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Small but important: The woody vegetation communities on the sandstone outcrops of Teyú Cuaré (Misiones, Argentina)

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Summary: Rock outcrops are commonly harsh environments that maintain important components of biodiversity because they are inhabited by endemic or relictual species. We studied the diversity and structure of the woody plant of rupestrian vegetation located in the San Ignacio department (Misiones, Argentina), and evaluated the beta diversity with respect to other neighbor vegetation formation (i.e. forest and savanna). We found 32 species, most of them were arboreal nonetheless of small size. *Qualea cordata* (Mart.) Spreng., *Monvillea euchlora* Backeb., *Ocotea lancifolia* (Schott) Mez and *Myrciaria delicatula* (DC.) O.Berg were the most important in the community structure. Rupestrian vegetation showed an intermediate woody species diversity compared to nearby forests and savannas. We found a high beta diversity between rupestrian formation and the other physiognomies mainly established by richness difference. Rock environments are high-priority conservation level because their singular plant communities inhabit specific edaphic and geomorphic conditions, occurring only in a restricted geographical range.

Key words: Rock outcrops, phytosociology, rupestrian vegetation, endemic species.

Resumen: Pequeños pero importantes: las comunidades de vegetales leñosas de los afloramientos de arenisca de Teyú Cuaré (Misiones, Argentina). Los afloramientos rocosos son ambientes comúnmente rigurosos que mantiene importantes componentes de la biodiversidad por estar habitados por especies endémicas o relictuales. El objetivo del presente estudio fue evaluar la diversidad y estructura de la planta leñosa de la vegetación rupestre ubicada en el departamento de San Ignacio (Misiones, Argentina) y evaluar la diversidad beta con respecto a otras formaciones vegetales vecinas (esto es bosque y sabana). Se encontraron 32 especies de plantas leñosas, la mayoría arbóreas de pequeño tamaño. *Qualea cordata* (Mart.) Spreng., *Monvillea euchlora* Backeb., *Ocotea lancifolia* (Schott) Mez y *Myrciaria delicatula* (DC.) O. Berg fueron las más importantes en la estructura de la comunidad. La vegetación rupestre del conjunto de afloramientos estudiados mostró una diversidad leñosa media en comparación con las formaciones de bosque y sabana, con una alta diversidad beta, principalmente estructurada por la diferencia de riqueza. Estos ambientes tienen una alta prioridad para la conservación, debido a que las comunidades vegetales son fisionómica y florísticamente singulares, además de estar en condiciones edáficas y geomorfológicas con una expresión geográfica restricta.

Palabras clave: Afloramientos rocosos, fitosociología, vegetación rupestre, especies endémicas.

Introduction

Rocky outcrops commonly present an extreme environment, characterized by water shortage, thermal fluctuation and a poor or absent soil mantle among others, that can generate stressful physiological conditions. Therefore, species can present adaptations to inhabit these sites (Scarano, 2007; Fernandes, 2016). Thus, this kind of environments was highlighted as important in maintaining endemic species (Medina & Fernandez, 2007; Porembski *et al*., 2016) and acts as vegetation refuge of relictual taxa (Pérez-García & Meave, 2004; Spezialea & Ezcurra, 2012). However, these environments are being disturbed by factors such as mining, urbanization or invasive alien species (Porembski *et al*., 2016).

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San Ignacio's flora, in Misiones province (Argentina), have attracted the botanical community, not only because of restricted plant distribution and endemic species, but also for its physiognomy, which previous researchers claim to represent a fragment of Brazil's Cerrado biome (Chébez, 1996; Biganzoli & Romero 2004; Velazco *et al*., 2018). The singularities of this region are not restricted to its flora, but also to geomorphology, derived from the sandstone outcrops of Solari Formation, a remarkable characteristic of the province since the most of its surface is covered by extrusive magmatic stones of the Serra Geral Formation (Aceñolaza, 2017). These outcrops emerged within a forest matrix, generating an environmental diversity that allowed the development of different plant communities, from simple and sparse herbaceous communities to shrub and arboreal elements, such as rupestrian savannas (i.e. a vegetation community composed by a herbaceous layer with sparse arboreal elements).

Some species registered in San Ignacio sandstone are only restricted to mentioned outcrops: *Blechnum asplenioides* Sw. (Blechnaceae), *Dicranopteris flexuosa* (Schrad.) Underw. (Gleicheniaceae), *Trichomanes pilosum* Raddi (Hymenophyllaceae), *Elaphoglossum pachydermum* (Fée) T. Moore (Lomariopsidaceae), *Clidemia biserrata* DC. (Melastomataceae; Biganzoli & Romero, 2004), and the recently discovered endemic species *Oxypetalum teyucuarense* (Farinaccio & Keller, 2014).

Considering the floristic and geological importance of San Ignacio, we aimed to identify the woody plant communities on these rock outcrops, by describing their floristic features and vegetation structure and comparing its diversity with other local communities, such as forests and savannas. Moreover, a partitioning of beta diversity is carried out in order to explore which process can be acting on local communities structuring.

