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Biogeography of the Monte Desert

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ABSTRACT

The Monte is a biogeographic province covers an extensive area from the subtropical northern part of Argentina at 24 degrees south, to the temperate northern region of Patagonia at 44 degrees south. Within the province, which is about 2000 km from north to south, lies the Monte Desert, on a strip of land that stretches along the eastern side of the Andes Mountains. The definition of the boundaries of the Monte Desert varies among authors. We present a division of the Monte Desert into three botanical districts: Northern, Eremean, and Southern districts. The Northern and the Southern districts are divided into subdistricts. Different hypotheses have been proposed for the origin of the Monte Desert biota. A few plant genera show a remarkable phylogenetic affinity with plants of the North American deserts of Mojave and Sonora. However, this is an exception because most of the Chaco and Patagonia. Second in importance is the group of taxa that originated in Patagonia, and the most enigmatic of all are the paleoendemic groups composed of relictual taxa of Pangeic or Gondwanic origin. The complexity of the biota of the Monte desert biota is probably a result of the extensive area of contact between the two South American biotas of South America: Brazilian biota (or tropical biota) and Patagonian biota.

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1. Introduction

The Monte is a Neotropical biogeographic province that belongs to the Chaco subregion (Cabrera and Willink, 1973; Morrone, 2000, 2001) or is considered as a part of South American Transitional Zone (Morrone, 2004, 2006).

The Monte province is physiognomically characterized by the presence of different shrubs genera mainly creosote bush *Larrea* Cav., *Aloysia* Ortega ex Juss., *Capparis* L., and *Parkinsonia* Zul. The distribution of these genera is not restricted to the Monte, and within the Americas they are primarily found in two areas which are geographically very far apart. One area is the Monte Biogeographical Province and other arid regions of the Southern Cone (Chile, Bolivia, and Peru) (Morello, 1958), and the other area includes the Sonoran and Mojave deserts of Mexico and southern USA. Besides this similarity, the taxa of the Monte are more closely related to those that inhabit the biogeographic provinces of the Pampa and Chaco and, in some cases, to other organisms occurring in the Patagonian and the Andean provinces.

The following is a brief historical description of the proposed boundaries of the Monte, the natural areas proposed within the Monte, and the relationships among its biota and the biota of other areas in the Americas.

2. The boundary area of the Monte

Several botanical contributions discuss the boundaries of the Monte with adjacent biogeographic provinces, such as Chaco (Morello, 1958; Roig and Roig, 1969), Patagonian Steppe (León et al., 1998; Morello, 1958; Ragonese and Piccinini, 1969; Roig et al., 1980; Roig, 1998; Soriano, 1949, 1950, 1952, 1956) and the Andean province (Martínez Carretero, 2000; Roig, 1972; Roig and Martínez Carretero, 1998). The boundary between the biogeographic provinces of the Monte and Patagonia (Fig. 1) has been particularly well studied, and assignment of the Valdés Peninsula (Fig. 1) to either province has been extensively debated. Early authors (e.g., Holmberg, 1898; Kühn, 1922, 1930; Lorentz, 1876) included the peninsula in Patagonia. Instead, Hauman (1920, 1926, 1931, 1947), who explored the surroundings of Puerto Madryn and entered the peninsula through Puerto Pirámides, included the peninsula within the Monte on account of "the extreme scarcity of truly Patagonian elements". Parodi (1934, 1945, 1951) and Castellanos and Pérez Moreau (1944) supported the assignment of the peninsula to the Monte. Cabrera (1951, 1953, 1958, 1971, 1976) and Morello (1958) instead assigned it to the Patagonia. However, Cabrera and Willink (1973) included the peninsula in the Monte (Ribichich, 2002). Ribichich (2002) also noted that Cabrera (1976) presented a map

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Fig. 1. The Monte Biogeographic Province with the districts and subdistricts proposed in the present contribution.

