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RESEARCH PAPER

NEOTROPICAL VEGETATION

Vegetation types of the Arid Chaco in Central-Western Argentina

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Abstract

Aims: We address the following questions: 1) Which are the main vegetation types that currently occur in the Arid Chaco? 2) Do those vegetation types differ in terms of floristic composition, endemism, chorotypes and life forms? and 3) Is there any spatial association between the vegetation types and the environmental heterogeneity of the Arid Chaco? **Study area**: The southwestern extreme of the Gran Chaco, in Central-Western Argentina. **Methods**: The survey was based on a dataset comprising 654 relevés collected according to the Braun-Blanquet method. Data were classified by the hierarchical ISOmetric feature mapping and Partition Around Medoids (ISOPAM), and ordinated through isometric feature mapping (ISOMAP). Bioclimatic and edaphic variables were related to the ISOMAP ordination. **Results**: We recorded 439 vascular plant species, 62 endemic at the national level and 22 endemic species restricted to the study and surrounding environments in Central-Western Argentina. A total of nine vegetation types, belonging to four major clusters, were identified. The most prominent chorotypes included species distributed in the Chaco region and in the Arid Chaco/Monte phytogeographic units. The predominant life forms were micro- and nano-phanerophytes, followed by hemicryptophytes, chamaephytes and mesophanerophytes. **Conclusions**: Major results highlighted that xerophytic shrublands are the most common vegetation types in this area as a result of the historical and present use, while old growth forests were constrained to areas with low anthropogenic disturbance in the last decades or to protected areas. Most vegetation types (with the exception of halophytic environments) are poorly differentiated from a floristic point of view; however, they clearly differ in physiognomy. The floristic composition of the vegetation types described revealed numerous species in common with other sectors of the Chaco of northern Argentina, Bolivia and Paraguay. Although the number of species restricted to the Arid Chaco was quite low, the most relevant chorotype included species with Western and Eastern Chaco distribution, conferring a clear Chaquenian identity to this area and discriminating it from other phytogeographic units.

Taxonomic reference: Catálogo de las Plantas Vasculares del Cono Sur (Zuloaga et al. 2008) and its online update (http://www.darwin.edu.ar).

Abbreviations: ISOMAP = isometric feature mapping; ISOPAM = isometric partitioning around medoids.

Keywords

Arid Chaco, *Aspidosperma* forest, chorotype, endemism, halophytic succulent, shrubland, species richness, vegetation classification

Introduction

The "Gran Chaco" or "Chaco" is a natural ecoregion in South America, comprising about 1,000,000 km^2, expanding in Argentina, Bolivia, Paraguay and a narrow strip in Mato Grosso do Sul, Brazil (Bucher 1982; Prado 1993; Navarro et al. 2006). This huge ecoregion has been traditionally classified into different subunits: Eastern (humid) Chaco, Central (sub-humid) Chaco, Western (dry) Chaco, Sierra (Mountain) Chaco and Austral Chaco (Morello and Adamoli 1968; Cabrera and Willink 1973; Bucher 1982; Prado 1993). Particularly the Western Chaco comprises a series of dry forests and shrublands that share numerous plant species throughout their distribution in northern Argentina, Bolivia and northern Paraguay (Spichiger et al. 1991; Cabido et al. 1993; Mereles 2005; Navarro et al. 2006). In Argentina, the southwestern extreme of the Gran Chaco corresponds to the Arid Chaco Woodland (Morello et al. 1985) which is the driest part of the Chaco ecoregion with the most pronounced xeromorphic vegetation (Morello and Saravia Toledo 1959; Prado 1993). Nowadays, due to domestic livestock grazing, logging and the conversion of forests into silvopastoral systems (Hoyos et al. 2013; Frate et al. 2015; Blanco et al. 2022), the vegetation of the Arid Chaco has been dramatically altered, thus a classification of its current vegetation types is urgently needed.

Over the last century, several phytogeographical synthesis were proposed for Argentina including also the Arid Chaco vegetation (Ragonese and Castiglioni 1970; Cabrera 1976, Oyarzábal et al. 2018, among others). Detailed vegetation studies are available only for restricted areas within the Arid Chaco, such as the Llanos de La Rioja province (Morello et al. 1985; Calella and Corzo 2006; Biurrun et al. 2012; Cabido et al. 2018a), the plains of western Córdoba province (Cabido et al. 1994; Cabido et al. 2018b), south-eastern Catamarca province (Morlans and Guichón 1998; De La Orden and Quiroga 2009), and northern San Luis province (Anderson et al. 1970; Peña Zubiate et al. 1998). Probably the only comprehensive description available today for the whole Arid Chaco vegetation is that of Karlin et al. (2013), but even this study is based on previous surveys comprising a low number of relevés and incomplete floristic records. One of the most interesting features of the Arid Chaco vegetation is the lack of the tree genus *Schinopsis* (red quebracho) and the dominance of the tree species *Aspidosperma quebracho-blanco* (white quebracho) (Sayago 1969; Ragonese and Castiglioni 1970; Morello et al. 1985; Prado 1993). Also, azonal communities such as *Prosopis* spp. woodlands, succulent communities dominated by the candelabra-like cacti *Stetsonia coryne*, and other edaphic vegetation, are frequent in the Arid Chaco (Sayago 1969; Morello et al. 1985; Cabido et al. 1994; Morlans and Guichón 1998; Calella and Corzo 2006; Karlin et al. 2013; Cabido et al. 2018a). Moreover, several endemic genera (*Mymozyganthus*, *Stenodrepanum*, *Setiechinopsis*) and numerous endemic species of the Gran Chaco are present in this area (Ragonese and Castiglioni 1970). As an intrusion of species from the deserts and semideserts of the Monte Phytogeographical Province has been evidenced, especially in the western extreme with drier and harsher environmental conditions (Morello 1958; Cabrera 1976; Morello et al. 1985; Prado 1993), there has been a long debate about the Chaquenian character of this area. Some authors suggested the inclusion of the Arid Chaco within the Monte province (Lorentz 1876; Hauman 1947; Parodi 1964; but see Prado 1993), while others reinforced the Chaquenian character of the Arid Chaco (Ragonese and Castiglioni 1970, Morello et al. 1985).

Formerly an almost continuous forest, the Arid Chaco vegetation has been fragmented and converted mostly into closed and open shrublands with only scattered emergent trees (Morello et al. 1985; Cabido et al. 1994; Zak et al. 2004; Calella and Corzo 2006; Hoyos et al. 2013; Cabido et al. 2018a). Therefore, current vegetation is a mosaic of forests, woodlands, and thorny shrublands, intermingled with cultivated fields and pastures (Cabrera and Willink 1973; Cabrera 1976; Dinerstein et al. 1995; Morrone 2000). The peak of forest exploitation of the Arid Chaco occurred during the last decades of the 19th century and the first four decades of the 20th century, coinciding with the expansion of the railroad network and internal and external demands (Río and Achával 1904; Terzaga 1963; Sayago 1969; Natenzon 1988; Natenzon and Olivera 1994; Karlin et al. 2013). Since about 1950 onwards there has been a slight vegetation recovery and the best-preserved forest patches that can be seen today date from that time (Sayago 1969). With respect to livestock exploitation, since the beginning of the 20th century there has been a general increase in the number of cattle, but also the replacement of cattle by goats. The rise of goat farming clearly increased land degradation focusing not only on the herbaceous communities, but also on the remaining forest patches, with strong impact on tree seedlings (Karlin et al. 2013). Today, most productive activities in the Arid Chaco are related to extensive cattle and goat raising (Blanco et al. 2005; Karlin et al. 2013; Quiroga et al. 2013), and the forage base in all cases is mostly the native flora (Blanco et al. 2005; Herrera et al. 2021). As a consequence, inappropriate logging with overgrazing have caused a slow but continuous degradation in plant communities (Blanco et al. 2005; Blanco et al. 2022). Management decisions, especially those related to biodiversity conservation, are currently being made without a comprehensive knowledge of its full floristic components and the distribution of vegetation types.

The aim of this study was to classify the main vegetation types occurring in the Arid Chaco of Central-Western Argentina. To accomplish this, the following questions were addressed: 1) Which are the main vegetation types that currently occur in the Arid Chaco? 2) Do those vegetation types differ in terms of endemic species, chorotypes and life forms? and 3) Is there any spatial association between the vegetation types and the environmental heterogeneity of the Arid Chaco?

Methods

Study region

The survey was conducted in the Arid Chaco, the south-western extreme of the Gran Chaco, extended across ca. 9.6 million ha in Central-Western Argentina (64°00' and 67°50'W – 28°20' and 34°00'S) (Ragonese and Castiglioni 1970; Morello et al. 1985; Karlin et al. 2013) (Figure 1). From the biogeographic point of view, the Arid Chaco is included in the Chaquenian Region (Región Chaqueña), and within it in the Southern Chaquenian Province (Provincia Chaqueña Meridional) (Rivas Martínez et al. 2011a). At the South American level, the study area is included in the lowland deciduous thorn woodland and shrubland geocomplex, and within this complex, it belongs to the Southern Chaco Province (Navarro et al. 2023). Within Argentina, the Arid Chaco belongs to the Chaco Phytogeographical Province (Morello et al. 1985; Biurrun et al. 2012) and has been recognized as a different district (Llanos District) by Ragonese and Castiglioni (1970) and, more recently, by Oyarzábal et al. (2018). In the international literature it has been defined as a thorn woodland (Beard 1955), as a dry subtropical wood (Sarmiento 1972), and also as xeric forests of the Southern Chaco (Bosques xéricos del Chaco Meridional) (Josse et al. 2003). On a global scale, the forests and shrublands of the Arid Chaco correspond to the tropical-subtropical dry forests and thickets within the tropical-subtropical forest biome (Keith et al. 2020). It borders the Monte Phytogeographical Province

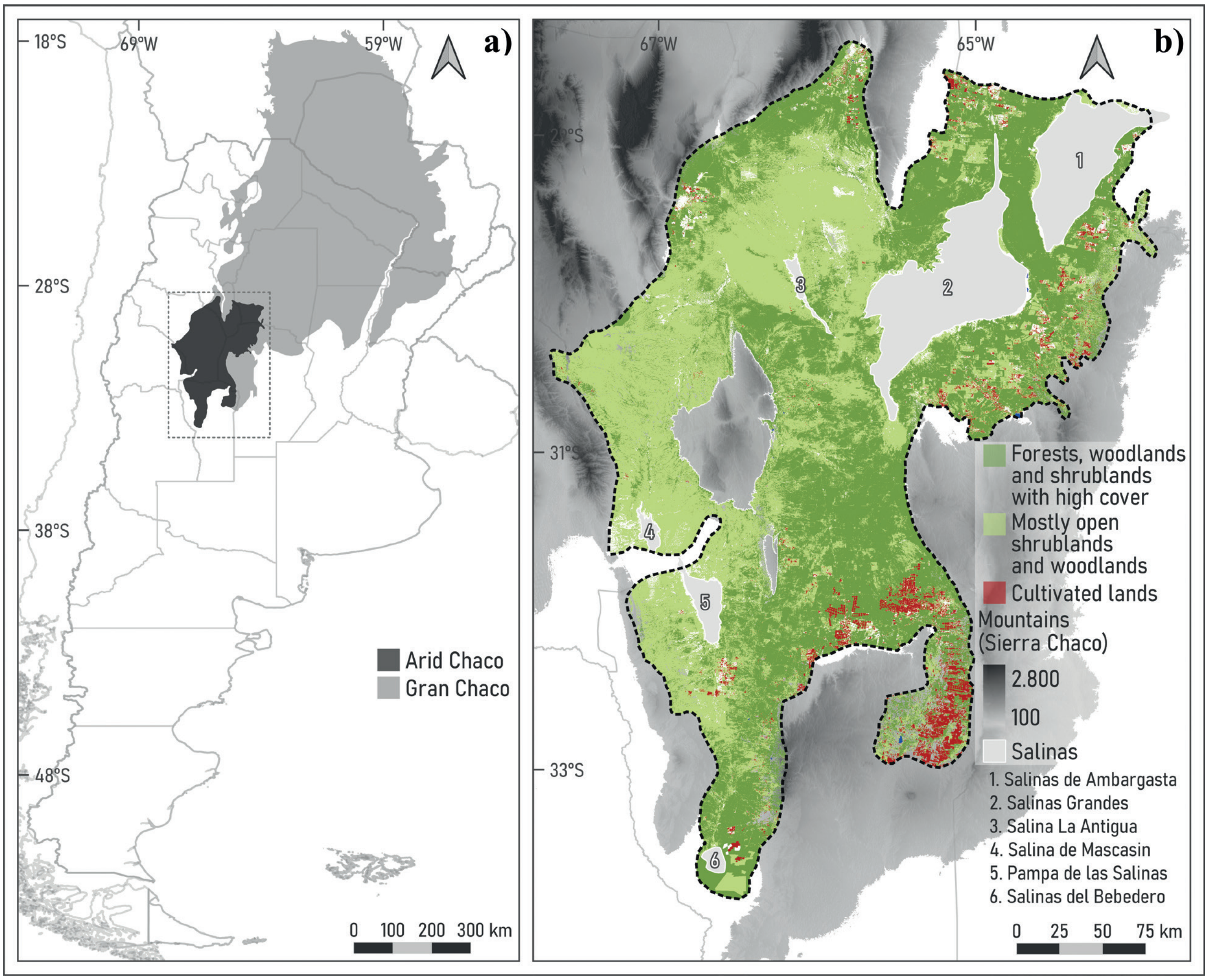

Figure 1. The study area: **a)** The location of the Arid Chaco in Argentina and within the Gran Chaco; and **b)** Arid Chaco and major features of the environment of the study region (in grey are shown the elevation gradient). Cover adapted from MapBiomas Chaco Project Collection 3.0 of the annual land use and land cover maps, accessed on December 2022. Datum: WGS 84, EPGS: 4326.

in the west and, to the south-east, the Espinal as well as the Western Chaco to the north-east (Morello et al. 1985); the surrounding mountain slopes belong to the Sierra Chaco or Mountain Chaco District (Karlin et al. 2013). The transition between the Arid Chaco and the Monte Phytogeographical Province has been a matter of controversy since decades ago (Lorentz 1876; Hauman 1947; Parodi 1964), until Morello (1958) traced the limit ca. along the 250 mm isohyet and pointed out the existence of a transitional belt where taxa of both units coexist.

