DESCOMPOSICIÓN Y RESPIRACIÓN EN SUELOS DE BOSQUES ALTOANDINOS EN DIFERENTES ESTADOS SUCESIONALES

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DECOMPOSITION AND RESPIRATION IN HIGH-ANDEAN FOREST SOILS AT DIFFERENT SUCCESSIONAL STAGES

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Declaración de responsabilidad

Yo, Catalina Franco Londoño, declaro que la presente tesis titulada "Explorando la respiración y descomposición en sucesiones de bosque altoandino: un enfoque de ecuaciones estructurales" es producto de mi trabajo original y es el resultado de mi esfuerzo personal. La investigación ha sido llevada a cabo bajo la supervisión de Beatriz Salgado Negret y Alejandro Salazar Villegas, y cumple con las normas y regulaciones establecidas por la Universidad Nacional de Colombia. Declaro que no he presentado esta tesis en ninguna otra institución para obtener un título académico. También declaro que he cumplido con las normas éticas establecidas en la investigación, y que he respetado los derechos de autor y la propiedad intelectual de terceros. Asumo toda la responsabilidad por cualquier error u omisión en esta tesis, y estoy dispuesto a hacer las correcciones necesarias en caso de ser requerido.

Firma: Catalina Fl

Fecha: 30 de Enero de 2023

Parte I
Agradecimientos

Agradezco de manera especial a mi familia, mis padres, mi hermana, mis abuelitos y mi novio por apoyarme incondicionalmente a lo largo de este camino, por estar a mi lado y motivandome siempre a hacer las cosas bien. Su presencia y motivación fueron fundamentales para superar los desafíos y alcanzar este resultado. Sus acciones, incluso aquellas que no se pueden medir, fueron de gran importancia para mi crecimiento tanto personal como académico. Les estoy eternamente agradecida.

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Parte II

Prefacio

La naturaleza es un enigma lleno de complejidades e interacciones que a menudo nos dejan maravillados. La investigación que presento en esta tesis tiene como objetivo tratar de desentrañar algunas de esas complejidades, enfocándose en los bosques y cómo los procesos y funciones del ecosistema dependen y coexisten en un equilibrio gracias a las comunidades de árboles y su estructura y función. Mi enfoque incluye tanto la estructura del bosque como hábitat, espacio y sistema, como también la ecología funcional, como mecanismo que integra diversos conceptos fisiológicos, mecánicos y ecológicos. Me interesan especialmente los misterios de la sucesión, una constante dualidad entre la entropía y la organización de la naturaleza. Espero a futuro seguir navegando en la ecología de los bosques y de las sucesiones.

Debido a que el suelo es el mayor reservorio de carbono de los ecosistemas forestales, la descomposición de hojarasca y la respiración, como flujos centrales de ingreso y emisión de carbono en los suelos de los bosques, resultan ser procesos fundamentales en el ciclo del carbono y como indicadores de un balance neto de su almacenamiento en los suelos, por lo que deben ser cuidadosamente estudiados para predecir y proteger las capacidades de los ecosistemas en este servicio. Actualmente, una de las grandes preguntas radica en comprender cómo varían estos procesos en respuesta a la sucesión, sobretodo porque los bosques secundarios dominan los ecosistemas actuales, y cuál es el estado y los factores ecológicos que determinan la dirección de este balance en los bosques altoandinos, ya que estudios previos se han enfocado en la biomasa aérea, dejando de lado la importancia de los suelos.

Estudiar estos procesos en los bosques Altoandinos de los alrededores de Bogotá, es urgente debido al gran impacto que ha producido la población de la ciudad y alrededores sobre este ecosistema, haciéndose necesario conocer sus capacidades para mantener estos procesos y almacenar carbono a largo plazo, información que permitirá entender el impacto de las sucesión en estos procesos y generar modelos predictivos que puedan ayudar a la toma de decisiones asociadas a la conservación de estos bosques remanentes. Todo esto, en favor de mitigar los efectos de la transformación del paisaje sobre el cambio climático. Además, este estudio se enmarca en un sistema de monitoreo a largo plazo de parcelas del Proyecto Rastrojos del Instituto de Recursos Biológicos Alexander von Humboldt, lo que abre la posibilidad de realizar futuros seguimientos y complementar con estudios adicionales que se realicen en el mismo sistema. Por todo lo anterior, se plantea la siguiente pregunta de investigación:

¿Cómo varían la descomposición y respiración en el suelo de dos estados sucesionales de bosques Altoandinos, y cuáles factores ecológicos explican el efecto de la sucesión sobre estos flujos de carbono?

Este estudio contribuye al campo de la ecología al aportar nuevos conocimientos sobre cómo la sucesión ecológica afecta los procesos de descomposición y respiración en el suelo en bosques altoandinos. Se investigaron los factores ecológicos que determinan las tasas de respiración y descomposición en el suelo, y se caracterizaron los factores estructurales y funcionales de la vegetación y las condiciones microclimáticas y edáficas en dos estados sucesionales de bosque altoandino. Los resultados de este estudio proporcionan una comprensión más profunda de cómo los procesos del suelo y la estructura del bosque están interrelacionados y cómo estos procesos están influenciados por la sucesión ecológica. Además, este estudio también tiene implicaciones para la conservación y el manejo de los bosques altoandinos, ya que proporciona información valiosa sobre cómo las diferentes etapas sucesionales afectan los servicios ecosistémicos proporcionados por los bosques. En general, este estudio es importante porque ayuda a entender cómo funciona un ecosistema y cómo estas funciones son afectadas por cambios en la estructura del bosque y por la sucesión ecológica.

Además de los objetivos científicos de esta investigación, también me propuse abordar algunos desafíos personales. En primer lugar, quería explorar y enfocarme en entender más a fondo la complejidad y el funcionamiento de los ecosistemas, y para ello decidí utilizar recursos estadísticos y matemáticos novedosos como el análisis de modelos de ecuaciones estructurales, lo que me permitió tratar a los ecosistemas como un todo complejo y no como partes aisladas. En relación con esto, también me propuse intentar sacar provecho de los recursos de computación actuales y afianzar mis destrezas de programación, así que decidí manejar todos los datos y análisis en R y escribir todo el documento en LaTeX. También quería presentar esta tesis en forma de artículo científico, para aprender a escribir mejor este tipo de documentos que son tan relevantes para la comunidad académica y que espero seguir produciendo a lo largo de mi carrera.

Con este trabajo tuve una gran cantidad de increíbles oportunidades. Tuve la suerte de formar parte del proyecto Rastrojos, una iniciativa maravillosa que buscaba investigar y destacar la belleza e importancia de los pequeños fragmentos de bosque que rodean la imponente metrópoli de Bogotá. El proyecto me brindó un gran apoyo y las bases para desarrollar la idea de esta investigación. También tuve la oportunidad de ser una de las primeras (hasta donde sabemos la primera) en utilizar el Tea Bag Index en Colombia, un innovador protocolo para medir la descomposición de forma estandarizada posibilitando su comparación alrededor de todo el mundo. Debido a esto, este proyecto de tesis se conecta con la red global, contribuyendo al haber sometido los primeros datos de Colombia, y además se beneficia de esta metodología usada y validada en todos los continentes. Además, presenté un póster en el Congreso de la ATBC en Cartagena, donde pude compartir y aprender sobre los resultados preliminares de mi proyecto.

A pesar de los desafíos que enfrenté, como limitaciones económicas y problemas logísticos (recordando especialmente que todo esto comenzó al mismo tiempo que las cuarentenas y restricciones por la pandemia), siempre conté con el apoyo de mi familia y de las personas que aportaron a la realización del proyecto. Gracias a ellos, logré superar todos los obstáculos y llegar a este resultado final. Espero que mi investigación contribuya a la comunidad científica y a aquellos estudiantes interesados en la conservación de los bosques y en el estudio de la sucesión y la dinámica del carbono. Este proyecto es solo un pequeño paso hacia el conocimiento y el cuidado de los ecosistemas que permanecen en este planeta.

Parte III

Artículo: Impacto de la sucesión en el suelo: la interacción de la estructura, la composición funcional y el microclima del bosque en la respiración y descomposición del suelo

Resumen

Se evaluó la respiración y la descomposición en los suelos comparando entre dos etapas sucesionales en bosques altoandinos. Estos procesos son una parte importante del balance de carbono global ya que están directamente ligados a la emisión y secuestro de carbono en el suelo. Sin embargo, no está claro cómo estos procesos pueden verse afectados por la etapa sucesional debido a las propiedades de la vegetación, como la estructura del bosque y la composición funcional. Medimos la respiración con un analizador de gases infrarrojo (IRGA, por sus siglas en inglés) y utilizamos el índice de bolsitas de té (TBI, por sus siglas en inglés) para medir la descomposición potencial de la hojarasca y el factor de estabilización. También medimos la estructura del bosque y la composición funcional a nivel de comunidad, así como la humedad, la temperatura y el pH del suelo. Luego, utilizamos un enfoque de modelo de ecuaciones estructurales para evaluar la cascada de efectos de la sucesión a los procesos del suelo, pasando a través de los atributos del bosque y el microclima. El modelo ajustado muestra que, mientras que la combinación de interacciones mutuamente compensatorias dio como resultado efectos totales neutrales sobre las tasas de respiración y descomposición del suelo, la sucesión juega un papel importante en la determinación de esto procesos del suelo. Este estudio brinda nuevas perspectivas sobre los mecanismos que impulsan el secuestro de carbono y la biodiversidad en los bosques de los Andes altos y destaca la importancia de considerar la sucesión en los esfuerzos de conservación y manejo de estos ecosistemas.

