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Phytogeography of the vascular páramo flora of Ramal de Guaramacal (Andes, Venezuela) and its ties to other páramo floras

by

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Abstract

Cuello, N.L., Cleef, A.M. & Aymard, G. 2010. Phytogeography of the vascular páramo flora of Ramal de Guaramacal (Andes, Venezuela) and its ties to other páramo floras. *Anales Jard. Bot. Madrid* 67(2): 177-193.

Ramal de Guaramacal is an outlier and lower elevation mountain range located at the northeastern end of the Venezuelan Andes. Phytogeographical patterns and affinities of the low altitude and wet vascular páramo flora of Ramal de Guaramacal, have been studied with emphasis in to the analysis of the floristic connections of the Guaramacal páramo flora with the neighboring dry páramos of the Sierra Nevada de Mérida and other páramo floras of the northern Andes and Central America. A total of 252 vascular plant taxa belonging to 150 genera and 69 families were recorded from the study area. The most species rich families are Asteraceae, Poaceae, Ericaceae and Orchidaceae, followed by the ferns families Grammitidaceae and Lycopodiacae. The most diverse genera are the ferns *Elaphoglossum*, *Huperzia* and *Hymenophyllum*. The analysis of generic phytogeographical composition of páramo flora showed that 52.8% of the genera are Tropical. The Temperate component is represented by 33.3% of the genera and the Cosmopolitan component is represented by 13.9% of the genera. The Neotropical montane element (38.9%) is high in Guaramacal páramo, the Páramo endemic element (1.9%) and the Andean alpine element (0.9%) and represented by only one genus *(Lachemilla)* are low compared to other páramo areas. The vascular flora of Páramo de Guaramacal is largely composed of (1) a group of Neotropical widespread distributed species (32%), (2) a group of Andean distributed species (49%), part of them confined to the Northern Andes and part widespread in the Andes from Colombia to Bolivia, and (3) a group of Venezuelan endemics (19%). From an eight páramo flora comparative dataset, the closest relationships among páramos is observed between the generic páramo floras of the Colombian Cordillera Oriental of Sumapáz and Sierra Nevada del Cocuy, which are both close-

Resumen

Cuello, N.L., Cleef, A.M. & Aymard, G. 2010. Fitogeografía de la flora vascular del páramo de Ramal de Guaramacal (Andes, Venezuela) y sus conexiones con otras floras de páramo. *Anales Jard. Bot. Madrid* 67(2): 177-193 (en inglés).

El Ramal de Guaramacal es una pequeña ramificación montañosa ubicada al extremo nororiental de los Andes venezolanos. Se estudiaron los patrones fitogeográficos y afinidades de la flora vascular de páramo húmedo y de baja altitud del Ramal de Guaramacal, con énfasis en el análisis de sus conexiones florísticas con páramos secos cercanos de la Sierra Nevada de Mérida y otras floras de páramo de los Andes del Norte y Centroamérica. En el área de estudio se han registrado un total de 252 táxones de plantas vasculares pertenecientes a 150 géneros y 69 familias. Las familias más ricas en especies son Asteraceae, Poaceae, Ericaceae y Orchidaceae, seguidas por las familias de helechos Grammitidaceae y Lycopodiacae. Los géneros más diversos son los helechos *Elaphoglossum*, *Huperzia* e *Hymenophyllum*. El análisis de composición fitogeográfica a nivel genérico de la flora de páramo mostró que el 52,8% de los géneros es Tropical. El componente Templado está representado por el 33,3% de los géneros; y el componente Cosmopolita, por el 13,9%. El elemento Montano Neotropical (38.9%) es alto en el páramo de Guaramacal; los elementos Endémico de Páramo (1,9%) y Alpino Andino (0,9%), representado sólo por un género *(Lachemilla),* son bajos en comparación con otras áreas de páramo. La flora vascular de Páramo de Guaramacal está integrada en gran medida por: 1) un grupo de especies de distribución amplia neotropical (32%), 2) un grupo de especies de distribución Andina (49%) –parte de ellas se limita a los Andes del Norte y parte se generaliza en los Andes desde Colombia hasta Bolivia– y 3) un grupo de especies endémicas de Venezuela (19%). De la comparación del conjunto de datos de flora de ocho páramos, las relaciones más cercanas entre éstos se observan entre las floras genéricas de los páramos de la Cordillera Oriental colombiana, Sumapáz y Sierra Nevada del Cocuy, los cuales están estrechaly related to that of the Sierra Nevada de Mérida in Venezuela. The generic páramo flora of Ramal de Guaramacal shows the closest relationship to southern Ecuador páramo flora of Podocarpus Biosphere Reserve. According to Detrended Correspondance Analysis and Principal Component Analysis ordination results, most of the variations in páramo floras may represent a response to differences in ambient humidity.

Key words: páramo flora, phytogeography, Andes, Venezuela, Talamancas.

mente relacionados con la Sierra Nevada de Mérida en Venezuela. La flora genérica de páramo del Ramal de Guaramacal muestra la relación más cercana con la flora de páramo de la Reserva de Biosfera Podocarpus al sur del Ecuador. Según los resultados de ordenación DCA y PCA, la mayoría de las variaciones en las floras de los páramos analizados pueden representar una respuesta a diferencias de humedad ambiental.

Palabras clave: flora de páramo, fitogeografía, Andes, Venezuela, Talamancas.

Introduction

Páramo is the open equatorial alpine vegetation located above the upper forest line (UFL) and below the permanent snow line from the northern Andes to Panamá and Costa Rica. However, páramo is also considered to be extended to the Amazon slopes of Bolivia (García & Beck, 2006; Rangel, 2006). Páramo flora is considered the high-mountain flora most rich in species of the world (Smith & Cleef, 1988). Phytogeographical studies at the generic level have shown that páramo flora has evolved mainly by immigration of cool-adapted plants from temperate regions (temperate elements) and, in relatively lower proportion, by adaptation of lower-elevation plants (tropical elements) to high-altitude environments and by speciation through repeated isolation in situ (Van der Hammen & Cleef, 1986; Smith & Cleef, 1988; Cleef & Chaverri, 1992; Ramsay, 1992; Ricardi & al., 1997; Sklenář & Balslev, 2007).

Páramo areas in Venezuela exhibit great environmental variability in climate at regional and local scales. Through the about 400 km southwest to northeast extension of the main Venezuelan Andean mountain chain, the Cordillera de Mérida, there is a wide range of páramo hydrological conditions, from dry páramos with 650 mm/year in a single rainy season, to permanently humid páramos with over 3000 mm distributed throughout the year (Monasterio & Reyes, 1980). The latter conditions characterize the páramo areas of Ramal de Guaramacal, an outlier and comparatively low elevation (3130 m) range located at the northeastern end of the Venezuelan Andes (Fig. 1).

North Andean páramo vegetation has been divided into several altitudinal zones (for a complete review we refer to Luteyn 1999). The Cuatrecasas (1934, 1958) altitudinal classification of superpáramo, páramo and subpáramo has since been widely adopted (Cleef, 1981; Acosta-Solís, 1984; Ramsay, 1992; Jørgensen & Ulloa, 1994; Luteyn, 1999; Hooghiemstra & al., 2006; Rangel-Ch., 2000a). For Venezuelan páramos, Monasterio (1980) recognises two altitudinal zones called 'pisos altitudinales': a High Andean zone or 'Piso Altiandino' (4000-4800 m) and the Upper Andean zone or 'Piso Andino Superior' (2800-4000 m).

Studies of phytogeography of the Venezuelan páramo flora started with a first approach of the worldwide distribution of Venezuelan páramo flora presented by Faría (1978) after the publication of the 'Flora de los Páramos de Venezuela' by Vareschi (1970). This very first flora of the páramos was not complete, but anyway representative.

Local floristic listings and phytogeographical analyses that include páramo areas such as those from Táchira and Trujillo states have appeared (Bono, 1996; Ortega & al., 1987; Rivero & Ortega, 1989; Aymard, 1999; Dorr & al., 2000). Bono (1996) also included a phytogeographical breakdown into geographic flora elements of the páramo flora of Táchira State, Venezuela.

More recent phytogeographical analyses of the Venezuelan páramo flora have been published by Ricardi & al. (1997, 2000). The first study deals with the phytogeography of the Mérida superpáramo; the second study highlights the Sierra Nevada de Mérida as a new phytogeographical subprovince of the northern Andes. Briceño & Morillo (2002, 2006) recently published a list of the flowering species of the Venezuelan Andean páramos, first the dicots, later followed by the monocots.

The aim of this study is to analyse the phytogeographical affinities of the low altitude and wet páramo of Ramal de Guaramacal in order to contribute to a better understanding of the distribution, origin, and diversity of its flora. A detailed analysis of phytogeographic composition of Ramal de Guaramacal páramo flora at a genus level is justified given the importance of this low, wet and relative isolated mountain range from the main Cordillera, which also shows a distinctive flora and vegetation composition (Cuello & Cleef, 2009b). Particular emphasis is given to the analysis of the floristic connections of the Guaramacal páramo flora with the neighboring dry páramos of the Sierra Nevada de Mérida and other páramo floras of the northern Andes and Central America.

One of our main objectives was to determine whether the phytogeographical analysis and patterns of the páramo flora of Ramal de Guaramacal are determined by temperature (a function of altitude) as has been established in previous studies (e.g. Cleef, 1979; Mérida Andes, Ricardi & al., 1997, 2000) or more by the overall humidity, which characterizes the Guaramacal bamboo páramo. We have some indications that ambient humidity may play a role, e.g. in the case of the bamboo páramo of Tatamá (Cleef, 2005), the páramos of Podocarpus National Park (PNP) in southern Ecuador (Lozano & al., 2009) and also in the Talamancas of Costa Rica (Cleef & Chaverri, 1992).

