Madera y bosques
ISSN: 1405-0471
ISSN: 2448-7597
Instituto de Ecología A.C.

Benedictto, Mariana N.; Gómez-Valencia, Bibiana; Torrella, Sebastián A.
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Madera y bosques, vol. 25, no. 2, e2521611, 2019
Instituto de Ecología A.C.

DOI: 10.21829/myb.2019.2521611

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doi: 10.21829/myb.2019.2521611

Madera y **Bosques** vol. **25**, núm. **2**, e**2521611** Summer **2019**

Scientific papers

Structural and functional characterization of the dry forest in central Argentine Chaco

Caracterización estructural y funcional del bosque seco en el Chaco central argentino

Mariana N. Benedictto[1], Bibiana Gómez-Valencia[1] and Sebastián A. Torrella[1*]

[1] Universidad de Buenos Aires. Facultad de Ciencias Exactas y Naturales. Grupo de Estudios de Sistemas Ecológicos en Ambientes Agrícolas. Buenos Aires, Argentina.

*Autor de correspondencia. sebatorrella@gmail.com

Abstract

Here, we studied the composition, structure and functioning of the woody vegetation of a 1000-ha area of the Central Argentine Chaco. First, we identified, through Landsat satellite image processing, three different vegetation classes: two forest types and a savanna. Each class was field surveyed to analyze the composition and structure of the woody plant community. Functioning was assessed through the enhanced vegetation index – a proxy of productivity – obtained from the MODIS sensor. The forest classes showed no differences in composition but some differences in structural attributes, particularly in the density of the dominant tree species in the area, *Aspidosperma quebracho-blanco*. As expected, the savanna showed less density and basal area of woody plants, with a relative high proportion of tree species seedlings and heliophilous shrubs. The forest class with less density of *A. quebracho-blanco* presented higher productivity. This could be related to a higher ability of the shrub layer to intercept radiation because shrubs are under an open canopy, as has been noted for early successional stages. Additionally, we found that annual mean productivity for the three classes showed a negative trend in the period 2000-2014. Our results provide valuable information since there are no studies addressing relationships between structural and functional attributes at local level in the Chaco Region.

Keywords: *Aspidosperma quebracho-blanco*, Chaco savanna, EVI, Modis; productivity.

Resumen

Se estudió la composición, estructura y funciones de la vegetación leñosa en un área de 1000 ha en el Chaco central argentino. En primer lugar, a través del procesamiento de imágenes satelitales Landsat, se identificaron tres clases de vegetación diferentes: dos tipos forestales y una sabana. Cada clase fue relevada a campo para analizar la estructura y composición de su comunidad de plantas leñosas. El aspecto funcional fue evaluado a través del Índice de Vegetación Mejorado – un estimador de la productividad – obtenido por el sensor MODIS. Las dos clases de bosque no mostraron diferencias en composición, pero sí en algunos atributos estructurales, particularmente en la densidad de *Aspidosperma quebracho-blanco*, la especie arbórea dominante. Como se esperaba, la sabana mostró menor densidad y área basal de plantas leñosas, con una proporción relativamente alta de renovales de árboles y arbustos heliófilos. La clase de bosque con menor densidad de *A. quebracho-blanco* presentó una productividad mayor. Esto puede estar relacionado con una mayor capacidad del estrato arbustivo para captar radiación, dado que se encuentra bajo un dosel más abierto. Por otro lado, se encontró que la productividad media anual para las tres clases de vegetación mostró una tendencia negativa en el período 2000-2014. Los resultados aquí obtenidos proveen valiosa información ya que no hay estudios que aborden relaciones entre estructura y atributos funcionales de la vegetación a escala local en la región Chaqueña.

Palabras clave: *Aspidosperma quebracho-blanco*, sabana, EVI, Modis, productividad.

Introduction

The Chaco region is a vast alluvial plain that occupies about 106 million hectares of South America, between north Argentina, west Paraguay, southeast Bolivia and a narrow strip in southwest Brazil. This region is naturally covered by a variety of plant physiognomies, such as thorny semi-deciduous forests, thorn dry forests, open forests, savannas, savannas with palm trees, and pastures (Morello & Adámoli, 1974; Prado, 1993). Currently, the region is one of the deforestation hotspots in the world (Hansen *et al.*, 2013). In the Argentine Chaco, about 4 million hectares of forest were lost between 2002 and 2010 (Piquer-Rodríguez *et al.*, 2015) because they were transformed into croplands or pastures.

The other productive activities carried out in the region, which are less intense but persistent, also have different effects on the forest structure. These include ranching (Trigo *et al.*, 2017), selective logging (Tálamo, López de Casenave, & Caziani, 2012), and exploitation for firewood and charcoal (Rueda, Baldi, Gasparri, & Jobbágy, 2015). This use of resources is not planned, causing forest degradation and sustained loss of the natural heritage in the region (Morello, Pengue, & Rodríguez, 2007). Therefore, there is a variety of forest conservation states, with varying degrees of impact and/or recovery levels, which will surely have their counterpart in functional aspects. However, the latter have been less studied.

Net Primary Production (NPP) is one of the most integrative descriptors of ecosystem functioning and represents the C gains by plants. Vegetation indices derived from satellite images like Enhanced Vegetation Index (EVI) and Normalized Vegetation Index (NDVI) are widely used to describe carbon gains and ecosystem functioning (Volante, Alcaraz-Segura, Mosciaro, Viglizzo, & Paruelo, 2012) because are closely related to above-ground net primary productivity (ANPP). Empirical relationships between vegetation indices and ANPP are well documented in the literature (Paruelo, 2008). Attributes like annual mean (an estimate of total C gains), annual relative range (description of the intra-annual variation of photosynthetic activity, an indicator of the seasonality of carbon fluxes), annual maximum and minimum (descriptor of vegetation phenology, indicating the intra-annual distribution of the period with maximum and minimum photosynthetic activity), derived from the seasonal curves of vegetation capture most of the variance in C gain dynamics across vegetation types (Cabello *et al.*, 2008; Volante *et al.*, 2012). These attributes can be considered synthetic variables describing the performance of vegetation and hence of ecosystem functioning focused on the dynamics of primary productivity (Paruelo, 2008). Functional characterization of vegetation based on remote sensing has been applied in different types of vegetation at regional scales (Brando *et al.*, 2010; Pennec, Gond, & Sabatier, 2011), but there are only a few studies at local scale. The functional characterization of vegetation, which is complementary to the structural characterization, is very important because the functional responses against different environmental changes are faster than the structural ones (Paruelo, 2008). Therefore, knowledge on the functioning of the vegetation, and not only on its structure, provides better information for the management and conservation of forests particularly at local level.

