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*Research article*

# Bamboo climatic tolerances are decoupled from leaf functional traits across an Andean elevation gradient

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Widespread changes in temperature and precipitation patterns present plant species with new and combined stresses that affect their performance and distribution. Functional traits are indicators of plant resource use–acquisition strategies and thus they are commonly used to understand the geographic distributions of plant species and species' potential responses to climate change. To date, most studies have targeted a few easy-to-measure leaf traits even though other traits, such as climatic tolerances, could provide valuable information directly related with species' current and future distributions. Here, we measured both leaf functional traits and indices of physiological tolerance to heat ($T_{50}$) and drought (cell membrane stability) in 28 woody bamboo populations from 22 narrow-ranged species along a > 3000 m elevation gradient in the southern Peruvian Andes. We found that bamboo leaf functional traits remain fairly constant with a combination indicative of an acquisitive strategy (low leaf mass area and high nitrogen per mass) along the elevation gradient, despite drastic changes in environment and fast species turnover. Heat and drought tolerances of bamboos varied widely along the gradient and were negatively correlated to each other. Drought tolerance of bamboo populations was positively related with elevation and with precipitation seasonality while heat tolerance decreased at higher, colder elevations. When analyzed for individuals within each species or for individuals within each elevation, the two metrics of climatic tolerances did not show a consistent relationship, contrasting with the expectation of a potential tradeoff between heat and drought tolerance. We also found that the measured leaf functional traits were not good predictors of climatic tolerances. Our results illustrate the diversity and complexity of the relationships between functional strategies and environmental gradients and highlight the limitations of using basic (i.e. 'soft') leaf traits to understand plant distributions and climatic tolerances.

Keywords: Andean forests, drought tolerance, ecological scales, elevation gradient, soft and hard traits, temperature tolerance, tropical forests

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## Introduction

Functional traits are widely used to characterize plant distributions in relation to stress tolerance and resource allocation strategies (Westoby and Wright 2006). Functional traits are characteristics of organisms that are important to their fitness and environmental responses; they generally represent the tradeoffs in resource allocation to growth, reproduction and defense (Violle et al. 2007), which ultimately defines where species occur. In other words, functional traits underpin species distributions and may provide crucial insight into plant responses to climate change.

Rapid change in conditions across elevations make mountains ideal natural laboratories to explore the adaptations of plants to climate and the consequences of climate change (Tito et al. 2020). Plant distributions are shaped by environmental requirements and biotic interactions; accordingly, a rapid turnover of plant species and communities along elevation gradients is frequently observed (Gentry 1988), which translates into a fast turnover of functional traits and strategies (Dalling et al. 2015). Although climatic and soil conditions do not always change uniformly across elevation gradients (Körner 2007), there is a general elevational pattern of plant functional strategies found mainly in trees (Körner et al. 1989, Apaza-Quevedo et al. 2015) but also in other plant forms (Dunbar-Co et al. 2009, Read et al. 2014). In general, low-elevation species tend to exhibit 'acquisitive' strategies (rapid growth and reproduction) with traits such as low leaf mass to area ratio (LMA), high nitrogen content per unit mass ($N_{mass}$) and low nitrogen content per unit area ($N_{area}$) (Moser et al. 2007, van de Weg et al. 2009, Asner et al. 2014, Read et al. 2014); whereas high-elevation species tend to have more 'conservative' strategies (slower growth and reproduction but greater stress tolerance in harsh conditions) with traits such as thicker and smaller leaves with less water content, lower photosynthetic rate and lower chlorophyll concentrations (Asner et al. 2014, Dalling et al. 2015).

The conditions that occur across elevation gradients are changing due to global warming. In the Tropical Andes Biodiversity Hotspot – which hosts about 15% of all plant species (Myers et al. 2000) and plays a large role in the global carbon cycle (Duque et al. 2021) – rising temperatures are reported to be causing upslope shifts in tree species ranges and changes in forest composition (Fadrique et al. 2018). Changes in precipitation patterns (total rainfall or distribution across the year – i.e. seasonality) (Urrutia and Vuille 2009, Esquivel-Muelbert et al. 2018) or cloud base elevation (Halladay et al. 2012) are also being studied as potential modulators of taxonomical and functional composition in the Andes and the adjacent Amazon. As a result, plants are facing new physiological stressors (Allen et al. 2010), or new combinations of stressors, raising questions about the ability of plants to cope with these new conditions and the traits that will determine their success.

Several studies purport that the most important driver of range shifts in Andean plants is elevated tree mortality due to hotter temperatures (Duque et al. 2015, Fadrique et al. 2018). Hotter temperatures increase leaf respiration rates, decrease photosynthetic rates and affect leaf thermoregulation, especially when in combination with limited water availability (O'sullivan et al. 2017). For example, tree mortality may peak in areas where temperature increases but rainfall decreases or becomes more seasonal, effectively extending the dry season. Thus, leaf-level temperature and drought tolerances are important determinants of a plants' ability to survive under increased heat or drought stress (O'sullivan et al. 2017, Brodribb et al. 2020). Along our study gradient from the Amazon to the high-elevation Andes, temperature decreases linearly with elevation while precipitation decreases from mid to higher elevations and becomes more seasonal. Based on these patterns and the climate variability hypothesis, which states that exposure to greater climatic variability favors organisms with broader tolerances (Janzen 1967, Stevens 1989), we should expect that plants in lower/warmer elevations with less exposure to drought are more tolerant to hot temperatures and less tolerant to drought than are plants in higher/colder elevations. Conversely, plants at high elevations should be more drought tolerant but less heat tolerant. This pattern suggests tradeoff between heat and drought tolerances due to large-scale climate gradients. However, at smaller spatial scales, such as within a given elevation, areas that are hotter due to sun exposure or topographic effects will also tend to be drier due to evaporation and increased vapor pressure deficit (Epron et al. 2006, Homeier et al. 2010). Thus, at smaller scales we may expect positive relationships between the heat and drought tolerances of plants. Within species, this positive relationship could be supported by the fact that heat and drought stress both affect membrane fluidity and cell metabolism, meaning that a more stable cell membrane could confer increased tolerances to both forms of stress (Los and Murata 2004).

Unfortunately, we still have little information about how temperature and drought tolerances are associated across either small- or large-scale environmental gradients, limiting our ability to predict how species will respond to climate change. This lack of information is especially severe in the tropics where high diversity and complicated logistics have hindered ecophysiological research. Here, we present one of the first-ever assessment of changes in both leaf traits and climatic tolerances (drought and temperature) along a tropical elevation gradient. Specifically, we investigated functional traits and climatic tolerances of plants distributed across a continuous elevation gradient from 400 to 3600 m a.s.l. in the Andes of south-eastern Peru (including lowland, premontane and montane forest, and puna grassland ecosystems).

