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Diversity, structure and dynamics of tropical montane forests: Insights from permanent-plot monitoring in the Venezuelan Andes

Maryam E. Sánchez[1,✉]; Luis D. Llambí[2,3]; Luis E. Gámez[4]; Gerardo Rodríguez[4]; Roxibell Pelayo[2]; Michele Ataroff[2] & Emilio Vilanova[5]

[1] Instituto de Investigaciones para el Desarrollo Forestal (INDEFOR), Facultad de Ciencias Forestales y Ambientales, Universidad de Los Andes. Mérida, Venezuela. [2] Instituto de Ciencias Ambientales y Ecológicas (ICAE), Universidad de Los Andes. Mérida, Venezuela. [3] Consorcio para el Desarrollo Sostenible de la Ecorregión Andina-CONDESAN. [4] Laboratorio de Dendrología, Facultad de Ciencias Forestales y Ambientales, Universidad de Los Andes. Mérida, Venezuela. [5] Wildlife Conservation Society (WCS).

Abstract. Tropical montane forests in the Andes are hotspots for species diversity and constitute important ecosystems for the provision of numerous services critical for local populations, including biomass/carbon accumulation and hydrological regulation. Additionally, in many countries in the region, these forests are being lost or degraded at alarming rates. Understanding their dynamics in terms of the composition, diversity, structure and function is a key challenge in the region that can inform policies for their sustainable management and conservation. This study focused on the use of monitoring data from ground-based permanent plots (part of the Andean Forest Network) in the two main mountain ranges of the Venezuelan Andes to analyze forest structure, diversity and dynamics over six years (2016-2023), and their potential drivers. We found that although the wetter forests of La Mucuy (northeast) and the more seasonal stands of San Eusebio (northwest) are very similar in terms of overall species richness, they show substantial differences in their species assemblages and their biogeographic origins. Both sites share similarities in tree dispersal strategies and stem turnover rates (mean=1.16%/year), but forests in La Mucuy are significantly more productive, with a mean annual woody productivity rate of 3.09±1.42 Mg C.ha^{-1}.y^{-1}, while this rate was 0.73±0.48 Mg C.ha^{-1}.y^{-1} in SEU plots. Interestingly, although species richness and composition has not shown significant changes during this 6-year period, both sites have increased their total aboveground biomass, acting as a significant carbon sink, which appears to be largely driven by the growth of large trees in these forests. These results emphasize the need of maintaining long-term monitoring efforts to be able to link more explicitly changes in composition, biodiversity and ecosystem services with changes in environmental drivers under climate change scenarios.

[Keywords: aboveground biomass, cloud forests, tree demography, dispersal syndromes, forest dynamics, species composition, tropical Andes]

Resumen. Diversidad, estructura y dinámica de los bosques montanos tropicales: Perspectivas del monitoreo de parcelas permanentes en los Andes venezolanos. Los bosques montanos tropicales de los Andes son hotspots de biodiversidad y constituyen ecosistemas importantes que proveen numerosos servicios para las poblaciones locales (e.g., acumulación de biomasa/carbono, regulación hidrológica). En países de la región, estos bosques se están perdiendo o degradando a tasas alarmantes. Entender su dinámica en términos de composición de especies, diversidad, estructura y función es un reto clave en la región, y serviría de base para políticas que favorezcan su conservación y gestión sostenible. En este estudio se usaron datos de monitoreo de parcelas permanentes (parte de la Red de Bosques Andinos) en las dos principales cordilleras de los Andes venezolanos para analizar la estructura, diversidad y dinámica de los bosques entre 2016 y 2023, y sus posibles elementos causales. Aunque los bosques más húmedos de La Mucuy (noreste) y los más estacionales de San Eusebio (noroeste) son similares en riqueza general de especies, difieren en la composición de especies y sus orígenes biogeográficos. Ambos sitios comparten similitudes en las estrategias de dispersión de los árboles y en las tasas de reemplazo de los tallos (promedio: 1.16%/año), pero los bosques de La Mucuy son significativamente más productivos (tasa media de productividad leñosa: 3.09±1.42 Mg C.ha^{-1}.y^{-1}), mientras que en las parcelas de SEU la tasa fue 0.73±0.48 Mg C.ha^{-1}.y^{-1}. Asimismo, aunque la riqueza y composición de especies no mostró cambios significativos durante los 6 años, ambos lugares incrementaron su biomasa aérea total, actuando como un importante sumidero de carbono, impulsado quizás por el crecimiento de grandes árboles en estos bosques. Los resultados enfatizan la necesidad de mantener los esfuerzos de seguimiento a largo plazo para vincular de forma explícita los cambios en la composición, biodiversidad y servicios ecosistémicos con los cambios en los factores ambientales bajo escenarios de cambio climático.

[Palabras clave: biomasa aérea, bosques nublados, demografía arbórea, síndromes de dispersión, dinámica del bosque, composición de especies, Andes tropicales]

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✉ maryam.elisa@gmail.com

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Introduction

Tropical forests around the world cover about one fifth of the globe´s terrestrial area. These forests are important for the provision of key ecosystem services, being global biodiversity hotspots, storing large amounts of atmospheric carbon and as pivotal resources in support of regional economies. Biome-wide changes in these functions could have profound consequences for biogeochemical cycles, with potential societal repercussions at multiple scales (Barlow et al. 2016; Lewis et al. 2015). Although occupying a less extensive area compared to their lowland counterparts, the so-called montane/cloud forests in the tropics are generally found above 1000 m above sea level (Spracklen and Righelato 2014), but their ecology and functioning reveal a unique role in the regional hydrological cycle and also as habitats supporting high levels of biological diversity. Moreover, there are multiple ecological interactions, including plant-animal relationships that are vital components of the ecology and dynamics of these forests (Bruijnzeel et al. 2011). Pollination, seed dispersal, herbivory and other symbiotic relationships all shape the structure and dynamics of cloud forest communities, interacting in multiple ways with environmental conditions such as high elevations, lower temperatures and often shallow and nutrient-poor soils (Salinas et al. 2021).

Human activities (i.e., deforestation, habitat fragmentation and climate change), pose significant threats to the stability of montane forests worldwide. It has recently been estimated that the area of montane forests in the tropics has been declining at a rate of 0.3% per year between 2001 and 2018 (or close to 32 million ha of total loss [He et al. 2023]), directly or indirectly disrupting key ecological processes and leading to biodiversity loss. Depending on the regional and local context, tropical montane forests are characterized by natural disturbances such as landslides, avalanches, volcanic activity, tree falls and windstorms driving their spatial and temporal dynamics, with effects in their structure and function. Understanding these multiple interactions is essential to understand the ecological processes and resilience of tropical montane forests.

The environmental controls on stand structure and dynamics in tropical forests include at least two major components. One is related to the edaphic factors, with soil phosphorus and cations positively influencing productivity, but with poorly structured soils associated to richer soil chemistry also promoting faster turnover rates (Quesada et al. 2012). The other is climatic, with a combination of higher temperatures and precipitation positively correlated with the total aboveground biomass (AGB) and with woody productivity (AGWP) (Johnson et al. 2016; Malhi et al. 2004; Vilanova et al. 2018). Parallel with these large-scale geographic patterns, differences within and between forests may also be modulated by species-level differences, with tropical trees experiencing a trade-off between growth and survival largely maintained by trait differences among the species (Wright et al. 2010). Yet, the role that demographic processes (e.g., dispersal, recruitment, mortality) and species diversity plays in these processes is not well understood.

Perhaps, nowhere the complexity of tropical montane forests is clearer than in the Andes of South America. The tropical Andes extend along the Northern and Central region of the longest mountain range on Earth along Venezuela, Colombia, Ecuador, Perú and Bolivia, and are recognized as one of the world's biodiversity hotspots (Myers et al. 2000). The ecology of the tropical Andes mountains is characterized by an altitudinal zonation, where distinct vegetation types are vertically distributed along the slopes (Malizia et al. 2020), and where the patterns of tree dynamics, productivity and structure vary considerably along the elevational gradients (Duque et al. 2021; Malhi et al. 2017). These effects also drive species diversity. For example, the tropical Andes may contain ~40.000 plant species and ~15% of the global total in only 1% of the world's land area (Pennington et al. 2010). From the lower mountain forests to the cloud forests, Puna and paramo ecosystems, the complex topography, varied climate and the geological history of the Andes drive the evolution of a remarkable array of tree species, with each zone displaying specific adaptations and species compositions.

