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Phytogeography of the vascular páramo flora of Podocarpus National Park, south Ecuador

Fitogeografía de la flora vascular del páramo del Parque Nacional Podocarpus, sur Ecuador

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Abstract

A plant ecological transect study of the páramos of the Podocarpus massif, southern Ecuador, was carried out between July 2001 and August 2004. Including herbarium records 187 vascular plant genera were found, which were used for the present phytogeographical analysis. Three geographic flora components were identified: tropical (55 %), temperate (38 %) and cosmopolitan (7 %). The neotropical-montane element, which belongs to the tropical component, has the largest number of genera, with 62 (33 %). A wide number of species are endemic to the forest-paramo «ecotone» of Podocarpus National Park (70 spp.). The Andean-alpine element was the least represented, with only eight genera (4 %). The wide temperate element and Austral-Antarctic of the temperate component show almost an equal representation with respectively 25 (13 %) and 26 (14 %) genera; the cosmopolitan component with 14 genera (7 %). Also a limited number of taxa with savanna affinity were found: 15 (8 %) genera. 40 genera (21%) are shared with the Puna. This first attempt to group generic elements is a contribution to the phytogeographic understanding of southern Ecuador. Wet climate and regional isolation seem to be key factors in the present-day phytogeographical distribution of the 187 paramo genera.

Key words: páramo; vascular flora; phytogeography; Podocarpus National Park, Ecuador.

Resumen

Se realizó la caracterización fitogeográfica en base de estudios de transectos de la vegetación de los páramos del macizo Podocarpus al sur del Ecuador, entre Julio 2001 y Agosto del 2004. Además se complementó con registros de los herbarios en Loja y Quito. 187 géneros de plantas vasculares fueron encontrados. Tres tipos de componentes geográficos florísticos fueron identificados: tropical (55 %), templado (38 %) y cosmopolita (7 %). El elemento neotropical, el cual pertenece al componente tropical, tiene la mayor representación genérica con 62 (33 %), donde un amplio número de especies son endémicas para la franja del «ecotono» bosque-páramo en el Parque Nacional Podocarpus (70 spp.). El elemento Andino-alpino es el menos representado con ocho géneros (4 %). El elemento austral-antártico y ampliamente templado que pertenecen al componente templado presenta una casi igual representación con respectivamente 26 (14 %) y 25 (13%) géneros; el componente cosmopolita con 14 género (7 %). Un número limitado de taxa de afinidad sabanera fueron encontrados con 15 (8%) géneros, además se presenta 40 géneros en común con la puna (21 %). Este primer intento de agrupar la fitogeografía genérica del sur del Ecuador es una contribución para entender de mejor manera sus afinidades fitogeográficas, en un área donde la geografía y el clima actúan como una barrera natural para la distribución de plantas. El clima muy húmedo y el aislamiento regional son considerados clave en la distribución geográfica actual de los 187 géneros del páramo.

Palabras claves: páramo; flora vascular; fitogeografía, Parque Nacional Podocarpus, Ecuador

Introduction

The Andes are the most salient orography of South America. The Cordillera borders the entire western side of the continent from Venezuela in the North to Tierra de Fuego in the South. A broad range of landscapes and climatic conditions is found within the Andes region, resulting in a megadiverse flora in the equatorial sector (Romero-Saltos *et al*., 2001; Duque *et a*l., 2001). This flora has been subject to drastic climatic fluctuations and environmental changes, which has led to continuous changes and adaptations of Andean plants and vegetation through time.

Studies of flora and biome development, especially in the northern Andes, have been based mainly on palynological and paleobotanical analyses (e.g., Van der Hammen (1988, 1991); Van der Hammen & Cleef (1986), Hooghiemstra (1984), Hooghiemstra & Cleef (1995), Torres (2006) and (Hooghiemstra *et al*., 2006)). References to paleoecological studies for Ecuador include Liu & Colinvaux (1985), (Bakker et al., 2008), (Bush *et al*., 1990), Colinvaux (1988, 1997), Graf (1992), van der Hammen et al. (2003), Hansen *et al.* (2003), Wille *et al*. (2002) and Moscol Olivera & Hooghiemstra (2008, in prep.). Niemann & Behling (2007, 2008) and Brunschön & Behling (2009) are presently the only Last Glacial-Holocene references for the Podocarpus study area, which is part of the Podocarpus National Park (further quoted as PBR). During the late Pleistocene, the area of El Tiro Pass (2810 m) in the northernmost sector of Podocarpus was grass páramo with azonal occurrences of *Plantago australis* and *P. rigida*, pointing to the presence of mires and bog. Subpáramo and (high) Andean forest gradually replaced the grass páramo during the early Holocene indicating slightly warmer site conditions. The humid Andean forest (with *Hedyosmum*, Podocarpaceae, *Myrsine* and *Ilex*) was present at El Tiro between 8900 and 3300 cal. yrs BP and corresponds to the hypsithermal. El Tiro has been under dense shrub páramo since 3300 cal. yr BP. Evidence suggests that fire became more frequent during the last 8000 years. This information may be extrapolated to the inmediate northern sector of PBR. New paleo-evidence is now also available from the southernmost part of the Podocarpus range (Brunschön & Behling, 2009).

Among the phytogeographic analyses for Ecuador, Ulloa & Jørgensen (1993) deal with woody genera above 2400 m, Lauer *et al*, 2001, with the high Andes East of Quito, and Sklenár & Balslev (2007) with an interesting phytogeographic breakdown of vascular genera of dry and humid superpáramos. Today we have better knowledge from the Andes of northern Ecuador (Moscol Olivera & Cleef, 2009 a, b), (Ramsay, 2001), but still little is known of páramos South of Quito.

Pleistocene records from the northern tropical Andes indicate a long sequence of glacial periods, with temperatures 6-8 ÚC lower than today (Hooghiemstra, 1984, van der Hammen, 1991, Hooghiemstra *et al*, 2006; Torres, 2006). According to Liu & Colinveaux (1985), the vegetation zones on the eastern slopes of the Andes of Ecuador may have been at least 700 m lower than today during the last glacial period. The beginning of the Holocene saw a gradual warming, reaching annual medium temperatures 1-2ÚC higher than today, especially during the middle Holocene (van der Hammen 1991, van der Hammen *et al*, 2003; Bakker *et al*, 2008). Palynological data show that during the Pleistocene tropical ecosystems were not stable. The high Andes experienced strong climatic changes, which influenced principally the upper forest line position and the extension of páramo in terms of repetitive connection and isolation (Van der Hammen & Cleef, 1986). In this way, processes of speciation were promoted. For plant species we can refer to e.g. Cuatrecasas (1969, 1986), Díaz Piedrahita (1999), Fernández Alonso (1995), Robson (1987, 1990), Romeroloux (1996), Von Hagen & Kadereit (2001, 2003); (Jørgensen et al., 1995), outlined a possible regional floristic division of the Ecuadorian páramo flora into four «quadrants», distinguished from one another by glacial and interglacial barrier-effects (Fig. 1).