Bioclimatically the study area belongs to the tropical xeric bioclimate (Rivas Martínez et al. 2011b). Annual rainfall ranges from over 500 mm in the east to 250–300 mm in the west of the area, with warm season rainfall (more than 70% of the rainfall falls from November to April) (Karlin et al. 2013). The decrease in rainfall is accompanied by the lengthening of the dry season from 5 to 7 months (Morello et al. 1985). In contrast with the pronounced precipitation gradient, the area shows a relative isothermal condition and mean annual temperatures vary between ca. 21 °C in the north and 18 °C in the south (Karlin et al. 2013). Absolute maximum temperatures may exceed 45 °C during the warmest months, while frosts may occur from May to August. Because of the high temperatures, intense solar radiation and low relative humidity, potential evapotranspiration is high, ranging from more than 1600 mm/yr^{-1} in the north and 900 mm/yr^{-1} in the southern extreme of the study area (Capitanelli 1979a; Karlin et al. 2013).

Previous authors have associated the distribution of the vegetation of the Arid Chaco in Argentina with topography and geomorphology (Cabido et al. 1994; Morlans and Guichón 1998; Calella and Corzo 2006; Karlin et al. 2013). On a broader scale, the association between the distribution of forests and shrublands in the Paraguayan and Bolivian Chaco with topography and, mainly, with soil internal drainage has been also highlighted (Spichiger et al. 1991; Mereles 2005; Navarro et al. 2006). The Arid Chaco occupies sedimentary basins, (locally named bolsones), which are sites of active deposition of sediments entirely surrounded by recently uplifted mountains (Carignano et al. 2014). These basins originated during the Tertiary as a consequence of the lowering of the crystalline shield and the uplifting of the Andes. The average elevation is ca. 300 m in the east and more than about 700 m in the western extreme, while in saline depressions altitudes hardly reach 200 m (Cabido et al. 1993). There are no permanent rivers, only temporary water courses. Different landforms can be recognized in the bolsones: the piedmont (transitional areas between the steep slopes and the plains, locally known as bajadas in their distal parts), fluvio-eolian plains, dry lakes (playas), salt flats (salinas) and muddy saline areas (barreales) (Capitanelli 1979b; Cabido et al. 1992; Cabido et al. 1994; Morlans and Guichón 1998; Karlin et al. 2013). Playas and barreales are low areas, with salty soils, while salinas are flat areas occupied by salt. Playas, barreales and salinas usually lack vegetation except on their perimeter (Karlin et al. 2013). Dune fields can also be found between the playas and salt flats, or scattered in the plains. Dunes are usually composed of relatively fine sands that are mostly stabilized by halophytic and xerophytic vegetation (Karlin et al. 2013). The most frequent soils in the Arid Chaco are aridisols and entisols (Peña Zubiate et al. 1998; Blanco et al. 2005). In general, the organic matter content is less than 1% and the texture varies from sandy to clayey soils (Gómez et al. 1993; Ayan et al. 2010). The water table at the foot of the mountains, in the distal bajada, is between 80 and 120 m deep, reducing the depth towards the lowlands to 8–12 m. In saline areas, the water table is almost at surface level, fluctuating according to rainfall between 0 and 5 m deep (Karlin et al. 2013).

Similar to what has been reported for other sectors of the Chaco in northern Argentina (Aguiar et al. 2022), Bolivia (Navarro 2011) and Paraguay (Mereles 2005; Navarro et al. 2006), and despite the association with topography and soils, the mosaic of plant communities that characterizes the Arid Chaco region today is heavily degraded and strongly influences to human activities (Morello and Saravia Toledo 1959; Sayago 1969; Bucher and Schoffield 1981; Morlans and Guichón 1998; Calella and Corzo 2006). The *Aspidosperma quebracho-blanco* forest, which most authors agree is the potential vegetation of the Arid Chaco, is currently very fragmented and reduced to few patches in protected areas or in isolated piedmont territories with little disturbance. The rest of the plains are covered by different phases of *Aspidosperma* forest degradation: low forests and woodlands, closed shrublands and thickets and patches with low plant cover and high percentages of bare soil, locally known as peladares (Morello et al. 1985; Cabido et al. 1992; Hoyos et al. 2018).

Vegetation sampling and environmental variables

A total of 654 phytosociological relevés were sampled during the last 20 years to represent the wide geographic, topographic and ecological heterogeneity comprised in the Arid Chaco. All vegetation plots can be found in Suppl. material 1. Relevés were performed during the rainy season (summer of Southern Hemisphere) and were taken following the criteria of physiognomic, floristic and ecological homogeneity. For each relevé (20 × 20 m) percentage cover of tree (>5 m to canopy height), shrub (0.5 to 5 m) and herb (<0.5 m) layers and bare soil were visually estimated. The complete list of vascular plants was registered including their abundance using the cover-abundance scale of Braun-Blanquet (Braun-Blanquet 1932). The distribution of the relevés is reported in Suppl. material 2: Appendix 1, figure S1.1. Endemic taxa at the national and more restricted levels (Arid Chaco and Monte regions), followed Zuloaga et al. (1994, 2008), Cabido et al. (1998), Zuloaga and Morrone (1999a, 1999b), Chiapella and Demaio (2015) and Giorgis et al. (2021). In addition, species were assigned to different chorotypes (groups of species with a similar distribution), following the criteria of Cabido et al. (1998): Southern-Brazilian/Paranaense, Western and Eastern Chaco, Espinal/Pampean, Arid Chaco and Monte, High and Andean Mountains/Puna, Patagonian and Ubiquitous (widely distributed in all Argentina and neighbor countries). Non-native species were also registered. Species were also classified into life forms following the scheme of Raunkiaer (1934), slightly adapted to the Chaco vegetation. The following categories were used: C, Chamaephytes (low shrubs, sub-shrubs, some perennial herbs); E, Epiphytes; F, Ferns; G, Geophytes; H, Hemicryptophytes; Kc: Columnar cacti; Ko, Opuntioid cacti; L: Climbers; P, Parasites and hemi-parasites; Ph, Phanerophytes (Phsa, sub-shrubs; Phs, shrubs; Phss, succulent shrubs; Pht, trees); T: Therophytes.

Bioclimatic variables were interpolated from the CHELSA (Climatologies at High Resolution for the Earth's Land Surface Areas) database (Karger et al. 2017), using the raster R-package (Hijmans et al. 2019). CHELSA provides high-resolution information on climatic conditions data of downscaled model output temperature and precipitation estimates of the ERA-Interim climatic reanalysis to a high resolution of 30 arc seconds. We selected bioclimatic variables previously reported as good predictors of floristic composition in previous studies in the same area (Cabido et al. 2018b; Zeballos et al. 2020): Annual Mean Temperature (AMT), Annual Precipitation (AP), and Precipitation seasonality (PS) (see O'Donnell and Ignizio 2012 for details concerning bioclimatic variables). We also obtained an Aridity index from the Climate Database v2 (Trabbucco and Zomer 2018). The Aridity index datasets provide high-resolution (30 arc seconds) global raster climate data for the 1970–2000 period, related to evapo-transpiration processes and rainfall deficit for potential vegetative growth, based upon implementation of a Penman Montieth Reference Evapotranspiration equation (Trabbucco and Zomer 2018). Finally, different soil variables related with soil texture and salinity were taken from the Global Map of Salt-Affected Soils (Omuto et al. 2020). Soil fractions in Clay, Silt and Sand (g/100g), were taken for the 0–15 cm soil depth (Schulz et al. 2022), while pH on water, electrical conductivity (dS/m) and exchangeable sodium percent (%) at depth interval of 0–30 cm (Rodríguez et al. 2021) both at 1000 m resolution, were also included in the analyses.

Data analysis

The data set of 654 plots and 439 species was classified into the major vegetation clusters using the ISOmetric feature mapping and Partition Around Medoids (ISOPAM) method (Schmidtlein et al. 2010; Černý et al. 2015), run on a Bray-Curtis dissimilarity matrix and cover-abundance transformed into central class values (van der Maarel 1979; Kent and Coker 1992). The maximum number of clusters on each hierarchical level was arbitrarily set to 10 and standardized G statistics to five. After that, diagnostic species were selected using the *phi* coefficient of fidelity for each vegetation type (Chytrý et al. 2002). For this, the fidelity of species to vegetation types was calculated with presence/absence data, with the *phi* coefficient applied to clusters of equalized size (Tichý and Chytrý 2006). We considered a species as diagnostic if *phi* > 0.1, had a constancy value equal or higher than 25% and a statistically significant ($p < 0.001$) association with a particular cluster according to Fisher's exact test. Clusters were named as vegetation types after species with: 1) *phi* ≥ 0.3 and a statistically significant ($p < 0.001$) association with a given cluster; and 2) constancy ≥ 45%. The species × relevés matrix was ordinated through isometric feature mapping (ISOMAP; Tenembaum et al. 2000; Černý et al. 2015), using the number of neighbors to the optimal value from the first hierarchical level of the ISOPAM classification. Environmental and soil variables were related to the ISOMAP ordination through the *envfit* function from the vegan R-package.

Incidence-based rarefaction and extrapolation (R/E) curves using sample size-based and coverage-based methods were performed to evaluate whether plant species from the different vegetation types classified by the ISOPAM method were well represented (Zeballos et al. 2020; Cantero et al. 2022). Non-parametric estimators for incidence data, and incidence-based rarefaction and extrapolation (R/E) curves were performed using the *SpadeR* and *iNEXT* R-packages (Chao and Chiu 2016; Hsieh et al. 2016), respectively.

Finally, one-way ANOVAs were performed in order to evaluate the differences in the mean percentage of life forms, endemic species and the mean percentage of each chorotype per vegetation type, as well as the differences in bare soil, height and cover of different layers among the vegetation types. The normality of the data and the homoscedasticity of variances were previously evaluated and when these requirements were not accomplished the data were natural log transformed. All statistical analysis and graphics were performed in R software version 4.0.2 (R Core Team 2021).

Results

Floristic composition of vegetation types

We recorded a total of 439 vascular plant species, distributed in 60 families and 241 genera (Table 1; Suppl. material 3). The richest family was Poaceae with 69 species, followed by Asteraceae (49 species), Fabaceae (34 species), Cactaceae (29 species), Solanaceae (26 species), Malvaceae (24 species), Euphorbiaceae (22 species), Amaranthaceae (20 species), Bromeliaceae and Verbenaceae (15 species each). The richest genus was *Tillandsia* with 13 species, followed by *Solanum* (11 species), *Euphorbia* (10 species), *Portulaca* and *Setaria* with nine species each.

We should note that 62 endemic species at the national level (14.0% of the total) and 22 (4.9%) endemic species restricted to the study area and surrounding environments of the Monte and the Western Chaco were recorded. The life-

Table 1. Summarized synoptic table obtained through the ISOPAM classification showing the vegetation types along with the percentage constancy and mean Braun-Blanquet cover-abundance values (as superscript) based on 654 relevés recorded in the Arid Chaco, Central-Western Argentina. Species are sorted by decreasing fidelity within each vegetation type. Dark, light dark, medium, light grey and low light grey indicate *phi* > 0.5, *phi* > 0.4, *phi* > 0.3, *phi* > 0.2 and *phi* > 0.1, respectively. Vegetation types are: 1.1, *Aspidosperma quebracho-blanco* forest; 1.2, *Larrea divaricata* shrubland; 1.3, *Prosopis flexuosa* woodland; 2.1, *Larrea cuneifolia* shrubland; 2.2, *Larrea cuneifolia – Bulnesia retama* shrubland; 3.1, *Mimozyganthus carinatus – Bulnesia foliosa* shrubland; 3.2, *Tricomaria usillo* shrubland; 4.1, *Suaeda divaricata – Atriplex argentina* shrubland; 4.2, *Heterostachys ritteriana – Allenrolfea patagonica* succulent shrubland. Only those species with constancy ≥ 25% in at least one vegetation type were included in the table. CT, chorotypes: Southern-Brazilian/Paranaense (1), Western and Eastern Chaco (2), Espinal/Pampean (3), Arid Chaco/Monte (4), High and Andean Mountains/Puna (5), Patagonian (6), Non-native (7), Ubiquitous (8). LF, Life forms: C, Chamaephytes (low shrubs, sub-shrubs, some perennial herbs); E, Epiphytes; F, Ferns; G, Geophytes; H, Hemicryptophytes; Kc: Columnar cacti; Ko, Opuntioid cacti; L: Climbers; P, Parasites and hemi-parasites; Ph, Phanerophytes (Phsa, sub-shrubs; Phs, shrubs; Phss, succulent shrubs; Pht, trees); T: Therophytes. Symbols: †, endemic species at the national level, and *, endemic species at more local level.

