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Forest Structure, above-Ground Carbon Stocks, and Productivity along an Elevational Gradient in the Ecuadorian Andes

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FOREST STRUCTURE, ABOVE-GROUND CARBON STOCKS, AND PRODUCTIVITY ALONG AN ELEVATIONAL GRADIENT IN THE ECUADORIAN ANDES

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ABSTRACT

The Andean forest provides a natural laboratory for evaluating long-term interactions between forests and variation in environmental parameters along elevational gradients. In particular, the mechanisms that control above-ground carbon stocks (AGC) and natural dynamics in mountain ecosystems constitute a potentially powerful tool for understanding the function of these ecosystems and their response to current climate change scenarios or past human disturbances. The present study integrates biotic (rarefied species richness and leaf traits) and abiotic (climate, soil properties and degradation) factors as possible drivers of AGC stocks, AGC net change (AGC_{nt}), AGC productivity (AGC_p) and AGC mortality (AGC_k), along an elevational gradient of ca. 3000 m in the montane forests of the Ecuadorian Andes. My findings show that AGC metrics respond to elevational gradients (climate conditions) and past human disturbances. I found that temperature constitutes the primary filter for forest structure, AGC stocks, AGC_{nt} and AGC_p along the elevational gradient, where abiotic factors such as degradation and soil properties represent the main drivers for AGC_k. This study provides insight into the processes that control patterns of AGC metrics in mountainous ecosystems, where temperature is likely the most important source of AGC variation in Andean forests.

INDEX WORDS: Andean forests, above-ground carbon, elevational gradient, climate, degradation, productivity, structural equation model

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“The philosophical study of nature endeavors, in the vicissitudes of phenomena, to connect the present with the past” – Alexander von Humboldt

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INTRODUCTION

Tropical forests store a large fraction of terrestrial carbon stocks and tree diversity (Bonan, 2008; Pan *et al.*, 2011; Slik *et al.*, 2015; Sullivan *et al.*, 2017; Requena Suarez *et al.*, 2019) and play an important role in the carbon cycle of the planet (Beer *et al.*, 2010; Poorter *et al.*, 2015). They store between 40% and 50% of the total carbon stocks in terrestrial ecosystems and between ca. 30% and 40% of the total net primary productivity comes from these forests (Phillips *et al.*, 1998; Townsend *et al.*, 2011; Phillips *et al.*, 2019); and both carbon stocks and productivity dynamics in these ecosystems constitute a keystone for climate regulation. The Tropical Andean Montane Forests of South America (Andean forests, hereafter), in particular, play a key role in their contribution to the Earth's biogeochemical cycles (Requena Suarez *et al.*, 2019) and the provision of ecosystem services, particularly those related to water (Bruijnzeel *et al.*, 2011) and climate regulation (Jarvis & Mulligan, 2011).

In Andean forest, most carbon is stored in above-ground biomass (AGC) and soil as organic carbon (SOC). These forests can hold up to 150 Mg C ha^{-1} at 1000 m asl in their above-ground biomass (Moser *et al.*, 2011; Phillips *et al.*, 2019) and up to 99 Mg C ha^{-1} above 3000 m of elevation (Grimm & Fassbender, 1981; Girardin *et al.*, 2010; Moser *et al.*, 2010; Román-Cuesta *et al.*, 2011); and between 95.3 and 323.6 Mg C ha^{-1} of SOC is stored within the first 30 cm of soil, at the same elevations (Iost, 2007; Gibbon *et al.*, 2010; Moser *et al.*, 2011; Zuniga-Escobar *et al.*, 2013). Over the last three decades, Andean forests have reported an AGC annual productivity of 0.67 ± 0.08 Mg C ha^{-1} y^{-1}, representing an important carbon sink compared to the

0.42 Mg C ha^{-1} y^{-1} estimated for lowland Amazonian forests (Duque *et al.*, 2021), 0.08 Mg C ha^{-1} y^{-1} for temperate forests, and 0.02 Mg C ha^{-1} y^{-1} for boreal forest (Keeling & Phillips, 2007). Here, estimates for forests are a fraction of those found for non-forested ecosystems (e.g., 1.5 Mg C ha^{-1} $year^{-1}$ for paramo (Calderón-Loor *et al.*, 2020), 2.9 Mg C ha^{-1} $year^{-1}$ for mangrove wetlands (Twilley *et al.*, 2017), and 4.6 Mg C ha^{-1} $year^{-1}$ for seagrass beds (Moriarty *et al.*, 1985)). However Andean forests, in particular, are suspected of playing an essential role in mitigating climate change by removing CO_2 from the atmosphere and transforming it into organic matter.

Andean forests contain about a tenth of all plant life in less than one percent of the world's land area (Myers *et al.*, 2000; Rodríguez-Machena *et al.*, 2004). These forests contain high levels of species diversity and endemism per unit area (> 15000 vascular plant species occurring only in this biome (Kessler & Kluge, 2008)) as a result of sharp environmental gradients associated with the tectonic complexity of the Andean range and their biogeographic and evolutionary history (Gentry, 1995; Gradstein *et al.*, 2008; Jørgensen *et al.*, 2011). Previous studies on the spatial diversity of different organisms along elevational gradients in the Andes found a general decrease in species diversity at higher elevations (Herzog *et al.*, 2005; Palin *et al.*, 2011), where species diversity peaked at mid-elevations, between 500 – 2000 m asl (Kessler, 2000, 2001; Herzog *et al.*, 2005; Salazar *et al.*, 2013). Due to their typically high species diversity and substantial environmental variation, Andean elevational gradients are ideal natural laboratories to evaluate carbon dynamics and the interactions between climate, soil, and species richness (Sundqvist *et al.*, 2013). Nevertheless, Andean forest represent one of the least studied terrestrial ecosystems (Girardin *et al.*, 2013; Mathez-Stiefel *et al.*, 2017), where most previous studies have focused on lowland forests (Brienen *et al.*, 2015; Hubau *et al.*, 2020). Although we know little about the mechanisms driving species diversity, carbon storage, and its dynamics along elevational gradients in Andean forests (Malhi, 2012), the rapid species turnover (beta diversity) with increasing elevation may be one of the main drivers of the high rates of gamma diversity typically found in Andean forests (Homeier *et al.*, 2010; Lippok *et al.*, 2014). In addition, the carbon dynamics in above-ground strata is controlled by biotic (e.g. species diversity, symbiotic associations), abiotic (e.g. microclimate, topography, soil properties) factors, and together with past human disturbances (e.g. timber extraction), may create a mosaic of different successional stages (Lohbeck *et al.*, 2015; Duque *et al.*, 2021) along Andean elevational gradients.

Biotic factors in tropical forests, such as species richness and plant resource acquisition strategies (Poorter *et al.*, 2017; Duque *et al.*, 2021), may control, in part, above-ground carbon (AGC) stocks and dynamics (van der Sande *et al.*, 2017a). Tree species richness (SR) and AGC within Andean forests typically decrease with increasing elevation, where their highest values are in the lowest elevational zones or piedmont forests (Lieberman *et al.*, 1996; Cui & Zheng, 2016; Pinto *et al.*, 2018). Leaf functional trait (LFT) variations among dominant tree species in tropical forest communities along environmental gradients are expected to determine ecological processes such as primary productivity, growth, nutrient cycling, and nutrient assimilation (Luo *et al.*, 2019b), but could also reveal competitive advantages independent of their dissimilarity (Mayfield & Levine, 2010; Kunstler *et al.*, 2012). In Andean forests, decreases in temperature, annual rainfall, and air humidity (Jarvis & Mulligan, 2011) with concomitant increases in solar and UV radiation at higher elevations (Cavelier, 1996; Halladay *et al.*, 2012; Fyllas *et al.*, 2017) can modify functional leaf trait strategies (Llerena-Zambrano *et al.*, 2021). For instance, at high elevations, trees develop thicker and smaller leaves than species at lower elevations (Velázquez-

Rosas *et al.*, 2002; van de Weg *et al.*, 2009; Bruijnzeel *et al.*, 2010; Fyllas *et al.*, 2017; van der Sande *et al.*, 2020) as a response to environmental filters, which can also affect the trait community assembly of species and their ecological functionality (Luo *et al.*, 2019a). Hooper *et al.* (2005) and Grime (1998) suggested that dominant trait community composition (Grime's mass-ratio hypothesis) instead of species richness may be a better predictor of AGC allocation and dynamics in forest ecosystems. However, this remains to be tested empirically in Andean forests.

Abiotic factors, such as climatic conditions and soil properties, may also substantially affect the composition of plant communities and carbon dynamics (Poorter *et al.*, 2017). These include AGC allocation and storage, which likely determine resource availability for plant growth and survival (van der Sande *et al.*, 2017a). For example, tropical forests on highly fertile soils show accelerated biomass dynamics (Baker *et al.*, 2009), which, together with high temperatures and water availability, exert a strong effect on forest biomass accumulation and dynamics. However, we know little about the effect of biotic and abiotic interactions over AGC dynamics in Andean forests. Although relatively few studies have evaluated the effects of abiotic factors on carbon dynamics along elevational gradients in Andean forests (Poorter *et al.*, 2017; van der Sande *et al.*, 2017a), such factors (i.e., local climate conditions and soil properties) are likely intertwined. More research is needed to disentangle the relative contribution of these factors to plant community composition and AGC patterns in Andean forests.

Global loss of forest cover is associated with an approximate 20% of CO_2 emissions from land-use and land-cover change, contributing to global warming (Parry *et al.*, 2007; Olsson *et al.*, 2019). Degraded forests cover about a quarter of the world's tropical forest area (Rutishauser *et al.*, 2015) and as high as 30% for the Neotropics (Grantham *et al.*, 2020), where in the last six decades, Andean forests, in particular, have degraded at an alarming rate of ~1% per year by logging and cattle grazing (Rodríguez Eraso *et al.*, 2013; Aide *et al.*, 2019). Forests clearing exerts increasing pressure on Andean forests in their ability to provide key ecosystem services (Jarvis *et al.*, 2010; Bustamante *et al.*, 2016), such as carbon stocks and water regulation dynamics, although the effect of such direct impacts can be complex. For example, while logging reduces above- and below-ground biomass stocks, the increased light exposure for lower tree strata may increase ecosystem productivity (Peña-Claros *et al.*, 2008). In addition, forest degradation may also alter soil-nutrient cycling rates, affecting carbon dynamics (van der Sande *et al.*, 2017b). Soil properties in the Andean mountains can vary significantly even over short distances (Moser *et al.*, 2011) due to heterogeneity within soil types and topography (van der Sande *et al.*, 2017b). Soil fertility also has indirect effects on soil organic matter (SOM) and its properties (C:N, N, P, K, Mg, Al and Ca), which might be correlated with AGC variations (Baker *et al.*, 2009; van der Sande *et al.*, 2017b). Given that Andean forests are particularly important for climate change mitigation (Leuschner *et al.*, 2013; Spracklen & Righelato, 2014; Duque *et al.*, 2021) and biodiversity conservation (Malizia *et al.*, 2020), understanding how biotic and abiotic factors affect Andean ecosystem function is essential to inform future science-based conservation actions.

The present study evaluates how abiotic, biotic conditions and past disturbances affect the AGC stocks and dynamics in forests of different successional stages along an elevational gradient in the Ecuadorian Andes. Specifically, I measured above-ground carbon stocks (hereafter AGC_{final}) and dynamics (AGC net change, AGC_{nc}; AGC productivity, AGC_{p}; AGC mortality, AGC_{k}), and addressed the following questions: 1) Do environmental conditions (air temperature, precipitation, and soil properties) control forest structure and composition (species richness) along an elevation gradient in Andean forests? 2) To what extent do abiotic factors (air temperature, precipitation, soil properties), biotic factors (species richness and functional leaf traits) and past human disturbance (Beta parameter) along an elevational gradient determine carbon stocks and changes in productivity? I hypothesize: 1) Environmental conditions, specifically air temperature and soil fertility, constitute the main filters for species richness. Here, I predict species richness will increase with increasing temperature and soil fertility (C/N, SOM, Ca, Mg, K, Al, and P); and 2) Temperature, soil properties and past human disturbances, with its subsequent forest successional stages, explain the carbon stocks and productivity rates along an elevational gradient. I predict that carbon stocks and productivity will be higher in warmer areas with fertile soils and advanced successional stages than colder areas, places with nutrient-poor soils, and earlier successional forests.

METHODS

Study site and experimental design

The study was carried out in the Pichincha forest dynamic monitoring transect established in 2015 (Pinto *et al.*, 2018; Teunissen van Manen *et al.*, 2020; Llerena-Zambrano *et al.*, 2021). This long-term study site consisted of 17 permanent plots (60 m x 60 m) located in the northwestern versant of the Ecuadorian Andes (0° 11' 17.8656" N, 0° 7' 36.21" S; -78° 34' 8.8566" W, -78° 54' 46.242" W). The plots were established along an elevational gradient of ca. 3000 m asl (632 m to 3507 m), each separated by ~300 m (±100 m) along the transect. To account for variation in forest structure, each plot included nine subplots (20 m x 20 m) for the census of trees (Chave *et al.*, 2003). The thermal amplitude (calculated by temperature sensors) and the precipitation range (calculated in the CHELSA platform), along the elevational gradient, are 7.43 to 23.43 ºC and 1250 to 2700 mm, respectively. The transect covers four montane forest ecosystems (MAE, 2012): Piedmont Forest (PMF), Lower Montane Forest (LMF), Montane Forest (MF), and Upper Montane Forest (UMF) (Gentry, 1995; Valencia *et al.*, 1999) (Figure 1); where the forest composition gradually changes along the elevation gradient.