Palabras clave: Respiración del suelo, descomposición de hojarasca, bosques secundarios, secuestro de carbono, rasgos funcionales, índice de bolsas de té, modelos de ecuaciones estructurales, bosques altoandinos.

Succession's Impact on Soil: The Interplay of Forest Structure, Functional Composition, and Microclimate on Soil Respiration and Decomposition

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Abstract

This study investigates the effects of succession on soil respiration and litter decomposition in high Andean forests. These processes are an important part of the global carbon budget as they are responsible for the emission and sequestration of carbon in the soil and can be affected by the successional stage due to the properties of vegetation, such as forest structure and functional composition. We measured actual soil respiration using an infrared gas analyzer and both potential litter decomposition and stabilization factor using the tea bag index. We characterized the stand structure and community-level functional composition. Microclimate variables, including soil water content, temperature, and pH, were also measured. A structural equation model approach was used to evaluate the cascade of effects from succession to soil processes, passing through forest attributes and microclimate. Results indicate that even though we did not find differences in the soil processes between the successional stages, succession plays an important role in determining soil process rates, but that the combination of mutually counterbalancing interactions results in neutral total effects. Our study provides insights into the mechanisms driving carbon sequestration and biodiversity in high Andean forests and highlights the importance of considering succession in conservation and management efforts in these ecosystems.

Keywords: Soil respiration, litter decomposition, secondary forests, carbon sequestration, functional traits, Tea Bag Index, structural equation models, high-andean forests.

Introduction

Soils are the largest long-term carbon reservoir in terrestrial ecosystems (Lal, 2004; Six et al., 2006; Pan et al., 2011; Sedjo and Sohngen, 2012). Soil carbon input and output fluxes are primarily controlled by soil processes such as litter decomposition and soil respiration, hence they are considered essential components of the global carbon budget (Luyssaert et al., 2007; Chapin et al., 2011; Sedjo and Sohngen, 2012; Le Quéré et al., 2016). However, the soil processes have suffered severe alterations due to the extensive human disturbances over tropical forests such as those caused by deforestation and land use change (Amoakwah et al., 2022; Ahmed et al., 2022). Reduction of forested lands due to economic activities increases the carbon flux from soils to the atmosphere up to 1.6 ± 0.8 Pg C/year (Lal, 2004), leading to soil carbon depletion and contributing to the increasing atmosphere CO_2 concentration (Lal, 2004; Amoakwah et al., 2022; Ahmed et al., 2022). Sometimes, when land use activities are abandoned, forests can naturally regrow, leading to a gradual replacement of mature tropical forests with an increasing coverage of regrown or secondary successional forests in the tropics (Chokkalingam and De Jong, 2001; Wright, 2010). Amid the fatal consequences of the mature forest loss scenario, the secondary forests opportunely appear to be able to recover the soil carbon storage capacity as compared to mature or undisturbed forests (Deng et al., 2013; Aryal et al., 2014) and decrease carbon efflux rates as compared to pasture or agricultural fields (Schedlbauer and Kavanagh, 2008; Bakker et al., 2011), but this topic remains under explored specially in tropical ecosystems. Thus, understanding how soil processes vary in secondary forests may be critical for predicting the recovery of the functioning of tropical ecosystems as future carbon refuges.

Following a disturbance event, a forest community typically experiences dynamic changes in its attributes as it undergoes the ecological succession process, which often involves tree growth, understory development, and species replacement, among the complex occurring biotic and abiotic interactions (Connell and Slatyer, 1977; McCook, 1994; Guariguata and Ostertag, 2001). Changes in forest attributes such as structure and functional composition across a successional gradient, can affect soil processes because they interact with the soil through nutrient, water, and energy flow or interception (Hardwick et al., 2015; Metzger et al., 2017), conditioning the environment through shading and providing substrate input to the soil (Raich and Tufekcioglu, 2000; Cornwell et al., 2008; Bakker et al., 2011). Some studies have highlighted the effect of changing forest attributes over these soil processes under fragmentation, invasion and forest management scenarios ((Søe and Buchmann, 2005; Hastwell and Morris, 2013; Mayer et al., 2017; Flores-Rentería et al., 2018; de Godoy Fernandes et al., 2021), but little efforts have been made on successional scenarios. Therefore, it is crucial to investigate the changes in forest attributes as the succession progresses, leading to altered soil biotic and abiotic factors and processes.

Respiration and decomposition rates have been found to both increase and decrease along succession, mediated, among others, by microclimatic conditions (Huang et al., 2011, 2016; Xiao et al., 2014; Lohbeck et al., 2015; Seidelmann et al., 2016; Rodtassana et al., 2021). These mixed results can be explained through the interaction of soil microclimatic changes along the succession which can be altered by the forest structure. The increase in vegetation biomass and canopy coverage as the forest stands grow in height and diameter and more complex canopy stratification (Guariguata and Ostertag, 2001; Lebrija-Trejos et al., 2010). Greater forest volume and canopy coverage reduces the radiation reaching the forest ground, decreasing soil temperature and moisture evaporation (Stoy et al., 2014; Kovács et al., 2017). However, higher temperatures in the soil can increase soil respiration and decomposition (Mayer et al., 2017; Salazar-Villegas et al., 2016; Gromova et al., 2020), as well as higher moisture, as they enhance microbial activity (Suseela et al., 2012; Xiao et al., 2014; Salazar-Villegas et al., 2016; Chen et al., 2018; Trivedi et al., 2018). This can lead to conflicting results in decomposition and respiration rates, as increased water availability in later-successional stages can cause decomposition to increase, but lower soil temperature can slow down microbial activity and cause decomposition to decrease, which points to the importance of additional investigation.

The species' replacement that occurs through succession is often explained in terms of species' adaptations to changes in resource availability and community interactions (Guariguata and Ostertag, 2001; Lebrija-Trejos et al., 2010; Arroyo-Rodríguez et al., 2017). During early-successional stages, when resources such as light are abundant, fast-growth species with efficient resource acquisition strategies tend to dominate and colonize these successional stages (Connell and Slatyer, 1977; Guariguata and Ostertag, 2001). These species are characterized by functional traits such as lower values of specific leaf area and higher nutrient concentrations in their leaves (Salgado-Negret et al., 2016). As the succession progresses, slow-growing, conservative species with high investment in dense and expensive tissues thrive in a longer-term and in a more light-limited competitive environment, typical from late-successional stages (Guariguata and Ostertag, 2001; Chazdon et al., 2007; Lohbeck et al., 2014; Huang et al., 2016). The shift in functional traits in the community level affects soil processes in various ways. First, it affects the quality of biomass input to soil through litter production, which serves as substrate for decomposition (Cornwell et al., 2008; De Deyn et al., 2008; Bakker et al., 2011; Jewell et al., 2017). Additionally, it can alter the soil's chemical properties, promoting or hindering microbial establishment and activity (De Deyn et al., 2008; Fang et al., 2015; Jewell et al., 2017). Studies in successional forests have found that litter decomposition rates decline through succession, as nutrient-rich soft leaves (acquisitive traits), primarily abundant in early successional stages, decompose more efficiently and faster (Quested et al., 2007; Eichenberg et al., 2013; Lohbeck et al., 2015). Also, this litter quality in early-successional stages improves soil nutrient availability and increases potential decomposition rates (Wardle et al., 2009; Fang et al., 2015).

Decomposition of litter and soil organic matter release CO_2 by respiration of soil decomposers, while also storing some in the soil as microbial biomass, soil organic matter, or recalcitrant material with longer decomposition rates (Berg and Meentemeyer, 2002; Sedjo and Sohngen, 2012). In this study, we explore how succession, forest structure and composition, and soil microclimatic conditions, influence soil processes related to carbon emission and storage. We focus on the carbon flux from the soil to the atmosphere through soil respiration, which also indicates the actual decomposition activity of the soil. Additionally, we assess the potential litter decomposition rate of the forest soil, and the soil's ability to turn litter into recalcitrant material, by using a standardized litter-bag decomposition protocol. This method measures the potential decomposition, independent of the chemical properties of the actual forest litter, as it utilizes a standardized substrate rather than actual forest litter. The forest attributes and soil conditions that favor microbial activity are expected to enhance both potential and actual decomposition processes, leading to a decrease in the stabilization factor, as the increased decomposition rate may result in less accumulation of recalcitrant organic matter. We hypothesized that changes in forest structure and functional composition between two successional stages will cause differences in soil decomposition processes and carbon sequestration through their effect on soil microclimatic and soil properties that determine decomposition activity. We predicted that soil respiration and potential decomposition rate will be higher in early-successional forests than in late-successional forests, due to greater radiation reaching the forest floor and higher soil temperature, increasing decomposition activity. We also expect that the stabilization factor will be higher in late-successional forests, because they have higher concentrations of conservative traits, which can lead to a slower decomposition rate and a higher stabilization factor.