Plant communities			1.1	1.2	1.3	2.1	2.2	3.1	3.2	4.1	4.2
Numbers of relevés			80	171	61	52	78	56	68	58	30
Species	CT	LF									
Justicia squarrosa	2	Fsa	65^{2}	13^{1}	8^{+}	2^{+}		2^{+}	1^{+}		
Senegalia gilliesii	4	Fs	83^{2}	23^{1}	11^{+}	15^{2}	4^{1}	14^{2}	3^{1}		
Sarcomphalus mistol	2	Ft	58^{1}	15^{+}	8^{+}	8^{+}		2^{+}	1^{+}		
Tillandsia duratii	2	E	73^{+}	27^{+}	10^{+}	35^{+}	6^{+}	13^{1}	13^{+}	7^{+}	
Tillandsia xiphioides	2	E	60^{+}	19^{+}	5^{+}	21^{+}	1^{+}	16^{+}	6^{+}	5^{+}	
Tillandsia aizoides	2	E	36^{+}	12^{+}	2^{+}	6^{+}	1^{+}	4^{+}	1^{+}		
Tillandsia pedicellata	2	E	46^{+}	17^{+}	2^{+}	17^{+}		11^{1}	3^{+}		
Tillandsia rectangula	2	E	26^{+}	7^{+}	3^{+}	2^{+}			1^{+}		
*Cardiospermum halicacabum**	1	T	25^{+}	5^{+}	2^{+}	10^{+}		4^{+}	3^{+}		
*Lycium elongatum**	4	Fs	54^{+}	28^{+}	16^{+}	19^{+}	13^{1}	16^{+}	22^{+}	5^{+}	
*Ayenia cordobensis**	2	Fsa	30^{+}	16^{+}	11^{+}	6^{+}		4^{+}	1^{+}		
Castela coccinea	2	Fs	36^{+}	15^{+}	8^{+}	10^{+}	3^{+}	5^{+}	12^{+}	5^{+}	3^{+}
Cleistocactus baumannii	2	Ko	31^{+}	12^{+}	2^{+}	12^{+}		9^{+}		9^{1}	3^{+}
Setaria lachnea	2	H	44^{1}	22^{+}	21^{1}	17^{+}	9^{1}	18^{1}	3^{+}	3^{+}	
Cereus forbesii	2	Kc	30^{+}	8^{+}	3^{+}	21^{+}		7^{+}	3^{+}	2^{+}	
Tragia hieronymii	2	Fsa	41^{+}	21^{+}	31^{+}	12^{+}	5^{+}	14^{+}	4^{+}		
Justicia xylosteoides	2	Fs	26^{+}	9^{+}	5^{+}	15^{+}	1^{+}	7^{1}	3^{1}		
Tillandsia myosura	8	E	34^{+}	19^{+}	8^{+}	21^{+}	4^{+}	9^{1}	6^{+}	2^{+}	
Deinacanthon urbanianum	2	H	51^{1}	31^{1}	11^{1}	29^{1}	21^{1}	11^{1}	6^{+}	41^{1}	7^{+}
Ephedra triandra	2	Fsa	26^{+}	17^{+}	26^{+}	13^{+}	6^{1}	13^{+}	1^{1}	2^{+}	
Digitaria californica	8	H	51^{+}	44^{+}	30^{1}	38^{+}	24^{+}	45^{1}	32^{+}	9^{+}	
*Neobouteloua lophostachya**	4	H	43^{+}	72^{1}	30^{2}	54^{1}	38^{1}	48^{+}	18^{1}	9^{1}	
Parkinsonia praecox	8	Ft	74^{1}	82^{1}	61^{1}	77^{1}	21^{+}	54^{1}	76^{+}	40^{1}	3^{+}
Sporobolus pyramidatus	8	H	60^{+}	70^{1}	34^{1}	54^{1}	35^{+}	46^{+}	16^{+}	59^{1}	50^{1}
Mimozyganthus carinatus	2	Fs	80^{2}	80^{2}	34^{1}	71^{1}	49^{1}	84^{3}	82^{2}	52^{2}	7^{1}
Sida argentina	2	H	15^{+}	26^{+}	20^{+}	12^{+}	8^{+}	27^{+}	7^{+}		
Aloysia gratissima	8	Fs	21^{+}	16^{+}	38^{1}	10^{+}	4^{+}	4^{+}	3^{1}	2^{+}	
Leptochloa crinita	8	H	65^{1}	61^{2}	77^{2}	65^{1}	28^{+}	38^{1}	12^{+}	59^{1}	37^{1}
Celtis pallida	2	Fs	68^{1}	27^{+}	43^{2}	8^{2}		2^{1}	3^{+}	2^{+}	
Selaginella sellowii	8	Pt	51^{2}	27^{2}	8^{2}	15^{2}	1^{4}	4^{1}			
Monteverdia spinosa	2	Fs	60^{+}	34^{+}	31^{1}	6^{+}	1^{+}	9^{+}	3^{+}	2^{+}	
Amphilophium carolinae	2	L	54^{+}	28^{+}	26^{+}	10^{+}	1^{+}	7^{+}			
Pseudabutilon pedunculatum	2	Fs	64^{+}	43^{+}	25^{+}	23^{+}	12^{+}	21^{+}	13^{+}		
Talinum polygaloides	2	G	50^{+}	33^{+}	11^{+}	27^{+}	5^{+}	9^{+}	1^{+}	9^{+}	
Atamisquea emarginata	8	Fs	81^{1}	57^{+}	82^{1}	60^{+}	15^{+}	39^{1}	34^{+}	41^{+}	3^{+}
Leptochloa pluriflora	8	H	35^{1}	32^{1}	7^{1}	8^{1}	3^{1}	13^{1}	7^{+}	17^{1}	3^{+}
Pappophorum caespitosum	4	H	39^{1}	35^{1}	16^{1}	15^{+}	9^{+}	11^{+}	13^{+}	5^{+}	3^{2}
Condalia microphylla†	4	Fs	65^{+}	40^{+}	61^{1}	12^{+}	4^{+}	16^{+}	9^{+}		
Prosopis flexuosa	4	Ft	70^{+}	80^{1}	93^{2}	75^{1}	71^{1}	59^{1}	24^{1}	41^{1}	
Lycium tenuispinosum†	4	Fs	8^{+}	16^{1}	31^{1}	10^{+}	13^{+}	7^{+}	7^{1}	33^{1}	13^{1}
Aspidosperma quebracho-blanco	2	Ft	94^{2}	80^{1}	64^{2}	90^{2}	51^{1}	71^{1}	90^{2}	36^{1}	
*Larrea cuneifolia**	4	Fs	5^{+}	19^{1}	7^{1}	100^{3}	99^{3}	30^{1}	13^{2}	21^{1}	
Setaria pampeana	8	H	49^{1}	51^{1}	30^{+}	63^{+}	33^{+}	36^{+}	28^{+}	45^{+}	20^{+}
Aristida adscensionis	8	T	10^{+}	18^{1}	16^{1}	15	60^{1}	38^{2}	15^{1}	10^{+}	3^{+}
Bulnesia retama	4	Ft	6^{2}	19^{1}	13^{1}	25^{1}	55^{1}	30^{1}	15^{+}	12^{+}	
Cottea pappophoroides	4	H	4^{+}	9^{1}		23^{+}	50^{1}	30^{+}	29^{+}	14^{+}	
Bougainvillea spinosa	4	Fs	1^{+}	6^{+}	3^{1}	15^{+}	35^{1}	13^{1}	9^{+}	9^{+}	
Bouteloua barbata	4	T		1^{+}	5^{+}	10^{1}	27^{1}	5^{1}	1^{+}	9^{+}	3^{+}
Bouteloua aristidoides	4	T	13^{+}	9^{2}	5^{2}	33^{1}	60^{2}	50^{2}	71^{1}	9^{1}	
Bulnesia foliosa	2	Fs	3^{+}	6^{1}	5^{+}	6^{+}	10^{1}	30^{2}	16^{1}	5^{+}	
Zinnia peruviana	8	C	5^{+}	12^{1}	11^{1}	21^{+}	19^{1}	30^{1}	13^{+}	3^{+}	
Aloysia ovatifolia†	2	Fsa	1^{+}	4^{1}	5^{2}	8^{1}	14^{1}	29^{1}	32^{+}		
Pappophorum krapovickasii	2	H	4^{+}	4^{+}		6^{+}	12^{1}	7^{1}	69^{1}	3^{+}	
Chloris castilloniana	2	H		1^{+}		2^{+}	8^{+}	5^{+}	47^{1}	3^{1}	
Aristida mendocina	4	H	43^{1}	40^{1}	26^{1}	23^{1}	37^{1}	52^{1}	97^{2}	5^{+}	
Gomphrena martiana	2	T		3^{1}	2^{1}	6^{1}	12^{1}	2^{+}	40^{1}	2^{+}	
Croton bonplandianus	1	Fsa	1^{+}	5^{+}	5^{+}	4^{1}	6^{+}	11^{+}	43^{+}	2^{+}	
Prosopis pugionata	2	Ft	30^{+}	32^{+}	15^{+}	21^{1}	33^{1}	14^{1}	82^{1}	21^{1}	7^{+}

Plant communities			1.1	1.2	1.3	2.1	2.2	3.1	3.2	4.1	4.2
Numbers of relevés			80	171	61	52	78	56	68	58	30
Species	**CT**	**LF**									
Vachellia aroma	2	Ft	30^{1}	16^{1}	15^{+}	6^{+}	8^{+}	23^{+}	63^{1}	2^{+}	
*Tricomaria usillo**	4	Fs	18^{+}	31^{1}	20^{1}	33^{1}	50^{1}	43^{1}	88^{2}	33^{1}	
Gaya parviflora	2	Fsa		4^{+}	2^{+}	4^{1}	6^{+}	14^{+}	26^{+}	2^{+}	
*Euploca mendocina**	4	C	1^{+}	1^{1}	2^{+}	2^{+}	10^{+}	13^{1}	25^{+}		3^{+}
Senna aphylla	4	Fs	28^{+}	60^{1}	48^{1}	67^{1}	65^{+}	61^{1}	85^{1}	60^{1}	
Gomphrena tomentosa	2	C	4^{+}	16^{1}	13^{+}	25^{+}	19^{1}	30^{1}	41^{1}	10^{1}	
Setaria hunzikeri	2	H	16^{1}	15^{1}	13^{1}	29^{1}	21^{+}	29^{+}	40^{+}		
Pseudabutilon virgatum	8	Fs	8^{+}	12^{+}	13^{+}	27^{+}	15^{+}	25^{+}	32^{+}		
Justicia gilliesii	2	Fsa	6^{1}	16^{1}	25^{1}	12^{+}	10^{1}	20^{+}	29^{1}	2^{+}	
Cordobia argentea	2	L	84^{1}	52^{+}	31^{1}	33^{1}	21^{1}	86^{1}	88^{2}	2^{+}	
Larrea divaricata	4	Fs	95^{2}	95^{3}	82^{2}	40^{1}	19^{1}	82^{2}	94^{2}	14^{2}	
Gouinia paraguayensis	2	H	73^{+}	68^{1}	61^{1}	54^{1}	35^{1}	73^{1}	79^{1}	2^{+}	
Ximenia americana	2	Fs	29^{+}	39^{+}	11^{+}	62^{+}	49^{+}	64^{+}	62^{+}	21^{+}	7^{+}
Pappophorum phillippianum	8	H	9^{+}	18^{1}	11^{+}	48^{+}	47^{+}	34^{1}	10^{+}	26^{1}	17^{+}
Opuntia sulphurea	4	Ko	36^{+}	29^{+}	10^{1}	42^{+}	10^{+}	9^{+}	4^{+}	41^{1}	10^{+}
Stetsonia coryne	2	Kc	23^{1}	13^{1}	2^{1}	31^{1}	1^{1}	5^{1}	6^{+}	31^{2}	17^{1}
Suaeda divaricata	4	Fss		2^{1}	3^{2}	6^{+}	19^{1}	2^{+}	1^{2}	72^{2}	10^{+}
Atriplex lampa†	4	Fss		1^{+}	2^{+}	2^{+}	5^{+}		1^{1}	28^{1}	10^{1}
Maytenus vitis-idaea	2	Fss	4^{+}	11^{1}	8^{1}	13^{+}	6^{1}	9^{+}	1^{+}	43^{1}	20^{2}
Lycium infaustum†	2	Fss	1^{+}	1^{+}	5^{+}	6^{+}	8^{1}	2^{1}		31^{1}	23^{1}
Strombocarpa strombulifera	4	Fs		1^{+}	2^{+}					19^{1}	13^{1}
Neltuma sericantha	4	Fs	3^{+}	26^{+}	18^{+}	29^{+}	10^{+}	7^{1}	10^{+}	45^{1}	3^{1}
Geoffroea decorticans	2	Ft	44^{+}	53^{1}	64^{1}	46^{1}	36^{1}	34^{+}	13^{1}	79^{2}	23^{1}
Echinopsis leucantha†	4	Ko	20^{+}	18^{+}	2^{+}	19^{+}	12^{+}	7^{+}	6^{+}	41^{+}	27^{+}
Atriplex argentina†	8	Fss		2^{+}	5^{2}	4^{1}	12^{1}	4^{+}		79^{2}	63^{1}
*Plectrocarpa tetracantha**	4	Fs	1^{+}	5^{1}	3^{1}	10^{1}	13^{1}	5^{+}	3^{+}	71^{1}	63^{1}
*Grahamia bracteata**	2	Fss		3^{+}	8^{1}	17^{+}	17^{+}	4^{1}	6^{+}	66^{1}	60^{1}
Ehretia cortesia	4	Fs	1^{+}	8^{+}	3^{+}	4^{+}	4^{+}	2^{+}	1^{+}	47^{1}	37^{1}
Cyclolepis genistoides	4	Fs	1^{+}	2^{+}	2^{+}	2^{+}	5^{+}	2^{+}		45^{1}	53^{1}
Lippia salsa	4	Fs		4^{+}	2^{+}	2^{+}	4^{+}	2^{+}	1^{+}	31^{+}	37^{1}
Strombocarpa reptans	2	Fs		1^{+}		4^{+}	4^{+}	2^{+}	1^{+}	38^{1}	70^{1}
Alternanthera nodifera	2	Fsa		2^{+}			6^{+}			28^{1}	43^{+}
Heterostachys ritteriana	8	Fss			2^{+}					5^{+}	83^{2}
Allenrolfea patagonica†	2	Fss								5^{1}	73^{3}
*Distichlis acerosa**	2	H			2^{+}					3^{+}	43^{1}

