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RESEARCH ARTICLE

Compositional shifts of alpine plant communities across the high Andes

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Abstract

Aim: Climate change is transforming mountain summit plant communities worldwide, but we know little about such changes in the High Andes. Understanding large-scale patterns of vegetation changes across the Andes, and the factors driving these changes, is fundamental to predicting the effects of global warming. We assessed trends in vegetation cover, species richness (SR) and community-level thermal niches (CTN) and tested whether they are explained by summits' climatic conditions and soil temperature trends.

Location: High Andes.

Time period: Between 2011/2012 and 2017/2019.

F. Cuesta and C. Tovar contributed equally to this study.

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Major taxa studied: Vascular plants.

Methods: Using permanent vegetation plots placed on 45 mountain summits and soil temperature loggers situated along a ~6800 km N-S gradient, we measured species and their relative percentage cover and estimated CTN in two surveys (intervals between 5 and 8 years). We then estimated the annual rate of changes for the three variables and used generalized linear models to assess their relationship with annual precipitation, the minimum air temperatures of each summit and rates of change in the locally recorded soil temperatures.

Results: Over time, there was an average loss of vegetation cover (mean = −0.26%/yr), and a gain in SR across summits (mean = 0.38 species m^2/yr), but most summits had significant increases in SR and vegetation cover. Changes in SR were positively related to minimum air temperature and soil temperature rate of change. Most plant communities experienced shifts in their composition by including greater abundances of species with broader thermal niches and higher optima. However, the measured changes in soil temperature did not explain the observed changes in CTN.

Main conclusions: High Andean vegetation is changing in cover and SR and is shifting towards species with wider thermal niche breadths. The weak relationship with soil temperature trends could have resulted from the short study period that only marginally captures changes in vegetation through time.

KEYWORDS

climate change, community thermal scores, latitude, mountains, species richness, thermophilization, vegetation dynamics

1 | INTRODUCTION

Due to anthropogenic climate change, some species are shifting their geographic distributions into newly suitable habitats and out of habitats that become unsuitable. Specifically, species tend to move to higher latitudes or higher elevations and into areas that were formerly 'too cold' and out of lower elevation or lower latitude areas that become 'too hot' (Spence & Tingley, 2020).

Given the high sensitivity of alpine flora to global warming and their anticipated range shifts, mountains are especially suitable systems for tracing climate-change impacts (Körner, 2021). For example, species range shifts, including leading-edge expansions and rear-edge contractions (Lenoir & Svenning, 2015), have resulted in increasing species numbers (Steinbauer et al., 2018) and compositional transformations of alpine plant communities across European mountain ranges (Gottfried et al., 2012; Lamprecht et al., 2018). In South America, studies have shown that high Andean plant communities of northern Argentina have also experienced changes in vegetation cover and species richness (Carilla et al., 2018), but overall we still lack regional analyses of changes along the Andean chain for high Andean communities.

As species' ranges shift due to climate change, local species richness and diversity may be affected. For example, an increase in species richness was documented on temperate to boreal mountain summits across Europe (+3.9 species/summit on average), whereas a decrease was found in Mediterranean mountains (−1.4 species/summit on average) between 2001 and 2008; the latter decrease might be due to a decrease in water availability in that region (Pauli et al., 2012). A more recent study across European mountains showed a rapid increase in species richness (+5.4 species/decade on average), occurring synchronously with rising temperatures (Steinbauer et al., 2018). For the high Andes, only one study exists that reported compositional changes of alpine plant communities based on resurveys of permanent plots in NW Argentina, and it found increases in species diversity in alpine and subnival summits (Carilla et al., 2018), but did not report on significant temperature changes. In the Himalayas, lower summits gained in species richness but the highest belt lost species (Hamid et al., 2020). These studies suggest differentiated responses of high-mountain plant communities along the elevation belts.

Widespread greening in the alpine area of the Alps, detected through remote sensing techniques (Choler et al., 2021; Rumpf et al., 2022), coincided with a general tendency towards increased vegetation cover in the Alps and the Apennines (Rogora et al., 2018). However, a decrease in vegetation cover was also observed in the central Alps (>2900 m), caused by a major reduction of cold-adapted species (Steinbauer et al., 2020). This reduction may have been caused by either direct climatic factors or by competitive displacement through advancing warmth-demanding alpine species from lower elevations. However, the overall decrease in vegetation cover suggests that the loss of cold-adapted species was faster than the colonization of other species (Steinbauer et al., 2020). In NW Argentina, a greening trend was also observed since 2013 (Carilla et al., 2023), corresponding with increased vegetation cover, particularly on the subnival summits, where plant cover doubled within a decade (Carilla et al., 2018). A similar trend was documented in the Himalayas due to the increased cover of shrubs, graminoids and forbs (Hamid et al., 2020).

The documented changes in species richness and vegetation cover across the European mountain summits were due to a measurable increase in the relative abundances of thermophilic (i.e. warmth-demanding) species that increased their cover area in situ or migrated into the summit areas from lower and warmer elevations along with a corresponding loss of cold-adapted species—a process called thermophilization (Gottfried et al., 2012). Thermophilization has been observed by many European studies (e.g. Rogora et al., 2018; Stanisci et al., 2016) due to an accelerating loss of subnival plant species (Lamprecht et al., 2018). In most cases, thermophilization has been assessed using the temporal changes in the community-weighted mean of the thermal optima of the constituent species in a community (i.e., Community Temperature Score, CTS). Associated with changes in CTS, thermophilization could also result in the increase of the community-weighted mean of the thermal niche breadth, and/or an increase in the community-weighted mean of the thermal minima, since species from lower elevations tend to have broader thermal niches and higher thermal minima.

Empirical evidence on climate change-driven shifts of alpine plant communities is based primarily on resurveys of temperate mountain ranges (e.g. Kelly & Goulden, 2008; Steinbauer et al., 2018, 2020). Significant gaps persist in our understanding of how global warming affects tropical, subtropical and temperate summit plant communities across the Andean range. Our previous study used thermal niche traits to infer vulnerability of high Andean species to climate change (Cuesta et al., 2020). We found that biogeographical species groups (e.g. Páramo endemics) that are distributed close to the equator and restricted to alpine regions showed narrower niche breadths than those with broader ranges (e.g. Andean alpine), which relates to an enhanced risk of changes in community composition (see also Rumpf et al., 2018). Since equatorial high-mountain plant communities prominently include species with narrow thermal niches, we expect compositional changes to be greater on low-latitude summits than at higher latitudes. Likewise, we expect that summit plant communities at higher latitudes should be less prone to compositional changes due to a higher representation of species with broader niches. Testing these vegetation changes is of utmost importance given the diversity and uniqueness of plant communities of Andean systems (Sklenář et al., 2014) and their potentially high susceptibility to climate change (Cuesta et al., 2020; Tovar et al., 2022).

To our knowledge, no study has yet assessed compositional changes of mountain summit plant communities on a pan-Andean scale. Indeed, evidence of climate change-driven modifications in high Andean plant communities is scarce and is primarily based on a few small-scale diachronic studies over centennial periods (i.e. 215, 210 and 140 years) using historical data (Moret et al., 2019, 2021; Morueta-Holme et al., 2015). For example, through a comparison to Humboldt's and Whymper's notes on floral altitudinal zonation in the Ecuadorian Andes, Morueta-Holme et al. (2015) and Moret et al. (2019, 2021) reported substantial upwards shifts of many subalpine and alpine species. While these studies provide valuable information about local changes, their historical idiosyncrasies complicate drawing general conclusions about climate change impacts across larger scales in tropical and subtropical mountains.

