

ORIGINAL ARTICLE

Relationship between woody vegetation and edaphic variables in natural forest formations of Paraguay

Relação entre a vegetação lenhosa e variáveis edáficas em formações florestais naturais do Paraguai

Lila Mabel Gamarra Ruiz Díaz¹ , Lucas Henderson de Oliveira Santos¹ , João Paulo Sardo Madi¹ , Lidia Florencia Pérez de Molas² , Édila Cristina de Souza³ , María Laura Quevedo Fernández² , Sílvia da Luz Lima Mota³ , Carlos Roberto Sanquetta¹ , Samuel de Pádua Chaves e Carvalho³ 

¹Universidade Federal do Paraná – UFPR, Curitiba, PR, Brasil

²Universidad Nacional de Asunción – UNA, San Lorenzo, Paraguay

³Universidade Federal de Mato Grosso – UFMT, Cuiabá, MT, Brasil

How to cite: Ruiz Díaz, L. M. G., Santos, L. H. O., Madi, J. P. S., Pérez de Molas, L. F., Souza, E. C., Quevedo Fernández, M. L., Mota, S. L. L., Sanquetta, C. R., & Carvalho, S. P. C. (2022). Relationship between woody vegetation and edaphic variables in natural forest formations of Paraguay. *Scientia Forestalis*, 50, e3861. <https://doi.org/10.18671/scifor.v50.21>

Abstract

Correlating vegetation data with environmental variables enables results that allow making inferences about the biological components present in these communities and thus contributing to their recovery. In this context, the objective of this study was to evaluate whether there is a correlation between soil variables, to determine whether these variables influence woody vegetation and which variables best explain this relationship. The study was carried out based on data obtained from the National Forest Inventory of Paraguay in 2015 in 5 forest strata: Dry Forest of the Chaco (BSCH), Sub-humid Flooded Forest of the Paraguay River (BSHIRP), Palmar Forest (BP), Sub-humid Forest of the Cerrado (BSHC) and Humid Forest of the Eastern Region (BHRO), totaling 36 ha sampled. Physical and chemical parameters of the soil and data of total height and diameter at 1.30 m in height ($d_{1.30}$) of all living shrub-arboreal individuals with $d_{1.30} \geq 5$ cm were used. For the sampled forest strata, the different soil variables influence the presence of the sampled species. Among soil variables, a strong positive correlation was observed between organic material and organic carbon, as well as silt and clay. In the BSCH, BSHC and BHRO strata, it was possible to attribute relationships between species and edaphic variables, where the edaphic variables that best explained these relationships were clay, sand, silt, organic material and organic carbon.

Keywords: Forest strata; Multivariate analysis; National Forest Inventory of Paraguay.

Resumo

Correlacionar dados de vegetação com variáveis ambientais viabilizam resultados que permitem realizar inferências sobre os componentes biológicos presentes nessas comunidades e assim contribuir para sua recuperação. Neste contexto, objetivou-se neste estudo avaliar se existe correlação entre variáveis do solo, determinar se essas variáveis influenciam na vegetação lenhosa, e quais variáveis explicam melhor essa relação. O estudo foi realizado a partir dos dados obtidos no Inventário Florestal Nacional do Paraguai do ano de 2015 em 5 estratos florestais: Floresta Seca do Chaco (BSCH), Floresta Sub-úmida Inundável do Rio Paraguai (BSHIRP), Floresta de Palmeiras (BP), Floresta Sub-úmida do Cerrado (BSHC) e Floresta Úmida da Região Oriental (BHRO), totalizando 36 ha amostrados. Foram utilizados parâmetros físicos e químicos do solo e dados de altura total e diâmetro a 1,30 m de altura ($d_{1.30}$) de todos os

Financial support: Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES.

Conflict of interest: Nothing to declare.

Corresponding author: lila.gamarra@agr.una.py

Received: 1 March 2022.

Accepted: 18 May 2022.

Editor: Mauro Valdir Schumacher.



This is an Open Access article distributed under the terms of the Creative Commons Attribution license, which permits unrestricted use, distribution, and reproduction in any medium, provided the scientific article is properly cited.

indivíduos arbustivo-arbóreos vivos com $d_{1,30} \geq 5$ cm. Para os estratos florestais, as diferentes variáveis do solo influenciaram a presença das espécies. Entre as variáveis do solo, foi observada uma forte correlação positiva entre material orgânico e carbono orgânico, além de silte e argila. Nos estratos BSCH, BSHC e BHRO foi possível atribuir relações entre espécies e variáveis edáficas, onde as variáveis edáficas que explicaram melhor essas relações foram argila, areia, silte, material orgânico e carbono orgânico.

Palavras-chave: Estratos florestais; Análise multivariada; Inventário Florestal Nacional do Paraguai.

INTRODUCTION

The natural forests of Paraguay have suffered great impacts and reduction of biodiversity during the last decades. According to the Reference Level of Forest Emissions from Deforestation (Paraguay, 2016) reported by Paraguay, the value identified as losses of the total gross forested area of the country for the period 2000-2015 represented 4,994,077.8 hectares, which corresponds to a loss of 18% of forest cover. This pressure has occurred mainly in the western region, due to the rapid expansion of cattle ranching given the promulgation of Law 2.524/04 in the eastern region and extended until 2030 according to Law 6.676/20, which "prohibits the transformation and conversion of areas with forest cover" (Paraguay, 2004, 2020).

This disturbance in this region of the country has transformed an important component of the system: the soil. In addition, water conditions suffer alterations, thus depleting important relationships within these environments and leaving a very small gap of valuable information on their operation, which, according to Ribas et al. (2003) can be used to support the establishment of relevant actions and policies for the use, management, conservation and recovery of the remaining natural environments.

Because forests have a great variation in floristic structure and composition, several parameters can be used for their analysis and relationship with environmental factors, where in addition to other factors such as the physical and chemical composition of the soil and/or topography (Oliveira-Filho et al., 1998; Moreno & Schiavini, 2001; Clark, 2002; Kotchetkoff-Henriques et al., 2005) are considered important in the distribution and structuring of forest formations.

The analysis of the relationship between vegetation and environment, based on quantitative parameters of species abundance, allows detecting the influence of environmental conditions on community structure, and to determine these relationships, even if indirect management methods are used (Ter Braak & Prentice, 1988; McGarigal et al., 2000; Felfili et al., 2007; Kent, 2012; Legendre & Legendre, 2012; Rorato, 2012).

Therefore, correlating this information turns out to be a fundamental matter, as it would allow inferences to be made about the biological components present in these communities and thus contribute to their recovery. In this context, the objective of this study was to evaluate whether there is a correlation between soil variables, to determine whether these variables influence woody vegetation and which variables best explain this relationship.

MATERIAL AND METHODS

Location and characterization of the study areas

The study was based on data obtained from the 2015 National Forest Inventory of Paraguay (IFN) of the Western and Eastern Regions (Figure 1), which were divided into five forest strata: Dry Forest of the Chaco - BSCH (21°34'26.96 "S 60°50'45.97 "W), Sub-humid Flooded Forest of the Paraguay River - BSHIRP (22°40'55.73 "S 58°16'46.46 "W), Palmar Forest - BP (22°55'0.87 "S 58°6'25.58 "W), Sub-humid Forest of the Cerrado - BSHC (22°26'13.96 "S 57°20'2.90 "W) and Humid Forest of the Eastern Region - BHRO (25°3'3.21 "S 55° 39'43.55 "W).

