

PHYTOBIOGEOGRAPHY OF THE SPECIES ASSOCIATED WITH DRY INTERMOUNTAIN VALLEYS IN THE CHAMA RIVER MIDDLE BASIN, MÉRIDA, VENEZUELA

Fitobiogeografía de especies asociadas a un valle intermontano seco en la cuenca media del río Chama, Mérida, Venezuela

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ABSTRACT

Dry intermountain valleys in the Andes constitute areas of ecological interest due to their unique climate, flora, and soils. In the state of Mérida (Venezuela), a xerophytic or semiarid enclave located in Ejido-Estanques in the middle basin of the Chama river was studied. The floristic inventory showed 28 families with 62 species (3 endemics) and seven new reports. The phytogeographic analysis indicates that all species belong to two floristic kingdoms, except for two cosmopolitan and cultivated species. Nine biogeographical regions and 37 provinces are represented, belonging to the Neotropical-Austroamerican kingdom, the Neotropical subkingdom. The most frequent are the Colombian Andean and Guajirean-Caribbean provinces, although other species have a Caribbean-Mesoamerican and Guayanan-Orinoquian origin. There are several natural ecosystems which suggest a drier climate in the past, with different floristic elements from those in adjacent more humid ecosystems.

Key words: Chama river, dry intermountain valley, Mérida, phytobiogeography, Venezuela

RESUMEN

Los bolsones xerofíticos de los Andes de Mérida constituyen enclaves de interés ecológico dadas sus condiciones únicas climáticas, edáficas y florísticas. En el estado Mérida (Venezuela) se estudió el bolsón xerofítico o enclave semiárido en Ejido-Estanques, en el valle medio del río Chama. El inventario florístico revela 28 familias, 62 especies, de las cuales tres son endémicas y siete son nuevos registros para la zona. El análisis fitogeográfico muestra dos reinos aunque hay dos especies cosmopolitas y cultivadas. Nueve regiones biogeográficas y 37 provincias están representadas, pertenecientes al reino Neotropical-Austroamericano, subreino Neotropical. Resaltan como frecuentes la provincia Andina Colombiana y la Guajireña-Caribeña de la Neogranadina; también se encontraron plantas de origen Caribe-Mesoamericano y de la región Guayana-Orinoquense. Hay varios ecosistemas naturales que revelan un clima seco en el pasado y elementos florísticos muy disímiles de los ecosistemas aledaños.

Palabras clave: Fitobiogeografía, Mérida, río Chama, valle intermontano seco, Venezuela

INTRODUCTION

Arid zones are common throughout the Andes, a consequence of low precipitation, the causes of which are varied. Dry conditions are often the result of being in a rain shadow, as is the case in Argentina (Sarmiento 1975), Ecuador (Emck *et al.* 2006), Chile (Di Castri & Hajek 1976), and Perú (López 2003). In other areas, low rainfall is a result of cold ocean currents, as is the case in the American Pacific Desert of Perú and Chile (Weberbauer 1945, cited by Emck *et al.* 2006; Koepcke 1961, cited by Sarmiento 1975; Rundel *et al.* 1991; Galan de Mera *et al.* 2011). Lower precipitation levels may also result from being situated in an inland valley, which prevents the entry of moisture-laden winds of oceanic origin. This is the case of the xerophytic or semiarid enclaves of the northern Andes, with examples in Colombia (Pamplonita, Chicamocha, and Magdalena) as well as in Venezuela (Cuatrecasas 1958; Sarmiento 1975; Rangel *et al.* 1997; Albesiano & Fernández-Alonso 2006; Visconti *et al.* 2013).

The most impressive xerophytic enclaves in Venezuela are located in the states of Trujillo, Táchira, Lara, and especially Mérida, where the Chama river valley between the towns of Ejido and Estanques (Croizat 1954; Bernardi 1956; Costa *et al.* 2007) constitutes a dry pluviseasonal inland valley, which is, in addition, subjected to a local dry wind known as the “Caldereta” (Bono 1997). This causes a significant drop in precipitation, thus favoring the formation of typical xerophytic vegetation.

In this context of local environmental conditions and considering the existence of several other areas in the Americas with similar ecological determinants, it proposes that the flora of this study sites should share a common biogeographic origin with other xerophytic areas in the continent.

Graham & Dilcher (1995) and Burnham & Graham (1999) emphasized that the isolation of South America from Central America and Africa during the Tertiary period left its imprint on the flora of the neotropics. In this context, Morrone (2001) notes that the taxa found in the western part of South America are commonly assigned broad characteristics that connect this area to Australia and New Zealand while those on the eastern side of the continent are assigned general characteristics connecting them to the tropics of the Old World (Morrone 2001). Morrone (1996) separates the western part of South America as the Andean subregion and later places it within the Austral kingdom (Morrone 2001). The rest of South America belongs to the Neotropical region, which also extends to Central America, the Antilles, and Mexico, where it borders on the Nearctic region (Morrone 2001).

On the basis of floristic elements and bioclimatology, Rivas-Martínez *et al.* (2011b) consider all of South America and the Caribbean to be within the Neotropical-Austroamerican Kingdom, but divided into three subkingdoms. The Neotropical subkingdom, which includes the northern central area of South

America along with the Caribbean, that is, those regions with a tropical flora and macrobioclimate, whereas the Austroamerican subkingdom includes the southern areas with a temperate, mediterranean, and boreal macrobioclimate and flora. Finally, the Circumantartic subkingdom includes the islands and regions arising from the Antarctic with a polar macrobioclimate. The Andes extend lengthwise throughout the two first subkingdoms, with the northernmost regions, the moist highlands (páramos), being included in the Neogranadian region, while the drier highlands (puna) are included in the Tropical South Andean region. The Southern Andes are situated in the Middle Chilean-Patagonian and Valdivean-Magellanian regions of the Austroamerican subkingdom. Prado & Gibbs (1993), Prado (2000) and Pennington *et al.* (2006) concluded that the present-day dry forests are vestiges of a much larger dry formation, the extension of which peaked in the dry and cold climatic period (between 18,000 and 12,000 BP), coinciding with the contraction of the distribution of wet tropical forests.

On the basis of this biogeographic scenario, the aim of this study was to carry out a phytogeographical analysis of the species associated with dry intermountain valleys in the Chama river middle basin in Mérida, Venezuela, evaluating their affinities with other xerophytic enclaves in the region.