Understanding large-scale patterns in the directions and rates of vegetative change across the high Andes, and the factors driving these dynamics, is fundamental to predicting the effects of ongoing global warming on these unique ecosystems. With this motivation, we used a series of permanent vegetation plots from the GLORIA-Andes network (Cuesta et al., 2017) combined with soil temperature loggers on mountain summits across the >6800 km N-S extension of the high Andes to assess (1) temporal trends in microclimatic soil conditions across high Andean summits over the last decade, (2) temporal trends in vegetation cover, species richness and plant communities' thermal composition and (3) whether vegetation trends are explained by summits' climatic conditions and microclimatic soil trends. Our a priori expectations were that Andean summit plant communities are experiencing microclimatic warming evidenced by the soil temperature dataloggers [H1, Vuille et al., 2015, 2018]. We also hypothesized increasing species richness and in vegetation cover over time across the Andean summits, driven by microclimatic warming trends and the local climatic conditions of the summits [H2, Pauli et al., 2012; Steinbauer et al., 2018]. Finally, due to warming, we expect an increase in the relative abundance of warm-adapted species and a decrease in the cold-adapted species over time across all summits [H3, Gottfried et al., 2012; Steinbauer et al., 2020].

2 | MATERIALS AND METHODS

2.1 | Study area and plant community data

This study used plant community data recorded in 720 permanent plots on 45 mountain summits representing 12 target regions across the high Andes (Table S1, Figure 1). Each target region has three or four summit sites. The plots were established by the GLORIA-Andes network (https://redgloria.condesan.org/) and span the entire Andes, from the Cordillera de Mérida in Venezuela (8.8° N) to Tierra del Fuego in Argentina (54° S) (Table S1). The GLORIA-Andes plot network covers a N-S latitudinal gradient of ca. 6870 km and an elevational gradient of nearly 4900 m (634 to 5498 m a.s.l.). Summits were classified as subalpine (n=5), alpine (n=9), subnival (n=19) and nival (n=12) according to their elevation and latitude (see [Cuesta et al., 2017; Lencinas et al., 2021] for details). The GLORIA-Andes network established 1 m^2 permanent vegetation plots in the upper area on each summit (i.e. in the area between the highest summit point and the 5-m contour line below summit). Each summit area contains 8 to 16 plots (mode=16 plots per summit), where each species' cover (%) was visually estimated following the GLORIA standard protocol (Pauli et al., 2015). All summit plots were surveyed twice between 2008 and 2019 (survey intervals ranged from 5 to 8 years; mode=5 years; Table S1). For our analyses,

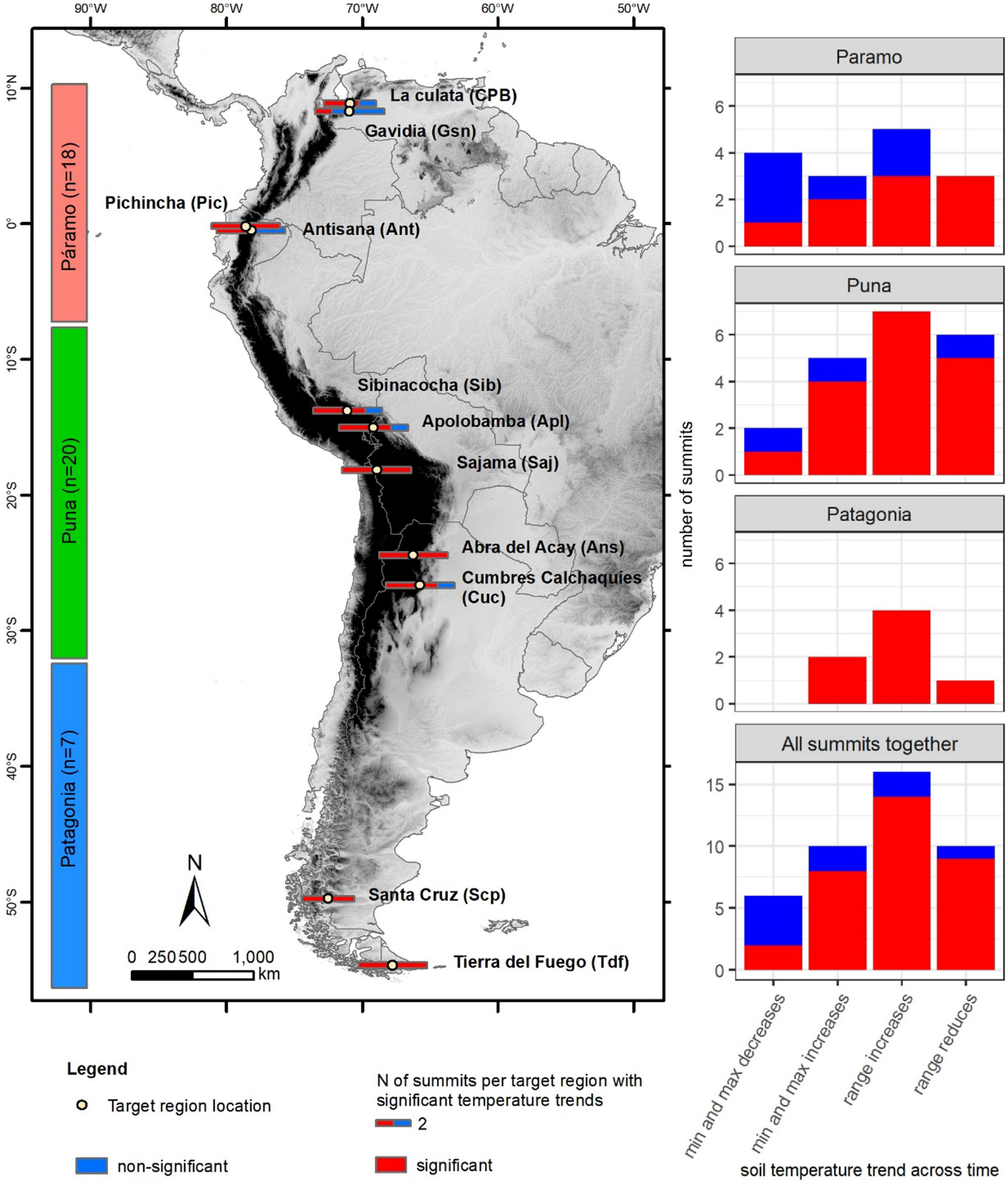

FIGURE 1 Summary of trends in daily soil temperature focusing on the temperature range (maximum and minimum) observed within the last decade across Andean summits. The map shows the number of summits with significant and nonsignificant trends for each category (notice the size of the horizontal bar corresponding to 2 summits in the legend) shown in the *x* axis of the bar plot per target region based on Mann-Kendal time series analyses. Bars in the right represent the number of summits for each category of trend, per biome and a total one (at the bottom). Red colour represents summits with significant trends, whereas blue represents nonsignificant trends. Detailed results of the time series analysis of each summit is found in Table S4. For exact length of time series per summit see Table S3.

we used the mean percent cover per species in each summit (i.e. 8–16 plots of 1 m^2) at each summit, and estimates of species richness based on the species lists of all corresponding plots.

