

Latitudinal and altitudinal patterns of plant community diversity on mountain summits across the tropical Andes

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The high tropical Andes host one of the richest alpine floras of the world, with exceptionally high levels of endemism and turnover rates. Yet, little is known about the patterns and processes that structure altitudinal and latitudinal variation in plant community diversity. Herein we present the first continental-scale comparative study of plant community diversity on summits of the tropical Andes. Data were obtained from 792 permanent vegetation plots (1 m²) within 50 summits, distributed along a 4200 km transect; summit elevations ranged between 3220 and 5498 m a.s.l. We analyzed the plant community data to assess: 1) differences in species abundance patterns in summits across the region, 2) the role of geographic distance in explaining floristic similarity and 3) the importance of altitudinal and latitudinal environmental gradients in explaining plant community composition and richness. On the basis of species abundance patterns, our summit communities were separated into two major groups: Puna and Páramo. Floristic similarity declined with increasing geographic distance between study-sites, the correlation being stronger in the more insular Páramo than in the Puna (corresponding to higher species turnover rates within the Páramo). Ordination analysis (CCA) showed that precipitation, maximum temperature and rock cover were the strongest predictors of community similarity across all summits. Generalized linear model (GLM) quasi-Poisson regression indicated that across all summits species richness increased with maximum air temperature and above-ground necromass and decreased on summits where scree was the dominant substrate. Our results point to different environmental variables as key factors for explaining vertical and latitudinal species turnover and species richness patterns on high Andean summits, offering a powerful tool to detect contrasting latitudinal and altitudinal effects of climate change across the tropical Andes.

The alpine life zone occurs in mountain regions above the climatic upper limit of forests, and is the only life zone that can be found at all latitudes (Smith and Cleef 1988, Körner 2003). The ecosystems contained within the alpine life zone are considered highly sensitive to climate change because their distribution has been closely linked to temperature (Sala et al. 2000, Halloy and Mark 2003, Pauli

et al. 2015) and precipitation patterns (Sklenář and Balslev 2005). Furthermore, the restricted altitudinal range that many species occupy within alpine ecosystems has been suggested to enhance sensitivity to climate change (Sklenář and Jørgensen 1999). Therefore, it is anticipated that climate change will force taxa to move upslope, or downslope, or from one slope to another (e.g. west – east), depending

on their ecological preferences (Nagy and Grabherr 2009, Corlett and Westcott 2013, Winkler et al. 2016). However, topographic variations and the predominance of rocky substrates can also generate a mosaic of microclimatic conditions on the slopes of the mountains that could buffer the effect of warming and retard migration (Scherrer and Körner 2011). Consequently, the alpine life zone provides an ideal 'natural laboratory' in which the relationship between vegetation diversity/dynamics and climatic drivers can be studied (Körner 2007).

Considerable research effort has been directed towards investigating alpine community assembly on mid- and high-latitude mountains (Körner and Spehn 2002, Körner 2003, Nagy and Grabherr 2009). However, relatively little work has been conducted at low tropical latitudes (Buytaert et al. 2011). The alpine life zone in the tropics is characterized by unique conditions including: 1) high levels of solar radiation, 2) low variability in yearly average temperatures, 3) high variability in daily temperatures, 4) inverted rainfall patterns along the elevation gradient above the treeline, and 5) the occurrence of marked precipitation gradients over short horizontal distances (Hedberg and Hedberg 1979, Halloy 1989, Rundel et al. 1994, Bader et al. 2007).

Within the tropics, the largest area of alpine life zone ecosystems occurs in the high Andes. Moreover, the alpine ecosystems in the high tropical Andes are outstandingly rich in plant species with a high level of endemism (Simpson and Todzia 1990, Sklenář et al. 2014). Extending more than 4500 km in a north-south direction, the tropical Andes show a prominent precipitation and temperature amplitude gradient (Fjeldså and Krabbe 1990) from the humid equatorial Andes to the xeric environments in the central Andes (Josse et al. 2011). The north-south precipitation/temperature gradient is paralleled by a remarkable change in topographic configuration from high fragmentation and continental insularity in the northern Andes to the large continuous alpine zone of the central Andes, including a high-elevation plateau (the Altiplano).

Previous research that has encompassed the full latitudinal extent of the high tropical Andes has mainly focused on the historical and evolutionary phytogeography of the flora (van der Hammen 1974, Simpson 1983, Simpson and Todzia 1990, Young et al. 2002). Consequently, little is known about the patterns and processes that influence plant community composition, species abundance patterns and species richness, and their relation with the environmental gradients that characterize tropical alpine ecosystems (but see Peyre 2015 and Peyre et al. 2015 for the Páramo vegetation). While some studies have evaluated large scale patterns in plant diversity by comparing country-scale floras (Jørgensen et al. 2011), the few studies based on community-scale field plots have been restricted to specific countries or regions (Sklenář and Ramsay 2001, Sklenář and Balslev 2005, Moscol and Cleef 2009, Londoño et al. 2014). Specifically, there is a lack of community data related to the vegetation on mountain summits in the tropical Andes, particularly in the subnival and nival belts, where vegetation could be more sensitive and exposed to climate change (Pauli et al. 2015). In addition, the plant communities at high elevation summits in the tropical Andes are the result of recent

and little understood community assembly processes after the last glacial maximum (Hansen et al. 1984, Vuille et al. 2008, Williams et al. 2011), and, in general, they have been affected less by human land use than zonal vegetation at lower elevations, allowing the analysis of the relationship between vegetation patterns and environmental drivers (Aldenderfer 2006, Llambí and Cuesta 2013).

The tropical Andes have been generally divided into a northern and a central section, in a sector where the chain is bisected by the Huancabamba depression in northern Peru at approximately 6°S (Clapperton and Clapperton 1993). This depression constitutes a barrier that divides biogeographically the Andes into two major phytogeographic units (ecosystems, hereafter): the Páramo, and the Puna (Cabrera and Willink 1973, Cleef 1979, Duellman 1979, Simpson 1983, Myers et al. 2000, Weigend 2002). The proposed classifications are based primarily on physiognomic analyzes that in many cases are correlated with the major climatic provinces of the Andes (Troll 1973). However, the Puna and Páramo ecosystems share many floristic elements and show a gradual change in community composition along the latitudinal gradient (Young et al. 2002). Although, a similar spatial pattern is expected in the plant community configuration of the high Andean summits, very few studies have focused on these communities, and those available are centered in a specific country (Sklenář and Balslev 2005) or region (Peyre 2015, Peyre et al. 2015).

Our general objective in the present study was to characterize patterns of change in plant community composition and structure in Puna and Páramo summits across the high tropical Andes using plant abundance data collected in permanent plots. Specifically, our aims were to: 1) assess the importance of geographic proximity and environmental gradients in explaining plant community patterns and beta diversity in all summits taken together and in Puna and Páramo summits analyzed separately and 2) to analyze the relationship between species richness, elevation and environmental drivers across all studied summits and in the Puna and Páramo summits.

To address these objectives, we conducted a continental-scale comparative study of plant community composition, species abundance patterns and species richness in summits along the full extent of high tropical Andes, from Venezuela (8°N) to northwestern Argentina (26°S). We used a standardized methodology to analyze data from 50 summits, located from just above the treeline to the upper limit of vegetation in the nival belt. The base-line data was collected in the context of the GLORIA-Andes network (Cuesta et al. 2012) for long-term biodiversity and climate monitoring, following the methodology of Pauli et al. (2015) for the global GLORIA network.

