

# Elevational range sizes of woody plants increase with climate variability in the Tropical Andes

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## Abstract

**Aim:** The climate variability hypothesis proposes that species subjected to wide variation in climatic conditions will evolve wider niches, resulting in larger distributions. We test this hypothesis in tropical plants across a broad elevational gradient; specifically, we use a species-level approach to evaluate whether elevational range sizes are explained by the levels of thermal variability experienced by species.

**Location:** Central Andes.

**Time Period:** Present day.

**Taxon:** Woody plants.

**Methods:** Combining data from 479 forest plots, we determined the elevational distributions of nearly 2300 species along an elevational gradient (~209–3800 m). For each species, we calculated the maximum annual variation in temperature experienced across its elevational distribution. We used phylogenetic generalized least square models to evaluate the effect of thermal variability on range size. Our models included additional covariates that might affect range size: body size, local abundance, mean temperature and total precipitation. We also considered interactions between thermal variability and mean temperature or precipitation. To account for geometric constraints, we repeated our analyses with a standardized measure of range size, calculated by comparing observed range sizes with values obtained from a null model.

**Results:** Our results supported the main prediction of the climate variability hypothesis. Thermal variability had a strong positive effect on the range size, with species exposed to higher thermal variability having broader elevational distributions. Body size and local abundance also had positive, yet weak effects, on elevational range size. Furthermore, there was a strong positive interaction between thermal variability and mean annual temperature.

**Main Conclusions:** Thermal variability had an overriding importance in driving elevational range sizes of woody plants in the Central Andes. Moreover, the relationship between thermal variability and range size might be even stronger in warmer regions, underlining the potential vulnerability of tropical montane floras to the effects of global warming.

## KEYWORDS

Andes, Bolivia, Climate variability hypothesis, Elevation, Forest plots, Madidi, Range size

## 1 | INTRODUCTION

Assessing the mechanisms shaping the distribution of species is essential to better understand the assembly of local communities and the potential consequences of environmental drivers on biodiversity patterns (Bellard et al., 2012; Nadeau et al., 2017). This is particularly urgent for mountain regions, areas of great importance for biodiversity conservation (Jung et al., 2021). Mountain ranges are characterized by high environmental heterogeneity across space and time (Rahbek, Borregaard, Antonelli, et al., 2019), and harbour roughly one-third of terrestrial living organisms, including many small-ranged species (Rahbek, Borregaard, Colwell, et al., 2019). Understanding the drivers of montane species ranges, particularly in the tropics, is critical given the threats that climate change and human modifications of the landscape poses to the distribution and persistence of species in these regions.

Although species distributions are often modelled as a function of average environmental conditions in a site or a region, temporal variation in these conditions can have profound effects on population and species adaptations, and consequently on their distribution. This idea underlies D. Janzen famous hypothesis that 'mountain passes are higher in the tropics' (1967). When thinking of the distribution of species in mountains at different latitudes, Janzen proposed that tropical mountains represent physiologically stronger filters for organisms than temperate mountains; he hypothesized that having evolved in less variable environments, montane tropical species likely had limited acclimation responses and, in consequence, smaller elevational ranges than species in temperate mountains. Increases in range size with latitude were later proposed as an 'ecological rule' (Rapoport, 1982) and the mechanism behind this rule was formally presented as the 'climate variability hypothesis' (Stevens, 1989). The climate variability hypothesis proposes that species subjected to wider temporal variation in climatic conditions will evolve tolerances to broader environmental niches, resulting in wider geographic distributions. Correspondingly, species experiencing stable environments would develop narrow tolerances and small geographic distributions.

Climatic variability, however, does not only characterize latitudinal gradients, but also elevational gradients, affecting range size (Chan et al., 2016). Within the tropics, for example, climatic variability can change significantly across elevation; daily temperature variation can be dramatic at high elevations, but only mild in the lowlands (McCain, 2009). If temporal variation in climate influences species distributions within tropical mountains, then species near mountain tops should have more extensive elevational distributions than species in the lowlands. This extension of the climate variability hypothesis to elevation (ECVH) was formalized by Stevens (1992).

The climate variability hypothesis across elevations (ECVH) has been tested in many taxa, producing conflicting results (Chan et al., 2016; McCain & Knight, 2013; Shah et al., 2021). Whereas some studies show increases in range size with latitude and elevation (e.g., Patterson et al., 1996; Pintor et al., 2015), others have

refuted these patterns (e.g., Hawkins & Felizola Diniz-Filho, 2006; Maccagni & Willi, 2022). Contradictory results have fuelled a debate regarding whether species responses to climate variation is only a local phenomenon or a consistent pattern (McCain & Knight, 2013; Rohde, 1996). Part of the reason for the inconsistent results among studies testing ECVH could be limitations to analyses or data. Geometric constraints in the distribution of species, for instance, have rarely been accounted for when testing ECVH hypothesis, resulting on strong criticisms on the statistical approaches and assumptions behind these studies (Macek et al., 2021; McCain, 2009; Ribas & Schoereder, 2006). Additionally, most studies of ECVH carry out assembly-level analyses, where the average range size for groups of species is used, and analyses focus on how these averages change across space (Rohde, 1992; Stevens, 1992). However, the evolution of climatic tolerances and responses to climatic variability are species-specific and, as such, require species-level analysis. Species-level and high-quality datasets are rare, particularly in diverse tropical regions, preventing species-level tests of ECVH in tropical mountains.

Studies testing predictions from the ECVH in vascular plants include only a few examples on the sub-tropical floras of the Himalayas (e.g., Liang et al., 2021; Macek et al., 2021) and the temperate Caucasus mountains (Mumladze et al., 2017), as well as studies focusing on smaller sets of temperate plants that extend ECVH predictions to other species characteristics (e.g., trait plasticity; Molina-Montenegro & Naya, 2012; Maccagni & Willi, 2022). To the best of our knowledge, the only study that has directly tested the climate variability hypothesis on Neotropical plants has focused only on alpine communities in the Andes (>3000m; Cuesta et al., 2020). This study found that tropical alpine species had narrower thermal niches than temperate species, supporting predictions derived from the classic CVH, but no significant effects of elevation. In consequence, whether temporal climatic variability shapes the distribution of tropical plant species along elevational gradients is yet poorly understood. A thorough analysis of the predictions of ECVH is necessary, particularly in tropical plants, to understand how species respond to climatic variability, and particularly, whether climatic variability can promote the formation of large geographic ranges.