High-Andean forests, are globally important carbon sinks and future carbon refuges (Duque et al., 2021), but they are also among the most fragmented ecosystems in the world (Armenteras et al., 2003). This is due to their high human population density and the presence of economic activities, which have led to extensive natural vegetation transformation in the region (Etter R. and Van Wyngaarden, 2000; Armenteras et al., 2011). The city of Bogotá, in particular, has a rich history of land use change (Anselm et al., 2018), and as a result, these forests are emerging as a potential repository for tropical biodiversity and ecosystem functions (Bongers et al., 2015; Arroyo-Rodríguez et al., 2017; Hurtado-M et al., 2022).

Methods

Study sites

This study was located in various hills surrounding the metropolitan area of Bogotá D.C in the southern region of the Bogota Savanna in Cundinamarca, Colombia. This is a high plateau valley at approximately 2600 m.a.s.l., and it is part of the eastern mountain range of the Colombian Andes, having a mean annual temperature of 14^oC and annual precipitation range from 600 to 12000 mm, with two rainy seasons from April to June and from September to November (Mendoza S. and Etter R., 2002).

We selected three study sites distributed in the Eastern and Western slopes of the mountain ranges that surrounds the high plateau valley: Reserva Encenillo, Guasca (Gu), Bosques de Canoas, Soacha (So) y El Silencio, San Francisco (Sf) (Figure 1). Each site exhibits different climatic and edaphic conditions (Table B1, see more details of the study area in Acuña (2013); Muñoz et al. (2017); Hurtado-M et al. (2020)). Each study site has six 20m x 20m plots, three of them located in early-successional forests, 10 ∼ 30 years and three in late-successional forests, ∼ +60 years, for a total of 18 permanent plots (Table B1 in Appendix A). Successional stages were classified based on the estimated minimal age provided by the land owners, and supported by physiognomy and structural data (see more in Hurtado-M et al. (2020)).

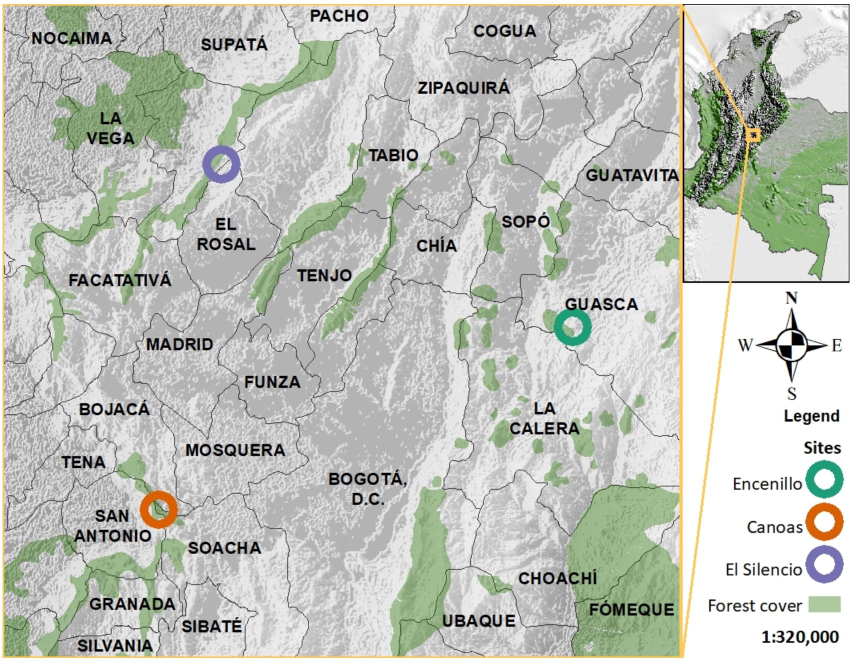

Figure 1. Map of the location of the study sites in the high-plateu valley of the city of Bogotá, Colombia Reserva Encenillo, Guasca (Gu, green), Bosques de Canoas, Soacha (So, orange) y El Silencio, San Francisco (Sf, purple)

Forest structure and functional composition

We estimated plot-level total basal area (BA) using the tree height and diameter at breast height (DBH) from the stand census performed in adult trees (DBH>2.5cm) in the plots between 2017 and 2021. We used cumulative basal area inflection height (EH) (Nakai et al., 2010) to measure the canopy height. It is the height at which the basal area of the trees in a stand reaches its maximum value, after which the basal area does not increase significantly with increasing height (Nakai et al., 2010). It marks the point at which the canopy is considered closed, and it is a measure of vertical structure and canopy closure in a forest stand. We calculated it by adjusting Richard's generalized logistic function with the R base package. To describe the canopy cover structure, we obtained the leaf area index (LAI), the cover fraction ($FCOVER$) and the gap fraction measured at 57^o ($P57$) by capturing the forest canopy with hemispherical photographs using the Redmi7A phone camera and a fisheye lens 180^o 0.4x Criacr, following the protocol of Pfeifer (2015). The LAI measures the total area of leaves per unit area of ground. It represents the amount of leaf area in a vegetation canopy and it is often used as a proxy for the canopy biomass; $FCOVER$ is the proportion of the ground covered by vegetation, it indicates how much the canopy covers the ground; and $P57$, is the fraction of the sky visible through a canopy which is the angle of the sun during solar noon at the equator. These three parameters are widely used in ecology and earth system science to represent the canopy structure, its relation to the underlying surface, and its impact on the light availability at the understory (Pfeifer, 2015). We later processed the images with the CAN-EYE software, which uses pixel information in the photographs to analyze and model the canopy (Weiss and Baret, 2017).

To estimate the functional composition per plot, we sampled five functional traits in three to five individuals of each species in each site: leaf area (LA), specific leaf area (SLA), leaf thickness (LT), leaf dry matter content ($LDMC$) and wood density (WD) (see units in Table C1 in Appendix C) following Salgado-Negret et al. (2016). Traits were selected based on their importance for plant growth and survival (Poorter et al., 2021) and their influence on litter decomposition rates (Cornwell et al., 2008). The community-weighted mean (CWM) for a functional trait is a good way to approach the functional composition of a community as it summarizes each trait per plot as a mean value weighted by their abundance or biomass as the more massive or abundant species may have more impact over the ecosystem (Díaz et al., 2007). Using species' abundance in each plot, we calculated the community-weighted mean (CWM) per plot using dbFD() of the FD package in R as

$$CWM_j = \sum_i^n p_{ij} T_{ij}, \tag{1}$$

where p_{ij} is the relative abundance of species i in plot j, and T_{ij} is the mean trait value of species i in plot j.

Soil conditions, and decomposition and respiration rates

We randomly distributed three permanent measurement points in each plot from which soil respiration, decomposition and microclimate data were collected as follows:

To measure respiration rates, we installed polyvinyl chloride cylinders embedded up to 8 cm in each measurement point, following Bekku et al. (1995). Soil respiration rate (R_s) was measured using a soil Infrared Gas Analyzer ($IRGA$, EGM-4 PP-Systems, Amesbury, MA, USA), with a SRC-1 Soil Respiration Chamber. Cylinders were inserted one month before R_s measurements. We took three to five readings of R_s per day at two different moments: November 2021 (rainy season) and February 2022 (dry season), which resulted in an average value per measuring point for each season.

Soil decomposition was studied using the Tea Bag Index (TBI) protocol. TBI is a globally comparable index, using commercial tea bags as standardized test kit, by using two different tea types with contrasting chemical and physical properties that affect decomposability (Keuskamp et al., 2013). At each point, we buried two sets of tea bags (each set consisting of one green and one rooibos tea bag) at a depth of 8 cm. Each set was left in the soil for 90 and 180 days, and the mass loss of the tea bags was then used to calculate the decomposition constant

(k) and stabilization factor (s), that indicate the soil's potential decomposition and stabilization capacity respectively, according to the method described by Keuskamp et al. (2013).

At each point, we also measured soil water content (SWC) using a moisture sensor (Field-Scout TDR 350) in the first 12 cm of soil depth, and soil temperature (ST) and pH with a pH-meter at 8 cm of soil depth (HANNA HI99121). They were all measured simultaneously in three different moments, August 2021 when tea bags were buried, and November 2021 and February 2022, when soil respiration was measured, and tea bags were recovered. We used mean SWC and mean ST as explanatory variables for decomposition rates, because they did not occur in a specific moment like respiration but throughout the months that tea bags were buried.

Data analysis

Before statistical analyses, all variables were centered and standardized using the base package in R (see raw means and ranges in Table C1 in Appendix C).

To reduce the number of structural and functional variables and to understand the correlation between them, we performed a principal component analysis (PCA) using the R base package. Then, we used the two first components of each PCA. $PC1_{Str}$ accounts for the variation of LAI, $FCOVER$ and $P57$ for which higher values represent more complex canopies and therefore more shaded forests, while the $PC2_{Str}$ accounts for EH and BA which indicate higher stand biomass (Figure 2a). On the other hand, $PC1_{Fun}$ is associated with higher values of LT, $LDMC$ and LA and with lower values of SLA at the community level (Figure 2b). This $PC1_{Fun}$ aligns with the acquisitive-conservative spectrum of leaf strategies. Additionally, $PC1_{Fun}$ also showed a slight association with higher wood density values. In comparison, $PC2_{Fun}$ was found to be mainly explained by higher values of wood density alone, and therefore it was considered unnecessary to include it in the further analysis as it did not add much additional information.