MATERIALS AND METHODS

Study area

Mérida is one state of the Venezuelan Andes (Fig. 1a). Approximately 14% of its surface experiences dry weather, and these areas concentrate 18% of the population of that state (Urbina 2012). This study was conducted specifically in the area between the town of Ejido, in the municipality of Campo Elías, and Estanques, in the municipality of Sucre. This state is characterized by a very rugged topography (Fig. 1b).

Geographically, the area of Lagunillas is disposed longitudinally along the inner groove of the Andes with a SW-NE orientation (Fig. 1b). This disposition channels the trade winds in the same direction so that they are present as south-westerly winds (Veillon 1989).

Bioclimatology

The methodology developed by Rivas-Martinez *et al.* (2011a) was followed to define the bioclimatic characteristics of the area based on data collected at weather stations in the state of Mérida (Table 1) and compiled by Aranguren (2009) and Aranguren *et al.* (2012). This data was provided by the Ministry of the Environment and Renewable Natural Resources (<http://www.minamb.gob.ve/>) and by the National Institute of Meteorology and Hydrology (<http://www.inameh.gob.ve/>) of Venezuela. The thermotypes and ombrotypes were constructed using the world bioclimatic classification system (<http://www.globalbioclimatics.org/>), found in the section on diagnostics and graphics.

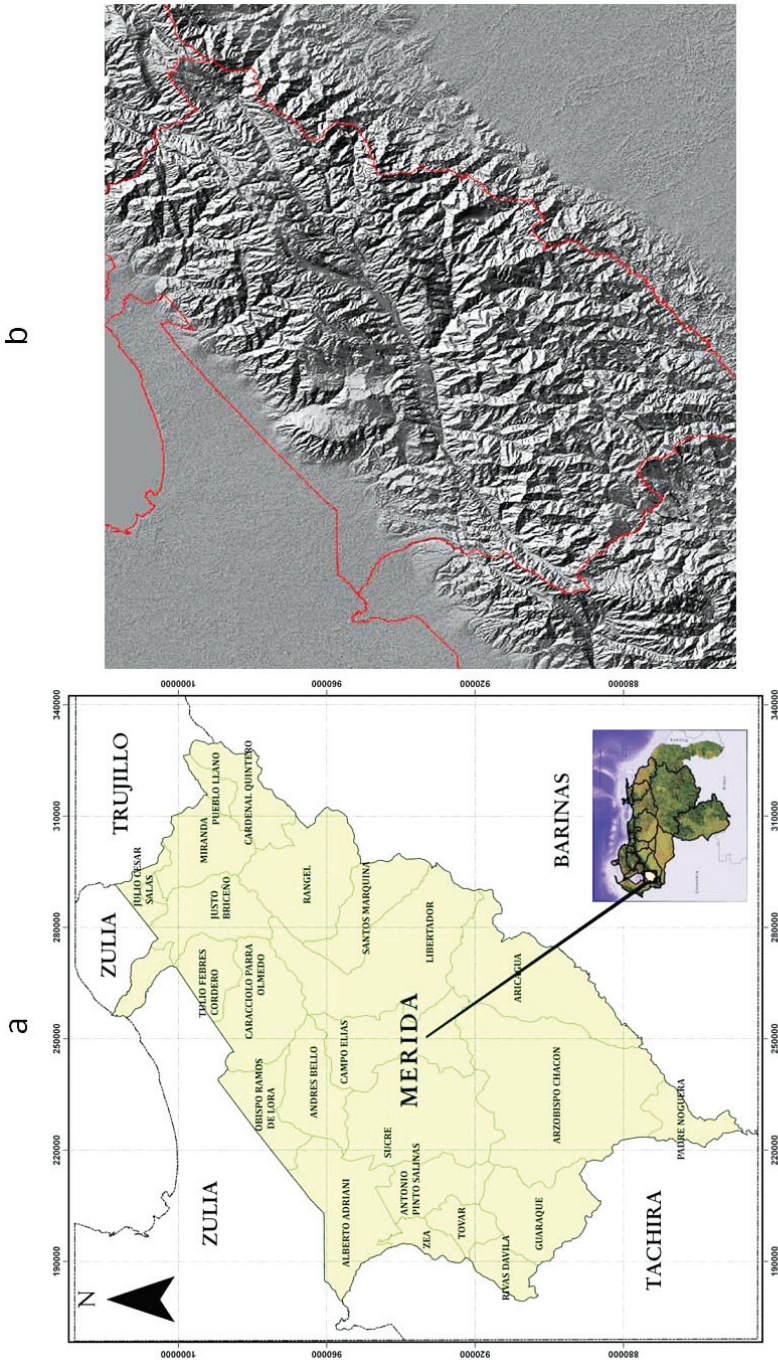


Fig. 1. a. Map showing the location of the study area. b. Radar image showing the mountainous terrain around the Chama river valley.

Table 1. Weather stations used to create the ombrothermic diagrams and rainfall analysis (Aranguren 2009).

Meteorological Station	WMO	Latitude	Longitude	Altitude (m asl)	Annual Mean precipitation (mm)	Measurement precipitation period	Annual mean temperature (°C)	Measurement temperature period
*Canaguá	803134	8°8'00" N	71°26'25" W	1560	1416.5	Oct 1968-Mar 1998	17.9	May 1981-Dec 1983
Chiguará	803053	8°29'32" N	71°32'07" W	1000	636.6	Jul 1950-Dec 1969	—	—
*Estanques	803054	8°27'32" N	71°31'56" W	452	506.6	Sep 1942-Dec 1969	23.9	Jan 1971-Dec 1976
El Molino	803023	8°12'15" N	71°33'00" W	1877	894.3	Jun 1966-May 1997	—	—
*La Palmita	808053	8°33'03" N	71°36'02" W	600	1224.1	Jan 1961-Dec 1995	28.2	Feb 1972-Mar 1984
Lagunillas	803055	8°30'25" N	71°23'14" W	1079	457.7	Jan 1950-Dec 1967	—	—
*Mérída- Airport	803047	8°35'00" N	71°11'00" W	1479	1738.0	Jan 1921-May 2007	19.0	Jan 1935-Dec 1990
*San Juan de Lagunillas	803170	8°30'40" N	71°21'13" W	1050	507.5	Oct 1970-Oct 1997	22.5	Feb 1972-Dec 1983
*Tovar	803067	8°20'31" N	71°45'00" W	952	1097	Sep 1942-Jan 1963	21.6	Mar 1969-Apr 1986