Materials and Methods

Study site

The studied outcrops are situated in department and municipality of San Ignacio, Misiones-Argentina (55°35'0.70" W, 27°16'55.46" S) at 75-185 m altitude (Fig. 1). The outcrops are near to Paraná River and divided into two protected areas, the Osununú Private Reserve and the Teyú Cuaré Provincial Park, both at the Köppen Cfa climate: humid, temperate with warm summers, and no distinct dry season (SAGyP-INTA, 1990). Mean annual temperature is 21.8 ºC and mean annual precipitation is 1,644 mm. Most of the rain is concentrated between October-February, and July-August is the driest period.

The predominant geological unit in this area is a sandstone of Solari Formation, which had its genesis in the Late Triassic (Aceñolaza, 2017). Mineralogical and diagenetic studies proved its high affinity to Botocatu Formation from Brazil (Tchilinguirián *et al*., 2005). The silicification of this rock is resistant to weathering and consequently gave rise to the current landscape feature, where areas with silicified sandstone created the steep cliffs with deep valleys and flat-topped hills of the region (Tchilinguirián *et al*., 2005). Many outcrops are located next to Paraná river, where the hills can reach as high as 120 m of elevation, determining a strongly undulating topography (CARTA, 1963).

The pedogenetic processes were delayed due to the characteristic of the parental material and the craggy features. Soils are scarce and commonly accumulated in rock fractures, or form a layer that normally does not exceed 25 cm in depth (Leptosols). Chemical and physical properties are poor, due to a low concentration of nutrients, a shallow soil horizon, a sandy texture, being excessively well drained and also highly susceptible to erosion (SAGyP-INTA, 1990; Velazco, 2014).

Regarding the phytogeography, following the Argentinean classification (Cabrera, 1994), the semideciduous seasonal forest prevails in the region and occurs within the Mixed Forest District (*Distrito de las Selvas Mixtas*). Site study is in the Laurel District (*Distrito de los Laureles*), which is characterized by the presence of Lauraceae species, such as *Nectandra megapotamica* (Spreng.) Mez and *Nectandra lanceolata* Nees & Mart. (Cabrera, 1994).

Survey and data analysis

We mapped areas for rupestrian plant communities through photointerpretation and field trips to the region. Photointerpretation was carried out by orthophoto of the year 2011, images of Google Earth of 2014, altimetric and slope maps.

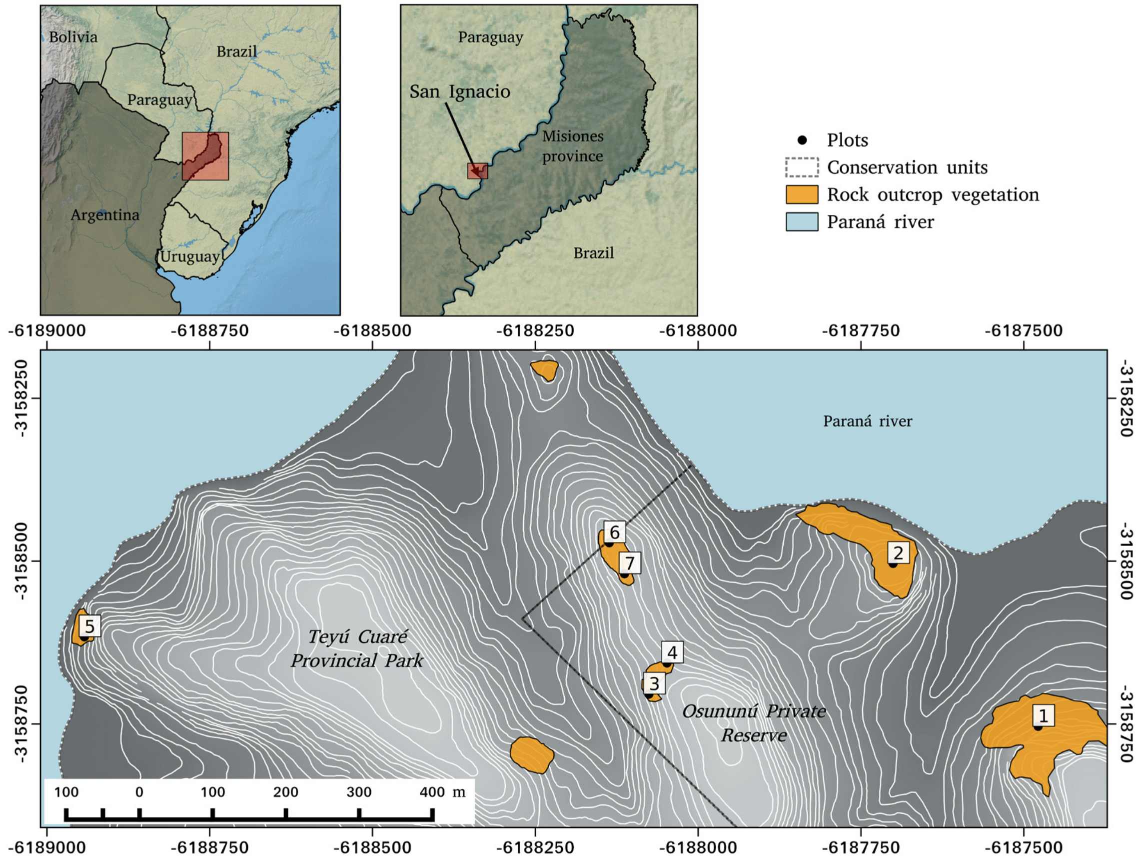

Fig. 1. Geographic location of the study area in San Ignacio, Misiones, Argentina. (Numbers in boxes indicate the fragments of rock outcrop vegetation and sites sampled).