Although the GLORIA protocol was designed for monitoring purposes and not explicitly for studying large-scale vegetation patterns, the GLORIA-Andes network has generated the first comprehensive, continent-wide dataset from long-term vegetation study plots suitable for analyzing plant community dynamics in both Punas and Páramos. The analysis of present-day patterns of summit plant communities is a valuable step forward for understanding their possible responses to climate change across the wide environmental gradients that characterize the tropical Andes.

Material and methods

Study area

The tropical Andes are the longest and widest high mountain region in the tropics, covering more than 1.5 million km² (11°N to 27°S) and containing complex topographic gradients (ca 600 m up to almost 7000 m a.s.l.) (Josse et al. 2011). The tropical Andes show a predominant north–south humidity gradient with specific localities of high annual rainfall along the Eastern Andean ridge in Peru and Bolivia (Killeen et al. 2007). However, at smaller spatial scales humidity exhibits highly heterogeneous patterns, in which over short distances conditions may vary from per-humid to semi-arid (Kessler et al. 2011). The actual treeline lies around 3500 m (\pm 400 m) near the equator and gradually decreases southwards (Körner 1998) to as low as 2500 m in the drier western versant of the central Andes (Navarro and Maldonado 2002, Beck 2003).

Previous studies divided the Páramo into four zones or altitudinal belts (Cleef 1981, van der Hammen and Cleef 1986, Ramsay and Oxley 1997): 1) the Subpáramo or subalpine belt extends from the treeline up to 3500 (\pm 400) forming an ecotone between the montane forest and the alpine ecosystems, 2) the alpine or Páramo belt extends from the Subpáramo up to 4200 m (\pm 200), 3) the subnival or Superpáramo belt extends up to 4600 m (\pm 100), and 4) from this point onwards the nival belt occurs (\sim 5000 m \pm 200). The alpine belt of the central Andes covers a larger area (\sim 283 865 km²) than the northern section (\sim 35 000 km²), has higher elevations, and is characterized by two major vegetation types reflecting a gradual increase in the length of the dry season towards the south of the Andean chain, the Mesic and the Xeric Puna (Josse et al. 2011). As in the Páramo, both Puna regions have been previously classified in altitudinal belts (Navarro and Maldonado 2002): 1) the alpine or Altiplano belt, between 3700 and 4400 m (\pm 200 m), 2) the subnival or Altoandino belt up to 5000 m (\pm 200) and 3) the nival belt above 5000 m.

Selected study sites

The regional initiative ‘climate change impacts on high-mountain biodiversity in the Andean region’ (Cuesta et al. 2012, <www.condesan.org/gloria>) promotes the establishment of long-term biodiversity-climate monitoring sites in the high tropical Andes. Here we analyze the vegetation baseline data from 13 of those sites, which comprise 50 summits along a 4200 km latitudinal gradient from 8°54′56″N (Mérida, Venezuela) to 26°41′24″S (Tucuman, Argentina), and with an elevation range from 3220 m (Piura, Peru) to 5498 m (Cuzco, Peru; Fig. 1b; Supplementary material Appendix 1, Table A1). The 50 summits selected were located across the latitudinal and elevation gradients with 26 summits in the Páramo, including 7 summits in the subalpine belt, 5 summits in the alpine belt, 10 in the subnival belt and 4 in the nival belt. The remaining 24 summits were located in the Puna with 4 summits in the alpine, 12 in the subnival and 8 in the nival belts. The vegetation data were collected between 2012 and 2013 during the most

favorable season for plant flowering (i.e. when most plants can be identified) for each site.

Sampling procedure

Each site is composed of four summits, except for Podocarpus (Ecuador) and La Culata–Piedras Blancas (Venezuela), with three summits each. We selected summits with different elevations at each site following the Gloria protocol (Pauli et al. 2015), from the subalpine to the nival belt (separated by an average elevation of 178 ± 90 m), excluding summits with permanent glaciers. On each summit, we established sixteen 1 \times 1 m permanent vegetation plots, four on each cardinal orientation, at the corners of a 3 \times 3 m quadrat design (Pauli et al. 2015). In each plot, we visually estimated the cover of each vascular plant species and of different substrate types (rock, scree, bare soil, above-ground decomposing necromass and total vascular plant cover). At the summit level, we recorded a complete plant species lists within the area included from 10 m below the summit up to the top of the summit. The summit area sampled ranged from 0.08 ha to 1.3 ha (mean = 0.4 ha, SD \pm 0.27 ha).

At each site, a reference collection was compiled, and the species were identified by the site taxonomist and the plant specialists of the corresponding associated herbaria (Supplementary material Appendix 1, Table A1). Additionally, we compared and validated the taxonomic information from all sites during two taxonomic workshops, held during 2012 in Quito (QCA Herbarium–Catholic Univ., Páramo sites) and La Paz (LPB Herbarium–San Andrés Univ., Puna sites). The voucher samples were contrasted among sites, and against the reference collections of both herbaria where the workshops took place. As a result of these meetings, we consolidated two regional reference collections for the central and northern Andes sites at LPB Herbarium in La Paz (Bolivia) and QCA Herbarium in Quito (Ecuador), respectively. Of the 968 morpho-species recorded, 505 taxa were identified at the species level, whereas 145 were identified at the genus level and 38 at the family level (Supplementary material Appendix 2). Currently the dataset contains 15 789 records from 920 permanent 1 \times 1 plots, 17 681 presence/absence records from 50 summits and contains information of 17 sites, yet only 13 of those were used for this publication as the other sites were installed later, or their data sets were not ready for analysis at the time this paper was drafted.

Data analysis

Community composition

We analyzed patterns of community composition (species abundance patterns) along altitudinal and latitudinal gradients, for which we constructed a matrix of the average cover of each vascular plant species, averaged over the sixteen 1 \times 1 m quadrats in each of the 50 summits. We standardized and squared root transformed species cover, to increase the weight of low-abundance species in the analysis (i.e. 10% of the species had a mean coverage higher than 3%). We then constructed a between-summits similarity matrix using Bray Curtis as floristic similarity metric and performed