form spectra showed a predominance of micro- and nanophanerophytes (16.6%), followed by hemicryptophytes (15.0%), chamaephytes (12.7%) and low trees (mesophanerophytes) (10.7%). The most relevant chorotype was the Eastern and Western Chaco (39.4% of all species), while the Arid Chaco and Monte (15.7%) and the Southern-Brazilian/Paranaense (11.1%) chorotypes were also represented. Ubiquitous species were also relevant (26.1%).

Although the sample-size based rarefaction showed that the curves of all the vegetation types had not yet reached the asymptote (Suppl. material 2: Appendix 2, figures S2.1, S2.2, S2.3, S2.4), the observed species richness reached a high percentage of the species estimated using the non-parametric estimators (Suppl. material 2: Appendix 2, tables S2.1, S2.2, S2.3, S2.4). The coverage-based rarefaction curves suggested that all the vegetation types identified were well represented because the sample coverage percentage varied from 0.93 to 0.98 in the different vegetation types (Suppl. material 2: Appendix 2, tables S2.1, S2.2, S2.3, S2.4).

Classification of vegetation types

The ISOPAM analysis divided the data set into four major clusters (Table 1). The number of species varied among the different clusters, ranging from 388 in the forests and shrublands of cluster 1 to 163 in the halophytic and sub-halophytic vegetation of cluster 4. Following, we present a general description of the four main clusters and the nine vegetation types, including a list of diagnostic species with fidelity values higher than 0.1 and constancy values higher than 25% (Table 1). The complete table presenting all diagnostic and non-diagnostic species is provided in Suppl. material 3. Where they exist, the local names of the vegetation types are given in inverted commas.

Cluster 1: This cluster comprised three vegetation types, two of them including forests, woodlands and shrublands with tree cover (mainly in Type 1.1 *Aspidosperma quebracho-blanco* forest and in Type 1.3 *Prosopis flexuosa* woodland) ranging from 30–40% to only scattered emerging individuals. The remaining type includes shrublands mainly dominated by *Larrea divaricata* (Type 1.2 *Larrea divaricata* shrubland). The floristic differentiation among these vegetation types was poor and mostly based in changes in the frequency and cover of a common set of species.

Type 1.1 *Aspidosperma quebracho-blanco* forest (locally named as "quebrachal") (Figure 2a)

Diagnostic species: *Justicia squarrosa*, *Senegalia gilliesii*, *Sarcomphalus mistol*, *Tillandsia duratii*, *Tillandsia xiphioides*, *Tillandsia aizoides*, *Tillandsia pedicellata*, *Tillandsia rectangula*, *Cardiospermum halicacabum*, *Lycium elongatum*, *Aspidosperma quebracho-blanco* (for the complete list of diagnostic species, see Suppl. material 3).

This vegetation type was mainly found on flat plains and lower bajadas in the eastern Arid Chaco with higher rainfall, but also in western humid sites located in the proximity of mountain ranges. The plains are homogeneous and have a gently to very gently undulating relief, with slopes of less than 1%. The sediments are very permeable so there is no defined drainage network. The direction of runoff is controlled by the central sectors or bottoms of the bolson. In the higher terrain the soils are loam, well drained and poorly developed (Torripsaments) while in the lower sectors silty-loam soils predominate (typical Camborthides) and the water retention capacity is greater.

This vegetation type included forests with a predominantly open tree canopy dominated by the evergreen tree *Aspidosperma quebracho-blanco*, and an open to close shrub understory, but also shrublands with scattered emergent trees. Other common deciduous trees were *Sarcomphalus mistol*, *Castela coccinea*, *Parkinsonia praecox* and *Prosopis flexuosa*. In the understory the most common shrubs were *Larrea divaricata*, *Justicia squarrosa*, *Senegalia gilliesii*, *Mimozyganthus carinatus*, *Celtis pallida*, *Monteverdia spinosa*, *Condalia microphylla* and *Atamisquea emarginata*. These shrubs may alternatively dominate in sites where the tree canopy is more open. A relevant feature in these forests was the presence of several epiphytic species of *Tillandsia*, as well as the bromeliad *Deinacanthon urbanianum*, as diagnostic of this vegetation type.

Type 1.2 *Larrea divaricata* shrubland (locally called "jarillal" or "fachinal") (Figure 2b)

Diagnostic species: *Larrea divaricata*, *Neobouteloua lophostachya*, *Parkinsonia praecox*, *Sporobolus pyramidatus*, *Mimozyganthus carinatus*, *Sida argentina* (for the complete list of diagnostic species see Suppl. material 3).

This vegetation type is a rather open to closed shrubland, nowadays highly widespread in the Arid Chaco. In some patches the cover of thorny shrubs may be over 75% turning the vegetation into a closed, inaccessible thicket. This vegetation type occurs in different geomorphological units in the alluvial and eolian plains, but in general on rather elevated sites with silty loam to sandy loam soils, well to excessively drained. This vegetation type frequently constitutes the replacement community of the *Aspidosperma quebracho-blanco* forest after anthropic disturbances and is therefore often found in similar habitats.

The dominant species is *Larrea divaricata*, an evergreen shrub widely distributed in north-western Argentina, with emergent individuals of the tree species *Aspidosperma quebracho-blanco* and *Prosopis flexuosa*. Alternatively, other deciduous thorny shrubs such as *Mimozyganthus carinatus*, *Parkinsonia praecox* and *Condalia microphylla*, and the evergreen shrub *Atamisquea emarginata*, may codominate in some relevés. Some C_4 grass species such as *Neobouteloua lophostachya*, *Sporobolus pyramidatus*, *Leptochloa pluriflora*, *Gouinia paraguayensis* and *Pappophorum caespitosum*, are diagnostic for this vegetation type.

Type 1.3 *Prosopis flexuosa* woodland (locally known as "algarrobal", "ralera")

Diagnostic species: *Aloysia gratissima*, *Leptochloa crinita*, *Celtis pallida*, *Prosopis flexuosa* (for the complete list of diagnostic species see Suppl. material 3).

The relevés of this vegetation type also occurred in mesic habitats in the eolian and fluvio-eolian plains and fluvial terraces, with a higher frequency in the wettest parts of the study area. Soils are well to moderately well drained and soil texture is predominantly silty to sandy loam. The algarrobal may also be found in a wide range of habitats across the entire Arid Chaco, such as lower sites with silty loam texture and the drainage are, at least temporarily, poor. The dominant physiognomy was that of low woodlands and tall shrublands.

The dominant species in the canopy was *Prosopis flexuosa*, a deciduous tree diagnostic to this cluster, but also *Aspidosperma quebracho-blanco* may codominate in some mixed woodland patches. The floristic composition of the shrub layer is similar to that of vegetation types 1.1 and 1.2, with *Aloysia gratissima*, *Celtis pallida*, *Atamisquea emarginata* and *Condalia microphylla* as diagnostic in this vegetation type. In lower sites, *Celtis pallida*, *Lycium chilense* and *Lycium tenuispinosum* may dominate in the understory.

Cluster 2: This cluster included shrublands dominated by *Larrea cuneifolia* and was further divided in two vegetation types (i.e., 2.1 and 2.2): the first one was characterized by widely distributed shrublands while the second one is confined to the drier parts of the study area and included characteristic species of the Monte deserts and semi-deserts.

Type 2.1 *Larrea cuneifolia* shrubland (locally named as "jarillal", "cardonal") (Figure 2c)

Diagnostic species: *Larrea cuneifolia*, *Setaria pampeana*, *Ximenia americana*, *Pappophorum phillippianum*, *Opuntia sulphurea*, *Stetsonia coryne* (for the complete list of diagnostic species see Suppl. material 3).

These shrublands were distributed across most of the Arid Chaco, especially in low areas in the alluvial and aeolian plains with moderately well to somewhat imperfectly drained soils consisting mainly of fine sediments and sands. The edaphic conditions are controlled by the micro- and meso-relief: in the higher sectors the soils have a higher percentage of sands and are less saline (typical Torripsaments), while in the intermediate and lower levels the soils are finer and somewhat saline (natric Camborthides).

The predominant physiognomy was that of a low and open shrubland. In sites where soils are well drained, *Aspidosperma quebracho-blanco* was frequent, also forming small forest patches. The dominant shrub was *Larrea cuneifolia*, an evergreen shrub, accompanied by other diagnostic species such as the deciduous shrub *Ximenia americana*, the columnar cacti *Stetsonia coryne* and the opuntioid cacti *Opuntia sulphurea*. Also, the aphyllous shrub *Senna aphylla*, though not diagnostic for this vegetation type, reached high cover values. In low-lying areas of the plains, where water retention capacity increases promoting the accumulation of salts by evaporation, *Stetsonia coryne* was dominant forming characteristic communities locally named "cardonales". The presence of this candelabra-like cacti is also conspicuous in some *Aspidosperma* *quebracho-blanco* forests ("quebrachal with cardón"), also included in this vegetation type.

Type 2.2 *Larrea cuneifolia – Bulnesia retama* shrubland ("jarillal")

Diagnostic species: *Larrea cuneifolia*, *Bulnesia retama*, *Aristida adscensionis*, *Cottea pappophoroides*, *Bougainvillea spinosa*, *Bouteloua aristidoides* (for the complete list of diagnostic species see Suppl. material 3).

This vegetation type was commonly found in the western driest parts of the Arid Chaco, on loessoid plains with well drained, loam to sandy loam soils. Some relevés were also recorded in the eastern part of the study area close to saline depressions and muddy saline areas, on imperfectly drained soils.

The characteristic physiognomy was that of low shrublands dominated by *Larrea cuneifolia*; however, many relevés exhibited also scattered emergent individuals of *Aspidosperma quebracho-blanco*. The main floristic difference with vegetation type 2.1 is the presence of several shrubs and small trees typical of the Monte Phytogeographical Province such as *Bulnesia retama*, *Bougainvillea spinosa* and *Zuccagnia punctata*, being the first two diagnostics for this vegetation type. Also, the presence of C_4 grasses widely distributed across northwestern arid Argentina, such as *Bouteloua barbata*, *Munroa mendocina* and *Bouteloua aristidoides*, among others, characterized this vegetation type.

Cluster 3: This cluster comprised the typical vegetation of highly disturbed sites, split into two vegetation types (3.1 and 3.2) and embracing open shrublands with high values of bare soil ("peladares") and a heterogeneous mosaic of xerophytic/thorny scrublands ("fachinales"), with the absence of trees or only very scattered individuals. We should note that the floristic differentiation between these two vegetation types was very poor (Table 1).

Type 3.1 *Mimozyganthus carinatus – Bulnesia foliosa* shrubland (locally known as "latal" and "iscayantal") (Figure 2d)

Diagnostic species: *Bulnesia foliosa*, *Zinnia peruviana*, *Aloysia ovatifolia* (for the complete list of diagnostic species see Suppl. material 3).

This vegetation type is widespread across the entire study area in flat to moderately sloped plains of different origin on well to excessively drained sandy loam soils formed from deposits of alluvial and eolian materials. On the flatter sites, this type may occupy areas where *Aspidosperma quebracho-blanco* forests probably thrived in the past. Patches of this vegetation type were also observed on stabilized dunes and distal parts of the bajadas, on excessively drained, sandy soils.

The prevailing physiognomy was that of a closed and medium height shrubland or scrubland, usually with scattered individuals of tree species such as *Aspidosperma quebracho-blanco*, *Prosopis flexuosa*, and *Parkinsonia praecox*, among others. Though not diagnostic for this vegetation type, the evergreen shrub *Larrea divaricata* and the deciduous shrub *Mimozyganthus carinatus*, were usually the dominants along with many other shrubs; however, in the central and northern parts of the study region, *Bulnesia foliosa* predominated. As in most of the clusters, C_4 grasses such as *Digitaria californica*, *Neobouteloua lophostachya*, *Sporobolus pyramidatus*, *Aristida adscensionis*, *Aristida mendocina* and *Gouinia paraguayensis* were frequent in the relevés of this vegetation type.