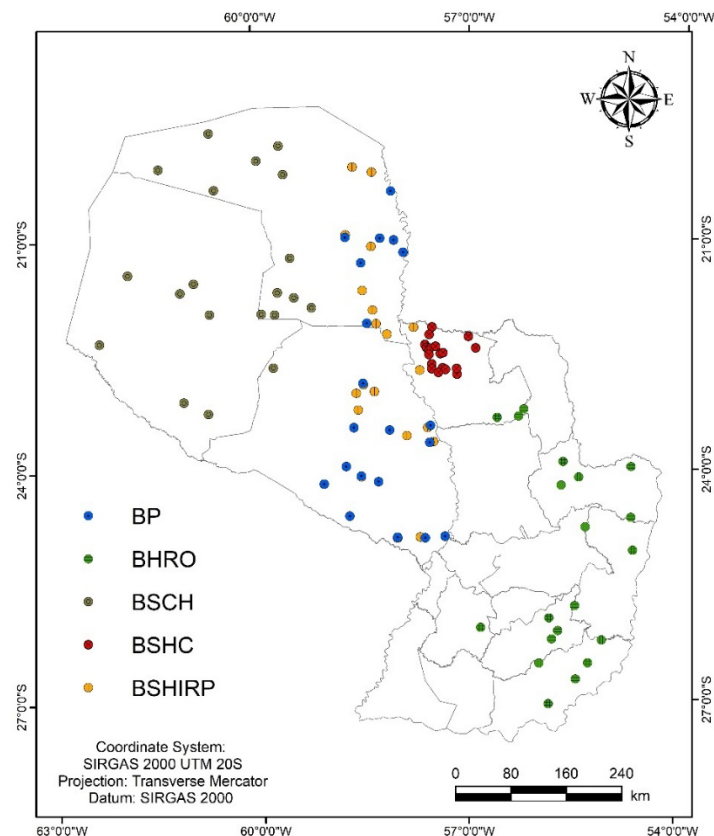


Figure 1: Map of the sampling units (SU) installed in each forest stratum.

The Dry Forest of the Chaco is characterized by small, leafy, deciduous trees with small and/or coriaceous leaves (xeroforms with stems adapted to store water), shrubs with the presence of spines, as described by different authors (Spichiger et al., 1991, 2005; Prado & Gibbs, 1993; Mereles, 2005; Navarro et al., 2011; Pérez, 2016). According to the Köppen's classification, the climate of most of the region is semi-arid/ steppe/warm, belonging to the specific variety "BSh" and the other small portion belongs to the variety "Aw", tropical/savanna. It has a total mean annual precipitation of 700 mm and a mean annual temperature of 20.5 °C (Pastén et al., 2001).

The Sub-humid Flooded Forest of the Paraguay River is characterized by being dominated by few species in the upper canopy, has a dense and sparse understory with the presence of bromeliads and other marginal species, i.e., it tolerates soil flooding for some time (Spichiger et al., 1991, 2005; Mereles, 2005; Navarro et al., 2011; Pérez, 2016). According to Pastén et al. (2001), considering the Köppen's Classification, the climate of half of the region is tropical/savanna, belonging to the specific variety "Aw", and the other half belongs to the variety "Cfa", temperate/no dry season/warm summer. It has a total average annual rainfall of 1200 mm and an average annual temperature of 19 °C.

The Palmar Forest is characterized by the presence of *Copernicia alba* throughout its extension, which is associated with herbaceous and woody plants, preferably in low, flooded and sometimes saline places (Spichiger et al., 1991; Mereles, 2005; Pérez, 2016). In accordance with Köppen's classification, the climate of half of the region is tropical/savanna, belonging to the specific variety "Aw", and the other half belongs to the variety "Cfa", temperate/no dry season/warm summer. It has a total mean annual precipitation of 1250 mm and a mean annual temperature of 20 °C (Pastén et al., 2001).

The Sub-humid Forest of the Cerrado is characterized by small trees, with tortuous branches and hard, thick bark, spaced shrubs and herbs, which according to Spichiger et al. (2005) corresponds to an ecotone area between the cerrados of southern Brazil and the forests of Paraná. According to Pastén et al. (2001), taking into account Köppen's classification,

the climate of the region is temperate without dry season and hot summer, belonging to the specific variety "Cfa". It has a total average annual precipitation of 1500 mm and an average annual temperature of 21°C.

The Humid Forest of the Eastern Region is characterized by its large trees, the tall forests constitute the typical formations of this region, however, the low forests are ecocline formations, in transition strips between the tall forests and the savannahs, riparian forests that penetrate the savannah zones and forest islands surrounded by herbaceous vegetation (Spichiger et al., 1992, 2005). Based on Köppen's classification, it is completely within the temperate climate/no dry season/warm summer, belonging to the specific variety "Cfa". It has a total mean annual precipitation of 1750 mm and a mean annual temperature of 17 °C (Pastén et al., 2001).

Edaphic variables

For each stratum, two soil samples for apparent density and carbon were collected at the SE and NW vertices of each sampling unit, using a 100 cc cylinder, according to the following depths: A (0-5 cm); B (25-30 cm) and C (45-50 cm). Samples from the SE vertex were mixed with those from the NW vertex, generating a composite sample for each depth and for each purpose.

The soil samples were analyzed at the laboratory of the Technological Company of Commerce and Agricultural Services TECSA S.A., in the Department of Itapúa, Paraguay. The soil chemical parameter was organic matter (O.M.) and for the physical and textural parameters were: granule size, % sand (Are), % clay (Arg), % silt (Sil), % apparent density (A.D.); and % organic carbon (O.C.), as indicated in the IFN Field Manual (Food and Agriculture Organization, 2015).

Woody vegetation sampling by stratum

The database used consists of quantitative information from 100 sampling units (SU) of 60 m x 60 m, distributed in the five tree strata (20 SU for each stratum), located throughout Paraguay, which were randomly selected, totaling 36 ha sampled.

Total heights and diameters at 1.30 m height ($d_{1.30}$) were recorded for all living shrub-arboreal individuals with $d_{1.30} \geq 5$ cm, only as an inclusion criteria. The total heights and diameters at 1.30 m ($d_{1.30}$) of all live shrub-tree individuals were recorded only as an inclusion criterion. All individuals were collected and subsequently identified based on literature and specialists as well as in the Herbarium of the Faculty of Chemical Sciences (FCQ), Department of Botany of the National University of Asuncion. Confirmation and updating of scientific names and families was performed according to the Missouri Botanical Garden database (Tropicos, 2021).

Data analysis

Correlation between vegetation data and edaphic data was performed using two matrices, where the first refers to the highest abundances of individuals of each species (>10), and the second refers to edaphic variables, both in the five strata sampled. According to Ter Braak (1987) and Nappo et al. (2000), the selection of species with a higher number of individuals is mainly justified by the fact that less abundant species have little or no influence on the results. The construction of both matrices was performed through a preliminary analysis to make the processing feasible, since, according to Borcard et al. (2011), it must have a smaller number of variables (rows) than the number of sample units (columns) with vegetation data.