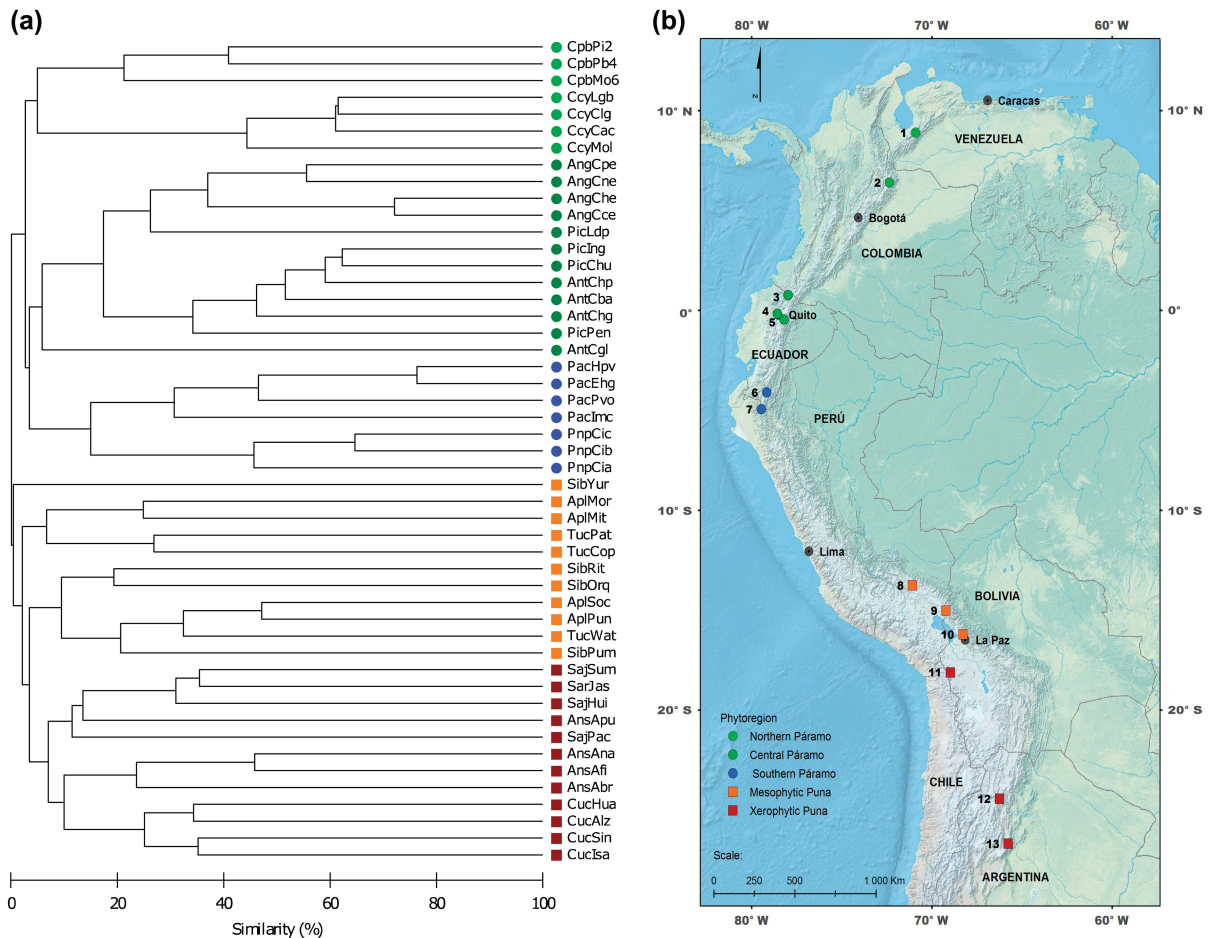


Figure 1. (a) Hierarchical cluster analysis (group average linkage) based on the Bray-Curtis similarity in plant species cover among the 50 studied summits. The Moraroni summit (APLMOR) was not included in the analysis since no vascular plants have been recorded. (b) Study area and distribution of the 13 monitoring sites that include the 50 studied summits. Each site comprises four summits except for Sierra de la Culata (Ve) and Podocarpus (Ec), with three summits each. The full names corresponding to each summit code are indicated in Supplementary material Appendix 1.

a hierarchical agglomerative cluster analysis using a group average linkage procedure (Primer ver. 6; Clarke and Gorley 2006). The Jasasuni summit (TUCJAS) was not included in the analysis since no vascular plants have been recorded up to 2012 (only bryophytes). Based on the cluster analysis, we used a similarity percentage procedure (SIMPER, Primer ver. 6) to determine which plant species characterized the groups in each node (up to a 50% contribution to the within group cumulative similarity).

Geographic distance and community turn-over

We analyzed the importance of geographic distance in explaining floristic distance between sites; for this, a presence-absence species matrix for each site was built based on the complete inventory carried out on each summit (see sampling procedure). Then, we calculated a Jaccard similarity matrix (at the species and genus level) between sites, which was correlated (Spearman rank) with a geographic distance matrix using the RELATE procedure in Primer ver. 6, and evaluated the significance of these correlations using a permutation procedure (9999 permutations). In addition, plant community turnover (i.e. beta diversity) within the

Páramo sites and within the Puna sites was quantified using the Whittaker index (Koleff et al. 2003) as follows:

$$b_w = \frac{S}{\bar{\alpha}} \quad (1)$$

where, S is the total number of species recorded for both sites ($S = a + b + c$); component a comprises the number of shared species between both sites, and components b and c comprise the number of species present exclusively in each of the two sites; $\bar{\alpha}$ is the average number of species found within the sites. The index was calculated for the Páramo and Puna sites separately in Past ver. 3.11 (Hammer et al. 2001).

Influence of habitat variables on species abundance patterns

We performed a canonical correspondence analysis (CCA) to assess the relationships between plant community structure and habitat variables, following Legendre and Anderson (1999). The analysis was performed in Past ver. 3.11 (Hammer et al. 2001), for all summits and for the Páramo and Puna sites separately.

The external environmental matrix used for the direct gradient analysis contained fine and broad-scale habitat variables. We collected fine-scale habitat data on average superficial substrate-type cover (rock, scree, bare-ground, above-ground decomposing necromass or litter) at each summit using the methods described above as part of the vegetation baseline (within the sixteen 1 × 1 m quadrats). The broad-scale habitat variables included climatic variables derived from WorldClim gridded datasets (Hijmans et al. 2005), extracted using the elevation and geographic location of each summit; these included: 1) total annual precipitation, 2) minimum temperature of the coldest month and 3) maximum temperature of the warmest month. To improve the characterization of the climatic conditions on each summit, the WorldClim temperature maps were downscaled from a 1 km to 90 m resolution using SRTM elevation data and a lapse rate of 5.4°C km⁻¹ (Bush et al. 2004, Ruiz et al. 2012). Precipitation maps were kept at 1km resolution due to interpolation limitations, since rainfall patterns in the Andes do not co-vary with elevation following consistent patterns across the region (Urrutia and Vuille 2009, Buytaert et al. 2010).

Patterns of species richness

We explored which environmental variables were important in explaining species richness patterns for all summits and for the Puna and Páramo summits analyzed separately. Richness was calculated as the total number of species found in the sixteen quadrats established in each summit, so that the sample area was the same in all summits. Some of the predictor environmental variables were log or square root transformed to address non-normality (Shapiro–Wilk test). We applied a quasi-Poisson generalized linear model (GLM), with species richness as the dependent variable, following Quinn and Keough (2002). Poisson GLM models were not used as they showed over-dispersion of model residuals (i.e. the residual deviance was larger than the available degrees of freedom). In all cases we selected the best model in terms of explanatory power based on the Adjusted Akaike's information criterion (AICc). Given the possible lack of independence of species richness in summits within each of the 13 sites, we evaluated the existence of spatial autocorrelation of the regression residuals (Moran's I index) for the best model in each case, using SAM ver. 4.0 (Rangel et al. 2010). Quasi-Poisson GLM regression was also used to analyze the relationship between species richness and summit elevation across all summits and in the Puna and Páramo summits separately. No significant spatial autocorrelation of model residuals was found in any of the GLM analyses carried out ($\alpha = 0.05$).

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.6qf10>> (Cuesta et al. 2016).

Results

Floristic composition

A total of 968 species, 269 genera and 76 families of vascular plants were identified in the entire summit sections surveyed (702 species were recorded within the 1 m² quadrats). Eleven families, from a total of 76, contained 67% of all the species recorded. Asteraceae (250 spp.) and Poaceae

(161 spp.) were the most diverse families (Supplementary material Appendix 2, Table A2). In the Puna 24 summits included in the study, the vegetation was composed of 45 families (133 genera, 443 species) of which 6 families contributed 72% of the species reported. The Puna families with the highest number of species were Asteraceae (128 spp.), Poaceae (95 spp.), Caryophyllaceae (30 spp.) and Brassicaceae (28 spp., Fig. 2a). In the 26 Páramo summits, a total of 63 families, 192 genera and 548 species were registered. In this case, the species were more evenly distributed between families. Eight Páramo families comprised nearly 57% of all the species recorded; the most diverse were: Asteraceae (127 spp.), Poaceae (69 spp.), and Orchidaceae (24 spp.) (Fig. 2a).