Here, we present the most thorough species-level test of the climate variability hypothesis across elevations (ECVH). Specifically, we evaluate whether species with populations experiencing high levels of temperature variation will have larger elevational distributions. For our study, we use data from the Madidi Project ([www.madidiproject.weebly.com](http://www.madidiproject.weebly.com)), a collaborative effort to document and study the plant biodiversity of the Tropical Andes, and possibly the most extensive dataset on tree occurrences in any tropical mountain. Using these data, we evaluate the effect of climate variability while controlling for the effects of potential confounding factors that have been proposed to affect range size such as geometric constraints, other climatic variables (temperature and precipitation), and species traits (plant size and local abundance) (e.g., Gaston & Blackburn, 1996; Peters & Peters, 1986). Our dataset and approach provide a unique opportunity to study the forces that drive the

distribution of tree species in one of the most species-rich regions of the planet.

## 2 | MATERIALS AND METHODS

### 2.1 | Vegetation data and elevational range sizes

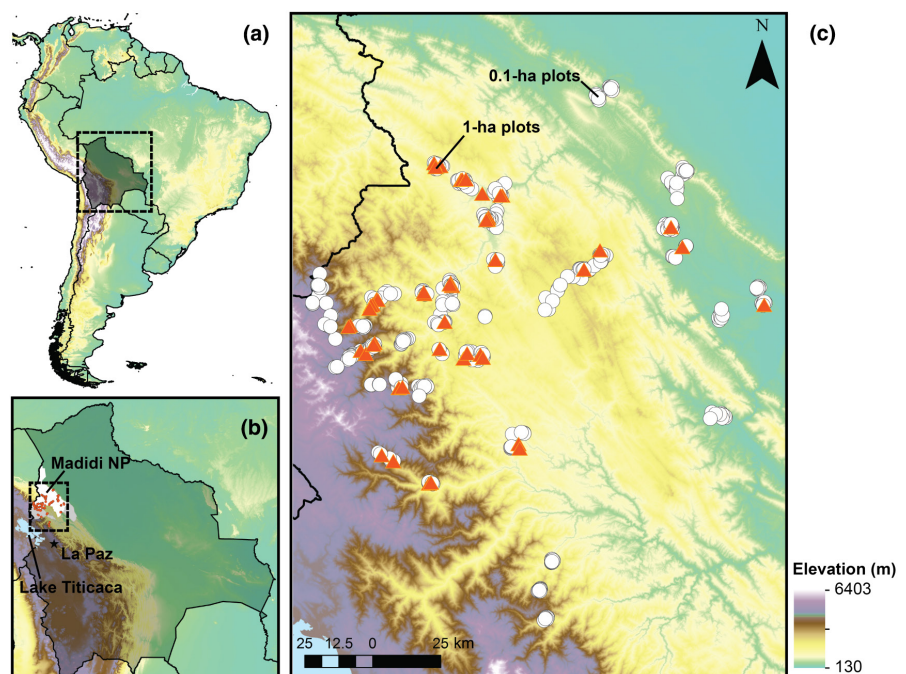
Species elevational distributions were determined based on a large network of forest plots distributed along the eastern slopes of the Bolivian Andes (Figure 1). The network consists of 48 1-ha plots (henceforth large plots) and 458 0.1-ha plots (small plots) ranging in elevation from 209 m (Amazon forests) to 4347 m (tree line). Within plots, all individuals of woody plant species with diameters at breast height (dbh) equal or above 10 cm (for large plots) or 2.5 cm (for small plots) were measured and identified. Each individual tree was assigned a species or morphospecies name (henceforth simply species), and extensive taxonomic work was conducted to ensure that names were applied consistently throughout all plots. For this study, we used version 5.0 of the Madidi Project plot database (<https://doi.org/10.5281/zenodo.5160379>). The species-level data and code necessary to replicate our analyses has been deposited and can be freely accessed in Dryad (Elevational range sizes of woody plants increase with climate variability in the Tropical Andes (<https://zenodo.org/uploads/10429518>)).

From these data, we removed all cacti (Cactaceae); bamboos (Poaceae), tree ferns (Dicksoniaceae and Cyatheaceae), gymnosperms (Podocarpaceae) and the non-native genera *Eucalyptus* and *Coffea*. We also removed plots above 3800 m in elevation, which were dominated by species of *Polylepis* and likely heavily shaped by human use. Because we only sampled individuals with a dbh 2.5 cm or larger, species that rarely reach this size might be included in our

