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Autor: López, Ramiro Pablo / Beck, Stephan

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Phytogeographical affinities and life form composition of the Bolivian Prepuna

RAMIRO PABLO LÓPEZ
&
STEPHAN BECK

ABSTRACT

LÓPEZ, R. P. & S. BECK (2002). Phytogeographical affinities and life form composition of the Bolivian Prepuna. *Candollea* 57: 77-96. In English, English and Spanish abstracts.

The Bolivian Prepuna is a summer-rain semidesert located in the Andes of southern Bolivia (20-22ºS, 2300-3300 m). This still not well known region is related to the Argentinean Prepuna; nonetheless, it shows a peculiar flora with an important number of endemisms. This study gathers all the available information on the Bolivian Prepuna's floristic composition and examines in detail its types of phytogeographical elements and life form spectrum. The phytogeographical elements were considered at genus and species levels. Three hundred and twenty-four species were recorded (two hundred and ninety-nine native). From the genus perspective, the Bolivian Prepuna has a strong influence of dry, (sub)tropical elements, both from the American dry tropics and from ancient pantropical elements originating principally in the Chaco region, and also of Andean elements given its mountain character. Cosmopolitan genera are also conspicuous. According to its species composition, the Prepuna mainly consists of a southern South American floristic stock (almost three quarters of its elements), in which predominate species exclusive to the whole Prepuna region (Argentinean and Bolivian) as well as Bolivian endemics (most of them exclusive to the Bolivian Prepuna), almost 50% of the species belonging to these two categories. This underscores the importance that this region has for conservation. Results of this study support the assertion that in South America a discontinuity exists between a tropical dry flora (from central Peru to Venezuela) and a subtropical-temperate one (the southern half of the continent). The life form spectrum is dominated by phanerophytes (shrubs and small trees). Hemicryptophytes (perennial herbs), succulents, and therophytes (annuals) are also important.

RESUMEN

LÓPEZ, R. P. & S. BECK (2002). Afinidades fitogeográficas y composición de formas vitales de la Prepuna boliviana. *Candollea* 57: 77-96. En inglés, resúmenes en inglés y en español.

La Prepuna boliviana es un semidesierto con lluvias estivales localizado en los Andes del sur de Bolivia (20-22ºS, 2300-3300 m) y relacionado con la Prepuna argentina; no obstante, muestra una flora peculiar en la que resalta un importante número de endemismos. Por lo demás, sigue siendo poco conocida. Este estudio reúne toda la información disponible en torno a la composición florística de la Prepuna boliviana, y examina en detalle sus tipos de elementos fitogeográficos y espectro de formas biológicas. Los elementos fitogeográficos se consideraron a nivel de géneros y especies. Se registran trescientos veinticuatro especies (doscientos noventa y nueve nativas). Desde la perspectiva genérica, la Prepuna boliviana tiene una fuerte influencia de elementos de los (sub)trópicos secos, tanto de los trópicos americanos como de elementos pantropicales ancianos, ambos provenientes de El Chaco, y también de elementos andinos dado su carácter montañoso. Asimismo, son conspicuos los géneros cosmopolitas. En términos de especies, la Prepuna está compuesta principalmente por un conjunto florístico del sur de Sudamérica (casi tres cuartos de sus elementos), donde resaltan especies exclusivas de toda la Prepuna (boliviana y argentina) así como endemismos bolivianos (la mayoría además exclusivos de la Prepuna boliviana); casi 50% de todas las especies pertenecen a estas dos categorías. Esto resalta la importancia de esta región desde la perspectiva de la conservación. Los resultados de este estudio apoyan la afirmación de que en Sud América existe una división entre una flora seca tropical (norte de Sud América, desde el centro de Perú hasta Venezuela) y otra subtropical-templada (en la mitad sur del continente). El

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espectro de formas biológicas está dominado por fanerófitos (arbustos y pequeños árboles); son también importantes los hemicriptófitos (hierbas perennes), suculentos y terófitos (anuales).

KEY-WORDS: Bolivian Prepuna – Summer-rain semidesert – Phytogeographic elements – Life forms – Southern South American dry flora.

Introduction

The Bolivian Prepuna is an Andean hot semidesert located in southern Bolivia (20-22ºS; Fig. 1). It is the northern-most extension of the Argentinean Prepuna, an arid mountain ecosystem related to the Monte Desert. The Bolivian Prepuna has been preliminarily characterized climatically, vegetationally, and floristically in a recent work (LÓPEZ, 2000).

Little is still known of this semidesert that is located at an altitude of 2300 to 3200-3300 m. Climatically, the average annual temperatures range between 14 and 20ºC, depending on altitude. Temperature fluctuations between the coldest and warmest months are from 8 to 10ºC. Maximum temperatures in summer may attain 35-41ºC. In winter, very cold temperatures can be reached at night (–10ºC and even lower), but, since there exists a great daily temperature variation (an

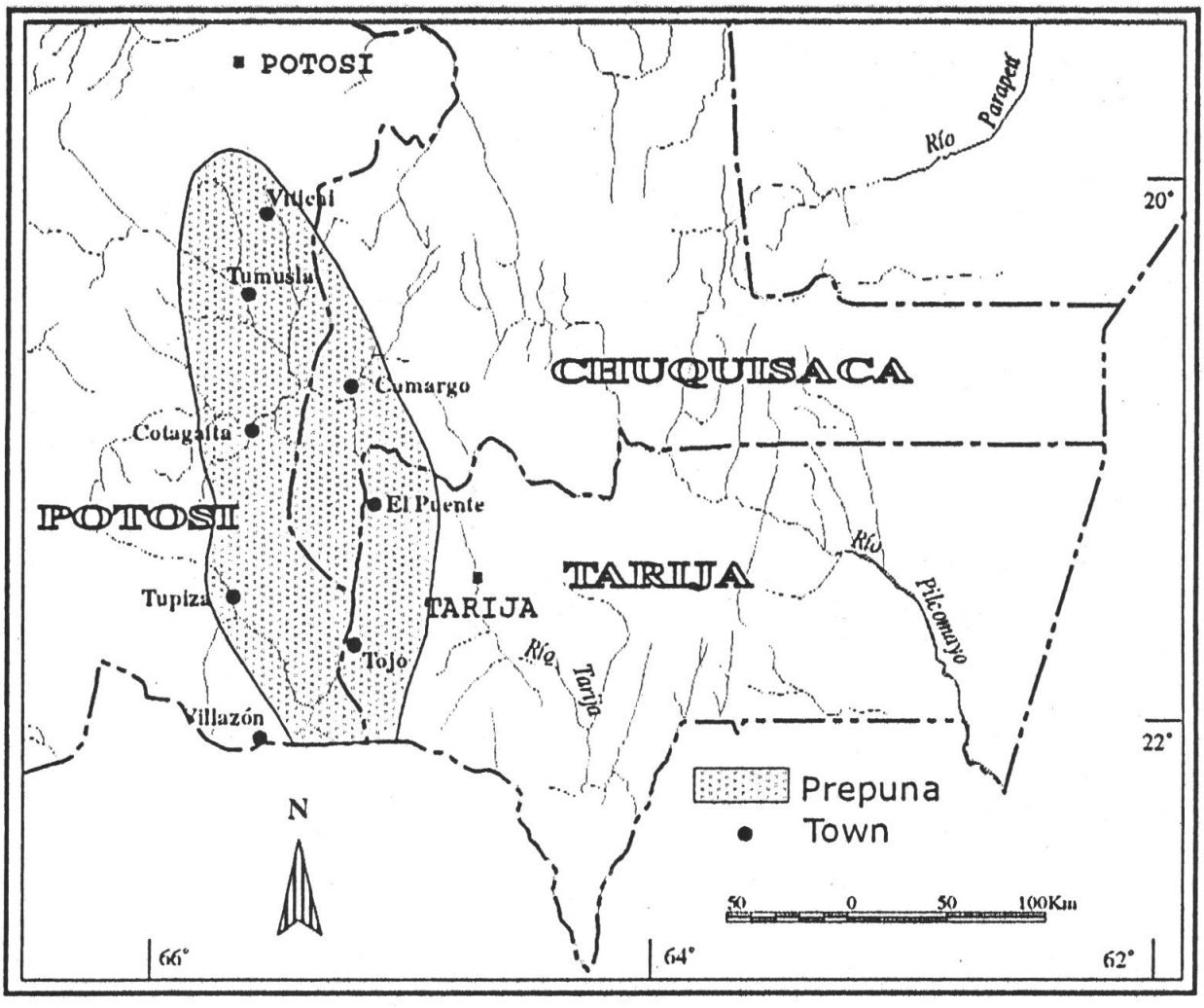

Fig. 1. - Approximate limits of the Bolivian Prepuna.

average of 20ºC, with maximum values that can exceed 30ºC in winter), mild and even warm temperatures are usual in the afternoon. The range of annual precipitation is from 200 to 370 mm. Relative humidity is very low (annual mean usually < 50%). The vegetation consists of open, thorn woodland or scrub in which Leguminosae (mainly mimosoids) and Cactaceae are predominant.