The main fragmentation or even isolation of páramo floras during the maximum extension of the Pleistocene glaciers follows the highest crest lines and is mostly meridionally oriented. In contrast, the interglacial and, to some extent, also glacial barriers follow the lowest dry valleys and bisect the Cordilleras on the East-West axis. Dissimilarity analyses highlight the Girón-Paute Valley, which is North of the PBR study area, as a main division line in southern Ecuador (Jørgensen & Ulloa Ulloa, 1994, Emck *et al*., 2006). A second major barrier for plant migration is situated in northern Peru: the Huancabamba depression (Cuatrecasas, 1949; Peña et al., 2006; Simpson, 1983; Simpson & Todzia, 1990; Richter *et al*., 2008). These two barriers isolate the Loja floristic province to some extent. They form the latitudinal limit for a number of taxa; other taxa, e.g. páramo-puna species cross from South to North and vice versa (Lozano, 2002; Van der Hammen & Cleef, 1986). Many specific taxa are limited to the area; their isolation can be traced to moist forest refuges located in dry basins, such as those of Catamayo or Huancabamba, as well as alongside and above the Rio Marañon (Richter *et al*., 2008). Peña et al. (2006) provided a first list of 252 vascular species (133 genera, 58 families) from low páramos (3000 -3560 m) in northern Peru, North of the Huancabamba depression.

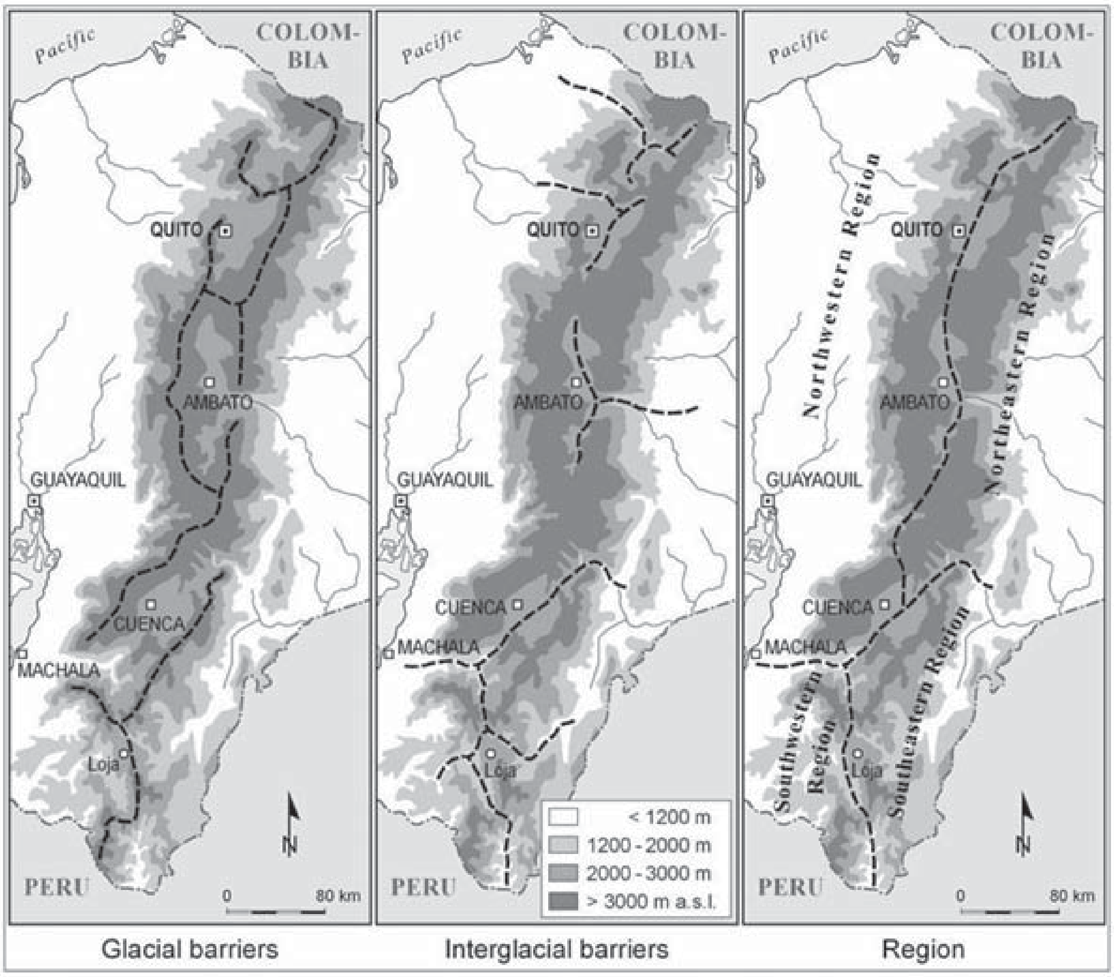

Fig. 1. Possible barriers for plant migration during interglacial and glacial periods in Ecuador, after Jørgensen et al. (1995). Reproduced with permission of P. M. Jørgensen and M. Richter. Girón-Paute Valley.

The present analysis aims at analyzing the phytogeographical elements of the vascular páramo flora of PBR. We hypothesize that the high presence of the tropical component in the most humid superpáramos of the northern part of Ecuador noted by Sklenár & Balslev (2007) might perhaps also be demonstrated for the world's wettest páramos (subpáramo, grass páramo) found in PBR (Bendix et al., 2008; Richter, 2008; Emck *et al*., 2006; Emck, 2009).