The establishment of plots within each ecosystem followed four main criteria: (1) away from accessible roads to protect the plot's integrity, (2) continuous forest coverage (>70% of tree-crown cover) containing three forest strata (i.e., understory, sub-canopy, and canopy), (3) no recent signs of anthropogenic disturbance, and (4) located within a private reserve to avoid near-future land-cover changes. These forests represent mid (i.e., secondary) and late successional stands disturbed by cattle grazing, burning, and timber extraction during the 1980s and 1990s. Forest plots were established in secondary successional forests between 30 to 40 years of recuperation, evidenced in the forest composition, structure, and forest strata configuration (Teunissen van Manen *et al.*, 2019; Llerena-Zambrano *et al.*, 2021).

Estimations of Above-ground Carbon in Biomass (AGC)

Biomass censuses in 16 plots were conducted in 2015, 2017, and 2019. AGB data were standardized in each plot according to Pinto and Cuesta (2019) and RAINFOR protocols (Metcalfe *et al.*, 2008). Every tree, palm, and tree fern with ≥ 5 cm of diameter at breast high (DBH), or 1.30 m of height, was measured and recorded, identified to species level, tagged, and tracked through time (Girardin *et al.*, 2014); the point of measure (POM) was marked for subsequent measurements. Tree total height (H), in meters, was estimated visually, and 10% of the population within each plot was randomly measured with the use of clinometers. This data was used to develop a tree H:DBH model at the plot level using the function *modelHD* of the

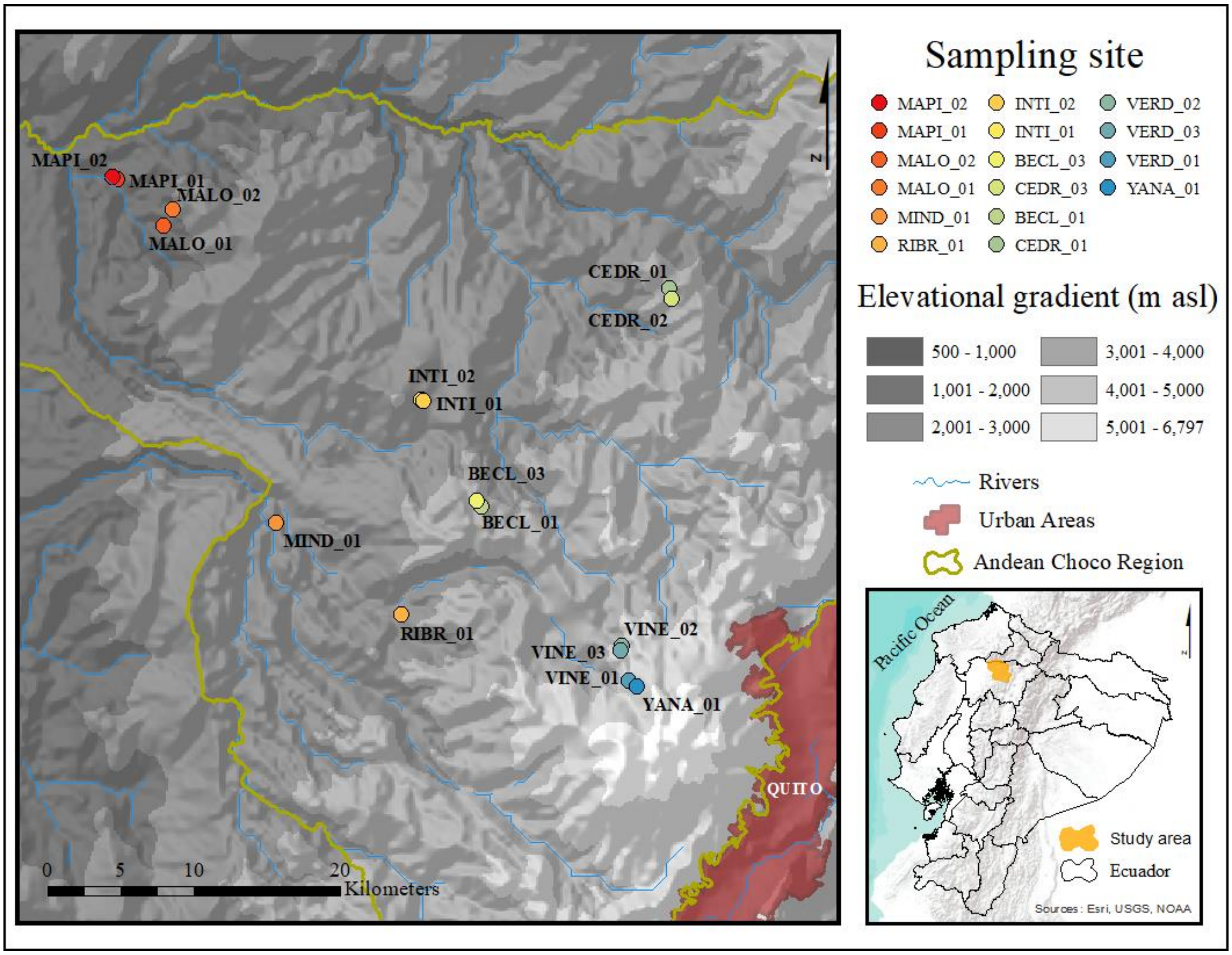


Figure 1. Long-term monitoring system in the western flank of the Ecuadorian Andes. Dots represent long-term permanent plots distributed in an elevational gradient, represented by the grayscale. The transect covers four montane forest ecosystems: Piedmont Forest (PMF; 500-1000 m asl), Lower Montane Forest (LMF; 1,001-2000 m asl), Montane Forest (MF; 2001-2900 m asl), and Upper Montane Forest (UMF; 2900-3600 m asl).

BIOMASS package in R (Réjou-Méchain *et al.*, 2017). The generation of a H:DBH model serves two roles: 1) it avoids under- and over-estimations of tree height at lowlands and highlands, respectively, and 2) it homogenizes above-ground biomass (AGB hereafter) estimates along the elevational gradient (Phillips *et al.*, 2019). The function utilizes four different models; two log-log polynomial models, a three-parameter Weibull model, and the two-parameter Michaelis-Menten model. The function with the lowest Residual Standard Error (RSE) and bias were considered the best estimate for each respective plot, following Duque *et al.* (2021) (Appendix A).

Carbon estimations were based on data integrated from all plots in the BIOMASS package (Réjou-Méchain *et al.*, 2017). The BIOMASS package first corrects and uses the last validated taxonomic names, and then determines the wood density values per species using the *getWoodDensity* function. This function assigned the WD values to each individual found in the plots according to available literature (Chave *et al.*, 2006; Zanne *et al.*, 2009). In cases where the WD value at the species level could not be assigned, the average value for the genus or family level was used. For individuals without a taxonomic identification, the average WD value of all other individuals found within the plot was used (Peña & Duque, 2013). Finally, for AGB estimates at the individual and plot level, the BIOMASS package uses a pantropical allometric equation developed by Chave *et al.* (2014) for tropical forests, defined as $AGB = 0.0673 \times (WD \times DBH^2 \times H)^{0.976}$. Individual tree values (Kg) were summed to estimate the biomass at the plot level, which were then scaled to megagram (Mg) at the hectare level. To obtain above-ground carbon (AGC hereafter), I multiplied the individual plot AGB value by a conversion constant of 0.465 (Martin *et al.*, 2018).

Estimations of Above-ground Necromass Carbon Stocks (NCS) and Soil Organic Carbon (SOC)

To estimate the total carbon allocated between censuses, and as a complement of AGC, two of the main carbon pools (necromass and soil) were evaluated in 2015 and 2019. All leaf litter, fine wood debris (FWD), and sticks (diameter < 10 cm), were collected within nine nested subplots (0.5 cm x 0.5 cm) per plot (Pinto *et al.*, 2018). Samples were stored in bags, dried in the laboratory, and weighed (g) once they reached a stable dry weight (Ananias, 1998, Womac *et al.*, 2005). The individual values per subplot were added and then transformed to Mg to estimate mass per hectare. The NCS calculated per plot was converted to carbon units by applying the conversion factor, 0.465 (Martin *et al.*, 2018)

Soil samples within three of the nine nested subplots (0.5 cm x 0.5 cm) were collected at two depths (i.e., the first two soil horizons, H and A), where the greatest amount of organic matter is concentrated. To determine the sampling depth along the gradient, soil pits of 1 m^3 were dug outside the plots, where soil horizons were defined and measured (Pinto *et al.*, 2018). Using a soil borer, the soil samples were collected and transported to the laboratory for processing. Soil samples for the first census were analyzed for C (%), N (%), and S (%) at the University of Amsterdam (UVA) using an Elementar-Organic Elemental Analysis (C / N elemental ratios of up to 7000:1 accuracy). For the 2019 census, macro-and micronutrient analyses were performed at Universidad de las Americas (UDLA) in Ecuador. To determine bulk density, I collected three undisturbed soil cores (4 cm of diameter x 5 cm in height) per plot, using Kopecky's still rings (Melo *et al.*, 2017), in an area free of litter and FWD. Soil Organic Carbon (SOC) was determined as C content (Mg ha^{-1}) = (ρ * h * C), where ρ = bulk density of the soil measured in g / cm^3, h = depth at which the sample was taken (cm), and C = percentage by weight of organic carbon in the soil (Hribljan *et al.*, 2016).

Leaf functional traits (LFT)

LFT were analyzed at a community scale to generate community indices (scores), where the weighted mean values for each functional trait were analyzed (Ackerly & Cornwell, 2007). Community-Weighted mean values of morphological leaf traits (CWM_LFT) were taken from Llerena-Zambrano *et al.* (2021) and linked to the ecological data associated with each plot. Specifically, the following leaf functional traits were included: (1) leaf area (LA), (2) specific leaf area (SLA), (3) leaf blade thickness (LBT), and (4) Leaf dry matter content (LDMC).

Climate data

Two temperature sensors were established (TidbiT® v2 Temp Logger) on each plot in 2015, one buried 10 cm below ground surface (BG_{10cm}) and the other 10 cm above the ground surface (AG_{10cm}) to record the air temperature. To measure relative humidity as a complement to the temperature data, a "HOBO Pro v2 Temp / RH" sensor was established at 1 m above the ground surface, this sensor also provides an additional above-ground temperature record (AG_{1m}). The reported values in this study correspond to the main ecological filters that facilitate nutrient assimilation in Andean forest species (Leuschner *et al.*, 2007; Salinas *et al.*, 2011) such as, the minimum (minDT), mean (meanDT) and maximum (maxDT) daily temperatures (Appendix B), calculated across a 2016-2020 period. The ordination technique (PCA) was used to reduce the number of temperature variables that describe a pattern ($PCA1_{Temp}$), instead of individual variables: six above-ground temperatures (three to 10 cm and three to 1 m), and three below ground (10 cm). Then the PCA axes values were used as one of the climatic explanatory variables in our analyses (Appendix B), reducing the multicollinearity and better captures the temperature variations along the elevational gradient (Báez *et al.*, 2015; Llerena-Zambrano *et al.*, 2021). Mean annual precipitation (MAP) was extracted from the CHELSA bioclimatic datasets at 30 ArcSecond resolution (~1km^2 at the equator) (Karger *et al.*, 2017; Teunissen van Manen *et al.*, 2020).

Statistical Analysis

Species Richness and forest structure

To estimate tree-species richness, while also accounting for differences along the elevational transect, I used observed species richness (SR) and rarefied species richness (Homeier *et al.*, 2010). I used the Gotelli and Colwell (2001) individual-based rarefaction method, which takes the number of species expected in a sample of 220 trees from a 3600 m^2 plot, where 220 corresponds to the smallest number of trees found in one of the 16 plots (Homeier *et al.*, 2010). Bivariate regressions were performed to assess relationships between richness with elevation, temperature and precipitation throughout the transect, and a non-metric multidimensional scaling analysis (NMDS) was done to evaluate the similarity of arboreal communities or plots along the elevational gradient. Additionally, basal area (BA), H, DBH, square root DBH (to provide equal representability to all diametric classes and reduce the biased effect of the biggest and smallest tree diameters), and WD were evaluated across the elevational gradient to determine structural plots variations.

Effects of disturbance on Above-ground carbon (AGC) stocks and dynamics

To assess the effect of past human disturbances on carbon stocks and productivity, a size-dependent parameter of mortality (β) was performed in RStudio, with a binomial error structure (Coomes & Allen, 2007). β derives from the logistic regression logit (pD) = $a+bD$, where pD is the probability of death and *D* is the initial stem size. This parameter discriminates plots as ranging from a) plots influenced by competitive thinning following internal disturbance (low β) to b) plots more influenced by active disturbances (high β) (Duque *et al.*, 2021).

