.42 ± 0.13, ranging from 0.22 to 0.70.

Similar to the species Spearman correlation analysis, we found strong negative relationships between modelled CWM K rate y^{-1} and traits measured for all 63 species for: CWM AdCT (P = 0.00011, R^2 = 0.72, n = 14, CI = [-0.08, -0.04]), CWM AbCT (P = 0.0021, R^2= 0.56, n=14, CI = [-0.16, -0.08]), CWM %AdCT (P = 0.0046, R^2 = 0.50, n = 14, C I= [-0.42, 0.19]), CWM %AbCT (P = 0.047, R^2 = 0.29, n = 14, CI = [-1.51, -0.26]), CWM VBD (P = 0.00061, R^2 = 0.64, n = 14, CI = [-0.005, -0.002]), CWM VBA (P = 0.018, R^2 = 0.38, n = 14, CI = [-0.00002,-0.0000007]), CWM LT (P = 0.046, R^2 = 0.29, n = 14, CI = [-0.003, 0.0002]), and CWM As PMc (P = 0.00031, R^2 = 0.68, n = 14, CI = [-6.53, -2.97]). In contrast, significant positive relationships were observed between CWM K rate y-1 and CWM As SMc (P = 0.036, R^2 = 0.32, n = 14, CI = [1.30, 7.06]), CWM PMI (P = 0.022; R^2 = 0.36, n = 14, CI = [0.02, 0.04]), CWM PMT/SMT (P = 0.00010, R^2 = 0.73, n = 14, CI = [0.58, 1.18]), and CWM %PM (P = 0.00031, R^2 = 0.68, n =14, CI = [0.02, 0.04]) (Figure 3).

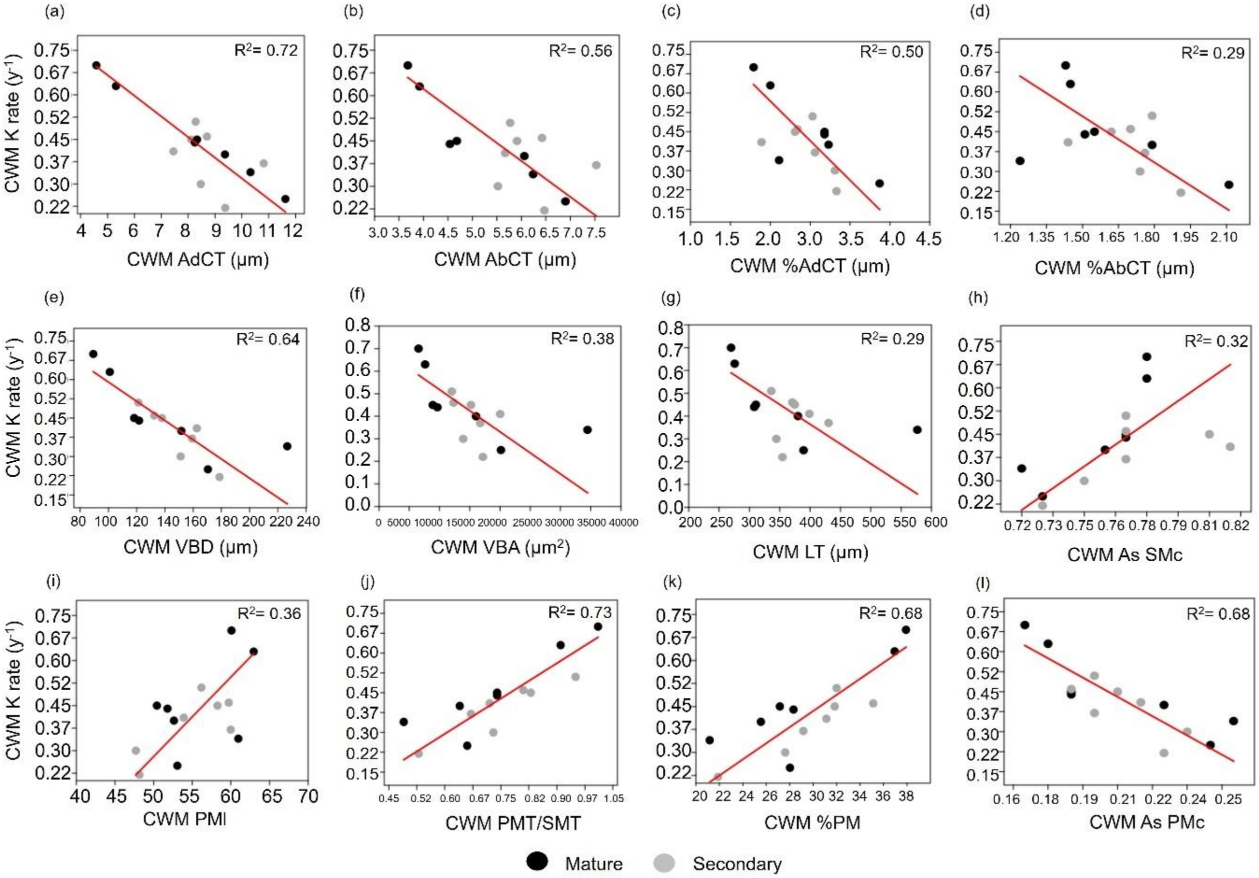

Figure 3. Reduced major axis regressions between Community Weighed Mean of decomposability (CWM K rate y^{-1}) and CWM of (a) Adaxial cuticle thickness (CWM AdCT, μm), (b) Abaxial cuticle thickness (CWM AbCT, μm), (c) %Adaxial cuticle thickness (CWM %AdCT), (d) %Abaxial cuticle thickness (CWM %AbCT), (e) Vascular bundle diameter (CWM VBD, μm), (f) Vascular bundle area (CWM VBA, μm^2), (g) Leaf thickness (CWM LT, μm), (h) Aspect ratio Spongy mesophyll cells (CWM As SMc), (i) Pallisade mesophyll cell length (CWM PMl, μm), (j) Pallisade mesophyll/ Spongy mesophyll ratio (CWM PMT/SMT), (k) %Pallisade mesophyll (CWM %PM), and (l) Aspect ratio Pallisade mesophyll cells (CWM As PMc). Dark dots represent mature forests and grey dots depict secondary forests. In the upper right corner of each plot the size effect is presented (R^2). Red lines indicate significant relations between variables ($P < 0.05$).

Functional diversity and decomposability along succession

Based on the multiple regression model with the anatomical traits that best predicted decay rates at the community level (i.e, CWM PMT/SMT and CWM %AbCT, $R^2 = 0.89$, Table 2), we calculated functional richness, functional evenness, functional divergence, and functional dispersion. Although CWM K rate y-1 ($P = 0.761$, $R^2 = 0.008$, n = 14, CI = [-0.02, -0.003]), functional divergence ($P = 0.313$, $R^2 = 0.08$, n = 14, CI = [-0.02, -0.002]), and functional dispersion ($P = 0.905$, $R^2 = 0.001$, n = 14, CI = [-0.03, 0.005]) did not correlate with AGB, we found that functional richness significantly increased with increasing AGB ($P = 0.0046$, $R^2 = 0.50$, n =14, CI = [0.06, 0.14]), while functional evenness significantly decreased with AGB ($P < 0.0001$, $R^2 = 0.77$, n = 14, CI = [-0.004, -0.002]) (Figure 4).

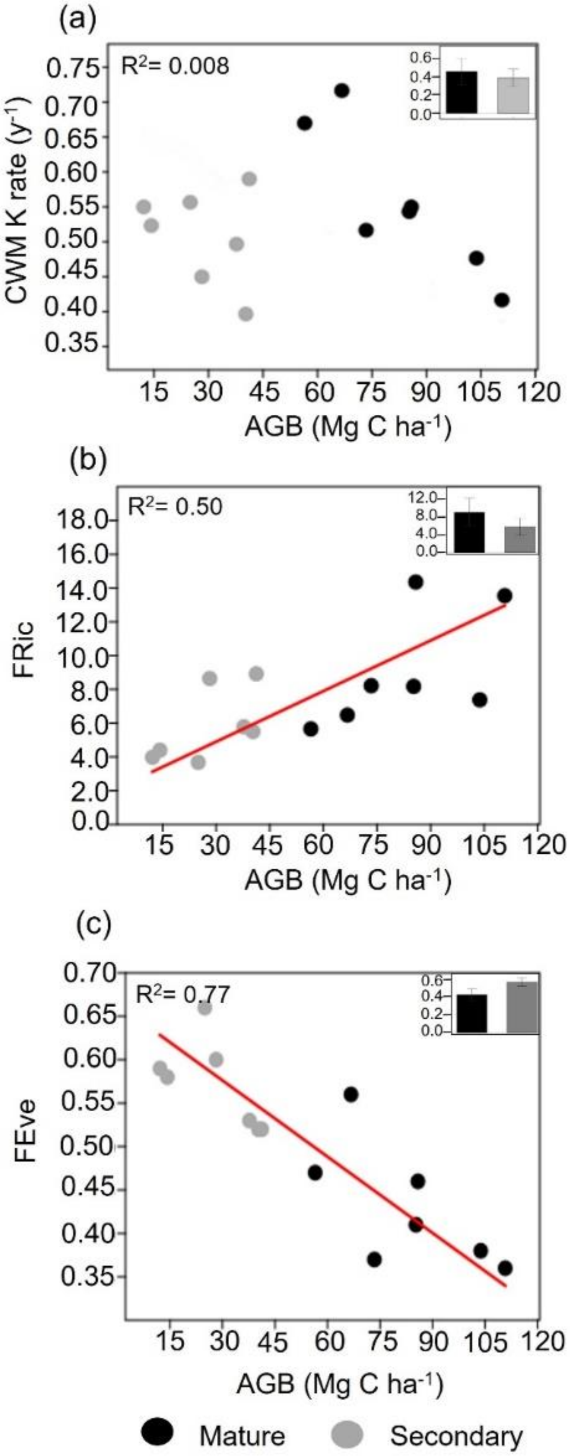

Figure 4. Reduced major axis regressions between aboveground biomass (Mg C ha^{-1}) as a proxy of succession and (a) Community Weighed Mean of decomposability (CWM K rate y^{-1}) (b) functional richness (FRic) and (c) functional evenness (FEve). In the upper left corner of each plot the size effect is presented (R^2). In the upper right corner, bar plots comparing mature and secondary forests are presented with 95% confidence intervals. Dark dots represent mature forests and grey dots depict secondary forests. Red lines indicate significant relations between variables ($P < 0.05$).

Table 2. Results from stepwise multiple linear regression model applied to decay rates (CWM K rate y^{-1}). The following covariates were considered but not included: CWM AdCT, CWM %PMT, CWM %AdCT, CWM As SMc, CWM As PMc, CWM PMl, CWM AbCT, CWM VBA, CWM VBD, and CWM LT. VIF represents the Variance Inflation Factor.

							Collinearity Statistics	
Model		**Unstandardized**	**Standard Error**	**Standardized**	**t**	**P**	**Tolerance**	**VIF**
Community level								
1	(Intercept)	0.424	0.035		11.996	< .001		
2	(Intercept)	-0.142	0.101		-1.405	0.185		
	CWM.PMT/SMT	0.760	0.134	0.854	5.689	< .001	1.000	1.000
3	(Intercept)	0.295	0.124		2.370	0.037		
	CWM.PMT/SMT	0.701	0.088	0.788	7.946	< .001	0.974	1.026
	CWM %AbCT.	-0.239	0.058	-0.411	-4.147	0.002	0.974	1.026
Model summary: R = 0.95, R^2 = 0.89, Adjusted R^2 = 0.88, RMSE = 0.047, P = 0.002								

Discussion

Our study consistently demonstrates that multiple leaf anatomical traits are strong predictors of litter decomposability at both species and community levels in tropical Andean montane forests. In addition to the well-known ‘soft’ leaf functional traits, we show that ‘hard’ anatomical traits including cuticles, mesophyll tissues, and vascular bundles, are highly correlated with decay rates. However, community-level decomposability showed no significant variation along the successional gradient, likely due to the counterbalancing effects of different dimensions of functional diversity, suggesting that distinct dynamics in community structure influence decay rates in secondary and mature forests.

Leaf anatomy and its connection to species decomposability

Our first hypothesis (H1) was supported as we found strong correlations between litter decomposability of individual species and fractions of tissue types from mesophyll, vascular bundles, and cuticle, with the exception of the epidermis. Specifically, we found significant negative correlations between decay rates and both abaxial and adaxial cuticle thickness (Figure 1a), which could be attributed to the mechanical and chemical resistance that the cuticle provides to the leaf. Acting as the outer protective layer of leaves, cuticles are composed of recalcitrant compounds like cutins, waxes, and polysaccharides, playing a fundamental role in shielding leaves from damage caused by different environmental and biotic stressors, such as wind, insects, pathogens, and microbial decomposers (Müller, 2006; Riederer & Mülller, 2006; Onoda et al., 2012). Thicker cuticles offer an important advantage in enhancing resistance due to their greater structural thickness and the strength of their constituent materials, resulting in longer leaf lifespans and a deceleration of decay rates (Onoda et al., 2012). Indeed, leaves with high cuticle thickness in both abaxial and adaxial side are strongly related to LMA (AdCT: P = 0.00019, R^2 = 0.67, n = 15, CI = [2.20, 14.97], AbCT: P = 0.0012, R^2 = 0.57, n = 15, CI = [6.40, 24.01]), which defines the plant ecological strategy along the LES (Figure 2, Wright et al., 2004). Furthermore, cutins decompose at a slower rate compared to other proteins and carbohydrates, and they exhibit long retention times in soil (Gallardo & Merino, 1993; Goni & Hedges, 1995; Onoda et al., 2012). This is mainly attributed to cutins being more resistant to chemical degradation (Schreiber & Schönherr, 2009), and given that the cuticle constitutes a significant fraction of leaf dry mass in plant species (Onoda et al., 2012), this anatomical structure appears to be crucial in determining the role of decomposition in ecosystem carbon cycling. In this sense, our findings corroborate the insights of Onoda et al. (2012), who emphasized the potential significant role of cuticle thickness in shaping carbon turnover and accumulation in ecosystems.

Contrary to our initial expectations, we found no correlation between the epidermis, expressed as thickness or a proportion of total leaf size, with decay rates in either the adaxial or abaxial layer (Figure 1a). While the leaf epidermis is traditionally recognized for its role in providing a protective barrier against mechanical injury, pathogens, and UV radiation, this tissue serves to other functions, including water conservation, osmoregulation, secretion of substances, reflecting and absorbing light, structural support, and even sensory functions (Dietz & Hartung, 1996; Glover, 2000; Javelle et al., 2011; Cavé-Radet et al., 2020; Galviz & Valerio, 2021). Given that the epidermis is the outermost layer of cells interacting with a plenty of environmental variables, and has multiple functions, its variations may respond to different trade-offs, potentially weakening its relationship with decay rates.

Significant negative associations were also observed between vascular bundle size and decay rates (Figure 1a). This finding can be explained due to the direct deposition of lignin within the cell walls of xylem and phloem tissues (Barros et al., 2015; Maceda et al., 2021), which facilitates long-distance water transport through the plant (Ménard et al., 2022). Consequently, plants with larger diameters and increased vascular bundle areas contain a substantial proportion of this recalcitrant polyphenolic polymer, making it difficult to degrade. Collectively, the presence of larger vascular bundles and thicker cuticles suggests that traits related to water use efficiency and mechanical resistance are integral components of plant ecological strategies (Figure 2), despite the higher construction costs associated with them (Xing et al., 2021; Ni et al., 2022). These strategies lead to extended leaf lifespans and slower decay rates.

Even though absolute palisade thickness showed no significant correlation with decay rates, the proportion of palisade tissue (%) and its ratio to spongy tissue thickness exhibited a strong positive relationship with decay rates (Figure 1). This result aligns with our initial hypothesis (H1), as palisade tissues contain chloroplasts with high concentration of nitrogen allocated to the photosynthetic machinery (Evans, 1989; Terashima et al., 2011; Onoda et al., 2017). Consequently, leaves with a high percentage of palisade tissue likely increase the litter quality, thus becoming particularly attractive to decomposers. This effect is likely to be magnified in ecosystems with pronounced nitrogen constraints, such as the tropical Andean montane forests (Vitousek et al., 1988; Tanner et al., 1998; Wilcke et al. ,2008; Myster, 2021), where decomposers actively seek out leaves with elevated nitrogen content due to its essential role in their metabolism (Bakker et al., 2011) and its scarcity in such environments (Vitousek et al., 1988; Tanner et al., 1998; Soethe et al., 2008). Interestingly, we also observed a negative relationship between the width of palisade cells and decay rates (Figure 1), suggesting that the shape of palisade cells may be linked to decomposability. The development of elongated and cylindrical cells is promoted by phototropins triggered by blue light (Watson, 1942; Kozuka et al., 2011). This unique cell shape maximizes photosynthesis by aligning perpendicularly to the epidermis (Terashima & Saeki, 1983; Terashima et al., 2006), which could potentially allocate more resources for decomposers. In line with this idea, we found a positive relation between palisade long and its thickness (P = 0.01, rho = 0.63, n =15). This effect is also consistent at the community level (see below).

Community-level relationships between leaf anatomy and decomposability

We confirm the same results observed at the species level concerning the negative correlations with cuticles and vascular bundles and the positive ones with palisade mesophylls, supporting our second hypothesis (H2, Figure 1 and 4). However, at the community level, we also found significant relationships with other anatomical structures. In particular, higher leaf anatomical thickness is negatively associated with decay rates (Figure 3g). Thicker leaves are also related to a higher LMA at both species (P = 0.002, rho = 0.72, n = 15) and community levels (P = 0.002, rho = 0.75, n = 14), which, in turn, can decrease decay rates (Wright et al., 2004; Onoda et al., 2012; Wang et al., 2025). Higher leaf thickness may result from increased mass investment in leaf tissues, which consequently increases LMA (John et al., 2017), as our findings show that leaf thickness is positively correlated with the thickness of nearly all tissues (Figure 1). Considering that studies in the upper Andean tropical forests have indicated that plant communities tend to exhibit more conservative strategies, characterized by leaves with high leaf thickness, high leaf toughness, and high LDMC (Homeier et al., 2021; Báez et al., 2022; Martínez-Villa et al., 2024), it is likely that these traits are also related to thicker leaf anatomical structures.

Interestingly, we found a positive relationship between the aspect ratio of spongy cells (CWM As SMc) and modelled community decay rates (CWM K rate y^{-1}), which means that circular spongy cells are related to faster litter breakdown. The spongy mesophyll is related to gas diffusion within the leaf and a thicker spongy mesophyll with larger intercellular spaces is assumed to enhance gas exchange (Terashima et al., 2011; He et al., 2018; Ni et al., 2022). The spongy mesophyll is also a photosynthetic tissue and cells with circular shapes likely maximize the surface area for gas exchange with the leaf intercellular spaces. Thus, rounder cells, which can allocate higher nitrogen concentrations, may be associated with a more acquisitive strategy that prioritizes maximizing photosynthesis, which is, in turn, positively correlated with decay rates (Figure 3).

Given that spongy and palisade tissues were inversely correlated (Figure 1b) and higher palisade/mesophyll ratio increases decay rates at both species (Figure 1c) and community levels (Figure 3j, Table 2), the mechanisms underlying the ratio between these mesophylls are needed to be further studied. One potential explanation is that a higher investment in spongy mesophyll can optimize photosynthesis by compensating for a lower investment in palisade tissue, thus effectively capturing scattered light, and this balance can vary depending on environmental conditions. In line with this idea, a recent study by Ni et al. (2022) reveals a trade-off in plants: species with thin leaves and a high palisade mesophyll optimize photosynthesis in higher latitudes and short growing seasons, while those with thick leaves and a high spongy mesophyll are better suited in lower latitudes under shaded and more scattered light conditions. Collectively, all these findings suggest that the dynamic balance between spongy and palisade mesophylls may shape crucial ecological functions, but further empirical evidence is needed to support this hypothesis.

Changes of functional diversity and decomposability along the successional gradient

When examining functional diversity along our gradient of forest succession, we observed that old-growth forests encompassed a wider functional richness but lower evenness for traits significantly related to decomposability, and that decay rates did not change along succession contrary to our third hypothesis (H3, Figure 4). Higher functional richness indicates that the range of values of anatomical traits related to decomposability increase as succession progresses, suggesting the occupation of various niches with the arrival of different species. The increase of species richness and the change in species composition with succession have long been demonstrated in tropical forests (Chazdon et al., 2014; Rozendaal et al., 2019; Poorter et al., 2021b; Elsy et al., 2024). This is particularly evident for rare species with new traits, which become more prevalent as succession advances (Elsy et al., 2024), thus contributing to increased functional richness (van der Sande et al., 2024). Nonetheless, in the later stages of succession, low functional evenness suggests that dominant plant species are distributed within specific combinations of leaf anatomical traits, unlike in the earlier stages. In accordance with our results, a comprehensive continental study of successional patterns in functional diversity has highlighted that functional evenness tends to decrease with succession primarily due to biotic processes such as competition (van der Sande et al., 2024). This results in the convergence of similar trait values of dominant species, while simultaneously allowing for the coexistence of a wide variety of rare species with distinctive functional traits (van der Sande et al., 2024). In our study, the opposite trends between functional evenness and functional richness could cancel out any discernible pattern of decay rates along the successional gradient (Figure 4). Higher functional evenness in early stages of succession may increase complementarity effects on decomposability within a constrained functional space. This is consistent with other studies that have shown complementarity effects on litter decomposition (García-Palacios et al., 2017) and nutrient cycling (Kahmen et al., 2006). By contrast, in mature forests, AGB is distributed in few dominant plant species with conservative traits, thereby increasing the functional redundancy, despite exhibiting a broader range of anatomical traits linked to decomposability in the whole community.

Limitations of the study

Although few studies have linked anatomical traits to decomposition, our findings highlight their significant role in this process by showing their association with species-level decomposability, supporting their inclusion in trait-based decomposition frameworks. However, a key limitation of our study is the potential for circular reasoning, given that foliar and anatomical traits—although distinct—are often correlated within the leaf economic spectrum (Somavilla et al., 2014; Harrison et al., 2021). While we used species-level foliar traits to estimate the decomposition rates of remaining species in the community, we also examined how anatomical traits relate to community-level decomposability. This raises concerns about potential circularity, although we assessed independently measured traits across ecological scales rather than testing the same variable against itself. Ideally, direct decomposition measurements for all species in the community—though requiring substantial experimental effort—would be preferable to estimations. While our approach provides a coherent and widely accepted estimation of decomposition rates according to the literature (Santiago, 2007; Bakker et al., 2011; de la Riva et al., 2019), its reliance on indirect measures based on foliar traits may introduce some imprecision. Future studies should address these limitations by incorporating direct decomposition measurements for all the species, expanding trait datasets, and employing more extensive experimental approaches to validate these associations.

Another important consideration is the use of CWM and functional diversity metrics, which are influenced by community structure. While this could introduce interdependence in our regression models, these metrics capture different ecological dimensions: CWM reflects the dominant functional strategy of the community (Garnier et al., 2004, 2016), whereas functional diversity indices describe the range and distribution of traits (Villéger et al., 2008; Schmera et al., 2023), providing insights into complementarity and redundancy. Despite these potential constraints, our approach allowed us to explore how shifts in community trait composition might shape decomposition patterns along succession.

Finally, while we demonstrated that leaf anatomy is a central factor influencing decay rates at both species and community levels, litter decomposition is a complex process shaped by multiple factors, including abiotic conditions (Salinas et al., 2011), litter quality (Castillo-Figueroa, 2024b; Castillo-Figueroa et al., 2025), decomposer communities (Castillo-Figueroa & Castillo-Avila, 2025), and non-additive effects (Castillo-Figueroa, 2024a), all of which can change along succession. Although these aspects are beyond the scope of this study, examining their interplay could further enhance our understanding of decomposition processes along successional gradients.

Conclusions

Our study integrates leaf anatomy into litter decomposability, revealing that traits such as cuticles, vascular bundles, palisade and spongy mesophylls play a pivotal role in predicting litter breakdown and may substantially influence carbon turnover in the ecosystems. Additionally, we found a strong correlation between leaf anatomical traits and decay rates at the community level. Specifically, plant communities with thicker protective leaf structures such as cuticles and larger vascular tissues displayed lower decay rates. Conversely, a higher proportion of palisade tissues relative to spongy tissues, along with a higher prevalence of cylindrical cells in palisade mesophylls and circular cells in spongy mesophylls, are related to increase decay rates. Remarkably, as succession progresses, predicted decay rates did not exhibit significant shifts. This finding could be explained by a balance between higher functional evenness in secondary forests within a narrow functional space, and lower functional evenness in mature forests within a broader functional space in the attributes linked to decomposability. This suggests that in tropical Andean montane forests, which are recognized as global carbon sinks, the dynamics driving functional diversity of leaf anatomical traits related to decomposability within plant communities vary between secondary and mature forests, thereby affecting the influence of succession on decay rates. Further studies should address limitations in circularity, interdependence between functional diversity metrics, and other biotic and abiotic factors varying along succession.

Acknowledgments

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Supplementary material

Figure S1. Study area where this study was conducted. The grey triangles indicate each of the four study sites in upper Andean tropical forests.

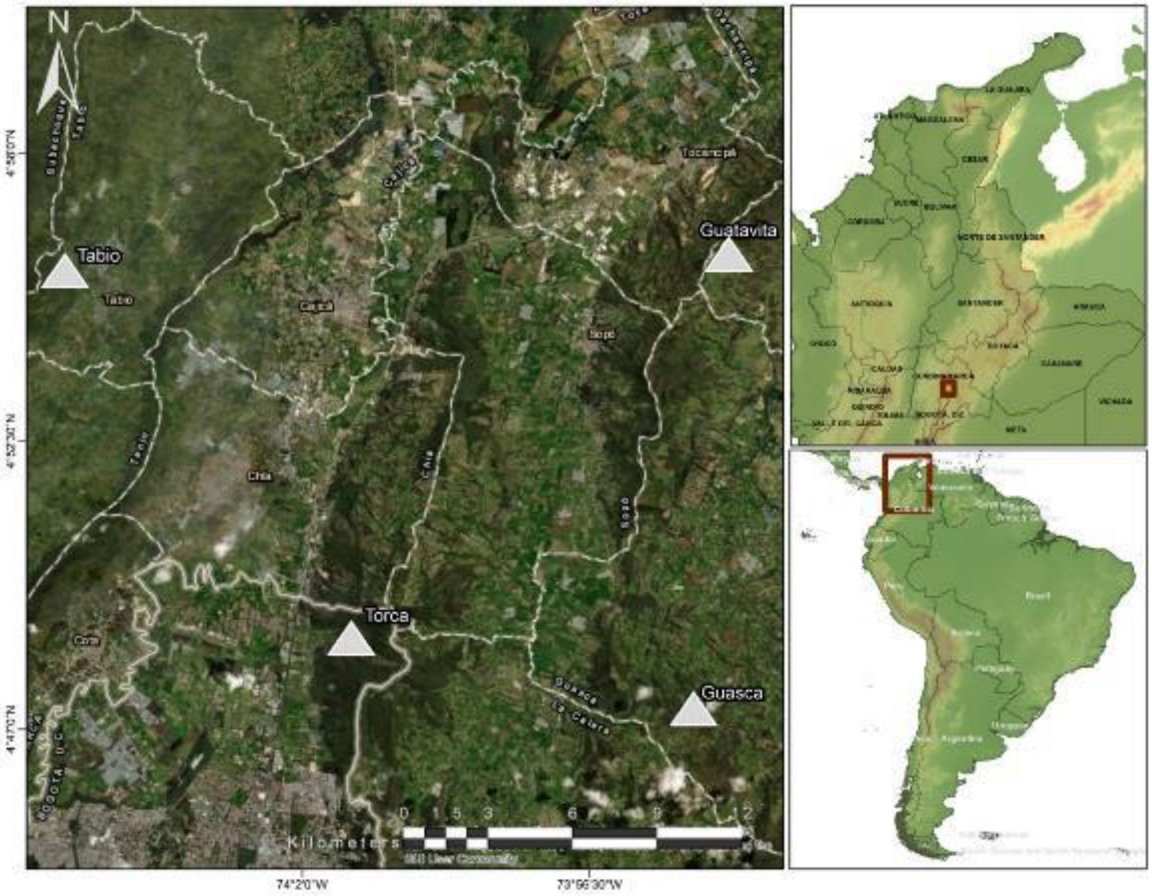

Figure S2. Light microscopy image of leaf transverse profile in *Clusia multiflora* showing the different anatomical traits measured in this study. Measurements on tissue sections (a) comprise the following acronyms: AdCT: Adaxial cuticle thickness (µm), AbCT: Abaxial cuticle thickness (µm), AdET: Adaxial epidermis thickness (µm), AbET: Abaxial epidermis thickness (µm), AdHT: Adaxial hipodermis thickness (µm), PMT: Pallisade mesophyll thickness (µm), SMT: Spongy mesophyll thickness (µm), AS: Air space (µm^2), VBA: Vascular bundle area (µm^2), VBD: Vascular bundle diameter (µm), LT: Leaf thickness (µm). Measurements on cell types (b) comprise the following acronyms: AdEw: Adaxial epidermis cell width (µm), AdEl: Adaxial epidermis cell long (µm), AdHw: Adaxial hypodermis cell width (µm), AdHl: Adaxial hypodermis cell long (µm), PMw: Pallisade mesophyll cell width (µm), PMl: Pallisade mesophyll cell long (µm), SMw: Spongy mesophyll cell width (µm), SMl: Spongy mesophyll cell long (µm), AbEw: Abaxial epidermis cell width (µm), and AbEl: Abaxial epidermis cell long (µm).

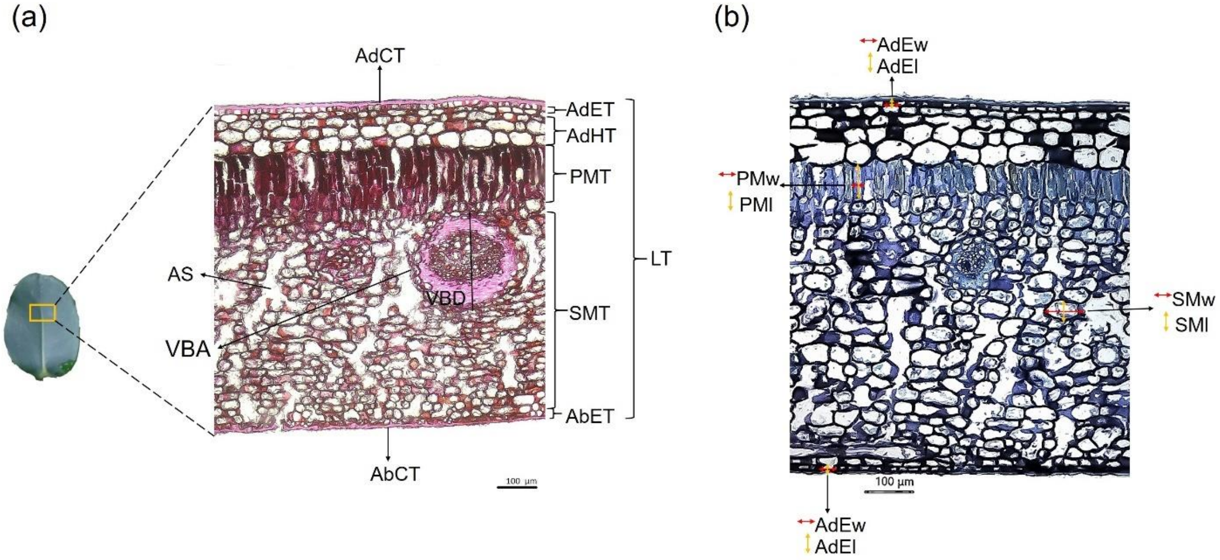

Table S1. Species dominance in the 14 permanent plots were this study was conducted.

Plot	Number od species	Number of total individuals	Species with highest dominance (ind, %)
1	19	172	*Myrcianthes leucoxyla* (63, 36.63%)
			Miconia squamulosa (24, 13.95%)
			Macleania rupestris (20, 11.63%)
			Vallea stipularis (12, 6.98%)
			Miconia ligustrina (11, 6.40%)
2	14	144	*Miconia squamulosa* (32, 22.22%)
			Myrcianthes leucoxyla (26, 18.06%)
			Macleania rupestris (16, 11.11%)
			Miconia ligustrina (15, 10.41%)
			Vallea stipularis (15, 10.42%)
3	16	119	*Weinmania tomentosa* (74, 62.18%)
			Cavendishia bracteata (7, 5.88%)
			Myrsine coriácea (6, 5.04%)
			Miconia ligustrina (6, 5.04%)
			Bejaria resinosa (6, 5.04%)
4	11	179	*Cavendishia bracteata* (120, 67.04%)
			Gaiadendron punctatum (24, 13.41%)
			Alnus acuminata (10, 5.59%)
			Weinmania tomentosa (8, 4.47%)
			Miconia ligustrina (5, 2.80%)
5	22	92	*Weinmania tomentosa* (37, 40.22%)
			Viburnum triphyllum (10, 10.87%)
			Myrsine guianensis (8, 8.79%)
			Myrsine coriácea (7, 7.61%)
			Cavendishia bracteata (5, 5.44%)
6	15	186	*Cavendishia bracteata* (70, 37.63%)
			Gaiadendron punctatum (26, 13.98%)
			Alnus acuminata (25, 13.44%)
			Myrsine coriacea (13, 6.99%)
			Diplostephium rosmarinifolum (10, 5.38%)

7	21	219	*Miconia squamulosa* (54, 24.66%)
			Daphnopsis caracasana (31, 14.16%)
			Myrcianthes leucoxyla (29, 13.24%)
			Ilex kunthiana (19, 8.68%)
			Cavendishia bracteata (14, 6.39%)
8	13	196	*Myrsine guianensis* (60, 30.61%)
			Daphnopsis caracasana (34, 17.35%)
			Miconia squamulosa (23, 11.73%)
			Morela parifolia (20, 10,.21%)
			Viburnum triphyllum (12, 6.12%)
9	19	76	*Miconia squamulosa* (22, 28.95%)
			Croton bogotanus (10, 13.16%)
			Xylosma spiculifera (9, 11.84%)
			Piper bogotensis (5, 6.58%)
			Daphnopsis caracasana (4, 5.26%)
10	18	148	*Viburnum triphyllum* (39, 26.35%)
			Miconia squamulosa (22, 14.86%)
			Daphnopsis caracasana (13, 8.78%)
			Critoniopsis bogotanus (12, 8.11%)
			Duranta mutissi (11, 7.43%)
11	16	70	*Clusia multiflora* (14, 20.00%)
			Drimys granadiensis (14, 20.00%)
			Weinmania tomentosa (7, 10.00%)
			Cavendishia nitida (7, 10.00%)
			Ilex kunthiana (5, 7.15%)
12	15	148	*Weinmania tomentosa* (64, 43.24%)
			Clusia multiflora (17, 11.49%)
			Bejaria resinosa (16, 10.81%)
			Cavendishia nitida (12, 8.11%)
			Myrsine coriacea (9, 6.08%)
13	22	133	*Miconia squamulosa* (43, 32.33%)
			Viburnum triphyllum (21, 15.79%)
			Palicourea lineariflora (13, 9.77%)

			Palicourea angustifolia (11, 8.27%)
			Oreopanax incisus (6, 4.51%)
14	15	158	*Clusia multiflora* (51, 32.28%)
			Weinmania tomentosa (46, 29.11%)
			Bejaria resinosa (13, 8.23%)
			Ilex kunthiana (11, 6.96%)
			Cavendishia bracteata (11, 6.96%)
			Cavendishia nitida (9, 5.70%)

Table S2. List of the 63 plant species in the 14 permanent plots and their scores to the first axis of the PCA based on litter functional traits. PCA was conducted based on seen traits: SLA = Specific Leaf Area, cm^2/g, LA = Leaf Area, cm^2, LDMC = Leaf Dry Matter Content, mg/g, LCC = Leaf Carbon Content, mg/g, LNC = Leaf Nitrogen content, mg/g, LT = Litter thickness, mm, LD = Leaf Density, mg/mm^3. Positive scores are related to conservative strategy, while negative scores are associated to acquisitive strategy. Biplot can be found in Castillo-Figueroa et al. (2025). In red the 15 species selected for the litter decomposition experiment.

Species names	**PC 1 (Functional spectrum)**
Abatia parviflora	-0.73718
Ageratina asclepiadea	0.085956
Ageratina fastigiata	0.099112
Ageratina glyptophlebia	-0.98637
Alnus acuminata	-0.71739
Aiouea dubia	1.012
Baccharis macrantha	-0.42052
Barnadesia spinosa	-1.468
Bejaria resinosa	0.43554
Bucquetia glutinosa	-0.21947
Cavendishia bracteata	1.00820
Cavendishia nitida	1.37300
Cedrela montana	-0.17349
Citharexylum sulcatum	0.65399
Clethra fimbriata	0.75867
Clethra lanata	0.39773
Clusia multiflora	0.49431
Critoniopsis bogotana	-0.57534
Croton bogotanus	-1.4909
Cybianthus iteoides	-0.18529
Daphnopsis caracasana	-0.2566
Diplostephium rosmarinifolium	0.013333
Drymis granadiensis	0.31206
Duranta mutisii	1.1189
Escallonia discolor	-0.45763
Gaiadendron punctatum	0.80424

Hedyosmum sp	-0.61753
Hesperomeles goudotiana	0.99902
Ilex kunthiana	1.2999
Lippia hirsuta	-1.4769
Macleania rupestris	0.66634
Macrocarpaea glabra	-1.6557
Maytenus laxiflora	0.86623
Miconia elaeoides	-0.57614
Miconia ligustrina	-0.16268
Miconia squamulosa	0.082214
Morella parvifolia	0.62294
Morella pubescens	0.26399
Myrcianthes leucoxyla	1.6843
Myrsine coriacea	0.89023
Myrsine dependens	-0.17641
Myrsine guianensis	1.0157
Ocotea calophylla	0.74866
Oreopanax bogotensis	0.91918
Oreopanax incisus	-0.0032272
Palicourea angustifolia	-0.32357
Palicourea demissa	-0.45296
Palicourea lineariflora	-0.3288
Piper bogotense	-1.7624
Prunus buxifolia	1.8857
Psychotria boqueronensis	-0.5217
Rhamnus goudotiana	-0.54881
Rhamnus sphaerosperma	-0.42132
Sessea corymbosa	0.17135
Symplocos theiformis	1.4416
Ulex europaeus	0.067323
Vallea stipularis	-0.6534
Varronia cylindristachya	-0.91304
Vasconcellea pubescens	-3.7274

Verbesina arborea	-2.0100
Viburnum triphyllum	-0.12204
Weinmannia tomentosa	0.97359
Xylosma spiculifera	0.97719

Table S3. Multiple regression analysis that predict decay rates ($P = 0.009$, $R = 0.84$, $R^2 = 0.71$) in the 15 plant species from the decomposition experiment. This model includes four traits: A_{max}, LNC, LCC and SLA. Decay rates from the 48 remaining species were estimated based on the coefficients and the intercept of the model.

	Coefficients	**Standard error**	**t**
Intercept	1.14630768	1.305887	0.87780006
A_{max} (μmol m^{-2} s^{-1})	-0.00016664	0.00944654	-0.01764051
LNC (mg g^{-1})	0.01013454	0.02898577	0.34963838
LCC (mg g^{-1})	-0.00244339	0.00200922	-1.2160892
SLA (cm^2 g^{-1})	0.00516302	0.00554969	0.93032652

Table S4. Descriptive statistics of the anatomical traits of the 15 plant species included in the litter decomposition experiment. The average and standard deviation of the remaining 48 species are also shown. Acronyms can be found in Table 1.

Species	**AdCT (μm)**	**AbCT (μm)**	**AdET (μm)**	**AbET (μm)**	**AdHT (μm)**	**PMT (μm)**	**SMT (μm)**	**AS (μm^2)**	**VBA (μm^2)**	**VBD (μm)**	**LT (μm)**
Alnus acuminata	4.21 ±0.84	2.78 ± 0.45	8.70 ± 1.45	10.92 ± 1.91	17.54 ± 5.65	98.51 ± 8.58	63.37 ± 8.24	1003.39 ± 571.25	2479.95 ± 988.28	66.40 ± 13.05	206.90 ± 12.84
Cavendishia bracteata	10.25 ± 2.64	7.44 ± 1.54	23.75 ± 5.61	13.77 ± 1.97	32.55 ± 7.47	53.88 ± 7.47	176.49 ± 28.03	3879.14 ± 1912.62	19537.68 ± 13947.34	200.88 ± 81.40	332.97 ± 38.88
Cedrela montana	4.59 ± 1.22	3.20 ± 0.57	10.12 ± 3.50	7.38 ± 1.40	0.00	99.21 ± 10.67	105.58 ± 18.72	4755.53 ± 1659.42	5938.36 ± 1951.74	89.45 ± 14.93	235.82 ± 19.37
Clusia multiflora	10.70 ± 1.51	6.89 ± 1.75	13.46 ± 2.36	15.18 ± 6.18	111.73 ± 12.95	115.49 ± 40.60	567.48 ± 72.26	8202.49 ± 4782.09	59821.36 ± 23937.55	331.40 ± 89.50	832.06 ± 106.02
Croton bogotanus	2.68 ± 0.46	2.30 ± 0.45	10.21 ± 1.58	9.09 ± 2.87	23.99 ± 10.73	72.95 ± 13.47	56.90 ± 11.72	1265.72 ± 816.22	1756.91 ± 947.17	49.68 ± 14.19	157.62 ± 17.35
Daphnopsis caracasana	4.74 ± 1.07	4.72 ± 1.02	38.19 ± 5.17	22.58 ± 3.44	0.00	122.73 ± 23.64	247.38 ± 36.48	7304.86 ± 2698.97	10784.26 ± 4701.47	124.78 ± 30.22	449.25 ± 62.40
Drymis granadiensis	10.10 ± 1.54	10.44 ± 1.86	16.99 ± 2.88	18.02 ± 5.06	18.01 ± 4.03	53.79 ± 21.31	96.38 ± 22.18	3445.60 ± 1143.51	7038.63 ± 2679.94	108.98 ± 26.25	226.73 ± 31.55
Ilex kunthiana	22.52 ± 3.55	13.14 ± 2.25	43.77 ± 11.03	18.06 ± 3.10	40.84 ± 10.87	174.97 ± 41.85	209.47 ± 25.28	6380.07 ± 2293.71	22663.36 ± 11273.61	191.64 ± 56.68	529.73 ± 24.16
Miconia squamulosa	5.87± 1.79	5.68 ± 1.49	13.50 ± 1.71	16.71 ± 4.60	24.72 ± 7.09	96.32 ± 10.32	129.00 ± 41.07	1438.68 ± 812.56	2844.96 ± 999.01	64.69 ± 12.69	304.20 ± 48.64
Morella parvifolia	7.15 ± 1.88	4.20 ± 0.61	12.55 ± 2.20	9.78 ± 1.69	0.00	84.01 ± 15.78	97.77 ± 17.70	5753.50 ± 1728.09	8343.10 ± 4227.85	116.93 ± 40.30	217.51 ± 34.93
Myrsine coriacea	9.49 ± 2.87	5.08 ± 1.15	16.08 ± 3.21	13.66 ± 2.64	0.00	70.65 ± 16.54	146.70 ± 55.03	4298.13 ± 1707.59	13086.38 ± 9328.39	146.45 ± 69.39	262.03 ± 61.54
Ocotea calophylla	9.43 ± 1.63	7.11 ± 1.64	19.88 ± 3.24	13.55 ± 2.08	32.11 ± 7.25	144.04 ± 9.65	176.98 ± 23.36	4373.68 ± 2280.03	28759.53 ± 19811.95	223.61 ± 64.57	402.67 ± 12.69
Piper bogotense	3.54 ± 0.56	2.37 ± 0.43	10.94 ± 2.45	10.79 ± 2.86	39.30 ± 6.65	73.97 ± 9.93	66.42 ± 13.04	702.88 ± 373.70	1287.80 ± 886.30	41.99 ± 13.96	206.60 ± 10.06
Prunus buxifolia	6.99 ± 1.18	4.99 ± 0.91	44.11 ± 15.12	17.78 ± 2.50	0.00	92.57 ± 10.58	174.65 ± 33.54	6104.71 ± 1993.01	17480.52 ± 11238.48	161.31 ± 64.02	340.63 ± 55.09
Vallea stipularis	3.68 ± 0.50	2.50 ± 0.37	16.85 ± 4.89	14.19 ± 2.72	0.00	105.76 ± 17.08	84.36 ± 20.43	1431.33 ± 1145.02	4103.69 ± 1831.47	81.87 ± 20.54	232.93 ± 33.60
15 Species	7.73 ± 5.08	5.52 ± 3.25	19.94 ± 13.05	14.10 ± 5.10	22.72 ± 28.89	97.26 ± 37.42	159.93 ± 126.4	4022.65± 3086.9	13728.43 ± 17840.92	133.34 ± 89.80	329.18 ± 173.09
48 remaining species	6.91 ± 4.27	4.65 ± 2.71	20.84 ± 8.34	12.37 ± 4.74	16.19 ± 27.54	95.37 ± 42.40	247.35 ± 105.70	3459.85 ± 3620.37	10909.36 ± 12188.22	121.68 ± 68.50	309.10 ± 159.53

Chapter 4

Drivers of soil fauna communities along a forest successional gradient in the upland Andes and their influence on decomposition rates.