WMO = World Meteorological Organization

* = stations with precipitation and temperature records

Vegetation

A general description of the plant communities was carried out (Table 2) from the alluvial fans adjacent to the Chama river (440 m asl) to the xerophytic communities in intermediate topographical positions, opposite the town of Estanques to Las Coloradas in the Sierra Nevada of Mérida (1200 m asl). In addition, two floristic samples were gathered in the seasonally dry forest, both in the area of Haciendas El Verdal (08°28'10.74" N, 71°33'19.62" W at 645 m asl) and El Corozo (08°27'2.8" N, 71°32'27.2" W at 600 m asl). In each case, a plot measuring one tenth of a hectare was delimited (Gentry 1982; Phillips & Miller 2002) and the individual trees and shrubs were identified. The floristic inventory was completed examining the entire area to corroborate the existence of other species outside the plot, as well as through a review of the literature (Meléndez 1995; Erazo 1999; Rondón 2001; Hernández *et al.* 2003). The botanical specimens collected by A. Aranguren under the numbers 06-388 were deposited in the herbarium MER for further studies and identification.

Table 2. Communities studied and geomorphology position.

Communities	Geomorphology position
Communities of <i>Typha dominguensis</i> - <i>Phragmites australis</i>	Alluvial fans
Communities of <i>Tessaria integrifolia</i>	Alluvial fans (Q0)
Matorrales de <i>Acacia-Crotalaria-Leucaena</i>	Alluvial fans (Q1)
Cardonales/Cactus scrub (<i>Cereus hexagonus</i> , <i>Stenocereus griseus</i> , <i>Pilosocereus tilianus</i>) and Espinares of <i>Acacia macracantha</i> and <i>Prosopis juliflora</i>	Alluvial fans (Q2) and high structural slopes
Seasonally dry forest (<i>Bursera simaruba</i> , <i>Triplaris americana</i> , <i>Croton ovalifolius</i>)	Interandean valleys 440-1200

Using the bioclimatic system of Rivas-Martínez *et al.* (2011a), the study area is defined by the thermotropical bioclimatic level, between the towns of Ejido and Estanques, which has a Tropical xeric bioclimate, low thermotropical upper semiarid (stations Estanques and San Juan de Lagunillas), which defines the weather characteristics of the xerophytic enclave. The studied area covers 310 km² and a total of 62 species were recorded (Aranguren 2009) including others reported by Hernández *et al.* (2003), summarized in Appendix 1.

Biogeography

For the plants collected in this study, it was obtained information on other collection sites along the Americas for each species reviewing Hokche *et al.* (2008), Mabberley (2008) and also W3 Tropicos (<http://www.tropicos.org>) and The Plant List and links (<http://www.theplantlist.org/>). From this data, a table was created with the biogeographic distribution of the collected species in accordance with the biogeographic units proposed by Rivas-Martínez *et al.* (1999, 2011b). This table established the proportion of floristic elements characterizing the vari-

ous biogeographic units (kingdoms, regions, and provinces) in order to determine the origin of the flora found in this area.

RESULTS

Bioclimatology

From a bioclimatic perspective (Rivas-Martínez *et al.* 2011a), the study area is located in a tropical pluvisesonal and xeric bioclimate with a thermotropical thermotype between its lower (between 543 and 716 lt) and upper (between 549 and 578 lt) limits. The two most characteristic ombrotypes in the area are dry (between 2.0 and 3.6 Io) and semiarid (between 1.0 and 2.3 Io) (Table 2, Fig. 2). Climate data for San Juan de Lagunillas (643 lt and 1.9 Io) and Estanques (690 lt and 2.2 Io) confirms these bioclimatic conditions. The aridity is attenuated at higher altitudes and on slopes that are more exposed to the influence of moist winds. This is the case in La Palmita, located 600 altitude meter with an average rainfall of 1227 mm and an ombrothermic index (Io) of 4.2, which has a pluvisesonal bioclimate and a subhumid ombroclimate. All of this gives rise to vegetation corresponding to that of a dry deciduous forest (Ataroff & Sarmiento 2003), while that in San Juan de Lagunillas and at the weather station in Estanques is thorn scrub (Table 3, Fig. 2).

Table 3. Bioclimate, Thermotype, Thermicity Index (It) and annual Ombrothermic Index (Io) from analyzed stations.

Station	Bioclimate	Thermotype	It	Ombrotype	Io
Canaguá 803134	Pluvisesonal	Upper thermotropical	526	Upper subhumid	6.6
Estanques 803054	Xeric	Upper thermotropical	690	Lower dry	2.2
La Palmita 808053	Pluvisesonal	Lower thermotropical	716	Lower subhumid	4.2
Mérida- Airport 803047	Pluvisesonal	Upper thermotropical	548	Lower humid	7.9
San Juan de Lagunillas 803170	Xeric	Lower thermotropical	643	Upper semiarid	1.9
Tovar 803067	Pluvisesonal	Low thermotropical	952	Upper semiarid	4.1

The attenuation of aridity can be clearly seen upon leaving the middle Chama river valley, where a semi-deciduous mountain forest becomes more common and widespread: for instance, in Tovar, at 952 m and with a tropical pluvisesonal bioclimate, average rainfall is 1077 mm, and shows a Io of 4.1, and a lower subhumid ombrotype prevails (Sarmiento *et al.* 1971; Ataroff & Sarmiento 2003). Mérida city, located at 1495 m and with a tropical pluvial bioclimate, average rainfall of 1770 mm, and an Io of 7.8, has a lower wet ombroclimate, while Canaguá, located at 1560 m and with a tropical pluvisesonal bioclimate, an average rainfall of 1411 mm, and an Io of 6.6, has an upper subhumid ombrotype (Table 3, Fig. 2).

