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Diversity and growth patterns of woody species in the Mediterranean Coastal range of Chile: A case study in Altos de Cantillana †

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Abstract

Background: The Altos de Cantillana mountain range (ACMR) in central Chile is composed of different vegetation communities, and is currently a priority site for conservation, due to its high endemism, high anthropogenic pressure and vulnerability to climate change. Research on biodiversity and carbon stocks in ACMR is essential to comprehend the resilience of these forests and to define conservation strategies. This study examines the spatial variability of biodiversity and tree biomass patterns along the entire altitudinal gradient of the ACMR.

Methods: Six tree species communities were studied in Altos de Cantillana Nature Sanctuary, along an altitudinal gradient ranging from 415 to 2010 m. Woody species regeneration and inventory plots, as well as dendrochronological sampling in ~150 trees were carried out. Diversity patterns were analyzed using the Jaccard index and alpha index. Growth patterns of dominant trees species were analyzed by ring-width and trunk biomass chronologies, focusing on the recent megadrought period since 2010.

Results: The forest inventory revealed a notable decline in alfa diversity patterns with increasing elevation. The moist sclerophyllous forest exhibited the highest diversity. However, we did not find a pattern between elevation and diversity (and abundance) at the seed regeneration inventory level. Additionally, we identified three clusters of woody species similarity: (i) sclerophyllous, shrubs and hygrophilous forest (<1,000 m.a.s.l.); (ii) high-elevation sclerophyllous forest (>1,500 m.a.s.l); and (iii) deciduous forests (~ 2,000 m.a.s.l). Furthermore, declining growth rates were observed in all communities studied beginning in the 1980s, with even a stronger reduction in radial growth (35% on average) and biomass accumulation (56% on average) when comparing the megadrought with six decades earlier.

Conclusions: We concluded that there is a negative correlation between woody species diversity and elevation. However, there are no altitudinal patterns in seedling regeneration diversity and abundance, which puts the natural succession in ACMR at risk. Additionally, we have determined that the accumulation of trunk biomass in dominant woody species has been significantly impacted by the recent megadrought period. This has affected the sink capacity of forest communities in ACMR. Therefore, our findings can significantly contribute to more efficient and timely decision-making processes regarding the conservation and restoration of this globally unique ecosystem.

Keywords: biodiversity hotspot, biogeographic gradient, dendroecology, forest inventory, megadrought, seedling density.

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Introduction

Mountains are considered an exceptional natural laboratory to study the effects of climate change on ecosystem structure, dynamics, and functions (Payne et al. 2017). Consequently, research on biodiversity and biomass patterns in mountain ecosystems is gaining relevance, as it contributes to understanding the resilience of forests to climate change and also plays a fundamental role in defining conservation strategies (Körner & Paulsen 2004; Nagy et al. 2023), especially in poorly researched ecosystems such as the coastal mountain range of central Chile.

Around 20,000 years ago, the last glacial advance began in South America, which kept the Andes Mountain range of Central Chile frozen (Rabassa & Clapperton 1990; Zech et al. 2008). As a consequence, there was a mass migration of ecosystems towards the Coastal Mountain range in Central Chile (31-35°S), which remained with more temperate conditions serving as a refuge for vegetation (Heusser 1990). Nowadays, these plant communities located in the Mediterranean climate of Central Chile provide fundamental ecosystem services to neighboring areas, such as nutrient cycling, carbon sequestration, soil protection, biodiversity conservation, climate regulation, and water supply (Martinez-Harms et al. 2017; Nocentini et al. 2022; Smith-Ramírez et al. 2023). One of the most outstanding refuges in South America is Altos de Cantillana mountain range (ACMR), located in the Mediterranean region of central Chile (Donoso 2008, 2015). ACMR is a priority site for conservation (MMA & PNUD 2015) and has been declared a biodiversity hotspot for having high species richness, a significant degree of endemism in flora and fauna, and a heightened vulnerability to landscape fragmentation (Arroyo et al. 1999; Myers et al. 2000). However, despite its high conservation importance, there are few scientific studies on its plant diversity (Romero-Gárate & Teillier 2009, 2014) and tree growth dynamics (Venegas-González et al. 2018, 2022).

Historically, the ACMR has faced various anthropogenic pressures, including urbanisation, agriculture, grazing, mining, and unsustainable extraction of natural resources (Alaniz et al. 2016; Cox & Underwood 2011; Montoya-Tangarife et al. 2023). More recently, it has encountered an unprecedented megadrought, characterised by an extended rainfall spanning from 2010 to 2022 (Cook et al. 2022, Garreaud et al. 2020). This perturbation period has been affecting the natural dynamics of native ecosystems, with drastic reduction on tree growth (Venegas-González et al. 2023, Venegas-González et al. 2018a), and also likely impacting plant biodiversity and recruitment in Central Chile (Fuentes-Castillo et al. 2019; Matskovsky et al. 2021).

Estimating biological diversity is the first step towards understanding ecosystem functioning (Magurran & McGill 2010). Knowing the composition, structure, and functionality of the diversity of communities is essential for the management and conservation of forest ecosystems, and also for taking political and administrative decisions (Larson 2003). On the other hand, tree growth is central to better understand forest dynamics and climate impacts on the carbon cycle (McDowell et al. 2020; Pugh et al. 2019), particularly considering that global carbon models do not capture current forest carbon dynamics (Koch et al. 2021). These changes in forest productivity dynamics in response to extreme climate have been observed in different parts of the world, and are impacting the carbon sequestration capacity of forest ecosystems worldwide (Reichstein et al. 2013; Zhao & Running 2010). Therefore, basic information on tree diversity, seedling regeneration, and tree growth is not only essential to generate conservation strategies in priority areas that have been poorly studied, such as ACMR; but also to better understand regional climate change (i.e., mitigation and adaptation) and terrestrial carbon sink expectations, providing key information to international agreements and new Chilean national policies related to climate change and biodiversity conservation (e.g., Climate Change Framework Law N°21,455 and Biodiversity and Protected Areas Service Law 21,600).

Here, we investigate the spatial variability of biodiversity and tree biomass patterns across the whole altitudinal gradient of the ACMR. Considering that tree species diversity changes along elevation gradients in response to underlying environmental and topographic conditions (Jump et al. 2012; Toledo-Garibaldi & Williams-Linera 2014), we hypothesise that the richness and abundance of tree species in ACMR are inversely correlated with elevation. This is attributed to harsher environmental conditions at higher elevations, such as colder temperatures, stronger winds, and the presence of snow in winter, in contrast to the relatively milder conditions at lower elevations. Moreover, studying individuals of woody species in the early stages of seedling regeneration is crucial for understanding patterns in the succession of plant communities (Rodà 1999), mainly in regions where the stress caused by summer drought conditions may impact the establishment of new individuals (Bacilieri et al. 1993; Holmgren et al. 2006). Thereby, our second hypothesis is that woody species regeneration by seeds (seedling) are negatively affected by the current conditions of climate change, finding lower regeneration diversity compared to established diversity of young and adult trees. This would modify the natural replacement of woody species, putting at risk the natural succession of the ACMR forests. Finally, given the prevailing conditions of the recent drought in central Chile (e.g. Garreuad et al. 2020; Barria et al. 2021) and the climate-sensitive nature of certain Mediterranean Chilean species (e.g. Venegas-González et al. 2023; Venegas-González 2018), our third hypothesis posits that the megadrought has led to a decline in the accumulation of forest biomass in ACMR. To address these hypotheses, we carried out a study based on prospective (inventory plots) and retrospective (dendrochronology) approaches in six forest communities across an altitudinal gradient. Specifically, we assessed: (i) change and similarities of tree diversity of woody species at different elevations; and (ii) annual variation of tree biomass accumulation of dominant species and their relationship to the current megadrought.