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Drivers of soil fauna communities along a successional gradient in upper Andean tropical forests and their influence on litter decomposition

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Abstract

Soils harbor over half of Earth's biodiversity, with soil fauna among the most diverse groups. However, the drivers shaping their diversity and their role in litter decomposition remain poorly understood. Upper Andean tropical forests are highly biodiverse but have experienced extensive historical transformations, resulting in landscapes with different forest successional stages. In this study, we analyzed soil fauna communities along a successional gradient in Colombia's Eastern Andean forests, identified key microclimatic, soil, and structural drivers, and evaluated their influence on litter decomposition. Soil fauna were sampled from 168 soil samples (30x30x5 cm) during wet and dry seasons across 14 permanent plots (20x20 m) distributed in four sites. Microclimate, soil nutrients, forest productivity, plant diversity, litter functional richness, body size traits, and decomposition rates were obtained at each plot. We observed marked soil fauna turnover among sites, reflecting their distinct floristic composition. Richness and abundance of soil fauna increased with succession, attributed to higher productivity and more suitable microclimatic conditions in mature forests. However, neither richness, abundance, nor body size traits significantly influenced the decomposition environment. Our findings suggest that the primary driver of soil fauna richness in tropical mountain Andean forests is the amount of energy (i.e, forest productivity), while soil fauna abundance is mainly influenced by thermal conditions. Additionally, factors framed within the physiological tolerance hypothesis (i.e., calcium, aluminum) and within the habitat heterogeneity hypothesis (i.e., litter functional richness, plant diversity) also play a role, albeit to a lesser extent. The lack of influence of soil fauna on decomposition may stem from the dominance of small-bodied fauna in these upper Andean forests. This study emphasizes the importance of examining forest recovery including soil fauna groups to understand successional patterns in tropical mountain forests, and highlights that their influence on decay rates is context-dependent and should not be generalized across all ecosystems.

Key-words: Andean forests, beta-diversity, ecological succession, human-induced landscape, plant-soil interactions, invertebrates, soil arthropods, litter decay.

Introduction

Soils account for about 59% of all species on Earth (Anthony et al., 2023). Due to this extraordinary biodiversity that remains largely unexplored, soils have been described as the third biotic frontier after oceanic abysses and tropical forest canopies (André et al., 1994; Hågvar, 1998; Briones et al., 2014). It has been estimated that soils are home of 30.4% of Arthropoda species, being Isoptera and Diplopoda the most soil-specialized groups with 84% and 76.8% of the total biodiversity, respectively (Anthony et al., 2023). Soil fauna plays a central role in ecosystem functioning by influencing litter decomposition and organic matter mineralization (Lavelle, 1996; Powers et al., 2009; Hedĕnec et al., 2022; Cheng et al., 2023), regulating primary production (González & Zou, 1999; Orgiazzi et al., 2016; Verhoef, 2004), maintaining soil structure and aggregation (Orgiazzi et al., 2016; Lavelle et al., 2006, 2020), redistributing organic matter from surface to subsoil (Wilkinson et al., 2009; Lavelle et al., 2006; Orgiazzi et al., 2016), aiding seed bank dynamics by transporting seeds along the soil profile (Forey et al., 2011; Orgiazzi et al., 2016) and regulating soil food webs (Orgiazzi et al., 2016; Cárdenas et al., 2017; Potapov et al., 2024). However, we still have a limited understanding about the main factors that determine the diversity of soil fauna communities.

Historically, several hypotheses have been proposed to explain biodiversity patterns. However, three main hypotheses have been extensively studied to gain a deeper understanding of spatial variations in biodiversity among plants and other aboveground organisms: (1) the energy hypothesis (Wright, 1983), (2) the physiological tolerance hypothesis (Currie et al., 2004), (3) and the habitat heterogeneity hypothesis (Tews et al., 2004). The energy hypothesis posits a positive relationship between energy and diversity, suggesting that an increase in energy, whether thermal, solar, or chemical, enhances diversity across trophic levels by affecting speciation rates and/or increasing the number and the size of species populations, thus mitigating local extinction (Evans et al., 2005; Wright, 1983; Calderón-Sanou et al., 2022). Plant productivity is a fundamental indicator of energy flux, as plants convert solar energy into biomass that then serves as the primary basal resource for heterotrophs (Currie et al., 2004; Evans et al., 2005; Calderón-Sanou et al., 2022). This includes the flux of litter to soils and litter depth, which reflect energy inputs and storage that drive the soil food web (Moore et al., 2004; Kaspari & Yanoviak, 2008). Thus, litter flux and accumulations serve as a basis for evaluating the energy hypothesis. Secondly, the physiological tolerance hypothesis posits that under favorable environmental conditions, biodiversity and/or abundance increase as a result of accommodating a wider range of strategies, thereby leading to more compact niche packing. Conversely, only a limited number of well-adapted species can endure stressful conditions (Currie et al., 2004; Spasojevic & Suding, 2012; Calderón-Sanou et al., 2022). Temperature is widely recognized as a primary factor limiting the thermal niche of soil organisms (Briones et al., 1997; Sulkava & Hutha, 2003). Additionally, soil organisms are strongly influenced by other abiotic factors such as water availability, heavy metal concentrations, soil nutrients, and pH levels, which can create stressful conditions, including drought, toxicity, and acidity (Gans, 2005; Xu et al., 2012; Calderón-Sanou et al., 2022; Mamabolo et al., 2024). Thirdly, the habitat heterogeneity hypothesis suggests that increasing habitat diversity provides a larger niche space, supporting a greater number of coexisting species (Stein et al., 2014; Tews et al., 2004). Although traditionally tested at the landscape scale, where biodiversity correlates with habitat or vegetation diversity (Stein et al., 2014), soils and litter exhibit a high degree of heterogeneity at much smaller scales, significantly contributing to their high biodiversity (Young & Crawford, 2004; Ettema & Wardle, 2002; Nielsen et al., 2010). However, these hypotheses have rarely been tested simultaneously for soil organisms (Decaëns, 2010; Thakur et al., 2020; Calderón-Sanou et al., 2022), and even less so for soil fauna communities, which remain poorly understood (Mathieu et al., 2022).

The upper Andean tropical forests stand out as one of the most biodiverse ecosystems on the planet (Malhi et al., 2010; Rahbek et al., 2019; Myster, 2021), hosting numerous endemic species (Myers et al., 2000; Orme et al., 2005; Castillo-Figueroa et al., 2024). Moreover, this region is characterized by a notable plant biodiversity turnover (Anthelme et al., 2014; Calbi et al., 2021; Hurtado-M et al., 2021), alongside heterogeneous and contrasting environmental conditions (Moser et al., 2011; Pierick et al., 2021). However, since the Spanish colonization, Andean forests have been subjected to significant transformation pressures due to human settlement and development (Etter & Wyngaarden; Etter et al., 2008, 2021). In Colombia, it is estimated that less than 20% of the high Andean forest coverage remains (Bax & Francesconi, 2019; Hurtado-M et al., 2021; Etter et al., 2021). Nevertheless, over the past decades, there has been a gradual increase in forest coverage in these ecosystems due to the abandonment of agricultural lands (Rubiano et al., 2017; Calbi et al., 2020), leading to the expansion of secondary forests. This context provides an ideal scenario to study changes in soil fauna communities along successional forest gradients and the biotic and abiotic factors driving these changes. Nevertheless, research on soil fauna diversity in upper Andean forests remains limited.

The inclusion of animal species, particularly soil fauna, in research focused on the ecological succession of tropical forests has received much less attention than research on plant communities (Acevedo-Charry & Aide, 2019; Poorter et al., 2023). In the tropics, aboveground biomass, tree canopy height, soil organic layer thickness, and nitrogen concentration in soils typically increase with succession with concomitant changes in microclimatic conditions, amount of energy, and habitat heterogeneity (Barberena-Arias & Aide, 2003; Pinho et al., 2018; Rosenfield et al., 2022; Poorter et al., 2021b, 2023, 2024). Changes along the successional gradient have been related to an increase in aboveground litter inputs to the soil with forest age (Brown & Lugo, 1990), which represent more energy in the system leading to more abundance and richness in soil fauna (Kattan et al., 2006; Mathieu et al., 2022). Even though studies in the Andean mountain region indicate higher richness and abundance of soil fauna in mature or advanced successional forests compared to other types of secondary forests or plantations (Kattan et al., 2006; Toledo et al., 2021; Tulande-M et al., 2018; Guarderas et al., 2022), much of the research has been primarily conducted through short-term sampling or focused on specific categories or taxa of soil fauna (Scheu et al., 2008; Illig et al., 2008; Illig et al., 2010; Marian et al., 2018, 2020). Therefore, to better explore the hidden biodiversity in the soil and to improve our understanding about how these communities are taxonomically structured in different successional stages of upper Andean forests, the inclusion of all groups of soil fauna across different climatic seasons is required (Cárdenas et al., 2017). In this regard, crucial questions arise about how variations in forest structural attributes, derived from the process of ecological succession, influence the structure and composition of soil fauna communities. Moreover, understanding changes in soil fauna communities along the forest successional gradient could provide key information for the conservation and planning of the restoration of the upper Andean tropical forests of the region (Morales-Márquez & Meloni, 2022; Auclerc et al., 2022).

Within the soil biota, the influence of soil fauna on litter decomposition at a global scale can accelerate the decay rates over a third (García-Palacios et al., 2013; Peng et al., 2023; Cheng et al., 2023; Zeng et al., 2024). Studies have found that the influence of soil fauna on litter decomposition are largely attributed to the activity of soil macrofauna due to their higher ingestion rates (Cárdenas et al., 2017; Four et al., 2019; Peguero et al., 2019) and 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 & Arancon, 2022), as well as the interactions with climatic conditions (Hättenschwiler et al., 2005; Sagi & Hawlena, 2024), suggesting that the effect of soil fauna on litter decay could be context-dependent. However, in upper Andean tropical 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 that go beyond assessing community structure and composition—such as analyzing body size traits—are needed to better understand the mechanisms underlying soil fauna communities and their effects on litter decomposition.

Therefore, the objective of this study was to analyze the structure of soil fauna communities along a successional gradient in the upper Andean tropical forests, identify the main drivers of their richness and abundance, and evaluate their influence on litter decomposition within these forests. Specifically, we aimed to (1) characterize soil fauna communities between different upper Andean tropical forest sites, (2) analyze the changes in soil fauna richness, abundance and composition in mature and secondary forests, (3) determine the main microclimatic, forest and soil conditions that drive the changes in soil fauna richness and abundance, and (4) analyze the effect of soil fauna richness, abundance and body size traits on decomposition environment. We hypothesized that (H1) soil fauna communities will exhibit a marked dissimilarity between study forest sites due to the high singularity of floristic composition in each of the forest sites; (H2) soil fauna richness and abundance will increase with forest succession and species composition will change between mature and secondary forests; (H3) amount of energy (energy hypothesis) will primarily influence soil fauna richness and abundance, more than microclimatic and soil conditions (physiological tolerance hypothesis) or litter functional richness and plant diversity (habitat heterogeneity hypothesis). This is because higher forest productivity, from both above- and belowground compartments, provides the essential energy needed to sustain large and diverse soil fauna communities. Although we anticipate that microclimate, soil factors, litter functional richness, and plant diversity will also affect these communities, their influence is expected to be less pronounced than that of amount of energy. Finally, (H4) we expect a positive effect of soil fauna richness and abundance on decay rates, given their key role in litter transformation, as well as a positive relationship between the Community Weighted Mean (CWM) of body size traits and the decomposition environment, due to increased litter ingestion by larger soil macrofauna.

Materials and methods

Study area

The research was carried out in the Andean region of Colombia, which is the economic center and the most densely populated region of the country, accounting for 70% of the total population (DANE, 2018). In the central part of the Andes the climate typically follows a bimodal pattern with two rainy seasons (April to June, and October to December) and two dry seasons (January to March and July to September) (IDEAM, 2024). We conducted this research in a set of permanent plots established in 2013 within upper Andean tropical forests of the Cundiboyacense Highplain, which encompass the capital city of Bogotá and its surrounding municipalities (Figure 1). These plots form an integral part of an extensive network comprising 36 plots measuring 20x20 m and eight plots measuring 50x50 m, situated at elevations ranging from 2685 to 3140 m (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023). Forests were classified as either secondary or mature, employing structural attributes such as basal area, tree height, tree density, and species composition (Castillo-Figueroa et al., 2023). The sites comprised in this study were:

- Torca (4° 48' 48.674'' N, 74° 0' 58.527'' W, 2708 – 2965 m, Figure 1): located in the eastern hills of Bogotá, it belongs to the *Floresta de la Sabana* urbanization and is part of the Productive and Protective Forest Reserve of the Bogotá river watershed. This site exhibits well-preserved mature forest fragments that are connected to the Regional Forest Reserve Area of Bogotá, as well as secondary forests near urbanization areas.

- Tabio (4° 55' 33.961'' N, 74° 6' 47.225'' W, 2696 – 2821 m, Figure 1): situated on private land in the rural area of Tabio, with extensive secondary forests and some patches of mature forests. Common economic activities in this site include crops of potato and corn and cattle ranching.

- Guasca (4° 47' 20.318'' N, 73° 54' 31.812'' W, 3085 – 3140 m, Figure 1): located in Encenillo Biological Reserve, a civil society reserve covering an area of 206 ha managed by the Fundación Natura (Fundación Natura, 2021). This site comprises secondary and mature forests that have, in part, grown over land previously used for lime mining.

- Guatavita (4° 56' 9.716'' N, 73° 53' 54.237'' W, 3028 - 3035 m, Figure 1): situated on private land in the rural area of *Tominé de Blancos* village. This site comprises secondary forests within an agricultural landscape dominated by crops of legumes and potatoes, and cattle ranching of sheep and cows.

In these study sites, 14 permanent plots measuring 20x20 m were established in secondary (7 plots) and mature (7 plots) upper Andean forests (Table 1): Torca (three for mature forest and one for secondary forest), Tabio (two for mature forest and two for secondary forest), Guasca (two for mature forest and two for secondary forest), and Guatavita (two for secondary forest). In these plots, the most common plants belong to the families Ericaceae, Melastomataceae, Cunoniaceae, Primulaceae, Clusiaceae and Asteraceae, with dominant genera including *Miconia*, *Weinmannia*, *Cavendishia*, *Myrsine*, and *Myrcianthes*, among others. A total of 63 species of shrubs and trees were identified in the study area, with *Cavendishia bracteata*, *Miconia squamulosa*, *Vallea stipularis*, *Piper bogotense*, and *Clusia multiflora* being some of the most common species. Plant richness and evenness did not differ significantly between study sites (Table S1); however, species composition varied across sites (Hurtado-M et al., 2021).

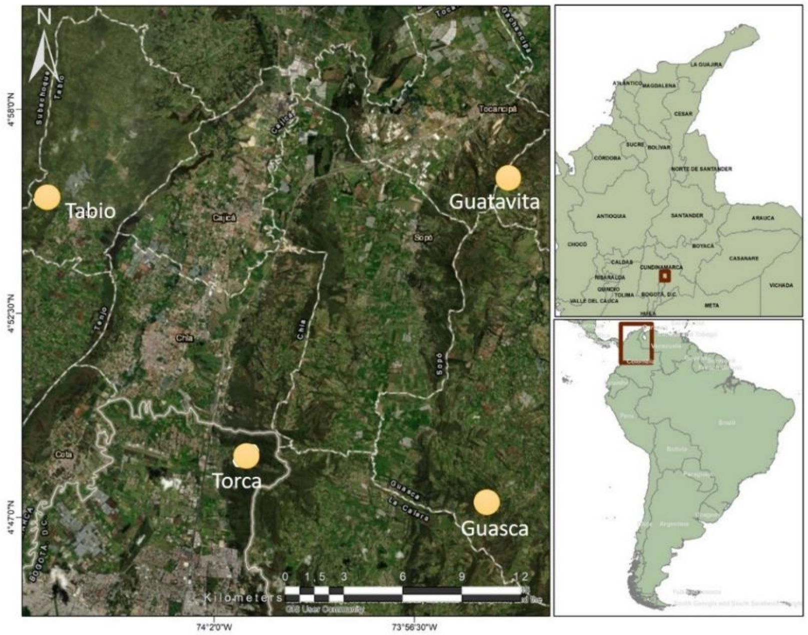

Figure 1 Map of the study area in the upper Andean tropical forests. Yellow circles show the locations where soil fauna sampling took place.

Soil fauna communities

To describe soil fauna, three soil samples measuring 30x30x5 cm depth were extracted from each of the 14 plots (n = 42). Each sample was associated with a decomposition experimental unit (litterbed), as a part of a litter translocation field experiment (see below). Soil fauna samplings were conducted over the four climatic seasons of 2022 (total n = 168) in January-February (dry season), April-May (rainy season), July-August (dry season), and October-November (rainy season). From each soil sample, two sub-samples were stored in plastic bags to distinguish fauna from (1) leaf litter and (2) soil depth at 0-5 cm (Anderson & Ingram, 1994; Toledo 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 hours, followed by a change to 70% alcohol as a preservative. Samples were examined under the Zeiss Stemi 305 stereoscope (Zeiss, Germany). All individuals were counted and taxonomically identified with the assistance of experts (see Acknowledgments), using original descriptions, and existing identification guides for the region, achieving the highest possible taxonomic resolution. Larvae of holometabolous insects that could not be associated with any adult species were classified as different morphospecies. Nymphs of hemimetabolous insects that differed morphologically but not in color from any adult morphospecies were considered as new morphospecies. This taxonomic resolution has been found sufficient to detect significant community composition patterns in temperate and tropical systems (Oliver & Beattie, 1996; Timms et al., 2013; Lamarre et al., 2016). Additionally, identification at the family level has provided ecologically suitable substitutes for species in ecological studies (Cardoso et al., 2011; Cárdenas et al., 2017). Morphospecies (henceforth species richness) and abundance were used to calculate diversity measures. Soil fauna was categorized into traditional functional groups according to Cárdenas et al. (2017). All soil fauna sampling was conducted under a national collection permit (ANLA - Resolución 530 del 27 de Mayo de 2014).

Litter functional traits

Functional traits of senescent leaves were measured on five individuals for each of the 63 species from the 14 permanent plots following the methods outlined by Bakker et al. (2011) and Pérez-Harguindeguy et al. (2013). We measured three key functional traits associated to the leaf economic spectrum (Wright et al., 2004): (1) leaf mass per area (LMA, g m^2), (2) litter nitrogen concentration (Litter NC, %), and (3) litter carbon concentration (Litter CC, %). To do this, one-sided leaf area (LA, cm^2) was measured by scanning leaves and analyzing the resulting images with ImageJ (Schneider et al., 2012, https://imagej.nih.gov/ij/). To determine fresh mass (g), leaves were rehydrated in plastic bags filled with moist paper for 24 to 48 hours at low temperature (4ºC) in the dark, following the complete rehydration method proposed by Garnier et al. (2001). Subsequently, each leaf sample was oven-dried at 60 ºC for 72 hours, and its dry mass (g) was determined to estimate the LMA. Litter NC, and Litter CC were measured using an elemental analyzer (FlashSmart™ Thermo Fisher Scientific, USA).

Measurement of environmental and soil variables

TMS-4 soil probes equipped with data loggers (TOMST, Czech Republic) were installed at the center of each of the 14 plots to record soil and air temperature and volumetric water content every 15 minutes throughout the year of soil fauna sampling in 2022. This device includes three temperature sensors at 15 cm above the soil surface, at the soil surface, and at 8 cm depth in the soil. At the bottom, it has a probe that measures the volumetric soil moisture at a depth of 14 cm (Wild et al., 2019).

Soil physicochemical characteristics were measured by collecting soil samples from each plot as part of another study (Posada et al., unpublished). To assess soil nutrient supply rates, Plant Roots Simulators probes (PRS®, Western AG), were installed at four random locations within each plot (n = 56 in total). These probes consist of ion-exchange membranes supported by plastic mounts, allowing for easy insertion into the soil to measure ion supply in the soil solution in situ, with minimal disturbance. Four anion and four cation probes were placed at each sampling point in the plots, which were subsequently pooled for laboratory analysis; these resulted in 16 probes deployed per plot for an effective statistical per plot (n = 4). Element concentrations were determined colorimetrically using automated flow injection for NO_3 and NH_4, and inductive plasma spectrometry for Ca, Mg, K, P, Fe, Mn, Cu, Zn, B, S, Pb, Al, and Cd at the Western AG laboratories (https://www.westernag.ca/). Probes were inserted vertically into the soil to a depth of 10 cm during the rainy season in November 2016 and retrieved after a 30-day period. Other measured variables included bulk density (g/cm^3), carbon and nitrogen concentration in soils (%), obtained by collecting five random soil samples from each plot at two depths (0-15 cm and 15-30 cm) (Posada et al., unpublished). Additionally, soil pH and texture (% silt, % sand, and % clay) were determined from composite samples of five soil cores collected from each plot at a depth of 10-30 cm (after removal of the top litter layer) (Hurtado-M et al., 2021) and were analyzed in the Laboratorio de Aguas y Suelos of the Universidad Nacional de Colombia (Bogotá) (Hurtado-M et al., 2021).

Indicators of forest succession

To estimate a multidimensional proxy of succession, we did a Principal Component Analysis (PCA) with aboveground biomass (AGB, Mg ha^{-1}), tree canopy height (m), nitrogen concentration in soils (%), and soil organic layer thickness (cm) from pre-existing measurements of the permanent plots. Previous studies have demonstrated that these four variables are good indicators of successional status (Brown & Lugo, 1990; Garnier et al., 2004; Poorter et al., 2021b; Rosenfield et al., 2022), allowing the establishment of a successional gradient from early to late successional forests. To estimate AGB, we used allometric equations formulated specifically for Andean mountain forests (Sierra et al., 2007; Pérez & Díaz, 2010). The height of trees and shrubs was measured using a clinometer or a telescoping measuring rod. Tree canopy height was then determined by calculating the weighted average of the upper quartile of all tree height measurements (Castillo-Figueroa et al., 2013). The thickness of the organic soil layer (O horizon) was measured by excavating soil pits out next to each plot using a shovel.

Forest productivity and energy flux

Litter productivity (Mg C ha^{-1} y-^{1}) was assessed in another study (Castillo-Figueroa et al., 2023), by collecting litterfall using 0.25 m^2 traps placed within the 14 plots (10 traps per plot, totaling 140 traps). These traps were constructed with 1/2-inch PVC tubes and covered with a 1 mm nylon mesh screen, elevated approximately 1 m above the ground. Litter collection occurred between May 2016 and April 2017 at intervals of 15-20 days to minimize decomposition-related losses (Castillo-Figueroa & Posada, 2025; Castillo-Figueroa et al., 2023). Subsequently, litter samples were oven-dried at 60 °C until reaching a constant weight and then weighed using an analytical scale. Branches with a diameter exceeding 1 cm were excluded from the analysis, while branches with a diameter less than 1 cm but wider than the trap were trimmed to match the trap's length. Additionally, annual stem productivity was assessed by measuring diameter at breast height (DBH) between 2013 and 2016 and calculating their increment.

Fine root productivity (Mg C ha^{-1} y^{-1}) was measured by installing nine root ingrowth cores, each consisting of mesh cages 11.5 cm in diameter and 30 cm in length, spaced 2 m apart from each other in a 3x3 m grid pattern, positioned 3 m away from the corner points (Castillo-Figueroa et al., unpublished). This arrangement allowed us to obtain 126 independent sampling points across the 14 plots. To prepare the cores, the surface soil litter was removed and then soil cylindrical cores were excavated with a post-hole digger to a depth of 30 cm, following the methodology outlined by Phillips et al. (2001). After extracting the roots from the soil samples, the rootless soil cores were returned to the ground. Root harvesting occurred over a one-year period, with collections at 6 and 12 months. Roots were manually removed over a 40-minute period for each root ingrowth core, divided into four intervals of 10 minutes each. Live fine roots (<2 mm) were separated using standard techniques (Metcalfe et al., 2007; Brassard et al., 2011; Marthews et al., 2012) and subsequently oven-dried at 60°C in the laboratory until reaching a constant weight. Dry weights were measured using an analytical scale accurate to 0.0001 g. To calculate the carbon found in all productivity measures, a conversion factor was used by multiplying by 0.5, considering that carbon constitutes approximately half of the dry weight (Petersson et al., 2012).

Finally, to estimate the amount of litter accumulated in the soil, we measured litter depth at each litterbed position where soil fauna was collected, with measurements taken at five random soil points using an electronic digital caliper (0.1 mm).

Litter decomposition field experiment

We conducted a reciprocal translocation field decomposition experiment within the 14 permanent plots over the period from October 2021 to April 2023 (Castillo-Figueroa et al., 2025). In this experiment, a set of 15 representative Andean species were selected based on their biomass and litter functional traits. This 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 (10x15 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).

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 (i.e., 14 permanent plots x 3 decomposition beds per plot x 15 litter species in each decomposition bed x 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).

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. 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-1070 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; 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 used them.

Data Analysis

We generated rarefaction curves based on samples covering the four climatic seasons sampled throughout the year to assess species richness. Species diversity index for soil fauna communities (plot diversity) was obtained from Hill numbers ($q = 0$, $q = 1$, $q = 2$) (Jost, 2006), with their corresponding 95% confidence intervals to analyze differences between the forest sites and successional stages (Table 1, Figure S1). To evaluate differences in community composition, we conducted analyses at both the plot level and the litterbed level (within the plots). Accordingly, we constructed a dendrogram to do a hierarchical clustering of the plots and successional stages and performed Non-metric Multidimensional Scaling (NMDS) to describe the similarity of community composition at the litterbed level across sites and successional stages. Both analyses were based on Bray-Curtis distances. In NMDS, Kruskal's stress is a measure of the difference between objects in the compressed matrix and the distances originally calculated (Illig et al., 2010), so stress below 0.2 was considered as an adequate representation in reduced dimensions (McCune & Gracia, 2002). To test for differences in community structure between sites and successional stages, a non-parametric permutation test (ANOSIM) was performed, where R values of +1 indicate total dissimilarity, and R values of -1 represent total similarity (Clarke, 1993). Test probability values are based on 9999 permutations (Clarke, 1993). This was complemented with a Similarity Percentage breakdown analysis (SIMPER) to analyze the taxa that most contributed to the dissimilarity between sites (Clarke, 1993).

Next, changes in soil fauna richness and abundance along the successional gradient were analyzed through Reduced Major Axis (RMA) regressions between: (1) the first axis of the PCA of succession (Figure S2) vs. soil fauna richness, and (2) the first axis of the PCA of succession vs. soil fauna abundance. Additionally, we analyzed changes in both abundance and richness for each functional group vs. the first axis of PCA of succession. To compare composition between mature and secondary forests, we did a second NMDS including all the sites in a single analysis.

To test the effect of variables related to the energy hypothesis, a second PCA was made using four variables: litter productivity, stem productivity, litter depth, and fine root productivity (Figure S3). These variables are indicators of energy flux and accumulation in the forests (Kaspari & Yanoviak, 2008; Brassard et al., 2011; Souza et al., 2019; Rosenfield et al., 2022). The scores of the primary axis from this PCA were selected to represent an environmental gradient indicating the amount of energy (energy hypothesis). These scores effectively summarized the observed data patterns and accounted for a significant portion of the data's variability, exceeding 60% (Figure S3). Consequently, they were deemed appropriate for incorporation into the multiple regression models outlined subsequently. In both PCAs, biplot eigenvectors were scaled by √dk as well as data points by 1/√dk following the method described by Legendre & Legendre (1998).

To test the influence of variables framed within the physiological tolerance hypothesis, we conducted RMA regressions between each soil and microclimatic variable and soil fauna richness and abundance. For each of the four microclimatic datasets obtained from the dataloggers over the year (i.e., air temperature, surface temperature, soil temperature, soil moisture), we derived nine statistical variables: mean, minimum, maximum, range, standard deviation, variance, 25th percentile, 50th percentile, and 75th percentile. This was done after cleaning the databases of any potential outliers resulting from the installation or data obtention of the dataloggers.

To test the influence of variables linked to the habitat heterogeneity hypothesis, we performed RMA regressions between plant diversity (measured by Fisher´s alpha index) and soil fauna richness and abundance. Additionally, we examined the relationship between soil fauna richness and abundance with litter functional richness for all plant species within each plot, which was based on three key traits related to the leaf economic spectrum (i.e., LMA, Litter NC, Litter CC, Wright et al., 2004). Functional richness represents the functional space occupied for all the species within a community (Mason et al., 2005). Hence, we computed this index using litter traits for each plot, as it provides a suitable measure that captures the heterogeneity of litter types encountered by soil fauna. We confirmed the homoscedasticity in all the RMA regressions using Breusch-Pagan statistic test (P > 0.05).

We conducted multiple regression analysis with the stepwise method to assess the influence of variables framed within the energy, physiological tolerance, and habitat heterogeneity hypotheses on both soil fauna richness and abundance. The response variables were soil fauna richness and soil fauna abundance per plot, while the explanatory variables consisted of the variables that showed a significant relation in the RMA regressions (see results). These variables include the amount of energy, temperature variables (mean, minimum, range, variance, 25th percentile), calcium and aluminum in soil solution, plant diversity, and litter functional richness. To address potential multicollinearity issues among predictors, we assessed the variance inflation factor (VIF) for each variable. We included variables with VIF values below 1.3, indicating no collinearity among predictors (Neter et al., 1990; Pinho et al., 2018). We estimated the Root Mean Squared Error (RMSE) and the Adjusted R^2 to select the best model for each explanatory variable. 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 & 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., 2013).

Finally, to evaluate the influence of soil fauna on litter decomposition, we analyzed the relationship between standard decomposition (i.e., decomposition environment)—estimated as the average decomposition rates of 15 litter species in each plot during the decomposition experiment—and both soil fauna richness and abundance. Additionally, we assessed the effect of body size by estimating the CWM of length, width, and biomass—weighted by the abundance recorded in each plot—and performed RMA regressions between these three body size traits and decomposition environment. All the analyses were conducted in JASP 0.14.1.0. (JASP Team, 2023), PAST v.4.14 (Hammer et al., 2001), iNEXT software (Hsieh et al., 2016), and R v. 4.3.3 (R core Team, 2024).

Results

Soil fauna communities in upper Andean tropical forests

We found a total of 6999 individuals that belonged to 351 morphospecies, 154 families and 41 orders of soil fauna during the year-long soil sampling in upper Andean tropical forests (Figure 2, Table S2). Over the half of the individuals collected belonged to the orders Polydesmida (Diplopoda), Coleoptera, and Sarcoptiformes (Acari), but different elusive and rare groups such as Schizomida, Embioptera, Nematomorpha, Zygentoma, Archaeognatha, among others, were also found in these forests (Figure 2, Figure S4). In terms of the soil fauna functional groups, litter transformers and detritivores account for approximately 3/4 of the relative abundance, while soil-borne pests, diseases and parasites represent less than 5% of the soil fauna communities (Figure 2, Figure S4, Figure S5).

In general, significant variations between sites and successional stages in species diversity were observed for all Hill numbers, as indicated by the 95% confidence intervals derived from the rarefaction curves (Table 1, Figure S1). Furthermore, striking differences in community composition were detected between forest sites, as demonstrated by NMDS (Stress = 0.16, Figure 3a), cluster dendrogram (Figure 3b), and ANOSIM tests ($P < 0.001$, $R = 0.92$, Table 2).

Table 1. Diversity of soil fauna communities for each plot and site. In the hill numbers (q = 0, q = 1, q = 2) 95% confidence intervals are shown in brackets.

Plot ID	Site	Succession	q = 0	q = 1	q = 2
1	Guatavita	Secondary	77 [61.86-92.14]	43.82 [37.90-49.73]	28.84 [24.79-32.89]
2	Guatavita	Secondary	67 [48.49-85.51]	46.03 [37.79-54.27]	34.19 [26.15-42.23]
3	Guasca	Mature	81 [67.14-94.86]	19.93 [17.08-22.78]	7.85 [7.75-8.95]
4	Guasca	Secondary	70 [70-50.31-89.69]	30.00 [25.99-34.01]	14.47 [10.95-18.00]
5	Guasca	Mature	75 [56.99-93.01]	32.64 [27.24-38.04]	15.27 [11.90-18.65]
6	Guasca	Secondary	61 [51.01-70.99]	21.56 [17.20-25.92]	7.97 [5.63-10.31]
7	Tabio	Secondary	84 [70.47-97.53]	39.53 [34.51-44.55]	21.58 [18.42-24.74]
8	Tabio	Secondary	63 [51.60-74.40]	23.76 [20.46-27.07]	14.19 [12.32-16.05]
9	Tabio	Mature	111 [82.51-139.49]	56.32 [50.42-62.23]	34.97 [30.99-38.95]
10	Tabio	Mature	99 [85.33-112.67]	39.34 [35.92-42.77]	20.01 [17.18-22.83]
11	Torca	Mature	99 [84.47-113.53]	37.20 [32.68-41.73]	17.82 [15.23-20.40]
12	Torca	Mature	91 [74.33-107.67]	26.23 [22.44-30.01]	10.36 [8.61-12.11]
13	Torca	Secondary	93 [73.09-112.91]	24.75 [21.69-27.82]	9.60 [8.17-11.03]
14	Torca	Mature	92 [81.30-102.70]	41.78 [36.97-46.60]	22.62 [19.49-25.75]

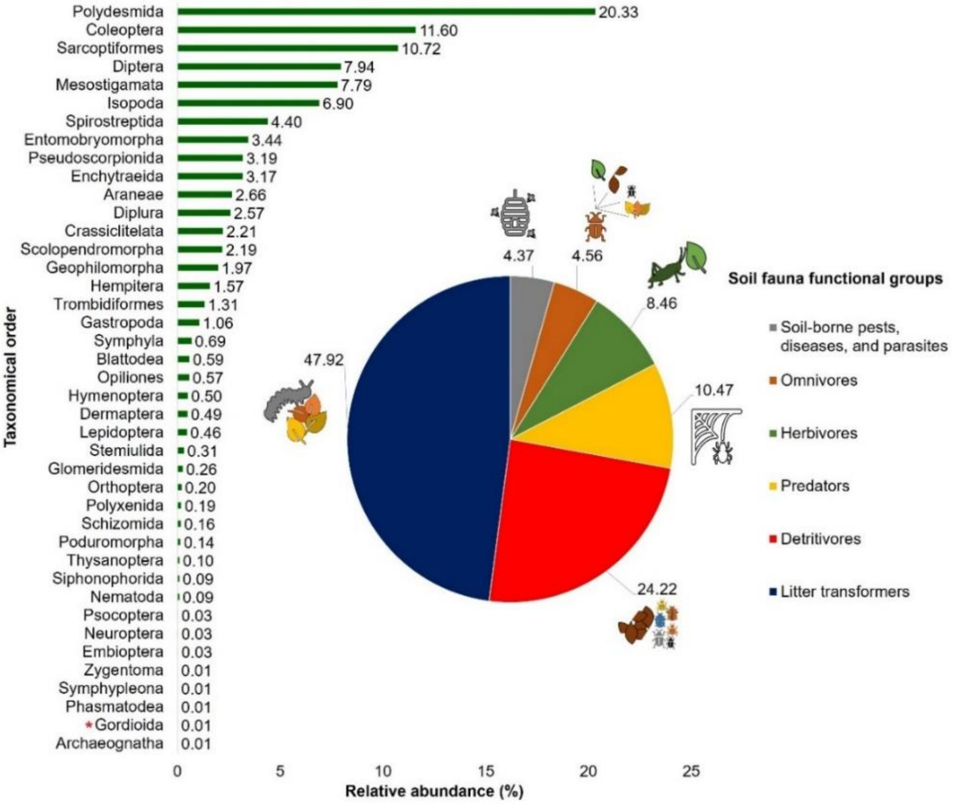

Figure 2. Soil fauna communities in upper Andean tropical forests are illustrated in the bar plot, showing the relative abundance of each taxonomical order found across all four sites. Note that the red asterisk (*) indicates the only group that does not correspond to a taxonomic order (Gordioda: Nematomorpha). The pie chart depicts the proportions of each soil fauna functional group.

Table 2. ANOSIM on morphospecies composition of soil fauna communities in four sites using a dissimilarity matrix based on Bray-Curtis similarity index. R values close to 1 indicate high differentiation between sites or successional stages.

Factor	R	P
Sites		
Between all sites	0.9204	0.0001
Guasca-Guatavita	0.9955	0.0001
Guasca-Tabio	0.9925	0.0001
Guasca-Torca	0.9932	0.0001
Guatavita-Tabio	0.9674	0.0004
Guatavita-Torca	0.9945	0.0002
Tabio-Torca	0.6514	0.0001
Succesion		
Between mature-secondary	0.172	0.001
Guasca mat-Guasca sec	0.6620	0.0027
Tabio mat-Tabio sec	0.5463	0.0058
Torca mat-Torca sec	0.5233	0.0217

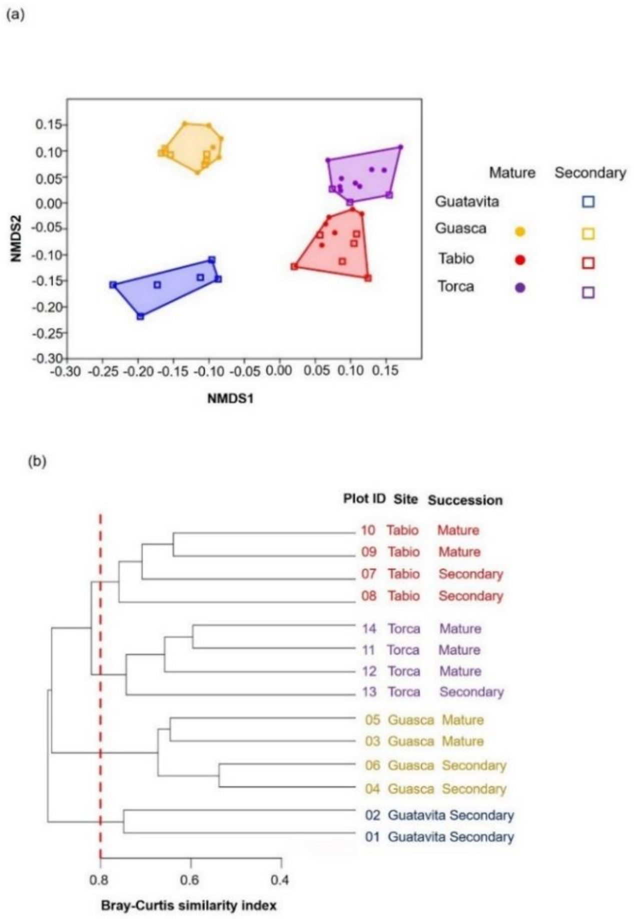

Figure 3. Structural differences in species composition between sites. (a) Non-metric multidimensional scaling (NMDS) showing differences in soil fauna composition between sites. Guatavita is represented in blue color, Guasca in yellow, Tabio in red, and Torca in purple. Filled circles depict mature forests and open squares represent secondary forests. Note that Guatavita only has young forests. Each filled circle/open square indicate the soil fauna community composition of each litterbed (n = 42). (b) Bray-Curtis similarity index including the plots of each site (n = 14). Note that plots are grouped consistently in successional stages within each site.

Soil fauna communities and succession

Proxies of succession made on the first axis of the PCA accounted for 75.53% of the variation and showed a positive correlation with aboveground biomass, nitrogen concentration in soils, tree canopy height, and soil organic layer thickness (Figure S2). We found a significant increase of both abundance (P = 0.023, n = 14, R^2 = 0.36, CI = [77.58, 251.34]) and richness (P = 0.015, n = 14, R^2 = 0.40, CI = [5.34-20.23]) with this axis of succession (Figure 4, Figure S6). In terms of the functional groups, only the litter transformers richness (P = 0.0006, n = 14, R^2 = 0.63, CI = [3.31, 6.19]) and detritivore abundance (P = 0.014, n = 14, R^2 = 0.40, CI = [43.93, 86.46]) increased with this axis of succession (Figure S7).

We also found a modest effect of succession on soil fauna composition when we pooled secondary and mature forests in an NDMS (Stress = 0.16, Figure 4a) and ANOSIM (P = 0.001, R = 0.172) (Figure S5). Yet, when the analysis of succession was conducted within each site, soil fauna composition exhibited a more pronounced differentiation between successional stages (Table 2, Figure 3b).

