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Thermal niche traits of high alpine plant species and communities across the tropical Andes and their vulnerability to global warming

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Abstract

Aim: The climate variability hypothesis (CVH) predicts that locations with reduced seasonal temperature variation select for species with narrower thermal ranges. Here we (a) test the CVH by assessing the effect of latitude and elevation on the thermal ranges of Andean vascular plant species and communities, and (b) assess tropical alpine plants vulnerability to warming based on their thermal traits.

*Carolina Tovar and Francisco Cuesta contributed equally to this study.

Location: High tropical Andes.

Taxon: Vascular plants.

Methods: Temperature data for 505 vascular plant species from alpine communities on 49 summits, were extracted from 29,627 georeferenced occurrences. Species thermal niche traits (TNTs) were estimated using bootstrapping for: minimum temperature, optimum (mean) temperature and breadth (maximum-minimum). Plant community-weighted scores were estimated using the TNTs of their constituent species. CVH was tested for species, biogeographical species groups and communities. Vulnerability to global warming was assessed for species, biogeographical species groups and communities.

Results: Species restricted to the equator showed narrower thermal niche breadth than species whose ranges stretch far from the equator, however, no difference in niche breadth was found across summits' elevation. Biogeographical species groups distributed close to the equator and restricted to alpine regions showed narrower niche breadth than those with broader ranges. Community-weighted scores of thermal niche breadth were positively related to distance from equator but not to elevation. Based on their TNTs, species restricted to equatorial latitudes and plant communities dominated by these species were identified as the most vulnerable to the projected 1.5°C warming, due to a potentially higher risk of losing thermal niche space.

Main conclusions: Our study confirms that the CVH applies to high tropical Andean plant species and communities, where latitude has a strong effect on the thermal niche breadth. TNTs are identified as suitable indicators of species' vulnerability to warming and are suggested to be included in long-term biodiversity monitoring in the Andes.

KEYWORDS

climate change, climate seasonality, endemics, mountains, niche breadth, thermal optimum

1 | INTRODUCTION

Some of the first evidence for a close relationship between temperature and vegetation was provided by Alexander von Humboldt whilst travelling in tropical America in the early 19th century (Romanowski & Jackson, 2009). In particular, Humboldt established a clear relation between elevation and the distribution of plant taxa in his seminal work 'Tableau Physique' and defined the concept of the vertical zonation of vegetation (Von Humboldt, 1807). Over the following two centuries, much effort had been dedicated to refining Humboldt's pioneering insights. In line with Humboldt's observations, decreasing temperature with increasing elevation has been found to be a globally common determinant of the distribution of alpine plant species and their community composition (Körner, 2003). A decrease in vascular plant species richness with increasing elevation above the tree line has been documented in both temperate and tropical mountains (Sklenář & Ramsay, 2001; Vetaas & Grytnes, 2002). As tropical alpine regions are exposed to large daily thermal amplitudes, including night-time freezing conditions, the ability of plants to resist these conditions has been proposed as one of the principal factors structuring tropical alpine plant communities and their species assembly along elevation gradients (Rundel, Smith, & Meinzer, 1994). Today, the patterns observed by Humboldt are considered to be fundamentally determined by the impact of low temperatures on the rate of metabolic processes during cell duplication and growth (Larcher, 2003).

Mean annual temperatures in the tropical Andes above 3,000 m a.s.l. have increased at a rate of approximately 0.13°C decade^{-1} over the past six decades (1950–2010; Vuille, Franquist, Garreaud, Lavado Casimiro, & Cáceres, 2015). Although a warming of this magnitude is expected to cause range shifts of species, empirical evidence from tropical alpine regions is scarce due to the absence of old-enough data from georeferenced plots (Buytaert, Cuesta-Camacho, & Tobón, 2011) and detailed species range data (Feeley & Silman, 2011). Among the few exceptions are a study that re-visited sites surveyed by Humboldt over 200 years ago (Morueta-Holme et al., 2015), and a comparison of Andean forest plots that had been censused on multiple occasions since the 1990s (Fadrique et al., 2018). Both studies found evidence of directional upward shifts in community composition related to warming.

To better understand the long-term effects of temperature changes on tropical alpine species and communities, improved knowledge of their thermal niches is essential. The vulnerability of

individual species, and possible responses to climate warming of tropical alpine plant communities as a whole, can be approximated by determining the thermal niche traits of species and plant communities across the Andean chain. Specifically, the determination of thermal niche traits allows the identification of: (a) species that are particularly prone to the effects of warming, and (b) communities with a higher risk of being subject to a warming-induced transformation of their species composition (Perez, Stroud, & Feeley, 2016).

Thermal niches comprise different components (hereafter thermal niche traits: TNT), such as the thermal optimum and niche breadth. The thermal optimum defines the temperature in which the species is most successful (Kleier & Rundel, 2009). The niche breadth describes the tolerance ranges, as narrow or broad. The narrower the range, the more specialized the species (Sierra-Almeida & Cavieres, 2012) and consequently the more vulnerable it is to temperature change (Inouye, 2008). This vulnerability would be particularly acute if the capacity of a species to shift its range was below the velocity of the climate warming (Lenoir & Svenning, 2015). Furthermore, species strongly adapted to low-temperature conditions would be more prone to suffer range contractions due to a topographically constrained upward displacement, as their distributions would be centred in the upper areas of usually conically shaped mountains (Pauli et al., 2012; Rumpf et al., 2018).

In tropical mountains, a further consideration on species ranges appears to be highly relevant. The climate variability hypothesis (CVH; Stevens (1989)) postulates that the non-seasonal climatic habitat conditions in the equatorial tropics select for narrower thermal tolerances, compared to habitats exposed to increasing seasonal climatic fluctuation with latitude, which favours broader thermal tolerances of species (Gaston & Chown, 1999; Spicer & Gaston, 1999). Janzen (1967), also linked the ideas behind the CVH to elevation gradients, suggesting that a more uniform tropical climate implies more effective dispersal barriers than seasonally fluctuating temperate climates, which should also be reflected in narrower elevation ranges of tropical species distributions. Recent studies on insect clades (Gill et al., 2016; Polato et al., 2018) documented that a reduced seasonality produces greater thermal stratification of taxa along tropical mountains compared to temperate ones, therefore limiting dispersal across tropical environmental gradients. Correspondingly, Chan et al. (2016) showed that both high seasonality and high daily temperature variability favour species with broader thermal niches. Most studies dealing with the CVH are based on animals (Chan et al., 2016; McCain, 2009), whereas, to the best of our knowledge, there are no previous studies on the variability of thermal niches of alpine plant species across the tropical latitudinal climate gradient.

