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Original Paper

Floristic structuring of woody plants from the Chaco in light of abiotic factors

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Abstract
The phytogeographic domains are structured by different geoclimatic (abiotic) factors, such as altitude, temperature and precipitation. Thus, our goal was to investigate the possible abiotic factors that are related to the floristic richness of the tree-shrub component throughout the Chaco remnants. This study is based on data of the presence and absence of species in different remnants related to geoclimatic data. In addition, World Wildlife Fund shapes were used to differentiate dry and wet Chaco. The database aggregated 36 areas and 522 species. The different clusters obtained by floristic affinity between groups in Chaco was mainly related to temperature, altitude and seasonality of precipitation. In remnants where the seasonality of precipitation and altitude were more evident, there is greater dissimilarity in the composition of the tree-shrub vegetation. On the other hand, the temperature gradient explained the floristic homogeneity in the humid Chaco. Thus, the richness of the tree-shrub component of the Chaco is mainly attributed to three geoclimatic factors. Dry Chaco presents greater floristic dissimilarity compared to Humid Chaco. Still, the seasonality of the precipitation and the altitude play a dominant role in the structuring of trees and shrubs in the Dry Chaco and the temperature in the most homogeneous formations that integrate the humid Chaco.
Key words: floristic similarity, precipitation, temperature, vegetation.

Resumo
Os domínios fitogeográficos são estruturados por diferentes fatores geoclimáticos (abióticos) tais como altitude, temperatura e precipitação. Assim, nosso objetivo foi investigar quais os possíveis fatores abióticos que estão relacionados à riqueza florística do componente arbóreo-arbustivo em remanescentes de Chaco, ao longo de sua extensão. O estudo é baseado em dados de presença e ausência de espécies em diferentes remanescentes relacionados com dados geoclimáticos. Somado a isso, foram utilizados shapes da World Wildlife Fund para diferir o Chaco seco do úmido. O banco de dados agregou 36 áreas e 522 espécies. A afinidade florística entre os grupos foi relacionada principalmente à temperatura, altitude e sazonalidade da precipitação. Em remanescentes onde a sazonalidade da precipitação e a altitude foram mais evidenciados, há maior dissimilaridade na composição da vegetação arbóreo-arbustiva. Por outro lado, o gradiente de temperatura explicou a homogeneidade florística no Chaco úmido. Assim, a riqueza do componente arbóreo-arbustivo do Chaco é atribuída principalmente a três fatores geoclimáticos. O Chaco seco apresenta maior dissimilaridade florística comparado ao Chaco úmido. Ainda, a sazonalidade da precipitação e a altitude têm papel preponderante na estruturação de árvores e arbustos no Chaco seco e a temperatura nas formações mais homogêneas que integram o Chaco úmido.
Palavras-chave: **s**imilaridade florística, precipitação, temperatura, vegetação.

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Introduction

The distribution of species among different phytogeographic domains can be evaluated by considering abiotic (geoclimatic) filters, such as soil type, precipitation and topography. Different filters can act in species selection according to the scale (Morello 1967; Lewis 1991; Oliveira-Filho & Fontes 2000), resulting in a heterogeneous environment. Thus, it is essential to consider scale when analyzing patterns in biological communities (Lewis 1991; Oliveira-Filho & Fontes 2000; Vellend 2010). Among spatial scales, local scales are often considered as those up to 10^2 km^2 in area and landscape or regional scales are those between 10^2 km^2 and 10^8 km^2 (Gurevitch *et al.* 2009).

The seasonally Dry Forests of South America (Caatinga, Chaco, Cerrado and Atlantic forest) are influenced by a gradient rainfall seasonality and/or decreasing soil moisture content (Oliveira-Filho *et al.* 2006). However, there is also substantial influence of temperature gradients, soil fertility and fire frequency, which results in distinct phytophysiognomies (Oliveira-Filho *et al.* 2006; Neves *et al.* 2015).

Among the different domains in South America, the Chaco is distinguished by its marked climatic seasonality (Pennington *et al*. 2000). The Chaco is a large sedimentary plain of ~1,000,000 km^2, extending north and south of the Tropic of Capricorn over northern Argentina, western Paraguay, eastern Bolivia and part of southeastern Brazil (Adamoli *et al.* 1990). The variation in annual rainfall separates the domain into two sectors: dry (500 to 700 $mm.yr^{-1}$) and wet (over 1,200 $mm.yr^{-1}$), which confers distinct floristic and phytophysiognomic types within the same domain (Ramella & Spichiger 1989; Adamoli *et al.* 1990; Prado 1993; Navarro *et al.* 2006). The dry portion occurs in Argentina, Bolivia, and Paraguay and the wet one in Argentina, Brazil, and Paraguay. According to Bueno *et al.* (2017), ecotonal regions in Paraguay present distinct species richness in the Chaco due to rainfall and soil, among other factors.