that includes the Valdés Peninsula in the Patagonian Province, but the definition of the area in the text includes the peninsula in the Monte. Morello (1958) also included Punta Ninfas, an area south of the Valdés Peninsula which is floristically similar to the Valdés Peninsula, within the Monte. Frenguelli (1940) considered the peninsula as an ecotone between the two provinces ("lateral Patagonia"). Soriano (1949, 1952) agreed that the peninsula was transitional between the two provinces, although he later (Soriano, 1956) included it in the Patagonian district of Chubutense because of its shrub-steppe physiognomy (resulting from the presence of *Chuquiraga avellanedae*). More recently, Bertiller et al. (1981) published a detailed map and species list of the vegetation of the Valdés Peninsula. Based on Bertiller et al. (1981), Roig (1998) included the peninsula in the Monte while noting the close floristic relationship between the northern Patagonian creosote bush shrublands (immediately south of the peninsula) and the vegetation of La Pampa province (immediately to the north). We follow Roig (1998) in recognizing an Atlantic Shrub District within the Monte Province that includes the Valdés Peninsula and Punta Ninfas, which together constitute an agroclimatic district defined by Beltramone and Del Valle (1981).

From a zoogeographic perspective, the Monte has been referred to as the Sub-Andean Zoogeographic Province. This zoogeographic province has been mostly based principally on patterns of vertebrate distribution, specifically mammals and birds, and its extent varies widely among authors (Cabrera and Yepes, 1940, 1950; Dabbene, 1910; Fittkau, 1969; Gollán, 1958; Müller, 1973; Ringuelet, 1961; Roig, 1962; Roig and Contreras, 1975; Redford and Eisenberg, 1992).

Cabrera and Willink (1973) gathered the botanical and zoological information to create a regionalization of Argentina that recognizes the biogeographic province of the Monte, and this same scheme has been used in subsequent studies (Morrone, 2004; Roig-Juñent et al., 2001).

3. Distribution of flora and fauna within the Monte

The boundaries of the Monte do not correspond to the area of distribution of a particular taxon, but do correspond with its physiognomic aspects and floristic characteristics (Morello, 1958). No plant species or genus has a range of distribution strictly coincident with the Monte area (Fig. 2). Even though the Monte is characterized by the presence of species of the genus Larrea, distribution of this genus in Argentina is broader than it is in the Monte (Fig. 2A–C). Some plant species whose area of distribution closely coincides with the area proposed for the Monte include Condalia microphylla Cav. (Fig. 2A), Parkinsonia praecox glaucum (Cav.) (Martínez Carretero, 1986) (Fig. 2D), and Montea aphylla (Fig. 2A). This last species was used by Morello (1958) to determine the boundary between the Monte and the Espinal. As with plants, there is no known insect taxon with a distribution that coincides strictly with the area of the Monte (Roig-Juñent et al., 2001). This is perhaps because some endemic insect species of the Monte are restricted to only a part of the province, such as the northern, central, or southern areas (Roig-Juñent et al., 2001). However, species widely distributed across the Monte have as well known occurrences outside the province particularly in areas of transition between the Monte and the biogeographic provinces of Espinal or Patagonia, as is the case with the genus Larrea. Two insect taxa are highly representative of the Monte, although their distribution extends into the ecotonal areas: Megelenophorus americanus Lacordaire, one of the country's largest tenebrionid beetles (Coleoptera); and the tribe Eucraniini (Scarabaeidae), dung beetles, whose species are endemic to the Monte, except for one that is found in ecotonal areas of Chaco (Ocampo and Philips, 2005).

Among reptiles, only the monotypic genus *Pseudotomodon* Koslowsky is exclusive to the Monte (*P. trigonatus* Leybold; Cei, 1993). All four species of the genus *Leiosaurus* (Duméril and Bibron) are present in the Monte as well in ecotonal areas (Cei, 1986; Laspiur et al., 2007). At species level, representatives of the region include *Liolaemus darwinii* (Bell), *L. gracilis* (Bell), *Homonota underwoodi* Kluge, *Amphisbaena angustifrons plumbea* (Gray), *Philodryas trilineata* (Burmeister), *Cnemidophorus longicaudus* (Bell) and, with a more restricted distribution, *Tupinambis rufescens* (Gunther) and *Leptotyphlops borrichianus* (Degerbol) (Cei, 1986; Tognelli et al., 2001; Scolaro, 2005, 2006).

4. The Monte as an area of independent evolution

The biological diversity of arid regions is considered poor compared to other hyperdiverse areas, such as tropical regions. Nevertheless, these measurements of biological diversity have been based on species richness without taking into account phylogenetic and biogeographic aspects (Navone et al., 2006). Mares (1992) showed that micromammal diversity is higher in deserts than in tropical regions when endemisms are included in the analysis.