Floristically, the Prepuna originated in the sub-tropical, dry Chaco forests of South America. These two regions share many genera and even some species. However, as can be expected, the Prepuna is also influenced by the overlying arid Puna region. Not much more is known of this plant formation. More systematic and detailed work is thus needed. This study aims at improving our knowledge of the Bolivian Prepuna's floristic composition and phytogeographical relationships, as well as determining the contribution that different life forms make to its vegetation. Besides the obvious biogeographic interest, this study also intends to show the importance of the region from a conservation point of view as well as to make comparisons with neighboring arid regions so as to better comprehend summer-rain deserts.

Methods

This study is inspired on a similar work carried out for the coastal desert of central Chile (ARMESTO & VIDIELLA, 1993), but, additionally, a biogeographical analysis was done down to species level. A species list was prepared that formed the base of the analysis; it was based on LÓPEZ (2000, and relevant references therein), on the authors' plant collections and field notes, and on the plant collection of the Herbario Nacional de Bolivia. Nomenclature is based mainly on ZULOAGA & MORRONE (1996, 1999), since there is no Bolivian plant catalogue to date. However, there exist taxonomic revisions for some taxa, and these were considered in the present study. For the *Cactaceae*, nomenclature follows KIESLING (1999 and pers. comm.) and NAVARRO (1996); for *Bromeliaceae*, KRÖMER & al. (1999); for *Gramineae*, RENVOIZE (1998). Names of species not found in Argentina and also that of *Helogyne tacaquirensis* are based on BRAKO & ZARUCCHI (1993); that of *Helogyne virgata* follows KING & ROBINSON (1987). *Bougainvillea berberidifolia* is based on HEIMERL (1930-1934); *Abutilon fuscicalyx*, on ULBRICH (1932); *Calandrinia punae*, on AÑÓN (1953); *Nicotiana cutleri*, on D'ARCY (1976), and *Iochroma cardenasianum*, on HUNZIKER (1977). *Agalinis tarijensis* follows CANNE-HILLIKER (1988); *Baccharis santelicis*, HELLWIG (1990); *Aloysia arcuifolia*, NESOM (1991), and *Acacia feddeana*, SALDÍAS (1993). *Pteromonnina* species names derive from ERIKSEN (1993); *Bulnesia rivas-martinezii, from* NAVARRO (1994), and, finally, *Polylepis tomentella* subsp. *tomentella* follows KESSLER (1995). The authors decided to keep *Neocracca* as a distinct genus.

Table 1. – Phytogeographical elements (genera) recognized in this study.

Cosmopolitan (Cosm)	Genera widely distributed in more than one continent, although not necessarily in all five continents
Pantropical (Pantr)	Genera common in the tropics and subtropics of at least two continents
Tropical American (TropAm)	Genera distributed mainly in the tropics and subtropics of the American continent
Amphitropical (Amphi)	Genera commonly found in the subtropics of North and South America (mainly in arid regions) but absent or very rare in the tropics in between. Here are included amphitemperate taxa as well
Andean (Andean)	Genera mostly distributed in the Andes or having originated in them
American (Am)	Genera distributed more or less uniformly in the Americas (temperate America as well). Exclusively South American genera, *Ligaria* and *Cortaderia*, are included here too, in order not to create another group for such a few species.

Table 2. – Phytogeographical elements (species) individualized in this study. Each number represents a different category. Elements 1-4 represent species exclusive of dry areas of the southern half of South America.	
1	Species endemic to Bolivia. The majority of the species falling in this category are found in the Prepuna region only.
2	Species of Bolivia and Argentina (a few also in northeastern Chile, in the Andes, in frontier regions with the aforementioned countries). Species distributed principally in dry zones of the Andes in southern Bolivia and northwestern Argentina. Many components of this element belong strictly to the Prepuna region, or to the Prepuna and the lower belt of the arid Puna, which overlies the Prepuna, or to Prepuna and other dry valleys (although more mesic than the Prepuna) of southern Bolivia and northwestern Argentina. Some taxa reach also the Monte desert.
3	Species found from southern Peru, central and southern Bolivia, northern Chile and northwestern Argentina, i.e., an extension specially northwards and eastwards of the previous category, and, in general, possessing more mesic conditions. Elements in this group are distributed in the Andean dry formations of the southern half of South America (obviousy, with the exclusion of species from element 2). Thus, this category includes interandean dry valleys in the cited countries and also the lower portions of the dry Puna (which is more mesic than the arid Puna) and even those of the semihumid Puna.
4	Species existing in Peru (mainly central-southern Peru), Bolivia, northern Argentina and Chile, Paraguay, southern Brazil and Uruguay, i.e., species from the southern half of South America not restricted to dry and predominantly mountain regions (unlike class 3)
5	Species restricted to Bolivia and Peru, mainly in dry parts of the Andes in these two countries
6	Species distributed in most of South America, tropical or temperate
7	Amphitropical or amphitemperate species of the American continent, i.e., species absent or rare in central America and northern South America
8	Species found from South to North America
9	Cosmopolitan and pantropical species, i.e., those found in most territories of the world or at least in the tropics and the subtropics of the planet
10	Introduced species subsequently naturalized (cultivated plants uncapable of autopropagation, via seeds or vegetatively, were not included)

Two levels of biogeographical analysis were considered: genera and species. Genera show Prepuna relations on a continental and global scale and have evolutionary significance. For the analysis, the number of species each genus possesses weighted the importance of genera. Six biogeographical classes or categories were recognized, quite similar to those chosen by ARMESTO & VIDIELLA (1993), so that direct comparisons are possible (Table 1). The modern geographic distribution of genera was based primarily on WILLIS (1973) and MABBERLEY (1989), but also on ARMESTO & VIDIELLA (1993), CABRERA (1978, for *Compositae*), and RENVOIZE (1998, for *Gramineae*). The only differences with ARMESTOS & VIDIELLA (1993)'s phytogeographical elements are those of the **American** (**Am**) elements of the present study, where taxa distributed in the whole continent or in part of it (*Ligaria*, *Cortaderia*) were included, and the endemics. The Bolivian Prepuna has no endemic genera, so that this class, very important in the isolated coastal desert of Chile, is absent here. Genera such as *Calandrinia* (found in most of the Americas) and *Baccharis* (predominantly in North and South America) were assigned to the Andean and Amphitropical elements, respectively, following Armesto & Vidiella's decision, in order to facilitate comparisons. In the analysis involving genera, only native taxa were considered.

By examination of species we can observe how genera diversified, but the phytogeographical territory involved becomes more restricted. The analysis at the species level pointed to more subtle distributional differences and it aimed at finding relationships of the Prepuna at a finer scale, inside South America. The distributional ranges of each species were examined and, from common patterns, ten categories or classes of phytogeographical elements were created. For

subespecies, the distribution of the subspecies was considered for assignation to a biogeographical element. Reference was made to the same literature mentioned for the case of nomenclature (first paragraph of this section) when determining the distribution of species. WOODSON, SCHERY & coll. (1943-1980), SHREVE & WIGGINS (1964), CABRERA (1978, 1983, 1993), and JORGENSEN & LEÓN-YÁNEZ (1999) were also consulted. The ten categories are shown in Table 2. Taxa whose identity was not confirmed (*aff.*, *cf.*) were not employed in the analysis.

The numbers represent phytogeographical elements. As we go from **1** to **10**, the elements are composed of species with succesively larger geographic ranges, except group **5**, which is a particular class that could be considered as belonging to a transition zone between southern and northern South America; here are included only species exclusive to southern Peru and Bolivia. Numbers **1** through **4** are the most relevant to the present study; they represent the austral species, exclusive to the dry southern half of South America, where the Prepuna belongs. Phytogeographical elements **1-3** are mostly dry Andean. Number **1** was chosen for Bolivian endemics. Most of the species in this group are moreover exclusive to the Prepuna. Number **2** includes Bolivian and Argentinean species, many of which are exclusively or predominantly Prepuna species. Number **3** is a larger group, covering the species of dry zones (specially the dry interandean valleys) in the Andes of the southern half of South America. As to number **4**, this denotes species of southern South America distributed in very differnt plant formations (e.g., moister Andean and lowland regions and dry lowlands, as the Chaco). From group or class **6** and on, again the groups include species with successively wider distributions (see Table 2).

There is no necessary relation between the two series of phitogeographical elements, that of genera and that of species (e.g., *Acacia*, a genus occurring in all the tropics and subtropics of the world, has species with very limited distributions, such as *A. feddeana*, a Bolivian endemic restricted to the Prepuna formation).