Another factor that likely interferes in the vegetation composition of the Chaco is altitude. In general, the topography of the Chaco is flat terrain and in its eastern portion the altitude does not exceed 100 m (Hueck 1972). However, in Chaco Serrano remnants the altitude varies from 1,000 to 2,600 m s.n.m. and represents 10% of Gran Chaco (Biani *et al.* 2006; Hernández & Giménez 2016). This portion of the Chaco is poorly studied, and little is known about the precise delimitation of its territory (Morales *et al.* 2019) and the influence of abiotic factors.

Regarding temperature, in the Chaco there is a decreasing gradient from north to south (Hueck 1972). In Santa Cruz, Bolivia and Porto Murtinho in Brazil, the average annual temperature is 25 °C (Hueck 1972; CEMTEC - Monitoring Center for Weather, Climate and Water Resources of the state of Mato Grosso do Sul, Brazil), while in Paraguay's central Chaco average annual temperatures between 23 and 24 °C are observed (Hueck 1972). In Santiago Del Estero, in northwest Argentina, it is 20.6 °C (Hueck 1972). In Tucumán, at the western limit of Chaco and in Córdoba, at the southern limit, 19 °C and 17 °C are recorded, respectively (Hueck 1972).

In the Neotropics the precipitation contributes positively to the diversity of species (Leigh Jr. *et al.* 2004; Esquivel-Muelbert *et al.* 2017). In seasonally dry tropical forest (SDTF) and Chaco woodland in the South American Dry Diagonal, the temperature followed by the precipitation contributed to the characterization of vegetation (Neves *et al*. 2015). The floristic affinity in the Argentine Chaco can be attributed to temperature variations in the north/south direction and to the east/west humidity gradient (Lewis 1991; Leigh Jr. *et al.* 2004). In the Paraguayan Chaco, precipitation contributes to species richness according to soil drainage and possible flooding events (Navarro *et al.* 2006). Studies of abiotic factors in the structuring of the woody vegetation of Chaco in Brazilian territory have revealed the important effect soil fertility has on vegetation (Assunção *et al.* 2020; Baptista *et al.* 2020). The Brazilian Chaco has the smallest territorial extension, ranging from 0.8% to 8% (Hueck 1972; Abdon *et al.* 2007) within the domain.

It is important to highlight that floristic structuring in the Argentine Chaco communities can be attributed to variations in the temperature and humidity gradient (Lewis 1991; Leigh Jr. *et al.* 2004), while precipitation and possible flooding events are determinants in the Paraguayan Chaco (Navarro *et al.* 2006) and the altitudinal variations affect floristic structuring in the Chaco Serrano (Biani *et al*. 2006). However, temperature was the factor that most influenced the flora of Chaco and SDTF (Neves *et al.* 2015). Based on this information, we assumed that Chaco is a heterogeneous domain and that abiotic factors can act on different scales in floristic structuring throughout Chaco remnants. Therefore, our goal was to investigate which and how abiotic factors are related to floristic structuring of woody vegetation (tree/shrubs) throughout the Chaco remnants. We expected that, among the variables, the higher the precipitation, the greater the dissimilarity in the vegetation within the entire South American domain since various studies (Ramella & Spichiger 1989; Lewis 1991; Leigh Jr. *et al.* 2004; Navarro *et al.* 2006) showed that precipitation directly influenced the structuring of vegetation in different regions of the domain.

Materials and Methods

Study areas and data collection

The study considered tree and shrub species recorded in floristic and phytosociological studies carried out in Chaco (Fig. 1). A database was obtained from studies performed in Brazilian Chaco remnants (Noguchi *et al.* 2009; Seleme 2010; Padilha 2011; Lima 2012; Carvalho & Sartori 2014; Assunção *et al.* 2020). Additionally, 29 other floristic lists from Oliveira-Filho (2014) were added to the data bank. Scientific names were checked. From the database, only presence and absence data for tree and shrub species were used. The database aggregated 36 areas and 522 species. Geoclimatic data were obtained for each Chaco domain remnant from the WORLDCLIM (Hijmans *et al.* 2005) with a resolution of 30 seconds.