Above-ground carbon (AGC) stocks and dynamics variation along the elevational gradient

Bivariate linear regression analyses were used to assess the variation of carbon stocks along the elevation gradient. I tested a series of different metrics for AGC stocks and productivity, such as AGC of 2019 census (AGC_{final}), AGC net change (AGC_{nc}), AGC productivity (AGC_{p}), and AGC mortality (AGC_{k}), as well as several possible predictor variables, which included climate factors, CWM_LFT, soil properties, and disturbance metrics (Appendix C). Environmental variables such as daily temperatures and annual precipitation were highly correlated (Pearson = -0.9816, p <0.000; Pearson = -0.8439, p <0.0001, respectively) with elevation, and thus elevation was not included in the bivariate analyses (Appendix D). The AGC net change (Mg ha^{-1} y^{-1}) was calculated as the difference between the AGC stocks in the last census (2019) and the AGC stocks in the initial census (2015); this value was then divided by the elapsed time period (4 years) (Duque *et al.*, 2021). To estimate the AGC productivity (Mg ha^{-1} y^{-1}) referred to as AGC growth of survivors and recruits between 2015 and 2019, I considered the growth of living trees between that 4-year period, the growth of 2017 recruits for a two-year period (2017-2019), and the recruits at the time of the last census in 2019 (Phillips *et al.*, 2019). To avoid overestimations of the overall increase in AGC due to recruitment (Feeley *et al.*, 2011), I subtracted the AGC corresponding to a tree of 4.99 cm per recruit or individuals with DBH ≥ 5 cm; in this way, I consider only the increment over 5 cm as growth in recruits (Talbot *et al.*, 2014). To annualize productivity, the individual growth values were summed to obtain a per plot value, which was then divided by the time interval between censuses (2 or 4 years). AGC mortality (Mg ha^{-1} y^{-1}) was calculated as the sum of the AGC of all individuals that died between censuses (Duque *et al.*, 2021), divided by the time between measurements.

Biotic and abiotic drivers of spatial variation of Above-ground carbon (AGC) stocks and dynamics

Structural equation model (SEM) analyses were performed to determine the influence of biotic, abiotic and disturbance factors as possible determinants of carbon stocks and productivity variation along the transect (Grace, 2006; Shipley, 2016; van der Sande *et al.*, 2017b). The SEMs included climate, CWM-LFT, soil properties, species richness, the Beta-parameter as a disturbance proxy, and the four different AGC metrics as exogenous variables. I performed a series of pair-wise Pearson-correlation analyses to determine explanatory variables to be used in the SEM, among all possible predictor values: AGC metrics, abiotic factors (temperature, precipitation, and disturbance parameter), and biotic factors (species richness and CWM-LFT) (Appendix E). To determine significant sources of variation in AGC stocks and dynamics across the gradient, I used five SEM models for ACG_{final}, nine for AGC_{nt}, six for $AGC_{p,}$ and three for AGC_{k} (Appendix F). I used the Akaike information criterion (AIC) and Root mean square error (RMSE) to identify the most parsimonious model per metric following Grace (2006).

To evaluate the significant relationships (total, direct and indirect effects) between endogenous and exogenous variables, I used a bootstrapping analysis that assesses the mean, and 95% confidence intervals (CI), of the selected AGC models (Appendix G to J). To assess the importance of each group of explanatory variables for explaining changes in the AGC stocks and dynamics along the elevational gradient, I used estimates of standardized coefficients in each path of the model and R^2 for each of the AGC endogenous variables. All statistical analyses were performed in JMP 8 (Inc., 2008), SPSS AMOS 27 (Arbuckle, 2006), PRIMER 6 (Clarke & Gorley, 2006), and R Studio statistical software (RCoreTeam, 2017).

RESULTS

Species richness (SR) and forest structure

A total of 7432 stems (dbh ≥ 5 cm) were measured and a total of 82 families, 205 genera, and 432 species were identified; 90% of the stems were identified at the species level, 7% at family and genus level, and only 3% were unidentified. The most abundant families in the transect were Lauraceae (32 spp.), Melastomataceae (31 spp.), Rubiaceae (29 spp.), Fabaceae (26 spp.), and Moraceae (26 spp.). The lowest section of the transect (piedmont forest [PMF] between 600 and 1000 m asl) was characterized by common lowland tree families such as Fabaceae, Rubiaceae, and Moraceae. At mid-elevation (between 1200 and 2900 m asl), Lauraceae and Melastomataceae families were dominant. In the upper montane forest (UMF; over 2900 m asl), Melastomataceae, Asteraceae, and Solanaceae contributed to the majority of species. *Dussia lehmannii* (632-2492 m asl), *Turpinia occidentalis* (632-3109 m asl), *Critoniopsis occidentalis* (1018-2932 m asl), *Guarea kunthiana*, *Miconia clathrantha* (653-3109 m asl), and *Miconia theaezans* (1018-3109 m asl) were the more common species, present in at least in 50% of the plots throughout the transect.

The bivariate regression analysis explained the SR variation along the elevational gradient (Figure 2). SR decreased as elevation increased ($R^2=0.69$, $p<0.0001$) (Appendix C), where MALO_02, at 800 m asl, was the plot with the highest number of species (113 spp.), and YANA_01, at 3500 m asl, showed the lowest number (18 spp.) (Table 1). Species richness

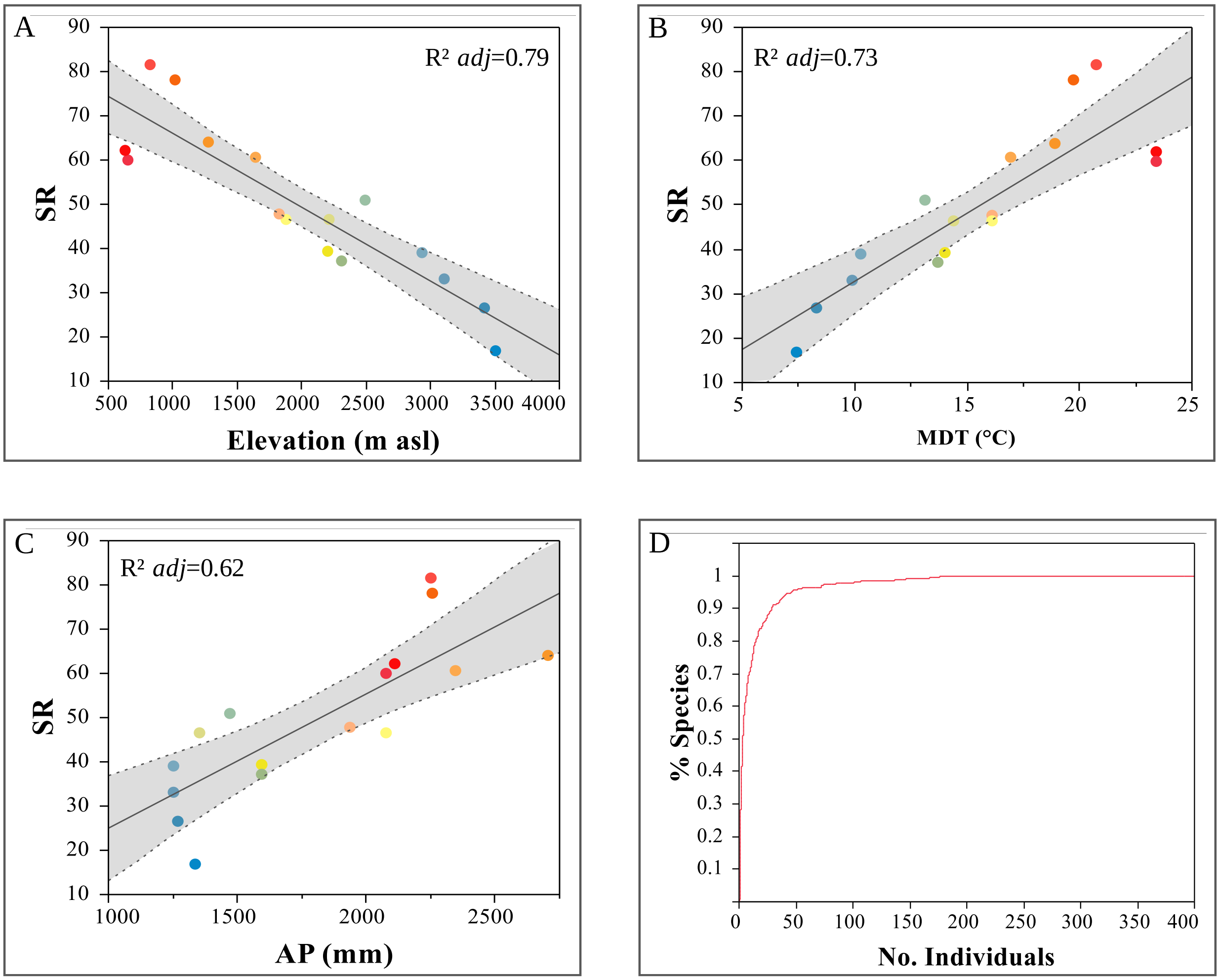


Figure 2. Bivariate relationships between rarefied species richness ($SR_{RAREFIED}$) and A) elevation, B) mean daily temperature (MDT), C) annual precipitation (AP), and D) a cumulative frequency curve of trees abundance and species percentage in the tropical Andean montane forests (TAMF) of Pichincha, Ecuador. R^2 *adj* = Adjusted coefficient of determination of the overall model.

Table 1. Climate and forest structure conditions of 16 permanent plots along an elevational transect in the western flank of the Ecuadorian Andes. The table also describes the observed species richness ($\mathrm{SR}_{\mathrm{OBSERVED}}$); rarefied species richness ($\mathrm{SR}_{\mathrm{RAREFIED}}$), absolute basal area (BA), tree density (TD), mean diameter at breast height (DBH), mean tree height (H), mean square root DBH ($\mathrm{DBH}_{\mathrm{SQR}}$), mean wood density (WD), annual temperature (AP), and mean daily temperature (MDT), and minimum mean daily temperature (minDT) per plot.

Plot ID	**Elevation (m asl)**	**SR OBSERVED**	**SR RAREFIED**	**TD (n)**	**BA (m2)**	**DBH (cm)**	**H (m)**	**$\mathrm{DBH}_{\mathrm{SQR}}$**	**MWD (g cm-3)**	**AP (mm)**	**MDT (°C)**	**minDT (°C)**
MAPI_02	632	79	62.04	364	8.55	13.45	13.39	3.48	0.50	2111	23.43	22.23
MAPI_01	653	77	59.93	356	8.84	14.05	13.75	3.55	0.51	2075	23.43	22.23
MALO_02	827	108	81.51	406	12.07	14.18	13.15	3.51	0.60	2253	20.72	19.65
MALO_01	1018	101	78.12	378	8.83	14.16	12.43	3.58	0.57	2255	19.70	18.79
MIND_01	1277	86	63.92	419	9.67	13.07	11.52	3.41	0.50	2704	18.88	17.23
RIBR_01	1640	86	60.65	537	8.60	12.14	10.55	3.37	0.55	2347	16.94	15.22
INTI_02	1829	73	47.66	561	9.02	11.42	10.72	3.22	0.37	1939	16.12	14.46
INTI_01	1879	60	46.49	435	10.68	13.59	10.86	3.47	0.42	2076	16.12	14.30
BECL_03	2203	42	39.25	256	6.87	15.06	10.04	3.69	0.54	1595	14.01	12.13
CEDR_03	2212	52	46.53	364	11.38	15.10	11.32	3.64	0.54	1351	14.40	12.66
BECL_01	2313	43	37.19	328	8.31	15.68	13.56	3.83	0.56	1595	13.72	12.14
CEDR_01	2492	66	50.97	474	11.13	13.98	10.08	3.56	0.54	1471	13.13	11.38
VERD_02	2932	51	38.98	473	7.84	12.21	10.79	3.36	0.52	1251	10.29	7.96
VERD_03	3109	39	33.13	464	8.93	12.63	8.51	3.37	0.53	1251	9.86	7.98
VERD_01	3421	31	26.68	625	10.65	12.54	8.01	3.42	0.55	1271	8.31	6.33
YANA_01	3507	17	17	220	9.77	18.64	11.25	4.07	0.59	1337	7.43	5.21
Mean (±SD)		63 (±18)	49 (±5)	416.25 (±106.75)	9.45 (±1.41)	13.87 (±1.74)	11.25 (±1.70)	3.53 (±0.21)	0.52 (±0.06)	1805 (±468)	15.41 (±4.99)	13.74 (±5.32)
R2 adj		0.75	0.79	-0.05	-0.07	-0.03	0.50	-0.008	-0.04	0.69	0.99	0.99
p value		<0.0001	<0.0001	0.64	0.98	0.46	<0.01	0.37	0.57	<0.0001	<0.0001	<0.0001

increased with temperature and decreased as air conditions became colder (Figure 2A). A similar trend was observed with annual precipitation (Figure 2B). After comparing rarefied species numbers and observed species, the regression trend was similar but the slope curve was not as steep because of the slightly higher tree densities at lower elevations (Homeier *et al.*, 2010). Additionally, the frequency curve shows no oligarchic species or the dominance of species over the rest (Figure 2D), suggesting a high species turnover between plots, along the transect. The NMDS confirmed the aggregation of the species composition in four major groups (Figure 3), related to the type of forest and suggesting a high dissimilitude rate and high rareness species patterns.