The hypothesis that the Monte is an impoverished area compared to Chaco has been traditionally accepted (Stange et al., 1976). This idea was mainly based on the lower diversity and fewer endemic species of Monte Desert vertebrates. Stange et al. (1976) found that several insect genera present in Chaco are also present in the Monte, although with fewer species. Roig-Juñent et al. (2001), on analyzing the distribution of 16 insect families and considering the total number of neotropical species in these families, confirmed that the Monte has 50% less diversity than Chaco (3.41% and 6.2% of diversity of neotropical species, respectively), showing a trend of decreasing biodiversity with increasing aridity from Chaco to the Monte.

However, because of the presence of numerous reptiles and insects endemic to the Monte, this area should be considered as an independent evolutionary center (Roig-Juñent et al., 2001; Rundel et al., 2007). The degree of endemicity varies depending on the taxonomic group. There are numerous endemic genera or tribes of insects and other arthropods, such as Solifugae (Arachnidae), with very high endemicity (almost 100%) (Maury, 1998; Roig-Juñent et al., 2001). In general, endemicity of arthropods has been found to average 30% (Roig-Juñent et al., 2001). Among vertebrates, reptiles have a similar percentage of endemicity, about 30% (Rundel et al., 2007), with the genera Leiosaurus and Pseudotomodon being the most representative of the Monte (Cei, 1986). Endemicity of mammals and birds is lower, about 21% and 12%, respectively (Rundel et al., 2007), with the rodents Tympanoctomys Yepes, Pipanococtomys Mares, Octomys Thomas and Salinomys Braun and Mares being the most remarkable endemic genera of mammals.

5. Natural areas of the Monte

Earlier studies failed to recognize the existence of natural areas of endemicity within the Monte (e.g. Cabrera, 1953; Hauman, 1920; Morello, 1958; among others). Roig (1998) proposed the existence of an Atlantic Shrub District on the Patagonian coast of Chubut. León et al. (1998) proposed the existence of a West and East Monte in northern Patagonia. Based on the broad latitudinal distribution of the Monte and the distribution patterns of its entomofauna, five areas of endemism have been defined: North, Center, Uspallata-Calingasta Valley, South, and the Valdés Peninsula (Roig-Juñent et al., 2001; Rundel et al., 2007). Also based on the distribution of insects, Roig-Juñent et al. (2002) conducted a Parsimony Analysis of Endemicity (PAE), which recognizes not only the areas proposed above but also new possibilities for areas within the Monte that should be analyzed in detail with additional taxa.

Based on vegetation, We propose three districts Northern, Eremean, and Southern districts, which match the entomological areas proposed by Roig-Juñent et al. (2001). The Northern district corresponds to the Northern and Central Monte, the Eremean district corresponds to the area of endemism of the Uspallata-Calingasta Valley, and the Southern district corresponds to the Southern Monte and the Valdés Peninsula.

A division of the area of the Monte into areas of vertebrate endemisms has not yet been proposed (Müller, 1973; Ringuelet, 1961). Nevertheless, based on the analysis of the distribution of herpetofauna, we recognized several endemic species for each district.

6. Districts of the Monte

The Eremean District (Fig. 1) covers a narrow strip along the length of the high pre-Andean valleys of Mendoza and San Juan.



Fig. 2. Area of distribution of: (A) Larrea divaricata (after Ezcurra et al., 1991), Montea aphylla, and Condalia micophylla; (B) Larrea cuneifolia (after Ezcurra et al., 1991); (C) Larrea nitida and L ameghinoi (after Ezcurra et al., 1991); (D) Parkinsonia praecox glaucum (After Martínez Carretero, 1986). Grey area shows the Monte Biogeographic Province.

Annual precipitation is between 50 and 100 mm, sometimes lower. Contracted vegetation is present. Characteristic species include *Larrea divarivata subsp. monticellii* (Perrone et Caro) Roig, *Puna clavarioies* (Pfeiff.) R. Kiesling, and *Cistante densiflora* (Barnéourd) Hershk.The only known endemic reptile to this area is *Homonota* *andicola* and endemic insects can be checked in Roig-Juñent et al. (2001).

