

Temporal shifts in the functional composition of Andean forests at different elevations are driven by climate change

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Abstract

Aim: Andean forests are a global biodiversity hotspot. They harbour many species living within narrow climate ranges and a high functional diversity of trees. It remains still unclear how such hotspots respond to climatic changes over time. We investigated whether Andean forests are changing their functional composition over time along an elevational gradient by assessing changes in species composition, abundance and functional traits.

Location: An elevational gradient in Colombia's northern Andes.

Time Period: Species composition changes were studied two to four times from 2006 to 2017, and functional composition from 2016 to 2017.

Major Taxa Studied: A total of 1104 tropical tree species with in situ traits characterization.

Methods: We used seven morphological leaf traits and wood density values to analyse the functional trait dynamic over 10 years along an elevational gradient. By analysing changes in species composition, abundance and trait representation, we inferred the magnitude and direction of changes in functional composition. Then, we assessed if the functional change was related to climate change and demography.

Results: With increased minimum temperature and vapour-pressure deficit, we found a decrease over time in mean values for leaf area and specific leaf area and increases in leaf thickness and leaf dry matter content. Long-term temperature increases are smaller with increasing elevation, but the magnitude of trait changes is greater than in lowlands.

Main Conclusions: The functional composition is changing towards more conservative strategies over time across the elevation gradient, with the strongest changes observed at the highest elevations. This pattern is explained by the change in species turnover within communities due to higher recruitment rates of species with high leaf dry matter content values and low leaf area values. These shifts may be related to communities' responses to higher evapotranspiration demand and thermal stress, mainly at higher elevations.

KEYWORDS

Andean forests, climate change, elevational gradient, forest plots, functional turnover, trait distributions, trait driver theory, trait-based ecology

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1 | INTRODUCTION

Andean forests, one of the most important global hotspots of diversity (Orme et al., 2005), are facing unprecedented climatic changes, but our understanding of how these changes will impact the functioning of their tree communities remains unclear (Payne et al., 2017). One plausible way to improve our knowledge of how forests respond to environmental changes is through the Trait Driver Theory (TDT) (Enquist et al., 2015). The TDT provides a theoretical framework focused on the shape of organismal trait distributions, which are expected to underlie the response of plant communities to environmental changes at the local scale (Enquist et al., 2017; Wiczynski et al., 2018). By quantifying the central moments of trait distribution, such as mean, variance, kurtosis and skewness,

we can infer the local predominant phenotype (optimum), functional dispersion, evenness and trait abundance (distribution bias) respectively (Figure 1, details in the method section) (Enquist et al., 2015). Therefore, the shape of the distribution of phenotypes can give us insights into the ecological dynamic of the community.

In mountain systems, the variation in functional composition has been studied primarily by evaluating how functional traits change along a natural gradient of temperature with elevation increase (Homeier et al., 2021; Ochoa-Beltrán et al., 2021). These studies have found that tree communities along elevational gradients tend to vary from acquisitive strategies (plants with fast-growth rates and low construction costs) in lowlands to conservative strategies (plants with high construction costs) in highlands (Maharjan et al., 2021; Ochoa-Beltrán et al., 2021). However, the temporal change in the

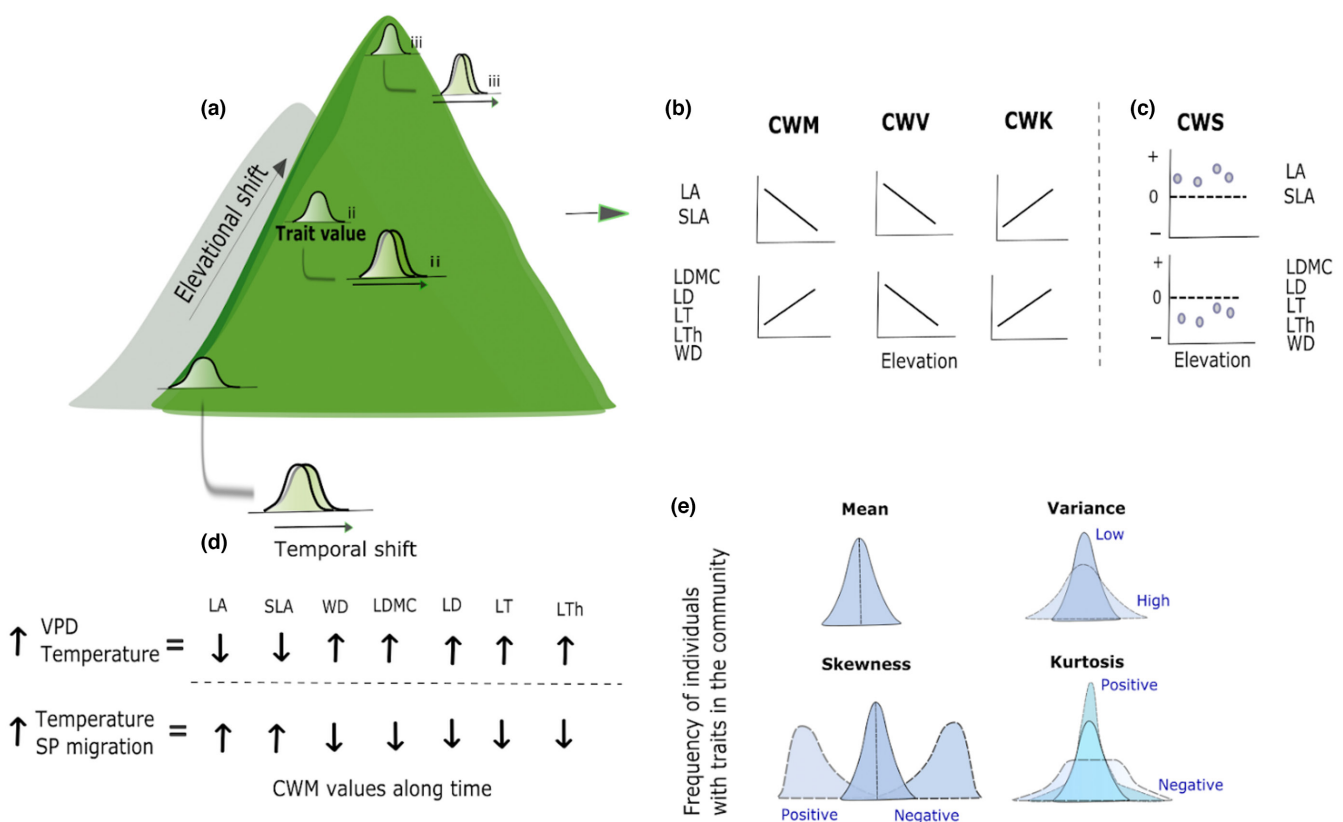


FIGURE 1 Representation of hypothesis on how functional composition would change along elevation and over time. (a) Along elevation trait distributions are expected to shift from acquisitive to conservative strategies. This will indicate (b) decreases in mean values (CWM) of leaf area (LA) and specific leaf area (SLA), and increases in mean values of leaf dry matter content (LDMC), leaf density (LD), leaf thickness (LT) and leaf toughness (LTh) and wood density (WD). At higher elevations, we expect lower values of trait variance (CWV) and a more peaked distribution with positive CWK related to strong environmental filtering due to lower temperatures at high elevations. (c) Community-weighted skewness (CWS) indicates the bias of the community trait distribution due to responses to rapid environmental changes in local communities and the dynamic of functional trait distribution over time. For instance, in a community affected by changes in climate, trait distributions will shift to reflect the changing optimal trait value. However, the mean will lag behind, resulting in a distribution bias. Those communities that are shifting in trait mean values should be characterized by positive or negative skewness. With warming, for those traits increasing across a temperature gradient (LA, SLA), we would predict positive skewness as the community shifts to the new optimal trait value. In contrast, with warming, trait distribution of those traits negatively correlated with temperature will be characterized by negative skewness as the community shifts to the new optimal trait value (Enquist et al., 2015, 2017) (see Figure 4 Wiczynski et al., 2018). (d) Hypothesized temporal changes in seven community-weighted mean traits in response to (i) increased VPD and temperature and (ii) increased temperature and upslope species migration. (e) The four central moment distributions; moments are compared with a normal distribution.

functional composition of plant communities in response to changes in climatic conditions remains poorly understood. Thus, assessing trends in species composition, demographic rates and trait characterization over time will improve our understanding of the mechanisms that control climate change-driven community trait shift.