To evaluate the differences of each soil process (R_s, k and S) between successional stages, linear mixed models were fitted using lme4 package in R. As we acknowledge the non-independence of plot statistical units due to the presence of unobservable and uncontrolled environmental differences between the sites (e.g. see Figure B1 in Appendix B), we included the sites as a random effect for the intercept in the models. The successional stage, on the other hand, was included as the fixed effect variable as we are controlling and evaluating its effects on soil processes. The differences in the soil processes between the forest succession were tested with the ANOVA analysis in lmerTest package and the fitted model was visualized using the ggeffect package in R.

In order to evaluate a hypothesized causal network that explains the direct and indirect effects of succession, forest structure, forest function and soil microclimate upon soil processes, we implemented Structural Equation Model (SEM)s. We used the PiecewiseSEM package in R (Lefcheck, 2016) that incorporates mixed effects, considering the potential site-specific environmental conditions that may have random effects on the interactions in the analysis. For the models, we hypothesized that the succession stage would cause variation in $PC1_{Str}$, $PC2_{Str}$ and $PC1_{Fun}$. Then $PC1_{Str}$ and $PC2_{Str}$ would have an effect on mean SWC and mean ST due to the constant effect of shade of the vegetation over the soil, while ST and SWC in a specific moment would be predicted by the general averaged soil microclimate, as well as by a seasonal random effect that captures fluctuations in moisture levels caused by more specific temporary factors. Also, $PC1_{Fun}$ would have an effect on pH due to the chemical differences in the input of litter. Furthermore, we hypothesized that ST, SWC and pH would have an effect over R_s; while mean ST, mean SWC and pH would affect S and k. Finally, we included different combinations of additional direct interactions between succession stage and the process variables (R_s, S and k), and between $PC1_{Fun}$ or $PC2_{Fun}$ and k or S, because we are aware that these interactions might exist without them being mediated by any of the explanatory variables that were included in this study. We ran 32 different models models and for each trial model, we checked the goodness of fit with the Fisher C and we ensured that all tests of directed separation were non-significant (p>0.05) (Lefcheck, 2016). Finally, the best-fitted model was selected according to AIC information criteria as it is the an appropriate method for choosing a Structural Equation Model (SEM) with a low sample size (Lin et al., 2017) (see model comparison in Table D1 in Appendix D).

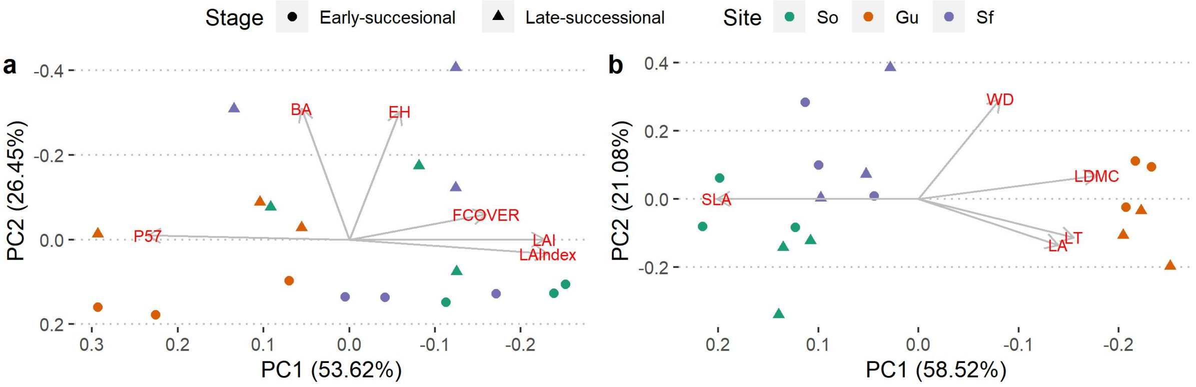

Figure 2. PCA for the evaluated vegetation structure (a) and for the functional composition variables (b).Symbols used: Reserva Encenillo, Guasca (Gu), Bosques de Canoas, Soacha (So), El Silencio, San Francisco (Sf), leaf area index (LAI), cover fraction ($FCOVER$), gap fraction measured at 57^o ($P57$), total basal area (BA), cumulative basal area inflection height (EH), specific leaf area (SLA), leaf area (LA), leaf thickness (LT), leaf dry matter content ($LDMC$) and wood density (WD).

Results

The selected model revealed numerous significant effects at all levels of interactions in the forests, from the successional stages to soil processes such as respiration and decomposition, mediated by forest attributes and soil properties such as soil water content (SWC), soil temperature (ST) and pH (Figure 3). Our results confirm that the hypothesized model adequately described the data, because we achieved a high explanation percentage for most variables (>50%) when considering both the fixed and the random effects. The soil processes (soil respiration rate (R_s), soil decomposition rate constant (k) and stabilization factor (S)) were explained up to 50%, 53% and 29% respectively by a complex interaction of succession, forest attributes, microclimate and soil pH (Figure 3; marginal R^2 in Table 1), and 97% in the case of S when considering the random effect of the site unaccounted differences (conditional R^2 in Table 1).

Structure and functional composition

As expected, the succession stage had a positive effect on forest stand biomass ($PC2_{Str}$) (Figure 3; marginal R^2=0.57 Table 1; Figure A1 in Appendix A), with late-successional forests displaying higher above-ground biomass than early-successional forests, as trees have had more time to grow in height and DBH. However, the succession stage did not affect canopy complexity and shade ($PC1_{Str}$) nor functional leaf spectrum ($PC1_{Fun}$). Instead, the site (a random-effect variable in our models) was what best explained the variation canopy complexity and shade ($PC1_{Str}$) and in functional leaf spectrum ($PC1_{Fun}$), as they were highly explained by the random effects (conditional R^2=0.66 and 0.98, respectively).

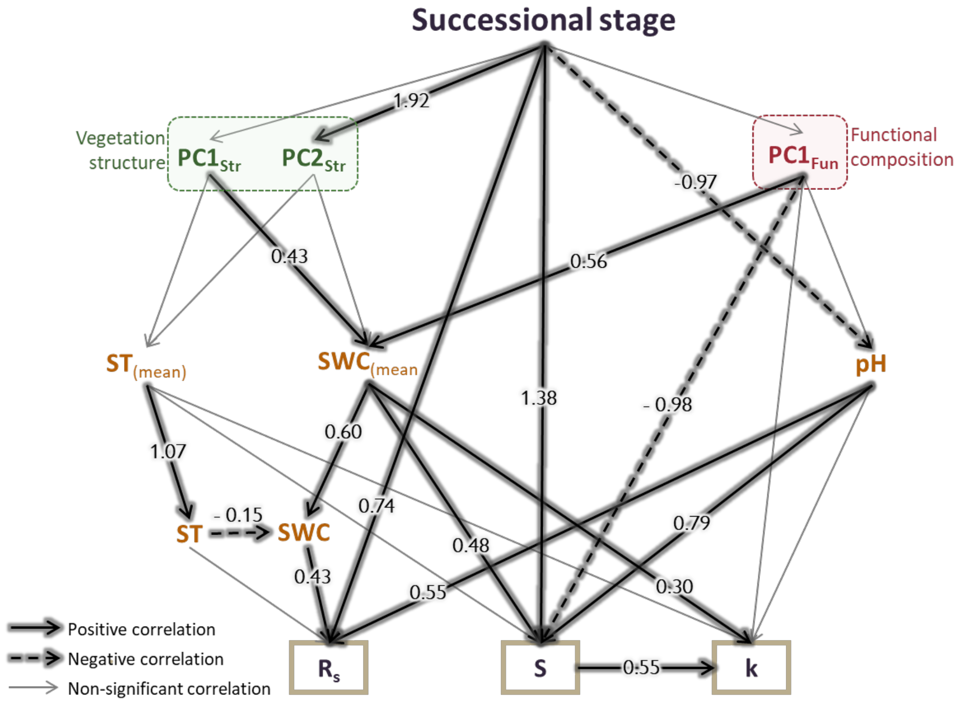

Figure 3. Selected SEM. Goodness of fit Fisher's C = 64.076; p-value = 0.872. It represents all considered interactions between variables; significant interactions are highlighted and have their standardized coefficients; positive interactions are shown as solid lines; negative interactions as dashed lines. See Table 1 for R^2. Forest attributes: canopy complexity and shade ($PC1_{Str}$), forest stand biomass ($PC2_{Str}$) and functional leaf spectrum ($PC1_{Fun}$); soil microclimate: soil temperature (ST), soil water content (SWC) and pH; soil processes: soil respiration rate (R_s), stabilization factor (S) and soil decomposition rate constant (k).