The Northern District (Fig. 1) encompasses the largest extent of land, from Salta and Tucumán provinces to the south of Mendoza. Climate is characterized by subtropical rainfall showing a marked seasonal rhythm and dry winters. Annual precipitation is between 200 and 400 mm. This district is subdivided into three subdistricts. Endemic reptiles to this area are *Liolaemus salinicola*, *L. scapularis*, *L. riojanus*, *L. anomalus*, *L. pseudonomalus*, *L. olongasta*, *L. duellmani*, *L. cuyanus*, *L. laurenti*, *Elapomorphus cuyanus* and *Leiosaurus catamarcensis*. Endemic insects can be checked in Roig-Juñent et al. (2001).

The Tucumán-Salta Subdistrict (Fig. 1) comprises a narrow strip in the northwest of Tucumán and South of Salta, and penetrates into the north of Catamarca. It is characterized by a closed canopy riparian forest with Chacoan trees, such as *Prosopis nigra* (Gris.) Hieron., *P. alba* Griseb, *Acacia visco* Lorentz ex Griseb as well as by diverse shrubs, such as *Krameria lappacea* (Dombey) Burdet et B. Simpson, *Senna crassiramea* (Benth.) H. Irwin et Barn., and *Pletrocarpa rougesii* Descole, O'Don. et Lourteig. Annual precipitation ranges between 200 and 300 mm.

The Central Subdistrict (Fig. 1) stretches over a large part of the Monte Biogeographic Province, from Catamarca to southern Mendoza. Landscapes feature are foothills, valleys and plains. Annual precipitation is around 200 mm. There are closed canopy riparian forests and marginal to them *Prosopis flexuosa* DC forests. *Bulnesia retamo* (Gillies ex Hook. et Arn) Griseb reaches its southern boundary on the border with the Pampa Subdistrict. Characteristic or typical species include *Prosopis alpataco* Phil., *P. argentina* Burkart, *Ephedra boelckei* Roig, *Heliotropium curassavicum* var. *fruticulosum* I.M. Johnst., and *H. ruizlealii* I.M. Johnst.

The Pampa Subdistrict (Fig. 1) begins in southern Mendoza stretches eastwards to include the west and southeast ports of La Pampa Province. Landscapes consist of plains, scarcely developed valleys, and basalt flows. To the east, the Pampa Subdistrict mixes with the forests of *Prosopis caldenia* of the Espinal Phytographic Province. Annual precipitation ranges from 200 to 400 mm. Differential species include *Junellia connatibracteata* (Kuntze) Mold., *Shhinus johnstonii* Barcley, and *Gutierrezia spathulata* (Phil) Kurtz. In some areas, there are sand dune areas with *Elionurus viridulus* (Spreng) Kunth.

The Southern District (Fig. 1) lies south of the Colorado River. Landscapes made up of Patagonian plateaus. Annual rainfall, ranges between 100 and 500 mm. The *Larrea* community makes up the lowest vegetation layer, and a second layer is rich in Patagonian species. The rainfall regime is typical of Mediterranean area with rains generally occurring throughout the year. Winters in the area are typically wet. Characteristic or differential species include *Larrea ameghinoi*, *Aylacophora deserticola* Cabrera (Neuquén), *Chuquiraga avellanedae* Lorentz, *Tetraglochin caespitosum* Phil., *Chuquiraga rosulata* Gaspar, and *Maihuenia patagonica* (Phil.) Britt. et Rose, with a lower layer rich in winter therophytes. It is divided into three subdisricts. Endemic reptiles to this area are *Liolaemus goetschi*, *L. donosobarrosi*, *L. melanops*, *L. martorii*, *L. gununakuna*, and *Amphisbaena angustifrons plumbea*. Endemic insects can be checked in Roig-Juñent et al. (2001).

The Northern Patagonia Subdistrict (Fig. 1) comprises the creosote bush shrublands of Río Negro and Neuquén provinces. Annual precipitation is between 150 and 250 mm. Characteristic or differential species include *Larrea ameghinoi*, *Maihuenia patagonica*, and *Nardophyllum deserticola* (Cabrera) G. Nesom. Shrub species are dominant and tree species, such as *Geoffroea decorticans* (Gill. ex H. et A.) Burkart and *Prosopis flexuosa* var. *flexuosa*, are scarce.

The Southern Patagonian Subdistrict (Fig. 1) includes *Larrea* Communities of the Chubut Province. Low shrublands alternate or mix with Patagonian elements, notable among which is *Chuquiraga avellanedae*. There are no trees. Annual precipitation is low, ranging between 150 and 200 mm.