In the past six decades, the temperature in the tropical Andes has increased between 0.03 and 0.04°C/year, exceeding global average warming rates (Pabón-Cañedo et al., 2020). Species have responded to these increases by migrating up slopes but at a rate much slower than warming (Feeley et al., 2011). Therefore, there may exist an expansion in the distribution range of lowland species in the highlands. Nevertheless, as the climate warms and precipitation becomes more variable in the tropical Andes, vapour-pressure deficit (VPD) also increases (Barkhordarian et al., 2019; Pabón-Cañedo et al., 2020), which may exacerbate plant thermal and water stress due to water loss through evapotranspiration (Grossiord et al., 2020). Studies have shown that plants with acquisitive strategies have low-stress tolerances (Reich, 2014) and high sensitivity to increased temperature and VPD. If so, those species within the community with high-stress tolerances and conservative traits will tend to be maintained in the face of climate change (in this study defined as the rate of change in temperature [mean, minimum and maximum], and VPD in the elevational gradient over 30 years in the study area). In any case, we expect that species responses to climate change will also change trait distributions by shifting the relative abundances of phenotypic frequencies in local communities. If climate change leaves a fingerprint on the functional composition of trees, increases in temperature and VPD will show the most detectable changes in the communities (Wieczynski et al., 2018). For example, a reduction in both leaf area (LA) and specific leaf area (SLA) will lead plant communities towards more conservative strategies over time.

Additionally, shifts in the trait composition of the community might depend on the demographic species' response (Violle et al., 2007). Previous studies have reported increased mortality rates of heat-sensitive species and increased recruitment rates of heat-adapted species (Duque et al., 2015; Fadrique et al., 2018). If climate-induced alterations in species composition and population dynamics are occurring, they may also entail modifications in functional composition. Recent studies suggest that increases in tree mortality risk in the tropics are driven mainly by the long-term increase in VPD and temperature (Bauman et al., 2022). The negative effects of these changes are exacerbated in species with acquisitive strategies such as low wood density and high SLA (Bauman et al., 2021). With climate change, it is likely that remaining and recruited species in the communities will have more stress-tolerant conservative traits. Overall, we expect the alteration of dominant plant traits in space and time to represent changes in forest functioning (Ruiz-Benito et al., 2017; Violle et al., 2014). Nevertheless, the direction of this alteration remains still unclear, and thus longitudinal studies across large environmental gradients are imperative.

In this study, we use nine 1-ha permanent plots to evaluate shifts in the functional composition of tree communities along an elevation

gradient of more than 2500 m in the Andean forest. We use the TDT framework to assess changes in the trait distributions and their dynamics using seven plant morphological traits of 1104 tree species. First, we evaluated how trait distribution changes along the elevational gradient and how climatic conditions affected these changes. Due to the considerable decrease in temperature with increasing elevation, we expect a higher abundance of species with conservative traits at higher elevations. This implies progressive changes in the value of local predominant traits (mean) with temperature decreases, such as lower leaf area (LA) and specific leaf area (SLA), but higher leaf dry matter content (LDMC), leaf thickness (LT), toughness (LTh), density (LD) and wood density (WD). With elevation, we also expect an overall decrease in the variance and an increase in kurtosis values of all the traits, indicating high environmental filtering promoting convergence of traits around the predominant local phenotype (Figure 1a,b). Second, we tested whether trait compositions in the nine communities along the elevational gradient shifted in the last decade (Figure 1c,d). We expect shifts in trait distributions and central moments. For example, for those traits related to the temperature showing decreases in mean values over time (e.g. LA or SLA), a positive skew distribution is expected because of changes in trait dominance within the community (Figure 1c). If our hypothesis is correct, these traits will have a higher rate of change in functional composition at higher elevations where species are cold adapted. Third, we assessed the climatic and demographic drivers associated with temporal changes in trait composition. Here, we expect that if increases in temperatures and VPD are modulating the changes in functional composition, higher mortality rates would be found in fast-growth species than in species with more conservative strategies. On the other hand, increased temperature and upward migration could lead communities to more acquisitive strategies over time along elevation (Figure 1d).

2 | METHODS

2.1 | Study area

The study area is located in the northwest region of Colombia between 5°50' and 8°61' North and 74°61' and 77°33' West (Figure S1). We used nine permanent plots of 1-ha (100 m × 100 m) belonging to the Red de Bosques Andinos, which have been monitored for the last decade (Duque et al., 2021; Malizia et al., 2020). The plots were established in Andean tropical forests along an elevation gradient from 50 to 2850 m with an average distance among plots of 146.9 km. All plots were established in areas showing minimal evidence of human disturbance where no fires had been recorded (except Carepa [-58 m], established in a small forest fragment [-50 ha]). The plots range in temperature from 27.7°C to 13°C from the lowest to the highest elevation. Along the elevational gradient, the plots vary significantly in solar radiation, VPD and potential evapotranspiration (Table S1).

2.2 | Abundance data set and censuses

In each of the nine plots, all shrubs and trees (hereafter trees) with a diameter at breast height (DBH) ≥ 10 cm were mapped, tagged and measured. Near the centre of each plot, all trees with a DBH ≥ 1 cm were inventoried in a 40 m \times 40 m subplot (0.16-ha). Voucher specimens were collected for potentially unique species in each plot, and identification was confirmed by consulting taxonomy specialists and comparing the specimens with herbarium material. The specimens that could not be identified at the species level were classified as morphospecies (hereafter species). All plots were established between 2006 and 2009 and were censused two to four times between 2016 and 2019 (Table S2).

2.3 | Climate data collection

We retrieved mean climate data for each plot using climatic layers at high resolution (30 arcsec) available in WorldClim 2.1 (Fick & Hijmans, 2017) and CGIAR-CSI 2.0 (Zomer et al., 2008). The following variables were obtained: mean annual temperature (MAT), mean annual precipitation (MAP), isothermality (ISO), temperature seasonality (TS), precipitation seasonality (PS), saturated vapour pressure (SVP), potential evapotranspiration (PET), wind speed and solar radiation (Solar rad) (Table S1). Vapour pressure deficit (VPD) was calculated as saturated vapour pressure minus vapour air pressure. To evaluate whether there was climate change in the study area, we retrieved historical climate data from the last 38 years, from 1980 to 2017, for MAT, maximal temperature (T_{\max}), minimal temperature (T_{\min}) and MAP from the Worldwide Energy Resource database (POWER-NASA) (<https://power.larc.nasa.gov>) with a resolution of 0.5°. Historical VPD was calculated using the long-term record of vapour air pressure (VAP) of the last 38 years retrieved from the Climate Research Unit (CRU-TS) version 4.04 (Harris et al., 2020). We then used these historical climate data to calculate the annual rate of climatic variables in the last four decades (Figures S7 and S8). We acknowledge that the choice of 38 years is arbitrary, but our criteria for choosing this time period were mainly related to the data availability. Although undisturbed forests such as those sampled in this study may take longer to show responses to climate changes, 38 years have been enough to find directional shifts in composition in some tree species located in the same study area (Fadrique et al., 2018).