To reduce the potential effects of including species from different phylogenetic lineages, we focus on one single lineage of abundant, diverse and ecologically important plants in the study area: bamboos (Fadrique et al. 2020). Woody bamboos (family Poaceae, subfamily Bambusoideae, tribe Bambuseae) are a native and conspicuous element of many forests from the lowland Amazon up to 4000 m a.s.l. in the Andes (Judziewicz et al. 1999). Bamboo species usually occur in narrow elevation belts and thus show high turnover along elevation gradients. This fast elevational replacement makes

bamboo an ideal focal group to study within-taxa variation in functional traits and climatic tolerances. Bamboo species display a variety of habits and life history strategies and they have an important role in community dynamics; for example, in the lowlands, tall canopy *Guadua* species form the bamboo-dominated forests where embedded tree patches show altered regeneration, community composition and dynamics (Griscom and Ashton 2006, Griscom et al. 2007, Fadrique et al. 2021a). In the cloud forest, areas with high density of understory *Chusquea* or *Aulonemia* show different forest structure with lower tree density, basal area and tree regeneration (Veblen 1982, Fadrique et al. 2021b). As opposed to other grasses, bamboos are believed to have evolved in forest ecosystems and use the C3 photosynthetic pathway (Strömberg 2011). In general, they are on the acquisitive end of the leaf economic spectrum, showing lower LMA and higher $N_{mass}$ than surrounding trees and lianas (Asner and Martin 2012, Montti et al. 2014, Supporting information).

We measured leaf functional traits and climatic tolerances of woody bamboos across a > 3 km elevation gradient in the Andes with three aims: 1) to assess the distribution of functional traits of bamboo across the elevation gradient, 2) to determine how climatic tolerances of bamboo vary along environmental (elevation, temperature and precipitation seasonality) gradients and 3) to explore the relationship between heat and drought tolerance at multiple scales to test for a potential tradeoff. Finally, while climatic tolerances can be measured in the field, they require significant investments of effort, time and money. Given that leaf shape and size are related to leaf thermodynamics (Givnish 1988, Knight and Ackerly 2003), and leaf mass, thickness and nitrogen content (as an osmoregulator) are linked to leaf drought tolerance (Abrams et al. 1994, Saneoka et al. 2004), we tested if 4) some of these 'soft' traits can serve as indicators of heat and drought tolerance in the Andean bamboos. If that is the case, we would be better equipped to understand current patterns of species' tolerances and the potential impacts of climate change. Given the consistent relationships between elevation and functional traits observed in many trees and other plant groups (Craine and Lee 2003, Kessler et al. 2007, Dunbar-Co et al. 2009), and the previous findings on bamboo leaf morphology change with elevation (Guo et al. 2018), we predicted bamboos to shift towards more conservative traits (i.e. increased LMA, $N_{area}$ and thickness and decreased leaf area and $N_{mass}$) at higher elevation. We also predicted a negative correlation between the heat and drought tolerances of bamboos across the large-scale elevation gradient, but a positive correlation between heat and drought tolerances both within elevations and within individual bamboo species.

## Material and methods

### Study area

Data collection took place in and around Manu National Park on the eastern slopes of the Peruvian Andes. Most of the data collection was performed along a transect of permanent forest monitoring plots in the Kosñipata Valley that are maintained by the Andean Biodiversity Ecosystem Research Group (ABERG; <www.andesconservation.org>). We focused efforts on seven elevations along this transect (3600, 3400, 3000, 2500, 1700, 1400 and 1000 m a.s.l.) and also included an area in an adjacent valley (Tono valley – 1000 m a.s.l.) (Supporting information). The lowland portion (400 m a.s.l.) of the study was carried out in the Amazonian section of Manu National Park along the Madre de Dios River near the Cocha Cashu Biological Station. Average annual precipitation varies from approximately 5000 mm $year^{-1}$ in the premontane forest to 2000 mm $year^{-1}$ in the higher elevations (Rapp and Silman 2012) and ~2500 mm $year^{-1}$ in the lowest elevations (Terborgh 1990). Mean annual temperature decreases with elevation at an adiabatic lapse rate of approximately 4.3°C $km^{-1}$ from ~25°C at 400 m a.s.l. to 10°C at 3600 m a.s.l. Mean daily maximum temperature of the warmest month decreases from ~32°C at 400 m a.s.l. to ~19°C at 3600 m a.s.l. (WorldClim ver. 2 BioClim5). According to recent research, temperature has increased in the region by 0.03–0.05°C $year^{-1}$ (Feeley et al. 2011) but no local record of precipitation change is available.

### Selection of focal individuals

Field work was conducted in 2016 and 2017 during the local dry season (July–September). In order to capture within-elevation heterogeneity, we selected two or three sites at each focal elevation adjacent to one of the forest monitoring plots. At each site, we searched for woody bamboo species growing in the plot and in the surrounding areas. For each species occurring at a site, we found at least four individuals for sampling (due to processing problems, in a few cases we only measured three individuals of a focal species at a given elevation: *Chusquea intipaqariy* at 3600 m a.s.l., *Chusquea scandens* at 3400 m a.s.l., *Chusquea aff. inamoena* at 2400 m a.s.l. and *Guadua sp6* at 1400 m a.s.l.). We grouped the individuals into 'populations' defined as conspecific individuals occurring at a single elevation belt. All species had narrow elevation ranges, leading to one or two populations per species. Sampling elevations, number of sites, individuals and species are tabulated in the Supporting information

Given the extreme difficulties in determining whether bamboo stems are connected underground by their rhizomes, we only sampled conspecific culms separated by ≥ 15 m (hereafter referred to as 'individuals'). The selected individuals were mature (leaves expanded across the culm), with no sign of being broken or diseased, and were located under a canopy cover typical for their species (for example, semi-exposed individuals for the cloud forest scandent species or exposed individuals for puna short-stature species). We visually estimated percentage of canopy exposure (i.e. % of sky that was unobstructed by overtopping leaves or branches) in half of the individuals (n = 119) and we found a non-linear relationship between average canopy exposure and elevation, such that the bamboo populations occurring below the cloud base or in the puna were more exposed than the

cloud-forest populations, which typically inhabit the understory (Supporting information). The latitude and longitude coordinates for each sampled individual were recorded with a handheld GPS.

### Leaf functional traits

For each bamboo individual, ~30 green, fully expanded and mature leaves (5 for traits and 25 for climatic tolerances measurements) with no signs of disease, infection or herbivory were collected from the upper third of the culm (but below the tip section) and placed with moist paper towels inside a closed plastic bag until processing (usually leaves were processed within 4 h of collection and in no case were leaves held > 12 h before processing).

