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THE ARID AND DRY PLANT FORMATIONS OF SOUTH AMERICA AND THEIR FLORISTIC CONNECTIONS: NEW DATA, NEW INTERPRETATION?

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Abstract. López, R. P., D. Larrea Alcázar & M. J. Macía. 2006. The arid and dry plant formations of South America and their floristic connections: new data, new interpretation? *Darwiniana* 44(1): 18-31.

In this study we aimed at testing two hypothesis about the biogeography of South America: (1) the existence of a marked discontinuity in the Andes of central Peru that separates the floras of northern and southern South America and (2) the occurrence of a more or less continuous semi-deciduous forest in South America during the Pleistocene. We conducted a search for different sources of published information on the flora (inventories) of 19 dry regions in South America as well as one region in Central America and another in North America. In order to analyze the data, we employed ordination and classification techniques, which give a more objective picture of the phytogeographical relationships. Additionally, we evaluated similarity scores between the regions. We found 1,421 woody and herbaceous genera for the 21 regions. These regions form two groups: one mostly in northern South America and the other one restricted to the southern half of the hemisphere. Within the latter, further subdivisions are discernible. Almost all the northern group is made up of tall, deciduous and semi-deciduous forest types. The southern group regions mainly range from very dry forests to desert scrub. Our results support the existence of a floristic discontinuity in relation to the drier flora of the Andes. The southern flora (from southern Peru to northern Argentina and Chile) constitutes a floristic group quite different from that of northern South America. The Chaco region, although more floristically related to the southern group, seems to constitute the connecting link between these northern and southern floras. Within the flora of southern South America, the coastal desert seems to be the connection between hot and cold semi-deserts. Our data also support the hypothesis of the existence of pleistocenic lowland forests in most parts of South America which, however, probably extended up to Mexico.

Keywords. Dry floras, floristic discontinuity, northern flora, pleistocenic lowland forest, southern flora, Andes, Chaco.

Resumen. López, R. P., D. Larrea Alcázar & M. J. Macía. 2006. Las formaciones vegetales áridas y secas de Sudamérica y sus conexiones florísticas: nuevos datos, ¿nueva interpretación? *Darwiniana* 44(1): 18-31.

En este estudio nos trazamos el objetivo de poner a prueba dos hipótesis sobre la biogeografía sudamericana: (1) la existencia de una marcada discontinuidad en los Andes del centro de Perú que separa las floras del norte y sur de Sudamérica y (2) la existencia de un bosque semideciduo más o menos continuo en Sudamérica durante el Pleistoceno. De esta manera, intentamos profundizar nuestra comprensión de las relaciones de la flora sudamericana. Realizamos una búsqueda de diferentes fuentes de información publicada sobre las floras (inventarios) de 19 regiones secas de Sudamérica así como una de Centroamérica y otra de Norteamérica. A fin de analizar los datos, empleamos técnicas de ordenación y clasificación, las cuales brindan información más objetiva sobre las relaciones fitogeográficas. Además, evaluamos índices de similitud entre las regiones. Encontramos 1.421 géneros leñosos y herbáceos en las 21 regiones. Éstas forman dos grupos: uno mayormente en el norte de Sudamérica y el otro restringido a la mitad austral del continente. Dentro del último se pueden distinguir ulteriores subdivisiones. Casi todo el grupo norteño está compuesto por bosques altos, semideciduos. Las regiones

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del grupo sureño van de bosques muy secos a matorral desértico. Nuestros resultados apoyan la existencia de una discontinuidad florística en relación con la flora seca andina. La flora sureña (del sur de Perú al norte de Argentina y Chile) constituye un grupo florístico bastante diferente del presente en el norte de Sudamérica. El Chaco, aunque florísticamente más afín al grupo del sur, parece constituir el nexo de conexión entre las floras norteña y sureña. Dentro de la flora de Sudamérica, el desierto costero parece conectar a los semidesiertos calientes y fríos. Nuestros datos también respaldan la hipótesis de la existencia de bosques pleistocénicos de tierras bajas en la mayor parte de Sudamérica. Posiblemente estos se extendieron incluso hasta México.

Palabras clave. Floras secas, discontinuidad florística, flora norteña, bosque pleistocénico de tierras bajas, flora sureña, Andes, Chaco.

INTRODUCTION

Different dry plant formations occur disjunctly from Argentina and Chile in South America to Mexico in North America. They contain a high biological diversity, both in species richness and endemism as well as in life forms. These zones span from true deserts and semi-desert shrublands through deciduous forests with a severe dry season in winter to evergreen forests with a strong summer drought (mediterranean-type forests). Although some of these dry regions are separated by thousands of kilometers and show different climatic conditions, they nonetheless show suggestive floristic connections that seem to point to a common history of contacts and divergences.

A number of studies have addressed the distribution of South America's dry biomes. Here we are interested in two approaches with major significance for the biogeography of South America: the hypothesis of Sarmiento (1975), on the one hand, and of that of Prado & Gibbs (1993), Prado (2000), and Pennington et al. (2000), on the other.

Sarmiento (1975) made a first attempt to determine the degree of interrelations of different South American dry regions. His most important conclusion was that there existed a floristic discontinuity in the Peruvian Andes, one that separated a northern, tropical South American flora from a southern, more temperate one. The second hypothesis by Prado and Gibbs (1993) proposed the existence of semideciduous forests in the lowlands of Pleistocenic South America, relicts of which would even extend into the southern part of the continent. Later, Prado (2000) even suggested that it should be given a more concrete biogeographical status: the tropical seasonal forests region which includes three provinces. The possible existence of these pleistocenic, deciduous forests was later extended to most of the Neotropic (Pennington et al. 2000). These forests would have occupied regions which today are covered by Amazonian tropical rain forest vegetation. At present, the seasonal formations are found in fragmented patches distributed in different parts of the continent.

The aims of this paper are twofold: to test the two hypothesis mentioned above and to evaluate the general biogeographical patterns in dry plant formations of South America.