During the past decade, permanent vegetation plots were established in alpine habitats across the entire tropical latitudes of the Andes as baseline to monitor effects of climate change on the species composition above the tree line (GLORIA-Andes; Cuesta et al., 2017). All plots were established using the same sampling design (Pauli et al., 2015). By focusing on summit habitats, which include all topographic aspects within a small area, and their arrangement along an elevation gradient in each of the 13 study regions, these data constitute a representative sample of the regional alpine floras occurring on mountain summits above the tree line across the tropical Andes.

Based on the GLORIA-Andes datasets that contain vascular plant species data from mountain summits distributed from Venezuela to northwest Argentina, plus plant distribution data extending beyond this area, the aims of this paper were (a) to test the CVH on the relationship between temperature seasonality and the observed thermal traits (thermal niche breadth, optima, minima) of tropical alpine species and communities along (1) latitudinal and (2) elevation gradients and (b) to assess the vulnerability of plant species to climate warming based on their observed thermal niche traits.

Regarding the CVH, we hypothesized that (1) Plant species and communities restricted to areas near the equator have a narrower thermal niche breadth, higher thermal minimum and higher thermal optimum than those located further away from the equator (Figure 1) and (2) Plant species and communities from lower elevations have a broader thermal niche breadth along with a higher thermal optimum and higher thermal minimum than those located at higher elevations (Figure 1). Moreover, we assessed the potential vulnerability of species and communities to climate warming using the estimated proportion of species niche breadth contraction under a moderate climate change scenario by the end of the century.

2 | MATERIALS AND METHODS

2.1 | Study area and plant community data

The study is based on plant community data of 49 high Andean summits (>3,000 m a.s.l) distributed in 13 regions across the entire extent of the tropical Andes, ranging from 8°54′56″ N to 26°41′24″ S (see Figure S1 in Appendix S1). Our study area includes 26 non-seasonal summits distributed along the equatorial Páramos of the Northern Andes, between 8.9 °N and 4.9 °S, and 23 seasonal summits distributed across the Punas of the Central Andes, between 13.7 °S and 26.7 °S (Table S1 in Appendix S1).

Along the 4,200 km latitudinal transect, 784 permanent vegetation plots (1 m^2) on 49 summits were set-up in the years 2008–2013, as part of the GLORIA-Andes network (Cuesta et al., 2017), upon which the plant community data were built (see Appendix S1). Plant community data were derived from the eight-sixteen 1-m^2 permanent plots established on each of the 49 summits, following the GLORIA protocols (Pauli et al., 2015). From each permanent plot, we obtained a complete species list and visually estimated the cover of each vascular plant species (Table S1 in Appendix S1).

We recorded 507 fully identified species in the 49 summit communities that were classified into biogeographical species groups. Biogeographical species groups are a set of taxa within the flora of a given region that show similar overall distribution patterns (McLaughlin, 1994). Here, species were grouped into seven biogeographical species groups (adjusted from Sklenář and Balslev (2007); see Figure 1d) based on the locations of their georeferenced records (see section Estimating Species TNTs):
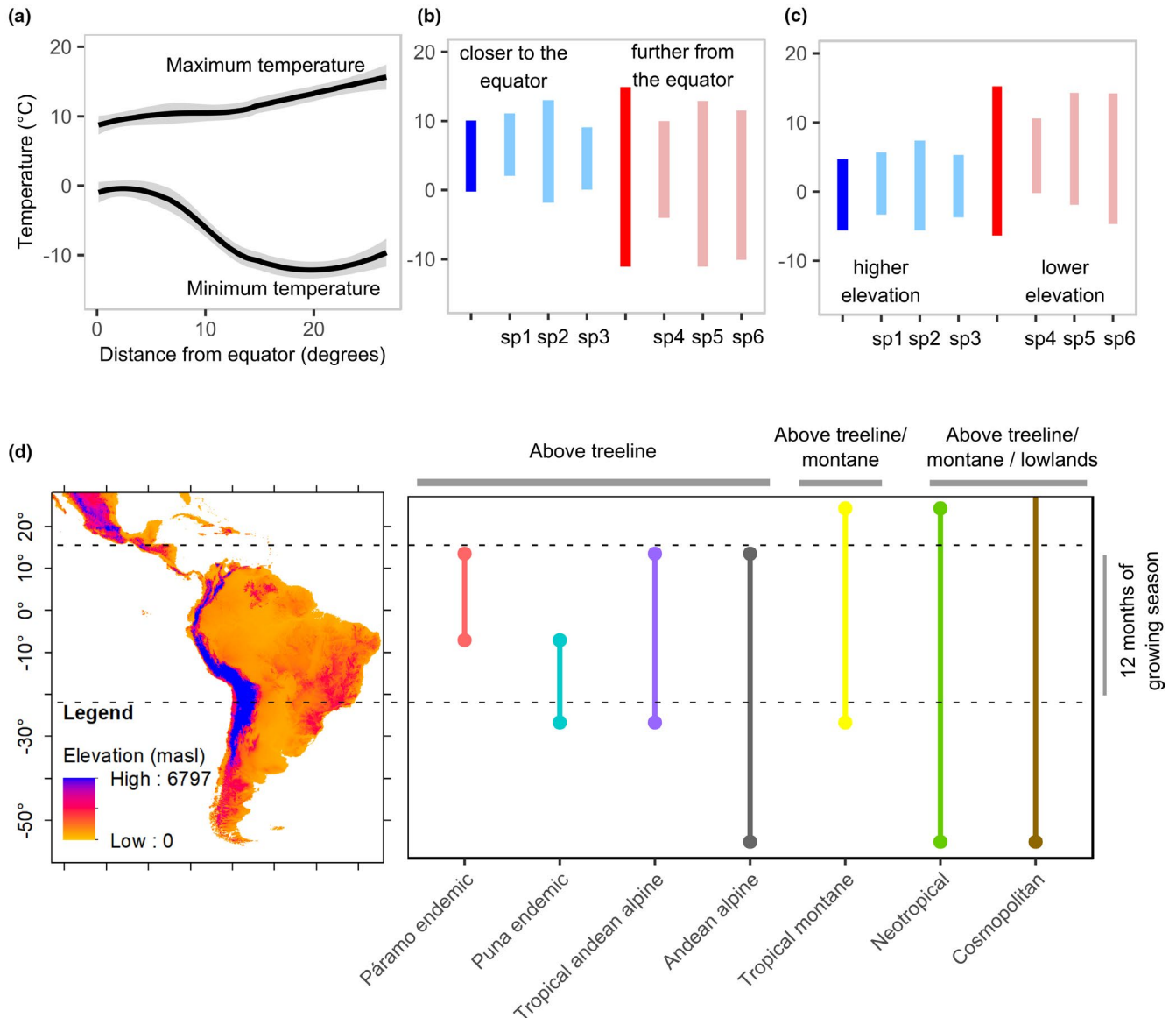
FIGURE 1 Environmental and biogeographical patterns of high Andean summits and its relationship on hypothesized thermal niche traits of vascular plant species and communities along the gradients in latitudinal and of summit elevations. (a) Minimum and maximum monthly air temperature on our summits derived from the Worldclim database (Hijmans et al., 2005). (b) Expected thermal niche of characteristic vascular plant species and their community-weighted scores on high Andean summits, along the latitudinal gradient. (c) Expected thermal niche of characteristic vascular plant species and their community-weighted scores on high Andean summits of different elevations. (d) Latitudinal distribution of the biogeographical species groups described in this study