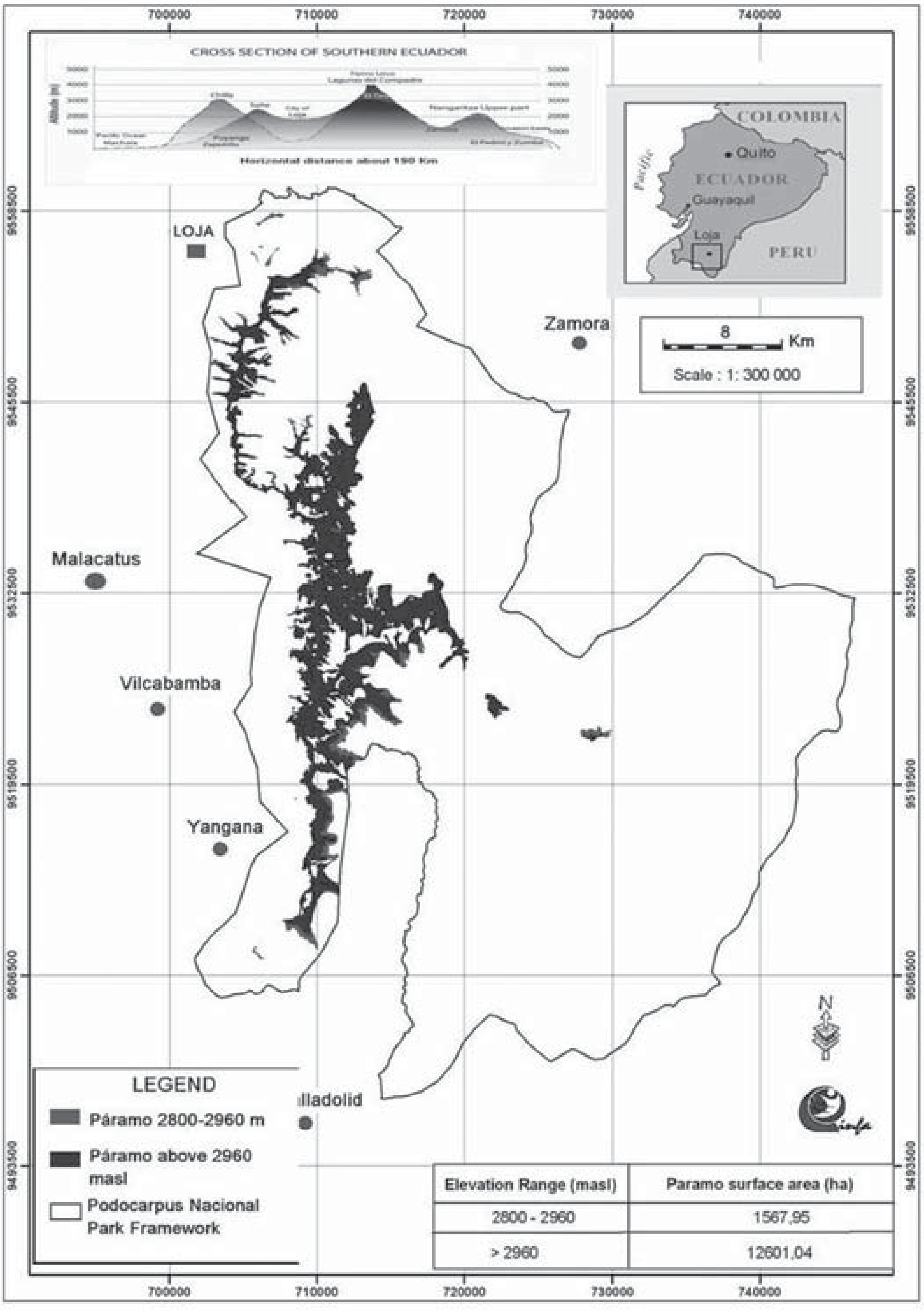

Fig. 2. Páramo Distribution Along North to South and Schematic West-East cross-section from the Pacific coast to the Amazon flood plain at the latitude of Loja.

Study area

PBR is located in South Ecuador (Fig. 2). It is situated at the most important continental divide that serves as watershed for the whole region, discharging both to the Pacific and Atlantic Ocean. PBR is also part of the low transition zone to the high Peruvian Andes (Richter et al., 2008) see fig. 2. The altitudes of the range are between 960 and 3800 m. An area of 146,280 ha is covered by PBR and represents the only public protected area in South Ecuador. According to Becking et al. (2004), PBR includes sixteen types of ecosystems; four of them belong to different types of páramo which belongs to « Zonal herbaceous and shrub on metamorphic and intrusive rocks in grass páramo and subpáramo, as well as azonal herbaceous communities on cretaceous sand, volcanic and rocky substrates. Bussmann (2002) described 5 associations of páramo from the northernmost part of PBR. The average annual precipitation is > 5000 mm (Bendix, 2000; Bussmann, 2001; Richter et al., 2008). Recent data reveal that the eastern slope of the Podocarpus range probably contains the wettest páramos in the Andes, because the angle and funnel shape of the main chains force the trade winds to release a bulk of their moisture here (Richter, 2003; Richter et al., 2008). The páramos of Cajanuma (central/western slope) even show annual amounts of rainfall in excess of 6000 mm (Richter et al., 2008).

The páramos of Ecuador cover about 65,000 hectares (Becking et al., 2004); of this 14,169 hectares (21,5%) are situated in PBR. The páramo region of PBR extends 45,5 km from North to South; its maximal width is 17,6 km. 1,567.9 hectares of azonal páramo are located between 2800-2950 m, and 12,601.04 hectares of zonal páramo above 2950 m; the highest altitude is between 3600 m and 3800 m (Fig. 2). Páramos are present between 04°10´56´´S, 79°10´26´´E (northern part, El Tiro) and 04°26´40´´S, 79°80´59´´E (southern part, Sabanilla), between Loja and Zamora Chinchipe province

The main zonal páramo vegetation type is bamboo páramo (sensu Cleef, 1981; Becking et al., 2004). This bamboo páramo is dominated mainly by bamboo species, either of *Neurolepis* or of *Chusquea*, both with a substantial woody component. Other typical páramo growth forms, such as cushion plants and bunch grasses among others, are also present (see Fig. 3). Most prominent, however, are the low evergreen small-leaved shrubs (and treelets), which are conspicuously present and represent the most important plant cover of the páramo zone. Espeletioid stem rosettes are absent (Cuatrecasas, 1986).

The low altitude páramo-forest ecotone (2800-3000 m) or upper forest line (UFL) is one of the most important physiognomic and floristic features of the Podocarpus range. Among the characteristic abiotic factors are permanent high humidity and acidic soils (Richter et al., 2008; Bussmann, 2001; Becking et al., 2004). There is a high rate of endemism; 70 endemic vascular species are found (Lozano et al., 2003, see also Fig. 4), almost half of the estimated total number of vascular plants (150 species.) This richness in endemic species is not only an attribute of the input in the past from the surrounding humid tropical montane forests, but also results from the high variety of neighbouring habitats. They range from per-humid in PBR to semi-arid in deep valleys and dry lands West of PBR (Young et al., 2002; Richter & Moreira-Muñoz, 2005). Most of the species found in the forest ecotone are also represented in open páramo vegetation. The genera *Brachyotum, Centropogon,* and *Lysipomia* are most rich in endemic species (Lozano et al., 2003). The geographic position of Podocarpus range is crucial because the National Park and its páramo flora are part of the transition zone between the humid northern Andes and the drier puna, with its related flora, of Peru and Bolivia. However, humid páramo-like plant communities are also found along the humidity exposed upper forest line in Peru and Bolivia fringing the Amazon basin (Beck, 1995; García & Beck, 2006; Weberbauer, 1911, 1945).