Trait measurements followed the protocols established in Baraloto et al. (2010) and Perez-Harguindeguy et al. (2013). First, we scanned each of the five leaves (after cutting their pseudopetioles) with a portable scanner to obtain leaf area ($cm^2$). We then took measurements of leaf thickness (mm) near the leaf bottom, middle and tip using a micrometer and avoiding midveins. After measurements, each leaf was placed in a labeled paper envelope and buried in silica gel and/or placed in a drying oven until dry. The dried leaf was then weighed for leaf mass (g) and leaf mass area (LMA) (g $m^{-2}$) was calculated as the ratio of leaf mass (dry) to fresh leaf area. For the nutrient analysis, we ground and mixed pieces from the same five leaves to obtain one homogenous sample per individual. We performed the nutrient analyses at the University of Miami's Laboratory of Stable Isotope Ecology of Tropical Ecosystems (LSIETE, Coral Gables, FL, USA) using an automated elemental analyzer to obtain percentage of nitrogen per mass ($N_{mass}$) (%). The values from $N_{mass}$ were converted to nitrogen per leaf area ($N_{area}$) (g $cm^{-2}$) by relating the percentage to leaf mass and then to LMA.

### Climatic tolerances

We calculated cell membrane stability (CMS) for each individual as a metric of relative drought tolerance (Blum and Ebercon 1981, Premachandra and Shimada 1987, Bajji et al. 2002). Cell membrane stability was measured by submerging leaf pieces in a hyperosmotic solution (50% polyethylene glycol 3500; PEG) that creates an extreme osmotic stress (~ −8 MPa) and measuring the subsequent cell damage based on the percentage of solute leakage. Increased osmotic stress creates membrane dysfunction and increases cell permeability leading to a high efflux of electrolytes to the solution. The osmotic pressure that leaves were exposed to in this experiment was more extreme (more negative) than what occurs during natural drought events. In other words, our measurements were not intended to quantify the response of plants to a simulated drought; rather, we employed this method as a rapid assessment of individuals' relative leaf membrane stability – a factor that may be associated to relative drought tolerance.

To measure relative membrane stability, four sets of three '½' circular leaf pieces each were prepared per individual. One leaf set was placed in distilled water (20 ml) (control) and three leaf sets were submerged in PEG solution (20 ml). After 12 h, the leaf pieces were washed and placed into distilled water (20 ml) for 12 h for solute leakage induction. Conductivity was measured at the beginning (Ci) and end (C1) of this induction period with a conductimeter. Finally, leaf pieces were placed in closed Falcon tubes in a boiling water bath for 30 min in order to fully lyse the membranes and extract all solutes. Twelve hours after boiling, final conductivity was measured (C2) and the final CMS index was calculated as:

$$\mathrm{CMS} = 100 - \left(\left(\left(\mathrm{C1} - \mathrm{Ci}\right) / \left(\mathrm{C2} - \mathrm{Ci}\right)\right) \times 100\right) \quad (1)$$

The CMS per individual was calculated as the mean of the CMS values for the three replicate treatment sets. Higher CMS values represent more stable membranes and therefore higher resistance against drought-induced cell damage.

We estimated heat tolerance (T50) for each individual using a modification of the protocol described in Krause et al. (2010). T50 is determined by measuring leaf fluorescence (Fv/Fm) in leaf samples exposed to different temperature treatments. For each individual, we first estimated the pre-treatment status of five leaves by measuring their initial fluorescence emission (Fo) and maximum total fluorescence (Fm) using an OS30p+ handheld fluorometer after 15 min of dark adaptation. Fv/Fm was then calculated as the ratio of maximum variable to maximum total fluorescence (Fv = Fm − Fo). Then, three 0.5 inch diameter circular leaf pieces were placed in individual Miracloth fabric pouches (three layers of fabric on the abaxial side and one on the adaxial side; to prevent anaerobiosis) and inserted into waterproof plastic bags. Each of these bags was submerged for 15 min in one of ten pre-heated circulating water baths maintained at set experimental temperatures. The experimental gradient included ambient 'room temperature' and a range of nine temperatures from 40 to 60°C with an increased concentration of temperatures appropriate to each sampling elevation (i.e. more temperature treatments between 40 and 50°C for samples collected from higher elevations, and more treatments between 46 and 56°C for samples collected from the lowlands). The temperature gradients were established based on preliminary tests to determine the approximate temperature treatment that caused the dead of the leaf pieces. After 15 min of treatment, all leaf disks were taken out and placed in petri dishes with moist paper towels for 24 h, to allow for recovery.

For the final measurement, each leaf disk was dark-adapted for 15 min and then Fv/Fm was measured. Fv/Fm of a healthy leaf is typically ~0.8 (Demming and Björkman 1987); as heat stress increases, photosystem damage (caused by increased fluidity of the thylakoid membranes) leads to higher fluorescence and reduces the Fv/Fm ratio. Using a logistic non-linear least squares model with the *nls* function in R (<www.r-project.org>), we modeled the relationship of Fv/Fm versus treatment temperature for each individual. The experimental temperature that caused a 50% reduction in

Fv/Fm compared to the initial value was then set as the individual's T50. We resampled the Fv/Fm versus temperature data within each individual (with replacement) and recalculated the corresponding T50; this process was reiterated 1000 times to generate bootstrapped estimates of the mean T50 with 95% confidence intervals for each individual.

### Environmental variables

The elevation for each collection site was estimated based on the recorded coordinates and the Shuttle Radar Topography Mission (SRTM) 1 ArcSec Global V3 (<https://lta.cr.usgs.gov>) 30 m-resolution digital elevation model (DEM). Mean annual temperature (MAT), precipitation seasonality (coefficient of variation in monthly precipitation values – higher seasonality values indicate greater relative changes in precipitation within a year) and maximum temperature of the warmest month at each collection point were estimated based on the coordinates and the WorldClim ver. 2 (30 arcsec resolution ~1 km at study area, 1970–2000) Bioclim1, Bioclim15, Bioclim5 variables respectively (Fick and Hijmans 2017) (Supporting information). Annual Precipitation was estimated using a polynomial regression to extrapolate ground data obtained from high precision gauges installed at 3600, 2750, 2100, 1700 and 500 m a.s.l. in the study area by the ABERG group during 2012 and 2013 (Silman, unpubl.) (Supporting information).

### Analysis

#### *Bamboo leaf functional trait distribution along the elevation gradient*

First, we calculated population (species × elevation) averages for the leaf traits. We performed linear regressions between the mean population values for each of the leaf traits and the mean sample elevations. All populations (n = 28) had data for all traits except *Chusquea sp5_L* which was not processed for nutrient analysis and therefore lacks $N_{mass}$ and $N_{area}$ values. To identify potential phylogenetic effects, we also performed the same regressions separately for only the populations of the bamboo genus *Chusquea*.

#### *Climatic tolerances variation with environmental gradients*

To investigate elevational and climatic patterns of drought and heat tolerance, we performed linear regressions between population averages of CMS and the populations' mean 1) elevation, 2) precipitation seasonality and 3) annual precipitation. Similarly, we performed linear regressions between the populations' mean T50 values and their mean 1) elevation and 2) MAT. In addition, we calculated an approximation to the safety margin as the difference between the population's mean maximum temperature of the warmest month (WorldClim) and its mean T50. Finally, in order to identify a potential tradeoff between the two climatic tolerances, we investigated the relationship between T50 and CMS at the population level using a Pearson correlation. As above, we also performed the same analysis for only the populations of the bamboo genus *Chusquea*.