- Páramo endemic: Species recorded only within the Páramo biome.
- Puna endemic: Species recorded only within the Puna biome.
- Tropical Andean alpine: Recorded in both Páramo and Puna biomes but not elsewhere.
- Andean alpine: Confined to alpine habitats with records occurring both within and outside of the tropical Andes.
- Tropical montane: Species with occurrences ranging from montane forest to the alpine zone in Páramos and/or Punas. It also includes species occurring in tropical montane forest outside the Andes (e.g. Central America).
- Neotropical: Species widely distributed in the Neotropics including lowland forests.

- Cosmopolitan: Species occurring worldwide, including records outside of the Neotropics. Yet, the derived thermal traits for these species were obtained only for the subset of records distributed within the study area (i.e. Neotropics).

2.2 | Estimating species TNTs and community-weighted temperature scores

Thermal niche traits (optimum temperature, minimum temperature and niche breadth) were estimated for each species. We used all available georeferenced records of each species to extract monthly mean temperatures for each location record. We

collected 29,627 species records from online databases that were clean and South American herbaria, including 1,388 records from the summit sites (see Appendix S1). Mean monthly temperature maps were obtained from WorldClim gridded datasets (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and then were downscaled to a 90 m pixel resolution. For this we used the Shuttle Radar Topography Mission Digital Elevation Model (SRTM DEM; http://www2.jpl.nasa.gov/srtm/) with a lapse rate of 0.54°C 100 m^{-1} (Bush, Silman, & Urrego, 2004).

To estimate the species TNTs, we first calculated the mean, minimum and maximum temperature of each location record only using the months of the growing period. The length of the growing period (active season) varies along the latitudinal gradient (Körner, Paulsen, & Spehn, 2011). Around the equator the growing season is all year round. Moreover, significant inactive seasons in terms of prolonged periods with low temperatures are exceptional for most of the entire tropical area involved. For transitional areas (i.e. 15–18 °N; 23–27 °S) and outside of the tropics (>27 °S), the 'inactive season' was defined as the months where mean air temperature is equal or below 0°C (see Figure S2a and Table S2 in Appendix S1). We performed two analyses to identify growing season periods along the latitudinal gradient before deriving the TNTs for each species (see Appendix S1).

Second, we used the estimated values of mean, minimum and maximum temperatures of all records per species to obtain 1,000 bootstrapped observations of the mean, minimum and maximum temperatures per species. Then we estimated the mean of the bootstrapped observations to obtain unique values for each of the three temperature values per species and obtained the following species thermal niche traits: optimum temperature (mean), minimum temperature and niche breadth (maximum–minimum temperature).

Third, for those species which had less than five records but with at least five records of congeneric individuals (n = 21), we used the TNTs calculated at genus level as a way to increase the number of locations per species (Feeley, Hurtado, Saatchi, Silman, and Clark (2013); see Table S3 in Appendix S1). Finally, we excluded from our analyses two species (*Plagiocheilus peduncularis* and *Polystichum pycnolepis*) which had less than five records and no other records from congeneric individuals. Our final number of species for all the following analyses was 505.

We then calculated a community-weighted temperature score (CTS; °C) for each of the 49 summits, as the average of the thermal optimum for the constituent species, weighted by their percentage cover (Feeley et al., 2013). Following the same procedure, we estimated a community-weighted niche breadth score (CBS; °C) and a community-weighted minimum temperature score (CMS; °C).

2.3 | Statistical analysis to test the CVH

We first tested our hypotheses at the species level. For this we used the species TNTs and those estimated by biogeographical group. First, we performed linear mixed-effects models ('nlme' R package, Pinheiro & Bates, 2000) for each TNT using species maximum distance to the equator and species mean elevation as fixed factors and biogeographical species group as a random variable. Maximum distance from the equator and mean elevation for each species were extracted using their georeferenced records. Second, we tested the differences between the TNTs of the different biogeographical species groups by using a Games-Howell test (Domingues, Martinelli, & Ehleringer, 2007) because sample sizes between groups and variances were not equal, and we also controlled by multiple comparisons ('user friendly science' R package, Peters (2015).