The mean tree-height across the gradient was 11.25 ±1.70 m, with the tallest trees being present in the lowlands, 13.18 ± 0.56 m, below 1000 m asl. Tree-height significantly decreased as elevation increased (Table 1), where the smallest trees (9.64 ± 1.62 m) were observed over 2900 m asl. The mean basal area in the transect was 9.45 ±1.41 m^2, and I did not observe significant differences along the elevation gradient (Table 1). The mean WD and DBH for all plots was 0.52 ± 0.06 g cm^{-3} and 13.87 ±1.74 cm, respectively. I did not observe significant differences along the elevation gradient for WD and DBH (Table 1).

Above-ground Carbon stocks and dynamics

Most of the AGC metrics, except AGC_k, showed a significant relationship with climate ($p < 0.05$) (Table 2). The mean AGC_{final} reported for the 16 plots was 81.4 ± 25.9 Mg C ha^{-1}, reaching its highest values, 157.6 Mg C ha^{-1}, at 800 m asl and decreasing up to 46.4 Mg C ha^{-1} at 3100 m asl, indicating that AGC_{final} stocks significantly increased concomitantly with temperature. The mean AGC_{nc} and AGC_p across the transect were 1.20 ± 0.89 Mg ha^{-1} y^{-1} and

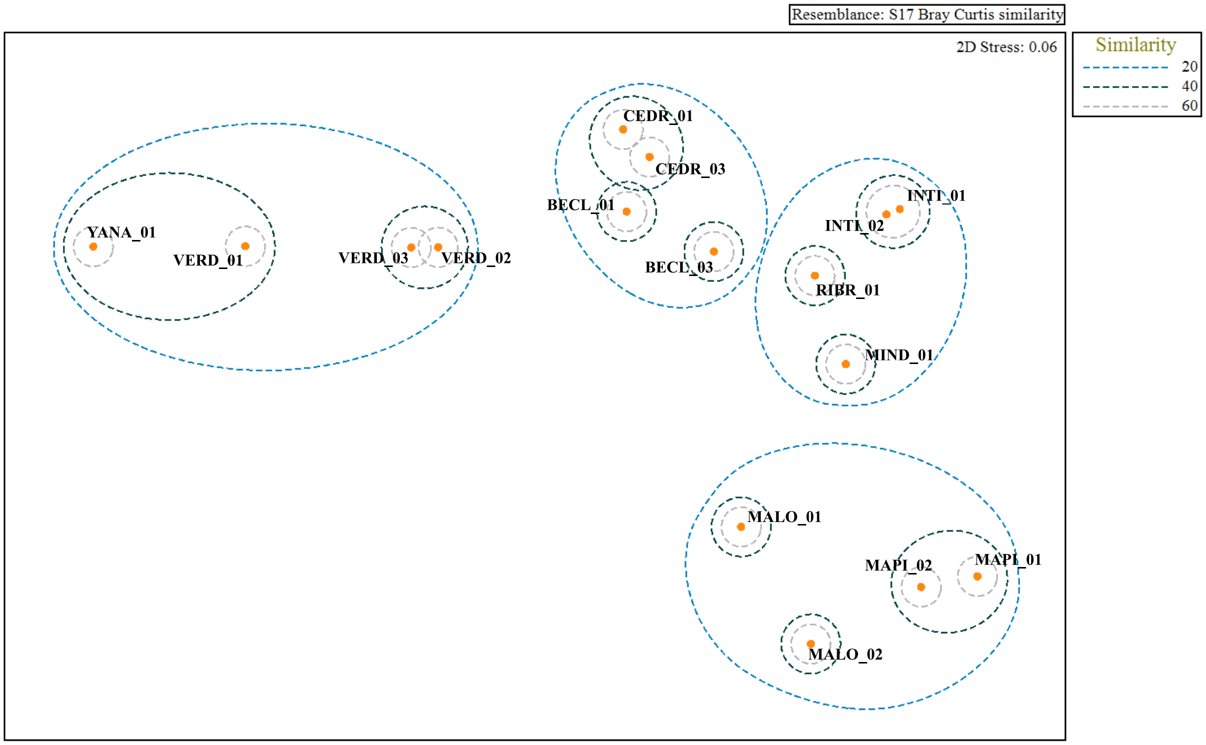


Figure 3. Non-metric multidimensional scaling analysis (NMDS) to evaluate the similarity of arboreal communities (plots) along an elevational gradient in the Andean forest in the west flank of Pichincha province. The similarity distance used is Bray-Curtis with the presence-absence scores of the species as the main grouping criterion.

Table 2. Above-ground biomass stocks variations for 16 permanent plots along an elevational transect during three censuses in a long-term monitoring system in the northwest flank of Pichincha province in the Ecuadorian Andes. AGC1= above-ground biomass in 2015, AGC_{final}= above-ground biomass in 2019, AGC_{nc}= above-ground biomass net change, AGC_p= above-ground biomass productivity, and AGC_k= above-ground biomass mortality.

Plot ID	**Elevation (m asl)**	**AGC_1 (Mg ha^{-1})**	**AGC_{final} (Mg ha^{-1})**	**AGC_{nc} (Mg ha^{-1} y^{-1})**	**AGC_p (Mg ha^{-1} y^{-1})**	**AGC_k (Mg ha^{-1} y^{-1})**
MAPI_02	632	73.30	80.07	1.69	2.11	0.40
MAPI_01	653	76.68	84.80	2.03	3.04	1.02
MALO_02	827	147.91	157.57	2.42	2.77	0.44
MALO_01	1018	92.90	96.58	0.92	2.87	2.14
MIND_01	1277	84.96	91.79	1.71	2.56	0.79
RIBR_01	1640	62.87	67.83	1.24	3.54	2.42
INTI_02	1829	62.90	66.79	0.97	1.65	0.83
INTI_01	1879	87.29	93.61	1.58	1.66	0.31
BECL_03	2203	58.34	63.28	1.23	1.80	0.62
CEDR_03	2212	94.27	99.60	1.33	3.10	1.27
BECL_01	2313	61.19	73.64	3.11	3.55	0.62
CEDR_01	2492	84.04	84.89	0.21	1.81	1.33
VERD_02	2932	45.10	46.57	0.37	0.70	0.36
VERD_03	3109	44.91	46.43	0.38	0.77	0.53
VERD_01	3421	68.52	69.26	0.19	1.70	1.10
YANA_01	3507	75.92	75.42	-0.13	1.08	0.51
Mean (±SD)		76.32 (±24.39)	81.4 (±25.95)	1.20 (±0.89)	2.16 (±0.92)	0.92 (±0.62)
R^2 Adj		0.20	0.28	0.39	0.32	-0.03
***p* value**		0.049	0.019	0.006	0.013	0.499

2.16 ± 0.92 Mg ha^{-1} y^{-1}, respectively. Plots from the lower end of the transect, on average, showed a higher AGC_{nc} (1.7 ±0.6 Mg ha^{-1} y^{-1}) and AGC_p (2.7 ±0.4 Mg ha^{-1} y^{-1}) than plots at higher elevations (> 2900 m), 0.2 ± 0.2 Mg ha^{-1} y^{-1} and 1.1 ± 0.5, respectively (Table 3). The mean AGC_k was 0.92 (±0.62) Mg ha^{-1} y^{-1} and did not change significantly across the elevational gradient (Table 3). The net increase was the result of 1.07 Mg ha^{-1} y^{-1} greater mean in AGC productivity (1.99 Mg ha^{-1} y^{-1}) than the mean AGC mortality (0.92 Mg ha^{-1} y^{-1}).

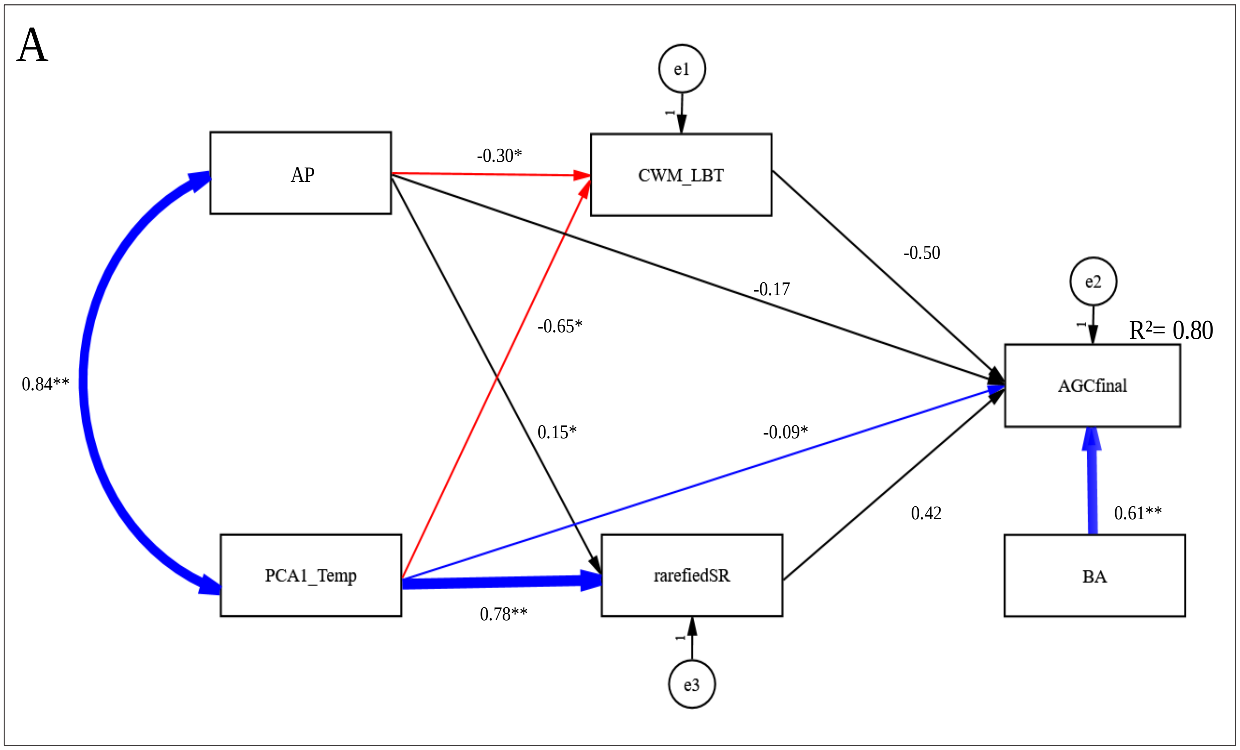
Given that $PCA1_{Temp}$ and AP were highly correlated with elevation (Appendix E), I only used *Climate* variables to explain variations in these variables across the elevational gradient, also AP presented a high correlation with $PCA1_{Temp}$ in all models ($r=0.83, p<0.01$). In addition, no significant differences were found for NCS and SOC between census ($p > 0.05$) or for biotic and abiotic sources of variation. The mean NCS and SOC for all plots was 6.25 ± 2.43 Mg ha^{-1} and 96.54 ± 29.60 Mg ha^{-1}, respectively (Appendix C). Given these results, NCS and SOC were considered as explanatory variables for AGC stocks and dynamics in this study.

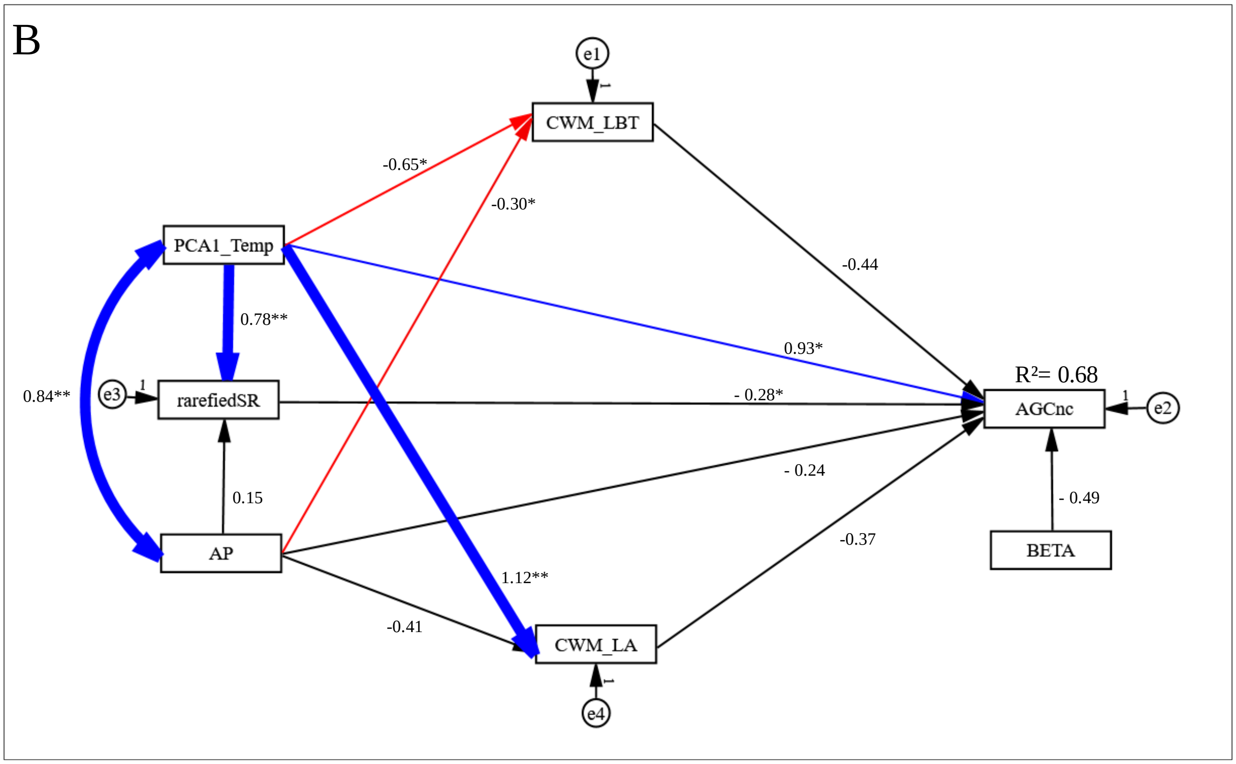
The best fit SEMs for AGC metrics were $PCA1_{Temp}$, AP, rarefied SR, and CWM_LBT in three of the four metrics used in this analysis (Appendix F). The selected model for AGC_{final} (lowest AIC and RMSE values) showed a positive significant relationship with BA ($p < 0.01$) and $PCA1_{Temp}$ ($p < 0.05$), where rarefied SR, CWM-LBT, and AP did not have a significant effect on AGC_{final} (Appendix G). However, rarefied SR was positively related ($p < 0.01$) to $PCA1_{Temp}$ (Figure 4A), and both $PCA1_{Temp}$ and AP showed a significant negative effect ($p < 0.05$) with CWM-LBT (Appendix G).