While many forests in the Andes still function as active carbon sinks (e.g., Duque et al. 2021), some studies showed that rising temperatures can lead to an upward shift of vegetation zones (Bax et al. 2021), causing changes in species distributions and potentially reducing habitat suitability for specialized montane species in a process known as 'thermophilization' (Fadrique et al. 2018; Feeley et al. 2011).

Moreover, changes in rainfall patterns and the intensity of extreme weather events can also disrupt the hydrological cycle, affecting water availability and potentially leading to increased drought stress (Bradley et al. 2006). This, in turn, can influence forest productivity, species composition, and thus long-term resilience of the ecosystem.

In the case of the cloud forests of the northern Andes in Venezuela, the effects of elevation on turnover rates, woody productivity and carbon storage in the aboveground biomass (AGB) are less clear than other studies conducted in elevational gradients in the Andes. Situated in the northern region of South America, the Venezuelan Andes encompass a range of elevations, from lower montane forests to cloud forests, and harbor a rich combination of plant and animal species. The ecological processes in these systems are characterized by relatively small and low intensity disturbances in contrast to other cloud forests in the Caribbean and Central America where hurricanes and other large-scale and severe disturbances are more common (Schwarzkopf et al. 2011) (Figure 1). Available research suggests that stands located at higher elevations can achieve high AGB while having low rates of productivity and turnover (Vilanova et al. 2018), but this evidence is limited to permanent plots located in a single study site in the case of the Venezuelan Andes.

Monitoring efforts are needed to increase our understanding of the dynamics, structural characteristics and functions of these ecosystems under climate change scenarios. This is why the Andean Forests Network (redbosques.condesan.org) was created in 2012 with the purpose of monitoring montane forests at a regional scale through the establishment and monitoring of permanent plots located throughout the South American continent, including 6 permanent plots in the Venezuelan Andes (Kessler 2002; Malizia et al. 2020). This information is key to consolidating evidence-based conservation and management strategies, which are essential for the long-term preservation of these unique ecosystems. In addition, they constitute an important contribution to monitoring efforts within protected areas of the Venezuelan Andes (including the emblematic Sierra Nevada

Figure 1. General view of montane forests in the two main mountain ranges of the Venezuelan Andes. High tree density and species richness, and unique species composition, and a key role of plant-animal interactions —such as zoochoric seed dispersal— are some of the many characteristics of these ecosystems. Left panel: San Eusebio forests, in the Sierra de La Culata range in Western Mérida state. Right panel: La Mucuy montane forests, in the Sierra Nevada national park. Photo credits: Luis Gámez.

Figura 1. Vista general de los bosques montanos de las dos principales cadenas montañosas de los Andes venezolanos. La elevada densidad y riqueza de especies arbóreas, la composición única de especies y el papel clave de las interacciones entre plantas y animales —como la dispersión zoocórica de semillas— son algunas de las muchas características de estos ecosistemas. Panel izquierdo: bosques de San Eusebio, en la Sierra de La Culata, al oeste del estado de Mérida. Panel derecho: bosques montanos de La Mucuy, en el parque nacional de Sierra Nevada. Fotos: Luis Gámez.

National Park), where official monitoring programs are lacking.

Using data collected between 2016 and 2022 in permanent plots that are part of the Andean Forest Network (Malizia et al. 2020), this study aims to characterize the structure, diversity and dynamics over a 6-year period in the two main mountain ranges of the Cordillera de Mérida in Venezuela (Sierra Nevada and Sierra de La Culata). Our focus is to describe the community-level differences in forest structure and dynamics of two contrasting and rather poorly studied mountainous areas of the northern Andes region of South America. Our approach includes an assessment of how the environmental conditions of both sites may influence the ecology of these forests with the goal of generating a baseline for future monitoring of the dynamics of Andean forests in Venezuela. We addressed the following questions: 1) What are the main differences in tree species composition, diversity, biogeographic origin, structure (i.e., stem density, size distribution, aboveground biomass, AGB) and dispersal strategies comparing forest sites in the two main mountain ranges of the Cordillera de Mérida?; 2) Are compositional and structural differences between these forests linked to contrasting environmental conditions within and between regions?; 3) Are these relatively mature montane forests showing evidence of changes in species composition and richness, and in their structural properties including tree density, total basal area and AGB within the last six years?, and 4) How do these changes in structure and composition relate to differences in tree demographic processes (mortality, recruitment, turnover)? Are they in line with longer-term trends linked to climate change that have been identified for the northern Andes?

Considering the environmental and biogeographic differences between both mountain ranges (for example, soils, climate), we expected the structure and composition to be very different when comparing both study sites. In relation to forest dynamics, given the relatively short monitoring period evaluated (2016-2022), we did not expect to find marked temporal changes in species diversity or composition. However, in tune with recent trends observed in other Andean sites that have experienced rapid changes in turnover and productivity, we expected to be able to detect changes in key structural properties such as above ground biomass, supporting the general idea that Andean forests are acting as an active carbon sink.

Materials and Methods

Study area

The study was carried out in two sectors of the Cordillera de Mérida (Mérida State), Venezuela: La Mucuy (MUC) —in the eastern Sierra Nevada— and San Eusebio (SEU) —in the Sierra de La Culata to the west—. This area of western Venezuela is inserted in a rather high and narrow mountain range with variability in climate driven by a large thermic gradient, with the configuration of the Cordillera in two long mountain ranges and two long intermontane valleys (Chacón-Moreno et al. 2021) (Figure 2). The information about the historical land use of these two areas is sparse, and records of both natural, but mostly anthropogenic disturbances are not well-known. At both study sites, forests may have been subject to some form of selective logging before the 1950's when the Sierra Nevada National Park (~2700 km^2) was officially created in 1952 (where La Mucuy site is located), and the ~360 ha of the San Eusebio Experimental Forest (1959) became a research station managed for educational and scientific purposes (Lamprecht 1954; Schwarzkopf et al. 2011). To the best of our knowledge, both sites are representative of the mature stage of the montane forests of the Venezuelan Andes. From the stand point of climate, there is a prominent rain shadow influencing the distribution of precipitation across Cordillera de Mérida as moisture becomes concentrated along a southeast to northwest axis along the Mérida Andes (Stansell et al. 2005).

Mean annual air temperatures in MUC ranges between 12 and 14 °C and total annual precipitation is between 2800 and 3300 mm, while in SEU, mean temperatures range between 13 and 14 °C and average annual precipitation is considerably lower than MUC with ~1800 mm/year (Vera 2006; Linares 2008; Azuaje 2019) (Supplementary Material-Table S1). Precipitation is high most of the year, especially at MUC, and more seasonal in SEU, with two peaks of precipitation (typically exceeding 200 mm/month in April-May and October-November), while the lowest rainfall occurs between January-February (without a true dry season). Canopy rainfall interception can exceed 50%, including high horizontal precipitation (fog interception), which can represent more than 9% of total atmospheric