First, Pearson correlation analysis was performed between the edaphic and Principal Component Analysis (PCA) variables with the six soil analysis variables for all the sampled plots (20 SU) in each stratum (5) in the three depths (A, B, C), resulting in a matrix with 60 rows (samples) and six columns (soil variables) (Ter Braak & Prentice, 1988). The depth that presented the highest correlation in the analysis (>30%) was chosen (Henderson, 2003).

To determine whether edaphic variables influence the presence of the species, Canonical Correlation Analysis (CCA) was performed, where two matrices were used: a main vegetation matrix, composed of the abundance of the species that presented above 50% of the importance value in the 20 SU of the BSCH, BSHRP, BSHC and BHRO strata, the matrices being composed

of 20 rows (SU) and 18, 12, 10 and seven columns (species), respectively, and for the BP stratum, a single species already accounted for over 80% of the importance value, so a matrix composed of the abundance (>10 individuals) of three species (columns) and a secondary matrix of edaphic variables with 20 rows (SU) and six variables (columns) were used.

These matrices were standardized using the Hellinger transformation, proposed by Legendre & Gallagher (2001) and considering that the rank of the data matrix must be less than the number of rows minus one ($n-1$). Canonical Redundancy Analysis was also performed to evaluate whether there are variables that have a greater influence on individuals (Felfili et al., 2011; Legendre & Legendre, 2012).

R software was used for the analyses (R Core Team, 2013), with the *vegan* (Oksanen et al., 2019), *factoextra* (Kassambara & Mundt, 2017), *ellipse* (Murdoch & Chow, 2018), *ggplot2* (Wickham, 2016), *MASS* (Venables & Ripley, 2002) and *FactoMineR* packages (Lê et al., 2008).

RESULTS AND DISCUSSION

According to the classification of Santos (2007), in the BSCH stratum a low positive correlation between Sil and Arg with O.M. was observed, a fact that also occurs in the BSHIRP, BSHC and BHRO strata, that is, the presence of these variables does not contribute to the increase or decrease of the sampled organic matter (Figure 2), which corroborates the results obtained by other authors, on the relationship between these variables (Rangel et al., 2007; Valladares et al., 2008; Carmo & Silva, 2012).

As for the variables Are and Sil presented a strongly negative correlation in the BSCH and BSHIRP strata, therefore, they present an inverse correlation, which means that the increase in the content of one influences the decrease in the content of the other. In the BP, BSHC and BHRO strata, the variables that presented a strong negative correlation between them were Are and Arg (Figure 2), which supports their opposite characteristics, either physical or chemical.

In all strata, the variable O.C. presented a strongly positive correlation with O.M., i.e., directly proportional, the presence of one contributes in the presence of the other.

For the ACP, considering the three soil depths in all the strata sampled, the lowest and highest values for dimension 1, respectively are 39 and 57.9%, while for dimension 2, they are 22 and 31.4%. Depth A was selected because it showed a higher correlation and had a greater influence on the analysis. Depths B and C showed low correlation (<30%) (Henderson, 2003) and were located near the origin, therefore, they contribute little or almost nothing to the analysis, being the most stable, so they were eliminated from the analysis (Figure 3).

For the canonical correlation analysis (CCA), the vegetation (Y) and edaphic variables (X) matrices for the BSCH, BSHIRP, BP, BSHC and BHRO strata presented the ranks seven and six, 10 and six, three and six, 12 and six, and 18 and six, in addition to accepting that the rank of the matrix must be less than the number of rows minus one, $\max(7.6) \leq 20-1$, $\max(10.6) \leq 20-1$, $\max(3.6) \leq 20-1$, $\max(12.6) \leq 20-1$, $\max(18.6) \leq 20-1$, respectively.

For the BSCH stratum, the variability of edaphic variables explains 44% of the species variability ($R^2 X|Y = 0.44$), while the inverse is weak ($R^2 Y|X = 0.29$), for BSHIRP, 33% ($R^2 X|Y = 0.33$) and ($R^2 Y|X = 0.25$), for BP, 13% ($R^2 X|Y = 0.13$) and ($R^2 Y|X = 0.19$), for BSHC, 71% ($R^2 X|Y = 0.71$) and ($R^2 Y|X = 0.27$) and for BHRO, 99% ($R^2 X|Y = 0.99$) and ($R^2 Y|X = 0.31$). These results corroborate other studies that have demonstrated the existence of distribution patterns associated with edaphic variables (Oliveira-Filho & Fontes, 2000; Espírito Santo et al., 2002; Camargos et al., 2008; Carvalho et al., 2009; Maraschin-Silva et al., 2009; Santos et al., 2012; Abreu, 2003; Martins et al., 2013; Braga et al., 2015; Oliveira et al., 2015).

These results indicate, with the exception of BHRO, that edaphic variables partially explain the floristic-structural variations in the other sampled strata. Nappo et al. (2000) and Machado et al. (2008) state that the remaining variance may occur due to stochasticity of the phenomena of establishment and growth of the species or be associated with unrecorded environmental variables, such as canopy openness, proximity to seed and propagule sources, topographic position, among others. Ter Braak (1987) and Ter Braak & Prentice (1988) state that unexplained disturbances are considered natural and do not compromise the significance of the correlations found.

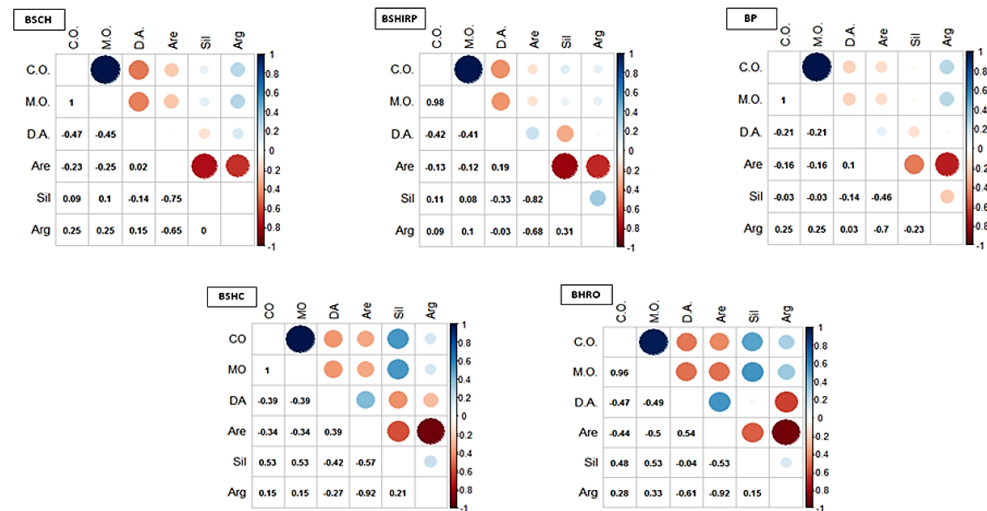


Figure 2: Pearson correlation matrix between the edaphic variables: Organic Carbon (O.C. or C.O.), Organic Material (O.M. or M.O.), Apparent Density (A.D. or D.A.), Sand (Are), Silt (Sil) and Clay (Arg), for 100 plots in the five forest strata of Paraguay (BSCH, Dry Forest of the Chaco; BSHIRP, Sub-humid Flooded Forest of the Paraguay River; BP, Palmar Forest; BSHC, Sub-humid Forest of the Cerrado; BHRO, Humid Forest of the Eastern Region).