2.4 | Trait sampling

We focused on six leaf morphological traits that capture the essential leaf economics: leaf area: LA (mm^2); specific leaf area: SLA (mm^2/mg); leaf density: LD (g/cm^3); leaf dry matter content: LDMC (mg/g); leaf toughness: LTh (Newton/mm); leaf thickness: LT (mm) and wood density: WD (g/cm^3) (Appendix S1). Size-related plant traits with power-law growth rates of the form

$Y = ax^b$, such as LA and LT, were \log_{10} transformed to normalize trait distributions and reduce the influence of outliers (Kerkhoff & Enquist, 2009).

We measured plant traits during 2016–2017 following standard protocols (Pérez-Harguindeguy et al., 2013). In each plot, we collected five leaves from five healthy individuals per species (three individuals in Angelópolis, Anorí and Segovia plots, due to the high number of species) for the most abundant species contributing to 80% or more of total species abundance. In addition, we sampled one to two individuals for those remaining species that contribute to less than 80% of the total species abundance (remaining species). Thus, nearly all species were sampled within each plot (Table S2). Shared species among plots were measured in each local community. We analysed 1104 species (of which 60% [610] were identified at the species level) distributed over 361 genera and 103 families. We sampled ~10,470 individual leaves belonging to ~2297 individuals. To collect WD, we took one sample of ~3 cm in diameter and ~10 cm long from one mature branch per individual. Due to some species being presented just in small size individuals (~18%), it was not possible to measure WD directly. Thus, we filled in the missing values hierarchically. First, the missing WD values per individual were assigned based on the average value of the same species in other plots. If the value was not available at the species level, the value by either genus or family was used.

2.5 | Trait distributions and central distribution moments

Using the TDT framework, we focused on the four central moments of trait distribution. The community-weighted mean (CWM) represents the distribution's average (predominant) trait value. Community-weighted variance (CWV) reflects the dispersion of trait values and can be interpreted as a measure of functional diversity. Community-weighted kurtosis (CWK) reflects the peakedness of the trait distribution; the higher the peakedness, the higher the dominance of specific traits. High positive kurtosis reflects more peaked distributions relative to a normal distribution due to reduced outliers and the high abundance of functionally similar species (Huang et al., 2021). Low or negative kurtosis reflects platykurtic distributions resulting from a wide range of trait values due to contrasting ecological strategies within the community. Values equal to -1.2 represent a complete evenness. Finally, negative or positive community-weighted skewness (CWS) reflects a strong right- or left-skewed distribution, which means extreme trait values at the ends of the distribution tails (Enquist et al., 2015; Wiczyński et al., 2018). An asymmetrical distribution results from changes in the frequency of trait values as a response to rapid environmental changes or rare species advantages within communities; this could be interpreted as a fingerprint of climate change (Enquist et al., 2015).

Based on the abundance-weighted kernel density distributions estimated for each trait and community, we quantified the four

central moments weighted by species abundance. To calculate density distributions that better represent the community and the variation in trait values, we incorporated intra-specific variability for those species with the largest numbers of sampled individuals. We ran statistical non-parametric bootstrapping to resample (with replacement) individuals' trait values in proportion to the species abundance to generate a set of new distributions (Maitner et al., 2023) (Appendix S1). The following equations define the central abundance-weighted moments:

$$\begin{aligned} \text{CWM} &= \frac{\sum w_i x_i}{\sum w_i} \\ \text{CWV} &= \frac{\sum w_i (x_i - \text{CWM})^2}{\sum w_i} \\ \text{CWK} &= \frac{\sum w_i x_i \frac{x_i - \text{CWM}}{\sqrt{\text{CWV}}}^4}{\sum w_i} - 3 \\ \text{CWS} &= \frac{\sum w_i x_i \frac{x_i - \text{CWM}}{\sqrt{\text{CWV}}}^3}{\sum w_i} \end{aligned}$$

where w_i is the abundance of species i in the local community and x_i is the local mean trait value for species i (Huang et al., 2021; Wieczynski et al., 2018).

2.6 | Patterns of change in functional composition over time along the elevational gradient

To analyse community changes in trait composition, we initially plotted the abundance-weighted density estimates for each trait for each plot and census. Next, we quantified the abundance-weighted moments (CWM, CWV, CWK and CWS) corresponding to the trait distribution of the first and the last census. To do this, we used the traits measured and matched trait values with species composition and abundance in the first and last census (8–10 years on average) (Table S2). Finally, to quantify the shift and the direction in functional composition over time, we calculated the trait velocity index (TV) (which represents the annual rate of change for each trait moment) (Trugman et al., 2020) as the difference between the last and the first community-weighted moment, divided by the length of the census period (TV_CWM, TV_CWV, TV_CWK, TV_CWS). Because these data do not involve repeated measures of traits over time, we could not assess functional plasticity, so we assumed that trait values were stable over time. Consequently, we focus on the effect of demographic responses on the communities' functional structure. Pairing trait data with species abundance by censuses provides insights into understanding temporal changes based on shifts in community composition and abundance (Aguirre-Gutiérrez et al., 2019; Swenson et al., 2020).

2.7 | Potential drivers of temporal changes in forest functional composition

2.7.1 | Climatic changes

We calculated the annual rate of change of MAP (ΔMAP in mm y^{-1}), MAT (ΔMAT in $^{\circ}\text{C y}^{-1}$), T_{max} (ΔT_{max} in $^{\circ}\text{C y}^{-1}$), T_{min} (ΔT_{min} in $^{\circ}\text{C y}^{-1}$) and VPD (ΔVPD in Kpa y^{-1}) as the slope of the linear least-square regression between the values of each climatic variable and time (Figure S7). To estimate climate change, we first used two different regressions to estimate the slopes as a measurement of the annual rate of change for the different variables. The first one used the 1980–2017 data set (data availability at power.larc.nasa.gov). The second one used the 1995–2017 data set following Fadrique et al., 2018, who used a similar timeframe to calculate the climatic rate in the Andes. We did a t -test for comparing slopes between the two periods, as slopes remain similar ($p > 0.05$ for all variables and plots), we considered climate change from 1980 because, although arbitrary, we believe that in mature forests the lag between climate change and community response can be decades (Alexander et al., 2018; Block et al., 2022). It is important to remark that we refer to climate change as the long-term changes mainly in temperature (mean, minimum and maximum) and VPD.

2.7.2 | Demographic tree rates

We calculated annual mortality and recruitment rates by plot following Phillips et al. (1994) as:

$$\text{Mortality rate (\%)} = \text{Ln} \left[\left(\frac{N_o}{N_s} \right) \right] / \Delta\text{time}$$

$$\text{Recruitment rate (\%)} = \text{Ln} \left[\left(\frac{N_f}{N_s} \right) \right] / \Delta\text{time}$$

where N_o is the initial number of individuals in the first census, N_f is the final number of individuals in the last census and N_s is the number of original individuals surviving until the final inventory. Mortality and recruitment rates were calculated for canopy individuals with $\text{DBH} \geq 10\text{cm}$ in the plots and understory individuals with $1\text{cm} \leq \text{DBH} < 10\text{cm}$ in the 0.16-ha subplots.