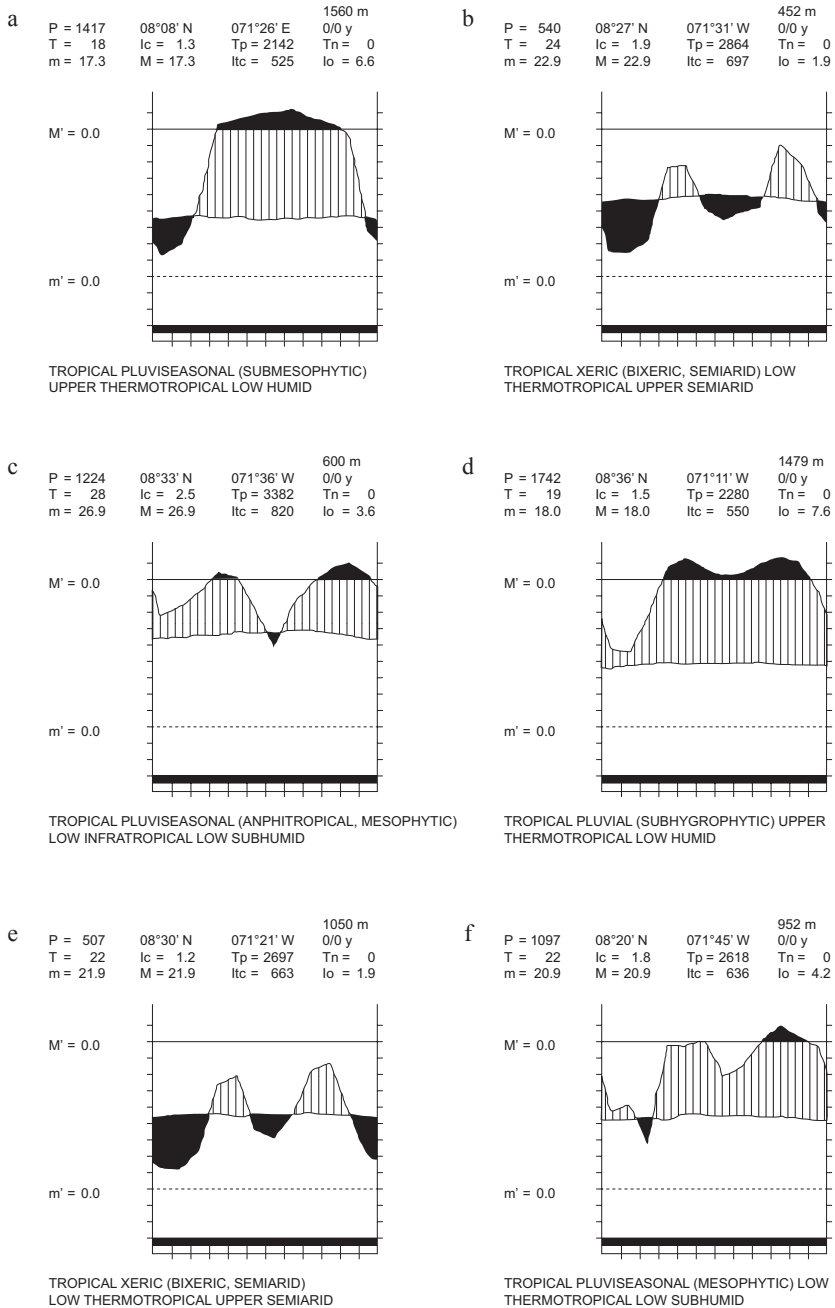


Fig. 2. Ombrothermic diagrams of Canaguá, Estanques, La Palmita, Mérida Airport, San Juan de Lagunillas, and Tovar.

It should be noted that because of its bioclimate, the town of San Juan de Lagunillas is characterized by thorn scrub vegetation rather than by a seasonal forest, which has occasionally been recorded (Ataroff & Sarmiento 2003). Moreover, regardless of the climatic characteristics of the area, the aridity is attenuated in the valley bottoms by the presence of moisture generated by rivers and streams, which leads to the growth of azonal edapho-hydrophilic vegetation in these areas.

In the arid areas of the middle Chama river valley, with its tropical xeric and pluvisseasonal bioclimate, low rainfall, seasonality, and sparse vegetation cover, all of which are associated with the steep slopes in this area, laminar erosion processes have occurred, with a high degree of rills and gullies leaving scarcely altered parental material exposed. In several places heterometric sediments have accumulated directly on exposed rock that in situ show no signs of pedogenetic evolution. In other words, this landscape is dominated by an erosive phase that considerably limits both soil formation (on the hillsides) and soil evolution (on the cones and terraces). The youngest terraces have been cut by streams and small tributaries of the Chama River itself.

Research conducted to date has recognized that the terraces (comprising less than 5% of the slopes) contain soil with signs of pedogenic evolution, with the formation of an argyillic (Bt) horizon and characterized by an abundance of stones or a skeleton formed by conglomeratic sedimentary rocks wrapped in a matrix that varies between coarse sandy loam to sandy clay loam. The reddish color is indicative of materials proceeding from the Jurassic formation "La Quinta" (<http://www.pdvs.com/lexico/lexico.htm>) with a high degree of weathering.

The bioclimatic characteristics of the area favor the accumulation of salts in the soil, mainly Ca^{2+} and Na^{+} . This leads to a basic soil pH. Soil type varies depending on the age of the sediments, but soils with sodium and calcium endopods dominate. These can be classified as Typic Natrustalfs and Type Haplustalfs (Calcis or Haplic Luvisol), the latter one present in the study area.

At an altitude of 580 m, Typic Ustorthents (Entisol) develop on alluvial fans with a great deal of drainage located in the late Precambrian formation of Sierra Nevada (<http://www.pdvs.com/lexico/lexicoh.htm>) with its igneous and metamorphic rocks; the predominant vegetation is of the thorn scrub type.

Located at an altitude of 588 m on structured, steep slopes with good drainage is the Cretaceous formation "Colon" (<http://www.pdv.com/lexico/lexicoh.htm>), which is characterized by calcareous shale and sandstone. The soil Lithic Ustorthents (Entisol) type, and instead of thorn scrub, the vegetation is typical of a dry seasonal forest.

Vegetation

The plant communities (Fig. 3) follow the changes noted between the alluvial fans of the Chama river (400 m) and the small town of Las Coloradas at 2000 m on the road connecting the southern towns of the state of Mérida (Cegarra 2006).

At an altitude of 450 m, a plant community of *Typha domingensis* Pers. and



Fig. 3. Transect of vegetation in the middle Chama river valley in the town of Estanques.