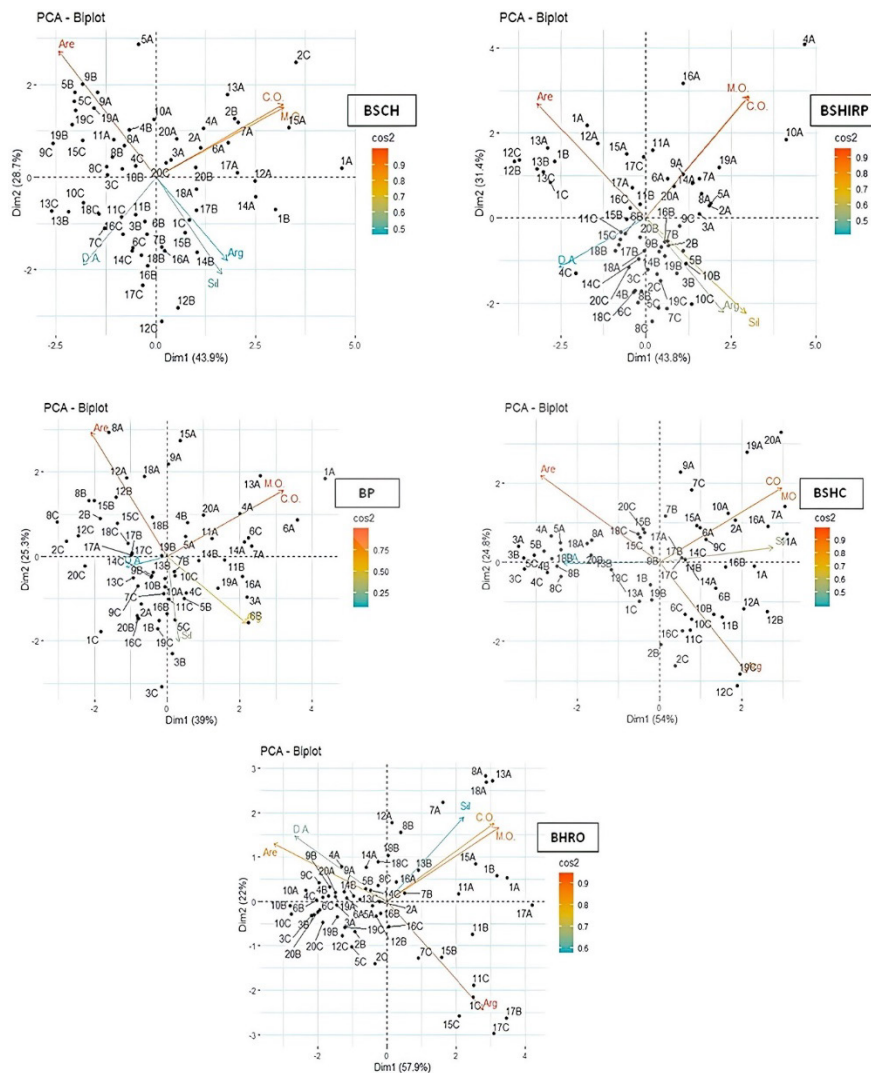


Figure 3: ACP of the three soil depths: A (0-5 cm); B (25-30 cm) and C (45-50 cm), for 100 plots in the five forest strata of Paraguay (BSCH, Dry Forest of the Chaco; BSHIRP, Sub-humid Flooded Forest of the Paraguay River; BP, Palmar Forest; BSHC, Sub-humid Forest of the Cerrado; BHRO, Humid Forest of the Eastern Region).

According to Borcard et al. (2011), the longer the length of a vector, the more influential the analysis, therefore, the species *Tabebuia nodosa* (Griseb.) Griseb. (Tnod), *Ceiba chodatii* (Hassl.) Ravenna (Ccho) and *Schinopsis lorentzii* (Griseb.) Engl. (Slor) and the edaphic variables clay (Arg) and sand (Are) are the most influential in the BSCH stratum. While, for BSHIRP, the species *Parapiptadenia rigida* (Benth.) Brenan (Prig), *Tabebuia nodosa* (Tnod), *Calycophyllum multiflorum* Griseb. (Csmu) and *Lonchocarpus leucanthus* Burkart (Lleu) and the variable apparent density (A.D.) were the most influential (Figure 4).

Similar results were obtained by Spichiger et al. (1991, 2004, 2005), Prado & Gibbs (1993) and Mereles (2005), in which these species were described in association with specific and intermediate edaphic conditions, in which species such as *Tabebuia nodosa* and *Calycophyllum multiflorum*, which, depending on the edaphic substrate, may be present in the "xerohygrophytic", "gallery hygrophytic" or "periodically flooded xerophytic" formation of the BSCH and BSHIRP strata, where soils are rich in clay and salt, highly structured and hard when dry, with low water availability and subject to temporary flooding.

It is difficult to find vegetation types or units whose distribution is absolutely independent of climatic conditions, especially when the level of detail in the delimitation of units is greater (Luebert & Plischoff, 2006). The zonal units of the humid Chaco (BSHIRP) may occur in the dry Chaco (BSCH), being, in this case, extrazonal vegetation units (Spichiger et al., 1991).

In the case of BP, *Tabebuia nodosa* (Tnod) and *Schinopsis balansae* Engl. (Sbal) are the most influential, as are the variables organic matter (O.M.), organic carbon (O.C.) and silt (Sil) (Figure 4). According to Spichiger et al. (1991) and Mereles (2005), they are part of the humid Chaco formation or mesoxerophytic unit, where *Copernicia alba* Morong is the dominant species. They are associated with the latter and are considered characteristic species of this type of forest formation, where the soils are sandy and the climate is arid.

For the BSHC stratum, the species that most influenced are *Cordia americana* (L.) Gottschling & J.S. Mill. (Came), *Myroxylon peruiferum* L. f. (Mper) and *Maclura tinctoria* (L.) D. Don ex G. Don (Mtin), besides the variables sand (Are), clay (Arg) and silt (Sil) (Figure 4). According to Mendoza et al. (2017), soils may or may not present drainage problems and species may be associated with small springs, as well as *Cordia americana*, which is usually present in the upper stratum of riparian forests.

In the BHRO stratum, the species *Machaerium paraguariense* Hassl. (Mpar), *Plinia rivularis* (Cambess.) Rotman (Priv) and *Jacaratia spinosa* (Aubl.) A. DC. (Jspi); and the edaphic variables organic carbon (O.C.), clay (Arg) and silt (Sil) are the most influential for CCA (Figure 4). Spichiger et al. (1992) mentioned that the soils of this type of forest formation are well drained and have a high clay content. Some species of the Myrtaceae family, such as *Plinia rivularis*, usually occur in tall forests with drainage problems (swampy substrates) and are characteristic of ecocline formations (Spichiger et al., 2005).

The species and edaphic variables whose vectors were located closest to the origin were the least influential in the analysis. This suggests that the data were homogeneous. And the closer the dots of the species and edaphic variables are to the sampling units, the more associated they are with them.