Summits are distributed over three main biomes in the high Andes: the Páramo (5 target regions, 18 summits), the Puna (5 target regions, 20 summits) and Patagonian high Andes (2 target regions and 7 summits) that correspond to the northern, central and southern Andes, respectively (Pérez-Escobar et al., 2022; Simpson, 1983). The Páramo constitutes a humid nonseasonal tropical high Andean grassland distributed between 8° N and 7° S (Sklenář & Balslev, 2005). The Puna is a seasonal high Andean grassland system that occurs from 8° S to 29–30° S and is characterized by a dry and wet seasonal climate due to a pronounced cold dry season occurring from May through September (Cuesta et al., 2017; Tovar et al., 2022). The Patagonian high Andes occur from 32–39° S to 56° S (northern limit is under discussion), and are characterized by a marked seasonality with a narrow summer window (December–February), when the maximum precipitation is reached (Lencinas et al., 2021).

2.2 | Species data

2.2.1 | Taxonomy and biogeographic groups

A total of 585 taxa of vascular plants were identified at species (570) or infraspecies (15) level and 37 taxa were identified at the genus level, following validation of species names using the Checklist of the Vascular Plants of the Americas (Ulloa et al., 2017) and the World Flora Online (www.worldfloraonline.org/). For subsequent analysis, we used the species level for all taxa identified at the infraspecies level and of the 37 taxa identified to the genus level, we excluded *Hymenophyllum* sp, *Gnaphalium* sp, *Polypodium* sp, *Maxillaria* sp, *Myrteola* sp, and *Stelis* sp because we did not have any recorded species within those genera.

We classified species into 11 biogeographic groups based on species' geographic distributions according to occurrence records and the country catalogues available in TROPICOS (www.tropicos.org). Seven of these groups are the same as those described in Cuesta et al. (2020), (Table 1).

2.2.2 | Species occurrences data, estimation of species thermal niche traits and community-weighted temperature scores

We collected occurrence records for 582 of the 585 identified taxa (Table S2). We used the records collected by Cuesta et al. (2020), obtained from GBIF, TROPICOS, La Paz herbarium (LPB) and ULA-Merida herbarium. These records mostly represent species recorded during the first survey conducted at each of the summits. New GBIF data were downloaded on 6 October 2020 and 19 June 2021 for the new species. This new download included data for the species

TABLE 1 Biogeographic species groups based on species' geographic distributions according to occurrence records and the country catalogues available in TROPICOS (www.tropicos.org).

Biogeographic region	*Number of species*	Description
Andean alpine	13	Species present in the alpine region of both the tropical and temperate Andes
Andean montane	3	Species present in both the alpine and forest ecosystems in the tropical and temperate Andes
Cosmopolitan	23	Species with a broader distribution than the neotropics
Neotropical	31	Species distributed in lowlands and highlands within the neotropical region
Páramo endemic	94	Species only present in the Páramo
Patagonia	46	Species present in both the highlands and lowlands of Patagonia
Patagonia highland endemic	15	Species only present in the highlands of Patagonia
Puna endemic	143	Species only present in Puna
Tropical alpine	6	Species present in the alpine belt in the Andes, Central America, and Mexico
Tropical Andean alpine	66	Species present in both the Páramo and the Puna
Tropical montane	142	Species present in the tropical region in both, the alpine and forest biomes. That could include or not the Andes (e.g. Central America and Mexico)

registered in the three new target regions not included in Cuesta et al. (2020) (Gavidia, Santa Cruz, and Tierra del Fuego), and for those species that were renamed, since their identification has been revised by taxonomic authorities after the publication by Cuesta et al. (2020). These new data records were cleaned using the R package *CoordinateCleaner* (Zizka et al., 2019) to remove duplicated coordinates, country centroids, records located in botanical/biodiversity institutions and those with coordinates erroneously located outside the study area at sea level. In addition, we visually inspected each species' records in ArcMap 10.5 (ESRI, 2022) to identify and remove obvious georeferencing errors. The final clean data set, containing only records within the Neotropics (28° N in Mexico as the northern limit), included a total of 32,526 records (mean = 55 records per species, median = 23). An additional 1567 species occurrences were added from our permanent plots across the South American GLORIA sites.

Monthly mean air temperatures were downloaded from WORLDCLIM 1 (Hijmans et al., 2005) and then downscaled to 90m^2 using elevation and assuming an adiabatic lapse rate of 0.54°C/100 m (Cuesta et al., 2020). These downscaled temperatures were used to estimate species thermal niche traits (see below). We used this data set instead of the CHELSA data set (Karger et al., 2017) because they represent the mean climate between 1960 and 1990, which is the approximate period when most of the species' occurrences were originally collected.

Thermal niche traits [i.e. optimum (mean) temperature, minimum temperature, and niche breadth (maximum–minimum temperature)] were estimated for each species following Cuesta et al. (2020), which is based on monthly air temperatures at the location of each occurrence record for species with at least 10 records. For taxa identified at the genus level, we used the combined occurrence data from the species belonging to a given genus to estimate its thermal niche. We also used the genus level thermal niches for species with less than 10 records. For 10 species, we found less than five records with no other congeneric species (Table S2). For these species, we assigned the mean thermal score of each community where they occurred (see below).

We then calculated a community-weighted temperature score (CTS; °C) for each summit, as the average of the thermal optima for the constituent species weighted by their percent cover at that survey [analogous to the 'community temperature score' of Feeley et al., 2013]. Following the same procedure, we estimated a community-weighted niche breadth score (CBS; °C) based on the statistical range and a community-weighted minimum temperature score (CMS; °C).

2.3 | Temperature data

2.3.1 | Soil temperatures locally recorded at the summits

On every focal summit, temperature loggers (GeoPrecision, Onset Stowaway Tidbit or Onset Hobo Pendant UA-001-64 Temperature/Alarm) were installed at each cardinal direction (N, E, S and W), buried at 10-cm substrate depth in vegetation plot sections (Pauli et al., 2015). A total of 174 loggers yielded soil temperature series at hourly intervals for the period between plot installation and the final vegetation survey (Table S3). Soil temperature data were processed as follows: (1) the day when the sensor was installed was removed to avoid days with incomplete data and to allow the sensor to acclimatize; (2) unusual temperatures anomalies were eliminated in two cases: (a) when records were three times higher or lower than the standard deviation of the daily mean temperature; (b) after plotting every logger's time series, we visually identified anomalous periods (e.g. very high temperatures, possibly due to the logger being unearthed by erosion or other local processes and exposed to high radiation); in this latter case, we eliminated the entire day of data. Using the cleaned sensor dataset for years that had at least 11 months of data, we merged the four temperature time series of each summit and estimated daily mean, maximum and minimum soil temperatures for every summit for the entire recorded period.

2.3.2 | Climate data

We downloaded the minimum temperature of the coldest month (BIO6) and the total annual precipitation (BIO12) layers from the CHELSA dataset (Karger et al., 2017) to represent the present-day climate of each summit. Given that the CHELSA data set covers the period 1979–2013, and the first vegetation surveys were done between 2008 and 2012, it best represents the ambient temperatures and precipitation conditions on the summits prior to and during the beginning of the study period. Furthermore, we compared the locally recorded soil temperatures and the CHELSA data set and found high consistency between both (Figure S1).

2.4 | Analyses

2.4.1 | Time series analyses of soil temperature

We conducted time series analyses of soil temperature data at each summit to identify significant trends in daily mean, minimum and maximum temperatures. As these data were not available for the three summits of the Podocarpus target region (PNP- Páramo Biome) and one from Abra del Acay (AnsAna), we analysed the remaining 41 summits across the Andean range. The significance of the trends was analysed using the Mann–Kenndal test (Pohlert et al., 2020) in R using the package *Kendall* (McLeod, 2005). Furthermore, we performed a linear regression to the trend data and derived the slope of the fit that represented the increase (positive) or decrease (negative) in degrees per day for the whole time series of each studied summit (i.e., soil temperature rate).