The San Jorge Gulf and Punta Ninfas or Atlantic Shrub Subdistrict (Fig. 1) is a territory surrounded by the Atlantic Ocean, which accounts for the higher precipitation (200–250 mm). Even though the species of *Larrea* disappear in these areas, other elements of the Monte persist, such as *Condalia microphylla*, *Prosopis flexuosa* DC var. *depressa* Roig, and *Schinus fasciculata* (Gris.) I.M. Johnst.. Characteristic or differential species include *Brachycladus lycioides* D. Don, *Baccharis triangularis* Hauman, *Stipa papposa* Nees, *S. longiglumis* Phil., and *Chuquiraga avellanedae*, this last one being frequently dominant.

7. Origin of the Monte biota

7.1. Age of different biogeographic components of the desert

The ensemble of organisms inhabiting a biogeographic region during a specific time is known as biogeographic component (Morrone, 2004; Roig-Juñent et al., 2008). Overall, the biogeographic components of an area have multiple origins. Deserts, for example, show biogeographic components from different geologic ages which are related to different biotas but that currently coexist in the same area (Navone et al., 2006; Roig-Juñent et al., 2008). The existence of deserts dates back to very old geologic times: large desert areas are known to have existed in Pangea. Throughout time, organisms have evolved which have become adapted to deserts, constituting in many cases genetic reservoirs of superior taxa now extinct in other parts of the globe. The existence of very primitive groups shows another very important feature of deserts, their persistence throughout the history of life on Earth (Shmida, 1985).

From the phylogeny and distribution of flora and fauna we can infer the age of the different groups of desert areas in South America.

7.1.1. Paleorelicts: South American desert taxa with related groups in other continents

Ages have been proposed for several arid lands of the South Hemisphere. Barnard (1998) proposes that the Namib Desert has been arid from at least 55 mya and that the region, isolated between the ocean and an escarpment, is a constant island of aridity surrounded by a sea of climatic change (Armstrong, 1990). Although it has been proposed that this desert was created 55 mya, it is very likely that arid conditions started before the continental split of West Gondwana, 80 mya, when the central part of Gondwana was an immense desert. Likewise, one part of South America was a desert during this period. The taxa that originated at this time, before the break-up of Gondwana, should currently show a distribution pattern of endemic taxa in different world deserts, and the phylogeny of each group should show clear vicariant events. Some plant groups have evolved since the Mesozoic in arid regions of the South Hemisphere and are presently found with a disjunct distribution (Shmida, 1985). Such as the case of the Zygophyllaceae, which show two clear clades, one African and the other American (Lia et al., 2001). Also Prosopis is also a taxon that shows a clear vicariant event between African-Asian and American species. Regarding insects, the same pattern can be found in the tribe Cicindini, with two species. This tribe is a basal group of Carabidae (Coleoptera), a family having some 40,000 species in the World. One species of this tribe, Cicindis bruchi Horn, occurs in the Salinas Grandes of Argentina, and the other one in Iran. This relictual distribution of these species, together with its basal position in the family, has led to the postulation that it must have originated in the central area of the Pangea (Roig-Juñent et al., 2008). Another example is the Karumiinae (Coleoptera: Dascillidae), a small group of seven genera that inhabit deserts of Iran-Afghanistan, Argentina, western USA, northern Africa, and Chile (Roig-Juñent and Lagos, 2008). Other arthropods also show this pattern, such as the Daesiidae (Solifuga), with representatives in South Africa, Spain, and the Near East, and the genera Syndaesia Maury and Valdesia Maury restricted to the Monte (Maury, 1998).