METHODS

Data collection

We conducted a search for different sources of published information on the flora of dry regions of South America as well as one region in Central America and another one in North America. This analysis was undertaken at the level of genera (see, for example, Sarmiento (1975) and Prado (2000) for similar analysis) because the comparisons were at a continental level, where the affinities of the species can be presumed as very weak. A comparison at the generic level gives more meaningful results because 1) the number of common genera is high enough to allow statistical analyses, 2) it implies greater taxonomic reliability (many species have uncertain status), and 3) the analysis is placed under wider evolutionary perspective (Sarmiento 1975). Moreover, more complete inventories can be obtained at the genus level. The dry regions are understood as all those spanning from true deserts up to deciduous and semi-deciduous forests with a severe dry season lasting many months. The Cerrado, in which sometimes woodlands occur, was not included as

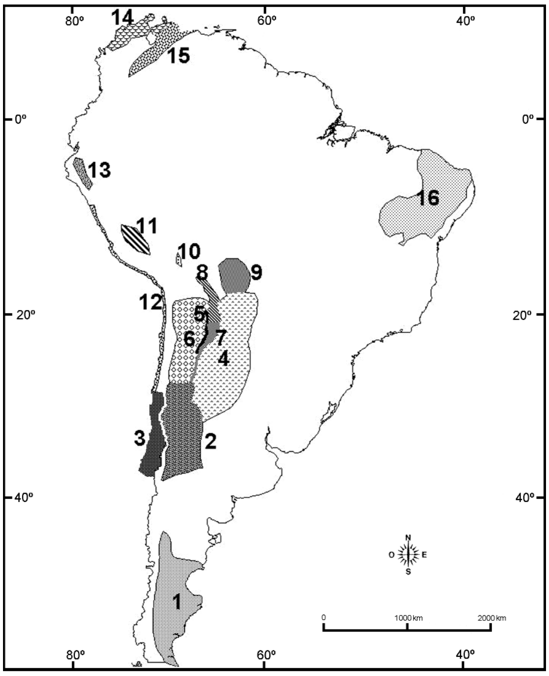

Fig. 1. The South American regions considered in this study. Areas are roughly delimited to only provide a general idea of their loctation and spatial relantionships. 1, Patagonia; 2, northern Monte Desert; 3, mediterranean region of Chile; 4,Chaco; 5, Prepuna; 6, arid Puna; 7, Argentinean Chaco Serrano; 8, Bolivian Chaco Serrano; 9, Chiquitania; 10, deciduous forests of northern La Paz; 11, dry Andean valleys of southern Peru; 12, coastal desert; 13, deciduous forests of northern Peru; 14, Guajira; 15, Venezuelan deciduous forests; 16, Caatinga.

it belongs mainly to the savanna vegetation types, which have different ecology and biogeography.

The regions considered (Fig.1) and the main sources of information were as follows acronyms as used in ordination graph appear beside name; number of genera included for the regions appear at the end of each description).

Deciduous and semi-deciduous forests

Chiquitania (**CHIQUITA**) (tropical deciduous forests of lowland Bolivia): Gentry (1993a, b), Saldías (1991), Killeen et al. (1998); 181 genera are included.

Deciduous forests of northern La Paz, Bolivia (**TUICHI**) (Tuichi, Machariapo, etc.; tropical forests occurring at intermediate altitudes in the Andes of central-northern Bolivia): Kessler & Helme, 1999; 279 genera.

Argentinean Chaco Serrano (**SERR ARG**) (one of Cabrera's (1976) biogeographical provinces): Cabrera (1976), Novara (1985); 350 genera.

Bolivian Chaco Serrano (**SERR BOL**) (known locally as the dry inter-Andean valleys): López (2003a); 497 genera.

Chaco Serrano of Cochabamba (**COCHAB**) (a drier and colder division of the Bolivian Chaco Serrano, occurring at higher altitudes-above 2400 m): Pedrotti et al. (1988), Ibisch & Rojas (1994), de la Barra (1998); 220 genera.

Dry Andean valleys of southern Peru (**PERU SOU**): Weberbauer (1948); 243 genera.

The Chaco (**CHACO**): Cabrera (1976), Hueck (1978), Ramella & Spichiger (1989), Spichiger et al. (1991), Prado (1993a, b), Navarro (2002); 207 genera.

Argentinean Chaco (**CHACO AR**) (the southernmost division of the Gran Chaco): Morello (1958), Cabrera (1976), Hueck (1978); 107 genera.

Caatinga (**CAATINGA**): Cabrera & Willink (1973), Hueck (1978), Schnell (1987), Prado & Gibbs (1993), Sampaio (1995), Pennington et al. (2000); 140 genera.

Venezuelan deciduous forests (**VENEZUEL**): Gentry (1982), Hueck (1978); 83 genera.

Deciduous forests of northern Peru (**PERU NOR**) (both Andean and lowland; includes Andes of Ecuador): Weberbauer (1945), Acosta-Solís (1968), Bridgewater et al. (2003); 227 genera.

Chilean dry mediterranean forests (**CHILE ME**): Cepeda et al. (2000); 145 genera.

Chamela deciduous forest, México (**CHAMELA**): Lott (1985); 430 genera.

Guanacaste, Costa Rica (**GUANACAS**): Gentry (1982); 72 genera.

Semi-desert shrublands

Prepuna (**PREPUNA**): Ruthsatz (1977), López & Beck (2002); 198 genera.

Arid Puna of southern Bolivia and northern Chile (**PUNA**): Navarro (1993), Teillier (1998); 134 genera.

Sonoran desert, Vizcaíno, México (**SONORA**): León de la Cruz et al. (1995); 248 genera.

Monte Desert (**MONTE**): Morello (1958), Roig (1980); 168 genera.

Patagonia (**PATAGONI**): Cabrera (1976); 111 genera.

Guajira scrubland of Venezuela/Colombia (**GUAJIRA**): Cabrera & Willink (1973), Hueck (1978), Rico et al. (1996); 124 genera.

Deserts

Coastal desert of Atacama (**COAST DE**): Rundel et al. (1991); 169 genera.

