



Cerrados in Argentina? Structure, diversity and biogeography of the woody component of a savanna in the Misiones Province

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Abstract

The Teyú Cuaré field, in Misiones province, Argentina, has been renowned for its flora and physiognomy, which led researchers to indicate that it could be a relict of Cerrado biome. We analyzed the floristic structure of the woody component of a savanna community in this site, and discussed the processes that could contribute to the permanence of this vegetation type over time. Perimeter and height of all woody individuals ≥ 10 cm of perimeter at soil height were collected in 12 square plots (400 m² each one). We found 15 families and 17 species in our site and compared the woody flora surveyed at this site with the flora of other Cerrado areas from Brazil and Paraguay. *Leptolobium elegans* had the highest importance value. The woody flora of the area is closely related to the Cerrado areas from Paraná state in Brazil and Canindeyú and Amambay in Paraguay. This site probably reflects old open physiognomies which were predominant in Misiones and Southern of Brazil in the late Pleistocene and middle Holocene. We inferred that the permanence of open physiognomies at Teyú Cuaré is probably related to mechanisms that act at different levels, such as geological, edaphic, anthropic, and fire disturbance.

Key words: *Leptolobium*, Cerrado, fire, phytosociology, relicts.

Resumo

O campo de Teyú Cuaré no departamento de San Ignacio, na província de Misiones, Argentina, tem se destacado pela sua flora e fisionomia, o que levou a pesquisadores a indicar que poderia ser um relict do bioma Cerrado. Analisou-se a florística e a fitossociologia do componente arbóreo-arbustivo de uma comunidade savânica, discutindo-se os processos que a originaram e contribuem para a permanência desta fitofisionomia. Em 12 parcelas quadradas de 400 m² foram mensurados o perímetro e a altura de todos os indivíduos lenhosos com perímetro ≥ 10 cm ao nível do solo. Avaliamos a similaridade florística entre a área estudada e outras áreas de Cerrado do Brasil e do Paraguai. No total foram detectadas 15 famílias e 17 espécies, onde *Leptolobium elegans* foi a de maior importância estrutural. A flora lenhosa da área é mais fortemente associada com as áreas de Cerrado do Paraná e Canindeyú e Amambay no Paraguai. A vegetação do local possivelmente é um reflexo da expansão das fisionomias abertas do Pleistoceno tardio e Holoceno médio, dominantes em parte da província e do Sul do Brasil. A permanência desta unidade campestre provavelmente está relacionada à atuação de mecanismos de natureza geológica, pedológica, antrópica e por perturbações pelo fogo.

Palavras-chave: *Leptolobium*, Cerrado, fogo, fitossociologia, relictos.

Introduction

Savanna vegetation is mainly characterized by the presence of a grass layer with woody elements, such as tall shrubs, trees or palm trees, in open formation (Sarmiento 1984). Neotropical savannas in the Caribbean and Central America are

distributed in Cuba, Belize, Guatemala, Mexico, and Nicaragua. In South America, they are found in Colombia, Venezuela, Guiana, Brazil, Bolivia and Perú (Pennington *et al.* 2006). The largest Neotropical savannas are the Cerrado, distributed in Brazil, Bolivia and Paraguay; and the Llanos,

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in Venezuela and Colombia. The Cerrado is considered one of the most diverse savannas in the world with more than 12,000 vascular plants (Mendonça *et al.* 2008). Despite being the second major biome in Brazil, its geographical domain suffered changes of expansion and retraction throughout the Quaternary period (Durigan 2006).

The presence of vegetation types that are different from the main landscape is an evidence of the spatial dispute perpetrated by different biomes (Ledru 2002; Mayle 2006; Cox & Moore 2011). Savannas in South America experienced cycles of expansion and retraction because of climate fluctuation (Werneck *et al.* 2011; Rull *et al.* 2013). When climate got drier, it favored the expansion of open physiognomies, such as savannas and grassland, and when climate got wetter, savannas suffered contraction, because climate was suitable for the closed formation (Sanaiotti *et al.* 2002; Ab'Sáber 2003; Alizadeh *et al.* 2015). Regarding Cerrado, relict and disjunction of this biome can be found as far from its current distribution area as in the Brazilian states of Roraima, Amapá, Piauí, Maranhão, São Paulo and Paraná (Ab'Sáber 2003; Ratter *et al.* 2003; Moro *et al.* 2015), as well as in other countries, in Bolivia and Paraguay (Villarroel *et al.* 2009; Mereles 2013).

In the Misiones province (Argentina), the flora comprises mainly forests, savannas, and grasslands. With one-third of the total number of vascular plants registered in Argentina (c. 3,400 species), it is one of the most biodiverse areas of the country (Zuloaga *et al.* 1999; Flora del Conosur <<http://www.darwin.edu.ar/Proyectos/FloraArgentina/fa.htm>>). Within Misiones, San Ignacio department has been highlighted for its floristic attributes due to the presence of taxa that, even though they have major distributions in other places, are restricted around the country, as well as high endemism levels (Cabrera 1987; Filgueiras 1990; Biganzoli & Romero 2004; Fontana 2005; Krapovickas 2012a; Krapovickas 2012b; Keller 2015; Keller & Tressens 2016). Less than 3 km to the southwest of the city of San Ignacio exist a singular vegetation locally known as Teyú Cuaré field. Due to its scenic and ecological relevance (Fontana 2005), it is considered an important Argentinian grassland and savanna site, closely related to Uruguay and Southern Brazil vegetation (Bilenca & Miñarro 2004).