Methods

Study site

The study was conducted during the summer (January) of 2021 in Altos de Cantillana Nature Sanctuary (SAC), located in the Coastal Mountain range of Central Chile (Figure 1). This site represents the northernmost part of the ACMR, with an altitudinal gradient ranging from 377 to 2282 m. It encompasses various vegetation formations under a Mediterranean climate regime characterised by a marked seasonality of rainfall, with cold (mean temperature ~ 11.4 ^{0}C) and rainy (accumulated precipitation ~ 300 mm) winters (June-July-August) and dry (accumulated precipitation ~ 5 mm) and warm (mean temperature ~ 23.4 ^{0}C) summers (December-January-February). Climate data were extracted from the TerraClimate (~ 4 km spatial resolution) by the Google Earth Engine (GEE) Cloud platform from 1958 to 2022 (Abatzoglou et al. 2018). In general, the soils of the Coastal Mountain originate from granitic and metamorphic rocks (Thrower & Bradbury 1973). Due to the intense weathering endured over millions of years, hillsides with soil of vibrant red hues and clayey horizons (Alfisols) are observed. These are associated with soils undergoing more significant leaching during their development, primarily due to water erosion (Inceptisols) (Pfeifer et al. 2018; Schaller et al. 2018). According to the classification by Roberts & Díaz (1960), the prevalent soils in the central zone of Chile include Non-calcium Brown in well-drained areas, characterised by low organic matter content and low nitrogen and phosphorus fertility. Gramusols are found in the lower and gently undulating areas, derived from sedimentary and basaltic rocks, occasionally featuring a high-water table. Specifically, the soils at the study site have a texture that moves between sandy loam and clay loam. They are shallow and exhibit abundant rock fragments, making them highly susceptible to erosion, especially given the steep slopes (Thrower & Bradbury 1973). These soils have a granitic origin with coarse and permeable textures on sunny and shaded slopes, although there is greater depth and organic matter content on south-facing slopes (Quintanilla 2011; Soto et al. 2006).

Sampling

Six tree communities along an altitudinal gradient were sampled during a 15-day field campaign, covering a walking distance of over 50 km (Figure 1). The forest communities from lowest to highest elevations are: (i) hygrophilous forest dominated by *Cryptocarya alba* (Molina) Looser (hygrophilous community; C1 = 415 m.a.s.l); (ii) sclerophyllous forest dominated located at southern exposure (moist conditions) by *Peumus boldus* Molina (moist sclerophyllous community; C2 = 815 m.a.s.l); (iii) ecotone between thorny shrubs and

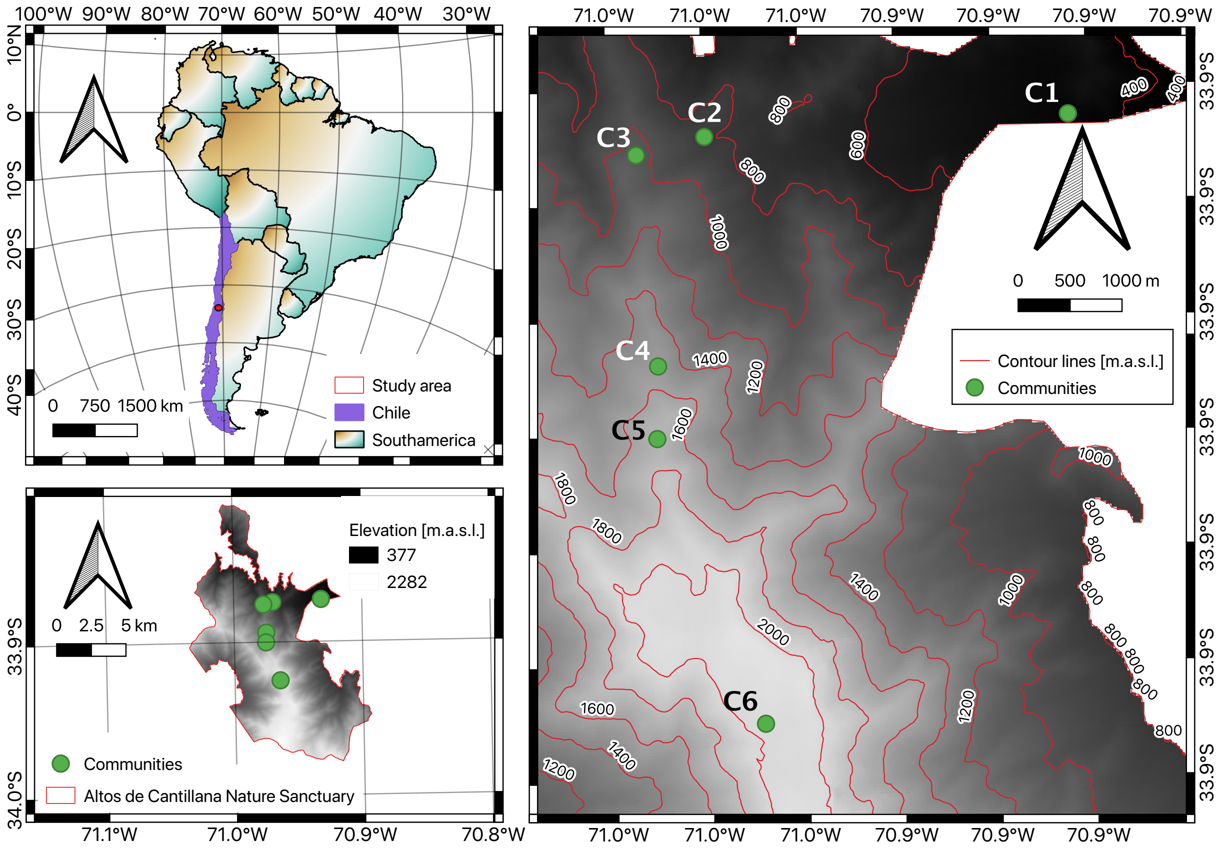

FIGURE 1: Location of the study area in South America (top left). Study area at Altos de Cantillana Nature Sanctuary (bottom left). Communities studied and elevation isolines (right).

sclerophyllous forest trees dominated by *Vachellia caven* (Molina) Seigler & Ebinger (ecotone shrub-trees community; C3 = 1032 m.a.s.l); (iv) sclerophyllous forest located at northern exposure (dry conditions) dominated by *Quillaja saponaria* Molina (dry sclerophyllous community; C4 = 1515 m.a.s.l); (v) montane sclerophyllous forest dominated by *Kageneckia angustifolia* D.Don (montane sclerophyllous forest community; C5 = 1,710 m.a.s.l); and (vi) the tree lines represented by the deciduous forest of *Nothofagus macrocarpa* (A.DC.) F.M. Vázquez & R.Rodr. (deciduous forest community; C6 = 2,010 m.a.s.l). Two 500 m^2 plots and 20 1-m^2 subplots were established in each community. The larger plots focused on woody species at later life stages, specifically trees and shrubs with a diameter at breast height (DBH measured at 1.3 m) or diameter at stump height (DSH measured at 0.10 m) ≥5 cm. In each plot, the woody individuals were counted, their species recorded, and their diameters and heights measured. For trees with buttresses, the DBH was measured immediately above them. The regeneration inventory targeted woody species at early life stages, particularly seedling regeneration with a height < 1 m. In the case of regeneration, the diameter was recorded in mm and was measured at collar height (DCH).

