Geographic flora elements in the Ecuadorian superpáramo

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Abstract

The superpáramo is an island-like ecosystem located on the highest mountain-tops in the equatorial Andes and its flora is composed of genera that are distributed in both tropical and temperate areas. We were interested in studying: (1) whether the proportions of tropical and temperate genera change along the altitudinal gradient of the superpáramo and (2) whether the proportions of tropical and temperate genera correlate to ecological conditions (dry vs. humid) of the superpáramo. We studied the generic composition in 18 isolated superpáramo sites of Ecuador and analyzed the proportions of eight geographic flora elements in: (1) the entire superpáramo flora, (2) eight altitudinal superpáramo flora samples between 4100 and 4800 m, and (3) the superpáramo flora samples divided into three humidity types, i.e., dry, humid, and very humid superpáramos. Of the total of 144 genera encountered, more than a half are predominantly distributed in temperate regions whereas about $\frac{2}{5}$ are predominantly distributed in tropical regions and only 2% are endemic to the páramo. When distinguishing only tropical and temperate genera their numbers along the altitudinal gradient do not depart from the expected values based on the entire superpáramo flora. But when breaking the temperate and tropical genera down into their constituent geographic flora elements, significant departure from the expected values is found above 4500 m altitude, which corresponds to a transition zone between the lower and upper superpáramo. Genera from the Wide temperate, Holarctic, and Andean alpine elements significantly increase along the altitudinal gradient whereas Neotropical montane, Austral-Antarctic, Páramo endemic, and Cosmopolitan elements significantly decline with altitude, and the proportion of genera from the Wide tropical element do not show correlation to altitude. Tropical genera are better represented in humid superpáramo types and temperate genera are more common in dry superpáramo type. Although the proportion of elements differs among dry, humid, and very humid superpáramo sites, their composition does not depart significantly from that in the entire superpáramo flora. We conclude that ecological predispositions of genera from their implied areas of origin predict their distribution within and among equatorial superpáramo.
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Introduction

Floras of mountain ecosystems have developed through combined processes of plant immigration and subsequent in situ evolution. Historic events, such as orogeny, volcanism, and glaciations, strongly affect plant

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distributions and add another dimension to the observed patterns of species richness and composition among mountain floras. Understanding how mountain floras have evolved is important because it can provide clues to how biodiversity originates (e.g., Comes and Kadereit, 2003; Hedberg, 1969; Kitayama, 1996; Knox and Palmer, 1995; Price, 2004; Van der Hammen and Cleef, 1986; Winkworth et al., 2005). Alpine floras of tropical mountains, which create "islands" of cold climate in the tropics, are of predominantly temperate (immigrant) origin whereas recruitment by adaptation from tropical lower altitude taxa has been relatively low (Smith and Cleef, 1988). Repeated Pleistocene climatic oscillations altered the geographic extent of these islands and strongly influenced the richness and distribution of their biota (Simpson, 1974; Vuilleumier, 1971; Vuilleumier and Monasterio, 1986). We here try to shed some light on the processes that have shaped the flora of the isolated superpáramo ecosystem in Ecuador by studying the relative proportions of geographic flora elements along an altitudinal gradient and by comparing the composition of plant genera in superpáramos with different humidity regimes.

The superpáramo ecosystem lies between the tree-less grass páramo and the perpetual snow on the highest altitudes of the tropical Andes from Venezuela to Ecuador, usually between 4100 and 4800 m (Cleef, 1981; Cuatrecasas, 1968; Monasterio, 1979; Sklenář and Balslev, 2005). The superpáramo has fragmented vegetation with open soil in between the plant cover which consists mostly of small rosulate herbs, prostrate dwarf-shrubs and short-stem grasses. Because the superpáramo occurs only on the highest tops of the mountains it is geographically divided and forms an insular system (Luteyn, 1992; Simpson, 1975; Sklenář and Balslev, 2005). The environment of the superpáramo is perhaps the most extreme within the tropics and it becomes increasingly harsh with increasing altitude. The climatic conditions impose very strong selection pressures on plants which must resist large diurnal changes in temperature and humidity, often involving both frost and frost-free conditions on a daily cycle. These conditions are strikingly different from the cool tropical and warm tropical vegetation surrounding the superpáramo and also different from the World's temperate zones where freezing is seasonal on an annual cycle with a long frost-free growing season (Rundel, 1995; Sarmiento, 1986).