Materials and methods

Study area

Ramal de Guaramacal is located south of the town of Boconó, Trujillo state, approximately 120 km Northeast of Mérida, in the centre of the Sierra Nevada de Mérida (Fig. 1). Páramo areas of the summit of Ramal de Guaramacal are found between 2800-3100 m, in the surroundings and between of 'Las Antenas' area (9°14'1.02" N; 70°11'6.47" W) and Páramo El Pumar (9°12'45.6" N; 70°12'5.55" W), 2.5 km Southwest of 'Las Antenas'.

The climate is very humid. According the first climatic records of the Davis Pro 2 climate station installed near the summit of Guaramacal (3100 m) by the first author beginning in December 2006, there are over 290 days/year of rain. Maximum precipitation occurs during April-July. Yearly precipitation is high, reaching over 3200 mm/year and relative humidity attains 100% most of the year. Temperatures remain low throughout the year with a diurnal temperature variation from 4-6 ºC to 14-16 ºC; mean minimum temperature of 5.3 ºC and mean maximum of 12.3 ºC; the lowest temperatures recorded being between – 0.1-1.3 ºC in the month of January; the highest between 17.8-18.3 ºC in the month of March, with mean yearly temperature of 8.1-8.6 ºC for the period from December 2006 - July 2009. Dominant wind directions are of ESE, SE and WNW, with a registered average speed of 3.9-5.8 km/h. Maximum wind speed registered has been of 77.2 km/h, SE in the month of July 2008.

The vegetation of the Páramo of Guaramacal is characterized by a mosaic of subpáramo formations (shrub páramo, bunchgrass páramo, most common bamboo páramo), intermingled with patches of dwarf forests (Subalpine Rain Forest or SARF sensu Grubb 1977), distributed between 2800 and 3130 m (Cuello & Cleef, 2009a, b). For detailed information on forest and páramo vegetation of Guaramacal and other aspects of the study area we refer to Cuello & Cleef (2009a, b, c) and Cuello (1999).

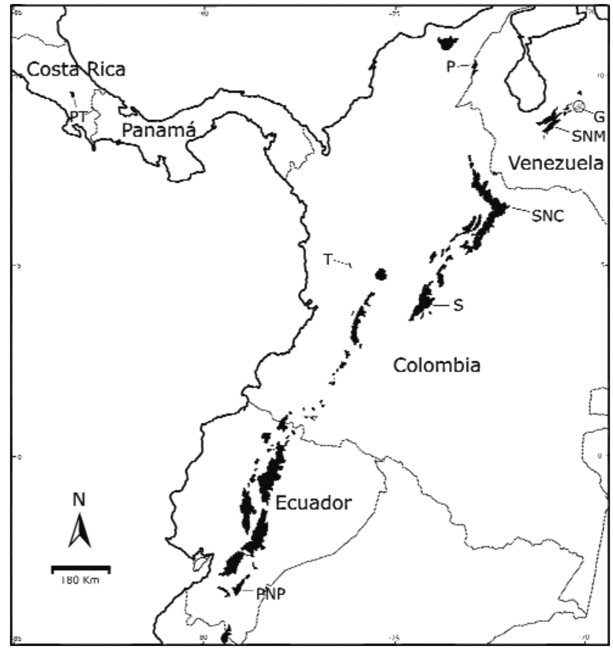

Fig. 1. The location of Guaramacal páramo study site (**G**) and the other páramo areas in northern South America and Central America which floristic comparison are made: Sierra Nevada de Mérida (**SNM**) in Venezuela, Talamancas páramos (**PT**) in Costa Rica-Panamá; Sierra Nevada del Cocuy (**SNC**), Serranía de Perijá (**P**), Tatamá massif (**T**) and Sumapaz páramo (**S**) in Colombia; Podocarpus National Park (**PNP**) in southern Ecuador.

The study and full inventory of the flora of the whole Ramal de Guaramacal range is still ongoing. Preliminary accounts of the vascular flora were first presented by Ortega & al. (1987) and later by Dorr & al. (2000). After that, several new records for the flora as well as new species to science have been documented for Guaramacal (Taylor, 2002; Stergios & Dorr, 2003; Stančík, 2004; Niño & al., 2005; Cuello & Aymard, 2008). A species inventory from páramo areas, including, páramo and subpáramo-connected dwarf forest vegetation islands is presented in this study (Appendix 1).

Methods

Páramo data were collected from phytosociological studies (Cuello & Cleef, 2009b, c) and 585 numbers of general plant collections made by the first author from páramo areas of Ramal de Guaramacal. Additional information was obtained from herbarium collections and database of Herbario Universitario PORT, UNELLEZ in Guanare. The total inventory included 255 vascular plant taxa belonging to 153 genera and 69 families that are listed in Appendix 1. Three exotic weedy taxa *(Polypogon elongatus*, *Rumex acetosella* and *Sonchus oleraceus)* present in disturbed areas, are listed in the Appendix 1, but excluded for the analyses.

For each vascular genus listed the present geographical distribution has been determined on basis of Mabberley (2008); occasionally also recent phylogenetic studies (e.g. Chacón & al., 2006: *Oreobolus;* von Hagen & Kadereit, 2003: *Halenia;* Meudt & Simpson, 2007: *Ourisia,* etc.). Species distribution was also determined by literature and by the W3Tropicos database. Plant genera have been grouped into different phytogeographical elements belonging to three mayor components according to Cleef (1979, 1981, 2005) and Cleef & Chaverri (1992).

1) The Tropical component is made up of four flora elements: (a) Wide tropical (WTR) taxa; (b) Andean alpine (NT-AA) taxa; (c) Páramo endemics (P); (d) Neotropical montane elements (NT-M). Thus, the former 'Other Neotropical elements' (Cleef, 1979), viz. 'Neotropical-montane element' (Cleef & Chaverri, 1992) is subdivided into the Andean alpine element (NT-AA) and Neotropical montane element (NT-M) following Simpson & Todzia (1990) and Sklenář & Balslev (2007).

2) Temperate component contains three flora elements: (a) Widely distributed temperate (WTE) taxa; (b) Holarctic (HO) groups; (c) Austral-Antarctic (AA) taxa.

3) Cosmopolitan component consists of only the Cosmopolitan taxa (CO).

For a biogeographical analysis into species level, overall species distribution was grouped into ten different geographic elements, adapting from previous phytogeographical studies in the Andean region such as those used by Kelly & al. (1994) and Schneider (2001). From the total 252 taxa recorded for the Guaramacal summit area, for the specific biogeographical analysis we used only 229 species with a defined distribution (those which were determined to species and/or infraespecific level), including all open páramo and dwarf forest islands (of Subalpine Rain Forest or SARF sensu Grubb 1977) vegetation species.

Floristic relationships of Guaramacal páramo generic flora to other páramo floras of the northern Andes and Central America were assessed using ordination (Detrended Correspondance Analysis - DCA, Principal Component Analysis - PCA) and classification (Cluster analysis) methods for seven additional available different páramo flora datasets. Floristic lists from each páramo site were obtained from literature or unpublished data from authors (see Table 1). The accounts on the different páramo floras were carefully screened by the authors for taxonomic update and true forest taxa were deleted. Two dataset were considered for these analyses, A) one which included the Guaramacal list of total genera of 150 from páramo & SARF combined, and B) the other that includes Guaramacal list of 108 genera from open páramo only. For these analyses, both data matrices A (404 genera × 8 sites) and B (347 genera × 8 sites) of presence/absence of genera in the eight páramo floras were analyzed using program PC-Ord 4 (McCune &

Table 1. Reference information for the eight páramo flora dataset used for comparative multivariate analysis.

Páramo	**Max. Elev.** (m)	**Aprox. Prec.** (mm/year)	**Area** (ha)	**Number of genera considered**	**Source of floristic data**
Sierra Nevada del Cocuy, Colombia	5330	1300-ca. 3000	112 418	213	Cleef, unpubl. data
Sierra Nevada de Mérida, Venezuela	4980	813 - 1811	69 100	149	Ricardi & al., 1997; Berg & Suchi, 2001
Sumapaz, Cordillera Oriental, Colombia	4250	~1200-3000	102 945	211	Cleef, 1979; Franco & Betancur, 1999; Pedraza-Peñaloza & al., 2004; Rangel-Ch., 2000b
Tatamá massif, Cordillera Occidental, Colombia	4100	>3000	5000	114	Cleef & al., 2005; Cleef, 2005
Serranía de Perijá, Colombia	4100	~2000	4560	137	Rivera-Díaz, 2007
Talamancas, Costa Rica/Panamá	3850	2000-4000	15 205	177	Barrington, 2005; Vargas & Sánchez, 2005
South Ecuador: Podocarpus National Park (PNP)	3695	~5000 mm	14 169	201	Lozano & al., 2009; Bussmann, 2002; Keating, 1999
Guaramacal, Venezuela	3130	>3200 mm	~400	150/109	This study

Mefford, 1999). Cluster analyses of shared genera used Sørensen (Bray-Curtis) as distance measure method and Group Average as group linkage method.

Results

Flora characteristics

To date, the vascular flora of summit areas of Ramal de Guaramacal is composed of a total of 252 taxa; 17 families, 28 genera, and 68 species of ferns, and 52 families, 122 genera and 184 species of angiosperms. In general, the most species rich families are Asteraceae, Poaceae, Ericaceae and Orchidaceae, followed by the ferns families Grammitidaceae and Lycopodiacae.

The most diverse genera are the ferns *Elaphoglossum*, *Huperzia* and *Hymenophyllum.* Of the 252 taxa considered, only 169 species belonging to 108 genera have been registered for proper subpáramo-páramo vegetation, excluding the SARF vegetation (Table 2).