2.4.2 | Vegetation dynamics

We compared species richness and their per cent cover for each summit between vegetation surveys to estimate annual rates of vegetation change. Then, we performed a binomial probability test to determine whether the number of summits with a positive trend in species richness and vegetation cover values differed significantly from the null expectations of equally positive and negative changes. We also analysed changes in vegetation cover (%) and species richness by biome, and by biogeographic category within each biome by estimating annual rates of change for each of these levels. To estimate the change by biome, we first estimated the annual rate of change for each species on each summit (%/yr.); second, we estimated the total annual rate of vegetation change by summit by summing all species' rates of change. Third, we estimated the mean annual rate of vegetation change and species richness per biome by averaging the rate of change of all summits within a given biome. We tested the differences between biomes by using a Games–Howell test (Domingues et al., 2007).

To estimate the change per biogeographic category for each biome, we first estimated the annual rate of change for each biogeographic group within each summit (%/yr.) by summing the vegetation cover of all species belonging to each biogeographic category (or counting the number of species for species richness). Then, within each biome, we estimated the average rate of change for each category using summits where the biogeographic category was present.

2.4.3 | Estimation of thermophilization rates

To assess thermophilization rates (TR) of each summit over time, we calculated the annualized difference in CTS between surveys for each summit: $TR=[(CTS_{t2}-CTS_{t1})/\text{years between surveys}]$. We also estimated the TR for CBS, and CMS. We used a binomial probability test to determine whether the number of summits with positive TR values differed significantly from the null expectations of equal positive and negative changes.

2.5 | Analysing potential drivers of vegetation dynamics

To identify the main climatic drivers structuring plant community thermal composition before analysing the effects of recent temperature changes along environmental gradients, we performed a correlation analysis between community-level thermal niches and the following summits' climatic conditions: minimum temperature of the Coldest Month (Tminair) and total annual precipitation (Annpp) from CHELSA and daily maximum, minimum and mean soil temperatures recorded on each summit for the period between surveys.

Subsequently, we used generalized linear models to assess whether changes in vegetation cover, richness, and TRs (TR_{CTS}, TR_{CBS} and TR_{CMS}) of each summit were explained by the corresponding rates of change in the locally recorded soil temperatures (using the slope of the trend), and present-day summits' climatic conditions (i.e. $Tmin_{air}$ and Annpp). Regression assumptions were visually inspected to ensure that normality and homogeneity of variance of the residuals were met. Since not all the summits had soil temperature data, only 41 summits were used for this analysis (Table S3). Lastly, we performed a correlation analysis at the biome level (i.e. Páramo, Puna and Patagonia) to assess whether the pan-continental trends differ from changes analysed separately for each biome (Figure S2). We did not use generalized linear models due to the limited number of summits for each biome (especially for Patagonia, *n* = 7).

3 | RESULTS

3.1 | Changes in soil temperatures across high Andean summits

Over the last decade, we found heterogeneous changes in soil temperatures across the Andean summits. Overall, one-third of the summits showed a significant increase in their thermal amplitude due to an increase in their maximum temperatures and a decrease in minimum temperature (Figure 1). Increases in thermal amplitude were the most common pattern in all three biomes but was especially marked on the Patagonia and Puna summits. Interestingly, 10 out of the 45 summits showed a contraction in their thermal amplitude due to a significant increase in their minimum temperatures and a significant decrease in maximum temperature (Figure 1). Likewise, 22 of the study summits exhibited significant increases in their daily maximum soil temperatures (range = 0.0002–0.023°C/day), and 21 exhibited significant increases in daily minimum soil temperatures (range = 0.00013–0.020°C/day; Table S4, Figure S3). Conversely, 17 summits registered significant decreases in their daily minimum soil temperatures (range = −0.0023 to −0.0001°C/day) (Table S4).

3.2 | Vegetation dynamics across the high Andean summits

Overall, there was a mean net-loss in vegetation cover (mean = −0.26%/yr) and a net-increase in species richness (mean = 0.38 species /m^2/yr) over time across the Andean summits. Nonetheless, the number of summits with increments over time in species richness and vegetation cover was significantly greater than expected due to random fluctuations (binomial probability = 0.049).

Most summits (*n* = 29) showed increases in vegetation cover between surveys, while 16 summits had decreases in vegetation cover. The mean annual rate of change on summits that lost vegetation cover was −3.79%/yr, whereas the rate of change on summits that gained vegetation cover was 1.69%/yr (Table S6). Remarkably, comparing between elevation belts, on average, the subalpine summits gained vegetation cover whereas the alpine, subnival and nival summits lost vegetation cover (Table S6). Across latitudes, more than half of the Páramo summits (55%) decreased in vegetation cover. In contrast, few summits in the Puna (*n* = 4) and Patagonia (*n* = 2) biomes decreased in vegetation cover, respectively (Figure 2a). However, we did not find significant differences for rates of change

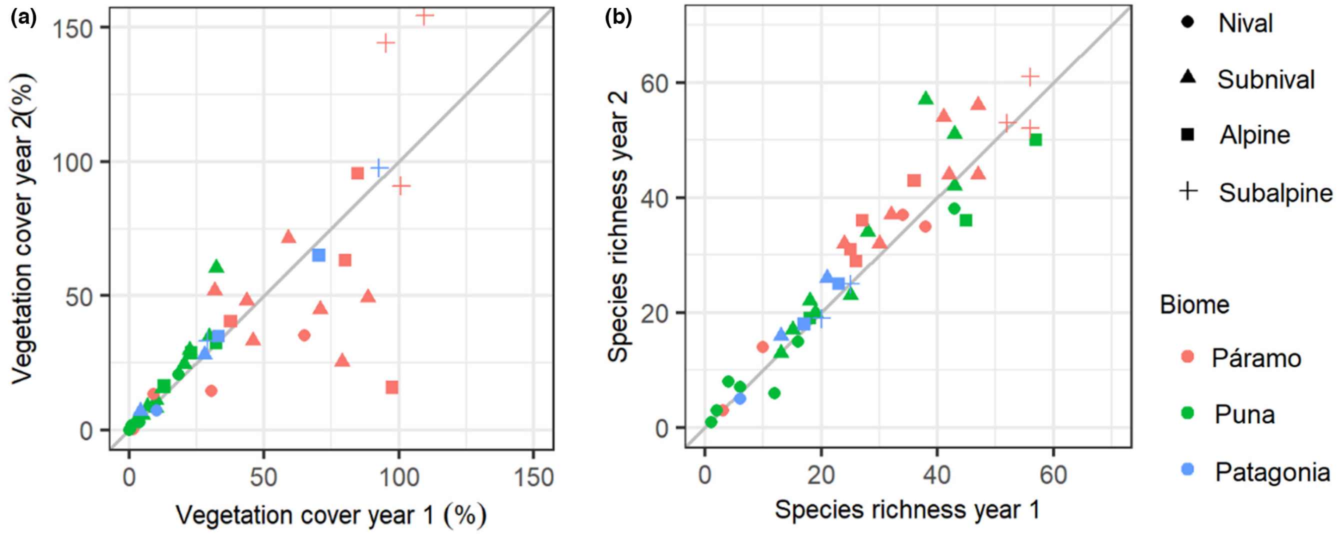

FIGURE 2 Comparison between the first survey and the second survey (5–8 years apart, see details in Table S1) for vegetation cover (a) and species richness (b) for 45 summits located in the High Andes. Points above the line indicate higher vegetation cover or richness in the second survey, and those below the line indicate lower values in the second survey in comparison to the first one. Points on the diagonal line represent values that were similar for both surveys.