The evolution of the páramo flora of the tropical Andes is closely related to the Andean orogeny. The northern Andes reached above the upper forest line near the end of the Pliocene 3–5 million years ago (Van der Hammen, 1974). Since then, the páramo and superpáramo floras have derived their species from two major sources (Simpson, 1983; Van der Hammen and Cleef, 1986). One is Neotropical genera, predominantly of the montane forest, from which certain elements have gradually adapted to the conditions at high altitudes above the upper forest line, for example, as demonstrated by the radiation within the endemic subtribe *Espeletiinae* CUATREC. (Asteraceae), in which branched shrubs and trees in the montane forest gave rise to monocaul taxa in the páramo (Cuatrecasas, 1986; Panero et al., 1999). The other source is genera from temperate zones north and south of the tropics, from which species have immigrated into and along the Andes sometimes followed by speciation or radiation, for instance, in such genera as *Valeriana* (Valerianaceae), *Halenia* and *Gentianella* (Gentianaceae) (Bell, 2004; Von Hagen and Kadereit, 2001, 2003). Such immigration started early and initially contributed to the so-called "prepáramo" flora of which about one half was of temperate affinity already during the Late Pliocene/ Early Pleistocene period (Van der Hammen and Cleef, 1986). The present-day proportion of temperate genera in a number of different páramo floras varies from 48% to 67% with the remainder being of tropical affinity (Cleef, 1979, 2005; Cleef and Chaverri, 1992; Ramsay, 1992; Salamanca, 1992; Van der Hammen and Cleef, 1986).

The flora that colonized the Andean habitats above the tree line had to adapt to a mosaic of ecological niches that had been formed by interaction of several environmental factors, of which the most prominent ones were the temperature gradients caused by altitude and the humidity and seasonality gradients caused by differences in latitude (Sarmiento, 1986; Troll, 1959; Weberbauer, 1945). Environmental changes related to the altitudinal gradient result in vegetation belts characterized by different sets of species. In the Ecuadorian Andes, a major change in species composition occurs at 3500 m (Jørgensen and León-Y., 1999), roughly along the forest line-páramo ecotone; another ecotone is the transition between páramo grasslands and superpáramo (Ramsay, 1992; Sklenář and Ramsay, 2001), and there is an additional change in the superpáramo belt at about 4500 m (Jørgensen and León-Y., 1999; Sklenář, 2000, 2006).

Spatial gradients in the Andes operate at various geographic scales and often are less consistent than the altitudinal gradient. At a continental scale aseasonal humid conditions in the equatorial Andes change to seasonal, warm–cool and dry–humid altiplano at mid-latitudes and seasonal, cool, humid temperate Andes further south (Cabrera, 1968; Simpson, 1983; Troll, 1959, 1968). This latitudinal gradient is accompanied by pronounced floristic differences which lead to delimitation of major phytogeographical units of the high Andes, such as páramo, jalca, and puna. In the high Andes of Ecuador we find a spatial environmental gradient at much smaller (regional) scale. The superpáramo there forms three distinct floristic types related

to the gradient of humidity and the regions are accordingly called dry, humid, and very humid super-páramos (Sklenář and Balslev, 2005).

It has been predicted that in the high Andean flora Neotropical genera would be best represented in humid tropical habitats and least prominent in arid habitats of southern Andes and that the relative proportion of Holarctic and cosmopolitan genera would be higher in the central and southern Andes than in the northern Andes (Simpson, 1983). The distribution of Andean taxa that occur above the forest line, indeed, tends to follow ecological similarities of habitats rather than geographic distance to the source area, and therefore there is a higher proportion of Holarctic genera in dry puna (Argentina) than in humid tropical páramo (Colombia) whereas there are more austral (southern-hemisphere temperate) taxa in páramo than in puna (Simpson and Todzia, 1990).

In this paper we analyze the generic composition of the superpáramo flora of Ecuador and relate it to the geographic distribution of the genera, employing the geographic flora element approach (Cleef, 1978, 1979; Hedberg, 1965). We use altitudinally stratified floristic data to investigate whether the altitudinal gradient of the superpáramo imposes a stronger pressure on distribution of genera with mainly tropical distribution, i.e. we test whether the proportion of tropical genera declines with altitude. Finally, we examine whether the distribution

patterns of the geographic elements observed on continental scales can be seen at a regional scale, i.e., we compare whether the dry Ecuadorian superpáramos have higher proportion of Holarctic and cosmopolitan genera than the humid ones, and whether the humid ones have higher proportions of Neotropical genera.

Methods

We collected our data in 18 superpáramo sites in northern and central Ecuador during May–December 1995, June–September 1997, and June–July 1999. The study sites included mountains built from volcanic as well as metamorphic rocks, several mountains topped with a glacier, and some active volcanoes (Fig. 1); more details about the study sites are given in Sklenář (2000) and Sklenář and Balslev (2005).