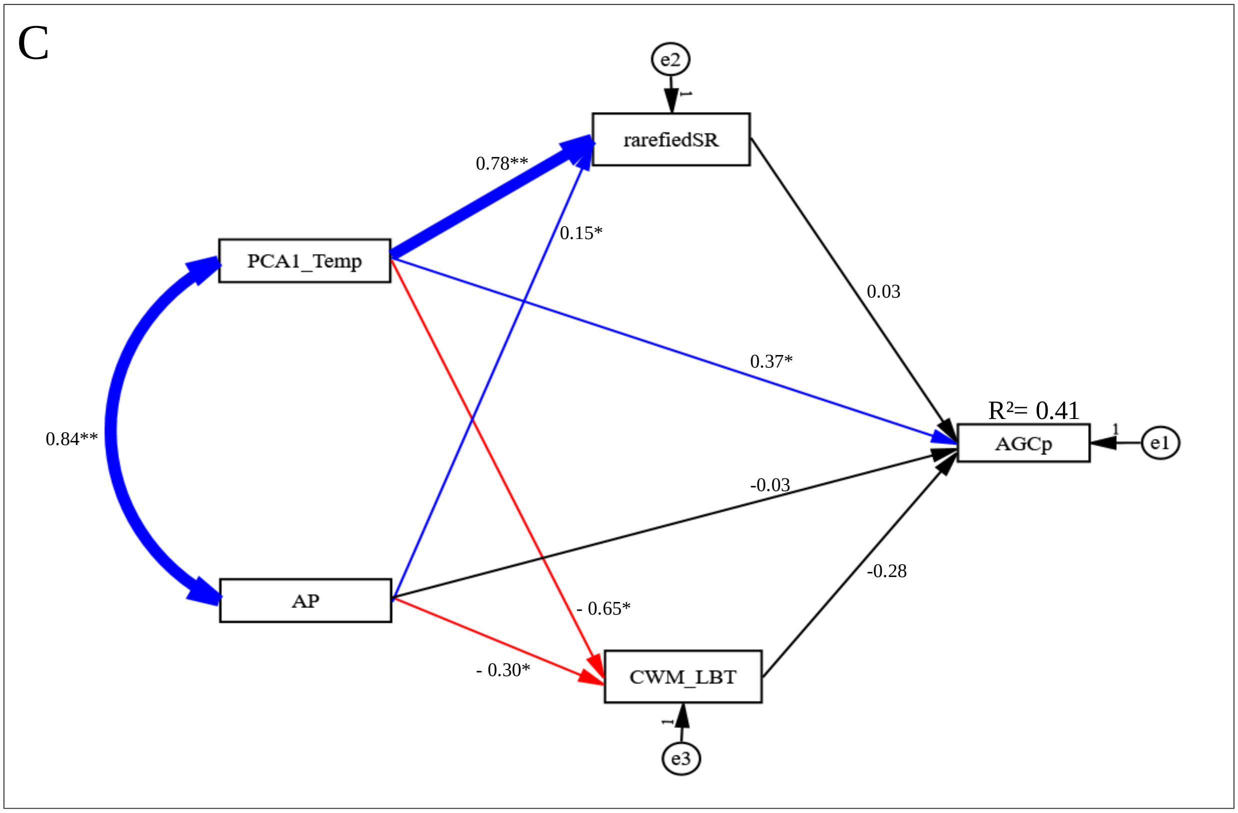
Only abiotic parameters such as $PCA1_{Temp}$ determined the main sources of variation in most of the ACG dynamics variables, which has a positive and direct significant effect over AGC_{nc} ($p < 0.05$) (Figure 4B) and AGC_p ($p = 0.05$) (Figure 4C). AGC productivity did not have a

Table 3. Mean above-ground biomass stocks (± SD) variations by elevation range in four years period in a long-term monitoring system in the northwest flank of Pichincha province in the Ecuadorian Andes. AGC_1= above-ground biomass in 2015, AGC_{final}= above-ground biomass in 2019, AGC_{nc}= above-ground biomass net change, AGC_p= above-ground biomass productivity, and AGC_k= above-ground biomass mortality.

Elevation range (m asl)	**AGC_1 (Mg ha^{-1})**	**AGC_{final} (Mg ha^{-1})**	**AGC_{nc} (Mg ha^{-1} year^{-1})**	**AGC_p (Mg ha^{-1} year^{-1})**	**AGC_k (Mg ha^{-1} year^{-1})**
600-1000	97.7 (±34.6)	104.8 (±35.9)	1.7 (±0.6)	2.7 (±0.4)	1.0 (±0.8)
1001-2000	74.5 (±13.5)	80.0 (±14.7)	1.4 (±0.3)	2.4 (±0.9)	1.1 (±0.9)
2001-2900	74.5 (±17.5)	80.4 (±15.6)	1.5 (±1.2)	2.7 (±0.9)	1.0 (±0.4)
2901-3500	58.6 (±16.0)	59.4 (±15.1)	0.2 (±0.2)	1.1 (±0.5)	0.6 (±0.3)


A
e1
1
AP
-0.30*
CWM_LBT
-0.50
-0.17
-0.65*
e2
1
R²= 0.80
0.84**
AGCfinal
0.15*
-0.09*
0.61**
0.42
PCA1_Temp
rarefiedSR
BA
0.78**
1
e3


B
e1
1
CWM_LBT
-0.65*
-0.30*
PCA1_Temp
-0.44
0.78**
0.93*
R²= 0.68
0.84**
e3
1
rarefiedSR
- 0.28*
AGCnc
1
e2
- 0.24
0.15
- 0.49
AP
-0.37
BETA
1.12**
-0.41
CWM_LA
1
e4


C
e2
1
rarefiedSR
0.78**
0.15*
PCA1_Temp
0.03
0.37*
0.84**
R²= 0.41
AGCp
1
e1
-0.03
-0.28
AP
- 0.65*
- 0.30*
CWM_LBT
1
e3

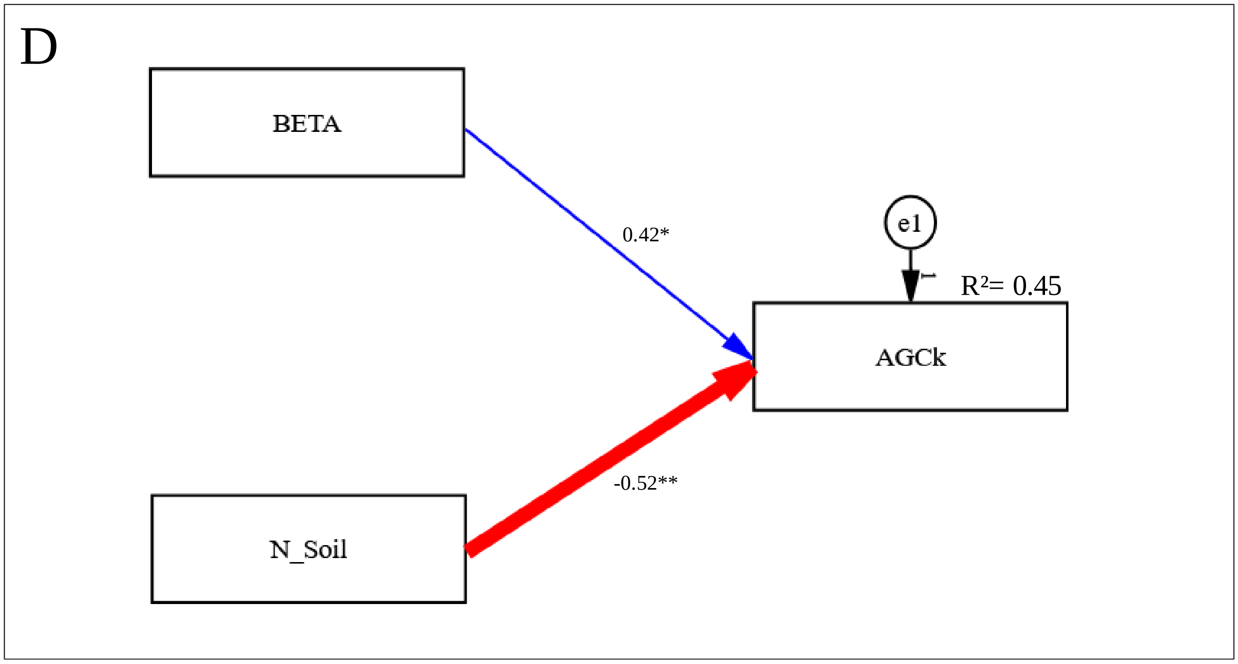

D
BETA
0.42*
e1
1
R²= 0.45
AGCk
-0.52**
N_Soil

Figure 4. Structural equation models (SEMs) used to evaluate the effects of biotic, abiotic, and the size-dependent probability of mortality (β) on above-ground carbon dynamics. A) AGC_{final} = above-ground carbon stock in 2019, B) AGC_{nc} = above-ground carbon net change (Mg C ha^{-1} y^{-1}), C) AGC_{p} = above-ground carbon productivity (Mg C ha^{-1} y^{-1}), and D) AGC_{k} = above-ground carbon mortality (Mg C ha^{-1} y^{-1}). Where, $PCA1_{Temp}$ = mean daily temperature, AP = annual precipitation, BA = basal area, rarefied SR = rarefied species richness per plot, CWM_LBT = community weighted mean leaf blade thickness, CWM_LA = community weighted mean leaf area. The values over the arrows correspond to the linear coefficients of the predictor variables. Positive numbers and blue arrows represent positive relationships, negative numbers with red arrows determine negative relationships, and black arrows illustrate non-significant relationships between variables. Thickest arrows define highly significant relationships ($p \leq 0.01$), thinner arrows determine significant relationships ($0.01 < p \leq 0.05$). R^2 = Coefficient of determination of the overall model.

significant association with the biotic predictor variables (Appendix I), and both rarefied SR and CWM-LBT were positive and negatively correlated to $PCA1_{Temp}$ ($p < 0.05$) respectively (Figure 4C and Appendix I). AGC_{nc} presents a similar pattern (Appendix H and Figure 4B). CWM-LBT and CWM-LA were not significant predictors of AGC_{nc} spatial variation along the elevation gradient ($p > 0.05$). Yet, CWM-LBT was negatively affected by $PCA1_{Temp}$ and AP ((p < 0.01), where CWM-LA and rarefied SR were positively affected by $PCA1_{Temp}$ ($p < 0.01$) (Figure 4B). This emphasizes the positive relationship between AGC dynamics and temperature, and a negative non-significant relationship between AGC_{nc} and AGC_p with precipitation along the gradient. The β-parameter showed a negative non-significant tendency with AGC_{nc} in the model (p=0.06) (Appendix H; Figure 4B). Unlike AGC_{nc} and AGC_p, AGC mortality was not correlated with climate nor with the biotic explanatory variables in the model (Appendix E). AGC_k showed a significant association with N_{Soil} and the β parameter (Appendix J, Figure 4D). AGC_k was positively associated with the β parameter ($p < 0.05$), and highly negatively related to soil nitrogen ($p < 0.01$).