The Teyú Cuaré field is an open vegetation patch located inside a forest matrix. It covers around 200 ha and is in the buffer zone of two protected

area, the Osununú Private Reserve and Teyú Cuaré Provincial Park. There are more than 179 plant species in Teyú Cuaré (Biganzoli & Romero 2004; Fontana 2005), of which *Leptolobium elegans* Vogel (= *Acosmium subelegans* (Mohlenbr.) Yakovlev) (Fabaceae) and *Allagoptera campestris* Kuntze (Arecaceae) are remarkable, because of their restricted distribution into Argentina. In Teyú Cuaré field coexist grassland and savanna physiognomies. The population of *Leptolobium elegans* has a dense distribution to the north of the Teyú Cuaré field, and in the same way as other species, it emerges from the herbaceous layer as tortuous small tree, being responsible for the transitional grassland to savanna appearance of the landscape. This physiognomy associated with floristic composition led researchers to indicate that it is a relict of Cerrado biome (Martínez-Crovetto 1963; Chébez 1996; Biganzoli & Romero 2004). The persistence of relictual vegetation can be associated with several factors, such as local climate (Moro 2012); geomorphology variation (Pérez-García & Meave 2004; Moro 2012; Speziale & Ezcurra 2012), edaphic conditions (Miranda *et al.* 2002; Carneiro Filho 1993), fire frequency (Behling & Pillar 2007) or human activities (Iriarte & Behling 2007). Those environmental factors could be acting in the apparently relictual Teyú Cuaré field. Thus, we aimed to study the flora and structure of the woody component of the savanna portion of this area and to discuss some processes that gave rise to this vegetation type and contribute to its permanence in the region.

Material and Method

Study area

The study site is located in San Ignacio Department, Misiones, Argentina (Fig. 1) at 75–185 m a.s.l. (longitude: 55°33'26.62"W; latitude: 27°16'42.17"S). The majority of the Teyú Cuaré field is covered by grassland, so the plots for our phytosociological survey was placed on the northern part of this site, which presents a larger abundance of woody elements and savanoid physiognomy. The climate is Köppen, *Cfa*, humid temperate with warm summers and cold winters, no distinguished dry season (INTA 1990). Mean annual temperature is 21.86 °C and mean annual rainfall is 1,644 mm; rainiest period comprises October to February. The mean annual number of frost days is nine, occurring from May to August (Martínez-Crovetto 1963).

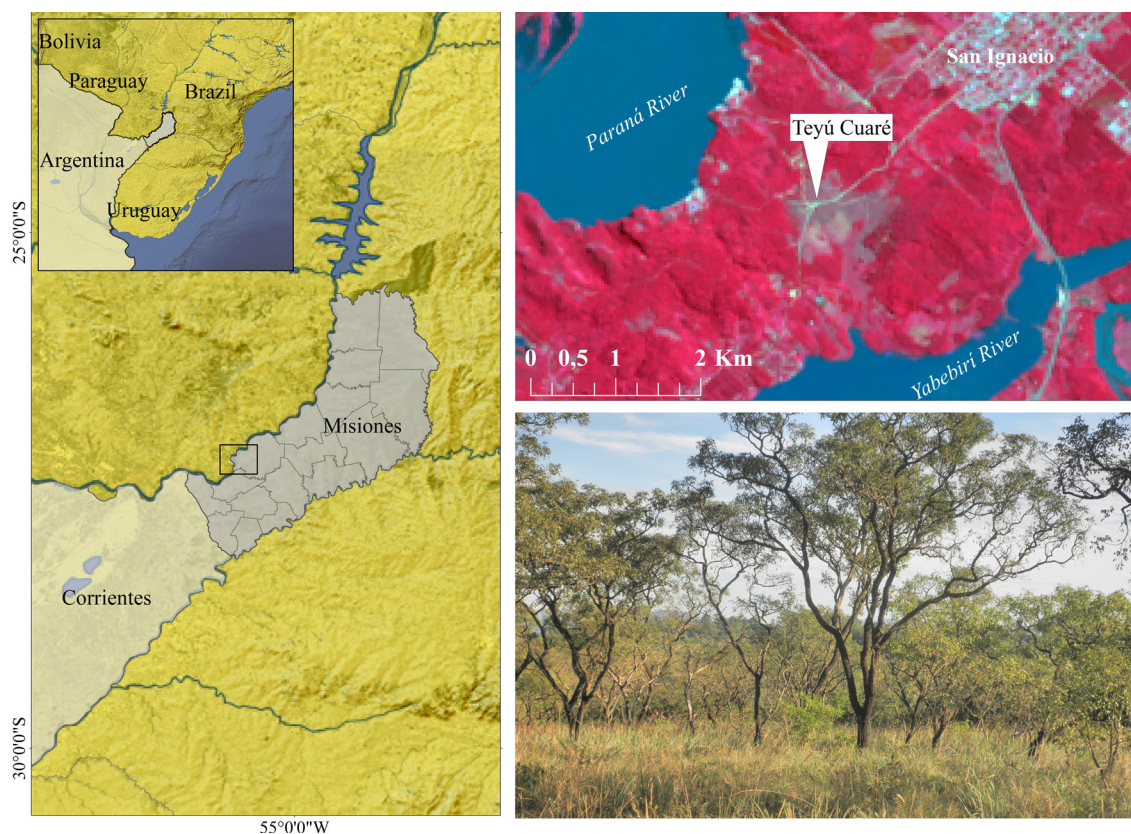


Figure 1 – Location of the research area in San Ignacio, Misiones - Argentina, and study site overview (bottom right).

The sandstone of Solari formation is predominant, which is notable considering that the province is mainly covered by basalt of the Serra Geral formation (Tchilinguirán *et al.* 2005). This sandstone relates to the Brazilian Botucatu formation (Teruggi 1970), as it is located above the Independência Series and under the eruptive Serra Geral (Harrington 1950). Posadas formation is also found in the site, with tholeiitic basaltic rocks (Teruggi 1970; Garrasino 1995). The study area shows a slightly undulate relief, with patches of sandstone outcrops.

Psamment and Entisol (IUSS 2015) are the predominant soils. The sampled soil profile (see supplementary material 1: <<http://dx.doi.org/10.6084/m9.figshare.5238961>>) has > 65% of sand fraction, is acid, with low base saturation and cationic exchange capacity. Due to the sandy composition, with single-grain structure and very friable granules, the soil is highly susceptible to erosion.