A. Chama river. B. Capatú lagoon

1. Formation of *Typha domingensis* and *Phragmites australis*. 2. Formation of *Tessaria integrifolia*. 3. First terrace with *Acacia macracantha* with *Cyperus* sp., *Panicum maximum* and *Arundo* sp. 4. Dry slopes with *Acacia macracantha* without moisture indicator plants. 5. Thorn scrubs with columnar cacti (cardones), *Stenocereus griseus* and *Cereus hexagonus* among others. 6. Seasonally dry forest with *Bursera simaruba*, *Triplaris americana*, *Croton ovalifolius* and *Duranta repens* among others. 7. Closed forest more moisture requirement with *Brugmansia arborea*, *Cecropia telenitida*, *Cordia alliodora* and *Inga oerstediana* among others. 8. Cloud forest with *Cyathea arborea*, *Ocotea calophylla* and *Clinopodium foliolosum* among others. 8. Cloud forest with *Cyathea arborea*, *Ocotea calophylla* and *Clinopodium foliolosum* among others.

Phragmites australis (Cav.) Trin. ex Steud. can be observed; this permanently flooded community is associated with the watercourse of the Chama river (Fig. 3). It has catenal contact with vegetation dominated by *Tessaria integrifolia* Ruiz & Pav, which can endure long periods of flooding and the extreme conditions caused by river flooding (Fig. 3). Slightly farther from the river, on the first terrace (Q1), there is a plant community comprised of *Acacia macracantha* Willd., *Clitoria* sp., *Crotalaria incana* L., *Cyperus* sp., *Leucaena leucocephala* (Lam.) de Wit, *Galactia* sp., *Panicum maximum* Jacq., *Pithecellobium dulce* (Roxb.) Benth., *Ricinus communis* L., *Serjania* sp., *Senna* sp., and *Stylosanthes viscosa* Sw. This community occupies the floodplain of the river and can withstand long periods of drought, but is also influenced by the phreatic level (Fig. 3). Together, these three zones represent the edapho-hygrophilous vegetation of the area.

Outside of the floodplain terrace and without the influence of the water table of the river there is a community similar to that last community, but there are no plants indicating the hygrophilous nature of the soil such as *Panicum maximum* Jacq., *Cyperus* sp., or *Arundo donax* L. In this community, new species of the thorn scrub type appear (Fig. 3). On steeper slopes with spurs as well as on alluvial fans it was found the typical thorn scrub of the lower thermotropical, upper semiarid level of the middle section of the Chama River Basin, in which columnar cacti forming “cardonales” (Cactus scrub) predominate, accompanied by thorny Mimosaceae with a stumpy appearance, locally known as “cujíes” (Fig. 3). Noteworthy in this plant community is the presence of *Agave americana* L., *Bastardia viscosa* (L.) Kunth, *Bromelia pinguin* L., *Bursera simaruba* (L.) Sarg., *Quadrella odoratissima* (Jacq.) Hutch., *Cereus hexagonus* (L.) Mill., *Chloris* sp., *Croton ovalifolius* Vahl, *Duranta mutisii* L.f., *Lippia moritzii* Turcz., *Maclura tinctoria* (L.) D.Don ex Steud., *Mammillaria mammillaris* (L.) H.Karst., *Cylindropuntia caribaea* (Britton & Rose) F.M.Knuth, *Opuntia elatior* Mill., *Pilosocereus tillianus* R.Gruber & Schatzl, *Passiflora* sp., *Pereskia guamacho* F.A.C.Weber, *Plumeria alba* L., *Prosopis juliflora* (Sw.) DC., *Stenocereus griseus* (Haw.) Buxb., *Tillandsia fasciculata* Sw., *Tillandsia recurvata* (L.) L., *Trixis* sp., *Vanilla* sp. and *Waltheria indica* L. On some extremely steep slopes and spurs, these species act as edaphoxerophilous vegetation.

Above the cardonales, at approximately 670 m asl (Fig. 3), there is a seasonally dry forest (Aranguren 2009) occupying the oldest terraces of the river and its more steeply sloped (>40%) banks. This forest contains *Calliandra magdalenae* (DC.) Benth., *Bursera simaruba* (L.) Sarg., *Quadrella odoratissima* (Jacq.) Hutch., *Cynophalla verrucosa* (Jacq.) J.Presl, *Capparis tenuisiliqua* Jacq., *Mallothus rhamnifolius* (Willd.) Müll.Arg., *Cordia curassavica* (Jacq.) Roem. & Schult., *Jatropha gossypifolia* L., *Guapira pacurero* (Kunth) Little, *Machaerium biovulatum* Micheli, *Myrcia splendens* (Sw.) DC., *Praecereus euchlorus* subsp. *smithianus* (Britton & Rose) N.P.Taylor, *Pilosocereus tillianus* R.Gruber & Schatzl, *Piptadenia* sp., *Stenocereus griseus* (Haw.) Buxb., and *Handroanthus ochraceus* (Cham.) Mattos (Aranguren 2009).

Above 1200 m there is a seasonally dry forest with a closed canopy and transitional plant species adapted to the change from a seasonal condition and greater water availability (Fig. 3, 7), with species such as *Alsophila engelii* R.M. Tryon, *Brugmansia arborea* (L.) Steud., *Bursera simaruba* (L.) Sarg., *Cecropia telenitida* Cuatrec., *Cordia alliodora* (Ruiz & Pav.) Oken, *Croton gossypifolius* Vahl, *Cyathea* sp., *Duranta erecta* L., *Ficus* sp., *Geonoma undata* Klotzsch, *Gunnera brephogea* Linden & André, *Inga oerstediana* Betnth., *Mallotus rhamnifolius* (Willd.) Müll.Arg., *Miconia meridensis* Triana, *Myrcia splendens* (Sw.) DC., *Ocotea* sp., *Palicourea buntingii* Steyerem., *Triplaris americana* L. and *Zanthoxylum rhoifolium* Lam.

The cloud forest appears at 1700 m (Fig. 3) and extends up to 2500 m asl. Common species in this formation include *Cyathea arborea* (L.) Sm., *Ocotea calophylla* Mez, *Clinopodium foliolosum* (Benth.) Govaerts, *Cecropia telenitida* Cuatrec., *Alsophila* sp., *Aphelandra runcinata* Klotzsch ex Nees, *Gleichenia* sp., and *Bocconia frutescens* L., among others. At higher altitudes, the cloud forest begins to include plants that clearly indicate the transition to the paramo, such as *Libanothamnus neriifolius* (Sch.Bip. ex Sch.Bip.) Ernst, *Calycolpus moritzianus* (O.Berg) Burret, and *Vaccinium floribundum* Kunth, among others. It is well known that in an area less than one hectare, 25% of the flora registered for the entire xerophytic enclave can be found, along with 14.4% of the plant species inventoried by Ricardi (1996) and Rico *et al.* (1996). This represents perhaps the highest phytodiversity in a plant community for this xeric area.