At the genus level, 20 out of 268 genera contained 33% of the total vascular plant diversity. *Senecio*, *Deyeuxia* and *Poa* were the richest genera, comprising 104 species altogether. The Puna summits were dominated in terms of cover by *Deyeuxia*, *Senecio*, *Poa* and *Nototriche*, whereas, in the Páramo summits the most abundant genera in terms of cover were *Diplostephium*, *Lachemilla*, *Senecio*, and *Calamagrostis* (Fig. 2b; Supplementary material Appendix 2, Table A2).

Cluster analysis based on Bray Curtis floristic similarity clearly separated the Páramo summits from their Puna counterparts (Fig. 1a). The species involved in separating the Páramo summits from the rest included *Calamagrostis intermedia*, *Pernettya prostrata*, *Hypochaeris sessiliflora* and *Disterigma empetrifolium* among others; the Puna node showed high abundance values of *Deyeuxia lagurus*, *Festuca orthophylla*, *Belloa schultzei* and *Senecio adenophyllus* (Table 1).

Within the Páramo, three floristic summit groups were defined along a latitudinal gradient (Fig. 1a): 1) the northern Páramo (Venezuela and Colombia), 2) the central Páramo (northern and central Ecuador) and 3) the southern Páramo (southern Ecuador and northern Peru). The first group was defined by the dominance of *Espeletiopsis colombiana*, *Castilleja fissifolia*, *Agrostis boyacensis*, *Coespeletia timotensis* and *Rumex acetosella* (an exotic herb, which is particularly abundant in two of the Venezuelan summits). The second group was dominated by *Calamagrostis intermedia*, *Hypochaeris sessiliflora*, *Baccharis caespitosa*, *Azorella aretioides* and *Xenophyllum humile*. The third group showed high abundances of *Hypericum lancioides*, *Vaccinium floribundum*, *Rhynchospora vulcani*, *Disterigma empetrifolium* and *Calamagrostis tarmensis*.

The Puna summits were subdivided in two sub-groups (Fig. 1a): 1) the xeric summits of northern Argentina and western Bolivia (Sajama) were separated from, 2) the mesic summits of eastern Bolivia and Southern Peru (Sibinacocha). The xeric summits were characterized by a predominance of *Festuca orthophylla*, *Deyeuxia lagurus*, *Azorella compacta* and *Mulinum axilliflorum*, while the mesic summits were dominated by *Stipa hans-meyeri*, *Nototriche obtusata*, *Pycnophyllum tetrastichum*, *Poa gymnantha* and *Deyeuxia minima*.

Geographic distance and community turn-over

The matrix correlation analysis between the floristic and the geographic distance produced a Rho of 0.775 ($p = 0.0001$). When we analyzed the Páramo summits separately, the Rho

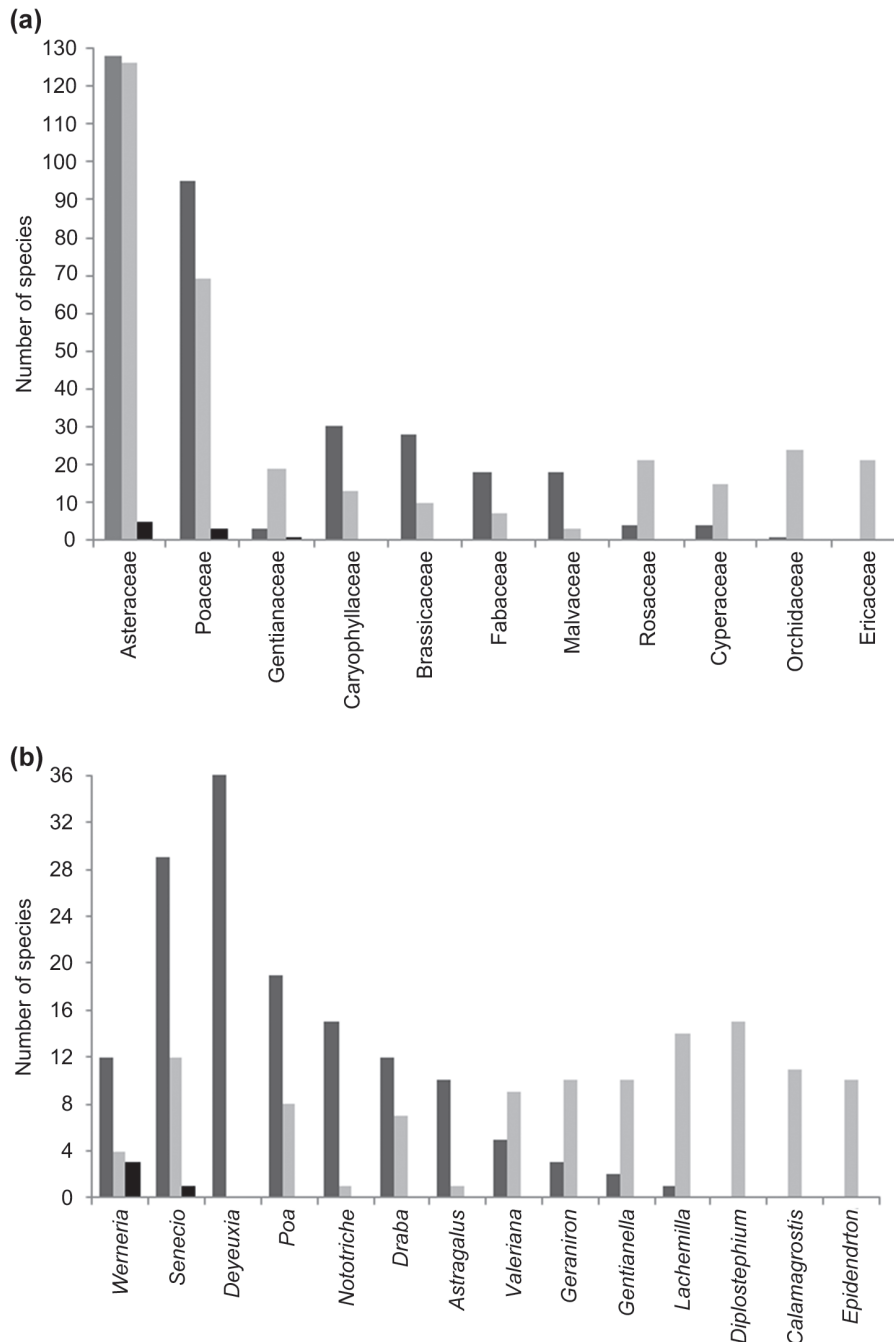


Figure 2. Number of species per (a) family and (b) genus for the 50 summits studied along the Puna (dark grey) and Páramo (light grey), and species shared between both regions (black). Only those families and genera with at least 15 species recorded were included.

was 0.571 ($p = 0.0145$); for the Puna summits, the correlation between floristic and geographic distance was lower and non-significant ($Rho = 0.425$, $p = 0.0736$). When floristic similarity at the genus level was correlated with geographic distance the correlation including all summits was weaker ($Rho = 0.555$, $p = 0.0005$). A similar value was obtained when the Páramo summits were analyzed separately ($Rho = 0.550$, $p = 0.0240$). Again, in the case of the Puna, the correlation between generic similarity and distance between summits was lower than in the Páramo and non-significant ($Rho = 0.457$, $p = 0.0866$).