DISCUSSION

Forest composition and structure

I found that tree species richness decreased with increasing elevation, a pattern found in previous studies aimed at assessing spatial patterns of plant diversity in Andean forests along elevation gradients (Gentry, 1995; Lieberman *et al.*, 1996; Young *et al.*, 2002; Homeier *et al.*, 2010). I recorded the highest levels of species richness in the piedmont forests under 1000 m asl, which coincides with the warmest and wettest area along the transect (Table 1). A decline in tree species richness with elevation was related to declining temperatures and a reduction in annual precipitation (Figure 2). Water availability and temperature are essential for plant growth because they inject the energy input into ecosystems, and a limitation of these resources influences richness patterns and community configuration (Kessler & Kluge, 2008); previous findings suggest strong environmental filtering at both low and high elevations (Chase & Leibold, 2002; Rahbek, 2005; Colwell *et al.*, 2008; Luo *et al.*, 2019a). The observed decline in species richness and increased dissimilarity in community composition above 1200 m asl, according to NMDS analysis, evidently involves other environmental factors that influenced our results (Figure 3). For example, a reduction in land area with increasing elevation (Jiménez-Castillo *et al.*, 2007), coupled with increased cloud cover (Jarvis & Mulligan, 2011; Fyllas *et al.*, 2017), likely reduced the photosynthetic capacity of species at high elevation sites (Malhi *et al.*, 2017). In the same forests at my study site, Llerena-Zambrano *et al.* (2021) found a marked shift in species resource acquisition strategies, where species with acquisitive strategies dominate the lower end of the transect, whereas species with more conservative strategies dominate the upper section of the transect. Here, species with acquisitive strategies have a short leaf lifespan with large specific leaf area (SLA) (i.e., efficient deployment of leaf area per unit biomass invested), high nitrogen (N) concentration, and thus, high assimilation and respiration rates. Alternatively, species with conservative strategies show low SLA and slow metabolic rates (Llambí *et al.*, 2003; Poorter & Bongers, 2006). Collectively my results most likely represent a combined strategy conferring tolerance to wind dryness and low-temperature stress together with lower energy availability (Niinemets, 2001; Vendramini *et al.*, 2002). Moreover, I did not find that oligarchic species, or the dominance of species, over the rest along the gradient, which agrees with the hypothesis of high species turnover along the elevational gradient (Hall *et al.*, 1998; Homeier *et al.*, 2010). This result suggests that even under mid successional stages, the turnover of species as a response to intrinsic local environmental conditions is still evident in Andean forests (Stephenson & van Mantgem, 2005). However, further empirical studies are needed to confirm this possible source of variation.

Our results also showed that the height of trees decreased as elevation increased, a trend similar to those found in other studies (e.g., Lieberman *et al.* (1996)). I observed a decrease in the tree height from ca. 13.2 m on average at piedmont (600 - 1000 m asl) to ca. 9.5 m at the upper montane forest over the 2900 m asl. This result is similar to those found by Homeier *et al.* (2010), who report a decrease in tree height from ca. 14 m at 1800 m asl to ca. 7 m at 2450 m asl. Collectively, these findings highlight the importance of the inclusion of tree height in AGC estimations in Andean forests, where height is likely the dominant factor influencing reported declines in above-ground carbon stocks with increasing elevation (Girardin *et al.*, 2010; Feldpausch *et al.*, 2012); other estimators (e.g., DBH, BA, WD) do not typically change across elevational transects (Peña *et al.*, 2018). The absence of a climate effect on WD found in my study may be explained by the age of the secondary successional forest, dominated by mid- and late-successional species. Overall, these results confirm those of other studies that also show a lack of association between climate and BA and DBH, where Girardin *et al.* (2014) found no trend for changes in the basal area across elevational transects in Bolivia, Peru, and Ecuador, and Leuschner *et al.* (2013) who also found no significant decrease in BA and DBH with an increase in elevation.

AGC stocks and dynamics variation along elevational gradients in Andean forest

AGC stocks patterns along elevational gradients in Andean forest

According to SEM analysis, AGC_{final} increased linearly with $PCA1_{Temp}$ (Figure 4A), which agrees with previous studies in Andean forests (Girardin *et al.*, 2010; Moser *et al.*, 2011;

Girardin *et al.*, 2014; Phillips *et al.*, 2019). This result indicates that understanding how temperature influences AGC stocks and dynamics may be primarily based on variation in elevation (Muller-Landau *et al.*, 2021). Although most of the temperature variation across the gradient was explained by elevation (r = -0.98, $p < 0.01$) (Peña *et al.*, 2018), our SEM analysis revealed a unimodal pattern for AGC_{final} along our elevational gradient, with peak values at 1000 m asl (PMF), under warmer conditions, and lower values at higher elevations. Minimum daily temperature (minDT) acts as one of the main environmental filters for plant processes in Andean forests, reducing the root nutrient uptake capacity of the species (Engels & Marschner, 1990) through a decrease in the nutrient availability (Leuschner *et al.*, 2007; Salinas *et al.*, 2011). In addition, the effects of minDT can make xylem and phloem transportation difficult due to changes in the water viscosity or freezing (Cavender-Bares (2005). Taken together, the observed AGC_{final} values over 2900 m asl, or in the upper montane forest (UMF), found in this study are likely a response to colder temperatures (MDT between 7 ºC and 10 ºC), lower BA (Homeier *et al.*, 2010) and the stunted stature of trees (Slik *et al.*, 2010).

The results of this study seem to confirm that BA stands as a good predictor for AGC since it integrates the effect of both the number and size of trees (Burrows *et al.*, 2000). BA showed a strong positive correlation with AGC_{final} that is similar to findings from other studies (Slik *et al.*, 2010; Slik *et al.*, 2015), where BA represents the main source of change in AGC stocks along an elevational gradient in Borneo, although the opposite trend has been found in the Andean region (Girardin *et al.*, 2014; Malhi *et al.*, 2017). This discrepancy may underscore a complex relationship between BA and AGC stocks that certainly deserves more evaluation. Malhi *et al.* (2017) suggested that this variability is strongly associated with a variation in forest stature, rather than changes in basal area, and Vitousek and Farrington (1997) stated that variations in BA and its relationship with AGC stocks seem to be limited by nutrient shortage variations along the elevational gradients. We know that minDT indirectly affects some ecological mechanisms in nature, such as cloud formation (Eller *et al.*, 2020), and Grubb & Whitmore (1966) highlight that in Andean forests, there is a gradation in cloud cover, which ranges from almost insignificant in the PMF, frequent in the MF, to constant in the UMF. In the Andean forest at my study site, the cloud immersion zone could lead to a reduction in solar radiation that, in turn, causes a decrease in the photosynthetic capacity rates of trees (Malhi *et al.*, 2017), with a concomitant reduction in their capacity to accumulate biomass at higher elevations. Future studies should increase efforts to understand the underlying effects of the frequency of clouds over AGC stocks by increasing spatial and temporal sampling regimes.

AGC dynamics patterns along elevational gradients in Andean forest

The temperature may also be the main driver of AGC dynamics at my study site because of its direct and positive effect over AGC_{nc} and AGC_p, which increased significantly when temperature also increased across the elevational gradient. Duque *et al.* (2021) reported an AGC net change of 0.67 ± 0.08 Mg C ha^{-1} y^{-1} for an Andean forest plot network, almost two times lower than the mean annual net change AGC found in the present research (1.20 ± 0.89 Mg C ha^{-1} y^{-1}). In addition, both mean AGC_{nc} and AGC_p (2.16 ± 0.92 Mg C ha^{-1} y^{-1}) found in the present study represent just a small portion of the AGC_{nc} and AGC_p reported for an Andean Colombian forest; 2.21 ± 0.51 Mg C ha^{-1} y^{-1} and 5.54 ± 0.23 Mg C ha^{-1} y^{-1}, respectively (Peña *et al.*, 2018). However, due to climate change and the increasing temperatures, the productivity rates could change due to the upslope migration of species, or thermophilization effect, while adapting to their thermal optima. Tropical plants may be especially susceptible to climate change because of their narrow thermal niches (Perez *et al.*, 2016). An increase in temperature that provokes species migration will also affect the rates of biomass productivity along elevational gradients in the TMF. But in mountainous ecosystems, the presence of distinct ecotones represents the main barrier for this migration. For example, the transition from montane rainforest to cloud forest at mid-elevations and the transition from closed-canopy forest to open alpine grasslands at high elevations could limit the translocation of species. Ultimately, such temperature effects can potentially reduce establishment success of colonizers and favour stability of incumbent communities.

Approximately 70% of the annual net gain in Andean forests are related to an increase in both temperature and CO_2 deposition (McMahon *et al.*, 2019), and temperature regulates both plant photosynthesis and metabolism (Sundqvist *et al.* (2013), which directly controls the metabolic processes essential for the production of new tissues (leaves and bark). For example, in the Andean forest, high elevations with low temperatures can decrease tree investment in fine roots, which in turn causes a decline in wood production (Leuschner *et al.*, 2007; Moser *et al.*, 2010; Malhi *et al.*, 2017). Such MinDTs could play a key role over AGC dynamics at my study site, which is also known to decrease nitrogen availability (Salinas *et al.*, 2011). N_{Soil} constituted the most consistent driver of AGC_k, which reflects that the N_{soil} limitation or a decrease in N_{soil} in the Andean forests reduce the capacity of root formation (Moser *et al.*, 2010) and thus a reduction in nutrient assimilation and a concomitant increase in mortality. For instance, in the lowlands, the high mortality rates can contribute to lower nitrogen accumulation in soils due to a significant increase in AGC_p ($p = 0.06$). Whereas, at high elevations, due to low temperatures and high soil water content, nitrogen mineralization rates and the availability of nutrients in soils can also decrease (Benner *et al.*, 2010), which in turn can lead to a reduction in foliar nitrogen and the phosphorus necessary for photosynthesis (van de Weg *et al.*, 2009; Wittich *et al.*, 2012).

Nonetheless, Peña and Duque (2013) acknowledge that in secondary forests, the exclusive competition between species may not have occurred before canopy closure, which may reduce the importance of soil-fertility over mortality rates at my study site.

Most of the other soil properties in our study were not related to AGC dynamics, a result that is similar to Phillips *et al.* (2019) (although, see Poorter *et al.* (2017). This lack of signal for AGC dynamics suggests that it may be difficult to detect differences along the gradient, due in part to the effects of the land-use changes in the Andean forest on the west flank of Pichincha province. I found that disturbance and self-thinning modify the forest dynamics at my site. There was a positive significant correlation between β-parameter and AGC mortality and a marginally significant negative trend with AGC net change throughout the transect. The size-dependent variables, β-parameter and AGC_k, were intrinsically related because the death of big trees with high C stocks contributes to greater declines in AGC stocks on a large scale (Duque *et al.*, 2021). These results support the hypothesis that past human disturbances partially explain the carbon stocks and dynamics rates along an elevational gradient. β-parameter, which discriminates plots influenced by competitive thinning following internal disturbance (low β) to plots affected by active disturbances (high β), is considered as a determinant in AGC mortality in the Andean forest. It is essential to define the extent and magnitude of its effect (β-parameter) over natural dynamics with more studies in tropical montane forest ecosystems.

Notwithstanding, the information presented here points to the importance of measuring forest disturbances (β-parameter) in tropical forests as a key regulator of forest productivity. Here, it is evident that CO_2 fertilization, increasing temperatures, droughts, and the effect of disturbances may all impact tree growth and mortality (Hubau *et al.*, 2020). For example, the negative association between β and AGC_{nt} suggests that after human disturbances, the major gain in AGC_{nt} are related to the growth of big trees and an increase in the mortality of small trees due to competitive thinning (Coomes & Allen, 2007; Duque *et al.*, 2021). In addition, logging reduces above- and below-ground biomass carbon stocks but also increases light availability utilized by trees at different forest strata. As a result, there may be an increase in ecosystem productivity (Peña-Claros *et al.*, 2008; van der Sande *et al.*, 2017b) over the next 3 - 10 years until the canopy closes again in the PMF and UPM.

The positive relationship between $PCA1_{Temp}$ and AGC dynamics may be driven by species composition along elevation gradients at a large scale (Rapp *et al.*, 2012). Notwithstanding, I did not identify a significant association among AGC dynamics with rarefied species richness or leaf traits. Other studies have shown that different plant communities, in addition to the density of species, influence changes in edaphic conditions, like nutrients and organic matter availability in the soil (Veneklaas, 1990), thus affecting the productivity rates in time. The Andean forest has shown a strong capacity for long-term AGC increases and recovery due to the upslope migration of species, which further indicates that forest succession in the tropical Andes might significantly increase carbon accumulation in trees (Duque *et al.*, 2021). Collectively, SEM results suggest that diversity mechanisms may not universally apply throughout tropical forests (van der Sande *et al.*, 2017c). Studies that attempt to quantify productivity in Andean forests are limited in number. Additionally, the inclusion of different diversity metrics, like phylogenetic diversity, is also relevant and could help to elucidate this relationship. By linking phylogenetic diversity and dispersion to determine assembly mechanisms of forests (i.e., AGB storage and productivity), phylogenetic analysis can reveal aspects of biodiversity not ordinarily observable and improve our understanding of the ecology, evolution, and biogeography of plant communities in TMFs (Maherali & Klironomos, 2007; Cadotte *et al.*, 2008; Worthy *et al.*, 2019).

