J. Mt. Sci. (2022) 19(12): 3441-3457 e-mail: jms@imde.ac.cn http://jms.imde.ac.cn
https://doi.org/10.1007/s11629-022-7473-8

Original Article

Species, growth form, and biogeographic diversity of summit vegetation along an elevation gradient in the tropical Andes: a baseline for climate change monitoring

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Citation: Llambi LD, Gámez LE, Pelayo R, et al. (2022) Species, growth form, and biogeographic diversity of summit vegetation along an elevation gradient in the tropical Andes: a baseline for climate change monitoring. Journal of Mountain Science 19(12). https://doi.org/10.1007/s11629-022-7473-8

Abstract: Tropical alpine ecosystems exhibit outstanding plant diversity and endemism while being particularly sensitive to the impacts of climate change. Although understanding spatiotemporal changes in plant species composition, richness and community structure along tropical alpine altitudinal gradients is of primary importance, both the functional and historical/biogeographic dimensions of vegetation diversity remain largely unexplored. We used Generalized Linear Models and multivariate analyses to assess changes in species, growth forms, and biogeographic groups richness and abundance, in response to habitat variables along an elevation gradient in seven summits (3800 to 4600 m asl) in the Venezuelan Andes, studied using the standardized

Received: 27-Apr-2022
Revised: 20-Jul-2022
Accepted: 16-Aug-2022

approach of the GLORIA-Andes monitoring network. The habitat variables assessed were soil temperature (-10 cm), soil organic matter, slope inclination, and substrate cover. We found 113 species, representing 72 genera, 32 families, 13 growth forms, and seven biogeographic origins, that included 25% of endemic elements. We observed richer vegetation, both in terms of species and growth forms, in summits with higher soil temperatures and higher SOM content, as well as higher biogeographic origin richness with increasing soil temperatures. The presence of holarctic elements increased toward higher elevations, while the occurrence of austral antarctic elements increased toward lower elevations. Our results indicate that biogeographic and functional approaches to vegetation diversity capture well the effect of abiotic filtering on community structuring in these tropical alpine environments. These findings constitute an important baseline for monitoring vegetation dynamics linked to climate change in the Venezuelan Andes by highlighting the functional and historical perspective on vegetation analyses, in contrast with more traditional approaches, based only on taxonomic species diversity.

Keywords: Alpine vegetation; Biogeography; Elevation gradient; Functional diversity; Páramo; Soil organic matter; Temperature; Tropical Andes

1 Introduction

Mountains are considered unique biomes in terms of their high alpha and beta diversity, driven by marked topographic and environmental gradients over short distances. The impacts of climate change are expected to be particularly significant in high alpine ecosystems, given their geographical isolation, as well as the limited range size and unique adaptations to cold conditions of many of their constituent species (Pauli et al. 2007; Hoegh-Guldberg et al. 2008; Lamprecht et al. 2018). High exposure and vulnerability of alpine vegetation to global warming will potentially impact the species' abilities to adapt to the new abiotic and biotic conditions. These species may either migrate, vertically or horizontally, looking for more suitable habitats, or become extinct. Given the characteristic conical shape of most high mountain areas, migrations could cause the loss of habitat area for those species with thermal optima at the highest elevations (Pauli et al. 2007; Chen et al. 2011; Tomiolo and Ward 2018; Cuesta et al. 2020).

Tropical alpine ecosystems (TAEs) are cold equatorial environments in which the unique combination of abiotic conditions has filtered (in the ecological timeframe) and selected (in the evolutive timeframe) plants with distinctive adaptive strategies (Monasterio and Reyes 1980; Körner 2003; Rada et al. 2019). Tropical alpine plant communities, particularly in the Andes, are strongly structured by climatic gradients, topographical complexity, high habitat heterogeneity and multiple biogeographical origins, leading to outstanding levels of species richness and endemism compared to other extra-tropical alpine environments, even if they exhibit lower local species diversity than other lowland tropical systems such as rainforests (Myers et al. 2000; Körner 2003; Winkler et al. 2016; Elsen et al. 2018). These characteristics make them ideal natural laboratories for understanding and monitoring the effects of global warming on mountain biodiversity (Anderson et al. 2011; Krishnaswamy et al. 2014). However, TAE remain relatively understudied compared to alpine regions in Europe and North America (Urban 2015).

The high biodiversity of TAEs is not only reflected in their high species richness and endemism, but also in terms of the diversity of their growth forms and evolutionary/biogeographic origins (Sklenář et al. 2014; Rada et al. 2019). On the one hand, these ecosystems exhibit a unique physiognomy and an outstanding functional diversity compared to other extratropical alpine environments, with an array of plant growth forms which includes ferns, cushion plants, shrubs, graminoids, herbs, acaulescent and giant stem rosettes (Hedberg and Hedberg 1979; Ramsay and Oxley 1997). These different growth forms show a wide spectrum of morphological, physiological and biochemical adaptations to cope with low temperatures and wide daily thermal oscillations, seasonal water stress, low nutrient availability and partial pressures of CO_2 and O_2, and high radiation income (Azócar and Rada 2006; Rada et al. 2019). Interestingly, even when TAEs are isolated one from another, behaving as biogeographical "sky islands" (Hooghiemstra and Van der Hammen 2004; Flantua et al. 2019), most key environmental drivers are shared, leading to similar evolutionary "solutions" to life between tropical mountains, with many striking examples of evolutionary convergence such as the giant stem rosettes in Andean and Afro- Alpines systems

(Hedberg and Hedberg 1979; Rundel et al. 1994; Rada 2016).

TAEs have been the scenario for some of the most recent plant radiations on Earth, and are among the world's fastest evolving floras (Diazgranados and Barber 2017; Valencia et al. 2020). Alpine floras originated by a combination of evolution and migration during the late tertiary and Pleistocene on new mountains (Billings 1974). The long Andean cordillera provided a pathway for ample latitudinal migrations of alpine species, especially during cold periods in the Pleistocene, when mountain forests retreated (Hooghiemstra et al. 2006; Sklenář et al. 2014; Nürk et al. 2020). Besides endemic taxa evolved in the cold tropics (e.g. the Espeletinae tribe), many other groups have migrated and colonized from the tropical lowlands and from temperate latitudes, including species/genera with holarctic, austral antarctic and wide temperate origins (Cleef 1979; Van der Hammen and Cleef 1986; Sklenář et al. 2011).

More than two decades ago, the GLORIA network initiated a global effort for monitoring the impact of climate change on plant diversity in mountain summits through a worldwide long-term observation network (Pauli et al. 2015). With its multi-summit approach along elevation gradients, this methodology captures an important proportion of the plant species and functional diversity in each target region, quantifying spatiotemporal changes in plant abundance and composition, together with temperature data (Gottfried et al. 2012; Hamid et al. 2020). Moreover, this approach provides standardized data on alpine vegetation patterns allowing a better understanding of the responses to large-scale environmental gradients and offering sensitive indicators for monitoring climate change impacts (Pauli et al. 2015; Cuesta et al. 2020).

The GLORIA-Andes network is the South American node of this global monitoring system, generating continent-wide information for analyzing vegetation structure and dynamics. Cuesta et al. (2017) presented the first comparative study of plant community diversity, using data from 49 summits between 3,220 and 5,498 m asl from Argentina to Venezuela. Total annual precipitation, maximum temperature, and substrate cover were the main predictors of community dissimilarities at the continental-scale, discriminating the more humid equatorial páramos from the drier and more seasonal punas (the most important high mountain biomes of the tropical Andes). Moreover, they found a clear trend for species richness to decrease both in the punas and páramos along the elevation and hence thermal gradient (Cuesta et al. 2017).