Type 3.2 *Tricomaria usillo* shrublands

Diagnostic species: *Aristida mendocina*, *Pappophorum krapovickasii*, *Gomphrena martiana*, *Chloris castilloniana*, *Croton bonplandianus*, *Prosopis pugionata*, *Tricomaria usillo*, *Vachellia aroma*, *Senna aphylla*, *Gomphrena tomentosa* (for the complete list of diagnostic species see Suppl. material 3).

This vegetation type was mainly found in the central and western part of the Arid Chaco, in dune fields or sand dunes, semi-stabilized or stabilized, alternating in the lowlands with forests and shrublands described in Cluster 1. The dunes are generally low, with maximum heights between four and six meters, and the materials that gave rise to the dunes have been deposited by the wind. The soils have a sandy loam to sandy texture and are very poorly developed. They are excessively drained and are very susceptible to erosion when vegetation cover is lost. In the lowlands the soils have a loamy texture and are somewhat more developed (Camborthides ustólicos); this development indicates a relatively long time of stabilization of the system.

The prevailing physiognomy was that of open shrublands, though shrub cover reached up to 80% in some relevés. The number of tree species was low and sometimes only individuals of *Aspidosperma quebracho-blanco* were present. The dominant shrubs were the diagnostic shrubs *Tricomaria usillo* (with ephemeral leaves) and *Senna aphylla* (a leafless species) and the no diagnostic shrubs *Larrea divaricata* and *Mimozyganthus carinatus*, while the woody climber *Cordobia argentea* was also relevant. The C_4 grasses *Pappophorum krapovickasii*, *Chloris castilloniana*, *Aristida mendocina* and *Gouinia paraguayensis* exhibited high constancy values in this vegetation type.

Cluster 4: This cluster included halophytic and sub-halophytic vegetation and was further split into two groups: vegetation type 4.1 represented mostly the vegetation locally known as "barreales" (muddy saline areas), while vegetation type 4.2 comprised succulent shrublands in the outer perimeter of salt flats and playas. Both vegetation types were characterized by halophylous and sub-halophylous species widely distributed across the whole Chaco and Monte Phytogeographical Provinces.

Type 4.1 *Suaeda divaricata – Atriplex argentina* shrubland ("jumeal", "cachiyuyal", "cardonal", "zampal") (Figure 2e)

Diagnostic species: *Suaeda divaricata*, *Atriplex lampa*, *Maytenus vitis-idaea*, *Lycium infaustum*, *Prosopis sericantha*,

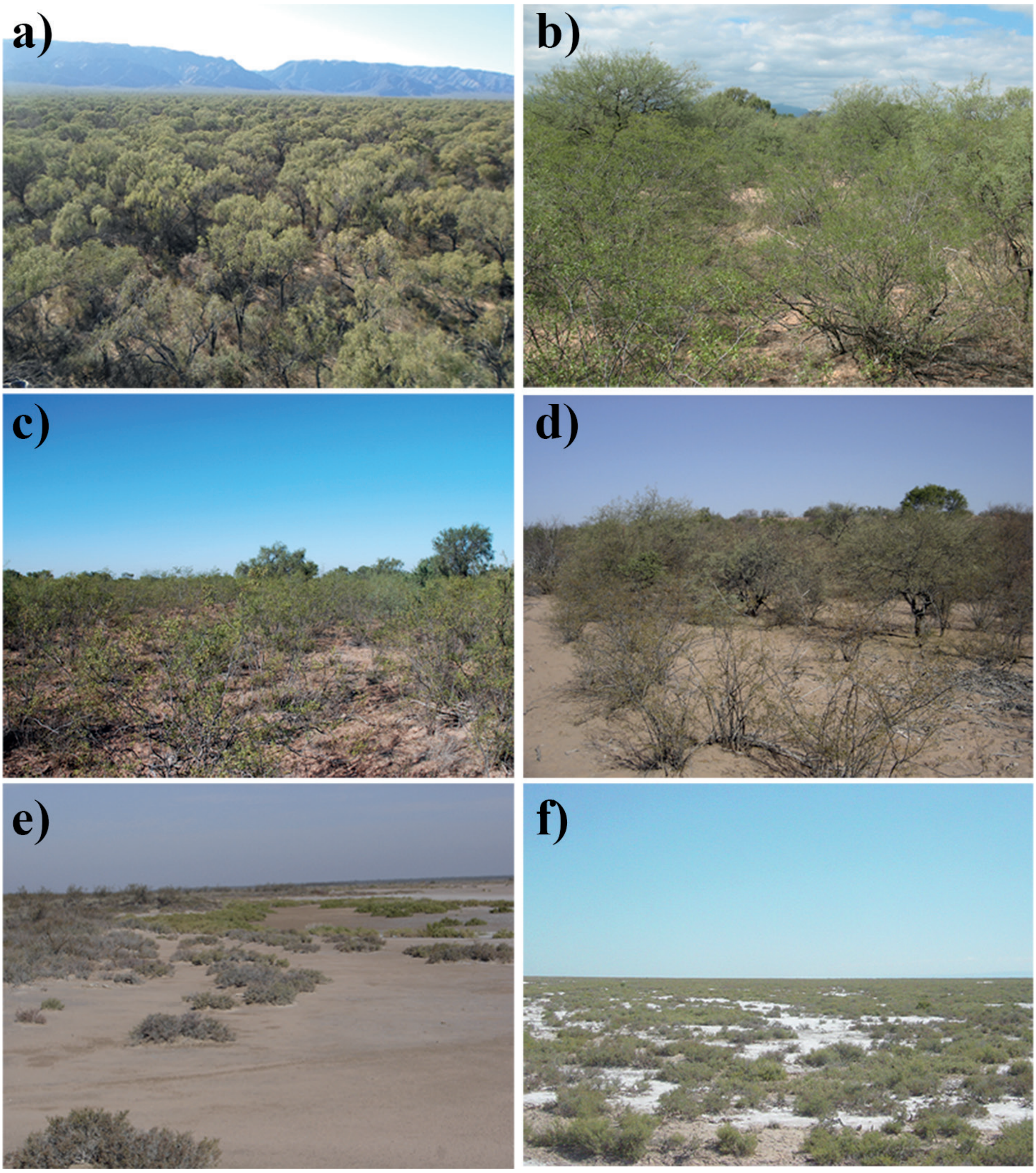

Figure 2. Some of the most representative vegetation types in the Arid Chaco in Central-Western Argentina belonging to: a) Type 1.1 *Aspidosperma quebracho-blanco* forest in fluvio-eolian plains; b) Type 1.2 *Larrea divaricata* shrubland (with emergent low trees) in sandy plains; c) Type 2.1 *Larrea cuneifolia* – *Bulnesia retama* shrubland in western sites; d) Type 3.1 *Mimozyganthus carinatus* – *Bulnesia foliosa* shrubland on stabilized dunes; e) Type 4.1 *Suaeda divaricata* – *Atriplex argentina* shrubland in muddy saline areas; and f) Type 4.2 *Heterostachys ritteriana* – *Allenrolfea patagonica* succulent shrubland in saline depressions. Photo credits: A. Cuchietti and G. Conti (a); S.R. Zeballos (b); M.R. Zak (e); W.D. Agüero (f).

Geoffroea decorticans, (for the complete list of diagnostic species see Suppl. material 3).

This vegetation type was found across the entire Arid Chaco, but confined to the margins of low-lying areas, mostly muddy saline areas (barreales), and also in the outer perimeter of playas and salinas. The mudflats receive runoff water, loaded with fine sediments that accumulate in the lower areas. Therefore, the soil is of alluvial origin, formed by the deposition mainly of silts and clays, and the drainage is almost impeded.

From the central, more saline sector of barreales and playas devoid of vegetation, up to the contact with the fluvio/aeolian plains, a vegetation zonation with communities gradually replacing each other, developing a series of rings around the salty playas and barreales, was found. This sequence comprised the following communities: a) open succulent shrubland with *Heterostachys ritteriana* and *Allenrolfea patagonica* (see vegetation type 4.2); b) "zampales" (dominated by *Atriplex lampa*), "cardonales" (dominated by the candelabra-like columnar cacti *Stetsonia coryne*), "cachiyuyales" (dominated by other species of *Atriplex*), and, mostly, shrublands dominated by *Suaeda divaricata* and some succulent species; c) mixed shrublands ("chañarales", "latales") with sub-halophylous species (they tolerate moderate salt concentrations) and other taxa shared with clusters 1 and 2, but frequently dominated by shrubs such as *Geoffroea decorticans* and *Mimozyganthus carinatus*; and d) *Aspidosperma quebracho-blanco* forests and *Larrea divaricata* shrublands but still with the presence of a few halophyllous species. This vegetation type included mostly communities b) and c). Some relevés were also found in the base of sand dunes nearby saline depressions. In addition to the diagnostic species, the more relevant taxa were: *Stromobocarpa strombulifera*, *Strombocarpa reptans*, *Plectocarpa tetracantha*, *Grahamia bracteata*, *Cortesia cuneifolia*, *Cyclolepis genistoides*, *Lippia salsa*, and *Alternanthera nodifera*. All of these species are shared with vegetation type 4.2.

Type 4.2 *Heterostachys ritteriana – Allenrolfea patagonica* succulent shrubland ("jumeal") (Figure 2f)

Diagnostic species: *Heterostachys ritteriana*, *Allenrolfea patagonica*, *Distichlis acerosa*, (for the complete list of diagnostic species see Suppl. material 3).

This vegetation type was found in the perimeter of salt lakes and salt flats, on soils frequently flooded or wet during the rainy season (summer), but dry, hard and with white salt efflorescence in winter and spring. The salinas have all the characteristics of ephemeral salt lakes, originated by the conjunction of structuring (closed basins) and climatic (evapotranspiration higher than the water supply) factors. The water supply is provided by ephemeral streams that flow only occasionally during the rainy season. The degree of salinity is maximum among the nine vegetation types, limiting the establishment and development of plant species. However, a distinction is made between (a) the saline depressions with clay-loam sediments, occasionally floodable, with polygonal drying cracks and a superficial saline crust, and (b) sandy hills between the lower areas (bajos). This variability in the salinity conditions of the soils causes changes in the composition and physiognomy of the vegetation.

This vegetation type included open succulent shrublands (community a) in the zonation described in vegetation type 4.1, dominated by *Heterostachys ritteriana* and *Allenrolfea patagonica*, both succulent shrubs that tolerate high salt concentrations in the soil.

Diversity, endemism, non-native species and chorotypes distribution patterns across the vegetation types

The vegetation types differed significantly in their mean species richness per relevé ($F_{(8, 644)}$ 13.09; $p < 0.0001$; Figure 3). With 36.7 ± 0.9 species, Type 1.1 *Aspidosperma quebracho-blanco* forest accounted for the highest mean species number per relevé and differed from the other vegetation types. Type 4.2 *Heterostachys ritteriana – Allenrolfea patagonica* succulent shrubland showed the lowest mean species richness per relevé (12.2 ± 1.5), while the other vegetation types exhibited intermediate values (Figure 3). The average richness per relevé of both national and more restricted endemic species, differed significantly among vegetation types (Statistics and *p* values for the response variables analyzed are reported in Suppl. material 2: Appendix S3, table S3.1). The halophytic types (cluster 4) exhibited the highest averages and differed significantly from all the other types (see Suppl. material 2: Appendix S3, table S3.1).

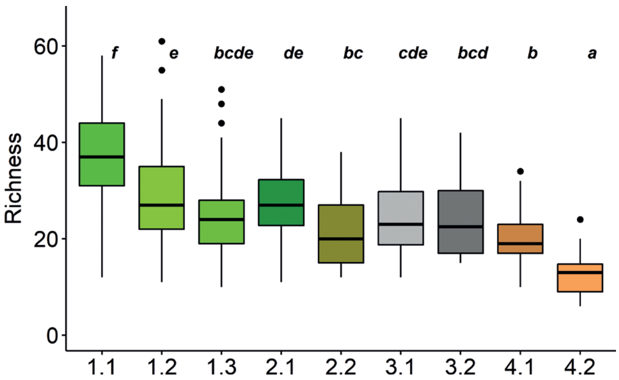

Figure 3. Mean species richness per relevé for the nine vegetation types recorded in the Arid Chaco, Central-Western Argentina. Vegetation types are those reported in Table 1. Different letters indicate significant differences between vegetation types pairs ($p \leq 0.05$).

In all the vegetation types described, significant differences in the representation of the different chorotypes were observed (Statistics and p values for the response variables analyzed are reported in Suppl. material 2: Appendix S4, table S4.1). Among all chorotypes, the Western and Eastern Chaco and the Arid Chaco and Monte were the best represented. Both differed significantly among the vegetation types. The former was prominent in all vegetation types except in Type 2.2 *Larrea cuneifolia – Bulnesia retama* shrubland, distributed in the western Arid Chaco, and in the halophytic Type 4.1 *Suaeda divaricata – Atriplex argentina* shrubland and in Type 2.1 *Larrea cuneifolia* shrubland. In these two vegetation types the Arid Chaco and Monte chorotype predominated. The Ubiquitous chorotype was also well represented in most vegetation types, differing significantly among them. The representation of the other chorotypes (Southern-Brazilian/Paranaense, Espinal/Pampean, and Patagonian) was poor. Despite the mean number of non-native species per relevé differing among the nine vegetation types, the total number of non-native species recorded was negligible (14 species, 3.1% of the total species registered).