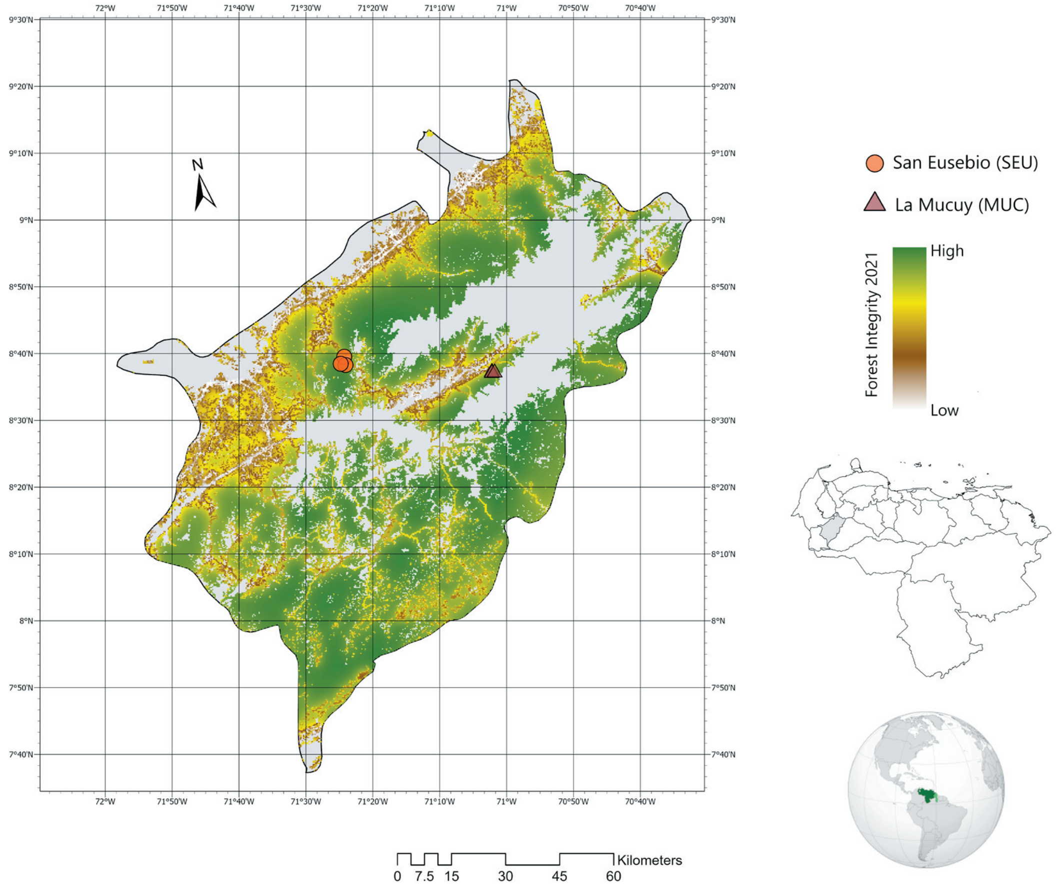

Figure 2. Location of the study plots in two sectors of the Andes of the state of Mérida, Venezuela. Map shows the 2021 extent of forest cover in Mérida state, classified by ecological integrity as defined by Grantham et al. (2020) (forestintegrity.com). Gray color represents non-forest areas. High integrity montane forests cover most of the mid-high elevation areas.

Figura 2. Ubicación de las parcelas de estudio en dos sectores de los Andes del estado Mérida, Venezuela. El mapa muestra la extensión de la cobertura forestal en 2021 en el estado de Mérida, clasificada por integridad ecologica según Grantham et al. (2020) (forestintegrity.com). El color gris representa las áreas no boscosas. Los bosques montanos de alta integridad cubren la mayor parte de las áreas de elevación media-alta mostradas en el modelo de elevación (panel derecho).

water inputs (Ataroff 2004; Pacheco and Ataroff 2001). Soils in both study areas are mostly young and poorly structured corresponding to inceptisols with a well-developed superficial O horizon that can reach depths between 20-35 cm, and predominately with sandy loamy to loamy textures (Azuaje 2019; Carey et al. 1994; Delaney et al. 1998; Pacheco and Ataroff 2005; Schwarzkopf et al. 2011). Soils are acidic (pH in the A horizon ranging from 3.76 to 3.94) and with high soil organic matter content (soil C in the A horizon ranging from 7.78 to 10.43%) (Supplementary Material-Table S1).

According to Ataroff and Sarmiento (2004), forests in La Mucuy correspond to the higher belt of the mountain cloud forests, consisting of dense evergreen vegetation with a complex stratified structure, average canopy tree height ranging between 18-22 m and emergent trees higher than 25 m. The forests of San Eusebio correspond to the lower belt of mountain cloud forests, with dense evergreen vegetation and at least three clearly differentiated strata. The upper/canopy stratum reaches 30 m, with emergent trees higher than 40 m. There is an intermediate stratum with tree heights between 20-25 m and a lower stratum with trees ranging between 10-15 m (Quevedo et al. 2016).

Data collection

We used six permanent plots (three per site) that are part of the Andean Forest Network (AFN) (Malizia et al. 2020; redbosques.condesan.org). In La Mucuy, plots were established in 2016 with a square shape (60x60 m, 3600 m^2)

and distributed along an elevation gradient from 2300 to 2500 (Supplementary Material-Table S1). A total of 1007 individuals were tagged in the first census of 2016 and followed for monitoring in a second re-census in 2022. In San Eusebio, we used the data collected from three 50x100 m (5000 m^2) permanent plots originally installed between 1961 and 1968 located almost at similar elevation levels (average of 2379 meters) (Supplementary Material-Table S1). During this ~50 year period of continuous monitoring (Min=47 y; Max=55 y), each plot has been resampled 30 times on average (Min=26; Max=34), being one of the longest records of forest monitoring in the tropics (Blundo et al. 2021). For MUC plots we used the base line data collected in 2016 and compared it with re-census data collected in 2022. To be able to compare both sites during the same time period, for SEU plots we restricted the analyses also to the 2016-2022 period. Since 2004, SEU plots have been part of the Amazon Forest Inventory Network (RAINFOR) (Malhi et al. 2002) and the data is stored and available at forestplots.net (López-González et al. 2011). Within each plot, data collection involved the measurement of all live stems from all species with diameter (D) of 10 cm at 1.3 m height, when possible, else above any stem deformation. Every individual was tagged and identified to the species level with botanical samples of each morphospecies collected in triplicate and deposited in the MER Herbarium (Facultad de Ciencias Forestales y Ambientales, Universidad de Los Andes, Venezuela). Species identification was based on the APG IV system (2016), and species names verified in the World Flora Online (2023) and the Missouri Botanical Garden webpage (tropicos.org 2023). During the 2022 census, we also accounted for all individuals that had died or were recruited during the interval including possible causes of death. The spatial location of each stem was also mapped at a 1 m resolution (details in Osinaga et al. 2014).

Analytical approach

Floristic and biographic diversity and species dispersal syndromes. Based on the data from each plot, we determined the total richness of species, genera and families present in each plot for the baseline (2016) and the re-census (2022). Since plot size was different within the two sites (3600 m^2 in La Mucuy and 5000 m^2 in San Eusebio), to adequately compare species richness between plots we used the individual rarefaction method proposed by Krebs (1989), using the software Past v.2.15 (Hammer 2012). We built species accumulation curves (with 1000 randomizations), increasing the number of individuals included in the sample for each plot and estimating the expected number of species for an equal number of individuals sampled. For this, we used the minimum common number of individuals among plots, which was 311 stems observed in MUC-02. We then calculated the Shannon and Simpson diversity indexes for each plot and compared them using the Compare Diversities Bootstrapping method (with 1000 randomizations of species total basal area for each pair of plots) implemented in Past v.2.15. We used a significance level α=0.01 to correct for multiple between-plot comparisons. We also compared the relative importance (in terms of number of species and total basal area) of phytogeographic groups in each plot, based on the classification of the origin of different genera present proposed by Cleef (1979), Webster (1985), Graham (1995), Van der Hammen and Cleef (1983) and Van der Hammen (2000). Species were classified as cosmopolitan, neotropical, wide tropical (pantropical, amfi-Pacific and amfi-Atlantic) and temperate (including holartic, austral-Antarctic and wide-temperate). We also described the relative importance of the different dispersal syndromes from the species present based on the classifications proposed by Van der Pijil (1982), Howe and Smallwood (1982) and Chain-Guadarrama (2005), classifying species as having zoochory, anemochory, barochory and hydrochory dispersal strategies.