Data analyses

The Jaccard Similarity Index (Mueller-Dombois & Ellenberg 1974) was used to calculate the similarity between the compiled areas. The grouping method used was the Unweighted Pair-Group Method (UPGMA), and the results were converted into a dendrogram (Sneath & Sokal 1973). Dry and humid Chaco were classified by plotting remnant coordinates in the QGIS Program using the shapes available at Olson *et al.* (2001) and the IBGE for Brazil (IBGE 2015). An ANOSIM nonparametric analysis (Clarke 1993) with 10,000 permutations was carried out to verify the significance of the groups formed. Environmental variables were selected by Principal Component Analysis (PCA) with only the least correlated between each other maintained (mean annual temperature, maximum temperature of the coldest month, temperature of the three coldest months of the year, annual precipitation, seasonality of precipitation and altitude). The climate gradient and the altitude of the remnants along the plots were obtained using the Canonical Correspondence Analysis (CCA). The analyses were performed using R software (R Core Team 2014).

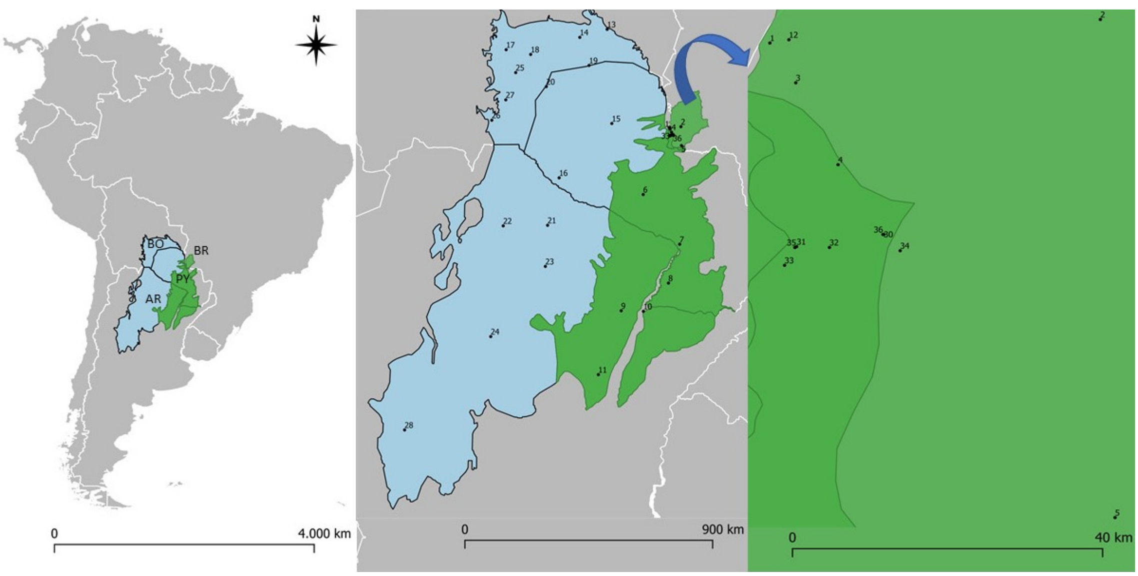

Figure 1 – a. map of South America. b. emphasis on the Chaco domain represented by the dry (blue) and humid (green) sector in relation to precipitation. c. details of some remnants measured. 1–36 represent different listings of woody species of Chaco. BR = Brazil; AR = Argentina; BO = Bolivia; PY = Paraguay.

Results

The evaluated remnants of Chaco domain formed five groups (values between S = 0.12 and S = 0.24), differing from one another (ANOSIM: R = 0.81, p < 0.0001), as seen in the dendrogram (Figs. 1; 2). The floristic affinity between groups was mainly related to temperature, altitude and seasonality of precipitation (Fig. 3).