We found that these communities developed on specific geomorphic and geological conditions, in shallow soils or in rock fractures, so it is possible to find them in small patches. Most of them are within the Teyu Cuare Provincial Park and Osonunú Natural Reserve. In 2014 we surveyed rupestrian vegetation using seven rectangular sample units of 10 x 20 m (200 m^2) throughout study area (Fig. 1). With a graduated stick, we measured the height of all trees and shrubs with a perimeter at ground height (PGH) $\geq$ 10 cm. For each sampled individual, we identified taxon at the species level. Scientific names and authors were updated according the Taxonomic Name Resolution Service V.4.0 (http://tnrs.iplantcollaborative.org/).

Sampling effort was assessed by the comparison between the individual-based rarefaction curve and the nonparametric richness estimators Chao 1 and ACE (Abundance Coverage-based Estimator). For the first criterion, a satisfactory survey is achieved when the values of richness estimators are approximately equal to the extreme value obtained in the species accumulation curve. For the other, based on a extrapolation curve, a sampling is sufficient when the increase of 10% of the sampling effort does not imply a richness increment greater than 10%. EstimateS software version 9.1.0 (Colwell, 2013) was used to generate species accumulation and extrapolation curves, Chao 1 and ACE.

We obtained absolute and relative phytosociological parameters of density, dominance frequency and relative importance value The last parameter is based on the sum of relative density, domain, and frequency divided by three (Mueller-Dombois & Ellenberg, 1974).

Diversity analysis

We compared the rupestrian community with the neighbor forest and savannas formation (Velazco *et al*., 2015, Velazco *et al*., 2018). Such comparisons were based on diversity profile (Jost, 2006) and beta diversity (Podani & Schmera, 2014) approaches. Commonly used diversity indexes (e.g. Shannon, Simpson, etc.) have a disadvantage: they are highly affected by the distribution of abundances among species in addition to the lack of criteria for selecting of a given index (Melo, 2008)diversity means variety of species, which may or not include information on the relative importance of each species. Diversity is one of the most important attributes in the study of communities and, as a result, many methods are available to its measurement. Among them, non-parametric diversity (or heterogeneity. Therefore, we used diversity profiles that calculate different diversity values by gradually changing of the "q" factor, which determines the sensitivity of the measure to the relative abundances of the species, i.e., calculates different diversity indexes for different weights of species abundance, thus allowing comparison of communities using all the information present in the data (Chao & Jost, 2015). Diversity profiles were constructed with "q" parameter ranging from 0 to 3. We used a presence-absence matrix for each community where columns represented the sampling units and rows the species. The confidence intervals were based on 100 randomizations. Variation in species composition among communities (i.e., beta diversity) can be partitioned into replacement and richness difference, which can be related to ecosystem processes (Legendre 2014). Species replacement refers to the fact that species tend to replace each other between communities, while richness difference refers to different communities including different species richness, for instance, caused by species nestedness (Legendre 2014). To evaluate the beta diversity between different vegetation formations, we calculated similarity (Sim, equivalent to the 1-Beta diversity), species replacement (Rempl) and richness difference (RichDiff), following Podani & Schmera (2014). We used the presence-absence matrix and Jaccard index.

Diversity analysis and graphics were performed in the R software v.3.4.1 (R Core Team, 2017). We used the packages *SpadeR* for diversity profiles, *adespatial* for the calculation of beta diversity, *ggplot2* and *ggtern* for graphics.

Results

Nonparametric richness estimators and extrapolation curves proved that the community was sufficiently sampled. The number of species, represented by the rarefaction curve, had a richness close to that predicted by the Chao 1 and ACE estimators; moreover, the extremes of those estimators fall within the confidence interval (Fig. 2). Based on the second criterion, an increment of 351 individuals - equivalent to three extra sampling units (117 individuals/plot) - estimates one additional species in the extreme of the extrapolation curve (Fig. 2).

We measured 823 individuals of 20 families, 28 genus and 31 species (Table 1). The most abundant

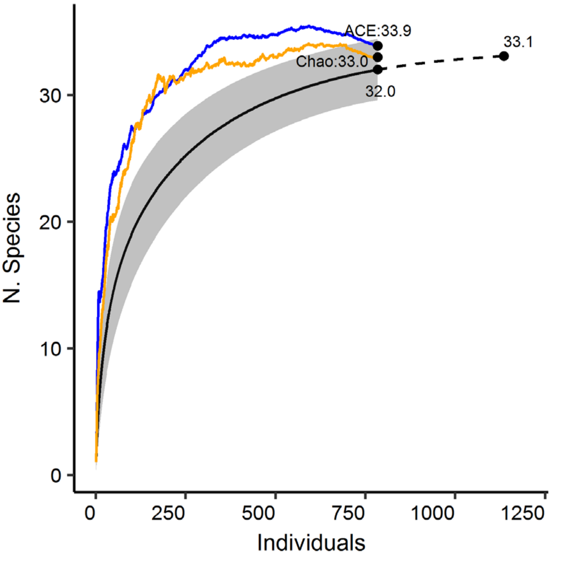

Fig. 2. Curves of species accumulation (black line), extrapolation (dashed line), confidence interval (95%; gray area), ACE and Chao 1 estimators, based on individuals sampled in the rock outcrop vegetation in San Ignacio, Misiones, Argentina.