However, these analyses have focused on species richness and composition, while the role of environmental filtering along elevation gradients on the abundance and diversity of growth forms (GFs) and biogeographic groups remain largely unexplored in the high tropical Andes. GFs constitute a functionally meaningful strategy to represent spatial and temporal changes in the abundance and distribution of plant species and to link their adaptive strategies with environmental gradients (Marini et al. 2012; Furze et al. 2013; Arzac et al. 2019). Hence, understanding the current and future distribution of GFs could provide a more consistent reference for comparing and interpreting the responses to climate change between regions with contrasting floristic composition, but similar adaptive/functional strategies (Scherrer and Körner 2011). Additionally, changes in GFs abundance can be linked with changes in functional trait diversity, which can constitute important drivers of ecosystem function (Pausas and Austin 2001). Significant efforts have been dedicated to characterize changes in GFs and functional traits along elevation gradients in extratropical systems (e.g. Halloy 1990, Wiemann et al. 1998, Pyankov et al. 1999, Blonder et al. 2017), but only a few studies have focused on the distribution of GFs along elevation gradients in the tropical Andes, mainly in páramo ecosystems of the northern Andes (Balslev and de Vries 1989; Ramsay and Oxley 1997; Arzac et al. 2019).

Regarding biogeographic aspects, previous research has mainly focused on the historical and evolutionary phytogeography of the tropical Andean flora (Simpson and Todzia 1990, Young et al. 2002; Sklenář et al. 2011). Recently, Cuesta et al. (2020) evaluated the thermal niche traits of plant species and biogeographic groups in GLORIA summits of the tropical Andes. Their results indicated that páramo endemics restricted to more equatorial latitudes and summit communities dominated by these species (particularly in the northern Andes of Venezuela and Colombia), showed the narrowest thermal niche breadth, and would be the most vulnerable under the projected 1.5°C warming scenario by the end of the century, due to a higher risk of losing thermal niche space. However, the patterns of change in the diversity and abundance of different biogeographic groups along elevation/environmental gradients remain largely unexplored. In this context, the niche-based hypothesis of community assembly (Losos 2008; Kraft et al. 2015) would indicate that as environmental conditions become more limiting and environmental filtering intensifies with elevation, the diversity of plant GFs and the biogeographic origins of the species able to cope with increasing environmental severity should be reduced, as the environment selects for more closely related species that are functionally/ecologically more similar (Venn et al. 2014; Gastauer et al. 2020).

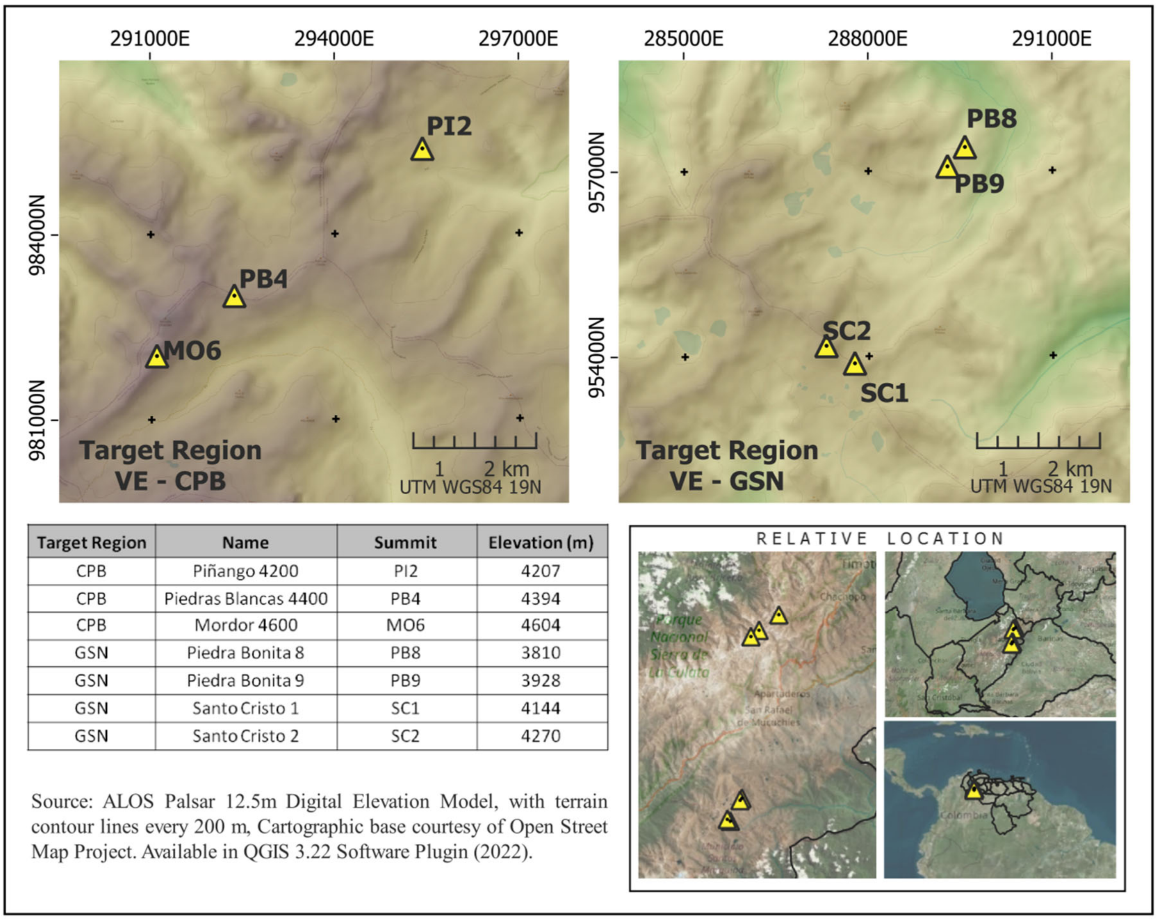
Our general objective in this paper was to analyze and compare spatial changes in plant community diversity in terms of the richness and abundance of plant species, growth forms, and biogeographic groups, and relate them to changes in key habitat variables in seven summits distributed along an elevation gradient between 3800 and 4600 m asl in the Venezuelan Andes (extending from the alpine to the nival belt, see Cuesta et al. 2017). The habitat variables assessed were monthly soil temperatures at – 10 cm below ground, soil organic matter (SOM), slope inclination, and substrate cover. For this we utilized the vegetation base-line data collected in each summit, and do not address here temporal changes in vegetation between this base-line and subsequent resurveys of these monitoring sites.

These summits are located in the two study areas (Sierra Nevada and Sierra la Culata) of the GLORIA-Andes network in Venezuela and were established as long-term monitoring sites using the standard GLORIA methodology (Pauli et al. 2015) between 2012 and 2014 (Gámez et al. 2020). Although there have been a few quantitative studies of changes in plant community structure with elevation in the Venezuelan páramos (e.g. Baruch 1984; see review in Llambí and Rada 2019), none has spanned the full elevational range from the alpine to the nival belt, or integrated taxonomic, functional and biogeographic approaches. Moreover, the available studies from the GLORIA-Andes network are based on temperature data derived from global databases (e.g. WorldClim gridded datasets, Cuesta et al. 2017, 2020), which can be appropriate for analyzing continental-scale patterns but lack the sufficient spatial resolution for interpreting patterns along elevation gradients at a more local regional/landscape scale. Here, we use and report instead data derived from superficial soil temperature data-loggers placed on each summit orientation following the GLORIA protocol, which provides particularly valuable and scarce thermal information from these elevations in the high Northern Andes (see Carilla et al. 2018 for summits in Northern Argentina). In addition, to explore the possible relations between soil development and vegetation patterns (see also Gastauer et al. 2020), we used data derived from complementary measurements of soil organic matter (0-10 cm) in each summit, which are only available in the case of the Venezuelan target regions within the GLORIA-Andes network. This should provide solid baseline for monitoring vegetation dynamics linked to climate change in the tropical Andes by highlighting the functional and historical perspective on vegetation structure patterns, in contrast with more traditional approaches, based only on taxonomic species diversity.