Finally, contrary to our expectations, our SEM results indicate that annual precipitation (AP) did not significantly affect AGC_{final}, $AGC_{nt,}$ AGC_{p}, or AGC_{k}. This result is similar to other studies that found that biomass productivity is weakly correlated with annual rainfall (e.g., Clark *et al.* (2001), Fehse *et al.* (2002), Del Grosso *et al.* (2008)). However, Poorter *et al.* (2017) hypothesized that AGC stocks and dynamics are strongly affected by water availability, where AGC should increase when water availability increases. Water is essential for the growth of trees (van der Sande *et al.*, 2015). In the forest canopy, in particular, large trees deal with higher radiation loads, vapour pressure deficits, and ultimately increased drought stress due to longer hydraulic paths (Bennett *et al.*, 2015). This result, coupled with those of my study, suggest the effect of AP on AGC stocks and dynamics could be masked by exogenous factors such as temperature ($PCA1_{Temp}$), which is highly correlated with AP at my study site.

CONCLUSIONS

The present study emphasizes that species richness, carbon stored in biomass, and its associated dynamics in the Andean forests, are subject to structuring mechanisms and ecological processes, including, soil nutriets, elevation and climate (Takyu *et al.*, 2003; Girardin *et al.*, 2010). This result supports the hypotheses that the main filters for species richness, AGC stocks and patterns of AGC dynamics along the elevational gradient are temperature, soil conditions and past human disturbance. The strong effect of temperature over the forest structure and AGC dynamics suggest that ongoing climate change could alter tree communities (Duque *et al.*, 2015; Fadrique *et al.*, 2018) and forest dynamics through changes in the dispersal strategies of tree species in the

Andean mountains (Llerena-Zambrano *et al.*, 2021). Supposing that species composition and distribution are, in part, determined by climate, an increase in global temperatures may cause upward shifts in tree communities in the Andean forest since temperatures decrease predictably with increasing elevation (Colwell *et al.*, 2008; Feeley *et al.*, 2011). Fadrique *et al.* (2018) acknowledged that rates of compositional change are average ten times slower than regional mean annual temperature changes, suggesting that many tropical tree species may already be occurring in sub-optimal conditions. However, the difference between climate change and thermofilization rates due to ecotonal barriers for migration may prove responsible for extinction and biodiversity loss because many species are unable to quickly respond to climate change (Bertrand *et al.*, 2011; Devictor *et al.*, 2012; Fadrique *et al.*, 2018).

The Andean region is a mosaic of natural habitats that are responsible, in part, for the spatial heterogeneity in AGC stocks and dynamics (Valencia *et al.*, 2004; Girardin *et al.*, 2010), due to human disturbances, which represents another important driver of AGC dynamics in our transect. However, it is essential to evaluate the disturbance effect over different forest components such as the soil and its similar effect in AGC stocks and dynamics. Soil conditions can change gradually with time (Terán-Valdez *et al.*, 2019), and sampling along the gradient is needed to determine the impact and direction of soil conditions over AGC dynamics under current degradation scenarios. Finally, the inclusion of additional sources of variation (e.g., cloud cover and phylogenetic diversity) as possible drivers of AGC and productivity variations along elevational gradients represent a key next step to complement gaps in our knowledge of the natural dynamics that determine Andean forest composition. Such knowledge will ultimately contribute to conservation initiatives for this increasingly threatened ecosystem.

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APPENDICES

Appendix A. Plot-based H:DBH allometries fitted for the 16 permanent plots surveyed in the tropical Andes. The best model was the one that minimizes the Residual Standard Error (RSE). Model selection was performed using the BIOMASS library for R.

PLOT_ID	PARAMETER			RMSE	RSE_{log}	Average bias	Selected model
	a	b	c				
INTI_01	41.260	32.200	0.000	5.514	0.000	-0.003	michaelis
BECL_03	28.710	23.810	1.520	4.324	0.000	-0.008	weibull
INTI_02	0.950	0.610	0.000	4.305	0.328	0.011	log1
MIND_01	2.139	-0.206	0.127	3.182	0.250	0.001	log2
RIBR_01	45.950	38.270	0.000	3.267	0.000	-0.002	michaelis
BECL_01	32.600	19.430	0.000	5.377	0.000	-0.004	michaelis
CEDR_01	0.864	0.569	0.000	2.768	0.208	-0.002	log1
CEDR_03	1.058	0.530	0.000	3.343	0.317	0.013	log1
MAPI_01	58.780	40.790	0.000	4.889	0.000	-0.002	michaelis
MAPI_02	65.420	46.660	0.000	3.091	0.000	-0.002	michaelis
MALO_02	54.090	37.340	0.000	2.936	0.000	0.004	michaelis
MALO_01	0.608	0.735	0.000	4.345	0.310	0.006	log1
VERD_01	19.984	18.205	1.494	2.849	0.000	-0.001	weibull
VERD_02	16.403	5.238	0.000	2.620	0.000	0.000	michaelis
VERD_03	1.216	0.384	0.000	2.332	0.282	0.006	log1
YANA_01	17.901	8.222	0.000	2.817	0.000	0.000	michaelis

Appendix B. Correlations values related to the first two axes of the principal component analysis (PCA) applied to temperature data from loggers established 10 centimeters and 1-meter above-ground (AG_{10cm} and AG_{1m}) and 10 centimeters below-ground (BG_{10cm}) in the monitoring system in NWPF. The abbreviations of the climatic variables are minimum daily temperature (minDT), mean daily temperature (meanDT), maximum daily temperature (maxDT). The most extreme values for both axes are represented in bold.

	PCA1 (88.6% of total variation)	**PCA2 (11.1% of total variation)**
meanDT_AG_{10cm}	**0.999382559**	0.002281603
maxDT_AG_{10cm}	0.996992733	-0.009324285
minDT_AG_{10cm}	0.998616256	0.003435414
meanDT_BG_{10cm}	0.999099836	0.00061158
maxDT_BG_{10cm}	0.997926768	0.033617457
minDT_BG_{10cm}	**0.126728778**	**0.991856367**
meanDT_AG_{1m}	0.997160124	-0.032975393
maxDT_AG_{1m}	0.991317408	**-0.100352945**
minDT_AG_{1m}	0.997191627	-0.023974105

Appendix C. Below-ground necromass carbon stocks (NCS) and soil organic carbon (SOC) monitored in two censuses, in 2015 or initial (e.g.NGC1) and 2019 o final (e.g. NCG_{final}), in a monitoring system in the Andean forest of Pichincha province in Ecuador.

PLOT	**Elevation (masl)**	**NGC_1 (Mg C ha^{-1})**	**NGC_{final} (Mg C ha^{-1})**	**SOC_1 (Mg C ha^{-1})**	**SOC_{final} (Mg C ha^{-1})**
MAPI_02	632	8.2	4.8	101.2	95.8
MAPI_01	653	8.2	6.0	75.8	73.0
MALO_02	827	3.9	11.5	128.4	98.6
MALO_01	1018	4.2	10.6	116.2	108.6
MIND_01	1277	6.3	4.1	167.7	74.6
RIBR_01	1640	5.9	3.5	52.9	74.6
INTI_02	1829	10.8	5.1	83.4	65.9
INTI_01	1879	8.5	8.7	154.7	138.9
BECL_03	2203	3.3	2.8	99.4	77.4
CEDR_03	2212	6.9	6.9	209.7	155.4
BECL_01	2313	8.1	4.9	71.6	99.3
CEDR_01	2492	6.1	5.7	114.9	143.4
VERD_02	2932	5.5	6.5	158.5	105.8
VERD_03	3109	6.4	7.6	165.7	107.1
VERD_01	3421	6.6	6.8	108.7	74.8
YANA_01	3507	8.7	4.3	61.2	51.4
Mean (±SD)		6.7 (±1.9)	6.2 (±2.4)	116.9 (±44.4)	96.5 (±29.6)
R^2 adj		-0.06	-0.02	-0.06	-0.07
***p* value**		0.77	0.43	0.77	0.97

Appendix D. Regression analysis for above-ground carbon final stock (AGC; DBH ≥ 5 cm) and AGC dynamics (Mg ha^{-1} y^{-1}) with predictor variables across an elevational transect in an Andean forest of Ecuador. AGC$_{nc}$ = above-ground carbon net change (Mg ha^{-1} y^{-1}), AGC$_{p}$= aboveground carbon productivity (Mg ha^{-1} y^{-1}), AGC$_{k}$= above-ground carbon mortality (Mg ha^{-1} y^{-1}), and AGC$_{final}$= above-ground carbon stock for the period 2019 (Mg ha^{-1}).

<table>
<tr><th colspan="5">AGC$_{final}$ (Mg ha^{-1})</th></tr>
<tr><th>Variable</th><th>R^2</th><th>R^2 Adj</th><th>RMSE</th><th>Prob>|ρ|</th></tr>
<tr><td>Elevation</td><td>0.33</td><td>0.28</td><td>21.98</td><td>0.0199</td></tr>
<tr><td>NCS$_{final}$</td><td>0.34</td><td>0.29</td><td>21.76</td><td>0.017</td></tr>
<tr><td>Rarefied SR</td><td>0.43</td><td>0.39</td><td>20.14</td><td>0.0054</td></tr>
<tr><td>BA$_{final}$</td><td>0.47</td><td>0.43</td><td>19.55</td><td>0.0034</td></tr>
<tr><td>CWM-LBT</td><td>0.42</td><td>0.38</td><td>20.43</td><td>0.0065</td></tr>
<tr><td>PCA1$_{Temp}$</td><td>0.34</td><td>0.29</td><td>21.85</td><td>0.0181</td></tr>
<tr><td>AP</td><td>0.24</td><td>0.19</td><td>23.36</td><td>0.0521</td></tr>
<tr><th colspan="5">AGC$_{nc}$ (Mg ha^{-1} y^{-1})</th></tr>
<tr><th>Variable</th><th>R^2</th><th>R^2 Adj</th><th>RMSE</th><th>Prob>|ρ|</th></tr>
<tr><td>Elevation</td><td>0.43</td><td>0.39</td><td>0.69</td><td>0.0055</td></tr>
<tr><td>Rarefied SR</td><td>0.24</td><td>0.19</td><td>0.80</td><td>0.0521</td></tr>
<tr><td>BETA</td><td>0.32</td><td>0.28</td><td>0.84</td><td>0.0213</td></tr>
<tr><td>CWM-SLA</td><td>0.28</td><td>0.23</td><td>0.86</td><td>0.0342</td></tr>
<tr><td>CWM-LBT</td><td>0.41</td><td>0.37</td><td>0.78</td><td>0.0073</td></tr>
<tr><td>CWM-LA</td><td>0.26</td><td>0.21</td><td>0.88</td><td>0.0424</td></tr>
<tr><td>PCA1$_{Temp}$</td><td>0.47</td><td>0.43</td><td>0.74</td><td>0.0033</td></tr>
<tr><td>AP</td><td>0.27</td><td>0.21</td><td>0.87</td><td>0.0406</td></tr>
<tr><td>Mg$_{Soil}$</td><td>0.23</td><td>0.19</td><td>0.89</td><td>0.0543</td></tr>
<tr><th colspan="5">AGC$_{p}$ (Mg ha^{-1} y^{-1})</th></tr>
<tr><th>Variable</th><th>R^2</th><th>R^2 Adj</th><th>RMSE</th><th>Prob>|ρ|</th></tr>
<tr><td>Elevation</td><td>0.38</td><td>0.32</td><td>0.76</td><td>0.0128</td></tr>
<tr><td>Rarefied SR</td><td>0.32</td><td>0.28</td><td>0.78</td><td>0.0213</td></tr>
<tr><td>CWM-LBT</td><td>0.38</td><td>0.34</td><td>0.75</td><td>0.0111</td></tr>
<tr><td>PCA1$_{Temp}$</td><td>0.39</td><td>0.35</td><td>0.74</td><td>0.0094</td></tr>
<tr><td>AP</td><td>0.30</td><td>0.25</td><td>0.80</td><td>0.0292</td></tr>
<tr><th colspan="5">AGC$_{k}$ (Mg ha^{-1} y^{-1})</th></tr>
<tr><th>Variable</th><th>R^2</th><th>R^2 Adj</th><th>RMSE</th><th>Prob>|ρ|</th></tr>
<tr><td>BETA</td><td>0.25</td><td>0.19</td><td>0.56</td><td>0.0498</td></tr>
<tr><td>C/N ratio</td><td>0.29</td><td>0.24</td><td>0.54</td><td>0.0321</td></tr>
<tr><td>N$_{Soil}$</td><td>0.34</td><td>0.29</td><td>0.52</td><td>0.0185</td></tr>
</table>

Appendix E. Correlation analysis for above-ground carbon final stock (AGC; DBH $\geq$ 5 cm) and AGC dynamics (Mg ha^{-1} y^{-1}) with predictor variables across an elevational gradient in an Andean forest in Ecuador. AGC$_{nc}$ = above-ground carbon net change (Mg ha^{-1} y^{-1}), AGC$_{p}$= above-ground carbon productivity (Mg ha^{-1} y^{-1}), AGC$_{k}$= above-ground carbon mortality (Mg ha^{-1} y^{-1}), and AGC$_{final}$= above-ground carbon stock for the period 2019 (Mg ha^{-1}).