The páramo of the PBR is characterized by extreme meteorological conditions. Podocarpus páramos are distinguished from most other páramos of Ecuador by the absence of (active) vulcanism, lower altitude and an impressive development of shrub páramo intermingled with «minitrees,» which are part of the canopy of the 2-3 m shrub layer. This is the altitudinal zone richest in species and endemism. The extreme ambient conditions and the extensive very dense shrub and dwarf shrub zone make geobotanical exploration difficult. Until now, the páramo zone of this massif has been poorly surveyed (Becking et al., 2004; Bussmann, 2001; Quishpe et al., 2002; Richter, 2003; Richter et al., 2008; Peters, 2009).

Methods

The páramo vascular plant genera of the PBR were grouped into geographic elements following Cleef (1979, 2005) and Cleef & Chaverri (1992). Data were collected

Fig. 3. Representative endemism páramo species of Podocarpus National Park. A. *Centropogon steyermarkii* Jeppesen; B. *Brachyotum incrassatum* E. Cotton; C. *Lysipomia caespitosa* T.J. Ayers; D. *Symplocos fuscata* B. Stålh; E. *Huperzia loxensis* B. Øllg.; F. *Neurolepis laegaardii* L.G.Clark. Especies de Páramo representativas del endemismo de la Reserva de Biosfera Podocarpus

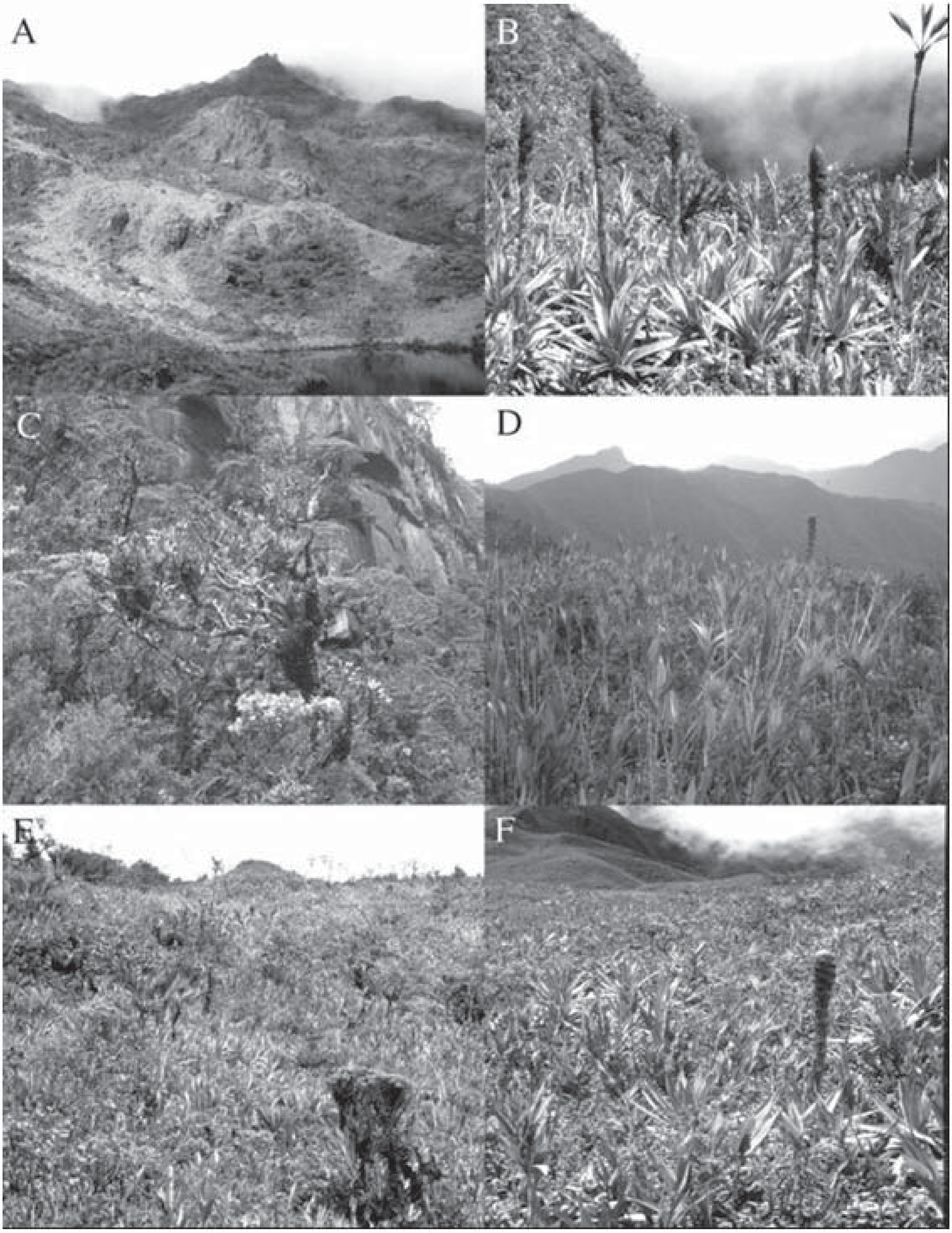

Fig. 4. Vegetation types at upper forest line and high Andean forest. A. Fowers of *Alzatea verticilata*; B. *Alzateetum veticillatae* association; C. Flowers of *Axinaea sp.*; D. *Clusietum latipedis* association; E. Elfin Forest; F. Purdiaeatum nutantis Floristic Association (Pictures and Description from Bussmann 2002). Tipos de vegetación en bosque de ceja de montaña del bosque alto andinos

during three years (2001-2004) of floristic-ecological field exploration along the west side of Podocarpus range only. The floristic inventory was based mainly on general páramo collections in herbaria in Loja and Quito. Own collections considered were gathered in the northernmost wet páramo extension near San Francisco, and in the southernmost páramos. Generic information was also derived from 45 plots (5 m x 5 m) established along the altitudinal gradient from high Andean dwarf forest (subalpine rain forest sensu Grubb, 1977) to the open páramo zone laid out in 30 transects from North to South on the West slope of Podocarpus massif. Presence / absence (including the cover percentage) of the species of herbs, shrubs, epiphytes, hemi-epiphytes, and treelets were recorded in each plot. Exotic and introduced species were not considered. Herborized material was pressed, dried, identified, and preserved in the herbarium (LOJA) of the Universidad Nacional de Loja, under the collection numbers of P. Lozano & R. Bussmann and P. Lozano, T. Delgado & B. Merino. Plant identification was mainly based on Harling & Andersson (1974-2003); plant names and their authorities were according to Jørgensen & León-Yánez (1999) and Luteyn (1999). The not identified collections (5 %) were also compared with vouchers at the herbarium of the Pontificia Universidad Católica Quito (QCA).