For the Canonical Redundancy Analysis (RDA), the coefficient of determination (R^2) and adjusted coefficient of determination (R^2_a) calculated between species with importance values (VI) higher than 50% and edaphic variables for the BSCH, BSHIRP, BP, BSHC and BHRO strata were 0.29 and -0.03; 0.25 and -0.10; 0.19 and -0.19; 0.27 and -0.06 and 0.31 and -0.01, respectively.

In the RDA results there are three entities in the plane: response variables (species - Y), explanatory variables (edaphic variables - X) and local (plots - sit) so they can be called "Triplot". According to Borcard et al. (2011), the cumulative contribution to the variation obtained by the canonical axes is the proportion of the total variance of the response data explained by the RDA.

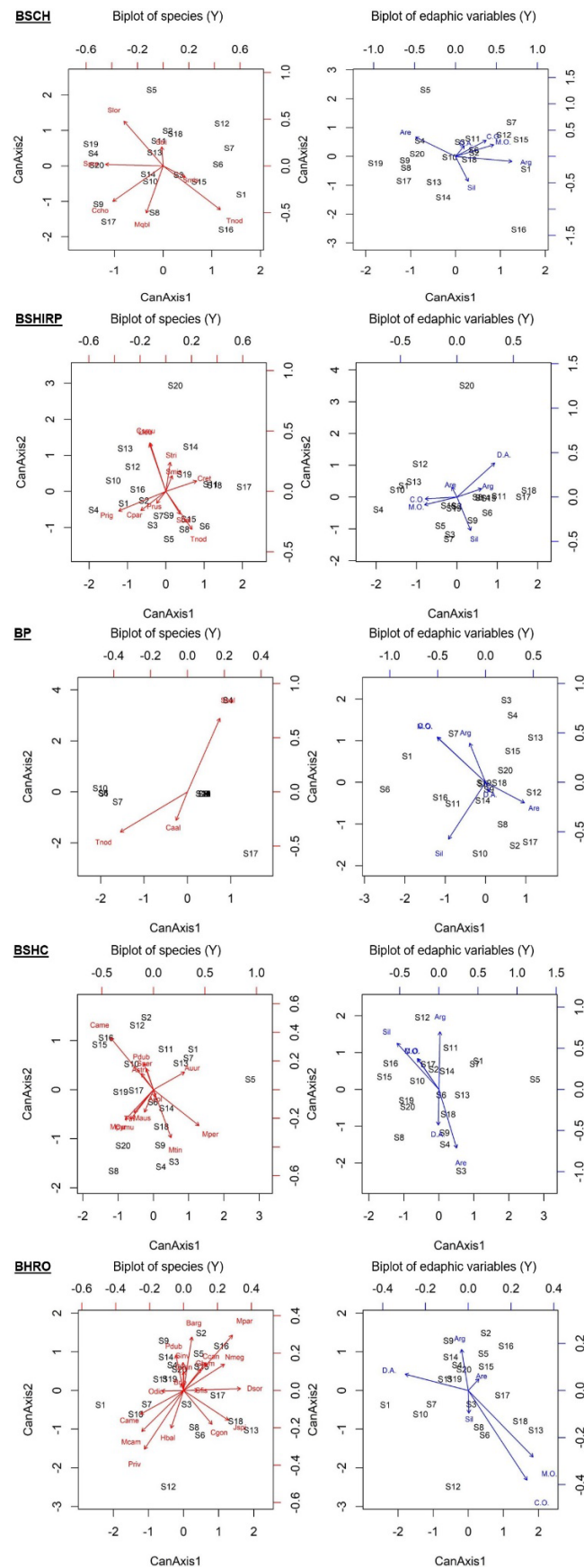


Figure 4: Biplots constructed by CCA of species with more than 50% of importance value (Y) and edaphic variables (X) for 100 plots in the five forest strata of Paraguay (BSCH, Dry Forest of the Chaco; BSHIRP, Sub-humid flooded Forest of the Paraguay river; BP, Palmar Forest; BSHC, Sub-humid Forest of the Cerrado; BHRO, Humid Forest of the Eastern Region).

Ter Braak (1995) explained that the proximity of the species to the arrows representing the edaphic variables results in the magnitude of the correlation between these variables, and the direction of the arrows infers the way in which the correlation occurs (direct or indirect). Species with arrows close to the origin have almost no influence on the analysis, and according to Borcard et al. (2011), species with no correlation with any edaphic variable indicate that they are present in most plots or related to intermediate ecological conditions, i.e., in the serial phase of ecological succession.

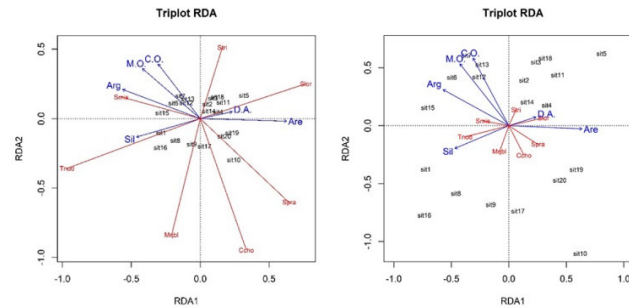
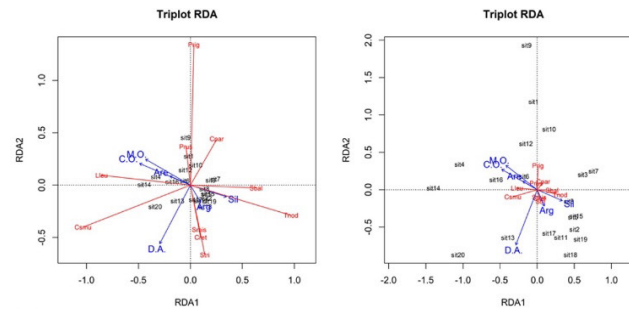
The first three canonical axes for the BSCH stratum explain 25.74% of the total cumulative variance in the weighted mean of the species with more than 50% of the importance value in relation to the edaphic variables analyzed. The restricted proportion of accumulated variance for the first three axes corresponded to 84.42%. Figure 5 shows that the soil variables O.M. and O.C. are very close, representing that they are highly correlated, a fact that also occurs in the BSHIRP, BP, BSHC and BHRO strata, and whose relationship has already been described by other authors (Rangel et al., 2007; Valladares et al., 2008; Carmo & Silva, 2012). *Sarcomphalus mistol* (Griseb.) Hauenschild (Smis) showed correlation with Arg, which could indicate the preference of this species to soils with higher porosity and high water retention. The species *Senegalia praecox* (Griseb.) Seigler & Ebinger (Spra) and *Ceiba chodatii* (Ccho) related to plots 10, 17, 19 and 20 are not characterized by any edaphic variable evaluated in this research, as well as *Aspidosperma quebracho-blanco* Schltdl. (Mqbl).

In the BSHIRP stratum, the first three axes explain the total cumulative variance of 19.48% in the weighted mean of the species in relation to the edaphic variables. The restricted proportion of the cumulative variance was 79.30%. The species *Prosopis ruscifolia* Griseb. (Prus), *Parapiptadenia rigida* (Prig), *Caesalpinia paraguariensis* (D. Parodi) Burkart (Cpar) and *Schinopsis balansae* (Sbal) related to plots 1, 3, 4, 6, 7, 9, 10, 10, 12, 13, 14, 16 and 20 are not correlated with any edaphic variable, as well as *Calycophyllum multiflorum* (Csmu) and *Lonchocarpus leucanthus* (Lleu) (Figure 5).