To test our hypotheses at the community level, we also evaluated the relationship between community-weighted TNTs and the distance to the equator and elevation of each summit community by implementing linear mixed-effects models ('nlme' R package, Pinheiro and Bates (2000)). The response variable was the community TNTs, whereas elevation (i.e. the highest point of that summit) and distance to the equator (i.e. latitude) were defined as fixed factors and target region (n = 13; see Figure S1 in Appendix S1) as a random factor. We verified that the assumptions of normality, homogeneity of variances and independence of samples were met. Only in the case of CBS, assumptions were met after removing elevation from the model.

2.4 | Species and community vulnerability to temperature increase

Species vulnerability to warming was based on the thermal niche breadth assuming that species with the narrowest niches are most at risk (Inouye, 2008). We estimated the percentage of the niche breadth that will be lost (i.e. loss of thermal niche space) under a moderate scenario of projected warming rate (departures from 1961–1990 mean) for the high tropical Andes by the end of this century (Vuille et al., 2018): 1.5°C air temperature increase from a moderate (Representative Concentration Pathway, RCP 4.5) emission scenario (Pachauri et al., 2014). We then classified species vulnerability to global warming using the 3-quantiles of the projected niche space loss as: high vulnerability (>12.97% lost), medium vulnerability (9.21%–12.96% lost) and low vulnerability (<9.21% lost).

Subsequently, we estimated the proportional representation of species classified as showing high, medium and low vulnerability to warming per community. Those communities with a higher prevalence of species classified as highly vulnerable were classified as such. In addition, we assessed the composition of each plant community by their biogeographical species group by calculating the proportional representation of vegetation cover of each biogeographical species group within each community to also assess vulnerability based on the composition of their biogeographical groups.

Finally, we estimated the observed warming rate for each of the 49 summits (see Appendix S2) using the time series data (1979–2013) from CHELSA v. 1.2 (Karger et al., 2017) as a way to identify plant communities with higher exposure to warming.
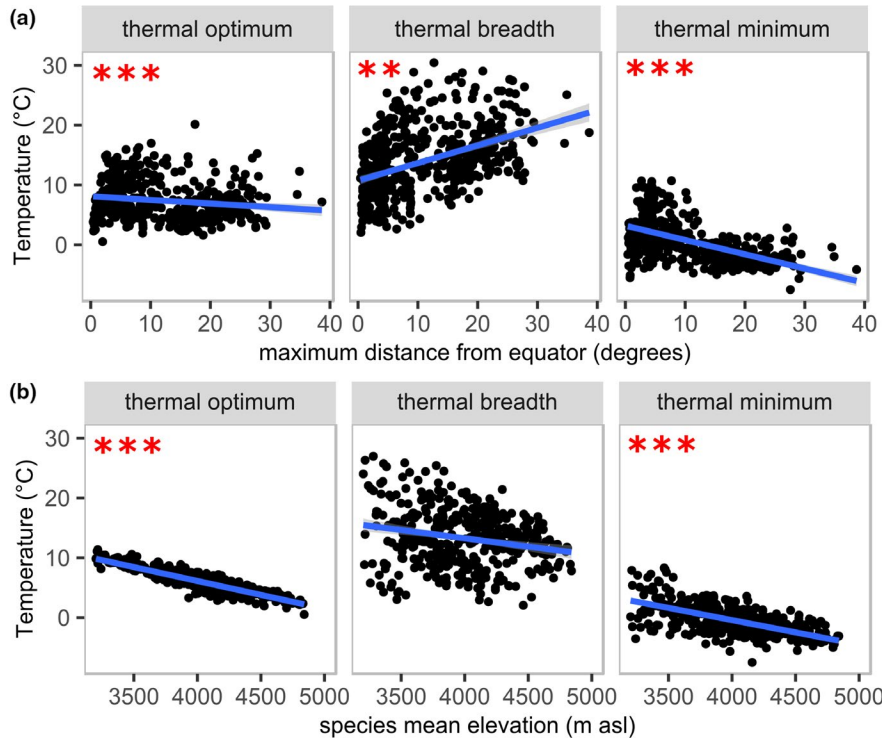
FIGURE 2 Thermal niche traits (TNTs) of 505 vascular plant species recorded in 49 summits along (a) the latitudinal and (b) elevation gradient of the tropical Andes. Maximum distance from the equator and mean elevation for each species were extracted using their occurrence records. Linear mixed-effects models were built for each TNT using distance to the equator and mean elevation as fixed factors and biogeographical species group as a random variable (Table S3). Asterisks represent a significant relationship: ***0.001 **0.01 *0.05

3 | RESULTS

3.1 | Species thermal niche traits (TNTs) and the CVH

Results of the linear mixed-effects model showed species with ranges restricted to near the equator had higher thermal optimum ($p < .001$) and thermal minimum ($p < .001$) than those distributed further from the equator. Species whose distributions are closer to the equator had narrower thermal breadth ($p < .01$) than those with further latitudinal distributions (Figure 2a; see Appendix S3). Likewise, plant species with a lower mean elevation had a significantly higher thermal optimum and thermal minimum than those species with higher mean elevation. We found no significant relationship between species thermal breadth and their mean elevation (Figure 2b, Table S3 in Appendix S1).

Additionally, species niche breadths differed among most biogeographical species groups with respect to their latitudinal and elevational distribution ($p < .01$). Páramo endemic species had the narrowest thermal niche breadth whereas Neotropical and Cosmopolitan species had the broadest ones (Figure 3). Minimum temperatures were more similar among biogeographical species groups, but Puna endemic species had a significantly lower value than Páramo endemic, Tropical Andean alpine and Tropical montane species ($p < .01$). All species of the 'alpine' biogeographical species groups (i.e. those with vertical distributions from the tree line upwards, see Figure 1d) had the same thermal optima irrespective of their latitudinal distribution, whereas the Neotropical, Cosmopolitan and Tropical montane species showed consistently warmer thermal optima (Figure 3).