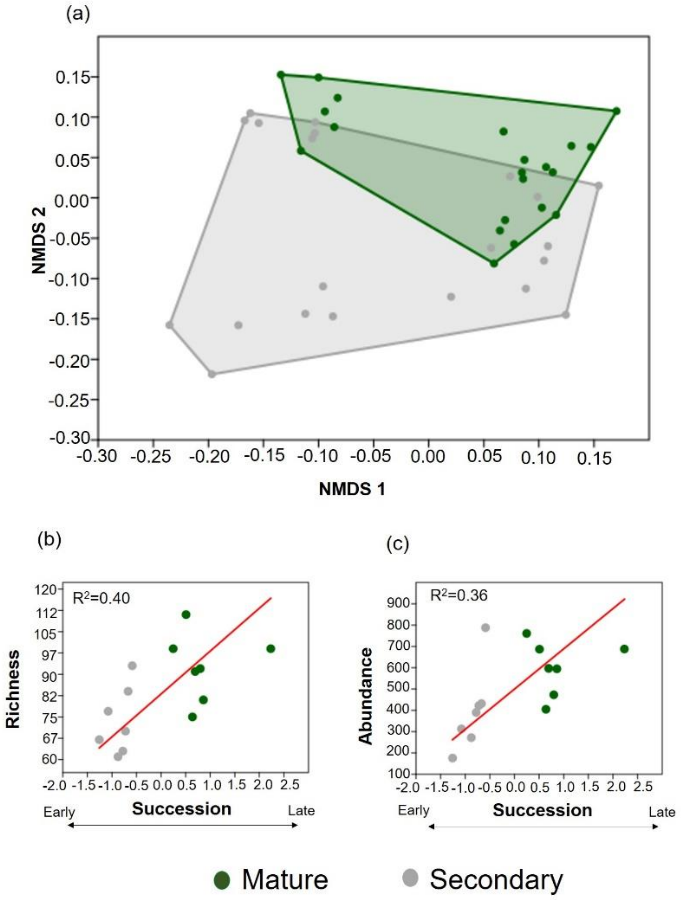

Figure 4. Changes of soil fauna along the successional gradient in upper Andean tropical forests. (a) NMDS comparing soil fauna communities between mature and secondary forests (b) RMA regressions between succession vs richness and (d) succession vs abundance. Green circles represent mature forest plots and grey circles-squares indicate secondary forest plots.

Drivers of soil fauna richness and abundance

We found significant positive relationships between minimum surface temperature and both soil fauna richness (P = 0.04, n = 14, R^2 = 0.30, CI = [6.15, 15.80], Figure 5) and soil fauna abundance (P = 0.01, n = 14, R^2 = 0.42, CI = [84.16, 178.6], Figure 6). Soil fauna abundance displayed significant negative associations with air temperature range (P = 0.02; n = 14, R^2 = 0.36, CI = [-59.12, -22.58]) and variance (P = 0.002, n = 14, R^2 = 0.56, CI = [-102.95, -37.18]), and a positive relationship with the 25th percentile of air temperature (P = 0.04, n = 14, R^2 = 0.30, CI = [110, 259]), unlike soil fauna richness, which showed no relation with these variables (P > 0.05; not shown). Among all soil variables, we only found an inverse relationship between soil fauna richness and aluminum (P = 0.02, n = 14, R^2 = 0.35, CI = [-1.03, -0.41]) and a positive one with calcium for both richness (P = 0.01, n = 14, R^2 = 0.40, CI = [0.01, 0.03]) and abundance (P = 0.04, n = 14, R^2 = 0.29, CI = [0.09, 0.91]).

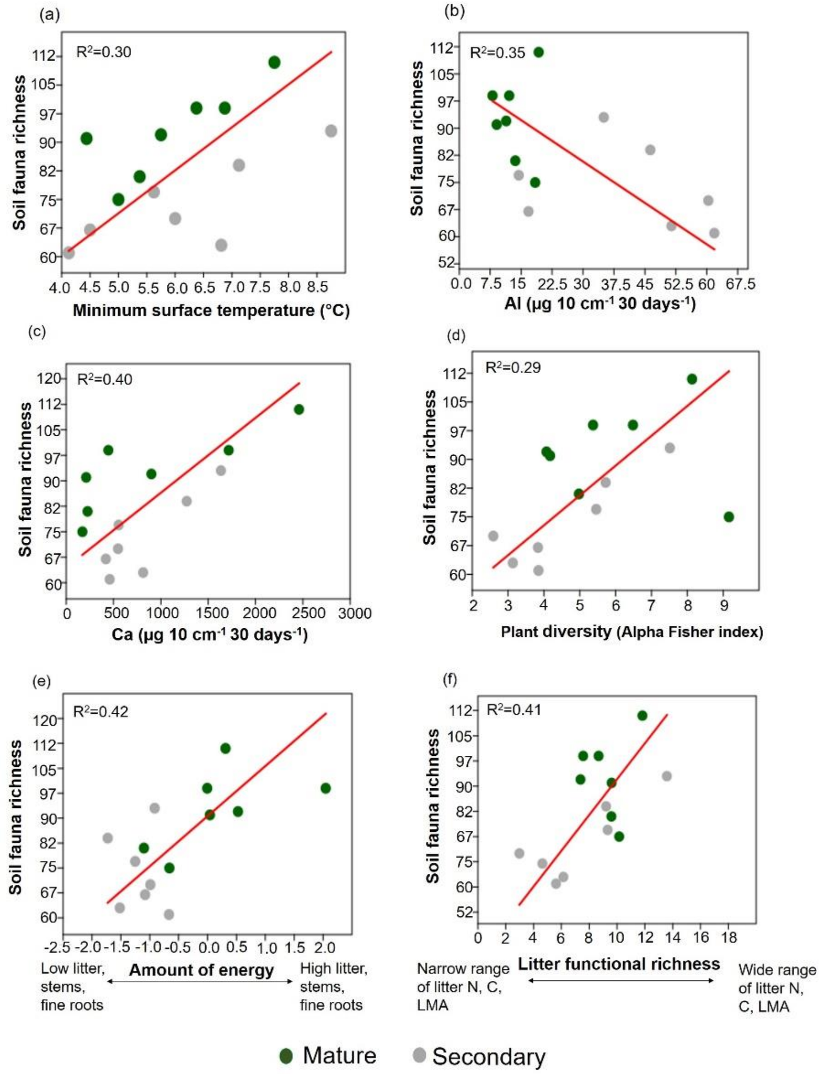

Figure 5. Drivers of soil fauna richness: (a) minimum surface temperature, (b) aluminum flux, (c) calcium flux, (d) plant diversity, (e) amount of energy, (f) litter functional richness. Green circles represent mature forest plots and grey circles indicate secondary forest plots.

The first axis of the PCA on amount of energy accounted the 67.17% of the variation, correlating positively with higher litter and stem productivity, thicker soil litter depth, and fine root productivity, and negatively with lower litter and stem productivity, thinner soil litter depth, and lower fine root productivity (Figure S3). We found an increase in soil fauna richness with this first PCA axis of amount of energy ($P = 0.01$, $n = 14$, $R^2 = 0.42$, CI = [2.10, 20.64]), yet this composed variable showed no correlation with soil fauna abundance ($P = 0.07$, $n = 14$, $R^2 = 0.25$, CI = [-21.69, 265.23]).

On the other hand, soil fauna richness increased with plant diversity ($P = 0.04$, $n = 14$, $R^2 = 0.29$, CI = [3.61, 10.64], Figure 5), but showed no relation with soil fauna abundance ($P = 0.11$, $n = 14$; $R^2 = 0.20$, CI = [29.94, 144.43]). Conversely, litter functional richness showed positive significant relations for both soil fauna richness ($P = 0.01$, $n = 14$, $R^2 = 0.41$, CI = [2.37, 7.26], Figure 5) and abundance ($P = 0.01$, $n = 14$, $R^2 = 0.41$, CI = [32.70, 87.88], Figure 6).

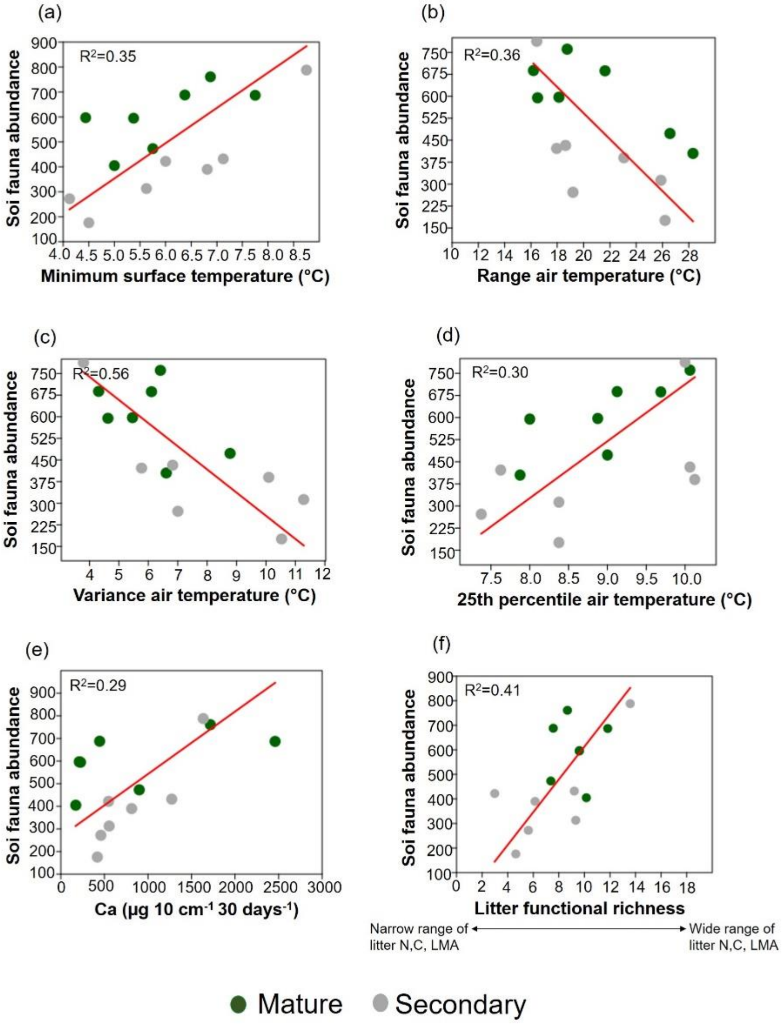

Figure 6. Drivers of soil fauna abundance: (a) minimum surface temperature, (b) range air temperature, (c) variance air temperature, (d) 25th percentile air temperature, (e) calcium flux, (f) litter functional richness. Green circles represent mature forest plots and grey circles indicate secondary forest plots.

Finally, in the multiple regression analysis, the final model that best predicted soil fauna richness (adjusted $R^2 = 0.84$, $P = 0.011$) included three main variables in the following order: (1) the amount of energy, (2) litter functional richness and (3) calcium in soils (Table 3). This result shows that although the amount of energy is the main driver of soil fauna richness, the other two hypotheses are partially supported. In the case of soil fauna abundance, the best model (adjusted $R^2 = 0.78$, $P = 0.003$) included two variables of air temperature: (1) variance and (2) 25th percentile. This suggests that thermal conditions play a fundamental role in determining soil fauna abundances within the communities.

Table 3. Multiple stepwise linear regression models showing the effects of the most important variables for soil fauna richness and soil fauna abundance. In the model of soil fauna richness, the following covariates were considered but not included: Fisher Alpha Index plants, soil aluminum, minimum surface temperature. Thus, amount of energy, litter functional richness and soil calcium on the soil fauna richness were the best factors explaining soil fauna richness ($n = 14$, $R^2 = 0.88$, adjusted $R^2 = 0.84$, RMSE = 6.02, $P = 0.011$). In the model of soil fauna abundance, the following covariates were considered but not included: litter functional richness, minimum surface temperature, range air temperature, and soil calcium. Thus, variance in air temperature, and 25th percentile air temperature were the best factors explaining soil fauna richness ($n = 14$, $R^2 = 0.81$, adjusted $R^2 = 0.78$, RMSE = 88.72, $P = 0.003$).

Model		**Unstandardized**	**Standard Error**	**Standardized**	**t**	**P**	**Tolerance**	**VIF**
	Soil fauna richness							
1	(Intercept)	83.071	4.029		20.616	< .001		
2	(Intercept)	83.071	3.208		25.897	< .001		
	Amount of energy	9.712	3.329	0.644	2.917	0.013	1.000	1.000
3	(Intercept)	57.002	6.899		8.262	< .001		
	Amount of energy	8.952	2.235	0.594	4.005	0.002	0.993	1.007
	Litter functional richness	3.140	0.790	0.590	3.976	0.002	0.993	1.007
4	(Intercept)	57.817	5.178		11.165	< .001		
	Amount of energy	8.676	1.678	0.575	5.170	< .001	0.990	1.010
	Litter functional richness	2.168	0.670	0.407	3.236	0.009	0.775	1.291
	Soil calcium	0.009	0.003	0.389	3.095	0.011	0.774	1.291
	Soil fauna abundance							
1	(Intercept)	499.929	50.509		9.898	< .001		
2	(Intercept)	918.482	113.174		8.116	< .001		
	Variance air temperature	-60.042	15.441	-0.747	-3.889	0.002	1.000	1.000
3	(Intercept)	31.742	240.755		0.132	0.897		
	Variance air temperature	-57.696	10.487	-0.718	-5.502	< .001	0.997	1.003
	25 percentile air temperature	97.825	25.175	0.507	3.886	0.003	0.997	1.003

Soil fauna communities and decomposition

We found no significant relationship with richness (P = 0.06, n = 14, R^2 = 0.26, CI = [0.003, 0.01], Figure 7a) or abundance (P = 0.13, n =14, R^2 =0.18, CI = [0.0002, 0.009], Figure 7b).

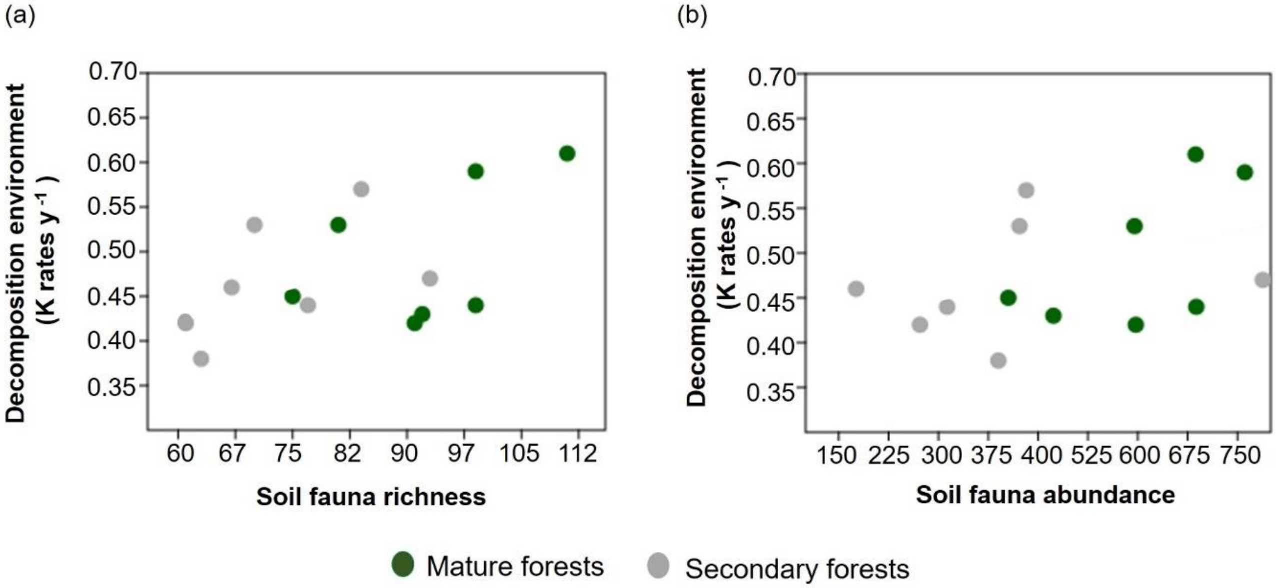

Figure 7. Reduced major axis regressions between decomposition environment and both (a) soil fauna richness and (b) abundances. Green circles represent mature forest plots and grey circles indicate secondary forest plots.

Overall, 863 individuals were measured from 327 morphospecies (93% of the total community). 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) (Figure 8a-c). The smaller animals were nematodes (1.49e-7 mg) and the larger ones were gastropods (481 mg). We did not find any relationship between decomposition environment and CWM width (P = 0.48, n = 14, R^2 = 0.04, CI = [-1.704, -0.251], Figure 8d), CWM length (P = 0.23, n = 14, R^2 = 0.12, CI = [-0.154, -0.001], Figure 8e), or CWM biomass (P = 0.305, n =14, R^2 = 0.09, CI = [0.086, 0.549], Figure 8f).

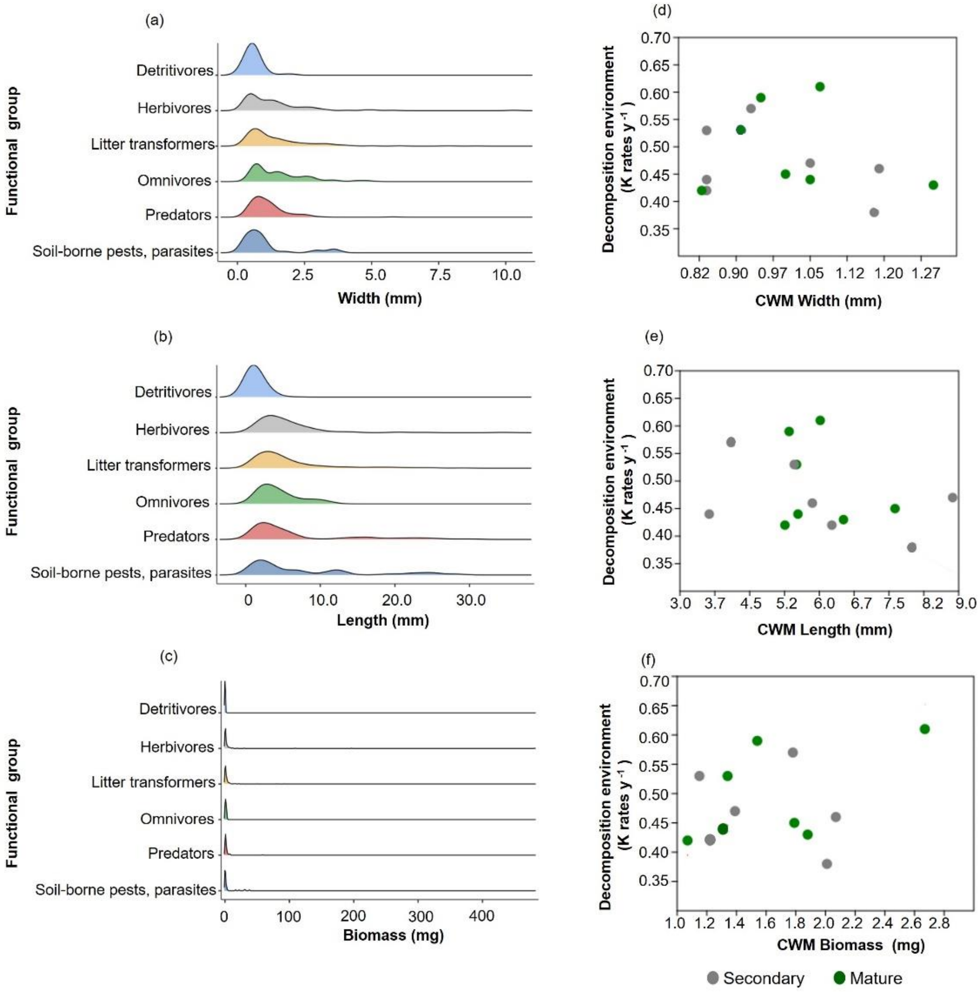

Figure 8. Density plots of each functional group in terms of (a) Length (mm), (b) Width (mm, (c) and Biomass (mg) and Reduced Major Axis regressions between decomposition environment and Community Weighted Mean (CWM) of (d) Width (mm), (e) CWM Length, and (f) CWM Biomass.

Discussion

Upper Andean tropical forests showcase remarkable biodiversity in soil fauna, which varies significantly from one forest site to another, despite substantial anthropogenic transformation. This result is consistent with prior research on plant communities in this region (Hurtado-M et al., 2021), underscoring an exceptional legacy in beta-diversity present in these tropical mountain forests. Notably, soil fauna communities increased in richness and abundance along succession and some rare groups such as arachnids, wasps, and ground beetles, were only found in old-growth forests. These changes in soil fauna communities are mainly attributed to the increasing amount of energy, which increase with succession (Figure S7). However, although the role of soil microclimatic conditions in driving these changes was modest for soil fauna richness, it exerted a significant influence on soil fauna abundance, suggesting a potential environmental filtering process. This could indicate an effect in excluding species less tolerant to cold temperatures and/or reducing their population sizes.

Litter functional richness and some soil nutrients such as calcium and aluminum also played a role in determining both soil fauna richness and abundance. Our results also showed that soil fauna had no effect on the decomposition environment, possibly due to the relatively low presence of large-sized soil fauna, which may have limited their contribution to decomposition. Altogether, our findings shed light on the fundamental role of forest structural attributes (i.e., aboveground biomass, tree canopy height, nitrogen concentration in soils, soil organic layer thickness) in shaping soil fauna communities in the tropical Andean mountains, providing valuable insights for the conservation and management of these ecologically significant ecosystems, which are threatened by habitat loss and degradation (Etter et al., 2021), with detrimental impacts on soil fauna (Decaëns et al., 2008; Nielsen et al., 2015; Parker, 2010).

Biodiversity turnover between upper Andean tropical forests

As expected in the first hypothesis (H1), we observed a pronounced dissimilarity in soil fauna among the four forest sites (Figure 3). This phenomenon can be attributed to the remarkable heterogeneity present in upper Andean tropical forests, which manifests across short distances due to varying topographical features (Pierick et al., 2021), climatic boundaries (Malhi et al., 2010), vegetation types (Calbi et al., 2021; Hurtado-M et al., 2021; Cedillo et al., 2023), and soil characteristics (Moser et al., 2011). Furthermore, the substantial variability in environmental conditions, coupled with different histories of anthropogenic disturbance and land use practices in the Colombian Andes (Etter et al., 2021), may exacerbate the distinctions observed in soil fauna communities.

Our findings are consistent with the previously observed high floristic distinctiveness within the same permanent plots (Hurtado-M et al., 2021). In this context, the high beta diversity in plant composition may exert significant influences on microenvironmental conditions associated with soil fauna. Recent studies have demonstrated that both the identity and richness of tree species can affect soil conditions (Zhang et al., 2024a), litterfall productivity (Joly et al., 2017; Ma et al., 2021), and microclimatic conditions (Díaz-Calafat et al., 2023; Zhang et al., 2022a), which are intricately linked to soil fauna communities (McGee et al., 2020; Lavelle et al., 2022).

These results suggest that each site represents a distinct biodiversity unit for conservation, as both the floristic and soil fauna composition exhibit unique characteristics. Certainly, our soil fauna sampling revealed the presence of rare, endemic, and newly discovered species exclusive to one of the sites (Castillo-Figueroa et al., 2024), emphasizing the distinctiveness of each forest surveyed. Our study strengthens the notion that upper Andean tropical forests in peri-urban areas are not only highly vulnerable due to widespread habitat loss, but also comprise small areas with high irreplaceability (Bax & Francesconi, 2019).

Effect of succession on soil fauna communities

Our second hypothesis (H2) was supported given that both soil fauna richness and abundance significantly increased with succession (Figure 4). As ecological succession progresses, different attributes of the forests, including aboveground biomass, tree canopy height, soil organic layer thickness, and nitrogen concentration in soils, tend to increase (Garnier et al. 2004; Pinho et al., 2018; Rosenfield et al., 2022; Poorter et al., 2021b, 2023, Figure S3). These changes are accompanied by shifts in species composition with conservative functional traits (e.g., high LMA, high LCC, low LNC), playing a key role in structuring the microhabitat complexity within the soil and litter layers (Barberena-Arias & Aide, 2003; Rosenfield et al., 2022; Poorter et al., 2021a). Additionally, the dynamics observed along the successional gradient often result in higher litter inputs to the soil in more mature forests (Brown & Lugo, 1990), enriching the ecosystem with larger amount of energy (Barberena-Arias & Aide, 2003; Rosenfield et al., 2022; Poorter et al., 2023, Figure S7). Consequently, this increased energy flux can promote greater abundance and richness in soil fauna communities (Kattan et al., 2006; Mathieu et al., 2022). In addition, mature forest coverage can regulate microclimatic conditions resulting in more stable temperature and soil moisture conditions (von Arx et al., 2013; Seidelman et al., 2016; De Frenne et al., 2019; De Lombaerde et al., 2022). Therefore, high species richness and abundance is often observed in environments with favorable conditions, allowing for the persistence of a wider range of strategies (Calderón-Sanou et al., 2022; Mathieu et al., 2022; Guarderas et al., 2022).

We found modest changes in species composition between mature and secondary forests when doing a general comparison between secondary and mature forest plots (Figure 4a, Table 2). This result is in agreement with previous studies that have found subtle differences in species composition between successional stages (Barberena-Arias & Aide, 2002, 2003). In our study, these small differences in species composition can be in part attributed to the lack of plots established in areas in the initial stages of succession, with no forest cover, which can display very contrasting conditions along the gradient in terms of composition (e.g., open pastures). However, we found species of beetles, wasps, oribatids, soil centipedes (e.g., Geophilomorpha), embiopterans, springtails, pygmy grasshoppers (e.g., Tetrigidae) and spiders exclusive of mature forests. According to the SIMPER analysis, 50% of the distinction between mature and secondary forests were attributed to species of millipedes (e.g., *Fuhrmannodesmus* sp.1, *Moojenodesmus* sp.1, Pseudonannolenidae sp.1, Trichomorphini sp.4., Pyrgodesmidae sp.3), arachnids (e.g., *Hoplophorella* sp.1) springtails (Isotominae sp.1) mites (*Allogalumna* sp.1, Tremturidae sp.1, *Macrocheles* sp.1, Uropodidae sp.1) flies (Tipulidae sp.1), isopods (*Prosekiini* sp.2, Scleropactidae sp.), oligochaetes (Enchytraeidae sp.1, Crassiclitellata sp.1), and centipedes (*Newportia stolli*). Some of these species exhibit narrow tolerance to soil nutrients or microclimatic conditions, yet there are many species of millipedes with widespread distribution and broad tolerances to various environmental conditions (Table S3).

Factors determining soil fauna richness and abundance

Our third hypothesis (H3) was partially accepted because amount of energy was the most important predictor of soil fauna richness according to the multiple regression analysis, but microclimate (i.e., variance and 25th percentile in air temperature) was the main driver of soil fauna abundance (Table 3). This finding suggests that forests in advanced state of succession perform a dual role in (1) providing total inputs from both above and belowground in the ecosystem largely determining soil fauna richness (Figure 5, Figure S7), but also, (2) a canopy cover that offer more stable thermal conditions that influence soil fauna abundance (Figure 6, Figure S8). Due to this, mature Andean forests need to be protected to safeguard soil fauna communities with high species richness and abundance, and unique species composition (Guarderas et al., 2022). Given the extensive forest transformation in the Andean region (Etter et al., 2021), it is a priority to conserve the scarce fragments of old-growth forests because they can act as source-patches that guarantee the recovery of soil fauna communities in secondary forests. Forest connectivity between mature and secondary forests is also required to maintain soil fauna biodiversity in this region.

As mentioned before, one of the main drivers of soil fauna communities is the amount of energy, especially for soil fauna richness (Table 3). In this sense, considering that roughly 3/4 of the soil fauna communities belonged to functional groups associated with litter and detritus (Figure 2), it is likely that the factors that determine these litter inputs also drive the organisms linked to these energy resources. Indeed, litter transformers richness and detritivore abundance increased strongly with increasing succession (Figure S7). At the same time, these results are in agreement with the successional patterns found as secondary forests showed the lowest litter productivity, litter depth, and aboveground biomass compared to old-growth forests (Figure 4, Figure S2, Figure S3, Figure S7). Overall, forests with a well-established tree canopy cover and standing biomass can provide higher litter resources in the soil that support richly diverse and abundant communities of litter transformers (Lavelle et al., 2022). Although some studies suggest that changes in litter quality can also influence soil fauna communities (Zhang et al., 2023; 2024b), we found no significant relationship between litter quality and soil fauna richness ($P = 0.19$; $R^2 = 0.13$; Figure S9) or abundance ($P = 0.11$, $R^2 = 0.19$, Figure S9). This reinforces the idea that the amount of energy in mature forests is a key driver of soil fauna communities.

Despite lesser influence of the variables framed within the physiological tolerance hypothesis and habitat heterogeneity hypothesis, we found that soil fauna richness is influenced by microclimatic conditions, aluminum and calcium in soils, as well as plant diversity and litter functional richness (Figure 5). Conversely, soil fauna abundance is mainly explained by microclimatic conditions, while calcium in soils and litter functional richness also play significant roles (Figure 6). In this sense, the highest species richness was found in forests with highest minimum temperatures (Figure 5), which also corresponded to mature forests with a well-developed canopy (Figure S8). Moreover, soil fauna abundance was diminished in secondary forests under unstable temperatures as well as low temperatures reaching the frost conditions, which has been reported in other studies (Briones et al., 1997; Coulson et al., 1996; Sulkava & Hutha, 2003). In this regard, we found that succession showed a positive relationship with minimum air temperature ($P = 0.035$, $R^2 = 0.32$, Figure S8), and an inverse relation with variance in air temperature ($P = 0.037$, $R^2 = 0.31$, Figure S8), which suggest that old-growth forests provide more stable thermal conditions that buffer frost conditions. However, it is important to note that although the altitudinal and temperature gradients in our study sites were narrow (<500 m, <3°C), we still found an effect of temperature on soil fauna suggesting that it is an important driver of soil fauna richness and abundance. Other studies have found that climate is a main driver of soil fauna communities at a regional or a global scale (Lavelle et al., 2022; Heděnec et al., 2022). Although our findings demonstrate a correlation between soil fauna communities and thermal conditions between plots, the broad response of these tropical Andean mountain forest communities to climate change requires further study. Therefore, conducting experimental studies that manipulate temperature is imperative to gain a deeper understanding of the thermal sensitivity of different groups of soil organisms.

The positive relationship between both soil fauna richness and abundance with calcium, could be attributed to its role as an essential micronutrient for invertebrates such as earthworms, millipedes, isopods, snails, and oribatid mites (Robertson, 1936; Gist & Crossley, 1975; Cromack et al., 1977; Ohta et al., 2014a; Mamabolo et al., 2024; Figure S10), which is needed in the development of body parts such as exoskeletons and shells (Ayuke et al., 2019; Parveen et al., 2020; Mamabolo et al., 2024). This finding is in line with previous studies demonstrating that higher soil calcium can influence different soil fauna groups, leading to an increase in their abundance (Hotopp, 2002; Reich et al., 2005; Skeldon et al., 2007; Ohta et al., 2014a, 2014b). Soil calcium is also important for soil structure and ecosystem functioning (Burstrom, 1968; Menta & Pinto, 2016). In particular, adequate calcium availability in soil promotes the formation of stable aggregates and improves permeability, thus creating favorable physical habitats for soil fauna activity (Wuddivira & Camps-Roach, 2007).

Conversely, high concentrations of aluminum in soil can represent significant challenges to soil fauna communities and thus negatively influence their richness (Figure 5). Toxic levels of aluminum can alter the absorption of essential nutrients by plants (Rout et al., 2001; Sade et al., 2016; Bojórquez-Quintal et al., 2017; Neenu & Karthika, 2019), indirectly affecting food availability and other resources for soil fauna such as the root system (Soethe et al., 2006). Aluminum toxicity can damage cellular structures and induce oxidative stress in soil organisms, reducing their viability and survival (Rengel, 2004). Furthermore, soil structure alteration due to high aluminum concentrations can affect plant root growth, leading to destabilization of soil aggregates, and soil compaction (Karabash et al., 2015; Bojórquez-Quintal et al., 2017), which limits soil fauna activity and available habitat.

Lastly, litter functional richness showed that soil fauna species richness and abundance is related to variability in the chemical and physical properties of litter inputs to the soil (Figures 5 and 6). This result is consistent with a recent study, which underscores the importance of plant diversity in the increasing of both richness and abundance of soil fauna (Zhang et al., 2022b). It is likely that the wide range of physical and chemical litter traits can create a high microhabitat heterogeneity in the soil where different species can specialize and proliferate (Madej et al., 2011; Mathieu et al., 2022). Various types of resources in the litter layer are likely to enhance food diversity, which can support a large number of species including rare ones (Wardle, 2006; Cavard et al., 2011; Madej et al., 2011). Additionally, these variety of resources can alter soil moisture and temperature (Liu et al., 2019b; Bello et al., 2019), thereby improving the microclimatic conditions for soil fauna (Zhang et al., 2022b). In this sense, plant species diversity and species composition with a broad spectrum in the litter functional space relate to a high diversity of soil fauna that occupy that space. This suggest that mixed forests with a wide range of litter traits can promote the conditions for increase the soil fauna diversity and abundance during succession.

Influence of soil fauna on decomposition environment

Contrary to our fourth hypothesis (H4), we found that soil fauna had no significant influence on decomposition environment. 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 this research has focused on macrofaunal exclusion experiments in tropical lowland forests. These ecosystems differ significantly from upper mountain regions in terms of 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), and some key decomposers, such as termites and social ants, which are crucial for litter decomposition worldwide (Zanne et al., 2022; Zeng et al., 2024), are absent in these highland forests (Guarderas et al., 2022). Instead, soil fauna communities from upper montane forests are predominantly composed of microarthropods and mesofauna, which, despite their importance in breaking down large litter fragments and dispersing microbial decomposers, are believed 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). Indeed, soil macrofauna was nearly absent from our samples, with mesofauna, including mites and small millipedes, dominating the community and having no effect on decomposition environment (Figure 8).

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 Cundiboyacence 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. Instead, soil microorganisms may play a more crucial role in litter decomposition in Andean mountain forests. 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.

Conclusions

Our study sheds light on the biodiversity of a largely overlooked group of soil organisms within the Upper Andean tropical forests of Colombia. We found that soil fauna communities exhibit significant biodiversity turnover between Andean forests sites, mirroring patterns observed in plant communities. This underscores the distinctiveness of plant and animal species composition at each site, emphasizing the exceptional irreplaceability and vulnerability of the Andean mountain forests around Bogotá. These sites may serve as refuges for specialized and endemic soil fauna species (Castillo-Figueroa et al., 2024), the loss of which could have negative consequences for ecosystem functioning, thus making them priority areas for conservation and restoration.

We observed that soil fauna richness and abundance increase with succession, attributed to higher productivity, litter inputs and more stable microclimatic thermal conditions in old-growth forests. Thus, our findings indicate that the primary driver of soil fauna diversity in tropical mountain Andean forests is the amount of energy (energy hypothesis), which promotes greater species richness. Nonetheless, other variables framed in the physiological tolerance hypothesis and habitat heterogeneity hypothesis also play a role, albeit to a lesser extent. Specifically, soil calcium, along with higher litter functional richness, create favorable conditions and greater habitat heterogeneity, supporting a higher number of coexisting species. For soil fauna abundance, more stable thermal conditions with no extreme cold temperatures emerge as primary favorable factors, suggesting that abundance is potentially determined by environmental filtering.

Finally, our study reveals that soil fauna exerts a limited influence on litter decomposition in upper Andean tropical forests. 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. This 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. Our study underscores the importance of analyzing functional recovery across different soil animal groups to improve our understanding of successional patterns in tropical Andean mountain forests and their relationship with decomposition.

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Supplementary material

Figure S1. Rarefaction curves between sites and succession for each of the Hill numbers of diversity (q = 0, q = 1, q = 2) in upper Andean tropical forests. Acronyms are as follows: GuaMat = Guasca mature, GuaSec = Guasca secondary, GutSec = Guatavita secondary, TabMat = Tabio mature, TabSec = Tabio secondary, TorMat = Torca mature, TorSec = Torca secondary.

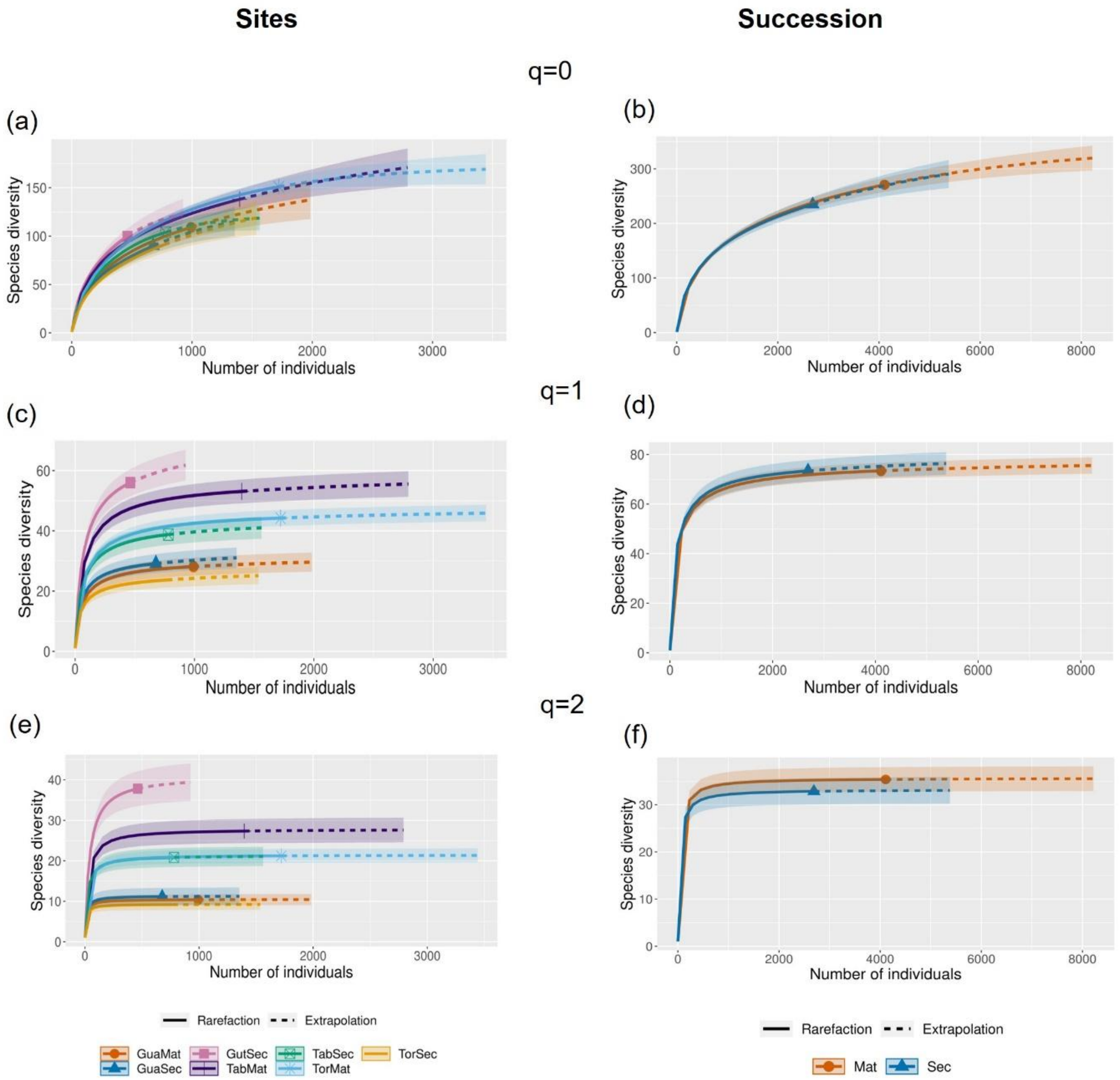

Figure S2. Principal component analysis including aboveground biomass (Mg ha^{-1}), tree canopy height (m), nitrogen concentration in soils (%), and soil organic layer thickness (cm) as proxies of succession. (a) Loading of each variable (b) Pearson correlations between each variable and the scores of the first axis of the PCA. Green circles represent old-growth forest plots and grey circles indicate second-growth forest plots.

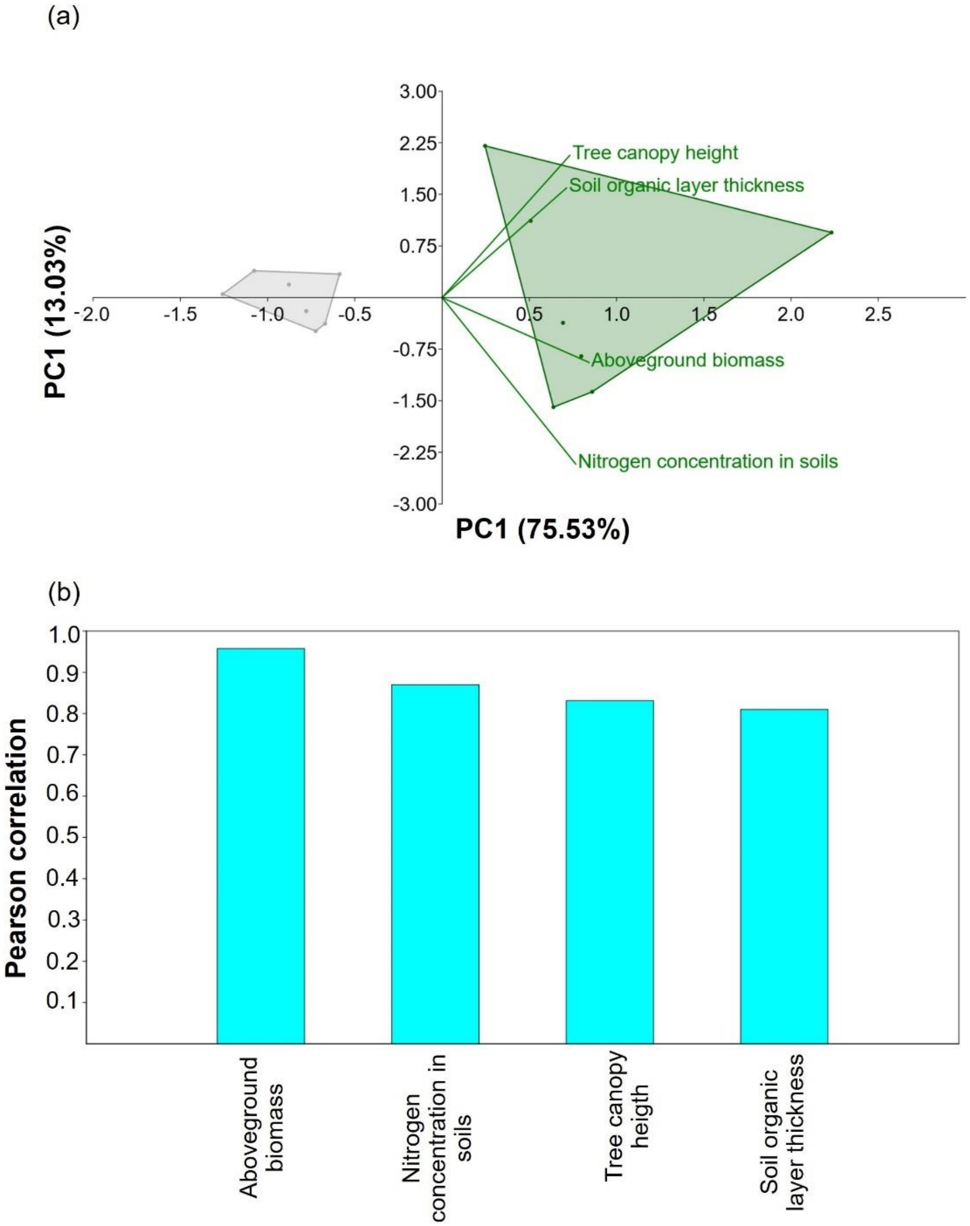

Figure S3. Principal component analysis including litter productivity (Mg C ha^{-1} y^{-1}), stem productivity (Mg C ha^{-1} y^{-1}), litter depth (cm), fine root productivity (Mg C ha^{-1} y^{-1}) as indicators of energy flux in the forests. (a) Loading of each variable (b) Pearson correlations between variables. Green circles represent old-growth forest plots and grey circles indicate second-growth forest plots.