According to Cleef (1979; 1981; 2005) and Cleef & Chaverri (1992) three main geographic groupings (i.e., components,) were considered to characterize the generic páramo flora:

(a) Tropical component, which includes the endemic páramo element, the neotropical-montane element, the Andean-alpine element, and the wide tropical element;

(b) Temperate component, which includes the Holarctic element, the Austral-Antarctic element and the wide temperate element;

(c) Cosmopolitan component and element which combines tropical and temperate distribution areas. Also subcosmopolitan genera rank here.

Following Simpson & Todzia (1990) and Sklenár & Balslev (2007), the neotropical flora element proposed by Cleef (1979) was split up into the Andean-alpine element and the Neotropical-montane element. Andean-alpine genera grow exclusively in the tropicalpine zone above the UFL, with some species also occurring outside the tropical Andes (e.g. *Lachemilla* in Guatemala, México and California; *Werneria nubigena* in Guatemala and Mexico). Neotropical-montane genera occur in the upper montane (Andean) and subalpine (high Andean) forests but grow also in the tropicalpine zone, even outside the páramo biome. As shown by Sklenár & Balslev (l.c.), this approach offers more resolution and is more meaningful in phytogeographic analysis. The endemic páramo element refers to generic endemicity in equatorial America, where most of the pearamos are based. Genera belonging to this flora element have a limited distribution, i.e. páramo and/or equatorial upper montane. Indeed most of the endemic páramo genera have a distribution, which includes mainly the Andean forest belt.

Finally, from the puna biome we have the first phytogeographic study of the vascular flora of the Central Andes of Peru (near Morococha and La Oroya), found between 3600 and 5200 m in the Cordillera Blanca (Gutte 1992). He distinguished Andean (~ neotropical montane, Andean alpine, puna endemics), tropical-subtropical(~ wide tropical), Holarctic, Austral-Antarctic and cosmopolitan (~ wide temperate, (sub-cosmpolitan) genera.

The percentages for the different phytogeographic components and elements have been calculated for the vascular genera of the PBR páramo. This approach has been followed in this study.

Results

Geographical flora elements of the páramos of the Podocarpus massif.

187 genera of the indigenous vascular páramo flora were found in the Podocarpus páramo (Fig. 5). They belong to eight geographic flora elements relevant to this area, and are distributed in three different components, as outlined above.

a) The tropical component includes the páramo, the neotropical-montane, the Andean-alpine and the wide tropical element, and represents with, the highest proportion (102 genera, 55 %).

Páramo element.- Includes 9 genera (5 %): *Ceratostema* Juss., *Chrysactinium* (Kunth) Wedd., *Dorobaea* Cass., *Semiramisia* Klotzsch, *Neurolepis* Meisn., *Niphidium* J.Sm, *Oreanthes* Benth, *Themistoclesia* Klotzsch, and *Tibouchina* Aubl.

The endemic páramo element is also represented in the forest zone below the páramo. For exemple: Ceratostema (2 species in páramo, 11 outside; Semiramisia (2 spp. In páramo, 3 outside), Niphidium (1 in páramo, 9 outside), Themistoclesia (8 spp. in páramo, 16 outside).

Neotropical-montane element. Includes 62 genera (33 %): *Aethanthus* (Eichler) Engl., *Ageratina* Spach, *Anthurium* Schott, *Antidaphne* Poepp. & Endl., *Arcytophyllum* Willd. ex Schult. & Schult. f., *Arracacia* Bancr., *Baccharis* L., *Bejaria* Mutis ex L., *Bomarea* Mirb., *Brachyotum* (DC.) Triana, *Campyloneurum* C. Presl, *Cavendishia* Lindl., *Centropogon* C. Presl, *Chaptalia* Vent., *Chusquea* Kunth, *Cybianthus* Mart., *Dendrophthora* Eichler, *Diplostephium* Kunth, *Disterigma* (Klotzsch) Nied., *Elleanthus* C. Presl, *Epidendrum* L., *Eriosorus* Fée, *Gaiadendron* G. Don, *Geissanthus* Hook. f., *Gomphichis* Lindl., *Greigia* Regel, *Guzmania* Ruiz & Pav., *Gynoxys* Cass., *Hesperomeles* Lindl., *Huperzia* Bernh., *Isidrogalvia* Ruiz & Pav., *Jamesonia* Hook. & Grev., *Lepidoploa* (Cass.) Cass., *Macleania* Hook., *Macrocarpaea* (Griseb.) Gilg, *Masdevallia* Ruiz & Pav., *Mezobromelia* L.B. Sm., *Miconia* Ruiz & Pav., *Monnina* Ruiz & Pav., *Monticalia* C. Jeffrey, *Moritzia* DC. ex Meisn., *Munnozia* Ruiz & Pav., *Nasa* Weigend, *Oligactis* (Kunth) Cass., *Oncidium* Sw., *Paepalanthus* Kunth, *Pachyphyllum* Kunth, *Palicourea* Aubl., *Pentacalia* Cass., *Peperomia* Ruiz & Pav., *Pitcairnia* L'Hér., *Puya* Molina, *Siphocampylus* Pohl, *Sphyrospermum* Poepp. & Endl., *Stelis* Sw., *Stemodia* L., *Stenorrhynchos* Rich. ex Spreng., *Symbolanthus* G. Don, *Thibaudia* Ruiz & Pav. ex J. St.-Hil., *Tillandsia* L., *Trichosalpinix* Luer., *Ugni* Turcz.

Andean-alpine element. Includes 8 genera (4 %): *Distichia* Nees & Meyen, *Lachemilla* (Focke) Rydb., *Loricaria* Wedd., *Lysipomia* Kunth, *Niphogeton* Schltdl., *Oritrophium* (Kunth) Cuatrec., *Werneria* Kunth, *Xenophyllum* V. A. Funk.

Wide tropical element. Includes 23 genera (12 %): *Achyrocline* (Less.) DC., *Bulbostylis* Kunth, *Clethra* L., *Conyza* Less., *Crassula* L.,*Elaphoglossum* Schott ex J. Sm., *Grammitis* Sw., *Hymenophyllum* Sm., *Ilex* L. (with few outliers in the northern hemisphere), *Maytenus* Molina, *Melpomene* A.R. Sm., *Mikania* Willd., *Myrsine* L., *Paspalum* L., *Passiflora* L., *Persea* Mill., *Phytolacca* L., *Pilea* Lindl., *Piper* L., *Sporobolus* R.Br., *Symplocos* Jacq., *Ternstroemia* Mutis ex L. f., *Trichomanes* L., *Xyris* L.

b) The temperate component includes 71 genera (38 %); the Holarctic, the Austral-Antarctic, and the wide temperate elements belong to the temperate component.