Response variable	Marginal R^2	Conditional R^2
$PC1_{Str}$	0.02	0.66
$PC2_{Str}$	0.57	0.72
$PC1_{Fun}$	0.01	0.98
$SWC_(mean)$	0.41	0.41
SWC	0.31	0.94
$ST_(mean)$	0.02	0.50
ST	0.63	0.86
pH	0.42	0.75
R_s	0.50	0.50
k	0.53	0.53
S	0.29	0.97

Table 1. Marginal and conditional R^2 for each response variable in the interactions included in the selected SEM model (Figure 3). Marginal R^2 shows the proportion explained by the fixed explanatory variables, while conditional R^2 includes random effects (site and season).

Soil microclimate and pH

Mean SWC was strongly influenced by forest attributes (marginal R^2=0.41; table 1). Both, higher canopy complexity and shade ($PC1_{Str}$) and more conservative values of functional leaf spectrum ($PC1_{Fun}$) resulted in higher mean SWC, as both had similar positive effects on SWC (Figure 3). In contrast, mean ST was poorly explained overall in the model (marginal R^2=0.02; table 1) and none of the forest attribute components significantly affected the mean ST. The forest stand biomass ($PC2_{Str}$) had no significant effect over soil pH or microclimatic variables (ST or SWC). Additionally, pH variation was also strongly predicted by the model (marginal R^2=0.42; table 1) and was significantly associated with forest succession directly, where late-successional forests tend to have more acid soils (Figure 3). Finally, both SWC and ST that were measured at a specific moment in time, were almost entirely predicted by the average soil microclimate, by a negative correlation between them, and by the specific site and seasonal conditions as captured by the random effects in our model (Figure 3, Table 1).

Soil respiration and decomposition

As previously stated, our model showed strong explanatory power for all three soil processes, as demonstrated by their high R^2 values (Table 1). All soil processes were positively correlated with the SWC, while ST did not significantly affect any of the soil processes (Figure 3). Additionally, we found that the pH had a positive impact on both R_s and S, while the soil decomposition rate constant (k) was unaffected by pH. Moreover, k was positively correlated with S, meaning that increased potential decomposition rate occurred with higher stabilization factor. We also discovered that the functional leaf spectrum ($PC1_{Fun}$) had a negative effect on S, which means that communities with more conservative leaf traits had lower stabilization factors (Figure 3).

On the other hand, we did not find significant differences in any of the three soil processes (R_s, S and k) between the two successional stages (Figure 4, p>0.05 in all cases). Despite that, when excluding the paths of interactions mediated by SWC, pH and $PC1_{Fun}$ that affect the soil processes, later-successional stages had increased R_s and S rates. Additionally, this direct (unmediated) positive effect of the successional stage was greater than the effect of soil microclimate or pH in both cases, as shown by the coefficients of each interaction of the model (Figure 3).

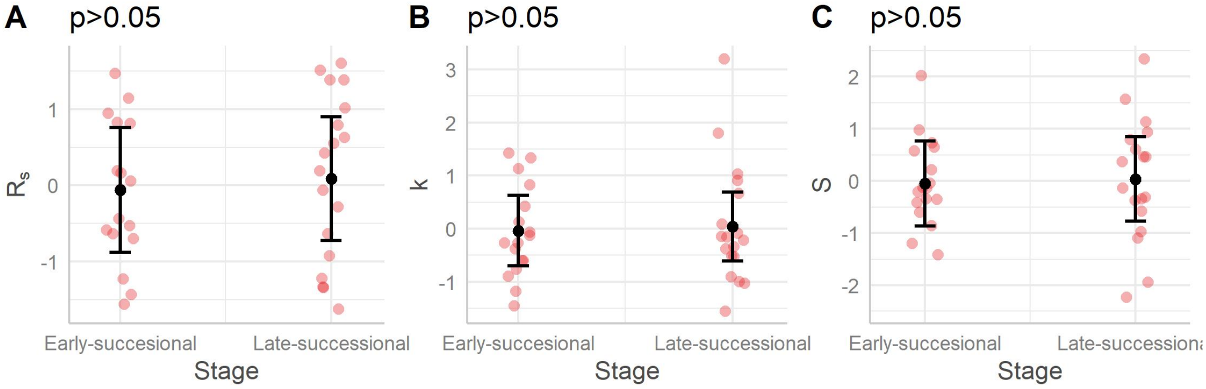

Figure 4. Fitted model of the effects of the successional stage over the soil processes. Symbols used: soil respiration rate (R_s), stabilization factor (S), soil decomposition rate constant (k), early-successional forests, 10 ∼ 30 years and late-successional forests, ∼ +60 years.

Discussion

Forest attributes between succession stages and effect on microclimate

When evaluating the forest structure, late-successional forests showed higher basal area and height as we expected. However, the structural differences did not imply changes in the canopy structure and shading. Probably, the early-successional forests considered in this study already have a well-established closed-canopy structure by the fast-growth species that establish and dominate this stage, and that is maintained between successional stages regardless of the species turnover of these forests (Hurtado-M et al., 2020). This structural similitude is coordinated with the functional similarity between successional stages. The functional leaf spectrum is not turning from a more acquisitive to a more conservative functional composition in the late-successional stages, as we were expecting. The absence of differences in the forest's structural and functional attributes regardless contrasting forest age, and their impact on soil processes, merits additional investigation.

The absence of differences in the canopy cover may explain the similar soil microclimatic conditions between the two successional stages (Figure A2 in Appendix A). The preservation of microclimatic regulation between the stages, illustrates how ecosystems can sometimes recover their function faster than any floristic recovery (Guariguata and Ostertag, 2001). Although the shade did not vary between the successions, it had an effect over soil water content, with higher values in more shaded forests. This was expected because shade limits water evaporation from the soil (Raich and Tufekcioglu, 2000; Hastwell and Morris, 2013; Metzger et al., 2017) and it implies that there is a significant level of heterogeneity in soil microclimate regulation between or even within forest plots, playing a key role in regulating soil microclimate. Surprisingly, soil temperature was unaffected by the canopy complexity and shade. The shading effect on soil temperature may not have been captured in this experiment due to a limited range of temperature variations. The High-Andean forests do not have contrasting temperature seasons, and all the sites had similar elevations, which means that soil temperature did not vary much between or within the sites. Additionally, the mean soil temperature and mean soil water content are averages taken over several months, so the effects of shading on temperature may have yet to be evident in these averages, as ST variation may be more pronounced within a short-term measurement, such as within a day, while the effect of radiation on SWC may take longer terms to be observed.

In addition to the shading effect, we also found a relationship between the functional leaf spectrum and the soil water content. Plots dominated by conservative species with dense and thick leaves showed higher SWC, which could be related to lower litter decomposition rates, promoting a thicker litter layer. This could reduce incident radiation, lowering the evaporation of soil water (Sayer, 2006; Quested et al., 2007; Cornwell et al., 2008; Wen et al., 2021). Additionally, a potential coupling or coordination in functional leaf and hydraulic traits in conservative species, may play a role in maintaining high soil moisture levels, as this is generally associated with narrow xylem vessels, low water efficiency, and low evapotranspiration rates (Markesteijn et al., 2011; Méndez-Alonzo et al., 2012).

We found a relationship between forest succession and soil pH, with later-successional forests having lower pH levels, consistent with other studies (Bautista-Cruz and del Castillo, 2005; Li et al., 2013; Sayer, 2006; You et al., 1999). It could be associated with high accumulation of soil organic carbon (SOC) in late-successional forests, which increases through forest growth or succession (Li et al., 2013; Aryal et al., 2014; Lewis et al., 2014; Deng et al., 2013; Flores-Rentería et al., 2018; Duan et al., 2020) and in relation to the presence of humic acids (You et al., 1999; Sayer, 2006). But further research into soil chemistry and properties may help to shed light on the mechanisms behind the decrease in soil pH in late-successional forests.

Effects on soil processes

All measured soil processes, R_s, k and S, showed a positive correlation with soil water content (as measured by either mean SWC for k and S, or SWC for R_s) and pH. These variables play a critical role in regulating microbial activity and processes such as respiration and decomposition, as they influence the availability of water and solubility of nutrients needed for growth and for the enzymatic processes of microorganisms (Aerts, 1997; Salazar-Villegas et al., 2016; Flores-Rentería et al., 2018; Trivedi et al., 2018). This finding aligns with previous studies in tropical ecosystems, which have shown the importance of SWC in driving changes in soil respiration rate and soil decomposition rate constant rates (Valentini et al., 2009; Jiang et al., 2016; Flores-Rentería et al., 2018; Rodtassana et al., 2021).

Although temperature can influence soil respiration and decomposition (Vargas-Terminel et al., 2022), in this study we did not find an effect of soil temperature on the soil processes. This could be due to the relatively constant temperatures in tropical ecosystems, which result in a small range of temperature variation compared to variations in precipitation regimes. The clear effect of soil water content and the lack of a noticeable effect of soil water content indicate that soil water content is a dominant factor driving changes in soil processes in this High-Andean forests. It is important to note that the temperature sensitivity of soil processes can vary throughout different stages of forest succession, influenced by interactive factors such as the microbial community composition, and temperature-water interactions (Suseela et al., 2012; Huang et al., 2016; Petraglia et al., 2019). Our study did not observe any significant differences in temperature or its impact on soil processes, however, it is possible that the temperature sensitivity of these processes may still vary with changing forest successional stages, a factor that was not assessed in this study.