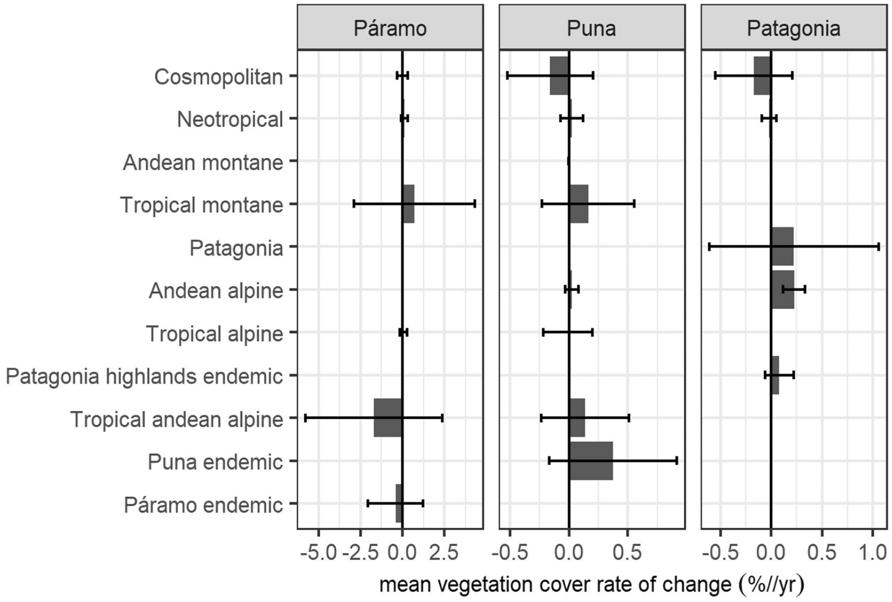

FIGURE 3 Mean rates of vegetation cover changes in each biogeographic species category (in the *y* axis) per biome (columns, names in top row) between the two surveys (5–8 years apart, see details in Table S1) on the high Andean mountain summits. Bars represent the mean rates of cover change and its dispersion (one standard deviation) per biogeographic category.

in vegetation cover between biomes [Games-Howell test: Páramo-Patagonia: $q = 1.28$, $p = 0.645$; Páramo-Puna: $q = 1.61$, $p = 0.505$; Puna Patagonia: $q = 1.51$; 0.55; Figure S4].

Most summits ($n = 29$) showed increases in species richness between surveys at a mean annual rate of 0.89 ± 0.7 species/m^2, whereas in fewer summits ($n = 12$), species loss occurred at a slower rate (mean = −0.71 ± 0.53 species/m^2/yr). The subnival summits showed the greatest increase in species richness (mean = 1.09 ± 0.78 species/m^2/yr). In contrast, the nival summits mostly showed a decrease in species richness through time (mean = −0.59 ± 0.40 species/m^2/yr). Across latitudes, most of the summits showed increases in species richness between surveys, particularly in the Páramo (Figure 2b). As in the trends for vegetation cover, we did not find significant differences in species richness between biomes [Games-Howell test: Páramo-Patagonia: $q = -2.45$, $p = 0.22$; Páramo-Puna: $q = -2.78$, $p = 0.13$; Puna-Patagonia: $q = -0.72$, $p = 0.87$; Figure S4].

When analysing the changes in vegetation cover for the different biogeographic groups in the different biomes, we observed that species from the 'Tropical Andean alpine' and 'Páramo endemic' biogeographic categories, on average, decreased in cover on the Páramo summits. In contrast, there was an increase in the rate of mean cover change for species from the 'Tropical montane' and 'Neotropical' categories (Figure 3). Only 'Cosmopolitan' species lost cover in the

Puna summits while most species from other biogeographic categories, particularly 'Tropical montane' and 'Puna endemic', gained in vegetation cover. Similarly, in Patagonia, 'Cosmopolitan' species lost cover while 'Patagonia', 'Patagonia highlands endemic' and 'Andean alpine' species increased in cover (Figure 3).

We found that vegetation cover trends were negatively related to minimum air temperature (Table 2). Summits with higher minimum temperatures (typically Páramo summits) tended to have greater losses in vegetation cover than summits with lower minimum temperatures (i.e. Puna and Patagonia summits), which on average, gained in cover (Figure 4). However, contrary to our initial expectations, changes in microclimate soil temperatures and annual precipitation were not significantly related to the observed changes in vegetation cover (Table 2).

TABLE 2 Regression models explaining thermophilization rates (TR) (based on annualized changes in community-level thermal niches), vegetation cover and species richness rates of change as a function of minimum air temperature and annual precipitation from the CHELSA global dataset, and the annual rate of change in soil maximum temperature obtained from locally installed data loggers (see methods).

	Estimate	Std. error	*t* value	Pr(>|t|)	
$\mathrm{TR}_{\mathrm{CTS}}$ (°C/yr)					
(Intercept)	3.47e−02	3.7e−02	0.946	0.350	
Minimum air temperature	3.35e−03	2.7e−03	1.24	0.224	
Annual precipitation	−1.1e−05	2.8e−05	−0.43	0.672	
Soil maximum temperature rate of change	3.48	8.35	0.42	0.679	
$\mathrm{TR}_{\mathrm{CBS}}$ (°C/yr)					
(Intercept)	6.09−02	0.103	0.591	0.558	
Minimum air temperature	7.59e−03	7.6e−03	0.998	0.325	
Annual precipitation	−5.5e−06	7.8e−05	−0.071	0.944	
Soil maximum temperature rate of change	−5.774	2.345	−0.246	0.807	
$\mathrm{TR}_{\mathrm{CMS}}$ (°C/yr)					
(Intercept)	−1.9e−03	2.4e−02	−0.081	0.936	
Minimum air temperature	8.8e−04	1.8e−03	0.497	0.622	
Annual precipitation	1.55e−05	1.8e−05	0.852	0.400	
Soil maximum temperature rate of change	10.42	5.455	1.909	0.064	.
Vegetation cover rate of change (%/yr)					
(Intercept)	−0.9950	2.1282	−0.468	0.643	
Minimum air temperature	−0.26522	0.1571	−1.688	0.0999	.
Annual precipitation	−0.00127	0.00162	−0.784	0.4378	
Soil maximum temperature rate of change	277.395	484.336	0.573	0.5703	
Species richness rate of change (#sp/m^2/yr)					
(Intercept)	6.69e−01	4.8e−01	1.40	0.1698	
Minimum air temperature	9.46e−02	3.5e−02	2.681	0.0109	*
Annual precipitation	2.07e−04	3.6e−04	0.570	0.5719	
Soil maximum temperature rate of change	2.232	1.088	2.053	0.0472	*

Note: $\mathrm{TR}_{\mathrm{CTS}}$, $\mathrm{TR}_{\mathrm{CBS}}$, and $\mathrm{TR}_{\mathrm{CMS}}$ correspond to the thermophilization rates of the community temperature score, the community niche breadth score and the community minimum temperature score, respectively. Asterisks represent a significant relationship: *0.05, whereas a point represents a marginal significance: ·0.1.