In order to explore the relationship between heat and drought tolerances at other spatial and ecological scales, we first performed Pearson correlations using all combined individual values (n = 159) and another one using the species' mean values (n = 22). Then, for each species with ≥ 5 individuals (n = 16), we performed independent correlations of the individual-level heat and drought tolerances. Finally, we aggregated the individuals co-occurring within elevation belts (n = 8) and performed separate correlations of the individual-level heat and drought tolerances.

#### *Relationships between climatic tolerances and leaf traits*

With the aim of testing whether soft leaf traits can serve as proxies of climatic tolerances, we explored the relationships between T50 and CMS and the leaf functional traits. Given the low number of observations and the inherent correlations between several of the leaf traits, we used a partial least square regression (PLSR) approach. We performed a PLSR analysis for each climatic tolerance (T50 and CMS) using $N_{area}$, leaf area, thickness, LMA, $N_{mass}$ and leaf mass as predictors. For each of the two climatic tolerances, we selected the leaf traits that had higher loads on the first and second components while being minimally correlated with each other. Then, we combined the selected leaf traits in a linear model to predict the climatic tolerances and examined the significance of each predictor. Finally, to assess the relative contribution of soft traits in predicting climatic tolerances, we combined the selected soft traits and the climatic variables (MAT for T50, and annual precipitation and precipitation seasonality for CMS) in the same model and performed a stepwise model selection process to obtain the 'best' model based on the AIC criterion.

## Results

### Bamboo species

We found 22 bamboo species in the study area which belonged to four genera, *Aulonemia*, *Chusquea*, *Guadua* and *Elytrostachys*. Only six species occurred at more than one elevation: *Guadua sp6* at 1000–1400 m a.s.l., *Chusquea sp22* and *Chusquea sp5* at 1400–1700 m a.s.l., *Aulonemia sp9* at 1700–2400 m a.s.l., *Chusquea aff.inamoena* at 2400–3000 m a.s.l. and *Chusquea scandens* at 3400–3600 m a.s.l. (Supporting information). Of the 22 species, eight were identified with the help of a taxonomical expert (Dr Lynn Clark, ISU) and two new species have been described based on the collections (Fadrique et al. 2019); twelve distinct morphospecies remain unidentified or undescribed but were included in the analyses. Based on the species occurrences at different elevations, we defined 28 populations of bamboo.

### Bamboo leaf functional trait distribution along the elevation gradient

The population means of $N_{mass}$ (slope = $1.4 \times 10^{-4}$; Adj. $R^2 = 0.13$, $p < 0.05$) and $N_{area}$ (slope = $1.7 \times 10^{-4}$; Adj. $R^2 = 0.15$, $p < 0.05$) increased with elevation, while leaf area

(slope = −0.01; Adj.$R^2$ = 0.13, $p < 0.05$) decreased with elevation (Fig. 1). We found a slightly positive but non-significant relationship between LMA (slope = 0.005; Adj.$R^2$ = 0.06, p = 0.11) and elevation. Leaf mass (slope = $-4.4 \times 10^{-5}$; Adj. $R^2$ = 0.08, p = 0.08) and leaf thickness (slope = $-5.7 \times 10^{-6}$; Adj.$R^2$ = −0.02, p = 0.456) also had non-significant relationships with elevation (Supporting information). When the subset of species in the genus *Chusquea* were analyzed separately, LMA (slope = 0.012; Adj.$R^2$ = 0.18, $p < 0.05$) and $N_{area}$ (slope = $3.7 \times 10^{-4}$; Adj.$R^2$ = 0.31, $p < 0.01$) increased with elevation while no significant effect of elevation was found for any of the other traits.

## Climatic tolerances variation with environmental gradients

The cell membrane stability (CMS) – our metric of relative drought tolerance – spanned almost the entire range of possible values, from 92.8% at high elevations to 15.7% at low elevations (high values are indicative of greater membrane stability and greater drought tolerance). CMS increased with elevation (slope = 0.017; Adj.$R^2$ = 0.65; $p < 0.001$), indicating that high-elevation bamboos are more tolerant of drought than low-elevation bamboos (Fig. 2a). There was also a strong positive relationship between CMS and precipitation seasonality (slope = 1.80; Adj.$R^2$ = 0.64; $p < 0.001$) indicating that bamboos in the more-seasonal areas are more tolerant of drought stress (Fig. 2b) than are bamboos in relatively aseasonal areas. Both relationships were equally strong when *Chusquea* populations were analyzed independently (elevation: slope = 0.016; Adj.$R^2$ = 0.48; $p < 0.001$ and precipitation seasonality: slope = 1.47; Adj.$R^2$ = 0.68; $p < 0.001$). CMS was not significantly related to annual precipitation (slope = −0.004; Adj.$R^2$ = 0.04; p = 0.15); however, for *Chusquea* populations there was a significant negative relationship with annual precipitation (slope = −0.008; Adj. $R^2$ = 0.35; $p < 0.01$) (Supporting information).

The T50 – our metric of heat tolerance – spanned from 44.4 to 52.7°C (higher temperatures indicate greater heat tolerance). T50 was negatively related to elevation (slope = −0.002; Adj.$R^2$ = 0.61; $p < 0.001$) and was positively related to mean annual temperature (MAT) (slope = 0.353; Adj.$R^2$ = 0.6; $p < 0.001$) (Fig. 2c, d) such that bamboos in the colder, higher elevations had lower T50 than the bamboos in the warmer, lower elevations. Both relationships were equally strong when *Chusquea* populations were analyzed