Biogeography

The distribution of the 62 species collected in Gentry transects applying the Rivas-Martínez biogeographically system (2011a) resulted in 359 different entries at the provincial level (4 regions with a total of 83 provinces were taken into consideration). The majority of the species identified were neotropical (74%), although there were also some pantropical species (19%), with 3% being cosmopolitan and another 3% having a paleotropical source. These species are distributed over nine American biogeographic regions (Table 4) in 37 different provinces.

Table 4. Lithological, geomorphological, and chemical characteristics of soil profiles.

	Profile 3	Profile 4	Profile 5
Formation	Sierra Nevada	Quinta	Colón
Geomorphology position	Alluvial fans	Alluvial fans	Structural slope
Altitude (m asl)	452	580	658
Slope (%)	< 5	< 5	>35
Drainage	External and internal excessively drained	External and internal well drained	Excessively drained
Texture	Sandy-loam	Clay-loam	Clay-loam
pH	5-5.5	7-7.6	6-6.5

Table 4. Continuation from previous page.

	Profile 3	Profile 4	Profile 5
% CO	< 1	0.8	3 %
P (ppm)	6	< 5	10
N (%)	0.2	< 0.2	0.3
K (Cmol/Kg soil)	0.2	< 0.2	0.2
CIC	5	18-20	2.5
% BS	< 20	>90	60
Typology	Entisols (Typic Usthorvents)	Alfisols (Typic Haplustalfs)	Entisols (Lithic Usthorvents)

The best represented regions are the Neogranadian, the Caribbean-Mesoamerican, and the Guayanano-Orinoquian (32, 22, and 20%, respectively) although another six American regions are also represented, albeit to a lesser degree (Table 5). These findings are in agreement with those of Croizat (1954) and Hernández *et al.* (2003), who consider the xerophytic flora of the Andes in Mérida to consist principally of Caribbean elements with the incorporation of floristic elements from other regions.

Currently, from a biogeographic perspective, the term “Caribbean” refers to two regions, namely the Caribbean-Mesoamerican and the Neogranadian zones (Rivas-Martínez *et al.* 2011b). In the middle Chama river valley, the flora of the Chiapan-Honduran (28%), Panamanian-Costa Rican (26%), Veracruzano-Yucatanian (21%) and Guajirano-Caribbean provinces (30%) are those with the greatest representation. Also, well represented are elements from the Colombian-Andean (34%) and Llanero (20%) provinces, which are characterized by plants that are well adapted to seasonal variation and xerophytic conditions (Aymard & González 2007).

Also, floristic elements from the pluviseasonal xeric areas of the region known as the Cerrado (West Cerrado: 39% and East Cerrado: 16%) as well as the Beniano (22%) are present. Both regions are marked by a tropical pluviseasonal bioclimate (Navarro & Maldonado 2002).

Moreover, a high percentage of species (60%) belongs to the Guaviareano-Orinoquian province, which includes the states of Bolívar and Amazonas. The presence of these species is due to the chaparral and savannah bush with these xeric floristic elements (Huber & Alarcón 1988).

To a lesser extent there are species originating from the following regions: Mexican Xerophytic (5%), Amazonian (4%), Madreño (3%), and Hyperdesertic Tropical Pacific (1%). These complete the set of biogeographic influences of this region and naturally share their pluviseasonal xerophytic characteristics.

Regarding endemic elements, only three species were found in the area: *Pilosocereus tillianus* R.Gruber & Schatzl (Rondón 2001), *Coursetia andina* Lavin (Lavin 1988), and *Ibatia pacifica* (G. Morillo, pers. com.). The first corresponds to a species mentioned by Croizat (1954), since this cactus is characteristic of

Table 5. Regions and provinces in which the reported species are found.

Region	%	Province	%
Neogranadian	31.8	Colombian Andean	34.5
		Guajiran-Caribbean	30.3
		Llaneran	20.4
		Guayaquilian-Ecuadorean	8.5
		Cordobesa-Lower Magdalena	4.9
		Colombian Pacific	1.4
		Insular Galapagos	0.7
Caribbean-Mesoamerican	21.7	Chiapan-Honduran	28.1
		Panamanian-Costa Rican	26.0
		Veracruzian-Yucatanian	20.8
		Lesser Antillean	10.0
		Cuban	8.3
Guyanan-Orinoquian	20.4	Floridan	6.3
		Guaviarean-Orinoquian	60.0
		Deltaic Orinoquian	24.4
Tropical South Andean	7.6	Guayanian	15.6
		Mesophytic Punenian	40.0
		Desert Peruvian-Ecuadorean	25.0
		Yungenian	20.0
Brazilian-Paranense	6.4	Bolivian-Tucumanean	15.0
		West Cerrado	38.9
		Benian	22.2
		East Cerrado	16.4
		Catingan	11.1
Mexican Xerophytic	4.5	Tocantins	11.1
		Tamaulipan	33.3
		Chihuahuana	26.7
		Baja California	13.3
		Sonoran	13.3
Amazonian	3.8	Sinaloan	13.3
		West Amazonian	60.0
		North Amazonian	40.0
Madrean	3.2	Balsas River and Southern Madrean	54.5
		Neovolcanic-Eastern Madrean	36.4
		Western Madrean	9.1
Hyperdesertic Tropical Pacific	0.6	Hyperdesertic North Peruvian	100

thorn scrub areas, but also forms part of the seasonally dry forest community both in Mérida and Táchira (Aranguren 2009). In contrast, *Coursetia andina* has only been collected in this area by Breteler (collection number 319), Ruiz Terán *et al.* (collection number 12647), and the acknowledged specialist in this genus, Lavin (collection number 5732 A). Another third species, *Ibatia pacifica*, generally found in arid and semi-arid areas, this particular species has only been found in this area (Morillo 2012). Other species with a more limited distribution associated with this semiarid enclave include *Mammillaria columbiana* Salm-Dyck, *Mammillaria mamillaris* (L.) H.Karst., and *Melocactus schatzlii* H.Till & R.Gruber, which are found only in Venezuela and Colombia and are classified as threatened (Llamozas *et al.* 2003; Trujillo, pers. com.). Finally, it is considered that *Bursera graveolens* (Kunth) Triana & Planch. should be included in future editions of the red book as a critically endangered species (Trujillo, pers. com.).