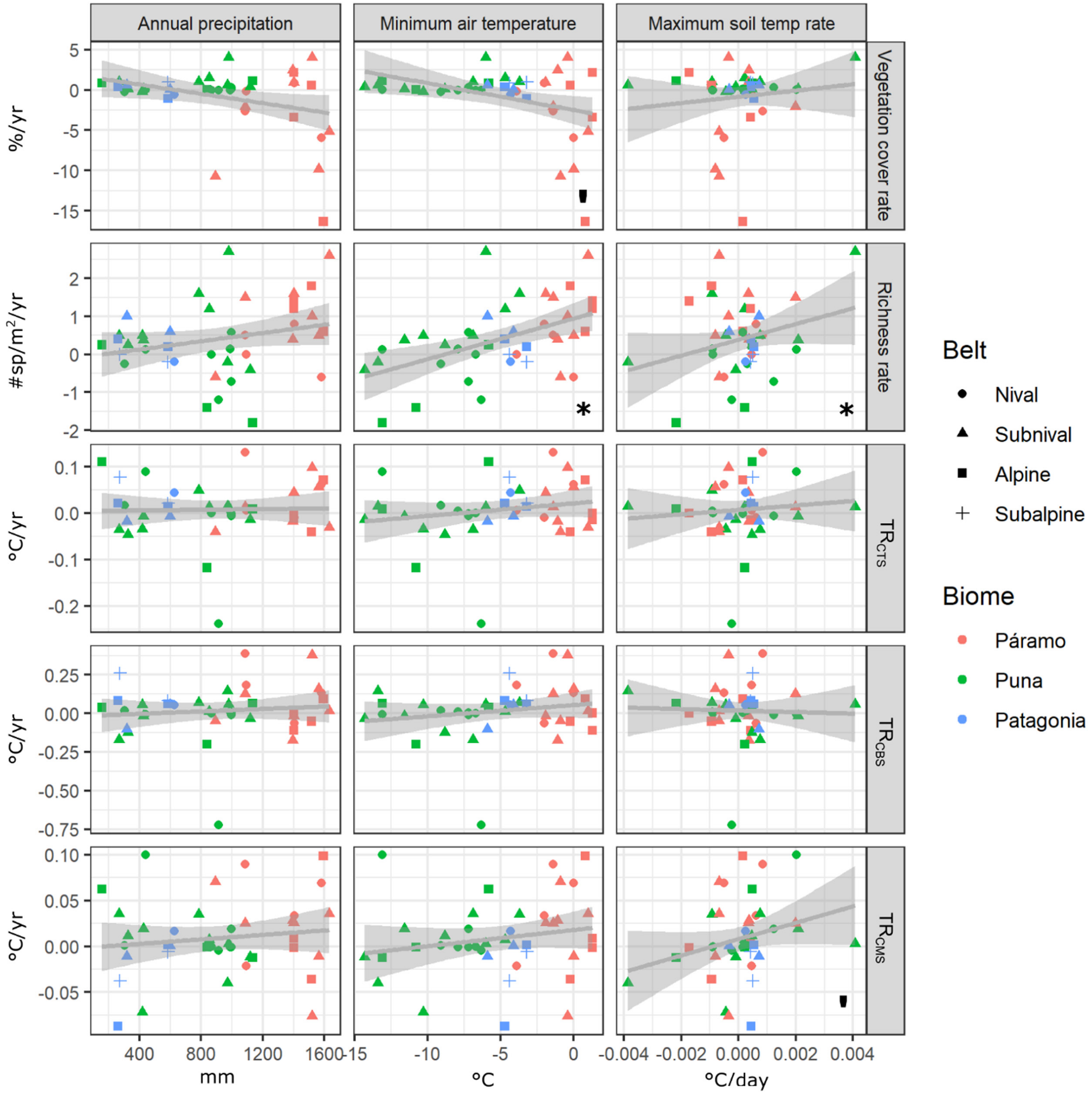

FIGURE 4 Rates of vegetation changes (vegetation cover, species richness, thermophilization) of high Andean summit plant communities in repeatedly surveyed plots along environmental gradients: total annual precipitation (left column), minimum air temperature (central column) extracted from CHELSA (average values for the period 1979–2013), and rate of change of the daily maximum soil temperature (right column), estimated from soil sensors' data over the last decade. Thermophilization rates of the community thermal optimum score (TR$_{CTS}$), community breadth score (TR$_{CBS}$), and community minimum temperature score (TR$_{CMS}$). Asterisks denote significant trends. Asterisks represent a significant relationship: *0.05. Marginal significance is shown as '(between 0.1 and 0.05).

We also found a significant positive relationship between minimum air temperature (current conditions), the change in daily maximum soil temperature over the study period, and the rate of change in species richness (i.e. summits closer to the equator, typically with higher minimum temperatures, showed more marked increases in maximum soil temperature and species richness). As in vegetation cover, annual precipitation had no effect on species richness trends (Table 2, Figure 4).

When the analyses were conducted at the biome level, we only found a significant positive correlation between rate of change in species richness and the summits' minimum temperature and annual rate of change in locally recorded soil temperature for the Puna summits (Figure S2).

3.3 | Changes in community-weighted thermal scores and TR of high Andean plant communities along environmental gradients

We found significant positive relationships between community-weighted temperature scores and the summits' climatic conditions, particularly with the daily maximum soil temperature and minimum air temperature of the coldest month ($Tmin_{air}$; Table 3).

For the TRs, we found that more than half of our studied summits ($n=27$) had a positive TR$_{\mathrm{CTS}}$, TR$_{\mathrm{CBS}}$ and TR$_{\mathrm{CMS}}$ (i.e., community-weighted scores increased between surveys, Figure 5). The positive thermophilization rates indicate an increasing relative abundance (i.e. per cent cover) of plant species from relatively warmer climates and with broader thermal niches. The number of summits with positive TR$_{\mathrm{CTS}}$ and TR$_{\mathrm{CBS}}$ were marginally significantly greater than expected due to random fluctuations in composition over time (binomial probability = 0.051). We found a similar pattern for the TR$_{\mathrm{CMS}}$ index, but only 25 summits (56%) showed increased community scores between surveys (binomial probability = 0.064). The overall mean TR$_{\mathrm{CTS}}$ and TR$_{\mathrm{CBS}}$ was 0.007°C/yr and 0.017°C/yr, respectively [95% confidence interval (CI) = −0.003 – 0.023°C/yr]. Nevertheless, 19 summits exhibited a negative TR$_{\mathrm{CTS}}$, indicating that cold-adapted species increased their coverage (Figure 4).

There was no relationship between TR$_{\mathrm{CTS}}$, TR$_{\mathrm{CBS}}$ or TR$_{\mathrm{CMS}}$ and the minimum air temperature or annual precipitation (Table 2). Likewise, thermophilization rates were not associated with the annual rate of change in soil maximum temperature, except for TR$_{\mathrm{CMS}}$, which had a marginally significant relationship (Table 2; Figure 4). When the analyses were conducted at the biome level, we found only in the Puna summits a significant positive correlation between the rate of change of soil maximum temperature and TR$_{\mathrm{CMS}}$ (Figure S2).

4 | DISCUSSION

4.1 | Soil temperature trends

Half of our study summits exhibited an increase in daily maximum temperatures, suggesting that these high Andean summits are experiencing a progressive warming in line with our first hypothesis and the general expectations of anthropogenic climate change. Interestingly, however, the daily minimum soil temperature decreased on half of the summits, leading to an expanded temperature amplitude on 18 out of the 41 summits.

The changes in soil temperatures were highly heterogeneous (Table S4), even within the same target region. This highlights the high climatic variability in the Andes induced by differences in local topography, macroclimates and external drivers such as ENSO (Garreaud, 2009; Sklenář et al., 2016). The position of the permanent plots within each summit (one in each of the four main cardinal orientations) and local slope inclinations most likely causes pronounced differences in the thermal input, significantly influencing vegetation physiognomy and composition (Carilla et al., 2018; Lencinas et al., 2021).