These 21 regions belong to different biogeographical hierarchies. Many of these are indeed biogeographical regions: Chaco, Caatinga, mediterranean Chile, Prepuna, Monte desert, Patagonia, Guajira, and coastal desert of Atacama. Others are major divisions of biogeographical regions: Bolivian and Argentinean Chaco Serrano, Argentinean Chaco, Venezuelan deciduous forests, Chamela, Guanacaste, dry Puna, Vizcaíno Sonoran Desert. The remaining have uncertain status, but could eventually qualify as subregions as well (Chiquitania, deciduous forests of northern La Paz, dry valleys of southern Peru, deciduous forests of northern Peru and even the Chaco Serrano of Cochabamba). This heterogeneity in the data set is inevitable as surveys of uniform methodology do not exist over such a wide geographic range and diversity of vegetation types. Further, there is still incomplete knowledge about many ot South America's floras, and thus an absence of a totally accepted biogeographical zonation of South America. Finally, the floristics lists of levels below the biogeographical region are included precisely because a comparison of their genus flora with other regions can shed light about their true floristic affinities.

Data analysis

Detrended Correspondence Analysis (DCA) is used to evaluate floristic relations across South America's dry regions. This ordination technique is more reliable for analysis of wide community gradients (Ludwig & Reynolds 1988). The analysis was carried out both for all present genera and for only the woody genera. In order to verify if some of the families gave way to similar patterns to those based on whole floras, the analysis was also conducted for three families which are among the most important in xeric regions: Leguminosae, Cactaceae, and Compositae. In such a case, any family with such characteristics could be used to predict relationships between other xeric regions, thus avoiding the need for complete floristic lists. In all cases, the default settings were used, i.e., axes were rescaled with a threshold of zero and the number of segments was 26.

It is recommended that more than one methodology be employed in order to verify the results of the first analysis (McCune & Grace 2002). Thus, we also evaluated the data through another ordination method, non-metric multidimensional scaling (NMS), and also through a classification method, TWINSPAN. In the case of NMS, the Sorensen (Bray-Curtis) method for distance measures was used. The maximum number of iterations was 400, the instability criterion was 0.0001, the number of real runs was 40, and randomized runs were 50. Finally, in order to make a direct floristic comparison between the dry regions studied, a similarity matrix between them was built using the Jaccard index. PC_ORD 4.10 (McCune & Mefford 1999) was used in all ordination and classification analyses.

RESULTS

We found 1,421 woody and herbaceous genera for the 21 neotropical regions, thus cosiderably improving the resolution level of the analysis as compared to Sarmiento's (1975) study (which encompassed 343 genera of primarily woody genera).

Fig. 2 shows the position of the 21 dry neotropical regions along axes 1 and 2 and 1 and 3 of the DCA ordination. Ordination conducted across all genera (1,421) showed that the cumulative percentage variance accounted for by axes 1 and 2 was 65% and 36%, and 65% and 23% when axes 1 and 3 were compared. Gradient length for axis 1 was 5.2, suggesting a good and coherent ordination.

Fig. 3 shows the position of the 21 dry neotropical regions along axes 1 and 2 and 1 and 3 when only the woody taxa (628 genera) were considered on the DCA ordination. The ordination carried out showed that the cumulative percentage variance explained by axes 1 and 2 was 63% and 36%, and 63% and 18% for axes 1 and 3. Gradient length for axis 1 was 5.1 showing a consistent ordination.

Finally, Figs. 4 and 5 show the results of DCA ordination undertaken only with Leguminosae (119 genera) and Compositae (154 genera), respectively. In the case of Leguminosae, the cumulative percentage variance accounted for by axes 1 and 2 were 53% and 26%, and 53% and 19% for axes 1 and 3. Gradient length for axis 1 was 4.2, suggesting a relatively good ordination. For the Compositae, the cumulative percentage variance explained by axes 1 and 2 were 66% and 49%, and 66% and 31% for axes 1 and 3. In this case, gradient length for axis 1 was 6.4, showing a good ordination; nevertheless, a strong tendency to arch distortion was observed in the ordination graphs. This suggests incongruence of the ordination method when only Compositae genera are analyzed. The ordination with Cactaceae (67 genera) did not show clearly discernible patterns, and is not presented here. With exception of the Compositae ordination, no arch distortion was observed showing independence of the second or third axis relative to the first axis.

A similar pattern was found in the DCA ordination of the 21 neotropical regions for all species (Fig. 2) or woody plants (Fig. 3), and even for the two families: Leguminosae (Fig. 4) and Compositae (Fig. 5) on their own. Two big clusters stand out: a group of northern South America and another one in the southern part of the continent (thereafter called northern and southern groups, respectively). We also observe this pattern when the first and third axes are analyzed (Figs. 2, 3). The groups are more evident along axis one. To the northern group belong the Caatinga, Guajira, Tuichi, Chiquitania, northern Peru, Venezuelan deciduous forests, and even Guanacaste and Chamela. In the second cluster appear Chaco Serrano, southern Peru, the Monte, the Prepuna, the coastal desert, the mediterranean forests of central Chile, the Puna, and Patagonia.

In the southern flora, there is a clear division between hot dry forests/semi-deserts (Chaco Serrano, southern Peru, Monte, Prepuna) from mediterranean formations and cold semi-deserts (central Chile, Puna, Patagonia). The coastal desert lies somewhere between the hot and cold types. The subgroup of Argentinean and Bolivian Chaco Serrano and southern Peru is quite consistent over all the ordinations, as is the one formed by the Monte, Prepuna and, possibly, the coastal desert. These two subgroups could unite to form a higher biogeographical unit. As for the second subgroup, the Patagonia and the Puna are never very close together.

Coincidentally, NMS and TWINSPAN reveal a very similar phytogeographical configuration as well: the two main groups (northern and southern floras) and the subdivisions within the southern group. Fig. 6 shows the NMS graph. In axis 1, the stress mean value in real data (40 runs) was 44.9 (15.7 - 54.87, min - max), while randomized data (50 runs) was 51.9 (44.7 - 54.9). In axis 2, the stress mean value in real data was 11.3 (9.1 - 37.5), while the stress mean in randomized data was 28.8 (26.6 - 32.1), suggesting a two-dimensional solution for our ordination. In fact, the cumulative percentage variance accounted for by axes 1 and 2 were 63% and 19%, which suggests a good ordination.

The subunits which were evaluated separately (Cochabamba and Argentinean Chaco) did not depart much from the general pattern of their corresponding regions. If anything, they lay closer to more arid types (the Chaco closer to the Monte desert and Cochabamba nearer the Prepuna; Figs. 2, 3).