Geographical composition of genera

The composition of genera of phytogeographic elements in páramo areas of Ramal de Guaramacal is presented in Table 3. A total of 150 genera is contained in Table 3, including 41 genera of woody, herbaceous and epiphytic plant species found inside the forest islands (of SARF vegetation) surrounded by páramo vegetation, and 27 genera present in azonal páramo vegetation. Proportions of phytogeographic elements and components of the studied data set are shown in Fig. 2, represented separately for: (a) all genera inclunding SARF vegetation, (b) all open páramo genera, and (c) for the genera present in azonal communities.

1. Tropical component

On the basis of 150 vascular plant genera more than half 61.3% (92 genera) are tropical. Neotropical montane element genera are those that range from montane forest into the supraforest zone. This element is represented by 64 genera (42.7%). Twenty two of them (including 10 herbaceous genera) correspond to SARF vegetation (Table 3). When considering only the genera recorded from páramo vegetation, the Neotropical montane element is represented by forty two genera (38.9%), four of them are found in azonal páramo (Fig. 2c).

Wide tropical element genera are widely distributed in the tropics, including those exclusively African-American and Asian-American. This element is represented by 24 genera (16%). Ten of them (including five herbaceous genera) were found in SARF islands (Table 3). When considering only páramo vegetation genera, the wide tropical element accounts for twelve genera (11.1%) and only one of them (*Xyris*) is found in azonal páramo.

Páramo endemic element genera are those confined to páramo (and sometimes also in the downslope Andean forests) and represented in the study area by 3 genera (2%), two of them small trees: *Liba-*

Table 2. Most diverse families and genera from the vascular flora of summit areas (including SARF and excluding exotic weeds) of Ramal de Guaramacal, Andes, Venezuela. For only proper páramo flora numbers of taxa are indicated in parenthesis.

FAMILY	Number Genus	Number spp.	Genus	Number spp.
Asteraceae	14(10)	24(17)	*Elaphoglossum*	11(5)
Poaceae	10	21(20)	*Huperzia*	8(6)
Ericaceae	10(8)	15(13)	*Hymenophyllum*	7(2)
Orchidaceae	9(4)	14(7)	*Chusquea*	7(6)
Grammitidaceae	6(3)	13(6)	*Rhynchospora*	6
Lycopodiaceae	3	14(10)	*Gaultheria*	5
Cyperaceae	4	10	*Hypericum*	4
Dryopteridaceae	2(1)	12(5)	*Blechnum*	4(2)
Rubiaceae	6(5)	7(6)	*Melpomene*	4
Hymenophyllaceae	1	7(2)	*Miconia*	4(1)
Melastomataceae	3	6(3)	*Pentacalia*	4(2)
Bromeliaceae	4	5	*Ruilopezia*	4
Myrsinaceae	3(2)	5(3)	*Weinmannia*	4(0)
Clusiaceae	1	4		
Rosaceae	3	4		
Blechnaceae	1	4(2)		
Cunoniaceae	1(0)	4(0)		
Totals 69(53) families	150(108) genera			252(169) species

nothamnus at the UFL and *Paragynoxys,* a species from SARF. Most spectacular are the 4 species of *Ruilopezia* (Espeletiinae), endemic for Venezuela. Only one Páramo endemic genus *(Ruilopezia)* is found in azonal páramo.

The Andean alpine element is represented by only one herbaceous genus (0.7%): *Lachemilla*, which is found mainly in azonal páramo.

2. Temperate component

Forty two genera are of temperate distribution (28%), including six genera from SARF. When considering only páramo vegetation genera, the temperate component is represented by 36 genera or 33.3%. These include 31 herbaceous genera, 16 of them counted from azonal páramo.

Widespread temperate element genera are distributed in temperate and cool regions from both hemispheres. This element is represented in the study area by twenty one genera (14%). The genus *Stellaria* was recorded from borders of SARF vegetation. When excluding this genus, the wide temperate element is represented by 18.5% for twenty páramo genera, eight of them counted from azonal páramo.

Austral-Antarctic element genera have southern temperate distribution. This element is represented by fifteen genera (10%). Among them, three genera were registered from SARF (Table 3). Twelve Austral-Antarctic element genera (including 8 herbaceous) of only páramo vegetation account for 11.1%. Eight genera are counted from azonal páramo.

Holarctic element genera have northern temperate

Table 3. Composition of genera of phytogeographic elements in páramo areas of Ramal de Guaramacal in the Venezuelan Andes. * Represents genera recorded from SARF vegetation.

Element	Genus
Tropical (TRO)	
Páramo endemics (P)	*Libanothamnus* Ernst, *Paragynoxys** (Cuatrec.) Cuatrec., *Ruilopezia* Cuatrec.
Andean alpine (NT-AA)	*Lachemilla* (Focke) Rydb.
Neotropical montane (NT-M)	*Ageratina* Spach, *Arcytophyllum* Willd. ex Schult. & Schult. f., *Aulonemia* Goudot, *Baccharis** (Less.) DC., *Bejaria* Mutis ex L., *Bomarea* Mirb., *Brachionidium** Lindl., *Campyloneurum* C. Presl., *Cavendishia* Lindl., *Centropogon* C. Presl., *Ceradenia* L.E. Bishop, *Cestrum** L., *Chusquea* Kunth, *Cochlidium** Kaulf., *Corynaea** Hook. f., *Cranichis** Sw., *Cybianthus* Mart., *Dendrophtora* Eichler, *Deprea* Raf., *Diplostephium* Kunth, *Disterigma* Sleumer, *Elleanthus* C. Presl., *Epidendrum* L., *Eriosorus** Fée, *Excremis* Willd., *Freziera** Willd., *Gaiadendron** G. Don, *Gamochaeta* Wedd., *Geissanthus** Hook. f., *Glossoloma** Hanst., *Gomphichis** Lindl., *Greigia* Regel, *Guzmania* Ruiz & Pavón, *Hesperomeles* Lindl., *Huperzia* Bernh., *Isidrogalvia* Ruiz & Pavón, *Jamesonia* Hook. & Grev., *Lellingeria** A.R. Sm. & R.C. Moran, *Macrocarpea** (Griseb.) Gilg, *Manettia* Mutis ex L., *Miconia* Ruiz & Pavón, *Monnina* Ruiz & Pavón, *Monochaetum* (DC.) Naud., *Munnozia* Ruiz & Pavón, *Myrcianthes** O. Berg, *Odontoglossum* Kunth, *Oreopanax** Decne. & Planch., *Pachyphyllum** Kunth, *Paepalanthus* Kunth, *Palicourea* Aubl., *Pentacalia* Cass., *Phoradendron** Nutt., *Pleurothallis** R. Br., *Psammisia** Klotzsch, *Pterichis* Lindl., *Puya* Molina, *Siphocampylus* Pohl, *Sphyrospermum* Poepp. & Endl., *Terpsichore** A.R. Sm., *Themistoclesia* Klotzsch, *Thibaudia** Ruiz & Pavón, *Tillandsia* L., *Tropaeolum* L., *Ugni* Turcz.
Wide tropical (WTR)	*Achyrocline* (Less.) DC., *Begonia** L., *Chaetolepis* (DC.) Miq., *Clethra** L., *Culcita** C. Presl., *Cyathea** Sm., *Elaphoglossum* Schott ex J. Sm., *Grammitis* Sw., *Hedyosmum** Sw., *Histiopteris* (J. Agardh) J. Sm., *Hymenophyllum* Sm., *Ilex* L., *Melpomene* A.R. Sm. & R.C. Moran, *Mikania** Willd., *Myrsine* L., Paesia J. St.-Hil., *Peperomia** Ruiz & Pavón, *Phytolacca* L., *Pilea** Lindl., *Plagiogyria** (Kunze) Mett., *Psychotria** L., *Sticherus* C. Presl., *Symplocos** Jacq., *Xyris* L.,
Temperate	
Austral-Antarctic (AA)	*Calceolaria* L., *Cortaderia* Stapf., *Cotula* L., *Drimys** J.R. Forst. & G. Forst., *Fuchsia** L., *Gaultheria* L., *Hypoxis* L., *Muehlenbeckia* Meisn., *Nertera* Banks ex Gaertn., *Oreobolus* R. Br., *Ortachne* Nees ex Steud, *Orthrosanthus* Sweet, *Pernettya* Gaudich., *Sisyrhynchium* L., *Weinmannia** L.
Holarctic (HO)	*Castilleja* Mutis ex L. f., *Diplazium** Sw., *Gentianella* Moench, *Halenia* Borkh, *Sibthorpia** L., *Vaccinium* L.
Wide temperate (WTE)	*Agrostis* L., *Arenaria* L., *Calamagrostis* Adans., *Carex* L., *Danthonia* DC., *Daucus* L., *Epilobium* L., *Festuca* L., *Galium* L., *Geranium* L., *Hieracium* L., *Hypericum* L., *Isoëtes* L., *Juncus* L., *Luzula* DC., *Plantago* L., *Poa* L., *Polypogon* Desf., *Stellaria** L., *Valeriana* L., *Viola* L.
Cosmopolitan (CO)	*Asplenium** L., *Blechnum* L., *Cynoglossum* L., *Eleocharis* R. Br., *Equisetum* L., *Gnaphalium* L., *Hydrocotyle* L., *Lycopodiella* Holub., *Lycopodium* L., *Ophioglossum* L., *Oxalis* L., *Polypodium* L., *Rhynchospora* Vahl, *Rubus* L., *Solanum* L., *Thelypteris* Schmidel, *Utricularia* L.

including Mediterranean climate distribution. Only six genera with Holarctic distribution (4%) were found in the study area. The genus *Sibthorpia*, which corresponds to a small herb species and the fern *Diplazium* have been found in borders of SARF vegetation or in the upper forest line. Excluding the SARF genera, the Holarctic element is represented by four genera (three of them herbaceous) or 3.7%. *Gen-*