For the case of biological spectra, species were assigned to the known life form classification of Raunkier's (BRAUN-BLANQUET, 1979) (Table 3). However, *Cactaceae* and *Bromeliaceae* were treated as a distinct life form, that of succulents.

Table 3. – Life forms. In parenthesis, equivalent terms also used in the text.

C	Chamaephytes (shrubs < 50 cm)
E	Epiphytes
G	Geophytes
H	Hemicryptophytes (perennial herbs)
M	Macrophanerophytes (trees)
N	Nanophanerophytes (shrubs > 50 cm)
P	(Hemi)parasites
S	Succulents
T	Therophytes (annuals)
V	Vines

Results

The plant list includes three hundred and twenty-four species of plants. These species are distributed in two hundred genera and sixty-one families (considering *Leguminosae* and *Pteridophyta* as one taxon). Corresponding values for native species only are two hundred and ninety-nine species, one hundred and eighty-three genera, and fifty-eight families. One species was identified to family level only (a *Verbenaceae*, perhaps *Diostea*).

Table 4. – Vascular plant species recorded for the Bolivian Prepuna, their life forms and biogeographical elements to which they belong. Names in boldface refer to Bolivian endemics found only in Prepuna. See Tables 1 through 3 for definitions.

Family	*Species*	*Life form*	*Phytogeographic element (genera)*	*Phytogeographic element (species)*	*Synonym([1])*
Pteridophyta	*Cheilanthes bonariensis* (Willd.) Proctor	–	–	–	
Pteridophyta	*Cheilanthes myriophylla* Desv.	–	–	–	
Pteridophyta	*Argyrochosma nivea* (Poir.) Windham var. *tenera* (Gillies ex Hook.) Ponce	–	–	–	*Notholaena nivea* (Poir.) Desv. var. *tenera* (Gillies ex Hook.) Griseb.
Pteridophyta	*Selaginella sellowii* Hieron.	–	–	–	
Ephedraceae	*Ephedra americana* Humb. & Bonpl. ex Willd.	N	Cosm	3	
Ephedraceae	*Ephedra breana* Phil.	N	Cosm	3	
Acanthaceae	*Justicia tweediana* (Nees) Griseb.	C	Pantr	2	
Acanthaceae	*Stenandrium dulce* (Cav.) Nees	H	TropAm	4	
Acanthaceae	*Alternanthera pungens* Kunth	H	Cosm	6	
Amaranthaceae	*Amaranthus hybridus* L.	T	Cosm	9	
Amaranthaceae	*Amaranthus muricatus* (Moq.) Hieron.	H	Cosm	4	
Amaranthaceae	*Gomphrena haenkeana* Mart.	H	TropAm	2	
Amaranthaceae	*Gomphrena meyeniana* Walp.	H	TropAm	3	
Amaranthaceae	*Gomphrena cf. phaeotricha* Pedersen	T	TropAm	–	
Amaranthaceae	*Guilleminea densa* (Willd. ex Roem. & Schult.) Moq.	H	Amphi	7	
Amaranthaceae	*Iresine diffusa* Humb. & Bonpl. ex Willd.	C	Cosm	2	*Iresine spiculigera* Seub.
Anacardiaceae	*Schinus molle* L.	M	TropAm	3	
Asclepiadaceae	*Asclepias barjoniifolia* E. Fourn.	H	Am	2	
Asclepiadaceae	*Sarcostemma* sp.	V	Pantr	–	
Begoniaceae	*Begonia* cf. *micranthera* Griseb.	G	Pantr	–	
Berberidaceae	*Berberis* sp.	N	Cosm	–	
Bignoniaceae	*Tecoma garrocha* Hieron.	N	Andean	2	
Boraginaceae	*Heliotropium microstachyum* Ruiz & Pav.	H	Cosm	6	
Cactaceae	*Austrocylindropuntia shaferi* (Britton & Rose) Backeb. *	S	Andean	2	
Cactaceae	*Austrocylindropuntia verschaffeltii* (Cels ex F.A.C. Weber) Backeb.	S	Andean	2	
Cactaceae	*Cleistocactus* aff. *hyalacanthus* (K. Schum.) Gosselin	S	Andean	–	
Cactaceae	***Cleistocactus tarijensis*** Cárdenas	S	Andean	1	
Cactaceae	***Cleistocactus tupizensis*** (Vaupel) Backeb.	S	Andean	1	
Cactaceae	***Corryocactus tarijensis*** Cárdenas *	S	Andean	1	
Cactaceae	*Echinopsis longispina* (Britton & Rose) Werderm.	S	Andean	2	*Echinopsis ferox* (Britton & Rose) Backeb.
Cactaceae	*Echinopsis mamillosa* Gürke	S	Andean	2	
Cactaceae	*Gymnocalycium spegazzini* Britton & Rose ssp. *cardenasianum* (Britton & Rose) Kiesling, Metzing & Meregali *	S	Andean	1	*Gymnocalycium cardenasianum* F.Ritter
Cactaceae	***Lobivia lateritia*** (Gürke) Britton & Rose *	S	Andean	1	*Echinopsis lateritia* Gürke
Cactaceae	*Lobivia pugionacantha* (Rose & Boed.) Backeb.	S	Andean	2	*Echinopsis pugionacantha* Rose & Boed.
Cactaceae	*Lobivia pygmaea* (R.E.Fr.) Backeb.	S	Andean	2	
Cactaceae	***Lobivia rauschii*** Zecher	S	Andean	1	*Echinopsis yuquina* D.R. Hunt
Cactaceae	*Opuntia albisaetacens* Backeb.	S	Am	1	
Cactaceae	*Opuntia ficus-indica* (L.) Mill.	S	–	10	
Cactaceae	*Opuntia soehrensii* Britton & Rose	S	Am	3	
Cactaceae	*Opuntia spinibarbis* F. Ritter	S	Am	2	
Cactaceae	*Opuntia sulphurea* Gillies ex Salm-Dyck	S	Am	2	

([1]) Only referred to some common species names that are now considered synonyms.
* Austral elements (genera), including amphitropical or amphitemperate taxa, or Andean (*Tarasa*) that go as far north as Peru only, or cosmopolitans (*Eupatorium*) that are absent from the northern South America dry flora. In the case of genera with more than one species, only the first species belonging to those genera is marked with the asterisk.

Family	*Species*	*Life form*	*Phytogeographic element (genera)*	*Phytogeographic element (species)*	*Synonym*
Cactaceae	*Oreocereus celsianus* (Lem. ex Salm-Dyck) Riccob. *	S	Andean	3	
Cactaceae	*Oreocereus trollii* (Kupper) Backeb.	S	Andean	2	
Cactaceae	***Parodia camarguensis*** Buining & F. Ritter *	S	Andean	1	
Cactaceae	***Parodia carrerana*** Cárdenas	S	Andean	1	
Cactaceae	*Parodia maassii* (Heese) A.Berger	S	Andean	2	
Cactaceae	***Parodia maxima*** F. Ritter	S	Andean	1	
Cactaceae	***Parodia occulta*** F.Ritter	S	Andean	1	
Cactaceae	***Parodia splendens*** Cárdenas	S	Andean	1	
Cactaceae	*Parodia subterranea* F.Ritter	S	Andean	1	
Cactaceae	*Parodia sutilihamata* F.Ritter	S	Andean	1	
Cactaceae	*Parodia tuberculata* Cárdenas	S	Andean	1	
Cactaceae	*Puna subterranea* (R.E.Fr.) R.Kiesling *	S	Andean	2	
Cactaceae	*Rebutia ritteri* (Wessner) Buining & Donald *	S	Andean	2	
Cactaceae	***Tephrocactus chichensis* Cárdenas ***	S	Andean	2	*Opuntia ferocior* (Backeb.) Rowley
Cactaceae	*Trichocereus atacamensis* (Phil.) Backeb. ssp. *pasacana* (Weber) Navarro *	S	Andean	2	*Trichocereus pasacana* (F.A.C. Weber) Britton & Rose
Cactaceae	***Trichocereus randallii* Cárdenas**	S	Andean	1	
Cactaceae	***Trichocereus tacaquirensis*** (Vaupel) Cárdenas	S	Andean	1	
Cactaceae	*Trichocereus tunariensis* Cárdenas	S	Andean	1	*Echinopsis camarguensis* Cárdenas
Cactaceae	*Trichocereus tarijensis* (Vaupel) Werderm.	S	Andean	2	
Cactaceae	***Trichocereus werdermannianus*** Backeb.(²)	S	Andean	1	
Cactaceae	***Weingartia fidaiana*** (Backeb.) Werderm. *	S	Andean	1	
Cactaceae	*Weingartia kargliana* Rausch	S	Andean	1	
Cactaceae	*Weingartia neumanniana* (Backeb.) Werderm.	S	Andean	2	
Cactaceae	*Weingartia westii* (Hutchinson) Donald	S	Andean	1	
Capparidaceae	*Capparis atamisquea* Kuntze	M	Pantr	2	*Atamisquea emarginata* Miers
Capparidaceae	*Cleome* sp.	H	Cosm	–	
Caricaceae	*Carica quercifolia* (A. St.-Hil.) Hieron.	M	TropAm	4	*Carica lanceolata* (A DC.) Hieron.
Caryophyllaceae	*Drymaria glandulosa* Bartl.	T	Cosm	3	
Caryophyllaceae	*Drymaria villosa* Cham. & Schltdl.	T	Cosm	8	
Caryophyllaceae	*Paronychia* sp.	H	Cosm	–	
Caryophyllaceae	*Spergularia* sp.	H	Cosm	–	
Chenopodiaceae	*Atriplex* cf. *semibaccata* R. Br.	N	–	10	
Chenopodiaceae	*Chenopodium album* L.	T	–	10	
Chenopodiaceae	*Chenopodium ambrosioides* L.	T	Cosm	4	
Chenopodiaceae	*Chenopodium graveolens* Willd.	T	Cosm	2	
Chenopodiaceae	*Chenopodium petiolare* Kunth	H	Cosm	3	
Chenopodiaceae	*Suaeda divaricata* Moq. *	N	Cosm	2	
Chenopodiaceae	*Suaeda* aff. *foliosa* Moq.	C	Cosm	–	
Compositae	*Aphyllocladus spartioides* Wedd. *	N	Andean	2	
Compositae	*Baccharis boliviensis* (Wedd.) Cabrera	C	Amphi	3	
Compositae	*Baccharis grisebachii* Hieron	N	Amphi	2	
Compositae	*Baccharis potosiensis* H. Robinson	N	Amphi	1	
Compositae	*Baccharis salicifolia* (Ruiz & Pav.) Pers.	N	Amphi	6	
Compositae	*Baccharis santelicis* Phil.	N	Amphi	3	*Baccharis incarum* Wedd.
Compositae	*Bidens exigua* Sherff	T	Cosm	3	
Compositae	*Chuquiraga acanthophylla* Wedd.	N	Andean	2	
Compositae	*Chuquiraga longiflora* (Griseb.) Hieron.	N	Andean	2	