Diversity analyses

Alpha diversity considers both the number of species (richness) and the number of individuals (abundance) of each species present in a specific area. However, the weighting of these variables determines the specific diversity at each site, which states the importance of a species due to its abundance, dominance, or the significance of a particular richness. To address this, we compared and estimated the effective number of species using the Hill series (q = 0, 1, and 2), which assesses the relative importance of rare versus abundant species (Hill 1973). Here, q = 0 corresponds to species richness, q = 1 represents common species (Shannon diversity, Shannon 1948), and q = 2 represents dominant species (Simpson diversity, Simpson 1949). For the numerical analysis, rarefaction curves were constructed, and their 95% confidence intervals (CI) were calculated, allowing to compare whether significant differences between communities exist (Cultid-Medina & Escobar 2019). If the 95% CIs overlap between samples, it is concluded that there is insufficient evidence to say that the estimates are significantly different below an alpha level of 0.05. Conversely, if the 95% CIs do not overlap, it is concluded that the estimates are significantly different from each other (Cumming et al. 2007). To construct the rarefaction curves, the formula of Chao and Jost (2012), available in the iNEXT package (Hsieh et al. 2015) for R was used. The curves consist of three parts: an observed (or interpolated) portion, an "observed" point, corresponding to the total observed richness and abundance, and an extrapolated portion after the observed point (Hsieh et al. 2015). To investigate the potential impact of altitudinal differences between the studied communities on species diversity, a linear regression analysis (LM) was conducted. In this analysis, species abundance and richness (dependent variables) were related to the elevation of each site (independent variable). In addition, we assessed the similarity between communities by calculating the Jaccard index, a measure based on qualitative data regarding the presence or absence of species in each site (Magurran 2004). All the statistical analyses were performed in R version 4.2.2 (R Core Team 2018).

Dendrochronological analysis

To study growth patterns, ~ 25 wood samples (i.e., increment cores and branches) of the dominant tree species (from C1 to C6: *C. alba*, *P. boldus*, *V. caven*, *Q. Saponaria*, *K. angustifolia*, and *N. macrocarpa*) were collected from each community, for a total of ~150 trees. It should be noted here that we analyses were performed at the population level, being considered as indicators of community biomass accumulation. In the case of *C. alba* and *N. macrocarpa*, we sampled only a few individuals in order to update the species chronologies that had been carried out previously (Venegas-González et al. 2023; Venegas-González et al. 2018). Classic dendrochronological techniques (Stokes & Smiley 1968) were followed for sample collection and processing. Age estimation was performed by counting the growth rings, and growth patterns were estimated by measuring the width of the rings using a Velmex Tree Ring Measuring System (model TA4021H1-S6, Velmex Inc, Bloomfield, USA). Samples were cross-dated to identify errors in the dating and measurement of the tree rings by calculating the moving correlations between the individual tree-ring series and an average master series using the program COFECHA (Holmes 1983). The temporal variability in the intensity of the common signal of the chronologies was assessed by the intercorrelation of the series, which represents the degree of association or similarity between two growth series, i.e., how common their growth and therefore the climatic signal is; with values over 0.4 considered as adequate (Fritts 1976).

After cross-dating and constructing annual ring width series, we estimated annual trunk biomass growth (AB) chronologies per tree species using the classical biomass formula., i.e., mean wood density * tree volume (Ortega Rodriguez & Tomazello-Filho 2019; Pompa-García et al. 2018). AB rates were derived from the difference in total AB values between two consecutive years. We did not consider *P. boldus* individuals as they were generally very young (Table S1).

To determine annual wood density, wood samples were scanned from bark to pith at 0.04-mm intervals using an X-ray densitometer (QTRS-01X Tree Ring Scanner; Quintek Measurement Systems, Knoxville, TN, USA). These data allowed us to observe changes in wood density in the pith-bark direction, and to obtain wood density values for heartwood and sapwood per individual. Second, the annual growth values from each tree ring were used to reconstruct the trees' historical diameters and volumes. The volume (V) for each species was calculated as: for *C. alba*, $V = 0.024819 + 6.28237\text{x}10^{-4}$ (DBH) (Benedetti Ruiz 2012a); for *V. caven*, $V = 0.0028 + 1.3065 (\text{DSH})^2$ (Benedetti Ruiz 2012b); for *Q. saponaria*, $V = 0.00641 + 0.00026293 (\text{DBH})^2$ (Godoy

Sáez 2007); and for *N. macrocarpa*, V = 0.000115439 (DBH) $^{2.48824}$ (Donoso et al. 2010). Since we did not find a volume formula for *K. angustifolia*, we used the same formula as for *Q. saponaria*. This decision was based on the close proximity of the populations and the similar characteristics of the individuals.

Results

Forest inventory and seedling regeneration

There were 18 woody species, with 94% of them being endemic across the six communities studied. In the forest inventory, which included individuals with DBH/DSH≥ 5 cm, 14 species were observed, belonging to 13 genera and 12 families. Regarding the woody species regeneration inventory, 16 species were recorded (Table S2). Linear regressions revealed a significant negative correlation between elevation and richness. However, insignificant relations were found at the regeneration level (Figure 2A). Neither relationships were found between the abundance of species and elevation (Figure 2B).

Woody species communities located below 1,000 m had the greatest richness compared to those at higher elevations (above 1,500 m), although abundance was independent with elevation (Table 1). The ecotone between thorny shrubs and sclerophyllous forest (~ 1,000 m) and deciduous forest community (~ 2,000 m), had the lowest mean abundance with 735 trees/ha. In the first case, there were only a few individuals for each species, which may be due to the more disturbed soil conditions. In the second case, there was only one dominant tree species (Figure 3A). In absolute numbers, *Q. saponaria* and *Colliguaja odorifera* Molina were the most and least abundant species, respectively. The communities at higher elevations are characterised by the exclusive presence of the *N. macrocarpa* and *K. angustiofolia* (Figure 3A). The presence of *N. macrocarpa* indicates the tree-line forest, while *K. angustifolia* marks the limit of the sclerophyllous vegetation.

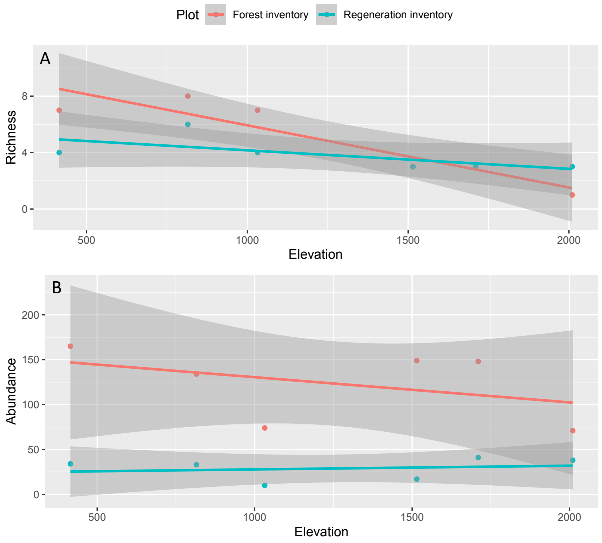

FIGURE 2: Linear relationship between elevation and species richness (numbers of species) and individual abundance for (A) tree and shrub inventory and (B) seedling regeneration inventory. The only significant relationship found was between elevation and species richness in the forest inventory ($r = -0.92$, $P < 0.01$, $R^2 = 0.85$). For abundance, we considered an area of 1000 m^2 for the tree and shrub inventory and 20 m^2 for the regeneration inventory.

With regard to regeneration, the highest communities (montane sclerophyllous and deciduous forest), presented the highest seedling density, with 20,500 and 19,000 seedlings per ha. Hygrophilous and moist sclerophyllous forests (<800 m) have intermediate values of seedling regeneration with ~17,000 seedlings per ha. The lowest values were found in the ecotone shrub-trees forest community with 5,000 seedlings per ha^{-1}. In absolute numbers, *N. macrocarpa*, *C. alba*, *K. angustifolia*, and *Lithraea caustica* Molina (Hook. & Arn.) (litre), were the most abundant species, while *K. oblonga*, *Q. saponaria*, and *Azara petiolaris* (D.Don) I.M.Johnst., were the least abundant species (Figure 3B).