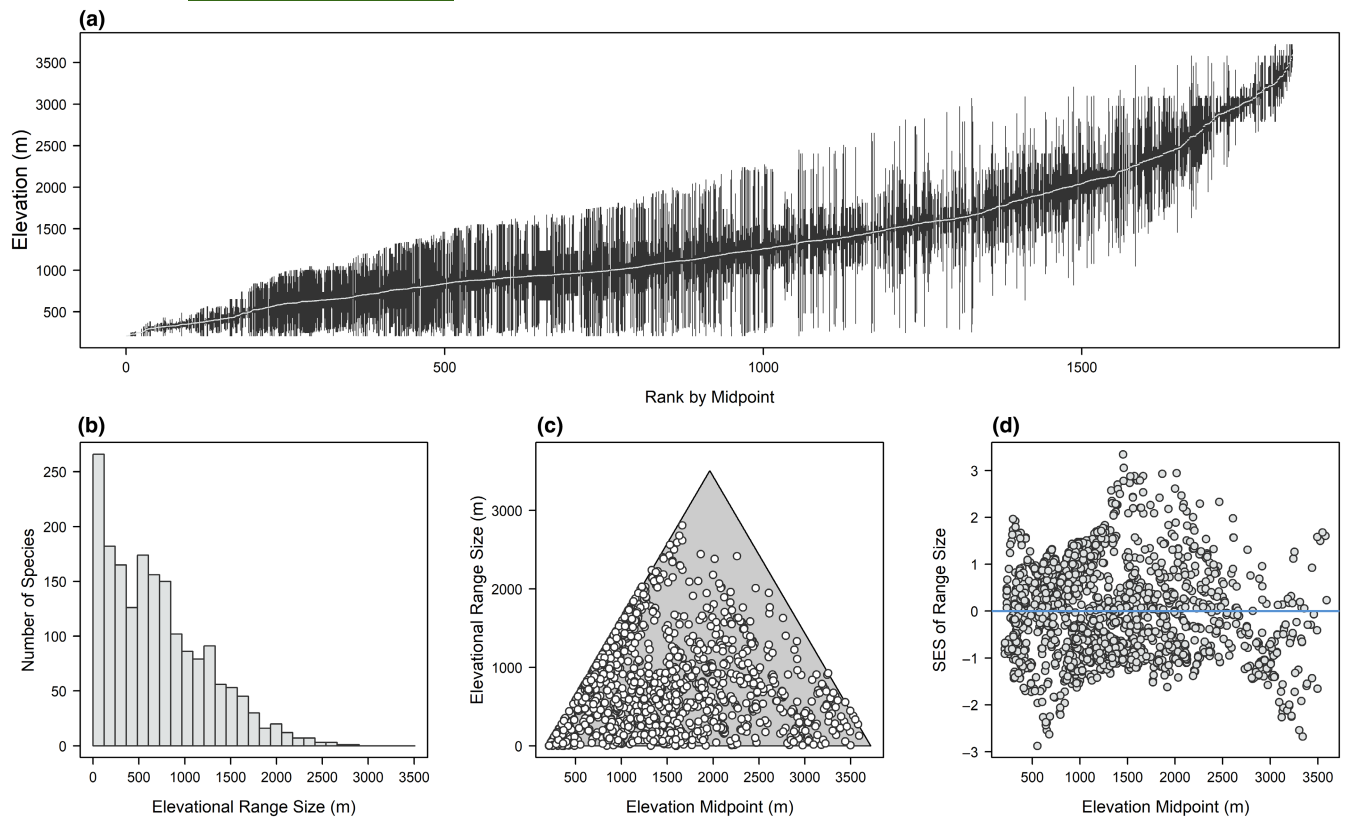
data but seriously under-represented relative to their true abundances. Thus, we examined the distribution of species-level maximum size values across our dataset and eliminated all species with maximum size below the lowest 5% of the distribution (this is, all species with maximum size less or equal to 3.24 cm; see Figure S1). Finally, we eliminated individuals that could not be assigned to species or morphospecies (<1% of individuals) and individuals from 16 additional species that could not be placed in the regional phylogeny (see below).

We estimated the elevational distribution of each species in our dataset by recording their highest and lowest elevation of occurrence (Figure 2a). Elevational range size was calculated as the difference in meters between these two points. Elevational position was characterized by the species' elevational mid-point (the mean between the maximum and minimum elevation of occurrence). For the estimation of elevational distributions, we merged the data from large and small plots with the objective of using all the available information for each species. After this process, we further excluded 461 species that were found in only one plot and thus could not be assigned to a reliable value of elevational range. After data curation, our dataset contained information on the distribution of 153,084 individuals belonging to 2292 species across 479 forest plots (48 large plots and 431 small plots).

To account for heterogeneity among species in range size estimation and ensure that our conclusions did not depend on the precise collection of species used, we repeated all analyses using two alternative subsets of species (Figure S2). In the second set of species, we included only species that were present in three or more sites or that had five or more individuals (1713 species); in the third set, we subsampled forest plots to reduce heterogeneity in sampling effort across elevations. We divided the elevational gradient (209–3717 m) into 20 equal-sized bands; in each band, we randomly selected 12 forest plots. This procedure reduced the



**FIGURE 1** Map of the study region and network of forest plots. (a, b) Location of the study region within and around Madidi National Park in Bolivia. (c) The forests' plots dataset used in our analyses include 48 large plots (1-ha in area) and 458 small plots (0.1-ha).



**FIGURE 2** Elevational ranges for woody plant species in the Andes of northwestern Bolivia. (a) Vertical lines connect the lowest and highest elevations recorded for each species used in our analyses. In this way, the lines describe the elevational extent of species' distributions (i.e., their elevational ranges). Species are ranked in the x-axis by their elevational mid-point. (b) Frequency distribution of elevational range sizes showing that most species have small ranges. (c) Relationship between elevational range size and elevational mid-point. The range size of each species is constrained geometrically by its position with respect to the upper and lower limits of the gradient. Species that have an elevational mid-point in the lowlands or highlands are constrained to having small ranges, while species that have a mid-point at intermediate elevations are free to have either small or large range sizes. The grey area shows the possible distribution of points; the black edges mark the geometric limits to this relationship. (d) Relationship between the standardized effect size of range size and elevational mid-point. Standardized effect size for a species was calculated by comparing its empirical range size to a subset of ranges of similar geometric constraints (see Section 2 for details; Figure 3). SES values greater than zero indicate ranges that are larger than expected by their constraints.

dataset to 1280 species. Despite considerable differences among these datasets, all analyses support the same conclusions. Thus, we present results for our complete dataset in the main text and provide results for the two subsets of data in the supplementary materials.