Contrary to the southern group, in northern and central South America no subgroups are clearly noticeable in the case of the all-species list. However, for the case of woody genera, Guanacaste, the Venezuelan deciduous forests, and Chamela occur close together (axes 1-2), which is no surprise given their proximity and similar climate (Figs. 3 and 6). Guajira, however, while more or less related to this group, is somehow isolated. Its much drier climate undoubtedly accounts for much of the difference with its northern neighbours. Its closest affinity, as shown by the similarity index, is with the Chaco and Chamela (0.25 and 0.23, respectively). Northern Peru appears in all of the ordinations separated from all other northern regions.

Finally, Table 1 shows Jaccard indexes for the

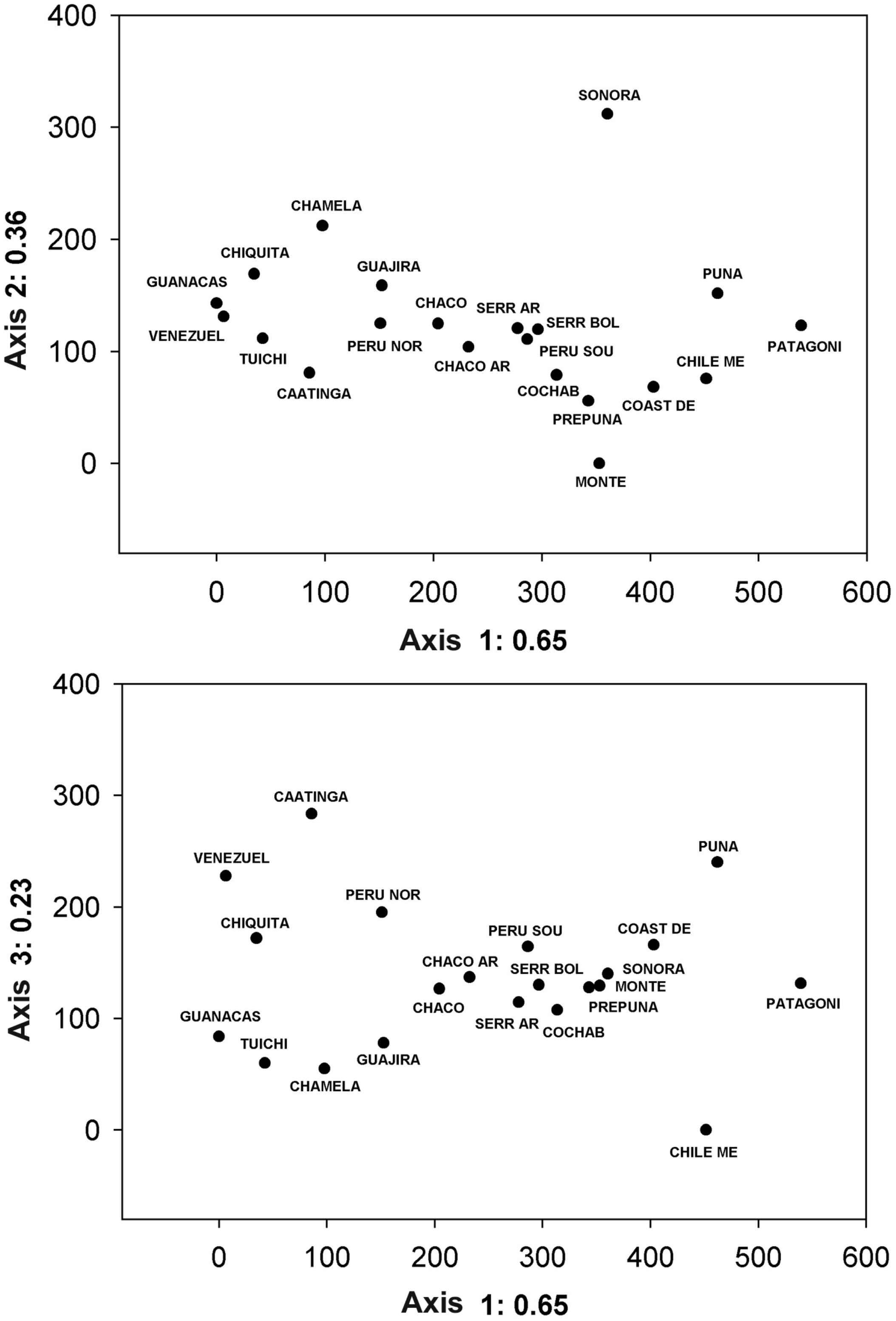

Fig. 2. Ordination graphs of the 19 dry regions plus two sub-regions considered in this study based on 1241 gene-