2 Methods

2.1 Study area

In western Venezuela, there are two target regions of the GLORIA-Andes network, both located in the Cordillera de Mérida, the largest central páramo complex of the country (Fig. 1, Table 1; Appendix 1). Following the standard GLORIA protocol, three to four summits were selected along an elevation gradient in each target region, in areas with as little human disturbance as possible (Pauli et al. 2015), although summits in both target regions are exposed to very extensive cattle and horse grazing with low animal loads, given their abrupt topography (see details of the definition of "summit" in Pauli et al. 2015). The target region Gavidia-Sierra Nevada (GSN, established in 2014), located in the Páramo of Gavidia within the Sierra Nevada National Park (declared in 1952), captures the transition between alpine and subnival belts, known in the Andes as páramo and superpáramo belts respectively (Cuatrecasas 1958; Monasterio 1980; Cleef 1981), with four summits between 3810 and 4270 m asl. The target region La Culata-Piedras Blancas (CPB, established in 2012), located in the Páramo of Piedras Blancas within the Sierra La Culata National Park (declared in 1989), captures the transition between subnival and nival belts (i.e. the transition between the superpáramo and the periglacial desert) with three summits between



Target Region	Name	Summit	Elevation (m)
CPB	Piñango 4200	PI2	4207
CPB	Piedras Blancas 4400	PB4	4394
CPB	Mordor 4600	MO6	4604
GSN	Piedra Bonita 8	PB8	3810
GSN	Piedra Bonita 9	PB9	3928
GSN	Santo Cristo 1	SC1	4144
GSN	Santo Cristo 2	SC2	4270

Source: ALOS Palsar 12.5m Digital Elevation Model, with terrain contour lines every 200 m, Cartographic base courtesy of Open Street Map Project. Available in QGIS 3.22 Software Plugin (2022).

Fig. 1 Maps with the location of the four summits in the Sierra Nevada target region (upper right), the three summits in the Piedras Blancas target region (upper left), and relative location in south América and Venezuela of both target regions of the GLORIA network in the Venezuelan Andes (bottom right). Maps by A. Albarran

Table 1 Environmental characteristics of summits established in the two target regions of the GLORIA network in the Venezuelan Andes. Correlations are also presented for the average of each variable with the 1st and 2nd axes of a Principal Components Analysis based on these environmental descriptors in each summit. Elevation shows a correlation of -0.963 with the 1st principal component (PC) and 0.003 with the 2nd PC (Values are mean ± standard deviation).

Target region	Summit code and elevation (m)	Slope (°)	Min temp (°C)	Mean temp (°C)	Max temp (°C)	SOM (%)	Scree (%)	Rock (%)	Bare ground (%)
Gavidia-Sierra Nevada (GSN)	PB8 3810	19.6±10.5	6.6±0.5	10.2±1.0	16.5±1.8	18.1±5.1	3.5±4.2	20.0±14.2	9.5±5.7
	PB9 3930	14.0± 0.8	6.2±0.6	10.1±0.5	16.8±2.1	13.2±2.1	4.7±0.8	25.3±15.0	12.1±7.6
	SC1 4145	20.4± 1.0	5.2±0.4	9.5±0.7	16.0±1.3	10.7±1.3	8.8±2.3	44.5±8.8	4.8±0.8
	SC2 4270	19.4±7.8	4.3±0.1	8.1±1.0	13.9±2.6	9.7±2.0	10.6±11.6	36.4±12.0	12.9±2.4
Culata-Piedras Blancas (CPB)	PI2 4207	11.2±1.5	4.9±0.7	8.3±0.7	13.2±1.7	15.4±2.6	3.8±2.7	11.4±20.8	14.3±20.5
	PB4 4400	19.1±4.9	3.7±0.8	7.0±0.9	12.3±1.9	8.9±0.9	33.6±11.8	25.7±12.1	7.5±7.3
	MO6 4604	14.8±1.6	1.7±0.6	5.5±0.4	11.9±0.9	4.0±1.7	43.6±31.6	34.5±14.8	13.1±11.4
1st PC		0.059	0.512	-	0.350	0.469	-0.474	-0.135	-0.368
2nd PC		-0.442	0.049	-	-0.350	0.188	-0.200	-0.672	0.391

Note: SOM, soil organic matter.

4207 and 4604 m asl (Appendix 1; Fig. 1; Monasterio 1979, 1980; Gámez et al. 2020).

In the Gavidia-Sierra Nevada site (GSN), precipitation is unimodal, with an average total annual rainfall of 1380 mm. The dry season extends between December and March, representing 7%-8% of total precipitation (Gavidia weather station, 3450 m asl, Sarmiento et al. 2003). Soils on the slopes are mainly inceptisols (with entisols occurring in the highest elevations), acid (pH ranging between 3.8 and 5.5), sandy to sandy-loam in texture, with between 8 and 22% organic matter contents in the first 10 cm of the soil profile, but with low mineral nutrient contents (Abreu et al. 2009; Llambí et al. 2014). The area is formed by non-volcanic Precambrian metamorphic rocks (Sierra Nevada association), with a predominance of banded gneiss, feldspathic quartz and schist (González 1998). Some of the summits in this study area were located below higher surrounding areas (i.e. they are prominences along a longer-higher ridge). This agrees with specifications of the GLORIA methodology (Pauli et al. 2015) as was necessary to construct a sequence of peaks with four orientations in the lower elevation areas where single standing summits are less common.

The Culata-Piedras Blancas site (CPB) is drier, influenced by the semi-arid enclave of the high Chama river basin, with a unimodal pattern and a total annual precipitation of 860 mm (Pico El Águila weather station, 4118 m asl). Less than 5% of this precipitation falls during the dry season, extending from December to March (Sarmiento 1986). Precipitation occurs mostly as rain, although snowfall can occur, particularly during the wet season (Monasterio 1979; Pérez 1995). The soils on the slopes are mainly entisols (with inceptisols in the lower elevations), formed from igneous and Precambrian metamorphic rocks, shallow and acidic (pH ranges between 4.5 and 5.2), with a coarse texture with a high content of gravel and sand, and variable soil organic-matter contents (typically ranging between 16% and 4% depending on local topography and elevation). The fine mineral fraction is mainly silt, with low clay contents. Frequent freeze-thaw cycles induce needle ice formation and superficial soil instability (Pérez 1995; Llambí et al. 2020).