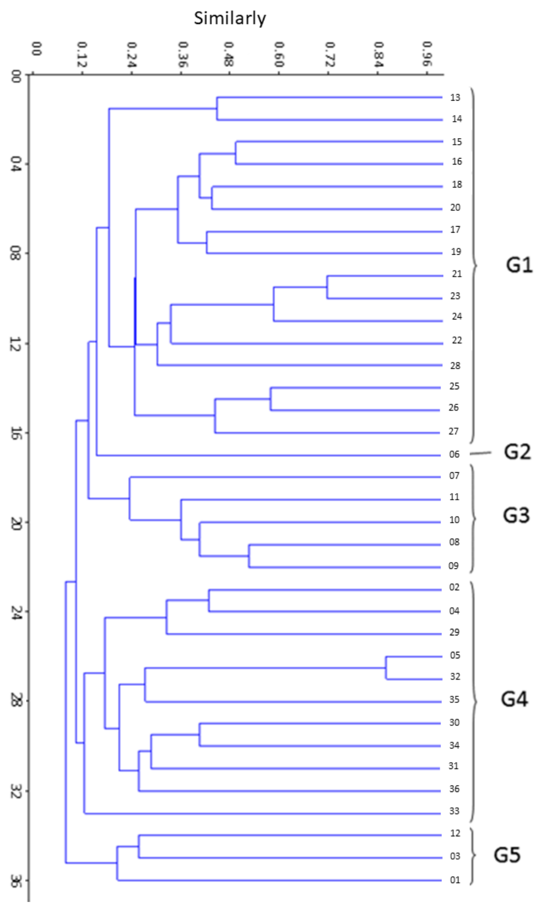

Figure 2 – Similarity dendrogram (Jaccard index) with UPGMA classification applied to woody species of the Chaco domain (Brazil, Bolivia, Argentina and Paraguay). 1–36 = each number in this range represents a list of the presence and absence of tree and shrub species obtained in the Chaco domain. From 1 to 28: Oliveira-Filho (2014); 29: Noguchi *et al.* (2009); 30: Carvalho & Sartori (2014); 31: Lima (2012); 32: Padilha (2011); 33: Seleme 1 (2010); 34: Seleme 2 (2010); 35: Assunção (2020 - Santa Vergínia Farm); 36: Assunção (2020 - Retiro Conceição Farm) (the index yielded a 0.71 cophenetic correlation coefficient). G1 to G5 represent the groupings.

The first two axes of the CCA covered 63.3% of the total variation. The areas represented by the G1 cluster were related to the seasonality of precipitation and altitude (from 130 to 867 m); G2 annual mean temperature; G3 mean annual temperature and average rainfall; G4 average temperature of the coldest month, average annual temperature, temperature of the three months plus cold and precipitation; and G5 all the previous plus precipitation, all the details of which can be found in Figures 1, 2 and 3 and Table 1. Using the World Wildlife Fund shapes that separate the Chaco domain according to precipitation, the floristic affinity indicated that the drier portion was more heterogeneous regarding floristic affinities than the humid portion.

Discussion

Temperature, seasonality of precipitation, and altitude were critical factors for determining floristic affinity among woody plants in different Chaco remnants. However, the affinity did not follow the same pattern observed for floristic affinity in the Argentine Chaco, where temperature contributes to the affinity of remnants in the north-south direction and precipitation contributes to it in the east-west direction (Lewis 1991).

The remnants with the highest elevation were those closest to the Andes, which are higher in altitude than the other areas (Biani *et al.* 2006). The altitude of the remaining remnants ranged from 62 to 867 m. In this range, the remnants between 130 and 867 m contributed to explain the heterogeneity of the flora of trees and shrubs together with the seasonality of precipitation. When evaluating the geographical ecology of the Arecaceae at different scales, Eiserhardt *et al.* (2011) observed that the altitude corresponded to the composition on a local and regional scale, possibly through the effects in conjunction with the hydrology and dynamics of the forest and soil. In other words, the altitude, together with other factors, likely contribute to explain the floristic dissimilarity on a regional scale.

Studies related to taxonomic diversity in Chaco remnants under different conditions and altitudes showed variations. In the Chaco Serrano in an intermediate successional stage above 1,800 m altitude, the Shannon (H') index was 2.65 (Hernández & Giménez 2016). In different remnants of "bosque chaqueño serrano," whose maximum altitude was 580 m above sea level, Varela *et al.* (2002) observed different values of diversity: "sur-Oeste" (H' = 2.97), "fondo de quebradas" (H' = 2.74), "cumbral area" (H' = 2.54), "piedemonte" (H' = 2.32) and "exposición nor-este" (H' = 2.30). In "Savana Estépica Arborizada" the diversity was H' = 2.02 (Lima 2012) and in "Savana Estépica Florestada" the values were higher than H' = 3 (Padilha 2011), both with an altitude of approximately 80 m. As a result, the diversity of the woody plant composition can likely be attributed to greater altitudinal differences (Biani *et al.* 2006), as well as to small elevations and depressions (between 10 to 20 m) (Ramella & Spichiger 1989), which contribute to vegetational particularities in the Chaco. However, it is important to note that the data from the studies mentioned above were obtained using different methods and performed on different phytophysiognomies.

Lewis (1991) pointed out that the more extreme the environmental factors, the more homogeneous Chaco rainforests are. Our evidence indicates that temperature contributed to the homogeneity found throughout the domain, unlike what was found when analyzing Chaco species in conjunction with SDTF, in which temperature explained the dissimilarity in woody plant composition (Neves *et al.* 2015). Therefore, the peculiarities of Chaco are observed when studied separately from the other domains present in South America.

As in other forest formations in Japan, diversity was negatively related to temperature (Mori 2018), which differed from the results observed by Butterfield & Munson (2016), who found that community structuring was attributed to temperature variation throughout a dry region in the southwestern United States.