The findings of this study suggest that soil water content has a positive effect on stabilization factor in agreement with other studies Sarneel et al. (2020); Orrego et al. (2022). However, this result contradicts our expectations that soil moisture would enhance decomposition, leading to a decrease in recalcitrant material. The positive correlation between stabilization factor, soil decomposition rate constant and soil water content in this study, may suggest that forests with more efficient decomposition processes have a higher potential to stabilize carbon compounds. This may align with Prescott and Vesterdal (2021), which explains that the higher residuals in decomposing litterbags are a result of both undecomposed litter material and the transformation of litter to recalcitrant products by decomposers. The latter is likely to increase with higher decomposition rates, since they are a byproduct of the decomposition process itself (Prescott and Vesterdal, 2021). However, this hypothesis requires further study to determine the exact mechanisms behind the positive correlation.

We reported a significant effect of the forest's functional composition on the soil's potential to stabilize carbon compounds (S), as demonstrated in our study using tea bags as a litter substrate. The results suggest that soils in forests with more conservative traits are less capable of accumulating organic matter, due to their fast decomposition rates. This interaction may be influenced by priming, the presence of certain organic compounds that inhibit decomposition and can lead to lower stabilization factor values (Six et al., 2006; Trivedi et al., 2018). Additionally, there is an effect of forest functional composition on the microbial community composition, with a potential coupling between the host forest functional traits and microbial functional composition. The presence of acquisitive species with high specific leaf area, leaf nitrogen concentration, and low leaf dry matter content is associated with soil microbial communities dominated by bacteria (low fungal:bacterial ratio) with rapid metabolic activities, and it is linked with poor carbon retention (Six et al., 2006; Rawat et al., 2015; Trivedi et al., 2018). Conversely, the dominance of conservative plant species with opposite functional promote soil microbial communities dominated by fungi with slow decomposing rates (high F:B ratio), usually linked with greater soil carbon storage (Rawat et al., 2015). It is worth noting that the characterization of microbial communities would provide a complete picture of these interactions.

Additionally, we observed a positive correlation between forest succession and soil respiration rate and stabilization factor. Although the underlying mechanisms of these correlations could not be directly established in our study, we can explore critical drivers of soil processes. For instance, late-successional forests, which have undergone more time for recovery, are likely to have a better-established microbial community with higher microbial biomass, which might increase in soil respiration rate (Salazar-Villegas et al., 2016, 2018). Furthermore, the accumulation of soil organic matter and certain nutrients over time in late-successional forests stimulates microbial activity. Additionally, the changes in carbon inputs, soil organic carbon and the quantity of litterfall with forest succession may provide more substrate for soil respiration rate (Lohbeck et al., 2015; Huang et al., 2016). On the other hand, the accumulation of soil organic carbon (SOC) through interaction with other soil chemical properties and increased organic matter input both above and below-ground in late-successional forests contribute to soil stabilization factors and improved carbon storage capacity (Deng et al., 2013; Orrego et al., 2022). Finally, it is likely that the observed positive correlation between succession and soil respiration rate is due to the inclusion of root respiration in our measurements, despite our efforts to exclude it by avoiding the presence of living roots. This can occur because superficial or fine root biomass can increase during succession (Hertel et al., 2006; Cavelier et al., 2015), leading to an increase in the proportion of root respiration contributing to total soil respiration, potentially offsetting any decrease in heterotrophic respiration that may occur (Wang et al., 2017).

Soil respiration and decomposition along succession, and neutralizing effects

Overall, the SEM results show that soil processes (R_s, k and S) were affected by soil variables, as well as by forest attributes. A direct effect of succession over R_s and S was also found, which mechanism operates independently from the considered forest structure and microclimate. But surprisingly, soil processes did not vary significantly between the successional stages (Figure 4). These results suggest that in high Andean forests, soil processes are probably being sustained throughout succession or even resist a disturbance. Lack of significant differences in litter decomposition with forest age has been reported (Xiao et al., 2014), but these results are opposing to most previous studies that reported increased soil respiration or litter decomposition rates in late-successional forests (Huang et al., 2016; Vargas-Terminel et al., 2022). All of these different results indicate that the effects of forest succession on soil respiration are context dependent to each ecosystem and its functioning properties.

The absence of differences in soil processes between successional stages may be explained through offsetting effects of multiple variables (neutralization of effects). First, a series of opposing or counterbalancing effects neutralize the variation between the two successional stages. For example, there is a positive effect from the successional stage and pH over both soil respiration rate and stabilization factor, but pH decreases with succession, leading towards the annulment of any significant difference in these soil processes that could be found between the stages. Second, the effect of the successional stage on soil processes is disrupted by the lack of continuity in the levels of interaction, as the successional stage has no significant influence on canopy complexity and shade and functional leaf spectrum, but rather it is these two factors that have any further impact on soil processes, as depicted in Figure 3.

Implications for soil carbon accumulation

Our have important implications for understanding the interactions between soil processes and forest succession. A key finding of our study is the invariability of the soil's potential soil decomposition rate constant (k) and stabilization factor (S) across successional stages in high Andean forests. It suggests that the soil has a stable capacity to decompose organic matter, regardless of changes in the forest successional stage. This stability of soil processes can play a significant role in maintaining the soil's carbon sequestration capacity and mitigating the effects of climate change. On the other hand, the findings also highlight the actual carbon fluxes (emission and sequestration) occurring in this ecosystem. The fact that the realized soil decomposition, as indicated by the actual soil respiration rate (R_s), is maintained at similar levels between successional stages suggests that changes in forest structure or microclimate do not significantly impact the carbon fluxes. This steadiness of carbon fluxes is essential, as changes in soil processes can considerably affect the balance between carbon sequestration and emissions. The maintenance of carbon fluxes in this forest ecosystem can therefore contribute to the mitigation of climate change and support the preservation of the ecosystem's carbon storage capacities.

It is important to acknowledge the limitations of this study. Firstly, the chronosequence approach is limited, as only two successional stages were considered in this study. This limits the potential for detecting patterns and trends over longer periods of forest succession. Additionally, chronosequence approaches in general have limitations in capturing the full range of variability and complexity of ecosystem dynamics over time (Chazdon et al., 2007). Secondly, the statistical power of the study was limited by the number of replicates, which prevented the inclusion of more relevant variables in the structural equation model, such as microbial community, biomass, soil chemical and physical properties. To further improve the understanding of the interactions between soil processes, forest attributes, microclimate, and pH in these ecosystems, future studies would benefit from a larger sample size and a more comprehensive set of variables.

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Parte IV

Apéndices

Appendix A Supplementary material

In this appendix, we present two supplementary figures (graphs) that display the results of linear mixed effect models. These models examine the effect of successional stage on the structural and functional components of the forest (Figure A1), as well as the effect on microclimatic variables (Figure A2). The models only include succession as a fixed variable and site as a random effect. The results show that there are no significant differences between successional stages, except for the forest stand biomass ($PC2_{Str}$) and the soil pH. The figures provide a clearer understanding of the structural equation model findings, which indicate that the forest structure or functional composition does not vary between stages, and that the microclimate also does not vary, despite the correlations observed between the structure, function, and microclimate of the forest.

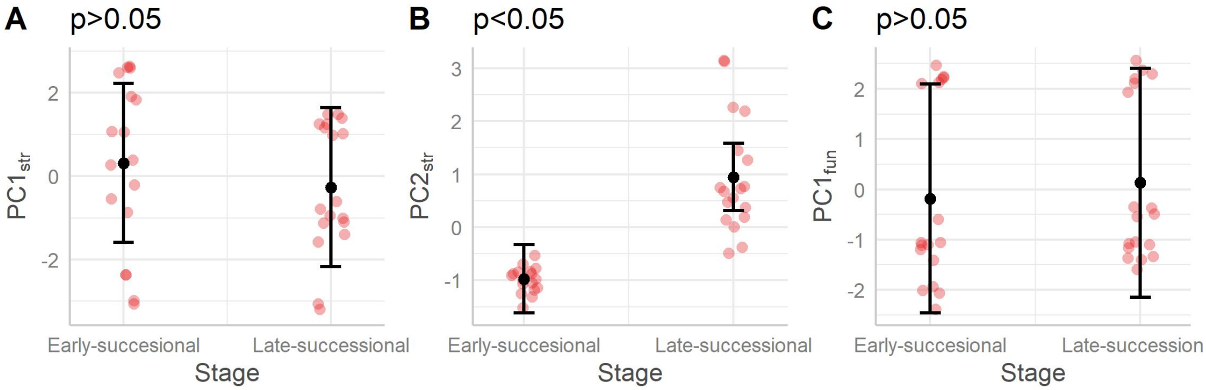

Figure A1. Fitted model of the effects of the successional stage over the structural and functional components of the forest. early-successional forests, 10 ∼ 30 years and late-successional forests, ∼ +60 years