At the upper-regional level, 45% of the species found belong to the Caribbean-Neogranadian area, which includes the Mesoamerican-Caribbean and Neogranadian regions. Of these, 8% have a distribution that extends to the Guiana massif while 36% are found only in the aforementioned super-region and only 8% are limited to the Venezuelan-Colombian Caribbean region.

Three of those endemic to the area are *Pilosocereus tilianus* Gruber & Schaltz (Cactaceae), *Coursetia andina* Lavin (Fabaceae) e *Ibatia pacifica* (Krings & Saville) Morillo (Apocynaceae), which means 4.83% of the studied flora and 1.15% of the 260 reported by Guevara for the semiarid enclave (updated Guevara, 2015). The distribution pattern of these endemic species is shown in Fig. 4.

Another important aspect to be considered is the presence of Caribbean species within the enclave, which allows us to infer the thermo-tropical upper floor as an upper limit of the Andean-Caribbean transition. In the study area distributional traces for *Amyris ignea* Steyerl. (Rutaceae), *Pereskia guamacho* (Cactaceae) and *Capparis tenuisiliqua* (Capparaceae) were found, three species distributed from the Caribbean coast of Venezuela and Colombia to the semiarid enclave in the eastern slopes of the Andes of both countries (Fig. 5). In the case of *Pereskia guamacho*, distribution extends to dry bioclimatic and pluvi seasonal regions (central Venezuelan Llanos) to some very humid regions as the Darien in Panama and Colombia, but in these last localities the species could be present as a cultivated plant. In the case of *Amyris ignea*, the species was also registered in the island of Trinidad (Fig. 5).

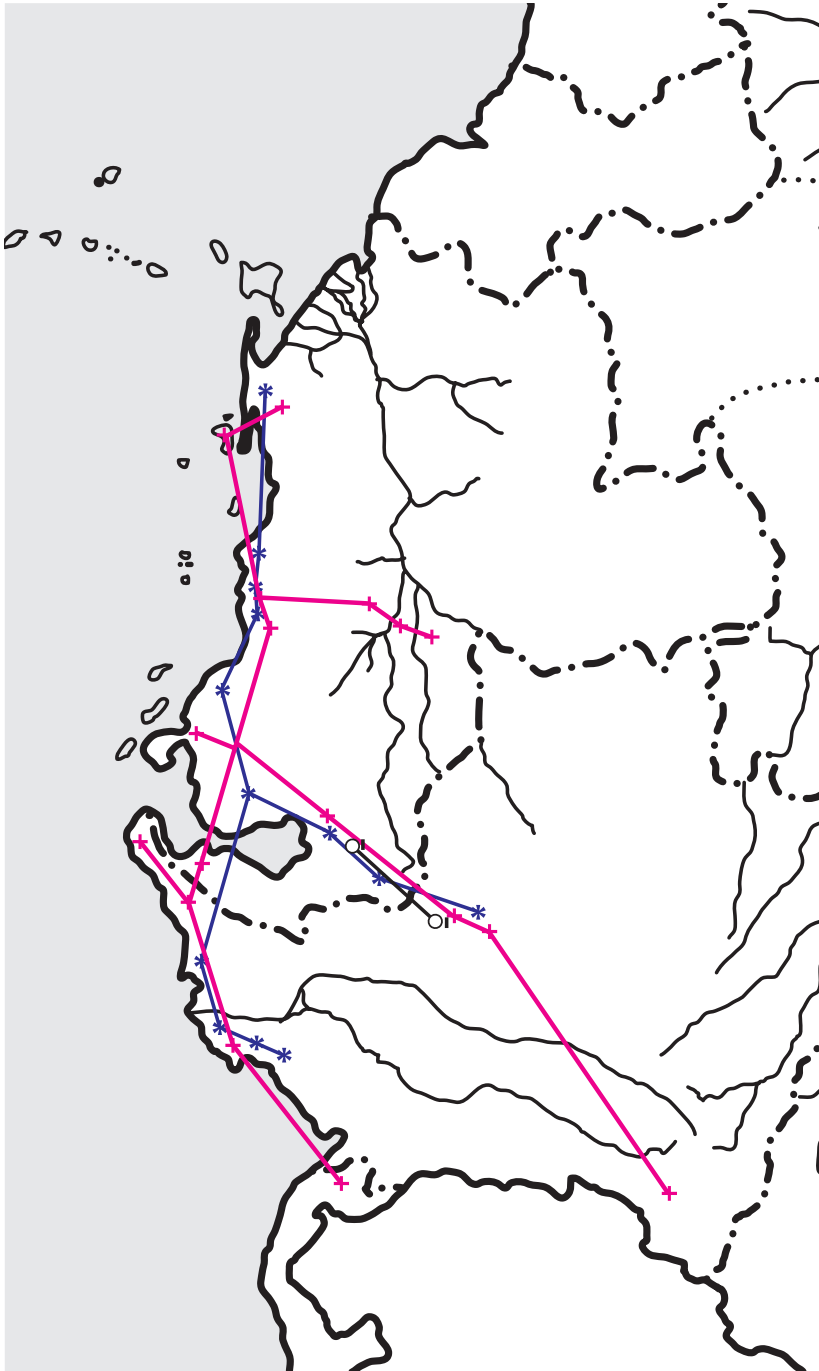


Fig. 4. Distribution of Andean-Caribbean species. * *Amyris ignea*; + *Pereskia guamacho*; o *Capparis tenuisiliqua*.



Fig. 5. Distribution of endemic species. **a.** *Coursetia andina*; **b.** *Pilosocereus tillianus*; **c.** *Ibatia pacifica*.

DISCUSSION

These results lead to the conclusion that, from a bioclimatic, floristic, and biogeographic perspective, this semiarid enclave is a unique ecosystem within the Andean context, one that has been biologically undervalued until now. To date, most research has focused on the lack of vegetative cover and erosion levels (Croizat 1954; Bernardi 1956; Watters 1971; Hernández *et al.* 2003), which has led to the view that this landscape has arisen from bad agricultural and cattle management. In contrast, the analysis presented here leads to propose that originally the climate was the decisive factor in shaping this region, although the anthropogenic influence has favored erosion and land degradation in the area.