2.8 | Data analyses

2.8.1 | Changes in trait distribution along the elevational gradient

To address our first aim of how trait distribution moments change along elevation and what climatic variables are involved, we regressed the central weighted moments of each trait for each plot and the climate conditions at each site for the last census.

To reduce the number of climatic variables to two main axes, we ran a principal component analysis (PCA) with all the climate data using the `princomp` function in R. All variables were standardized to a mean of zero and standard deviation of one before conducting the PCA. The first and second PCA axes explained 47.7% and 23% of the climatic variance respectively (Figure S2). The $PC1_{\text{climate}}$ axis was primarily determined by MAT, solar radiation, VPD and PET (Table S3). Notably, $PC1_{\text{climate}}$ is primarily negatively correlated with MAT ($p < 0.05$, $R = -0.87$) (Figure S3b) and positively correlated with elevation (Figure S3a). Precipitation seasonality (PS) determined the $PC2_{\text{climate}}$ axis ($r = 0.69$, $p < 0.05$) (Table S3) and was used as a surrogate of seasonality (Figure S3g). We then built simple linear models between the trait moment values and the $PC1_{\text{climate}}$ and $PC2_{\text{climate}}$ separately to quantify the relationship between climatic variation and community-weighted moments.

2.8.2 | Changes in trait distribution over time

To assess our second aim of whether functional composition of each local community changes over time, we first performed a Kolmogorov–Smirnov test between the distributions of the first and last census of each trait for each plot to test significant differences. To evaluate differences in central moments between the first and last census, we used a linear mixed model, with the census as a fixed factor and the plot as a random factor to account for the repeated censuses per plot (van der Sande et al., 2016). Finally, we performed a least-squares linear model between each TV trait and elevation to examine whether there are directional changes in the functional composition along the elevation.

2.8.3 | Assessing potential drivers of change in functional composition over time

To address the potential impact of climate change and species demography on functional changes over time (third question), we tested whether shifts in the community trait composition were related to temporal climatic variations and mortality/recruitment. We ran ordinary least-squares regressions between the TV per moment and trait (response variable) and changes in climate and demographic rates (ΔMAP , ΔMAT , ΔT_{max} , ΔT_{min} , ΔVPD , mortality and recruitment rate). To control significant false p -values when comparing multiple hypothesis tests, we adjusted the p -value of each regression using the false discovery rate (type I error) (Benjamini & Hochberg, 1995) with the function `FDR` in the `fuzzySim` R package (Barbosa, 2015). Due to the statistical restrictions of the small sample size, our models test the effect on one independent variable at a time in order to keep the statistical power of the data. All analyses were performed using R version 4.0.0 (R Core Team, 2010).

3 | RESULTS

3.1 | Variation in trait distribution along the elevational gradient

All the distributions showed a unimodal trend, reflecting one predominant phenotype or mean trait value for the community, except for the distribution of WD, which reflects two peaks in plots located at low elevations, suggesting two possible prevailing phenotypes (Figure S4).

As expected, the central moments showed that functional composition varies from strategies of fast resource acquisition to high construction costs along the climatic/elevational gradient ($PC1_{\text{climate}}$). Changes in CWM are primarily associated with a significant decrease in traits related to photosynthetic capacity (reduction in leaf area and specific leaf area) and an increase in leaf structural components for protection, such as thickness (Figure 2a). CWM of LDMC showed a humped-shaped relationship with the $PC1_{\text{climate}}$ (Figure 2a). Contrary to our expectations, CWV (which reflects functional diversity) did not decrease significantly for all traits along the $PC1_{\text{climate}}$. The CWV of wood density decreased with $PC1_{\text{climate}}$ and conversely, leaf thickness increased, indicating a broader spectrum of trait values at higher elevations (Figure 2b).

The analysis of the trait distribution shape (CWK) showed that all traits, except LDMC, were characterized by kurtosis values greater than zero, indicating a distribution with a reduction of more variable trait values and more peaked than expected from a normal distribution (Figure 2d). Only the CWK of the leaf toughness showed a significant increase with $PC1_{\text{climate}}$. None of the moments were significantly related to $PCA2_{\text{climate}}$ (Figure S5).

3.2 | Changes in trait composition over time

The Kolmogorov–Smirnov test showed significant shifts in trait distribution per plot between the first and the last census, particularly in plots located at high elevations (Figure 3). The fourth moment (CWS), which analyses the bias of the trait distribution and can be interpreted as a fingerprint of climate change, showed that photosynthetic traits such as leaf area and specific leaf area had a CWS greater than zero. This reflects a dynamic change in trait distribution towards lower values of the predominant phenotype. These results support our hypothesis that if the mean community trait increases across a temperature gradient (e.g. LA and SLA, negatively correlated with $PC1_{\text{climate}}$), warming would lead to communities characterized by positive skewness (Figures 1 and 2c). Leaf thickness, positively correlated with $PC1_{\text{climate}}$, showed some communities with negative skewness. Thus, it may be a trait with a slower response to heating than those related to the area.

According to the linear mixed model, which quantifies changes in time, leaf area showed significant differences between the first and the last census for the mean and variance, indicating that functional composition and diversity varied over time (Table 1). In comparison,