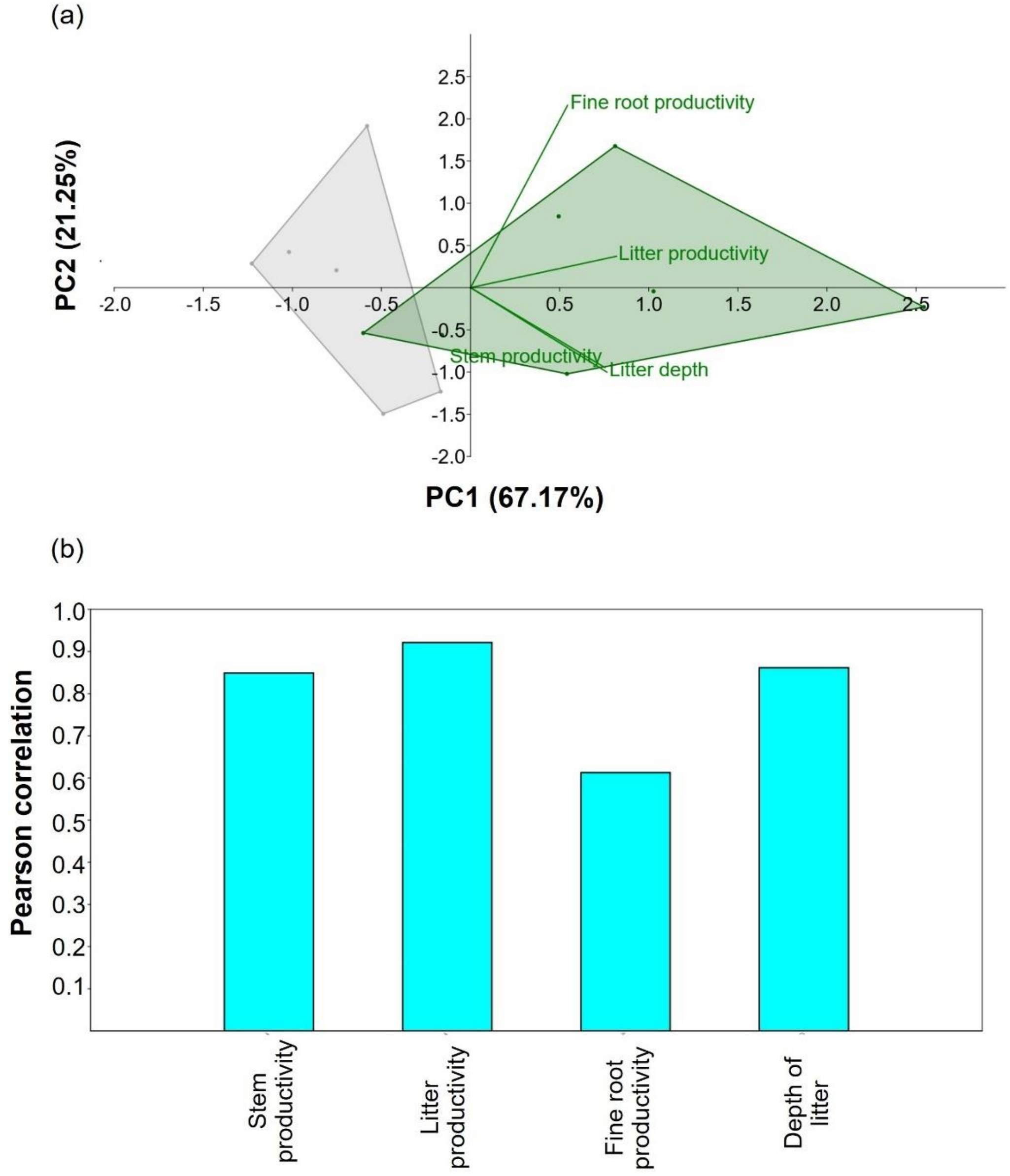

Figure S4. Soil fauna relative abundance in each of the upper Andean tropical forest sites per each (a) taxonomical group and (b) functional group.

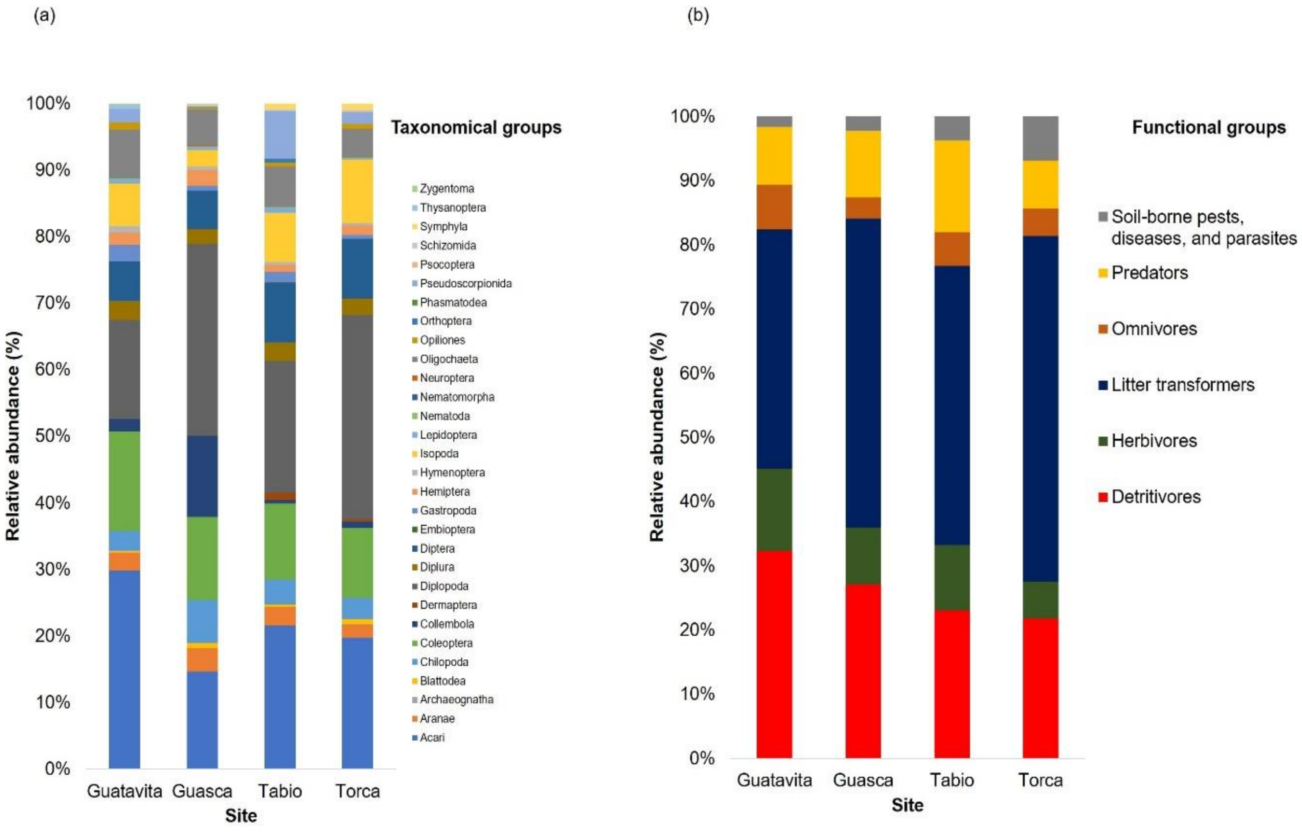

Figure S5. Soil fauna relative abundance in mature and secondary upper Andean tropical forests per each (a) taxonomical group and (b) functional group**.**

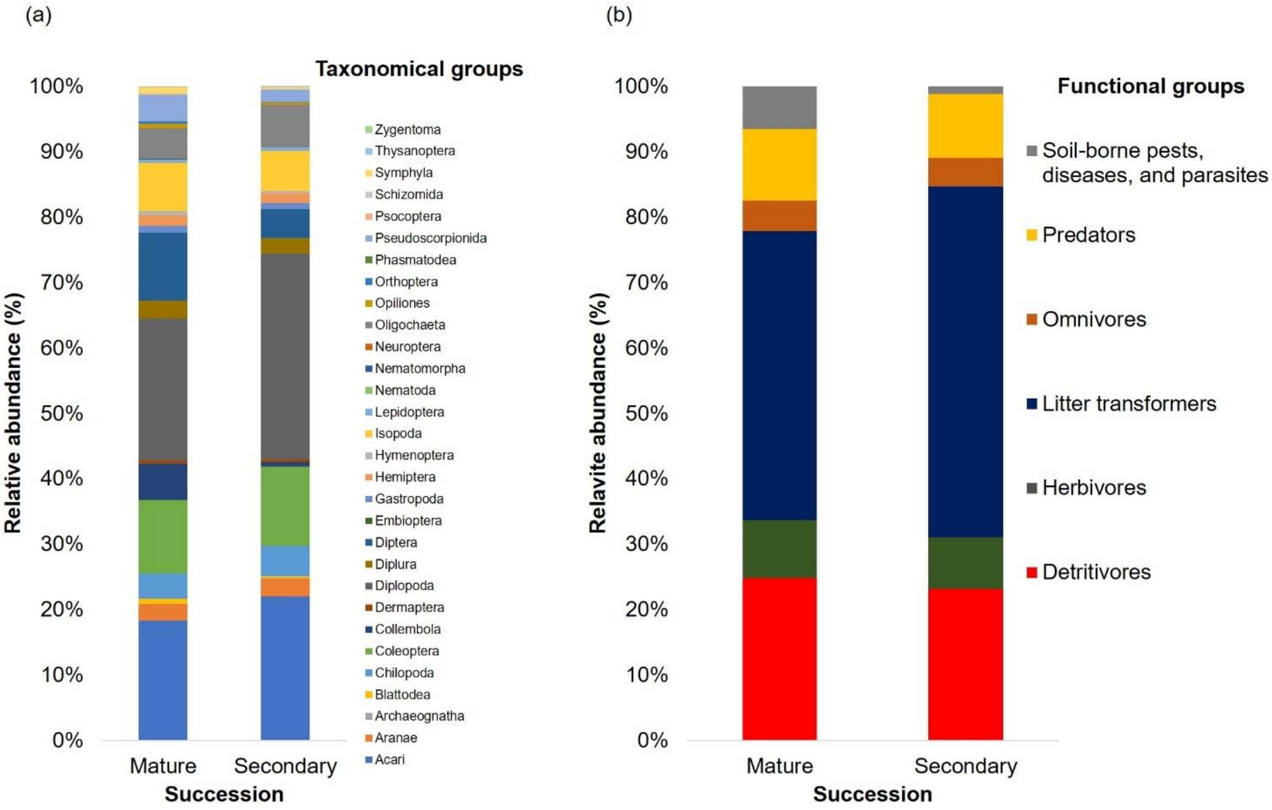

Figure S6. Rainclouds showing differences in species richness (t = 2.994, df = 12, Cohen´s d = 1.60, P = 0.011) and abundance between (t = 2.306, df = 12, Cohen´s d = 1.233, P = 0.040) mature and secondary in upper Andean tropical forests.

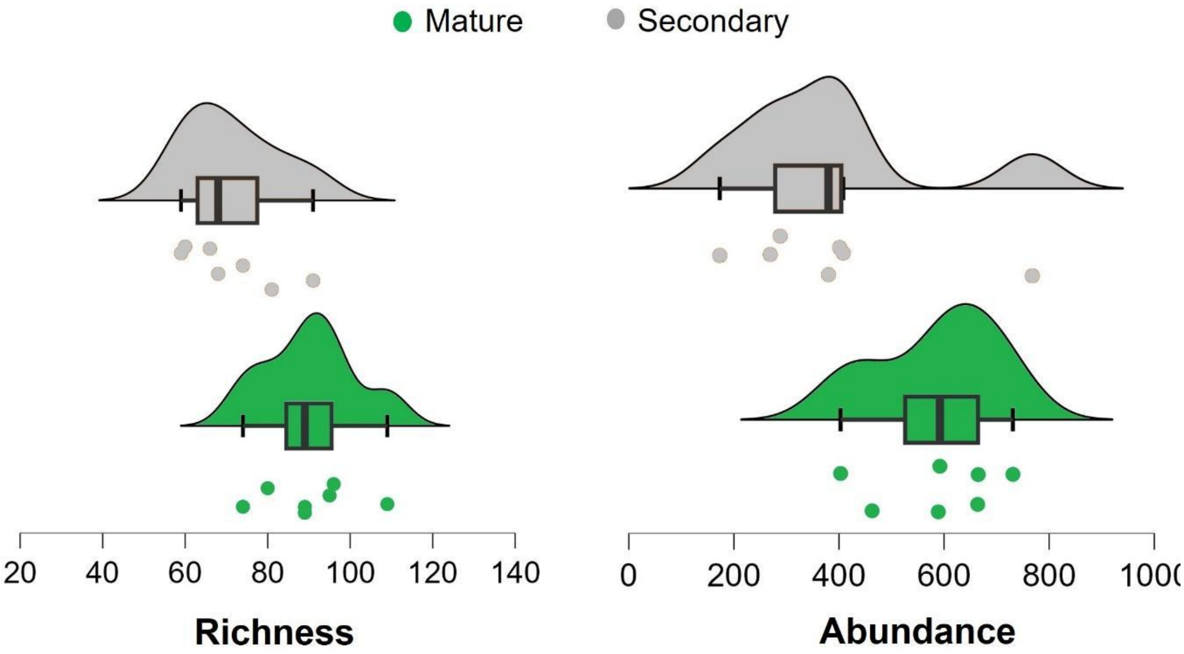

Figure S7. Soil fauna functional groups related to litter and detritus, and amount of energy along the successional gradient in upper Andean tropical forests. (a) litter transformers richness ($P = 0.0006$, $n = 14$, $R^2 = 0.63$, CI = [3.31, 6.19]), (b) detritivore abundance ($P = 0.015$, $n = 14$, $R^2 = 0.40$, CI = [43.93, 86.46]), and (c) amount of energy ($P = 0.0003$, $n = 14$; $R^2 = 0.68$, CI = [0.80, 1.32]).

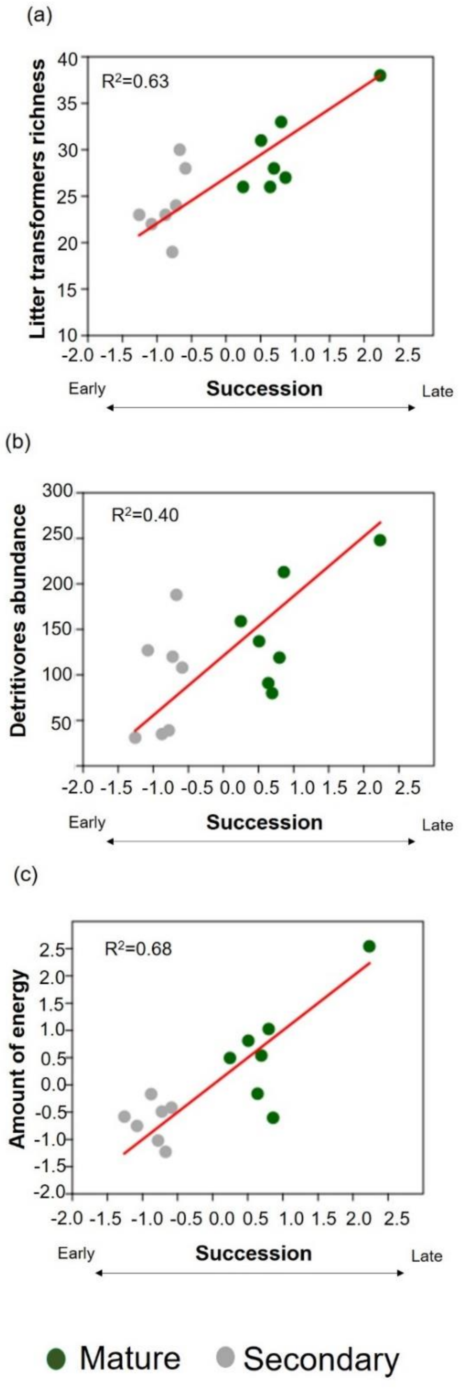

Figure S8. Microclimatic conditions along the successional gradient. (a) minimum air temperature (P = 0.035, n =14, $R^2 = 0.32$, CI = [0.78, 2.21]), (b) variance in air temperature (P = 0.037, n = 14, $R^2 = 0.31$, CI = [-3.44, -1.05]), (c) standard deviation of soil moisture (P = 0.01, n = 14, $R^2 = 0.40$, CI = [-0.02, -0.008]).

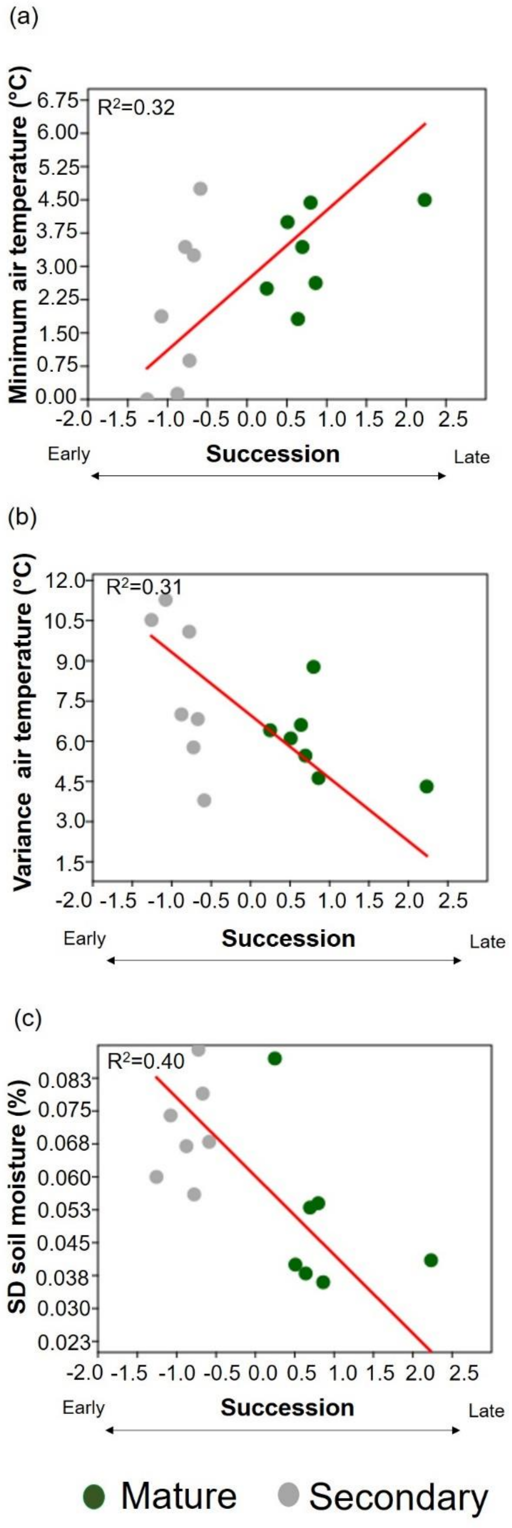

Figure S9. No relation between litter quality and soil fauna community attributes in upper Andean tropical forests. Community Weighted Mean (CWM) of leaf CN ratio was employed as a measure of litter quality and showed no relation with (a) soil fauna richness (P = 0.19, $R^2 = 0.13$, CI = [-6.16, -0.96]) nor with (b) soil fauna abundance (P = 0.11, $R^2 = 0.19$, CI = [-32.54, -3.02]).

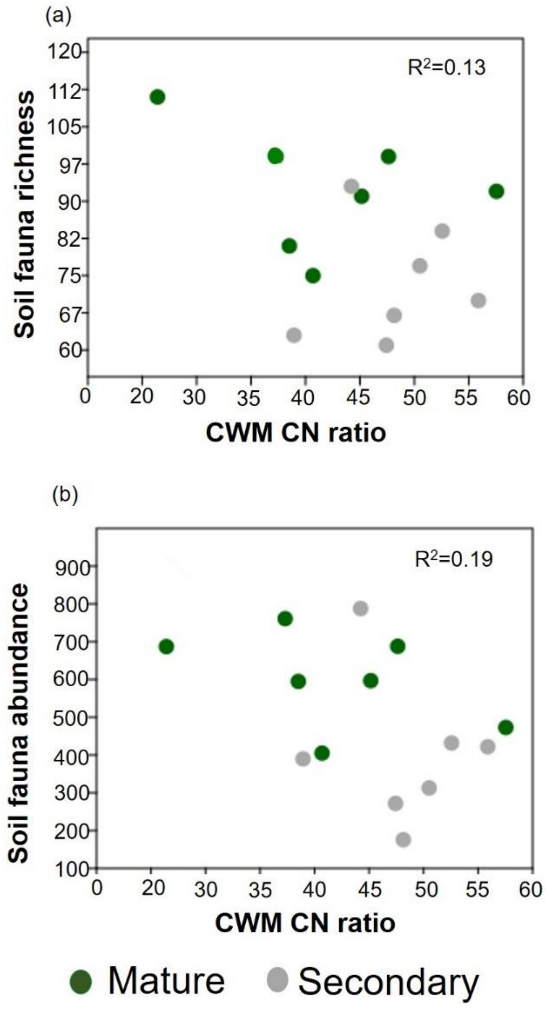

Figure S10. Calcium effects on (a) gastropoda abundance (P = 0.012, n = 14, R^2 = 0.42, CI = [0.002, 0.012]), (b) acari richness (P = 0.023, n = 14; R^2 = 0.36, CI = [0.001, 0.011]) in upper Andean tropical forests.

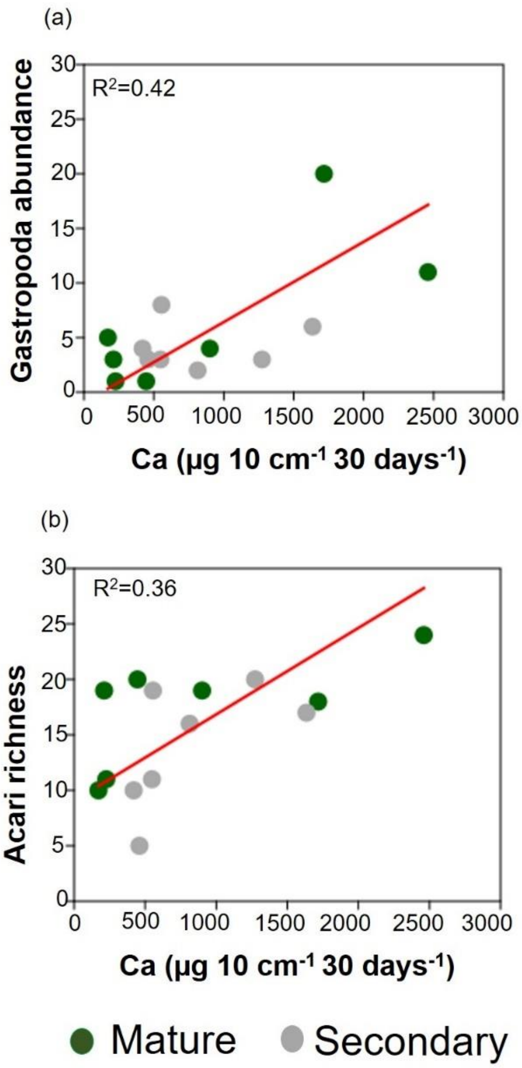

Table S1. Plant community attributes of Upper Andean tropical forests. More information about plant composition can be found in Hurtado-M et al. (2021) (see references).

Plant community attribute	Site	Coefficient of variation	Mean SD	P	Kruskal-Wallis tests (H)
Abundance	Torca	0.311	127.25 ± 39.53		
	Tabio	0.396	159.75 ± 63.18		
	Guasca	0.125	158.00 ± 19.80		
	Guatavita	0.319	144.00 ± 45.89		
				0.696	1.439
Species richness	Torca	0.198	17.00 ± 3.37		
	Tabio	0.192	17.75 ± 3.40		
	Guasca	0.214	16.50 ± 3.54		
	Guatavita	0.284	16.00 ± 4.54		
				0.943	0.388
Evenness (Pielou)	Torca	0.098	0.79 ± 0.08		
	Tabio	0.029	0.84 ± 0.02		
	Guasca	0.112	0.81 ± 0.09		
	Guatavita	0.187	0.67 ± 0.13		
				0.174	4.971
Diversity (Alfa Fisher)	Torca	0.308	5.60 ± 1.71		
	Tabio	0.366	5.58 ± 2.05		
	Guasca	0.247	4.65 ± 1.15		
	Guatavita	0.554	5.14 ± 2.85		
				0.843	0.839

Table S2. Taxonomic structure of each site in terms of abundance and species richness. N = abundance, S = morphospecies richness.

Taxonomical grouping	Guatavita		Guasca		Tabio		Torca		Total	
	N	**S**	**N**	**S**	**N**	**S**	**N**	**S**	**N**	**S**
Acari	146	22	248	20	490	28	503	31	1387	42
Aranae	13	6	60	8	63	11	50	20	186	31
Archaeognatha	0	0	0	0	0	0	1	1	1	1
Blattodea	1	1	13	1	8	4	19	5	41	7
Chilopoda	15	4	109	5	85	8	82	6	291	8
Coleoptera	73	26	212	38	260	47	267	49	812	108
Collembola	9	3	206	5	12	3	25	4	252	13
Dermaptera	0	0	0	0	25	1	9	1	34	1
Diplopoda	73	8	488	9	448	10	781	11	1790	22
Diplura	14	2	39	2	64	2	63	2	180	2
Diptera	29	4	97	13	202	12	228	11	556	23
Embioptera	0	0	0	0	2	1	0	0	2	1
Gastropoda	12	2	12	2	36	5	14	5	74	7
Hemiptera	9	3	40	5	24	6	37	7	110	12
Hymenoptera	5	4	10	6	10	3	10	7	35	18
Isopoda	31	4	41	3	168	3	243	4	483	6
Lepidoptera	3	2	8	4	17	8	4	3	32	16
Nematoda	1	1	1	1	3	1	1	1	6	1
Nematomorpha	0	0	1	1	0	0	0	0	1	1
Neuroptera	0	0	2	2	0	0	0	0	2	2
Oligochaeta	36	2	91	2	138	2	112	2	377	2
Opiliones	5	3	4	2	13	4	18	4	40	9
Orthoptera	0	0	2	1	12	2	0	0	14	3
Phasmatodea	0	0	0	0	1	1	0	0	1	1
Pseudoscorpionida	10	3	3	2	163	3	47	4	223	3
Psocoptera	0	0	0	0	0	0	2	1	2	1
Schizomida	0	0	0	0	6	1	5	1	11	2
Symphyla	0	0	4	2	19	2	25	2	48	2
Thysanoptera	3	2	3	2	1	1	0	0	7	5
Zygentoma	1	1	0	0	0	0	0	0	1	1
Total	489	103	1694	136	2270	169	2546	182	6999	351

Table S3. SIMPER analyses for each of the site pairwise comparisons of the soil fauna composition. For each comparison, the species that contributed to the 50% of the difference were included.

SIMPER Secondary-Mature: Overall dissimilarity: 80.1%

Taxon	Av. Dissimilarity	%Contribution	%Cumulative	Mean Secondary	Mean Mature
Fuhrmannodesmus sp1.	5.877	7.336	7.336	14.5	17.2
Moojenodesmus sp1.	4.917	6.138	13.47	8.52	10.6
Pseudonannolenidae sp1.	3.253	4.061	17.54	6.1	7.76
Tipulidae sp3.	2.928	3.656	21.19	0.0476	10.6
Allogalumna sp1.	2.926	3.653	24.84	3.05	10.4
Isotominae sp1.	2.738	3.418	28.26	0	9.05
Hoplophorella sp1.	2.009	2.508	30.77	1.43	7
Ideobisium sp1.	1.955	2.441	33.21	1.57	7
Prosekiini sp1.	1.799	2.246	35.46	4.29	3.9
Scleropactidae sp2.	1.782	2.225	37.68	1.71	5.76
Enchytraeidae sp1.	1.611	2.012	39.69	5.24	5.33
Trematuridae sp2.	1.328	1.658	41.35	3.33	3.14
Crassiclitellata sp1.	1.17	1.46	42.81	3.38	4
Macrocheles sp1.	1.168	1.458	44.27	4.76	1.62
Trichomorphini sp2.	1.141	1.425	45.7	1.52	2.86
Newportia stolli	1.095	1.366	47.06	2.62	3.48
Scleropactidae sp1.	1.049	1.31	48.37	0.476	3.19
Uropodidae sp1.	1.049	1.31	49.68	3.81	2.95
Pyrgodesmidae sp2.	0.9836	1.228	50.91	3	0.476

SIMPER Guatavita-Guasca: Overall dissimilarity: 87.29%

Taxon	Av. Dissimilarity	%Contribution	%Cumulative	Mean Guatavita	Mean Guasca
Moojenodesmus sp1.	14.85	17.01	17.01	0.167	33.4
Isotominae sp1.	5.486	6.285	23.3	0	15.8
Newportia stolli	2.736	3.134	26.43	0	6
Pergamasus sp1.	2.449	2.805	29.24	0.333	5
Hoplophorella sp1.	2.101	2.407	31.64	0.333	5.33
Macrocheles sp1.	1.923	2.203	33.85	5.33	2.33
Enchytraeidae sp1.	1.887	2.162	36.01	2	4.75
Crassiclitellata sp1.	1.714	1.963	37.97	4	2.83
Acaridae sp1.	1.557	1.783	39.76	3.5	0
Uropodidae sp1.	1.493	1.71	41.47	3.33	1.83
Trombidiinae sp1.	1.426	1.634	43.1	3.83	1
Stemmiulus sp1.	1.394	1.597	44.7	2.83	0
Fuhrmannodesmus sp2.	1.362	1.561	46.26	3.17	0
Pyrgodesmidae sp3.	1.337	1.531	47.79	2.83	0
Prosekiini sp2.	1.265	1.449	49.24	2.67	0
Allogalumna sp1.	1.174	1.345	50.58	2.33	1.33

SIMPER Guatavita-Tabio: Average dissimilarity 86.4

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Guatavita	Mean Tabio
Fuhrmannodesmus sp1.	7.733	8.95	8.95	0	22.1
Prosekiini sp1.	3.888	4.501	13.45	0	9.58
Ideobisium sp1.	3.73	4.317	17.77	0.667	11.6
Trichomorphini sp2.	2.901	3.357	21.13	0	7.67
Pyrgodesmidae sp2.	2.764	3.199	24.32	0	6.08
Trematuridae sp2.	2.588	2.996	27.32	0	8.33
Macrocheles sp1.	2.053	2.377	29.7	5.33	3.83
Enchytraeidae sp1.	2.039	2.36	32.06	2	6.33

Allogalumna sp1.	1.898	2.197	34.25	2.33	6.08
Alleculinae sp1.	1.826	2.114	36.37	0	4.08
Crassiclitellata sp1.	1.785	2.067	38.43	4	5.17
Uropodidae sp1.	1.61	1.863	40.3	3.33	4.92
Scleropactidae sp2.	1.519	1.758	42.06	0.333	3.75
Tipulidae sp3.	1.483	1.717	43.77	0	5.08
Acaridae sp1.	1.327	1.536	45.31	3.5	0
Stemmiulus sp1.	1.173	1.358	46.67	2.83	0
Trombidiinae sp1.	1.17	1.354	48.02	3.83	2.17
Fuhrmannodesmus sp2.	1.165	1.348	49.37	3.17	0
Pyrgodesmidae sp3.	1.131	1.309	50.68	2.83	0

SIMPER Guatavita-Torca: Average dissimilarity 88.74

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Guatavita	Mean Torca
Fuhrmannodesmus sp1.	10.5	11.84	11.84	0	33.4
Pseudonannolenidae sp1.	6.942	7.823	19.66	0	21.9
Allogalumna sp1.	4.377	4.933	24.59	2.33	15
Tipulidae sp3.	4.324	4.872	29.47	0	13.5
Scleropactidae sp2.	2.624	2.957	32.42	0.333	7.5
Hoplophorella sp1.	2.412	2.719	35.14	0.333	7.08
Scleropactidae sp1.	2.349	2.647	37.79	0	6.42
Enchytraeidae sp1.	2.002	2.256	40.05	2	6.42
Macrocheles sp1.	1.557	1.755	41.8	5.33	2.33
Crassiclitellata sp1.	1.299	1.464	43.26	4	2.92
Trichomorphini sp1.	1.281	1.444	44.71	0	3.83
Uropodidae sp1.	1.268	1.429	46.14	3.33	3.42
Newportia stolli	1.222	1.378	47.52	0	3.33
Acaridae sp1.	1.207	1.36	48.88	3.5	0
Trombidiinae sp1.	1.176	1.326	50.2	3.83	0.667

SIMPER Guasca-Tabio: Average dissimilarity 86.14

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Guasca	Mean Tabio
Moojenodesmus sp1.	10.39	12.06	12.06	33.4	0
Fuhrmannodesmus sp1.	6.433	7.468	19.53	0	22.1
Isotominae sp1.	4.072	4.728	24.26	15.8	0
Ideobisium sp1.	3.301	3.832	28.09	0	11.6
Prosekiini sp1.	2.917	3.387	31.48	1.58	9.58
Trichomorphini sp2.	2.393	2.778	34.26	0	7.67
Pyrgodesmidae sp2.	2.203	2.557	36.81	0	6.08
Trematuridae sp2.	2.124	2.466	39.28	0.667	8.33
Pergamasus sp1.	1.678	1.948	41.23	5	0.167
Allogalumna sp1.	1.678	1.948	43.17	1.33	6.08
Newportia stolli	1.574	1.827	45	6	1.33
Enchytraeidae sp1.	1.52	1.765	46.77	4.75	6.33
Alleculinae sp1.	1.473	1.71	48.48	0.0833	4.08
Hoplophorella sp1.	1.441	1.673	50.15	5.33	2.17

SIMPER Guasca-Torca: Average dissimilarity 84.52

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Guasca	Mean Torca
Moojenodesmus sp1.	9.603	11.36	11.36	33.4	0
Fuhrmannodesmus sp1.	8.891	10.52	21.88	0	33.4
Pseudonannolenidae sp1.	5.139	6.08	27.96	2.33	21.9
Allogalumna sp1.	3.993	4.724	32.69	1.33	15
Isotominae sp1.	3.82	4.519	37.21	15.8	0
Tipulidae sp3.	3.676	4.349	41.55	0	13.5
Scleropactidae sp2.	2.056	2.432	43.99	1.67	7.5
Scleropactidae sp1.	1.95	2.307	46.29	0	6.42
Hoplophorella sp1.	1.929	2.282	48.57	5.33	7.08
Enchytraeidae sp1.	1.606	1.9	50.47	4.75	6.42

SIMPER Tabio-Torca: Average dissimilarity 73.59

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Tabio	Mean Torca
Fuhrmannodesmus sp1.	5.401	7.339	7.339	22.1	33.4
Pseudonannolenidae sp1.	5.223	7.098	14.44	0	21.9
Tipulidae sp3.	3.964	5.386	19.82	5.08	13.5
Allogalumna sp1.	3.176	4.316	24.14	6.08	15
Prosekiini sp1.	2.403	3.265	27.4	9.58	3.17
Ideobisium sp1.	2.204	2.995	30.4	11.6	3.08
Trichomorphini sp2.	1.975	2.683	33.08	7.67	0
Scleropactidae sp2.	1.847	2.509	35.59	3.75	7.5
Pyrgodesmidae sp2.	1.768	2.402	37.99	6.08	0
Scleropactidae sp1.	1.727	2.347	40.34	0	6.42
Trematuridae sp2.	1.722	2.339	42.68	8.33	2.33
Hoplophorella sp1.	1.659	2.254	44.93	2.17	7.08
Enchytraeidae sp1.	1.543	2.097	47.03	6.33	6.42
Alleculinae sp1.	1.186	1.611	48.64	4.08	0
Crassiclitellata sp1.	0.9943	1.351	49.99	5.17	2.92
Trichomorphini sp1.	0.962	1.307	51.3	0	3.83

Chapter 5

Drivers of soil fungal communities along a forest successional gradient in the upland Andes and their influence on decomposition rates.

Under review in *Biotropica*

Drivers of soil fungal communities along a forest successional gradient in upper Andean tropical forests and their influence on decomposition rates

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Abstract

Soil fungi are vital in regulating ecosystem functions, yet their community changes along tropical mountain forest succession and roles in litter decomposition remain underexplored. This study investigates the main drivers of soil fungal communities along a successional gradient in upper Andean tropical forests and their influence on decomposition. Soil fungi were sampled from the topsoil in 14 permanent plots (20x20 m) across four forest sites in the Andean mountains surrounding Bogotá, Colombia. We collected data on microclimate, soil nutrients, plant diversity, forest biomass, litter functional richness, and decomposition from these plots. Using Illumina sequencing to amplify the ITS1 region, we analyzed data with OTUs as a proxy for species richness and calculated Hill numbers to assess fungal diversity ($q = 0$, $q = 1$, $q = 2$). ANOSIM and NMDS analyses indicated significant differences in fungal communities between forest sites. Reduced major axis regressions showed no changes in fungal diversity along the successional gradient, with aboveground biomass as a proxy of successional status. However, fungal diversity varied with minimum soil surface temperature, litter functional richness, plant diversity, and soil calcium. Fungal diversity was not related to decomposition rates, as relationships between fungal guilds and decay rates of each litter species neutralized this effect. Plant pathogen diversity appeared to negatively impact decomposition, likely due to metabolic responses in plants that slow down the process. Our findings reveal that each Andean forest site hosts distinct fungal communities and that anthropogenic changes in drivers like soil nutrients, plant diversity, and microclimate may affect their diversity and role in decomposition.

Key-words: Andean region, biodiversity, forest structure, fungi, litter decay, soil attributes, succession, tropical mountain forests.

Introduction

Fungi account for approximately 12 Gt of carbon globally (Bar-On et al., 2018) and represent a significant portion of soil microbial biomass (Janowski & Leski, 2022). They are essential for regulating key ecosystem functions, including litter decomposition (Tunlid et al., 2022; Li et al., 2022), nutrient cycling (Mayer et al., 2021), and promoting plant growth (Adedayo et al., 2023). Given their high turnover rates and sensitivity to land-use changes, soil fungal communities can serve as indicators of forest successional status (Gao et al., 2015; Li et al., 2020; He et al., 2022). However, the influence of forest structure, microclimate, and soil factors on fungal community composition and functional guilds along successional gradients remains understudied, particularly in tropical mountain ecosystems.

Over the last few decades, different studies have highlighted the influence of biotic and abiotic factors on soil fungal communities. Edaphic conditions, such as nutrient concentrations (Liu et al., 2019a; Geng et al., 2023b; Hogan et al., 2023), organic carbon (Zhang et al., 2022c), bulk density (Harris et al., 2003), pH (Zhang et al., 2022c; Zhang et al., 2016; Djemiel et al., 2024), and texture (Sarula et al., 2020; Sanchez-Tello & Corrales, 2024), directly influence fungal diversity and composition. Forest factors such as plant diversity and productivity, also shape soil fungal community structure (Adamo et al., 2021; Roy-Bolduc et al., 2016; Shen et al., 2021). Plant communities influence the composition of root-associated microorganisms (Hanif et al., 2019; Li et al., 2020), while the amount, quality, and diversity of litters provide essential substrates and habitat heterogeneity for soil fungi (Ochoa-Hueso et al., 2018). Additionally, microclimatic conditions including moisture (Manzoni et al., 2012; Chen et al., 2023), and temperature (Castaño et al., 2018) can impose physiological constraints, affecting fungal biomass and composition.

Litter decomposition is critical for carbon and nutrient cycling across terrestrial ecosystems (e.g., Berg & Mcglaugerthy, 2020; Castillo-Figueroa, 2021). Decomposition represents a complex process involving not only the breakdown of litter but also the transformation of other materials (Prescott & Vesterdal, 2021). Within this process, soil fungi play a primary role due to their enzymatic capacity to decompose plant litter, especially recalcitrant types (Tunlid et al., 2022; Ullah et al., 2023; Leifheit et al., 2024). Fungal saprotrophs, including litter, soil, wood, and dung saprotrophs, typically dominate litter horizons and are the most abundant fungal guilds (Tedersoo et al., 2014; Põlme et al., 2020), directly influencing decomposition (Li et al., 2022; Meng et al., 2024). Other groups indirectly influence decomposition through distinct mechanisms, such as ectomycorrhizal fungi by competing with saprotrophs (Averill & Hawkes, 2016; Tunlid et al., 2022), and fungal pathogens by affecting plant communities and their litter quality (Guo et al., 2025). Yet, most studies on fungal roles in decomposition have focused on temperate and boreal ecosystems where plant species diversity is generally lower than in the tropics. Furthermore, our understanding of fungal contributions to litter decomposition in tropical ecosystems, particularly in upper mountain regions, remains poorly known (Looby & Martin, 2020).

Upper Andean Tropical Forests (UATF) are among the world's most biodiverse mountain ecosystems (Rahbek et al., 2019; Myster, 2021). These forests host numerous endemic species (Myers et al., 2000; Castillo-Figueroa et al., 2024) and exhibit high biodiversity turnover across short distances (Hurtado-M et al., 2021; Cedillo et al., 2023; Barczyk et al., 2023). While significant progress has been made in understanding plant (Cuesta et al., 2017, 2023) and animal diversity in these ecosystems (Marian et al., 2018, 2020), soil microorganisms remain understudied. Around Bogotá, the capital city of Colombia, forests have been naturally recovering (Rubiano et al., 2017; Calbi et al., 2020; Hurtado-M et al., 2021), but the dynamics of soil fungal communities during succession are still poorly understood. Studying these changes is crucial for guiding restoration efforts and land-use management, especially in this region where less than 20% of the original forest cover remains (Etter et al., 2021).

Research on tropical forest succession has largely overlooked soil fungi when compared to plant communities (Poorter et al., 2023, 2024), and most studies have focused on lowland ecosystems rather than mountain regions (Adamo et al., 2021; Alves da Silva et al., 2023). Successional theories suggest that forest recovery leads to increased plant diversity, soil organic carbon content and increase in structural attributes such as canopy height, basal area, and aboveground biomass (Garnier et al., 2004; Poorter et al., 2021b, 2023). These shifts alter microclimatic conditions, soil properties, and fungal substrates (Castaño et al., 2018; Geng et al., 2023b). Studies indicate that soil fungal communities change with succession (Li et al., 2020; Adamo et al., 2021), driven by the arrival of conservative plant species with recalcitrant compounds in later stages (Poorter et al., 2021a). As succession advances, litter accumulates and the fungal channel becomes dominant over bacterial food webs (Frouz et al., 2013), suggesting an expected increase in fungal diversity and changes in fungal community composition along succession. These changes would likely influence decay rates, although responses may vary by fungal guild and are context-dependent (Shi et al., 2019; Adamo et al., 2021).

To uncover the hidden biodiversity of soil fungi and understand their taxonomic community structure during secondary succession in UATF, we conducted a comprehensive study incorporating microclimatic conditions, soil properties, and forest structural attributes from permanent plots. Our goal was to identity the main drivers of soil fungal communities and their influence on litter decomposition along a successional gradient. Specifically, we aimed to: (1) characterize soil fungal communities across sites, (2) examine changes in soil fungal diversity and composition between mature and secondary forests, (3) identify key environmental factors driving fungal diversity, and (4) assess the influence of fungal communities on litter decomposition. Our hypotheses were: (H1) soil fungal communities will vary between forest sites due to high habitat heterogeneity; (H2) fungal diversity will increase with succession, and species composition will change between secondary and mature forests due to higher litter accumulation in the latter, (H3) edaphic, microclimatic, and litter functional characteristics should be strong determinants of fungal diversity as they are related to fungal physiology, resource availability, and heterogeneity; and (H4) higher fungal diversity, especially in saprotrophs guilds, will enhance litter decay rates given its major role on decomposition.