Species abundance patterns. To analyze the patterns of change in similarity of species abundance, we used a matrix with the total basal area for each species in each plot in both sites and for both years of evaluation (2016-2022). Values were standardized based on the relative basal area for each species as plots sizes differed between sites. Data was also transformed using the square root of the relative abundance to increase the importance of those species with low and intermediate abundance. Using this matrix, we then calculated the Bray-Curtis similarity between plots as the basis for a cluster analysis (average linkage) and a Principal Coordinate Analysis (PCoA) ordination, using Primer v.6 (Clarke and Warwick 2001).

Forest structure and dynamics. For each plot and census year, we calculated the sum of the total density of individuals (D≥10 cm), total basal area and total aboveground biomass (AGB), and then extrapolated to one hectare to allow comparisons between plots, sites and with other studies. All stem data was also classified by size-classes of 10 cm to address the differences between sites and across the six-year period between censuses. Aboveground biomass (AGB) for each stem was estimated using the BIOMASS package in R (Réjou-Méchain et al. 2017), using the allometric equation for tropical forests developed by Chave et al. (2014):

$$AGB = \exp(-2.024 - 0.896 * E + 0.920 * \log[WD] + 2.795 * \log[D] - 0.0461 * \{\log[D]^2\})$$

Equation 1

where AGB is the aboveground biomass of each individual (megagrams, Mg); D is the diameter (cm); WD is the value of wood density obtained for each species (or genera/family when information was not available) from the globaldata base in Zanne et al. (2009), and E is an estimate of water stress obtained from global climate data sets. Results were summed for all individuals in each plot and expressed in terms of aboveground carbon content (AGC-MgC) multiplying AGB values by the IPCC conversion factor of 0.47 (Rozendaal et al. 2022). The lack of information <10 cm in diameter means that we may have slightly underestimated AGB in these old-growth forests. Nevertheless, trees between 5 and 10 cm in diameter tend to contribute little to AGB in old-growth forests (e.g., ~1.033 and 1.020 times higher AGB for tropical moist and wet forests, respectively) (Poorter et al. 2015). With the AGC estimates at both censuses (2016-2022), we also calculated the net change in AGC to obtain an approximation of the aboveground woody productivity (AGWP) for each plot, site and within the different size classes. The mean net AGC change (Mg $C.ha^{-1}.y^{-1}$) is calculated as the difference in the AGC stocks between 2016 and 2022 divided by the census interval (6 years). This metric allowed us to compare the productivity with other forest-types in Venezuela and the tropics, but it was especially useful to put our estimates in the context of the recent Duque et al. (2021) regional estimates of the carbon sink in Andean forests where no data from Venezuela was included. Demographic rates of recruitment and mortality were calculated for each plot based on the instantaneous rates (%$year^{-1}$) approach using the equations reported in several studies (Vilanova et al. 2018). Turnover rates were then calculated as the average of recruitment and mortality. Since demographic rates for heterogeneous populations are likely to be influenced by the length of census interval (Kohyama et al. 2018; Phillips et al. 2004; Sheil 1995), we standardized recruitment, mortality and turnover to annual rates using the correction proposed by Lewis et al. (2004) as $\lambda_{corr}=\lambda\ t^{0.0759}$, where λ_{corr} is the standardized annual rate, λ is the uncorrected average rate during the study period and t corresponds to the number of years between both census (6 years). As for the case of AGC, we calculated these rates for each of the size classes previously defined to better assess the dynamics of stem turnover.

The role of environmental variables. Although a small number of plots may limit the potential of capturing significant relationships between environmental variables and the characteristics of these forests in terms of structure and dynamics, we pursued an exploratory analysis in two main analytical steps. First, we applied individual simple correlations using Kendal's τ (tau) approach to examine overall relationships between all variables as it does not rely on a particular distribution of the variables involved. Second, we tested the relationships between three main response variables, namely turnover, AGC and AGWP with environmental descriptors using the scores of the first two axes obtained from a Principal Component Analysis (PCA) where all environmental attributes described in Supplementary Material-Table S1 were included. Following recommendations from McCune et al. (2002), all variables were normalized by range prior to the PCA analysis. These analyses were conducted using the vegan package version 2.6.4 (Oksanen et al. 2022) within the R software version 4.2.2 (R Development Core Team 2022).

RESULTS

Floristic diversity

In the three study plots in La Mucuy (MUC) combined, we registered a total of 61 species from individuals with D≥10 cm, which belong to 44 genera and 28 families. In San Eusebio (SEU), 71 species were recorded from 50 genera and 32 families, for a combined total of 103 species (61 genera, 37 families). In terms of richness, the best represented families in the two sites were Lauraceae (24 spp., 23.3%), Melastomataceae (14 spp., 13.6%), Rubiaceae (7 spp. 6.80%), Myrtaceae (6 spp., 5.8%), Araliaceae (4 spp., 3.9%) and Clusiaceae, Cyatheaceae, Euphorbiaceae, Meliaceae and Primulaceae (3 spp. each). The rest of the families were represented by only one or two species (Supplementary Material-Table S2). The best represented genera were *Miconia* (9 spp., 8.7%), *Ocotea* (7 spp., 6.8%), *Palicourea*, *Persea* (3 spp. each) and *Clusia*, *Nectandra* and *Ruagea* (2 spp. each), while the rest of the genera were represented by a single species. Floristically, there were differences in relation to the number of families, genera and species exclusive to each of the sites. From the total number of families reported, 13.5% are exclusive to MUC, 24.3% to SEU and 62.2% were common to both sites; 18% of the genera identified were found only in MUC and 27.9% in SEU. About 40.8% of the species identified are only found in SEU and 31.1% at MUC.

In the case of the biogeographic origin of the genera identified, at both study sites the proportion of the number of genera for each group was relatively similar (Supplementary Material-Figure S1). The highest proportion of species corresponds to those of Neotropical origin (51% in MUC and 57% in SEU respectively), followed by Pantropical species (36 and 33%), with fewer species of Holarctic and austral-Antarctic origins (between 10 and 3%). However, when we analyze the proportion of total basal area for the species included in each group, the austral-Antarctic group increases its relative importance in SEU to 20% (vs. 2% in MUC), and the pantropical becomes less important in SEU (19%) and more important in MUC (47%). Overall, the Neotropical group was the most abundant in both sites (48% in MUC and 59% in SEU), while the Holarctic group had the lowest relative basal area (2% at both sites). The increased importance of the austral-Antarctic group in terms of basal area, but not in terms of the number of species in SEU is linked to the presence of only three genera (*Podocarpus*, *Retrophyllum* and *Weinmannia*), two of which (the two Podocarpaceae species) were only found at this site, but with a relatively high number of individuals (≥20 in both cases) and large diameters.

A comparison of the number of species in all the plots shows relatively small changes between 2016 and 2022 (Supplementary Material-Table S2). In MUC-02, plot-level species richness changed from 39 to 38 species because of the loss of one rare species (*Cestrum lindenii*). In the other two plots (MUC-01 and MUC-03), richness remained constant at 38 species, with one species disappearing and one new species appearing in each case (Supplementary Material-Table S3). In the case of San Eusebio, observed species richness ranged between 38 and 47 species and was slightly more dynamic, with a net increase of two or three species in SEU-01 and SEU-03, resulting from the gain of five and three species and the loss of two and one species in each case and a net decrease of two species in SEU-02 (two species gained and four lost) (Supplementary Material-Table S3). However, when species richness is compared based on an equal sampling effort (i.e., SEU plots are larger than MUC plots), changes in richness between 2016 and 2022 were less evident as per the individual rarefaction index (S_{raref}) (Supplementary Material-Table S2). Moreover, estimated richness based on S_{raref} indicated that SEU-01 had the lowest number of species (33-34 spp. per plot); then, the three plots of MUC showed similar values (37-38 spp.) and the highest richness was estimated for SEU-02 and SEU-03 (ranging between 39 and 45 spp.) (Supplementary Material-Table S2). The comparison of species diversity based on Shannon's (H′) and Simpson's (Ds) indexes accounting for differences in the size of the sampling plots showed similar results (Supplementary Material-Table S2), with no significant differences in diversity between sampling years both in MUC and in SEU (P=0.01 in all pair-wise comparisons). When we compared H′ and Ds between plots, plots were arranged in the same order resulting from the rarefaction index: SEU-01<(MUC-01, MUC-02, MUC-03)<(SEU-02, SEU-03).