Table 1. Families and species from the rock outcrop vegetation in San Ignacio, Misiones - Argentina, with their respective life forms (Tr: tree; Sh: shrub), and dispersal syndrome (An: anemochoric; Au: autochoric; Zo: zoochoric).

Family / Species	Life form	Dispersal syndrome
APOCYNACEAE		
Tabernaemontana catharinensis A.DC.	Tr	Zo
ARECACEAE		
Syagrus romanzoffiana (Cham.) Glassman	Tr	Zo
BIGNONIACEAE		
Handroanthus heptaphyllus (Vell.) Mattos	Tr	An
Handroanthus pulcherrimus (Sandwith) S. O. Grose	Tr	An
CACTACEAE		
Cereus stenogonus K.Schum.	Sh	Zo
Monvillea euchlora Backeb.	Sh	Zo
CLUSIACEAE		
Rheedia brasiliensis (Mart.) Planch. & Triana	Tr	Zo
ERICACEAE		
Agarista paraguayensis (Sleumer) Judd	Sh	Au
EUPHORBIACEAE		
Alchornea glandulosa Poepp.	Tr	Zo
Alchornea triplinervia (Spreng.) Müll.Arg.	Tr	Zo
Sebastiania brasiliensis Spreng.	Tr	Au
FABACEAE		
Leptolobium elegans Vogel	Tr	An
Senna pendula (Humb. & Bonpl. ex Willd.) H.S.Irwin & Barneby	Tr	Au
LAMIACEAE		
Vitex megapotamica (Spreng.) Moldenke	Tr	Zo
LAURACEAE		
Ocotea lancifolia (Schott) Mez	Tr	Zo
MELIACEAE		
Guarea macrophylla Vahl	Tr	Zo
MYRTACEAE		
Eugenia hyemalis Cambess. var. *marginata* (O.Berg) D. Legrand	Tr	Zo
Eugenia moraviana O. Berg	Tr	Zo
Hexachlamys edulis (O. Berg) Kausel & D. Legrand	Tr	Zo
Myrcia palustris DC.	Tr	Zo
Myrciaria delicatula (DC.) O.Berg	Tr	Zo

Family / Species	Life form	Dispersal syndrome
Psidium guineense Sw.	Tr	Zo
PICRAMNIACEAE		
Picramnia sellowii Planch.	Tr	Zo
PRIMULACEAE		
Myrsine balansae (Mez) Otegui	Tr	Zo
RUBIACEAE		
Cordiera concolor (Cham.) Kuntze	Sh	Zo
Coutarea hexandra (Jacq.) K.Schum.	Tr	Zo
RUTACEAE		
Helietta apiculata Benth.	Tr	An
SALICACEAE		
Casearia sylvestris Sw.	Tr	Zo
SAPINDACEAE		
Matayba elaeagnoides Radlk.	Tr	Zo
SAPOTACEAE		
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	Tr	Zo
VOCHYSIACEAE		
Qualea cordata (Mart.) Spreng.	Tr	An

families were Vochysiaceae (22.0 %), Cactaceae (21.14%), Myrtaceae (17.6%) and Lauraceae (9.11%; Fig. 3A-E). According to biological forms, 29 species were categorized as trees and three as shrubs; 74.5% of individuals were trees and 25.5% were shrubs (Table 1). About dispersal syndrome, 67.6% of individuals were zoocoric, 28.1% anemocoric and 4.34% autocoric (Table 1).

Most individuals were between 1.5 and 3.5 m height, with the major frequency in the class from 2.0 to 2.5 m (Fig. 4A). The mean height of all individuals measured was 2.68 m. When diameter were evaluated, we found a mean diameter of 5.7 cm (Fig. 4B), and an inverted J-shaped curve distribution, with 75.6% individuals in the first class (3-8 cm PGH), which denotes the predominance of small individuals.

Species with the greatest relative importance were *Qualea cordata*, *Monvillea euchlora*, *Ocotea lancifolia* and *Myrciaria delicatula*, together they represented more than 60% of the total importance value; other species only reached values lower than 4.5 %. The relative importance value of the three first species are explained by their high dominance and density, however, for the others, the frequency parameter seems to be representative (Table 2). The whole community had a density of 4,571 ind/ha and a dominance of 29.1 m^2/ha.

The rupestrian vegetation showed an intermediate richness, the highest absolute density and dominance, and the lowest mean diameter and height when compared with other local phytophysiognomies such as forest and savanna (Table 3). Forest was the most diverse formation with 66 species, however, its diversity is similar to the rupestrian community at higher values of "q" with no significant difference. Savanna formation showed the lowest richness (17 species) and diversity for any value of "q" (Fig. 5A, and Table 3). Regarding beta diversity, rupestrian vegetation showed low average similarity (i.e. high beta diversity) with respect to forest and