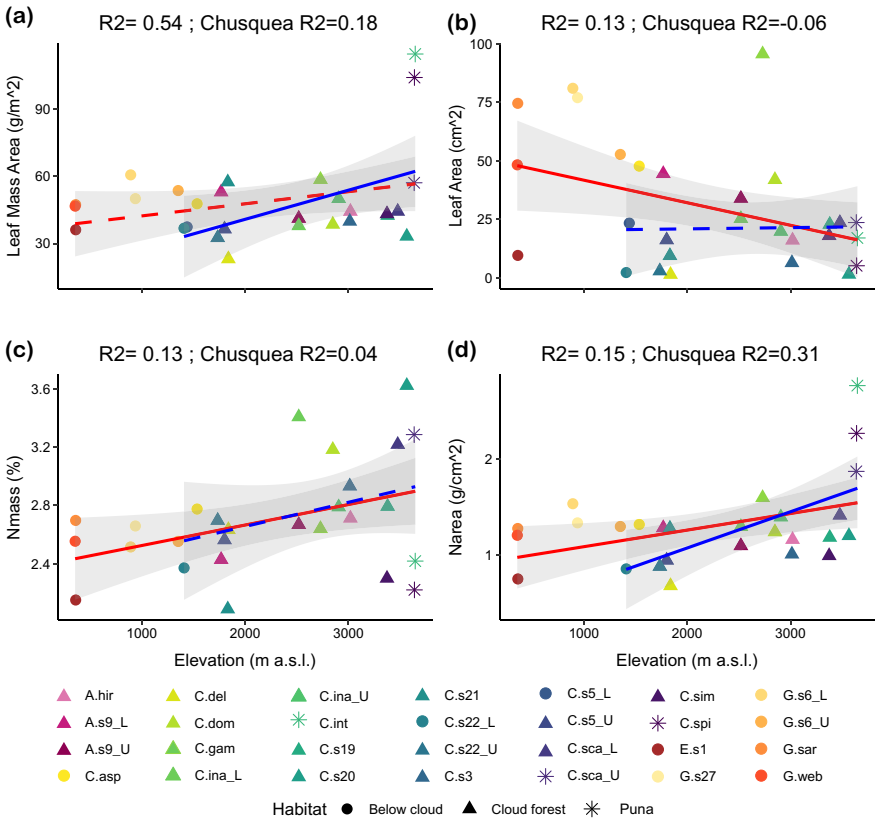


Figure 1. Relationship between population mean elevation and population averages of (a) leaf mass area (g $m^{-2}$) (b) leaf area ($cm^2$) (c) $N_{mass}$ (%) (d) $N_{area}$ (g $cm^{-2}$). Colors indicate populations, which correspond to unique combinations of species and elevation belts. Significant relationships ($p \leq 0.05$) are shown with solid lines and non-significant relations with dashed lines. Red line represents the entire dataset and blue line represents only the species in the genus *Chusquea*. Shade ribbons are 95% confidence intervals around the predicted relationship. Shapes represent the three habitats. For species identity in reference to legend codes see Supporting information.

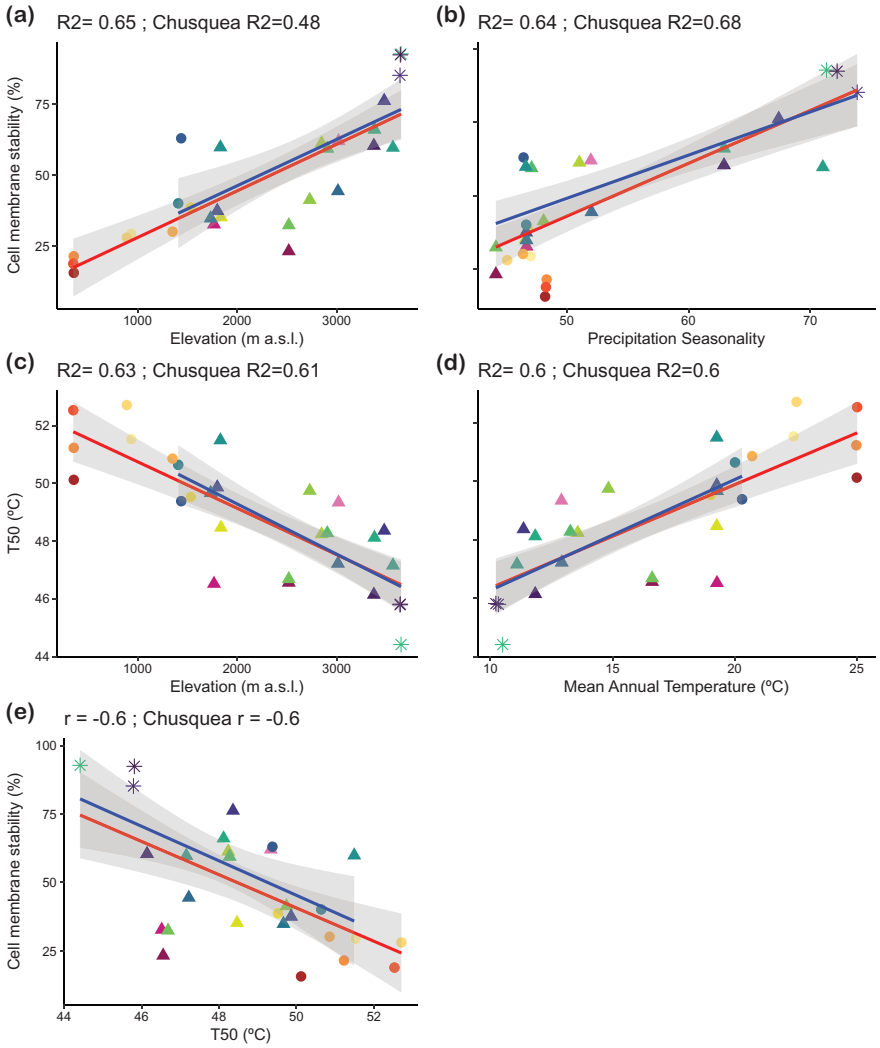


Figure 2. Relationship between population mean cell membrane stability (%) (a, b) or T50 (°C) (c, d) with mean population elevation (a, c), precipitation seasonality (b) and mean annual temperature (d), and between population means of T50 (°C) and cell membrane stability (%) (e). Colors indicate populations, which correspond to unique combinations of species and elevation belts. Shapes represent the three habitats. Color and shape legend can be found on Fig. 1. Significant relationships ($p \leq 0.05$) are shown with solid lines and non-significant relations with dashed lines. Red line represents the entire dataset and the blue line represents only the species in the genus *Chusquea*. Shade ribbons represent 95% confidence intervals around the predicted relationship.

separately (elevation: slope = −0.002; Adj.$R^2$ = 0.61; $p < 0.001$ and MAT: slope = 0.378; Adj.$R^2$ = 0.6; $p < 0.001$). MAT and maximum temperature of the warmest month declined at similar rates along the elevation gradient (0.432 and 0.407°C per 100 m respectively). However, the rate of T50 decline was slower (0.160°C per 100 m), leading to an increasing difference between climatological temperature and leaf temperature tolerances (= thermal safety margin) at higher elevations (Supporting information).

Population means of T50 and CMS were negatively correlated to each other (Pearson; r = −0.60; $p < 0.01$ for both the whole set and for just the *Chusquea* spp.). This tolerance gradient coincided with the elevation gradient. In other words, low-elevation bamboos showed higher T50 and lower CMS values than did high-elevation bamboos, which tended to have high CMS and low T50 values (Fig. 2e). The relationships between tolerances for the combined individual values (Pearson; r = −0.49; $p < 0.0001$) and for the species means (Pearson; r = −0.69; $p < 0.001$) (Fig. 3a) were both negative and significant. Within species, only *Chusquea s22* showed a negative significant relationship (Pearson; r = −0.49; $p < 0.05$) while relationships for other species were not significant (Fig. 3b). Within elevation belts, there were two positive significant relationships at 3400 (Pearson; r = 0.58; $p < 0.01$) and 400 m a.s.l. (Pearson; r = 0.52; $p < 0.05$), the other elevations belts showed non-significant relationships (Fig. 3c).