Some studies have addressed the relationships between structural and functional parameters of the vegetation in the Chaco region. Regarding productivity, there was observed a clear seasonality pattern with maximum values from December to April (Clark, Aide, Grau, & Riner, 2010; Zerda & Tiedemann, 2010) during the growing season, according to climatic patterns in the region. At the same time, forest showed higher values of NPP and lower seasonality than natural grasslands in the region (Volante *et al.*, 2012; Zerda & Tiedemann, 2010). For the semiarid Chaco forest, some authors have found a relationship between the normalized vegetation index (NDVI) in the dry season and above-ground biomass (Gasparri & Baldi, 2013), which could be explained by differences in the phenology of trees, shrubs and herbs (Gasparri, Parmuchi, Bono, Karszenbaum, & Montenegro, 2010). Although it has been suggested that studies of the structural and functional complexity of forests should be performed at different scales (Gasparri & Baldi, 2013), there are yet no studies addressing this issue at local level in the Chaco region.

Objectives

The aims of this work was: a) to establish a zonation of an area of native forests and savannas of the semiarid Chaco forest, based on the composition and structure of the woody plant community; b) to analyze the relationships between the structure of the community of woody plants and its productivity (estimated by the EVI). We expect to find higher values and lower seasonality in the ANPP of those vegetation classes with higher density and basal area of woody plants.

MATERIALS AND METHODS

Study area

The study was conducted within an agricultural-cattle establishment in Chaco Province, Argentina (61.5° W, 27.6° S), located in the Dry Chaco ecoregion within the "Chaco Subhúmedo Central" (Subhumid Central Chaco) complex (Morello, 2012a). Toward the south of the study area is the "Bajos Submeridionales" (Submerdional Lowlands) complex (Fig. 1). The establishment has near 1100 ha of natural cover, corresponding to native forests and savanna. Main productive activities in the establishment are breeding of cattle and cultivation of agricultural and forage crops. Forest and savanna are exposed, in some areas, to grazing and trampling due to the presence of cattle. Currently there is not timber extraction, but selective logging was carried out more than 60 years ago in the forest. According to this low anthropic pressure, forest presents a relatively well conserved structure.

The natural cover in the "Chaco Subhúmedo Central" consists of semi-deciduous forests on well-drained soils alternated with not floodable open savannas and flooded grasslands (Morello, 2012a). The area is one of the hotspots of agricultural expansion in the region (Vallejos *et al.*, 2015) and the current landscape is characterized by the presence of forest fragments, most of which are < 200 ha, immersed in an agricultural matrix (Torrella, Oakley, Ginzburg, Adámoli, & Galetto, 2011) (Fig. 1).

The climate has a marked seasonality with average temperatures of 27 °C in summer and 14 °C in winter, and an average annual rainfall between 900 mm and 1000 mm, concentrated mostly in spring-summer (Bianchi & Cravero, 2010).

Zonation

To identify differences within the study area, we performed an unsupervised classification of the Landsat 8 OLI image (228-79, November 3rd, 2014). The parameters of the classification were 50 classes, maximum 40 iterations and 0.99 convergence threshold, and isodata algorithm. The classes that corresponded to forests were identified by simultaneous comparison with a high-resolution satellite image (Google Earth – April 22nd, 2014). This area was selected from the original Landsat image to make a second classification, with 10 new classes. Based on this second classification and the spatial pattern obtained, homogeneous areas within the forest were identified. Finally, from the initial classification of 50 classes and observing the satellite image, we manually identified areas corresponding to savannas (a natural herbaceous matrix with scattered woody elements). Image classification and GIS analysis were performed in QGIS 2.4 (Quantum GIS development Team, 2014).

Vegetation sampling

We used a random stratified sampling with a total of 26 plots: 10 plots in each forest class and 6 in the savannas, given the small area that they occupy. Forest plots were located randomly in each class and with the following restrictions: avoiding roads and edges by at least 50 m, and distanced from each other by at least 150 m. In the case of the savannas, they were limited to the spatial location of the open areas.

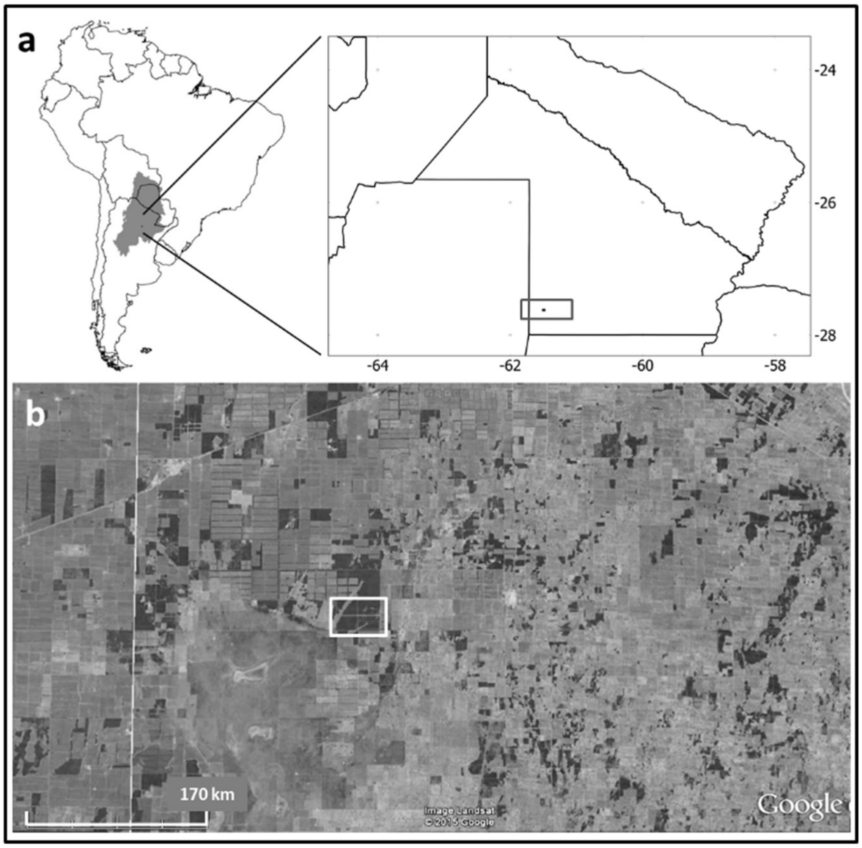

FIGURE 1. a. Chaco region in South America and location of the study area in Argentina. b. Satellite image of the area showing the forest fragments (dark gray) within an agricultural matrix (light gray).
The rectangle highlights the study area.

Sample units were 4 m × 100 m for individuals of tree species (any size) and individuals of shrubby species with a diameter at breast height (DBH) ≥ 5 cm, and 2 m × 50 m for shrubs with DBH < 5 cm, because of their high density (Tálamo & Caziani, 2003; Torrella *et al.*, 2011). We considered each stem as an individual and recorded the species and stem diameter for each individual. Individuals with DBH < 5 cm were measured at 10 cm from the soil (D10). Individuals with D10 < 1 cm were considered as not definitely established, and thus not taken into account.The number of individuals was used to calculate the density (individuals per hectare, ind ha^{-1}), and DBH and D10 were used to calculate the basal area (m^2 ha^{-1}). Taxonomic identification was carried out in the field. When that was not possible, we used a dichotomous identification key. All taxonomic names were checked with the Instituto de Botánica Darwinion [Iboda] (n.d.). Fieldwork was conducted between August 2013 and November 2014.