Concerning the Hill series of the forest inventory (Figure 4A), we observed that the interpolated portion of community 2 considerably exceeds the observed portions built for the other communities using the effective number of common species (q = 1) and abundant species (q = 2). Therefore, sclerophyllous moist forest represents the highest species diversity. In terms of species richness (q = 0), the richness observed for community 2 does not differ significantly from the richness observed for community 1 and community 3. The rarefaction curves for high-elevation sclerophyllous forest (>1,500 m.a.s.l., i.e., communities 4 and 5) showed that species diversity is always maintained below the lower-elevation forests using any diversity order (q). Since deciduous forests are monospecific (one tree species, Table 1), regardless of the value that q takes, it will always be below the rarefaction curves calculated for the other communities.

In terms of seedling regeneration inventory, all rarefaction curves showed the same pattern for community 2 (moist sclerophyllous forest). The interpolated portion of the curve considerably exceeded the observed portions constructed for the other communities, demonstrating the highest species diversity of this forest (Figure 4B). However, the other tree communities differ in their results in forest inventory because the hygrophilous forest (lowest elevation, community 1) had similar curves to the high-elevation sclerophyllous forest (communities 4 and 5). These results confirm that seedling regeneration is not limited by elevation, as demonstrated by linear regressions (Figure 2).

According to the Jaccard index, we identified three clusters of woody species with similar communities based on the species richness of the forest inventory: (i) thorn shrubs and sclerophyllous forest at lowest elevation (<1,000 m.a.s.l.); (ii) high-elevation sclerophyllous forest (>1,500 m.a.s.l.); and (iii) deciduous forests (~ 2,000 m.a.s.l.) (Figure S1).

TABLE 1: Characterisation of the six sampled communities. C1: hygrophilous forest community, C2: moist sclerophyllous forest, C3: ecotone shrub-trees forest community, C4: dry sclerophyllous forest community, C5: montane sclerophyllous forest community; C6: deciduous forest community.

Community features	**Community**					
	C1	**C2**	**C3**	**C4**	**C5**	**C6**
Topographic features						
Latitude (°S)	-33.86	-33.86	-33.86	-33.88	-33.89	-33.91
Longitude (°W)	-70.93	-70.97	-70.98	-70.97	-70.97	-70.96
Elevation (m.a.s.l.)	415	815	1032	1515	1710	2010
Aspect (degrees)	120	135	100	415	210	270
Slope (%)	11.0	50.0	22.5	38.5	32.5	36.5
Canopy cover (%)	67.5	69.1	31.7	57.7	21.3	62.8
Tree attributes						
Dominant height (m)	12.0	7.0	4.7	5.5	4.0	15.0
Understory dominant height (m)	2.8	2.5	1.9	2.2	2.0	4.3
Tree abundance (in 1000 m^2)	165	134	74	149	148	71
Richness	7	8	7	3	3	1
Mean DBH[1] ± SE (cm)	11.2±0.7	11.2±0.9	12.5±1.0*	13.3±0.8	9.3±0.3*	29.6±4.4
Mean height ±SE (m)	7.0±0.4	4.2±0.2	2.4±0.2	3.2±0.1	2.4±0.1	8.3±0.6
Regeneration features						
Mean DCH[2] ± SE (mm)	4.5±0.5	17.6±6.1	25.7±3.7	13.6±1.8	10.1±1.1	20.4±1.4
Mean height ± SE (cm)	22.1±3.3	39.5±6.3	103±14.4	109±17	37.7±3.1	55.6±6.0
Seedling abundance (in 20 m^2)	34	33	10	17	41	38
Richness	4	6	4	3	3	3

[1] DBH*:* diameter at breast height (1.3 m), **DSH:* diameter at stump height (0.10 m)*;* [2] DCH*:* diameter at collar height (0 m); SE*:* Standard error; C: community.

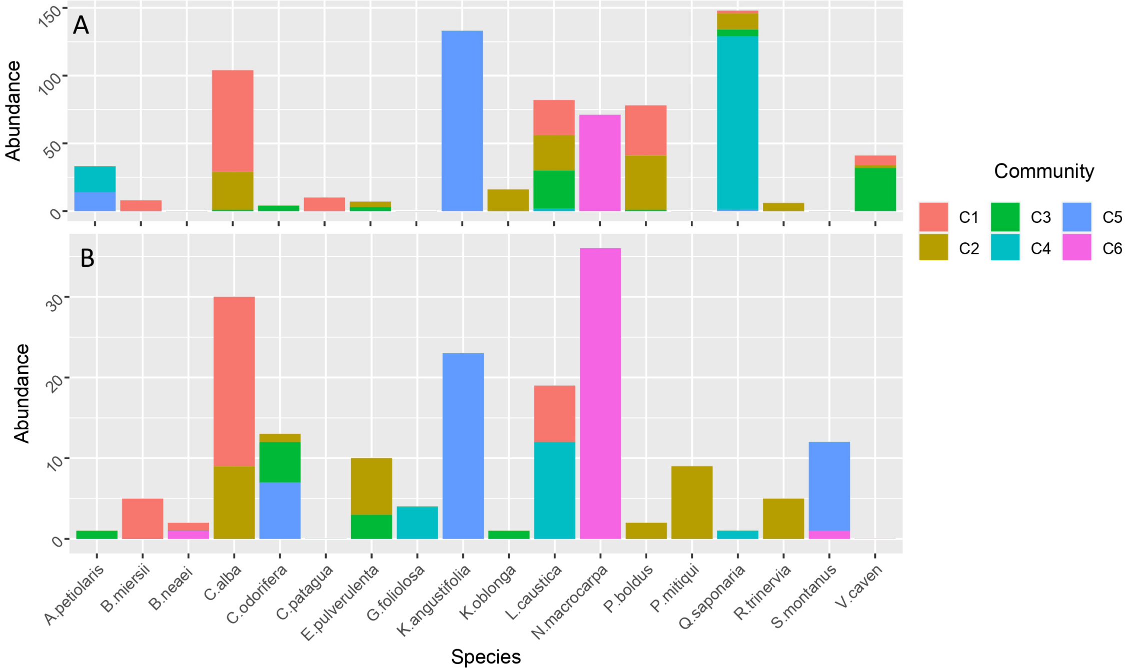

FIGURE 3: Abundance of individuals from forest inventory (A) and regeneration inventory (B) for each community. We considered the total area of the plot by community, i.e., 1000 m^2 for the forest inventory and 20 m^2 for the regeneration inventory.