Interestingly, Argentina presents different phytophysiognomies throughout its territory (Giménez *et al.* 2007) and presents Chaco flora that is most similar to the Bolivian flora (G1 of Fig. 2),

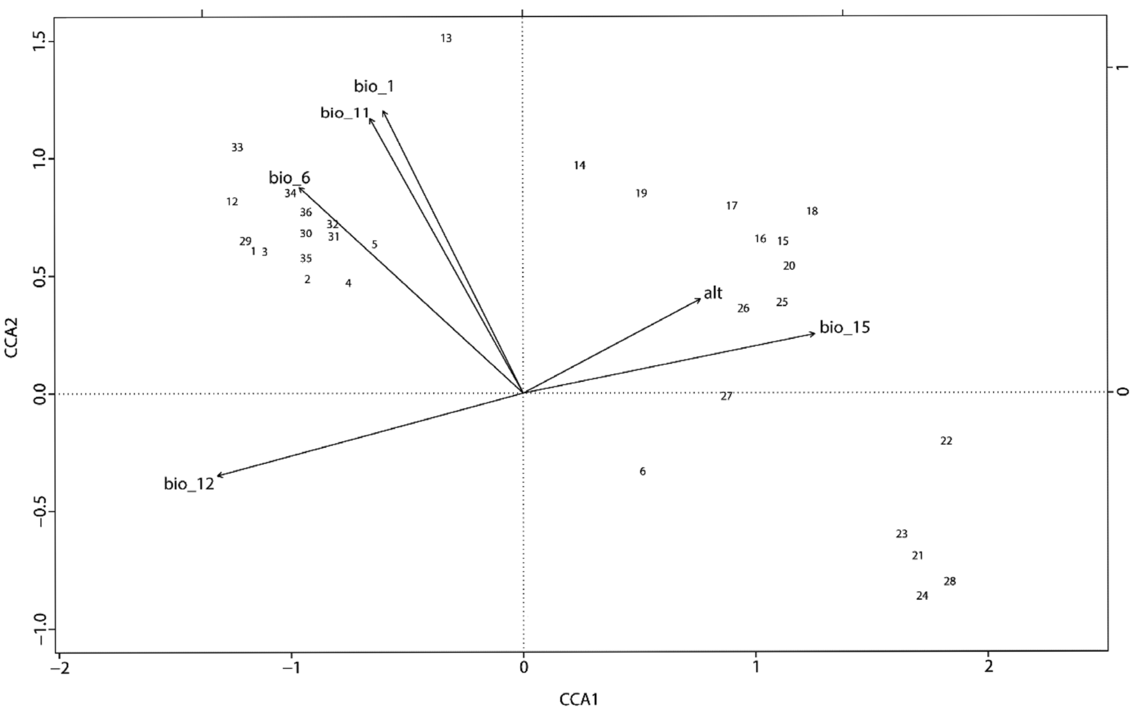

Figure 3 – Canonical Correspondence Analysis showing the ordering of the first two axes of 36 areas with the presence and absence of Chaco tree and shrub species related to environmental variables (bio_1 = average annual temperature; bio_6 = average temperature of the coldest month; bio 11 = temperature of the coldest three months of the year; bio 12 = annual precipitation; bio 15 = precipitation seasonality; alt = altitude). From 1 to 28: Oliveira-Filho (2014); 29: Noguchi *et al.* (2009); 30: Carvalho & Sartori (2014); 31: Lima (2012); 32: Padilha (2011); 33: Seleme 1 (2010); 34: Seleme 2 (2010); 35: Assunção (2020 - Santa Vergínia Farm); 36: Assunção (2020 - Retiro Conceição Farm). Blue circle represents the G1, Yellow G2, Red G4 and Green G5. G1 to G5 represent the groupings obtained from the Similarity dendrogram.

Table 1 – Relation of trees and shrubs in different remnants of Chaco domain, separated by humid and dry sectors according to precipitation in different countries and coordinates.