Functioning characterization of vegetation classes

We analyzed the time series of the enhanced vegetation index (EVI) produced by the MODIS MOD13Q1 product to evaluate the functioning of the vegetation classes obtained. The EVI is a spectral index developed to optimize the vegetation signal with a correction of atmospheric influence on the soil and vegetation (Huete *et al.*, 2002). The MODIS product has a spatial resolution of 250 meters and a temporal resolution of 16 days, using the maximum value composite of observations for each pixel. The EVI time series was analyzed for the period 2000-2014, obtained from the MODIS SUBSET platform (http://daacmodis.ornl.gov), for each hydrological year from September to August.We selected the MODIS pixels, which include at least 60% coverage of the vegetation class assigned during the mapping. For each class, we obtained the following attributes: the mean, minimum, maximum and relative range (RREL = [MAX - MIN] / Average) of each year. We used the command *r.series* of the Grass complement in QGIS to obtain the functional attributes and spatial query to obtain the values of each class.

We also obtained the total annual and mean monthly precipitation values for the period 2000-2014 (Administración Provincial del Agua, 2010). Also, we performed the annual curve (hydrological year) for each class of vegetation with the mean EVI values for the same period.

Data analysis

Using relative abundance, we elaborated rank-abundance curves to analyze community diversity of each class. In this way, we were able to graphically compare species richness, species relative abundances and evenness of the vegetation classes communities.

From the measurements taken in the plots, we calculated the total and per-species basal area (m^2 ha^{-1}) and density (ind ha^{-1}) for each vegetation class. Then, we evaluated the differences in structure and composition between classes using these estimates at both community and population level. For the analysis, we separated the data in: "adults" (tree and shrub species with DBH > 5 cm in 4 m × 100 m plots), "saplings" (tree species with DBH < 5 in 4 m × 100 m plots) and "shrubs" (shrub species with DBH < 5 cm in 2 m × 50 m plots).For all pixels of each class per year, we averaged the values of each functional attribute. We analyzed the temporal trend of the EVI for each class by using linear regressions. We made a correlation between the trend of the mean EVI and mean precipitation values in the period 2000-2010, according to Iglesias, Barchuk and Grilli (2010).

We used general linear models to compare the classes identified, both for the structural and functional attributes. Each of the attributes corresponded to the response variable, and vegetation classes were included as a fixed factor. For the structural attributes, different variance structures (varIdent, varPower and varExp) were tested. For the functional attributes, we included models with three structures of residual covariance: (i) independent residuals, (ii) compound symmetry and (iii) autoregressive order 1.

In all statistical analyses, we tested the assumptions of normality and homogeneity of variance with Shapiro-Wilk and Levene's tests, respectively. When necessary, we modeled heteroscedasticity. We compared different models and selected the best according to the lowest Akaike Information Criterion (AIC) value. For cases in which there was no adjustment of residues to a normal distribution, we used the non-parametric Kruskal-Wallis test. When we found differences among the three vegetation classes, we performed comparisons with the Post-hoc Tukey test. The significance level used was 0.05. The statistical analysis was performed in the R software (R Development Core Team, 2012).

RESULTS

Zonation

Three types of natural cover were identified: two classes of forest (forest A: 419.6 ha, and forest B: 592.3 ha) and a savanna (93.6 ha) (Fig. 2).

Composition and structure of the vegetation

We recorded a total of 4,178 individuals corresponding to 33 woody species belonging to 19 botanical families (Table 1). All species recorded are considered native in the region (Iboda, n.d.). We found 27 species in each forest class and 13 species in the savanna. The rank-abundance curves showed that the species composition of the two forest classes had no relevant differences in the number of species or in the curve shape (Fig. 3). However, they were different from the savanna curve, which also showed lower richness and evenness.

In the case of forests, a rift between the four most abundant species (which were the same in both classes) and the rest was highlighted in both curves.

TABLE 1. Species recorded in the sampling.

Species	Family	Abbreviation
Acacia aroma Gillies ex Hook. & Arn.	Fabaceae	Aca aro
Acacia caven (Molina) Molina	Fabaceae	Aca cav
Acacia praecox Griseb.	Fabaceae	Aca pra
Achatocarpus praecox Griseb.	Achatocarpaceae	Ach pra
Aloysia sp Paláu	Verbenaceae	Alo sp.
Anisocapparis speciosa (Griseb.) X. Cornejo & H.H. Iltis	Caparaceae	Ani spe
Aspidosperma quebracho-blanco Schltdl.	Apocynaceae	Asp q-b
Banara umbraticola Arechav.	Salicaceae	Ban umb
Caesalpinia paraguariensis (D. Parodi) Burkart	Fabaceae	Cae par
Capparicordis tweediana (Eichler) H.H. Iltis & X. Cornejo	Caparaceae	Cap twe
Capparis atamisquea Kuntze	Caparaceae	Cap ata
Castela coccinea Griseb.	Simaroubaceae	Cas coc
Celtis ehrenbergiana (Klotzsch) Liebm. var. *ehrenbergiana*	Celtidaceae	Cel ehr
Cereus forbesii Otto ex C.F. Först.	Cactaceae	Cer for
Coccoloba argentinensis Speg.	Polygonaceae	Coc arg
Cynophalla retusa (Griseb.) X. Cornejo & H.H. Iltis	Caparaceae	Cyn ret
Jodina rhombifolia (Hook. & Arn.) Reissek	Cervantesiaceae	Jod rho
Mimosa detinens Benth.	Fabaceae	Mim det
Moquiniastrum argentinum (Cabrera) G. Sancho	Asteracea	Moq arg
Moya spinosa Griseb.	Celastraceae	Moy spi
Opuntia quimilo K. Schum.	Cactaceae	Opu qui
Porlieria microphylla (Baill.) Descole, O´Donell & Lourteig	Zygophyllaceae	Por mic
Prosopis sp L.	Fabaceae	Pro sp.
Prosopis kuntzei Harms	Fabaceae	Pro kun
Schinopsis balansae Engl.	Anacardiaceae	Sch bal
Schinopsis heterophylla Ragonese & J. Castillo	Anacardiaceae	Sch het

Schinopsis lorentzii (Griseb.) Engl.	Anacardiaceae	Sch lor
Schinus fasciculatus (Griseb.) I.M. Johnst. var. *fasciculatus*	Anacardiaceae	Sch fas
Schinus sp L.	Anacardiaceae	Sch sp.
Sideroxylon obtusifolium (Roem. & Schult.) T.D. Penn.	Sapotaceae	Sid obt
Solanum argentinum Bitter & Lillo	Solanaceae	Sol arg
Trithrinax schizophylla Drude	Arecaceae	Tri sch
Ziziphus mistol Griseb.	Rhamnaceae	Ziz mis