2.2 Sampling design

In each summit, the sampling followed the design of the GLORIA standard protocol (Pauli et al. 2015). This protocol uses two types of sampling areas:

(a) Clusters of 3m × 3m, establishing one per cardinal orientation (N, E, W, S) that are subdivided in 1-m^2 quadrats, where field measurements describing vegetation targeted the 1-m^2 quadrats located in each cluster corner. At each of these 16 1-m^2 quadrats per summit, plant species composition, species cover and substrates cover (scree, rock, and bare ground) were recorded using the point-quadrat method (Greig-Smith 1983). For this, the contact of each species and substrate with a thin metal rod was recorded in 100 sampling points distributed in a regular square grid. Soil samples were collected at each corner of the cluster, from March-April in 2015 in GSN and October-November in 2016 in CPB, preserved in plastic bags and transported to the lab to determine the content of organic matter in soil (SOM) using the gravimetric method adapted from Miyazawa et al. (2000). In the center of each cluster, a HOBO-TidbiT v2 logger recorded soil temperature at -10 cm, every hour since November 2012 in CPB and April 2015 in GSN. Because the soil-temperature series recorded between January 2016 and December 2018 are complete for all the seven summits, we built the environmental matrix used to perform the analysis of environmental determinants of vegetation richness (see data processing and analysis section) using climate data series for this time span.

(b) Summit areas sections (SAS), establishing two per cardinal orientation, dividing the summit in eight sections: the superior section, from the highest summit point (HSP) to 5 m below in elevation and, the inferior section, from 5 m to 10 m below the HSP. Within these sections we measured the general slope using a Suunto PM-5/360 PC clinometer. In the SAS, all the vascular plant species present were recorded, and the cover of all vascular plants present was estimated visually (using the standard scale proposed in the GLORIA field manual, see Pauli et al. 2015). Also, we quantitatively estimated the cover of the vascular plants and substrates (scree, rock, and bare ground), using the point-quadrat method, with 100 sampling points distributed along a 100 m linear transect per SAS. We used the mean cover of the species obtained in the two transects (at each SAS per orientation), and complemented it with our visual estimation for species present in each SAS but not touched by the sampling points along each transect (mostly rare and very rare species with covers below

5%). With this more comprehensive data set we built the vegetation matrix used in the multivariate analysis of changes in vegetation composition / structure (see data processing and analysis section).

All vascular plant species present were collected in the surroundings of the summits, and deposited in MER, the Herbarium of the Universidad de los Andes after their taxonomic identification (see Gámez et al. 2020 for details, including an identification key for the studied species).

2.3 Classification of species in growth forms and biogeographic groups

We assigned each recorded species to a growth form following the detailed system proposed by Muriel et al. (2020) for the GLORIA-Andes network. This growth form classification is an adaptation of the one proposed for páramo plants by Ramsay and Oxley (1997), allowing to encompass the growth form diversity present in TAEs along the whole Andean chain. Thirteen growth forms were recorded: erect shrubs, prostrate shrubs, cushions, turf grasses, disperse grasses, tussock grasses, ferns, erect herbs, prostrate herbs, acaulescent rosettes, basal rosettes, caulescent rosettes and succulents (Appendix 2). We also assigned each recorded species to the biogeographical origin of its genus following Sklenář et al. (2011). Seven biogeographical origins were recorded: austral antarctic, cosmopolitan, holarctic, neotropical, páramo endemic, wide temperate and wide tropical (Appendix 2).

2.4 Data processing and analysis

2.4.1 Plant diversity

We calculated three measurements of plant diversity: species richness, growth form richness (number of different GFs found in each quadrat), and richness of biogeographical origin (number of different biogeographical groups found in each quadrat), from the field measurements describing vegetation (i.e. at the 1 m^2 sampling quadrat level). To analyze the relation of these richness measurements with key habitat variables, we compiled a matrix containing, together with elevation, substrate cover (scree, rock, and bare ground), vascular plant cover, soil organic matter (SOM), and the temperature variables, including: annual average temperature, minimum temperature of the coldest month, and maximum temperature of the warmest month for each year, as well as multiannual average temperature, minimum multiannual temperature (average of the minimum temperature of the coldest month values), and maximum multiannual temperature (average of three maximum temperature of the warmest month values) for the 3-years period. Soil temperature variables summarized four data series per summit (one per cardinal orientation), i.e., the four 1 m^2 quadrats on the same orientation of a summit have the same soil temperature values from the thermometer logger in that orientation.

Based on a correlation analysis (Appendix 3), we reduced the set of environmental predictors to those with significant correlation (p<0.001) and $|\text{rho}| \geq 0.03$ with the response variable, and orthogonal between them. Then, we fitted generalized linear models (GLM) using the reduced set of environmental predictors, corresponding to minimum multiannual temperature and SOM, to predict species richness, growth form richness, and richness of biogeographical origin. We used a Poisson error distribution to linearize the regression (Bolker 2008) because the response variables were numeric and discrete and both growth form richness and richness of biogeographic origin were not distributed normally (Shapiro-Wilk normality test: W=0.96, p=0.002 and Shapiro-Wilk normality test: W=0.92, p<0.001, respectively); species richness showed a normal distribution (Shapiro-Wilk normality test: W=0.98, p=0.114). We fitted these GLM with the glmer function of the "lme4" R package (Bates et al. 2015) and the link log. The best model was selected using the Akaike information criteria corrected for small sample sizes (AICc; Anderson and Burnham 2002), and models with ΔAICc<2 were considered equivalent.

2.4.2 Multivariate analyses of plant community structure

To analyze changes in plant community structure in the different summits/elevations, we constructed a matrix with the average cover of each species taking together the two-summit area sections for each summit orientation (which we used as our sampling unit for this analysis), for a total of four average cover values for each species in each summit (north, south, east and west). Similar matrices were built with the average cover in each orientation of each summit of the different plant growth forms and the biogeographic groups. These matrixes were standardized, and square-root transformed, to increase the weight of low-abundance species in the analysis (Ter Braak 1995). We then constructed a similarity matrix using Bray Curtis as floristic distance metric and performed a Principal Coordinate Analysis (PCoA) ordination of the 4 sampling units for all summits using Primer ver. 6 (Clarke and Gorley 2001).

2.4.3 Influence of habitat variables on plant community structure

To compare the relationship between abiotic habitat variables and plant community structure (biotic variables) analyzed in terms of species, growth forms and biogeographic origin, we used the matrices of the average cover of species, growth forms and biogeographic groups (standardized and square-root transformed), and an environmental matrix containing, for each orientation in each summit (see Table 1): slope inclination; average of the monthly minimum temperature (Tmin), average of the monthly maximum temperature (Tmax), and average temperature for the 3-years period; SOM; and the cover of rocks, scree and bare ground. Average temperature was excluded from further analyses as it was strongly correlated with Tmin and Tmax.

Then, we calculated separately the Spearman rank correlations (r_s) between the Bray-Curtis similarity matrices (BCM) for species, growth forms and biogeographic origin and the Euclidean distance matrix (EDM) based on the normalized environmental variables using the RELATE procedure in Primer v6 (non-parametric equivalent to the Mantel test). A total of 999 permutations were used to calculate the significance of the r_s coefficient in each case. We then selected the combination of environmental variables that produced the higher correlation between the EDM and the BCM in each case (for species, growth forms, and biogeographic origin), using the *best* procedure in Primer v6. Finally, we carried out direct gradient ordinations to compare community-habitat relations based on species, growth forms and biogeographic origin separately, using distance-based redundancy analyses (dbRDA), with the normalized environmental matrix as our external matrix in all cases (Primer 6.0 software, Anderson et al. 2008).