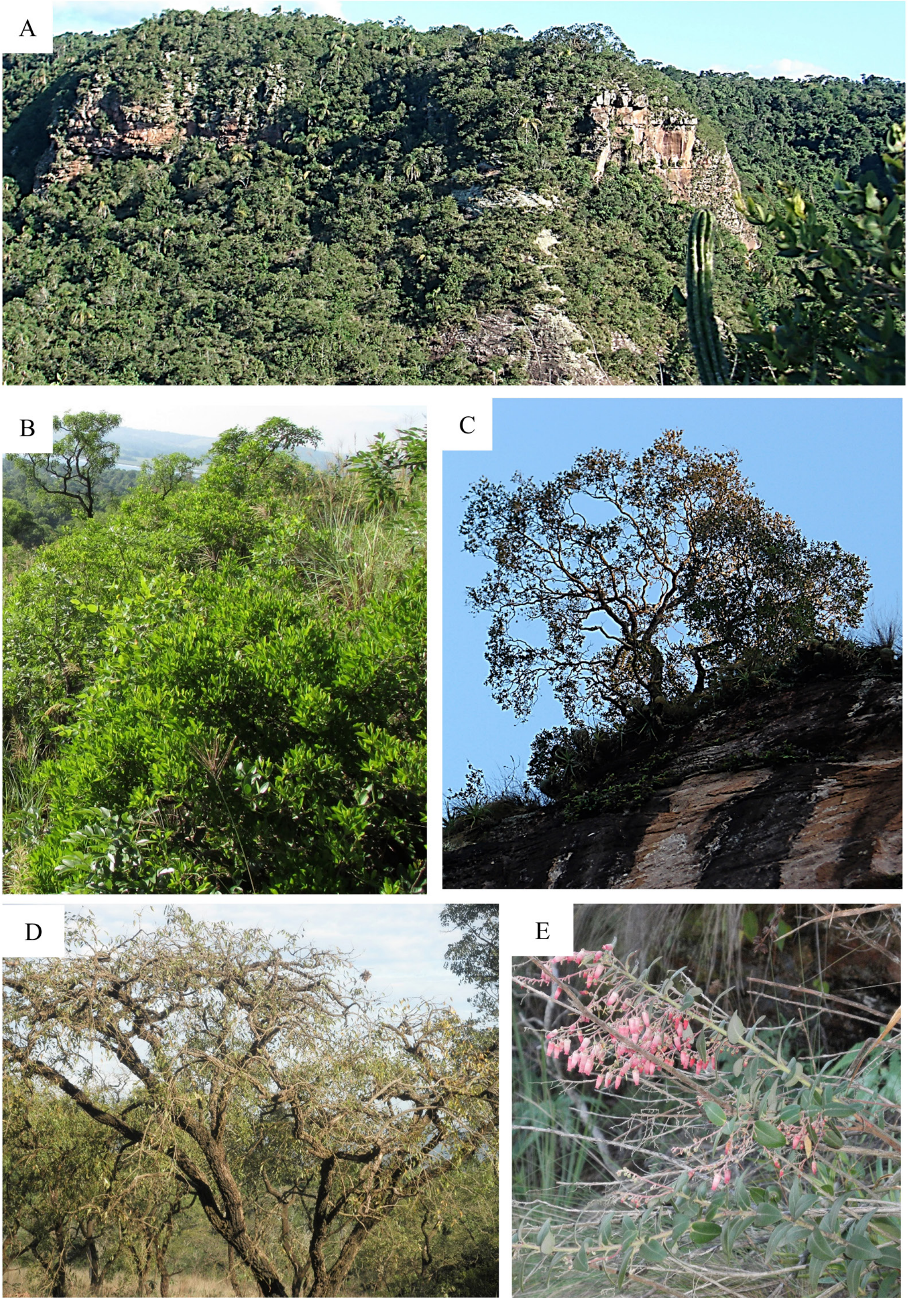

Fig. 3. A: Rock outcrop vegetation among the forest. **B**: Individuals of *Cordiera concolor* (Cham.) Kuntze. **C**: *Qualea cordata* (Mart.) Spreng. **D**: *Leptolobium elegans* Vogel. **E**. *Agarista paraguayensis* (Sleumer) Judd.

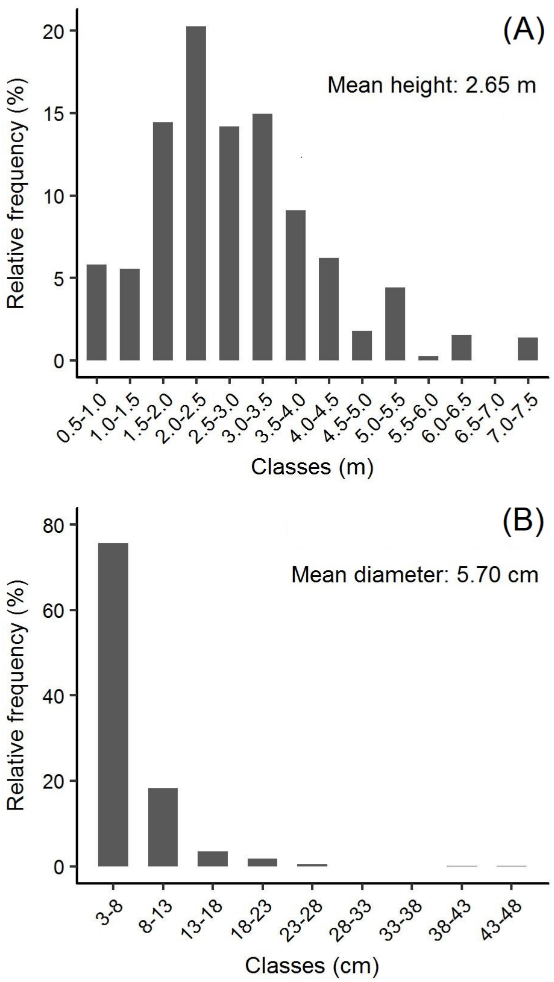

Fig. 4. Relative frequencies of vegetation height (**A**) and diameter (**B**) of rock outcrop vegetation in San Ignacio, Misiones, Argentina.

savanna. Mean richness difference between forest and rupestrian vegetation was c. 50%, however, between rupestrian vegetation and savanna it was 60% (Fig. 6B, C).