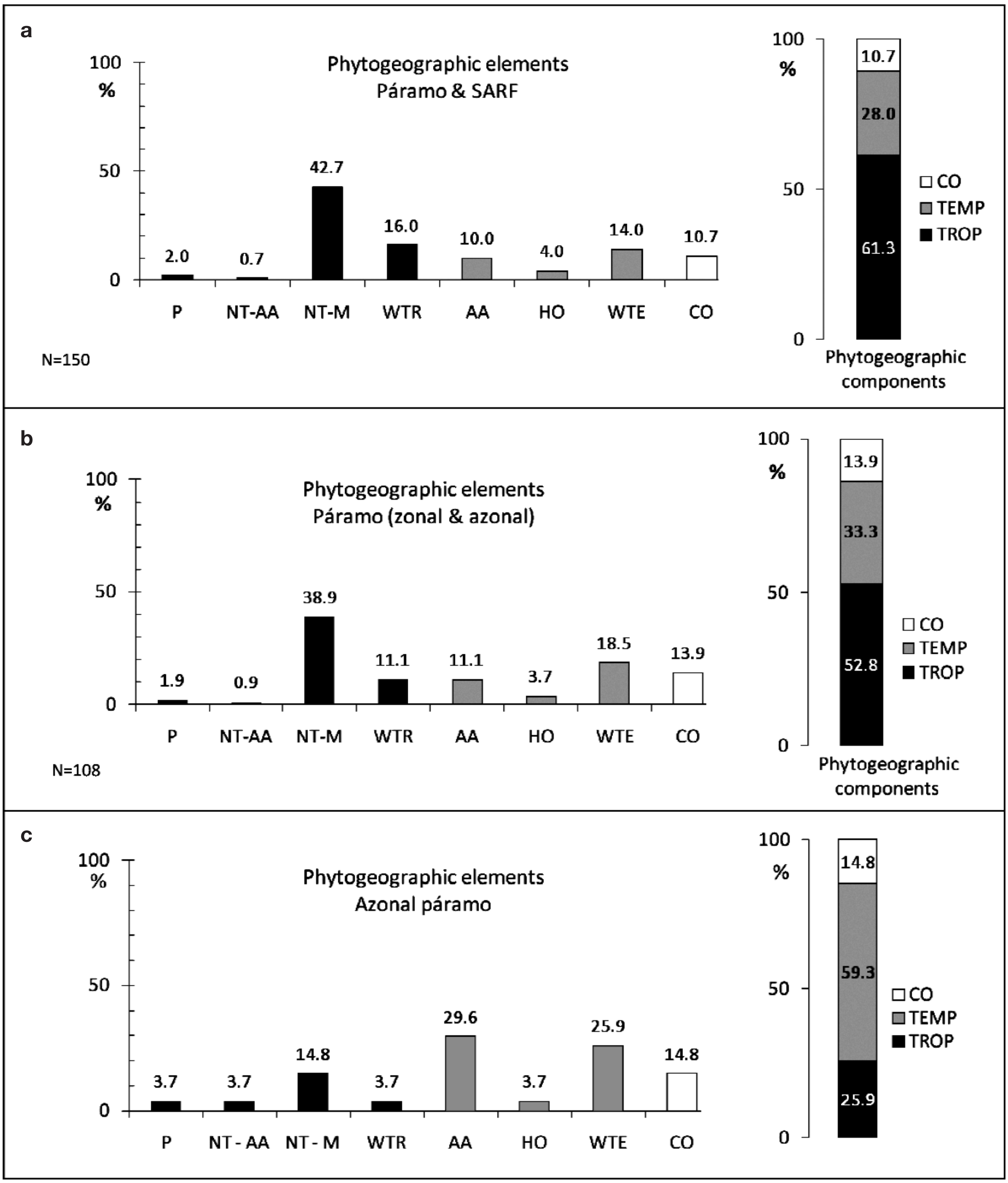

Fig. 2. Proportions (%) of phytogeographic components and elements of (**a**) genera of páramo and SARF, (**b**) of all páramo genera, and (**c**) the genera from azonal communities from Ramal de Guaramacal, Andes, Venezuela.

tianella was the only Holarctic genus counted from azonal páramo.

3. Cosmopolitan component

Cosmopolitan element genera are those with worldwide, or nearly so, distribution. The Cosmopolitan element is represented in the study area by sixteen genera (10.7%). The fern genus *Asplenium*, represented by the species *A. serra*, is found in the understory of SARF vegetation. The Cosmopolitan component for only fifteen páramo genera (13 of them herbaceous) is represented by 13.9%. In the azonal páramo the Cosmopolitan component is represented by four genera.

Species geographical range

The geographical range of the vascular species present in páramo areas of Ramal de Guaramacal, grouped in ten major groups (or distribution types), is shown in Table 4. Neotropical widespread distributed species all over in the whole Neotropics or in a wide range from Central America to Bolivia are broken down into five (1-5) groups. Andean distributed species are split into groups 6 to 9. Venezuelan endemic species (group 10) is divided into four subgroups. The number of vascular species, by taxonomic groups (ferns and Angiosperms) and percentages of the total are presented for each distribution category. From the total 229 taxa determined to species, only 156 species belong to proper páramo/subpáramo vegetation.

Páramo flora relationship

Fig. 3 shows the dendrograms of generic similarity among páramo sites resulting from the cluster analyses. In both graphs, over fifty percent of similarity, four main groups can be recognized. The closest relationships (about 90%) among páramos is observed between the generic páramo floras of the Colombian Cordillera Oriental of each Sumapaz and Sierra Nevada del Cocuy, which are both closely related to Sierra Nevada de Mérida in Venezuela. The generic páramo flora of Ramal de Guaramacal shows the closest relationship to southern Ecuador páramo flora of Podocarpus National Park, with more than 50% similarity, when considering Guaramacal generic flora from

Table 4. Analysis of the geographic range of the páramo flora based on 229 taxa with a defined geographical range in Appendix 1. **F,** ferns and fern allies; **A,** angiosperms; %, percentage of total vascular species. Numbers in parentheses are percentages of total Venezuelan endemics.

Group	Description	Number of páramo species				Number of páramo & SARF species combined			
		F	A	Total	%	F	A	Total	%
1.	Widespread in the Neotropics and also occurring elsewhere	4	10	14	9.0	5	10	15	6.6
2.	Widespread in the Neotropics	4	10	14	9.0	9	13	22	9.6
3.	Widespread in Tropical South America	0	3	3	1.9	0	3	3	1.3
4.	Widespread in Central America, northern (western) South America and the West Indies	11	3	14	9.0	12	4	16	7.0
5.	Central America, northern and western South America, including the Guyana highlands	2	3	5	3.2	3	5	8	3.5
6.	Widespread from Costa Rica to Bolivia	5	24	29	18.5	15	31	46	20.1
7.	Widespread in the Andes from Col. to Bolivia	5	16	21	13.5	13	25	38	16.6
8.	Confined to Venezuela, Colombia and Ecuador	1	9	10	6.4	1	12	13	5.7
9.	Confined to Venezuela and Colombia	3	13	16	10.3	3	19	22	9.6
10.	Endemic to Venezuela:								
	10.1. Andean region and Coastal cordillera	0	2	2	1.3(6.7)	0	4	4	1.7(8.7)
	10.2. Andean region and Venezuelan Guayana (highlands)	1	2	3	1.9(10)	3	2	5	2.2(10.9)
	10.3. Endemic to Andean region of Venezuela	0	15	15	9.6(50)	0	25	25	10.9(54.3)
	10.4. Endemic to Guaramacal	0	10	10	6.4(33.3)	0	12	12	5.2(26.1)
	Total Venezuelan endemics	1	29	30	19.2(100)	3	43	46	20.1(100)
	Species Totals	36	120	156	100	64	165	229	100.0

páramo and SARF combined (Fig. 3a), however no relationship of Guaramacal to any other páramo flora is observed when taking into account only the open generic páramo flora of Guaramacal.

Fig. 4 shows the resulting DCA (a, c) and PCA (b, d) ordination diagrams for both A (a, b) and B (c, d) datasets of presence/absence of genera and 8 páramo floras analyzed. An altitudinal gradient may be represented on axis 1 of DCA (a) and axis 2 of PCA (d), while a humidity gradient is mainly captured by axis 2 of PCA (b).

The results of ordination also show that for dataset A (that includes the páramo and SARF genera from Guaramacal) páramos with greatest values of humidity and rainfall according to Table 1 are grouped in line to the lower right corner on both DCA(a) and PCA(b) diagrams (e.g. Tatamá massif, 4100 m, ~2000-3000 mm/year (Cleef & al., 2005); South Ecuador, PBR, 3695 m, ~5000 mm/year (Lozano & al., 2009); and Guaramacal, 3100 m, > 3200 mm/year and relative humidity of 100% during most part of the year), while drier and higher elevation páramos are grouped to the lower left corner of DCA(a) and upper left corner of PCA(b). However, that humidity relationship is not obvious for dataset B (that with Guaramacal only open páramo genera), where páramo sites seem to be arranged mainly in relation to an altitudinal gradient in axis 2 of PCA(d).

Compared to other generic páramo floras (Table 5), Guaramacal shows the greatest proportion of Neotropical montane element genera and the lowest proportion of Andean-Alpine element genera. The proportion of the Holarctic element is the lowest of all páramo floras compared, but the Cosmopolitan element is the highest.