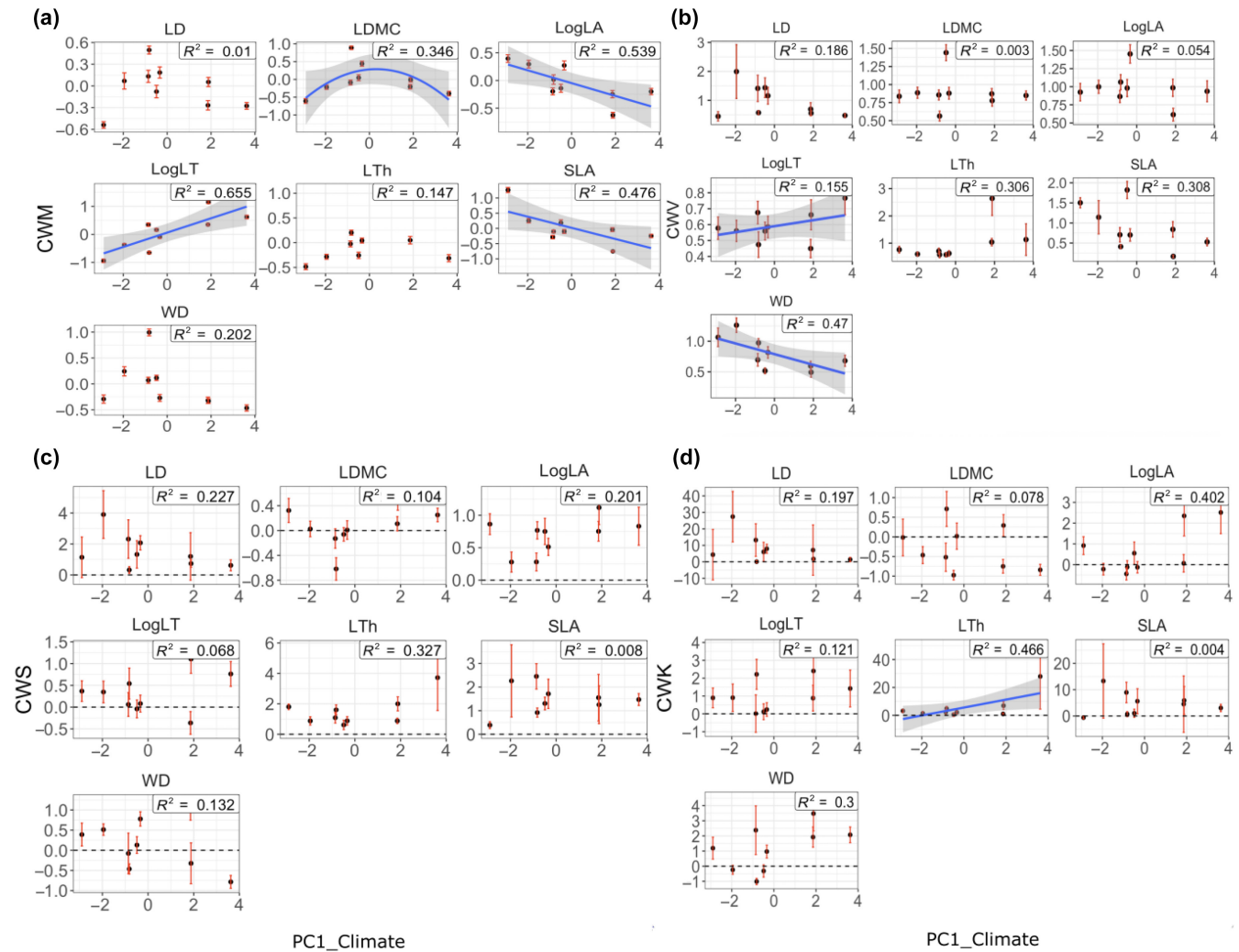


FIGURE 2 Shifts in the abundance-weighted community of (a) mean (CWM), (b) variance (CWV), (c) skewness (CWS) and (d) kurtosis (CWK) of each trait along the climatic gradient (PC1_{climate}, mainly correlated with temperature and elevation) for leaf area (LA), specific leaf area (SLA), wood density (WD), leaf dry matter content (LDMC), leaf density (LD), leaf thickness (LT) and leaf toughness (LTh). Size-related plant traits with power-law growth rates of the form $Y = ax^b$, such as LA and LT, were \log_{10} transformed. CWM and CWV were standardized with mean zero and variance one to compare traits. Significant relationships with PC1_{climate} axes are shown with the trend line. The 95% confidence intervals (red lines) are reported for each plot and trait per moment. Confidence intervals were calculated based on 1000 bootstrap replicates for each plot. Values of zero represent a normal distribution. $CWS \neq 0$ represents strong left or right tails. $CWK = -1.2$ represents an even distribution. Note that PC1_{climate} is negatively correlated with temperature. So, for a CWM trait value that is positively correlated with PC1_{climate} (negatively correlated with temperature such as SLA and LA), we would predict positive skewness. In contrast, when a CWM trait value is negatively correlated with PC1_{climate} (positively correlated with temperature, such as LT), we would predict negative skewness. In general, we do see support for these predictions.

thickness had changes in skewness values; specific leaf area and LDMC in the kurtosis (Table 1). Our analyses found a directional shift of functional composition along elevation for one trait. The changes over time in mean values (TV_CWM) of LDMC and the strong tendency of change for leaf area presented a positive and negative relationship with elevation, respectively (Figure 4), indicating an increment in the magnitude of the change in functional composition when elevation increases. Remarkably, nearly all the plots showed decreases over time in mean values of leaf area (negative values) and

increased LDMC regardless of elevation (Figure 4). Furthermore, the changes over time in variance (TV_CWV) had a positive relationship with elevation for WD (Figure S6). Thus, communities have a broader spectrum of trait values for this trait over time. Finally, changes over time in skewness (TV_CWS) of WD and leaf area significantly decreased along the elevational gradient (Figure S6c). This result indicates that the bias of the trait distribution decreases over time, probably because communities are achieving new values of predominant phenotypes.

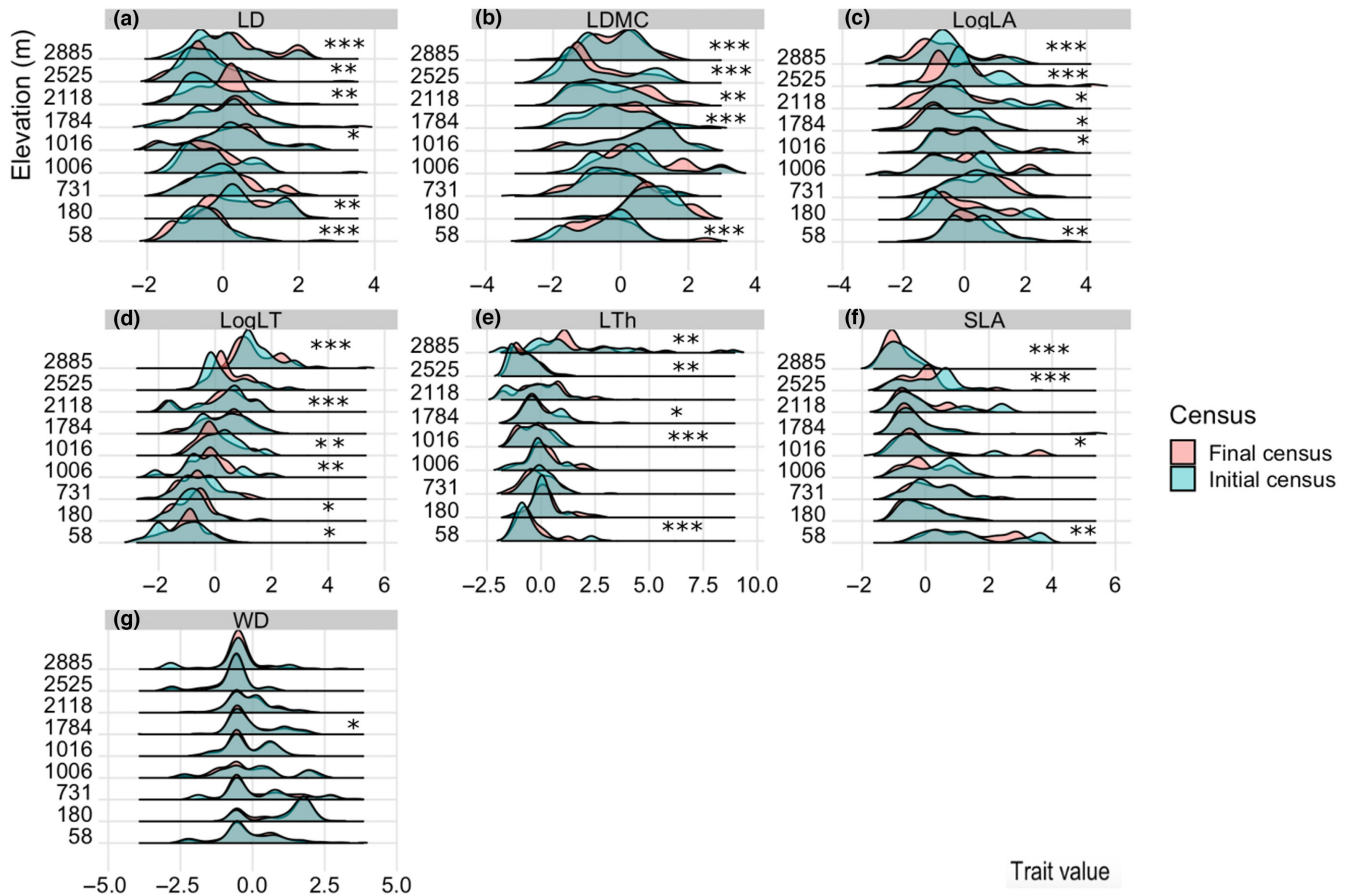


FIGURE 3 Abundance-weighted Kernel density estimates of each trait across the elevational gradient in each census. Each elevation represents a tree community, and each colour represents a census. Traits are (a) leaf density (LD), (b) leaf dry matter content (LDMC), (c) leaf area (LogLA), (d) leaf thickness (LogLT), (e) leaf toughness (LTh), (f) specific leaf area (SLA) and (g) wood density (WD). Size-related plant traits with power-law growth rates of the form $Y = ax^b$, such as LA and LT, were \log_{10} transformed. Results represent p -values from the Kolmogorov-Smirnov test between the trait distribution of the first census and the distribution of the last census ($* < 0.05$, $** < 0.01$, $*** < 0.001$). Data were standardized with mean zero and variance one to compare traits.