Discussion

The rupestrian communities are distributed in a dispersed pattern on the convex top or dissected areas of the study site. They are mainly dominated by *Qualea cordata* (Mart.) Spreng., *Monvillea euchlora* Backeb., *Ocotea lancifolia* (Schott) Mez and *Myrciaria delicatula* (DC.) O.Berg and presented an average diversity compared to the nearby forest and savanna formations. Beta diversity between rupestrian vegetation and the other vegetation types was high and mainly caused by richness difference.

It was challenging to compare our results against other researches, because of the variety of methods used to study this kind of vegetation community (Moura *et al*., 2011). However, research on rocky vegetation in the Cerrado biome indicated that *Qualea*, *Matayba*, *Myrcia*, *Syagrus*, *Cordiera* and *Leptolobium* are the most common genera (Miranda *et al*., 2007; Pinto *et al*., 2009; Moura *et al*., 2010; Gomes *et al*., 2011; Maracahipes *et al*., 2001), the same as those found in our study sites. Plant richness and diversity of previous studies were always greater than ours, this fact could highlight that in our site the number of species that can inhabit rock outcrop is low, possible because the rarity of this kind of environment in the region.

The frequency of individuals between 2.0-2.5 m high is coincident with other results in rupestrian savannas in Brazil (Amaral *et al*., 2006; Ribeiro & Walter, 2008; Pinto *et al*., 2009; Lima *et al*., 2010; Gomes *et al*., 2011). However, individual density and basal area in San Ignacio were greater than sites with the same vegetation (Miranda *et al*., 2007; Pinto *et al*., 2009; Moura *et al*., 2010; Lima *et al*., 2010; Gomes *et al*., 2011), which reveals that ours is a denser community. This could be a consequence of the inclusion of *Monvillea euchlora* (Cactaceae), while in the other sites, non-woody species were not considered.

We found two species restricted to this rocky environment: *Agarista paraguayensis* (Sleumer) Judd. and *Cordiera concolor* (Cham.) Kuntze. The particular environmental conditions of these sites, very different to the sorrounding forest, make them potential for rare or endemic species (Major, 1988; Moura *et al*., 2010; Ribeiro & Walter, 2008). The low frequency of *A. paraguayensis* may be due to its size, as a shrub rarely reached the inclusion diameter. However, this species occurs in rockiest places, apparently in the sunniest areas. This is the only place where this species was reported in Argentina, its distribution is mostly limited to the rocky areas, cliffs and steep slopes in eastern Paraguay and San Ignacio (Judd, 1995). Its narrow geographic range and very specific environmental requirements make it considered a vulnerable species.

Table 2. Phytosociological variables of absolute and relative Density (AD, RD), Dominance (ADo, RDo), and Frequency (AF, RF) for species of rock outcrop vegetation in San Ignacio, Misiones, Argentina, sorted by their Relative Importance Value (RIV).

Species	AD (ind/ha)	RD (%)	ADo (m^2/ha)	RDo (%)	AF (%)	RF (%)	RIV (%)
Qualea cordata	1292.9	22.0	8.2	28.3	100.0	7.3	19.2
Monvillea euchlora	1207.1	20.5	4.8	16.6	100.0	7.3	14.8
Ocotea lancifolia	535.7	9.1	4.3	14.7	71.4	5.2	9.7
Myrciaria delicatula	600.0	10.2	1.4	4.7	100.0	7.3	7.4
Syagrus romanzoffiana	78.6	1.3	1.7	5.8	85.7	6.3	4.5
Myrcia palustris	257.1	4.4	0.8	2.9	57.1	4.2	3.8
Guarea macrophylla	178.6	3.0	0.6	2.0	71.4	5.2	3.4
Myrsine balansae	192.9	3.3	0.5	1.6	71.4	5.2	3.4
Alchornea triplinervia	85.7	1.5	1.1	3.9	57.1	4.2	3.2
Cordiera concolor	157.1	2.7	0.2	0.8	71.4	5.2	2.9
Leptolobium elegans	192.9	3.3	0.9	3.2	28.6	2.1	2.8
Rheedia brasiliensis	107.1	1.8	1.0	3.4	42.9	3.1	2.8
Sebastiania brasiliensis	207.1	3.5	0.8	2.9	14.3	1.0	2.5
Cereus stenogonus	35.7	0.6	0.4	1.4	57.1	4.2	2.1
Eugenia hyemalis	121.4	2.1	0.2	0.5	28.6	2.1	1.6
Coutarea hexandra	50.0	0.9	0.1	0.4	42.9	3.1	1.5
Eugenia moraviana	28.6	0.5	0.2	0.7	28.6	2.1	1.1
Helietta apiculata	35.7	0.6	0.1	0.2	28.6	2.1	1.0
Chrysophyllum marginatum	21.4	0.4	0.1	0.2	28.6	2.1	0.9
Casearia sylvestris	14.3	0.2	0.0	0.1	28.6	2.1	0.8
Matayba elaeagnoides	42.9	0.7	0.1	0.4	14.3	1.0	0.7
Handroanthus heptaphyllus	28.6	0.5	0.1	0.3	14.3	1.0	0.6
Agarista paraguayensis	28.6	0.5	0.0	0.2	14.3	1.0	0.6
Hexachlamys edulis	14.3	0.2	0.1	0.3	14.3	1.0	0.5
Picrasma crenata	14.3	0.2	0.1	0.2	14.3	1.0	0.5
Handroanthus pulcherrimus	21.4	0.4	0.0	0.1	14.3	1.0	0.5
Tabernaemontana catharinensis	14.3	0.2	0.0	0.1	14.3	1.0	0.5
Psidium guineense	14.3	0.2	0.0	0.0	14.3	1.0	0.4
Alchornea glandulosa	7.1	0.1	0.0	0.1	14.3	1.0	0.4
Picramnia sellowii	7.1	0.1	0.0	0.0	14.3	1.0	0.4
Senna pendula	7.1	0.1	0.0	0.0	14.3	1.0	0.4
Vitex megapotamica	7.1	0.1	0.0	0.0	14.3	1.0	0.4
Dead	271.4	4.6	1.2	4.1	85.7	6.3	5.0
Total	**5879**	**100**	**29.09**	**100**	**1371**	**100**	**100**