(²) It could be a variety of *T. atacamensis* (Kiesling, pers.comm.).

Family	Species	Life form	Phytogeographic element (genera)	Phytogeographic element (species)	Synonym
Compositae	*Conyza* sp.	–	Cosm	–	
Compositae	*Dasyphyllum hystrix* (Wedd.) Cabrera	N	TropAm	5	
Compositae	*Eupatorium patens* D.Don ex Hook & Arn. *	N	Cosm	4	
Compositae	*Eupatorium schickendantzii* Hieron.	H	Cosm	2	
Compositae	*Flaveria bidentis* (L.) Kuntze	T	TropAm	8	
Compositae	*Flourensia fiebrigii* S.F. Blake *	N	Amphi	2	
Compositae	*Galinsoga urticifolia* (Kunth) Benth.	T	TropAm	6	*Galinsoga quadriradiata* Ruiz & Pav.
Compositae	*Galinsoga* sp.	T	TropAm	–	
Compositae	*Gamochaeta deserticola* Cabrera	T	Cosm	2	
Compositae	*Gamochaeta pensylvanica* (Willd.) Cabrera	T	Cosm	8	
Compositae	*Gochnatia cardenasii* S.F. Blake *	N	TropAm	2	
Compositae	*Gutierrezia mandonii* (Sch. Bip.) Solbrig *	C	Amphi	2	
Compositae	*Helogyne straminea* (DC.) B.L.Rob. *	N	Andean	5	
Compositae	*Helogyne tacaquirensis* Hieron.	N	Andean	3	*Eupatorium tacaquirensis* (Hieron.) B.L. Robinson
Compositae	*Helogyne virgata* (Rusby) B.L. Rob.	N	Andean	1	
Compositae	*Heterosperma nanum* (Nutt.) Sherff	T	TropAm	3	
Compositae	*Heterosperma tenuisectum* (Griseb.) Cabrera	T	TropAm	3	
Compositae	*Hyaloseris camataquiensis* Hieron. Ex J. Kost. *	N	Andean	2	
Compositae	*Hymenoxys robusta* (Rusby) K.L. Parker	T	Am	3	
Compositae	*Lophopappus cuneatus* R.E. Fr. *	N	Andean	2	
Compositae	*Lophopappus foliosus* Rusby	N	Andean	3	
Compositae	*Mutisia orbignyana* Wedd.	N	Andean	3	
Compositae	*Nardophyllum armatum* (Wedd.) Reiche *	N	Andean	2	
Compositae	*Parthenium hysterophorus* L.	H	Amphi	7	*Parthenium glomeratum* Rollins
Compositae	*Pectis sessiliflora* (Less.) Sch.Bip.	T	TropAm	3	
Compositae	*Porophyllum lanceolatum* DC.	C	TropAm	4	
Compositae	*Porophyllum ruderale* (Jacq.) Cass.	T	TropAm	8	
Compositae	*Proustia cuneifolia* D. Don *	N	Andean	3	
Compositae	*Schkuhria degenerica* (Kuntze) R.E. Fr.	T	TropAm	2	
Compositae	*Schkuhria multiflora* Hook. & Arn.	T	TropAm	7	
Compositae	*Senecio hieronymi* Griseb.	C	Cosm	2	
Compositae	*Senecio potosianus* Klatt	C	Cosm	1	
Compositae	*Senecio* sp.	N	Cosm	–	
Compositae	*Sigesbeckia jorullensis* Kunth	T	Pantr	9	
Compositae	*Sonchus oleraceus* L.	T	–	10	
Compositae	*Stevia* cf. *bangii* Rusby	C	TropAm	–	
Compositae	*Tagetes minuta* L.	T	TropAm	4	
Compositae	*Tagetes multiflora* Kunth	T	TropAm	3	
Compositae	*Taraxacum officinale* L.	T	–	10	
Compositae	*Tessaria absinthioides* (Hook. & Arn.) DC.	N	TropAm	4	
Compositae	*Trichocline auriculata* (Wedd.) Hieron.	G	Am	2	
Compositae	*Viguiera pazensis* Rusby	H	TropAm	3	
Compositae	*Viguiera procumbens* (Pers.) S.F. Blake	H	TropAm	3	
Compositae	*Viguiera tucumanensis* (Hook. & Arn.) Griseb. var. *oligodonta* (Blake) Cabrera	H	TropAm	2	
Compositae	*Xanthium catharticum* Kunth	T	–	10	
Compositae	*Zinnia peruviana* (L.) L.	T	TropAm	8	
Convolvulaceae	*Cuscuta cf. grandiflora* Kunth	P	Cosm	–	
Convolvulaceae	*Dichondra argentea* Humb. & Bonpl. ex Willd.	H	Pantr	2	