7.1.2. South American desert taxa with related groups only in America

Even though there are taxa that are common to almost every desert in the world, many taxa have evolved in each arid region of their own continent. For example, Kuschel (1964) showed that a large proportions of the insect fauna of arid regions of South America, Africa, and Australia have no direct phylogenetic relationships among them. This supports the idea that these taxa must have evolved after the break-up of Gondwana break-up. Within this group of taxa in America we can recognize two different cases, an old element that shows ancient relationships with northern deserts, and elements that show recent relationships. One group that shows old relationships among the American desert areas after the Gondwana break-up is Cactaceae. The Cactaceae with about 1500-1800 named species show a basal split between North and South American clades (Edwards et al., 2005) and this separation is prior to the Opuntiodea and Cactoideae clades that could have originated about 20-25 my a (Edwards et al., 2005). Also proposed for early diversification after the Gondwana break-up is the American clade of Prosopis (Burghardt and Espert, 2007), which comprises two groups of species, Strobocarpa and Alganobia. These authors conclude that all the species of both groups growing in North America and South America centers of distribution comprise an ancestral palaeoflora, and that diversification had taken place before the separation of both areas, since the North American species of Prosopis do not form a monophyletic group. Other authors have also proposed a Cenozoic arid biota for America. Solbrig (1976) proposed that the Monte and Chaco were a savanna at the beginning of the Cenozoic, made up of Tertiary-Chaco-Paleoflora. During the lower Cenozoic, South America had one of its wettest periods. Nevertheless, palynological data have shown the existence of a small area with semi-arid conditions in centralwestern Argentina in the Eocene (Volkheimer, 1971). For the Pliocene, we have evidence of the existence of more or less extensive areas of semi-desert, which have persisted to the present day, although they may have changed considerably in extent. The major factor generating this semi-arid condition was the uplift of the Andes Mountains, which produced a slow decrease in precipitation in the regions to the west. This process, along with the rise of the Sierras Peripampásicas that blocked the winds of the Atlantic, resulted in the formation of xeric shrubland landscapes, such as the Monte. Therefore, the dry habitat area has changed in size as a result of climate changes, especially during the Cenozoic. During dry periods, the Monte was larger than it is today and included current areas of the Chaco in the Salinas Grandes (Mares et al., 1985).

In addition to those groups showing an old relationship in all the American deserts, there are some particular taxa that have a different age. This is the case of Larrea (Zygopyllaceae), a genus endemic to America, distributed in the southwest of North America, Argentina, specifically in the Monte, and in small areas in Chile and Bolivia. In the Monte, Mojave and Sonoran deserts, Larrea species are an important element of the community. Because of this similarity, Johnson (1940) and Roig and Rossi (2001) postulated the existence of a land connection between these deserts and, therefore, a common origin for their biota. Nevertheless, a comparison of taxa is not sufficient to establish a criterion of similarity between the different floras, because that existence of common genera cannot reveal whether the species occurring in both deserts are closely or distantly related phylogenetically related (Solbrig et al., 1977). Lia et al. (2001) have shown that Larrea tridentata DC, the sole North American species, is the sister species of Larrea divar*icata* Cav. and that both make up the sister group of the remaining species. These authors conclude that the genus Larrea originated in South America and that subsequent long-distance dispersal to North America of the ancestor of Larrea divaricata-L. tridentata caused allopatric divergence. Two different ages have been proposed for this event. The first one is considered to have occurred during the last glacial episode, with later expanded distribution in to North America (Cordo and DeLoach, 1993; Schultz et al., 1977; Schultz and Floyd, 1999). This assumption is supported by other studies that show that the oldest fossil of Larrea in North America is about 18,700 years BP (Van Devender, 1990). Nevertheless Cortés and Hunziker (1997) estimate the speciation event of Larrea divaricata-L. tridentata on the basis of isoenzymes between 1.2 and 0.6 mya and, more recently, on the basis of rbcl substitution rates between 4.2 and 8.4 mya (Lia et al., 2001). We agree with the hypothesis of Lia et al. (2001) that the phenomenon of dispersal of L. tridentata was much earlier than 18,000 years BP because of the presence of at least 30 monophagous insect species on this plant species (Schultz et al., 1977) which have coevolved with it. Furthermore, no herbivorous insect species that feeds on *Larrea* is common to both areas (Cordo and DeLoach, 1993; Schultz et al., 1977). Not only is it interesting that there are no species in common, but also that neither the generic and some supra-generic taxa show no similarities between deserts. This is the case with the Naupactini (Curculionidae), which show high richness of genera and species endemic to Argentina but are completely absent in North America. All insects associated with creosote bush in North America are of North American origin and did not migrate from South America with this shrub; instead, their speciation processes presumably evolved as a response to the introduction and eventual dominance of this new resource (Schultz and Floyd, 1999).

Another case similar to that of *Larrea* is shown by the American species of *Parkinsonia*. This genus has the greatest species diversity in North American deserts, and only one species in Argentinean deserts, *Parkinsonia praecox*. Haston et al. (2005) developed a phylogenetic analysis that found that most of North American species are basal, and that *P. praecox* belongs to a North American and South American clade, this species being the adelphotaxon of the North American species a recent event of speciation within the genus.