Species dispersal syndromes

The assessment of the different dispersal strategies showed that both sites, despite being in contrasting conditions, share similar syndromes. For instance, most species in both sites (82 in total) had seeds dispersed by animals (Zoochory syndrome, 82% in MUC and 80% in SEU), including species of the families Lauraceae (*Nectandra*, *Ocotea*, *Persea* and *Aniba*), Melastomataceae (*Miconia*), Euphorbiaceae (*Alchornea* and *Sapium*) and Rubiaceae (*Palicourea*). Species with heavy fruits (e.g., *Billia ros*ea in SEU) comprise barochory-dispersed species which represent 13-14% in MUC and SEU (for a total of 14 species), respectively. Finally, anemochory and hydrochory species corresponded to 5-6% in the two sites, with three species in total included in each group (Supplementary Material-Figure S2).

Patterns of species abundance

Based on a Bray Curtis floristic similarity approach, the largest differences in species abundances were observed between the two study sites (MUC vs. SEU), which were clearly separated along the first ordination axis of the PCoA (which captured 60.4% of total variation), with the plots in each site being grouped in two different clusters (Figure 3, Supplementary Material-Figure S3). In fact, the average Bray-Curtis similarity between plots in the two sites was only 30.3%. The differences between the two sites were mostly associated with a higher relative importance of species such as *Hedyosmum racemosum*, *Clethra fagifolia*, *Billia rosea*, *Weinmannia lechleriana* and *Guettarda crispiflora* in La Mucuy, while in San Eusebio, species such as *Retrophyllum rospigliosii*, *Aniba robusta*, *Hieronyma fendleri*, *Cyathea pauciflora*, *Ficus velutina* and *Geissanthus fragrans* were more important (or were absent in MUC plots).

In La Mucuy, the second ordination axis organized plots along elevation, with the higher plot at 2700 m (MUC-03), with higher abundances of species such as *Beilschmiedia tovarensis*, *Cyathea parvifolia*, *Clethra fagifolia* and *Ocotea macropoda*, and being clearly separated from the two plots at lower elevations (MUC-01 and MUC-02). These showed a higher floristic similarity and a higher basal area of *Alchornea grandiflora*, *Myrcia splendens* and *Zanthoxylum melanostictum*. Across the two censuses however, there were relatively few changes in species abundances in the plots between the base line (2016) and the re-census (2022), being grouped in all cases very close in the ordination space and in the cluster analysis, showing more than 80% of Bray-Curtis similarity between them in all

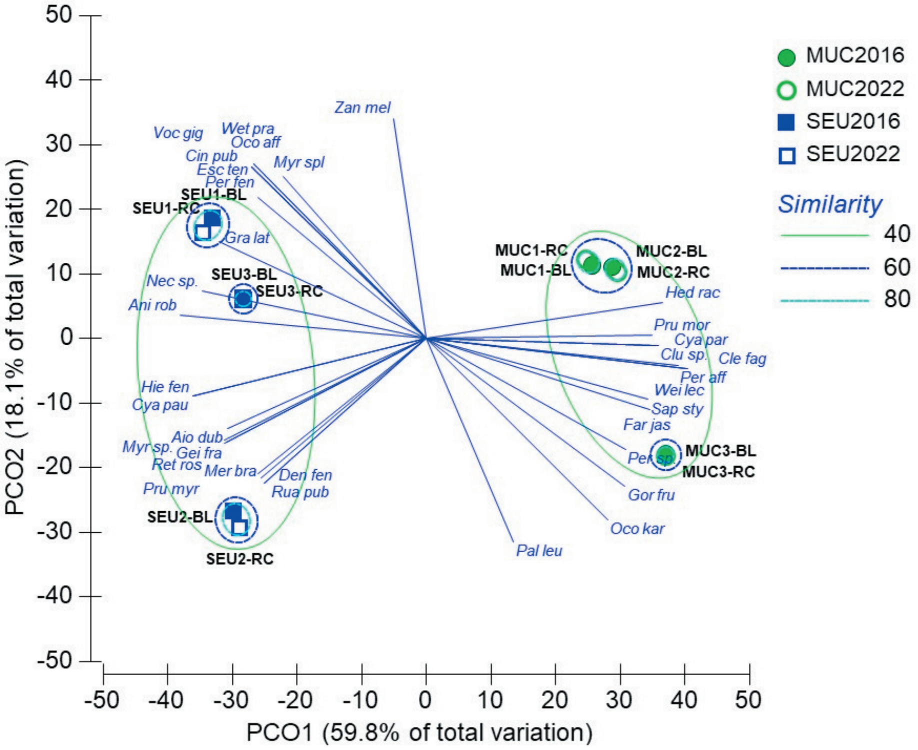

Figure 3. Principal coordinate analysis ordination based on Bray-Curtis similarity calculated from a matrix of basal area for each species for permanent plots in La Mucuy (MUC) and San Eusebio (SEU) for the years 2016 (base line; BL) and 2022 (re-census; RC). The first two ordination axes are presented. Vectors represent the Spearman rank (r_s) correlation of the total basal area of each species with the first two ordination components (we include species with $r_s \geq 0.80$). We overlayed results from a cluster analysis (average linkage) on the same Bray-Curtis similarity matrix (groups correspond to 40, 60 and 80% similarity). For a detailed description of the species see Supplementary Material-Table S3.

Figura 3. Ordenación del análisis de coordenadas principales basado en la similitud de Bray-Curtis calculada a partir de una matriz de área basal para cada especie para parcelas permanentes en La Mucuy (MUC) y San Eusebio (SEU) para los años 2016 (línea base; BL) y 2022 (re-censo; RC). Se presentan los dos primeros ejes de ordenación. Los vectores representan la correlación de rango de Spearman (r_s) del área basal total de cada especie con los dos primeros componentes de ordenación (incluimos especies con $r_s \geq 0.80$). Superpusimos los resultados de un análisis de conglomerados (vinculación media) en la misma matriz de similitud de Bray-Curtis (los grupos corresponden a 40, 60 y 80% de similitud). Para una descripción detallada de las especies, ver Supplementary Material-Tabla S3.

cases (Figure 3, Supplementary Material-Figure S3).

Characterization of forest structure

We observed high values of total stem density and aboveground carbon (AGC) in all plots, but no clear differences between the two study sites were found, although a higher variability was evident in San Eusebio plots. Mean values of density in 2016 were 903±250 stems/ha (SD) for SEU increasing to 962±281 stems/ha in 2022. In the case of MUC, 2016 mean density was 900±49 stems/ha and increased to 933±95 stems/ha in 2022. While average density was very similar among both sites, AGC was higher in La Mucuy compared to San Eusebio in both years. In 2016, MUC had, on average, 195.4±40.3 (SD) Mg C/ha in the AGC, increasing six years later to 213.9±38.9 Mg C/ha. Between 2016 and 2022, AGC in San Eusebio forests increased from 187.4±77.1 to 191.8±80.9 Mg C/ha (Figure 4). The observed increase in AGC occurred considerably faster in MUC plots, with a mean annual rate of 3.09±1.42 MgC.ha^{-1}.y^{-1}, while this rate was 0.73±0.48 Mg C.ha^{-1}.y^{-1} in SEU plots.