Family	*Species*	*Life form*	*Phytogeographic element (genera)*	*Phytogeographic element (species)*	*Synonym*
Convolvulaceae	*Dichondra sericea* Sw.	H	Pantr	4	
Convolvulaceae	*Evolvolus* cf. *nummularius* (L.) L.	H	TropAm	–	
Convolvulaceae	*Evolvulus sericeus* Sw.	H	TropAm	8	
Convolvulaceae	*Ipomoea* cf. *aristolochiaefolia* G. Don	V	Cosm	–	
Crassulaceae	*Crassula connata* (Ruiz & Pav.) A. Berger	T	Cosm	6	*Tillaea connata* Ruiz & Pav.
Cruciferae	*Capsella bursa-pastoris* (L.) Medik.	T	–	10	
Cruciferae	*Lepidium aletes* J.F. Macbr.	T	Cosm	4	
Cruciferae	*Lepidium* sp.	H	Cosm	–	
Euphorbiaceae	*Croton* sp.	C	Pantr	–	
Euphorbiaceae	*Euphorbia peplus* L.	T	–	10	
Euphorbiaceae	*Euphorbia hypericifolia* L.	T	Cosm	8	*Euphorbia boliviana* Rusby
Euphorbiaceae	*Jatropha clavuligera* Muell.Arg.	N	Pantr	5	
Euphorbiaceae	*Ricinus communis* L.	N	–	10	
Geraniaceae	*Erodium cicutarium* (L.) L'Hér. Ex Aiton	T	–	10	
Hydrophyllaceae	*Nama dichotomum* (Ruiz & Pav.) Choisy	T	Amphi	7	
Hydrophyllaceae	*Phacelia nana* Wedd. *	T	Amphi	3	
Hydrophyllaceae	*Phacelia pinnatifida* Griseb. ex Wedd.	H	Amphi	4	*Phacelia boliviana* Brand
Krameriaceae	*Krameria lappacea* (Dombey) Burdet & B.B. Simpson	C	Amphi	6	
Labiatae	*Salvia gilliesii* Benth.	C	Cosm	2	
Ledocarpaceae	*Balbisia integrifolia* R. Knuth *	N	Andean	2	
Ledocarpaceae	*Balbisia* cf. *meyeniana* Klotzsch	N	Andean	–	
Leguminosae-Caes.	*Caesalpinia mimosifolia* Griseb.	N	Pantr	2	
Leguminosae-Caes.	*Caesalpinia pumilio* Griseb.	C	Pantr	2	
Leguminosae-Caes.	*Cercidium andicola* Griseb.	M	TropAm	2	
Leguminosae-Caes.	*Hoffmannseggia viscosa* (Ruiz & Pav.) Hook. & Arn. var viscosa *	G	TropAm	6	*Caesalpinia viscosa* (Ruiz & Pav.) J.F. Macbr.
Leguminosae-Caes.	*Senna birostris* (Domb. ex Vog.) H.S. Irwin & Barneby var. *hookeriana* (Hook.) H.S. Irwin & Barneby	N	Cosm	2	
Leguminosae-Caes.	*Senna crassiramea* (Benth.) H.S. Irwin & Barneby	N	Cosm	2	
Leguminosae-Mim.	*Acacia caven* (Molina) Molina	M	Pantr	4	
Leguminosae-Mim.	***Acacia feddeana*** Harms	M	Pantr	1	
Leguminosae-Mim.	*Acacia macracantha* Humb. & Bonpl. ex Willd.	M	Pantr	6	
Leguminosae-Mim.	*Acacia visco* Lorentz ex Griseb.	M	Pantr	3	
Leguminosae-Mim.	*Prosopis alba* Griseb.	M	Pantr	4	
Leguminosae-Mim.	*Prosopis ferox* Griseb.	M	Pantr	2	
Leguminosae-Mim.	*Prosopis flexuosa* DC.	M	Pantr	2	
Leguminosae-Mim.	*Prosopis laevigata* (Humb. & Bonpl. ex Willd) M.C. Johnston var. *andicola* Burkart	M	Pantr	3	
Leguminosae-Pap.	*Coursetia brachyrrachis* Harms	N	TropAm	2	
Leguminosae-Pap.	*Dalea boliviana* Britton	C	Am	3	
Leguminosae-Pap.	*Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart	M	TropAm	4	
Leguminosae-Pap.	*Melilotus albus* Desr.	C	–	10	
Leguminosae-Pap.	*Neocracca heterantha* (Griseb.) Speg. *	T	Andean	2	*Coursetia heterantha* (Griseb.) Lavin.
Loasaceae	*Mentzelia cordovensis* Urb. & Gilg	C	Amphi	2	
Loasaceae	*Mentzelia parvifolia* Urb. & Gilg	G	Amphi	2	
Loganiaceae	*Buddleja aromatica* J. Rémy	N	Cosm	2	
Loganiaceae	*Buddleja hieronymi* R.E. Fr.	N	Cosm	2	
Loganiaceae	*Buddleja tucumanensis* Griseb.	N	Cosm	2	
Loranthaceae	*Ligaria cuneifolia* (Ruiz & Pav.) Thieg. *	P	Am	4	

Family	Species	Life form	Phytogeographic element (genera)	Phytogeographic element (species)	Synonym
Malvaceae	***Abutilon fuscicalyx*** Ulbr.	N	Cosm	1	
Malvaceae	*Pseudabutilon virgatum* (Cav.) Fryxell	C	TropAm	6	*Abutilon virgatum* (Cav.) Sweet
Malvaceae	*Sida cordifolia* L.	N	Pantr	6	
Malvaceae	*Sphaeralcea* sp. *	H	Amphi	–	
Malvaceae	*Tarasa* sp. *	T	Andean	–	
Myrtaceae	*Eucalyptus globulus* Labill.	M	–	10	
Nyctaginaceae	*Allionia incarnata* L. *	H	Amphi	7	
Nyctaginaceae	*Boerhavia* sp.	H	Pantr	–	
Nyctaginaceae	*Bougainvillea berberidifolia* Heimerl	N	TropAm	1	
Nyctaginaceae	*Bougainvillea spinosa* (Cav.) Heimerl	N	TropAm	3	
Nyctaginaceae	*Mirabilis jalapa* L.	H	Amphi	7	
Nyctaginaceae	*Mirabilis prostrata* (Ruiz & Pav.) Heimerl	V	Amphi	6	
Olacaceae	*Menodora* sp. *	C	Amphi	–	
Oxalidaceae	*Oxalis cotagaitensis* R. Knuth	T	Cosm	2	
Papaveraceae	*Argemone* sp.	H	Am	–	
Passifloraceae	*Passiflora foetida* L.	V	TropAm	8	
Plantaginaceae	*Plantago* sp.	T	Cosm	–	
Polygalaceae	*Pteromonnina rusbyi* (Chodat) Eriksen	T	Andean	2	*Monnina rusbyi* Chodat
Polygalaceae	*Pteromonnina wrightii* (A. Gray) Eriksen	T	Andean	3	*Monnina wrightii* A. Gray
Polygonaceae	*Rumex conglomeratus* Murr.	H	–	10	
Portulacaceae	*Calandrinia punae* R.E. Fr.	G	Andean	2	*Talinum punae* (R.E. Fr.) Carolin
Portulacaceae	*Portulaca elongata* Rusby	T	Pantr	3	
Portulacaceae	*Portulaca oleracea* L.	T	–	10	
Portulacaceae	*Portulaca perennis* R.E. Fr.	H	Pantr	3	
Ranunculaceae	*Clematis* sp.	V	Cosm	–	
Rhamnaceae	*Kentrothamnus weddellianus* (Miers) M.C. Johnst. *	N	Andean	2	
Rosaceae	*Kageneckia lanceolata* Ruiz & Pav. *	M	Andean	3	
Rosaceae	*Polylepis tomentella* Wedd. Ssp. *tomentella*	M	Andean	3	
Rubiaceae	*Heterophyllaea lycioides* (Rusby) Sandwith *	N	Andean	5	
Salicaceae	*Populus deltoides* Bartram	M	–	10	
Salicaceae	*Populus nigra cv. Italica* (Münchh.) Koehne	M	–	10	
Salicaceae	*Salix babylonica* L.	M	–	10	
Salicaceae	*Salix humboldtiana* Willd.	M	Cosm	8	
Sapindaceae	*Cardiospermum corindum* L.	V	TropAm	8	
Sapindaceae	*Dodonaea viscosa* Jacq.	N	Pantr	9	
Sapindaceae	*Urvillea* sp.	V	TropAm	–	
Saxifragaceae	*Escallonia* sp. *	N	Andean	–	
Scrophulariaceae	***Agalinis tarijensis*** (R.E. Fr.) D'Arcy	H	Am	1	
Solanaceae	*Iochroma australe* Griseb.	N	TropAm	2	
Solanaceae	***Iochroma cardenasianum*** Hunz.	N	TropAm	1	
Solanaceae	*Lycianthes lycioides* (L.) Hassl.	N	Cosm	6	
Solanaceae	*Lycium chilense* Miers ex Bertero	N	Cosm	2	
Solanaceae	*Nicotiana glauca* Graham	N	TropAm	3	
Solanaceae	***Nicotiana cutlerii*** D'Arcy	H	TropAm	1	
Solanaceae	*Solanum chamaesarachidium* Bitter	T	Cosm	2	
Solanaceae	*Solanum palitans* C.V. Morton	H	Cosm	3	
Solanaceae	*Solanum tripartitum* Dunal	H	Cosm	2	
Solanaceae	*Vassobia fasciculata* (Miers) Hunz. *	N	Andean	5	