Remnant	Longitude	Latitude	Sector	Country
1	-57.914	-21.449	Humid	Brazil
2	-57.531	-21.42	Humid	Brazil
3	-57.884	-21.498	Humid	Brazil
4	-57.835	-21.599	Humid	Brazil
5	-57.514	-22.034	Humid	Brazil
6	-58.759	-23.626	Humid	Paraguay
7	-57.573	-25.244	Humid	Paraguay
8	-57.938	-26.509	Humid	Paraguay
9	-59.476	-27.409	Humid	Argentina
10	-58.753	-27.428	Humid	Argentina
11	-60.22	-29.488	Humid	Argentina
12	-57.892	-21.445	Humid	Brazil
13	-59.933	-18.253	Dry	Bolivia
14	-60.824	-18.513	Dry	Bolivia
15	-59.78	-21.316	Dry	Bolivia
16	-61.497	-23.084	Dry	Bolivia
17	-63.222	-18.915	Dry	Bolivia
18	-62.423	-19.068	Dry	Bolivia
19	-60.521	-19.426	Dry	Bolivia
20	-61.914	-20.116	Dry	Bolivia
21	-61.873	-24.628	Dry	Argentina
22	-63.317	-24.647	Dry	Argentina
23	-61.945	-25.966	Dry	Argentina
24	-63.723	-28.249	Dry	Argentina
25	-62.91	-19.659	Dry	Bolivia
26	-63.689	-21.209	Dry	Bolivia
27	-63.234	-20.546	Dry	Bolivia
28	-66.528	-31.288	Dry	Argentina
29	-57.885	-21.701	Humid	Brazil
30	-57.782	-21.685	Humid	Brazil
31	-57.883	-21.700	Humid	Brazil
32	-57.845	-21.701	Humid	Brazil
33	-57.897	-21.723	Humid	Brazil
34	-57.763	-21.705	Humid	Brazil
35	-57.885	-21.701	Humid	Brazil
36	-57.783	-21.685	Humid	Brazil

a fact corroborated by López (2003), who observed that the flora of the Bolivian dry valleys was similar to the Andean flora in northern Argentina. In other words, even with different phytophysiognomies, the specific regions with less precipitation were more similar compared to the others that were analyzed.

In the clusters where the seasonality (G1) and precipitation average (G3) was higher (Figs. 2; 3), we observed greater heterogeneity in species composition. Leigh Jr. *et al.* (2004) pointed out that rainfall contributes to the higher tree species diversity in the tropics. The positive relationship between tree richness and precipitation also occurred in remnants in the Neotropics (Esquivel-Muelbert *et al.* 2017). The woody vegetation of Paraguay (Oakley & Prado 2011) is distributed according to the climatic seasonality marked by a well-defined dry season with varied duration.

It is interesting to note that for Leguminosae in the Chaco Morales *et al.* (2019) mentioned that the highest percentages of exclusive specific and infraspecific taxa correspond to the dry Chaco and sierra Chaco (23% and 12%, respectively, and ca. 16% in species growing simultaneously in both subregions), whereas the percentage in humid Chaco is lower (ca. 22%). The same authors mentioned that this is likely due to their more demanding and harsh environmental conditions which limit the dispersion of generalists or intrusive-invading species. Another aspect to be considered refers to the seasonality of precipitation that can be considered in different time scales (days, years, decades) or seasonal scales (seasons), with the seasonality of precipitation becoming unpredictable in extreme climates (Gurevitch *et al.* 2009).

In addition, the formation of two groups (G2 and G3 in Fig. 2) in Paraguay is likely justified by soil fertility (Oakley & Prado 2011). The proximity of these groups with the Brazilians groupings (G4 and G5 in Fig. 2) is due to the influence of the Missiones Nucleus in Brazil, which allows common species (Oakley & Prado 2011). Also, the clusters formed in Brazil are probably due to their geographical proximity to Cerrado and Dry Forests.

The species shared with these areas in Mato Grosso do Sul include *Astronium urundeuva* (M.Allemão) Engl., *Handroanthus heptaphyllus* (Vell.) Mattos, *Anadenanthera colubrina* (Vell.) Brenan, *Guazuma ulmifolia* Lam., *Helicteres brevispira* A.St.-Hil., *Psidium guajava* L., *Chomelia obtusa* Cham. & Schltdl. and *Randia armata* (Sw.) DC. The Chaco portion with the highest mean precipitation also presents more exorheic rivers (Ramella & Spichiger 1989); that is, diaspores could come from species in other domains following the flow of the river, with favorable conditions facilitating their establishment.

From our study, we attribute the floristic affinity of the different Chaco remnants in Chaco domain to variations in precipitation, altitude and temperature, which is in contrast to our expectations regarding precipitation as the predominant factor in species richness and structure. In addition, in remnants where the seasonality of precipitation and altitude are highest, there is greater dissimilarity in the richness of woody vegetation.

Temperature played a greater role in remnants with more floristic homogeneity. In general, it can be said that the heterogeneity verified in the Chaco is influenced by different factors, where the seasonality of precipitation and altitude prevail in the structuring of trees and shrubs in the dry Chaco and the temperature in more homogeneous formations that make up the humid Chaco.