## 2.2 | Temperature and precipitation data and species-level predictors

Using the coordinates of each forest plot, we extracted temperature data from WorldClim 2.1 (at ~1 km resolution; Fick & Hijmans, 2017). We considered other alternative climate datasets (e.g., Chelsa 1.2; Karger et al., 2017), but we found that WorldClim 2.1 was the closest match to field measurements of temperature (Figure S3). We extracted precipitation data from TRMM 2b31-Based Rainfall Climatology Version 1.0 at ~1 km resolution (Mulligan, 2006). For each plot, we obtained data on mean annual temperature (MAT),

total annual precipitation (TAP), annual temperature range (ATR) and diurnal temperature range (DTR). Our initial inspection of predictive variables showed DTR is closely correlated with ATR (Figure S4D), and thus, we used only data on ATR in our analyses. We present similar models using DTR instead in the supplementary materials (Table S1).

For each species, we estimated the degree of temperature variation that individuals experience by using the maximum value of ATR at a site across all occupied plots (Max. ATR). Additionally, we calculated other species-specific predictors that could be important determinants of elevational range size, which were used as co-variables in our analyses. We calculated abundance-weighted mean annual temperature (w-MAT) and total annual precipitation (w-TAP). For these calculations, plot-level values of MAT or TAP contribute to the species mean as a function of the abundance of the species in each plot. These variables represent the most typical environmental conditions occupied by each species. Finally, we calculated species-level maximum size as the 90% quantile of the distribution of dbh

for each species, and species abundance as the maximum value of relative abundances of each species across all occupied plots.

### 2.3 | Statistical tests of the ECVH hypothesis

The climate variability hypothesis across elevations (ECVH) predicts that species with populations experiencing high levels of temperature variation will have larger elevational distributions. To evaluate this prediction, while accounting for shared evolutionary history among species, we used a phylogenetic generalized least squares (PGLS) regression model. In this analysis, species elevational range size was the dependent variable and maximum annual temperature range (max. ATR) was the main predictor of interest. In PGLS, the covariance structure among species (the errors) is given by a particular evolutionary model, often a Brownian motion model. In this study, we used a Pagel correlation structure, which is more flexible than a Brownian correlation as it allows deviations from a perfect phylogenetic structure in the data (Pagel, 1999). In this way, using a Pagel correlation structure allows for the simultaneous estimation of the regression model, as well as the strength of the phylogenetic signal in the predictor and response variables (Revell, 2010).

Phylogenetic relationships among our species are based on Smith and Brown's (2018) mega-phylogeny, accessed using the R package V.PhyloMaker (Jin & Qian, 2019). Species that were not found in the base phylogeny were added using taxonomic information at base of the branch of the corresponding genus or family using the 'S1' option in V.PhyloMaker. While this phylogeny is a coarse description of evolutionary relationships, it allows us to construct phylogenetic regressions that would otherwise be impossible. We used Ives' proposed R2resid metric to characterize the amount of variance in the data explained within a phylogenetic regression model (Ives, 2019); rr2 R package: (Ives & Li, 2018). PGLS models were performed with function gls in R package nlme (Pinheiro et al., 2020).

To account for the effects of other potentially important covariates, the PGLS model also included mean annual temperature (w-MAT) and total annual precipitation (w-TAP) as well as species-level characteristics including maximum size (i.e., 90th percentile of dbh distribution per species) and species maximum local abundance. To meet model assumptions, elevational range size was square-root transformed, while maximum size and species abundance were log-transformed. Other variables remained untransformed. All predictors were centred to a mean of zero and standardized to a standard deviation to 1 before analyses. In this way, regression coefficients are comparable and measure the relative importance of each predictor in the model. Finally, the model also included the interactions of temperature variability with mean temperature (max. ATR × w-MAT) and annual precipitation (max. ATR × w-TAP). We evaluated collinearity among predictors in our PGLS model using variance inflation factors (VIF) using function vif in the R package car (Fox et al., 2022). Most variables had VIFs less than five indicating that collinearity is low in our models (Table 1).

### 2.4 | Accounting for geometric constraints and sampling effects on elevational range sizes

Geographic ranges are subject to geometric constraints given by the limits of the domain over which species are distributed. In our study, the domain is the elevational gradient ranging from Amazon forests at 209 m in elevation and the timberline at 3717 m. Species in our study are constrained to be distributed between these elevations (Figure 2c). The effect of this constrained domain is expressed in the relationship between elevational position and elevational range size. Species with distributions centred in the lowlands (low elevational mid-points) or in the highlands (high elevational mid-points) cannot have large elevational ranges. Species with distributions centred at intermediate elevations, on the other hand, are free to have small or large elevational distributions. This constraint is potentially problematic for our analysis and could mask the effects of environmental or biological variables on the extent of the geographic distribution of species.

To account for this potential effect, we calculated an alternative metric of range size that is less affected by these geometric constraints, and repeated our analyses with this new response variable. First, for each species, we calculated the distance between its elevational mid-point to the closest edge of the elevational domain (i.e., to 209 m or 3717 m whichever is closest; Figure 3a). This distance (hereafter *d value*) determines the strength of the geometric constraint on a species' distribution; as this distance decreases, species are located closer to the edges of the domain and have a narrower set of possible values of range size (Figure 3a). Then, we found a pool of other species under similar geometric constraints. This pool was defined as all species with *d* values equal to that of the focal species  $\pm 50$  m (Figure 3a,b). For each species, we calculated a standardized effect size (SES) that compares its elevational range size to those of the other species in its pool (Figure 3b). SES was calculated as the difference between the elevational range size of the focal species and the mean range size of all other species in its pool divided by the standard deviation of the range sizes in the pool. A positive SES value indicates that the focal species has a distribution that is larger than other species under similar constraints, while a negative value means the species has a smaller distribution. Using these SES of range size, we repeated all statistical analyses as described above.

Finally, it is possible that relationship between range size and climate variability could be spuriously produced by a sampling effect; species with large elevational ranges might also occupy many sites (high occupancy). In turn, species present on many sites are able to sample the environmental space better and - by chance - find higher values of climatic variability (e.g., max. ATR). To account for this potential effect, we (1) examined the relationships between species occupancy (number of plots with presence of the species) and elevational range size and max. ATR, and (2) repeated our PGLS regressions including occupancy as a covariate.