Family	*Species*	*Life form*	*Phytogeographic element (genera)*	*Phytogeographic element (species)*	*Synonym*
Sterculiaceae	*Melochia* sp.	–	Pantr	–	
Tropaeolaceae	*Tropaeolum seemanii* Buchenau	V	TropAm	5	*Tropaeolum rectangulum* Buchenau
Umbelliferae	*Bowlesia* sp.	–	Andean	–	
Verbenaceae	***Aloysia arcuifolia*** G.L. Nesom	N	Amphi	1	
Verbenaceae	*Aloysia gratissima* (Gillies & Hook.) Tronc.	N	Amphi	4	
Verbenaceae	*Aloysia virgata* (Ruiz & Pav.) Juss.	N	Amphi	4	
Verbenaceae	*Diostea* cf.	C	–	–	
Verbenaceae	*Junellia bisulcata* (Hayek) Moldenke *	C	Andean	2	
Verbenaceae	*Lantana balansae* Briq.	C	Pantr	4	
Verbenaceae	*Lippia* sp.	C	Pantr	–	
Verbenaceae	*Verbena* sp.	H	Cosm	–	
Viscaceae	***Phoradendron liga*** (Gillies) Eich.	P	Am	4	
Zygophyllaceae	***Bulnesia rivas-martinezii*** G. Navarro *	C	Andean	1	
Zygophyllaceae	*Kallstroemia boliviana* Standl.	H	TropAm	5	
Zygophyllaceae	*Larrea divaricata* Cav. *	N	Amphi	7	
Zygophyllaceae	*Porlieria microphylla* (Baill.) Descole, O'Donell & Lourteig *	C	Andean	4	
Zygophyllaceae	*Tribulus terrestris* L.	H	–	10	
Bromeliaceae	***Deuterocohnia bracteosa*** W. Till & L. Hrom. *	S	Andean	1	
Bromeliaceae	*Deuterocohnia digitata* L.B. Sm.	S	Andean	2	
Bromeliaceae	*Deuterocohnia lorentziana* (Mez)M.A. Spencer & L.B.Sm.	S	Andean	2	
Bromeliaceae	***Deuterocohnia scapigera*** (Rauh & L. Hrom.) M.A. Spencer & L.B. Sm.	S	Andean	1	
Bromeliaceae	*Deuterocohnia strobilifera* Mez	S	Andean	2	
Bromeliaceae	*Puya hofstenii* Mez	S	Andean	2	
Bromeliaceae	*Puya humilis* Mez	S	Andean	1	
Bromeliaceae	*Puya stenothyrsa* (Baker) Mez	S	Andean	1	
Bromeliaceae	***Puya trollii*** L.B. Sm.	S	Andean	1	
Bromeliaceae	***Puya weddelliana*** (Baker) Mez	S	Andean	1	
Bromeliaceae	*Tillandsia aizoides* Mez	E	TropAm	2	
Bromeliaceae	*Tillandsia caliginosa* W. Till.	E	TropAm	4	
Bromeliaceae	***Tillandsia camargoensis*** L. Hrom.	E	TropAm	1	
Bromeliaceae	*Tillandsia capillaris* Ruiz & Pav.	E	TropAm	6	
Bromeliaceae	*Tillandsia cardenasii* L.B. Sm.	E	TropAm	1	
Bromeliaceae	***Tillandsia cotagaitensis*** L. Hrom.	E	TropAm	1	
Bromeliaceae	*Tillandsia gilliesii* Baker	E	TropAm	3	
Bromeliaceae	***Tillandsia hasei*** Ehlers & L. Hrom.	E	TropAm	1	
Bromeliaceae	***Tillandsia hegeri*** Ehlers	E	TropAm	1	
Bromeliaceae	*Tillandsia hirta* W. Till & L. Hrom	E	TropAm	2	
Bromeliaceae	*Tillandsia lorentziana* Griseb.	E	TropAm	4	
Bromeliaceae	*Tillandsia lotteae* H. Hrom	E	TropAm	1	
Bromeliaceae	*Tillandsia muhriae* W. Weber	E	TropAm	2	
Bromeliaceae	*Tillandsia myosura* Griseb. ex Baker	E	TropAm	4	
Bromeliaceae	*Tillandsia sphaerocephala* Baker	E	TropAm	2	
Bromeliaceae	*Tillandsia virescens* Ruiz & Pav.	E	TropAm	4	
Bromeliaceae	*Tillandsia xiphioides* Ker-Gawler	E	TropAm	4	
Cyperaceae	*Cyperus* cf. *andinus* Palla ex Kük.	G	Cosm	–	
Gramineae	*Aristida adscencionis* L.	T	Cosm	9	
Gramineae	*Aristida antoniana* Steud. ex Döll	H	Cosm	3	*Aristida enodis* Hack.
Gramineae	*Aristida friesii* Hack.	H	Cosm	1	

Family	Species	Life form	Phytogeographic element (genera)	Phytogeographic element (species)	Synonym
Gramineae	*Arundo donax* L.	M	–	10	
Gramineae	*Bothriochloa barbinodis* (Lag.) Herter	H	Pantr	8	
Gramineae	*Bouteloa curtipendula* (Michx.) Torr.	H	Am	8	
Gramineae	*Bromus catharticus* Vahl	T	–	10	
Gramineae	*Chloris halophila* Parodi.	G	Pantr	6	
Gramineae	*Chondrosum simplex* (Lag.) Kunth	T	Am	8	*Bouteloa simplex* Lag.
Gramineae	*Cortaderia* sp.	H	Am	–	
Gramineae	*Cottea pappophoroides* Kunth	H	Amphi	7	
Gramineae	*Danthonia secundiflora* J. Presl	H	Cosm	6	
Gramineae	*Digitaria californica* (Benth.) Henrard	G	Cosm	8	
Gramineae	*Distichlis spicata* (L.) Greene	G	Amphi	7	
Gramineae	Eleusine indica *(L.) Gaertner*	T	Pantr	10	
Gramineae	*Elionurus muticus* (Spreng.) Kuntze *	H	Pantr	4	
Gramineae	*Enneapogon desvauxii* P. Beauv. *	H	Amphi	7	
Gramineae	*Eragrostis cilianensis* (All.) Vignola ex Janch.	T	–	10	
Gramineae	*Eragrostis nigricans* (Kunth) Steud.	T	Cosm	6	
Gramineae	*Eragrostis virescens* J. Presl	T	Cosm	6	
Gramineae	*Erioneuron avenaceum* (Kunth) Tateoka *	H	Amphi	7	*Tridens avenacea* (Kunth) Hitchc.
Gramineae	*Leptochloa dubia* (Kunth) Nees	H	Pantr	8	
Gramineae	*Lycurus phleoides* Kunth	H	TropAm	7	
Gramineae	*Melica chilensis* C. Presl	H	Amphi	2	*Melica adhaerens* Hack.
Gramineae	*Melinis repens* (Willd.) Zizka	T	–	10	*Rhynchelytrum repens* (Willd.) C.E. Hubb.
Gramineae	*Microchloa indica* (L.f.) P. Beauv.	T	Pantr	9	
Gramineae	*Microchloa kunthii* Desv.	H	Pantr	9	
Gramineae	*Muhlenbergia asperifolia* (Nees & Meyen) Parodi	T	Cosm	8	
Gramineae	*Muhlenbergia rigida* (Kunth) Kunth	H	Cosm	8	
Gramineae	*Munroa argentina* Griseb. *	T	Amphi	2	
Gramineae	*Pappophorum caespitosum* R.E. Fr.	H	TropAm	4	
Gramineae	*Pappophorum philippianum* Parodi	H	TropAm	4	
Gramineae	*Paspalum* cf. *prostratum* Scribn. & Merr.	T	Pantr	–	
Gramineae	*Pennisetum chilense* (Desv.) B.D. Jack.	G	Pantr	2	
Gramineae	*Pennisetum villosum* R. Br. ex Fresen.	G	–	10	
Gramineae	*Setaria barbinodis* Herrm.	H	Cosm	1	
Gramineae	*Setaria macrostachya* Kunth	H	Cosm	8	
Gramineae	*Sporobolus indicus* (L.) R.Pr. var. *andinus* Renvoize	H	Cosm	5	
Gramineae	*Sporobolus pyramidatus* (Lam.) Hitchc.	T	Cosm	8	
Gramineae	*Stipa holwayi* Hitchc.	H	Cosm	2	
Gramineae	*Stipa ichu* (Ruiz & Pav.) Kunth	H	Cosm	8	
Gramineae	*Stipa* cf. *illimanica* Hack.	H	Cosm	–	
Gramineae	*Stipa rupestris* Phil.	H	Cosm	6	
Gramineae	*Tragus berteronianus* Schult.	T	–	10	
Gramineae	*Tripogon spicatus* (Nees) Ekman	H	Pantr	8	
Iridaceae	*Sisyrinchium* sp.	G	TropAm	–	
Juncaceae	*Juncus* cf. *tenuis* Willd.	G	Cosm	–	
Liliaceae	*Anthericum* sp.	G	Cosm	–	
Liliaceae	*Nothoscordum* sp.	G	Am	–	

Table 5. – Bolivian Prepuna's most important plant families. Total number of species: 324. Total number of native species: 299.

a) All species *Family*	*n° spp*	*%*	*b) Native species* *Family*	*n° spp*	*%*
Compositae	55	17.0	Compositae	52	17.4
Gramineae	45	13.9	Cactaceae	41	13.7
Cactaceae	42	13.0	Gramineae	38	12.7
Bromeliaceae	27	8.3	Bromeliaceae	27	9.0
Leguminosae	19	5.9	Leguminosae	18	6.0
Solanaceae	10	3.1	Solanaceae	10	3.3
Verbenaceae	8	2.5	Verbenaceae	8	2.7
Amaranthaceae	7	2.2	Amaranthaceae	7	2.3
Chenopodiaceae	7	2.2	Nyctaginaceae	6	2.0
Nyctaginaceae	6	1.8	Convolvulaceae	6	2.0
Convolvulaceae	6	1.8	Chenopodiaceae	5	1.7
Zygophyllaceae	5	1.5	Malvaceae	5	1.7
Malvaceae	5	1.5	Zygophyllaceae	4	1.3
Euphorbiaceae	5	1.5	Caryophyllaceae	4	1.3

Table 6. – Phytogeographic elements (genera) of the Bolivian Prepuna.
a) Importance of genera given by the number of species possessed.
b) Without considering number of species included within each genus. For definitions of biogeographic elements, see Table 1.