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References

Abdon MM, Silva JSV, Souza IM, Romon VT, Rampazzo J & Ferrari DL (2007) Desmatamento no bioma Pantanal até o ano 2002: relações com a fitofisionomia e limites municipais. Revista Brasileira de Cartografia 59: 17-24.

Adamoli J, Sennhauser E, Acero JM & Rescia A (1990) Stress and disturbance: vegetation dynamics in the dry Chaco region of Argentina. Journal of Biogeography 17: 491-500.

Assunção VA, Silva DM, Dalponti G, Sartori ALB, Casagrande JC & Mansano VF (2020) Environmental filters structure plant communities in the Brazilian Chaco. Acta Botanica Brasilica 34: 746-754.

Baptista MSP, Assunção VA, Bueno ML, Casagrande JC & Sartori ALB (2020) Fabaceae species representativeness in restrictive soils explains the difference in Chaco vegetation structuring. Acta Botanica Brasilica 34: 559-569.

Biani NB, Vesprini JL & Prado DE (2006) Conocimiento sobre el gran Chaco Argentino en el siglo XX. *In*: Goya JF, Frangi JL & Arturi MF (eds.) Ecología y manejo de los bosques de Argentina. Universidad de La Plata, La Plata. Pp. 1-24.

Bueno ML, Rezende VL, Pontara V & Oliveira-Filho AT (2017) Floristic distributional patterns in a diverse ecotonal area in South America. Plant Ecology 218: 1171-1186.

Butterfield BJ & Munson SM (2016) Temperature is better than precipitation as a predictor of plant community assembly across a dryland region. Journal of Vegetation Science 27: 938-947.

Carvalho FS & Sartori ALB (2014) Reproductive phenology and seed dispersal syndromes of woody species in the Brazilian Chaco. Journal of Vegetation Science 26: 302-311.

Clarke KR (1993) Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18: 117-143.

Eiserhardt WL, Svenning JC, Kissling WD & Balslev H (2011) Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. Annals of Botany 108: 1391-1416.

Esquivel-Muelbert A, Baker TR, Dexter K, Lewis SL, ter Steege H, Lopez-Gonzalez G, Mendoza AM, Briene R, Feldpausch TR, Pitman N, Alonso A, van der Heidjen G, Peña-Claros M, Ahuite M, Alexiaides M, Dávila EA, Murakami AA, Arroyo L, Aulestia M, Balslev H, Barroso J, Boot R, Cano A, Moscoso VC, Comiskey JA, Cornejo F, Dallmeier F, Daly DC, Dávila N, Duivenvoorden JF, Montoya AJD, Erwin T, Fiore AD, Fredericksen T, Fuentes A, García-Villacorta R, Gonzales T, Andino JEG, Coronado ENH, Huamantupa-Chuquimaco I, Killeen TJ, Malhi Y, Mendoza C, Mogollón H, Jørgensen PM, Montero JC, Mostacedo B, Nauray W, Neill D, Vargas PN, Palacios S, Cuenca WP, Camacho NCP, Peacock J, Phillips JF, Pickavance G, Quesada CA, Ramírez-Ângulo H, Restrepo Z, Rodriguez CR, Paredes MR, Sierra R, Silveira M, Stevenson P, Stropp J, Terborgh J, Tirado M, Toledo M, Torres-Lezama A, Umaña MN, Urrego LE, Martinez RV, Gamarra LV, Vela CIA, Torre EV, Vos V, von Hildebrand P, Vriesendorp C, Wang O, Young KR, Zartman CE & Phillips OL (2017) Seasonal drought limits tree species across the Neotropics. Ecography 40: 618-629.

Giménez AM, Hernández P, Gerez R & Ríos NA (2007) Diversidad vegetal en siete unidades demostrativas del Chaco semiárido argentino. Madera y Bosques 13: 61-78.

Gurevitch J, Scheiner SM & Fox GA (2009) Ecologia vegetal. 2. Ed. Ed. Artmed, Porto Alegre. 592p.

Hernández P & Giménez AM (2016) Diversidad, composición florística y estructura en el Chaco Serrano, Argentina diversity, floristic composition and structure in the Chaco Serrano, Argentina. Madera y Bosques 22: 37-48.

Hijmans RJ, Cameron SE, Parra JL, Jones PG & Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978. <https://doi.org/10.1002/joc.1276>

Hueck K (1972) As florestas da América do Sul. Polígono, São Paulo. 466p.

IBGE - Instituto Brasileiro de Geografia e Estatística (2015) Índices de mapas interativos. Available at <https://portaldemapas.ibge.gov.br/portal.php#homepage>. Access on 20 August 2021.