3 Results

3.1 Plant diversity

In total we identified 113 species in the seven summits studied. We found a total of 88 species in the Gavidia-Sierra Nevada target region, distributed in 66 genera and 32 families, while the total number of species in Piedras Blancas-La Culata was 71 species (53 genus and 24 families). Asteraceae, Poaceae, Rosaceae and Brassicaceae were the families better represented, comprising 60% of all species recorded for all summits. Total and average species richness showed a significant trend to decrease along the elevation gradient; the same was found for GFs richness and the number of biogeographic origins (Appendix 4). Erect shrubs, erect herbs and tussock grasses were the categories with more species (20 for the first two and 16 for the last), followed by acaulescent rosettes (12 spp.), prostrate herbs (10 spp.) and caulescent rosettes (9 spp.), then ferns (6 spp.), cushions, prostrate shrubs and turf grasses with 4 spp. each; the less represented GFs were basal rosettes with two species and there was only one succulent species (Appendix 5). While erect herbs and shrubs are always represented in the seven summits, GFs like ferns, turf and disperse grasses, prostate shrubs and succulents disappear in the highest elevations (Appendix 5). Most of the species found belong to genera of wide temperate (39 spp.) or neotropical origin (28 spp.); 16 of the species have holarctic origin and 12 of them are páramo endemic species, while wide tropical, austral antarctic and cosmopolitan genera were less represented in terms of the number of species, with seven, six and three species respectively (Appendix 6). Categories like wide temperate and neotropical were present along the whole elevation ranges, while austral antarctic and holarctic species have opposite trends, with the abundance and richness of austral antarctic elements decreasing with elevation, while holarctic elements where the most important group in terms of richness and cover in the highest summit (4600 m, Appendix 6).

Species richness and GFs richness decreased with decreasing temperatures and a reduction in soil organic matter (Table 2), with a significant interaction between the two predictors ($p<0.001$). For these richness measurements, the best model equals the full model (Table 3) and explained 46% of the variance for species richness (AICc=515.79) and 51% of the variance for GFs (AICc=419.12). In turn, the best model for biogeographical origin richness explained 27% of the variance (AICc=379.16) and indicated that

Table 2 Model coefficients of the best generalized linear model (GLM) fit to assess the effect of key habitat variables and their interaction on species, growth form, and biogeographic origin richness across seven GLORIA network summits in the Venezuelan Andes. OM: Organic Matter; TMin: Minimum multiannual temperature; β: coefficient estimates; SE: standard error; P: significance. Correlation among key habitat variables are in Appendix 3. Note that the best GLM for Biogeographic Origin richness has two components, the intercept and OM as the only predictor.

Model component		Species richness			Growth form richness			Biogeographic origin richness		
		β	SE	P	β	SE	P	β	SE	P
Intercept		2.12	0.039	<0.001	1.66	0.049	<0.001	0.92	0.105	<0.001
Key habitat variable	OM	0.14	0.045	0.002	0.13	0.056	0.023			
	TMin	0.19	0.047	<0.001	0.20	0.06	<0.001	0.21	0.05	<0.001
Interaction	OM × TMin	-0.222	0.040	<0.001	-0.17	0.048	<0.001			

Table 3 Comparison among null, full and best models fitted for species, growth form and biogeographical origin richness in seven summits established in the two target regions of the GLORIA network in the Venezuelan Andes. DF: Degrees of freedom; AICc: Akaike information criteria corrected for small sample size; Variance explained = 1 - (Residual deviance. Best/ Residual deviance.Null)×100. * Best model equals full model.

Fit model	Species richness			Growth form richness			Biogeographical origin richness		
	DF	Residual deviance	AICc	DF	Residual deviance	AICc	DF	Residual deviance	AICc
Null	106	597.58	601.58	106	461.84	465.8419	106	391.52	395.52
Full	103	505.79	515.79	103	409.12	419.122	103	368.33	378.33
Best	*	*	*	*	*	*	107	373.16	379.16
Variance explained	46%			51%			27%		

the number of biogeographical origins present increased with increasing values of minimum multiannual temperature ($\beta = 0.21$, $p < 0.001$, Table 2).

3.2 Plant community structure of high Andean summits along environmental gradients

The PCoA ordination of species cover in each summit orientation showed marked changes in species composition among summits, while the 4 orientations within each summit consistently occur close together in the ordination (indicating a higher floristic similarity between orientations within each summit, Fig. 2a). Summits were organized in terms of their elevation and target region along the first two PCoA axes, with the two lowest summits from the GSN target region (PB8 and PB9, 3810 and 3930 m asl) in the extreme low-right corner, then the next two higher summits from GSN towards the center (SC1 and SC2, 4145-4270 m asl), and then the two summits located between 4207-4400 m in the CPB target region (PI2 and PB4) towards the upper-left corner of the ordination space. The highest summit in CPB at 4604 m asl (MO6) showed the highest dissimilarity due to is different species composition and is located far from all the rest in the lower-left corner of the ordination. Interestingly, the ordination analyses based on the cover of GFs and biogeographic origin showed a similar configuration of the summits along the first two ordination axes (Fig. 2b and 2c), although in general there is a higher overlap between the different summits on the ordination space, indicating a higher similarity in community structure between summits when the analysis is based on GFs or biogeographic abundance patterns.

The position of the Spearman correlation vectors of the cover of species, GFs and biogeographic groups in the ordinations (Figs. 2a, 2b; Appendix 7) indicates that the two lowest summits in GSN, located within the alpine/páramo belt are characterized by the highest abundance of tussock grasses (e.g. *Calamagrostis effusa, Cortaderia hapalotricha*), prostrate shrubs (e.g. *Gaultheria myrsinoides*), erect shrubs (e.g. *Arcytophyllum nitidum*) and ferns (e.g. *Elaphoglossum mathewsii*). As we move to higher elevations between 4000 m and 4300 m in the subnival/superpáramo belt (SC1 and SC2 in the GSN site, and PI2 in the CPB site) erect shrubs (e.g. *Hypericum laricifolium*) and tussock grasses remain important, while other growth forms increase in relative cover including acaulescent rosettes (e.g. *Acaena cylindristachya*), disperse grasses (e.g. *Luzula racemosa*), caulescent rosettes (e.g. *Espeletia schultzii*), mat-forming grasses (e.g. *Aciachne acicularis*) and postrate herbs (e.g. *Bidens triplinervia*). Then, the 4400 m summit in the upper portion of the superpáramo (PB4) show high relative abundance of the giant caulescent rosette *Espeletia timotensis,* erect herbs (e.g. *Castilleja fissifolia*, *Gnaphalium meridanum*, the exotic *Rumex*