3.2 | Community-weighted temperature scores and the CVH

Using all plots within each of the 49 summits we estimated community-weighted temperature scores. Results of the linear mixed-effects model (see Appendix S4) for each community-weighted temperature score showed a significant positive relationship between distance to the equator and Community Breadth Score ($p = .0018$), and a negative one with the Community Minimum Score ($p = .0343$; Figure 4a). As expected, summit elevation was negatively related with the Community Temperature Score ($p < .00001$) and the Community Minimum Score ($p = .0162$), but we found no relationship with the Community Breath Score ($p > .05$).

3.3 | Species and community vulnerability to warming

The majority of the species belonging to the Páramo endemic, Tropical Andean alpine and Puna endemic biogeographical groups had a lower thermal optimum and narrow thermal niche breadth, suggesting higher susceptibility to climate warming (Figure 5a, Table S3 in Appendix S1). Under a moderate warming scenario, RCP 6.5, all species groups showed a potential thermal niche contraction that ranged from 6.4% to 22.5%. Páramo endemic species were projected to have the highest niche contraction amongst all biogeographical groups, whereas Puna endemics were projected to have the lowest niche contraction among the 'alpine' biogeographical species groups (Figure 5b). Most of the species classified as highly vulnerable belonged to the Páramo endemic and Tropical Andean alpine species groups (Table 1); nearly 82% of all Páramo endemic species, and

FIGURE 3 Thermal niche traits of 505 vascular plant species recorded on 49 summits along the tropical Andes grouped by biogeographical species groups. Different letters represent a significant difference between biogeographical species groups (*p* < .01) based on Games-Howell test. The *n* values indicate the number of species included in each group
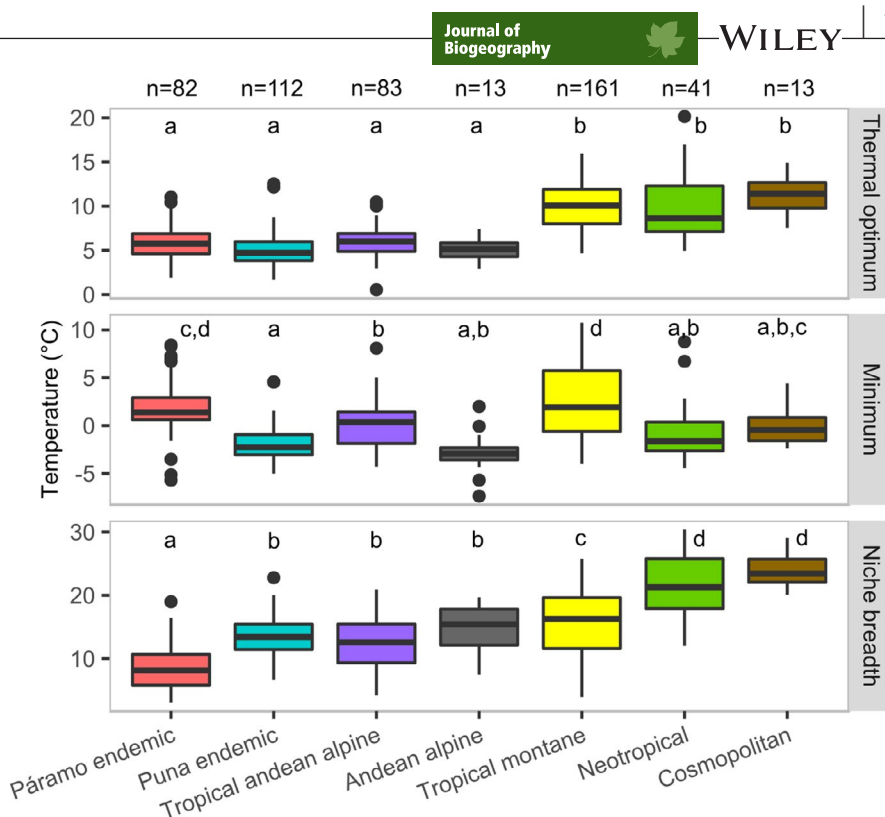

64% of Tropical Andean alpine species respectively, were included in this category. In contrast, 50% and 83% of all Tropical montane and Neotropical species respectively, were classified as showing low vulnerability (Table 1).

For the vulnerability analyses of summit communities, we aggregated species of all plots within a summit to define a community and used i) the vulnerability of each species within a community and the

vulnerability of the community based on the species biogeographical group. These analyses showed that the majority of summit communities located further from the equator, in the central Andes, were dominated by Puna endemic species, whereas the equatorial summit communities were composed by a more heterogeneous array of different biogeographical species groups (Figure 5c). Equatorial summits at higher elevations in Venezuela and Colombia were generally