Páramos of Colombian Cordillera Oriental (S.N. Cocuy and Sumapaz) and Sierra Nevada de Mérida show the most similar proportions of phytogeographic elements among them. Páramos of Costa Rica/Panama

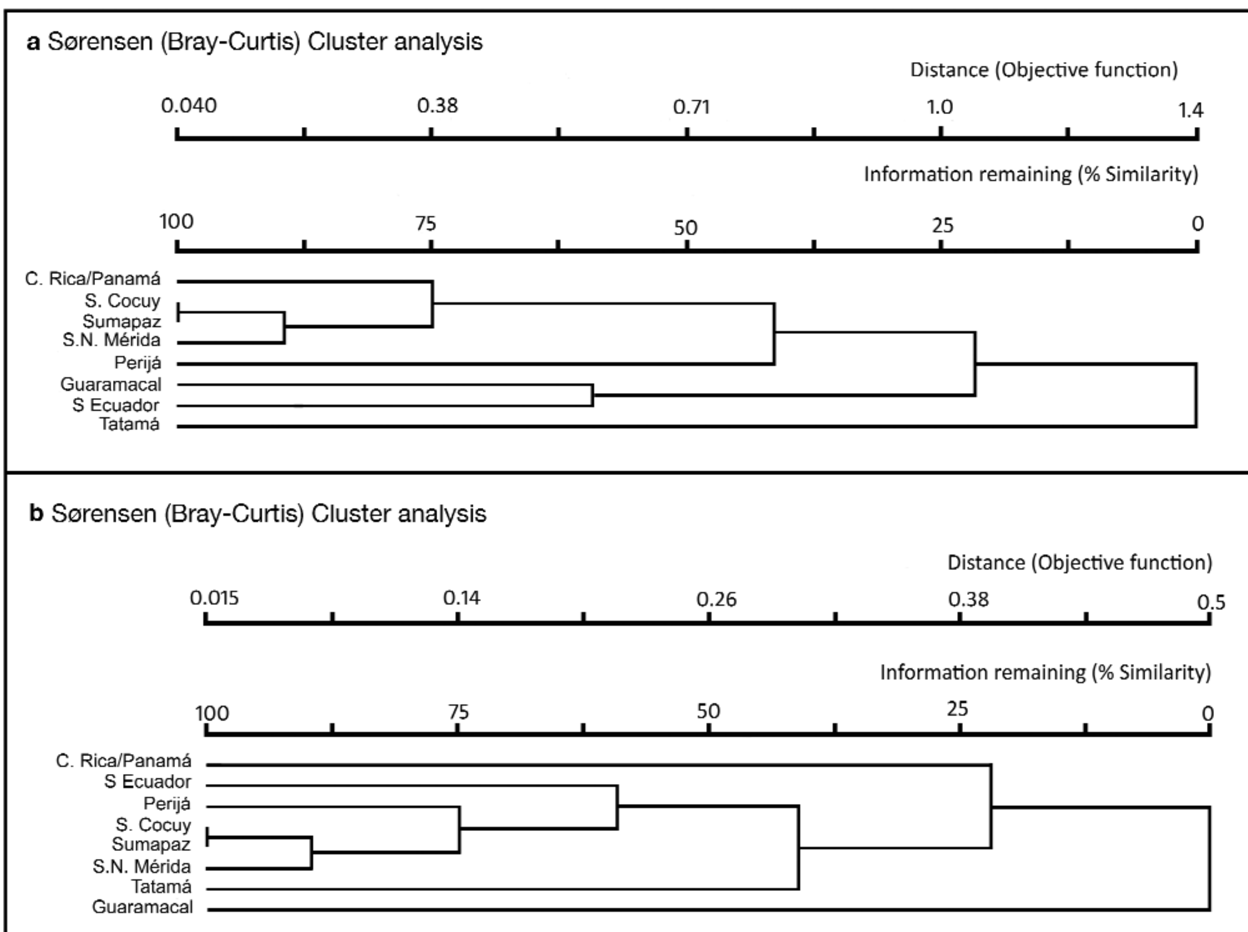

Fig. 3. Sørensen (Bray-Curtis) cluster analysis dendrogram of floristic similarity among 8 páramo sites based on (**a**) the presence/absence of 404 genera (including páramo & SARF genera from Guaramacal), (**b**) the presence/absence of only 347 genera (including only proper páramo genera from Guaramacal).

and Tatamá show the lowest proportion of Páramo endemic genera. Páramos of South Ecuador and Guaramacal show both more similar (the highest) proportions of Neotropical genera and also the lowest proportions of Holarctic genera.

Discussion

Floristic features

As in almost all páramo and other alpine floras (Rangel-Ch., 2000b; Vargas & Sánchez, 2005; Rivera-Díaz, 2007; Rangel-Ch. & al., 2008; Briceño & Morillo, 2002, 2006; Lozano & al., 2009), Asteraceae and Poaceae rank as most dominant in terms of genera and species (Table 2). Remarkable for the páramo of the study area is the third position of Ericaceae with 10(8) genera and 15(13) species. Orchids and Grammitidaceae take the 4th and 5th position respectively in the general flora list, but for proper páramo flora only, Lycopodiaceae is more diverse. The relative importance of pteridophytes under wet climate is also sup-

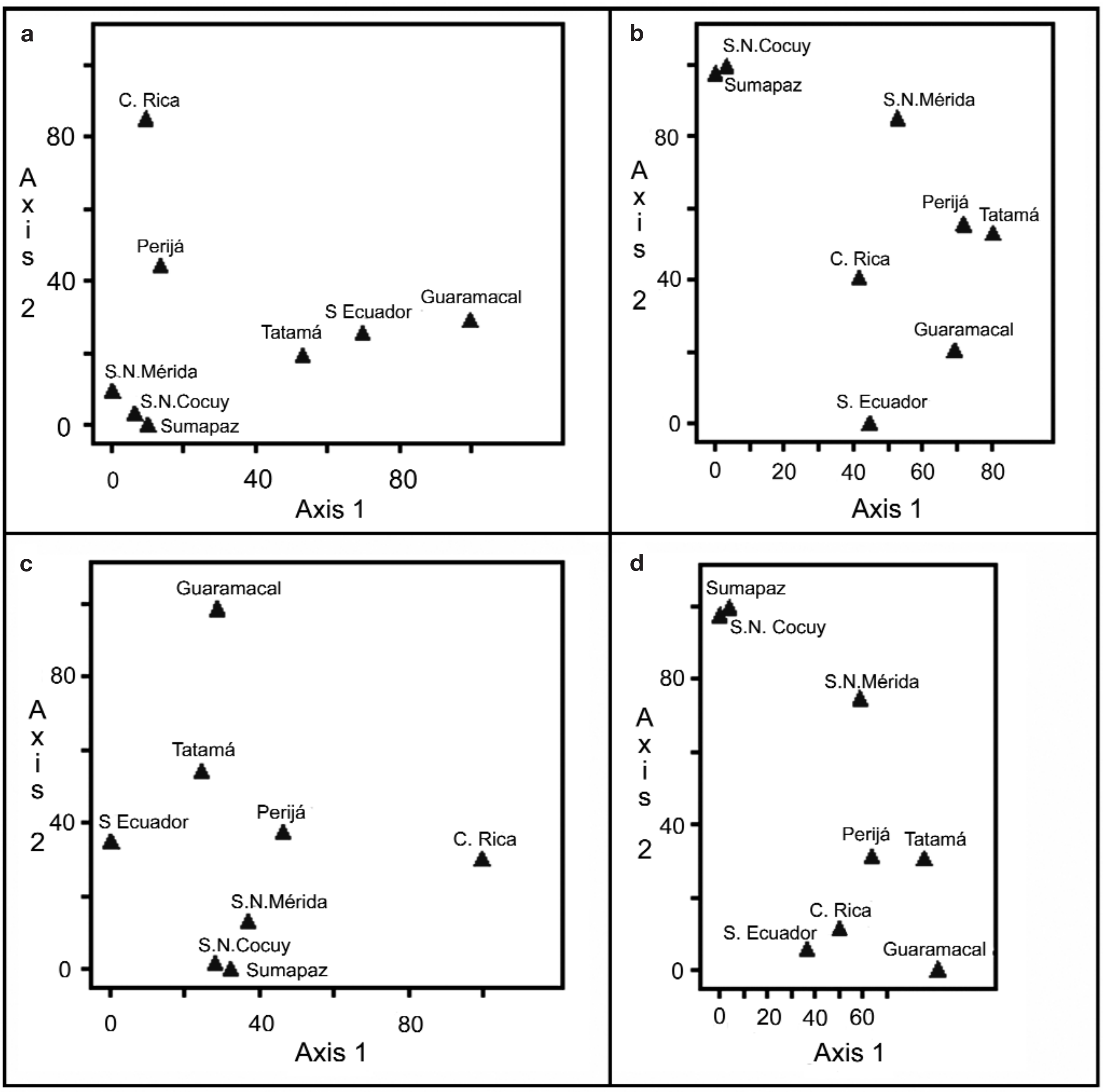

Fig. 4. DCA (**a, c**) and PCA (**b, d**) Ordination diagrams of 404 (**a, b,** including páramo & SARF genera from Guaramacal) and 347 (**c, d,** including only proper páramo genera from Guaramacal) genera for 8 páramo floras datasets. **a,** DCA Axis 1 Eig = 0.422; Axis 2 Eig = 0.321; **b,** PCA Axis 1 Eig = 473.827; Axis 2 Eig = 121.424; **c,** DCA Axis 1 Eig = 0.223; Axis 2 Eig = 0.189; **d,** PCA Axis 1 Eig = 803.377; Axis 2 Eig = 87.539.

ported by Dryopteridaceae with *Elaphoglossum* displaying 11(5) species and Hymenophyllaceae with *Hymenophyllum* containing 7(2) species.