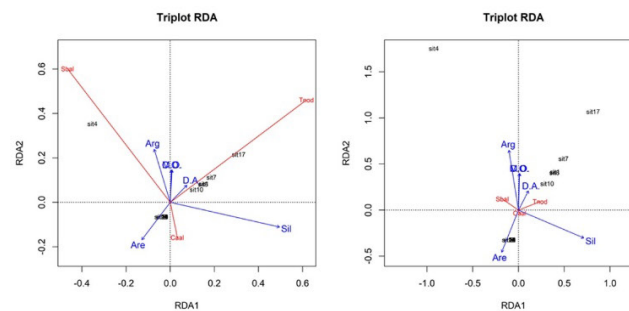
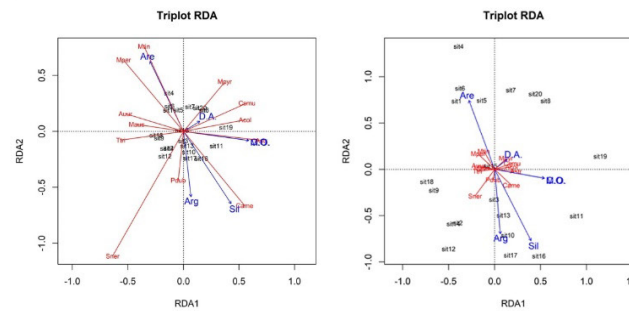
In the case of BP, the first three axes explain 18.57% of the total accumulated variance in the weighted mean of the species in relation to the soil variables. The restricted proportion of the cumulative variance for the first three axes corresponded to 100%. Figure 5 shows that the species *Schinopsis balansae* (Sbal) and *Tabebuia nodosa* (Tnod), related to plots 1, 4, 6, 7, 10 and 17 are not correlated with any soil variable evaluated in this study.

Whereas, for BSHC, the first three canonical axes explain 23.85% of the total cumulative variance in the weighted mean of the species related to the analyzed edaphic variables. The restricted proportion of cumulative variance for the first three axes was 87.21%. The species *Maclura tinctoria* (Mtin) presented correlation with the variable Are, which is an indication of the preference of this species to soils with lower porosity and low water retention. The correlation of the variables O.M. and O.C. with *Astronium* sp. evidences a high nutritional requirement of this species, and the variable Sil with *Cordia americana* could indicate soils with higher water retention, therefore, with lower drainage. The species *Sebastiania nervosa* (Müll. Arg.) Müll. Arg. (Sner), *Terminalia triflora* (Griseb.) Lillo (Ttri), *Macaglia australis* (Müll. Arg.) Kuntze (Maus) and *Astronium urundeuva* (Allemão) Engl. var. *urundeuva* (Aaur) related to plots 1, 2, 4, 5, 5, 6, 9, 12, 14 and 18 do not correlate with any edaphic variable evaluated in this study (Figure 5).

For the BHRO stratum, the first three axes explained 23.47% of the total cumulative variance in the weighted mean of the species in relation to the soil variables. The restricted proportion of accumulated variance for the first three axes corresponded to 75.75%. In Figure 5, it is possible to verify that the soil variables Sil and Arg are very close, representing that they are highly correlated, which evidences certain levels of weathering (Pedroso Neto & Lopes, 2009; Marcatto & Silveira, 2017; Silva et al., 2018) also associated with the species *Cedrela fissilis* Vell. The species *Machaerium paraguariense* (Mpar), *Peltophorum dubium* (Pdub), *Cabralea canjerana* (Vell.) Mart. (Ccan), *Ocotea diospyrifolia* (Meisn.) Mez (Odio), *Diatenopteryx sorbifolia* Radlk. (Dsor), *Nectandra megapotamica* (Spreng.) Mez (Nmeg), related to plots 16, 19 have no correlation with any soil variable, as well as *Muellera campestris* (Mart. ex Benth.) M.J. Silva & A.M.G. Azevedo (Mcam), *Cordia americana* (Came) and *Plinia rivularis* (Priv).

BSCHBSHIRP

BP

BSHC

BHRO

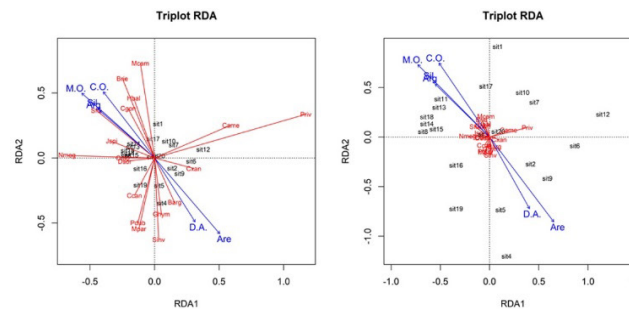


Figure 5: Distance (Scale 1) and correlation (Scale 2) triplots constructed by RDR with the eigenvectors of species with more than 50% of importance value (Y) and edaphic variables (X) after Hellinger transformation, for 100 plots in the five forest strata of Paraguay (BSCH, Dry Forest of the Chaco; BSHIRP, Sub-humid flooded Forest of the Paraguay river; BP, Palmar Forest; BSHC, Sub-humid Forest of the Cerrado; BHRO, Humid Forest of the Eastern Region).

Variance not explained by soil variables ("noise") did not compromise the results, as correlations were significant. Noise can be common in vegetation data and can be explained by variables not included in the analysis, especially in very heterogeneous areas (Ter Braak, 1987). Nappo et al. (2000) and Dalanesi et al. (2004) say that this high remaining variance is expected in community studies, considering the complexity of the factors involved in determining the floristic structure and composition of plant communities.

CONCLUSIONS

The different soil variables influence the presence and behavior of the sampled species. There are visible relationships between edaphic variables. The strong correlation between organic matter and organic carbon, in addition to silt and clay, stands out.

In the BSCH stratum, it was possible to attribute relationships between *Sarcomphalus mistol* and clay; while in the BSHC stratum, *Maclura tinctoria* showed a correlation with sand, *Astronium* sp. with organic material and organic carbon and *Cordia americana* with silt; in the BHRO stratum, *Cedrela fissilis* was correlated with silt and clay. It was not possible to assign relationships between species and edaphic variables in the BSHIRP and BP strata. The edaphic variables that best explained these relationships were clay, sand, silt, organic material and organic carbon.