Trait	CWM	CWV	CWS	CWK
	Census	Census	Census	Census
SLA	0.3 (-0.14)	0.1 (-0.36)	0.1 (0.31)	0.04 (3.33)
LogLA	0.05 (-0.06)	0.009 (-0.08)	0.9 (-0.006)	0.3 (0.23)
LDMC	0.1 (0.11)	0.6 (0.01)	0.4 (-0.08)	0.02 (0.5)
LD	0.1 (0.07)	0.2 (0.19)	0.2 (0.46)	0.1 (3.57)
LTh	0.2 (0.14)	0.4 (-0.08)	0.07 (0.49)	0.2 (3.55)
LogLT	0.5 (0.08)	0.1 (-0.23)	0.01 (0.30)	0.2 (0.45)
WD	0.2 (0.01)	0.7 (0.06)	0.6 (0.02)	0.4 (-0.11)

Note: The plot was included as a random effect to account for the census as repeated measures per plot.

TABLE 1 p -Values and coefficients (in parenthesis) from the linear mixed effect models between each community-weighted moment and census.

3.3 | Potential drivers of change in functional composition over time

Over the last 38 years, the temperature and VPD have increased significantly in the nine plots. The ΔT_{\min} and ΔVPD have a

negative relationship with elevation, which means that lowlands are experiencing more significant warming and more water stress (Figures S7 and S8). We found that negative changes over time for traits associated with photosynthesis (leaf area and specific leaf area) and positive changes for traits associated with leaf structure

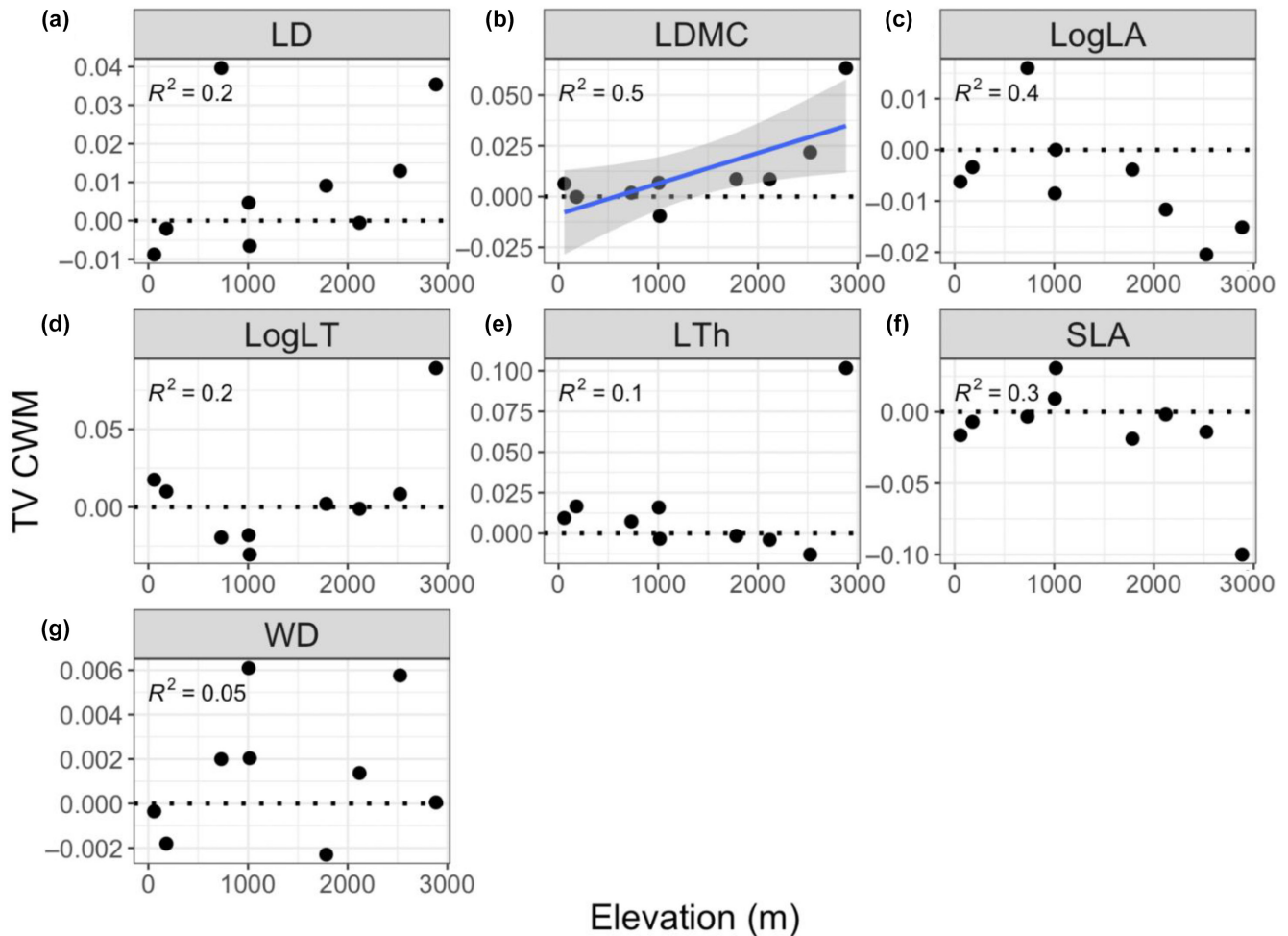


FIGURE 4 Trait velocity index of community weighted-mean (TV_CWM) of each trait (y-axis) along the elevational gradient (x-axis). TV_CWM represents the annual rate of change for each trait moment, which indicates the direction and magnitude of the functional change. TV_CWM equal to zero represents no change over time. Positive values mean an increase in the trait community value over time. Negative TV values mean a decrease in community trait value over time. The further the TV value is from zero, the higher the magnitude of the change. A significant relationship between TV_CWM with elevation is presented with the linear regression trend line. Traits are (a) leaf density (LD), (b) leaf dry matter content (LDMC), (c) leaf area (LogLA), (d) leaf thickness (LogLT), (e) leaf toughness (LTh), (f) specific leaf area (SLA) and (g) wood density (WD). Size-related plant traits with power-law growth rates of the form $Y = ax^b$, such as LA and LT, were \log_{10} transformed.

(leaf thickness and LDMC) had a relationship with increases in minimum temperature and VPD at high elevations (Figure 5a,b). Climatic changes in the mean, maximal temperature, and precipitation were unrelated to mean trait changes over time (Figure S9). Overall, temperature changes significantly affect changes over time for the variance of leaf area and specific leaf area (Figure S10), indicating that this factor affects the functional diversity over time. Significant changes over time in skewness were present mainly in WD and leaf thickness and were modulated specifically by ΔT_{\min} (Figure S12). Finally, the potential climatic drivers did little to explain the changes over time for kurtosis values (TV_CWK) (Figure S11).