At each site we prepared a species list from: (1) stratified-randomly located plot-samples of zonal vegetation with three replicates at each 100 m altitudinal levels between 4100 and 4800 m (a total of 240 plot-samples were recorded), and (2) additional surveys for species in zonal vegetation outside the plot-samples and in azonal vegetation such as rocky outcrops, cushion mires, lake shores, etc. Introduced species that were naturalized in the superpáramo vegetation were included.
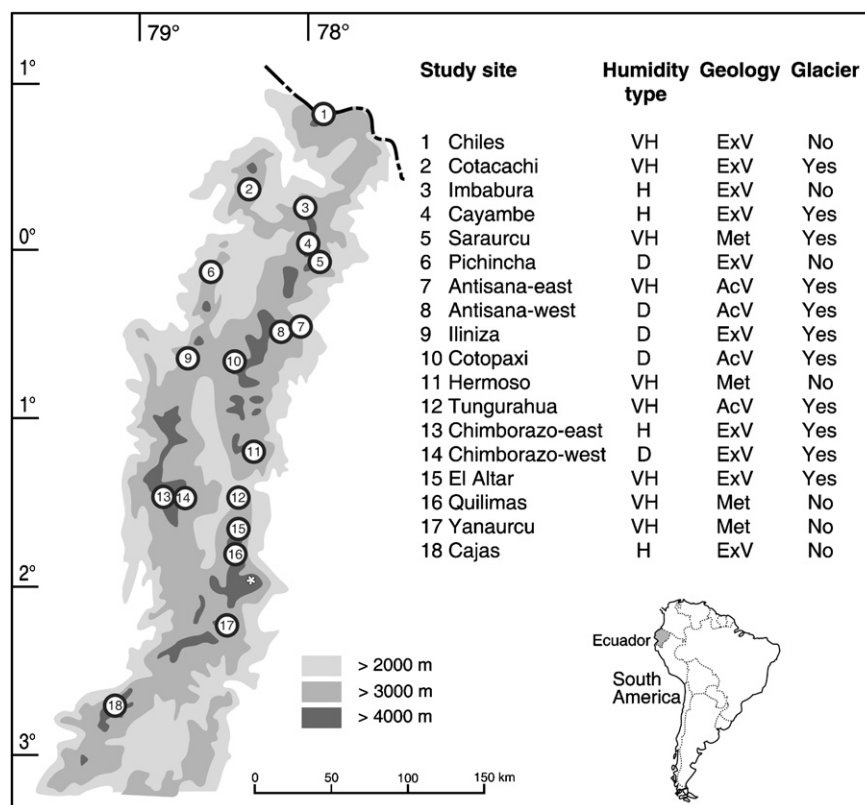

Fig. 1. Location of study sites in the Andes of Ecuador and their basic characteristics; Humidity types: D – dry, H – humid, VH – very humid; Geology: ExV – extinct volcano, AcV – active volcano, Met – metamorphic basement.

We classified all genera recorded into geographic flora elements (Table 1), and calculated the relative importance of each element for the entire superpáramo and for each altitude range of 100 m from 4100 to 4800 m. A genus was considered present at all altitudes between its maximum and minimum recorded presence. Finally, we calculated the percentages of each geographic flora element for five dry, four humid, and nine very humid superpáramos separately.

The observed frequencies of the elements in the altitudinal floristic samples were tested for departure from frequencies estimated for the entire Ecuadorian superpáramo flora, i.e., in floristic data obtained from both zonal and azonal habitats. Deviation from the expected frequencies was measured by log-likelihood test, or *G*-test (Sokal and Rohlf, 1995). Correlation analysis (Spearman-rank correlation coefficient) was used to test whether or not proportions of individual elements were constant along the altitudinal gradient. Direct ordination analysis (CCA) was performed to test the overall correlation between the composition of elements and altitude employing program CANOCO (Ter Braak and Šmilauer, 1998), the significance of the resulting ordination was evaluated by Monte Carlo permutations.

Nomenclature follows Luteyn (1999) with updates from Sklenář et al. (2005).

Results

Geographic flora elements in Ecuadorian superpáramo

Among 144 genera of vascular plants encountered in the Ecuadorian superpáramo (Table 1), almost three-fifths are distributed predominantly in the temperate zones of the World and about one-third are distributed predominantly in tropical zones (Table 2). Also among the widespread genera there are many more temperate ones (Wide temperate element; 31%) than tropical ones (Wide tropical element; 5%). About 17% of the genera occur in alpine habitats above the forest line in the tropical or temperate Andes (Andean alpine element) and about 6% of the genera have nearly worldwide distributions (Cosmopolitan element). The proportions of each element in the total superpáramo flora (Table 2, bottom line) were used to calculate the expected numbers of genera in the following tests.

Altitudinal distribution of geographic flora elements

Of the 144 genera, 121 that were registered in the stratified plot-samples were used to analyze the altitudinal distribution patterns. The relative proportion of tropical and temperate genera is fairly constant in the middle part of the altitudinal gradient, with only modest variations at the lower and the upper ends, but without significant departures from the expected frequencies (based on proportions of 37.5 vs. 56.2) at any altitude (Table 2). Correlation analysis confirms those results for the tropical genera indicating that there is no significant change in their proportions (decline) along the gradient (Spearman $r = -0.357$, $p = 0.39$) but we find a significant increase with increasing altitude in the temperate genera (Spearman $r = 0.81$, $p = 0.015$).

When the elements in the altitudinal samples are considered individually, no significant departure from the expected frequencies is found below 4500 m. The altitude of 4500 m is marginally non-significant, whereas the three highest altitudes (4600–4800 m) depart significantly (Table 2). All elements except the Wide tropical element correlate significantly to altitude; Páramo endemic, Neotropical montane, Austral-Antarctic, and Cosmopolitan elements significantly decline, whereas Andean alpine, Holarctic, and Wide temperate elements significantly increase with increasing altitude (Table 2, Fig. 2). Altitude is thus a significant factor which accounts for 76% of the variation in the composition of elements in the altitudinal samples; CCA: *F*-ratio = 19.336, $p = 0.002$, 499 permutations.