Physiognomy and life form spectra across vegetation types

The average total cover differed significantly among the vegetation types (Statistics and p values for the response variables analyzed are reported in Suppl. material 2: Appendix S5, table S5.1). Type 1.1 *Aspidosperma quebracho-blanco* forest, exhibited the highest average vegetation cover (80.9%), while the lowest value was registered in Type 4.2 *Heterostachys ritteriana – Allenrolfea patagonica* succulent shrubland (61.1%) (see Suppl. material 2: Appendix S5, table S5.1). Cover and height of trees also varied significantly among vegetation types, with Type 1.1 *Aspidosperma quebracho-blanco* forest (27.9% tree cover) and 1.3 *Prosopis flexuosa* woodland (30.0%), differing significantly from the rest of the vegetation types (see Suppl. material 2: Appendix S5, table S5.1). Type 4.2 *Herterostachys ritteriana – Allenrolfea patagonica* succulent shrubland, occupying saline depressions, exhibited the lowest tree cover (0.5%), differing from the other vegetation types (see Suppl. material 2: Appendix S5, table S5.1). The shrub layer exhibited the highest cover among the different layers in all the vegetation types and its cover differed significantly among them. Type 1.1 *Aspidosperma quebracho-blanco* forest showed the highest shrub cover (64.5%) while Type 3.2 *Tricomaria usillo* shrubland exhibited the lowest cover (50.0%) (see Suppl. material 2: Appendix S5, table S5.1). Shrub height did not differ among the vegetation types. Shrubs reached the maximum average height in Type 4.1 *Suaeda divaricata – Atriplex argentina* shrubland (4.42 ± 0.57 m) and the minimum in the other type within cluster 4, Type 4.2 *Heterostachys ritteriana – Allenrolfea patagonica* succulent shrubland (see Suppl. material 2: Appendix S5, table S5.1). Herbs cover differed significantly among vegetation types being maximum in the vegetation types included in clusters 1 and 3, and minimum in the halophytic vegetation of cluster 4. Bare soil exhibited the highest values in the halophytic vegetation types (cluster 4) and in shrublands dominated by *Larrea cuneifolia* (cluster 2) (see Suppl. material 2: Appendix S5, table S5.1). Bare soil percentages also differed significantly among clusters, recording the maximum values in Type 4.2 *Herterostachys ritteriana – Allenrolfea patagonica* succulent shrubland and the minimum in Type 1.1 *Aspidosperma quebracho-blanco* forest (see Suppl. material 2: Appendix S5, table S5.1).

Life forms spectra varied significantly among vegetation types (Statistics and p values for the response variables analyzed are reported in Suppl. material 2: Appendix S6, table S6.1), but shrubs were the most prominent life form in all the types, with average number of species per relevé ranging from 9.8 in Type 1.1 *Aspidosperma quebracho-blanco* forest to 3.2 in Type 4.2 *Heterostachys ritteriana – Allenrolfea patagonica* succulent shrubland (see Suppl. material 2: Appendix S6, table S6.1). In the latter, succulent shrubs were the most abundant life form. Epiphytes, trees, sub-shrubs, hemicryptophytes, and climbers, were more prominent in Type 1.1 *Aspidosperma quebracho-blanco* forest and their number of species decreased towards the halophytic vegetation types included in cluster 4. Columnar cacti showed in general low percentages, while opuntioid cacti exhibited the highest average number of species per relevé in Type 1.1 *Aspidosperma quebracho-blanco* forest and in Type 4.1 *Suaeda divaricata – Atriplex argentina* shrubland. All the life forms showed significant differences among the vegetation types (see Suppl. material 2: Appendix S6, table S6.1).

Vegetation types and their relationship with environmental and edaphic variables

The ISOMAP ordination (Figure 4) displays the four clusters and nine vegetation types observed in Table 1. The overall floristic composition was related to electrical conductivity (EC; $r^2 = 0.29$, $p = 0.001$), sand content ($r^2 = 0.27$, $p = 0.001$), aridity index (AI; $r^2 = 0.27$, $p = 0.001$), annual mean precipitation (AP; $r^2 = 0.22$, $p = 0.001$), exchangeable sodium percent (ESP; $r^2 = 0.22$, $p = 0.001$), precipitation seasonality (PS; $r^2 = 0.21$, $p = 0.001$), clay content ($r^2 = 0.17$, $p = 0.001$), silt ($r^2 = 0.16$, $p = 0.001$), elevation ($r^2 = 0.12$, $p = 0.001$), pH ($r^2 = 0.1$, $p = 0.001$) and annual mean temperature (AMT; $r^2 = 0.09$, $p = 0.001$). Differences among vegetation types could be partially explained by differences in environmental and soil conditions. That is, the vegetation types included in cluster 2 were distributed mostly in the west part of the study area, in sites with higher aridity index, lower precipitation, higher precipitation seasonality and higher elevation (Type 2.2 *Larrea cuneifolia – Bulnesia retama* shrubland), or low-lying areas in the rest of the Arid Chaco (Type 2.1 *Larrea cuneifolia* shrubland). The soils in the relevés included in this cluster showed high sand content, exchangeable sodium percent and pH values with low clay and silt content (Figure 4). On the other side, Type 1.1 *Aspidosperma quebracho-blanco* forest and partially shrublands with open tree canopy included in cluster 3, were associated with sites with higher annual precipitation, lower aridity index, and soils with low pH, electrical conductivity and exchangeable sodium percentage. The variability within cluster 3 can be partially explained by the higher elevation of some of the relevés of Type 3.2 *Tricomaria usillo* shrubland, distributed towards the west of the study area on soils with higher sand content. Finally, it could be noted also that the halophytic vegetation (Type 4.1 *Suaeda divaricata – Atriplex argentina* shrubland and Type 4.2 *Heterostachys ritteriana – Allenrolfea patagonica* succulent shrubland) was associated to salty soils (i.e., high electrical conductivity values), and that its relationship with climatic factors is less clear.

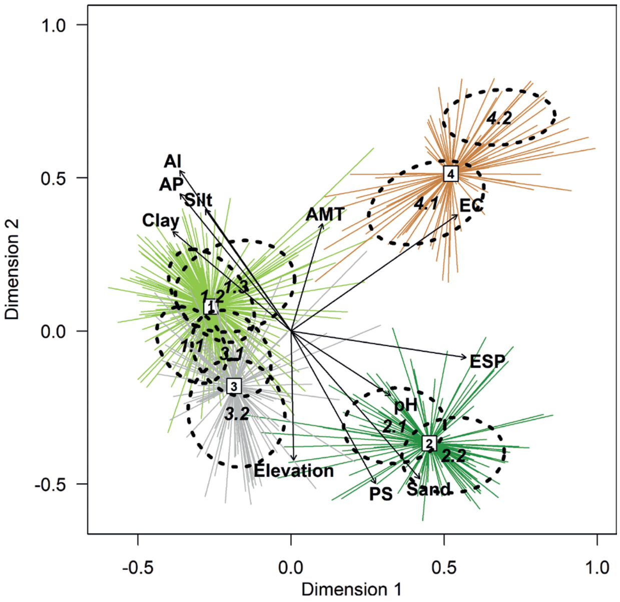

Figure 4. Isometric feature mapping plot (ISOMAP), based on Bray-Curtis dissimilarity of 654 relevés × 439 plant species matrix corresponding to the Arid Chaco, Central-Western Argentina. Vegetation types codes as in Table 1. Environmental variables significantly correlated with the sample scores in the ordination space are also reported. Environmental and soil variables abbreviations: AI: Aridity Index; AMT: Annual Mean Temperature; AP: Annual mean Precipitation; EC: Electrical Conductivity; ESP: Exchangeable Sodium Percent; and PS: Precipitation Seasonality.

Discussion

In this study we classified the vegetation of the Arid Chaco located in Central-Western Argentina and recognized four main clusters comprising nine vegetation types. With the exception of the halophytic vegetation, the floristic differentiation among the remaining vegetation types described was quite poor. The vegetation types differed in the relative abundance of species and in their physiognomy, ranging from forests to open shrublands. Despite the floristic composition of the different vegetation types was related to elevation, climate and soil variables, the strong impact of human activities on the original *Aspidosperma quebracho-blanco* forests could have become one of the main drivers determining the physiognomy and composition of the current vegetation of the Arid Chaco. Although the number of species restricted to the Arid Chaco was quite low, the most relevant chorotype included species with Western and Eastern Chaco distribution, conferring a clear Chaquenian identity to this area and discriminating it from other phytogeographic units. Therefore, the floristic composition of the vegetation types described revealed numerous species in common with other sectors of the Chaco of northern Argentina, Bolivia and Paraguay.

Floristic patterns

The most recent phytogeographical scheme at the national level recognized the Arid Chaco as a separate unit, the "xerophyte forest with *Aspidosperma quebracho-blanco* in transition to steppe" (Oyarzábal et al. 2018). The vegetation types described in our study revealed, at least at the level of the dominant species, a floristic composition similar to that reported for specific sectors of the Arid Chaco by several authors (Morello et al. 1985; Cabido et al. 1992; Morlans and Guichón 1998; Peña Zubiate et al. 1998; Calella and Corzo 2006). Moreover, the floristic composition of the vegetation types proposed here was also similar to those of the major communities in the Western Chaco (Morello and Saravia Toledo 1959; Cabrera 1976). However, in the Arid Chaco the lack of the important tree species *Schinopsis lorentzii*, a dominant tree in the Western Chaco, stands out. In addition, our vegetation types also share species with the Espinal phytogeographic province, but important characteristic elements of the Espinal, such as *Prosopis caldenia*, (Peña Zubiate et al. 1998), were absent in the relevés collected in the southern extreme of the Arid Chaco in close contact with the Espinal. Another relevant feature is the floristic relationship between the Arid Chaco and the Monte phytogeographic province. Our results revealed that the presence of species characteristic of the Monte phytogeographic province, such as *Bougainvillea spinosa*, *Zuccagnia punctata*, *Bulnesia retama*, among others, was prominent in Type 2.2 *Larrea cuneifolia* – *Bulnesia retama* shrubland, but they were almost absent in the remaining vegetation types. Those floristic relationships have been extensively discussed in the past (Morello 1958; Morello et al. 1985), and the Arid Chaco has been alternatively defined as a floristic ecotone between the phytogeographic provinces of Chaco and Monte, or a phytogeographic entity in itself, with the predominance of species with a Chaquenian character (Morello et al. 1985). Although Chaco and Monte share numerous species (Solbrig 1976; Roig et al. 2009), the floristic composition recorded in this study highlights the distinctive Chaquenian character of the Arid Chaco. When our floristic lists are compared with those provided for the Paraguayan (Mereles 2005; Navarro et al. 2006) and Bolivian (Navarro 2011) Chaco, remarkable similarities emerge, which confirm the Chaquenian character of our study area. Moreover, the best represented chorotype (39% of all species) in our survey is the one that includes species widely distributed in the Chaco of northern Argentina, Bolivia and Paraguay.

Many authors have reported that different types of shrublands with a similar composition to ours, constitute the current most widespread vegetation type in the Arid Chaco (Roig 1963; Sayago 1969; Anderson et al. 1970; Ragonese and Castiglioni 1970; Luti et al. 1979; Morello et al. 1985; Callela and Corzo 2006; Cabido et al. 2018a, b; Blanco et al. 2022). In agreement with the authors cited above, seven of the nine vegetation types described in this study corresponded to shrublands. In addition to a few tree species such as *Aspidosperma quebracho-blanco*, *Prosopis flexuosa*, *Sarcomphalus mistol* and *Senegalia praecox*, a group of thorny (*Senegalia gilliesii*, *Celtis pallida*, *Condalia microphylla*, *Mimozyganthus carinatus*, *Parkinsonia praecox*, *Monteverdia spinosa*) and non-thorny (*Larrea divaricata*, *Larrea cuneifolia*, *Aloysia gratissima*) shrubs may locally predominate. Another striking floristic feature that should be noted in the Arid Chaco is the presence of 13 species of the epiphytic genus *Tillandsia*, representing 25% of the 52 species reported for Argentina (Zuloaga et al. 2019). These species were mostly recorded in the *Aspidosperma quebracho-blanco* forest. Several of the species belong to the subgenus *Diaphoranthema*, reported as confined to xerophytic habitats in north-western Argentina, Bolivia and north-western Paraguay (Barfus et al. 2016; Donadio et al. 2022).