TABLE 1 Testing for the effect of temperature variability and other predictors on size of elevational distributions.

Response	Predictor	Coeff.	p-value	VIF	Obs.-pred. corr.	R <sup>2</sup> <sub>resid</sub>	LR	LRT: p-value
ERS	Intercept	27.011	<0.001		0.618	0.389	890.6	<.001
	log(Max. Size)	1.688	<0.001	1.054				
	log(Max. Abund.)	3.033	<0.001	1.156				
	w-MAT	1.730	<0.001	2.069				
	w-TAP	2.602	<0.001	1.952				
	Max. ATR	9.592	<0.001	4.071				
	w-MAT × Max. ATR	3.735	<0.001	5.877				
	w-TAP × Max. ATR	0.309	0.310	3.591				
SES	Intercept	0.237	<0.001		0.647	0.419	994.5	<.001
	log(Max. Size)	0.136	<0.001	1.055				
	log(Max. Abund.)	0.252	<0.001	1.157				
	w-MAT	0.474	<0.001	2.035				
	w-TAP	0.257	<0.001	1.946				
	Max. ATR	0.968	<0.001	4.014				
	w-MAT × Max. ATR	0.280	<0.001	5.806				
	w-TAP × Max. ATR	0.018	0.494	3.550				

Note: Phylogenetic generalized least-square regressions (PGLS) were used. Elevational range size (ERS) or a standardized effect size for range size (SES) were modelled as the response variable in separate models. Regardless of the response used, we found that maximum annual temperature range (max. ATR) was a strong predictor and had a significant interaction with abundance-weighted mean annual temperature (w-MAT). Additional predictors included species maximum size, maximum abundance among occupied plots, and abundance-weighted total annual precipitation (w-TAP). For each predictor, we report standardized coefficients, p-values and variation inflation factors (VIF). Model fit is characterized by Ives' residual R<sup>2</sup> value for phylogenetic modes, as well as Pearson's correlation between observed and model-predicted values of the response variable. Finally, we used a likelihood ratio test (LRT) to obtain a model-wide p-value by contrasting each PGLS against a null model. The null model had only an intercept and the same phylogenetic structure estimated for the main PGLS model. Details on univariate models and other competing models are detailed in Table S1.

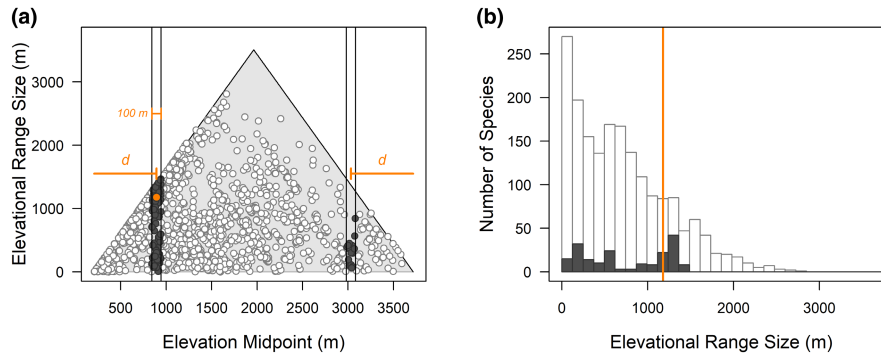
### 3 | RESULTS

Elevational ranges varied greatly across species, having a strongly skewed frequency distribution (Figure 2b). Most species had very small ranges and very few had broad elevational distributions. The mean and median of elevational range size were 702 and 607m, respectively; the maximum was 2812m. Environmental characteristics also varied greatly across the network of plots. Mean annual temperature decreased dramatically across elevations from 25.4 to 9°C (Figure S4A). Similarly, estimates of total precipitation ranged from 3819 to 197 mm per year. Although temperature variability generally increased with elevation (Figure S4B), the pattern was non-linear: ATR showed a small initial dip towards intermediate elevations (with a minimum around 1250m), before a steep increase towards the highlands. These gradients in climate suggest that populations of species in the highlands experience a higher degree of temperature fluctuations than in the lowlands. The distribution of plots across environmental gradients is depicted in Figures S5 and S6. Our results provide strong evidence that elevational range sizes are shaped by temporal variation in climate, particularly temperature. We found that max. ATR was the strongest predictor included in our models (Table 1) and had a clear positive effect on elevational range size (Figure 4). Species exposed to higher temperature variability have broader geographic distributions. This effect was highly consistent across our different

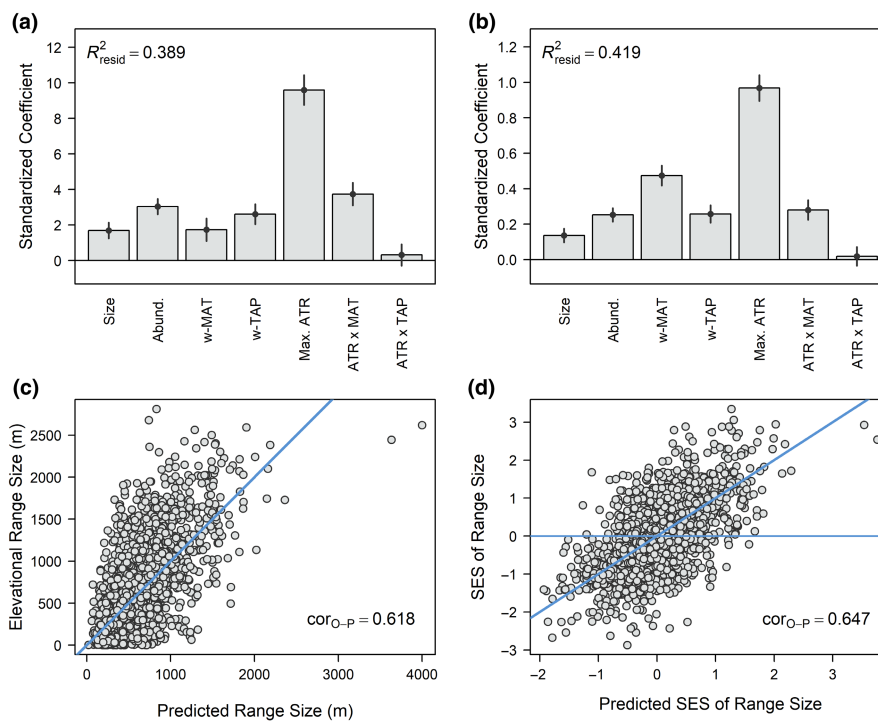
analyses; max. ATR had a strong positive effect whether raw elevational range size or standardized effect sizes (SES) were used as response variables (Figure 4; Figure S7). When repeating our analyses with alternative datasets, we found further support to our results; max. ATR had a consistent positive effect when elevational distributions were characterized using species with at least two occurrences (Figure 4; Table S1), or when using species with at least three occurrences or five individuals (Figure S8; Table S2), or with a dataset that has been reduced to homogenize effort across elevations (Figure S9; Table S3).