Distribution of geographic flora elements in dry and humid superpáramos

Of the 144 genera encountered in the Ecuadorian superpáramos, 112 occur in dry, 105 in humid, and 113 in very humid sites (Table 3), and among them 30 genera are restricted to dry and 18 genera are restricted to humid/very humid sites. Although the proportions of elements differ among the three superpáramo types, their overall distribution in any of the types does not depart significantly from the frequencies found in the entire superpáramo flora (dry superpáramos: $G = 4.79$, $p = 0.69$, humid superpáramos: $G = 3.86$, $p = 0.80$, very humid superpáramos $G = 1.5$, $p = 0.98$).

There is a clear trend in the proportion of tropical genera to increase from dry to very humid superpáramos and this is also evident in the Páramo endemic and Neotropical montane elements (Table 3). *Floscaldasia* and *Neurolepis* from the Páramo endemic and *Arcytophyllum*, *Puya*, *Brachyotum*, and *Miconia* from Neotropical montane elements as well as some fern genera (e.g., *Hymenophyllum*, *Hypolepis*) from the Wide tropical element were found only in humid or very humid superpáramos. On the other hand, *Conyza*, a Wide tropical element, was found only in dry superpáramos. The Andean alpine element is comparably frequent in dry and humid superpáramo and drops slightly in very humid superpáramo, although certain genera (*Aciachne* and *Jalcophila*) were found only in the latter.

Table 1. The generic composition of geographic flora elements in the Ecuadorian superpáramo

Element	Definition	Genus
Tropical		
Páramo endemic	Confined to páramo	*Chrysactinium* (KUNTH) WEDD. (D), *Floscaldasia* CUATREC. (H), *Neurolepis* MEISN. (H)
Andean alpine	Confined to supraforest habitats but unlike páramo with species occurring also outside the tropical Andes	*Aa* RCHB.f., *Aciachne* BENTH. (H), *Aphanactis* WEDD., *Brayopsis* GILG & MUSCHL. (H), *Cuatrecasasiella* H.ROB., *Distichia* NEES & MEYEN, *Eudema* HUMB. & BONPL., *Hypsela* C.PRESL (D), *Jalcophila* M.O.DILLON & SAGÀSTEG. (H), *Lachemilla* (FOCKE) RYDB., *Laestadia* KUNTH EX LESS. (H), *Loricaria* WEDD., *Lucilia* CASS., *Luciliocline* ANDERB. & S.E.FREIRE (= *Belloa* REMY), *Lysipomia* KUNTH, *Myrosmodes* RCHB.f., *Niphogeton* SCHLTDL., *Nototriche* TURCZ., *Oritrophium* (KUNTH) CUATREC., *Perezia* LAG., *Phylloscirpus* C.B.CLARKE (D), *Plagiocheilus* ARN. EX DC., *Werneria* KUNTH, *Xenophyllum* V.A.FUNK
Neotropical montane	Genera that range from montane forest to the supraforest zone, distributed also outside páramos	*Arctophyllum* WILLD. EX SCHULT. & SCHULT.f. (H), *Baccharis* L., *Bomarea* MIRB., *Brachyotum* (DC.) TRIANA (H), *Campyloneurum* C.PRESL (D), *Chuquiraga* JUSS., *Diplostephium* KUNTH, *Disterigma* (KLOTZSCH) NIED., *Gamochaeta* WEDD., *Gynoxys* CASS., *Hesperomeles* LINDL. (H), *Huperzia* BERNH., *Jamesonia* HOOK & GREV. (H), *Lasiocephalus* WILLD. EX SCHLTDL., *Lellingeria* A.R.SM & R.C.MORAN (H), *Miconia* RUIZ & PAV. (H), *Pentacalia* CASS., *Pterichis* LINDL. (H), *Puya* MOLINA (H), *Terpsichore* A.R.SM.
Wide tropical	Widely distributed, also in the Palaeotropics	*Achyrocline* (LESS.) DC., *Conyza* LESS. (D), *Elaphoglossum* SCHOTT EX J.SM., *Hymenophyllum* SM., *Hypolepis* BERNH., *Melpomene* A.R.SM.
Temperate		
Austral-Antarctic	Southern temperate distribution	*Azorella* LAM., *Calandrinia* KUNTH, *Calceolaria* L. (H), *Colobanthus* BARTL., *Cortaderia* STAPF (H), *Cotula* L., *Escallonia* MUTIS EX L.F. (H), *Gaultheria* L., *Gunnera* L., *Lilaea* BONPL. (D), *Lilaeopsis* GREENE (D), *Muehlenbeckia* MEISN., *Nertera* BANKS& SOL. EX GAERTN. (H), *Oreobolus* R.BR. (H), *Oreomyrrhis* ENDL., *Ourisia* COMM.EX JUSS., *Pernettya* GAUDICH., *Rostkovia* DESV. (H), *Sisyrinchium* L., *Uncinia* PERS.
Holarctic	Northern temperate and mediterranean distribution	*Astragalus* L. (D), *Bartsia* L., *Castilleja* MUTIS EX L.f., *Cerastium* L., *Draba* L., *Erigeron* L., *Halenia* BORKH., *Hypochaeris* L., *Lupinus* L., *Muhlenbergia* SCHREB. (D), *Potentilla* L. (D), *Ribes* L., *Satureja* L., *Saxifraga* L., *Sibthorpia* L., *Silene* L., *Stachys* L.
Wide temperate	Temperate and cool regions of both hemispheres	*Agrostis* L., *Arenaria* L., *Bromus* L., *Calamagrostis* ADANS., *Callitriche* L., *Caltha* L., *Cardamine* L., *Carex* L., *Crassula* L., *Cystopteris* BERNH., *Dryopteris* ADANS. (H), *Elatine* L. (H), *Ephedra* L., *Epilobium* L., *Festuca* L., *Galium* L., *Gentiana* L., *Gentianella* MOENCH, *Geranium* L., *Gnaphalium* L., *Hieracium* L., *Hypericum* L. (H), *Isoëtes* L., *Juncus* L., *Lepidium* L., *Limosella* L., *Luzula* DC., *Montia* L., *Plagiobothrys* FISCH.& C.A.MEY (D), *Plantago* L., *Poa* L., *Polystichum* ROTH., *Ranunculus* L., *Rumex* L., *Sagina* L. (D), *Senecio* L., *Stellaria* L., *Stipa* L. (D), *Thelypteris* SCHMIDEL (H), *Trisetum* PERS., *Urtica* L., *Valeriana* L., *Veronica* L. (D), *Viola* L., *Vulpia* C.C.GMEL. (D)
Cosmopolitan	Worldwide, or nearly so, distribution	*Asplenium* L. (D), *Bidens* L. (D), *Blechnum* L. (H), *Eleocharis* R.BR. (D), *Eryngium* L., *Hydrocotyle* L. (H), *Lycopodium* L. (H), *Ophioglossum* L., *Rhynchospora* VAHL (H)