TABLE 3 Correlations between community-level thermal niches (CBS, community niche breadth score; CMS, community minimum temperature score; CTS, community temperature score), minimum air temperature of Coldest Month ($Tmin_{air}$), total annual precipitation (Ann pp), daily maximum, minimum and mean soil temperature ($Tmax_{soil}$, $Tmin_{soil}$, $Tmean_{soil}$) obtained from data loggers on each summit (see methods).

	CTS	CBS	CMS	$Tmin_{air}$	Ann pp.	$Tmax_{soil}$	$Tmean_{soil}$	$Tmin_{soil}$
CTS	– –							
CBS	0.72*** <0.001	– –						
CMS	0.7*** <0.001	0.05 0.77	– –					
$Tmin_{air}$	0.33* 0.032	0.11 0.47	0.69*** <0.001	– –				
Ann pp	0.004 0.98	0.39* 0.01	0.40** 0.01	0.56*** <0.001	– –			
$Tmax_{soil}$	0.6*** <0.001	0.44** 0.004	0.35* 0.03	0.03 0.83	0.08 0.63	– –		
$Tmean_{soil}$	0.26 0.10	0.28 0.08	0.10 0.55	0.17 0.28	0.10 0.52	0.66*** <0.001	– –	
$Tmin_{soil}$	0.06 0.73	0.23 0.14	0.42** 0.006	0.86*** <0.001	0.50*** <0.001	0.09 0.57	0.34* 0.03	– –

Note: Air temperature and annual precipitation were extracted from CHELSA (average values for the period 1979–2013). Asterisks represent a significant correlation: ***0.001; **0.01; *0.05.

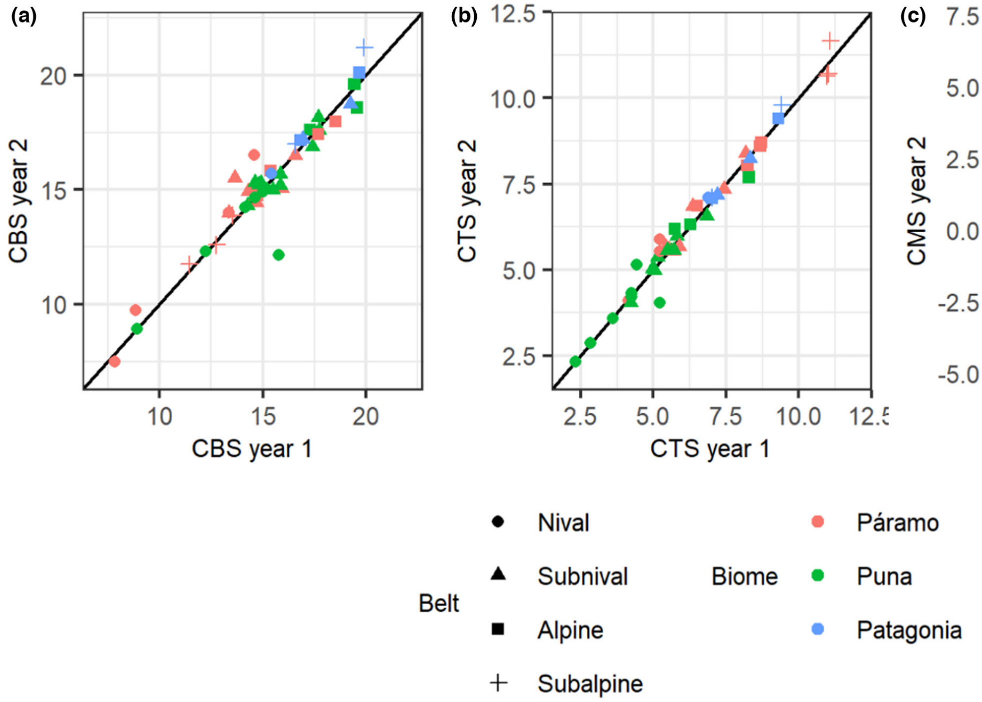

FIGURE 5 Comparison of community-level thermal niches between the first and second survey (5–8 years apart, see details in Table S1) for 45 summits located in the High Andes. (a) Community niche breadth score (CBS), (b) Community temperature score (CTS), and (c) Community minimum temperature score (CMS). Points above the line indicate a higher value in the second survey in comparison to the first survey and vice versa for those below the line. Points on the diagonal line represent constant community-weighted thermal scores. The specific dates of each survey for each summit are found in Table S1.

4.2 | Vegetation dynamics across the high Andean summits

We found two contrasting patterns of changes over time across the Andean summits. On average, at a continental scale, summits are losing vegetation cover (particularly alpine to nival summits) and, concurrently, are experiencing an increase in species richness (Figures 2 and 5). However, most individual summits showed increments over time in species richness and vegetation cover. These changes are in line with our second hypothesis (Table S5).

4.2.1 | Vegetation cover

On average, Páramo summits tended to lose the largest proportions of vegetation cover while increasing in species richness. The loss of vegetation cover could be linked to the potential higher vulnerability of Páramo communities to climate change. Páramo summits are dominated by species with narrow niche breadths (Figure S5), such as 'Páramo endemics' and 'Andean alpine' biogeographic groups (Cuesta et al., 2020; Llambi et al., 2022). Greater thermal specialization may make these species more vulnerable to changes in temperature (Janzen, 1967). In consistency, species restricted to equatorial latitudes, and plant communities dominated by these species, were identified as the most vulnerable to a projected 1.5°C warming, due to a potentially higher risk of losing thermal niche space (Cuesta et al., 2020).

In contrast to the Páramo summits, plant communities located on the Puna and Patagonia summits were composed of species with broader thermal niches and have mostly undergone an increase in their vegetation cover over time (e.g. Puna endemics, Patagonia highlands). The greater differences between species' thermal minima and maxima suggests a larger capacity to cope with novel climates (Figure S5). Compared with the equatorial tropics, the seasonal tropical and temperate situation of the Puna and Patagonia biomes are expected to favour species' adaptation to a wider range of thermal conditions (Baied & Wheeler, 1993).

Remarkably, the major losses in vegetation cover were concentrated in the alpine and nival belts (Table S6), similar to the declines in the subnival and nival belts reported from the Austrian Alps (Steinbauer et al., 2020). The continued losses in vegetation cover in the high Alps were strongly attributed to diebacks of narrow-ranged cold-adapted species, suggesting an increasing maladaptation of subnival–nival species to warmer habitat conditions, instead of growth reduction driven by competition (Lamprecht et al., 2018; Steinbauer et al., 2020). In the equatorial South American mountains, increasing maladaptation of specialized cold-adapted plants (e.g., low propagation rates) could have led to similar reductions of vegetation cover in the upper alpine to nival zones, although the specific driving mechanisms of maladaptation require further studies.

4.2.2 | Species richness

We found widespread increases in plant species richness across the high Andean summits that were more pronounced on summits with higher increases in soil temperature. Most of these summits were from the subnival belts and located at lower latitudes. The observed trend could be related to: (1) a progressive expansion of species from the Tropical Andean alpine biogeographic group and other, more warmth-demanding taxa with high thermal optima (Figure S5), as evidenced by the observed increase in CTS and CBS between surveys; (2) an overall reduction in vegetation cover, leaving space for plant colonization in available niches mediated by more favourable conditions, as previously reported for European mountains (Pauli et al., 2012; Rogora et al., 2018; Steinbauer et al., 2020). Colonization of species with good dispersal mechanisms (e.g. wind-dispersed small herbs and grasses) is well-documented for primary succession in deglaciated forelands in the Andes (Llambí et al., 2021; Zimmer et al., 2018). These species could colonize quickly and increase local richness.