### Relationships between climatic tolerances and leaf traits

The first component of the partial least square regression (PLSR) (Fig. 4) explained 64% of the variation in CMS and 51% of the variation in T50. The leaf traits with higher loads in the first PLSR component were $N_{area}$ and LMA (highly correlated with each other) for CMS and leaf mass and leaf area (highly correlated with each other) for T50. For CMS, the second component, with much lower explanatory power (6%) had the highest loads from leaf mass, leaf area (highly correlated with each other) and leaf thickness. For T50 the second component explained 2% of the variation and was mainly influenced by $N_{area}$. Based on these results, $N_{area}$, leaf area and leaf thickness were included as predictors of CMS in a linear model analysis (Adj.$R^2 = 0.69$). The overall model was significant ($p < 0.001$) as well as the $N_{area}$ ($p < 0.001$) and leaf area ($p < 0.01$) parameters (Supporting information). For T50, leaf area and $N_{area}$ were included as predictors in the linear model analysis (Adj.$R^2 = 0.40$). The overall model was significant ($p < 0.001$) as well as the $N_{area}$ ($p < 0.01$) and leaf area ($p < 0.01$) parameters (Supporting information).

To assess the relative contribution of soft traits in predicting CMS and T50, we performed separate stepwise model selection processes that started with the complete model including climate (annual precipitation and precipitation seasonality for CMS and MAT for T50) and traits ($N_{area}$, leaf area and thickness for CMS and $N_{area}$, leaf area for T50). The selected CMS model (Adj.$R^2 = 0.77$, $p < 0.001$) retained just precipitation seasonality, $N_{area}$ and leaf area as predictors (Supporting information). The selected T50 model (Adj. $R^2 = 0.60$, $p < 0.001$) retained only MAT as a predictor (Supporting information). The results of the model selection did not vary significantly if the interaction between leaf area and $N_{area}$ was included in the complete model.

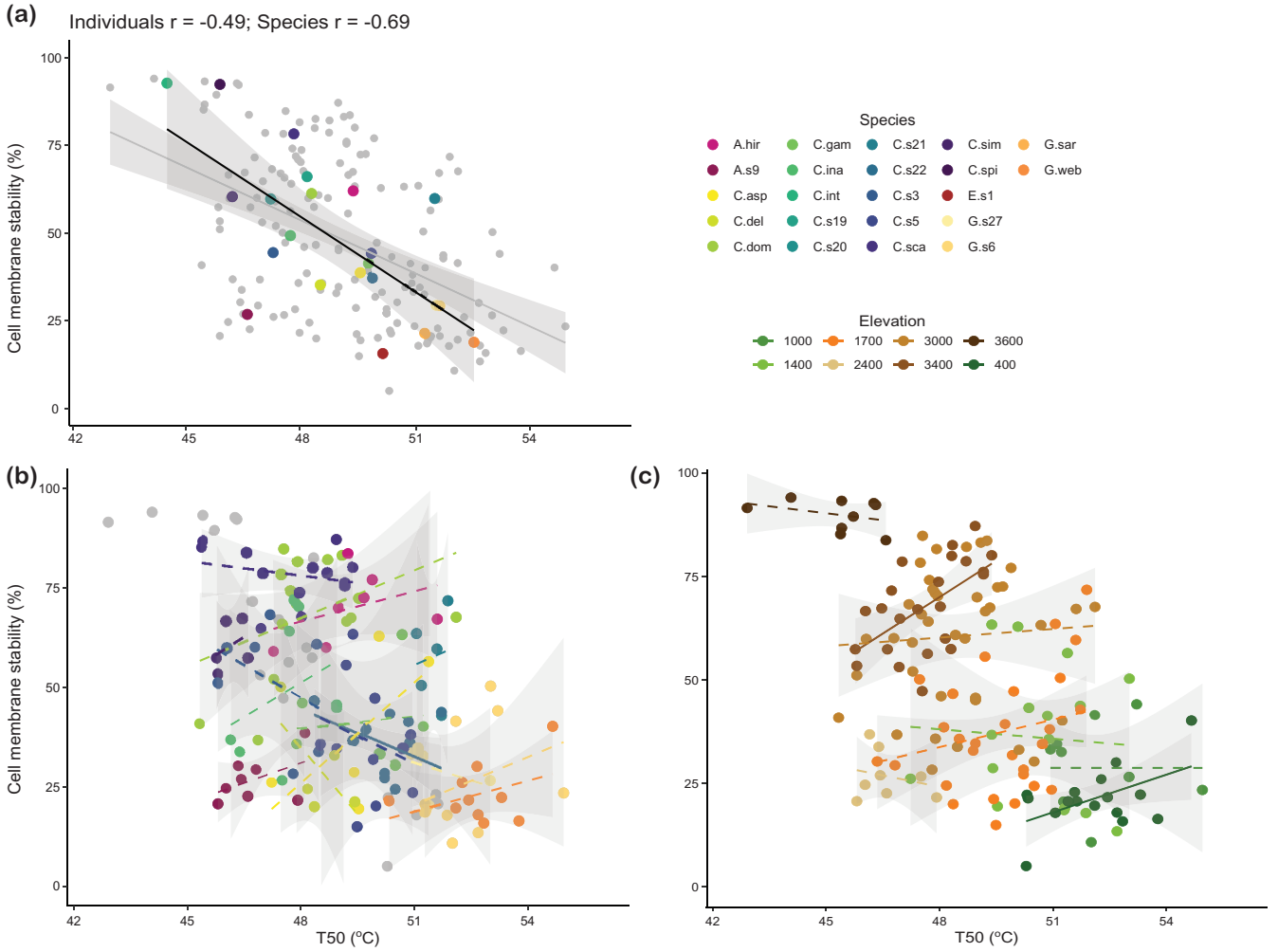


Figure 3. Relationship between cell membrane stability (%) and T50 (°C) for (a) all individuals combined (grey points and line), and species means (coloured points and black line), (b) individuals within species (species with ≥ 5 individuals), (c) individuals within elevation belts. Significant relationships ($p \leq 0.05$) are shown with solid lines and non-significant relations with dashed lines. Shade ribbons are 95% confidence intervals around the predicted relationship.

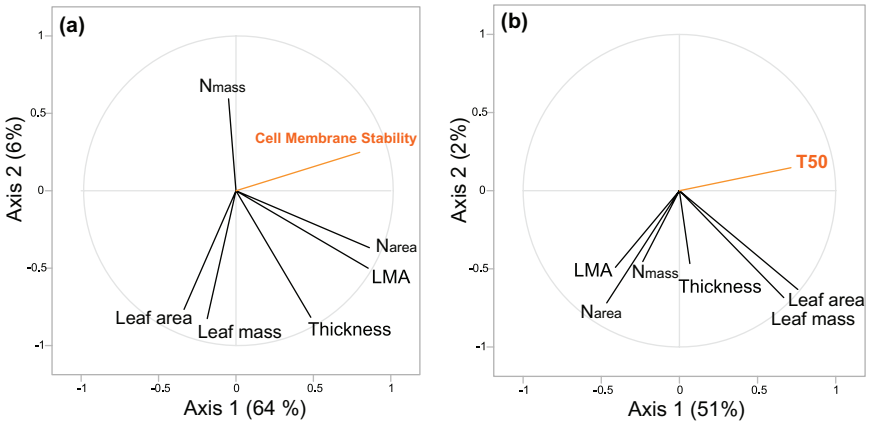


Figure 4. Results from the partial least squared regression for (a) cell membrane stability and (b) T50. Axis explanatory power is shown in brackets.