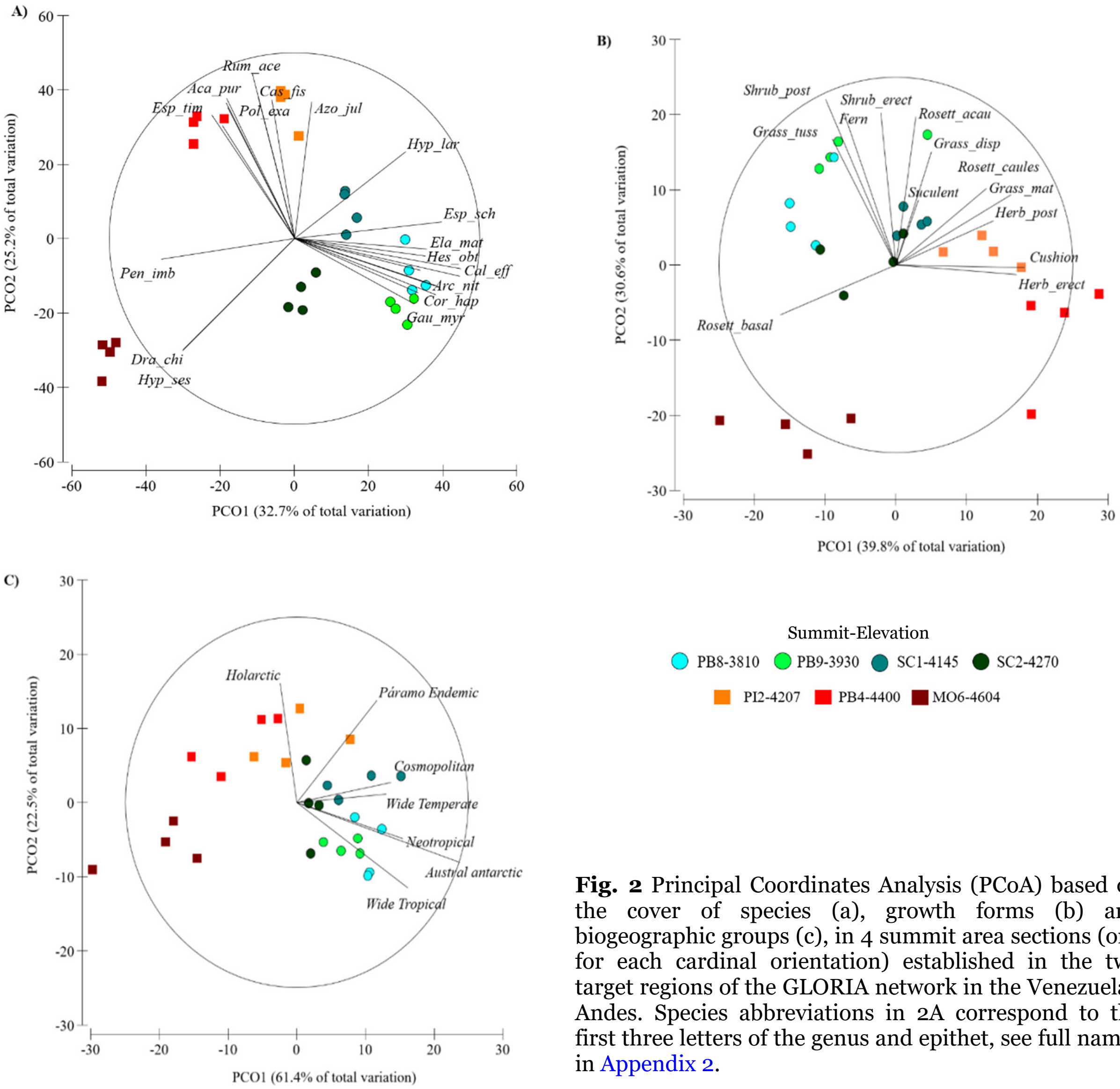


Fig. 2 Principal Coordinates Analysis (PCoA) based on the cover of species (a), growth forms (b) and biogeographic groups (c), in 4 summit area sections (one for each cardinal orientation) established in the two target regions of the GLORIA network in the Venezuelan Andes. Species abbreviations in 2A correspond to the first three letters of the genus and epithet, see full names in Appendix 2.

acetosella) and cushions (e.g. *Azorella julianii*). Finally, the MO6 summit in the nival/periglacial belt (4604 m asl) is characterized by the highest abundance of basal rosettes (e.g. *Draba chionophilla*), while a few small erect shrubs (e.g. *Pentacalia imbricatifolia*) and disperse grasses are also important (e.g. *Festuca fragilis*).

These changes were accompanied by a shift in the relative importance of different biogeographic groups (Fig 2c, Appendix 7), with austral antarctic, neotropical and wide tropical elements having higher cover values in the lowest summits; wide temperate and páramo endemics increased in relative importance at intermediate elevations; finally, holarctic species increase in relative importance with elevation and become dominant at the highest summit.

3.3 Influence of habitat variables on plant community structure

The Spearman correlations (r_s) between the abiotic matrix (Euclidean Distance Matrix, EDM) and the biotic similarity matrixes (Bray-Curtis Matrixes, BCM), showed similar values when using species, GFs or biogeographic origin, being statistically significant in all cases ($p \leq 0.001$). The highest correlation was obtained between abiotic EDM and the species BCM (r_s=0.658), then with the biogeographic origin BCM (r_s=0.602) and then with the growth forms BCM (r_s=0.555). Interestingly, when the best combination of abiotic variables is selected, monthly minimum temperature and the cover of rocks, scree and/or bare ground were consistently included among the selected variables, and the r_s values increase (ranging between 0.726 with the species matrix and 0.671 for growth forms matrix).

This result is consistent with the results of the direct gradient analysis ordination using dbRDA, which shows similar results when based on species, growth forms of biogeographic groups (see Fig. 3 for the case of the ordination based on the species data). In this analysis, monthly minimum temperature showed the strongest positive correlation with the first ordination axis (0.601), and substrate cover of scree and bare ground, the strongest negative correlation with this axis (-0.438 and -0.402, see Table 4), indicating this axis is capturing the elevation gradient. In fact, the lowest elevation summits (PB8, PB9) occupy the extreme right-hand side of the diagram, associated higher monthly minimum temperatures, while the summits at the highest elevations (PB4, MO6) occupy the left-hand side of the diagram, associated with a high cover of scree and bare ground. Interestingly, the summits with intermediate elevations (SC1 and SC2 in the Gavidia-Sierra Nevada site and PI2 in the Culata-Piedras Blancas site) are separated along the 2nd axis, which is strongly associated with a gradient of rock cover (which shows a positive correlation of 0.833 with the 2nd axis, Table 4). Hence, this 2nd axis separates the rockier high summits in Gavidia from the less rocky, more sandy summits in La Culata. Finally, SOM tends to increase towards the summits at lower elevations and with a lower rock cover, but the correlation of this variable with these two first ordination axes is relatively low (0.356 with the 1st and -0.348 with the 2nd).

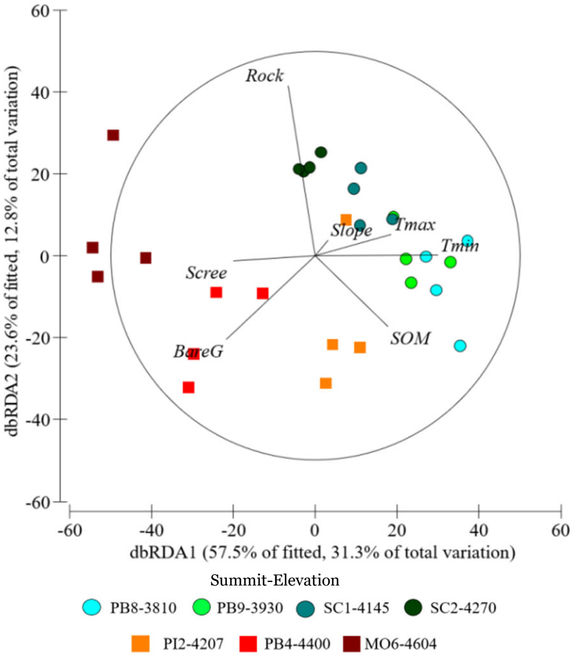


Fig. 3 Distance-based Redundancy Analysis (dbRDA) of the cover of species vs. environmental variables measured in summit area sections (one for each cardinal orientation) in seven summits established in the two target regions of the GLORIA network in the Venezuelan Andes. The elevation of each summit (m asl) is indicated in the legend. Tmax: average of the monthly maximum temperature; Tmin: average of the monthly minimum temperature.

Table 4 Correlation coefficients between distance-based Redundancy Analysis (dbRDA) axes and environmental variables. Performed for the dbRDA based on species cover and environmental variables measured in the summits established in two target regions of the GLORIA network in the Venezuelan Andes. Values on bold indicate significant correlations between the variable and the axis.