It is possible that the observed increases in species richness are transient events, reflecting a growing 'extinction debt' caused by a lag in the rate of local extinctions (i.e. of cold-adapted specialists) relative to the speed of modern climate change (Rumpf et al., 2019). The mechanisms related to the posited 'extinction debt' are related to the interaction of demographic inertia and time lags in alpine plant replacement by novel species spreading upwards from lower elevation (Nomoto & Alexander, 2021; Rumpf et al., 2018). Both upper and lower range margins of species in the Alps, however, have been found to move upwards at a similar pace, which may rapidly switch transitional gains in species numbers to local extinction of species (Rumpf et al., 2018). However, these range displacement processes and their long-term consequences remain to be explored in more detail in the unique and complex bio-geoclimatic scenario of the Andes (Cuesta et al., 2019).

4.3 | Thermophilization rates of high Andean plant communities

We expected widespread increases of thermophilic species combined with decreases in cold-adapted species as a consequence of warming microclimatic conditions, as has been previously observed on European mountain summits (Gottfried et al., 2012). We found that most of the studied plant communities did increase their thermal optimum (CTS) and thermal breadth (CBS) over time (positive TRs), suggesting an ongoing thermophilization process on the Andean summits. The increase in CBS is related to the progressive colonization of species from warmer/lower elevations with broader thermal niches such as those from the 'Tropical montane' biogeographic group (Figure S5). The increase in CTS could be attributed to a reduction in coverage of cold-adapted species and an increase in species with higher thermal optima. However, contrary to our hypothesis, rates of change of soil temperatures did not explain TRs, except for a marginal positive relationship between TR_{CMS} and trends in daily soil maximum temperatures.

While more than half of the summits ($n = 27$) had positive increase in TR_{CBS} and TR_{CTS}, we also found a heterogeneous pattern across the Andes. More than a third of the study summits (38%) exhibited decreases in their CTS and CBS (i.e. negative TRs). Similar to observations from Andean forests (Fadrique et al., 2018), TRs of high Andean plant communities are expected to differ along latitudinal and elevation gradients because environmental conditions vary along these gradients. For example, we found that communities at warmer habitats (higher minimum temperatures) had higher thermophilization rates compared with summits exposed to colder conditions (lower minimum temperatures). There are several other potential explanations for the high spatial heterogeneity in TRs observed on mountain summits across the high Andes. First, there could be a considerable variation among regions in the proportions of species exhibiting a wide thermal breadth. In regions with a larger proportion of species with a broad thermal niche, similar warming rates would yield weaker thermophilization signals than in other regions. Second, many of our mountain summit species may show a truncated niche (Feeley & Silman, 2010) due to the existence of sharp ecotonal boundaries and orographical differences in soil development relative to rock cover. Such sharp boundaries, for example, occur between alpine and lower elevation habitats in the dry environments of the Puna (e.g. Sajama) and the northern relatively dry Páramos of Venezuela.

Contrary to our expectations (H3), TRs were not clearly associated with changes in soil maximum temperature. The lack of association could be due to a time lag in plant communities' responses to the observed microclimatic trends (Nomoto & Alexander, 2021). Long-lived species, including many high Andean plants (De Witte et al., 2012; García et al., 2016), can persist through periods of unsuitable climatic conditions, where obvious reductions in coverage and reproductive failure may only occur over prolonged periods. Thus, our study time span could have been too short to accurately quantify compositional changes. Concurrently, several plant species from the high Andes are small and changes in their species cover may have little influence on TRs, compared to larger or more-dominant species (many of which are very long lived, e.g., cushions, giant rosettes). Nevertheless, we found a high correlation between community-weighted temperature Scores of the last survey and the climatic conditions of the respective summits (Table 3), which suggests that the temperature regime strongly determines the composition of the Andean plant communities. Similar relationships have been found across European mountain summits (Gottfried et al., 2012). Longer term studies of both alpine and subnival vegetation in Europe showed accelerating compositional changes leading to faster TRs (Lamprecht et al., 2018; Steinbauer et al., 2020).

The data from the 45 summits studied here represent the largest standardized vegetation data set of the Andes above the upper forest line, which also includes repeated surveys. Nonetheless, it is relatively limited with respect to the extremely high variability of the alpine vegetation across the Andes—the planet's largest and most diverse mountain system in terms of latitudinal extent, topography, climate variability and biodiversity (Hazzi et al., 2018; Pérez-Escobar et al., 2022). The resulting shortage of replicates probably influenced the detection of a stronger directional signal of compositional changes, at least over the rather short study periods of less than a decade. Therefore, the GLORIA-Andes network is planned to be expanded to yield a better coverage in each biome, if possible equipped with soil humidity sensors, and resurveyed at regular intervals that are conducive to a long-term monitoring evaluation.

5 | CONCLUSIONS

We here provide the first continent-scale analysis of microclimatic and compositional changes of mountain summit plant communities across the high Andes. We showed that most of the Andean summits are experiencing significant but heterogeneous changes in soil temperatures (i.e. increase and contraction in their thermal amplitude and overall increase). We also observed an average decrease in vegetation cover, and an increase in species richness. The increase in species richness was widespread and exceptionally fast on summits with higher rates of daily maximum soil temperatures, especially on subnival Páramo summits. We also observed that more than half of the summits experienced thermophilization (positive TRs) probably due to a gradual expansion of taxa with high thermal optima and broader thermal ranges. This is most likely combined with a reduction of narrow-ranged cold-adapted species. We, however, also showed that a considerable share of the summits (38%) exhibited decreases in their CTS and CBS (negative TRs).

This heterogeneity in TRs is influenced by the strong environmental gradients across the high Andes. Indeed, we found that TR_{CMS} tends to be higher on summits with warmer air temperatures, closer to the equator. However, other factors, such as the high turnover in species composition among summits and their thermal niche traits, will also likely influence TRs. Future studies focussing on specific biomes, summits' aspects and elevation belts as additional predictive variables could provide a deeper understanding of high Andean plant communities' responses to warmer conditions. Lastly, contrary to a priori expectations, the changes in soil temperature during the assessed period did not explain the changes in vegetation cover or TRs. However, changes in soil temperature did explain species richness trends (positive relationship). A potential explanation is that the 5- to 8-year intervals do not yet, or only marginally, capture changes in vegetation through time (as with TRs). We expect a vegetation time lag in response to changes in temperature, owing to the ability of many high Andean species to persist in varied climatic conditions, their commonly slow growth rates, and long life spans (Cotto et al., 2017).

Tracing and understanding the development of tropical high mountain plant communities in response to modern climate change requires long-term ecological networks. The GLORIA-Andes network is well poised for continued vegetation change studies on a continental scale, spanning the only high mountain system uninterruptedly extending from the equator to the temperate biome.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article. Likewise, our derivate data and codes upon which the main figures were based can be accessed in Dryad: The following DOI has been assigned: doi:10.5061/dryad.b2rbnzsk7. https://datadryad.org/stash/share/uf5yFau-2pSm7YMAh1abAvi7nE0ytoXxzpUYS63ojg4.

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BIOSKETCH

The GLORIA-Andes network is a research platform created in 2008 that supports the establishment of permanent monitoring sites on high Andean summits to study the effect of climate change on the Andean mountains (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 19 GLORIA sites (Target regions) following the same protocol and data management standards established by the global GLORIA network (http://www.gloria.ac.at/).

SUPPORTING INFORMATION

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

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