Holarctic element. Includes 20 genera (11 %): *Bartsia* L., *Berberis* L., *Castilleja* Mutis ex L.f., *Clinopodium* L., *Draba* L., *Gentiana* L., *Gentianella* Moench, *Halenia* Borkh., *Hypochaeris* L., *Lupinus* L., *Lysimachia* L., *Muhlenbergia* Schreb., *Oenothera* L., *Pedicularis* L., *Pinguicula* L., *Ribes* L., *Salvia* L., *Silene* L., *Stachys* L., *Vaccinium* L.

Austral-Antarctic element. Includes 26 genera (14 %): *Acaena* Mutis ex L., *Azorella* Lam., *Calceolaria* L., *Cortaderia* Stapf, *Cotula* L., *Dendrophorbium* (Cuatrec.) C. Jeffrey, *Desfontainea* Ruiz & Pav., *Escallonia* Mutis ex L.f., *Fuchsia* L., *Gaultheria* L., *Gleichenia* Sm., *Gunnera* L., *Hydrocotyle* L., *Lilaea* Bonpl., *Lilaeopsis* Greene, *Muhlenbeckia* Meisn., *Myrteola* O. Berg, *Nertera* Banks & Sol. ex Gaertn., *Oreobolus* R. Br., *Orthrosanthus* Sweet, *Ourisia* Comm. ex Juss., *Pernettya* Gaudich., *Rostkovia* Desv., *Sisyrinchium* L., *Sticherus* C. Presl, *Uncinia* Pers.

Wide temperate element. Includes 25 genera (13 %): *Agrostis* L., *Calamagrostis* Adans., *Cardamine* L., *Carex* L., *Equisetum* L., *Galium* L., *Geranium* L., *Gnaphalium* L., *Hieracium* L., *Hypericum* L., *Juncus* L., *Luzula* DC., *Oxalis* L., *Plantago* L., *Poa* L., *Polystichum* Roth, *Ranunculus* L., *Rubus* L., *Rumex* L., *Senecio* L., *Stellaria* L., *Stipa* L., *Thelypteris* Schmidel, *Valeriana* L., *Viola* L.

c) The cosmopolitan component

Cosmopolitan element. Includes 14 genera (7 %): *Asplenium* L., *Blechnum* L., *Eleocharis* R. Br., *Eriocaulon*

L., *Eryngium* L., *Isoëtes* L., *Isolepis* R.Br., *Lycopodiella* Holub, *Lycopodium* L., *Ophioglossum* L., *Pteris* L., *Rhynchospora* Vahl, *Selaginella* P. Beauv., *Solanum* L.

Discussion

Main features

Until now, we have recorded 187 vascular genera for the páramo of the Podocarpus National Park. They have been assigned to the different phytogeographic components (3) and elements (8) as outlined above (Fig. 3). 102 genera (55 %) belong to the tropical component and 72 genera (38 %) belong to the temperate component. 14 genera (7 %) have been assigned to the cosmopolitan component and element.

As also reported in previous accounts, it remains a question of debate which genera should be included in the páramo flora. We have accepted a number of tree genera as well (such as *Escallonia*, *Gaiadendron, Gynoxys, Hesperomeles* and *Myrsine*), which are found as low shrub, or treelets in subpáramo, or at protected sites in terrain pockets, or near rock outcrops in grass páramo, as well as trees in Andean and high Andean forest. We have left out tree species such as *Clusia, Oreopanax,* and *Schefflera.* The case of *Lomatia* and *Weinmannia*, both Austral-Antarctic elements, remains doubtful. However, *Weinmannia* is represented in quite a number of páramo releves (Bussmann, 2002), where high Andean forests gradually transitions into open páramo with a dense bamboo-shrub vegetation as transitional zone.

A recent study by Izco et al. (2007) of the páramos of the northernmost outliers of PBR (Nudo de Loja), directly connected to the PBR páramos by mountain ranges 2000 and 3000 m in elevation, revealed the presence of nine additional genera not reported to date from the Podocarpus páramos. They include: *Habenaria, Lobelia, Morella (Myrica), Oreomyrrhis, Roupala, Scirpus, Stevia, Triniochloa*, and *Trisetum.* Taking into account the lowering of the UFL during glacial periods (Niemann & Behling, 2007, 2008), Podocarpus páramos without doubt have been repeatedly united with those of the northernmost outliers bordering the deep Girón-Paute valley system. Species belonging to these nine genera are also supposed to occur in the Podocarpus páramos. The general proportions of the flora elements in this study will hardly change, adding three genera to the Neotropical-montane element, one genus to the Holarctic, two genera to the wide temperate element, two genera to the wide tropical and one genus to the Austral-Antarctic element. *Morella* (previously *Myrica*) has presently a wide tropical distribution (Parra-O, 2002); *Myrica* remains exclusively holarctic in distribution area.

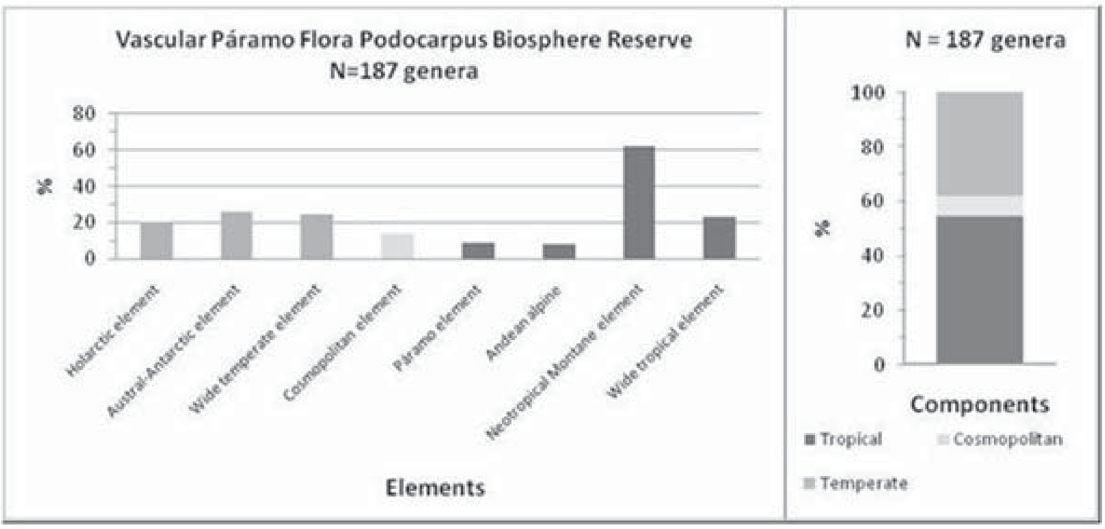

Fig. 5. Phytogeographic distribution in percentages for 187 vascular genera of the páramo flora of Podocarpus National Park in South Ecuador.