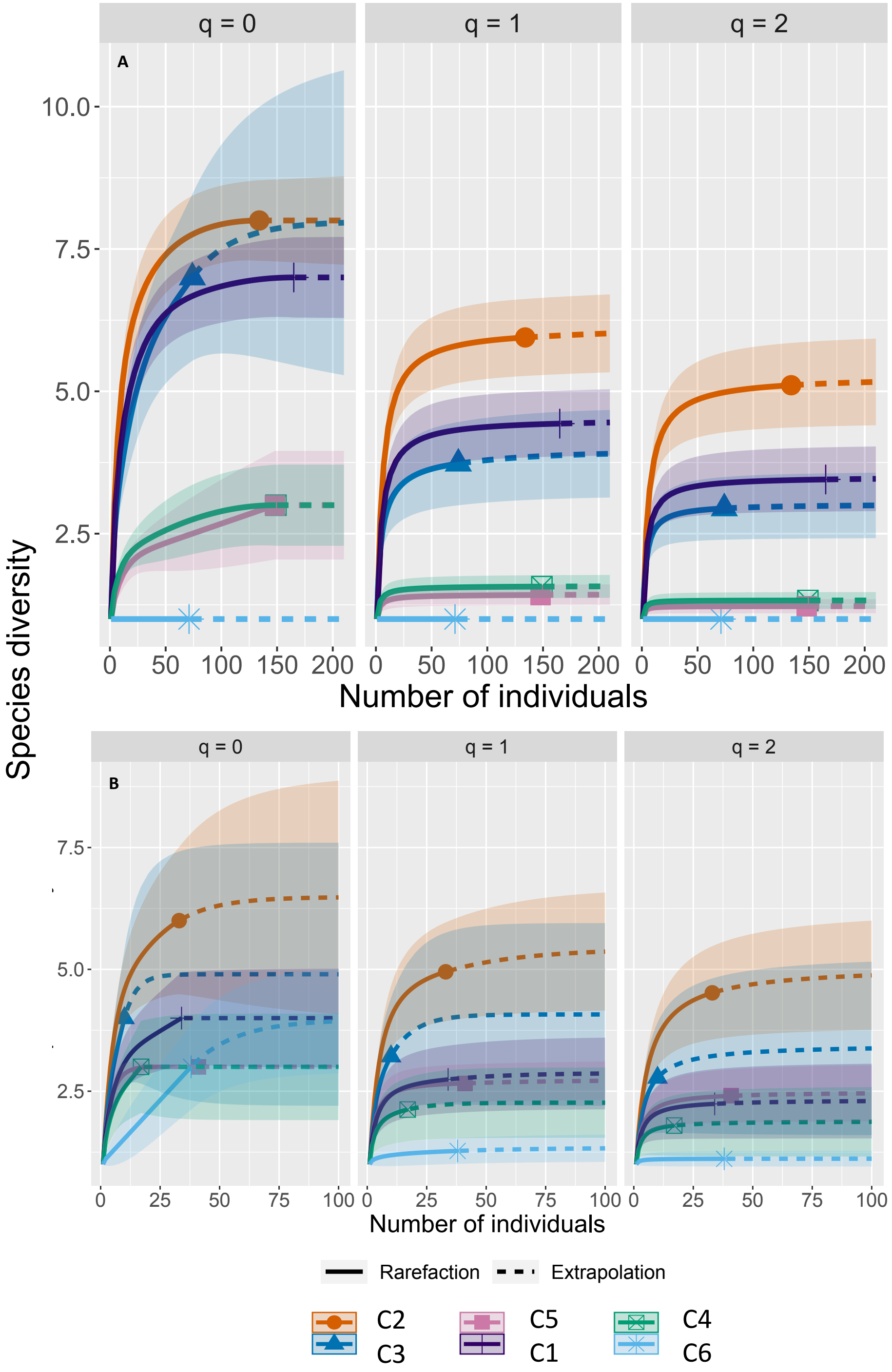

FIGURE 4: Rarefaction curves were constructed based on individuals and their corresponding sampling communities: C1, C2, C3, C4, C5, and C6 (Table 1 and 2). (A) show the number of species from the forest inventory while (B) seed regeneration of woody species. Figures are displayed in the format offered by iNEXT: an interpolated or observed portion of the curve; a point that marks the richness observed in each community, and a portion of the curve extrapolated from the maximum richness and abundance observed in each community. The q-order of diversity is shown at the top of each panel: 0 = richness, 1= effective number of common species, and 2 = effective number of highly abundant species. The bands around the curves correspond to the 95% confidence intervals (CI).

TABLE 2: Radial growth per tree (RW, mm) and annual trunk biomass growth per tree (AB, kg yr^{-1}) rates by decades for the 1950-2019 period for each community: C1: hygrophilous forest community, C2: moist sclerophyllous forest, C3: ecotone shrub-trees forest community, C4: sclerophyllous dry forest community, C5: montane sclerophyllous forest community; C6: deciduous forest community.

Decade	**Community**											
	C1		**C2**		**C3**		**C4**		**C5**		**C6**	
	RW	**AB**	**RW**	**AB**	**RW**	**AB**	**RW**	**AB**	**RW**	**AB**	**RW**	**AB**
1950s	1.3	0.8	1.4	-	1.8	0.9	1.9	1.2	0.7	0.6	3.1	2.7
1960s	1.1	1.5	1.2	-	2.0	1.0	1.0	1.4	1.0	0.4	2.2	2.4
1970s	1.5	1.6	1.9	-	1.8	0.5	0.7	1.2	1.3	0.7	2.6	3.5
1980s	1.0	1.2	1.1	-	1.7	0.7	0.8	1.4	0.7	0.4	1.6	1.6
1990s	1.2	0.9	1.0	-	1.4	0.6	0.6	1.6	0.6	0.5	1.2	2.0
2000s	1.4	1.1	0.7	-	1.0	0.5	0.5	1.3	0.6	0.5	1.5	2.6
2010s	0.8	0.8	0.5	-	0.4	0.4	0.4	0.7	0.4	0.4	0.9	1.8
Mean*	1.25	1.18	1.22	-	1.62	0.70	0.92	1.35	0.82	0.52	2.03	2.47
% decrease**	**-36.0**	**-32.2**	**-59.0**	**-**	**-75.3**	**-42.9**	**-56.5**	**-48.2**	**-51.2**	**-23.1**	**-55.7**	**-27.1**

* Baseline period (1950-2009) of growth rate before megadrought period (2010-2019). **Percentage decrease during the megadrought concerning the baseline period mean. RW: radial growth; AB: annual trunk biomass growth

Growth patterns and biomass

From the 221 ring-width series measured, we constructed six tree-ring chronologies of dominant species in DBH (DSH) of the tree community analyzed in the previous item. The intercorrelation coefficients between the series indicate a common tree growth pattern among the individuals of each community ($r > 0.44$, $P>0.01$). The high mean sensitivity (> 0.44) demonstrates that the chronologies are responsive to climate. The oldest trees were found in deciduous forests, while the youngest forest were observed in the community dominated by *P. boldus*. The hardest wood was *V. caven*, in the ecotone community (Table S2).

Overall, we did not observe significant variations in growth rate across the studied gradients, which ranged from 0.82 to 2.03 mm/year. However it seemed as trees in Community 6 showed the highest ring-width growth, while trees in community 5 had the lowest radial growth rates (Table 2). The forests of communities 1, 4, and 6 (lowest, middle, and highest elevation) exhibited the highest average annual biomass accumulation in the trunk between 1980 and 2019 (Figure 5).

We did not observe differences in tree growth and trunk biomass patterns in response to the megadrought, since all tree communities studied showed a reduction in the values during the period 2010–2019. The radial growth decreased an average of 56%, with the ecotone between thorny shrubs and sclerophyllous trees (C3) being the one that had the greatest reduction (75%). Regarding annual trunk biomass growth per tree (AB), we observed an evident decline in the annual accumulation of this variable including the last years in all communities studied (Figure 5). During the megadrought period, an average of 35% less annual biomass was observed, with tree communities <1,500 m.a.s.l. being the most affected.

Discussion

There is very limited published information about the flora of the Coastal Mountain Range of central Chile, even less with an integrated landscape-level perspective of tree diversity, growth patterns, and trunk biomass accumulation. We aimed to understand diversity and growth patterns along an elevation gradient (~ 400 to 2,000 m.a.s.l.) of the northernmost forest ecosystems of Altos de Cantillana Mountain Range (ACMR). Our results revealed the negative impacts of the current conditions of climate change on the patterns of seed regeneration and tree growth, putting at risk the natural succession and carbon stock of these ecosystems.

Diversity patterns

Our results showed that tree species richness decreases with elevation, when considering only individuals in the established life stage (DBH/DSH >5cm, forest inventory) (Figure 2A). This coincides with many other studies that found a decline in number of plant species with increasing elevation (e.g. Lopez-Angulo et al. 2018; Rahbek 1995; Vetaas & Grytnes 2002). Elevation plays a key role in shaping these habitats, leading to changes in vegetation types, microclimates, and ecological processes (Tito et al. 2020). Typically, as elevation increases, there is a decrease in species richness and biodiversity. However, this pattern can vary depending on specific factors such as climate, and habitat type (McCain & Grytnes 2010). We did not find significant results at the regeneration inventory level (Figure 2B).