In terms of number of species (Table 2) *Elaphoglossum, Huperzia* and *Hymenophyllum* and *Chusquea* take the first four positions in the general flora list. For páramo flora only, *Chusquea*, *Huperzia* and *Rhynchospora* with six species are the most diverse genera. The high diversity of *Rhynchospora* is remarkable. *Rhynchospora* sect. *Paniculatae* is supposed to be derived from lowland savanna stock (Wayt Thomas, pers. comm.). Earlier it was supposed that the ascent to the Andean páramos from savanna flora was most likely from the lower ranges of the eastern extreme/end of the Andes of Venezuela (Cleef & al., 1993). *Rhynchospora oreoboloidea* Gómez-Laur. of the Holarctic sect. *Oreoboloides,* a common species of the lower páramos in the northern Andes and in the Talamancas*,* is absent in the Guaramacal páramo. In Colombian páramos hardly there are found 6 different species of *Rhynchospora* in one study site.

Chusquea is considered here including three species formerly belonged to *Neurolepis* (Fisher & al., 2009). One páramo species, *Chusquea steyermarkii*, has vicariant bamboo communities on the tepuies.

In conclusion, the taxa listed in Table 2 are almost all indicative of wet páramo climate. *Hypericum* and *Pentacalia* contain species thriving both under wet and drier páramo climate.

Phytogeographical composition at genus level

Based on the studies of the Tatamá páramo flora (Cleef, 2005) or that of the Talamancas in Costa Rica (Cleef & Chaverri, 1992) we expected that humidity would play a role in determining the floristic composition of the Guaramacal range. In fact values for the Neotropical montane element (38.9%) are high in the Guaramacal páramo, as well as for the Austral-Antarctic element (11.1%). Increased values for the Austral-Antarctic element also have been observed in the Podocarpus National Park, Tatamá and Talamanca páramos. However the substantial proportion of the Neotropical montane element may also be related to the low altitude of the Guaramacal range, 3000 m more or less, and one summit at 3130 m. Páramo endemic genera rank low (2%), probably also because of the general low altitude and one predominant humid climate type. There are also fewer distinct habitats in the Guaramacal páramo, as caused by the limited altitudinal amplitude of maximally about 200 m, but most of the range even less. It is striking that the Andean-alpine element is represented only by one genus *(Lachemilla)* and that the Holarctic element only accounts for 3.6%. Genera belonging to both these elements are mostly herbaceous and favoured by higher altitude. Further they are well adapted to periodical stress by dryness (Gutte, 1992). We suppose that bamboo páramo has been present in the summit area of Ramal de Guaramacal since Holocene times and that the prevailing wet climate served as a kind of filter preventing the arrival or survival of dry páramo species from the Mérida páramos.

Another interesting feature is the relative isolation of the Guaramacal páramo from the main cordillera of the Sierra Nevada de Mérida. A small connection is found on the northern side at about 2200 m. During glacial times the summit areas of Guaramacal range were glaciated; remnants of former glacial lakes with terminal moraines are still present at different sites in the páramo belt as well as at lower altitude of about 2000 m near the Park headquarters. Páramo vegetation actually occurred during glacial times at lower altitude along the very steep slopes. In the uppermost part of Guaramacal range with a type of superpáramo, which is completely absent today. *Isoëtes karstenii*, a submerged species found from grass páramo up to the

Table 5. Proportions (%) of phytogeographic elements of páramo genera for seven additional páramo floras compared to Guaramacal. (**a**) SARF and páramo genera combined, (**b**) páramo genera only.

Phytogeographic element	Guaramacal		South Ecuador	Perijá	S. N. Cocuy	S. N. Mérida	Sumapaz	Tatamá	Costa Rica
	(a)	(b)							
P	2.0	1.9	4	5.8	6.5	5.4	4.8	1.8	1.7
NT-AA	0.7	0.9	5.5	3.6	8.4	8.1	7.1	8.0	3.4
NT-M	42.7	38.9	32.5	27.0	27.6	22.3	25.7	25.7	27.7
WTR	16	11.1	12	12.4	7.9	8.1	8.6	9.7	8.5
AA	10	11.1	13	10.2	10.7	10.8	12.4	14.2	12.4
HO	4.0	3.7	10.5	13.9	12.1	14.2	11.9	8.8	16.4
WTE	14.0	18.5	13.5	20.4	18.2	23.0	18.6	22.1	19.2
CO	10.7	13.9	9	6.6	8.4	8.1	11.0	9.7	10.7
Total %	100	100	100	100	100	100	100	100	100
Total genera	150	108	200	137	214	148	210	113	177

highest lakes in the superpáramo in Colombia (Cleef, 1981; Salamanca & al., 2003) and Venezuela (Fuchs-Eckert, 1982; Small & Hickey, 2001) has been found in a small lake in the Guaramacal páramo. Its presence in a glacial lake in the modern páramo of Ramal de Guaramacal can probably be considered as a 'glacial relict'. The Temperate component is best represented in azonal páramo vegetation *(Sphagnum* bogs) on top of Ramal de Guaramacal (Fig. 2c).

When the genera of the SARF vegetation in the Guaramacal bamboo páramo are taken into account the overall proportion of the Tropical component rises from 53.6% to 61.6%, mainly because of more Neotropical montane and Wide tropical genera. For comparison with other páramo floras (Table 5), the taxa from SARF vegetation (column a) have not to be considered, though, sometimes this is difficult to do as well. Looking at the case of the extremely humid páramos of Podocarpus National Park in southern Ecuador (Lozano & al., 2009), with a gradual transition of SARF into shrub páramo, it is noticeable that even the trees adapt to the general structure of shrub páramo vegetation (Bussmann, 2002; Richter & Moreira-Muñoz, 2005; Peters, 2009, Lozano & al., 2009; Cleef, pers. obs.).

Species geographic range

The tropical American part of the vascular flora of Páramo de Guaramacal is largely composed of (1) Neotropical widespread distributed species all over the Neotropics or in a wide range from Central America to Bolivia, (2) a group of Andean distributed species, part of them confined to the northern Andes and part widespread in the Andes from Colombia to Bolivia, and (3) a group of Venezuelan endemics (Table 4).

There is quite a difference between the 156 species with defined geographical distribution range reported for the Guaramacal páramo and the 229 species for the páramo including the SARF islands of Guaramacal. However, the phytogeographical proportions change slightly between both data bases: they maintain rather the same percentages. Looking more closely at the three main distribution types of the Guaramacal páramo flora *(sensu stricto,* without the SARF islands) we can state that there are 50 species, i.e. ca. 32%, for the groups or distribution types 1-5 (e 4), these species displaying a more wide Neotropical distribution. The second and largest species group includes the distribution types 6-9 and is basically tropical Andean in distribution and accounts for seventy six species or about 49%. Group 10 contains thirty species (about 19%) all endemic to Venezuela. Ten species (6.4%) are narrow endemics of the Guaramacal páramo. They include 3 species of Espeletiinae stem rosettes: two species of *Ruilopezia*, and one species of *Libanothamnus.* Also, two species of *Miconia,* one species each of *Bomarea*, *Epidendrum*, *Festuca, Ilex* and *Rhynchospora*.

About 70 species or about 30% of the Guaramacal páramo species are shared with Central America - surprising given the distance and remoteness of Ramal de Guaramacal, although 30 of them correspond to ferns (Table 4). In contrast, only 3 species (1.9%) are shared with the Guayana Highlands which are at much closer distance indicating lack of exchange between these two areas. Most remarkable is the northernmost extension of the bamboo species *Chusquea steyermarkii.*

Páramo flora relations

We found a strong floristic similarity and similar phytogeographical composition among the páramo floras of Sierra Nevada del Cocuy, Sumapáz and Mérida páramos (Figs. 3, 4; Table 5). These mountain chains are contiguous in geographical position and display similar climatic characteristics with regard to the exposition of the ascending trade winds loaded with atmospheric water and the drier wind shadow areas. The Central American páramos of Panamá and Costa Rica, which are more humid, present about 75% similarity of páramo flora with those of the Mérida and Colombian Eastern Cordillera páramos (Fig. 3a). The Colombian Perijá páramo (drier side) ranks with about 40% similarity versus the wet páramo cluster of Guaramacal and PNP in S. Ecuador. Both remote páramo floras are similar at about a 60% value, which is most remarkable, because of the large distance between both areas. The similarity between the páramo floras of Guaramacal and PNP of South Ecuador is observed only when considered the páramo and SARF genera of Guaramacal (Fig. 3a). When considered only open páramo genera of Guaramacal (Fig. 3b), the páramo flora of Guaramacal is not related to any other of the paramo floras analyzed, and in this case PNP (South Ecuador) flora appears to be rather related with the group formed by the páramo of Perijá and the group of drier and higher paramos of S. Cocuy, Sumapáz and S.N. Mérida, conversely, in this case, the páramo flora of Costa Rica/Panama has little relationship with this group. On the other hand, in the DCA and PCA ordinations, when SARF genera of Guaramacal are not included (Fig. 4c, d), the relationship to a humidity gradient is not so obvious, and an altitudinal gradient seem to prevail in PCA (Fig. 4d), while in the DCA (Fig. 4c) the relationship to those environmental variables is not so clear, and instead of them a latitudinal gradient may be detected.

Judging from the results it is most clear that the wet páramos floras are more similar to each other than to seasonally dry páramos (containing both dry bunchgrass páramo and bamboo páramo). In the case of the exclusively wet páramos it appears that humidity is more important than a temperature gradient. In fact the Ecuadorian Podocarpus National Park and Guaramacal páramos are similar in that both are relatively low in altitude with a maximum of about 200 m altitudinal amplitude in Guaramacal and about 400-500 m in the Podocarpus National Park although the highest core area of the latter reaches ~3700 m in elevation. That the ambient humidity gradient apparently overrules that of temperature (viz. altitude), seems also confirmed by the DCA en PCA ordination diagrams of Fig. 4 (a, b), which are based on a comparison of eight páramo floras.