The definitions of the elements are based on Cleef (1979), Van der Hammen and Cleef (1986), Cleef and Chaverri (1992), and Luteyn (1999) with modifications. The major modification is the division of Neotropical element into Neotropical montane and Andean alpine elements (see also Simpson and Todzia, 1990), but we also reclassified those genera for which results of phylogenetic studies corrected the knowledge about their origin in the páramo flora (i.e., *Halenia*, *Huperzia*); (H) and (D) indicate exclusive occurrence in humid/very humid and dry superpáramo sites, respectively.

Holarctic and Wide temperate elements, which are mainly responsible for the higher representation of temperate genera in dry superpáramos, decline from dry to very humid superpáramos and some genera (e.g., *Astragalus*, *Muehlenbergia*, and *Potentilla* from Holarctic, and *Plagiobothrys* and *Stipa* from Wide temperate

Table 2. Proportions (%) of geographic flora elements of the entire flora of Ecuadorian superpáramo (last row), and in altitudinal floristic samples; p = significance level

| Altitude (m)	Number of genera	Number of samples	Tropical				Temperate			Cosmopolitan	G test	p	Tropical total	Temperate total	G test	p
			Páramo endemic	Andean alpine	Neotropical montane	Wide tropical	Austral-Antarctic	Holarctic	Wide temperate							
4100	72	15	1.4	18.1	18.1	4.2	15.3	11.1	26.4	5. 6	1.781	*0.97*	41.7	52.8	0.295	*0.59*
4200	103	48	1	16.5	13.6	3.9	12.6	14.6	32	5.8	1.834	*0.97*	35	59.2	0.401	*0.53*
4300	104	52	1	17.3	15.4	3.8	13.5	14.4	31.7	2.9	4.196	*0.76*	37.5	59.6	0.121	*0.73*
4400	89	47	1.1	19.1	13.5	4.5	11.2	14.6	33.7	2.2	5.157	*0.64*	38.2	59.6	0.373	*0.54*
4500	72	33	1.4	19.4	15.4	4.2	9.7	15.3	34.7	0	11.748	*0.07*	40.3	59.7	0.082	*0.77*
4600	54	23	0	20.4	14.8	5. 6	9.3	18.5	31.5	0	12.213	*0.03*	40.7	59.3	0.109	*0.74*
4700	33	15	0	21.2	12.1	0	3	21.2	42.4	0	16.635	*<0.01*	33.3	66.7	2.233	*0.13*
4800	19	3	0	26.3	10.5	0	0	21.1	42.1	0	13.216	*<0.001*	36.8	63.2	1.774	*0.19*
Spearman r			–0.712	0.929	–0.738	–0.325	–0.976	0.952	0.714	–0.913			–0.357	0.81		
p			*0.05*	*<0.001*	*0.04*	*0.43*	*<0.001*	*<0.001*	*0.05*	*<0.01*			*0.39*	*0.02*		
Total zonal superpáramo 4100–4800	121	240	1.7	15.7	14	5.8	13.2	14	30.6	5			37.2	57.8		
Total superpáramo	144	–	2.1	16.7	13. 9	4.9	13. 9	11.8	30. 6	6.2			37.5	56.2		
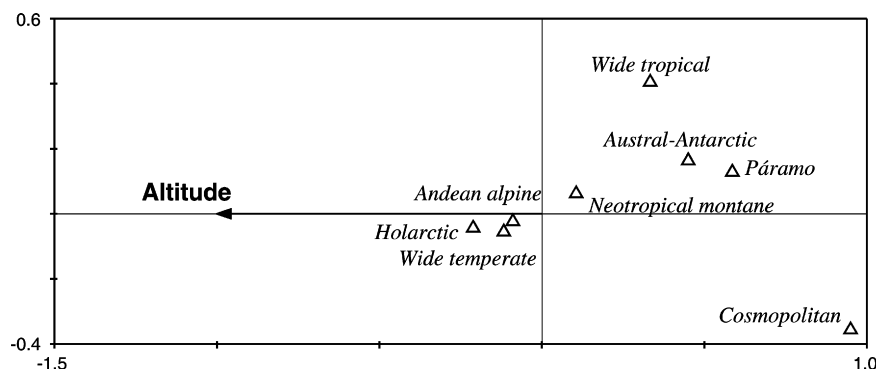
Fig. 2. CCA ordination diagram indicating the correlation between geographic elements and altitude; $\lambda_1 = 0.071$, $\lambda_2 = 0.015$, total inertia = 0.093, altitude accounts for 76.3% of data variability.