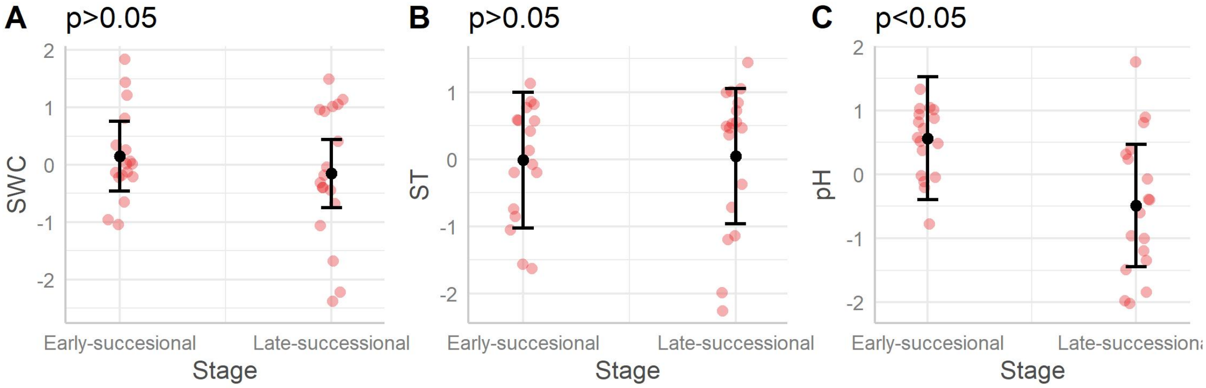

Figure A2. Fitted model of the effects of the successional stage over the microclimate (soil water content (SWC) and soil temperature (ST)) and pH. early-successional forests, 10 ∼ 30 years and late-successional forests, ∼ +60 years.

Appendix B Sites and plot details

In this appendix, we present details of the three study sites. First, a table of coordinates, elevation, and soil general characteristics of each site is provided. This information provides a baseline understanding of the location and environmental conditions of each site and offers insights into the results and future research opportunities, complementary to the visual information provided in Figure 1. For example, we observe in the table that the plots in Reserva Encenillo, Guasca (Gu) have a higher elevation with a difference of up to 500 meters.

Additionally, we want to highlight the distinct land use transformation histories of each site. Reserva Encenillo, Guasca (Gu) was once a lime mine and has since become a research and ecotourism site as part of a restoration and conservation project. On the other hand, Bosques de Canoas, Soacha (So) and El Silencio, San Francisco (Sf) have long been privately-owned lands with a history of cattle raising and, in the case of Bosques de Canoas, Soacha, flower cultivation. Today, El Silencio, San Francisco also focuses on research and ecotourism, albeit to a lesser extent than Reserva Encenillo, Guasca. Both Bosques de Canoas, Soacha and El Silencio, San Francisco have land use patterns that consist of a mix of forest fragments and cattle pastures. This suggests that Reserva Encenillo, Guasca has undergone more severe historical transformation due to the impacts of mining on the soil, while the other sites have undergone less severe, but still important, historical transformation as a result of conversion to pastures.

Site	Plot	Successional stage	Coordinates	Elevation (m)	Bulk density	Clay content
Gu	P03	*Late – successional*	4°47’20,318"N 73°54’31,812"W	3141	Med	Med
	P04	*Early – successional*	4°47’28,667"N 73°54’25,886"W	3086	High	High
	P05	*Late – successional*	4°47’24,124"N 73°54’31,332"W	3107	Low	Low
	P06	*Early – successional*	4°47’26,609"N 73°54’25,904"W	3095	High	Med
	P15	*Early – successional*	4°47’05,2"N 73°54’13,8"W	3115	Med	Med
	P16	*Late – successional*	4°47’16.5"N 73°54’15.4"W	3075	Med	Low
So	P23	*Late – successional*	4°36’55.54"N 74°18’8.32"W	2673	Med	Med
	P24	*Early – successional*	4°36’59.82"N 74°18’2.42"W	2665	Med	Low
	P25	*Late – successional*	4°36’46.74"N 74°18’6.39"W	2671	Low	Low
	P26	*Early – successional*	4°36’55.22"N 74°18’2.68"W	2666	Low	Med
	P27	*Late – successional*	4°37’7.25"N 74°18’17.97"W	2682	Med	Med
	P28	*Early – successional*	4°37’8.46"N 74°18’8.98"W	2651	Med	Med
Sf	P29	*Late – successional*	4°56’37.61"N 74°14’32.96"W	2634	Med	High
	P30	*Early – successional*	4°56’43.31"N 74°14’25.44"W	2658	High	High
	P31	*Late – successional*	4°57’17.91"N 74°14’14.25"W	2804	High	High
	P32	*Early – successional*	4°57’6.52"N 74°14’23.30"W	2668	High	High
	P33	*Late – successional*	4°56’45.91"N 74°14’46.64"W	2713	Med	Low
	P34	*Early – successional*	4°56’46.33"N 74°14’43.80"W	2717	Low	Med

Table B1. Detailed information of the permanent plots where the study was performed. Reserva Encenillo, Guasca (Gu, green), Bosques de Canoas, Soacha (So, orange) y El Silencio, San Francisco (Sf, purple)

We also present a principal component analysis (PCA) (Figure B1) that displays the first two multivariate components of climatic variables previously obtained for the plots of our study (See more in Hurtado-M et al. (2020). The figure clearly shows a clustering of the plots into the three study sites, indicating greatly contrasting climate conditions. This climatic contrast between the sites, together with the spatial distribution of the plots in different and distant hills and the differing transformation histories and situations of each site, were the main reasons why we included the site as a random effect variable in all our statistical models. This helps us to account for the potential impact of differences in local climate, geography, and human transformation between the sites on the results, as all of them are likely to influence other uncontrolled variables such as taxonomic composition, diversity, (as in Hurtado-M et al. (2020) and soil chemical and physical properties, all of which might definitely influence the soil processes and interactions being evaluated.

Finally, we present a figure that depicts the precipitation regimes of the three study sites (Figure B2), based on mean data from 2010 to 2018 obtained from external sources (GEOPORTAL de datos abiertos, IDEAM). The figure shows the seasonal patterns of precipitation in each site, which are bimodal for all sites. It also indicates that the site of Reserva Encenillo, Guasca has a different precipitation regime compared to the other two sites, as one of the two dry seasons is not as pronounced, and it seems like it has in general more total annual precipitation. Of particular note is the contrasting precipitation between November (the rainy season) and February (the dry season), the months during which we conducted our soil process measurements. However, during our field study, we noticed that February 2022 had an unusual amount of precipitation, likely due to increased precipitation levels in the entire year of 2022. Since we did not measure precipitation directly, we are unable to determine its exact effect on our results. Nevertheless, we still included season as a random effect variable for both h and t at specific moments in time, accounting for this uncontrolled variation between measurement events. These details provide a more complete understanding of the study sites' climatic conditions and their potential influence on our results.

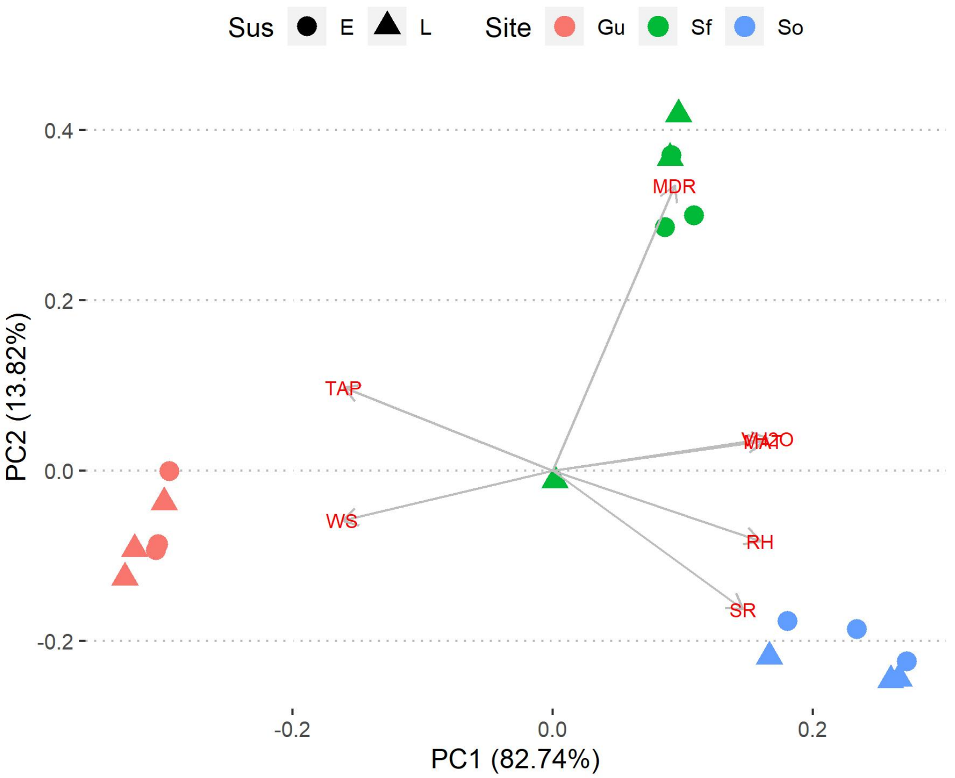

Figure B1. PCA of climate variables for each plot. Sites: Bosques de Canoas, Soacha (So),Reserva Encenillo, Guasca (Gu),El Silencio, San Francisco (Sf). Successional stages: early-successional forests, 10 ∼ 30 years (E), late-successional forests, ∼ +60 years (L). Climatic variables: solar radiation (SR), mean annual values of diurnal range temperatures (MDR), mean annual temperature (MAT), total annual precipitation (TAP), relative humidity (RH), water vapor pressure (VH2O), and wind speed (WS).