REFERENCES

- Abreu, K. M. P. (2003). *Estrutura, florística e diversidade de fragmentos de floresta estacional semidecidual no norte-noroeste fluminense* (Tese de doutorado). Universidade Estadual do Norte Fluminense Darcy Ribeiro, Campo dos Goytacazes.
- Borcard, D., Gillet, F., & Legendre, P. (2011). *Numerical ecology with R* (306 p.). New York: Springer.
- Braga, A. J. T., Borges, E. E. L., & Martins, S. V. (2015). Influência dos fatores edáficos na variação florística de Floresta Estacional Semidecidual, em Viçosa, MG. *Revista Árvore*, 39(4), 623-633.
- Camargos, V. L., Silva, A. F., Meira Neto, J. A. A., & Martins, S. V. (2008). Influência de fatores edáficos sobre variações florísticas na Floresta Estacional Semidecidual no entorno da Lagoa Carioca, Parque Estadual do Rio Doce, MG, Brasil. *Acta Botanica Brasílica*, 22(1), 75-84.
- Carmo, D. L., & Silva, C. A. (2012). Métodos de quantificação de carbono e matéria orgânica em resíduos orgânicos. *Revista Brasileira de Ciência do Solo*, 36, 1211-1220.
- Carvalho, J., Marques, M. C. M., Roderjan, C. V., Barddal, M., & Sousa, S. G. A. (2009). Relações entre a distribuição das espécies de diferentes estratos e as características do solo de uma floresta aluvial no Estado do Paraná, Brasil. *Acta Botanica Brasílica*, 23(1), 1-9.
- Clark, D. B. (2002). Los factores edáficos y la distribución de las plantas. In M. R. Guariguata & G. H. Kattan (Eds.), *Ecología y conservación de Bosques Neotropicales* (pp. 193-221). Cartago: Ediciones LUR.
- Dalanesi, P. E., Oliveira-Filho, A. T., & Fontes, M. A. L. (2004). Flora e estrutura do componente arbóreo da floresta do Parque Ecológico Quedas do Rio Bonito, Lavras – MG, e correlações entre distribuição das espécies e variáveis ambientais. *Acta Botanica Brasílica*, 18(4), 737-757.
- Espírito-Santo, F. D. B., Oliveira-Filho, A. T., Machado, E. L. M., Souza, J. S., Fontes, M. A. L., & Marques, J. J. G. S. M. (2002). Variáveis ambientais e a distribuição de espécies arbóreas em um remanescente de Floresta Estacional Semidecidual Montana no Campus da Universidade Federal de Lavras, MG, Brasil. *Acta Botanica Brasílica*, 16(3), 331-356.
- Food and Agriculture Organization - FAO. (2015). *Manual de Campo: Procedimientos para la planificación, medición y registro de información del Inventario Forestal Nacional del Paraguay "Medir para decidir". Programa Nacional Conjunto ONU-REDD*. Asunción, Paraguay: FAO.
- Felfili, J. M., Carvalho, F. A., Libano, A. M., Venturoli, F., Pereira, B. A. S. (2007). *Análise multivariada em estudos de vegetação* (Comunicações Técnicas Florestais, Vol. 9, No. 1). Brasília: Departamento de Engenharia Florestal, Universidade de Brasília.
- Felfili, J. M., Carvalho, F. A., Libano, A. M., Venturoli, F., Pereira, A. S., & Machado, E. L. M. Análise multivariada: princípios e métodos em estudos de vegetação. In J. M. Felfili, P. V. Eisenlohr, M. M. R. F. Melo, L. A. Andrade & J. A. A. Meira Neto (2011). *Fitossociologia no Brasil: métodos e estudos de casos* (Vol. 1, pp. 122-155). Viçosa: Universidade Federal de Viçosa.
- Henderson, P. A. (2003). *Practical methods in ecology* (174 p.). London: Blackwell.

- Kassambara, A., & Mundt, F. (2017). *factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.5*. Vienna: R Foundation for Statistical Computing. Retrieved in 2022, March 1, from <https://CRAN.R-project.org/package=factoextra>
- Kent, M. (2012). *Vegetation description and analysis: a practical approach* (2nd ed., 438 p.). London: John Wiley & Sons.
- Kotchetkoff-Henriques, O., Joly, C. A., & Bernacci, L. C. (2005). Relação entre o Solo e a Composição Florística de Remanescentes de Vegetação Natural no Município de Ribeirão Preto, SP. *Revista Brasileira de Botânica*, 28(3), 541-562.
- Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: a package for multivariate analysis. *Journal of Statistical Software*, 25(1), 1-18. <http://dx.doi.org/10.18637/jss.v025.i01>.
- Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129, 271-280.
- Legendre, P., & Legendre, L. (2012). *Numerical ecology* (3rd ed., 990 p.). Amsterdam: Elsevier.
- Luebert, F., & Pliscoff, P. (2006). *Sinopsis bioclimática y vegetal de Chile: biodiversidad* (323 p.). Santiago de Chile: Editorial Universitaria
- Machado, E. L. M., Oliveira-Filho, A. T., Van Den Berg, E., Carvalho, W. A. C., Souza, J. S., Marques, J. J. G. S. M., & Calegário, N. (2008). Efeitos do substrato, bordas e proximidade espacial na estrutura da comunidade arbórea de um fragmento florestal em Lavras, MG. *Revista Brasileira de Botânica*, 32(2), 287-302.
- Maraschin-Silva, F., Scherer, A., & Baptista, L. R. M. (2009). Diversidade e estrutura do componente herbáceo-subarbustivo em vegetação secundária de Floresta Atlântica no sul do Brasil. *Revista Brasileira de Biociências*, 7(1), 53-65.
- Marcatto, F. S., & Silveira, H. (2017). Relação entre as propriedades físicas e hídricas e os tipos de uso da terra em Neossolos Regolíticos da bacia hidrográfica do rio Pirapó-PR. *Caderno de Geografia*, 27(50), 427-440.
- Martins, R., Jarenkow, J. A., Giehl, E. L. H., Citadini-Zanette, V., & Santos, R. (2013). Estrutura de uma floresta brejosa em substrato turfoso, sul de Santa Catarina, Brasil. *Revista Árvore*, 37(2), 299-309.
- McGarigal, K., Cushman, S., & Stafford, S. (2000). *Multivariate statistics for wildlife and ecology research* (283 p.). New York: Springer Science and Business Media.
- Mendoza, C. R., Jiménez, M. V., & Arrúa, R. D. (2017). Plantas nativas del Cerrado de Aguará Nú, Reserva Natural del Bosque Mbarakayú, Paraguay. *Rojasiana*, (3), 1-244.
- Mereles, M. F. (2005). Una aproximación al conocimiento de las formaciones vegetales del Chaco Boreal, Paraguay. *Rojasiana*, 6(2), 5-48.
- Moreno, M. I. C., & Schiavini, I. (2001). Relação entre vegetação solo em um gradiente florestal na Estação Ecológica do Panga, Uberlândia (MG). *Revista Brasil. Bot.*, 24(4), 537-544.
- Murdoch, D., & Chow, E. D. (2018). *ellipse: functions for drawing ellipses and ellipse-like confidence regions. R package version 0.4.1*. Vienna: R Foundation for Statistical Computing. Retrieved in 2022, March 1, from <https://CRAN.R-project.org/package=ellipse>
- Nappo, M. E., Oliveira-Filho, A. T., & Martins, S. V. (2000). A estrutura do sub-bosque de povoamentos homogêneos de *Mimosa scabrella* Benth, em área minerada, em Poços de Caldas, MG. *Ciência Florestal*, 10(2), 17-29.
- Navarro, G., Molina, J. A., & Vega, S. (2011). Soil factors determining the change in forests between dry and wet Chacos. *Flora*, 206, 136-143.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'hara, B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *vegan: Community Ecology Package. R package version 2.5-4*. Vienna: R Foundation for Statistical Computing. Retrieved in 2022, March 1, from <https://CRAN.R-project.org/package=vegan>
- Oliveira, M. L. A. A., Grings, M., Richter, F. S., & Backes, A. R. (2015). Composição, estrutura e fatores edáficos condicionantes da distribuição das espécies do componente arbóreo em Floresta ribeirinha do rio Ibirapuitã, Bioma Pampa. *Iheringia. Série Botânica*, 70(2), 245-263.
- Oliveira-Filho, A. T., & Fontes, M. A. L. (2000). Patterns of Floristic differentiation among Atlantic Forests in southeastern Brazil and the influence of climate. *Biotropica*, 32(4B), 793-810.
- Oliveira-Filho, A. T., Curi, N., Vilela, E. A., & Carvalho, D. A. (1998). Effects of canopy gaps, topography and soils on the distribution of woody species in a Central Brazilian deciduous dry forest. *Biotropica*, 30, 362-375.