The overall community turnover between plant communities from high Andean summits was higher for Páramo sites with respect to the Puna sites (mean value of Whittaker's indices: 0.88 ± 0.12 and 0.76 ± 0.09 , respectively) (Table 2a). The dissimilarity decreased at the genus level between sites; 37% of the recorded genera were shared across all sites (mean value of Whittaker's index 0.63 ± 0.17) and increased to 44 and 56% shared species in the Páramo and Puna summits respectively (mean value of Whittaker's index: 0.56 ± 0.14 and 0.44 ± 0.09 , respectively) (Table 2b).

Table 1. Plant species with the highest contribution (average cover) to the Bray Curtis similarities within each group (up to a 50% contribution to the within group cumulative similarity) based on a Similarity Percentage procedure (SIMPER, Primer ver. 6).

Species	Av. abund	Contrib. %	Cum. %
Páramo summits			
<i>Calamagrostis intermedia</i>	2.13	14.95	14.95
<i>Pernettya prostrata</i>	0.68	7.08	22.03
<i>Hypochaeris sessiliflora</i>	0.8	6.34	28.37
<i>Disterigma empetrifolium</i>	0.91	4.96	33.34
<i>Calamagrostis aff. effusa</i>	1.12	3.39	36.73
<i>Vaccinium floribundum</i>	0.62	3.33	40.05
<i>Hypericum lancioides</i>	0.82	2.92	42.97
<i>Baccharis caespitosa</i>	0.78	2.86	45.83
<i>Azorella aretioides</i>	0.63	2.84	48.68
<i>Xenophyllum humile</i>	0.78	2.46	51.14
Puna summits			
<i>Deyeuxia lagurus</i>	1.01	14.47	14.47
<i>Festuca orthophylla</i>	1.31	11.72	26.19
<i>Belloa schultzei</i>	0.63	6.99	33.18
<i>Senecio adenophyllum</i>	0.67	4.33	37.51
<i>Azorella compacta</i>	0.69	4.08	41.59
<i>Pycnophyllum tetrastichum</i>	0.65	3.95	45.54
<i>Mulinum axilliflorum</i>	0.66	3.85	49.39
<i>Pycnophyllum convexum</i>	0.87	3.76	53.15

Community composition and the influence of habitat variables

The CCA indicated a clear relationship between plant community assemblages and habitat variables (Table 3). The first two CCA axes accounted for 20.91% and 19.75% of the fitted variation in community similarity. The variables with a significant correlation ($p < 0.05$) with these two CCA axes included precipitation, maximum air-temperature, and the cover of rocks and bare soil. A precipitation gradient discriminated the Puna summits (located in the lower right-hand side) from the Páramo counterparts, with the relatively dry Páramo summits from Venezuela occupying an intermediate position (Fig. 3a). Lower precipitation values were strongly associated with lower minimum air-temperatures in the less equatorial Puna summits. However, the two variables were highly correlated (Spearman's rank correlation = 0.774), so minimum air-temperature was not included in the analysis to avoid co-linearity. We excluded minimum air-temperature instead of annual precipitation since the model that included air-temperature and not precipitation explained a lower variation of the data. The rainfall gradient was also negatively associated with increasing bare-soil and rock cover from the Páramo to the Puna summits (Fig. 3a). An orthogonal maximum air-temperature gradient was also evident, with the summits being distributed from the sub-alpine and alpine belts towards the high end of the temperature vector, while the subnival and nival summits tended to occupy the lower end (Fig. 3a); this was more evident in the Páramo than in the Puna summits, where there was higher overlap between elevation belts.

The CCA performed solely with the Puna summits, defined two major bioclimatic units (Fig. 3b). The first ordination axis accounted for 21.28% of the fitted variation and separated the mesic summits of eastern Bolivia and southern Peru (right-hand side of the diagram), from the xerophytic

summits of Argentina and western Bolivia, along a precipitation and maximum air-temperature gradient (Table 3). The 2nd axis accounted for 17.95% of the variation and ordered summits with mid to high percentage of bare soil and rock cover at the low end of the diagram, whereas summits with high percentage of scree cover were placed at the opposite end of the diagram (Fig. 3b).

In the case of the Páramo summits, the 1st CCA axis explained 22.92% of the fitted variation in the plant cover data and discriminated the summits along a thermal gradient (Table 3) generating two major groups: 1) the subalpine summits of southern Ecuador and northern Peru, and 2) the alpine, subnival and nival summits of Ecuador and Colombia (Fig. 3c). The 2nd axis accounted for 22.92% of the variation, defining a substrate-cover type gradient (scree-rock cover) which separated a third group of summits from the rest, the Piedras Blancas summits in Venezuela, which were located towards the right-hand side of the diagram. In these summits scree cover was particularly high (Table 3).

Species richness patterns

The Quasi-Poisson GLM indicated that species richness decreased linearly with increasing elevation in all summits taken together and in the Puna and Páramo summits analyzed separately (Fig. 4). The best quasi-Poisson GLM using environmental variables as predictors contained 3 out of 7 habitat variables, and explained 44.6% of total variation ($AIC_c = 93.8$, $R^2 = 0.446$). This model indicated that species richness increases with maximum temperature and above ground necromass and decreases with scree cover (Table 4). The best model generated using the Puna summits alone explained 58.6% of the variation ($AIC_c = 52.4$, $R^2 = 0.586$), and indicated a positive relationship of richness with precipitation and maximum temperature and a negative relationship with scree cover. In the case of the Páramo summits, the best regression model explained 51% of variation ($AIC_c = 50.1$, $R^2 = 0.510$). This model indicated a positive relationship between richness and precipitation and a negative relationship with scree (Table 4). In all GLM models, the analysis of the change in Moran's I index with the distance between summits showed no statistically significant spatial autocorrelation of model residuals ($p > 0.05$).

Discussion

Community composition

At the family level, many elements were common between Puna and Páramo summits; for example, Asteraceae and Poaceae were the dominant components in both environments as previously documented (Simpson and Todzia 1990, Luteyn 1999, Sklenář and Ramsay 2001, Peyre 2015). A few genera contained most of the species present in the Puna and Páramo summits (Fig. 2). High species richness within genera has also been reported for the Páramo flora of the eastern cordillera (Simpson and Todzia, 1990) and for the superpáramo of Ecuador (Sklenář and Balslev 2005). Simpson and Todzia (1990) and Sklenář and Balslev (2005)

Table 2. Plant community turnover (i.e. Beta diversity) between sites based on Whittaker's index (Koleff et al. 2003) using (a) species data, and (b) genus data. Ccy = Cocuy, Ang = El Ángel, Ant = Antisana, Pic = Pichincha, Pnp = Podocarpus, Pac = Pacaipampa, Cpb = Piedras Blancas, Ans = Abra del Acay, Cuc = Cumbres Calchaquíes, Apl = Apolobamba, Saj = Sajama, Tuc = Tuni Condoriri, Sib = Sibinacocha.