Our results show that temperature variability interacts with MAT, but not with TAP (Figure 4a,b). While the effect of temperature variability is always positive, the strength of this effect is greater for species with distributions in warmer climates (Figure 5a,b). On the other hand, the effect of ATR is consistent regardless of levels of precipitation (Figure 5c,d). Finally, species' characteristics had a significant effect on elevational range size, but the effect sizes were small (Figure 4; Figure S7). As expected, range size increased for larger species (maximum size), and species that were more locally common (maximum abundance). These results were also robust when using alternative datasets (Tables S2 and S3).

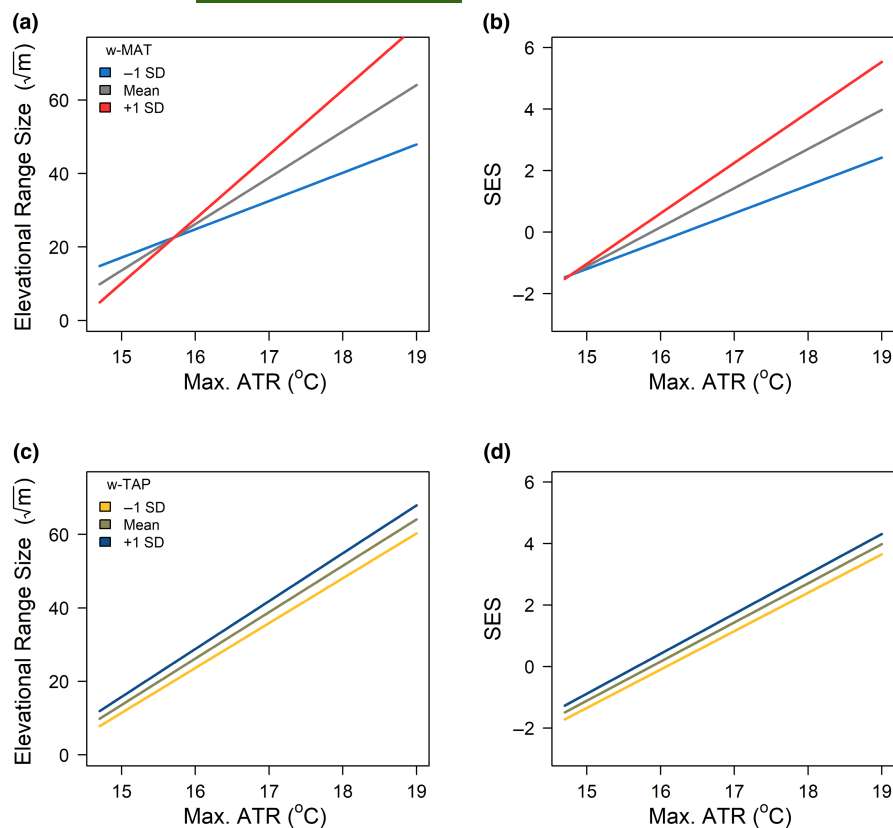
Finally, we found no evidence of potential sampling bias in our analyses; while high occupancy does lead to larger ranges



**FIGURE 3** Calculation of standardized effect sizes of range size. To account for geometric constraints on elevational distributions, we compared the range size of each species to the range sizes of all other species that suffer from a similar constraint. In the example shown here, the range size and midpoint of a focal species is indicated by the orange circle in (a) and the vertical orange line in (b). All species that suffer a similar constraint to the focal species are indicated by dark grey circles in (a) and grey bars in (b). All other species are shown in white. Species with a similar constraint to the focal species are those that (1) have a midpoint in a region 50m above or below the midpoint of the focal species, or (2) have a midpoint 50m above or below an elevation that is equidistant from the opposite edge of the gradient (distance  $d$ ). The range sizes of all species in these elevational bands represent a pool of potential values that the focal species could take given its midpoint. Thus, to calculate a standardized effect size, we (1) sampled 1000 values of range size from the pool of similar species, and then (2) subtracted the mean of the random values from the empirical range size and divided this by the standard deviation of the random distribution. In this way, a standardized effect size measures the breadth of elevational distribution while accounting for geometric constraints. A positive value indicates a range size that is larger than other ranges with similar constraints; a negative value indicates a range size that is smaller than other similar ranges.



**FIGURE 4** Effects of climate variability and other predictors on the breadth of elevational distributions. (a) Standardized coefficients showing the effect of each predictor on elevational range size. The height of each bar indicates the coefficient estimate, while the lines show the 95% confidence interval. Ives'  $R^2_{resid}$  is also shown. (b) Same as (a), but where the response variable was the standardized effect sizes of range size (i.e., range size after accounting for geometric constraints). (c) Empirical values of range size plotted against predictions made by the regression model in (a). The 1:1 correspondence is indicated by the solid blue line. (d) Same as (c), but where the response variable was the standardized effect sizes of range size (regression model in (b)). Size, maximum size (90th percentile of diameter at breast height); Abund., maximum local relative abundance; w-MAT, abundance-weighted mean annual temperature; w-TAP, abundance-weighted total annual precipitation; ATR, maximum annual temperature range.