When analysing richness and abundance, i.e., patterns of alpha diversity, our results evidenced at the forest inventory level that diversity decreased as elevation increased (Figure 4A). In agreement with other studies (Martin et al. 2021; Monge-González et al. 2020; Wani

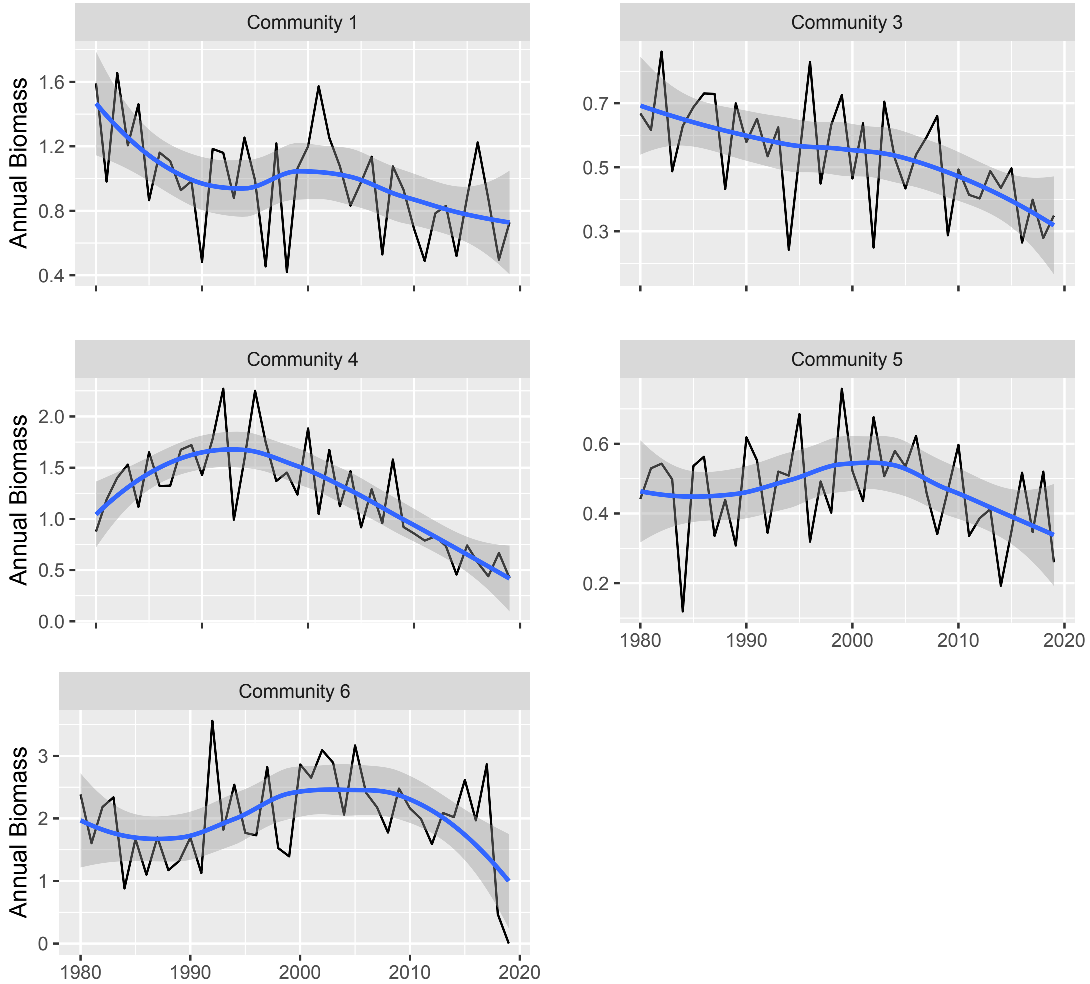

FIGURE 5: Annual woody biomass in the trunk per tree (kg yr^{-1}) for the period 1980-2019 (black line) and trend line (blue line) for five communities. C1: hygrophilous forest community, C3: ecotone shrub-trees forest community, C4: sclerophyllous dry forest community, C5: montane sclerophyllous forest community; C6: deciduous forest community.

et al. 2023) the hypothesis proposed by Rahbel (1995), suggests a general decrease in the number of species with increasing elevation. This is often referred to as the "altitudinal gradient of biodiversity" (e.g., Beck et al. 2008; Hobohm et al. 2014; Zhao et al. 2019). As elevation increases, environmental conditions become more extreme, with lower temperatures, higher winds, and reduced availability of resources such as water and nutrients. These conditions can limit the number of species that can survive and thrive (Young 2009). In this case, the forest at the tree line (i.e., *N. macrocarpa* forest, community 6) is composed solely of the dominant species, *N. macrocarp*a (Figure 4A). Despite having the lowest woody species diversity, this forest stands out for having the highest genetic diversity in the entire distribution (Mathiasen et al. 2020; Venegas-González et al. 2022). This is demonstrated, among other variables, by the observed heterozygosity, with higher values compared to other *Nothofagus* species (Torres-Díaz et al. 2007).

To validate the findings presented in Figures 4A, we employed the Jaccard index to cluster the communities that showed greater diversity at the forest inventory level. The analysis revealed that the forests located at lower elevations, specifically the hygrophilous, moist sclerophyllous, and ecotone shrubs-trees forests (Figure S1), exhibited the highest diversity. However, it is noteworthy that these communities have experienced a decline in species richness at the seedling regeneration scale, with values of 25% (C1), 25% (C2), and 43% (C3) as compared to the established tree diversity. This decline could be attributed to the dry conditions of the last few decades (Garreaud et al. 2020) and the significant increase in heat waves in central Chile since 1980 (González-Reyes et al. 2023), so that the current drier regime would be affecting the seedling recruitment of some sclerophyllous woody species (Velasco & Becerra 2020). Therefore, the diversity of natural forest succession would be affected by these changes. It is worth noting that the ecotone shrub-tree forests dominated by *V. caven,* showed lower richness and abundance values, exhibiting low germination and seedling establishment. Holmgren et al. (2000) documented the limitations of regenerating this species 20 years ago, a finding that was recently corroborated by Becerra et al. (2022).

Our study found that the diversity of seedling regeneration was not affected by elevation. This suggests that most extreme weather conditions, specifically lower temperatures, do not influence seedling regeneration (Figure 4B). Generally, seeds require specific conditions to germinate, which may vary depending on the plant species. In general, these conditions include moisture, temperature, oxygen, light, and the absence of inhibitors (Egley 2017; Toole et al. 1956). It is important to note that different plant species have different germination requirements, and these conditions can vary widely. Therefore, it is necessary to further study the germination of each target species and monitor the subsequent establishment. Additionally, we should note that the data collection was done during summer (warm and dry season), so it is possible that some seeds germinated in late winter and early spring but did not establish until summer and therefore were not accounted for.

Growth patterns and biomass

Regarding growth patterns, a consistent negative trend has been observed across all communities since the 1980s, particularly during the megadrought period (56% less radial growth on average). This has resulted in a strong reduction in trunk biomass growth both in lower and higher elevations (35% less annual biomass on average). In addition, we have observed a 19% tree mortality rate, mainly below 1,500 m, which poses a risk to the region's role as a carbon sink for these ecosystems. Therefore, our study provides valuable insights into the variations and similarities of forest communities along an altitudinal gradient in terms of woody species diversity and tree growth patterns, given the ongoing climate change in central Chile and the uncertain response of mountain ecosystems to projected climate scenarios.

The higher annual trunk biomass accumulation per tree was found in the *N. macrocarpa* forests from community 6, which represents the oldest forest of ACMR, and possibly, of all species distribution (Venegas-González et al. 2018a). This forest has an uneven-aged structure (Venegas-González et al. 2018b) and lower anthropogenic interventions (Venegas-González et al. 2019). The other population with high annual values of biomass accumulation was *C. alba*. This community correspond to the hygrophilous forest, which also contains other large tree species, such as *Beilschmiedia miersii* (Gay) Kosterm, *Persea lingue* Nees and *Crinodendron patagua* Molina (Figure 3, Romero-Gárate & Teillier 2014).