Materials and methods

Study area

Our study took place in the Colombian Andes, which covers 24.5% of the country (Etter & Wyngaarden, 2000) and is a highly deforested region due to agriculture, livestock, urbanization, and mining (Antonio-Fragala & Obregón-Neira, 2011; Etter et al., 2021). This region is Colombia's most densely populated area, harboring 70% of the nation's population (DANE, 2018). Its capital is Bogotá and, together with its surrounding municipalities, has over 11 million residents (World Population Review, 2024). Our research focused on a successional gradient in the Eastern mountain range, specifically in the Cundiboyacense high plains, at elevations between 2685 and 3140 m. The climate near Bogotá exhibits mean annual temperature of 14.78ºC and a mean annual rainfall of 975 mm (Anselm et al., 2020).

In 2013, a set of permanent plots were established in peri-urban areas around Bogotá across five municipalities (Guasca, Guatavita, Tabio, San Francisco, and Soacha) to monitor long-term carbon cycling, biodiversity and resilience (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023, 2024). These included 36 20x20 m and eight 50x50 m plots. For our study, we focused on 14 of the 20x20 m plots, where we had access to extensive data on community and ecosystem ecology (Figure S1). Forests were classified as secondary or mature based on structural attributes like basal area, canopy height, stem density, and species composition from previous studies (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023). The 14 plots were located in four sites: Torca (2708–2965 m), Tabio (2696–2821 m), Guasca (3085–3140 m), and Guatavita (3028–3035 m) (Castillo-Figueroa, 2024a; Figure S1). In these plots, vegetation is dominated by plants from the families Ericaceae, Melastomataceae, Cunoniaceae, Primulaceae, Clusiacea and Asteraceae, which together account for over half of all individuals with a basal diameter greater than 5 cm (the basal diameter was taken 5 cm aboveground; see Hurtado-M et al., 2021 for more details). A total of 63 species of shrubs and trees were identified in the study area, with *Weinmannia tomentosa*, *Cavendishia bracteata*, *Miconia ligustrina*, *Miconia squamulosa*, and *Myrcianthes leucoxyla* being among the most common species (Clerici et al., 2016; Castillo-Figueroa et al., 2023).

Litter functional traits

We quantified litter functional richness for each plot as a proxy of habitat heterogeneity for soil fungi, given that functional richness reflects the range of functional traits present within a community (Mason et al., 2005). We measured functional traits of senescent leaves for each of the 63 species by sampling five individuals per species across the 14 permanent plots. Measurements were conducted according to methodologies outlined by Bakker et al. (2011) and Pérez-Harguindeguy et al. (2013). To calculate litter functional richness, we focused on three key functional traits that are in part related to the leaf economic spectrum (Wright et al., 2004): leaf mass per area (LMA, g/m^2), litter nitrogen content (Litter NC, %), and litter carbon content (Litter CC, %). To determine one-sided leaf area, leaves were scanned and analyzed using ImageJ (Schneider et al., 2012). Each leaf sample was then oven-dried at 60 ºC for 72 hours to measure dry mass (g) and estimate LMA. Litter NC and Litter CC were analyzed using an elemental analyzer (FlashSmart™ Thermo Fisher Scientific, USA).

Estimation of forest biomass

Aboveground biomass (AGB) per plot was estimated by measuring the diameter at breast height (DBH) for individuals with a diameter at 'ankle' height (DAH, 5 cm above the soil surface) 5 cm or higher, following the method described by Hurtado-M et al. (2021). This approach facilitated the inclusion of shrubs that typically branch near the ground, as well as individuals with twisted stems, which are common in mountain forests. AGB was estimated using two allometric equations specifically developed for Andean mountain ecosystems (Sierra et al., 2007; Pérez & Diaz, 2010). We used AGB as a proxy for forest successional status (Brown & Lugo, 1990; Garnier et al., 2004; Poorter et al., 2021b, 2023). We also used aboveground net primary production (NPP) and fine root production (FRP) from previous studies conducted in these same plots (Castillo-Figueroa & Posada, 2025; Castillo-Figueroa et al., 2023).

Measurement of environmental and soil microclimatic variables

TMS-4 soil probes with data loggers from TOMST (Czech Republic) were placed in the center of each of the 14 plots to monitor soil temperature and volumetric water content every 15 minutes throughout 2022. Each probe has three temperature sensors: one 15 cm above the soil surface, one at the surface, and one at a depth of 8 cm. A separate sensor measures volumetric water content at 14 cm deep (Wild et al., 2019). For this study, we used surface temperature data, as soil fungi were collected from the topsoil (see below). After cleaning the databases of potential outliers from datalogger installation or data collection, we derived nine statistical variables for surface temperature and volumetric water content: mean, minimum, maximum, range, standard deviation, variance, and the 25th, 50th, and 75th percentiles.

Soil physicochemical characteristics was assessed by collecting samples to evaluate nutrient supply rates using plant roots simulators (PRS®) probes from Western AG. These ion-exchange membrane probes were positioned in four random locations within each plot (n = 56) to capture environmental variability with minimal disturbance. Each location had four anion and four cation probes, which were pooled for laboratory analysis, resulting in 16 pairs of probes per plot. Nutrient concentrations were determined through colorimetric analysis for NO_3 and NH_4, and inductively coupled plasma spectrometry for elements like Ca, Mg, K, P, Fe, Mn, Cu, Zn, B, S, Pb, Al, and Cd at Western AG laboratories. The probes were inserted vertically into the soil to a depth of 10 cm during the rainy season in November 2016 and retrieved after 30 days.

Bulk density (g/cm^3) was measured by collecting five random soil samples from each plot at two depths (0-15 cm and 15-30 cm). Soil texture (% silt, % sand, % clay) was assessed from composite samples of five soil cores taken at a depth of 10-30 cm after removing the top litter layer.

Litter decomposition experiment

Litter decomposition was estimated through a reciprocal translocation field experiment involving multiple Andean species conducted between October 2021 and April 2023 (Castillo-Figueroa et al., 2025). The experiment spanned the 14 plots, each containing three litter decomposition beds spaced at least 5 meters apart. We used 15 different litter species (Table S1), subjected to four decomposition periods (3, 6, 12, and 18 months), resulting in a total of 2,520 litterbags (14 plots x 3 beds x 15 species x 4 harvest times). The litterbags measured 10x15 cm and were made from 2 mm mesh fiberglass that allowed entry for micro- and mesofauna. After collection, the litterbags were brushed to remove mineral soil particles. The remaining litter was oven-dried at 60°C for 72 hours and weighed on an analytical scale (0.0001 g, LX 220A scs). We calculated K rates (y^{-1}) for each species as a standard measure of decomposition according to Olson (1963).

Soil fungal sampling

In June 2022, we collected three soil subsamples from beneath the litter layer associated with each litterbed in the decomposition experiment. To account for spatial heterogeneity (Smith et al., 2015), these subsamples were combined into a single composite soil sample per plot. After collection, the samples were stored in freezers at -30°C and shipped to the Faculty of Natural Sciences at the University of El Rosario in Bogotá, Colombia. In the lab, DNA was extracted using the DNeasy PowerSoil Pro Kit (QIAGEN, Hilden, Germany) following the manufacturer's instructions. The resulting DNA concentration was quantified in (ng/µl) in a NanoDrop2000 (Thermo Fisher Scientific, USA). The ITS1 region was PCR-amplified and sequenced on an Illumina HiSeq2500 PE250 by Novogene Bioinformatics Technology Co. Ltd. (Beijing, China) using the fungal specific primers ITS5-1737F (GGAAGTAAAAGTCGTAACAAGG) and ITS2-2043R (GCTGCGTTCTTCATCGATGC). The sequences were processed into operational taxonomic units (OTUs) as a measure of richness, and fungal guilds were analyzed based on their primary lifestyles at the genus-level using the Fungal-Traits database (Põlme et al., 2020).

Bioinformatics

The Illumina MiSeq data was analyzed with AMPtk v1.3.0 (Palmer et al., 2018), following the protocol published by Corrales & Ovrebo (2020). MiSeq reads were demultiplexed according to the AMPtk documentation (https://amptk.readthedocs.io/en/latest/pre-processing.html). Sequences shorter than 150 bp were discarded. Reads were clustered at 97% similarity to generate OTUs, which were then assigned taxonomic classifications using the AMPtk taxonomy algorithm (Palmer et al., 2018) and the UNITE database (Version 18.07.2023; Abarenkov et al., 2023). Non-fungal OTUs and those with fewer than 10 sequences were excluded from the dataset (Sanchez-Tello & Corrales, 2024).

Data analysis

We did rarefaction curves based on soil samples collected from each plot. Plot species diversity indexes for plant and soil fungal communities were based on Hill numbers, which encompass species richness ($q = 0$), exponential Shannon diversity ($q = 1$), and inverse Simpson diversity ($q=2$) (Jost, 2006; Djemiel et al., 2024). To assess differences in fungal community composition between sites (H1) and successional stages (H2), we conducted two non-metric multidimensional scaling (NMDS) analyses based on Bray-Curtis distances. Kruskal's stress in NMDS measures the difference between objects in the compressed matrix and the original distances, with values below 0.2 considered acceptable (McCune & Gracia, 2002). We tested for differences in fungal community composition using a non-parametric permutation test (ANOSIM), where R values of +1 indicate total dissimilarity and -1 indicates total similarity (Clarke, 1993). This analysis was complemented by a redundancy analysis (RDA) to examine whether fungal community composition could be explained by environmental parameters. The biological matrix consisted of soil fungi (OTUs) weighted by abundance, while the environmental matrix included, soil environmental parameters, microclimatic variables, and litter functional characteristics. To analyze changes in soil fungal diversity along the successional gradient (H2), we performed reduced major axis regression (RMA) between the diversity indices and AGB, as a proxy for succession (Garnier et al., 2004; Poorter et al., 2021b; Castillo-Figueroa et al., 2023). We also conducted these analyses for diversity measures of each fungal guild with succession.

To analyze the factors driving soil fungal diversity (H3), we conducted RMA between the three diversity measures and all the soil, microclimatic, and litter functional characteristics from the plots. We calculated 95% bootstrapped confidence intervals for the slopes ($n=1999$). We used multiple stepwise linear regressions to identify the main factors influencing each soil fungal diversity index (response variables). We included as independent variables those that showed a significant relationship with each diversity index in the RMA regressions (see results). To address multicollinearity, we assessed the variance inflation factor (VIF), retaining only variables with VIF values below 1.3 (Neter et al., 1990). Model selection was based on root mean squared error (RMSE) and Adjusted R^2; RMSE quantifies predictive accuracy, while Adjusted R^2 accounts for the number of predictors and penalizes irrelevant variables (Montgomery et al., 2012; Chatterjee & Hadi, 2015). Additionally, we analyzed significant correlations between diversity measures of each fungal guild and environmental variables using Spearman correlation matrices.

Finally, we analyzed the role of soil fungal communities on litter decomposition (H4) by conducting RMA between the three diversity indices and decomposition ‘environment’ as the average decomposition rate per plot of the 15 species that were used in the decomposition experiment (see above). We also examined the influence of the diversity of specific fungal guilds on the decomposition environment. For a more detailed analysis, we constructed a Spearman correlation matrix to assess relationships between diversity measures of each fungal guilds and decay rates of litter of each species. All analyses were performed using JASP 0.14.1.0 (JASP Team, 2023), PAST v.4.14 (Hammer et al., 2001), and R v.4.3.3 (R Core Team, 2024).

Results

Composition of soil fungal communities

A total of 1,476,568 valid reads were obtained with an average 105,469 reads per sample. We identified 4,982 OTUs, with an average of 1,159 per sample (Figure S2). Overall, we found 15 phyla, 44 classes, 225 families, and 516 genera (Figure S3), with Tabio showing the highest number of OTUs, followed by Torca, Guasca, and Guatavita (Figure 1). Strong differences in fungal composition between the four forest sites were observed in both NDMS (stress = 0.13, Figure 2a, Figure S4) and ANOSIM tests (P = 0.0035, R = 0.43, Table 1). However, RDA analysis indicated that the availability of nutrients, soil microclimate conditions, and litter functional richness did not explain the changes in composition of soil fungal communities across sites (P = 0.19, F =1.67, R^2 Adjusted = 0.382, Figure S5). The most abundant primary lifestyles were soil saprotrophs (37.21%), followed by wood saprotrophs (18.13%), root endophytes (11.43%), litter saprotrophs (8.98%), plant pathogens (8.78%), and mycoparasites (6.26%), with variations across sites (Figure 2b).

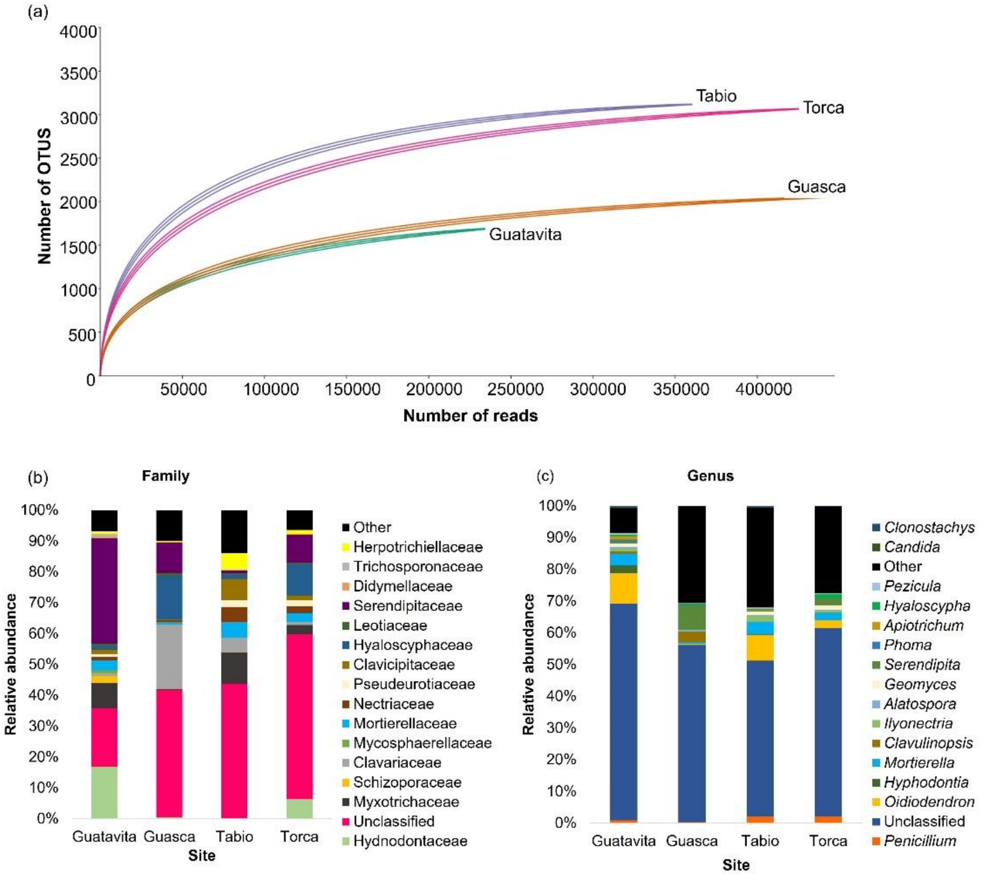


Figure 1. Fungal community variation in the four upper Andean tropical forest sites of Colombia. (a) Rarefaction curves with 95% confidence intervals show the representativeness of the sampling. The relative abundance of fungi from samples obtained in 14 permanent plots. Each bar height represents the relative abundance, and color represents a particular fungal (b) family and (c) genus.

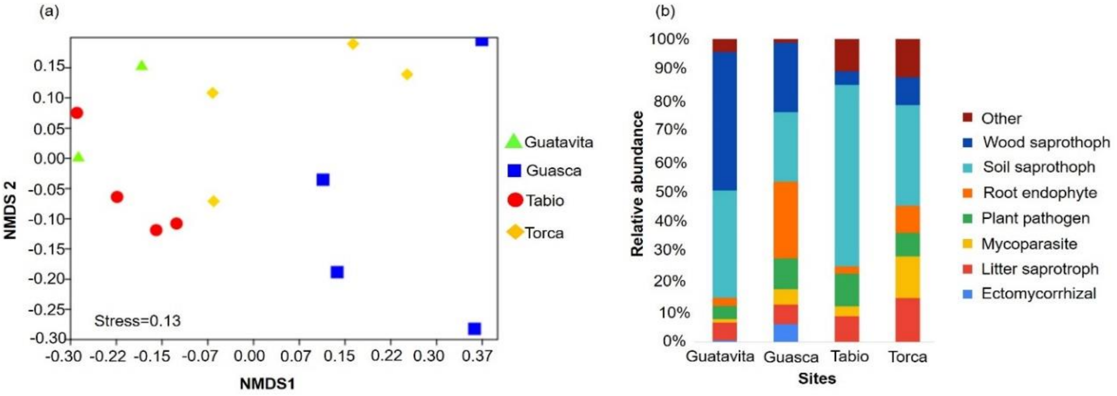


Figure 2. Changes of fungal communities across the four upper Andean tropical forest sites. (a) NMDS comparing soil fungal communities between Guatavita (green triangles), Guasca (blue squares), Tabio (red circles) and Torca (gold diamonds) (b) relative abundance of the different functional guilds from each site. Guilds were classified according to the primary lifestyle based on Fungal-Traits database. Guilds are represented in different colors.

Influence of succession on soil fungal communities

The overall soil fungal communities showed no significant changes along the successional gradient (i.e., AGB). Moreover, fungal composition did not change when comparing mature and secondary forest plots, as indicated by the ANOSIM test ($P = 0.097$, $R = 0.136$, Table 1, Figure 3a). Additionally, we found no relation between fungal richness ($P = 0.62$, $R^2 = 0.021$, CI = [-13.74, 1.28], Figure 3b), exponential Shannon diversity ($P = 0.95$, $R^2 = 0.0003$, CI = [0.26, 1.89], Figure 3c), and inverse Simpson diversity ($P = 0.76$, $R^2 = 0.007$, CI = [0.091, 0.55], Figure 3c), with AGB. However, when analyzing fungal guild separately, we observed a decline in litter saprotrophs with succession for exponential Shannon diversity ($P = 0.03$, $R^2 = 0.33$, CI = [-0.09, -0.02], Figure S6) and inverse Simpson diversity ($P = 0.03$, $R^2 = 0.37$, CI = [-0.06, -0.02], Figure S7), along with unspecified saprotrophs for exponential Shannon diversity ($P = 0.03$, $R^2 = 0.33$, CI = [-0.09, -0.03], Figure S7). Overall, fungal guilds showed similar relative abundances in both forest types (Figure S6).

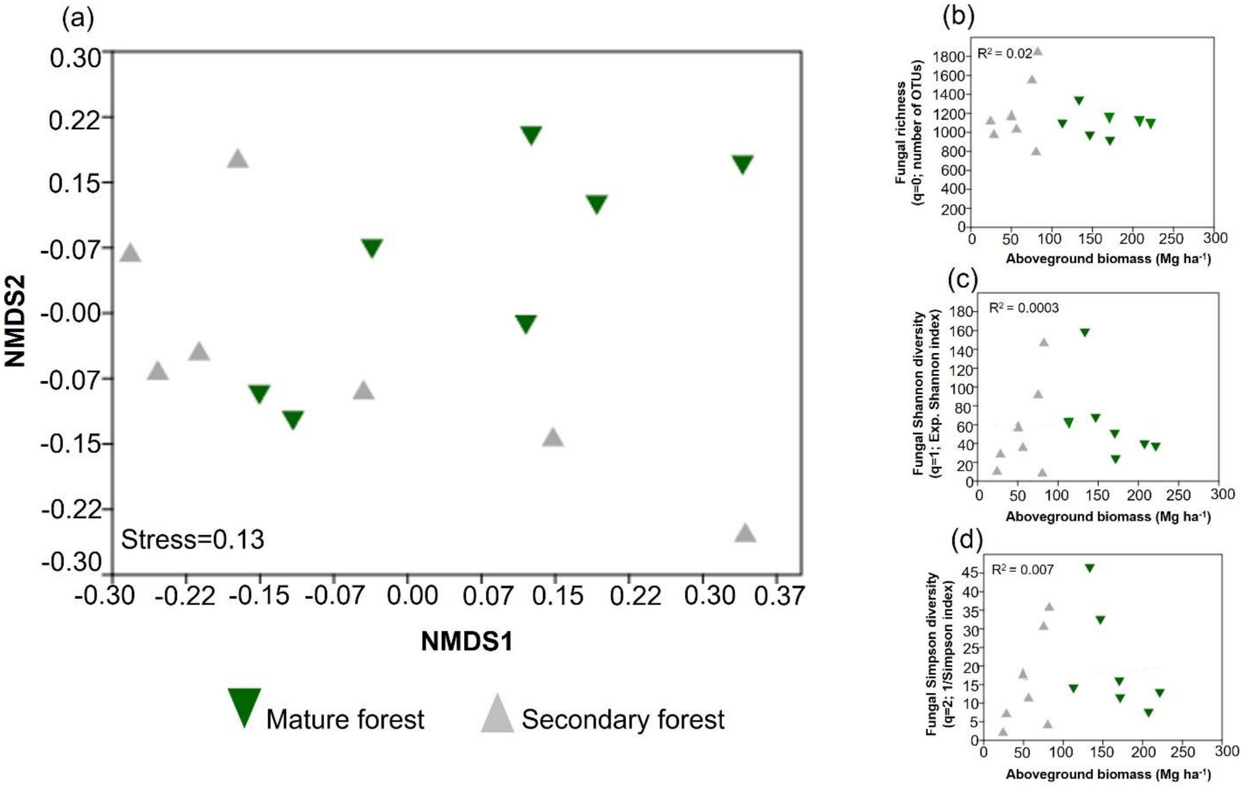


Figure 3. Changes of fungal communities along the successional gradient in upper Andean tropical forests. (a) NMDS comparing fungal communities between mature and secondary forests. RMA regressions between aboveground biomass vs (b) fungal richness (q = 0, number of OTUS), (c) fungal exponential Shannon diversity (q = 1, Exp. Shannon index) and (d) fungal inverse Simpson diversity (q = 2, 1/Simpson index). Inverse green triangles represent mature forest plots and grey triangles indicate secondary forest plots. Plots with no red line indicate no significant relation ($P > 0.05$).

Table 1. ANOSIM on OTUs composition of soil fungal communities in four sites using a dissimilarity matrix based on Bray-Curtis similarity index. R values close to 1 indicate high differentiation between sites or successional stages**.**

Factor	**R**	**P**
Sites		
Between all sites	0.4284	0.0035
Guasca-Guatavita	0.7500	0.0683
Guasca-Tabio	0.7708	0.0294
Guasca-Torca	0.0625	0.2616
Guatavita-Tabio	0.2037	0.4286
Guatavita-Torca	0.1429	0.3979
Tabio-Torca	0.4688	0.0289
Succesion		
Between mature-secondary	0.1361	0.0979

Drivers of fungal communities

Significant positive relationships were observed between minimum surface temperature and fungal richness ($P = 0.004$, $R^2 = 0.52$, CI = [125.3, 308.6], Figure 4a), exponential Shannon diversity ($P = 0.002$, $R^2 = 0.57$, CI = [20.5, 49.23], Figure 4b), and inverse Simpson diversity ($P = 0.03$, $R^2 = 0.34$, CI = [5.5, 28.6], Figure 4c). Litter functional richness was also positively related with fungal richness ($P = 0.02$, $R^2 = 0.38$, CI = [51.9, 244.8], Figure 4d), exponential Shannon diversity ($P = 0.001$, $R^2 = 0.59$, CI = [6.5, 11.3], Figure 4e), and inverse Simpson diversity ($P = 0.002$, $R^2 = 0.55$, CI = [1.9, 3.3], Figure 4f). Plant richness was positively related to fungal richness ($P = 0.008$, $R^2 = 0.46$, CI = [47.3, 122.3], Figure 4g), and plant exponential Shannon diversity was positively related to fungal exponential Shannon diversity ($P = 0.02$, $R^2 = 0.39$, CI = [4.5, 28.6], Figure 4h), yet no relationship were found between plant and fungal inverse Simpson diversity ($P = 0.19$, $R^2 = 0.14$, CI = [2.9, 19.3], Figure 4i). NPP and FRP showed no relationship with any fungal diversity indices ($P > 0.05$), and only when analyzed separately with fungal guilds, such as saprotrophs and parasites, were some significant relationships observed (Figure S8-10).

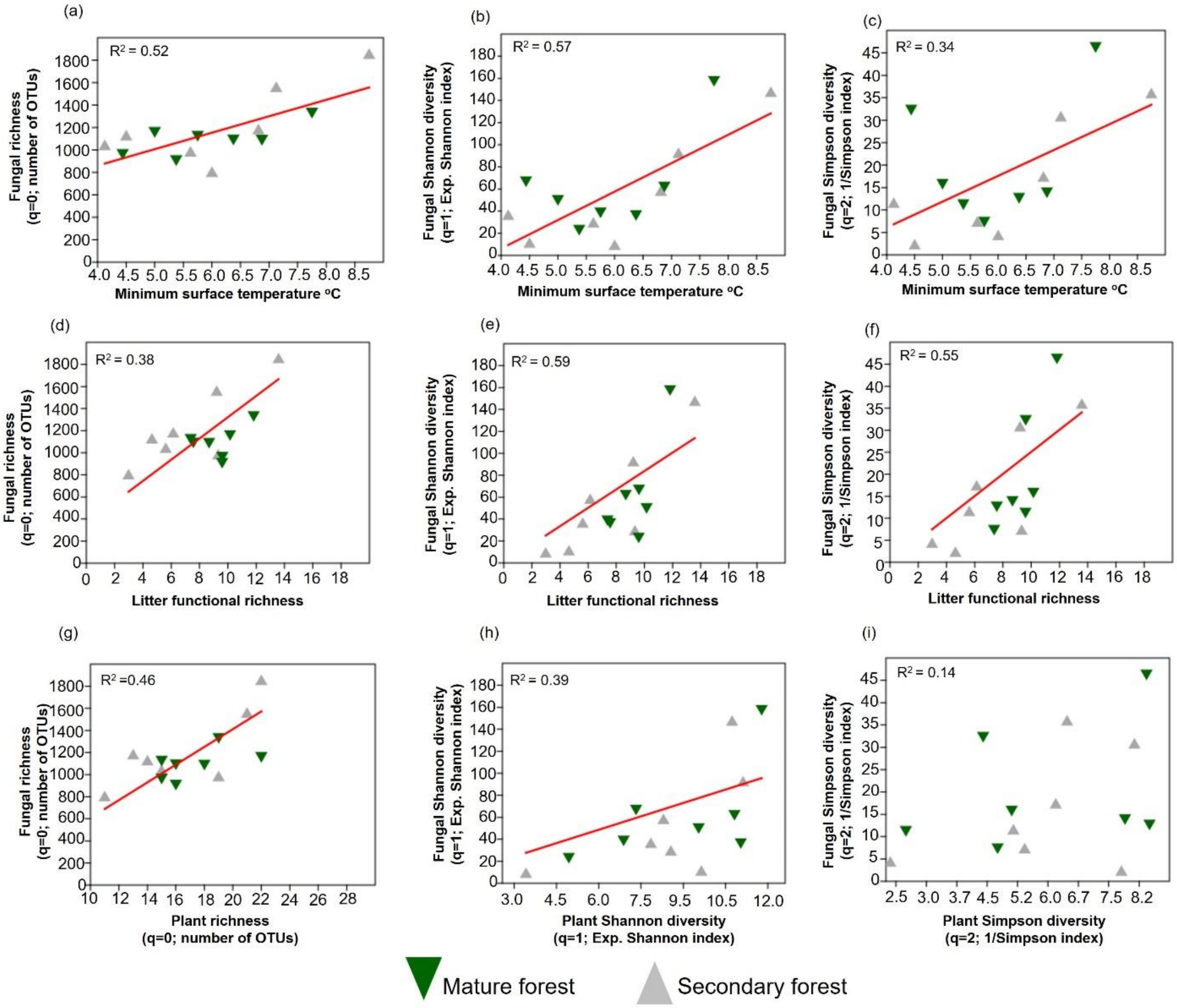


Figure 4. Microclimatic and litter functional drivers of soil fungal diversity. Reduced major regressions between fungal diversity (q = 0, q = 1, q = 2) and (a-c) minimum surface temperature, (d-f) litter functional richness, (g-i) plant diversity. Inverse green triangles represent mature forest plots and grey triangles indicate secondary forest plots. Plots with no red line indicate no significant relation (P > 0.05).

Regarding soil nutrients, calcium flux showed strong positive correlations with fungal richness ($P = 0.02$, $R^2 = 0.36$, CI = [0.1, 0.6], Figure 5a), exponential Shannon diversity ($P = 0.0004$, $R^2 = 0.66$, CI = [0.04, 0.09], Figure 5b), and inverse Simpson diversity ($P = 0.01$, $R^2 = 0.42$, CI = [0.011, 0.06], Figure 5c). Sulfur flux was not associated with fungal richness ($P = 0.06$, $R^2 = 0.26$, CI = [0.19, 7.5], Figure 5d), but it exhibited significant positive relationships with exponential Shannon diversity ($P = 0.006$, $R^2 = 0.47$, CI = [0.33, 1.21], Figure 5e) and inverse Simpson diversity ($P = 0.03$, $R^2 = 0.33$, CI = [0.12, 0.34], Figure 5f). Magnesium flux was positively related to exponential Shannon diversity ($P = 0.009$, $R^2 = 0.44$, CI = [0.20, 0.56], Figure 5g), but showed no significant relationship with fungal richness ($P = 0.07$, $R^2 = 0.25$, CI = [0.58, 3.5], Figure 5h) or inverse Simpson diversity ($P = 0.06$, $R^2 = 0.26$, CI = [0.07, 0.32], Figure 5i).

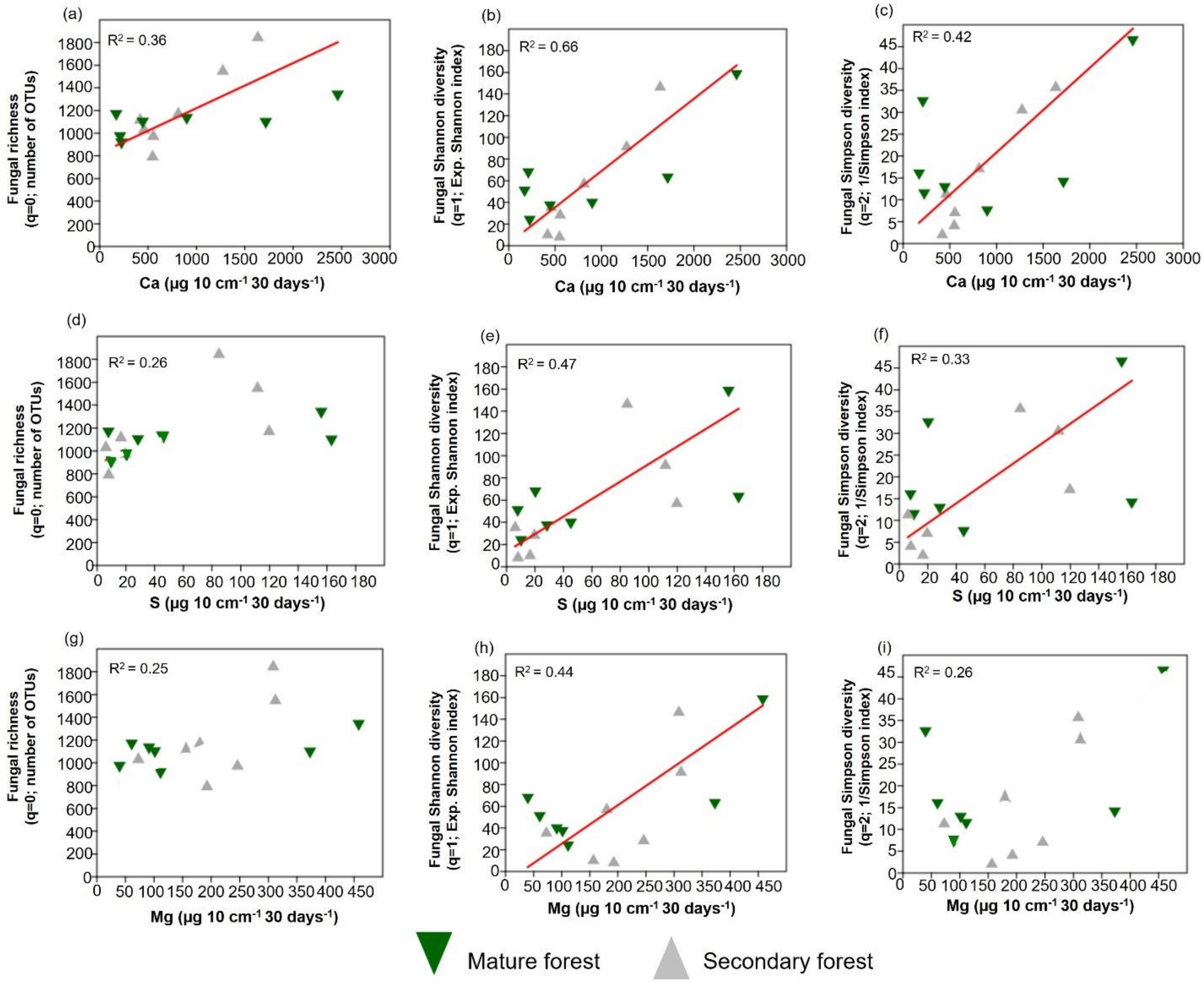


Figure 5. Soil environmental drivers of soil fungal diversity. Reduced major regressions between fungal diversity (q = 0, q = 1, q = 2) and (a-c) Ca flux, (d-f) S flux, and (g-i) Mg flux. Inverse green triangles represent mature forest plots and grey triangles indicate secondary forest plots. Plots with no red line indicate no significant relation (P > 0.05).

The multiple linear regression revealed that the best predictor for soil fungal richness was minimum surface temperature and plant richness ($R^2 = 0.68$, Adjusted $R^2 = 0.62$, RMSE = 167.786, $P = 0.038$, Table 2). For exponential Shannon diversity, the best predictors were litter functional richness and calcium flux ($R^2 = 0.85$, Adjusted $R^2 = 0.83$, RMSE = 19.117, $P = 0.003$, Table 2), while for inverse Simpson diversity litter functional richness was the strongest predictor ($R^2 = 0.55$, Adjusted $R^2 = 0.51$, RMSE = 9.265, $P = 0.002$, Table 2).

Table 2. Multiple stepwise linear regression models showing the effects of the most important variables for soil fungal richness (q = 0), soil fungal exponential Shannon diversity (q = 1), and soil fungal inverse Simpson diversity (q = 2). In the model of soil fungal richness (q = 0), the following covariates were considered but not retained by the analysis: Ca, litter functional richness. Minimum surface temperature and plant richness were the best factors explaining soil fungal richness (n = 14, $R^2 = 0.68$, adjusted $R^2 = 0.62$, RMSE = 167.786, P = 0.038). In the model of fungal exponential Shannon diversity (q = 1), the following covariates were considered but not retained by the analysis: Minimum surface temperature, Mg, S. Variance in Ca and litter functional richness were the best factors explaining soil fungal exponential Shannon diversity (n = 14, $R^2 = 0.85$, adjusted $R^2 = 0.83$, RMSE = 19.117, P = 0.003). In the model of fungal inverse Simpson diversity (q = 2) the following covariates were considered but not retained by the analysis: Minimum surface temperature, S and Ca. Litter functional richness was the best factor explaining soil inverse Simpson diversity (n = 14, $R^2 = 0.55$, adjusted $R^2 = 0.51$, RMSE = 9.265, P = 0.002).

							Collinearity Statistics	
Model		**Unstandardized**	**Standard Error**	**Standardized**	**t**	**P**	**Tolerance**	**VIF**
Fungal richness (q = 0, number of OTUS)								
1	(Intercept)	1159.071	72.811		15.919	< .001		
2	(Intercept)	274.609	252.253		1.089	0.298		
	Minimum surface temperature	146.536	40.872	0.719	3.585	0.004	1.000	1.000
3	(Intercept)	-90.062	264.790		-0.340	0.740		
	Minimum surface temperature	106.626	38.711	0.523	2.754	0.019	0.808	1.237
	Plant Species richness, q0	35.923	15.251	0.447	2.355	0.038	0.808	1.237
Fungal exponential Shannon diversity (q = 1, Exp. Shannon index)								
1	(Intercept)	58.578	12.212		4.797	< .001		
2	(Intercept)	12.778	12.076		1.058	0.311		
	Ca ug 10cm 30days	0.054	0.011	0.811	4.810	< .001	1.000	1.000
3	(Intercept)	-40.791	16.395		-2.488	0.030		
	Ca ug 10cm 30days	0.038	0.009	0.576	4.372	0.001	0.777	1.287
	Litter functional richness	8.055	2.125	0.499	3.790	0.003	0.777	1.287
Fungal inverse Simpson diversity (q = 2, 1/ Simpson index)								
1	(Intercept)	17.823	3.541		5.034	< .001		
2	(Intercept)	-10.958	7.933		-1.381	0.192		
	Litter functional richness	3.466	0.908	0.741	3.819	0.002	1.000	1.000

Soil fungal communities and litter decomposition

Decomposition ‘environment’ (i.e., average litter decomposition rate per plot) varied from 0.38 to 0.61 (K rates y^{-1}). No significant relationships were found between decomposition environment and fungal richness (P = 0.30, $R^2 = 0.09$, CI = [-0.0009, 0.00012], Figure 6a), exponential Shannon diversity (P = 0.57, $R^2 = 0.028$, CI = [-0.004, 0.00067], Figure 6b), or inverse Simpson diversity (P = 0.57, R^2 = 0.027, CI = [-0.017, -0.0009], Figure 6c). However, plant pathogen diversity showed a negative relationship with decomposition environment for exponential Shannon diversity (P = 0.02, R^2 = 0.36, CI = [-0.015, -0.003], Figure 6def) and inverse Simpson diversity (P = 0.01, R^2 = 0.39, CI = [-0.03, -0.008], Figure S11). Spearman correlations revealed both positive and negative relationships between fungal guild diversity and the decay rates of the 15 species (Figure S11).

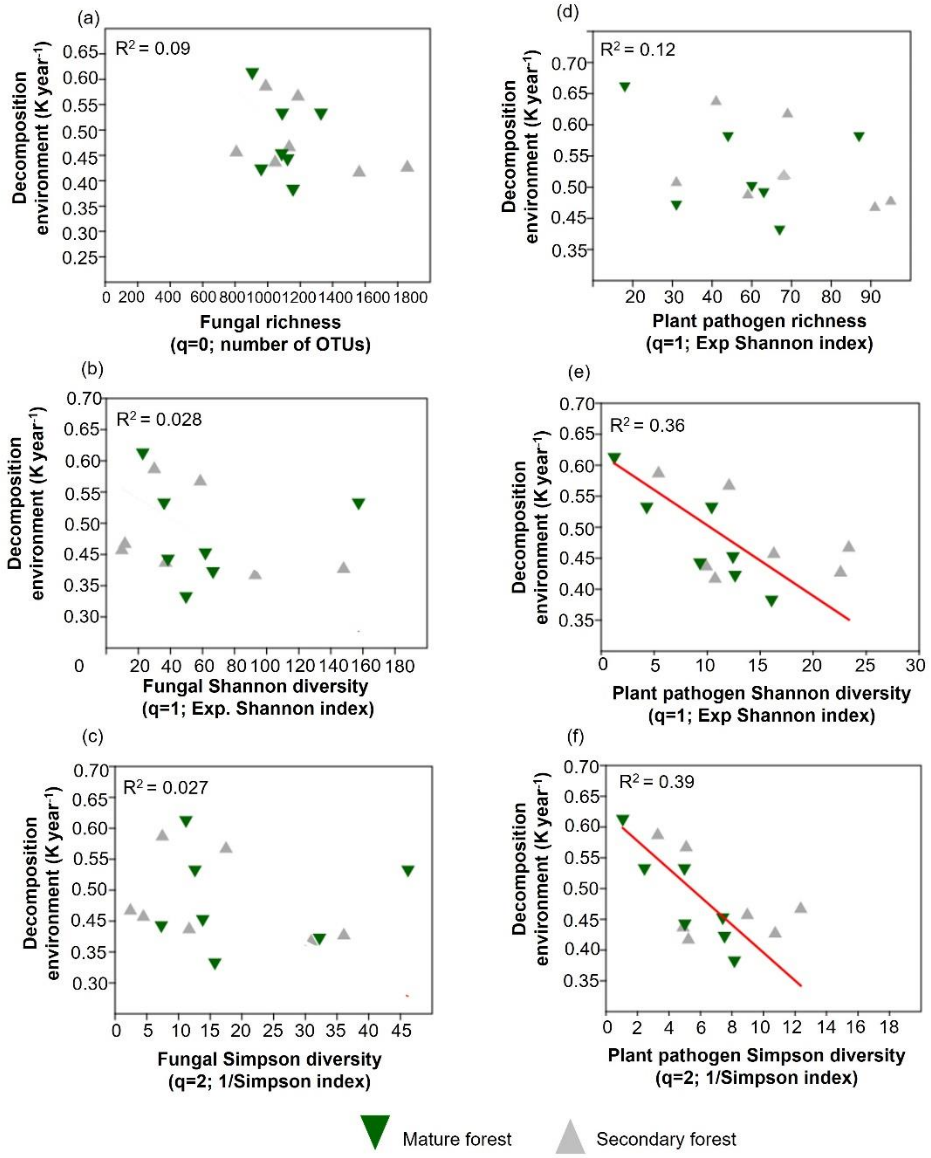


Figure 6. Reduced major regressions between decomposition environment and (a) fungal richness (q = 0, number of OTUS), (b) fungal exponential Shannon diversity (q = 1; Exp. Shannon index), (c) fungal inverse Simpson diversity (q = 2, 1/Simpson index), (d) plant pathogen richness (q = 0, number of OTUS) (e) plant pathogen exponential Shannon diversity (q = 1, Exp. Shannon index) and, (f) plant pathogen inverse Simpson diversity (q = 2, 1/Simpson index). Inverse green triangles represent mature forest plots and grey triangles indicate secondary forest plots. Plots with no red line indicate no significant relation (P > 0.05).

Discussion

Diversity patterns of soil fungi along succession remain understudied in tropical montane forests, despite their importance for understanding forest recovery and key processes such as decomposition. Our study sheds light on the main determinants of soil fungal communities along succession in Andean mountain forests and its relations to decay rates, integrating data from both aboveground and belowground compartments. We found that soil fungal communities exhibited marked compositional differences between sites but did not change along the successional gradient, suggesting that site land-use history may play an important role. Fungal diversity was influenced by soil nutrients, microclimatic conditions, and litter functional characteristics. However, fungal diversity did not affect average plot decomposition rates, likely due to specific relationships between fungal guilds and litter decay rates, which may have offset or obscured any broader effects on decomposition along succession. Only pathogen diversity appeared to decrease decomposition, possibly by reducing litter quality.