(a)

Páramo sites							
	Ccy	Ang	Ant	Pic	Pnp	Pac	Cpb
Ccy	0	0.87597	0.93778	0.93133	0.9542	0.89764	0.82648
Ang	0.87597	0	0.77436	0.72414	0.88793	0.85714	0.94709
Ant	0.93778	0.77436	0	0.45882	0.9799	0.95812	0.9359
Pic	0.93133	0.72414	0.45882	0	0.94203	0.88945	0.92683
Pnp	0.9542	0.88793	0.9799	0.94203	0	0.74561	0.98964
Pac	0.89764	0.85714	0.95812	0.88945	0.74561	0	0.95676
Cpb	0.82648	0.94709	0.9359	0.92683	0.98964	0.95676	0

Puna sites						
	Ans	Cuc	Apl	Saj	Tuc	Sib
Ans	0	0.67136	0.86473	0.73563	0.82659	0.85116
Cuc	0.67136	0	0.81203	0.74249	0.80172	0.81752
Apl	0.86473	0.81203	0	0.79736	0.54867	0.64179
Saj	0.73563	0.74249	0.79736	0	0.81347	0.85532
Tuc	0.82659	0.80172	0.54867	0.81347	0	0.64957
Sib	0.85116	0.81752	0.64179	0.85532	0.64957	0

(b)

Páramo sites							
	Ccy	Ang	Ant	Pic	Pnp	Pac	Cpb
Ccy	0	0.42282	0.56522	0.53642	0.6	0.51553	0.43939
Ang	0.42282	0	0.49606	0.41429	0.55556	0.53333	0.57025
Ant	0.56522	0.49606	0	0.24031	0.84962	0.69784	0.58182
Pic	0.53642	0.41429	0.24031	0	0.72603	0.60526	0.57724
Pnp	0.6	0.55556	0.84962	0.72603	0	0.39744	0.81102
Pac	0.51553	0.53333	0.69784	0.60526	0.39744	0	0.71429
Cpb	0.43939	0.57025	0.58182	0.57724	0.81102	0.71429	0

Puna sites						
	Ans	Cuc	Apl	Saj	Tuc	Sib
Ans	0	0.40299	0.54386	0.42308	0.53398	0.57983
Cuc	0.40299	0	0.47368	0.42254	0.44681	0.52866
Apl	0.54386	0.47368	0	0.44262	0.28926	0.28467
Saj	0.42308	0.42254	0.44262	0	0.38739	0.49606
Tuc	0.53398	0.44681	0.28926	0.38739	0	0.36508
Sib	0.57983	0.52866	0.28467	0.49606	0.36508	0

proposed that the skewed taxonomic composition towards a few highly diverse genera indicated a high degree of a recent local speciation driven by geographic isolation between high alpine 'continental islands' or complexes. In fact, (Madrinán et al. 2013), report that the average net diversification rates of Páramo plant lineages are faster than any of the documented recent speciation processes in other ecosystems.

Patterns of community similarity indicated three groups for the Páramo and two for the Puna summits (Fig. 1a). These groups were composed of different plant community assemblages, probably as a result of past geological–biogeographical events (Sklenář and Balslev 2005, Sklenář et al. 2014), and current environmental conditions (Jørgensen et al. 2011, Kessler et al. 2011). The differences in plant community composition and abundances between high

Andean summits investigated in this study supports previous findings that compared the Puna and Páramo regions (Simpson 1983, Sklenář et al. 2011, Smith and Cleef 1988). However, the high level of community dissimilarity identified between summits could also have been influenced by the limited numbers of study sites together with a relatively low surface area sampled on each summit. If a higher number of more evenly distributed summits across the Andes could be incorporated, a more gradual change in species composition and a more representative view of vegetation patterns along summits in the tropical Andes could be obtained. Incorporate Páramo summits from Colombia and Venezuela (particularly in more humid regions), as well as for the mesic Puna in central Peru would be particularly important, as they are underrepresented in the currently available data set.

Table 3. Correlation coefficients between environmental variables and axis scores from a canonical correspondence analysis (CCA) based on all plant species recorded on 49 high Andean summits. Significant correlations ($p < 0.05$) are represented in bold with an asterisk. Signs reflect arbitrary selection of gradient direction by PAST.

Variable	All summits		Puna summits		Páramo summits	
	1st axis	2nd axis	1st axis	2nd axis	1st axis	2nd axis
LogPrec	-0.845*	0.678*	0.862*	0.258	-0.460	0.476
Tmax	0.646*	0.384	-0.749*	0.186	-0.944*	0.102
Rock	0.565*	-0.629*	-0.373	-0.438	0.397	-0.626*
Bsoil	0.323	-0.636*	0.036	-0.510*	0.491	-0.380
Log(DNec)	-0.132	-0.070	-0.518*	-0.070	0.317	-0.016
Scree	0.287	0.233	0.178	0.169	0.132	-0.601*
Lat	-0.335	0.133	0.242	-0.150	0.098	-0.189
Long	0.174	-0.156	0.010	0.043	0.156	0.135

At a continental scale, floristic similarity between summits declined with geographical distance, as previously documented in the Páramos (Londoño et al. 2014, Sklenář et al. 2014). Moreover, there was a higher correlation between floristic and geographic distance in the Páramos than in the Punas at species and genus level. Our results support the idea of continental insularity (i.e. the fragmentation of alpine areas separated from each other by forests) as an important driver of high levels of species turnover, particularly in the

northern Andes (Anthelme et al. 2014). The studied Páramo sites showed higher values of community turnover, something that could be linked with the differences in landscape connectivity of high elevation areas between the more insular Páramos and the more continuous Punas. The observed pattern could have important consequences for long-term biodiversity dynamics in high Andean regions, as land use practices and climate anomalies are expected to increase the effects of continental insularity in the coming years,