The dry intermountain valley analyzed here is currently under great pressure from human activity as it has become an area of urban and industrial expansion for the cities of Mérida, Ejido, and Tovar. Not only have many great industries relocated there, but just recently the customs offices of the city of Mérida opened in this region, in association with the tax-free port referred to as the Duty Free Area for Science and Technology (Zona Libre de Ciencia y Tecnología or ZOLCIT). All of these will bring more service companies competing for land to the area. In addition, the solid waste dumps of the city of Mérida and the surrounding towns have also been established in this area, with the corresponding environmental impact that this entails (Cegarra 2006).

The presence of the Chama river and the formation of alluvial deposits have led to the development of significant agricultural activity in this area since ancient times. However, the region is being transformed into an industrial area and urban development in more recent times. The areas with the steepest slopes, which represent a high percentage of the total land in this region, are being divided into small lots and used in accordance with the slope of the land, but most of the agricultural activity is situated in the lower lying areas. In these areas, a great number of crops are grown, especially tomatoes (*Lycopersicon esculentum* Miller), peppers (*Capsicum annuum* L.), onions (*Allium cepa* L.), sugar cane (*Saccharum officinarum* L.), and many others that require the use of irrigation systems (Cegarra 2006).

In Mérida, as in other parts of the world, xeric areas are not adequately valued. Because their uniqueness and natural value are generally overlooked, they tend to be used for all kinds of marginal activities (Pozzobon *et al.* 2004). From a biological point of view, however, these dry enclaves constitute important areas of migration for various species in times of major environmental changes such as those reported for the glacial and interglacial periods. In his analysis of the dry formations of South America, Sarmiento (1975) mentions that the Andean range has served as a biogeographic migration route of drought-resistant species, acting as a continental bridge joining the dry formations of North America and the tip of South America.

After their analysis of the distribution of species in the seasonally dry forests of South America, this research agrees with Prado & Gibbs (1993), Prado (2000)

and Pennington *et al.* (2006) who concluded that the present-day dry forests are vestiges of a much larger dry formation, the extension of which peaked in the last dry and cold climatic period (between 18,000 and 12,000 BP), coinciding with the contraction of the distribution of wet tropical forests.

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Appendix 1. Species analyzed in this study

<i>Acacia tortuosa</i> (L.) Willd.	<i>Handroanthus serratifolius</i> (Vahl) S.O. Grose
<i>Acacia genistifolia</i> Link	<i>Heliotropium indicum</i> L.
<i>Acanthocereus tetragonus</i> (L.) Hummelinck	<i>Hibiscus phoeniceus</i> Jacq.
<i>Adenaria floribunda</i> Kunth	<i>Lantana fucata</i> Lindl.
<i>Ageratum conyzoides</i> (L.) L.	<i>Machaerium biovulatum</i> Micheli
<i>Amyris ignea</i> Steyerem.	<i>Maclura tinctoria</i> (L.) D.Don ex Steud.
<i>Anthurium crassinervium</i> (Jacq.) Schott	<i>Mallotus rhamnifolius</i> (Willd.) Müll.Arg.
<i>Astronium graveolens</i> Jacq.	<i>Malpighia glabra</i> L.
<i>Baccharis nitida</i> (Ruiz & Pav.) Pers.	<i>Melicoccus bijugatus</i> Jacq.
<i>Berberis bicolor</i> H.Lév.	<i>Melochia villosa</i> (Mill.) Fawc & Rendle
<i>Bromelia pinguin</i> L.	<i>Momordica charantia</i> L.
<i>Bursera graveolens</i> (Kunth) Triana & Planch.	<i>Myrcia splendens</i> (Sw.) DC.
<i>Bursera simaruba</i> (L.) Sarg.	<i>Pereskia guamacho</i> F.A.C. Weber
<i>Calliandra magdalenae</i> (DC.) Benth.	<i>Pilosocereus tiliannus</i> R. Gruber & Schatz
<i>Capparis tenuisiliqua</i> Jacq.	<i>Praecereus euchlorus</i> subsp. <i>smithianus</i> (Britton & Rose) N.P.Taylor
<i>Capsicum annum</i> L.	<i>Prosopis juliflora</i> (Sw.) DC.
<i>Cardiospermum</i> aff. <i>grandiflorum</i> Sw.	<i>Quadrella odoratissima</i> (Jacq.) Hutch.
<i>Cereus hexagonus</i> (L.) Mill.	<i>Sida abutifolia</i> Mill.
<i>Chrysophyllum argenteum</i> Jacq.	<i>Solanum bicolor</i> Willd. ex Roem & Schult.
<i>Clusia minor</i> L.	<i>Stachytarpheta cayennensis</i> (Rich.) Vahl
<i>Cnidoscopus urens</i> (L.) Arthur	<i>Stenocereus griseus</i> (Haw.) Buxb.
<i>Commelina diffusa</i> Burm. f.	<i>Stylosanthe hamata</i> (L.) Taub.
<i>Cordia curassavica</i> (Jacq.) Roem. & Schult.	<i>Talinum paniculatum</i> (Jacq.) Gaertn.
<i>Coursetia andina</i> Lavin	<i>Tecoma stans</i> (L.) Juss. ex Kunth
<i>Croton billbergianus</i> Müll. Arg.	<i>Tillandsia flexuosa</i> Sw.
<i>Cynophalla hastata</i> (Jacq.) J.Presl	<i>Tillandsia recurvata</i> (L.) L.
<i>Cynophalla verrucosa</i> (Jacq.) J.Presl	<i>Trichilia havanensis</i> Jacq.
<i>Euphorbia tithymaloides</i> L.	<i>Waltheria indica</i> L.
<i>Ficus obtusifolia</i> Kunth	<i>Wedelia fruticosa</i> Jacq.
<i>Guapira</i> aff. <i>pacurero</i> (Kunth) Little	<i>Wigandia urens</i> var. <i>caracasana</i> (Kunth) D.N.Gibson
<i>Handroanthus ochraceus</i> (Cham.) Mattos	<i>Zanthoxylum fagara</i> (L.) Sarg.