7.1.3. Endemic South American desert taxa

Several higher rank taxa are endemic to the South American deserts and have their sister groups in mesic or humid tropical areas of the Netropics.Such is the case of endemic tribes of coleopteran insects, like Cnemalobini (Carabidae), Eucranini (Scarabaeidae), and Allidostomatinae. For some of these tribes their existence throughout the Cenozoic was proposed (Roig-Juñent et al., 2008).

7.1.4. Neoendemic desert taxa

This is a term proposed by Shmida (1985) for those endemic taxa that have undergone recent rapid speciation in desert environments.-Neo-endemisms can be detected by first checking whether the sister groups occur in the neighboring non-desert regions, and second by determining whether these neo-endemisms are terminal species of the cladogram. A clear example is given by the lizards of the genus Pristidactylus Fitzinger. This genus probably originated in the mesophylla forests of southern Chile, a habitat that is now occupied by the primitive and treedwelling Pristidactylus torquatus (Philippi) (Cei, 1986; Scolaro et al., 2003). This genus was proposed to have undergone speciation, following "vanishing refuge" theory, resulting in species of rocky areas of Patagonia, extra-Andean mountains, or of shrublands of the Monte, and whose final phase of ecogeographic speciation is represented by Pristidactylus fasciatus (D'Orbigny and Bibron), a species that is representative of arid environments of the Monte (Cei, 1986; Lamborot and Díaz, 1987; Scolaro et al., 2003).

Therefore, we find that the biota of Monte is composed of an assemblage of organisms of different origins, mostly Neotropical and Patagonian, as well as of older groups from before Pangea fragmentation and a few ones of recent holarctic origin.

7.2. Relationships with other American deserts

The old elements of American deserts show a common origin and evolution of this desert biota such as Cactaceae, Prosopis, Zygophyllaceae, among others. The close relationships with some North American deserts have been discussed above, considering that most species in the Monte and in the deserts of southwestern North America are not vicariant, that is to say that they do not come from a common ancestry. Other data support this idea. Solbrig (1976) stated that all 51 plant genera in common to these two deserts are also distributed in the rest of Tropical America, and that the species present in both deserts are not closely related phylogenetically with one another. This same situation occurs with insects since, for example, none of the species of Apoidea is shared (except for the introduced Apis melifera), and the species of the 12 genera occurring in both areas their species are not closely related phylogenetically. Also few species of vertebrates are common to both areas, 10 birds and 6 mammals, some of which are introduced and the remainder are widely distributed Throughout America (Solbrig, 1976). Among reptiles, there are few genera common to both North and South America, all widespread across in the Americas. This is the case with Crotalus Linnaeus, Leptotyphlops Fitzinger, and *Cnemidophorus* Wagler, the last being primarily distributed in arid and semiarid zones (Blair et al., 1976; Wright, 1993). Therefore, the similarity between the floras of these two areas may be the result of adaptations to arid zones involved in processes of parallel or convergent evolution. In both types of evolution, the flora may have evolved from groups that are widely distributed in tropical regions (Solbrig, 1976) and the distribution of Larrea, Parkinsonia, and Prosopis should be treated as special cases for these particular genera and not for the entire biota.

Different biogegraphic analyses have proposed a close relationship between the Monte with Chaco and Pampa biogeographic provinces. A biogeographic study using track analysis shows that the Monte biota is more related to that of Chaco-Caatinga (Roig-Juñent et al., 2006), whereas cladistic biogeographic analyses show that Monte and Chaco are closely related, with Chaco being strongly related to the northern area of Monte (Morrone, 1993; Roig-Juñent et al., 2006).

8. The Monte and its location in biogeographical schemes

South America is characterized by the existence of two different biotas. These two biotas have been recognized as Patagonian (=Paleeantartic, Notogeic) and Brazilian (=Inabrésic) (Jeannel, 1942, 1967; Kuschel, 1964, 1969; Ringuelet, 1956, 1961). The tropical biota of South America is related to the tropical biota of other austral continents whereas the austral biota is related with the biota of southern Australia, Tasmania and New Zealand (Crisci et al., 1991; Jeannel, 1967; Ringuelet, 1961). It has been well documented that these two biotas were in contact and underwent displacements principally as an outcome of large climate changes during the Cenozoic. For this reason, Morrone (2004, 2006) recognized the Monte as one of the biogeographic provinces that make up of the South American Transition Zone.