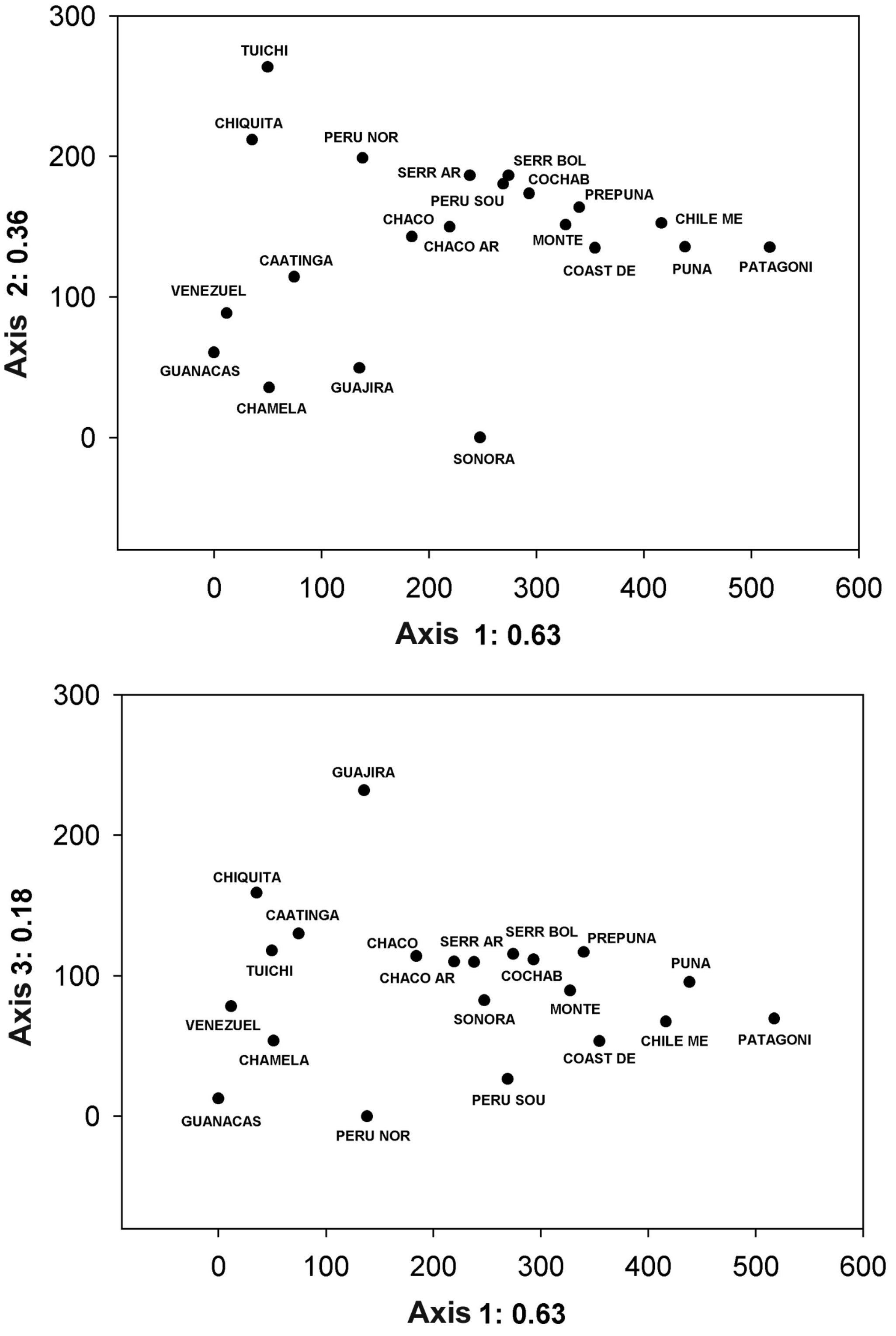

Fig. 3. Ordination graphs of the19 dry regions plus two sub-regions considered in this study based on 628 woody genera.

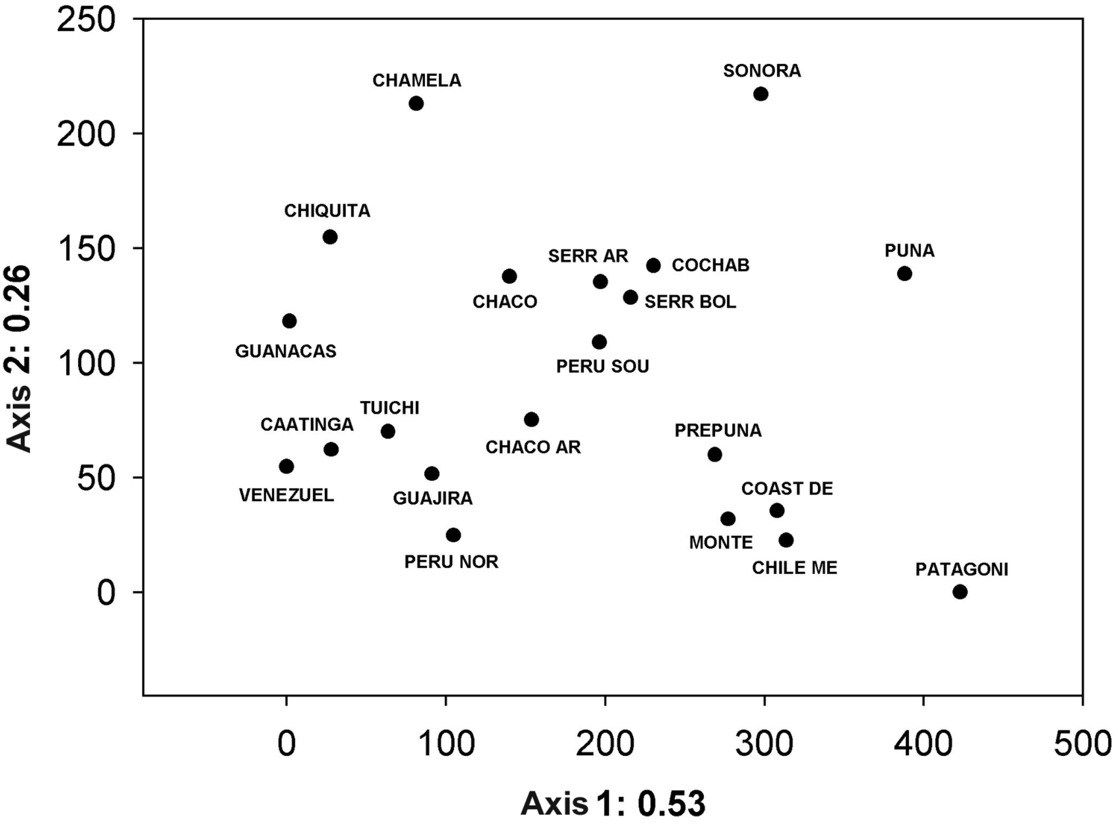

Fig. 4. Ordination graph of the 19 dry regions plus two sub-regions considered in this study based on 119 genera of legumes. Only axes 1 and 2 are shown.

woody genera of 21 dry neotropical regions, which were recorded between zero, for Patagonia with Guanacaste and Venezuelan deciduous forests, to 0.59 for Argentinean and Bolivian Chaco Serrano. The higher the value, the stronger the similarity.