Soil fungal communities in Andean forests

Our results reveal significant differences in soil fungal community composition between forest sites, supporting our first hypothesis (H1). This agrees with the high biodiversity turnover observed in plants (Hurtado-M et al., 2021) and soil fauna (Castillo-Avila et al., 2025) within the same plots. Hence, each locality in the Andean mountain forests serves as a unique biodiversity reservoir shaped by contrasting environmental conditions. Numerous studies indicate that UATF exhibit pronounced spatial heterogeneity, with notable variations in topography (Pierick et al., 2021), microclimate (Malhi et al., 2010; Castillo-Figueroa, 2024b), vegetation types (Calbi et al., 2021; Cedillo et al., 2023), soil properties (Wilcke et al., 2008; Moser et al., 2011; Barczyk et al., 2024), and nitrogen availability (Pierick et al., 2024) over short distances that contribute to a high beta diversity. Our RDA results further suggest that environmental characteristics are not strongly associated with fungal composition, indicating that other unmeasured variables, including biotic interactions with plants, and belowground soil microbial community, or dispersal limitations, could be related to these changes in fungal composition (Shi et al., 2019; Liu et al., 2023). Alternatively, this lack of association could indicate a more random distribution influenced by stochastic processes rather than deterministic environmental filtering, consistent with other studies on fungal communities (Adamo et al., 2021; Kutos et al., 2023; Djemiel et al., 2024).

The distinct anthropogenic disturbance histories and land use practices at each study site—such as livestock in Tabio, urbanization and forest degradation in Torca, lime mining in Guasca, and agriculture in Guatavita—may further amplify the differences in soil fungal communities. Previous research indicates that soil fungal communities are sensitive to small-scale environmental changes (Waring et al., 2016; Kutos et al., 2023) and human disturbances (Shi et al., 2019; Fox et al., 2021; Centenaro et al., 2024). These compositional changes are also evident in the variation of fungal guilds across forests, which can influence different ecosystem functions through their interactions with a range of resources (Põlme et al., 2020).

Soil fungal communities along succession

Our second hypothesis (H2) was rejected, as we found no significant changes in fungal diversity or composition with succession. We only observed a decrease in saprotrophs with succession, consistent with previous studies (Li et al., 2020; Geng et al., 2023b). This decline may result from higher litter quality in early succession (Poorter et al., 2021a), which favors litter saprotrophs, or from competition with other guilds in later successional stages (Li et al., 2020). Although shifts in plant species composition and forest productivity during succession can alter the soil microenvironment through increased litter input (Poorter et al., 2021b, 2023) and root exudates (Smith et al., 2015; Han et al., 2021)—both of which support soil fungal diversity—these factors did not emerge as primary drivers for fungal communities. This finding contrasts with studies that reported changes in soil fungal diversity across different successional stages (Dang et al., 2018; Shi et al., 2019; Tomao et al., 2020; Zhu et al., 2024). Two non-exclusive reasons may explain the lack of association with forest succession: (1) contrasting soil characteristics across sites may obscure a successional effect, or (2) the analyzed gradient included only intermediate and late-stage forests, lacking early-stage representation.

Studies indicate that fungal communities can exhibit significant variability at small scales (Kutos et al., 2023). Given the high heterogeneity of Andean mountain soils (Wilcke et al., 2008), edaphic variability may obscure relationships between forest structural and process variables—such as AGB and productivity—and fungal community composition and diversity. Thus, it is likely that fungal communities differ more between sites than across successional stages in our study. Additionally, the absence of early successional stages, like abandoned open pastures—which experience contrasting microenvironmental conditions in soil temperature and humidity due to a lack of cover (Paudel et al., 2015; Shi et al., 2019)— may have prevented the detection of significant changes in fungal community structure along the gradient. In contrast, studies that observed shifts in fungal communities during succession typically included a wider range of habitats, spanning both early and late stages (Dang et al., 2018; Geng et al., 2023b).

Edaphic, microclimatic and litter functional determinants of soil fungal diversity

Our third hypothesis (H3) was generally supported, as we found significant relationships between soil fungal diversity and soil nutrients (calcium, magnesium, and sulfur), but also microclimatic conditions (temperature) and litter functional characteristics (litter functional richness, and plant diversity). In Andean mountain forests, cold temperatures significantly shape plant (Squeo et al., 1991; Rehm & Feeley, 2015) and animal communities (Mani, 1968). Numerous studies indicate that thermal conditions notably influence soil fungal diversity, biomass, and community composition (Castaño et al., 2018; Baldrian et al., 2022; Kumar et al., 2023; Li et al., 2024). Temperature affects fungal enzymatic activity and growth (Finestone et al., 2022), with lower temperatures potentially imposing physiological constraints on soil fungi (Newsham et al., 2015). Our findings support these results, as we observed a positive relationship between minimum surface temperature and fungal diversity. This suggests that lower temperatures may filter out thermophilic species, leaving only those adapted to colder conditions, thereby reducing overall species richness.

Litter functional richness indicates that fungal richness, exponential Shannon diversity and inverse Simpson diversity are influenced by heterogeneity in the chemical and physical properties of litter inputs. Studies show that microhabitats in the humus layer are vital for maintaining local fungal diversity (Wang et al., 2021; Yamauchi et al., 2021). The diverse sizes, shapes, and nutrient content of litter create various microhabitats with a range of substrate qualities, which should allow different fungal species to specialize and diversify. Evidence suggests that litter composition strongly influence soil fungal community structure (Habtewold et al., 2020; Meng et al., 2024). Additionally, litter heterogeneity can affect soil moisture and temperature (Liu et al., 2019b), enhancing microclimatic conditions for fungi (Zhang et al., 2022a). Interestingly, similar patterns were observed in soil fauna from the same plots (Castillo-Avila et al., 2025), suggesting that similar mechanisms may apply to multitude of soil organisms in UATF.

Plant diversity influenced both fungal richness and exponential Shannon diversity, potentially reflecting direct plant-fungal interactions, such as substrate-specific litter decay, mutualistic mycorrhizal relationships, or antagonistic pathogens, which are often characterized by high specificity between plant host and fungi (Adamo et al., 2021). Alternatively, plants may indirectly affect fungal communities by altering soil structure, nutrient levels, and litter substrates; at the same time, fungi may exert both negative feedbacks by influencing seedling mortality or positive feedbacks through enhanced nutrient acquisition (Adamo et al., 2021; Geng et al., 2023b).

Among the nutrients, calcium was the most influential factor in determining exponential Shannon diversity, and it also correlated with richness and inverse Simpson diversity, consistent with global patterns of soil fungal diversity (Tedersoo et al., 2014). Calcium is crucial for soil fungi, as it is found in cell walls, vacuoles, and organelles, playing a key role in plant-fungi associations (Moreau, 1987). Fungal growth is particularly dependent on soil calcium levels in acidic soils, like those in Andean forests (Gramss & Bergmann, 2007; Wilcke et al., 2008). Furthermore, calcium supports hyphae formation, enhancing plant litter colonization, increasing carbon use efficiency, and fostering associations between minerals and microbial byproducts, thereby indirectly boosting soil fungal diversity (Shabtai et al., 2023; Hogan et al., 2023).

Other nutrients positively associated with exponential Shannon and inverse Simpson fungal diversity included sulfur and, to a lesser extent, magnesium. Soil fungi can assimilate various sulfur compounds—both inorganic (e.g., methionine, homocysteine) and organic (e.g., sulfate, thiosulfates)—which are necessary for amino acid and cofactor synthesis, as well as energy metabolism (Marzluf, 1997; Linder, 2018). Sulfur addition has also been shown to increase the abundance of root-associated fungal pathogens (Wu et al., 2021).

Magnesium acts as a cofactor for enzymatic reactions involved in nutrient uptake and photosynthesis in plants (Marschner, 1995), indirectly influencing root exudates and litter resources that support fungal growth and diversity (Lehmann & Rillig, 2015; Hogan et al., 2023). However, some studies have reported no significant relationship between magnesium levels and soil fungal diversity (Yang et al., 2023).

The role of soil fungi on decomposition

Our fourth hypothesis (H4) was rejected, as soil fungal diversity was not related to decomposition, even when focusing on saprotrophs guilds. Previous research suggests that litter quality is the primary driver of decomposition, more so than climate or decomposer communities (Cornwell et al., 2008; Makkonen et al., 2012). In fact, studies on the same plots indicated that litter quality explained over 60% of decomposition across all decay stages (Castillo-Figueroa et al., 2025). While soil fungi significantly contribute to organic matter decomposition (Tunlid et al., 2022; Ullah et al., 2023), their capacity to degrade plant litter vary widely (Leifheit et al., 2024). Consequently, specific relationships between fungal guilds and decomposition of different litter species may blur broader diversity-decomposition relationships. Interestingly, our analyses revealed that plant pathogens related negatively to average decomposition rates (Figure 6). This may result from pathogens triggering plant defense responses, which can alter litter quality by increasing secondary metabolite accumulation, such as terpenoids, alkaloids, and polyphenols, potentially inhibiting microbial activity during decomposition (Pusztahelyi et al., 2015; Chomel et al., 2016; Guo et al., 2025).

Another possible reason for the limited influence of soil fungal communities on litter decomposition is that the harsher environmental conditions of Andean mountain forests—characterized by low temperatures and high soil moisture—may inhibit the activity of lignin-degrading enzymes such as laccase, lignin peroxidase, and manganese peroxidase. Research indicates that temperature and moisture significantly affect the production, activity, and stability of these ligninolytic enzymes (Snajdr & Baldrian, 2007; Asgher et al., 2011). Future studies should incorporate transcriptomic, proteomic, and metabolomic approaches to accurately assess the functional genes involved in decomposition within soil fungal communities in UATF.

Conclusions

Our study revealed that soil fungal communities varied more between sites than across successional stages, with each forest site hosting a unique fungal composition. This pattern aligns with studies on plant and animal communities, highlighting UATF as crucial reservoirs of mountain biodiversity. The pronounced microenvironmental heterogeneity, stochasticity, and differing historical land-use practices likely contribute to the significant site-to-site differences that we observed. The lack of detectable changes in soil fungal communities along succession, could also be due to the absence of early successional stages in our gradient. The main determinants of soil fungal diversity included minimum surface temperature, litter functional richness, plant diversity, and soil calcium levels, suggesting that these variables are key at fostering conditions that promote fungal coexistence. Despite these findings, fungal diversity did not significantly influence decomposition rates, likely due to specific relationships between fungal guilds and the decay rates of individual litter species. Pathogen diversity was the only guild inversely related to decay rates, likely by reducing litter quality. Furthermore, although various saprotrophic groups were present, the lower temperatures and high soil moisture typical of UATF may have limited the activity of ligninolytic enzymes necessary for litter degradation. Future studies should employ omics approaches to further explore the fungal mechanisms involved in litter decomposition within UATF.

Acknowledgements

This study was part of the Small grant project "*Dinámicas de regeneración y descomposición de hojarasca en un gradiente sucesional de bosque Altoandino*" funded by Universidad del Rosario (Project ID: IV-FPD003) lead by JMP and partially-developed by DC-F. The study also benefited from funding of the project "*Estudio de dinámicas socio-ecológicas ante escenarios de cambio climático en bosques secundarios periurbanos Altoandinos*" lead by JMP and funded by MINCIENCIAS (No.FP44842-046-2017). Permanent plots have been installed and monitored thanks to the financial support of Universidad del Rosario, Pontificia Universidad Javeriana, and Minciencias under the leadership of Natalia Norden and JMP. We thank Brayan Polania-Camacho for his collaboration in the field trips and lab assistance. We are in debt to the owners of the private areas where we conducted this research for their generosity and hospitality.

Supplementary material

Figure S1. Upper Andean tropical forests plots where soil fungi sampling was conducted. Hexagons indicate the location of the plots located around Bogotá, the capital city of Colombia. The characteristics of each site are summarized on the left-hand side.

Guatavita
Elevation: 3028-3035m
Mean soil temperature: 11.55 °C
Mean soil moisture: 39.47%

Guasca
Elevation: 3085-3140m
Mean soil temperature: 9.89 °C
Mean soil moisture: 33.81%

Tabio
Elevation: 2696-2821m
Mean soil temperature:12.75 °C
Mean soil moisture: 42.14%

Torca
Elevation: 2708- 2965m
Mean soil temperature: 11.76 °C
Mean soil moisture: 37.97%

Figure S2. Species accumulation curves (OTUs) for each permanent plot sampled in the upper Andean tropical forests plots.

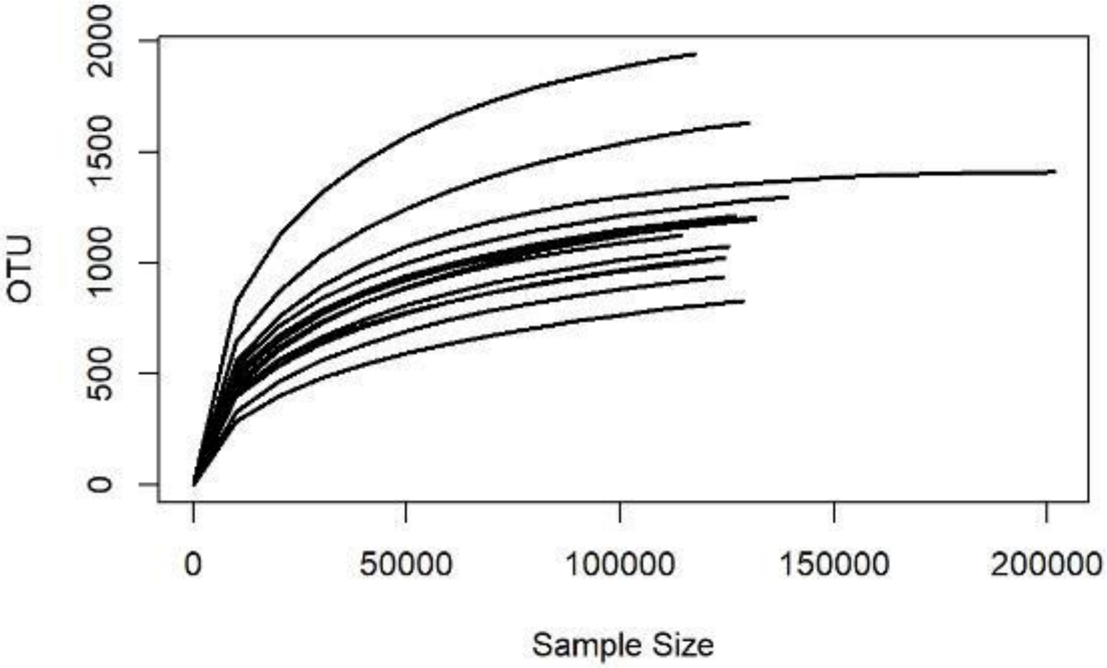


Figure S3. Relative abundance of (a) phyla and (b) classes of soil fungi in upper Andean tropical forests. Each phylum or class is represented with a different color.

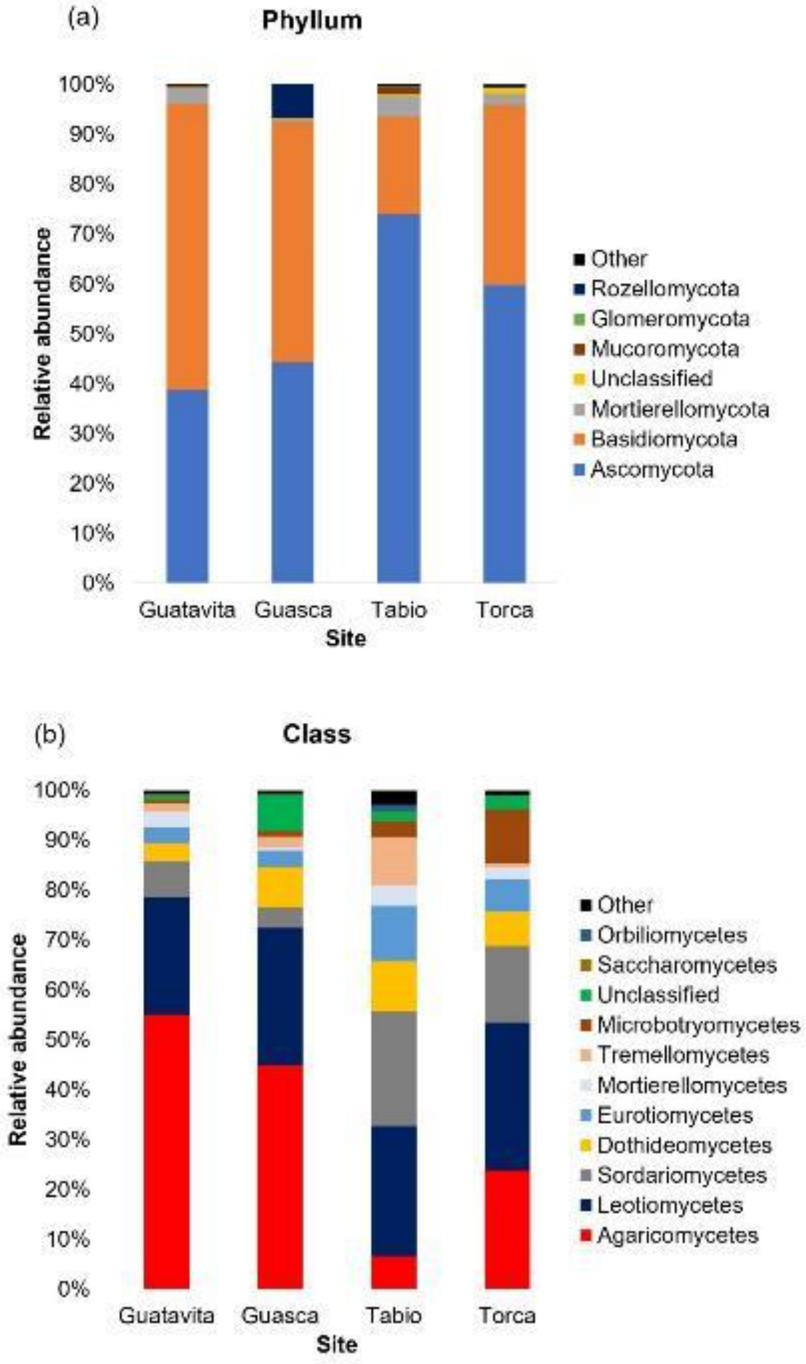


Figure S4. Sheppard plot showing the obtained vs observed (target) ranks that indicates the quality of the NMDS between sites. Note that points minimal deviated from the straight ascending line 1:1, which suggest a good representation of the analyzed distances between objects without significant distortion.

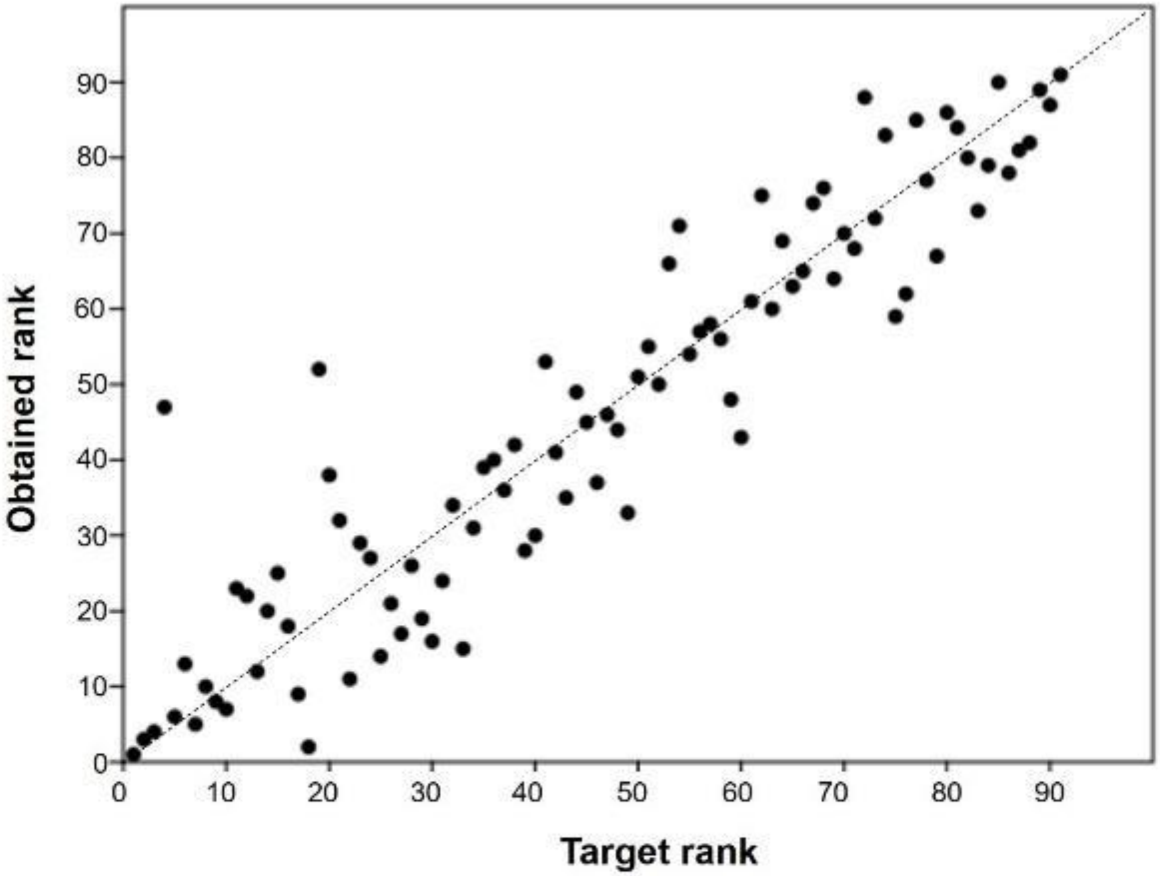


Figure S5. Redundancy analysis (RDA) biplot depicting the (a) relationship between the fungal communities and main environmental parameters of the four different sites. Note that there is no clear relation between sites and variables as RDA was non-significant (P = 0.19, F = 1.67, R^2 Adjusted = 0.382). Loadings of environmental variables are shown in plot (b). Abbreviations of variables: Litter Functional Richness (Litter FR), mean Surface Temperature (ST), mean Soil Moisture (SM) %Nitrogen (N), nutrient flux in µg 10 cm^{-1} 30 $days^{-1}$ of Manganese (Mn), Calcium (Ca), Zinc (Zn), Potassium (K), Boron (B), Phosphorus (P), Aluminum (Al).

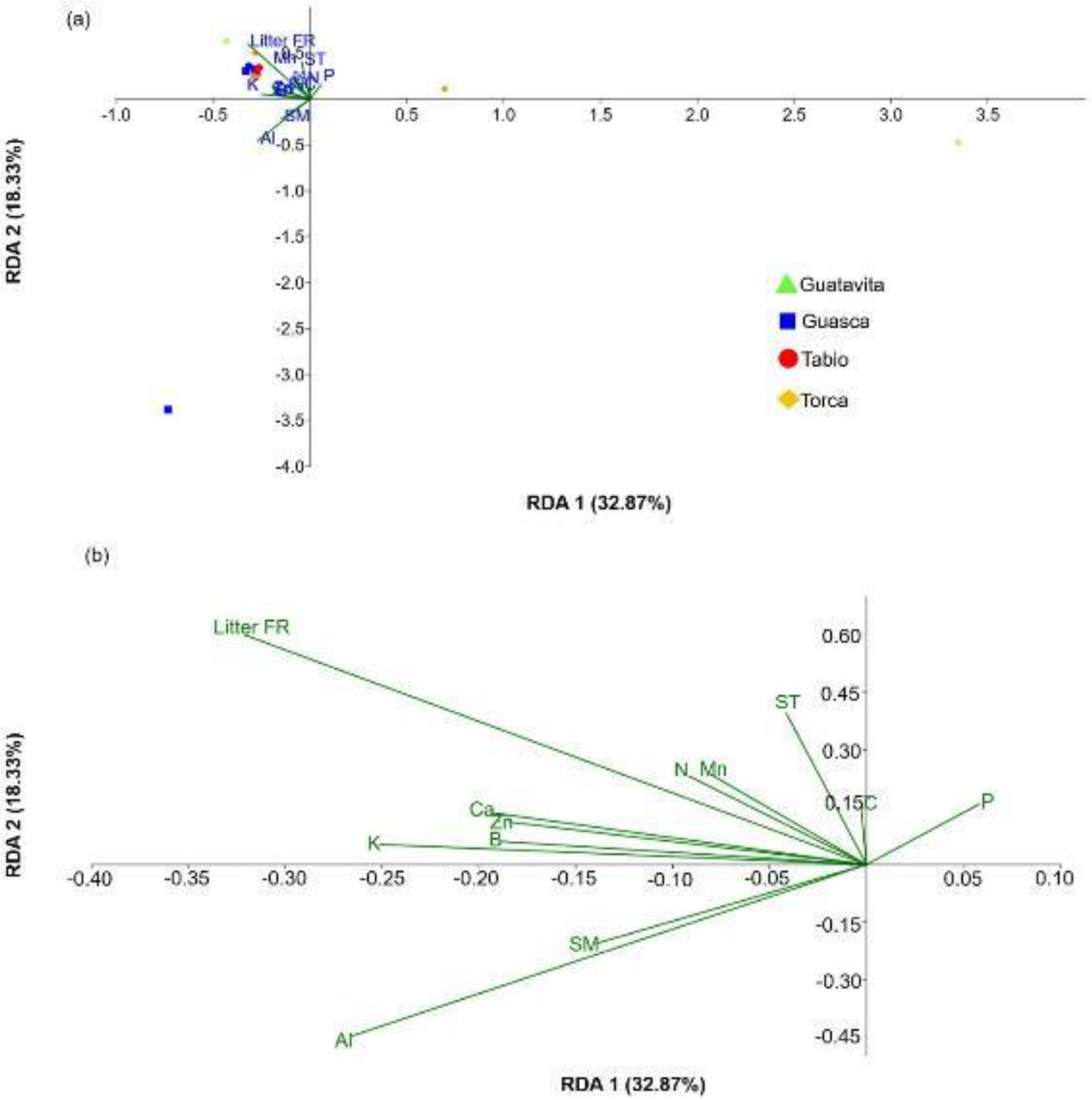


Figure S6. Relative abundance of the different functional guilds in mature and secondary forests. Guilds were classified according to the primary lifestyle based on fungal traits database. Sites and guilds are represented in different colors.

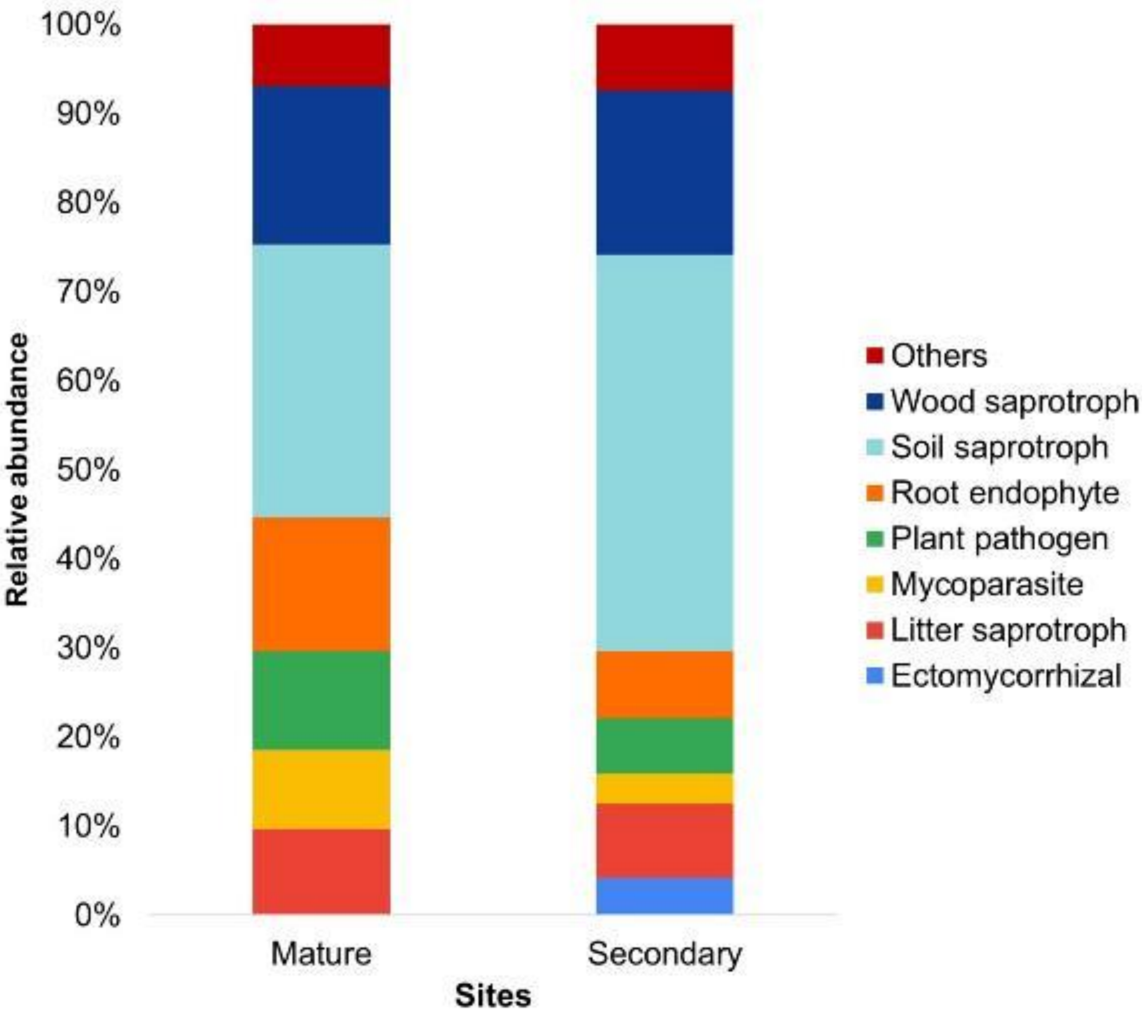


Figure S7. Changes of litter (a-b) and unspecified saprotrophs (c) along succession. The other functional groups did not exhibit changes along succession. Green inverse triangles represent mature forests and grey triangles depict secondary forests.

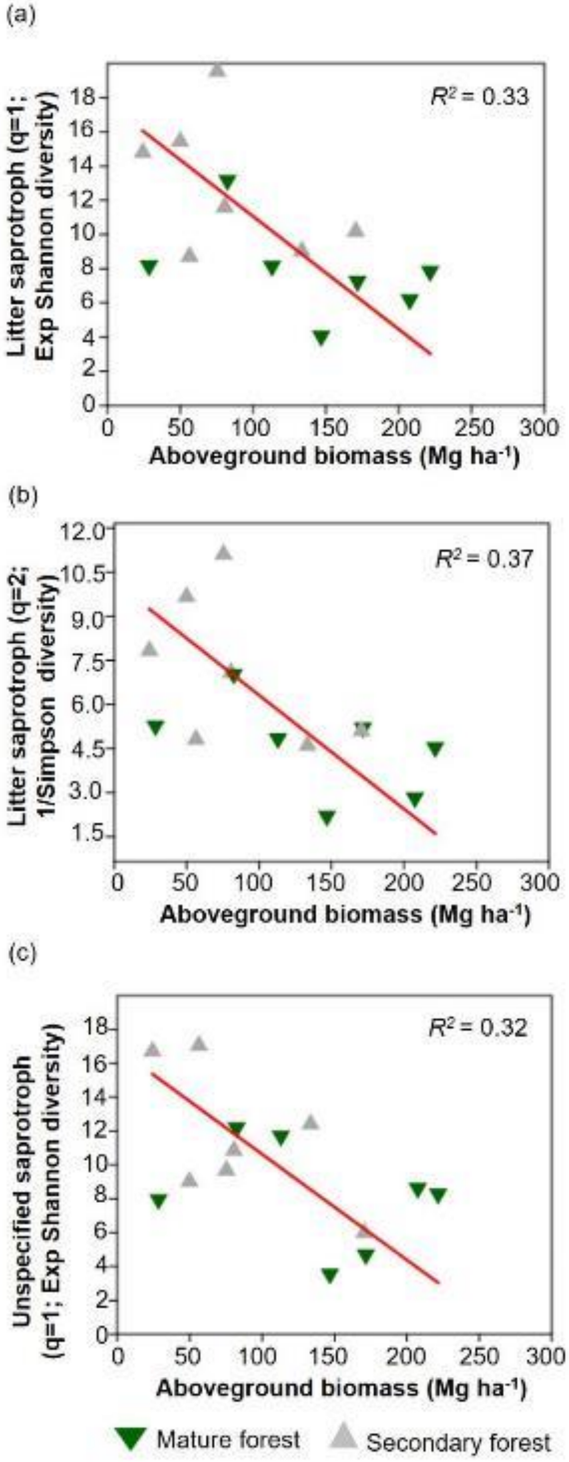


Figure S8. Spearman correlation matrix showing the relationships between environmental variables and the number of OTUs (q = 0, OTU richness) for each soil fungal guild. Blank cells indicate no significant correlations (P > 0.05). Red-orange ellipses represent significant positive correlations, while blue ellipses indicate significant negative correlations. Environmental variables are shown in green, and soil fungal guilds (q = 0) are displayed in brown.

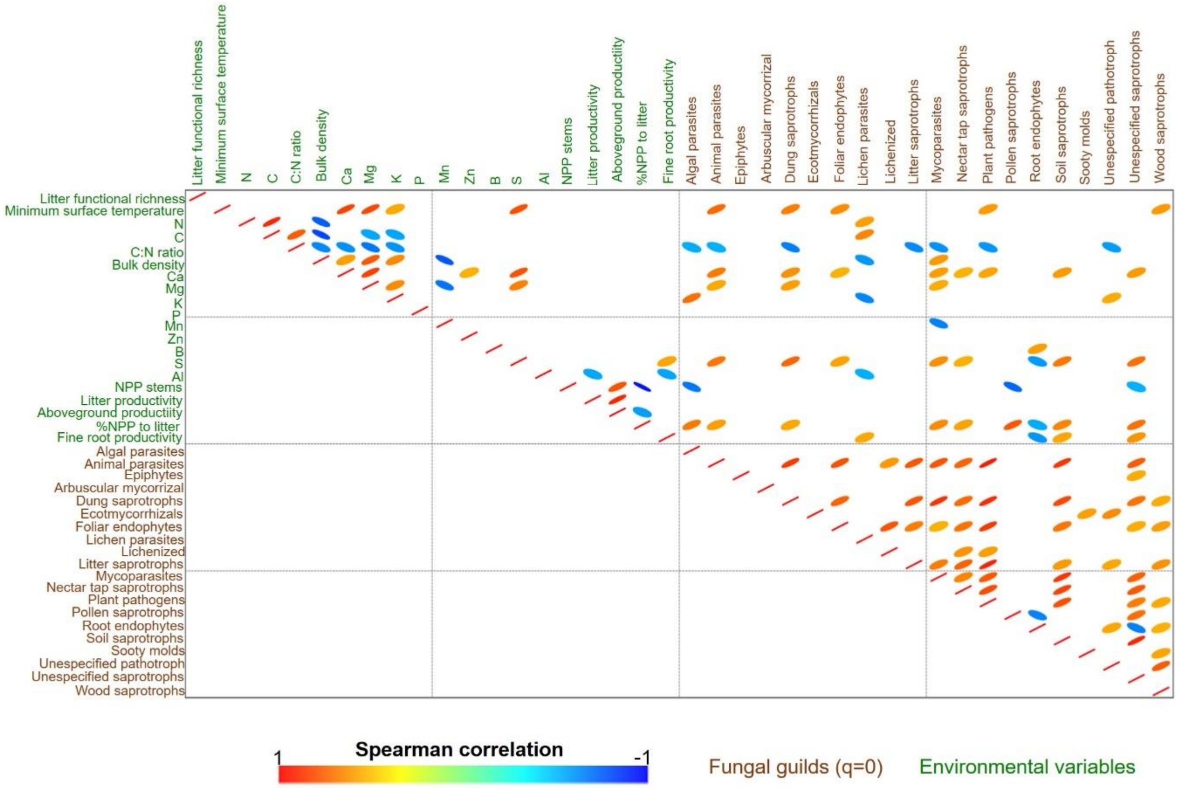


Figure S9. Spearman correlation matrix showing the relationships between environmental variables and the number of OTUs (q = 1; Exp Shannon index) for each soil fungal guild. Blank cells indicate no significant correlations (P > 0.05). Red-orange ellipses represent significant positive correlations, while blue ellipses indicate significant negative correlations. Environmental variables are shown in green, and soil fungal guilds (q = 1) are displayed in brown.

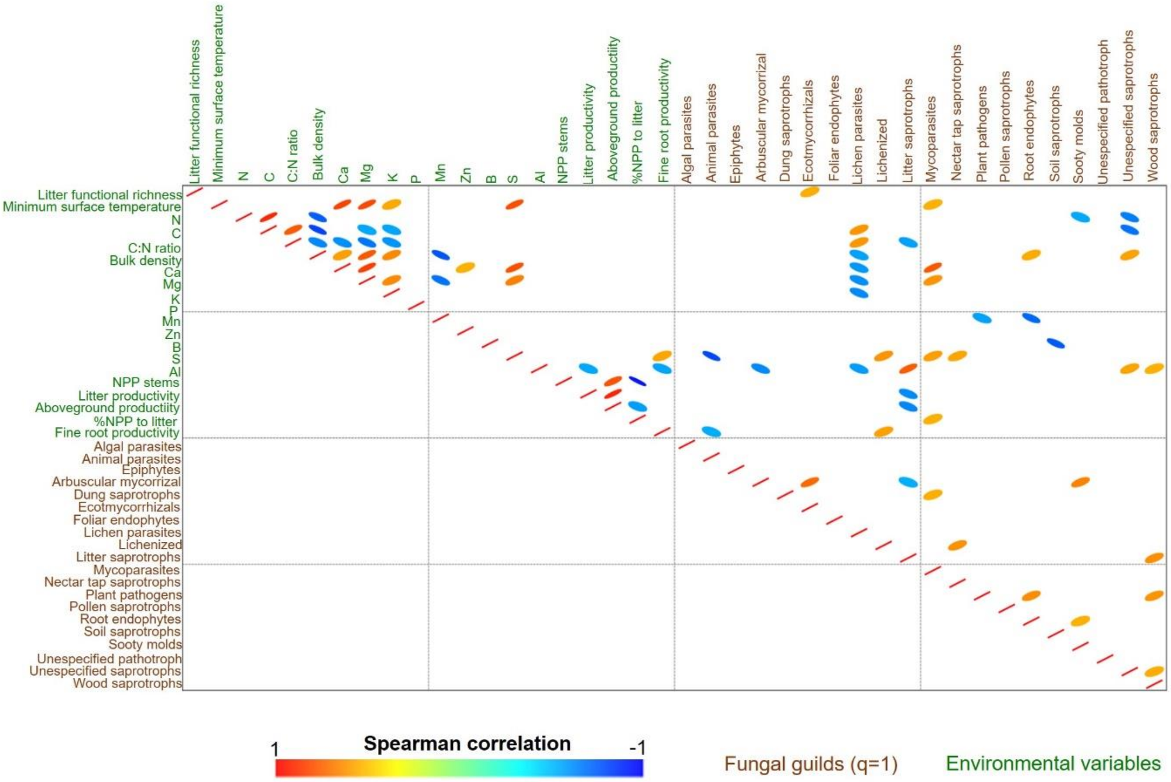


Figure S10. Spearman correlation matrix showing the relationships between environmental variables and the number of OTUs (q = 2; 1/Simpson index) for each soil fungal guild. Blank cells indicate no significant correlations (P > 0.05). Red-orange ellipses represent significant positive correlations, while blue ellipses indicate significant negative correlations. Environmental variables are shown in green, and soil fungal guilds (q = 2) are displayed in brown.

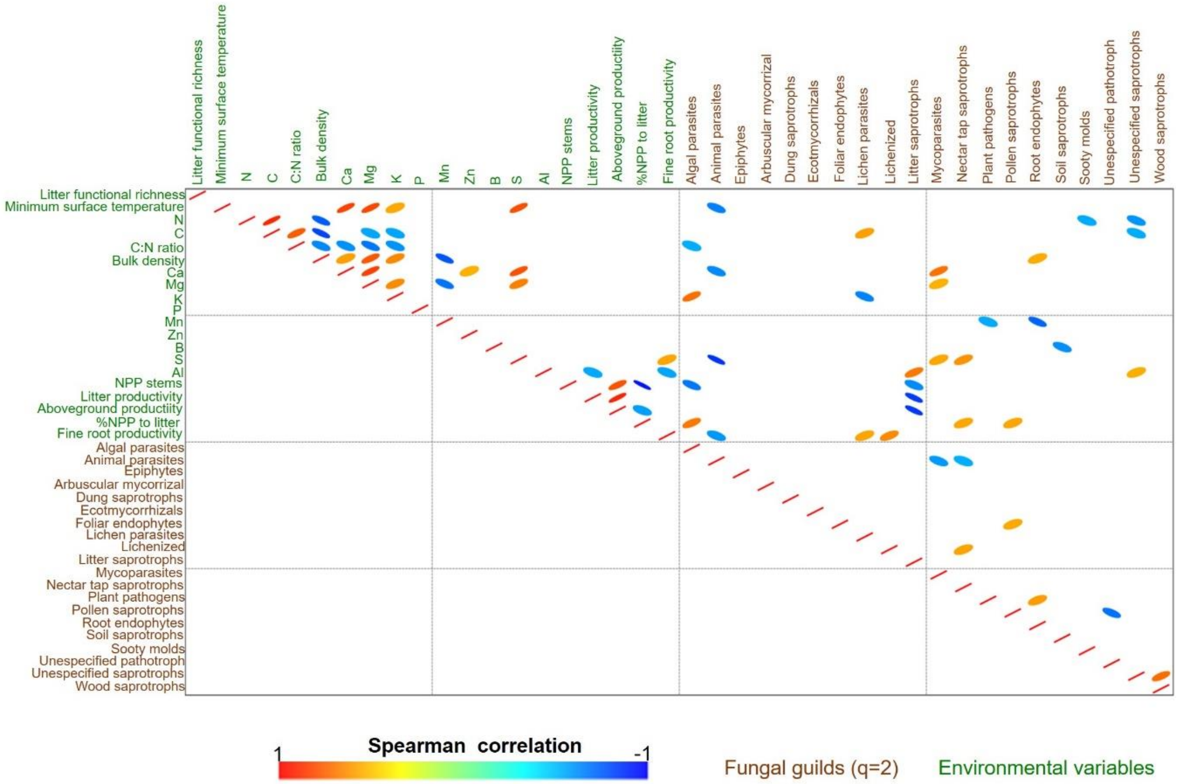
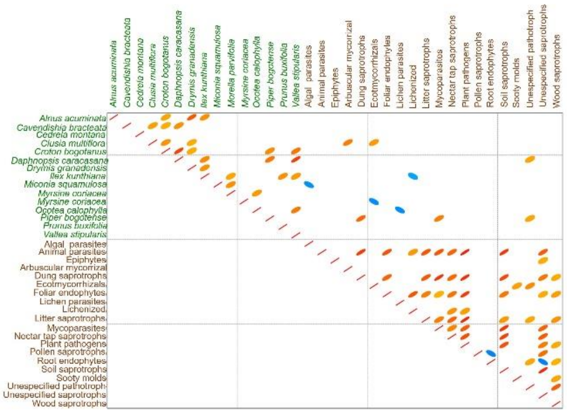


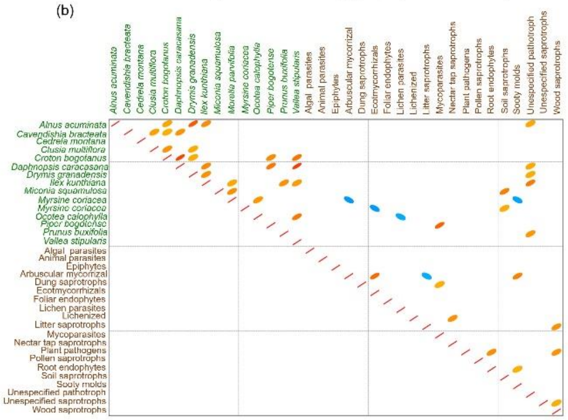
Figure S11. Spearman correlations between fungal guild diversity (brown) and each litter species (green) are shown for (a)fungal richness, (b) fungal exponential Shannon diversity (q = number of OTUs) and, (c) fungal inverse Simpson diversity (q = 2). Orange ellipses represent significant positive correlations, while red ellipses indicate significant negative correlations. Blank cells indicate no significant correlations (P > 0.05).