FIGURE 4 Community-weighted scores (community-weighted mean of thermal niche traits, TNTs) of 49 summits along the (a) latitudinal and (b) elevation gradient of the tropical Andes. Linear mixed-effects models were built for Community Temperature Score, Community Breadth Score and Community Minimum Score using distance from equator and elevation of the community location as fixed factors and summit site location (see Table S1) as a random variable. For Community Breadth Score the best model did not include elevation which was not significant. Asterisks represent a significant relationship: ***0.001 **0.01 *0.05
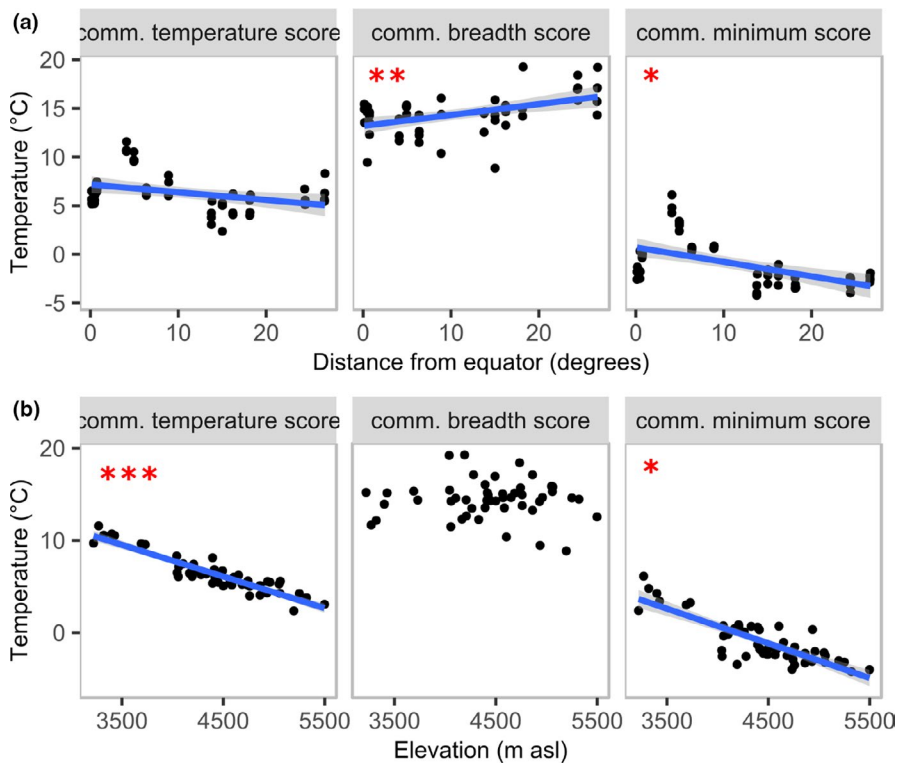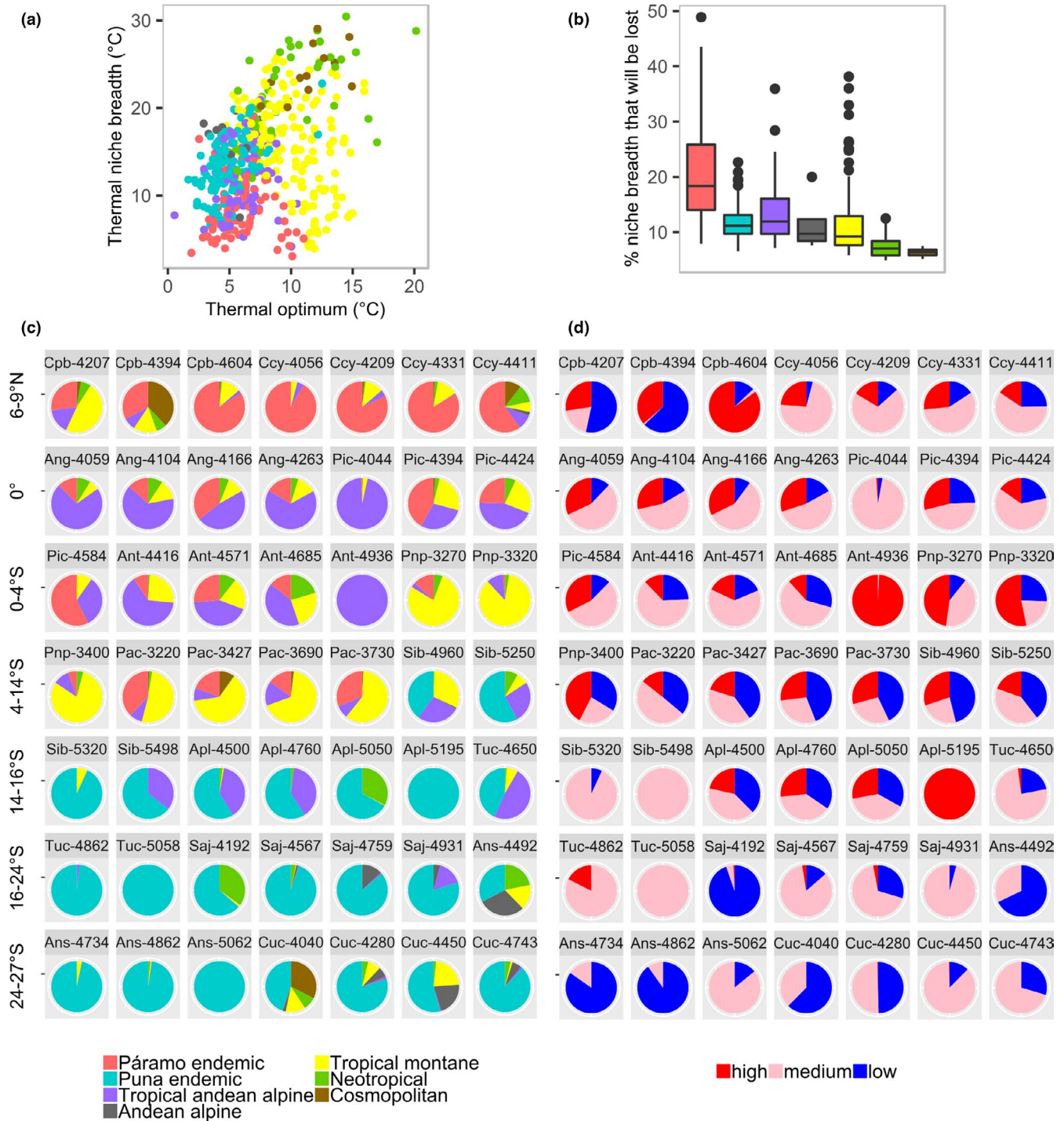
FIGURE 5 Vulnerability to climate change. (a) Scattergram showing the thermal optimum and niche breadth of 505 vascular plant species recorded on 49 summits of the tropical Andes. Species are classified by their biogeographical groups (based on their current geographical distribution, see methods). (b) Percentage (%) loss of thermal niche space under a moderate warming scenario (1,5°C increment - RCP 4.5) by the end of the 21st century per biogeographical species group. (c) Community composition by their biogeographical species groups. (d) The vulnerability of 49 high Andean summits plant communities based on the proportion of species with different levels of vulnerability. Each species was classified as high, medium or low vulnerability based on the proportion of the thermal niche that each species is projected to lose under a 1.5°C warming scenario (see methods). Abbreviations of the summit names and elevations are shown. Information on the summit position and climate data are shown in Table S1.1

dominated by species classified with high and medium vulnerability to warming (Figure 5d), many of which correspond to Páramo endemic species (Figure 5c). High elevation summits in northern