To further understand the potential role of stem mortality as a driver of the changes of both AGC and density, we explored their relationships via simple regression disaggregating these estimates in 10-cm size classes (Figure 5). While these relationships appeared weak or absent, a consistent pattern was observed in terms of the highest AGC change occurring within the largest size class (≥60 cm) in both sites. For example, at MUC, this was estimated at 2.39±0.67 Mg C.ha^{-1}.y^{-1} or close to ~77% of the total AGC change, followed by the 50-60 cm (Mean AGCch=0.31 Mg C.ha^{-1}.y^{-1}) and 10-20 cm trees (Mean AGCch=0.28 Mg C.ha^{-1}.y^{-1}). Only the intermediate size classes (30-50 cm) had a decline in AGC between 2016 and 2022. In SEU, the proportion of change in AGC from large trees was even higher with a mean AGCch of 0.61±0.11 Mg C.ha^{-1}.y^{-1} or close to ~84% of the total AGC change, followed by the 10-20 cm (Mean AGCch=0.52 Mg C.ha^{-1}.y^{-1}) and 50-60 cm classes (Mean AGCch=0.27 Mg C.ha^{-1}.y^{-1}). Contrary to MUC plots, trees between 20 and 50 cm in size had, on average, a decline in AGC as high as -0.51 Mg C.ha^{-1}.y^{-1} (Supplementary Material-Figure S5).

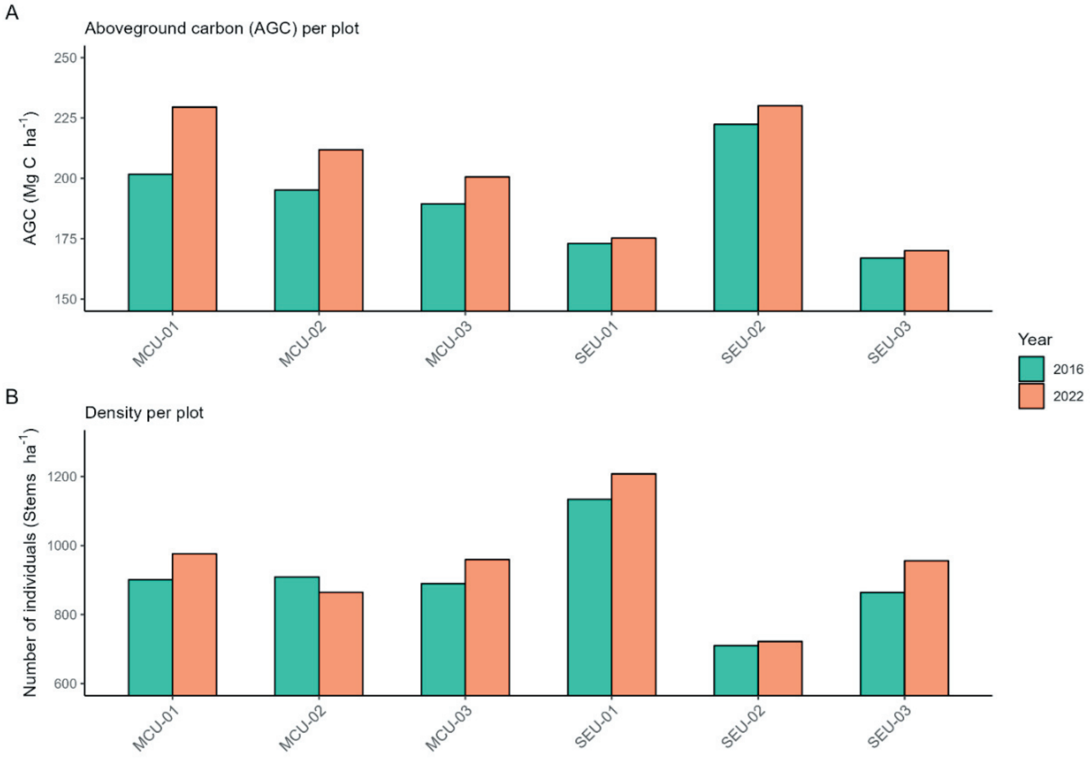

Figure 4. Aboveground carbon (AGC) (A) and stem density (B) for each plot between 2016 and 2022. MCU=La Mucuy (Sierra Nevada Mountain range). SEU=San Eusebio (La Culata range).

Figura 4. Carbono sobre el suelo (AGC) (A) y densidad de tallos (B) para cada parcela entre 2016 y 2022. MCU=La Mucuy (Sierra Nevada). SEU=San Eusebio (La Culata).

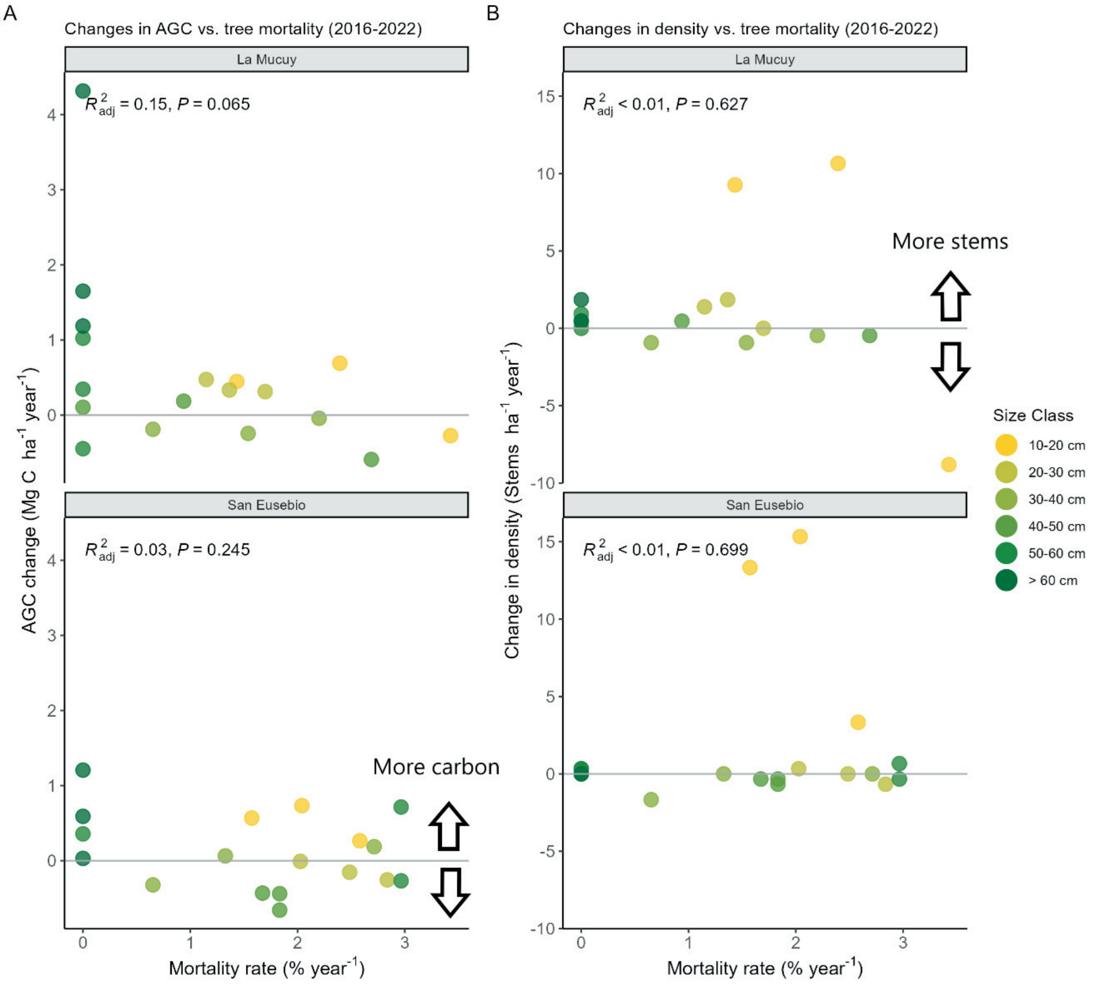

Figure 5. Mean annual change in AGC (A) and stem density (B) between 2016 and 2022 as a function of mortality rates by size classes. The gray horizontal line intersecting zero in each figure serves as a threshold to indicate gains or losses in carbon and density over the study period.

Figura 5. Cambio promedio anual en AGC (A) y densidad de tallos (B) entre 2016 y 2022 en función de las tasas de mortalidad por clases de tamaño. La línea horizontal gris que intercepta el cero en cada figura sirve para indicar las ganancias o pérdidas de carbono y densidad durante el periodo de estudio.