Variable	dbRDA1	dbRDA2	dbRDA3	dbRDA4
Tmax	0.372	0.105	0.558	0.2
Tmin	**0.601**	0.001	0.13	0.479
SOM	0.356	-0.348	0.371	-0.575
Slope	0.062	0.076	-0.243	0.496
Rock	-0.133	**0.833**	0.309	-0.169
Scree	-0.402	-0.025	0.483	0.222
Bare ground	-0.438	-0.41	0.382	0.276

4 Discussion

4.1 Plant Diversity

The studied summits comprise a very good representation of the flora in the Venezuelan páramos; according with Briceño and Morillo (2002, 2006), there are 520 species of monocots and 917 species of dicots in the Venezuelan Andes above 2500 m of elevation. Gámez et al. (2020) indicate that approximately 308 species are present in the Venezuelan páramos above 4000 m asl, while we recorded a total of 113 species in the studied summits (located between 3800 and 4600 m); 25% of this species are endemics for the Venezuelan Andes (Gámez et al. 2020). This good representation of the flora of the region is interesting, given the particular environmental conditions associated with mountain summits compared to flatter surrounding areas (a comparison that would be interesting to develop in further studies). However, the "summit approach" used by GLORIA offers several advantages including:

1) They can be easily located for further surveys; 2) they are well defined topographic units providing comparable conditions and all slope aspects within a small area; 3) they are less prone to severe human induced disturbance or debris falls/avalanches (Pauli et al. 2015).

Our results showed a general decrease in species richness with increasing elevation. This agrees with what has been generally found for vascular plants along elevation gradients in other regions of the world (Lomolino 2001, McCain and Grytnes 2010; Gastauer et al. 2020), and with what has been previously described for GLORIA summits in puna and páramo environments of South- America (Cuesta et al. 2017; Carilla et al. 2018). The observed decrease in species richness could be related to the increment of abiotic constraints with elevation, including thermal and water stress (Körner 2003). In general, the richness trends found in our summits suggest a strong abiotic regulation and an increase in the importance of environmental filtering of plant diversity at higher elevations, as has been suggested for other environments like subarctic mountain tundra (Naud et al. 2019).

Nevertheless, comparisons between taxonomic, functional and biogeographic richness along elevational gradients are extremely scarce in the literature, and as far as we know this is the first study that integrated these different approaches in TAEs. Interestingly, the trend for a decline in species richness with elevation was also observed for the richness of plant growth forms and biogeographic species groups, suggesting that abiotic filtering does not only reduce taxonomic diversity but also the functional and biogeographic diversity of the species present with increasing elevation. This results in the absence of some growth forms (ferns, postrate shrubs, disperse grasses) and biogeographic groups (austral-antarctic and cosmopolitan) in the permanent plots from the two highest summits.

Our results showed that minimum temperature and soil organic matter content were the main predictors associated with the decrease along the elevation gradient of both, taxonomic and functional richness (in terms of GFs), while in the case of richness of biogeographic origins minimum temperature was the only significant abiotic predictor. Carilla et al. (2018) also report a positive relation between species richness and minimum soil temperature along an elevational gradient in four GLORIA summits in NW Argentina; at continental scale, while Cuesta et al. (2017) report maximum temperature (correlated with minimum temperature), aboveground necromass and scree cover as the main abiotic variables associated with the decrease of species richness along elevation in the 49 summits of the GLORIA-Andes network in South America.

A direct relationship between soil organic matter and richness along elevational gradients is less documented in the literature, but if we consider SOM as a proxy of ecosystem productivity (Laughlin et al. 2007), we do find that the idea that there is a clear relationship between productivity and richness is widely recognized (Waide et al. 1999). This would agree with the previous result of aboveground necromass (also linked with productivity) being associated with species richness in the GLORIA summits at a continental scale (Cuesta et al. 2017). However, the mechanisms involved and the direction of the relationship between richness and productivity (i.e unimodal, positive or negative), has been a matter of dispute (Rosenzweig 1995). In any case, since soil organic matter contributes directly to soil fertility and the water holding capacity of soils (Lehmann and Kleber 2015), a decrease in the number of species with low SOM values as elevation increases and temperature decreases could be expected, particularly in an ample elevation gradient such as the one studied here, that spans the transition between the alpine, subnival and nival belts.

An important consideration is that the summits in our two study regions do not only differ in elevation but also in total annual precipitation (being 38% higher in the lower elevation summits in the GSN site, than in the drier summits of CPB). Hence, a reduction in richness between the lower summits of GSN and the higher summits of CPB could be partially due to this difference in rainfall. However, a more robust quantitative assessment of this effect would require more detailed precipitation data along the whole elevation gradient (only data from two meteorological stations is currently available, and they are some distance apart from the studied summits).

4.2 Plant community structure of high Andean summits along environmental gradients

Results of the multivariate analyses (PCoA) indicate that the elevation gradient is associated with clear changes in community structure in terms of the patterns of abundance of species (see also Cuesta et al. 2017; Carilla et al. 2018), growth forms and biogeographic groups, while slope orientation in each summit had no clear/consistent effects on the ordinations. Interestingly, a similar ordination was evident when community structure was analyzed in terms of species, growth forms and biogeographic groups, indicating that the functional and biogeographic responses to elevation agree with the more classic floristic analysis, capturing in all cases the main patterns of variation in vegetation structure along the first ordination axis (although there was lower overlap/similarity between sampling units in the different summits when the responses of individual species were considered).

The patterns of change in species and GFs abundance agree with the characteristic changes in plant physiognomy from the páramo belt to the superpáramo and the periglacial desert in the northern Andes (i.e. the alpine, sub-nival and nival belts respectively), corresponding with a transition from vegetation dominated by tall shrubs and tussock grasses in the páramo summits, to a predominance of giant stem rosettes and erect herbs in the superpáramo and finally an increase in relative importance of basal rosettes together with small erect herbs and shrubs in the periglacial desert (see also Baruch 1984; Balslev and de Vries 1989; Ramsay and Oxley 1997; Llambí et al. 2014).

The array of growth forms that plants adopt indicates diverse strategies to cope with abiotic stress. In TAEs, the functional/morphological diversity of plants is mainly related with ecological adaptations to low temperatures, recurrent night frosts throughout the year, low nutrient availability and seasonal water stress (Hedberg and Hedberg 1979; Rundel et al. 1994; Rada et al. 2019). For example, stem rosettes, with freezing avoidance adaptations, are abundant at low and intermediate elevations, possibly responding to less harsh thermal conditions compared with those found at the highest extreme of the gradient (where freezing tolerance strategies are more common, see Goldstein et al. 1985; Rada 2016; Rada et al. 2019). In the case of erect shrubs, although they were present along the whole elevation gradient, their species identity changed. In the lower summits the dominant species are characterized by a higher leaf area (e.g. *Bacharis prunifolia*, *Hesperomeles obtusifolia*), while at highest elevations the shrub species present have smaller leaves (e.g. *Hinterhubera columbica*, *Pentacalia imbricatifolia*); this decrease of leaf area in shrubs has been previously reported for páramos above the treeline ecotone, and has been related with changes in drought resistance mechanism (Arzac et al. 2019); at higher elevations, water can become a more limiting resource, because of a lower water retention capacity in soils and because soil water tends to be frozen during the first hours of the day, and cannot be absorbed by the roots (Rada et al. 2019).