DISCUSSION

The dry flora of South America appears separated in two main groups. The disjunction found in the present study between northern and southern floras supports Sarmiento's (1975) conclusion of the existence of a floristic discontinuity in the Andes of central/southern Peru. This assertion has also been backed by other studies (e.g., Gentry, 1995; Kessler & Helme, 1999; Linares-Palomino et al., 2003; López 2003b). However, this separation would apply mainly to the drier vegetation types, as some vegetation zones more similar to the northern group penetrate into the southern neotropics as well, along the Andes foothills in Bolivia and northwest Argentina and in northeastern Argentina and southern Brazil (Hueck 1978; Brown et al. 1985; Prado & Gibbs 1993), favoured by the orographic effect of the Andes which promote more rain in an otherwise dry climate. To the northern group belong principally the more mesic, taller, semi-deciduous forests of the kind described by Murphy & Lugo (1986) or Gentry (1995). The exception are the drier Guajira-type scrub and other semi-arid plant formations occurring in dry valleys of Ecuador and Colombia. Failure to spot affinities between regions within this group is due in great part to the more incomplete floristic lists for Guanacaste, Guajira, and Venezuelan deciduous forests. No doubt these regions possess many more genera, but we were unable to

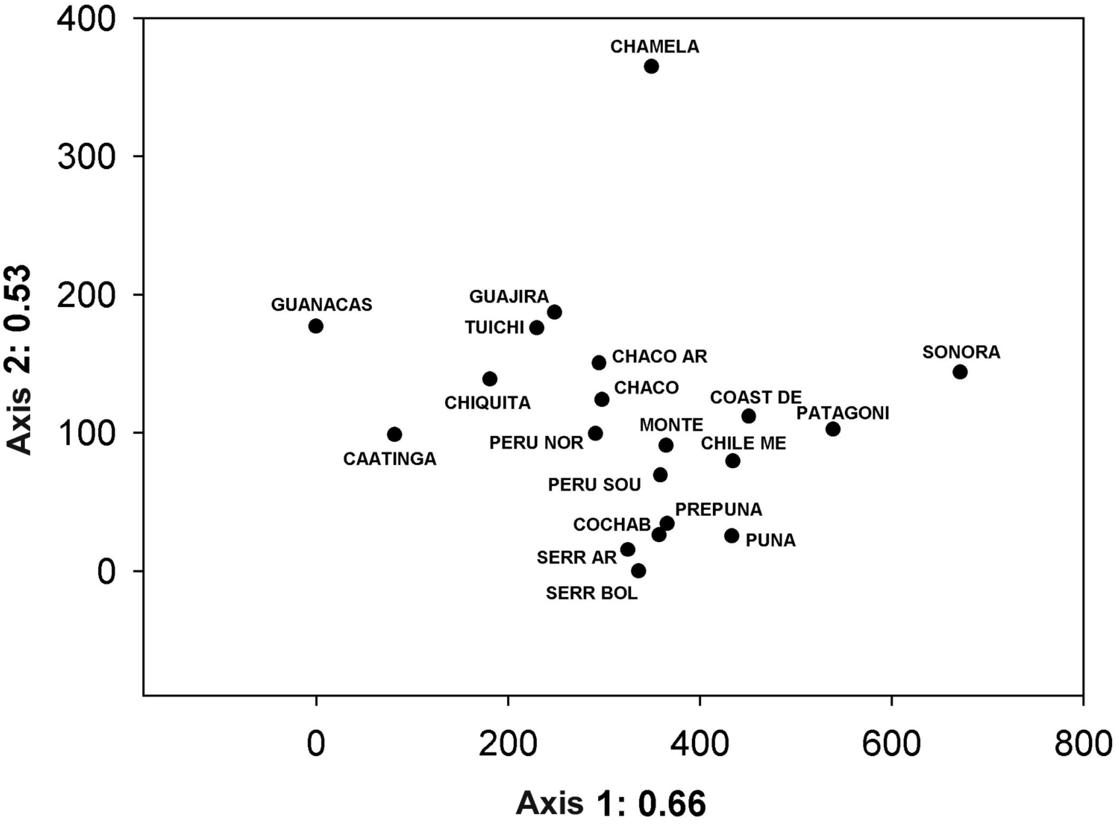

Fig. 5. Ordination graph of the 19 dry regions plus two sub-regions considered in this study based on 154 compositae genera. Only axes 1 and 2 are shown. No Compositae genera appeared in the lists of deciduous forests of Venezuela employed in this work.

find more information regarding their flora. The Venezuelan deciduous forests, for example, are floristically very similar to the Chamela forests of Mexico and both contain similar number of genera (G. Sarmiento, personal communication). Nevertheless, in spite of the differences in their botanical information, both dry regions showed consistent floristic affinities in our ordinations (Figs. 2-6).

The southern group regions mainly range from very dry, temperate forests to desert scrub. Exceptions are certain more mesic parts of Chaco Serrano (sometimes referred to as humid Chaco Serrano), but these medium-height forests are located at higher altitudes than any other regions in the northern group. Most of the northern group tends to be located nearer the equator, where more mesic conditions prevail. Thus, different precipitation and relative humidity conditions would partly explain this floristic division, but the crucial difference amongst them consists of the much colder conditions in the southern group, since its members are not only located at higher latitudes but also, generally, at higher altitudes.

The results of the present study support the hypothesis of the existence of semi-deciduous forests in most of South America (and the Neotropic in general) in glacial periods of the Pleistocene (the northern group). Prado (2000) lists many genera that are exclusive or almost exclusive of these deciduous forests. Hence, the high affinities between Tuichi and Chiquitania in Bolivia with Chamela in Mexico stand as one of the most remarkable facts supporting this statement. This shows that distance is not always an indicator of dissimilarity, as is suggested by de Oliveira & Nelson (2001) for the Brazilian rain forests. Several taxa mentioned in Prado & Gibbs's (1993) are