(a) Category	*n° spp*	*%*	*(b) Category*	*n° spp*	*%*
Andean	77	26.1	Cosm	45	25.0
Cosm	70	23.7	Andean	39	21.7
TropAm	65	22.0	TropAm	35	19.4
Pantr	37	12.5	Pantr	27	15.0
Amphi	30	10.2	Amphi	21	11.7
Am	16	5.4	Am	13	7.2
TOTAL	295	100.0.	TOTAL	180	100.0

Compositae, *Cactaceae*, *Gramineae*, *Bromeliaceae* and *Leguminosae* are the most speciose families (Tables 4 and 5). The ranking is quite similar whether or not introduced species are considered in the analysis.

Andean elements share a greater percentage of the phytogeographic spectrum of genera, with a little more than a quarter of the species belonging to predominantly Andean genera (Tables 4 and 6a). Cosmopolitan and Tropical American genera rank second and third, respectively, not far from Andean elements. However, if all tropical elements (Tropical American and Pantropical) are summed up, this group becomes dominant (almost 35% of the species). If we examine relative proportions of genera without considering the number of species each genus possesses, cosmopolitans stand out as the most important group (one quarter of the genera), and Andean and Tropical American elements demonstrate lower relative proportions compared with the case

Table 7. – Phytogeographic elements (species) of the Bolivian Prepuna. See Table 2 for definitions.

All species *Category*	*n° spp*	*%*	*Native species* *Category*	*n° spp*	*%*
2	78	28.0	2	78	30.7
1	47	16.8	1	47	18.5
3	36	12.9	3	36	14.2
4	28	10.0	4	28	11.0
10	25	9.0	8	21	8.3
8	21	7.5	6	18	7.1
6	18	6.4	7	12	4.7
7	12	4.3	5	8	3.1
5	8	2.9	9	6	2.4
9	6	2.1			
TOTAL	279	100.0	TOTAL	254	100.0

Table 8. – Life form spectra (%) for the Bolivian Prepuna and other South American dry formations. Numbers in parenthesis refer to number of species. H = hemicryptophytes, S = succulents, T = therophytes, N = nanophanerophytes, C = chamaephytes, M = macrophanerophytes, E = epiphytes, G = geophytes, V = vines, P = (hemi)parasites, He = helophytes.

	H	*T*	*N*	*S*	*C*	*M*	*E*	*G*	*V*	*P*	*He*	*TOTAL*
Bolivian Prepuna (1)	19.6 (62)	18.3 (58)	18.0 (57)	16.4 (52)	7.6 (24)	6.6 (21)	5.4 (17)	4.7 (15)	2.5 (8)	0.9 (3)	– –	100.0 (317)
Bolivian Prepuna (native species) (1)	20.5 (60)	15.4 (45)	18.8 (55)	17.5 (51)	7.9 (23)	5.5 (16)	5.8 (17)	4.8 (14)	2.7 (8)	1.0 (3)	– –	100.0 (292)
Argentinean Prepuna (2)	29	18.5	28.2	8.1	8.1	2.4	3.2	2.4	–	–	–	100.0
Ñacuñán (3)	20	32	25	3	6	4	–	6	4	–	–	100.0
Llanos de la Rioja (3)	18	30	14	2	10	12	4	5	5	–	–	100.0
Coastal desert (4)	20.8	33.1	33.1	–	–	–	–	12.3	–	0.6	–	100.0
Argentinean Puna (2)	44.2	12.6	16.1	6.3	8.2	0.6	1.2	9.6	–	–	–	100.0
Argentinean Puna (5)	39.1	14.0	16.0	3.4	10.2	0.3	1.1	13.3	–	–	2.1	100.0

(1) This study
(2) RUTHSATZ & MOVIA (1975) AND RUTHSATZ (1977)
(3) ROIG (1971)
(4) ARMESTO & VIDIELLA (1993)
(5) CABRERA (1957)

where number of species is included (Table 6b). This suggests that these two groups either radiated more and/or had lower extinction rates than the other classes.

As to the species, exclusively Prepuna elements (class **2**) are by far the most important component with near to one third of the species (Table 7). Bolivian endemics are also conspicuous; the majority of these are not distributed outside the Bolivian Prepuna (twenty-nine out of fourty-seven) (Table 4). Most of the endemisms are Andean. Classes **1** and **2** contain almost 50% of all the species. The other elements of southern South America (classes **3** and **4**) are also worth mentioning. Each of the other classes contributes less than 10 percent of the species number.

The life form spectrum shows the dominance of hemicryptophytes, nanophanerophytes, succulents, and annuals in the vegetation of the Bolivian Prepuna (Table 8). Of these, only

Table 9. – Life form spectra for phytogeographic elements (%).
H = hemicryptophytes, S = succulents, T = therophytes, N = nanophanerophytes, C = chamaephytes, M = macrophanerophytes, E = epiphytes, G = geophytes, V = vines, P = (hemi)parasites.
See Table 1 for definitions of phytogeographical elements.

	H	*T*	*S*	*N*	*C*	*E*	*M*	*G*	*V*	*P*	*TOTAL*
Andean	–	5.3	61.8	25.0	3.9	–	2.6	1.3	–	–	100.0
TropAm	20.0	20.0	–	13.8	4.6	26.1	6.1	3.1	6.1	–	100.0
Cosm	33.3	27.5	–	20.3	7.2	–	1.4	5.8	2.9	1.4	100.0
Pantr	25.0	13.9	–	11.1	13.9	–	25.0	8.3	2.8	–	100.0
Amphi	33.3	10.0	–	30.0	16.7	–	–	6.7	3.3	–	100.0
Am	31.2	12.5	25.0	–	6.2	–	–	12.5	–	12.5	100.0

Table 10. – Distribution of phytogeographic elements among life forms (%).
H = hemicryptophytes, S = succulents, T = therophytes, N = nanophanerophytes, C = chamaephytes, M = macrophanerophytes, E = epiphytes, G = geophytes, V = vines, P = (hemi)parasites.
See Table 1 for definitions of phytogeographical elements.

	Andean	*TropAm*	*Cosm*	*Pantr*	*Amphi*	*Am*	*TOTAL*
H	–	21.7	38.3	15.0	16.7	8.3	100.0
S	92.2	–	–	–	–	7.8	100.0
T	8.7	28.3	41.3	10.9	6.5	4.3	100.0
N	34.5	16.4	25.4	7.3	16.4	–	100.0
C	13.6	13.6	22.7	22.7	22.7	4.5	100.0
G	7.1	14.3	28.6	21.4	14.3	14.3	100.0
M	12.5	25.0	6.2	56.2	–	–	100.0
V	–	50.0	25.0	12.5	12.5	–	100.0
E	–	100.0	–	–	–	–	100.0
P	–	–	33.3	–	–	66.7	100.0

annuals and trees increase in importance when exotic species are included, overtopping succulents and nanophanerophytes and becoming the second most important life form. If in the group of shrubs we incorporate that of small trees (M), which often take a shrubby growing form, the woody habit becomes the most important (one quarter of the species). In fact, most Prepuna vegetation is dominated by a woody physiognomy, which indicates the importance of small trees and shrubs also from the perspective of cover. The other life forms are represented by relatively low species numbers.

With regard to the relation between biogeographic elements and life forms (Table 9), hemicryptophytes, the most abundant life form, are important in all categories except the Andean. Annuals and shrubs are also more or less well represented in almost all classes. Annuals contribute little to the Andean elements. In turn, most of shrubs are Andean, as are the great majority of succulents (Table 10). Andean succulents are composed of endemics or exclusively Prepuna elements (classes **1** and **2**, respectively). Moreover, succulents also contribute significantly to the American elements (Table 9). Epiphytes make a substantial contribution to the Tropical American category (Table 9); in fact, all epiphytes are Tropical American (Table 10). However, all the species of *Tillandsia* come from a southern stock (classes **1** through **4**), as attested by distributional ranges of the species [see column of biogeographical elements (species), Table 4]. Finally, small trees are important for Pantropical elements.