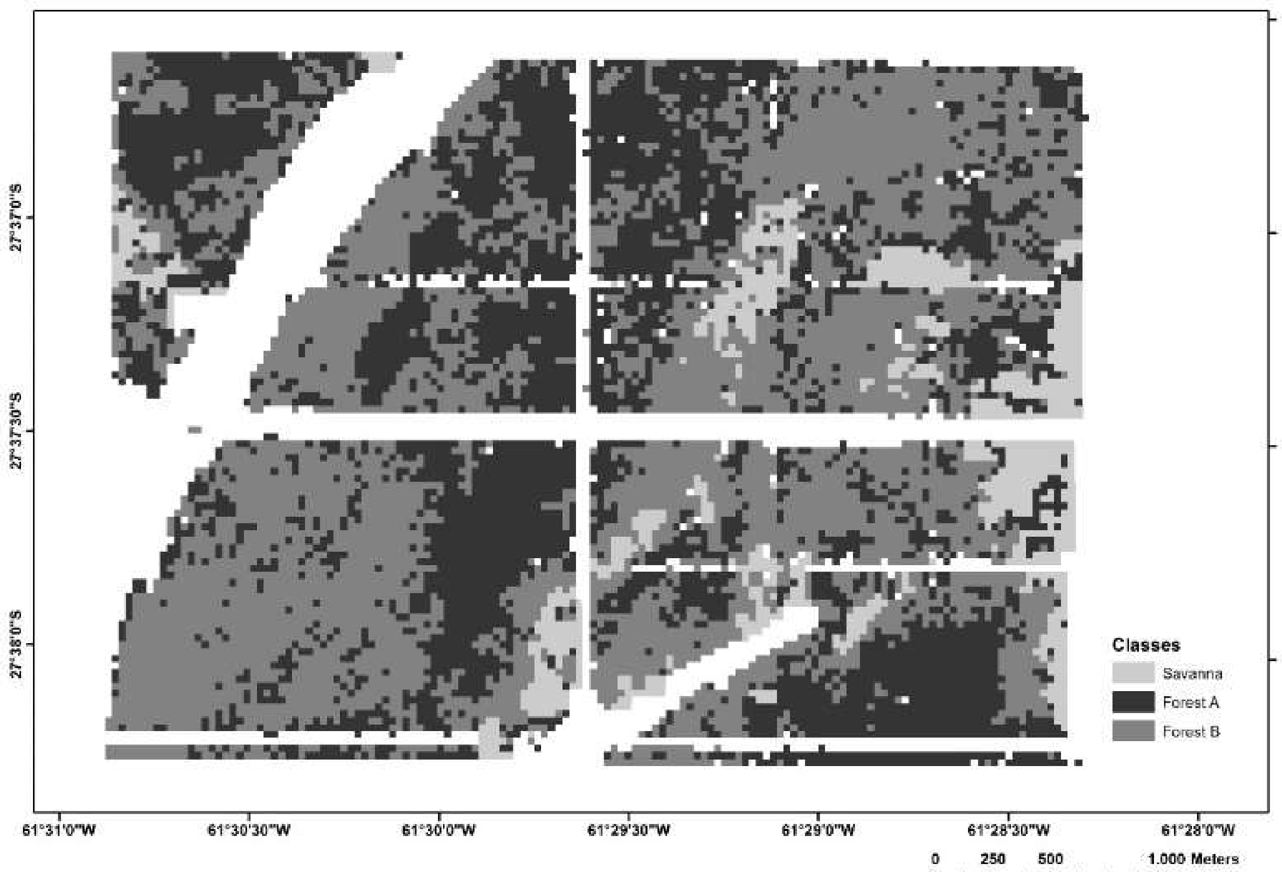

FIGURE 2. Zonation of the natural vegetation of a 1105 ha area of the Central Argentine Chaco from the Landsat 8 OLI image.
In white: Areas of crops and roads.

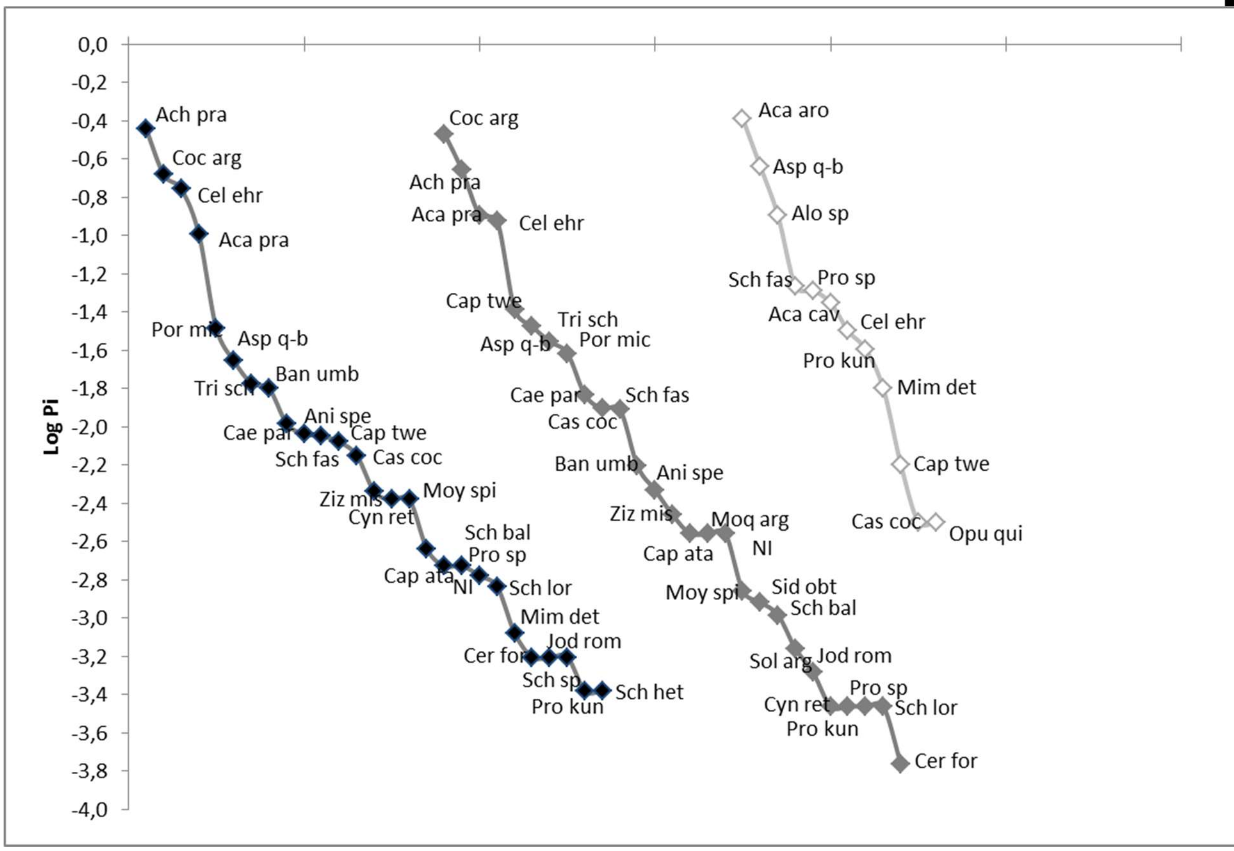

FIGURE 3. Rank-abundance curves for each vegetation class.
Black = Forest A (n = 10), dark gray = Forest B (n = 10), light gray = Savanna (n = 6). The abbreviations of the names are those given in table 1.