The condition of the PBR páramo is special because of the exceptionally low upper forest line, which can be explained by its exposure to stormy trade winds (Bendix, 2000; Beck et al., 2008; Richter et al., 2008; Emck, 2008), and as a consequence a strong top effect (Grubb, 1971). On the other hand, PBR páramos are also characterized by the presence of a dense shrub-treelet layer marking the subpáramo Richter (2003); Niemann & Behling (2007, 2008); Izco et al. (2007); Peters (2009); Schönbrun & Behling (2009). This condition is probably typical to superwet páramos (Cleef et al., 2005), where soils allow for a gradual ecotone transition from high Andean forest to open páramo. It is interesting to note that even scattered low trees of a *Persea* species, are part of the 2-3 m subpáramo shrub layer. Lauraceae are predominant in subandean or lower montane forests; some trees are present in Andean and high Andean forests, such as species of *Aiouea, Aniba, Ocotea*, and *Persea* (Ulloa Ulloa & Jørgensen, 1993; Rangel, 2000). Previously the family was not reported from shrub páramo. During a recent visit to Cerro Toledo also *Freziera minima*, a *Podocarpus* endemic, has been found as a treelet (4-5 m) in the uppermost Andean rain forest, as well as 1-2 m low treelets in shrubby páramo.

Most of the equatorial páramo floras based on >150 genera have been reported with about equal proportions of the tropical and temperate component (Cleef, 1979, 2005; Cleef & Chaverri, 1992; Ulloa Ulloa & Jørgensen, 1993; Sklenár & Balslev, 2007), though slight differences may be observed between the different sites (to be discussed below).

This is also true for the 240 genera of the puna flora of a sector of the Cordillera Blanca in Peru. Gutte (1992) calculated for the tropical component (Andean and Tropical genera) 47,3% versus 44,6% for the temperate component, 35,4% for Holarctic and 9,3% for Austral-Antarctic genera. Cosmopolitan genera account for 8,0%. The author did not publish full lists, but it is clear that the Holarctic genus group contains mostly genera of the wide temperate element. This is supported by the statements of Simpson & Todzia (1990) noting an increased presence of Holarctic and wide temperate elements in the dry puna, as compared to the humid páramos, which are much closer to the northern source areas. However, we suppose that a substantial proportion of the wide temperate element has entered South America in the past from the North, a view that is supported by the very low plant diversity in the (sub-)Antarctic zone (Cleef, 1979; Moore, 1983a). From gentianaceous herbs such as species of *Gentianella* (von Hagen & Kadereit, 2001) and *Halenia* (von Hagen & Kadereit, 2003), it has been shown that their origin is in Central Asia and that they migrated via Alaska to the Andes. On the other hand Chacón et al. (2006) have shown that *Oreobolus* species reached southern South America from Australasia. Meudt & Simpson (2007) in contrast demonstrated that *Ourisia* species (in the past Scrophulariaceae, today Plantaginaceae) reached Australasia spreading from southern South America.

Sklenár & Balslev (2007) studied Ecuadorian superpáramos and found remarkable differences between the tropical and the temperate components. In very humid superpáramos, the proportion of the tropical component is greater compared to dry superpáramos. This pattern seems also to hold for the lower altitude grass páramo and subpáramos of the PBR study area. The proportions of the tropical (55%) vs. the temperate component (38%) of the PBR páramo flora indicate indeed a strong tropical character. Though generic data of Peña et al. (2006) for northernmost low altitude páramos of Peru are not complete, a first glance suggests, that these páramos are also rich in species and include at least 15 local endemic species. It is difficult to understand the criteria used for the delimitation of (sub-)páramo and (high) Andean forest. Forest taxa found in their list include: *Alnus acuminata, Hedyosmum racemosum* and *Morella (Myrica) pubescens,* further species of *Axinaea, Clusia, meriania, Oreopanax, Schefflera* and *Weinmannia*. They are present in the interface between forest and páramo, when the natural transition is gradual on slightly sloping ground, or remain after cutting, burning and grazing (Moscol Olivera & Cleef, 2009 a, b), even since pre-Colombian time (Schjellerup, 1992). The following taxa have been documented for these páramos: 29 species of pteridophytes, 47 species of monocots (in 30 genera) and 176 dicots (in 90 genera). Orchidaceae, Poaceae, and Liliaceae are the most common families among the monocots, and Asteraceae, Ericaceae, and Melastomataceae among the dico ts. The most species-diverse are *Senecio* and *Valeriana* (each 8 spp.), *Miconia*

(7 spp.), and *Arcytophyllum, Baccharis*, and *Huperzia* (5 spp. each). In conclusion: there is substantial affinity with the páramos of the PBR study area not so far away.

The tropical component

In the Podocarpus páramo the proportion of the tropical component is 55 % versus 38 % of the temperate component. The 62 genera of the neotropical-montane element (33%) are responsible for the high proportion of the tropical component in the Podocarpus páramo. We suppose that this is caused by the elevated proportion of woody genera (34 vs. 28 herbaceous), which constitute a gradual transition from the high Andean dwarf forest or subalpine rain forest into the dense shrub formations (with a number of species of treelets forming part). This is the most species rich zone, the dense-stemmed shrub belt transition from high Andean or subalpine dwarf forest to open páramo. The PBR massif in South Ecuador lacks high altitude area above 3900 m; «Lagunas del Compadre», is just near 3800 m. superpáramo is absent. This limits slightly the proportion of the temperate component in the vascular flora. Shrubby subpáramo formations cover most of the supraforest area. This could explain the low proportion of Andean-alpine genera (4 %), which are more bound to open dry bunchgrass páramo and dry superpáramo. Especially in the puna, species and genera of the Andean-alpine element represent about 30% (Gutte, 1992).

In contrast, the proportion of neotropical-montane genera is highest with 33 %. Ancestors of woody páramo species are mainly found in the montane forests of the equatorial Andes: e.g., *Baccharis* (Cuatrecasas, 1967), *Calceolaria* (Molau, 1978, 1988), *Diplostephium* (Cuatrecasas, 1969)*, Disterigma* (Pedraza-Peñalosa, 2008), *Macleania* (Luteyn, 1983), *Miconia* (Uribe Uribe, 1972). The shrub páramo apparently contains a number of typical forest genera that here have adapted to the subpáramos zone; examples include *Anthurium, Antidaphne, Cavendishia, Guzmania, Macleania, Munnozia, Palicourea, Persea, Pitcairnea, Siphocampylus, Sphyrospermum, Thibaudia*, and *Weinmannia*. This is a special condition of the Podocarpus shrub páramo, thus far not reported elsewhere. A slightly higher proportion of the tropical component has also been observed in the Colombian Tatamá bamboo páramo,of the Western Cordillera (Cleef, 2005). In the rainy Tatamá páramo the neotropical-montane elements are represented by 36 genera (26,9%) and the Andean-alpine element by 10 genera (7,4%) out of a total of 134 páramo genera.