We observed that tree growth patterns in response to the megadrought did not vary across the altitudinal gradient. All populations showed a reduction in radial growth and biomass rate for the period 2010-2019 compared to the baseline (Table 2, Figure 5). Drought events in Mediterranean regions have been shown to have significant impacts on forest ecosystems, including changes in trunk biomass accumulation and tree growth patterns (Babst et al. 2014; Reichstein et al. 2013). Venegas-González et al. (2018) found an abrupt decline in radial growth for *N. macrocarpa* since 1980 related to the decrease in rainfall and the increase in temperatures, as observed for biomass since the megadrought in this study (Figure 5, Community 6). In the lowest elevation (community 1), Venegas-González et al. (2023) observed an abrupt change in the tree growth of this forest since 2002, which was related to an increase in drought, the same year in which some trunk biomass chronologies also began to decrease (Figure 5). Therefore, the effects of climate change appear to be affecting the different communities regardless of their altitudinal position.

For both the short and long term, a general decrease in forest growth, as well as in carbon stocks, promotes conditions of massive tree mortality (Cailleret et al. 2017). Drought-induced water stress can negatively impact tree growth, leading to reduced trunk biomass accumulation and narrower tree rings, which can be used as indicators of reduced growth rates (e.g., Larysch et al. 2022). In our study, we identified that 19% of the total trees sampled had evident mortality signs, i.e. >75% of crown transparency (Dobbertin 2005), mainly from hygrophilous forests to sclerophyllous dry forests (Figure S2). According to Miranda et al. (2020), approximately one-third of the Chilen Mediterranean forest exhibited browning conditions between 2010 and 2017. Notably, the semi-arid sclerophyllous forest, characterised by drought-tolerant species, displayed the most severe degree of browning, aligning with our findings. In our research, communities 3 and 4 demonstrated the highest percentage of mortality trees compared to other communities (Figure S2).

Previous research has suggested that deciduous tree species may be more resilient to drought compared to evergreen species in Mediterranean forests (e.g., Gazol et al. 2018). A similar situation was observed in community 6, where the dominant species, *N. macrocarpa*, presented a lower reduction in aerial biomass during the megadrought compared to the evergreen communities (Table 3). Furthermore, research has shown that the impacts of drought on trunk biomass accumulation and tree growth may persist even after the drought event has ended, resulting in delayed recovery or long-term changes in growth patterns (e.g., Jiao et al. 2021). Drought can disrupt the physiological processes of trees, leading to long-lasting effects on tree growth and annual trunk biomass growth, even after the return of normal precipitation levels (Pereira et al. 2007; Tague et al. 2019). If this is the situation for long-established communities in the ACMR, uncertainties arise for restoration initiatives and carbon sequestration plans associated with existent and potential forest ecosystems. The results presented here, along with other studies in Central Chile show the increasing vulnerability of these special ecosystems and the research gaps that will require urgent attention in the short term.

Conclusions

We concluded that the diversity of woody species, with DBH/DSH >5 cm, in the northernmost ecosystems of Altos de Cantillana Mountain Range (ACMR) is negatively correlated with elevation. The moist sclerophyllous forest (~ 800 m.a.s.l.) exhibited the highest biodiversity both in the established life stage and the early life stage (forest inventory and regeneration inventory). However, there are no altitudinal patterns in the abundance of individuals, both in trees/shrubs > 5cm DBH and seedling regeneration, being the ecotone between thorn shrubs and sclerophyllous forest (~ 1,000 m.a.s.l.) the one with the lowest density. Hence, it appears that the alteration of woody species within altitudinal levels is underway, posing a potential threat to the natural succession of the forests in ACMR. Woody species communities display similar richness and diversity patterns, which can be classified into three main groups: (i) thorny shrubs, sclerophyllous and hygrophilous forest (<1,000 m.a.s.l.), (ii) high-elevation sclerophyllous forest (>1,500 m.a.s.l.), and (iii) deciduous forests (~ 2,000 m.a.s.l.). Finally, we concluded that the biomass accumulation in the trunk of dominant woody species has been strongly affected by the recent megadrought period, affecting the sink capacity of forest communities in ACMR. Therefore, findings in tree biodiversity and biomass accumulation can significantly contribute to more efficient and timely decision-making processes regarding the conservation and restoration of this globally unique ecosystem.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

SGC and AVG carried out the sampling, participated in the study design, performed the statistical analysis, and wrote the manuscript. AOM participated in the interpretation and discussion of results. All authors have read and approved the final version of manuscript.

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Supplementary data

TABLE S1: Characteristics of tree-ring width chronologies for each community.

TABLE S2: Species list with family, vernacular name and origin.

FIGURE S1: Jaccard similarity among six trees communities.

FIGURE S2: Frequency of live (L) and dead (D) individuals by size class (DBH), for each community.

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Supplementary Data

TABLE S1: Characteristics of tree-ring width chronologies for each community: C1: hygrophilous forest community, C2: moist sclerophyllous forest, C3: ecotone shrub-trees forest community, C4: dry sclerophyllous forest community, C5: montane sclerophyllous forest community; C6: deciduous forest community.

Variables	**Community**					
	C1	**C2**	**C3**	**C4**	**C5**	**C6**
N° of samples	23	18	25	43	49	63
N° of trees	19	12	21	30	25	34
Chronology period	1913-2019	1955-2019	1949-2019	1919-2019	1949-2019	1789-2019
Mean (max) age	67 (105)	36 (65)	46 (71)	54 (101)	50 (71)	123 (308)
Mean RW[1] (mm)	2.14	0.79	0.73	1.54	1.08	1.37
Mean WD[2] (Kg/cm^3)	526.9	-	804.4	563.9	586.3	514.1
Mean sensitivity	0.44	0.56	0.50	0.48	0.56	0.49
Series intercorrelation	0.60	0.54	0.54	0.44	0.53	0.52

[1] mean radial growth*;* [2] WD = wood density

TABLE S2: Species list with family, vernacular name and origin.

Family	Species	Vernacular name	Origin
Salicaceae	*Azara petiolaris* (D.Don) I.M.Johnst.	Corcolén, Lilén, Maquicillo	Endemic
Lauraceae	*Beilschmiedia miersii* (Gay) Kosterm.	Belloto del Norte	Endemic
Euphorbiaceae	*Colliguaja odorifera* Molina	Colliguay	Endemic
Elaeocarpaceae	*Crinodendron patagua* Molina	Patagua	Endemic
Lauraceae	*Cryptocarya alba* (Molina) Looser	Peumo	Endemic
Escalloniaceae	*Escallonia pulverulenta* (Ruiz & Pav.) Pers.	Corontillo, Lun, Siete camisas	Endemic
Rosaceae	*Kageneckia angustifolia* D.Don	Frangel	Endemic
Rosaceae	*Kageneckia oblonga* Ruiz & Pav.	Bollén	Endemic
Anacardiaceae	*Lithraea caustica* (Molina) Hook. & Arn.	Litre	Endemic
Nothofagaceae	*Nothofagus macrocarpa* (A. DC.) F.M.Vázquez & R.Rodr.	Roble de Santiago	Endemic
Monimiaceae	*Peumus boldus* Molina	Boldo	Endemic
Quillajaceae	*Quillaja saponaria* Molina	Quillay	Endemic
Rhamnaceae	*Retanilla trinervia* (Gillies & Hook.) Hook. & Arn.	Tevo, Trevo	Endemic
Fabaceae	*Vachellia caven* (Molina) Seigler & Ebinger	Espino	Native
Asteraceae	*Podanthus mitiqui* Lindl.	Mitique	Endemic
Asteraceae	*Gochnatia foliolosa* (D.Don) D.Don ex Hook. & Arn. var. *fascicularis* (D.Don) Cabrera	Miramira	Endemic
Anacardiaceae	*Schinus montanus* (Phil.) Engl.	Litrecillo	Endemic
Asteraceae	*Baccharis neaei* DC.	Baccharis	Endemic