Variable	by Variable	Spearman ρ	Prob>|ρ|
AGC$_{nc}$	Elevation	-0.7059	0.0022
AGC$_{p}$	AGC$_{nc}$	0.7735	0.0004
AGC$_{p}$	Elevation	-0.6765	0.004
AP	CWM_LA	0.595	0.015
AP	AGC$_{nc}$	0.5965	0.0147
AP	AGC$_{p}$	0.7128	0.0019
AP	CWM_LDMC	0.7982	0.0002
AP	PCA1$_{Temp}$	0.8312	<.0001
AP	CWM_LBT	-0.8539	<.0001
AP	Elevation	-0.8439	<.0001
AP	Mg$_{Soil}$	-0.7237	0.0015
AP	K$_{Soil}$	-0.6441	0.0071
BA$_{final}$	AGC$_{final}$	0.6118	0.0118
C$_{Soil}$	AGC$_{final}$	0.649	0.0065
COS$_{final}$	AGCN	0.6402	0.0076
CWM_LA	AGC$_{nc}$	0.6382	0.0078
CWM_LA	Elevation	-0.8412	<.0001
CWM_LA	CWM_LBT	-0.7104	0.002
CWM_LA	Mg$_{Soil}$	-0.6814	0.0037
CWM_LA	K$_{Soil}$	-0.6726	0.0043
CWM_LA	BETA	-0.6353	0.0082
CWM_LBT	K$_{Soil}$	0.6445	0.007
CWM_LBT	Mg$_{Soil}$	0.7581	0.0007
CWM_LBT	Elevation	0.8622	<.0001
CWM_LBT	AGC$_{final}$	-0.6603	0.0054
CWM_LBT	AGC$_{p}$	-0.6323	0.0086
CWM_LBT	C$_{Soil}$	-0.6062	0.0128
CWM_LBT	AGC$_{nc}$	-0.6043	0.0132
CWM_LDMC	CWM_LBT	-0.7133	0.0019
CWM_LDMC	Elevation	-0.6588	0.0055
CWM_SLA	AGC$_{nc}$	0.5882	0.0165
K$_{Soil}$	Elevation	0.7697	0.0005
Mg$_{Soil}$	Elevation	0.7314	0.0013
Mg$_{Soil}$	AGC$_{p}$	-0.6343	0.0083
PCA1$_{Temp}$	CWM_LDMC	0.6358	0.0081
PCA1$_{Temp}$	AGC$_{p}$	0.6623	0.0052

$\mathbf{PCA1_{Temp}}$	AGC_{nc}	0.6755	0.0041
$\mathbf{PCA1_{Temp}}$	CWM_LA	0.8021	0.0002
$\mathbf{PCA1_{Temp}}$	Elevation	-0.9816	<.0001
$\mathbf{PCA1_{Temp}}$	CWM_LBT	-0.851	<.0001
$\mathbf{PCA1_{Temp}}$	K_{Soil}	-0.7865	0.0003
$\mathbf{PCA1_{Temp}}$	Mg_{Soil}	-0.729	0.0014
Rarefied SR	Elevation	-0.8824	<.0001
Rarefied SR	AGC_{p}	0.6559	0.0058
Rarefied SR	Mg_{Soil}	-0.8079	0.0002
Rarefied SR	CWM_LBT	-0.8769	<.0001
Rarefied SR	CWM_LA	0.7	0.0025
Rarefied SR	CWM_LDMC	0.6235	0.0099
Rarefied SR	$\text{PCA1}_{\text{Temp}}$	0.911	<.0001
Rarefied SR	AP	0.8719	<.0001
Rarefied SR	$\text{AGC}_{\text{final}}$	0.5824	0.0179
Rarefied SR	AGC_{nc}	0.5529	0.0263
BETA	AGC_{nc}	-0.5206	0.0387
BETA	AGC_{k}	0.5578	0.0248

Appendix F. Structural equation models (SEMs) for above-ground carbon (AGC) stocks and dynamics: AGC of the last census (AGC$_{final}$), AGC net change (AGC$_{nc}$), AGC productivity (AGC$_{p}$), and AGC mortality (AGC$_{k}$), and the effects of abiotic and biotic factors. The endogenous and exogenous variables are presented, as well as R^2, AIC, and RMSE values are shown to determine the best model.

Response Var.	Model	Endogenous var.	Exogenous var.	Chi-square	*p*	R^2	RMSE	AIC
AGC$_{final}$	**1**	AGC$_{final}$, CWM_LBT	PCA1$_{Temp}$, AP, rarefied SR, BA$_{final}$, NCS$_{final}$	12.087	0.208	0.805	0.151	50.087
	2	AGC$_{final}$, CWM_LBT	PCA1$_{Temp}$, AP, rarefied SR, BA$_{final}$	2.684	0.612	0.788	0.000	36.684
	3	AGC$_{final}$, CWM_LBT	PCA1$_{Temp}$, AP, rarefied SR, BA$_{final}$	32.245	0.000	0.735	0.449	58.245
	4	AGC$_{final}$, CWM_LBT	PCA1$_{Temp}$, AP, rarefied SR, BA$_{final}$	3.465	0.749	0.775	0.000	33.460
	5	AGC$_{final}$, CWM_LBT, rarefied SR	PCA1$_{Temp}$, AP, BA$_{final}$	4.226	0.517	0.80	0.000	36.226
AGC$_{nc}$	**1**	AGC$_{nc}$, CWM_SLA, CWM_LBT, CWM_LA	BETA, Elevation, rarefied SR, PCA1$_{Temp}$, AP	38.547	0.000	0.911	0.362	102.547
	2	AGC$_{nc}$, CWM_SLA, CWM_LDMC, CWM_LBT, CWM_LA, PCA1$_{Temp}$, AP	BETA, Elevation	23.933	0.047	0.864	0.217	85.933
	3	AGC$_{nc}$, CWM_LDMC, CWM_LBT, CWM_LA, rarefied SR	BETA, Elevation, PCA1$_{Temp}$, AP, CWM_SLA	126.477	0.000	0.937	0.534	188.477
	4	AGC$_{nc}$, CWM_LDMC, CWM_LBT, CWM_LA, rarefied SR	BETA, Elevation, PCA1$_{Temp}$, AP, CWM_SLA	39.405	0.009	0.865	0.242	107.405

Response Var.	Model	Endogenous var.	Exogenous var.	Chi-square	*p*	R^2	RMSE	AIC
	5	AGC$_{nc}$, CWM_SLA, CWM_LBT, CWM_LA, rarefied SR	BETA, PCA1$_{Temp}$, AP, CWM_LDMC	43.642	0.001	0.693	0.294	95.642
	6	AGC$_{nc}$, CWM_SLA, CWM_LDMC, CWM_LBT, CWM_LA, rarefied SR	BETA, PCA1$_{Temp}$, AP	33.233	0.011	0.727	0.252	89.233
	7	AGC$_{nc}$, CWM_SLA, CWM_LBT, CWM_LA	BETA, PCA1$_{Temp}$, AP, rarefied SR	8.413	0.493	0.714	0.000	62.413
	8	AGC$_{nc}$, CWM_SLA, CWM_LBT, CWM_LA, PCA1$_{Temp}$, AP	BETA, rarefied SR	11.097	0.435	0.727	0.024	77.097
	9	AGC$_{nc}$, CWM_LBT, CWM_LA, rarefied SR	BETA, PCA1$_{Temp}$, AP,	5.142	0.742	0.68	0.000	45.142
AGC$_p$	**1**	AGC$_p$, CWM_LBT, Mg$_{Soil}$	PCA1$_{Temp}$, AP, rarefied SR	0.000	NA	0.523	0.614	54.000
	2	AGC$_p$, CWM_LBT, Mg$_{Soil}$	PCA1$_{Temp}$, AP, rarefied SR	1.029	0.310	0.52	0.044	41.029
	3	AGC$_p$, CWM_LBT, Mg$_{Soil}$	PCA1$_{Temp}$, AP, rarefied SR	0.000	NA	0.523	0.614	42.000
	4	AGC$_p$, CWM_LBT, Mg$_{Soil}$	PCA1$_{Temp}$, AP, rarefied SR	48.320	0.000	0.493	0.859	94.320
	5	AGC$_p$, CWM_LBT, Mg$_{Soil}$, PCA1$_{Temp}$, AP	rarefied SR	3.771	0.438	0.522	0.000	49.771
	6	AGC$_p$, CWM_LBT, rarefied SR	PCA1$_{Temp}$, AP	0.133	0.715	0.41	0.000	28.133
AGC$_k$	**1**	C/N$_{Soil}$, N$_{Soil}$, AGC$_k$	BETA	0.637	0.727	0.486	0.000	24.637

Response Var.	**Model**	**Endogenous var.**	**Exogenous var.**	**Chi-square**	***p***	**R²**	**RMSE**	**AIC**
	2	AGC_k	BETA	0.000	NA	0.248	0.000	10.000
	3	AGC_k	BETA, N_{Soil}	0.602	0.438	0.447	0.000	10.602

Appendix G. Standardized prediction coefficients for each causal path in the above-ground biomass final stock (AGC_{final}) reported by structural equation modeling analysis (see Figure 4A). Red numbers determine significant relationships between variables and black numbers represent no significant relationships.

EFFECT	**Endogenous** / **Exogenous**	**$PCA1_{Temp}$**	**AP**	**BA_{final}**	**Rarefied SR**	**CWM_LBT**
Total	**Rarefied SR**	0.78	0.15	0.00	0.00	0.00
	CWM_LBT	-0.65	-0.30	0.00	0.00	0.00
	AGC_{final}	0.59	0.02	0.61	0.38	-0.45
Direct	**Rarefied SR**	0.78	0.15	0.00	0.00	0.00
	CWM_LBT	-0.65	-0.30	0.00	0.00	0.00
	AGC_{final}	0.00	-0.17	0.61	0.38	-0.45
Indirect	**Rarefied SR**	0.00	0.00	0.00	0.00	0.00
	CWM_LBT	0.00	0.00	0.00	0.00	0.00
	AGC_{final}	0.59	0.19	0.00	0.00	0.00
***p* value**	**Rarefied SR**	0.002	0.234	...	...	...
	CWM_LBT	0.017	0.042	...	...	...
	AGC_{final}	0.023	0.432	0.001	0.201	0.131

Appendix H. Standardized prediction coefficients for each causal path in the above-ground biomass net change (AGC$_{nc}$) reported by structural equation modeling analysis (see Figure 4B). Red numbers determine significant relationships between variables and black numbers represent no significant relationships (SEM).

EFFECT	**Endogenous** **Exogenous**	**PCA1$_{Temp}$**	**AP**	**BETA**	**CWM_LA**	**Rarefied SR**	**CWM_LBT**
Total	**CWM_LA**	1.12	-0.42	0.00	0.00	0.00	0.00
	Rarefied SR	0.78	0.15	0.00	0.00	0.00	0.00
	CWM_LBT	-0.65	-0.30	0.00	0.00	0.00	0.00
	AGC$_{nc}$	0.58	0.01	-0.49	-0.37	-0.28	-0.44
Direct	**CWM_LA**	1.12	-0.42	0.00	0.00	0.00	0.00
	Rarefied SR	0.78	0.15	0.00	0.00	0.00	0.00
	CWM_LBT	-0.65	-0.30	0.00	0.00	0.00	0.00
	AGC$_{nc}$	0.93	-0.24	-0.49	-0.37	-0.28	-0.44
Indirect	**CWM_LA**	0.00	0.00	0.00	0.00	0.00	0.00
	Rarefied SR	0.00	0.00	0.00	0.00	0.00	0.00
	CWM_LBT	0.00	0.00	0.00	0.00	0.00	0.00
	AGC$_{nc}$	-0.35	0.25	0.00	0.00	0.00	0.00
***p* value**	**CWM_LA**	0.002	0.125	...	...	...	...
	Rarefied SR	0.002	0.229	...	...	...	...
	CWM_LBT	0.018	0.039	...	...	...	...
	AGC$_{nc}$	0.047	0.476	0.089	0.084	0.330	0.111

Appendix I. Standardized prediction coefficients for each causal path in the above-ground biomass productivity (AGC_p) reported by structural equation modeling analysis (see Figure 4C). Red numbers determine significant relationships between variables and black numbers represent no significant relationships (SEM).

EFFECT	**Endogenous** / **Exogenous**	**AP**	**PCA1$_{Temp}$**	**Rarefied SR**	**CWM_LBT**
Total	**Rarefied SR**	0.15	0.78	0.00	0.00
	CWM_LBT	-0.30	-0.65	0.00	0.00
	AGC_p	0.06	0.58	0.03	-0.28
Direct	**Rarefied SR**	0.15	0.78	0.00	0.00
	CWM_LBT	-0.30	-0.65	0.00	0.00
	AGC_p	-0.03	0.38	0.03	-0.28
Indirect	**Rarefied SR**	0.00	0.00	0.00	0.00
	CWM_LBT	0.00	0.00	0.00	0.00
	AGC_p	0.09	0.20	0.00	0.00
***p* value**	**Rarefied SR**	0.216	0.002	...	...
	CWM_LBT	0.038	0.014	...	...
	AGC_p	0.465	0.050	0.465	0.325

Appenxi J. Standardized prediction coefficients for each causal path in the above-ground biomass mortality (AGC_k) reported by structural equation modeling analysis (see Figure 4D). Red numbers determine significant relationships between variables and black numbers represent no significant relationships (SEM).

EFFECT	**Endogenous** **Exogenous**	**N_{Soil}**	**BETA**
Total	**AGCk**	-0.52	0.42
Direct	**AGCk**	-0.52	0.42
Indirect	**AGCk**	0.000	0.000
***p* value**	**AGCk**	0.007	0.040