The total density of adult trees was higher in forest B than in forest A (1047.5 ind ha^{-1} ± 262.6 ind ha^{-1} and 837.5 ind ha^{-1} ± 285.6 ind ha^{-1}, respectively), although these differences were not statistically significant (Supplement 1). We found no adult trees in the savanna class. The most abundant species in the forest were *Aspidosperma quebracho-blanco*, *Trithrinax schizophylla*, *Acacia praecox*, *Achatocarpuspraecox* and *Caesalpinia paraguariensis*. The density of adults was significantly different between the forest classes A and B only in *A. quebracho-blanco*, *Schinopsis lorentzii* and *T. schizophylla*, with higher values in forest B (Fig. 4 and Supplement 1).

Regarding the basal area of adult individuals, we also found higher values in forest B than in forest A. *A. quebracho-blanco* was the species with highest values in the two forest classes and had significantly higher basal area in forest B than in forest A (Fig. 5 and Supplement 1).

The total density of tree saplings showed no statistically significant differences between the two forest classes and the savanna, except for *Prosopis kuntzei*, which was more abundant in the latter (Fig. 6 and Supplement 1). However, there were notable differences in the species composition of the sapling assembly between the two forest classes and the savanna (Fig. 6).

Among the shrub strata, the savanna class was distinguished from both forest classes, showing lower values of density and basal area (Figs. 7 and 8). Between forest A and B, we found significant differences in *Castela coccinea*, *Coccoloba argentinensis* and *Capparicordis tweediana*, with higher values in forest B (Figs. 7, 8 and Supplement 1).

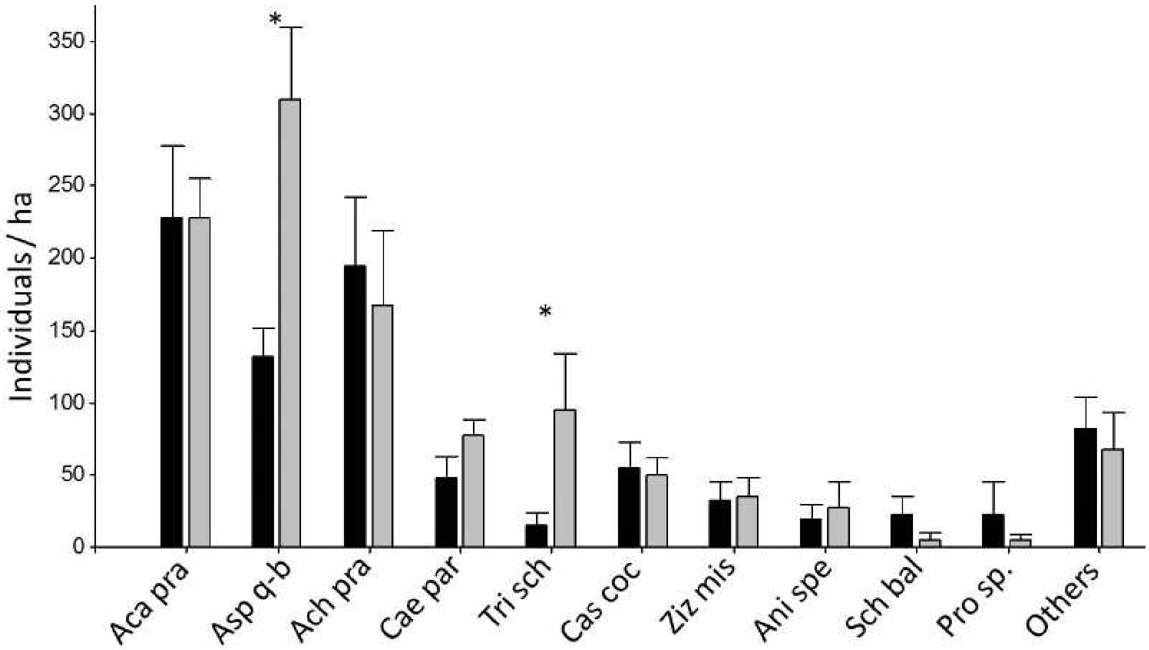

FIGURE 4. Density of adult individuals (DBH > 5 cm) of woody species in 4 m × 100 m plots (Mean ± SE).
Black: Forest A (n = 10), dark gray: Forest B (n = 10). * indicates that means differ significantly at p = 0.05 (linear model or Kruskal-Wallis test). Detailed data of all species are provided in Supplement 1.

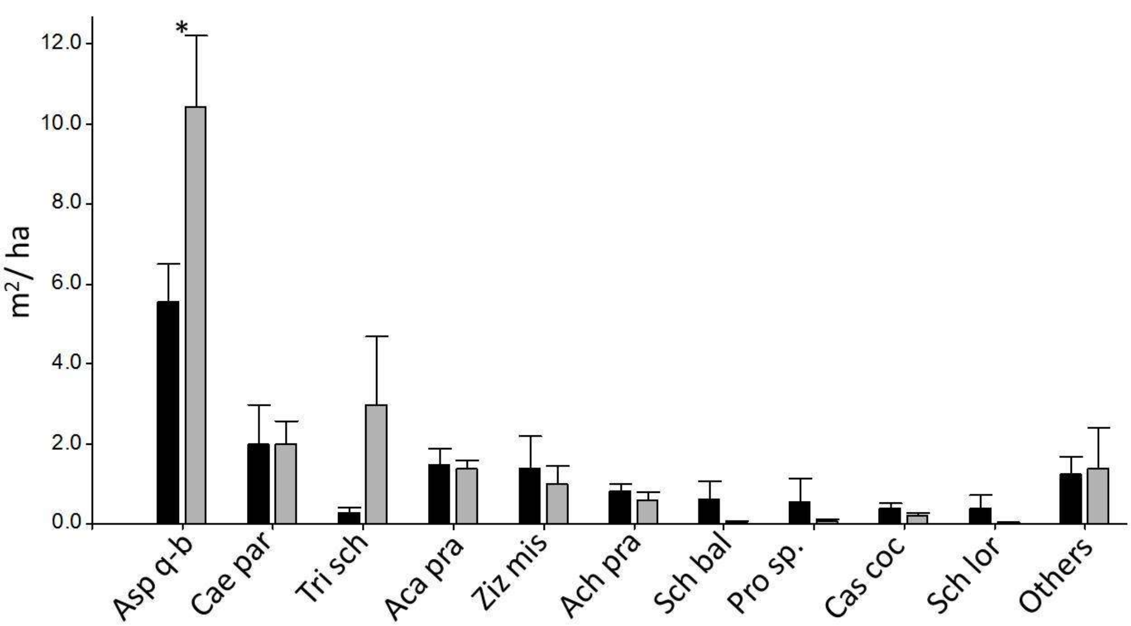

FIGURE 5. Basal area of adult individuals (DBH > 5 cm) of woody species in 4 m × 100 m plots (Mean ± SE).
Black: Forest A (n = 10), dark gray: Forest B (n = 10). * indicates that means differ significantly at p = 0.05 (linear model or Kruskal-Wallis test). Detailed data of all species are provided in Supplement 1.