Deciduous and semi-deciduous dry forests are the most common vegetation type in the region, and grasslands and savannas in the Southwest of

the province gradually replace them. Based on the Martínez-Crovetto (1963) vegetation classification system, the study area comprises Distrito de los laureles, characterized by the presence of Lauraceae as *Nectandra megapotamica* Mez and *Nectandra lanceolata* Nees & Mart, and the Distrito del Urunday, with *Astronium balansae* Engl. as the main species. Up to date, there are eight endemic species recognized for the Teyú Cuaré site: *Austrochthamalia teyucarensis* (Apocynaceae) (Keller 2015), *Gaya kelleri* Krapov. (Malvaceae) (Krapovickas 2012a), *Hedeoma teyucarensis* (Lamiaceae) (Keller & Tressens 2016), *Hyptis australis* Epling (Lamiaceae) (Epling 1949), *Lessingianthus teyucarensis* (Cabrera 1987), *Mesosetum comatum* Swallen (Poaceae) (Filgueiras 1990), *Oxypetalum teyucarensis* Farinaccio & Keller (Apocynaceae) (Farinaccio & Keller 2014), and *Sida rhizomatosa* Krapov. (Malvaceae) (Krapovickas 2012b).

Survey and data analysis

We established 12 square plots of 20 × 20 m (400 m²) randomly in the northern part of the open

vegetation patch and measured all individuals with perimeter at soil height ≥ 10 cm. Sampling sufficiency was assured by two criteria. The first was based on the individual-based rarefaction curve and its relationship with nonparametric species estimator Chao 1 and ACE (Abundance Coverage-based Estimator). A satisfactory survey is achieved when the sampled richness is equivalent or close to these estimators (Colwell 2013). Cain criterion (Mueller-Dombois & Ellenberg 1974) was applied too, in which a satisfactory survey is reached when an increase of 10% in the sampling effort does not imply in a richness increment greater than 10%. For this, we used the extrapolation curve (Colwell *et al.* 2012). We used EstimateS software v. 9.1.0 (Colwell 2013) to calculate Chao 1 and ACE estimators and perform the rarefaction and extrapolation curve with 100 individual randomizations.

Species names and their authors were updated according to the database of International Plant Name Index (<<http://www.ipni.org/index.html>>). Dispersion type and the habit were listed too. Community structure parameters (density, dominance, frequency and importance value) and Shannon diversity index using natural logarithms, Simpson's reciprocal and Berger-Parker's reciprocal were calculated (Mueller-Dombois & Ellenberg 1974).

Comparison with other study sites

We performed ordination and cluster analysis in order to evaluate patterns of floristic similarity among the flora surveyed in Teyú Cuare and other savannah sites in the core and marginal Cerrado areas. Thus, we combined previous scientific publications of phytosociology and floristic lists with surveys of the Cerrado Domain in Brazil closer to the study site (states of Paraná, São Paulo, and Mato Grosso do Sul) and eastern Paraguay (departments of Amambay and Canindeyú) (Locations of the floristic surveys are depicted in the Figure 5, for more description for each site see supplementary material 2: <<http://dx.doi.org/10.6084/m9.figshare.5238961>>). Our database encompassed 513 species and 66 areas, which 53 were sourced by the Conservation and Management of the Biodiversity of the Cerrado Biome Project (<<http://cerrado.rbge.org.uk/cerrado/index.php>>), published by Ratter *et al.* (2003). For the floristic studies, we just considered trees and large shrubs. The accepted names of taxa were verified using Taxonomic Name Resolution Service Version 1.1.

(Boyle *et al.* 2013) prior to analysis. Ordination and cluster analysis included those species that occurred in two or more sites (*i.e.*, unicates were not considered); consequently, the final presences/absences matrix comprised 354 species (see supplementary material 3: <<http://dx.doi.org/10.6084/m9.figshare.5238961>>).

For ordination, we performed a Principal Coordinate Analysis (PCoA) based on Sørensen distance index. For cluster analysis, we applied Ward's hierarchical method with the same distance index used in the ordination. The best number of groups was assessed varying the number of cluster from 2 to 5 and performing the silhouette coefficient, in which the best is one that has the greatest coefficient value. The ordination and cluster analysis were performed in R v. 3.3.2 (R Core Team 2016) with the *vegan* package.

Results

In the phytosociological study we measured 493 individuals, distributed in 17 species, 17 genera and 15 families (Tab. 1). Individual-based rarefaction and extrapolation curves, and ACE and Chao estimators, proved the sampling was satisfactory (Fig. 2). The asymptotic trend of the curve is proved by the proximity of the value of rarefaction curve and Chao 1 estimator, and to a lesser degree by the ACE estimator. For both estimators, the end of the rarefaction curve is within the confidence interval. The extrapolation curve predicts a weak richness increment with 500 additional individuals, again attesting a satisfactory sample (Fig. 2). Diversity values were 1.13 nats, 1.73 and 1.32 for the Shannon, Simpson's reciprocal and Berger-Parker's reciprocal index respectively.

Leptolobium elegans had the highest density (66.53% of individuals), followed by *Tabernaemontana catharinensis* (14.20%). All other species had values up to 3.85%. *Leptolobium elegans* was the most dominant (89.55%) and frequent species (24.49%) too. Following it, *Tabernaemontana catharinensis* and *Helietta apiculata* were the species that shown the highest frequencies. Thus, *L. elegans* encompasses more than half the relative importance, followed by *T. catharinensis* and *H. apiculata* (Tab. 1).

The mean diameter of the woody plant community was 8.72 cm, and the J-shaped distribution pattern of diameters was similar to sampled *L. elegans* individuals alone. This species showed the largest diameters (28–31 cm) (Fig. 3a).

Table 1 – Families and species included in the survey sorted by relative importance (RI), with their habit (H; Tr: tree; Sh: shrub), dispersion syndrome (D; An: anemocoric; Au: autocoric; Zo: zoocoric), successional group (SG; P: pioneer, ES: early-secondary, LS: late-secondary), and phytosociological parameters. N: number of individuals; AD: absolute density (ind/ha); RD: relative density (%); ADo: absolute dominance (m²/ha); RDo: relative dominance (%); AF: absolute frequency (%); RF: relative frequency (%).