Ecuador were primarily composed by species classified with medium vulnerability to warming that generally belongs to the Andean alpine biogeographical group (Figure 5c,d). The lower elevation summits in

TABLE 1 Expected vulnerability of high Andean vascular plant species aggregated into seven biogeographical species groups, based on the species thermal niche traits (TNTs)

Biogeographical species group	Vulnerability			Total species number
Vulnerability class	High	Moderate	Low	
Páramo endemic	67 (82)	13 (16)	2 (2)	82 (16.2)
Puna endemic	30 (27)	63 (56)	19 (17)	112 (22.2)
Tropical Andean alpine	34 (41)	36 (43)	13 (16)	83 (16.4)
Andean alpine	1 (8)	6 (46)	6 (46)	13 (2.6)
Tropical montane	40 (25)	41 (25)	80 (50)	161 (31.9)
Neotropical	0 (0)	7 (17)	34 (83)	41 (8.1)
Cosmopolitan	0 (0)	0 (0)	13 (100)	13 (2.6)
Total	172 (34)	166 (33)	167 (33)	505 (100)

Note: Table shows the observed number and percentage (in parentheses) of species in each biogeographical species group. Species vulnerability was assessed as the expected percentage loss of thermal niche space under a moderate warming scenario (1,5°C increment - RCP 4.5) by the end of the 21st century.

the central Andes, further away from the equator, were dominated by species with low vulnerability to warming (Figure 5d). The species that characterize these communities belong to a diverse array of biogeographical groups, primary Tropical montane, Neotropical and Andean alpine species (Figure 5c). High elevation summits in the central Andes were dominated by species classified with medium to high vulnerability to climate warming, many of which belong to the Puna endemics biogeographical species group (Figure 5d).

We found that most of the summits have undergone an increase of temperature during the period 1979–2013 with a median increase of 0.021°C per year while the maximum observed increase was of 0.061°C (see Appendix S2). Further, we found that the summits located at higher latitudes have undergone stronger temperature increments than the equatorial summits, with some negative trends in the latter. Nearly one third, 18 out of 49 summits, showed a decrease in temperatures for the analysed period (see Appendix S2).

4 | DISCUSSION

4.1 | The CVH: species TNTs and community-weighted scores across the Andes

This study provides a first assessment on how different tropical climates (non-seasonal equatorial to seasonal tropical) and elevation gradients are related to the thermal traits of species occurring in high Andean summit habitats and communities (where a community-weighted score is estimated using all plots within a summit). Non-seasonal climate conditions on alpine summits closer to the equator were associated with plant species and communities with narrower thermal tolerances, whereas summits further from the equator were characterized by species and communities with broader thermal tolerances, lower thermal optima and minima. In addition, biogeographical species groups restricted to alpine habitats and closer to the equator (e.g. Páramo endemics) had a narrower thermal niche breadth than those groups restricted to alpine environments that are located further from equatorial latitudes

(e.g. Puna endemics). The geographic trend found in niche breadth amplitudes is likely due to the effect of the gradual transition towards a more seasonal climate with lower air temperature minima during the dry season in the central Andes (Baied & Wheeler, 1993), i.e. larger annual temperature variation (see Appendix S1, extended methods). Our findings support the applicability of the CVH (Spicer & Gaston, 1999) to high elevation plant species and communities along a latitudinal gradient within the tropical Andes, which supports our first hypothesis (Figure 1b), in accordance with a recent study on aquatic insects (Polato et al., 2018).

The association of narrow thermal niche breadths of tropical alpine species with non-seasonal climates, might be enhanced due to the combined effects of topographic and evolutionary factors. First, there is a higher degree of fragmentation of the equatorial alpine areas compared to the alpine areas of the central Andes (Josse et al., 2011). Second, a more fragmented landscape may constrain dispersal of Páramo endemic species (Young, Ulloa, Luteyn, & Knapp, 2002), thus limiting their distribution and potential thermal niche breadth. Third, alpine habitats in the Central Andes reach higher elevations, and the tree line is located higher up than in the Northern Andes, which contributes to a lower minimum temperature and a broader thermal amplitude (Körner, 2012). Fourth, high frequency of speciation events possibly due to changes in the extent of alpine environments following the Pleistocene glacial-interglacial cycles (Flantua & Hooghiemstra, 2018) and rapid diversification (Hughes & Eastwood, 2006) could mean that many of the species are still expanding their niches.

While thermal optimum of species decreases with distance from equator, no trend is found for biogeographical species groups distributed further from the equator such as Puna endemics or Andean alpine and groups distributed around the equator (e.g. Páramo endemics). These could be related to the fact that many of the endemic species of the Páramo and Puna biogeographical groups had narrow-range distributions restricted to the subnival and nival habitats (See Annex 1, Table S3). Therefore, the thermal optimum of such species is similar for both cases, masking the effect of the seasonal thermal gradient.

Further, our findings of a monotonic decrease in the thermal optima and lower minima of species and communities located at higher elevations, partially confirms our second hypothesis (Figures 2b and 4b). Yet, we found no relationship between species niche breadths and elevation nor with community breadth score and elevation, as opposed to Janzen's hypothesis (Janzen, 1967) and the results recently reported for cryptic aquatic insects (Gill et al., 2016). This suggests that the seasonality gradient is more strongly associated with species and community thermal niche breadth than summit elevation in tropical alpine systems. The absence of relationship could be caused by the high cover of tropical Andean alpine and Andean alpine species in many summit communities at different elevations (Figure 5c). Those species share similar niche breadths (Figure 3), which translates into similar Community Breadth Score values in summits with dissimilar elevations across latitudes. We suspect the lack of annual thermal seasonality in equatorial mountain summits creates more constant conditions throughout the year, which could allow the presence of a more diverse array of biogeographical species groups including Tropical montane, Tropical Andean alpine and Páramo endemic species (Figure 5c). Complementary, the results of Gill et al. (2016) that shows the effect of the CVH along the elevation gradients became evident when only the cryptic species were considered in the analyses. Thus, a similar pattern could arise in our dataset if we only look at narrow-range species restricted to alpine habitats across the Andes. Additionally, the lack of a significant relationship between species and community breath scores and elevation could be related to the fact that we used monthly mean values instead of daily temperature records (see Appendix S5). Chan et al. (2016) and McCain (2009) documented the influence of annual and daily thermal variation on species thermal ranges for endothermic and ectothermic vertebrates. Both studies evidenced the importance of annual and daily temperature variability to shape species niche breadths and argue that pronounced daily temperature variation can be of a similar magnitude to temperate annual variability. Future work, however, is needed in order to accurately assess the influence of daily temperature variation on the thermal niche traits of tropical alpine plants along latitudinal and elevation gradients (see Appendix S5).