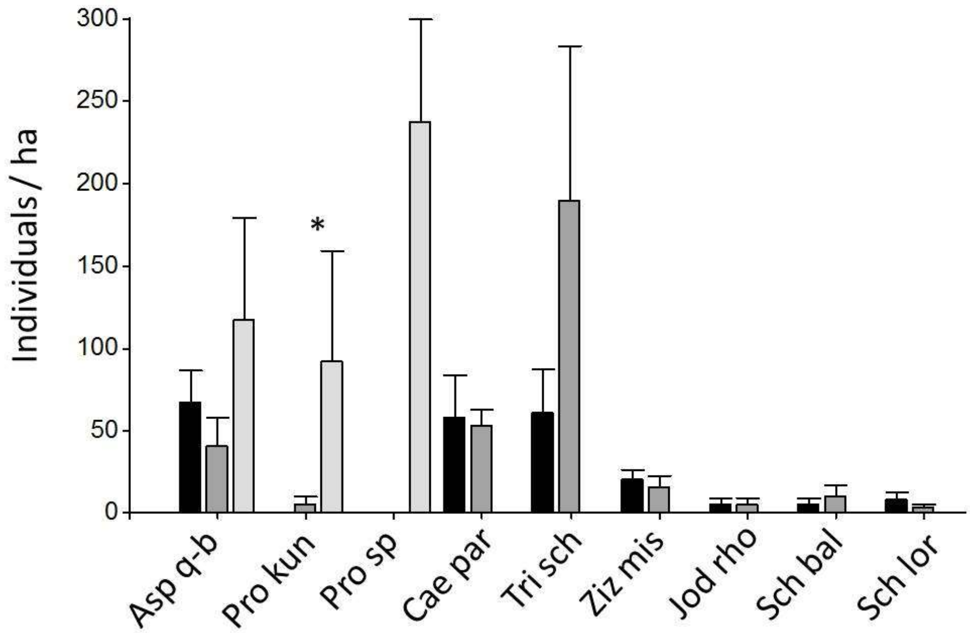

FIGURE 6. Density of sapling individuals (DBH < 5 cm) of tree species in 4 m × 100 m plots (Mean ± SE).
Black: Forest A (n = 10), Dark gray: Forest B (n = 10), light gray: Savanna (n = 6). * indicates that means differ significantly at p = 0.05 (linear model or Kruskal-Wallis test). Detailed data of all species are provided in Supplement 1.

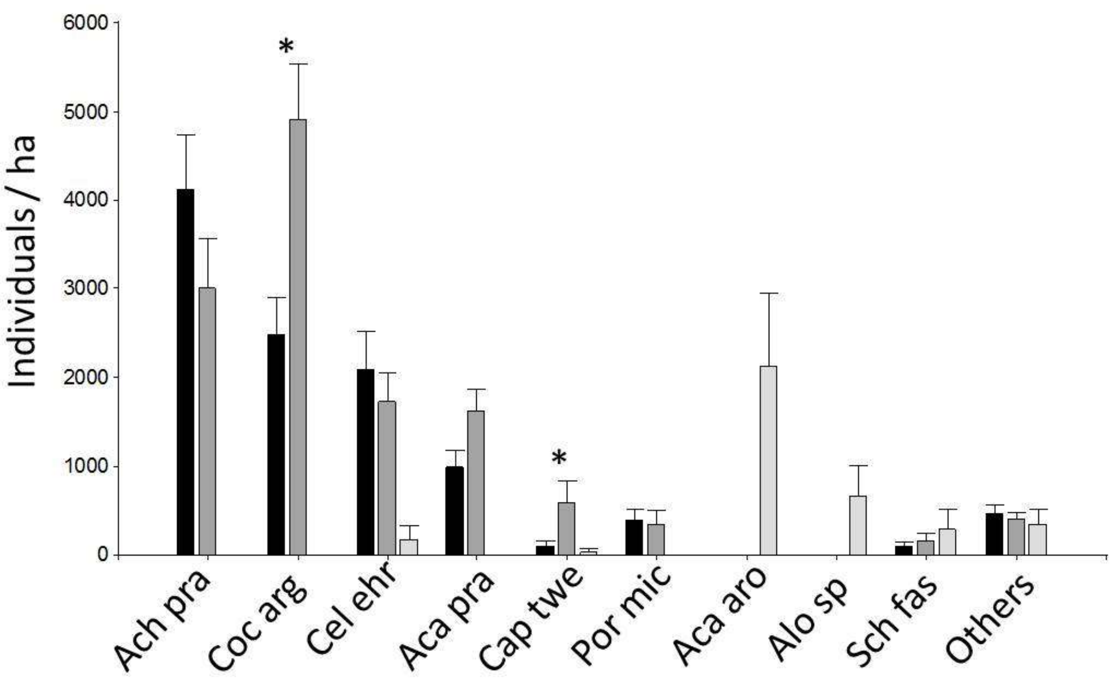

FIGURE 7. Density of shrub individuals (DBH< 5 cm) in 2 m × 50 m plots (Mean ± SE).
Black: Forest A (n = 10), Dark gray: Forest B (n = 10), light gray: Savanna (n = 6). * indicates that means differ significantly at p = 0.05 (linear model or Kruskal-Wallis test). Detailed data of all species are provided in Supplement 1.