Family	Species	H	D	SG	N	AD	RD	ADo	RDo	AF	RF	RI
Fabaceae	<i>Lepotobium elegans</i> Vogel	Tr	An	P	328	683	66.53	8.43	89.55	100.00	24.49	60.19
Apocynaceae	<i>Tabernaemontana catharinensis</i> A.DC.	Tr	Zo	P	70	145	14.20	0.51	5.46	66.67	16.33	12.00
Rutaceae	<i>Helietta apiculata</i> Benth.	Tr	An	ES	11	22	2.23	0.03	0.32	41.67	10.20	4.25
Salicaceae	<i>Casearia syvestris</i> Sw.	Tr	Zo	P	19	39	3.85	0.06	0.68	25.00	6.12	3.55
Erythroxylaceae	<i>Erythroxylum deciduum</i> A.St.-Hil.	Tr	Zo	ES	12	25	2.43	0.09	0.95	16.67	4.08	2.49
Rubiaceae	<i>Cordia concolor</i> (Cham.) Kuntze	Sh	Zo	LS	11	22	2.23	0.03	0.27	16.67	4.08	2.20
Voehysiaceae	<i>Qualea cordata</i> Spreng.	Tr	An	-	13	27	2.64	0.15	1.59	8.33	2.04	2.09
Myrtaceae	<i>Hexachlamys edulis</i> (O. Berg) Kausel & D. Legrand	Tr	Zo	P	4	8	0.81	0.03	0.28	16.67	4.08	1.72
Cactaceae	<i>Morvillea euchlora</i> (F.A.C. Weber ex K. Schum.) Backeb.	Sh	Zo	-	3	6	0.61	0.01	0.14	16.67	4.08	1.61
Lauraceae	<i>Ocotea lancifolia</i> Mez	Tr	Zo	ES	2	4	0.41	0.01	0.11	16.67	4.08	1.53
Sapindaceae	<i>Matayba elaeagnoides</i> Radlk.	Tr	Zo	ES	2	4	0.41	0.01	0.07	16.67	4.08	1.52
Euphorbiaceae	<i>Sebastiania brasiliensis</i> Spreng.	Tr	Au	ES	7	14	1.42	0.02	0.20	8.33	2.04	1.22
Primulaceae	<i>Myrsine balansae</i> (Mez) Otegui	Tr	Zo	ES	4	8	0.81	0.01	0.08	8.33	2.04	0.98
Solanaceae	<i>Solanum granulolum-leprosum</i> Dunal	Tr	Zo	P	2	4	0.41	0.00	0.04	8.33	2.04	0.83
Rubiaceae	<i>Coutarea hexandra</i> (Jacq.) K.Schum.	Tr	An	ES	1	2	0.20	0.00	0.03	8.33	2.04	0.76
Asteraceae	<i>Calea pinnatifida</i> Banks ex Steud.	Sh	An	-	1	2	0.20	0.00	0.02	8.33	2.04	0.75
Sapindaceae	<i>Cupania vernalis</i> Cambess.	Tr	Zo	ES	1	2	0.20	0.00	0.02	8.33	2.04	0.75
Dead	-	-	-	-	2	4	0.41	0.02	0.20	16.67	4.08	1.56
Total					493	1022	100	9.40	100	391.67	100	100

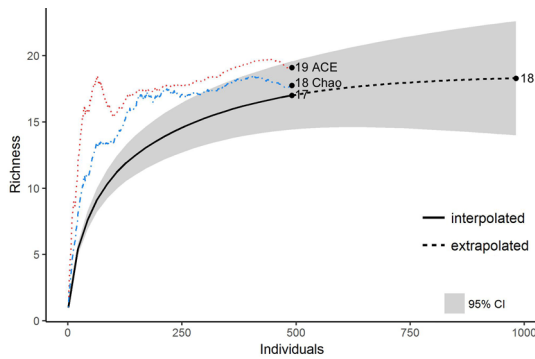


Figure 2 – Rarefaction and extrapolation curves, confidence interval at 95%, ACE and Chao estimator, based on individuals surveyed in San Ignacio, Misiones, Argentina.

The mean height of the community was 3.30 m. For the whole community and for other species the highest value was for the third class of height, while for *L. elegans* was the second class (Fig. 3b). *Leptolobium elegans* had the largest basal diameter mean and diametric range, followed by *Qualea cordata* and *Erythroxylum deciduum*. *Cordia concolor* and *Helietta apiculata* presented the lowest values. This pattern was different regarding height, as *Helietta apiculata* and *L. elegans* showed the highest mean values, followed by *Hexachlamys edulis* and *Erythroxylum deciduum*. The lowest mean height was found in *Qualea cordata* and *Cordia concolor*. *Leptolobium elegans*, *T.*

catharinensis and *Q. cordata* were the species with largest height range (Fig. 4).

The ordination and cluster analysis revealed that the study site is strongly associated with the disjunct Cerrado patches from Paraná state in Brazil and those from Canindeyú and Amambay in Paraguay. It is possible to infer that the first ordination axis represents a latitudinal gradient (Figs. 5; 6a). Four groups were defined in the cluster analysis, which had a mean silhouette coefficient of 0.18: Group I - represented mostly by sites from the north and central Mato Grosso do Sul state; Group II - sites located near to the group in the south of Mato Grosso do Sul; Group III - the most spread group in geographical terms, all areas located at Southern study region, comprising sites from Argentina, Paraná state, and Paraguay; Group IV - sites from São Paulo state, to the East of the study site (Figs. 5; 6b).