**FIGURE 5** Interactions between temperature variability and mean temperature or total precipitation. Each panel shows the effect of temperature variability (maximum annual temperature range; max. ATR) on elevational range size (left column) and standardized effect sizes (right column) for different values of mean annual temperature (top row) and total annual precipitation (bottom row). In each case, the grey line depicts the effect of max. ATR for the mean value of the interacting variable. The coloured lines depict the effects of max. ATR for values one standard deviation above and below the mean of the interacting variable. These results demonstrate that increases in mean temperature significantly amplify the effect of temperature variability (a, b). On the other hand, increases in total precipitation do not modify the effects of temporal variability (c, d).

(Figure S10A), high occupancy does not necessarily imply larger values of temperature variability (Figure S10B). Moreover, the main conclusions of our analyses did not vary when including occupancy as a covariate in our PGLS models (Table S4).

## 4 | DISCUSSION

### 4.1 | Thermal variability and mean temperature interact to determine elevational range size

Using species-specific responses for ~2300 plant species to climate variability across an extensive elevational gradient in the Central Tropical Andes, we found strong support for the climate variability hypothesis across elevations (ECVH; Janzen, 1967; Stevens, 1992). Our findings show a strong positive relationship between local climate variability, particularly in temperature, and the elevational range size of woody plants (Table 1). In fact, the effect of variability in temperature is stronger than that of any other factor considered in our models. Importantly, our results were robust to all variations in analyses to account for potential biases related with species rarity and range size variability, uneven sampling across elevations and geometric constraints. The overall trend for elevational restricted species to occupy less climatically variable environments, regardless of their elevation of occurrence (i.e., not limited to lower elevations), suggests that elevational range restriction in Andean trees is likely related to narrow thermal tolerances rather than to biotic interactions or habitat specificity, two processes hypothesized to be more

prevalent at lower elevations (Brown et al., 1996; MacArthur, 1984; Paquette & Hargreaves, 2021).

Previous studies have tested for the relationship between thermal variability and elevational range size, independent of the elevation of occurrence. Like ours, these studies found this relationship to be positive, despite using different methods of assessing climatic variability and focusing on different taxa (Beck et al., 2016; Maccagni & Willi, 2022; Pintor et al., 2015). Only a few studies have, however, tested predictions from the ECVH in vascular plants and their conclusions have been limited by their data or analyses. For instance, using a large empirical dataset on plant elevational distributions in the Western Himalaya, Macek et al. (2021) found no support for the ECVH. As recognized by the authors, the lack of relationship between climate variability and elevational ranges in their study might result from the fact that the lowest elevation in their study is ~2650 m a.s.l., and thus their dataset lacks information of lowland species and lower elevation climatic variability. A similar reason might have caused the lack of relationship between thermal niche breadth (maximum – minimum temperature a species experienced) and elevation in alpine plants (>3000 m a.s.l.) of the Andes in the study by Cuesta et al. (2020). Here, we take advantage of a naturally extreme elevational gradient (~200–3750 m a.s.l.) in the Central Tropical Andes and can extend our hypothesis testing to the whole set of woody plants. To the best of our knowledge, no other comparable dataset exists for tropical plants where sampling of species has been as intensive and systematic over a large elevational gradient, and empirical data were obtained with standardized and homogeneous taxonomic information across species and sites. When including a full gradient of



climatic variability, we found a strong positive relationship between thermal variability and elevational range sizes.

While we found that climate variability has a strong positive effect on elevational range size, we also found that the magnitude of this effect depends on whether species are distributed in warmer or colder regions (i.e., a significant interaction between max. ATR and w-MAT). Specifically, the positive effect of climate variability was stronger for species in warmer regions (e.g., lower elevations) than for species in colder regions (e.g., higher elevations). This finding is consistent with previous studies that found that both mean climatic conditions and climate variability are important drivers of species' range sizes in different taxa (e.g., Chan et al., 2016; Liang et al., 2021; Luo et al., 2011). Although studies in terrestrial vertebrates have considered the interaction between average environmental conditions and climate variability (Chan et al., 2016), to the best of our knowledge, our study is the first one on woody plants to include these effects when testing the ECVH. For example, Liang et al. (2021) considered mean environmental variables besides thermal variability in their study of plant elevational ranges. They found that both MAT and mean annual precipitation had a significant relationship with plant elevational ranges; they did not, however, consider interactions among these and climate variability in their analyses. Similarly, Mumladze et al. (2017), examined the correlations between the thermal range size of plant species (and not directly its elevational range) and the maximum temperature seasonality in two elevational gradients of the Caucasus. In their paper, Mumladze et al. (2017) separately tested the correlation with precipitation ranges and precipitation seasonality but did not test for interactions nor examined the relative importance of different environmental variables on species ranges. Our study, therefore, is the first one to show how average environmental conditions modulate the effect of climate variability on the climatic tolerances and range size of plant species.

Although we argue that the most direct way to test predictions of the ECVH is to study the response of individual species to different levels of climate variability, most studies use the average range size of co-occurring species as response variable (e.g., Liang et al., 2021; Macek et al., 2021; Mumladze et al., 2017). These studies average the range sizes of all species occurring at a given site or elevational band (i.e., the 'Steven's method') or average the range size of species whose distributional middle point falls within a given elevational band (i.e., the 'midpoint method'). Because species relationships with climate variables is idiosyncratic (McCain & Knight, 2013), this aggregation of species responses could be a confounding factor, resulting in inconsistent results. Assemblage-level averages hide important variation among species. In a study with mayflies, for example Gill et al. (2016) found great variability in elevation range sizes even among closely related species that was likely related with variation in species physiological and dispersal traits. Species-specific differences in traits may result in large variation in elevational ranges across plant clades that co-occur at any given elevation, variability that could be dismissed when using assemblage-level metrics. Thus, conclusions reached with assemblage-level analyses should be taken cautiously.