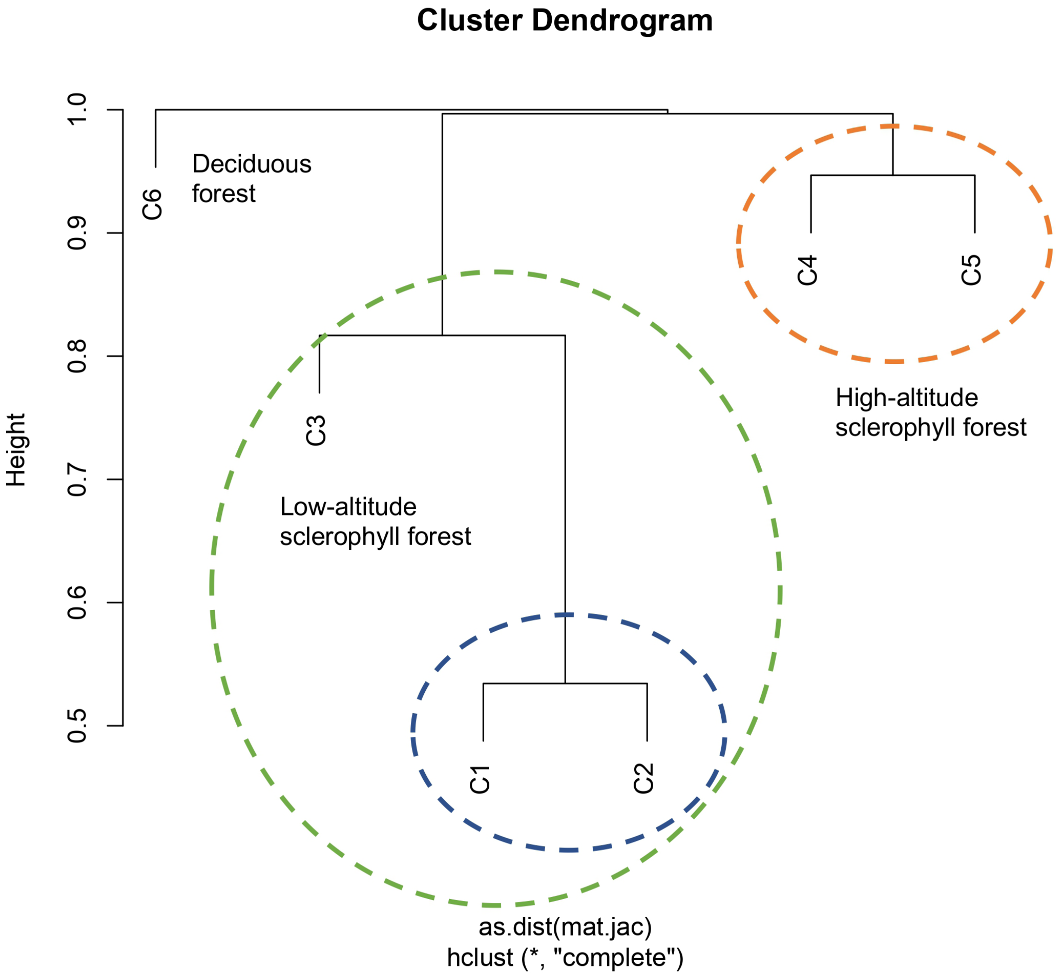

FIGURE S1: Jaccard similarity among six trees communities (C). C1: hygrophilous forest community, C2: moist sclerophyllous forest, C3: ecotone shrub-trees forest community, C4: dry sclerophyllous forest community, C5: montane sclerophyllous forest community; C6: deciduous forest community.

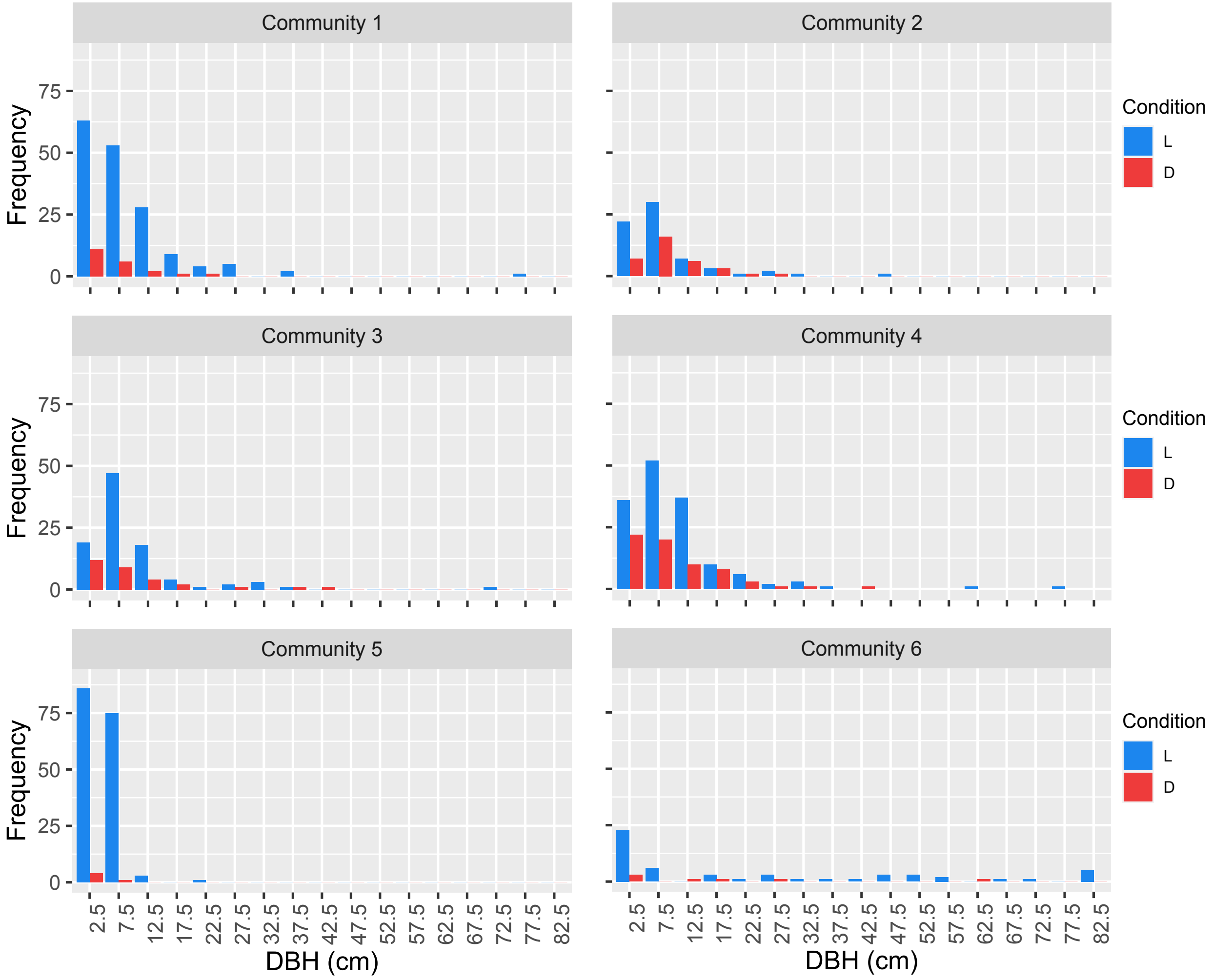

FIGURE S2: Frequency of live (L) and dead (D) individuals by size class (DBH), for each community: C1: hygrophilous forest community, C2: moist sclerophylloust forest, C3: ecotone shrub-trees forest community, C4: dry sclerophyllous forest community, C5: montane sclerophyllous forest community; C6: deciduous forest community.