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Appendix 1

Species list range

Species list from páramo areas [zonal (Pzo) and azonal (Paz) páramo vegetation, including, subpáramo (SP) and páramo-connected dwarf forest (SARF) vegetation islands] present in the summit of Ramal de Guaramacal in the Venzuelan Andes. Species distribution group (1-10.4) as presented in Table 3, Group 0 for unknown distribution. Introduced species indicated with asterisk (*).

FAMILY/SPECIES	Distr. Group	VEG.
ASPLENIACEAE		
Asplenium serra Langsd. & Fisch.	2	SARF
BLECHNACEAE		
Blechnum aff. *atropurpureum* A.R. Sm.	10.2	SP
B. auratum (Fee) R.M. Tryon & Stolze	6	SARF/Pzo
B. binervatum (Poir) C.V. Morton subsp. *fragile* (Desv). R.M. Tryon & Stolze	2	SARF
B. schomburgkii (Klotzsch) C. Chr.	5	Pzo/SARF
CYATHEACEAE		
Cyathea fulva (Mart. & Gal.) Fee	6	SARF
DENNSTAEDTIACEAE		
Histiopteris incisa (Thunb.) J. Sm.	1	Pzo
Paesia acclivis (Kunze) Kuhn	7	Pzo/SARF
DICKSONIACEAE		
Culcita coniifolia (Hook.) Maxon	2	SARF
DRYOPTERIDACEAE		
Diplazium hians Kunze ex Klotzsch	2	SP/SARF
Elaphoglossum andicola (Fee) T. Moore	7	SARF
E. appressum Mickel	7	Pzo
E. cf. *lingua* (C. Presl) Brack.	4	Pzo
E. cuspidatum (Willd) Moore	6	SARF
E. latevagans Mickel	7	UMRF/SARF
E. minutum (Pohl ex Fee) T. Moore	4	Pzo
E. muscosum (Sw.) T. Moore	4	Pzo
E. nigrocostatum Mickel	7	SARF
E. paleaceum (Hook. & Grev.) Sledge	4	Pzo
E. papillosum (Baker) H. Christ.	6	SARF
E. rhynchophyllum H. Christ.	10.2	SARF/Pzo
EQUISETACEAE		
Equisetum bogotense Kunth	2	Pzo
GLEICHENIACEAE		
Sticherus revolutus (Kunth) Ching	4	Pzo
GRAMMITIDACEAE		
Ceradenia intonsa L.E. Bishop, ined	8	SP/Pzo
Cochlidium pumilum L.E. Bishop	7	SARF
Grammitis leptopoda (C.H. Wright) Copel.	5	Pzo
G. xanthotrichia (Kl.) A.R. Sm.	10.2	SARF
Lellingeria major (Copel.) A.R. Sm. & R.C. Moran	7	SARF/Pzo
L. myosuroides A.R. Sm. & R.C. Moran	1	SARF/Pzo
Melpomene flabelliformis (Lag. ex Sw.) A.R. Sm & R.C. Moran	1	Pzo
M. moniliformis (Lag. ex Sw.) A.R. Sm & R.C. Moran	4	Pzo
M. xiphopteroides (Liebm.) A.R. Sm.	4	Pzo
M. sp.	0	Pzo
Terpsichore cultrata (Bory ex Willd.) A.R. Sm.	2	SARF

FAMILY/SPECIES	Distr. Group	VEG.
T. longisetosa (Hook.) A.R. Sm.	6	SARF
T. semihirsuta (Kl.) A.R. Sm.	6	SARF/SP
HYMENOPHYLLACEAE		
Hymenophyllum aff. *apiculatum* Mett. ex Kuhn	5	SARF
H. fucoides (Sw.) Sw.	2	SARF
H. karstenianum J.W. Sturm	7	SARF
H. myriocarpum Hook.	6	SARF/Pzo
H. sp.	0	Pzo
H. tegularis (Desv.) Proctor & Lourteig	6	SARF
H. trichomanoides Bosch.	2	Pzo
ISOETACEAE		
Isoëtes karstenii A. Braun	9	Paz
LYCOPODIACEAE		
Huperzia amentacea (B. Øllg.) Holub	6	Pzo
H. cf. *capellae* (Herter) Holub.	7	Pzo
H. eversa (Poir.) B. Øllg.	6	Pzo
H. molongensis (Herter) Holub.	7	SARF/Pzo
H. ocanana (Herter) Holub	9	Pzo
H. riobambensis (Herter) B. Øllg.	9	Pzo
H. rufescens Hook. Trevis	7	Pzo
H. sp.	0	SARF
Lycopodiella cernua (L.) Pic. Serm.	1	SP
L. pendulina (Hook.) B. Øllg.	6	SP
L. riofrioi (Sodiro) B. Øllg.	6	B-P
Lycopodium clavatum subsp. *contiguum* Kl.	6	Paz/Pzo
L. jussiaei Desv. ex Poir.	4	B-P
L. thyoides H. & B. ex Willd.	2	Pzo
OPHIOGLOSSACEAE		
Ophioglossum crotalophorioides Walter	1	Paz/Pzo
PLAGIOGYRIACEAE		
Plagiogyria pectinata (Liebm.) Lellinger	4	SARF/Pzo
POLYPODIACEAE		
Campyloneurum amphostenon (Kunze ex Klotzsch) Fée	4	Pzo
Polypodium funckii Mett.	7	Pzo
P. sp.	0	Pzo
PTERIDACEAE		
Eriosorus flexuosus (Kunth) Copel. var. *flexuosus*	4	SARF/Pzo
Jamesonia imbricata (Sw.) Hook. & Grev.	7	Pzo
THELYPTERIDACEAE		
Thelypteris cheilanthoides (Kunze) Proctor	4	Pzo
T. frigida (H. Christ) A.R. Sm.	6	Pzo/SP
T. prolatipedis Lellinger	6	SARF
APIACEAE		
Daucus montanus H. & B. ex Spreng.	1	Pzo
Hydrocotyle venezuelensis Rose ex Mathias	10.1	Pzo/SARF
AQUIFOLIACEAE		
Ilex guaramacalensis Cuello & Aymard	10.4	Pzo/SARF
ARALIACEAE		
Oreopanax discolor (Kunth) Decne. & Planch.	9	SARF
O. sp.1	0	SARF
O. sp.2	0	SARF
ASTERACEAE		
Achyrocline moritzianum Klatt	8	Pzo
A. vargasiana DC.	3	SP
Ageratina theifolia (Benth.) R.M. King & H. Rob.	9	Pzo/SARF
Baccharis prunifolia Kunth	7	SP/SARF
Cotula mexicana L.	2	Paz
Diplostephium obtusum S.F. Blake	10.3	Paz/Pzo/SARF

FAMILY/SPECIES	Distr. Group	VEG.
D. venezuelense Cuatrec.	10.3	Pzo
Gamochaeta americana (Mill.) Wedd.	1	Pzo
Hieracium avilae Kunth	8	Paz/Pzo
H. erianthum Kunth	7	Pzo
Libanothamnus griffinii (Ruiz-Terán & Lóp. Fig.) Cuatrec.	10.4	Pzo/SARF
Mikania nigropunctulata Hieron.	5	LMRF/SARF
M. stuebelii Hieron.	7	SARF
Munnozia senecionidis Benth.	6	Pzo
Paragynoxys cuatrecasasii Ruiz-Terán & López-Fig.	10.3	SARF
Pentacalia cachacoensis (Cuatrec.) Cuatrec.	9	Pzo/SARF
P. greenmaniana (Hieron.) Cuatrec.	10.3	Pzo/SARF
P. theaefolia (Benth.) Cuatrec.	7	SARF
P. vicelliptica (Cuatrec.) Cuatrec.	10.3	SARF
Ruilopezia jabonensis (Cuatrec.) Cuatrec.	10.3	Paz/Pzo
R. lopez-palacii (Ruiz-Terán & López-Figueiras) Cuatrec.	10.4	Paz/Pzo
R. paltonioides (Standl.) Cuatrec.	10.3	Pzo/SARF
R. viridis (Aristeguieta) Cuatrec.	10.4	Pzo
Sonchus oleraceus L.*		
BALANOPHORACEAE		
Corynaea crassa Hook.f	6	SARF
BEGONIACEAE		
Begonia formosissima Sandwith	10.3	SARF-Pzo
B. lipolepis L.B. Sm. var. *luteynorum* (L.B. Sm. & Wassh.) Dorr	10.3	SP/SARF
BORAGINACEAE		
Cynoglossum amabile Stapf & J.R. Drumm.	1	Pzo
CAMPANULACEAE		
Centropogon aff. *elmanus* E. Wimm.	10.3	SARF
C. lanceolatus E. Wimm.	10.3	SP/Pzo
Siphocampylus odontosepalus Vatke	7	Pzo/SP
CARYOPHYLLACEAE		
Arenaria venezuelana Briq.	9	Paz/Pzo
Stellaria cuspidata Willd. ex Schltdl.	2	SARF
CHLORANTHACEAE		
Hedyosmum translucidum Cuatrec.	7	SARF
CLETHRACEAE		
Clethra fagifolia Kunth var. *fagifolia*	6	SARF/UMRF
CLUSIACEAE		
Hypericum cardonae Cuatrec.	6	Paz/Pzo
H. juniperinum Kunth	9	Paz/Pzo
H. juniperinum × *cardonae*	10.4	PAz
H. paramitanum N. Robson	10.3	Pzo/SARF
CUNONIACEAE		
Weinmannia auriculata D. Don	7	SARF
W. fagaroides Kunth	2	SARF
W. karsteniana Szyszyll.	9	SARF
W. lechleriana Engl.	7	SARF
ERICACEAE		
Bejaria aestuans L.	6	Pzo
Cavendishia bracteata (Ruiz & Pavon ex St.-Hil.) Hoerold	6	Pzo/SARF
Disterigma acuminatum (Kunth) Nied.	3	Pzo
D. alaternoides (Kunth) Nied.	6	Pzo/SARF
Gaultheria anastomosans (L.f.) Kunth	6	Pzo/SARF
G. buxifolia Willd.	7	Pzo
G. erecta Vent.	2	Pzo/SARF
G. glomerata (Cav.) Sleum.	7	Pzo
G. hapalotricha A.C. Sm.	7	Pzo
Pernettya prostrata (Cav.) DC.	2	Pzo/Paz
Psammisia hookeriana Klotzsch.	9	SARF