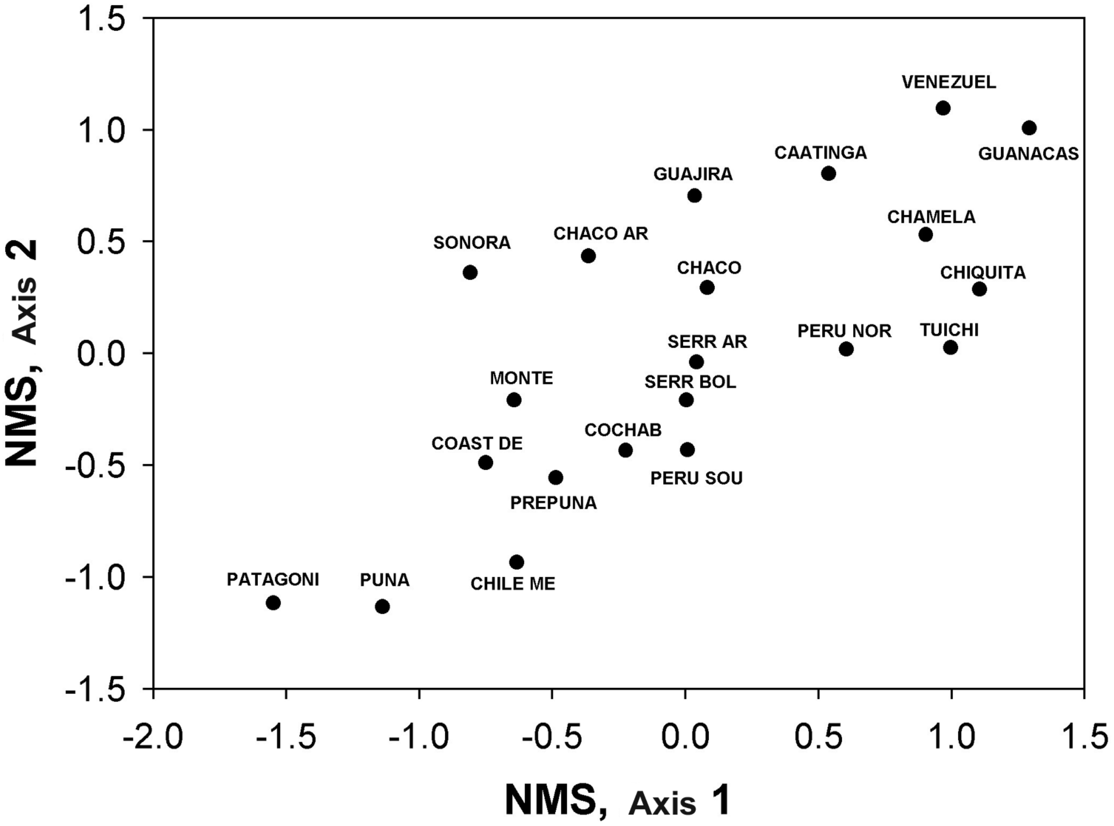

Fig. 6. Results of non-metric multidimensional analysis. Only the case for woody genera (axes 1-2) is shown as it is based on more complete lists for all 21 regions.

involved as common elements of these more mesic, disjunct forests (e.g., *Anadenanthera*, *Astronium*, *Enterolobium*, *Phyllostylon*, etc.), but there are still more. Moreover, as no genera with amphitropical distributions are implicated in these affinities, this huge semi-deciduous plant formation would have had stronger floristic connections than previously thought, sharing many other genera and even some species. The distribution of these deciduous forests would have paralleled today's distribution of the neotropical rain forests which exhibit similarities from Bolivia to southern Mexico. It is interesting, in this connection, to notice that some elements contributing to the similarity of deciduous forests of the northern group throughout most of their range are genera of humid forest types too (e.g., *Cordia*, *Nectandra*, *Dalbergia*, *Strychnos*). These Amazonia-related elements are absent from the southern group. It seems plausible to unite these seasonal forests into a high rank phytogeographical unit (Prado 2000) but, because of their apparently greater geographical extent, it can be postulated that more provinces than the three originally proposed would compose this region.

The Chaco seems to connect the southern and northern floras as it shares different sets of genera with both groups. Nonetheless, its strongest affinities are with the southern group (Chaco Serrano and the Monte, Table 1), as expected given its geographical location (which entails a different climate; for example, frosts in winter, compared with the tropical northern group). It appears that the Chaco (and not central Chile or the sierra formation as Sarmiento (1975) had found; as a matter of fact, the true Chaco is absent from Sarmiento's analysis) constitutes the link between the northern and southern groups (i.e., it shows more or less strong generic affinities with both). The Chaco is related to the southern group

Table 1. Similarity matrix of the woody genera in the 21 dry to arid regions of the Neotropic. Jaccard index.