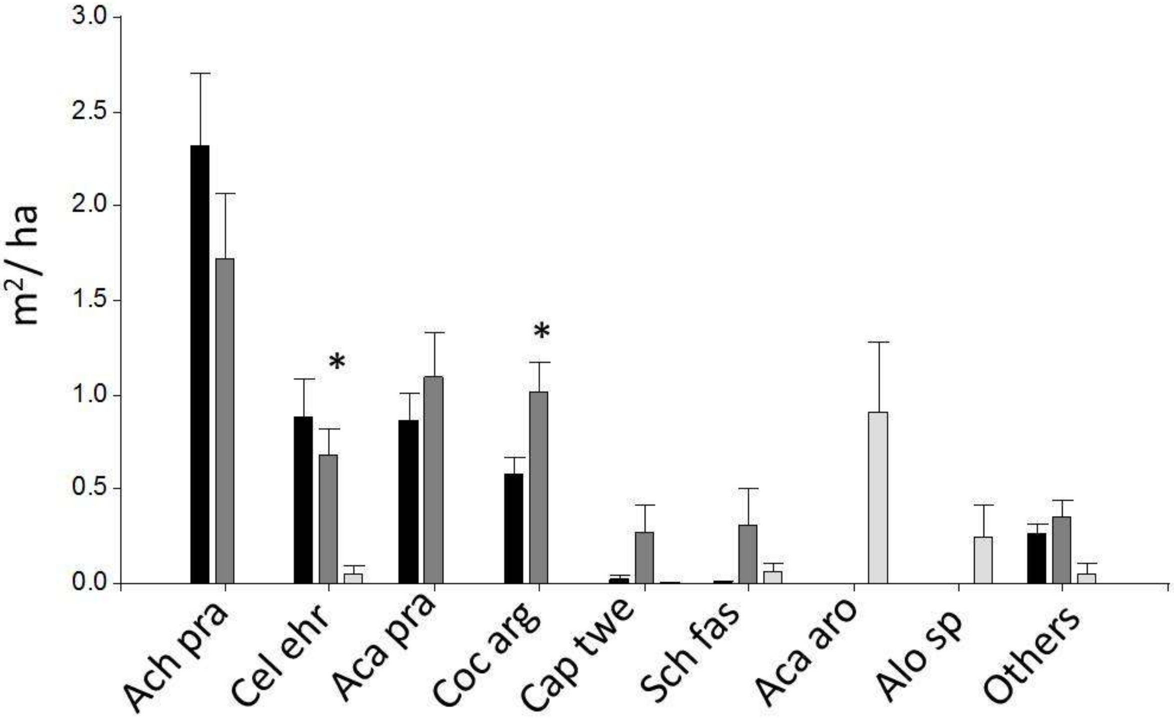

FIGURE 8. Basal area of shrub individuals (DBH< 5 cm) in 2 m × 50 m plots (Mean ± SE).
Black: Forest A (n = 10), Dark gray: Forest B (n = 10), light gray: Savanna (n = 6). * indicates that means differ significantly at p = 0.05 (linear model or Kruskal-Wallis test). Detailed data of all species are provided in Supplement 1.

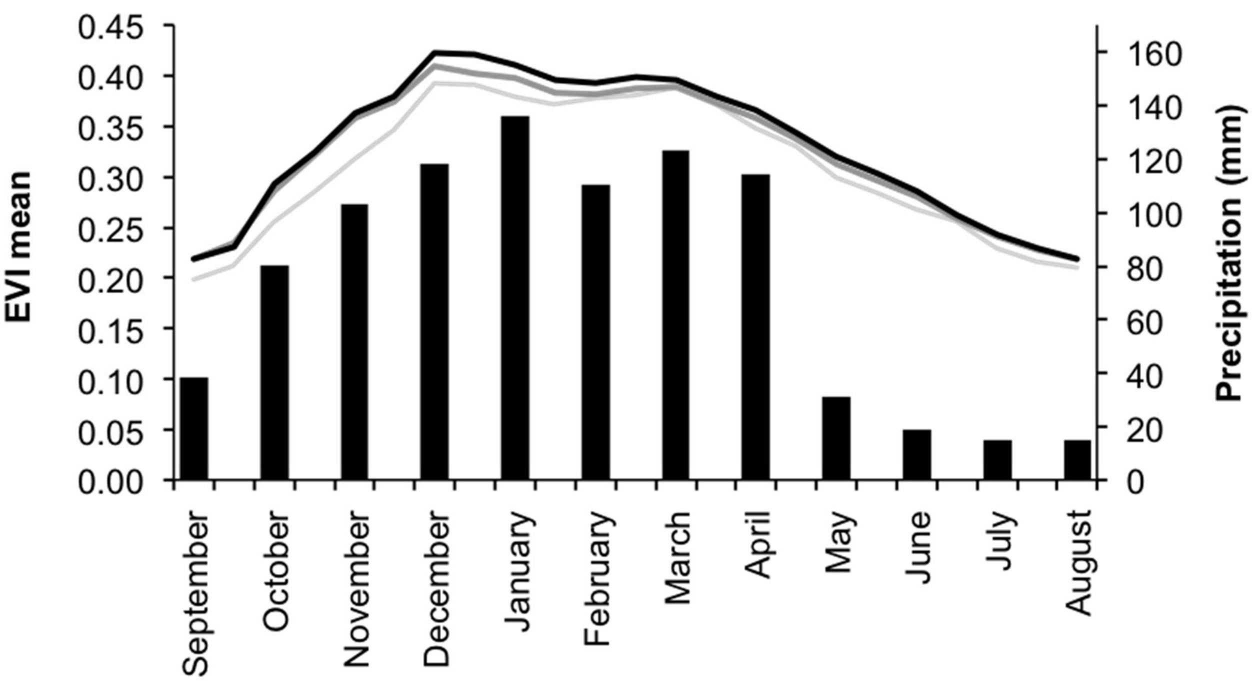

FIGURE 9. Mean EVI profile of the three vegetation classes analyzed and monthly precipitation values.
Black = Forest A, dark gray = Forest B and light gray = Savanna.

Functional characterization

Seasonal curves (EVI) for the three vegetation classes were unimodal. As from September, the EVI mean value increased and reached the maximum during the summer. As from March, the photosynthetic activity decreased until winter, when it reached the minimum values, following the pattern of precipitation (Fig. 9). The number of pixels analyzed was 39 for forest A, 75 for forest B and 3 for the savanna.

We observed a negative trend in the mean EVI values for the three vegetation classes along the period 2000-2014 (Forest A: R2 = 0.53, p <0.01; forest B R2 = 0.48, p <0.01, avanna C R2 = 0.47, p <0.01), with a reduction of 15%. No relationship was observed between the trend of mean EVI values and the precipitation values for the period 2000-2010 (Forest A: $R^2 = 0.27$, p = 0.1; forest B: $R^2 = 0.23$, p = 0.1; savanna C: $R^2 = 0.34$, p = 0.06).

The best model for each of the functional attributes included the autoregressive model (AR1) in residues except for the relative range (Supplement 1). Significant in the annual mean EVI values ($F_{2,42} = 9.14$, $p < 0.01$) and minimum EVI values ($F_{2,42} = 11.5$, $p < 0.01$) between the three vegetation classes; the maximum EVI values showed no significant differences ($F_{2,42} = 11.5$, p = 0.93). Forest A had the highest annual mean EVI values, followed by forest B and the savanna. The relative range presented a marginally significant difference between the savanna and the forest classes ($F_{2,42} = 2.88$, p = 0.06) (Fig. 10).

DISCUSSION

Our study shows that there are differences in the composition and structure of the community of woody plants between the forest and the savanna in the study area. The density and basal area of adults and shrubs were naturally lower in the savanna, where the density of saplings was higher. In terms of composition, all the tree species found in the savanna were also recorded in the forest, but some tree species (e.g. *Schinopsis balansae*, S. *lorentzii* and *Caesalpinia paraguariensis*) were found only in the forest classes.

The total density of saplings was markedly higher in the savanna, a difference due to the saplings of *A. quebracho-blanco*, *Prosopis sp.* and *P. kuntzei*. *Prosopis* saplings were almost absent in both forest classes, in agreement with their heliophilous condition (Tortorelli, 2009).The shrub layer showed differences in species composition: while five species were present both in the forests and the savanna, *Aloysia* sp., *Acacia aroma*, *A. caven* and *Opuntia quimilo* were found only in the savanna. This could be explained because the last three species are heliophilous and acacias are dispersed by cattle (Demaio, Karlin & Medina, 2002; Mereles & Degen, 1997).