(a) Fungal richness (q=0; number of OTUs)



Fungal Shannon diversity (q=1; Exp. Shannon index)

(b)



(c)

Fungal Simpson diversity (q=2; 1/Simpson index)

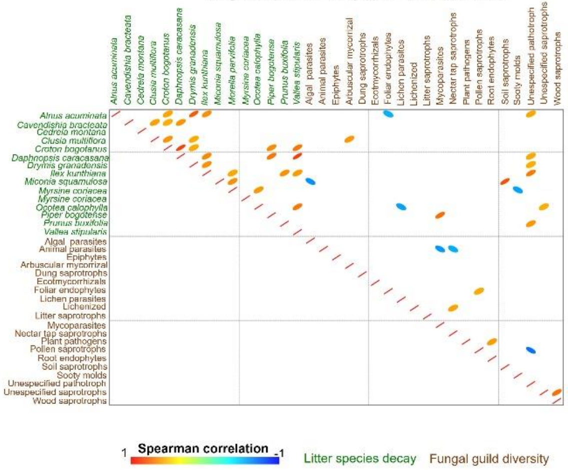


Table S1. Species selected for litter decomposition experiment showing the corresponding **ORDER**, Family and *Species* and picture of their litter.

Taxa	Picture
AQUIFOLIALES Aquifoliaceae *Ilex kunthiana* Triana	
ERICALES Ericaceae *Cavendishia bracteata* (Ruiz & Pav. ex J. St.-Hil.) Hoerold	
Primulaceae *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult	
MALPIGHIALES Clusiaceae *Clusia multiflora* Kunth.	
Euphorbiaceae *Croton bogotanus* Cuatrec.	
LAURALES Lauraceae *Ocotea calophylla* Mez	

ROSALES Rosaceae *Prunus buxifolia* Koehne	
OXALIDALES Elaeocarpaceae *Vallea stipularis* L. f.	
MYRTALES Melastomataceae *Miconia squamulosa* (Sm.) Triana	
FAGALES Betulaceae *Alnus acuminata* Kunth	
Myricaceae *Morella parvifolia* (Benth.) Parra-Os.	

SAPINDALES Meliaceae *Cedrela montana* Moritz ex Turcz.	
MALVALES Thymelaeaceae *Daphnopsis caracasana* Meisn.	
PIPERALES Piperaceae *Piper bogotense* C. DC.	
CANELLALES Winteraceae *Drimys granadensis* L.f. 1782	

Chapter 6

Changes in soil organic matter along a forest successional gradient in the upland Andes and the influence of decomposition.

In preparation for publication.

Soil organic horizon is related to aboveground productivity rather than decomposition along a successional gradient in upper Andean tropical forest

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Abstract

Soils play a major role in global carbon storage, particularly in tropical forests. However, extensive landscape transformation has resulted in the expansion of successional forests, prompting shifts in carbon pools within soils. Upper Andean tropical forests (UATF) are crucial ecosystems for global carbon regulation, yet few studies have delved into the drivers influencing soil organic horizon (SOH) in these ecosystems. In this study, we analyze the main determinants of SOH as well as their effects in soil properties along a successional gradient in UATF. To do this, we measured carbon inputs (aboveground and fine root productivity), carbon outputs (decomposition and decomposability) their drivers (soil biota, microclimate, and leaf anatomical traits) and effects in soil properties (carbon, nitrogen, and bulk density) in 14 permanent plots (20x20m) around Bogotá (Colombia), across a successional gradient of UATF. Our findings indicate a significant correlation between SOH and litter inputs from aboveground productivity, which increase with succession. Surprisingly, decomposition environment and decomposability exhibited no association with SOH. Decomposability was strongly related to leaf anatomical traits linked to litter quality (palisade/spongy thickness ratio, adaxial cuticle thickness), while decomposition environment showed no relation with soil biota richness nor with microclimatic conditions. The lack of variation in decomposability and decomposition environment along the successional gradient partially explains the absence of a relationship with SOH. Our study reveals that SOH is driven by litter inputs rather than litter decomposition across the successional gradient and highlights the importance of conserving different forest successional stages to uphold carbon in UATF.

Key-words: Andean mountains; Carbon cycle; Ecological succession; Forest productivity; Soil conditions; Tropical forest.

Introduction

Soils are pivotal in the carbon cycle since most terrestrial carbon is stored within this compartment (Schmidt et al., 2011; Jackson et al., 2017). Indeed, the carbon stock in soils store around three times more carbon than in the atmosphere with approximately 3000 Pg C according to the Harmonized World Soil Database (FAO, 2012; Scharlemann et al., 2014). Due to this, soils play a major role when it comes to achieving many of the United Nations sustainable development goals (Filser et al., 2016). Understanding the drivers of soil carbon is fundamental to better predict potential shifts in global carbon cycling in future scenarios (Trumbore & Czimczik, 2008; Filser et al., 2016; Jackson et al., 2017).

Tropical forests play a crucial role in the global carbon cycle, accounting for 30% of the total carbon sink (Harris et al., 2021) and storing 40% of the carbon in soil and living plants worldwide (Phillips, 1998). While tropical lowland forests can allocate over 60% of their carbon to the aboveground compartment (Malhi et al., 2011; Raich et al., 2014), tropical montane forests exhibit a different pattern. In these forests, over 70% of the total carbon can be stored in soils (de la Cruz-Amo et al., 2020). Furthermore, despite a 70% decrease in aboveground net primary productivity and a 20-fold decline in wood production between 1000- and 3000-meters elevation (Moser et al., 2011), the size of the soil organic horizon (SOH) increases seven to nine times (Wilcke et al., 2008; Moser et al., 2011). This increase is mainly due to lower mean annual temperatures that slow down decomposition and enhance the carbon storage potential of tropical montane forests (Spracklen & Righelato, 2014; Malhi et al., 2017; Salinas et al., 2021). Indeed, the high proportion of carbon stored in soils is often associated with the development of a thick SOH (Liu et al., 2016), which is particularly sensitive to land-use changes due to its lack of protection by mineral associations (Grosse et al., 2011).

Forest conversion to agricultural and productive systems is a major driver of soil organic carbon decline (Harris et al., 2021; Smith et al., 2016). Recent estimates show that the area of tropical montane forests has been declining at a rate of 0.3% per year between 2001 and 2018, equating to a total loss of 32 million hectares—almost three times faster than the rate observed in temperate forests (He et al., 2023). Notably, some of these deforested areas are then abandoned, as part of the complex deforestation-reforestation transitions that characterize the region (Meyfroidt et al., 2010), resulting in a mosaic of secondary forests and small remnants of mature forests (Calbi et al., 2020; Hurtado-M et al., 2021). These forest transitions impact soil carbon by affecting both the inputs of carbon to soils, through above and below-ground productivity, and its outputs, through decomposition and erosion.

Regarding carbon inputs to the soil system, previous studies have shown that in early successional stages, tropical montane forests can act as carbon sinks in their aboveground compartment as they recover (Paulick et al., 2017), while in later stages, the aboveground compartment reaches a steady state (Duque et al., 2021). However, during these late successional stages, increases in biomass and productivity (Poorter et al., 2021b, 2023; Castillo-Figueroa et al., 2023) can contribute to the accumulation of thick layers of undecomposed litter that increase the size of SOH (Castillo-Figueroa & Posada, 2025). This organic matter accumulation is linked to higher soil carbon and nitrogen concentration (Cristóbal-Acevedo et al., 2019; Suhaili et al., 2021). Bulk density also shifts with forest development (Poorter et al., 2021b), showing an inverse relationship with soil organic matter (Yimer et al., 2006; Bhomia et al., 2016). Consequently, as succession advances in tropical montane forests, soil carbon and nitrogen concentration are expected to increase, while bulk density follows the opposite trend.

Regarding carbon outputs through decomposition, successional changes can influence all controlling factors: environmental conditions for decomposition, litter quality, and the decomposer community (Swift et al., 1979; Bradford et al., 2016; Joly et al., 2023). As succession progresses from abandoned fields and trees become more abundant and denser, the most immediate changes are reflected in the microclimate (Paudel et al., 2015; Seidelmann et al., 2016). Increased biomass and forest cover may lead to reduced solar radiation reaching the soil, which decreases soil temperature and increases soil moisture (Reiners et al., 1994; De Frenne et al., 2019). In terms of litter quality, as succession progresses, fast-growing, acquisitive species are replaced by larger, slow-growing, conservative trees, whose lower litter quality can slow down decomposition (Seidelmann et al., 2016; Pinho et al., 2018; Poorter et al., 2021a; Aryal et al., 2022). In turn, changes in both microclimate and litter quality can alter the composition and activity of decomposers (Garnier et al., 2007; Fortunel et al., 2009; Poca et al., 2015). In tropical montane forests, recent evidence suggests that soil fauna richness increases with succession, driven by energy availability, litter functional diversity, and soil calcium (Castillo-Avila et al., 2025). In contrast, soil fungal richness exhibits no variation along the gradient and is influenced by microclimatic conditions and plant diversity (Castillo-Figueroa et al., under review).

Upper Andean Tropical Forests of Northern South America (UATF - 2600-3200 m *sensu* Cuatrecasas, 1989) are part of a global hotspot of biodiversity (Myers et al., 2000; Olson & Dinerstein, 2002; Orme et al., 2005; Myster, 2021), characterized by rapid-human transformation (Etter et al., 2008, 2021), extraordinary local endemism (Myers et al., 2000; Castillo-Figueroa et al., 2024) and high rates of beta-diversity (Anthelme et al., 2014; Hurtado-M et al., 2021; Cedillo et al., 2023). Additionally, UATF are key ecosystems to counteract climate change by serving as global carbon sinks (Duque et al., 2021; Salinas et al., 2021; Vento et al., 2023). However, our understanding about soil carbon in UATF is very limited (Malhi et al., 2011; Castillo-Figueroa, 2021) given that research has mostly focused on the aboveground compartment (Yepes et al., 2015, 2016; Duque et al., 2021). Although studies on leaf litter decomposition (Pinos et al., 2017; Marian et al., 2017; Ostertag et al., 2022; Castillo-Figueroa, 2024a, 2024b) and aboveground productivity (Paulick et al., 2017; Castillo-Figueroa et al., 2023) have been conducted separately in UATF, a comprehensive framework that examines how carbon inputs and outputs influence soil organic matter along succession is still lacking.

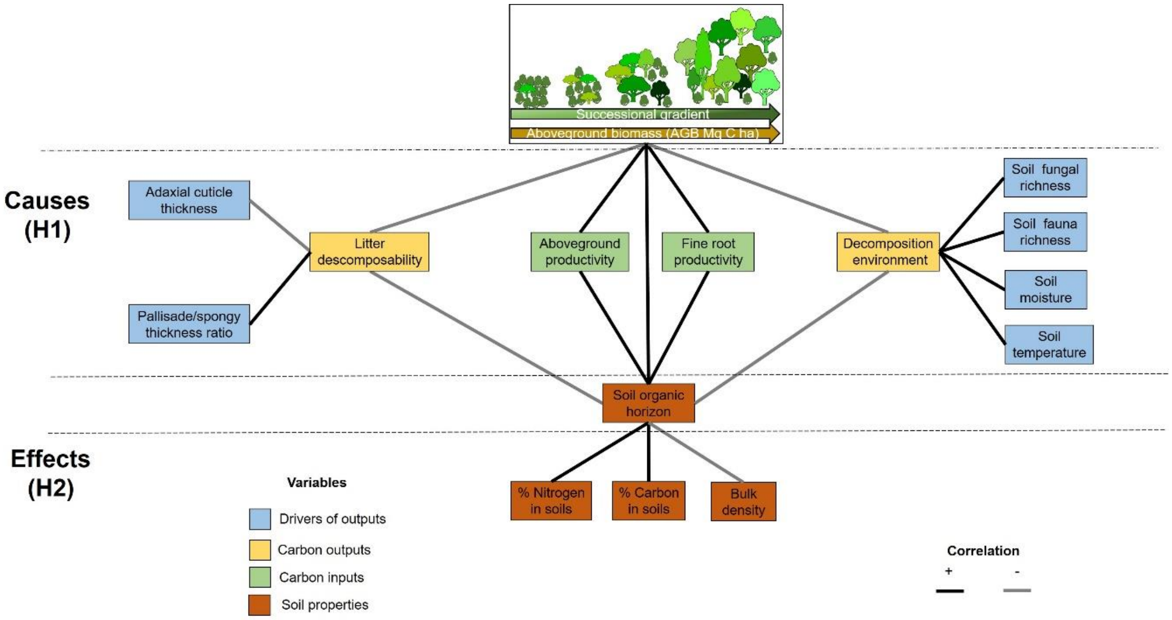

Figure 1. Conceptual model of the main drivers of soil organic horizon along a successional gradient of Upper Andean tropical forests of Colombia. The scheme shows the two-hypothesis tested in this study: H1 about the drivers of SOH and, H2 about the associated effects of SOH on soil physicochemical properties. Green boxes represent variables associated to carbon inputs, yellow boxes to carbon outputs, brown boxes to soil properties, and blue boxes to drivers of carbon outputs.

The objective of this paper was to examine changes in SOH along a successional gradient in UATF and determine whether these changes are influenced by the carbon inputs and outputs to the soil (causes) and their key relationships with soil physicochemical properties (effects). Specifically, we analyzed in the main causes if the SOH was related to: i) aboveground and fine root productivity, ii) decomposability (as an indicator of litter quality), and iii) decomposition environment. We also assessed in the effects if the SOH was related to: i) soil carbon concentration, ii) soil nitrogen concentration and iii) bulk density. We hypothesized that SOH will increase with succession due to higher ecosystem inputs (i.e., greater aboveground and fine root productivity) and reduced carbon outputs through decomposition (H1) (Figure 1). This reduction in decomposition will occur not only under conditions that slow-down decomposition (i.e., low temperature, low soil moisture, and less diverse decomposer communities), but also due to less decomposable litter (i.e., traits reflecting lower litter quality). Additionally, given that soils with high organic matter typically have higher soil carbon and nitrogen concentration in mature forests and are negatively associated with bulk density, we predict that as SOH increases with succession, soil carbon and nitrogen concentration will increase, whereas bulk density will decrease along the successional gradient (H2) (Figure 1).

Materials and methods

Study area

The Andean region encompass 24.5% of Colombia's territory (Etter & Wyngaarden, 2000), and constitutes the most densely populated area, hosting 70% of the total population (DANE, 2018). It is the economic center of the country with over the half of national domestic product (DANE, 2024). Our study focused on a successional gradient in the Eastern Colombian Andes, specifically at the Cundiboyacense high plains, within Andean mountain forests situated at elevations ranging from 2685 to 3140 m. Dominant land use activities in this region include agriculture, livestock grazing, urbanization, and mining (Antonio-Fragala & Obregón-Neira, 2011; Etter et al., 2021). Around the capital city of Bogotá, the climatic conditions feature an average annual atmospheric temperature of 14°C, with mean annual precipitation varying from 600 mm in the central valleys to 1200 mm in the western sectors (Clerici et al., 2016). The high plain experiences a distinctive bimodal precipitation regime, characterized by two rainy seasons occurring from April to June and October to December, interspersed with two dry periods from January to March and July to September (IDEAM, 2024).

To conduct this research, in 2013, 14 permanent plots (20x20 m) were established across four study sites within secondary (7 plots) and mature Andean mountain forests (7 plots) around Bogotá. These plots are part of a larger network in the region ("Rastrojos project", see acknowledgments), which includes a total of 36 20x20m plots and eight 50x50m plots (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023). Forests were categorized as secondary or mature based on their structural attributes such as basal area, tree height, tree density, and species composition (Hurtado-M et al., 2021; Castillo-Figueroa et al., 2023). The 14 plots where we focused this study were distributed in four sites as follows: Tabio (two per successional stage), Guasca (two per successional stage), Torca (three from mature forest and one from secondary forest) and Guatavita (two from secondary forest). Soil texture exhibit a considerable variation between sites: Guatavita (clay = 10%, silt = 15%, sand=74%), Guasca (clay = 25.5%, silt = 25%, sand = 48.5%), Tabio (clay = 24%, silt = 37%, sand = 39%), Torca (clay = 23.5%, silt = 31.5%, sand = 45%).

In these plots, some of the most common plant families are Ericaceae, Melastomataceae, Cunoniaceae, Primulaceae, and Asteraceae, representing 56% of all individuals with a diameter at 'ankle height' above 5 cm (see below). The five dominant genera are *Miconia*, *Weinmannia*, *Cavendishia*, *Myrsine*, and *Myrcianthes*, representing 51% of all individuals. A total of 63 species of shrubs and trees were identified in the study area; among them the five dominant are *Weinmannia tomentosa* Linnaeus filius 1782, *Cavendishia bracteata* Hoerold 1909, *Miconia ligustrina* Triana 1872, *Miconia squamulosa* Triana 1872, and *Myrcianthes leucoxyla* McVaugh 1963 (Clerici et al., 2016).

Data on aboveground biomass (AGB), forest productivity (aboveground and fine root productivity), and soil variables (soil carbon concentration, soil nitrogen concentration, SOH, and bulk density) were obtained from the “Rastrojos Project.” Additionally, data on litter decomposition and its associated biotic and abiotic drivers came from a decomposition project conducted in the same plots. The following sections detail the measurement of each variable.

Forest biomass

To quantify AGB per plot, diameter at breast height (DBH) was measured for individuals with a diameter at 'ankle' height (DAH, 5 cm above the soil surface; as described by Hurtado-M et al., 2021) equal to or larger than 5 cm. This method was used to encompass shrubs that typically branch near the ground or individuals with twisted stems (Hurtado-M et al., 2021). AGB was estimated by averaging two allometric equations specifically developed for Andean mountain ecosystems (i.e, Sierra et al., 2007; Pérez & Diaz, 2010). To convert the biomass into carbon, biomass was multiplied by 0.5 considering that carbon constitute approximately half of dry weight (Penman et al., 2003). Thus, AGB was used as a surrogate for succession to establish the gradient from secondary forests with low AGB to mature forests with high AGB (Brown & Lugo, 1990; Garnier et al., 2004; Poorter et al., 2021b, 2023).

Carbon inputs: forest productivity

To estimate the inputs of carbon to soils, both aboveground productivity and fine root productivity were calculated . Aboveground productivity was estimated as the sum of litterfall productivity and trunk growth; new recruits and tree death were treated following the methodology outlined by Clark et al. (2001). Litterfall productivity was estimated by collecting litter from 0.25 m^2 traps every 15-20 days between May 2016 and April 2017 (10 per plot, 140 in total) (Castillo-Figueroa & Posada, 2025; Castillo-Figueroa et al., 2023). Litter traps were made of ½ inch PVC tubes and 1 mm mesh nylon screen and set up 1 m above-ground. Branches exceeding 1 cm in diameter were excluded, while those narrower than 1 cm but wider than the trap were trimmed to match the trap length. In the lab, litter samples were oven-dried at 60°C until reaching a constant weight, after which they were weighed using an analytical scale accurate to 0.0001 g (LX 220A scs). Stem growth was estimated by measuring changes in DBH between 2013 and 2016.

To estimate fine root productivity, nine root-ingrowth cores were installed in each plot (11.5 cm in diameter and 30 cm in length), totaling 126 independent sampling units across the 14 plots. To prepare the cores, the surface soil litter was first removed and then used a post-hole digger to excavate cylindrical cores to a depth of 30 cm, as described by Phillips et al. (2001). After extracting all roots from the soil samples, root-free soil was encased in mesh cages and reinserted them into the ground. Root harvesting took place over a one-year period. Roots were manually extracted from each core during 40-minute sessions, divided into four 10-minute intervals. Fine roots (<2 mm) were separated using standard techniques (Metcalfe et al., 2007; Brassard et al., 2011; Marthews et al., 2012), and were then oven-dried at 60°C in the laboratory until they reached a constant weight. Dry weights were measured with an analytical scale.

Carbon outputs: decomposition environment and litter decomposability

To determine the effect of biotic and abiotic conditions on litter decomposition, a reciprocal translocation field experiment was conducted involving multiple species between October 2021 and April 2023 (Castillo-Figueroa et al., 2025). The experiment was established in the 14 plots, each containing three litter decomposition beds (total n = 42), with a minimum distance of 5 m between beds. Within these beds, 15 different litter species were employed, each subjected to four decomposition periods (3, 6, 12, 18 months), resulting in a total of 2,520 litterbags (14 plots x 3 beds x 15 species x 4 harvest times). The litterbags, measuring 10 x 15 cm, were constructed from flexible fiberglass fabric with a mesh size of 2 mm, allowing for the entry of micro- and mesofauna. During placement, areas with forest gaps, topographic depressions, and highly irregular soil conditions were avoided. Upon collection, the litterbags underwent gentle brushing to remove mineral soil particles. All contents of the litterbags, except for the soil fauna, were processed, while the fauna was carefully collected and preserved in 70% ethanol (Castillo-Figueroa et al., unpublished work). Then, the litter material was oven-dried at 60°C for 72 hours and weighed using a precision scale. Decomposition rates (mass loss % y^{-1}) was calculated based and Njoroge et al. (2022). Decomposition environment was estimated based on the average mass loss of the 15 litter species used as standard material in each plot during the experiment.

Abiotic (soil microclimate) and biotic factors (soil fauna and fungi richness) were measured in each plot. To obtain soil microclimate, TMS-4 soil probes equipped with data loggers (TOMST, Czech Republic) were installed at the center of each of the 14 plots to record soil temperature and volumetric water content every 15 minutes throughout the year 2022. Each device includes three temperature sensors, one located 15 cm above the soil surface, one at the soil surface, and one at 8 cm depth in the soil. Additionally, a probe at the bottom measures volumetric soil moisture at a 14 cm depth (Wild et al., 2019).

To collect soil fauna, three soil samples (30x30x5 cm) were extracted from each plot, with each sample corresponding to a litterbed from the decomposition experiment (n = 42). These samples were taken across four climatic seasons (n = 168): January-February (dry season), April-May (rainy season), July-August (dry season), and October-November (rainy season) of 2022 (Castillo-Figueroa et al., 2024; Castillo-Avila et al., 2025). 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 hours, followed by transfer to 70% alcohol as preserver. Samples were observed using a stereoscope (Zeiss Stemi 305, Germany), and taxonomically identified to the highest possible taxonomic resolution with the help of experts, original descriptions, and available identification guides for the region. Larvae of holometabolous insects that could not be linked to any adult species were classified as distinct morphospecies (Castillo-Avila et al., 2025). Morphospecies were used to assess soil fauna richness.

To collect soil fungi, three soil subsamples per plot were taken to a depth of 5 cm after removal of the surface litter, next to each litterbed of the decomposition experiment (Castillo-Figueroa et al., under review). These three subsamples were homogenized, resulting in a single composite soil sample per plot (total n = 14). After collection, soil samples were stored in freezers at -30°C. In the lab, DNA extraction was performed using the DNeasy® PowerSoil® Pro Kit (QIAGEN, Hilden, Germany). The ITS1 region was PCR-amplified and sequenced on an Illumina HiSeq2500 PE250 by Novogene Bioinformatics Technology Co. Ltd. (Beijing, China) using the fungal specific primers ITS5-1737F (GGAAGTAAAAGTCGTAACAAGG) and ITS2-2043R (GCTGCGTTCTTCATCGATGC). The Illumina MiSeq data was analyzed with AMPtk v1.3.0 (Palmer et al., 2018), in accordance with the methodology of Corrales & Ovrebo (2020). MiSeq reads were demultiplexed according to the AMPtk documentation (https://amptk.readthedocs.io/en/latest/pre-processing.html), and sequences shorter than 150 bp were discarded. Fungal richness was assessed using operational taxonomic units (OTUs), with reads clustered at 97% similarity to define OTUs. Taxonomic classification was performed using the AMPtk taxonomy algorithm (Palmer et al., 2018) and the UNITE database (Version 18.07.2023; Abarenkov et al., 2023). Non-fungal OTUs and those with fewer than 10 sequences were removed from the dataset (Sanchez-Tello & Corrales, 2024).

To estimate litter decomposability (i.e., litter quality), community weighted mean of mass loss (% y^{-1}) was estimated from all the species present in each plot. To do this, decomposability was predicted based on previous analyses using parameters from a multiple linear regression that included SLA (mg g^{-1}), leaf carbon content (mg g^{-1}), leaf nitrogen content (mg g^{-1}), and leaf photosynthetic capacity (A_{max} µmol g^{-1} $s^{-}1$). These foliar traits are linked to litter quality (Bakker et al., 2011; de la Riva et al., 2019) and were the best predictors of litter decomposition in the experiment (R = 0.85, R^2 = 0.71, Castillo-Figueroa & Posada, 2025). Leaf anatomical traits were also measured from sunny leaves of all 63 plant species, collected from three individuals per species within the permanent plots. Transverse sections of the leaves were cut using a microtome (Leica RM2255) to obtain a flat surface for subsequent estimation of cell fractions after gradual dehydration in an ethanol series (50%, 70%, 85%, 95%, 100%) and paraffin hot infiltration, following standardized methodology (He et al., 2018; Harrison, 2021). Measurements of anatomical traits included the thickness of cuticle, epidermis, palisade and spongy mesophylls, and vascular bundles diameter as well as their relations (e.g., palisade/spongy ratio); image analyses were conducted using ImageJ (Schneider et al., 2012, https://imagej.nih.gov/ij/). Based on previous analyses, the adaxial cuticle and the palisade/spongy thickness ratio were key traits that strongly predicted litter decomposability (Castillo-Figueroa & Posada, 2025).

Therefore, these two traits were used as measures of decomposability and scaled to the plot level using community weighted means (Figure 1).

SOH and its effects on soil physiochemical properties

Depth of the SOH (cm), and their effects on soil physicochemical properties such as soil carbon (%), soil nitrogen (%), and bulk density (g/cm^3) were measured in the 14 plots. SOH was measured by excavating a soil pit next to each plot using a shovel. To measure carbon and nitrogen concentrations, samples were taken at five random points in each plot using a soil corer at a depth of 0-15 cm ($n = 70$). Bulk density was estimated on the same samples based on the known volume cylinder method (Robertson et al., 1999). Element concentrations were measured with an auto-analyzer at the Max Planck Institute for Biogeochemistry (Jena, Germany).

Data analysis

To analyze the changes in SOH and their associated physicochemical properties along succession, reduced major axis regressions (RMA) were conducted between SOH, soil carbon concentration, soil nitrogen concentration, bulk density and AGB as a proxy for succession. To assess the changes in carbon inputs and outputs along the successional gradient, RMA were performed using both aboveground productivity and fine root productivity as carbon inputs, and decomposition environment and litter decomposability as carbon outputs, in relation to AGB. In all the RMA, we calculated the 95% bootstrapped confidence intervals of the slopes ($n = 1999$). Breusch-Pagan test was applied to confirm homoscedasticity in each linear regression model.

The Shapiro-Wilk test for multivariate normality confirmed normality ($P = 0.611$). To synthetize the factors that are related to SOH, Pearson correlations were made between all the variables included in the conceptual model outlined in the Figure 1. A multiple linear regression model was conducted using the stepwise method to determine how carbon inputs, outputs and drivers (explanatory variables) better explain the SOH (response variable). Based on our first hypothesis (H1) depicted in Figure 1, we included for each response variable the following explanatory variables: decomposition environment, litter decomposability, aboveground productivity, fine root productivity, and AGB. We included models with Variance Inflation Factor (VIF) below 3.0 to prevent multicollinearity (Neter et al. 1990). To select the best model for each explanatory variable, we used the Adjusted R^2 and Root Mean Squared Error (RMSE). Adjusted R^2 offers a relative measure of model fit by accounting for the number of predictors and penalizing the inclusion of unnecessary variables, thus helping to prevent overfitting (Kutner et al., 2004; James et al., 2013). RMSE, on the other hand, provides an absolute measure of model accuracy by quantifying the average deviation of predicted values from actual values in the same units as the dependent variable (Montgomery et al., 2012; Chatterjee & Hadi, 2015).

Finally, to examine the relationships between SOH and soil physicochemical properties, associations with soil carbon concentration, soil nitrogen concentration, and bulk density were analyzed according to the second hypothesis established in Figure 1 (H2). All the analyzes were conducted in JASP 0.14.1.0 (JASP Team, 2023) and PAST 4.14 (Hammer et al., 2001).

Results

SOH and their associated soil physicochemical properties along succession

We observed a substantial variation in the SOH, ranging from 2.3 cm to 44.5 cm along the successional gradient. Additionally, soil carbon concentration varied from 8.24% to 50.69%, while soil nitrogen concentration ranged from 0.59% to 1.78%. In mature forests, the average SOH (18.61 ± 10.45 cm), soil carbon concentration (34.75 ± 16.36 %), and soil nitrogen concentration (1.39 ± 0.45 %) were approximately two-fold than that of secondary forests (SOH: 6.98 ± 4.93, soil carbon concentration = 13.57 ± 2.06, soil nitrogen concentration = 0.745 ± 0.15, Table S1). Accordingly, we found an increase in the thickness SOH ($P = 0.01$, $R^2 = 0.41$, $n = 14$, CI = [0.17, 0.53], Figure 2a), soil carbon concentration ($P < 0.0001$, $R^2 = 0.73$, $n = 14$, CI = [0.37, 0.62], Figure 2b), and soil nitrogen concentration ($P < 0.0001$, $R^2 = 0.80$, $n = 14$, CI = [0.001, 0.01]; Figure 2c) with increasing AGB.

Bulk density varied widely, from loose soils with 0.047 g/cm^3 to compact soils with 0.733 g/cm^3. Average bulk density in secondary forests (0.51 ± 0.081 g/cm^3) was two-fold than that of mature forests (0.26 ± 0.25 g/cm^3). Along the successional gradient, bulk density decreased significantly with increasing AGB ($P = 0.001$, $R^2 = 0.57$, $n = 14$, CI = [-0.008, -0.004], Figure 2d). Furthermore, bulk density had an inverse relationship with soil carbon concentration ($P < 0.001$, $R^2 = 0.87$, $n = 14$, CI = [-87.25, -59.68], Figure S1), and soil nitrogen concentration ($P < 0.001$, $R^2 = 0.79$, $n = 14$, CI = [-2.45, -1.50], Figure S1).

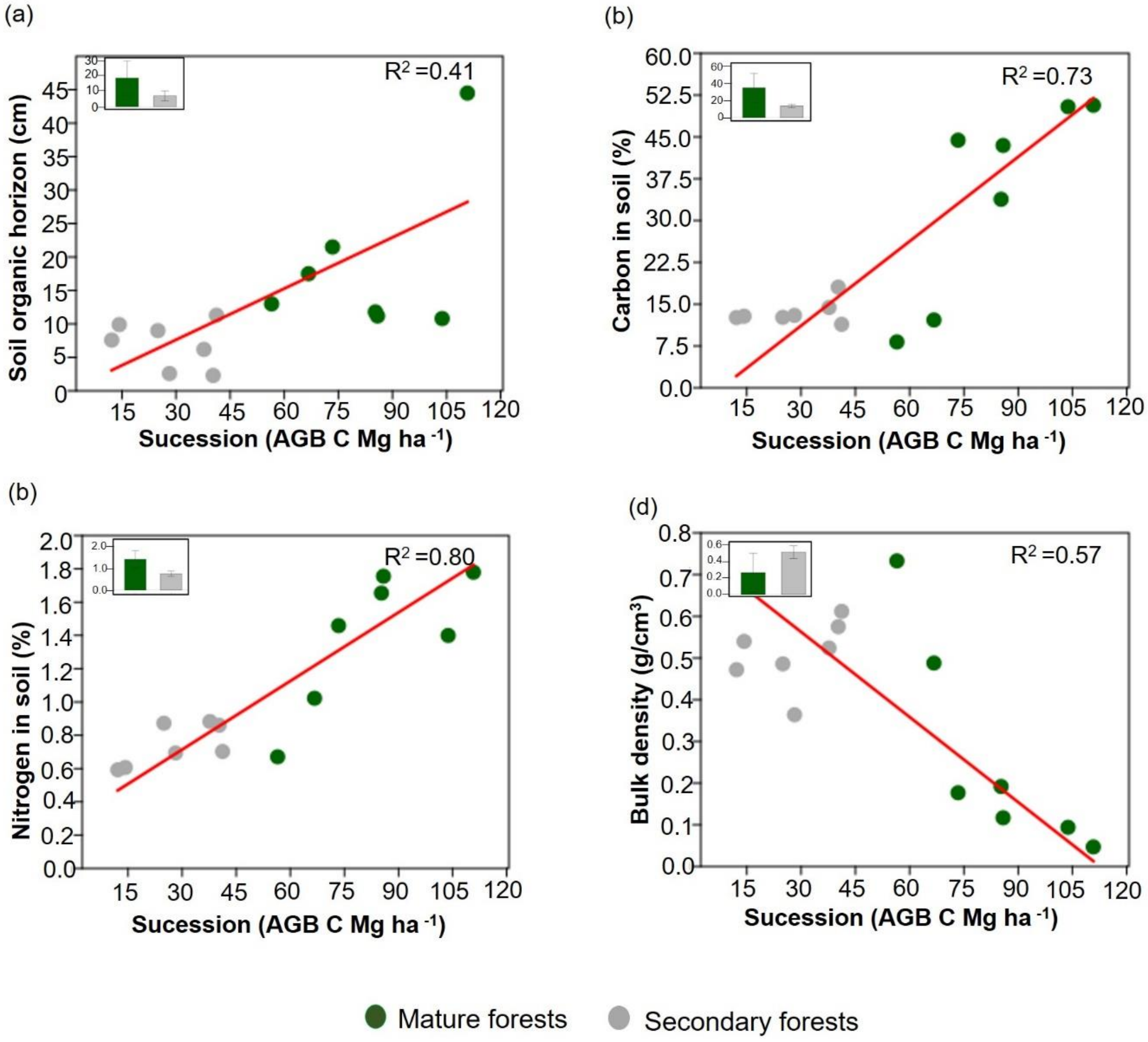

Figure 2. Reduced major axis regressions between Aboveground Biomass (AGB C Mg ha^{-1}) as proxy of succession and (a) Soil organic horizon (cm) (b) Carbon in soil (%) (c) Nitrogen in soil (%) and (d) bulk density (g/cm^3). In the right corner of each plot, the R^2 value is displayed, and in the left corner, a bar plot shows data for mature and secondary forests along with their respective 95% confidence intervals. Mature forests are depicted in green colors, while secondary forests are represented in gray colors.

Carbon inputs along succession

Aboveground net primary productivity increased significantly with AGB (P = 0.003; R^2 = 0.52, n = 14, CI = [0.04, 0.09], Figure 3a), ranging from 1.90 to 9.43 Mg C ha^{-1} y^{-1}. Mature forests showed higher values (5.38 ± 1.95 Mg C ha^{-1} y^{-1}) than secondary ones (3.06 ± 1.09 Mg C ha^{-1} y^{-1}, Table S1). However, fine root productivity did not change with AGB (P = 0.47, R^2 = 0.04, n = 14, CI = [0.02, 0.91], Figure 3b) and ranged between 0.78 and 2.85 Mg C ha^{-1} y^{-1}. For this input, mature forest (1.72 ± 1.06 Mg C ha^{-1} y^{-1}) showed similar values than secondary forests (1.62 ± 0.86 Mg C ha^{-1} y^{-1}, Table S1).

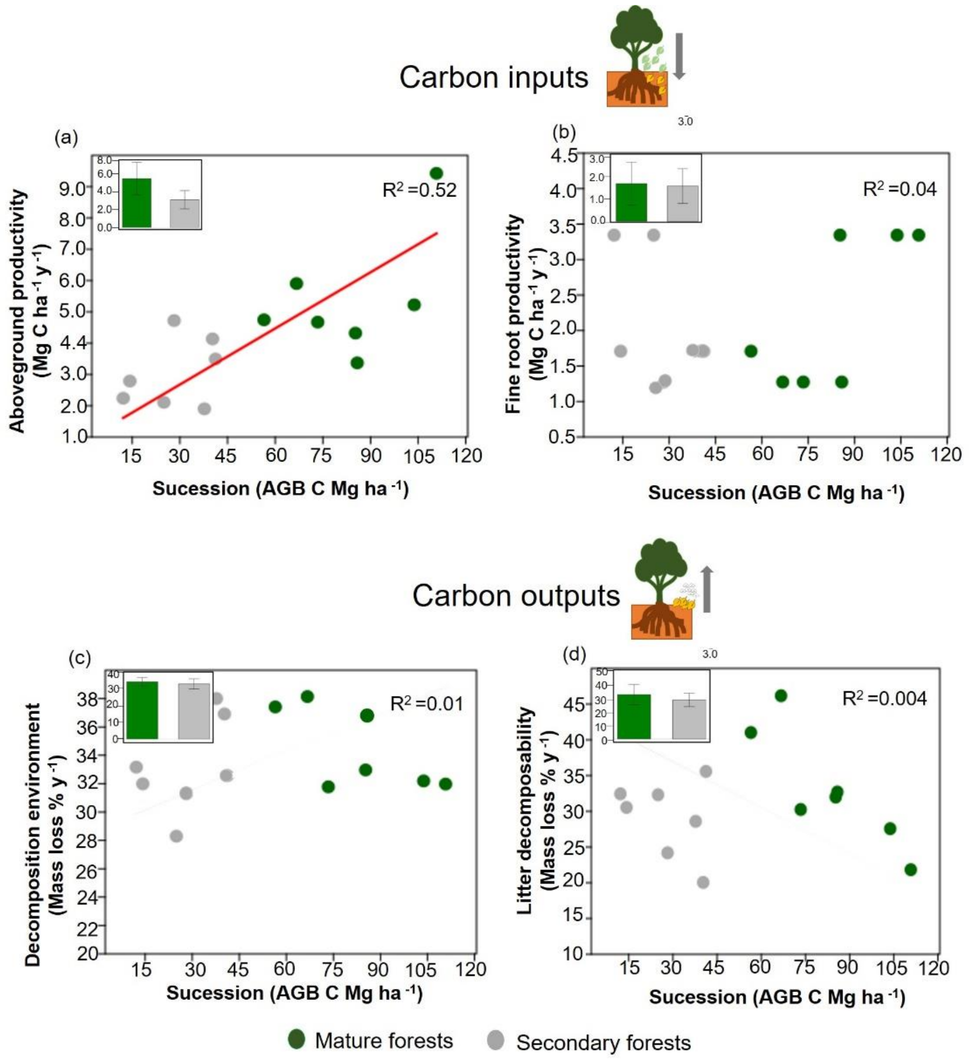

Figure 3. Reduced major axis regression between Aboveground Biomass (AGB C Mg ha^1) as a proxy of succession and (a) aboveground productivity, (b) fine root productivity, (c) decomposition environment (mass loss% y^{-1}) and, (d) litter decomposability (mass loss% y^{-1}). In the right corner of each plot, the R^2 value is displayed, and in the left corner, a bar plot shows data for mature and secondary forests along with their respective 95% confidence intervals. Mature forests are depicted in green colors, while secondary forests are represented in gray colors. Plots without red line indicate no significant relationship (P > 0.05).

Carbon outputs along succession

Standard decomposition rates from the environment showed minimal variation along the successional gradient (P = 0.71, R^2 = 0.01, n = 14, CI = [0.04, 0.30], Figure 3c), ranging from 28.30 to 38.14 mass loss (% y^{-1}). Overall, we found similar values in the average decomposition environment in both mature forests (34.45 ± 2.84 % y^{-1}) and secondary forests (33.18 ± 3.32 % y^{-1}, Table S1). Litter decomposability ranged from 20.05 to 46.17 % y^{-1} and also did not change with ABG (P = 0.83, R^2 = 0.004, n = 14, CI = [-0.78, -0.14], Figure 4d), showing similar values in both mature forests (33.08 ± 8.17 % y^{-1}) and secondary forests (29.11 ± 5.35 % y^{-1}, Table S1).

Importantly, neither microclimatic variables nor soil biota richness were correlated with decomposition environment (Figure 4), however, soil fauna richness was positively related to SOH (P = 0.02, r = 0.60, Figure S2). In terms of litter quality, litter decomposability was negatively associated with adaxial cuticle thickness (P < 0.0001, r = -0.84) and positively associated with palisade/spongy thickness ratio (P < 0.0001, r = 0.83) (Figure 4). Interestingly, adaxial cuticle thickness showed a positive relation with soil carbon concentration (P = 0.03, r = 0.57, Figure S2), while palisade/spongy thickness ratio exhibited a negative relation with the same variable (P = 0.03, r = 0.60, Figure S2). However, neither decomposition environment nor litter decomposability were associated with ABG nor with the thickness of the SOH (Figure 1).

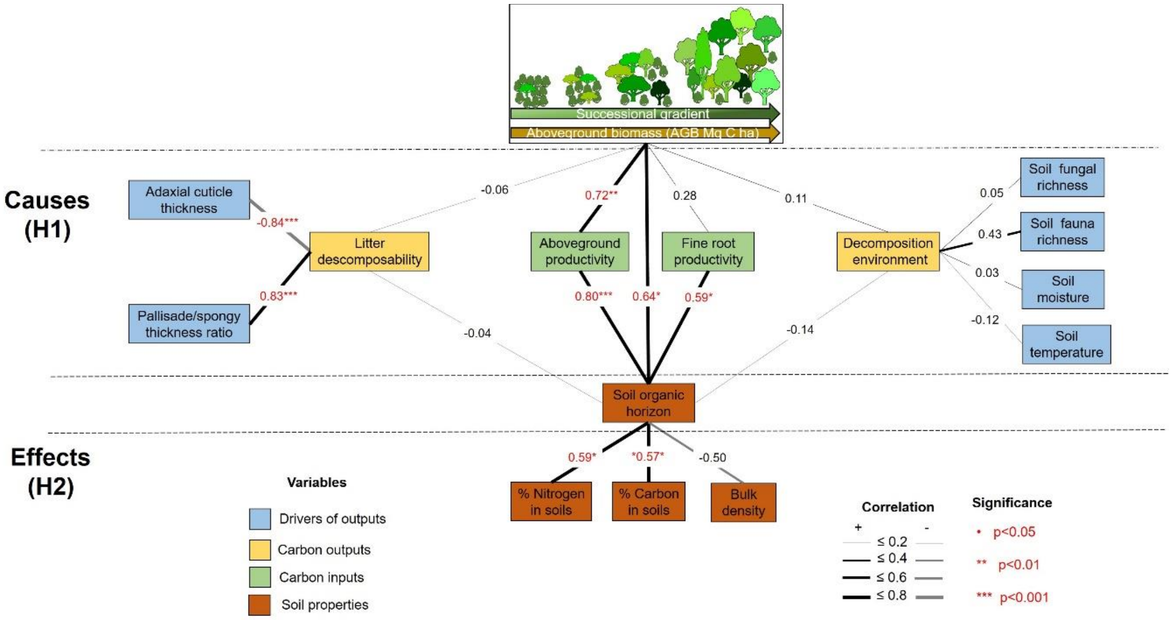

Figure 4. Pearson correlations between variables related to litter decomposability, decomposition environment, soil organic horizon, %C in soils and %N in soils. Black lines represent positive relations, while gray lines depict negative relations. Red colors display significant relations. Green boxes represent variables associated to carbon inputs, yellow boxes to carbon outputs, brown boxes to soil properties, and blue boxes to drivers of carbon outputs.