- Paraguay. (2004). Ley nº 2.524, de 11 de diciembre de 2004. Que prohíbe las actividades de transformación y conversión de superficies con cobertura de bosques en la Región Oriental. *Biblioteca y Archivo Central del Congreso de la Nación*, Asunción.
- Paraguay. (2020). Ley nº 6.676, de 13 de diciembre de 2020. Que amplía la Ley 2.524/04 "Que prohíbe las actividades de transformación y conversión de superficies con cobertura de bosques en la Región Oriental". *Biblioteca y Archivo Central del Congreso de la Nación*, Asunción.
- Paraguay. Programa Nacional Conjunto – PNC. Organización de las Naciones Unidas para la REDD+ – ONU REDD+. Secretaría del Ambiente – SEAM. Instituto Forestal Nacional – INFONA. Federación por la Autodeterminación de los Pueblos Indígenas – FAPI. (2016). *Nivel de Referencia de las Emisiones Forestales por Deforestación en la República del Paraguay para pago por resultados REDD+ bajo la CMNUCC*. Asunción: FAO/PNUD/PNUMA, 76 p.
- Pastén, M., González, A. V., & Espínola, C. F. (2001). *Clasificación climática del Paraguay utilizando los métodos de Köppen y Thornthwaite* (43p.). San Lorenzo: Universidad Nacional de Asunción. Facultad Politécnica. Informe final.
- Pedroso Neto, J. C., Lopes, E. W. (2009). Caracterização física do Latossolo vermelho distrófico da Fazenda Escola da FAZU. *FAZU em Revista*, (6), 11-52.
- Pérez, L. F. (2016). *Manual de familias y géneros de árboles del Paraguay* (216 p.). San Lorenzo: Organización de las Naciones Unidas para la Alimentación y la Agricultura
- Prado, D., & Gibbs, P. (1993). Patterns of distributions in the Dry Seasonal Forests of South America. *Annals of the Missouri Botanical Garden*, 80(4), 902-927.
- R Core Team (2013). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Retrieved in 2022, March 1, from <http://www.R-project.org/>
- Rangel, O. J. P., Silva, C. A., & Guimarães, P. T. G. (2007). Estoque e frações da matéria orgânica de Latossolo cultivado com cafeeiro em diferentes espaçamentos de plantio. *Revista Brasileira de Ciência do Solo*, 31, 1341-1353.
- Ribas, F. R., Meira Neto, J. U. A., Silva, A. F., & Souza, A. L. (2003). Composição florística de dois trechos em diferentes etapas gerais de uma floresta estacional semidecidual em Viçosa, Minas Gerais. *Revista Árvore*, 27, 821-830.
- Rorato, D. G. (2012). *Fitossociologia de espécies nativas de mata ciliar no entorno do Reservatório Divisa, São Francisco de Paula, RS* (Dissertação de mestrado). Programa de Pós-graduação em Engenharia Florestal, Centro de Ciências Rurais, Universidade Federal de Santa Maria, Santa Maria.
- Santos, C. (2007). *Estatística descritiva: manual de autoaprendizagem*. Lisboa: Lisb Ed.
- Santos, R. M., Oliveira-Filho, A. T., Eisenlohr, P. V., Queiroz, L. P., Cardoso, D. B. O. S., & Rodal, M. J. N. (2012). Identity and relationships of the Arboreal Caatinga among other floristic units of seasonally dry tropical forests (SDTFs) of north-eastern and Central Brazil. *Ecology and Evolution*, 2(2), 409-428.
- Silva, W. T. M., Alves, F. J. B., Leonardo, F. A. P., Santos, R. V., & Farias Junior, J. A. (2018). Levantamento da textura do solo e da relação silte/argila em regiões semiáridas do Nordeste. *Agropecuária Científica no Semiárido*, 414(4), 266-272.
- Spichiger, R., Bertoni, B. S., & Loizeau, P. A. (1992). Los bosques del Alto Paraná en Paraguay. *Candollea*, 47, 219-250.
- Spichiger, R., Calenge, C., & Bise, B. (2004). Geographical zonation in the Neotropics of tree species characteristic of the Paraguay-Parana. *Journal of Biogeography*, 31, 1489-1501.
- Spichiger, R., Calenge, C., & Bise, B. (2005). Discriminant analysis of the spatial distribution of plant species occurrences: II. Distribution of major tree communities in Paraguay. *Candollea*, 60(2), 577-593.
- Spichiger, R., Ramella, L., Palese, L., & Mereles, F. (1991). Proposición de leyenda para la cartografía de las formaciones vegetales del Chaco Paraguayo: contribución al estudio de la flora y de la vegetación del Chaco. III. *Candollea*, 46, 541-564.
- Ter Braak, C. J. F. (1987). The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetation*, 69, 69-77.
- Ter Braak, C. J. F. (1995). Ordination. In R. H. G. Jongman, C. J. F. Ter Braak & O. F. R. Van Tongeren (Eds.), *Data analysis in community and landscape ecology* (pp. 91-173). Cambridge: Cambridge University Press.
- Ter Braak, C. J. F., & Prentice, I. C. (1988). A theory of gradient analysis. *Advances in Ecological Research*, 18, 271-317.
- Tropicos. Missouri Botanical Garden. (2021). Retrieved in 2022, March 1, from <https://www.tropicos.org/home>

- Valladares, G. S., Pereira, M. G., Dos Anjos, L. H. C., & Ebeling, A. G. (2008). Caracterização de solos brasileiros com elevados teores de material orgânico. *Magistra*, 20(1), 95-104.
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). New York: Springer. Retrieved in 2022, March 1, from <https://www.stats.ox.ac.uk/pub/MASS4>
- Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag. Retrieved in 2022, March 1, from <https://ggplot2.org>

Authors' contributions: LMGRD: conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, supervision, validation, visualization, writing - original draft, writing - review & editing; LHOS and JPSM: conceptualization, data curation, formal analysis, software, supervision, writing - review & editing; LFPM: formal analysis, investigation, supervision, validation, visualization, writing - review & editing; CS, SLLM, CRS: formal analysis, supervision, validation, visualization; MLQF: formal analysis, supervision, validation, visualization, writing - review & editing; SPCC: data curation, formal analysis, resources, supervision, validation, visualization, project administration.