Taking into account that the forests in the region and in the "Chaco Subhúmedo Central" complex are dominated or co-dominated by species of the genus *Schinopsis* (Morello, 2012a; Morello & Adámoli, 1974; Prado, 1993; Torrella *et al.*, 2011), the relative low abundance of this genus in the forests studied here is of note. This could be the result of selective logging; however, we found no evidence of recent or intensive logging. In fact, the current owners of the property ensure that no logging has been performed for about 60 years. Then, the explanation could be linked to the soil or topographical features possibly related to the proximity of the study site to the "Bajos Submeridionales" complex, a zone characterized by flooding and saline soils (Morello, 2012b).

A. quebracho-blanco was the most abundant tree species in our study area, with higher density values in forest B. It is well known that this species presents environmental plasticity against *Schinopsis*, having a wide distribution that includes areas with severe environmental conditions (Morello, 2012a; Prado, 1993). In forest B, we also found a notably higher density of *T. schizophylla*, a palm species highly associated with clay soils and flood sites (Moraes, Ríos-Uzeda, Moreno, Huanca-Huarachi, & Larrea-Alcázar, 2014; Navarro, Molina, & Vega, 2010). Then, the soil characteristics may explain the differences in the densities of *T. schizophylla* and *A. quebracho-blanco*.

doi: 10.21829/myb.2019.2521611
Madera y **Bosques** vol. **25**, núm. **2**, e**2521611** Summer **2019**

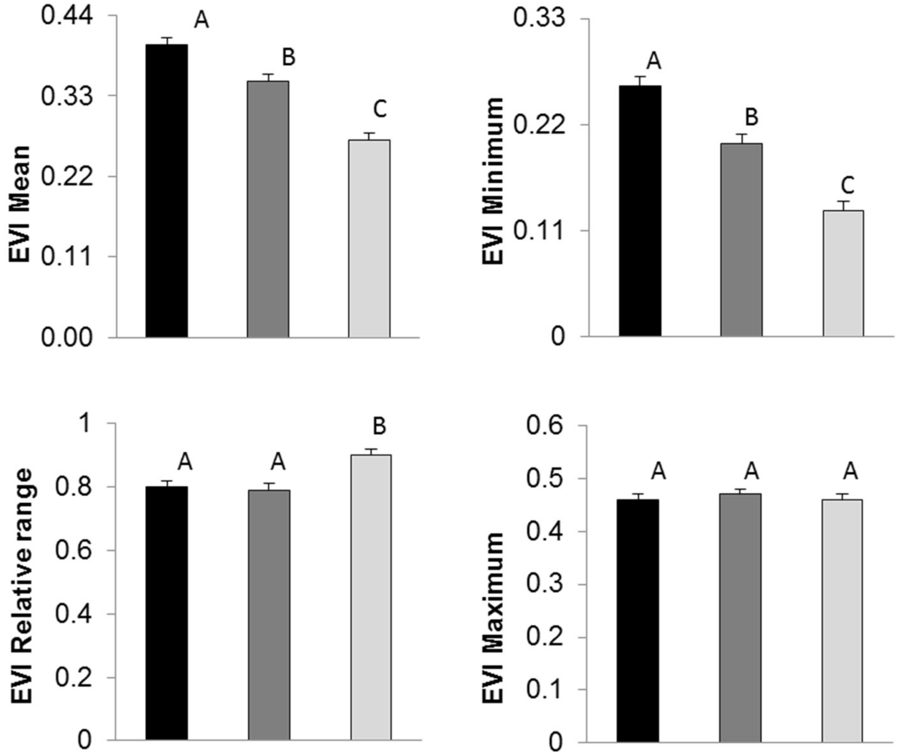

FIGURE 10. Adjusted values of the functional attributes of the three vegetation classes.
Black = Forest A, dark gray = Forest B and light gray = Savanna. Different letters indicate a p value < 0.05 (Linear Model).

The seasonal vegetation curve corresponded to that previously described for the woody vegetation in the Chaco region (Clark *et al*., 2010; Zerda & Tiedemann, 2010). The negative trend of the productivity in the period 2000-2014 was not related to the precipitation values. Gaitán, Bran, and Azcona (2015) also find a negative trend in the NPP (using NDVI as a proxy) for many areas in the region in the same period. The authors attribute this result to the land use change and deforestation process, since NPP of the native Chaco forest is higher than cultivated areas (Volante *et al*., 2012). Interestingly, in our study site, the forest area did not change in the analyzed period, thus, the negative trend in NPP would be promoted by other process and is not necessarily related to forest degradation. In general, along a secondary succession, productivity is higher in early stages, then decrease and tends to an asymptote (Curiguata & Ostertag, 2001). This could be the case in the study area, if some intense disturb occurred many years ago, like selective logging (that was carried out more than 60 years ago) or woody fire.

Most studies about relationships between ANPP and forest structure have been developed at a large scale and some have found a positive relationship between vegetation indices and coverage (Gaitán *et al*., 2013) and density of trees (Gillespie, Zutta, Early, & Saatchis, 2006; Pau, Gillespie & Wolkowich, 2012). However, not many studies have evaluated the relationships between forest structure and ANPP through the EVI at local scale. Some have noted that ANPP is higher in situations where the shrub layer has greater influence on the spectral properties, like in the open forest (Gond *et al*., 2013) and in early successional stages (Hernandez-Stefanoni & Dupuy, 2007), when the canopy is not yet dense. According to expected, NPP of the savanna, with lower basal area and density, is lower than the NPP in forest. This is also consistent with that reported in other regions (Borges & Sano, 2014).

Between forest classes, although we did not find statistically significant differences in basal area nor density, the forest with higher values in these structural parameters (forest B) showed lower values of ANPP, contrary to expected. This difference in ANPP could be given by other factor not directly related with the attributes measured here, like foliar area, deciduousness, or successional stage. Other studies reported that mature forests show lower vegetation index values than secondary forest (Hartter, Ryan, Southworth, & Chapman, 2011; Hernandez-Stefanoni & Dupuy, 2007) because they invest in woody biomass rather than in foliar biomass. In our study site, the higher density of *A. quebracho-blanco* in forest B could be related with a successional stage relatively mature which would explain the observed differences in ANPP.

CONCLUSIONS

The methodology allowed establishing a zonation of the area and quantitatively describing the community of woody plants in two different forests and a savanna. We could not identify a clear pattern in the relationship between woody vegetation structure (i.e. basal area and density) and ANPP. Our general prediction (higher ANPP values with higher density and basal area) was fulfilled only when comparing forest and savannas; but not between forest classes. This issue should be further explored to find general patterns to predict the vegetation structure by using satellite data in other sectors within the region, and it would also be necessary to explore other vegetation features (e.g. foliar area, deciduousness) and attributes of the herbaceous layer. Future research should analyze whether the negative trend detected in the EVI for the period 2000-2014 is a general pattern in the forests of the region and if is related to degradation or to changes in functionality along a post-disturbance recovery.

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Received: 29 July 2017

Accepted: 29 November 2018

Published: 19 August 2019

This paper must be cited as:

Benedictto, M. N., Gómez-Valencia, B., & Torrella, S. A. (2019). Structural and functional characterization of the dry forest in central Argentine Chaco. *Madera y Bosques*, *25*(2), e2521611. doi: 10.21829/myb.2019.2521611

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