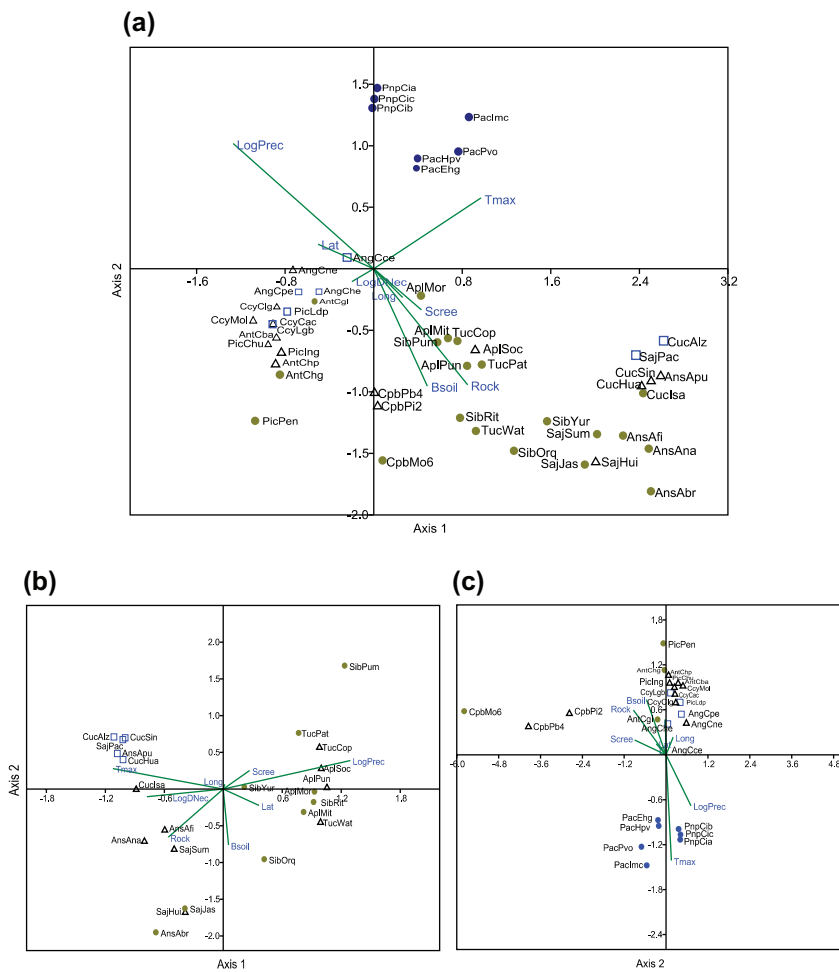


Figure 3. Biplots from canonical correspondence analysis (CCA) based on plant community similarity (Chi-square distance) in plant species cover among the 49 studied summits and its relation with normalized habitat variables: (a) all summits; (b) Puna summits; (c) Páramo summits. Summits are classified into vegetation belts based on their recorded elevation. Dot-dark blue = subalpine, square-light blue = alpine, triangle-black = subnival, dot-olive = nival.

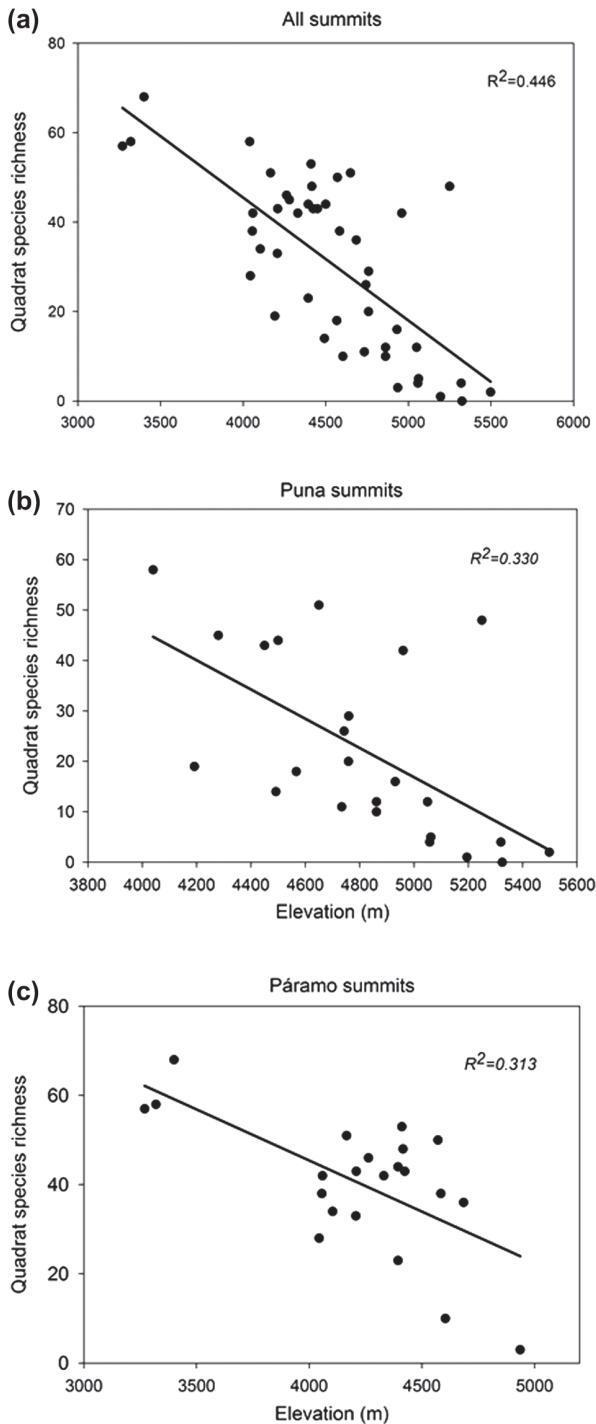


Figure 4. Change in quadrat species richness with elevation in high Andean summits: (a) all summits; (b) Puna summits; (c) Páramo summits. GLM quasi-Poisson regression model fitted to the data in each case. There was no significant spatial autocorrelation of model residuals.

especially by reducing the permeability of the lowland matrix that encloses tropical alpine summits (Anthelme et al. 2014). Nevertheless, Sklenář and Balslev (2005) found environmental similarity (i.e. humidity) between superpáramo areas were more important for species distribution than other factors, such as geographic distance. Hence, at smaller geographic scales climatic factors could be more relevant

for explaining community assemblages than biogeographic processes. Our results also indicate that processes linked with environmental factors (e.g. correspondences in precipitation regimes) also influence patterns of community similarity at continental scales, particularly across the Puna summits; for example, the xeric summits of Sajama in Bolivia, showed higher community similarity with the xerophytic Puna sites in northern Argentina than with the other, geographically closer, but more mesic sites in Bolivia.

Plant communities and the influence of habitat variables

The importance of environmental variables in explaining community similarity patterns was supported by results from the CCA. Annual precipitation, maximum temperatures and substrate types, mostly rock and scree, were the most important variables explaining plant community structure across the summits (Table 3), as has been reported for vascular plants at global, regional and local scales (Dufour et al. 2006, Krefl and Jetz 2007, Crous et al. 2013). A strong latitudinal precipitation gradient separated the Páramo summits from their Puna counterparts. This was associated with a stronger thermal seasonality in the Punas, which have a less equatorial distribution than the Páramos. A second, temperature gradient discriminated the summits according to their elevation belt (from the subalpine to the nival), this being particularly evident across the Páramo summits (Fig. 3a).

The ordination performed only with the Puna summits confirmed the existence of a marked precipitation gradient that divided the xeric summits from the mesic ones. Further, a maximum temperature gradient separated the alpine summits (all xeric Puna summits) from the subnival and nival counterparts. The CCA analysis performed only for the Páramo summits, diverged from the analysis based purely on floristic information (cluster analysis). In this case, the summits were ordered according to a strong temperature gradient and to a lesser degree following a precipitation gradient (Fig. 3c). Hence, the summits were organized according to their elevation belt, with the subalpine summits (southern Páramos), followed by the alpine, then subnival and then nival summits (irrespective of their geographic distribution along the central and northern Páramos); the Piedras Blancas summits of Venezuela were separated from the rest due to their lower annual precipitation and the predominance of scree and rock as the dominant substrates; the presence of very extensive cattle grazing could also be a factor linked with this separation, which could in turn be linked with the high cover of the exotic species *Rumex acetosella* in the two lower Venezuelan summits.

It is important to take into account the geographic specificities of our summit based data-set for the purpose of analyzing environment–floristic relationships; on the one hand, the lowest (mean = 3416 m) and more humid (mean = 3089 mm yr⁻¹) summits in our Páramo data were geographically clumped, as they were all located in southern Ecuador and northern Peru, where the cordillera is at one of its lowest elevations throughout the Andes. On the other hand, within the xeric Puna we had a lower frequency of nival summits than in the mesic Puna. This obviously

Table 4. Generalized linear model – GLM (quasi-Poisson) – of plant species richness as a function of environmental variables in the summits studied along the tropical Andes and in the Puna and Páramo summits analyzed separately. The parameters selected on the basis of the AICc criteria for the best model are presented in each case. Significant relations are represented with an asterisk: ***highly significant, **significant, *marginally significant.