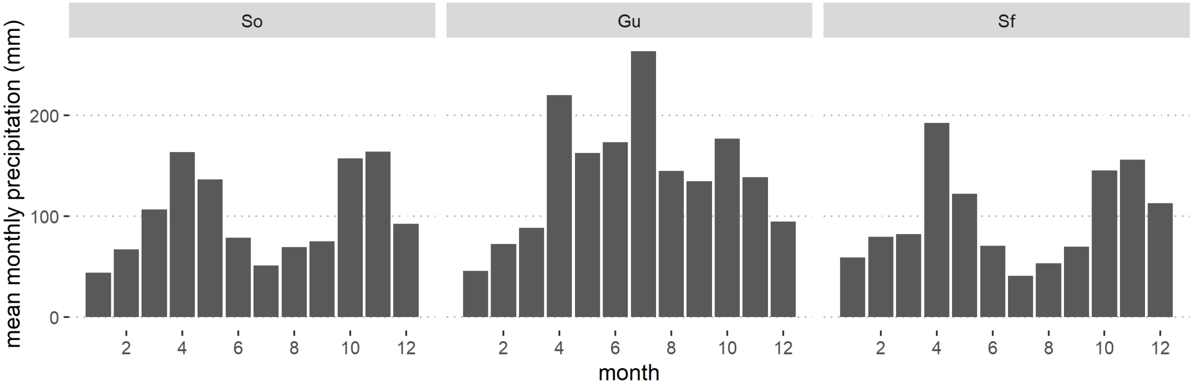

Figure B2. Precipitation regimes in the sites according to data from 2010 to 2018 (Ideam). Bosques de Canoas, Soacha (*So*),Reserva Encenillo, Guasca (*Gu*),El Silencio, San Francisco (*Sf*). 1 to 12 represent the 12 months of the year from January to December

Appendix C Variables information

In this appendix, we present a table containing additional information about the variables used, including the units and the means and ranges of the untransformed variables. During the statistical analysis, we standardized all the variables, and we used principal components to reduce some of them, which results in standardized intercept coefficients. This raw information allows for comparison with other studies and provides a clearer understanding of the high-Andean forests. We also tested for normality for our variables even though this is not a necessary assumption for the linear mixed effect models we performed, including the ones in the piecewise Structural Equation Model.

Variable	Units	Mean	Min value	Max value	Normality test
EH	m	10.2	3.81	26.3	0.016*
BA	m^2ha^-1	0.329	0.174	0.760	0.010*
$P57$	-	0.07	0.02	0.12	0.056
LAI	-	2.99	2.29	4.18	0.071
LAIindex	-	5.34	4.15	6.55	0.622
$FCOVER$	-	0.834	0.509	0.941	0.000*
$LA_{(}CWM)$	cm^{-2}	99.6	37.9	222.0	0.096
$LT_{(}CWM)$	mm	0.418	0.329	0.515	0.615
$SLA_{(}CWM)$	cm^2g^{-1}	91.6	57.5	121.0	0.005*
$LDMC_{(}CWM)$	mg g	352	303	410	0.089
$WD_{(}CWM)$	g cm^3	0.513	0.438	0.61	0.710
SWC	%	14.0	1.37	26.5	0.211
ST	^oC	13.3	9.96	16.4	0.068
$SWC_{(}mean)$	%	19.8	9.4	27.2	0.107
pH	-	4.64	2.7	6.34	0.071
$ST_{(}mean)$	^oC	13.4	10.8	15.1	0.103
R_s	g_{CO_2} m^{-2} $Hour^{-1}$	0.549	0. 293	0.791	0.055
k	-	0.0162	0.0065	0.0350	0.307
S	-	0.226	0.088	0.356	0.899

Table C1. Details of the variables used in this study: Units, raw mean, raw min and max values and Shapiro-Wilk normality test p-values ($p<0.05$ normality is rejected).

Appendix D Structural Equation Models selection

As described in the methods section of the main article, we ran 32 different models as described in the methods. In all models, we included the hypothesized interactions even if they resulted to be non-significant, and we additional interaction combinations. The indicators of significance and fitness of these models are seen in table D1. Fischer's C estimator indicates the goodness of fit of the model, which is tested by the p-value > 0.05. The number of independence claims in the tests of directed separation (K) reflect the number of residual covariance or correlation parameters that need to be included in the model to account for the interdependence between variables. A low number of significant (p<0.05) independence claims suggests that the model fits the data well and captures the interdependence structure of the variables adequately, while a high number of significant claims means that there are still correlated variables even after including the indirect interactions. The chosen model, "sem.29", had the lowest AIC and BIC, had a general p-value > 0.05 and was the only model with zero significant tests of directed separation (K*), which indicates that apparently there are no missing associations and the model provides a good fit to the data.

ID	Fisher.C	df	P.Value	AIC	BIC	K	K*
sem.29	64.076	78	**0.872**	**186.076**	**280.952**	61	**0**
sem.23	117.424	86	0.014	213.424	**288.081**	48	3
sem.30	114.419	48	0.000	212.419	288.631	49	5
sem.32	143.994	58	0.000	231.994	300.429	44	8
sem.19	77.968	74	**0.354**	**203.968**	301.955	63	1
sem.18	87.412	76	**0.175**	211.412	307.844	62	3
sem.24	152.560	94	0.000	240.560	308.995	44	7
sem.17	85.427	76	**0.215**	213.427	312.969	64	3
sem.14	96.879	74	0.038	220.879	317.311	62	4
sem.16	86.856	74	**0.146**	222.856	328.620	68	4
sem.20	154.846	68	0.000	262.846	346.835	54	7
sem.13	98.053	82	**0.109**	268.053	400.258	85	3
sem.15	85.939	74	**0.162**	263.939	402.365	89	2
sem.21	79.039	70	**0.215**	261.039	402.576	91	2
sem.11	196.482	114	0.000	344.482	459.578	74	5
sem.6	227.716	114	0.000	375.716	490.812	74	7
sem.5	227.450	114	0.000	387.450	511.878	80	7
sem.4	252.740	120	0.000	406.740	526.502	77	9
sem.8	242.803	132	0.000	426.803	569.895	92	8
sem.9	242.803	132	0.000	426.803	569.895	92	8
sem.10	212.956	108	0.000	420.956	582.712	104	5
sem.7	248.360	132	0.000	486.360	671.446	119	7
sem.3	427.152	168	0.000	607.152	747.133	90	15
sem.1	479.998	206	0.000	659.998	799.979	90	18
sem.2	447.837	182	0.000	651.837	810.483	102	16

Table D1. Structural Equation Model (*SEM*) comparative of the indicators of fitness and significance used to determine the best fitted model. The chosen model and the best fitting indicators are highlighted in bold.

Acronyms

R_s	soil respiration rate. 12–16, 18–20, 33
k	soil decomposition rate constant. 13–16, 18–20, 33
S	stabilization factor. 13–16, 18–20, 33
PCA	principal component analysis. 2, 13, 14, 30
SEM	Structural Equation Model. 2, 13–15, 19, 33, 34
$IRGA$	Infrared Gas Analyzer. 12
TBI	Tea Bag Index. 12
So	Bosques de Canoas, Soacha. 11, 14, 30–32
Gu	Reserva Encenillo, Guasca. 11, 14, 30–32
Sf	El Silencio, San Francisco. 11, 14, 30–32
$Early-successional$	early-successional forests, 10 $\sim$ 30 years. 11, 16, 29–31
$Late-successional$	late-successional forests, $\sim$ +60 years. 11, 16, 29–31
BA	total basal area. 11, 13, 14, 33
DBH	diameter at breast height. 11, 14
$FCOVER$	cover fraction. 12–14, 33
EH	cumulative basal area inflection height. 11, 13, 14, 33
LAI	leaf area index. 12–14, 33
$P57$	gap fraction measured at 57^o. 12–14, 33
LA	leaf area. 12–14, 33
$LDMC$	leaf dry matter content. 12–14, 18, 33
LT	leaf thickness. 12–14, 33
SLA	specific leaf area. 9, 12–14, 18, 33
WD	wood density. 12, 14, 33
CWM	community-weighted mean. 12
$PC1_{Fun}$	functional leaf spectrum. 13–17, 19
$PC2_{Fun}$	second principal component for functional traits. 13, 14
$PC2_{Str}$	forest stand biomass. 13–16, 29
$PC1_{Str}$	canopy complexity and shade. 13–17, 19
SWC	soil water content. 13–18, 29, 33
ST	soil temperature. 13–18, 29, 33