## 4.2 | Limitations of our study and recommendations for future analyses

A potential caveat of our study is the use of climate information from global databases. The coarse resolution of global databases might result in inaccurate information in mountain regions (e.g., Browoski & Schickhoff, 2017). For example, the complex landscape of the Andes likely adds to thermal variability; adjacent areas with different topographic exposures may differ notoriously in temperature and thermal variability, creating contrasting micro-habitat variation (Jackson & Forster, 2010). This small-scale spatial variability might be better captured with local climatic information obtained from data-loggers installed across elevations. We partially address this concern by comparing the climatic patterns in global datasets with a few data-loggers located in the study region (Figure S3). We found WorldClim v.2.1 matched most closely the climate patterns we detected in situ with data-loggers. Furthermore, the use of highly localized climate data collected by data-loggers has its own limitations. With a forest canopy that might surpass 30 m of height, environmental information obtained from sensors located below 3 m (where most data loggers are set due to logistical constraints; Bach et al., 2003) might represent poorly the thermal environment that most trees experience. Indeed, it has been shown that climatic conditions experienced by understory versus canopy species can vary substantially (Frey et al., 2016), with canopies potentially experiencing greater temperature variability (De Frenne et al., 2019). Future studies might explore the differences in climate variability experienced by understory and canopy species and how these further affects species' distribution across environmental gradients.

Furthermore, it is important to consider that although we found range sizes to be strongly associated with climate variability, other mechanisms might also act as determinants of Andean plant species' ranges. We found a significant effect of tree size and local abundance, both of which had a positive effect on range size. These results are consistent with other studies on the ecological factors shaping the size of species distributions (Stahl et al., 2014). Moreover, other processes that we did not consider in our analyses could also be important. Biotic interactions such as specialized mutualisms or competitive interactions have been found to shape species ranges across latitudes and elevation (Brooker et al., 2007; Jankowski et al., 2010; Wisz et al., 2013). Dispersal abilities or dispersal history might also play a role in the realized range size of plants, with climate stability potentially having a stronger effect on groups with lower dispersal capacities (Xu et al., 2018). Finally, phenotypic plasticity or local adaptation can both contribute to shaping elevational range sizes (Bradshaw, 1965; Buckley et al., 2019; Van Nuland et al., 2017). Indeed, species along elevational gradients might have undergone genetic divergence and populations might represent cryptic divergence with more restricted elevational ranges than assumed at a species-level analysis like ours (Gill et al., 2016; Guarnizo et al., 2015). Future studies should focus on disentangling which and how these mechanisms

might further restrict or extend species' elevation distributions in tropical mountains.

### 4.3 | Implications for environmental change

Understanding how climate shapes species distributions along environmental gradients is becoming increasingly urgent in a rapidly changing world, particularly because many tropical species are responding to global warming through range shifts (Fadrique et al., 2018; Freeman et al., 2018; Nadeau et al., 2017). Our study points to the overriding importance of thermal variability in driving elevational range sizes in woody plants in the Central Tropical Andes. Moreover, we found evidence suggesting that in warmer mountains the relationship between thermal variability and range size might be even stronger. Our results have implications not only to understand drivers of range size, but to predict how environmental change might impact biodiversity (Nadeau et al., 2017).

Combined, our findings highlight the great vulnerability of tropical floras to the enhanced effects of climate change in mountain ranges (Sentinella et al., 2020). Under a climate warming scenario, species with smaller thermal tolerances (often in warm, tropical regions) might be more vulnerable as their distributions seem to be strongly related with their climatic stability. Furthermore, species at low elevations not only have narrower climatic tolerances and small ranges, but they often also experience temperatures closer to their upper tolerance limits (Colwell et al., 2008). This could mean that species inhabiting tropical lowlands will likely face greater impacts of warming temperatures. Species might respond to such changes in local conditions either by tracking suitable climates and moving upslope to match their historical niches (e.g., Feeley et al., 2011), by persisting in situ in thermally buffered micro-habitats created by topography and other physiographic features (e.g., Suggitt et al., 2018), potentially resulting in fragmented populations, or by decreasing in abundance and potentially going extinct. By the same logic, species that are adapted to more variable environments and have broader distributions might be best able to cope with significant environmental change. On the other hand, as thermal variability along elevation is mostly determined by variation in minimum rather than maximum temperatures (lower temperatures decrease at a faster rate), species adapted to highly variable climates may struggle surviving in habitats with temperatures closer to their maximum tolerances. Having no place to 'escape' from higher temperatures, high elevation floras in the tropics might be particularly vulnerable to rising temperatures. Climate variability, its effect on species climate tolerance and spatial distribution, can provide important clues into how species, communities and ecosystems will change in response to environmental shifts.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study is deposited in Dryad repository (DOI: [10.5061/dryad.31zcrjdt0](https://doi.org/10.5061/dryad.31zcrjdt0)).

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## BIOSKETCH

**Flavia A. Montano-Centellas** has a background in tropical ecology and conservation. She is broadly interested in the theoretical and empirical aspects that cause and maintain biodiversity. Currently Flavia is a postdoctoral researcher at Louisiana State University, where she focuses her research on the drivers of biodiversity across environmental gradients. **Sebastián Tello** is a scientist at the Missouri Botanical Garden interested in the function, conservation and restoration of tropical forests, particularly across the Andes. His research focuses on how individuals, communities and ecosystems respond to environmental change, and how these insights can inform conservation and restoration practice. All authors belong to the Madidi Project—a long-term collaboration between the Missouri Botanical Garden, the Herbario Nacional de Bolivia and various other researchers. For over 20 years, the Madidi Project has documented and monitored plant biodiversity in and around the Madidi National Park in Bolivia, supporting research, conservation and capacity building.

**Author contributions:** JST conceived the idea, FMC and JST performed data analyses and wrote the first draft of the manuscript, AF, LC, MM, GA, MIL, BNA and JST collected and curated the data. All authors contributed to manuscript editing.

#### SUPPORTING INFORMATION

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

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