Table 3. Proportions (%) of geographic flora elements in the flora of three humidity types of Ecuadorian superpáramos (as described by Sklenář and Balslev, 2005)

Element	Dry superpáramos $N = 5$	Humid superpáramos $N = 4$	Very humid superpáramos $N = 9$
Total genera	112	105	113
Tropical			
Páramo endemic	0.9	1.9	1.8
Andean alpine	17.8	18.1	15.9
Neotropical montane	10.7	14.3	16.8
Wide tropical	3.6	2.9	4.4
Tropical total	33	37.1	38.9
Temperate			
Austral-antarctic	11.6	14.3	15.9
Holarctic	15.2	13.3	10.6
Wide temperate	35.7	32.4	29.2
Temperate total	62.5	60	55.8
Cosmopolitan	4.5	2.9	5.3

elements) were encountered only in dry superpáramos. The Austral-Antarctic element increases from dry to very humid superpáramos and, for instance, *Cortaderia*, *Gaultheria*, *Nertera*, *Oreobolus*, and *Rostkovia* were not found in dry superpáramos. Some genera from the Cosmopolitan element, which is highest in very humid and lowest in humid superpáramos, also demonstrate preferences among the regions, e.g., *Bidens* and *Asplenium* were found only in dry and *Blechnum* only in humid superpáramos.

Discussion

The geographic flora elements

We found that close to three-fifths of genera in the superpáramo flora of Ecuador has an affinity to temperate regions, which is similar to proportions that were found in the superpáramo in Colombia (Van der Hammen and Cleef, 1986) and Venezuela (calculated from Berg, 1998). This is consistent with the general finding that the tropical alpine floras are predominantly of temperate origin (Smith and Cleef, 1988). In Ecuador, the southern temperate element is slightly more abundant than the northern temperate element, whereas in Colombia and Venezuela it is the northern temperate element that is more abundant, nevertheless the differences are small. The Páramo endemic element is less common in Ecuador than in Colombia and Venezuela; several genera from the endemic subtribe *Espeletiinae* reach into the superpáramo belt in the two latter countries whereas they are absent from that belt in Ecuador.

A study of the superpáramo flora that analyzes the relative proportions of genera with different geographic distributions must take into account that a species may be derived from any part of the distributional area

covered by the genus it belongs to (Simpson, 1988; Simpson and Todzia, 1990). The concept of geographic flora elements therefore has some limitations (Cleef, 1979; Hedberg, 1965) and a true understanding of origin of the flora should include knowledge of the phylogenetic relationships and geographical areas of closely related taxa (e.g., Winkworth et al., 2005).

For widespread taxa it would be necessary to understand their phylogeographic structure to determine from which part of the distribution area the superpáramo taxon originated. Phylogenetic studies indicate, for example, that *Huperzia* colonized páramo habitats with taxa from the tropical montane forest (Wilkström et al., 1999) so using a genetic criterion the genus belongs to the Neotropical montane element and not to the Cosmopolitan element to which it was classified in the past (Cleef, 1979; Van der Hammen and Cleef, 1986). *Plantago* in our sample comprises species with affinities to both southern temperate and northern temperate regions (Cleef, 1979; Rahn, 1996) so genetically it represents both Holarctic and Austral-Antarctic elements. Additionally, immigration to the equatorial high Andes may have occurred repeatedly, such as in *Halenia* (Von Hagen and Kadereit, 2003). Unfortunately such detailed evolutionary information is lacking for most of the superpáramo taxa. Ideally, to be helpful in understanding the origin of the superpáramo flora, phylogenetic studies should include páramo populations. *Caltha*, for instance, is widely distributed in temperate regions of both hemispheres and the only páramo species, *C. sagittata* CAV., is also present at the southern tip of South America. This species may have arrived to tropical high Andes from temperate South America after the formation of páramo habitats, or the páramo plants may represent relictual populations from the late Cretaceous/early Paleocene migration of the genus to the Southern hemisphere from North America (Schuettpelz and Hoot, 2004; Schuettpelz, 2004, personal communication). Without studying the phylogenetic relationships of the (super)páramo populations to populations in temperate South America and temperate North America we cannot know from which source area the superpáramo *Caltha* originated.