FAMILY/SPECIES	Distr. Group	VEG.
Sphyrospermum buxifolium Poepp. & Endl.	5	Pzo
Themistoclesia dependens (Benth.) A.C. Smith	8	Pzo/SARF
Thibaudia floribunda Kunth.	7	SARF
Vaccinium corymbodendron Dunal	7	Pzo/SARF
GENTIANIACEAE		
Gentianella nevadensis (Gilg.) Weaver & Rüdenberg	8	Paz/Pzo
Halenia sp.	0	Pzo
Macrocarpaea bracteata Ewan	10.3	UMRF/SARF
GERANIACEAE		
Geranium stoloniferum Standl.	10.3	Paz/Pzo
GESNERIACEAE		
Glossoloma chrysanthus (Pl. & Tr.) J. Clark	10.3	SARF
LENTIBULARIACEAE		
Utricularia alpina Jacq.	2	Pzo
LORANTHACEAE		
Dendrophtora sp. A.	0	Pzo/SARF
Gaiadendron punctatum (R. & P.) G. Don	5	UMRF/SARF
Phoradendron sp.	0	Pzo/SARF
MELASTOMATACEAE		
Chaetolepis lindeniana (Naudin) Triana	9	Pzo/SARF
Miconia arbutifolia Naud.	10.1	SARF/SP
M. elvirae Wurdack	10.4	SARF
M. jahnii Pittier	8	SARF
M. tinifolia Naud.	8	Pzo/SARF
Monochaetum discolor H. Karst.	10.3	Pzo/SARF
MYRSINACEAE		
Cybianthus laurifolius (Mez) Agost.	9	SARF
C. marginatus (Benth.) Pipoly	7	Pzo/SARF
C. stapfii (Mez) Agostini	9	SARF
Geissanthus andinus Mez	8	SARF
Myrsine dependens (R. & P.) Spreng.	6	Pzo/SARF
MYRTACEAE		
Myrcianthes myrsinoides (Kunth) Grifo	7	SARF
Ugni myricoides (Kunth.) O. Berg.	4	Pzo
ONAGRACEAE		
Epilobium denticulatum Ruiz & Pavon	6	Pzo
Fuchsia membranacea Hemsl.	10.3	SARF
OXALIDACEAE		
Oxalis sp.	0	Pzo
PHYTOLACCACEAE		
Phytolacca rugosa A. Braun & C.D. Bouche	6	Paz
PIPERACEAE		
Peperomia acuminata Ruiz & Pavon	4	SARF
P. sp. 1	0	SARF
P. sp. 2	0	SARF
PLANTAGINACEAE		
Plantago australis L.	2	Pzo
POLYGALACEAE		
Monnina meridensis Planch. & Lind. ex Wedd	10.3	Pzo
M. sp.1	0	SARF
M. sp.2	0	SARF
POLYGONACEAE		
Muehlenbeckia tamnifolia (Kunth) Meisn.	2	Pzo
Rumex acetosella L.*		
ROSACEAE		
Hesperomeles obtusifolia (Pers.) Lindl.	6	Paz/Pzo/SARF
H. sp.	0	Pzo/SARF
Lachemilla verticillata (Fielding & Gardner) Rothm.	6	Paz
Rubus acanthophyllos Focke	7	Pzo
RUBIACEAE		
Arcytophyllum nitidum (Kunth) Schltdl.	9	Pzo

FAMILY/SPECIES	Distr. Group	VEG.
Galium hypocarpium (L.) Endl. ex Griseb.	6	Pzo
Manettia lindenii Sprague	10.3	Pzo
M. moritziana (K. Schum.) Werham.	10.1	Pzo/SP
Nertera granadensis (Mutis ex L.f.) Druce	1	Paz/Pzo
Palicourea jahnii Standl.	10.3	Pzo/SARF
Psychotria dunstervilleorum Steyerm.	10.3	SARF
SCROPHULARIACEAE		
Calceolaria tripartita R. & P.	2	Pzo
Castilleja fissifolia L.f.	2	Pzo
Sibthorpia repens (L.) Kuntze	6	SARF/Pzo
SOLANACEAE		
Cestrum buxifolium Kunth	9	SARF/SP
Deprea paneroi Benitez et Martinez	10.4	Pzo/SARF
Solanum macrotonum Bitter	5	Pzo
SYMPLOCACEAE		
Symplocos tamana Steyerm.	10.3	SARF
THEACEAE		
Freziera serrata A.L. Weitzman, ined.	10.3	UMRF/SARF
TROPAEOLACEAE		
Tropaeolum deckerianum Moritz & H. Karst.	8	Pzo
URTICACEAE		
Pilea sp.	0	SARF
VALERIANACEAE		
Valeriana quirorana Xena	10.3	Pzo
VIOLACEAE		
Viola stipularis Sw.	4	Pzo
WINTERACEAE		
Drimys granadensis L.f.	6	SARF
ALSTROEMERIACEAE		
Bomarea amilcariana Stergios & Dorr	10.4	Pzo
B. edulis (Tussac) Herb.	2	SARF
BROMELIACEAE		
Greigia sp.	0	Pzo
Guzmania squarrosa (Mez & Sodiro) L.B. Sm. & Pittdn.	7	Pzo/SARF
Puya aristeguietae L.B. Sm.	8	Pzo
Puya sp. nov.	10.4	Pzo
Tillandsia complanata Benth	4	SP
CYPERACEAE		
Carex bonplandii Kunth	1	Paz/Pzo
C. jamesonii Boott	6	Pzo
Eleocharis acicularis (L.) Roem. & Schult.	1	PAz
Oreobolus venezuelensis Steyerm.	6	Paz/Pzo
Rhynchospora gollmeri Boeck.	10.2	Paz/Pzo
R. guaramacalensis M. Strong	10.4	Pzo
R. cf. *lechleri* Steud.	5	Pzo
R. macrochaeta Steud. ex Boeck.	6	Pzo
R. ruiziana Boeck	6	Pzo
R. sp.	0	Pzo
ERIOCAULACEAE		
Paepalanthus pilosus (Kunth) Kunth	6	Paz/Pzo
HYPOXIDACEAE		
Hypoxis decumbens L.	1	SP
IRIDACEAE		
Orthrosanthus acorifolius (Kunth) Ravenna	9	Paz/Pzo
Sisyrinchium tinctorium Kunth	6	Pzo
S. sp.	0	Paz

FAMILY/SPECIES	Distr. Group	VEG.
JUNCACEAE		
Juncus bufonius L.	1	Pzo
J. stipulatus Nees & Meyen	3	Pzo
Luzula gigantea Desv.	6	Pzo
LILIACEAE		
Excremis coarctata (Ruiz & Pav.) Baker	7	Pzo
ORCHIDACEAE		
Brachionidium tuberculatum Lindl.	7	SARF
Cranichis antioquensis Schltr.	6	SARF
Elleanthus aurantiacus (Lindl.) Rchb.f	2	Pzo
E. flavescens (Lindl.) Rchb.f.	7	Pzo
E. maculatus (Lindl.) Rchb. f.	6	Pzo
Epidendrum frutex Rchb.f.	7	Pzo
E. guaramacalensis Hagsater	10.4	Pzo
Gomphichis costaricensis (Schltr.) Ames, F.T. Hubb. & Schweinf.	6	SP/SARF
Odontoglossum megalophium Lindl.	7	SARF
O. ramosissimun Rchb.f.	7	Pzo
O. schillerianum Rchb.f.	9	SARF
Pachyphyllum crystallinum Lindl.	6	SARF
Pleurothallis glossopogon Rchb. f.	8	SARF
Pterichis multiflora (Lindl.) Schltr.	8	Pzo
POACEAE		
Agrostis basalis Luces	10.1	PAz
A. perennans (Walter) Tucker	1	PAz
A. sp. B	0	PAz
Aulonemia ximenae L.G. Clark, Judz. & C.D. Tyrrell	9	SP
Calamagrostis bogotensis (Pilg.) Pilg.	6	Paz/Pzo
C. planifolia (Kunth) Trin. ex Steud.	7	Pzo
C. sp. A	0	Paz/Pzo
Chusquea aff. *fendleri* Munro	9	Pzo
C. angustifolia (Soderstr. & C.E. Calderón) L.G. Clark	9	Pzo/Paz/SARF
C. mollis (Swallen) L.G. Clark	9	Pzo/SP
C. spectabilis L.G. Clark	8	Pzo/SP
C. spencei Ernst.	9	Pzo/SARF
C. steyermarkii L.G. Clark	10.2	Pzo
C. tessellata Munro	7	Pzo
Cortaderia hapalotricha (Pilg.) Conert.	6	Paz/Pzo
Danthonia secundiflora J. Presl. subsp. *secundiflora*	2	Pzo
Festuca guaramacalana Stancik	10.4	Pzo
Festuca sp.	0	Pzo
Ortachne erectifolia (Swallen) Clayton	6	PAz
Poa annua L.*	1	Pzo
Polypogon elongatus Kunth*		
TOFIELDIACEAE		
Isidrogalvia robustior (Steyerm.) Cruden.	10.3	Pzo
XYRIDACEAE		
Xyris subulata Ruiz & Pav. var. *acutifolia* Heimerl.	6	Paz/Pzo

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