At the scale of the whole Chaco, our vegetation types share numerous species with communities described for the northern Paraguayan (Ramela and Spichiger 1989; Spichiger et al. 1991; Mereles 2005; Navarro et al. 2006) and boreal Bolivian (Navarro 2011) Chaco. In general, tree species richness is lower in the forests and shrublands of the Arid Chaco (studied here) than in the xeromorphic forests of the Chaco of northern Argentina, Paraguay and Bolivia. Another important difference is the absence of species of the genus *Schinopsis* in the *Aspidosperma quebracho-blanco* forests of the Arid Chaco. This is one of the main criteria by which Morello et al. (1995) and Ragonese and Castiglioni (1970) separated the Arid Chaco or Los Llanos District from the Western Chaco of Cabrera (1976). The vegetation formations of the Paraguayan Chaco have been divided by Spichiger et al (1991) into "Dry Chaco" and "Humid Chaco". Some of the zonal vegetation units described for the Dry Chaco exhibit floristic relationships with the vegetation types of the Arid Chaco. Specifically, the xeromorphic forest of *Aspidosperma quebracho-blanco* and *Chorisia insignis* (quebrachal de quebracho blanco) described by Ramella and Spichiger (1989) and Spichiger et al. (1991) as the climax community of the Paraguayan Dry Chaco, exhibits numerous species in common with the forests of the Arid Chaco, such as *Castela coccinea*, *Cercidium praecox*, *Sarcomphalus mistol*, *Stetsonia coryne*, among others. Also, for the boreal Paraguayan Chaco, Mereles (2005) described non-flooded xerophytic formations among which some communities with certain floristic relationships with the forests of the Arid Chaco are reported. Among them, it is worth mentioning the semi-deciduous dense xerophytic forest ("Bosque xerofítico denso semi-caducifolio") and the semi-deciduous dense xerophytic forest in transition ("Bosque xerofítico denso semi-caducifolio en transición"). Both formations occur on imperfectly drained, clay soils, although in the second case there is a predominance of sands on the surface (Mereles 2005). Although most of the dominant species are not present in the Arid Chaco, *Aspidosperma quebracho-blanco* is a co-dominant and there are numerous species in common, such as *Stetsonia coryne*, *Mimosa detinens*, *Prosopis sericantha*, *Bulnesia bonariensis*, *B. foliosa*, *Prosopis nigra*, *Sarcomphalus mistol*, *Jatropha excisa*, *Ximenia americana*, *Acacia aroma*, *Opuntia quimilo*, and pioneers such as *Cercidium praecox* and *Castella coccinea*, among others.

Navarro et al. (2006) also reported for the Chaco of northern Paraguay some xeromorphic forests that harbor species in common with our forests, although with higher richness of tree species and the presence of *Schinopsis* species. Some of these forests are the "quebracho blanco forest of the Parapetí old alluvial fan on rather poorly drained soils" and the "xerophytic forest on vertic soils with dominant clay and lime textures, poorly drained in the lower horizons". One of the emergent trees in this forest is *Aspidosperma quebracho-blanco*. In addition, Navarro reported "xerophytic forest on fairly well-drained soils", distributed in the north of the Pilcomayo old alluvial plain, with species in common with our vegetation types such as *Monteverdia spinosa* and *Mimozyganthus carinatus*.

The vegetation types of the Arid Chaco also maintain floristic relationships with the Northwestern Chaco Sector of the Bolivian Chaco (Navarro 2011). From the detailed and comprehensive description of the Bolivian Chaco by Navarro (2011), it is clear that the vegetation types described in this study share plenty of species with the vegetation of well to moderately well-drained soils of the Bolivian Chaco. The "xeric forests of the ancient alluvial plains of the western northern Chaco", which constitute the zonal climax vegetation of the northwestern Bolivian Chaco, share with the forests and shrublands of the Arid Chaco at least 30% of the species mentioned by Navarro (2011) as a characteristic combination of these forests. In addition, the Quebrachal of white quebracho (Quebrachal de Quebracho Blanco) on imperfectly drained soils" described by Navarro (2011) exhibits some floristic similarities with the *Aspidosperma quebracho-blanco* forests of the Arid Chaco, especially with those that occupy lower areas with higher clay content in the soil where the presence of *Geoffroea decorticans* is conspicuous. All these floristic relationships reinforce the real Chaquenian character of the Arid Chaco.

The vegetation types occurring in saline habitats correspond to the phytosociological class *Suaedetea divaricatae* and the order *Stenodrepano-Prosopietalia reptantis*, described for the warm saline desserts of north-western Argentina (Martínez Carretero 2001). Some of the characteristic species of these units were also discriminated as diagnostic in our analyses. However, the position of the succulent shrublands (our Type 4.2) is not entirely clear in the phytosociological scheme of Martínez Carretero (2001). Therefore, we consider that the floristic and phytosociological information available for the Arid Chaco and phytogeographically related regions is still very preliminary and insufficient to attempt a valid syntaxonomic synopsis.

As stated by Navarro (2011), these halophytic vegetation types develop also in the saline and seasonally flooded soils of the northern Chaco, in Bolivia, Paraguay and northern Argentina. A zonation similar to that described in this work from the Chaco Forest to the saline playa at the bottom of the bolsón, is reported by Navarro (2021) for Bolivia and by Spichiger et al. (1989) and Mereles (2005) for the northern Paraguayan Chaco. When the silty clay and/or sandy soils of the xeromorphic forest become saltier, species with some tolerance to salt appear, such as *Maytenus vitis-idaea*, *Cyclolepis genistoides*, *Lycium* spp., etc., until the playas with saline efflorescence and devoid of vegetation are reached (Spichiger et al. 1989). The floristic similarity between the vegetation of barreales and salinas (Types 4.1 and 4.2) with that of saline sites of the Bolivian and Paraguayan Chaco is surprising. A large group of taxa of the genera *Maytenus*, *Grabowskia*, *Cyclolepis*, *Atriplex*, *Portulaca*, *Sesuvium*, *Heliotropium*, *Sclerophylax*, *Holmbergia*, *Heterostachys* and *Sarcocornia* is shared by saline shrublands and scrublands along the Chaco from Bolivia to its southern extreme in the Arid Chaco.

Physiognomy and life form spectra across vegetation types

As stated above, one of the relevant physiognomic features of the Arid Chaco is the dominance of shrublands and scrublands. However, some physiognomic variations could be observed among the different shrubland types, possibly related to edaphic variations and different intensities of disturbance (Blanco et al. 2005; Calella and Corzo 2006; Biurrun et al. 2015). The highest tree cover was recorded in vegetation Type 1.1 *Aspidosperma quebracho-blanco* forest and Type 1.3 *Prosopis flexuosa* woodland. The cover of the herb (grasses and forbs) layer not only exhibited a high variability among the different vegetation types, but also within them which has been related to differences in water availability and grazing intensity (Blanco et al. 2005; Calella and Corzo 2006; Karlin et al. 2013; Quiroga et al. 2013).

In accordance with the dominant physiognomy in the Arid Chaco, shrubs were the most prominent life form in terms of cover and average number of species per relevé in all the vegetation types. Different kinds of shrubs (microphyllous, both evergreen and deciduous, aphyllous, thorny and non-thorny) have been reported for the Arid Chaco vegetation (Morello et al. 1985). Specifically, we recorded: evergreen shrubs with *sclerophyllous* leaves such as *Larrea divaricata* and *Larrea cuneifolia*, thorny deciduous shrubs with soft leaves such as *Senegalia gilliesii*, *Mimozyganthus carinatus*, *Celtis pallida*, *Parkinsonia praecox* and *Ximenia americana*; non-thorny deciduous shrubs such as *Atamisquea emarginata* and even mostly aphyllous shrubs like *Senna aphylla* or with ephemeral leaves such as *Bulnesia retama* and *Tricomaria usillo*. In the halophytic vegetation types, succulent-leaved shrubs such as *Heterostachys ritteriana*, *Allenrolfea patagonica*, *Grahamia bracteata* and *Suaeda divaricata*, among others, were recorded. As far as hemicryptophytes are concerned, different morpho-functional grasses have been recognized by Morello et al. (1985) in the Arid Chaco: perennial tussocks, annual grasses and very short grasses and all of them were recorded in our study. Regarding trees, the dominant *Aspidosperma quebracho-blanco* is evergreen, although under exceptional conditions, may lose its leaves (Morello et al. 1985). Some other important deciduous trees are microphyllous (*Prosopis flexuosa* and *Senegalia praecox*), or with larger leaves (*Celtis tala* and *Sarcomphalus mistol*). As expected, epiphytes and climbers, were particularly abundant in the *Aspidosperma quebracho-blanco* forest. Most shrubland types almost lack epiphytes and climbers and, when present, are restricted to the scattered emergent trees, with the exception of *Cordobia argentea*, which is likely to thrive on low shrubs. Finally, three other outstanding life forms were the cacti, the reviviscent fern *Selaginella sellowii* and the epiphytic bromeliads of the genus *Tillandsia*, already mentioned above. The former included columnar cacti (*Stetsonia coryne* and *Cereus forbesii*), as well as opuntioid species, mostly included within the genus *Opuntia*. Opuntioids like *Opuntia sulphurea* and species of *Tephrocactus*, are usually very abundant in disturbed and degraded sites, with high percentages of bare soil (Morello and Saravia Toledo 1959; Cabido et al. 1994). *Selaginella sellowii* forms a carpet-like cover colonizing degraded soils in the initial phases of secondary successions (Morello et al. 1985).

Plant richness, endemism, non-native species and chorotypes distribution patterns across the vegetation types

Previous studies revealed that not only plant diversity, but also arthropod richness, was reported highest in forests and woodlands in relation to scrublands and very open shrublands in the Arid Chaco (Gardner et al. 1995). This high species richness was associated with the structural diversity (mainly vertical and horizontal heterogeneity) of vegetation (Gardner et al. 1995). Our findings confirmed those results with the highest floristic richness registered in the *Aspidosperma quebracho-blanco* forest and the lowest in open shrublands and scrublands. Also, halophytic vegetation types exhibited low species richness, which is common in saline communities (Ruiz Posse et al. 2007).

It has been proposed that the low number of endemism reported for the Gran Chaco was related to the lack of geographical barriers separating the Chaco from other phytogeographical regions such as the Espinal, the Pampa and the Cerrado (Bucher 1982). However, and perhaps as a response to climatic barriers, this study revealed the presence of 62 endemic species at the national level and 22 restricted to the Arid Chaco and neighboring phytogeographic provinces such as the Monte and Prepuna. The halophytic vegetation exhibited the highest proportion of restricted endemic species which is probably related to the isolated character of saline depressions. However, the number of species strictly restricted to the Arid Chaco was very low. Despite the study area is surrounded by mountain systems, these do not probably constitute geographic barriers as revealed also by the occurrence of species belonging to the Western and Eastern Chaco, the Southern-Brazilian/Paranaense and Espinal/Pampean chorotypes. In this way, the dominant chorotype in the Arid Chaco was the Eastern and Western Chaco (39.4% of all the species recorded) while species included in the Arid Chaco and Monte chorotype comprised only 15.7% of the total species. However, in the other districts of the Gran Chaco in Argentina (Western, Eastern and Mountain Chaco, according to Cabrera 1976), the Arid Chaco and Monte chorotype is almost lacking (Cabido et al. 2018b; Zeballos et al. 2020). Patagonian species were also scarce and the same was true for non-native species. These figures reflect the Chaquenian character of the Arid Chaco and confirm the identity revealed previously by Ragonese and Castiglioni (1970) and Morello et al. (1985).

Vegetation types and their relationship with environmental variables

The ISOMAP ordination revealed some trends of floristic change that were weakly, though significantly, related to elevation, climate and soil. The limited explanatory power of the bioclimatic variables and elevation suggested that the entire Arid Chaco region exhibits a certain climatic (mainly thermal) uniformity.

Previous surveys in other sectors of the Gran Chaco have also revealed the influence of climate, geomorphology and soils, mostly soil drainage, on the composition, physiognomy and distribution of vegetation (Prado 1993b; Ramella and Spichiger 1989; Spichiger et al. 1991; Mereles 2005; Navarro et al. 2006; Navarro 2011). The zonal vegetation of the Arid Chaco are the xeromorphic forests with *Aspidosperma quebracho-blanco* and perhaps the psammophilous variants on sand dunes and sand fields. In addition to the climax vegetation, the remaining vegetation types described are grading into one another along a topographic gradient or topo-sequence from the distal bajadas to the bottom of the bolsón (Figure 5a).

Studies of the vegetation in specific sites of the Arid Chaco associated the spatial distribution of vegetation to geomorphological and edaphic characteristics (Morello et al. 1985; Cabido et al. 1992, 1994; Morlans and Guichón 1998; Peña Zubiate et al. 1998; Calella and Corzo 2006; De La Orden and Quiroga 2009; Karlin et al. 2013). In general, these authors did not recognize climatic differences within the region as determinants of vegetation types. Our results partially agree with those previous findings: Type 1.1 *Aspidosperma quebracho-blanco* forest was described in the fluvio-eolian plains, although the most widely distributed vegetation types throughout the plains of the Arid Chaco were shrublands and scrublands (mostly relevés included in Types 1.2, 1.3, 3.1 and 3.2), alternatively dominated by different species. These vegetation types thrived mainly on loamy soils, well to moderately well drained (see topo-sequences in Figure 5a). In the distal sectors of the bajadas, with soils well to excessively drained soils, there was a predominance of thorny scrublands with some emergent trees. The foothills and the apical sectors of the bajadas, comprising habitats with unstable substratum and surface runoff, were occupied mainly by thorny scrublands dominated by *Mimozyganthus carinatus*, *Senegallia giliesii* and *Larrea divaricata* (vegetation type 3.1) and only scattered emergent trees were seen. This pattern was previously observed in the northern and western parts of the Arid Chaco where *Bulnesia foliosa* is also dominant (Morlans and Guichón 1998; Calella and Corzo 2006; De La Orden and Quiroga 2009; Cabido et al. 2018a). Some of the shrublands dominated by *Larrea cuneifolia* (Cluster 2) were associated with imperfectly drained soils with, high pH, mostly in the vicinity of saline depressions and in western sectors of the study area, with lower rainfall.