Regarding species demography, the recruitment rate of individuals increased with elevation (Figure S8g). The analyses of demographic rates related to changes over time in trait composition of LDMC and leaf area indicated that the higher the recruitment, the

higher the LDMC and the lower the leaf area (Figure 5c). Similarly, recruitment also affected the changes over time for mean trait values and variance of WD (Figure S10e) and the changes in the skewness of leaf thickness (Figure S12e). Mortality was not significant with changes over time in mean values (Figure 5d).

4 | DISCUSSION

Previous studies have suggested a functional shift over time along elevation in the Andean forests related to climate change (Duque et al., 2021; Fadrique et al., 2018). However, few have evaluated this hypothesis by integrating plant traits and species demography (see Báez et al., 2022). Here, we assessed how functional composition changes along elevation and over time and investigated what environmental variables drive these changes. Our results

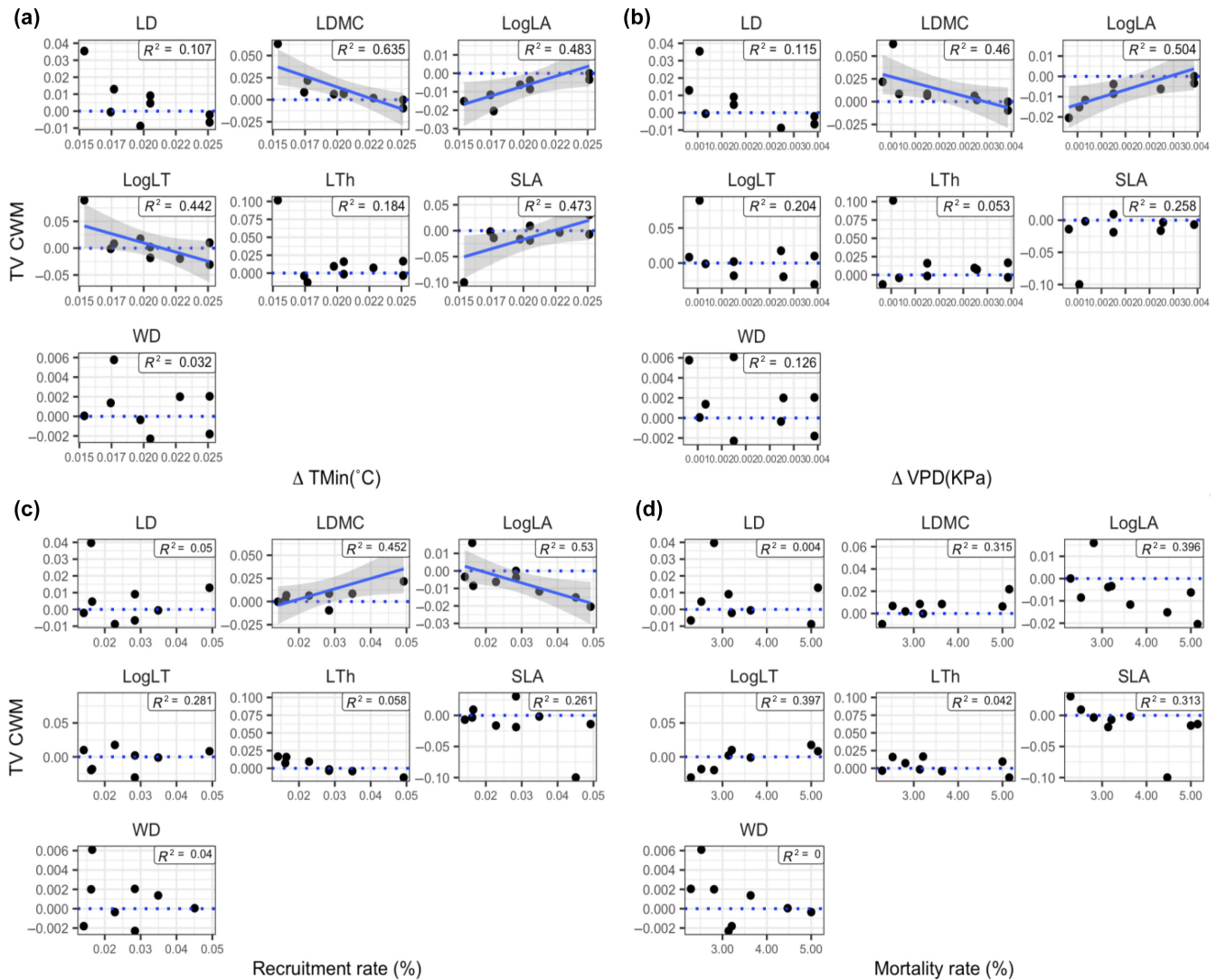


FIGURE 5 Linear regressions between trait velocity of community weighted-mean (TV_CWM) of each trait and the (a) annualized rate of change of minimum temperature (ΔT_{\min}), (b) vapour-pressure deficit (ΔVPD), (c) recruitment and (d) mortality of individuals (%). TV_CWM equal to zero represents no change over time. Positive values mean an increase in the trait community value over time. Conversely, negative TV_CWM values mean decreases in community trait value over time. A significant relationship between changes in functional composition and changes in climate or demography is denoted by a linear trend. TV_CWM values were standardized with mean zero and variance one to compare traits. The traits are wood density (WD), leaf dry matter content (LDMC), specific leaf area (SLA), leaf toughness (LTh), leaf density (LD), leaf area (LogLA) and leaf thickness (LogLT). Size-related plant traits with power-law growth rates of the form $Y = ax^b$, such as LA and LT, were \log_{10} transformed. TV values were standardized with mean zero and variance one to compare traits.

show that shifts in trait composition along elevation and over time are related mainly to changes in temperature and vapour-pressure deficit (VPD). Over time, functional changes show a decline in mean community values of leaf area and specific leaf area and an increase in LDMC and thickness, mainly at higher elevations (Figure 5). Our results agree with previous studies identifying changes in VPD and temperature as drivers of change in species composition (Bauman et al., 2021; Feeley et al., 2011), community plant traits (Fadrique et al., 2018) and plant abundance (Duque et al., 2021; Peña et al., 2018) in the tropical forest. Thus, our trait-based approach can help to understand the potential direction of future changes in Andean forest dynamics with continuous climate change.

4.1 | Variation in functional composition along the elevational gradient

Changes in the functional composition along the $\text{PC1}_{\text{climate}}$ were defined by the variation in community mean values from high to low values of leaf area and specific leaf area and from low to high values of leaf thickness. The reduction of leaf area and specific leaf area and the increase in leaf thickness towards higher elevation seems to be related to the marked decrease in temperature and high levels of solar radiation since this morphology allows plants to maximize water use efficiency and conserve heat in cold environments with high radiation (Llerena-Zambrano et al., 2021). These changes reveal a shift from communities characterized by acquisitive strategies

in the lowlands to conservative strategies in the highlands. These trends are widely reported in tropical mountain forests (Homeier et al., 2021; Maharjan et al., 2021; Ochoa-Beltrán et al., 2021) and are related to a gradient of the leaf resource investment and return (Wright et al., 2004).