Discussion

Structure, diversity and similarity

Stabilization of the rarefaction curve, as well as the values of the richness estimators, suggest that the sampling effort was enough to ensure correct description of species richness of the woody component. We sampled a richness constituted by 17 species, *Leptolobium elegans* was the main taxon that contributes the most to the structure of this savanna, with more than half of the relative

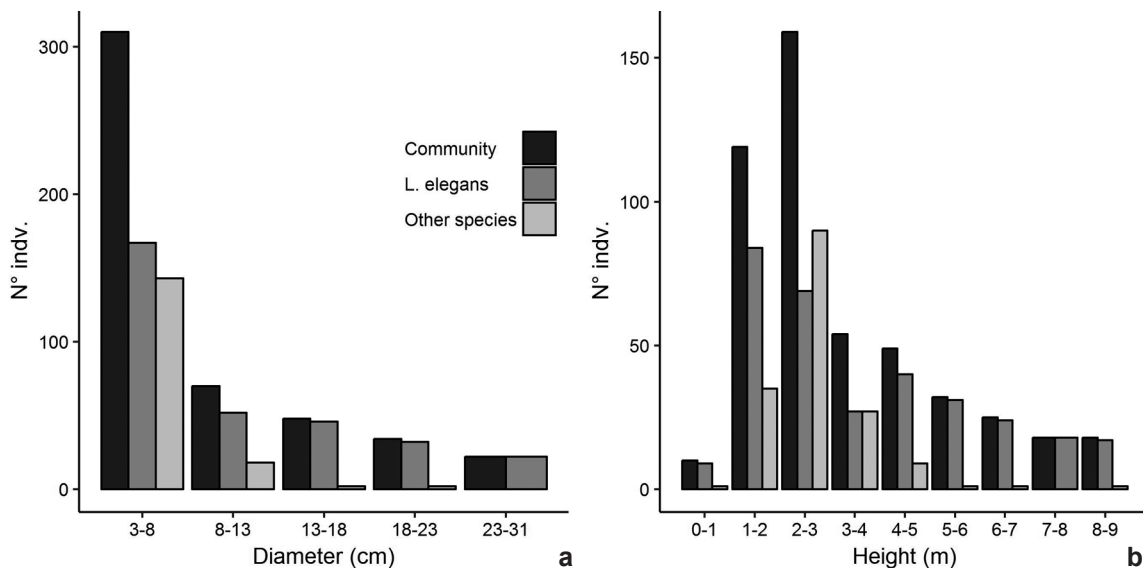


Figure 3 – Absolute frequency distribution of diameter (a) and height (b) classes for the community species (17 species), *Leptolobium elegans* individuals only, and other species than *Leptolobium elegans* (16 species).

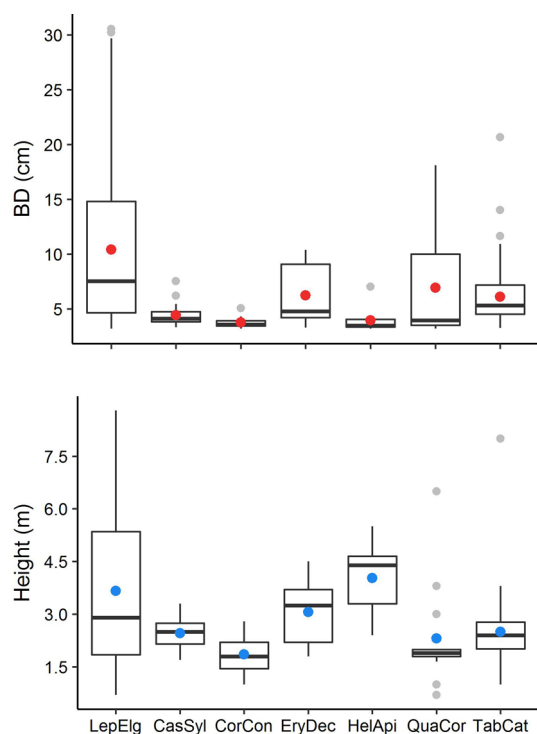


Figure 4 – Mean (points), median and quartile of the basal diameter (BD) and height of the most abundant species. LepElg: *Leptolobium elegans*, CasSyl: *Casearia sylvestris*, CorCon: *Cordia concolor*; EryDec: *Erythroxylum deciduum*, HelApi: *Heliopsis apiculata*, QuaCor: *Qualea cordata*, TabCat: *Tabernaemontana catharinensis*.

importance, with the largest mean diameter and mean height. The low values of diversity and evenness are the result of the high dominance of *L. elegans* and the low number of woody species. *L. elegans* is a heliophytic species that inhabits different physiognomies mainly distributed in central-western Cerrado region (Ratter *et al.* 2003). It can withstand drought periods, as well as poor and well-drained soil (Burkart 1952; Lorenzi 2000; Rodrigues & Tozzi 2012). *Leptolobium elegans* and *Casearia sylvestris* are two of the 11 key-species in shrub-grassland and rupicolous Cerrado in Paraná and São Paulo states in Brazil (Moro 2012). Although *Leptolobium elegans* stood out in all phytosociological parameters, we also detected forest pioneer species, such as *Tabernaemontana catharinensis*, *Casearia sylvestris*, and *Solanum granulatum-leprosum*, and early secondary such as *Heliopsis apiculata*, *Cupania vernalis* and *Matayba elaeagnoides*.

Regarding *Leptolobium elegans* importance value, other studies achieved similar results. The species was one of the six more important in open grassland and typical Cerrado physiognomies in Paraná (Uhlmann *et al.* 1998) and São Paulo (Meira Neto 1991; Durigan *et al.* 2002; Toppa 2004; Ishara 2010; Ishara & Maimoni-Rodella 2010; Prado Júnior *et al.* 2012). A typical Cerrado represents a savanna with sparse short arboreal elements of gnarled trunk and branches. Open grassland (*campo limpo*, in Portuguese) has a denser herbaceous vegetation with almost any arboreal component when compared to the typical Cerrado (Cerrado *sensu stricto*, Ribeiro & Walter 2014). Regarding absolute dominance values (the area covered by the transection of all trunks present in the site), the data was similar to the dominance found in some areas of typical Cerrado (Uhlmann *et al.* 1998; Durigan *et al.* 2002; Ishara 2010), although we found lower values than other sites (Toppa 2004; Ishara & Maimoni-Rodella 2010). Absolute density was similar to closed field (*campo cerrado*, in Portuguese) in Paraná (Uhlmann *et al.* 1998) and typical Cerrado in São Paulo (Durigan *et al.* 2002), and lower than other sites in São Paulo (Ishara 2010; Ishara & Maimoni-Rodella 2010; Carmo *et al.* 2012). Most of the sampled individuals were included in the same height class identified in several other studies (Uhlmann *et al.* 1998; Toppa 2004; Ishara 2010; Ishara & Maimoni-Rodella 2010). However, the studied community shows a different structure and diversity when compared with nearby forest environments (Velazco *et al.* 2015).