Turnover rates and stem dynamics

Estimated mortality, recruitment and turnover rates for the six-year period analyzed here were relatively low and similar between all studied plots. Mortality rates ranged between 1.23 and 2.58%/year in La Mucuy (mean=1.92±0.67%/year SD), corresponding to 92 trees dying between 2016 and 2022. In San Eusebio, they ranged between 1.92 and 2.31%/year (mean=2.05±0.22%/year SD), with 135 individuals dying during the 2016-2022 period. Recruitment rates were slightly higher in MUC (n=128 individuals), ranging between 0.37 and 0.38%/year (mean=0.38±0.01%/year SD), while in SEU (recruits=167) varied between 0.23 and 0.35%/year (mean=0.29±0.06%/year SD). Finally, turnover rates were similar in the two study sites, with a general average in all plots of 1.16%/year (Supplementary Material-Table S5, Supplementary Material-Figure S4).

As expected, recruitment and mortality were both concentrated in the most abundant species in these forests. In La Mucuy for example, recruited and dead trees detected in 2022 were mostly from *Hedyosmum racemosum*, *Myrcia splendens* and *Eugenia tamaensis*, and two arboreal fern species *Cyathea parvifolia* y *Alsophila engelii*. In the case of San Eusebio, ingrowth of new individuals and the associated mortality rates were largely concentrated in *Cyathea pauciflora*, *Wettinia praemorsa*, *Myrcia* sp. and *Eugenia tamaensis*. Although in the section below we are describing the structural characteristics of both sites in more detail, it is important to indicate that large trees (>50cm in La Mucuy and >60cm in San Eusebio) did not experience any mortality during this six-year period. In fact, individuals of the species indicated earlier with the highest mortality rates were found in the 10-20 cm size class in La Mucuy (mean=2.42%/year; range=1.43-3.42%/year), while in San Eusebio, the highest mortality occurred in the 20-30 cm class (mean=2.52%/year; range=2.02-2.83%/year).

The role of environmental conditions

The principal component analysis (PCA) conducted on a set of environmental variables showed two major axes which explained more than 80% of the environmental variability in this dataset (Supplementary Material-Figure S6). A first axis captured 52.3% and was negatively correlated with three soil-related variables (i.e., soil pH, %loam content, %nitrogen) and with all temperature-based estimates (i.e., Tmin, Tmax, Tmean). This first axis was positively correlated with elevation, slope, %sand, %organic carbon and mean annual precipitation (MAP). The second axis described 28.9% of the variation with elevation and %loam negatively correlated, while positively correlated with the rest of the variables. This simple approach allowed us to differentiate both sites largely due to higher levels of precipitation, higher slope and higher proportion of clay in soils in La Mucuy plots. Overall, when using the scores of the first two axes of the PCA as predictors of AGC, AGWP, turnover rates (i.e., mortality and recruitment) and species richness, very weak to non-existent correlations were found. Nevertheless, PCA1 was significantly and negatively correlated with AGWP and species richness, but positively with recruitment rates. On the other hand, PCA2 was only significantly (and positively) correlated with AGWP (Supplementary Material-Figure S7).

Discussion

Our study explored tree species composition, structure and short-term dynamics of two sites in the two main mountain ranges of the Venezuelan Andes. Our first working hypotheses of clear differences between both sites and the lack of significant trends in species diversity and composition were confirmed. In relation to our first research question about the main differences in species diversity and their associated dispersal syndromes across two montane forest sites in the Venezuelan Andes, three main messages emerge. First, taking both sites together, species richness of individuals ≥10 cm in diameter are in the low side of the range reported across other forests of the tropical Andes (Malizia et al. 2020). Despite being in the tropical region, the geographical location of our study sites towards the northern portion of the Andes (and north of the equator), relative to other Andean forests with more equatorial latitudes, could be the first large-scale factor driving the relatively low diversity found in our plots. Overall, a higher number of species towards the equator is consistent with the latitudinal diversity gradient (LDG) theory (Liang et al. 2022; Saupe et al. 2019). Also, in the younger Andean highlands towards the north, a shorter time for species establishment may explain the lower richness of lineages, as well as the increased tendency for closely related species to coexist (Ramírez et al. 2019). In addition, our study sites are also located in an elevation belt (>2000 m a. s. l.) closer to the cloud-immersion zone where species diversity is generally lower in many Andean forests (Girardin et al. 2014; Griffiths et al. 2021). Indeed, most if not all of the abundant species found in our plots are species with unique adaptations to persist, survive and grow slowly under shade and relatively cool temperatures (Quevedo-Rojas et al. 2016). Another factor to consider is that the Andean forests in Venezuela have a floristic composition influenced by the Orinoquia region, which tends to be drier and less diverse, whereas, for example, Andean forests of Perú, Bolivia and Ecuador are connected to the wetter and more diverse Amazonian ecoregion (Kessler et al. 2011; Trujillo-C and Henao-Cárdenas 2018).

Secondly, the composition of these forests align well with the findings of Gentry (1995), who reported a predominant abundance of Neotropical families such as Lauraceae, Melastomataceae and Myrtaceae (Supplementary Material-Table S3) across many montane tropical forests, including the Andes. The presence of a high number of Lauraceae species in the Andes (24 different species out of 103 identified in the case of MUC and SEU combined (Supplementary Material-Table S3) was noted by Gentry (1988) as an evidence of the replacement of the Leguminosae family, highly dominant at lower elevations, as the most species-rich family at intermediate elevations. Lauraceae species often develop monospermic, fleshy fruits or large succulent diaspores (sensu Kelly et al. 1994) with zoochory dispersed mechanisms (Supplementary Material-Figure S1, Supplementary Material-Table S3), which are an important food source for the high diversity of birds and some species of bats and rodents found in the Andes. With a similar dispersal form as berries, drupes or arillate seeds, the majority of Melastomataceae, Myrtaceae, Rubiaceae, Viburnaceae and Solanaceae tree species are also dispersed by many mammals, birds, reptiles and ants in several montane forests of the Venezuelan Andes (Kelly et al. 1994). In a recent study comparing several seed-dispersal networks in the Andes, Dehling et al. (2020) found that the similarity in functional roles, despite the high species turnover, suggests that the ecological process of seed dispersal is organized similarly along the Andes, with similar functional roles fulfilled locally by different species assemblages. This also aligns with our findings of both sites having a great proportion of species with zoochory dispersal syndromes (Supplementary Material-Figure S1, Supplementary Material-Table S3), in which many bird species are needed to maintain the seed-dispersal process along the Andes.

While we found that about a quarter of the species identified are shared between both sites (Supplementary Material-Table S3), there are clear differences in the main species assemblages (Supplementary Material-Figure S1). This could be linked with abiotic factors (i.e., environmental filters), such as climate, soils or topography. In fact, the location of plots in the multivariate space (Figure 3, Supplementary Material-Figure S6) appears to show a combined effect of differences in precipitation, slope and the proportion of clay in the soil between the two study sites. Higher values for all these variables (in terms of the PCA axes) seem to be associated with lower species richness in MUC plots (Supplementary Material-Table S1). However, past selective logging or deforestation, particularly in La Mucuy forests, may have played an additional role in shaping current diversity patterns and merits further analysis. In montane forests of Central America, for example, floristic similarity was negatively correlated with differences in elevation, horizontal precipitation, temperatures and soil conditions between plots, which suggests that beta-diversity (i.e., the variation or turnover of species composition across different habitats) can be largely driven by species with narrow spatial ranges, due to the interactions between topography, climate and soil formation processes, especially around the wind-exposed and cloud covered ridge areas (Häger 2010).