But ecologically speaking, not all details of the phylogenetic history of a taxon are necessarily important. By classifying *Plantago* and *Caltha* into the Wide temperate element, the amount of evolutionary information is reduced, but the two genera still represent a temperate genetic stock in the superpáramo flora. In the tropical alpine flora of New Guinea, there is a significant correlation between certain ecological parameters and floristic elements, defined on taxonomic and distribution criteria (Smith, 1977). Until we know more about the phylogeny of (super)páramo taxa an approach using distribution areas is the only one that is feasible to suggest geographic and ecological origins of the flora.

Obviously the patterns observed should be further examined as more detailed phylogenetic information concerning the taxa becomes available.

Altitudinal distribution of geographic flora elements

Páramo endemic and Neotropical montane elements and so the total tropical element have their highest values at 4100 m (the lowest altitude examined in this study) while Holarctic and Wide temperate elements have their lowest values there. The transition from grass páramo to lower superpáramo, which coincides with this altitude, therefore seems to act as a filter for species belonging to genera of tropical distribution. This is consistent with the situation reported for Colombia (Van der Hammen and Cleef, 1986).

We expected a gradual change in the proportion of the elements along the altitudinal gradient within the superpáramo; i.e., that temperate genera would increase because of their presumed pre-adaptation to the colder climate whereas tropical genera would be at a disadvantage and decrease at higher altitudes. This scenario is not seen when tropical and temperate elements are examined. Even if there appears to be a response to altitude it is not fully supported by the significance tests (Table 2). When looking at the relative proportions of individual geographic elements distinct changes are encountered at 4500 m, however. Below that altitude, the elements are basically constant and their relative proportions do not significantly depart from that in the entire superpáramo flora (Table 2). Above 4500 m, the proportions of most elements change and their composition significantly departs from that in the entire superpáramo. The transition from the lower superpáramo to the upper superpáramo occurs at altitudes between 4400 and 4500 m (Jørgensen and León-Y., 1999; Sklenář, 2000, 2006) and the composition of generic elements seems to reflect it. Our finding of a rather abrupt change agrees with the results of a study of the grass family in the páramos of Venezuela. Although encompassing a longer gradient of altitude (2400–4200 m), more or less step-wise rather then gradual change in the relative proportions of tropical and temperate grass genera was found there (Márquez et al., 2004).

Most of the geographic flora elements show a significant response to altitude. Páramo endemic genera disappear above 4500 m possibly because the humid superpáramos, where they are mostly found, were not well-represented in our sample at such high altitudes. The distribution of *Floscaldasia*, for instance, is confined to humid superpáramos (Sklenář and Robinson, 2000) and it is very possible that *Floscaldasia azorelloides* SKLENÀŘ & H.ROB. could be found at altitudes above 4500 m in poorly explored humid mountains, such as

Altar. In contrast to our results, páramo endemic genera do occur well above 4500 m in Venezuela (*Coespeletia* CUATREC. and *Hinterhubera* SCH.BIP. EX WEDD.) and Colombia (*Raouliopsis* S.F.BLAKE) (Berg, 1998; Luteyn, 1999; Monasterio, 1979). Neotropical montane and Wide tropical elements are rather evenly represented over much of the altitudinal gradient, although the former tends to decline and the latter eventually disappears above 4600 m. It seems that climatic and/or edaphic factors do not discriminate much against Neotropical montane genera, many of which are shrubs, and they appear to be capable of inhabiting the highest altitudes of the superpáramo zone along with the temperate genera.

The proportions of Holarctic and Wide temperate elements increase significantly with altitude, although they remain fairly stable through a large portion of the gradient (4200–4600 m). This supports the hypothesis that temperate genera would be better suited to higher altitudes and is similar to the pattern observed in Colombia (Van der Hammen and Cleef, 1986). Their increase compensates for the decline of Austral-Antarctic and Cosmopolitan elements (which eventually disappear at the highest altitudes), so that the total temperate element remains unchanged through most of the gradient.

The Andean alpine element also significantly increases with altitude but this group should be interpreted with caution. Unlike other elements, in which the included genera can be expected to have fairly similar evolutionary histories, the Andean alpine element comprises genera that may have immigrated from temperate or subtropical Andes and radiated in the tropical alpine environment, such as *Lysipomia* (Ayers, 1999), and genera that may have spread along the Andes from equatorial latitudes, such as *Oritrophium* and *Niphogeton* (Baumann, 1988; Cuatrecasas, 1997). The history of the genera in the Andean alpine element cannot be inferred without further support from phylogenetic studies and this presently prevents further interpretation of the observed patterns. Nevertheless, the opposite altitudinal distribution of the Andean alpine element as compared to the Neotropical element, to which the genera were classified in the past (Cleef, 1979; Van der Hammen and Cleef, 1986), justifies our recognition of Andean alpine genera as a separate element (see also Simpson and Todzia, 1990).