Striking with respect to the endemic páramo element is the low representation of Asteraceae (only 2 genera) compared to the northern Andes, where 7 genera of the endemic Espeletiinae predominate the páramo element, together with a number of other endemic asteraceous genera, such as *Aequatorium, Blakiella, Chionolaena, Floscaldasia, Hinterhubera, Jaramilloa, Laestadia* and *Scrobicaria.* In the Podocarpus páramos Ericaceae, with three genera, is the leading family of the páramo element. *Ceratostema, Semiramisia* and *Themistoclesia* characterize (sub) páramo shrub under very humid to wet climate. The high diversity in Ericaceae also reflects the extreme humidity of the Podocarpus páramo.

On the very wet Chocó slope of the West Cordillera in Colombia and northern Ecuador, Ericaceae are also highly diverse (Salinas & Betancur, 2005). In contrast with the species richness of asteraceous *Pentacalia* and *Monticalia* (shrub and dwarf shrub) in the Colombian páramos and in the eastern Andes of Peru, their presence in PBR páramos is limited in terms of species (Díaz Piedrahita & Cuatrecasas, 1999, Izco et al., 2007). The páramo endemic genera *Chrysactinium* and *Oreanthes* are absent elsewhere in the northern Andes.

The wide tropical element is well represented with 23 genera (12%). This flora element contains most genera of the so-called savanna relationship (Cleef et al., 1993): e.g., *Bulbostylis*, *Paspalum, Sporobolus*, and *Xyris*. Also the eriocaulaceous genera *Paepalanthus* and *Syngonanthus* belong here, though *Paepalanthus* species are rare in Neotropical savannas, and *Syngonanthus* is only represented by two species in páramos of southern Ecuador and northern Peru (Jørgensen & Ulloa Ulloa, 1994; Luteyn, 1999).

The Temperate Component

The Austral-Antarctic element is slightly better represented with 26 genera (14%) than the Holarctic element with 20 genera (11%). In the rainy Tatamá bamboo páramo, in the Colombian Western Cordillera 20 Austral-Antarctic genera outnumbered the 10 Holarctic genera. This phenomenon has recently also been supported for Ecuadorian superpáramos (Sklenár & Balslev, 2007) and was readily observed by Simpson & Todzia (1990) when comparing páramo and puna floras. Apparently permanent humidity at high altitude reduces the occurrence of frost at soil level (Ramsay 2001, Sklenár & Balslev, 2007), which is advantageous for lesser frost adapted Austral-Antarctic species. Humid and very humid superpáramos evidence more ground cover of much more species than in dry superpáramos (Cleef, 1981,2008).

Holarctic genera thrive better under drier conditions with changing humidity and are better frost-adapted; most of them are herbaceous. They are generally better represented on the drier páramo slopes of the northern Andes. Sklenár & Balslev (l.c.) demonstrated that the proportion of Holarctic genera rises markedly in the dry superpáramo compared to lower altitude. Genera of the tropical component are poorly represented in dry superpáramos (Sklenár & Balslev, 2007).

This phenomenon is also strongly corroborated by the phytogeographic analysis of an area of (dry) puna flora including the subnival belt (3600-5200 m) near Morococha and La Oroya in the Central Andes of Peru by Gutte (1992). Holarctic genera are over three times more represented than Austral-Antarctic genera (35,4 % vs. 9,3 %), but in reality the Holarctic proportion is lower, since a number of wide temperate genera has also been included in the Holarctic element judging from the examples referred to by Gutte (1992). The increased proportion of the temperate component, as documented in superpáramo (Sklenar & Balslev, 2007), is also registered in the subnival zone of the Central Andes of Peru by Gutte (1992).

Most remarkable in this context is the report by Simpson & Todzia (1990) that 26 Holarctic genera or 23,6% are present in the vascular flora of Tierra del Fuego (Moore 1983 a, b), more prevalent than, for instance, in Colombian páramo, which is much closer to the North American source area. This is explained by the high similarity of climatic conditions and by dispersal by migrating sea birds (e.g., the case of *Empetrum* (Simpson & Todzia l.c.).

In the wide temperate element are also genera which migrated from the North, e.g. *Valeriana.* (Bell & Donughue, 2005). Migration from southern latitudes occurred of the wide temperate species such as, *Calamagrostis* sect. *Deyeuxia* and *Plantago* (Rahn, 1996). The 26 genera of the Austral-Antarctic element represent almost fully this element in the páramo flora of the equatorial Andes. *Rostkovia*, thus far, has not been documented from Colombia, but is probably also present on the volcanoes of southern Colombia. *Rostkovia magellanica* grows in mires on the southern slopes of volcano Chiles, close to the Colombian border. This species has also been recorded on the Malvinas and other subantarctic islands (Balslev, 1979). *Ourisia* species, now Plantaginaceae, have their origin in temperate South America and spread first to New Zealand and later on in South America to equatorial latitudes (Meudt & Simpson, 2006, 2007).

The cosmopolitan component and element is represented by 14 genera. Striking is the presence of *Stipa.* Species of this genus generally occur at warmer and more arid habitats.

Though present at lower elevation, close to 3000 m, they do not form part of the Colombian and Venezuelan páramo flora under natural conditions as far as we know.

In conclusion, the phytogeographic spectrum of the Podocarpus study area is that of a rain páramo, lacking the superpáramo of higher elevations. This is supported by a very large proportion of the neotropical-montane element versus a limited proportion of the Andean-alpine element. Furthermore, the large proportion of the Austral-Antarctic or wide temperate element versus a smaller proportion of the Holarctic element characterizes the wet Podocarpus páramo. Similar patterns have also been found by Sklenár & Balslev (2007) comparing very humid and dry superpáramos in Ecuador.

The generic relationship with the puna is limited, though some 40 genera (or about 21 % of the generic flora) are shared with the puna of Peru. The wet climate probably does not allow for a greater presence, in spite of the relatively short distance. A substantial affinity exists with northernmost Peruvian páramos, situated north of the Huancabamba depression. Few genera document the savanna relationship (Cleef & Chaverry, 1992); theseaffinityrelationship (Cleef et al., 1993); these genera belong to the wide tropical and cosmopolitan element. The Podocarpus massif shares many genera and species with the neighbouring Cordillera del Condor, which also harbors a number of Tepuian genera and species (e.g., *Stenopadus andicola*). Except for the cyrillidaceous low tree *Purdiaea nutans* of the high Andean Podocarpus forest belt, tepuian genera seem absent in the PBR páramo (Mandl et al., 2008).

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