	chiquitania	sonora	chamela	coastdes	chilemed	perusouth	guanacaste	venezuela	chacoarg	cochab	patagonia	caatinga	tuichi	perunorth	serrarg	serrbol	prepuna	monte	puna	guajira	chaco
chiquitania	1	0,078	0,273	0,06	0,05	0,103	0,193	0,215	0,12	0,111	0,005	0,251	0,352	0,218	0,191	0,152	0,063	0,077	0,016	0,131	0,235
sonora	0,078	1	0,148	0,19	0,123	0,183	0,042	0,058	0,175	0,176	0,093	0,102	0,092	0,111	0,183	0,166	0,182	0,192	0,136	0,214	0,181
chamela	0,273	0,148	1	0,066	0,034	0,142	0,223	0,23	0,092	0,13	0	0,207	0,267	0,221	0,185	0,176	0,08	0,072	0,022	0,229	0,188
coastdes	0,06	0,19	0,066	1	0,33	0,237	0,033	0,037	0,155	0,295	0,159	0,075	0,077	0,086	0,209	0,207	0,296	0,296	0,188	0,132	0,128
chilemed	0,05	0,123	0,034	0,33	1	0,189	0,029	0,033	0,115	0,227	0,231	0,061	0,058	0,099	0,168	0,186	0,276	0,252	0,217	0,085	0,108
perusouth	0,103	0,183	0,142	0,237	0,189	1	0,052	0,077	0,167	0,358	0,086	0,139	0,131	0,3	0,317	0,42	0,342	0,236	0,135	0,184	0,193
guanacaste	0,193	0,042	0,223	0,033	0,029	0,052	1	0,322	0,074	0,033	0	0,195	0,153	0,142	0,095	0,067	0,027	0,038	0	0,147	0,134
venezuela	0,215	0,058	0,23	0,037	0,033	0,077	0,322	1	0,099	0,056	0	0,269	0,19	0,189	0,117	0,084	0,038	0,041	0,008	0,157	0,15
chacoarg	0,12	0,175	0,092	0,155	0,115	0,167	0,074	0,099	1	0,165	0,065	0,181	0,111	0,152	0,315	0,21	0,172	0,34	0,054	0,197	0,56
cochab	0,111	0,176	0,13	0,295	0,227	0,358	0,033	0,056	0,165	1	0,107	0,116	0,141	0,17	0,399	0,465	0,457	0,289	0,181	0,161	0,195
patagonia	0,005	0,093	0	0,159	0,231	0,086	0	0	0,065	0,107	1	0	0,014	0,019	0,058	0,077	0,155	0,191	0,298	0,027	0,043
caatinga	0,251	0,102	0,207	0,075	0,061	0,139	0,195	0,269	0,181	0,116	0	1	0,175	0,213	0,216	0,18	0,088	0,102	0,02	0,22	0,231
tuichi	0,352	0,092	0,267	0,077	0,058	0,131	0,153	0,19	0,111	0,141	0,014	0,175	1	0,262	0,228	0,184	0,087	0,102	0,024	0,156	0,184
perunorth	0,218	0,111	0,221	0,086	0,099	0,3	0,142	0,189	0,152	0,17	0,019	0,213	0,262	1	0,262	0,269	0,143	0,121	0,033	0,198	0,224
serrarg	0,191	0,183	0,185	0,209	0,168	0,317	0,095	0,117	0,315	0,399	0,058	0,216	0,228	0,262	1	0,586	0,282	0,289	0,093	0,212	0,372
serrbol	0,152	0,166	0,176	0,207	0,186	0,42	0,067	0,084	0,21	0,465	0,077	0,18	0,184	0,269	0,586	1	0,387	0,249	0,137	0,182	0,304
prepuna	0,063	0,182	0,08	0,296	0,276	0,342	0,027	0,038	0,172	0,457	0,155	0,088	0,087	0,143	0,282	0,387	1	0,411	0,28	0,15	0,186
monte	0,077	0,192	0,072	0,296	0,252	0,236	0,038	0,041	0,34	0,289	0,191	0,102	0,102	0,121	0,289	0,249	0,411	1	0,191	0,147	0,281
puna	0,016	0,136	0,022	0,188	0,217	0,135	0	0,008	0,054	0,181	0,298	0,02	0,024	0,033	0,093	0,137	0,28	0,191	1	0,045	0,05
guajira	0,131	0,214	0,229	0,132	0,085	0,184	0,147	0,157	0,197	0,161	0,027	0,22	0,156	0,198	0,212	0,182	0,15	0,147	0,045	1	0,253
chaco	0,235	0,181	0,188	0,128	0,108	0,193	0,134	0,15	0,56	0,195	0,043	0,231	0,184	0,224	0,372	0,304	0,186	0,281	0,05	0,253	1

by a set of genera which is different from the genera which unite it to the northern group. Thus, the Chaco does not seem to be as distantly related floristically to the northern group as implied elsewhere (e.g., Sarmiento 1975; Pennington et al. 2000), at least from a genus perspective, although these affinities are stronger with the drier types of northern South America (Guajira). At the species level, instead, the Chaco possesses a distinct flora (Prado, 1993a, b; Navarro, 2002). Some genera of the southern group (e.g., *Schinopsis*) may have evolved from an ancient Chaco floristic stock (Solbrig, 1976). Other austral elements probably appeared in connection with the rising of the Andes but could not migrate north and now are exclusive elements of the southern group (e.g., *Aphyllocladus*, *Athyanna*, *Kentrothamnus*, *Morella*, as well as several cacti genera).

Leguminosae appear to be a promising group for predicting floristic relations among neotropical xeric regions. It can be observed that the general patterns manifested in the case of the complete species lists, but especially in the case of woody plants, is reproduced to an important degree by the legumes. The Compositae do not appear to be as precise, but the general patterns are not contradicted either. Cactaceae could be useful only when comparing arid or semi-arid zones, where they comprise a great fraction of the flora.

To sort out affinities at a more regional level (for example, among the southern group), an analysis at the species level is needed. In that case, we can anticipate, for example, that southern Peru would split from the Chaco Serrano complex. This is already evident in some ordinations along axis three (Figures 2, 3). There exist genera in the southern valleys of southern Peru which do not occur at all in the Bolivian Chaco Serrano, such as the endemic *Haplorhus* (Anacardiaceae), *Eriotheca* (Bombacaceae), *Bursera* (Burseraceae), *Leucaena* (Leguminosae), *Matucana* (Cactaceae), *Pineda* (Flacourtiaceae), to name a few. These Peruvian dry valleys are in close contact with Yungas elements. This is not the case with the Chaco Serrano. Further, more than 50% of the species found in the Bolivian Andean dry valleys fail to reach Peru (López 2003a, b). As to the Patagonia-Puna differences, many genera of the Patagonia which are exclusive to this cold-temperate region explain this situation (e.g., *Brachyclados*, *Duseniella*, *Xerodraba*, *Lecanophora*, *Benthamiella*). On the other hand, the affinities of some South American regions with the Sonoran desert have been explained by long-distance dispersal (Raven 1963).

The present data may also be employed in testing current biogeographical maps of South America. Cabrera & Willink's (1973) is probably the most accepted interpretation of the biogeography of the continent. The main groups of his classification find support in the data presented here. The Monte and Prepuna are clearly more related to the Chaco than to the Puna, at least from the genus perspective, and their placement in the Chaco biogeographical region (Cabrera's *Dominium*) seems correct. The dry valleys of southern Peru could also join this region. The coastal desert, while remaining in the Andean-Patagonia unit, is clearly the link between the latter and the Chaco *Dominium*. Yet, some amendments could be done. His Paranense and Caatinga provinces (and probably the Guajira too), which Cabrera places in different biogeographical regions, should constitute provinces of a region, along with the other regions belonging to the northern group of this paper. This is what Prado (2000) already suggested. The Guajira and other very dry types of this region (and not the Caatinga) seem to constitute the connection with the Chaco.

Finally, Bolivia's deciduous forests are frequently misunderstood as to their real floristic connections. For example, the Tuichi and other related plant formations are placed together with the Chaco Serrano of southern Bolivia (the Chaco Serrano sensu Cabrera, 1976). The results presented here definitely reject that assertion, as other works had already suggested (e.g., López 2000).

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