Finally, during the 2016-2022 period considered in our study we did not find clear evidence of major changes in species composition and species richness/diversity in these forests. The most obvious explanation is that a significant alteration of species composition in these forests may require much longer timescales than the short 6-year interval considered here, a broader altitudinal gradient in the sample or a specific disturbance event capable of influencing species turnover. For example, widespread evidence of 'thermophilization' in mature and juvenile tree species in Andean forests have been reported for longer intervals of at least 15 years (Duque et al. 2015; Fadrique et al. 2018). While the potential compositional changes were not directly addressed, using the entire record of more than 50 years of data from San Eusebio plots, Vilanova (2019) found that these forests have been experiencing significant structural changes including an increase in mortality rates and a decline in the average tree size over time which possibly may have altered their composition. Ultimately, this serves as a sound justification for the continued monitoring of these sites as climate change continues to impact montane forests across the Andes, and the need to expand the monitoring efforts to establish new permanent plots at different elevations in the Venezuela Andes (Mata-Guel et al. 2023).

Structural and demographic attributes

The analysis of the structure and turnover rates of these contrasting montane forests of the Venezuelan Andes revealed interesting patterns. In terms of stem density for example, these forests contain a considerably higher number of individuals per area relatively to other forests in Venezuela and in the tropics, particularly compared to lowland forests in the Western plains and the Guiana Shield regions (Vilanova et al. 2018). These high densities are in fact a common feature of tropical and sub-tropical Andean forests particularly at elevations between 2000 and 3000 m a. s. l. (Girardin et al. 2014; Malizia et al. 2020; Baez et al. 2015) (Figure 4). Both sites also share a similar pattern of stem density across different size-classes following the standard reversed J-shaped form, with high numbers of small-stemmed trees and with an overstory of a relatively few scattered large trees that characterize the structure of mature forests (Oliver and Larson 1996) (Supplementary Material-Figure S5). These levels of density are also naturally associated with large carbon stocks attained in the aboveground biomass of tropical montane forests (Spracklen and Righelato 2014). In fact, 2022 AGC values across all plots (202.9±25.9 Mg C/ha) are among the highest across old-growth tropical forests even beyond montane ecosystems, often comparable to lowland forests (Cuni-Sanchez et al. 2021; Delaney et al. 1998; Duque et al. 2021; Rozendaal et al. 2022; Spracklen and Righelato 2014; Vilanova et al. 2018). In high elevation forests like those studied here, lower temperatures promote lower evapotranspiration and a much higher stem aboveground carbon residence time (Cuni-Sanchez et al. 2021; Girardin et al. 2010; Malhi 2012), which allows for high AGC accumulation. In addition, forest biomass density in northern South America has been shown to increase with increasing water availability and precipitation (Alvarez-Davila et al. 2017), which can explain why the more humid MUC plots have, on average, ~10% higher AGC values compared to SEU plots in 2022 (Figure 4).

Demographic rates of mortality and recruitment (i.e., turnover) in our study fall well within the range of values reported for other tropical montane forests (Báez et al. 2015; Carey et al. 1994; Vilanova et al. 2018), usually showing that these ecosystems have a relatively slower stem dynamics compared to their lowland counterparts. The rates at which trees/stems from these ecosystems die and recruit new individuals is determined by both successional status (i.e., age), where most tropical mature stands have typically lower rates of turnover (Phillips et al. 2004) and dynamics of the disturbance regime. Other than large-scale landslides, which tend to have a lower frequency compared to other disturbances (Freund and Silman 2023), in Andean montane forests natural disturbances are frequent and generally occur over small spatial scales, typically less than 200 m^2 (Asner et al. 2014). Also, our interval between measurements of only six years (2016-2022) does not allow us to fully capture the nature of the potential effect of disturbance events on turnover rates. Yet, as indicated above, our results show a high and significant correlation between the environmental conditions most strongly associated with the compositional differences between MUC and SEU (i.e., precipitation, slope, %clay) (Supplementary Material-Figure S6) with recruitment rates (Supplementary Material-Figure S7). Although recruitment rates are generally low, these are higher in MUC plots, where moisture deficit is not a major limiting factor (Schwarzkopf et al. 2011), thus, creating favorable conditions for species establishment and survival.

With a few exceptions, higher mortality rates were largely concentrated in the low to medium size-class trees across both sites, a common pattern in old growth tropical forests (Oliver and Larson 1996), but did not show a clear relationship with the observed changes in AGC that occurred between 2016 and 2022 (Figure 4). One plausible explanation is that the lack of a large sample size may have impeded the detection of statistically significant relationships. For example, using a higher number of plots, Johnson et al. (2016) and Duque et al. (2021) showed that mortality rates were major drivers of the variation of AGC across Amazonian and Andean forests, respectively. In addition, mortality rates were not correlated with any of the environmental parameters considered here (Supplementary Material-Figure S7), also likely as a result of insufficient spatial replication. Length of dry season, longer in the case of SEU, has been found to drive tree mortality across the tropics (Phillips et al. 2010).

Our overall estimates of the net increase in AGC or aboveground woody productivity (AGWP) over the six-year period considered here (3.09±1.42 Mg C.ha^{-1}.y^{-1} at MUC; 0.73±0.48 Mg C.ha^{-1}.y^{-1} in SEU) support our second hypothesis and are consistent with recent findings showing that Andean forests have been net carbon sinks over the last few years (Duque et al. 2021). However, at least for MUC, this change seems to have occurred considerably faster, on average, than in many other forests in the Andes. One hypothesis that needs to be considered and further investigated is that plots in La Mucuy may be in an advanced secondary succession stage where faster growth is common (Poorter et al. 2016), although we do not have direct evidence of human use, except for limited selective logging before the creation of these forest reserves in the 1950s. Furthermore, there seems to be a disparate role of tree size across all plots in driving this change, with small and large classes having the highest positive changes in AGC (Figure 4), especially in SEU plots where the total stocks of large trees are remarkably higher than in MUC plots (Supplementary Material-Figure S5). Under the right environmental conditions, the increases in total leaf area as trees age can outpace the declines in productivity per unit of leaf area and thus act not only as senescent carbon reservoirs but actively fix large amounts of carbon over time (Slik et al. 2013; Stephenson et al. 2014). This ultimately highlights the relevance of large trees as major components of forest structure and dynamics.

Conclusions

In this study we provide a general overview of the compositional and structural characteristics and recent dynamics of cloud forests in the two main mountain chains of the Venezuelan Andes. While limitations regarding the spatial and temporal coverage do need to be acknowledged, our goal was to establish a regional baseline for continuous monitoring of these diverse and complex forests. Both sites studied show contrasting patterns of species diversity, largely driven by their ecological conditions, particularly higher precipitation in MUC plots. These compositional differences between the two sites (which were also reflected in differences in the biogeographic composition of both forests), emphasize the large beta-diversity that results from the presence of two distinct sierras in the Venezuelan Andes, emphasizing the importance of protecting forest diversity at a regional scale (which is aided by the presence of one large national park in each of them). Moreover, the strong prevalence of zoochoric seed dispersal emphasizes the importance of conserving the bird and mammal communities associated with these forests for the long-term resilience of these ecosystems.

In the short interval considered here, we did not find evidence of significant compositional changes and these areas have both a relatively slow dynamics reflected in rather similar rates of turnover, but with San Eusebio plots attaining lower carbon stocks (probably also as a result of lower total rainfall at this site). Yet, both areas have shown an increase in their AGC stocks between 2016 and 2022 capturing a significant amount of carbon dioxide from the atmosphere thus serving as an active sink, pointing to carbon accumulation as a key service provided by these ecosystems. Interestingly, this function appears to be largely driven by the largest tress in both sites, that account for the highest proportion of stocks in both periods.

Considering that these are highly threatened ecosystems limited to higher elevations within protected areas (where official monitoring programs are urgently needed), we think the expansion and a long-term and sustained effort for monitoring of these forests is a fundamental priority for evidence-based decision making and conservation efforts. In this context, our results provide insights into the ecological drivers and habitat conditions that shape species composition and dynamics in montane forests of the Venezuelan Andes. Understanding these relationships and interactions is crucial for conservation and management efforts, as these helps identifying areas of high biodiversity, prioritize conservation actions and anticipate potential impacts of climate change on species distributions.

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