Discussion

Floristic relations

From the perspective of genera, the Prepuna is dominated by a dry (sub-)tropical stock (the tropical elements together constitute 35% of the species). This points to the affinities that the Bolivian Prepuna has with the Chaco region. CABRERA (1976) mentioned the Chacoan origin of the Argentinean Prepuna. On the other hand, in the Prepuna the importance of Andean elements is remarkable, totaling more than a quarter of the species. This indicates the influence of the Puna region.

SARMIENTO (1975) found that the dry flora (genera) of South America presented a clear discontinuity in central Peru. His analysis holds when considering overall floristic relations or only genera of *Cactaceae*. In both cases, two groups appear: one, from central Peru northwards (the tropical dry areas); the other, from southern Peru, to Bolivia, Chile and Argentina (the subtropical or austral dry areas). Perhaps this separation recurs for more mesic plant formations as well. KESSLER & HELME (1999), when working in semideciduous forests in northwestern Bolivia, found that species composition of some plant families of those semidry plant formations have more in common with equivalent ecosystems in southern Bolivia, southern Brazil and northern Argentina than with those occurring in Peru and further north.

While at the generic level the distance between the Bolivian Prepuna and dry plant formations from northern South America does not seem to be as great as that found by SARMIENTO (1975) between northern and southern South American floras, nonetheless clear differences do exist. Of the one hundred and eighty-two native genera identified in this study (the unidentified *Verbenaceae* is excluded), fourty-five (one quarter of the total) are austral South American elements (Table 4). Herbs increase the similarity between Prepuna and northern South America floristic types given their generalist character (Tables 9 and 10). However, in his comparison, SARMIENTO (1975) principally considered woody taxa (succulents included). If only woody elements are selected from the list presented in this study (i.e., C, M, N and S), eighty-two genera are shown. Of these, thirty-four belong to the austral group. The exclusive austral elements now constitute 41.5% of the genera occurring in Prepuna, i.e., a considerable number of woody genera from the Bolivian Prepuna are really exclusive southern elements. If, as SARMIENTO did, only genera of Cactaceae are examined, the floristic difference between Bolivian Prepuna and the northern portions of the continent doubles: almost 80% of the cacti genera are exclusive austral elements. [From ARMESTO & VIDIELLA (1993)'s study, one hundred and twenty-three native genera can be extracted; of these fifty-six (45%) belong to austral South America. If only shrubs are considered, this value falls to little less than 40%. The isolation of this ecosystem induced rapid differentiation of taxa in all their life forms, including herbs.]

At the species level the discontinuity is very evident. The Bolivian Prepuna is unequivocally related to the dry flora of southern South America. By uniting classes **1**, **2**, **3** and **4** (the austral elements), three quarters of the species considered (naturalized species are excluded in this computation) are covered (Table 7). Notice the importance of class **2** (> 30% of native species), which underlines the strong connections of the Bolivian Prepuna with the driest parts of southern South America, mainly the Monte Desert and the Argentinean Prepuna.

SARMIENTO (1975) ascribes this discontinuity to the fact that there was a gap between forests from which South American tropical and subtropical (austral) dry areas arose. The semidry forests extending from southern Mexico to northern Peru would have given place to the tropical arid formations, and those of a subtropical-temperate character would have originated from subtropical dry forests like the Chaco. Similarly, CABRERA (1976) considers that the Chaco gave rise to the Prepuna, the Monte and other semiarid regions of southern South America.

But not only different floristic sources do explain this segregation of the flora; different climates as well (SARMIENTO, 1975). The tropical or thermally constant zone barely reaches 17-18 degrees of latitude in some Andean areas (SARMIENTO, 1986). In fact, from as far north

as central Bolivia (17°S) some seasonality can be felt: there exist a marked colder and very dry period in which below zero temperatures are recorded in mountainous regions at intermediate altitudes (1500-3000 m), the rest of the year being characterized by frost-free conditions. Therefore, different environmental conditions must have fostered the existence of more or less different floras.

At family level, the Prepuna shows the great importance of *Compositae*, *Cactaceae*, *Gramineae* and *Bromeliaceae* (Table 5). Composites and grasses are among the most important families in virtually all deserts; cacti and bromeliads characterize American deserts (SHMIDA, 1985). Moreover, the abundance of cacti in the Bolivian Prepuna is striking, even from a physiognomic point of view. No other phytogeographic unit or plant formation type in South America is similarly characterized by this family. If the Prepuna is compared with the Puna region, in the latter composites are even more abundant: 18 to 33% of all species belong to this family; grasses rank second, ranging from 12 to 19% (ARROYO & al., 1982, as cited in ARMESTO & VIDIELLA, 1993; OSTRIA, 1987; BECK & VALENZUELA, 1991; NAVARRO, 1992; VARGAS, 1992; IBISCH & ROJAS, 1994; LÓPEZ, 1996). Unlike Prepuna, in the Puna the *Cactaceae* have little importance and other families become more abundant: e.g., *Caryophyllaceae*, *Cruciferae*, *Scrophulariaceae*, among others. In the Puna, *Solanaceae* and *Leguminosae* may have relative proportions similar to those in the Prepuna, but, in the case of the latter family, most of the species belong to the subfamily *Faboideae*. Thus, floristically the dissimilarities are evident, with the Puna being more characterized by a floristic stock in which many temperate elements intrude.

Life forms

Bolivian Prepuna's life form spectrum is dominated by four habits (Table 8). Note that what most distinguishes this region, as compared to the others regions shown, is the importance of succulents (most of them *Cactaceae*). This could indicate the possibility of comparatively more reliable rainfalls. Cacti are more common in regions with more reliable, summer precipitation (SHMIDA & al., 1985; MOURELLE & EZCURRA, 1996). If, on the other hand, nano- and macrophanerophytes are united (a more realistic option since the latter category, taxa, normally adopt a shrubby appearance), the Bolivian Prepuna life form spectrum generally matches that of the Argentinean Prepuna. The preponderance of woody elements in dry formations in South America is a fact already emphasized by ARROYO & al. (1988, 1993). Compared to the Monte Desert in Ñacuñán and a dry formation in La Rioja (both in Argentina), it is noted that annuals are more important and succulents very scarce in the Argentinean formations. As to the other life forms, there are strong similarities in the relative proportions.

The life form spectrum differs from that of the coastal desert in central Chile in much the same way as it does in the Ñacuñán and La Rioja cases. The coastal desert differs also from the continental South American deserts in that geophytes are clearly more important and succulents absent in the former. Shrubs are apparently also better represented in Chile, but in this case true shrubs are put together with small ones (chamaephytes), and this confuses the comparison. At a more distant similarity level is the dry Puna. Here, hemicryptophytes and geophytes are proportionally much greater, and succulents, annuals, and shrubs are less well represented. The different biological spectra of Puna and Prepuna shows the great climatic differences of these two arid zones: the first a cold desert; the second, a hot one.

The relative importance of annuals in the Prepuna flora is less than in other deserts. As in the case with the coastal desert in Chile, annuals increase in importance a little when exotic species are included in the analysis. It seems, however, that therophytes are not only scarcer in the Prepuna but in South America in general. Exceptions exist in the extreme southern portion of the coastal desert in Chile in which annuals constitute more than 60% of all the species present (ARMESTO & al., 1993) and in certain dune habitats in parts of the Monte desert with a representation of annuals of up to 46% (ROIG, 1971). Values for other world deserts indicate relative

proportions of therophytes ranging from 40 to 70% (ORSHAN, 1986; KEMP, 1989; VENABLE & al., 1993).

Importance for conservation

Despite its floristic and vegetational singularity, the Prepuna region in Bolivia and, as far as I know, Argentina, lacks even a small protected area. This forgotten ecological region presents many endemisms, especially among the *Cactaceae* (all the family is included in the CITES) and *Bromeliaceae*. In fact, almost all the species of succulents considered here are endemic to Bolivia or to the whole Prepuna floristic region (including Argentina). These two families also have very important endemism levels in other dry areas (although more mesic than Prepuna) of Bolivia (KESSLER & al., 1998). The as yet incomplete knowledge of the Bolivian Prepuna should stimulate the implementation of more floristic (and ecological) studies there. The Bolivian Prepuna presents large areas still well preserved that could be studied to better understand summer-rain deserts structure and dynamics.

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Address of the authors: RPL and SB: Herbario Nacional de Bolivia, Campus Universitario, calle 27, Cotacota s/n, La Paz, Bolivia.

RPL, also: Casilla (PO Box) 3-35121, La Paz, Bolivia. E-mail: rplopez@ceibo.entelnet.bo