Drivers of soil SOH and their associated soil physicochemical properties

We found that SOH was primarily associated with aboveground productivity (P < 0.001, r = 0.80) and fine root productivity (P = 0.02, r = 0.59). Moreover, SOH exhibited a positive relationship with carbon (r = 0.57, P = 0.03) and nitrogen concentration (P = 0.03, r = 0.59), but surprisingly, it was not significantly related to bulk density (P = 0.06, r = -0.50) (Figure 4). We did not observe a significant relationship between SOH and either decomposition environment (r = -0,14, P = 0.62) or decomposability (r = -0.04, P = 0.89). Lastly, multiple regression analysis showed that the best predictor for SOH was aboveground productivity (P < 0.001, Adjusted R^2 = 0.61,Table 1).

Table 1. Multiple stepwise regression through showing the effects of the most important variables for soil organic horizon: aboveground productivity, fine root productivity, decomposition environment, litter decomposability, and aboveground biomass (AGB) as a proxy of succession. Values of correlation (R), size effect (R^2), Root Mean Square Error (RMSE) significance (P value), and Variance Inflation Factor (VIF) are depicted for each model.

Model		Unstandardized	Standard Error	Standardized	t	P	Tolerance	VIF
Soil organic horizon (R = 0.801, R^2 = 0.642, Adjusted R^2 = 0.612, RMSE = 6.51, P < 0.001)								
1	(Intercept)	12.800	2.793		4.582	< .001		
2	(Intercept)	-5.457	4.301		-1.269	0.229		
	Aboveground productivity	4.327	0.932	0.801	4.641	< .001	1.000	1.000

Discussion

Tropical lowland forests are widely recognized for their significant role in the global carbon cycle, primarily due to the substantial carbon storage in their AGB (Mills et al., 2023). In contrast, tropical montane forests have been much less studied, despite potentially serving as important carbon reservoirs (Spracklen & Righelato, 2014). A large portion of their carbon is stored in soils, which provide a more stable long-term carbon stock compared to vegetation. Our study reveals that the thickness of the SOH in UATF is primarily influenced by litter inputs from aboveground productivity, which increases with succession. Soil carbon and nitrogen concentrations are, in turn, influenced by SOH and forest succession. Contrary to part our working hypothesis, decomposition was not correlated with the thickness of the SOH nor with carbon and nitrogen concentrations and did not change along the successional gradient. Our study supports the notion that SOH and litter decomposition are modulated by different mechanisms along succession.

SOH and carbon inputs along succession

On average, secondary forests had a 39% lower soil carbon concentration than mature forests, partially confirming our first hypothesis (H1) (Figure 2). Previous research has indicated that disturbed secondary forests can contain up to 45% less soil organic carbon than mature undisturbed forests (Naldini et al., 2023) and that soil organic carbon increase as succession progresses (Yang et al., 2016). The increase in the SOH was behind the increase in concentrations of nitrogen and carbon, both of which were also positively correlated with AGB (Figure 4), as indicated by previous studies (Chua & Potts, 2018; Badalamenti et al., 2019; Duan et al., 2020; Poorter et al., 2021b). However, contrary to our expectations, the increase in the SOH with succession was mainly explained by aboveground productivity rather than decomposition (Figure 4, Table 1).

Although soil organic matter typically results from the balance between litter mass remaining and the soil microbial transformation of plant debris (Lehmann & Klever, 2015; Prescott & Vesterdal, 2021; Naldini et al., 2023), our study revealed no significant correlation between litter decomposition and the formation of the SOH (Figure 4). This finding could be attributed to the minimal variation in decomposition along the successional gradient (Figure

3, but see below), highlighting the predominant role of inputs over outputs in influencing the accumulation of soil organic matter in UATF. The positive relationship observed between aboveground productivity, succession, and the SOH (Figures 3 and 4) reinforces the idea that carbon accumulation in soils is mainly driven by aboveground processes including photosynthesis, litterfall, stem growth, and aboveground carbon sequestration. In this sense, high aboveground productivity leads to greater fluxes of plant necromass, which in turn increases the size of the SOH and the carbon concentration, as reported in previous studies (Frank et al., 2012; Osland et al., 2018; Jackson et al., 2017; Augusto & Boča, 2022).

We found that fine root productivity also contributed to the formation of the SOH, albeit its role was less clear than aboveground inputs (Figure 4, Table 1). Although fine roots are primarily concentrated in the first 10 cm of soil depth (Soethe et al., 2007, 2008), decompose more slowly than thicker roots (Fan & Guo, 2010; Sun et al., 2013), and their production and turnover increase above 2500 m elevation in UATF (Leuschner et al., 2007; Graefe et al., 2008a, 2008b), their main contributions lie in nutrient cycling and water acquisition rather than organic matter accumulation in the soil (Soethe et al., 2007). Additionally, fine root productivity did not vary along the successional gradient as SOH did (Figure 3), diminishing its influence on soil organic matter.

Carbon outputs along succession

In our study, litter decomposability was highly related with anatomical traits associated to litter quality (Figure 4). Anatomical traits such as cuticle and palisade/spongy thickness ratio can influence litter decomposability by shaping leaf traits that underlies the leaf economic spectrum (Castillo-Figueroa & Posada, 2025). The inverse relation between cuticle thickness and decay rates could be attributed to the recalcitrant chemical composition of cuticles including cutins, waxes and polysaccharides, that prevent the degradation by microbial decomposers (Müller, 2006; Onoda et al., 2012). Conversely, palisade/spongy thickness ratio reflects the inversion in photosynthetic tissues which concentrate nutrient-rich resources such as nitrogen (Terashima et al., 2011; Onoda et al., 2017), which are preferred by decomposers (Bakker et al., 2011). These anatomical characteristics are promising ‘hard’ functional traits for disentangle litter decomposability at both community and ecosystem scales, and they could also play a key role in soil carbon dynamics. Indeed, the significant relationships found between soil carbon, adaxial cuticle thickness, and palisade/spongy thickness ratio (Figure S2) suggest that forests dominated by species with conservative leaf anatomical traits may influence the accumulation of less decomposable material, potentially increasing carbon levels in the soil. However, the lack of significant relationships between these anatomical traits and SOH (Figure S2) reinforces the key role of aboveground inputs in shaping SOH.

Decomposition environment, defined as average decomposition rates for 15 representative species placed in all plots, was not significantly influenced by microclimate nor by soil biota richness (Figure 4). This suggest that biotic and abiotic variables vary in opposite directions along the successional gradient, leading to an overall lack of effect on litter decay. For instance, we found a positive correlation between soil fauna richness and

AGB (P = 0.02; r = 0.58), but a negative relation between moisture and AGB (P = 0.048, r = -0.52), while soil fungal richness (P = 0.62, r = -0.14) and temperature were unrelated to AGB (P = 0.61, r = -0.15) (Figure S3). This variability in the patterns of biotic and abiotic variables may help explain their limited influence on the decomposition environment. Another potential explanation is that other unmeasured environmental factors need to be considered to account for the variation in litter decomposition in these forests. Soil nutrients and litter substrate quality, for example, have been related to litter decomposition under natural conditions (Ge et al., 2013).

As previously mentioned, decomposition environment and litter decomposability did not change along the successional gradient (Figures 3 and 4). Although mature forests exhibited higher mean values than secondary forests, both decomposition environment and decomposability did not decrease with succession, contrary to our prediction. In a previous study conducted in the same plots, we demonstrated that succession was a weak predictor of litter decomposition, with only some species showing changes between forest successional stages (Castillo-Figueroa et al., 2025). In the case of litter decomposability, it is possible that functional traits do not change significantly towards conservative strategies along the gradient. In our study site, we identified a decrease in wood density along the successional gradient (Castillo-Figueroa et al., 2023), in contrast to the pattern observed in the lowland tropical rain forests (Poorter et al., 2021a); the decrease in wood density in upper Andean forests was primarily attributed to high proportion of shrubs early in succession that declined as forest mature and gain more biomass. Alternatively, it is possible that our successional gradient included only intermediate and late successional stages, without the initial disturbance stages (i.e., open pastures with no cover), thereby reducing the range of variability in environmental conditions for decomposition.

Consequently, this lack of change in decomposition environment along succession could partially explain the absence of a relationship between decomposition and the SOH, which exhibits a pronounced increase with succession (Figures 2 and 4). Moreover, the SOH and decomposition may occur on different time scales. While decomposition in this study was measured over a period of 18 months, the formation of the SOH results from decades of organic matter accumulation from both aboveground and belowground compartments. This temporal mismatch suggests that short-term decomposition rates do not immediately result in SOH accumulation, as organic matter stabilization depends on slow-acting processes such as the formation of stable humic substances, the development of organo-mineral associations, and long-term root turnover (Six et al., 2002; Schmidt et al., 2011; Lehmann & Kleber, 2015).

Causes and associated effects of SOH in Andean forests

Our results corroborate the fact that aboveground productivity increases SOH by litter inputs (Lohbeck et al., 2018), supporting part of our first hypothesis (H1) (Figure 1 and 4). Studies in different contexts, however, indicate that AGB does not always contribute to soil organic matter, either because it is not necessarily linked to aboveground productivity or due to other influencing factors. For instance, in the lowland Andes, higher nutrient cycling and plant growth influenced by warmer temperatures result in higher AGB but lower soil organic carbon (de la Cruz-Amo et al., 2020). In Southeast Asia, soil organic matter is determined by species diversity and functional diversity rather than AGB and productivity (Satdichanh et al., 2019, 2023).

Regarding the effects of SOH on soil properties, we found that soil carbon and nitrogen concentrations were positively related to SOH, whereas bulk density showed a negative but non-significant trend with SOH, partially supporting our second hypothesis (H2) (Figure 4). Nonetheless, bulk density decreased with increasing soil carbon and nitrogen concentration (Figure S1), which, in turn, increased along succession (Figure 2). This suggests that in mature forests, organic matter occupies more space within the soil, as organic particles are less dense than mineral particles. This organic matter promotes the formation of stable soil aggregates, which enhance both soil structure and porosity (Six et al., 2002; Bronick & Lal, 2005). The formation of these aggregates creates air-filled spaces within the soil, reducing bulk density (Gupta & Germida, 2015). Soils with low bulk density exhibit higher porosity (Kakaire et al., 2015), which positively influences microbial activity (Gupta & Germida, 2015), fostering greater organic matter accumulation (Kakaire et al., 2015) and carbon stabilization (Six et al., 2002) through microbial synthesis and necromass formation (Cotrufo et al., 2015). In this sense, mature forests in UATF exhibit an improvement in soil structure, which is crucial for ecosystem services related to soil biodiversity, fertility, and water regulation (Gaglio et al., 2017; Tito et al., 2022).

Lastly, SOH was positively related to soil carbon and nitrogen concentrations through the effect of increasing productivity along succession (Figure 4). This implies that conserving mature forests, which have a more developed SOH rich in carbon and nitrogen, may be relevant for maintaining the forest organic matter balance. Considering that mature forests exhibited 2.5 times higher soil carbon concentration than secondary forests, the conservation of these forests could be important for climate change mitigation at local and regional scales, as they are key carbon reservoirs (Duque et al., 2021; Castillo-Figueroa, 2021). Nevertheless, secondary forests also have the potential to store carbon in the soils over the long-term (Chazdon et al., 2016). Therefore, improving connectivity between early successional forests and mature forests may help accelerate functional recovery and long-lasting carbon gain in the former. The recovery time of soil organic carbon in early successional forests will depend on local factors, including climate (e.g., temperature, precipitation), soil properties (e.g., texture, land-use history), and plant composition (e.g., monoculture vs. mixed species) (Xu et al., 2024). In sum, each successional stage may contribute to maintaining key ecological functions related to carbon and nutrient cycling in the upland Andes, particularly under current and future environmental change scenarios.

Caveats and limitations of the study

Although we found significant relationships between SOH with succession, one limitation of our study concerns the sensitivity of the relationship between AGB and the thickness of the SOH to a single data point. One old-growth forest plot exhibited a markedly thicker SOH compared to the rest of the plots, which strongly influenced the observed positive association between succession and SOH (Figure 2). This same plot also had the highest aboveground productivity, which similarly biased the regression (Figure 3). These values are not due to measurement error, but reflect real field conditions, likely related to the fact that this is the most conserved and structurally mature forest in our dataset, where sustained aboveground productivity may have promoted organic matter accumulation. However, this plot did not exhibit similarly outlying values in other variables such as soil carbon and nitrogen concentrations, or bulk density, suggesting that local factors beyond successional age may have contributed to the exceptionally thick organic layer.

We retained this plot in our analyses, as it represents a real and ecologically meaningful condition within mature forests. Nonetheless, we acknowledge that this result should be interpreted with caution, given that when this data point is excluded, the relationship between AGB and SOH becomes non-significant despite remaining positive (P = 0.1088, r = 0.47, R^2 = 0.22, n = 14, CI = [0.0024, 0.015]). By contrast, the exclusion of this plot did not substantially affect the results of the other variables showed in Figure 3: aboveground productivity (P = 0.023, r = 0.62, R^2 = 0.39, CI = [0.019, 0.057]), fine root productivity (P = 0.768, r = 0.091, R^2 = 0.008, CI = [0.011, 0.100]), decomposition environment (P = 0.46, r = 0.22, R^2 = 0.049, CI = [0.042, 0.331]), and litter decomposability (P = 0.61, r = 0.156, R^2 = 0.024, CI = [0.043, 0.685]). This supports the conclusion that not all carbon inputs and outputs were driven by this outlier along the successional gradient.

Another key limitation of our study concerns the land-use heterogeneity among forest plots. Although the plots were selected to represent a gradient of successional stages, their selection was also influenced by logistical considerations and the permissions granted by private landowners. As a result, the plots vary in their land-use legacies and disturbance histories, including different degrees of past cattle grazing, fire exposure, and other human disturbances. This variability complicates the attribution of the observed patterns solely to successional processes. We therefore recommend caution in overinterpreting the effects of succession and acknowledge the potential influence of additional, confounding factors that may contribute to structural and soil variation across plots.

Finally, the unusually low bulk density values observed in some high-biomass plots may reflect the presence of volcanic ash in the soil matrix. Volcanic ash-derived soils are known to contain amorphous, non-crystalline minerals that strongly retain organic carbon, potentially affecting both carbon content and bulk density (Shoji et al., 1993; Torn et al., 1997). Although soil taxonomy data were not available for these plots, future research should assess mineralogical composition to better disentangle the influence of volcanic parent material from successional dynamics.

Conclusions

Our study reveals that aboveground processes and their inputs play an important role in the formation of the SOH, while decomposability and decomposition environment remain constant along the successional gradient in UATF. SOH was positively related to forest recovery, while both decomposition environment and litter decomposability were unrelated, suggesting different mechanisms behind organic matter accumulation and decomposition along succession. The increase in the SOH resulted in higher carbon and nitrogen concentration but showed a marginally significant inverse relationship with bulk density. Mature forests, which exhibit higher aboveground productivity and have a higher SOH should be conserved to contribute to carbon sequestration. However, secondary forests present a thinner SOH, but they have the potential to accumulate more carbon and nitrogen in the long-term if forest productivity recovers. In sum, although most of the carbon in UATF is stored in the soil, aboveground processes significantly influence this compartment, helping to sustain these stocks, which may contribute to climate change mitigation.

Acknowledgments

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Supplemental material

Figure S1. Reduced major axis regression plots showing the inverse relationship between bulk density (g/cm^3) and (a) Carbon in soil (%), and (b) and Nitrogen in soil (%) of Upper Andean tropical forests of Colombia. In the right corner of each plot the R^2 is presented. Mature forests are depicted in green colors, while secondary forests are represented in gray colors.

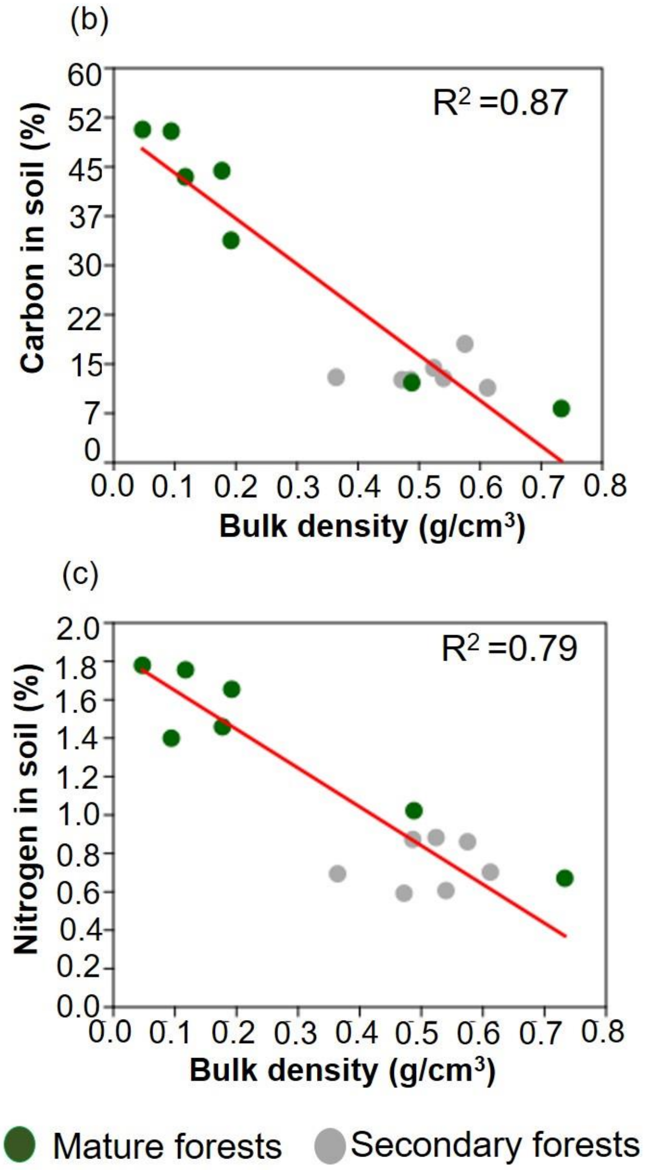

Figure S2. Pearson correlations between decomposition environment, litter decomposability and their drivers. Blanks represent no significant relationships (P > 0.05). Coefficients of the correlations are shown in the significant correlations.

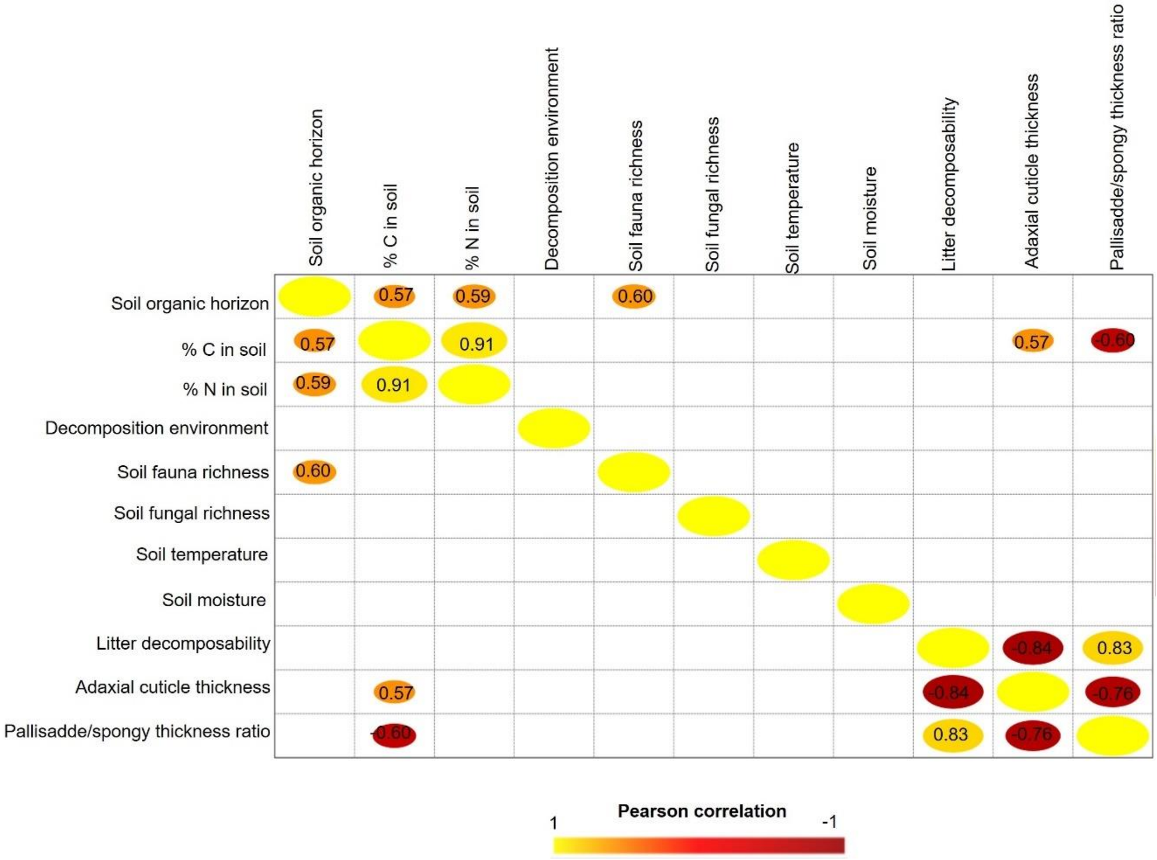

Figure S3. Pearson correlations between the drivers of decomposition environment and Above Ground Biomass (AGB). Blanks represent no significant relationships (P > 0.05). Coefficients of the correlations are shown in the significant correlations.

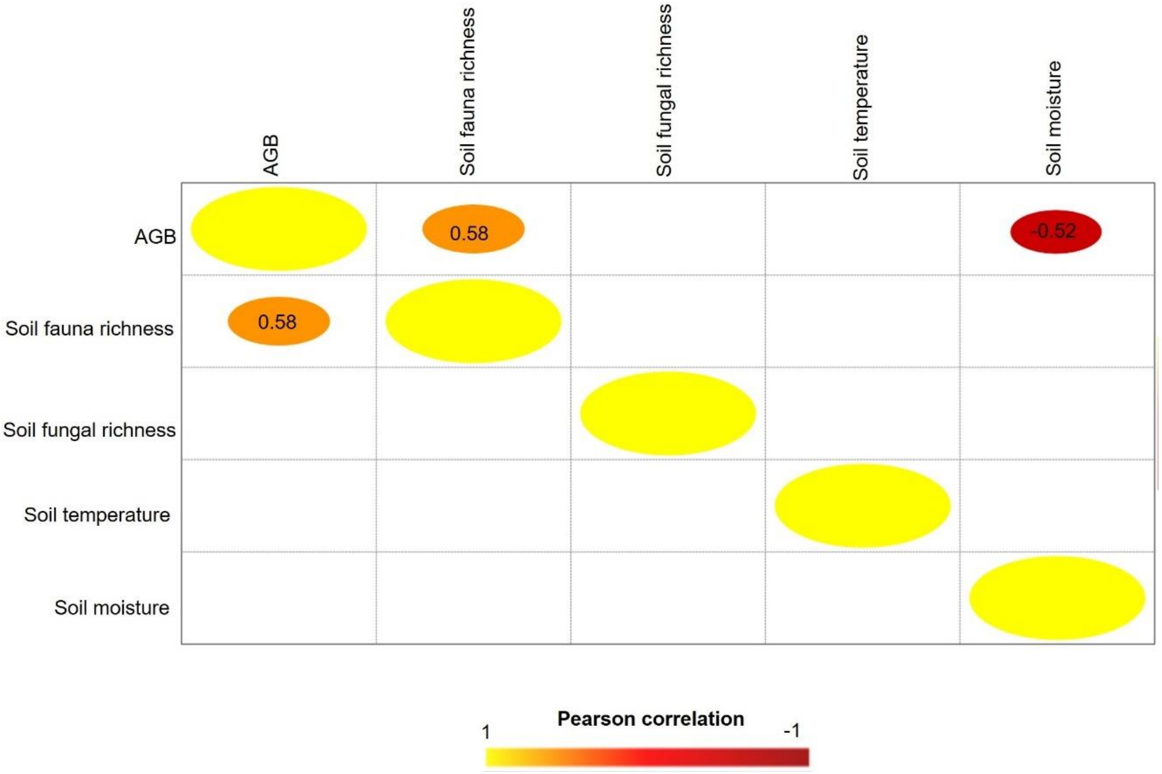

Table S1. Welch T-test for comparisons between mature and secondary forest for soil organic horizon, soil carbon content, soil nitrogen content, bulk density, aboveground productivity, fine root productivity, decomposition environment and litter decomposability. Significant p values ($P < 0.05$) are highlighted with “*”

Variable	**Welch T test**	**P value**	**Cohen's d ± SE**
Soil organic horizon (cm)	2.449	0.044*	1.309 ± 0.639
Soil carbon content (%)	3.140	0.019*	1.679 ± 0.698
Soil nitrogen content (%)	3.984	0.005*	2.130 ± 0.781
Bulk density (g/cm^3)	-2.466	0.042*	-1.318 ± 0.640
Aboveground productivity (Mg C ha^{-1} y^{-1})	2.758	0.021*	1.474 ± 0.664
Fine root productivity (Mg C ha-1 y^{-1})	1.578	0.141	0.843 ± 0.580
Decomposition environment (mass loss % y^{-1})	0.775	0.454	0.414 ± 0.546
Litter decomposability (mass loss % y^{-1})	1.076	0.306	0.575 ± 0.556

Chapter 7

General discussion and conclusions

General discussions and conclusions

Discussion and conclusion outline

The objective of this dissertation was to understand the biotic and abiotic drivers influencing leaf litter decomposition along a successional gradient in UATF. Additionally, this thesis examined how decomposition affects changes in soil organic matter throughout this gradient. Overall, I found that: (1) species identity and functional traits are the principal drivers of litter decomposition in UATF (Chapter 2); (2) leaf anatomical traits underlying the leaf economics spectrum are strongly associated with litter decomposability (Chapter 3); (3) soil fauna communities change significantly along the successional gradient but have a limited influence on litter decomposition (Chapter 4); (4) soil fungal communities did not change along the successional gradient, and the varying responses of fungal guilds to the decay rates of different litter species cancel out the overall effect on decomposition (Chapter 5); and (5) litter decomposition is not correlated with the soil organic layer thickness, while other factors related to forest productivity exert a stronger influence on the increase of soil organic matter accumulation (Chapter 6).

Patterns of litter decomposition in UATF

Nearly a century ago, Tenney & Waksman (1929) identified the primary factors controlling litter decomposition. Since then, climate and litter quality have been consistently highlighted as key drivers of this process, with substantial supporting evidence (e.g., Meentemeyer 1978; Melillo et al., 1989; Canessa et al., 2021). However, understanding the relative importance of these factors remains an active research topic, as the findings have been contradictory. Additionally, forest succession plays a role in modulating these drivers, as forest recovery shapes the environmental conditions in which litter decomposition occurs and determines the plant composition that affects litter quality. While components of the carbon cycle, such as carbon gain and accumulation (e.g., aboveground biomass), have been extensively studied along successional gradients, other aspects, like litter decomposition, have received less attention, particularly in tropical upland ecosystems (Castillo-Figueroa, 2021). This limits our understanding of how the carbon cycle shifts during forest recovery in UATF. Given the crucial role of Andean mountain forests as carbon sinks (Salinas et al., 2021; Duque et al., 2021; Vento et al., 2023) and their widespread habitat transformation that creates forest patches with different levels of recovery and disturbance (Etter et al., 2021; Hurtado-M et al., 2021), I aimed to assess how litter decomposition is influenced by functional traits and microclimatic conditions over time and along a successional gradient in UATF.

The findings of this chapter clearly demonstrate that functional traits are the primary drivers of litter decomposition in UATF at all stages of decay. Although soil microclimatic conditions did not significantly affect decomposition, this outcome could be attributed to the narrow climatic gradient in our study and/or the occurrence of La Niña event during the experiment that altered rainfall seasonality. Nevertheless, the strong influence of litter quality suggests that shifts in species composition, driven by anthropogenic changes, could profoundly impact carbon and nutrient cycles in these ecosystems characterized by substantial soil carbon storage and limited resources like nitrogen.

The results also supported the "after-life effect" of leaf traits and revealed significant changes in traits such as SLA, LNC, and LCC. Specifically, green leaves had lower SLA compared to senescent leaves, while LNC and LCC were higher in green leaves than in senescent ones. These changes reduce the quality of senescent leaves for decomposers, thereby slowing down decay rates from the outset of the decomposition process. Traditionally, low decomposition rates in mountain regions have been linked to factors such as low temperatures (Salinas et al., 2011; Ostertag et al., 2022), acidic soils (Wilcke et al., 2002), and nutrient-poor conditions (Soethe et al., 2008). Nevertheless, these findings indicate that shifts in leaf traits during senescence may be another key factor in slowing decomposition in UATF, as mechanisms like nitrogen resorption can reduce litter quality from the onset of the process.

In the context of global environmental change, where mountain regions are particularly vulnerable (Bradley et al., 2004; Thakur et al., 2021), this results suggest that shifts in species composition in UATF could potentially increase greenhouse gas emissions from litter if more acquisitive species become dominant, thereby altering soil carbon accumulation in one of the planet's most vital carbon sinks.

Leaf anatomical basis of decomposition

Litter decomposition is possibly one of the ecological processes in which functional traits have been most extensively studied (Garnier et al., 2016). The relationships between foliar traits such as SLA, LDMC, LNC, LCC, and litter decomposability (i.e., the potential decomposition based on its litter quality) have been well documented across different ecosystems (e.g., Bakker et al., 2011; Makkonen et al., 2012; Poca et al., 2014; Esquivel et al. 2020). However, a portion of the variance in litter decomposability remains unexplained by these traditional traits (Santiago et al., 2007). Therefore, investigating “hard” traits that underlie the leaf economics spectrum, including structural tissues and metabolic ('liquid phase') processes, is essential to better predict the underlying economics trade-offs related to decomposability (Shipley et al., 2006; Onoda et al., 2017). This need formed the basis of this chapter, which focuses on leaf anatomical traits and their connection to litter decomposability. This work represents one of the few studies globally that attempt to integrate leaf anatomy into the study of litter decomposability.

The findings of this chapter showed that traits such as cuticles, vascular bundles, palisade and spongy mesophylls thickness play a pivotal role in predicting decomposability and may significantly influence carbon turnover in ecosystems. Additionally, there was a strong correlation between leaf anatomical traits and decay rates at the community level. Specifically, community weighted means with thicker protective structures, such as cuticles, exhibited lower decay rates. While Onoda et al. (2012) previously suggested that cuticles might be linked to ecosystems carbon processes, this research provides experimental confirmation of this hypothesis 13 years later.

Conversely, a higher proportion of palisade tissues relative to spongy tissues, along with the prevalence of cylindrical cells in palisade mesophylls and circular cells in spongy mesophylls, were associated with higher decay rates. The trade-off between palisade and spongy tissues is intriguing and has been observed in other regions (Ni et al., 2022), although the underlying mechanism remains uncertain. However, this ratio should be related to important processes such as photosynthesis, which have a clear ”after-life effect” on decomposition. This study further emphasizes that cell shape plays a role in decomposition, offering new insights into how cell architecture influences litter decay at a fine scale. These findings represent a step toward future research focused on pinpointing where and how decomposition occurs within the leaf.

Notably, as succession progresses, decay rates did not show significant shifts, as discussed in Chapter 3. This can be explained by a balance between the higher functional evenness within a narrow functional space in secondary forests and lower functional evenness within a broader functional space in mature forests in attributes related to decomposability, as demonstrated by recent studies (van der Sande et al., 2024; Elsy et al., 2024). This suggests that in UATF, the dynamics of community structure driving the functional diversity of leaf anatomical traits related to decomposability vary between secondary and mature forests, influencing to the weak relationship between succession and decay rates.

Soil fauna biodiversity and its role on litter decomposition in UATF

In recent decades, research on the role of soil fauna in litter decomposition has grown exponentially (Berg & McClaugherty, 2020; Sagi & Hawlena, 2024; Zeng et al., 2024). However, most studies in the tropics comes from lowland regions (Peguero et al., 2019; Li et al., 2022), with limited studies examining the influence of soil fauna on decomposition in UATF. In fact, there are few surveys on soil fauna in these ecosystems, and little is known about its taxonomic and functional structure, as well as the main drivers influencing it across successional gradients. This gap in knowledge motivated me to investigate the mechanisms driving soil fauna changes along the gradient and to assess its role in litter decomposition, especially considering that, as discussed in Chapter 2 and 3, functional traits account for more than half of the variation in decomposition.

This chapter highlights the biodiversity of often-overlooked soil fauna organisms in UATF of Colombia. Remarkable alpha diversity was observed in the soil fauna, with 351 morphospecies and 154 families identified. Importantly, new genus records for the country were documented (Castillo-Avila & Castillo-Figueroa, 2024; Castillo-Avila, in prep.) and undescribed species of soil organisms were identified (Castillo-Avila et al., in prep.). These findings confirm that mountain forests are extraordinary reservoirs of biodiversity, as previously suggested (Rahbek et al., 2019; Myster, 2021). Additionally, striking beta diversity was observed, as soil fauna communities displayed significant biodiversity turnover across relatively short spatial distances in Andean forest sites, mirroring patterns seen in plant communities (Hurtado-M et al., 2021). This emphasizes the distinct species composition at each site, underscoring the irreplaceability and vulnerability of Andean mountain forests around Bogotá. These forests may serve as refuges for specialized and endemic soil fauna species (e.g., Castillo-Figueroa et al., 2024), whose loss could negatively impact ecosystem functioning. Therefore, UATF should be prioritized in conservation, restoration, and sustainable management efforts.

An increase in soil fauna richness and abundance with succession was observed. The primary driver of soil fauna richness in UATF was amount of energy (i.e., net primary production), supporting the energy hypothesis (Calderón-Sanou et al., 2022). However, other factors associated with the physiological tolerance hypothesis and habitat heterogeneity hypothesis also appear to play a role, albeit to a lesser extent (Mathieu et al., 2022). Specifically, higher soil calcium and higher litter functional richness create favorable conditions and enhance habitat heterogeneity, supporting more coexisting species. In contrast, soil fauna abundance was related to more stable thermal conditions without extreme cold temperatures. This suggests that dramatic temperature changes due to global warming may impact soil fauna abundance, although the extent of this effect will depend on the thermal sensitivity of each soil fauna group. Experimental studies that control for temperature can enhance the understanding of the vulnerability of different soil organism groups to climate change. Overall, this research underscores the importance of examining forest recovery across different soil fauna groups to better understand successional patterns in UATF, especially considering that most studies have primarily focused on plant communities.

Lastly, the findings of this chapter reveal that soil fauna did not significantly influence litter decomposition in UATF. While recent meta-analyses have highlighted the increasing importance of soil fauna in decomposition processes (Sagi & Hawlena, 2024; Zeng et al., 2024), this effect is highly context-dependent and should not be generalized across all ecosystems, as it appear to be less significant in UATF than in tropical lowland forests. The primary explanation for this pattern is the limited presence of soil macrofauna and the dominance of small-sized fauna in UATF, which contribute minimally to litter consumption. Future research should explore the indirect effects of soil fauna on decomposition in UATF, through its interaction with fungal and bacterial decomposers in soil food webs.

Soil fungal communities and the varying guild responses on decomposition

Soil fungi are key microorganisms in litter decomposition due to their enzymatic ability to break down recalcitrant materials (Tunlid et al., 2022; Ullah et al., 2023; Leifheit et al., 2024). Their rapid turnover and sensitivity to land-use changes also make them valuable indicators of forest successional stages (Gao et al., 2015; Li et al., 2020; He et al., 2022). However, fungal contributions to litter decomposition across tropical successional gradients, particularly in upper mountain regions, remain poorly understood (Looby & Martin, 2020). This knowledge gap in UATF soil fungal communities led me to further investigate biotic factors influencing decomposition, complementing the findings of soil fauna communities in Chapter 4.

This chapter uncovered remarkable fungal biodiversity, comprising 4,982 OTUs, 15 phyla, 44 classes, 225 families, and 516 genera. Unlike soil fauna, fungal communities did not change along the successional gradient, yet significant differences were observed between forest sites. The distinct fungal composition pattern aligns with previous research on plant and animal communities (Anthelme et al., 2014; Hurtado-M et al., 2021), reinforcing the role of UATF as vital biodiversity reservoirs. Factors such as microenvironmental heterogeneity, stochasticity, and different land-use practices likely contributed to these site-specific differences. The primary drivers of fungal diversity—minimum surface temperature, litter functional richness, plant diversity, and soil calcium—were similar to those affecting soil fauna richness, suggesting common mechanisms shaping soil biota diversity in UATF.

Fungal diversity did not significantly influence the decomposition environment (i.e., standard decomposition) due to specific relationships between fungal guilds and the decay rates of different litter species. The variation in litter decomposition observed across the 15 plant species analyzed in the experiment, as shown in Chapter 2, supports the coexistence of diverse fungal taxa within the forest ecosystem, consistent with previous research (Li et al., 2020). This highlights the high substrate specificity of soil fungi, where the balance of positive and negative interactions may cancel out their overall effect on the decomposition environment.

Notably, a negative effect of fungal pathogens on decomposition was found, likely caused by plant defense responses that increase secondary metabolite production, slowing down decomposition. Recent evidence indicates that pathogens indirectly affect decomposition by triggering metabolic changes that alter litter quality (Pusztahelyi et al., 2015; Chomel et al., 2016; Guo et al., 2025), which aligns with the results of this chapter. Overall, these findings suggest that decomposition in UATF is governed by more complex interactions than those described by the traditional decomposition triangle based on litter quality, climate, and decomposer organisms (Bradford et al., 2016). Although various saprotrophic groups were identified, the harsh environmental conditions of UATF— such as low temperatures and high soil moisture (Myster, 2021)—likely limited the activity of ligninolytic enzymes necessary for litter degradation. While enzymatic activity was not measured, this study marks an initial step toward understanding the role of soil fungal communities in litter decomposition in UATF. Future studies employing omics approaches are encouraged to further investigate the fungal mechanisms involved.

Litter decomposition is not related to the thickness of the soil organic horizon in UATF

UATF play a critical role in mitigating climate change by acting as global carbon sinks (Yepes et al., 2015, 2016; Duque et al., 2021). However, most research has focused on the aboveground compartment (Castillo-Figueroa, 2021), while belowground dynamics remain largely unexplored (Malhi et al., 2011). This gap is particularly important given that a substantial portion of carbon is stored in soils and tied to the formation of a thick organic horizon (Wilcke et al., 2008; Moser et al., 2011), which is especially vulnerable to land-use changes (Satdichanh et al., 2019, 2023). Understanding the drivers of soil organic matter dynamics is essential for predicting future shifts in global carbon cycling (Trumbore & Czimczik, 2008; Filser et al., 2016; Jackson et al., 2017). In this chapter, key results from previous chapters were synthesized to build a comprehensive framework that examines critical factors—such as forest productivity, microclimatic conditions, soil communities, and functional traits—and their relationship with soil organic matter in UATF.

The main findings of this research reveal that aboveground processes and all the inputs from this compartment are significantly related to the soil organic horizon, while decay rates are part of a separate process not directly linked to the formation of soil organic matter. The fact that soil organic horizon was positively related to aboveground biomass, while both decomposition and decomposability were unrelated, suggest that the gains by litter inputs determine the thickness in the soil organic horizon given that the carbon losses by decomposition do not change along the gradient. This contrasts with general ideas about carbon storage in tropical forests where it has been established that a higher carbon accumulation in mature forests is due to higher inputs but lower decomposition (Souza et al., 2019; Aryal et al., 2022). This also suggests that the mechanisms behind organic matter accumulation differ from those driving decomposition along the successional gradient in UATF.

Soil carbon and nitrogen concentrations, which are positively associated with the soil organic horizon, increase with forest succession but decrease as bulk density rises. Consequently, old-growth forests—characterized by higher aboveground productivity, greater soil carbon concentration, and thicker horizons with lower bulk density—should be prioritized for conservation to enhance carbon sequestration and nitrogen accumulation. However, secondary forests also have the capacity to store carbon in soils over the long-term (Chazdon et al., 2016), as their potential of biomass recovery can surpass those of old-growth forests (Chazdon, 2014; Hubau et al., 2020; Poorter et al., 2021b). Therefore, enhancing connectivity between early successional and old-growth forests may be important for accelerating functional recovery and long-term carbon gain in the former. In this context, both secondary and old-growth forests play a vital role in preserving key ecological functions related to carbon and nutrient cycling in the upland Andes, particularly considering current and future environmental change.

Finally, the framework developed in this chapter could enhance our understanding of carbon dynamics in UATF. Most existing conceptual models of the carbon cycle often exclude litter decay and are often focused on net primary productivity (Ise et al., 2010; Gottschalk et al., 2012). By incorporating several measured variables from both above- and belowground, including biotic and abiotic factors related to carbon inputs and outputs, a more comprehensive model is proposed as a reference for estimating carbon dynamics along successional gradients in tropical mountain ecosystems. Further research should include additional sites and plots to validate and refine this conceptual model.

Products derived from the project

Articles published in peer reviewed journals

- **Castillo-Figueroa, D.** (2021). Carbon cycle in tropical upland ecosystems: a global review. *Web Ecology*, 21, 109–136. https://doi.org/10.5194/we-21-109-2021
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- **Castillo-Figueroa, D.,** & Posada, J.M. (2025). The role of litterfall in understanding the ecological integrity of endangered upper Andean successional forests. In: Conservation of Andean forests. Springer Nature Switzerland, pp 59–76. https://doi.org/10. 1007/978-3- 031- 80805-0_3

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- Oral presentation at the *VII Latin American Congress of Arachnology* "Hábitat de dos especies de escorpiones látigo de cola corta (Arachnida: Schizomida) en los Andes tropicales del norte de Sudamérica". Bogotá, Colombia, Universidad del Rosario, June 16-21, 2024.

- Poster at the *III International Congress of Environmental Research and Innovation CNIIA 2022, 2nd International Forum on Climate Change and 4th National Meeting of Environmental Authorities* "Bosques y fauna del suelo: una relación necesaria para entender el cambio climático en la Sabana de Bogotá" Bogotá, Colombia, November 9 -11, 2022.

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