Table 3. Structural parameters of different vegetation formation in San Ignacio, Misiones, Argentina.

Vegetation formation	Absolute density (ind/ha)	Basal area (m²/ha)	Mean diameter (cm) ± SD	Mean height (m) ± SD
Forest	2,882	25.2*	8.3 ± 6.1*	6.5 ± 2.5
Savanna	925	9.4	8.1 ± 6.4	2.7 ± 1.9
Rupestrian	4,571	29.1	5.7 ± 2.9	2.5 ± 1.2

*base on perimeter at breast height

Structural parameters revealed that *Qualea cordata* was the species that characterized these environments. We consider this is an important fact as it is restricted to the San Ignacio municipality and is the only taxon of Vochyciaceae in Argentina (IBODA, 2014). This species grows in shallow soils and relatively dry environments (Yamamoto, 2009; Negrelle, 2011), and also occurs both in rupestrian grassland in the Brazilian cerrado (Lisboa, 2000) and in rocky substrates in Paraguay, in which is one of the most common Vochysiaceae in the Cerrado flora (Spichiger *et al*., 1995). The plasticity of *Q. cordata* allows it to be a shrub in rocky areas or to reach arboreal dimension in better edaphic conditions, as in the forest near to study site (Velazco *et al*., 2015). In rocky areas, we observed that it generates a coarsening in the trunk base, probably as a way of attachment to rocks.

The second most important species, *Monvillea euchlora*, is exclusive to the area, often forming a closed and dense population, which inhabits rocky soils or gaps in the forest (Biganzoli & Romero, 2004). Based on herbaria records, it is distributed in Argentina and Paraguay, with no occurrences in Brazil.

The abundance of *Ocotea lancifolia* denotes its capacity to live in this kind of site, although it was recorded in low frequency in local savanna and forest (Velazco *et al*., 2015; Velazco *et al*., 2018).

Myrciaria delicatula tree, like the previous one, had shrub dimension. It occurs commonly from riparian forests to rocky outcrops (Rotman, 1982), and was observed in rocky grassland in Guartelá Canyon in the Paraná state - Brazil (Silva, 2000).

It is important to mention the detection of *Leptolobium elegans*, a provincial natural monument, in rock outcrop sites one and three. Because of its presence, these sites has high conservation values for this species in the Osununú Private Reserve. This species was the most important in the Teyu Cuaré savanna (Velazco *et al*., 2018)

Cordiera concolor is a small tree characteristic of dense and mixed ombrophilous forest, as well as of natural forest patches on grassland from Brazil, Paraguay and Argentina (Bacigalupo, 1960; Delprete *et al*., 2004). In the last country, this species was recorded only in the San Ignacio municipality and is considered as exclusive to this region (Biganzoli & Romero, 2004).

An overview of the different vegetation formation of the Teyu Cuaré region reveals that rupicolous vegetation encompasses an intermediate woody diversity when compared to the forest and savannas. The gradual diversity decreasing from the forest, rupestrian vegetation to savanna, and the richness difference values obtained suggest the existence of ecological gradient, likely controlled by environmental filters. We suppose that the main factor structuring the woody flora can be related to edaphic condition and disturbance caused by fire. In the region, the savanna soil is nutrient poor with a sandy texture, while in the rupestrian environment the soil is scarce (see appendix in Velazco 2014). Fire is frequent in savanna (Velazco *et al*., 2018), so only fire-resistance species can prevail in that environment. Fire and soil are common factors that determine structure and composition of communities in rupestrian and savanna vegetation (Abadia *et al*., 2018; Fernandes, 2016; Dantas *et al*., 2015).

Conclusions

Despite the majority of individuals in rocky environments belonging to arboreal species, they are small, with a mean height of 2.7 m and PGH of 5.7 cm.