Leigh Jr. EG, Davidar P, Dick CW, Puyravaud JP, Terborgh J, Ter Steege H & Wright SJ (2004) Why do some tropical forests have so many species of trees? Biotropica 36: 447-473.

Lewis JP (1991) Three levels of floristical variation in the forests of Chaco, Argentina. Journal of Vegetation Science 2: 125-130.

Lima TE (2012) Perturbação ambiental em remanescentes de chaco e mecanismos de defesa em leguminosas. Dissertação de Mestrado. Universidade Federal de Mato Grosso do Sul, Campo Grande. 48p.

López RP (2003) Diversidad florística y endemismo de los valles secos bolivianos. Ecología en Bolivia 38: 27-60.

Morales M, Oakley L, Sartori ALB, Mogni VY, Atahuachi M, Vanni RO, Fortunato RH & Prado DE (2019) Diversity and conservation of legumes in the Gran Chaco and biogeograpical inferences. PLoS One 14: e0220151.

Morello J (1967) Bases para el estudio fitoecológico de los grandes espacios (el Chaco Argentino). Ciencia e Investigación 23: 252-267.

Mori AS (2018) Environmental controls on the causes and functional consequences of tree species diversity. Journal of Ecology 106: 113-125.

Mueller-Dombois D & Ellenberg H (1974) Aims and methods of vegetation ecology. Wiley & Sons, New York. 547p.

Navarro G, Molina JA & Molas LP (2006) Classification of the forests of the northern Paraguayan Chaco. Phytoecologia 36: 473-508.

Neves DM, Dexter KG, Pennington RT, Bueno ML & Oliveira Filho AT (2015) Environmental and historical controls of floristic composition across the South American Dry Diagonal. Journal of Biogeography 42: 1566-1576.

Noguchi DK, Nunes GP & Sartori ALB (2009) Florística e síndromes de dispersão de espécies arbóreas em remanescentes de Chaco de Porto Murtinho, Mato Grosso do Sul, Brasil. Rodriguésia 60: 353-365.

Oakley L & Prado DE (2011) El dominio de los Bosques Estacionales Neotropicales y la presencia del Arco Pleistocénico en la Reblica del Paraguay. Rojasiana 10: 55-75.

Oliveira-Filho AT, Jarenkow JA & Rodal MJN (2006) Floristic relationships of seasonally dry forests of Eastern South America based on tree species distribution patterns. *In*: Pennington RB, Lewis GP & Ratter JA (eds.) Neotropical savannas and seasonally dry forests: plant diversity, biogeography, and conservation. The Systematics Association Special Volume. Series 69. CRC Press, Boca Raton. Pp. 159-187.

Oliveira-Filho AT & Fontes MA (2000) Patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate. Biotropica 32: 793-810.

Oliveira-Filho AT (2014) NeoTropTree, flora arbórea da região neotropical: um banco de dados envolvendo biogeografia, diversidade e conservação. Universidade Federal de Minas Gerais. Available at <http://prof.icb.ufmg.br/treeatlan/>. Access on 20 October 2015.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P & Kassem KR (2001). Terrestrial ecoregions of the world: a new map of life on Earth. BioScience 51: 933-938.

Padilha DRC (2011) Fitossociologia e estimativas da biomassa aérea e de carbono em chaco florestado no Brasil. Dissertação de Mestrado. Universidade Federal de Mato Grosso do Sul, Campo Grande. 71p.

Pennington RT, Prado DE & Pendry CA (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography 27: 261-273.

Prado DE (1993) What is the Gran Chaco vegetation in South America? I. A review. Contribution to the study of the flora and vegetation of the Chaco. V. Candollea 48: 145-172.

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at <http://www.R-project.org>. Access on 20 October 2015.

Ramella L & Spichiger R (1989) Interpretación preliminar del medio físico y de la vegetación del Chaco boreal. Contribución al estudio de la flora y de la vegetación del Chaco. Candollea 44: 639-680.

Seleme EP (2010) Flora de remanescentes de chaco brasileiro: aspectos biológicos e etnobotânicos. Dissertação de Mestrado. Universidade Federal de Mato Grosso do Sul, Campo Grande. 75p.

Sneath PHA & Sokal RR (1973) Numerical taxonomy. W.H. Freeman and Co., San Francisco. 573p.

Varela O, Rossi de Ceballos E, Sidán M & Perera T (2002) Estructura, diversidad y relaciones florísticas de un bosque chaqueño serrano de Argentina. Contribución al estudio de la flora de la vegetación del Chaco. XIV. Candollea 57: 239-249.

Vellend M (2010) Conceptual synthesis in community ecology. The Quarterly Review of Biology 85: 183-206.

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