Basal rosettes, particularly *Draba chionophila*, showed a high relative cover in the highest summit. Interestingly, this species has been characterized as highly tolerant to freezing temperatures (Azócar et al. 1988). Grasses and herbs were abundant along the whole elevation gradient although their relative importance and species identities changed; given the predominance of tolerance to frost among herbaceous and grass growth forms (Rada et al. 2019), they can be particularly well adapted to these extreme environments, which could explain the high relative abundance of species such as *Festuca fragilis* or *Castilleja fissifolia* in the highest summits. Interestingly, grasses and small herbs have also been found among the pioneer species during primary succession at high elevations in the Venezuelan Andes (Llambí et al. 2021). Even when cushion plants are also frost tolerant, they were one of the least abundant growth forms in these communities (although they showed a high relative abundance in the superpáramo summits at 4400 m), something that could be related with dispersal limitations or with their low growth rates and plant height, which could make them more susceptible to competitive displacement or parasitism by taller shrubs, grasses and herbs (see Llambí et al. 2018); in fact, cushion plants only appear at high elevations in other superpáramo regions in the tropical Andes (Rada et el. 2019; Cuesta et al. 2019). Only a few ferns were found in the studied summits, and always with low abundances; the genus *Jamesonia*, one of the most abundant ferns found here, has been reported to exhibit adaptations to páramo environments, including coriaceous leaves and reduced pinnae (Sklenář et al. 2011).

Regarding biogeographic origin, previous studies indicate that in the páramos, approximately half of the species may be descendent from a lineage with temperate origin (Sklenář et al. 2011). In fact, we observed that species with wide temperate origin were present along the whole elevation gradient. Species with wide geographical distributions are generally successful in the colonization of new habitats, given their broader ecological tolerances, which allows them to have wide elevation ranges (Hedberg 1969; Cuesta et al. 2020). On the other hand, austral antarctic and holarctic elements showed opposite trends, with the austral antarctic species decreasing in abundance with elevation until they disappear at 4600 m, while the opposite occurred with the holarctic species, which showed the highest relative cover at 4600 m. Both elements are common among the páramo flora. According with Sklenář et al. (2011), austral antarctic elements migrated from the Southern Andes through the continuous mountain chain, while the presence of holarctic elements in the páramos indicates long-distance dispersal across land bridges in Central America (in the last two million years). Even when both elements are adapted to cold conditions, our results indicate that the species with holarctic origin are better suited for the extreme environments found at higher elevations in these tropical mountains. Endemics elements were present along the whole elevation gradient, with no clear trend in terms of their relative abundance. In the Bolivian Andes, Kessler (2000) reported an increase of species with endemic origin with elevation (but in a study comprising areas from much lower elevations). The radiation of new species that are restricted to páramo environments could be related with the high habitat heterogeneity in mountain regions that leads to isolation in populations (Kessler 2000; Sklenář et al. 2011). Neotropical elements showed similar abundances along the whole gradient, with a slight increase in the highest summit. These elements include species that can occur in other alpine habitats outside the tropical Andes (Sklenář et al. 2011). Cosmopolitan and wide tropical elements were the less represented in the communities described, probably because their lack of adaptations for unproductive/alpine environments.

4.3 Influence of habitat variables on plant community structure

The analysis of the relationship between abiotic variables and community structure, through dbRDA ordination and the correlation between abiotic and biotic similarity matrixes, showed consistent results when the community was characterized in terms of the cover of species, growth forms or biogeographic groups in each summit. Again, this indicates that biogeographic and functional classifications of species capture well the effect on abiotic filtering across elevations on plant community composition and structure in these tropical alpine environments.

Similar to what we found in the analyses for plant richness, minimum temperature was consistently the most important abiotic predictor of these changes in community structure along the elevation gradient. However, in this case, the cover of scree and bare ground (which both increase with increasing elevation) was more important than SOM as predictor variables. Interestingly, scree cover was also found to be an important variable for explaining changes in species richness and abundance across GLORIA-Andes summits at a continental scale, with scree increasing in cover from alpine to nival summits (Cuesta et al. 2017). Hence, a higher scree cover seems to be a good indicator of the most limiting conditions for vegetation development at high elevations given its direct link with the occurrence of periglacial conditions and frequent freezing temperatures inducing gelifraction processes (Monasterio 1986; Pérez 1987). This could explain its negative relation with Tmin in the ordination. Moreover, as Tmin decreases with elevation, it is to be expected that both, the cover of bare ground increases while SOM decreases, as climatic conditions become more limiting and soils become younger and less developed, probably reducing plant productivity.

Again, as in the case of our analysis for vegetation diversity, one additional factor that would need to be considered is the difference between our study regions in total annual rainfall, which could also contribute to explain the differences in community structure between the lowest-more humid summits in GSN, and the highest-drier summits in the CPB region.

5 Conclusions

Tropical alpine environments harbor one of the richest floras in the word, but they are still poorly studied in comparison with other alpine systems. This paper summarized changes in species, growth form, and biogeographic diversity and its relationship with key habitat variables in seven summits established along an elevation gradient from 3800 to 4600 in the tropical Andes. We found clear and consistent changes in diversity and community structure along elevation when the community was characterized in terms of species, growth forms or biogeographic groups in each summit. The same was true of the analysis of the abiotic variables associated with these changes in diversity and community structure, with minimum temperatures, SOM and scree cover being among the most important habitat variables explaining the observed patterns, SOM being more important in the case of richness and scree in the case of patterns of community similarity. Hence, our results indicate that biogeographic and functional classifications of species capture well the effect on abiotic filtering along elevation in these tropical alpine environments.

Emblematic elements such as the caulescent rosettes and cushions were not present in the periglacial desert (nival belt), while a basal rosette became dominant in the highest summit, possibly responding to differences in their ability to tolerate freezing temperatures; herbs and grasses were present along the whole elevation gradient, pointing to their importance in structuring these tropical alpine ecosystems. Endemic species were distributed along the whole elevation gradient, while holarctic and austral antarctic groups showed opposite trends in terms of cover: the first increased and the second decreased with elevation. These results constitute a unique base-line for monitoring changes in vegetation dynamics linked with climate change in the tropical Andes, offering a more functional and historical/evolutionary basis than more traditional approaches based only on the analysis of taxonomic/species diversity. Further challenges include the comparative analysis of vegetation dynamics between this base-line and subsequent re-surveys and a more detailed understanding on how changes in temperature and substrate conditions interact with spatial and temporal changes in precipitation.

Acknowledgments

We want to thank the financial support to the GLORIA-Andes network in Venezuela of CONDESAN and the Swiss Development Agency (SDC). The present synthesis analysis was financed by the Adaptation at Altitude Program (CONDESAN-SDC). We also want to thank the institutional support of ICAE and the MER Herbarium at ULA and INPARQUES and the detailed and insightful comments provided by the referees, which we are sure have contributed to improve the manuscript. The following researchers have actively participated during these years in field work, laboratory analyses, taxonomic identification, generation of maps and other key activities: Teresa Schwarzkopf, Eulogio Chacón, Manuel Fernández, Zulay Méndez, Julia K. Smith, Andrea Bueno, Magdalena Gerhardt, Benito Briceño, Alejandra Melfo, Cherry Rojas, Mariana Cárdenas, Rafael Pacheco, Mayanin Rodríguez, Ciro Soto, John Parra, Maryam Sánchez, Gerardo Rodríguez, Susana Rodríguez, Víctor Palomares, Anderson Albarran, Dominique Bednareck, Favián Vega and Gabriel Guirigay. Finally, we want to thank the kind support during field work in Gavidia of Leopoldo Ponte, the Torres Family and Manuel Moreno.

Electronic supplementary material: Supplementary material (Appendixes 1-7) is available in the online version of this article at https://doi.org/10.1007/s11629-022-7473-8.

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