These communities are structured by *Qualea cordata*, *Monvillea euchlora*, *Ocotea lancifolia* and *Myrciaria delicatula*, all adapted to this environment and rupestrian areas in Brazil and Paraguay.

We found evidence that these communities develop on fragile geomorphic and pedological conditions which are poorly represented in the

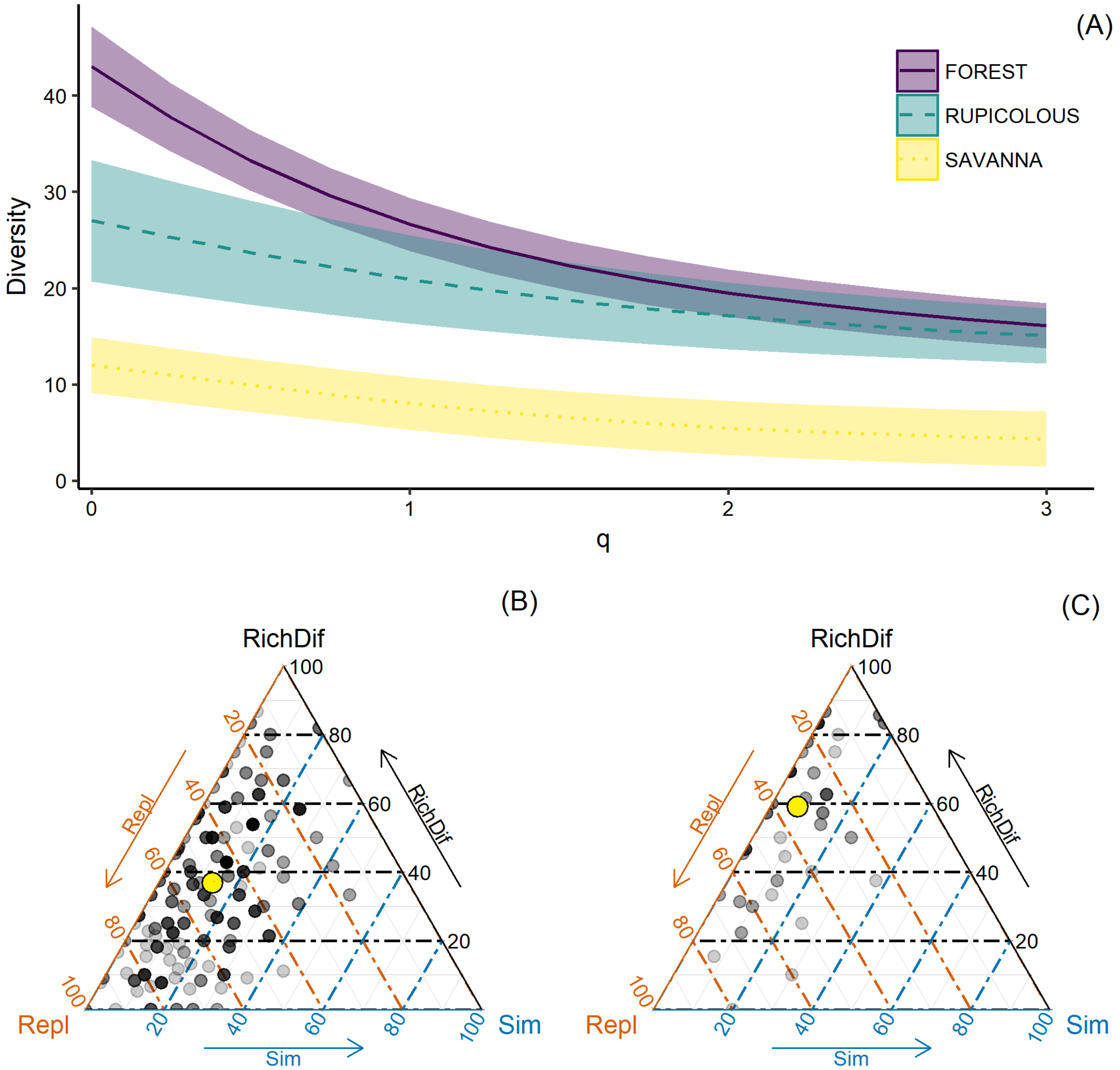

Fig. 5. Diversity profile for different phytophysiognomies in Teyu Cuare (**A**) and beta diversity component comparing rupestrian vegetation with forest (**B**) and savanna (**C**) in San Ignacio, Misiones, Argentina. Transparent colored areas depicted in the A panel represent 95% confidence interval. The ternary plots in the B and C panels show the relationship of the similarity (Sim), species replacement (Repl) and richness difference (RichDif). Large yellow points represent the average value.

region. Several of the species that compond its flora have restricted distribution in the country such as *Qualea cordata*, *Monvillea euchlora*, *Leptolobium elegans*, *Agarista paraguayensis* and *Cordiera concolor*. The flora and the sigular vegetation physiognomy of these environments reinforce the need to consider them as high-priority sites for conservation.

Rupestrian vegetation showed an average woody diversity compared to forest and savanna formation, with high beta diversity mainly structured by richness difference, possibly caused by several environmental filters, like fire and edaphic condition. Studies on environmental filters would be needed to better understand the mechanisms that structure the different communities.

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