It remains to be examined whether the mechanisms that enable the temperate genera to colonize the highest reaches of the superpáramo belt work on a physiological basis (Márquez et al., 2004), are related to their lower habitat limitations or to a superior competition potential (over the tropical genera), or a combination of these factors. The opposite reactions of the southern (Austral-Antarctic) and northern (Holarctic) temperate genera to altitude may be due to different habitat preferences or to physiological constraints. Austral-Antarctic taxa are generally abundant in azonal páramo habitats, such as cushion bogs or aquatic vegetation (Cleef, 1981, 2005; Van der Hammen and Cleef, 1986). Favorable habitats for growth, such as wet depressions, are less common at the highest altitudes, which may be the reason that Austral-Antarctic genera are less well represented there. In Ecuador, however, Austral-Antarctic genera also constitute an important component of zonal plant communities in the lower superpáramo zone, and locally they may be even more abundant than Holarctic, Andean alpine, and Neotropical montane elements (P. Sklenář, unpublished data). Therefore, increasing drought (absolute or physiological) at the higher altitudes may also contribute to the decline of Austral-Antarctic genera (see also below).

Distribution of geographic flora elements in dry and humid superpáramos

The generic compositions in dry and humid superpáramos in Ecuador are consistent with general predictions and findings regarding the distribution of tropical and temperate genera in the South American Andes (Simpson, 1983; Simpson and Todzia, 1990). Both the total tropical and the separate tropical elements (except Andean alpine) are more common in humid superpáramos whereas total temperate and often also the separate temperate elements are more common in dry superpáramos. The higher proportion of the Austral-Antarctic element in humid Ecuadorian superpáramos confirms earlier observations that several southern-temperate genera, such as *Azorella* and *Oreobolus*, which are abundant in very wet sub-antarctic islands, encounter favorable conditions in sufficiently humid habitats of the tropical Andes, whereas they are much less common in arid puna environments (Cleef, 1978; Simpson and Todzia, 1990; Troll, 1968). Consistent with Simpson's (1983) view, we find a higher proportion of Holarctic and Wide temperate elements in dry superpáramos.

The Páramo endemic element is least well represented in dry superpáramo which is consistent with its implied origin in habitats above the forest line of the humid equatorial Andes, although the number of genera is low in any of the superpáramo humidity type. The Andean alpine element has similar proportions of the genera in dry and humid Ecuadorian superpáramos but is less well represented in very humid ones, which may be due to the dual character of this element (see above). Its distribution may indicate that a large portion of it (e.g., *Lucilia*, *Lucilioline*, *Nototriche*, *Werneria*, and *Xenophyllum*) is related to dry and moderately humid environments of extratropical Andes, such as the puna.

Cosmopolitan genera are more frequent in the humid Colombian páramo than in the dry Argentinean puna (Simpson and Todzia, 1990). In the superpáramo of

Ecuador, the Cosmopolitan element is highest in very humid, but only slightly less common in dry, and least common in humid type. This rather inconsistent distribution pattern among superpáramo humidity types may reflect the ubiquitous character of this element.

Superpáramo species of *Plantago* exemplify that the correlation between the geographic elements and their ecology and distribution in the (super)páramo may be independent of the taxonomic rank, i.e., that consistent patterns may occur at lower taxonomic levels. *Plantago tubulosa* Decne. and *P. rigida* Kunth, from the "gondwanic" section *Oliganthos* Barnéoud of subgenus *Plantago* L. (Rahn, 1996), conform to the Austral-Antarctic element and occur in humid páramo regions (although *P. rigida* was found also in some dry superpáramos confined to humid azonal habitats there). *Plantago sericea* Ruiz and Pav., from the section *Gnaphaloides* Barnéoud of subgenus *Albicans* Rahn, would be classified among the Holarctic element and was found only in dry superpáramos.

Conclusions

Our analyses of altitudinally stratified floristic samples and samples based on distribution between dry and humid superpáramo regions point to some general patterns.

The ecotonal zone between grass páramo and superpáramo filters out genera of tropical affinity.

The proportions of genera with different areas of distribution, the so called geographic flora elements, do not change gradually with increasing altitude within the superpáramo belt, but instead the change occurs abruptly at around 4500 m, corresponding to the transition between the lower and upper superpáramo.

The tropical genera preferentially occupy humid superpáramos and their absence at the highest elevations may be either due to lack of habitats or lacking ability to adapt to the high elevation conditions.

The temperate genera have colonized the superpáramos in different ways depending on which geographic element they belong to. The Austral-Antarctic genera have mostly occupied humid superpáramo habitats whereas genera belonging to the Holarctic and Wide temperate elements have mostly occupied drier habitats and higher altitudes, presumably due to their adaptation to seasonal/drier climates experienced at higher latitudes gained by their ancestors.

Ecological predispositions (or habitat preferences) of genera from their implied areas of origin to a large degree determine their distribution among (super)páramo sites, i.e., among dry versus humid mountains. Or in other words, ecological parameters of the habitats determine the composition of particular floras. These relations appear to be similar at both continental and regional geographic scales although the mechanisms responsible for the observed distribution patterns remain to be determined.

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