Despite the low diversity of woody species in the Teyú Cuaré field, it was floristically more related to some of the disjunct patches of Cerrado savannas in the extreme southern Cerrado region, such as those sites from Paraguay and Paraná state in Brazil. Many studies in savanna relicts in Brazil far from the core area of the Cerrado also showed poor woody richness, as in the pre-litoranean plains from Ceará (Moro *et al.* 2011), a savanna in Rio Grande do Norte (Oliveira *et al.* 2012), the small patches in Paraná (Ritter *et al.* 2008; Moro 2012), or those found in Amapá, Pará, and Amazonas (Ratter *et al.* 2003). The southern region of the Brazilian cerrados are in a subtropical climate, facing frosts during the winter, and shorter dry season than in the core Cerrado biome (Durigan 2006), a quite similar condition to the Teyú Cuaré region.

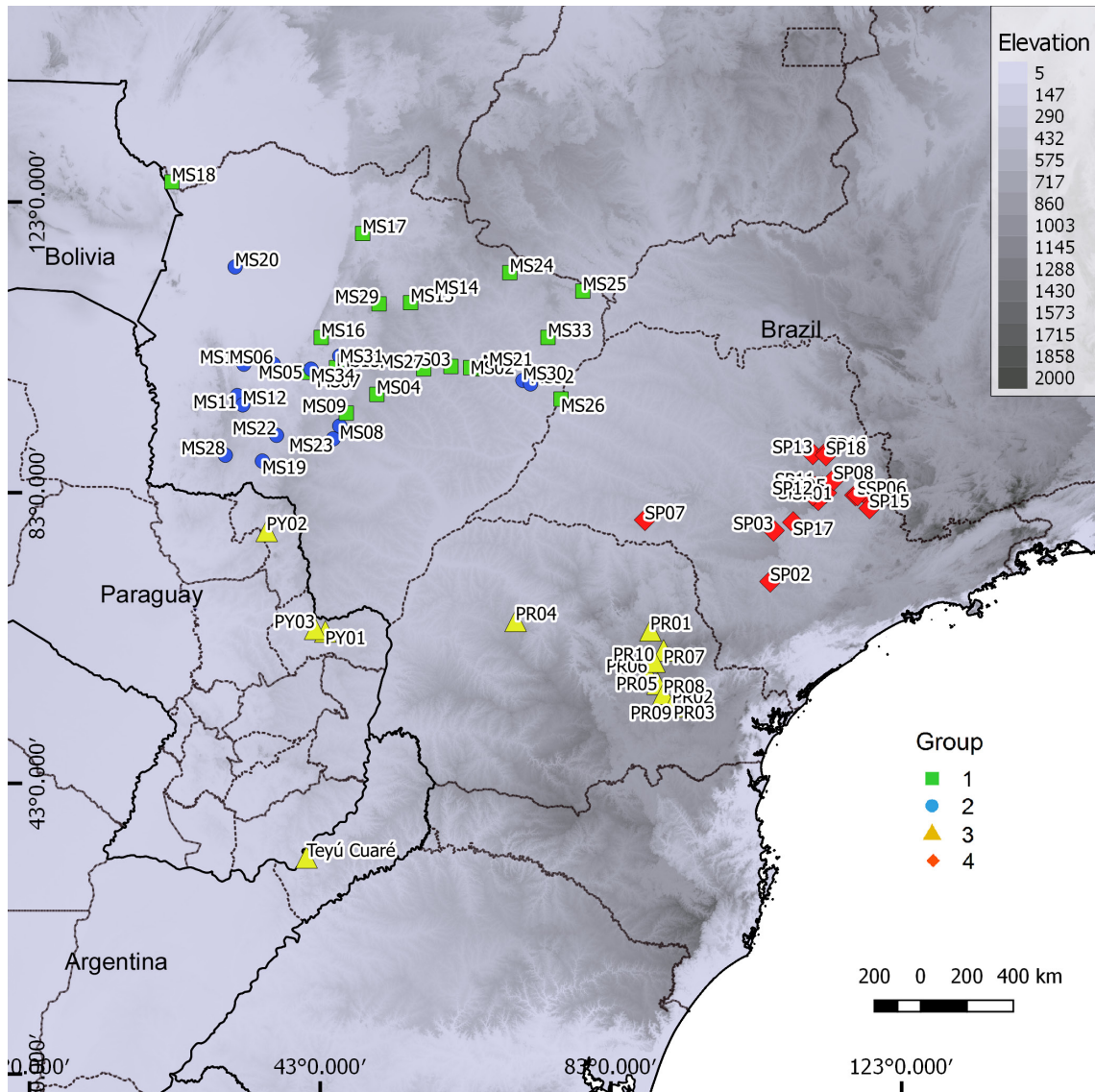


Figure 5 – Location of 66 floristic surveys of Cerrado's areas from Brazil, Paraguay, and Argentina –Teyú Cuaré–. Each color and shape represent different groups derived from the Ward's hierarchical method.