Regarding arthropods, we find a mixture of Patagonian and Brazilian elements that support this idea of a Transition Zone. Many of the insect groups are Brazilian (Roig-Juñent et al., 2001), but there are important arthropod groups that are related to the Patagonian fauna, such as the scorpions (Acosta and Maury, 1998). Reptiles also show a mixture of Patagonian and Brazilian elements. Those of Patagonian origin include the genus *Diplolaemus* Bell, of relatively recent speciation, which enters in ecotones of the Monte with *D. sexcinctus* Cei, Scolaro and Videla, whose northern boundary occurs in the central zone of the Monte (Mendoza Province) (Cei et al., 2003). The genus *Pristidactylus*, with several Patagonian species, is present in the Monte with *P. fasciatus* (D'Orbigny and Bibron) (Cei, 1986; Scolaro et al., 2003). *Leiosaurus*, a phylogenetically genus related to *Diplolaemus* and *Pristidactylus* (Frost et al., 2001), includes *L. bellii* Duméril and Bibron, which inhabits ecotonal areas of Monte-Patagonia and species more restricted to the Monte such as *L. paronae* Peracca, *L. catamarcensis* Koslowsky and *L. jaguaris* Laspiur, Acosta and Abdala. The genus *Phymaturus* Gravenhorst, typically Patagonian, comprises 20 species currently described, two of which are present in the shrub steppe of the Monte-Patagonia ecotone (Scolaro, 2005).

Among the reptiles of Brazilian origin, we should mention the Teidae, represented in the Monte by *Teius teyou* (Daudin), *Teius oculatus* (D'Orbigny and Bibron), and *Tupinambis rufescens* (Ávila, 2002; Cei, 1986), and the snakes *Leptotyphlops australis* Freiberg and Orejas Miranda, *L. unguirostris* (Boulenger), *Lystrophis semicinctus* (Duméril, Bibron and Duméril), *Oxyrhopus rhombifer bachmanni* (Weyenbergh), *Philodryas psammophidea* (Günther), *Micrurus pyrrhocryptus* (Cope), and *Bothrops neuwiedi diporus* Cope (Ávila et al., 1998; Cei and Roig, 1973; Scolaro, 2006). The amphibians present in the Monte are all of Chacoan origin, none from Patagonia, with the most representative being Odontophrynus occidentalis (Berg), *Pleurodema nebulosa* (Burmeister) and the widespread toad *Bufo arenarum* Hensel (Cei, 1980).

The Monte greatest floristic similarity is to its neighbor, the Chaco biogeographic province, with which it shares 60% of its species (Solbrig et al., 1977). Nevertheless, from a floristic perspective, the Monte biogeographic province is not the last transition area with the subantarctic biota. The vegetation of the Patagonia biogeographic province, specifically the Patagonian steppe, may have a Neotropical origin; therefore, it is the furthest south area in contact with the southern biota of Nothofagus. Other analyses support this idea. A Cladistic Biogeographic analysis based on plant and insects has shown that Patagonian steppe areas are more related to Chacoan subregion, such as the Pampean province, than to areas of Nothofagus forest (Roig-Juñent, 1994). Also a panbiogeographic analysis (Roig-Juñent et al., 2003) related the Patagonian steppe to Puna, which is another of the provinces considered by Morrone (2006) as part of the South American Transition Zone. Further studies have to consider the possibility of including the Patagonian steppe in the transition zone.

9. Conclusions

The concept of the Monte boundaries have changed throughout the history of scientific research. The numerous studies conducted for, both the Monte areas and for the different regions of the country, have established more precise boundaries that we summarize in this contribution. Even though it has been recognized that there are different areas within the Monte, a general classification of areas has not yet been accomplished. In this work, we propose dividing the Monte into three areas (districts), as well as into subdistricts. Península de Valdés is included as a subdistrict of the southern Monte.

The existence of paleoendemisms may indicate that the Monte-Chaco has existed since, at least, throughout the Cenozoic, which makes it an old arid zone. In this area, there are biogeographic elements of different origin, mainly Patagonian and Brazilian, which have undergone patterns of speciation within the area.

The Monte is a natural area, with at least 30% of its biota endemic to it. Its relationships are stronger with the Chacoan region, but it also shows faunal elements from the Patagonian biota. Due to the presence of different biogeographic elements we agree that the Monte could be considered, as was proposed, as a part of the South American Transition Zone.

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