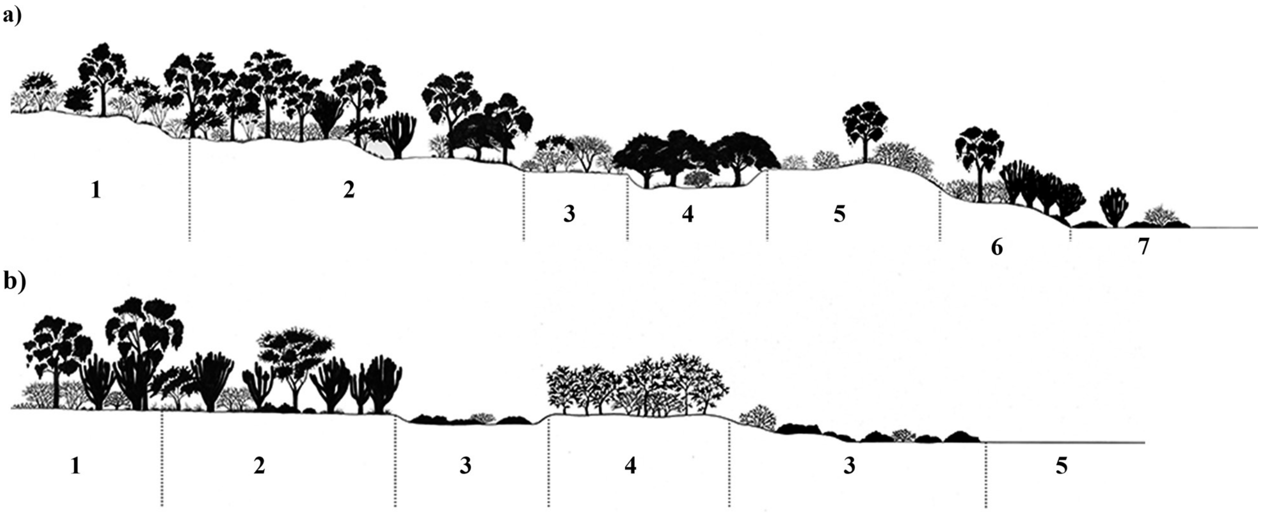

Figure 5. Schematic representation of the toposequence observed from the distal part of the bajadas to the saline bottom of the bolsón in the Arid Chaco of Central-Western Argentina. a) sequence from the bajada to the bottom of the bolsón showing the following vegetation types: 1) *Mimozyganthus carinatus – Bulnesia foliosa* shrubland; 2) *Aspidosperma quebracho-blanco* forest; 3) *Larrea divaricata* shrubland; 4) *Prosopis flexuosa* woodland; 5) *Tricomaria usillo* shrubland; 6) *Stetsonia coryne* shrubland; and 7) *Heterostachys ritteriana – Allenrolfea patagonica* shrubland. b) Detailed vegetation profile of saline environments: 1) *Aspidosperma quebracho-blanco* forest with *Stetsonia coryne*; 2) *Stetsonia coryne* shrubland; 3) *Suaeda divaricata – Atriplex argentina* shrubland; 4) *Geoffroea decorticans* shrubland; *Heterostachys ritteriana – Allenrolfea patagonica* shrubland; 5) saline playa. Art work: Fernando A. Gallará.

Saline soils occupy large areas in Central-Western Argentina and in some places, they are on the rise, mainly due to the use of inadequate management techniques (Martínez Carretero 2001). In the Arid Chaco there are several saline depressions and other sectors in which there is an accumulation of salts on the surface, such as the muddy areas (barreales). In these sites the vegetation was associated to soils with high electric conductivity. The vegetation zonation described in this survey from the saline playa to the *Aspidosperma quebracho-blanco* forest in the fluvio-eolian plains, coincided with previous descriptions for saline sectors of the Arid Chaco (Ragonese 1951; Sayago 1969; Ruiz Posse 2007). The sequence of plant communities along the zonation were included in our vegetation types 4.1 and 4.2 and is similar to the topo-sequence described by Spichiger et al. (1991) from xeromorphic forests to halophytic steppes in northern Paraguay (see Figure 5b).

Despite our considerations on the relationships between vegetation distribution and soils, a definitive explanation of the spatial patterns of vegetation will require the detailed study of the effects of disturbance (logging, livestock and fire) on vegetation cover, as well as the variability of soils at a higher spatial resolution than that used in this study.

Vegetation types and the role of disturbance

It has been proposed that the original landscape of the Chaco region consisted of patches of old-growth forest alternating with patches of grasslands resulting from fires set by the Amerindian people for their hunting activities (Morello and Saravia Toledo 1959; Bucher and Schofield 1981). Later, due to the introduction of European livestock with shifts in management and exploitation practices, grasslands were invaded by shrubs, losing their forage aptitude, and forests were dramatically altered. These changes resulted in the predominance of xerophytic and thorny scrubs (fachinales) or shrublands with a high percentage of bare soil (peladares) and low herbaceous cover (Morello 1970). Although the successional model developed by these authors corresponds to the Chaco of northern Argentina, where annual rainfall is higher, our results allow us to propose the application of a dynamic model (in fact, a regressive succession) also to the vegetation of the fluvio-eolian plains of the Arid Chaco (Figure 6). To the previous disturbances described here it must be added that the deforestation was linked to the expansion of the railway network since the end of the 19th century and the increased exploitation of livestock during the last century and so far, this century (Morlans and Guichón 1998; Britos and Barchuk 2008; Zak et al. 2008; De La Orden and Quiroga 2009; Karlin et al. 2013). The changes brought about by the disturbances are manifested rather in the vertical and horizontal structure and in the relative abundance of some species. In general, there is a reduction in the height of the upper strata which could even disappear as the intensity of the disturbance increases. Knowledge of the responses to disturbance of the vegetation of salt marshes, mudflats (Cluster 4) and sand dunes is still very preliminary, so any speculation on this subject is extremely risky.

The, preliminary outline of major trends of change representing different degradation stages of the original

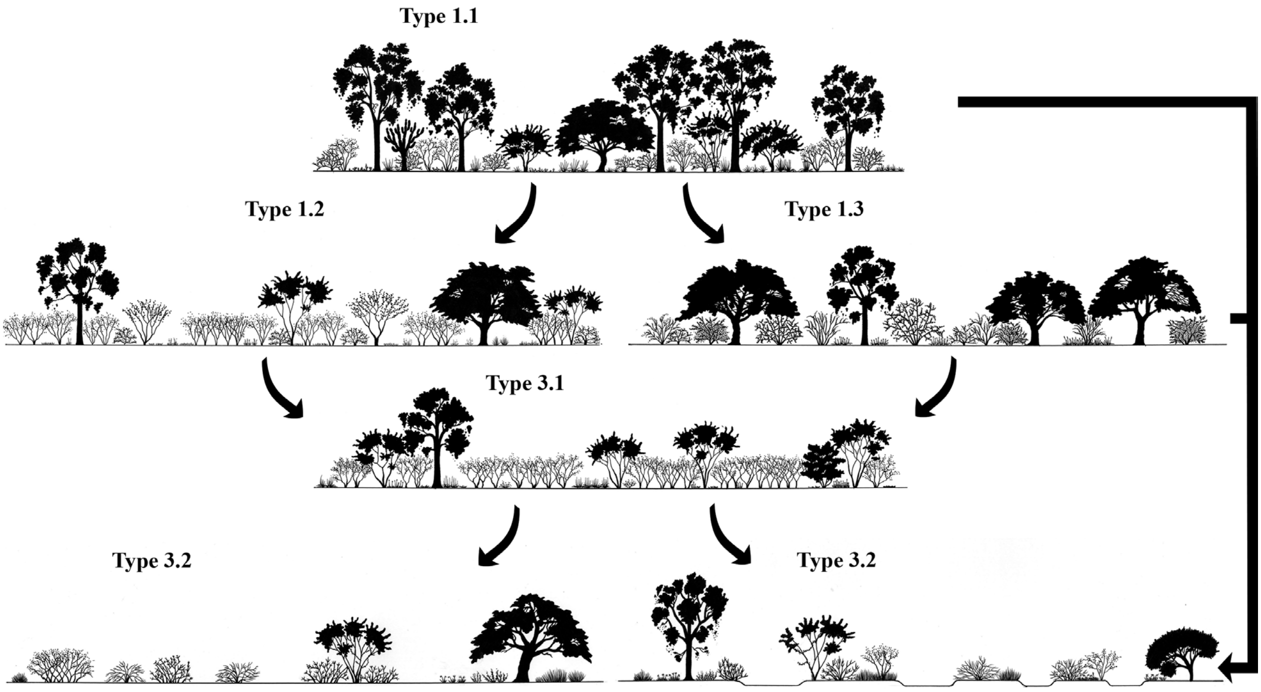

Figure 6. Stages in the degradation (regressive succession) of vegetation cover in the Arid Chaco. The figure shows in a simplified schematic form the regressive sequence from the *Aspidosperma quebracho-blanco* forest (vegetation type 1.1) to the vegetation types exhibiting the greatest degradation of vegetation (the peladares and fachinales represented by vegetation types 3.1 and 3.2). Vegetation types are those reported in Table 1. Art work: Fernando A. Gallará.

forest is presented in Figure 6. The Type 1.1 *Aspidosperma quebracho-blanco* forest is proposed as the old growth/potential natural vegetation. The other types within cluster 1 are interpreted as a result from low or medium intensity disturbances or occur in areas that have been free of severe disturbances for years and still conserve a tree layer, either as Type 1.2 *Larrea divaricata* shrublands with emergent individuals of *Aspidosperma quebracho-blanco*, or as low and closed Type 1.3 *Prosopis flexuosa* woodlands and also other type of shrublands. The vegetation types included in cluster 3 represent stages of further degradation of the original forests, characterized by closed to open thorny scrubs (Type 3.1 *Mimozyganthus carinatus – Bulnesia foliosa* shrublands), and also degradation phases on stabilized sand dunes and sandy soils where the Type 3.2 *Tricomaria usillo* shrublands thrives. The final stages of degradation of the *Aspiodosperma quebracho-blanco* forest consists of the peladares (areas with low cover and high percentages of bare soil), with scattered shrubs and a remarkable presence of cacti. Stages of maximum disturbance of the Arid Chaco Forest, caused by the combined action of logging, fire and grazing, is nowadays very common in the study area, especially in the vicinity of local people's dwellings. In these situations, the abundance of *Prosopis flexuosa*, *Vachellia aroma*, the opuntioid cacti *Opuntia sulphurea* and species of *Tephrocactus* among other species, is higher (some of the relevés included in Type 3.2 represent this final stage in the degradation of the original forests). The advance of species and communities from the Monte towards the east, may also be a consequence of disturbances on the *Aspidosperma quebracho-blanco* forest, as highlighted by Morello (1958), Morello and Saravia Toledo (1959) and Sarmiento (1972).

Conclusion and further perspectives

In this study we provide baseline information concerning the floristic heterogeneity of the vegetation of the Arid Chaco in Central-Western Argentina. Despite the studied region still includes communities in a good conservation status, most of the territory exhibits secondary communities (mainly shrublands and scrublands) replacing vegetation Type 1.1 *Aspidosperma quebracho-blanco* forest, as a consequence of human activities. Old growth forests are restricted to areas free from disturbances for decades or to protected areas (Cabido et al. 1992, 1994). It is likely that the loss of structural complexity and the decrease in the floristic richness of the most severely disturbed vegetation types, may impact in the remaining trophic levels, which is a matter of consideration in the face of biodiversity conservation and management. In view of the intense disturbance to which the vegetation of the Arid Chaco has been subjected, we emphasize the need to protect the few mature forests still present in the region.

Data availability statement

The database of occurrence records of the Arid Chaco vegetation in Central-Western Argentina is available in Suppl. material 1.

Author contributions

M.R.C, A.T.R.A, J.M., F.N.B. and L.J.B. planned the research; M.R.C., A.T.R.A., J.M., F.N.B., J.J.C., S.R.Z., L.J.B., W.D.A., R.J.A., M.G.A., D.N.A., A.Q. and R.E.Q. conducted the field work; S.R.Z. and M.R.C. performed the statistical analyses; S.R.Z. prepared the tables, figures 2 to 4 and the Supplementary materials; D.S.A. performed Figure 1 and figure S1.1, Supplementary material 2, Appendix S1; M.R.C., S.R.Z., J.J.C. and A.T.R.A led the writing; while all authors commented on the manuscript.

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Supplementary material

Supplementary material 1

Individual relevé matrix comprising 439 species × 654 plots (Table S1.1) recorded in the Arid Chaco, Central-Western Argentina.

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Supplementary material 2

Appendix S1: Distribution of relevés belonging to different vegetation types.

Appendix S2: Sample-size-based and coverage-based rarefaction, extrapolation sampling curves jointly with species observed and non-parametric estimators of species richness.

Appendix S3: National and regional percentage of endemic species (mean ± sd) per vegetation type.

Appendix S4: Mean (± sd) species percentage per relevé of all chorotypes and non-natives species.

Appendix S5: Mean cover and height with their respectively standard error and maximum and minimum cover values recorded for tree, shrub and herb layers.

Appendix S6: Life forms percentage (mean ± sd) per vegetation type in the Arid Chaco.

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Supplementary material 3

Floristic table. Table S1.1: extended synoptic table.

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