We hypothesized a decrease in the variance of all traits (narrow range of trait values) and an increase in kurtosis along the climatic/elevation gradient (represented by $PC1_{climate}$) related to strong environmental filtering. Contrary to our expectations, the variance of leaf thickness increases in high elevations (low temperatures), a pattern that has also been reported by other studies (Homeier et al., 2021). Furthermore, we only find a strong positive kurtosis (a more peaked distribution reflecting biotic exclusion) along the climatic/elevation gradient for leaf area and toughness. One possible explanation for this apparent lack of variance reduction and environmental filtering along elevation is the complex mountain topography, which at a small scale, creates different niches that enhance trait variability at high elevations (Homeier et al., 2021). A complementary explanation is given that high thickness and toughness confer advantages in low temperatures (Llerena-Zambrano et al., 2021). The high variance suggests the presence of multiple adaptative strategies within the community, such as diverse morphological responses to the specific environmental stress, which result in the over-dispersion of phenotypes (Enquist et al., 2015). These results show that it is critical to evaluate not just community mean values but other moments of trait distribution, such as variance and kurtosis, which give us information about ecological mechanisms shaping trait distribution along environmental gradients.

4.2 | Temporal patterns of change in functional composition

Historical increases in VPD, minimum temperature and recruitment rate mainly drive shifts in trait composition over time, particularly at high elevations (Figures 3–5). Temperature-related traits presented high positive skewness, such as leaf area and specific leaf area. These patterns are consistent with expected community directional shifts with an increase in VPD and temperature and have been reported in previous tropical mountain studies (Enquist et al., 2017; Wiczyński et al., 2018). The decline in mean values of leaf area and increase in LDMC at higher elevations indicates a potential shift in community functional composition towards more conservative and stress-tolerant strategies, partially supporting our hypothesis. Although this study did not assess the shift in trait plasticity, changes in species composition and dominance may indicate how increases in temperature and VPD modulate and filter species with certain traits, thus shaping the future functional composition.

We found long-term increases in VPD and minimum temperature in the study area, which are associated with high thermal and hydric stress due to high evapotranspiration demand (Grossiord

et al., 2020). These long-term changes in climatic conditions may explain some of our results in shifts in trait distribution and species demographic rates. In the most recent communities, the observed increases in LDMC and leaf thickness, along with the corresponding decreases in leaf area and SLA, with rising minimum temperature and VPD at high elevations, likely indicate the heightened susceptibility of tree species to these climatic factors. This susceptibility can be attributed to their lower thermal tolerances, as supported by previous studies (Cuesta et al., 2020; Feeley et al., 2020). Andean forests are highly adapted to low temperatures (Llerena-Zambrano et al., 2021), so they could be more sensitive to changes in minimum temperature than mean, maximum temperatures or precipitation (Konings et al., 2017), as shown in our results. In the same way, increased VPD is a risk factor that can increase mortality in species with more acquisitive strategies (Bauman et al., 2022) such as large leaf areas and high values of SLA. Considering that water vapour is a key factor for forest functioning (Yuan et al., 2019), mainly in mountain forests, increases in VPD substantially increase the water demand and decrease the photosynthetic rate (Grossiord et al., 2020). Thus, the effects of higher VPD and decreased cloud cover (Los et al., 2019) should filter species with traits more tolerant to higher solar radiation and with better water-use efficiency. Overall, selecting species with smaller and thicker leaves contributes to increased leaf lifespan, nutrient retention and water-use efficiency under higher temperatures and VPD (Ackerly et al., 2002). The decreases of mean values over time in leaf areas and increases in LDMC could also prevent leaf overheating (Meng et al., 2015) and water loss in cold-adapted species.

Many studies assessing the effects of climate change on tree communities focused mostly on temperature changes, and VPD tended to be neglected (Báez et al., 2022; Feeley et al., 2011). Nevertheless, in humid regions and cloud forests, changes in VPD may significantly impact the species' physiology and functioning, affecting their demographic responses and, subsequently, community functional composition. This factor, in addition to temperature, helps us to understand more mechanistically the effects of climate change on forest functioning. Although we recognize that our time framework to evaluate changes in the functional composition is short and could be arbitrary due to the data availability (e.g. 10 years), we found recruitment rates and functional shifts over time in four traits related to VPD and minimum temperature changes. We believe that it is a matter of time before other traits show changes in functional composition mainly due to the lag between climate change and the community response.

Changes in species composition are long-term accumulative responses (Alexander et al., 2018), and previous studies have shown increases in the recruitment of heat-tolerant species in the Andes (Duque et al., 2015). In our study, increases over time in LDMC and decreases in leaf area were related to higher recruitment rates at high elevations, which could reflect higher recruitment of species with conservative resource-use strategies and a

higher capacity to avoid overheating (Reich, 2014). If only warming occurs, we would expect a change towards more acquisitive traits. Nevertheless, increments in VPD and solar radiation (Los et al., 2019) are factors that may filter species with conservative traits. Studies have shown that the upslope migration of tree species in the Andes is significantly slower than the warming rate, which reduces the tracking of environmental changes (Feeley et al., 2011). Furthermore, the habitat loss and subsequent fragmentation of the forest and hence the loss of animals for seed dispersal could further limit tree species migration. Species with conservative traits exhibit higher tolerance to environmental changes, resulting in a slower migration rate compared to acquisitive species. Due to their ability to withstand climatic variations in their current habitats, conservative species have a greater likelihood of successful juvenile recruitment; thus, establishing and recruiting juvenile trees with more conservative traits may be strongly associated with local environmental and soil conditions that promote germination (Block et al., 2022).

Although Andean forests are one of the ecosystems most vulnerable to climate change, they remain an important carbon sink (Duque et al., 2021). The observed filtered traits over this short temporal window are those with the greatest ability to persist under climate change and more stressful environmental conditions (Reich, 2014). Through species demography (recruitment/mortality), those species would be expected to survive and recruit, leading communities towards more conservative strategies, mainly at high elevations.

5 | CONCLUSIONS

Our findings emphasize the relationship between shifts in functional composition over time along an elevational gradient in the Andean mountains and the responses of tree communities related to increases over time in vapour-pressure deficit and minimum temperature. Observed changes in functional composition suggest a shift in the community towards promoting species with conservative strategies such as decreases in mean community values of leaf area and specific leaf area and increases in LDMC and leaf thickness. This was also supported by our results of higher recruitment rates of individuals with more stress-tolerant traits. Although we found shifts in trait composition in four of the seven traits, if minimum temperature and vapour-pressure deficit continue increasing at the current rate, we could expect shifts in other plant traits as well with potential consequences for forest functioning. Longitudinal monitoring of permanent plots and in situ functional traits is needed to fully understand the effect of climate change on species' demographic and plastic responses to new conditions. Ongoing studies must include dispersal traits to quantify species' migration capacity along elevation and include an analysis of species mortality risk as a function of their traits.

AUTHOR CONTRIBUTIONS

Johanna Andrea Martínez-Villa, Sandra M. Durán and Brian J. Enquist designed and conceived the idea for the study; Alvaro Duque conceived Antioquia's Forest plot network; Johanna Andrea Martínez-Villa and Alvaro Duque designed and coordinated trait characterization sampling and forest inventory; Johanna Andrea Martínez-Villa performed the data analyses; Johanna Andrea Martínez-Villa wrote the manuscript with input from all authors. Johanna Andrea Martínez-Villa and Alain Paquette funded as part of the fieldwork. Alain Paquette and Christian Messier commented on and edited the manuscript. Alain Paquette and Christian Messier funded the PhD candidate studies. All authors provided critical feedback and helped shape the research, analysis and manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data and code deposition: The data and codes used in this study are available in the file "scripts and data_GEB.zip". Additionally, they are deposited on figshare ([10.6084/m9.figshare.24189045](https://doi.org/10.6084/m9.figshare.24189045)).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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