Factors related to the origin and permanence of open physiognomies

We hypothesize that the coexistence of an open vegetation formed by savanna and meadow and the surrounding forest is the result of historical and current factors affecting each physiognomy differently, such as: (1) Glacial-Interglacial Cycles: global climate cycles promoted the advance and retraction of open physiognomies, leaving relictual formations, which we consider responsible for originating the studied savanna patch. (2) The presence of ancient cultures: in Misiones province, archeological evidence

exists of the ancient population, some of them are related to open physiognomies and used fire as a tool to clear vegetation. (3) Edaphic conditions: the soil profile analyzed in the forest presented more concentration of some nutrient than in the savanna, where poor nutrient soils prevail with higher aluminum saturation (Velazco 2014, see supplementary material 1: <<http://dx.doi.org/10.6084/m9.figshare.5238961>>). (4) Disturbance events promoted by fire: in the studied area, burning is much more frequent in the savanna-meadows patch than in the forest surrounding it. Based on the Temaikèn foundation registries, in

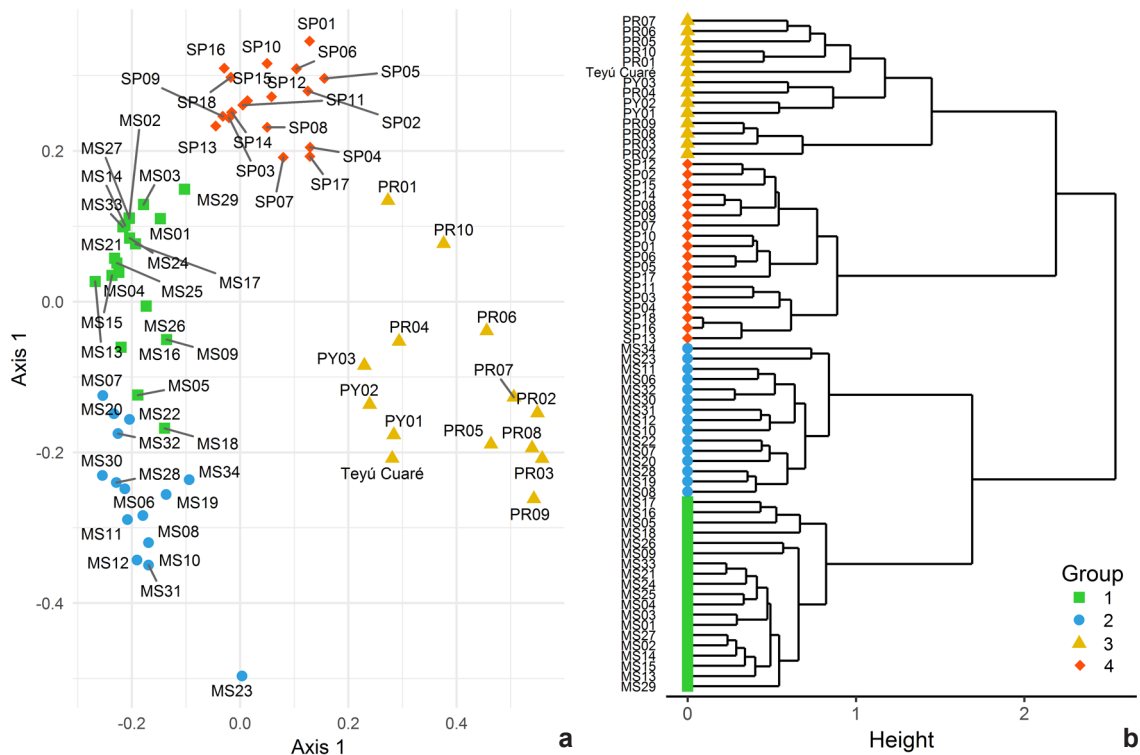


Figure 6 – Ordination diagram yielded by PCoA (a) and dendrogram (b) for trees and large shrubs of 66 Cerrado's area from Brazil, Paraguay, and Argentina -Teyú Cuaré-. Each color and shape represent different group derived from a the Ward's hierarachical methods.

the last five years, at least eight burnings were registered in the savanna, while the last forest fire occurred in 2002.

Permanence of distinct vegetation patches/islands (relicts) can be maintained by local factors such as lithology, hydrology, topography and paleobotany (Ab'Sáber 1962), but its origins can be explained by changing distribution of vegetation domains during the Quaternary (Ab'Sáber 2003). During this period, the biomes distribution was influenced by glacial and interglacial cycles (Cox & Moore 2011). According to Refuge Theory, distribution patterns of flora and fauna of tropical America are the consequence of spatial dynamics (i.e. expansion and retraction) due to climatic fluctuation (Haffer 1969; Ab'Sáber 1992; Haffer & Prance 2002). Considering this, it is possible to indicate that the current distribution of savannas and seasonally dry forest in the Neotropics is related to the climatic variations of the Quaternary (Pennington *et al.* 2000). Changes in the distribution of Neotropical savannas are well documented in the literature and proved by different approaches, such

as the use of carbon isotope (Sanaiotti *et al.* 2002), pollen studies (Behling 1995), paleodistribution modelling (Bueno *et al.* 2016) or combination of phylogeographical and species distribution modelling (Collevatti *et al.* 2012).

In the actual interglacial period, which started 10,000 years BP (Holocene), due to a warmer and wetter climate and ice retraction, many taxa have drastically changed their geographic distribution (Lomolino *et al.* 2010). Concerning the Quaternary, the Pleistocene climate was cold and dry, while the early and middle Holocene was warm and dry, becoming wetter and stable later (Gessert *et al.* 2011). It is possible that during the middle Holocene, grasslands, and savannas had covered the entire Southern Misiones. Carbon dating in Oberá town (Misiones - Argentina) determined that from 7,500 to 3,000 years BP there was an expansion of C4 plants along the S - N transect, indicating an increase of aridity in that period that changed after 3,000 years BP, when the climate became wetter (Zech *et al.* 2009). Other studies proved that in Southern Brazil and some

Misiones regions, the climate became wetter and less seasonal in the last 2,000 years, allowing the replacement of open vegetation types and dry forest (Misiones) with *Araucaria* forest (Behling 2002; Behling & Pillar 2007; Iriarte & Behling 2007; Gessert *et al.* 2011). This forest expansion was overlapped by the advance of farmers and potters of the Taquara/Itararé Tradition (Iriarte & Behling 2007), that reached Paraná state around 4,000 years ago (Parellada 2009).