4.2 | High summit plant species and community's vulnerability to climate warming across the andes

Páramo endemics, together with Tropical Andean alpine species, showed the highest vulnerability to warming among the seven biogeographical species groups (Figure 5b). The observed TNTs patterns suggest that the spatially more restricted species near the equator (e.g. Páramo endemics) are at the same time the most vulnerable to warming, similar to model projections for tropical and temperate mountain biomes (Engler et al., 2009; Tovar, Arnillas, Cuesta, & Buytaert, 2013). Spatially restricted cryophilic species (e.g. *Espeletiopsis colombiana*, *Coespeletia timotensis and Pycnophyllum tetrastichum*) would be particularly prone to a loss of climate niche space (Mavárez, Bézy, Goeury, Fernández, & Aubert, 2018), in agreement to the expected range contraction and loss in genetic diversity of Afrotropical alpine species suggested by model projections (Chala

et al., 2016). Additional pressures on thermal narrow-range specialists could arise from increases in seasonal temperature variability (IPCC, 2013), coupled with decreases in diurnal temperature variability due to faster night-time versus daytime warming (Easterling et al., 1997).

The observed warming trends (period 1979–2013) in our summits exhibited significant differences among them. The results suggest that summits located at higher latitudes and at higher elevations could be exposed to higher temperature increases in shorter periods of time (see Appendix S2). Thus, plant communities located in these summits are likely to suffer high impacts during the coming decades.

Although the global climate model outputs project an average increase of 1.5°C in global temperatures from a moderate-emission scenario (RCP 4.5) by the end of the century (Pachauri et al., 2014), inevitably there will be regional variations. The Andes, in particular, is a region of high climate variability induced by external drivers such as ENSO and the Pacific Decadal Oscillation, as well as local topography and microclimates (Garreaud, 2009), which may obfuscate warming trends (see Appendix S2).

Warming-driven dynamics have already been observed to be in progress across different groups of organisms, for example by the upward range shifts found for plants (Morueta-Holme et al., 2015), insects (Moret, Aráuz, Gobbi, & Barragán, 2016) and vertebrates (Seimon et al., 2017) across the high Andes. Similar directional dynamics have also been reported from the Mediterranean high mountain areas (Pauli et al., 2012), where narrow niche breadths of high elevation endemic floras pose a high risk of biodiversity loss through climate warming.

At the community level ($n = 49$, one community is represented by all 1-m^2 plots within an entire summit) vulnerability was assessed using both vulnerability of their species and the community composition of the biogeographical groups. Our results indicate that summit plant communities located at higher elevations and lower latitudes would have a higher susceptibility to warming (see Figure 5c-d). These particular summits are dominated by species with narrow thermal breadths and lower thermal optima, which relates to an enhanced risk of changes in community composition (Rumpf et al., 2018), compared to those summits located in lower elevations, at least in those regions where potential high elevation refugia are limited. Summit plant communities located further from the equator might be less prone to critical biodiversity losses through temperature increase, due to broader community-weighted breadth scores and the larger availability of potential refugia at higher elevations in the Central Andes, which cover nearly three times the size of the Northern Andes (Fjeldså & Krabbe, 1990; Josse et al., 2011).

Further, expected warming is likely to have a large impact on summit plant communities composed by a high proportion of narrow thermal range species due to: (a) changes in thermal habitat suitability, and (b) in biotic factors such as increased competition with species from lower elevations (Alexander, Diez, & Levine, 2015). Yet, this study focuses on temperature-related factors, because they are probably the strongest abiotic factor determining current high mountain plants distributions and range shifts in relation to climate

change (Steinbauer et al., 2018). Global warming may have direct (e.g. physiological stress) and indirect (e.g. facilitation and competition among species) effects on species abundance changes and range shift (Anthelme, Cavieres, & Dangles, 2014; Lamprecht, Semenchuk, Steinbauer, Winkler, & Pauli, 2018), which are enhanced by topographic complexity in alpine environments (Graae et al., 2018) and limitations of plant dispersal and colonization (Zimmer et al., 2018). Yet, we did not account for such differential effects, because the study focuses on a large and complex mountain region and included many species, where little, if anything, is yet known about their individual responses to ongoing climate change.

Our results suggest that the use of thermal niche traits could be an effective approach for assessing the warming-induced transformation of tropical alpine plant species compositions and the risk of biodiversity losses by means of repeated permanent plot surveys. Given that climate change impacts could be nonlinear (Carilla et al., 2018), it is important to strengthen long-term ecological observation networks. All plots used in this study were established as permanent plots of the GLORIA-Andes network. Resurveys of these plots will enable to assess if thermophilization of high Andean plant communities is occurring, as it has been documented for the montane forest of the Andes (Duque, Stevenson, & Feeley, 2015; Fadrique et al., 2018).

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BIOSKETCH

The GLORIA-Andes network is a research platform established in 2008 that supports the establishment of permanent monitoring sites on high Andean summits to study the effect of climate change on tropical mountain ecosystems (https://redgloria.condesan.org/). The network is made up of more than eight universities and research centres from the Andean countries. To this day, the network has promoted and assisted the establishment of 15 GLORIA sites (Target regions) following the same protocol and data management standards established by the global GLORIA network (http://www.gloria.ac.at/).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.