Summits	Parameter	Estimate	SD error	t value	p(> t)
All	Intercept	3.371	0.223	15.09	< 0.001***
	Tmax	0.053	0.016	3.295	0.002**
	Log(DNec)	0.259	0.125	2.073	0.045*
	Log(Scree)	-0.130	0.030	-4.341	< 0.001***
Puna	Intercept	-1.665	1.524	1.092	0.288
	Log(Prec)	1.218	0.379	3.213	0.005**
	Log(Scree)	-0.125	0.054	-2.310	0.032*
	Tmax	0.205	0.045	4.551	< 0.001***
Páramo	Intercept	1.683	1.073	1.568	0.133
	Log(Scree)	-1.147	0.059	-2.503	0.0216*
	Log(Prec)	0.740	0.324	2.284	0.0341*

increased the association between precipitation and temperature in our data, suggesting special care is needed when analyzing the interactions between these two climatic drivers, particularly when the Páramo and Puna summits are analyzed separately.

Moreover, climatic variables and substrate types did not account for all of the variability in community composition. This suggests that other factors such as biogeographical isolation, geological/edaphic heterogeneity and landscape history could also be important determinants of changes in vegetation structure (resulting from processes such as different histories of volcanism, glaciation or land use). For example, Londoño et al. (2014) reported high levels of flora dissimilarity in Páramo summits disconnected by less than 100 km in Colombia as previously reported for the eastern Andes realm by Cleef (1981). This is also the case in northern Argentina, where the Pampean mountains, of which Cumbres Calchaquíes are part, conform entirely distinct floristic compositions on each summit, separated by deep valleys but only a few dozen kilometers apart (Aagesen et al. 2012).

Patterns of species richness

We found a clear linear decline in species richness with elevation across all summits and in the Puna and Páramo analyzed separately. Moreover, richness was positively associated with maximum temperature in the GLM using environmental variables for all summits (Table 4). A monotonic decrease in species richness with increasing elevation above the treeline has been well documented in many mountain regions, including the Páramos of Colombia (Cleef 1981) and Ecuador (Sklenář and Ramsay 2001). In contrast, a hump-shaped pattern of richness with elevation has also been reported for humid Páramo areas (Sklenář and Balslev 2005). The upper condensation belt in the lower subnival belt (~ 4200 m) creates a humid climate enhancing species richness in these humid regions (Sklenář et al. 2008).

As suggested by Körner (2003) the inverse relationship between temperature/elevation and species richness may be partly due to the conical shape of high mountains, which result in an overall decrease in the size of the species pool as

the surface area decreases with altitude (other relevant factors include increased isolation of high elevation areas). Even so, the GLM model for species richness in all summits indicated a significant positive relationship with above-ground decomposing necromass (plant litter), which could be interpreted as a result of higher site productivity (Al-Mufti et al. 1977). Moreover, species richness in the summits increased monotonically with total plant cover in all summits and in the Puna and Páramo analyzed separately (Table 4). All of this suggests that environmental factors limiting productivity at high altitudes could also play a role in influencing species richness, as predicted for the low-end of productivity gradients in the classical humpback diversity–productivity model (Grime 1973, see Peyre 2015 for the Páramo region).

As for the relationship between precipitation and richness, this variable was not included in the best GLM model for all summits, but it was included as a positive effect in the models for the Puna and Páramo analyzed separately. In the case of the Páramo this could have been influenced by the lower elevation summits (Podocarpus, Ecuador) which show the highest observed species richness and annual rainfall in our data; at the other end, the driest summits in Venezuela, showed some of the lowest species richness values. In the case of the Puna summits, the positive relationship between richness and precipitation could be linked with higher overall richness in the more mesic summits than the more xeric ones (after accounting for differences in temperature/elevation in the GLM).

In addition, the regression models for all summits, and for the Puna and Páramo analyzed separately, indicated a significant negative relation between richness and scree cover. Scree and rocks were in fact the dominant substrates in nival and subnival summits, and appear to be indicative of limiting conditions for soil and vegetation development. The predominance of scree should have a direct link with the occurrence of periglacial conditions and frequent freezing temperatures inducing gelifraction processes (Monasterio 1986, Pérez 1986). Finally, the decline in species richness in high altitude summits can also be linked with the relatively recent retreat of glaciers and snow covered areas (i.e. after the Little Ice Age, Vuille et al. 2008). These dynamic historical changes in climatic conditions need to also be considered for explaining species richness patterns on high Andean summits.

Conclusions and implications for climate change research

Overall, our results indicate that community structure along tropical high Andean summits is influenced by the complex interaction of biogeographic processes, reflected in the patterns of association of floristic similarity and geographic distribution, and latitudinal/elevation gradients, which are in turn reflected in a strong association of climatic and substrate characteristics with community composition and species richness.

The large proportion of species belonging to a few highly diversified genera in combination with a high replacement of species composition between our study summits, is consistent with the general finding that vegetation in the high tropical Andes is characterized by many species with narrow distributions and high species turn-over (Sklenář and Balslev 2005, Sklenář et al. 2011, Anthelme et al. 2014). Consequently, vegetation in our summits might be highly sensitive to the effects of climate change, especially considering that tropical alpine environments are among the terrestrial ecosystems that are likely to experience higher warming rates during this century (Bradley et al. 2006), and there is growing evidence that the rate of warming is amplified with elevation (Mountain Research Initiative 2015). Moreover, species which occupy high summits will have limited space for vertical migration (Ramirez-Villegas et al. 2014), and high Andean plants appear to be shifting rapidly towards their upper elevation limit, as recently documented on the Chimborazo volcano, two centuries after Humboldt's visit (Morueta-Holme et al. 2015). Nevertheless, microclimatic refugia are common in alpine ecosystems and this might help to attenuate the expected trend in species vertical migration (Scherrer and Körner 2011, Valencia et al. 2016).

Our results also support the idea of continental insularity as driver of high levels of species turnover, particularly in the northern Andes (Anthelme et al. 2014). Even so, geographic proximity did not account for all the variation in community structure between summits. A general latitudinal gradient of precipitation and minimum air temperatures was strongly associated with differences in community composition between the Páramos and Punas. Variation in species richness across all summits was mainly explained by altitudinal changes in maximum air temperature, above-ground necromass, and scree cover.

Hence, our results point to different climatic drivers as key factors for explaining both vertical and latitudinal species turnover and species richness patterns in high Andean summits. This could offer a powerful tool to detect contrasting latitudinal and altitudinal effects of climate change across the tropical Andes. In particular, it raises interesting questions regarding the differential effect of temperature vs precipitation on summit community diversity at continental scales (Pauli et al. 2012). For instance, on European GLORIA summits, the documented recent increase in air temperature has been related to a shift towards a more thermophilous species composition (Gottfried et al. 2012) and to an increase of species richness on temperate and boreal summits, whereas on the drier Mediterranean summits a reduction in annual rainfall has resulted in stasis or decrease in richness (Pauli et al. 2012). Given that many models

predict a reduction in precipitation in the dry central Andes in the next few decades, but not in the northern Andes – except for the drier Venezuelan Páramos (Buytaert et al. 2010, Tovar et al. 2013), the monitoring system established in high Andean summits should provide a sensitive system of permanent sites to evaluate the possibility of diverging impacts of climatic changes on plant diversity and vegetation composition across the region.

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Supplementary material (Appendix ECOG-02567 at <www.ecography.org/appendix/ecog-02567>). Appendix 1–2.