## Discussion

Our study provides a novel assessment of both leaf functional traits and climatic tolerances (to heat and to drought) along a 3 km tropical elevation gradient. Overall, our results suggest that 1) bamboos are functionally distinct from other plant taxa and do not show the same trait pattern of gradually becoming more conservative with elevation as previously reported for trees or other plant groups; however, 2) heat and drought tolerances do follow similar patterns to those identified in trees and vary strongly along our study gradient. Heat and drought tolerances are negatively correlated across the gradient but 3) this negative relationship does not hold within species or elevation belts, contrasting expectations from a mechanistic tradeoff and likely related to the functional distinctiveness of bamboos. Finally, we show that for bamboos 4) 'soft' functional traits are poor predictors of climatic tolerances. Despite some ecophysiological differences can exist among bamboo species (Saha et al. 2009, Montti et al. 2014, Ely et al. 2019), working with a single plant lineage allowed us to control for phylogenetic effects and thus focus on the ecology of functional trait variation. While bamboo species were well suited for this study, it should be noted that they do have their peculiarities (e.g. clonal growth, lack of secondary growth, monocarpic flowering), divergent ecology and life histories that can influence their physiology and lead to patterns that may be distinct from what would occur in other taxonomic groups.

### Bamboo leaf functional trait distribution across the elevation gradient

The elevational patterns of $N_{mass}$, LMA and most of the other leaf traits in bamboo populations do not fully match the a priori expectations based on previous results reported for trees. Similar results were obtained for some leaf traits of *Pleioblastus amarus* bamboo along a 600 m elevation gradient in China (Guo et al. 2018). General predictions and specific studies of dominant trees along this elevation gradient indicate that as conditions become harsher at higher elevations, greater structural investment is needed and conservative strategies become more common, resulting in a decrease in leaf area and $N_{mass}$, and an increase in LMA, thickness and $N_{area}$ with elevation (Moser et al. 2007, van de Weg et al. 2009, Read et al. 2014, Fyllas et al. 2017). Yet, the increase in LMA with elevation in bamboo populations is weak and only significant within the *Chusquea* genus, and the slight decrease in leaf area is associated with the transition from *Guadua* spp. at lower elevations to *Chusquea* spp. at higher elevations. In accord with the limited elevational change in LMA and thickness, bamboos showed a significant increase in both $N_{mass}$ and $N_{area}$ with elevation. Despite the lack of strong trends, we note that the highland puna populations (above the treeline) do show comparatively higher LMA, $N_{area}$ and leaf thickness than the lowland populations (Poorter et al. 2009).

These weak and sometimes unexpected relationships between traits and elevation indicate that bamboos exhibit an overall acquisitive strategy throughout the gradient, despite the possible limitations imposed by stress and limiting resources (temperature, moisture, light, nutrients) at different elevations. We hypothesize that the extensive rhizome networks of bamboos allow them to exploit the water and nutrients available in multiple microenvironments at the different elevations, to store them (in rhizome or culms), and/or to translocate them to culms in resource-limited areas (Kleinhenz and Midmore 2001, Fang et al. 2019), thereby providing bamboos with a potential buffer against microclimatic environmental conditions. This process of physiological integration has been suggested to allow for successful growth of bamboo clones under different light environments (Yang et al. 2014). This process, or indeed its absence, could explain why puna bamboo populations, which form small short-statured clumps, have distinctive leaf traits, even when compared to the populations occurring in adjacent forests at just slightly lower elevations (3400 m a.s.l.) (Ely et al. 2011). We hypothesize that the smaller size and the clumping growth pattern of these species reduce their ability to take advantage of the resources available from different microenvironments. This constraint would eliminate any potential buffer and increase their exposure to the harsh high-elevation conditions

including high UV levels, strong winds, low temperature and higher precipitation seasonality. The combination of harsher conditions and a reduced buffer may contribute to the puna bamboo populations exhibiting more conservative traits such as relatively high LMA and small thick leaves.

## Climatic tolerances variation with environmental gradients

Drought tolerance of bamboo populations is positively related with elevation and with precipitation seasonality. This pattern concurs with the climate variability hypothesis (Janzen 1967, Stevens 1989). In our case, the larger intra-annual differences in precipitation found at higher elevations may increase the plants' exposure to seasonal drought and could therefore favor the development of greater drought tolerance. In contrast, lower elevations are less seasonal and thus plants are less likely to experience drought stress, thereby limiting the advantage to species with adaptations for tolerating drought conditions.

Although precipitation seasonality was the best predictor of CMS, there are multiple factors in tropical mountain forests (e.g. precipitation, slope, aspect, relative humidity, cloud cover, exposure, etc.) whose contribution to local water availability and thus, to leaf drought tolerance, remains poorly understood. While precipitation seasonality, extracted from a global climate dataset, may not represent the actual water availability at sample locations, it is a reasonable proxy for the variability experienced by the different populations. The values of precipitation seasonality within our study gradient only represent a small part of the potential variability of precipitation seasonality, with a moderately uniform annual rainfall up to ~2500 m and an increasing variability towards the higher elevations. Future studies along stronger and broader climatic gradients (including larger ranges of precipitation seasonality) will provide further insight into the relationship between climatic variability and drought tolerance.

Thermal tolerances of bamboos decrease with elevation as air temperatures get colder. In other words, low-elevation species experience higher air temperatures and are more heat-tolerant than the high-elevation species that normally experience colder temperatures. This positive relationship between leaf heat tolerance and air temperature was expected and has been previously shown for trees along an elevational gradients in Colombia and Panama using the same heat tolerance method (Feeley et al. 2020, Slot et al. 2021). A similar relationship was also found along the global latitudinal gradient for a broad range of plant species but using different measures of heat tolerance (O'sullivan et al. 2017). From the Equator to the Artic, heat tolerance decreased by more than 8°C over a > 20°C range of maximum air temperature (O'sullivan et al. 2017). In our study, bamboo heat tolerances varied by more than 8°C (44.4–52.7°C) over a 15°C mean temperature range. This comparison stresses the exceptional functional diversity of tropical montane plants and the invaluable potential that elevation gradients have for informing our understanding of macro-ecological patterns and phenomena.