Advance and retreat dynamics of these biomes and their relationship with different human cultures could have happened in Misiones, according to the rich archaeological evidence. It indicates that different old civilizations inhabited the region for thousands of years. Among the most ancient (8,000 years ago), there are archaeological remains of the Umbu Tradition, strongly associated with grasslands, and from hunter-gatherer groups, possibly related to the Humaitá Tradition (Dias & Hoeltz 2010). The Guarani group arrived in the region c. 1000 years ago (IPEC 2012), while the Jesuits settled close to Paraná river right after the Guayrá Exodus in 1631, founding San Ignacio Mini and Nuestra Señora de Loreto (Belastegui 2006). Despite the Guarani inhabiting sylvan environments, they have adapted to forest edges and grasslands, developing some hunting techniques associated with these kind of environments, as indicated by the use of *boleadeiras*, a tool that was found together with Guarani ceramics in San Ignacio (see supplementary material 4: <<http://dx.doi.org/10.6084/m9.figshare.5238961>>).

Transitional vegetation types between savanna vegetation and forest are controlled by chemical and physical soil properties such as cation capacity exchange (Veenendaal *et al.* 2015), potassium (Lloyd *et al.* 2015), aluminum saturation or clay (Ruggiero *et al.* 2002). In the Teyú Cuaré field, the soil profile of savannas shows higher concentration of aluminum saturation, and lower concentration of organic carbon, base saturation and phosphorous than the soil profile of forests, which could suggest that chemical soil conditions are different between those physiognomies. Despite that in both vegetation types the soil presents sandy texture. It has been proved that sandy and well-drained soil could act as an environmental filter, promoting more stressful condition for propagules of mesic species in open formations (Saporetti-Junior *et al.* 2012).

There are three dynamics between forest-savanna boundary zones: (i) the forest can advance

over the savanna; (ii) the savanna advances into the forest, (iii) or both are in equilibrium (Hopkins 1992). We inferred that the first of them is occurring in the studied site. We observed that the forest-savanna transition is almost abrupt, a normal characteristic of this physiognomy boundary (Hopkins 1992; Cole 1992). However, some patches were dominated by pioneer and early secondary species. An explanation for this arboreal pioneer colonization can be attributed to periodic burning (Fontana 2005) in those areas. We highlighted that the majority of plots showed traces of previous burns, evidenced by carbonized corks. Fire is a disturbance agent present at global level (Miranda *et al.* 2002; Walter *et al.* 2008; Hutley & Setterfield 2008) and is the second most important factor that controls this forest-savanna dynamic (Hopkins 1992). Many studies, in different Cerrado physiognomies, have shown the effect of burning on soil nutrient and woody-herb components; and how it helps to maintain open communities (Kaufmann *et al.* 1994; Pivello & Coutinho 1996; Felfili *et al.* 2000; Hoffmann *et al.* 2003; Miranda & Sato 2005; Moreira 2008; Pivello *et al.* 2010; Oliveras *et al.* 2013), acting as an important environmental filter (Carvalho & Batalha 2013). Thus, some researchers support the use of fire to maintain the diversity of this kind of vegetation (Ramos-Neto & Pivello 2000; Fontana 2005; Pivello 2005; Moreira 2008; Oliveras *et al.* 2013). In fact, another savanna patch allocated c. 1 km from the studied area (55°33'10.04"W and 27°15'54.19"S), the absence of fire promoted a denser woody vegetation.

The forest colonization rate depends on the severity and frequency of fire (Hopkins 1992; Pinheiro & Durigan 2009; Oliveras *et al.* 2013). The gradual conversion of open vegetation to shrub and forest areas would happen though the complete inhibition of burnings (Pinheiro & Durigan 2009), as fire precludes the establishment of arboreal seedlings and benefits herbaceous species or fire-adapted trees (Ferri 1973; Walter *et al.* 2008; Hutley & Setterfield 2008). This situation not only benefits grasslands but also the growth of grasses and promotes the subsequent combustible material accumulation (Hutley & Setterfield 2008). The opposite process occurs when arboreal species established in savanna, and in absence of fire, they gradually develop a dense canopy, which hampers light entry to the detriment of the herbaceous layer, helping the maintenance of the arboreal community (Hopkins 1992; Hutley & Setterfield 2008). The

previously explained process happens in the study area because there is evidence of recurrent burns (eight in the last five years), the most important species is a well adapted to fire, and many of the herbaceous species have fire resistant traits, such as subterranean or cork stems, xylopodium and clumped species. Also, there are species common in other savannas that apparently reach here their southern distribution limits: *Allagoptera campestris*, *Calliandra longipes*, *Ditassa acerosa*, *Eryngium juncifolium*, *Leptolobium elegans*, *Macrosiphonia virescens*, *Qualea cordata*, and *Sporobolus acuminatus* var. *longispiculus*.

Despite the need for more studies to elucidate accurately the biogeographical and historical processes that determined the peculiar flora of Teyú Cuaré field, it would be feasible to conclude that this grassland-savanna vegetation type is a vestige of the late Pleistocene and middle Holocene climate conditions. The maintenance of this vegetation type is related to geological and edaphic conditions, such as sandy, acid, dystrophic and strongly drained soils, combined with recurrent fires, possibly linked to ancient cultures and current burnings.

Conclusion

Leptolobium elegans stood out as the main woody species in the area, presenting the most important structural values. The structure of the savannah site was similar to other sites of typical Cerrado in Paraná and São Paulo states in Brazil.

The woody vegetation of this savanna is floristically closely related to that in the southern areas of Cerrado sites, mainly with Amambay and Canindeyú department in Paraguay, and Paraná state in Brazil. The vegetation of Teyú Cuaré field is probably an expression of the open formation that prevailed in Misiones province and Southern Brazil in the late Pleistocene and middle Holocene; this condition was probably reversed after 3,000 years BP when the climate became more favorable to forest development (Zech *et al.* 2009).

Considering the actual climate condition and the records of pioneer and late secondary species, the area exhibits a gradual advance of the forest through the grassland. However, the open physiognomies still remain through mechanisms that work at different levels, such as geological, edaphic and anthropological aspects, this last associated with fire. In this sense, the total inhibition of burns could reduce the herbaceous layer promoting a structural and floristic shift. For this reason, the use of fire could be a feasible tool

to maintain the characteristics of this particular and biogeographically valuable site.

In order to achieve more in-depth conclusions, we recommend additional studies comparing Teyú Cuaré floristics and vegetation structure with Cerrado areas from Paraguay and Brazil, but considering all life forms, specially taxa from the herb stratum.

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