A potentially valuable indicator of plants' vulnerability to global warming is their thermal safety margin (difference between heat tolerance and hottest temperatures experienced by a plant). We calculated an approximation to the thermal safety margin as the difference between the maximum temperature of the warmest month (MTWM) at a plant's location (extracted from WorldClim) and its T50. Based on this metric, low-elevation bamboos appear to have narrower safety margins and may be operating closer to their thermal limits than are high-elevation bamboos. A similar pattern was found for lowland forests in Panama which shown a narrower safety margin than pre-montane forests (Slot et al. 2021). Also in agreement with our results, a study of high-elevation paramo plant species in Colombia showed broad safety margins and reduced thermal stress in these alpine plants (Leon-Garcia and Lasso 2019). However, it is worth noting that in our study, the relatively coarse resolution of the MTWM data (30 arcseconds ~1 km) in relation to the steep slopes in our study area may lead to imprecision on the estimated temperatures for individual plants. Even at low elevations, bamboo T50 values exceed maximum temperatures by more than 20°C; however, leaf temperatures can be markedly hotter than air temperatures (Still et al. 2019), especially when leaves are exposed to direct sun. Therefore, it is reasonable to assume that low-elevation bamboo species, with high heat tolerances but narrower safety margins, may be more vulnerable to extreme temperatures than higher-elevation species (Perez and Feeley 2020).

### *Climatic tolerance tradeoff*

At large scales (i.e. across the entire study gradient), our results show that leaf thermal and drought tolerances are negatively correlated in bamboo populations. High-elevation bamboos are relatively drought tolerant (i.e. have higher cell membrane stability; CMS) but have low heat tolerances (lower T50); in contrast, low-elevation bamboos have higher thermal tolerances but lower drought tolerances. Nevertheless, when the relationship between heat and drought tolerances was evaluated for individuals within species or within elevation belts, we found no consistent results. Only one species showed a significant correlation indicating a negative relationship, and two elevation belts (400 and 3400 m a.s.l.) showed significant positive correlations. These contrasting results indicate that the large-scale negative relationship may be driven by the distribution of environmental conditions along the elevation gradient (hot temperatures and wet aseasonal conditions in the lowlands versus cold temperatures and seasonal precipitation in the highlands) and the consequent species replacement, rather than a tradeoff in the physiological mechanisms underlying heat and drought tolerances. We expected a positive correlation between the tolerances within species due to the important role that cell membrane stability can play in both cases; however, our results suggest that many other processes may be acting simultaneously to regulate the leaf-level climatic tolerances. For example, enzyme composition, or heat shock proteins can alter leaf heat tolerances (Wahid et al. 2007). Similarly,

plants can survive droughts by using different mechanisms for drought avoidance, drought delay and drought tolerance (Poorter and Markesteijn 2008). Indeed, at the organismal level, many bamboos have embolism-refilling capabilities via positive nocturnal root pressure that provides water recharge to cope with water deficit (Cochard et al. 1994, Saha et al. 2009, Wang et al. 2011, Yang et al. 2012, Zhao et al. 2017), minimizing the tradeoff between hydraulic conductivity and vulnerability to cavitation, which constrains many other fast-growing species. Finally, these cellular mechanisms may also be related to other physiological processes that we are not taking into account. For example, freezing avoidance on high elevation bamboos is usually achieved via supercooling (Ely et al. 2014, 2019). Supercooling can create cell dehydration which can lead to freezing damage (Pearce 2001). Leaf mechanisms that increase drought tolerance in high elevation bamboos are also linked to freezing tolerance (Ely et al. 2014) thus our results for puna species, showing high drought tolerance, may be influenced by simultaneous adaptations by these species for high tolerance to freezing.

### Relationships between climatic tolerances and leaf traits

Using the 'soft' functional traits measured in this study, we could not accurately estimate climatic tolerances. Prediction of hard traits from soft traits was also limited and complex when leaf area was used to evaluate plant's physiological response to drought along a soil moisture gradient (Belluau and Shipley 2018). Our results showed that the combination of leaf functional traits explained just 40 and 69% of the variation in heat and drought tolerances, respectively. Leaf nitrogen per area and leaf area were the two traits that explained most variation without being correlated among themselves (Ely et al. 2011). Leaf area is tightly related to the thermodynamics of a leaf such that larger leaves generally reach higher temperatures than smaller leaves and thus can generally tolerate higher temperatures (Knight and Ackerly 2003, Perez and Feeley 2020, Slot et al. 2021). Leaf nitrogen content has been related to drought tolerance given its osmoregulatory properties (Abrams et al. 1994, Saneoka et al. 2004); however, nitrogen availability has also been linked to large-scale climatic and edaphic gradients (Messier et al. 2017) making it difficult to discern its actual role in this process.

When functional traits were combined with the climate variables, the selection process left MAT as the only significant predictor of T50, explaining 60% of the variability. Similar to our results, MTWM and elevation plus latitude were O'Sullivan et al.'s best predictors of thermal tolerances along the global latitudinal gradient and the inclusion of leaf traits did not improve their models (O'sullivan et al. 2017). In the case of CMS, our model selected a combination of Precipitation Seasonality, leaf area and leaf $N_{area}$ as the best predictors, explaining a total 77% of the variability in drought tolerance. Here again, climate (in this case precipitation seasonality) was the single best predictor. In summary, at least in the case of bamboos, the mean annual temperature and precipitation seasonality where plants grow are better predictors of heat and drought tolerance than are the plant's leaf functional traits.

The limited potential of leaf traits to predict climatic tolerances is underpinned by the weak relationship between leaf traits and elevation, contrasting with the strong relationship between climatic traits and elevation. Bamboos may have physiological adaptations such as clonal growth and physiological integration, that allow them to display sub-optimal leaf trait combinations buffered from the environmental conditions. However, heat and drought tolerances seem to be directly related with climate. Therefore, leaf trait plasticity may not have direct consequences on leaf heat and drought tolerance, limiting the potential solutions for plants to deal with climate change. Despite the strong local climate-tolerance relationship, field measurements of heat and drought tolerance are still necessary to better understand the driving mechanisms and the relationship between them; however, the potential use of leaf traits to estimate these tolerances is not supported by our data. Repeated measurements to characterize the inter and intra-seasonal variability in leaf traits and tolerances, which could be a potential confounding effect in this study, would complement our findings and provide a more holistic insight into plant function. Finally, better characterization of climate, and especially microclimate, will be crucial to improve our understanding of plant–climate relationships and predictions on climate change responses and consequences.

The widespread use of leaf traits to understand plant distributions and responses to climate change is biased towards simple-to-measure traits in dominant tree species. Our results broaden the perspective of functional ecology by showing how an alternative group of plants exhibit a strategy that deviates from these predictions and by highlighting the potential limitations of using 'soft' traits to understand plant distributions and climatic tolerances.

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### Author contributions

**Belen Fadrique**: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Chris Baraloto**: Funding acquisition

(supporting); Methodology (supporting); Supervision (supporting); Visualization (supporting); Writing – review and editing (supporting). **Catherine H. Bravo-Avila**: Data curation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Kenneth J. Feeley**: Conceptualization (supporting); Funding acquisition (lead); Methodology (supporting); Supervision (lead); Writing – review and editing (supporting).

### Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cc2fqz68n> (Fadrique et al. 2022).

### Supporting information

The Supporting information associated with this article is available with the online version.

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