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Species representativeness of Fabaceae in restrictive soils explains the difference in structure of two types of Chaco vegetation

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ABSTRACT

The distributions of species of Fabaceae are strongly related to the soil. Their presence can alter restrictive conditions and favour the establishment of other species. However, it is still not known how the relationship between species of Fabaceae and edaphic factors interact in structuring woody Chaco vegetation. In this context, we aimed to test the hypothesis that restrictive edaphic conditions can explain the difference in floristic patterns of two types of vegetation through their species representativeness of Fabaceae. We analysed floristic consistency between wooded and forested Chaco to address how spatial and environment components might explain differences between them along with the effects of the interaction between Fabaceae and the soil. We observed that the association between environmental and spatial variables was more important than any individual factor in explaining the structuring of the communities. Both the percentage of species of Fabaceae present and the soil influence the structure of the two types of vegetation. Species of Fabaceae have greater potential as indicators in the wooded Chaco. Therefore, we suggest the interaction between soil types and species of Fabaceae plays a role during the structuring of the communities through the establishment of these species in more restrictive soils.

Keywords: Chaco vegetation, ecological success, environmental filtering, edaphic gradient Leguminosae, environmental seasonality, structural patterns

Introduction

The processes that determine species distribution are central to understand communities (Benkman 2013; McPeek 2017). Historically, the patterns observed have been associated with the mechanisms of niche theory (Hutchinson 1959) and neutral theory (Hubbell 2001). The niche theory predicts that communities are structured by deterministic processes (*e.g.* competition and environmental filtering), while the neutral theory, by stochastic processes (*e.g.* dispersion limitation). The consensus has been reached that these mechanisms work together, and the distribution patterns can be explained by environmental factors (John *et al*. 2007; Brunbjerg *et al*. 2012; Neves *et al*. 2017), by spatial stochastic mechanisms (Cottenie 2005; Wang *et al*. 2008) or by the interaction between them (Legendre *et al*. 2009; Neves *et al*. 2015; Bueno *et al*. 2017). The explanation of each process can vary substantially due to other factors such as species richness and primary productivity (Wang *et al*. 2016; Perry *et al*. 2017). Thus, stochastic mechanisms tend to be

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better fitted for tropical forests; while environmental filters for temperate forests (Myers *et al*. 2013). Moreover, niche processes are more evident on larger scales, and neutral processes on smaller scales (Chase 2014). The scale effect may change depending on the used variable. For example, at broader scales, species distribution may be related to soil types (Tuomisto *et al*. 1995). At smaller scales, on the same soil type, the patterns might be related to the variation of nutrients concentration (Young & Leon 1989; Poulsen & Baslev 1991). The distribution of species on a local scale (<1 km) was explained on several reports through the availability of resources below ground (John *et al*. 2007; Baldeck *et al*. 2013; Maia *et al*. 2019). This finding is important to understand niche mechanisms related to the interaction between species, such as the facilitation effect.

Some species play a key role in the maintenance of distribution patterns and on functioning of the ecosystem (Beierkuhnlein & Jentsch 2005; Hooper *et al*. 2005). For example, foundation species are able to establish themselves in restrictive environments (Ellison *et al*. 2005) and engineer species create locally stable conditions for the establishment of other species (Jones *et al*. 1994; Morrison 2009). Among plants, Fabaceae is recognized as an important group for the productivity and stability of the ecosystem (Spehn *et al*. 2002; Temperton *et al*. 2007; Marquard *et al*. 2009). Adaptations to weathered soils facilitate their establishment in restrictive environments (Crews 1999). They are, for example, more efficient in obtaining potassium, calcium and magnesium (McLean *et al*. 1956), and more tolerant to aluminium (Blamey *et al*. 1992; Yang & Goulart 2000) due to their higher cation exchange capacity (CEC) when compared to other species (Silva *et al*. 2010). Moreover, due to their ability to fix nitrogen through nodulation, Fabaceae assists the establishment of other species (Sprent 2007; Meira-Neto *et al*. 2017). The contribution of this family to the availability of nutrients, absorption and growth of neighbouring species is indeed well described throughout the scientific literature (*e.g.* Spehn *et al*. 2002; Marquard *et al*. 2009; Küchenmeister *et al*. 2012; Roscher *et al*. 2012). Furthermore, nitrogen fixation in the environment occurs more frequently in soils with nitrogen restriction (Sylvester-Bradley *et al*. 1980; Martinelli *et al*. 1999), and the facilitating effect of Fabaceae is more pronounced in situations of extreme climate (Khan *et al*. 2014).

Fabaceae is one of the botanical families with the largest number of species in the world (Lewis 2005; Chase *et al*. 2016) and are usually associated with seasonally dry or arid climate regions (Lavin *et al*. 2004; Pennington *et al*. 2004). For this reason, the family is quite diverse in the Neotropics, mainly in the South America Dry Diagonal Zone (Gentry 1995; Lima *et al*. 2015). This zone presents extreme seasonal climate changes, and water restriction during part of the year. It also includes different plant domains such as Cerrado, Caatinga and Chaco (Neves *et al*. 2015). Species of Fabaceae were identified as key indicator species to differentiate these vegetation types (Lima *et al*. 2017). The highest rates of diversity and endemism in Fabaceae assemblages are found in Chaco (Lima *et al*. 2015), which is distinguished from other regions by its harsher climatic seasonality (Pennington *et al*. 2000). The term Chaco or "Gran Chaco" is used to describe vegetation that covers the vast plains of north-central Argentina, southeastern Bolivia, western Paraguay and a small portion in western Brazil (Prado *et al*. 1992; Prado 1993). In the Chaco region, Fabaceae is the most representative family in the wooded stratum, and some of its species can help the recognition of different types of vegetation (for example, *Prosopis rubriflora* in wooded Chaco – Sartori 2012 and *Mimosa hexandra* in forested Chaco – Baptista *et al*. 2017). Some species are monodominant in environments where soil fertility is a restrictive factor (for example, *Parkinsonia praecox* – Baptista *et al*. 2016). However, it is not clear how the differences in the edaphic component in the environment can cause changes in the assemblage of species of Fabaceae, which could have effects on the entire community.

In landscape-scale, the topography and soil moisture are important factors that determine the distribution of woody species in the Gran Chaco, mainly in the eastern portion of the region (Barberis *et al*. 2005). In a local scale, edaphic and floristic differences shape Chaco's diversity patterns; there are, however, indications that environmental filters may act as structuring processes of these communities (Assunção 2016). According to the literature, species of Fabaceae can be grouped according to the different types of soils on which they grow (Dludlu *et al*. 2017). Thus, it is possible to identify assemblages whose occurrence indicates the soil's predominant conditions in a specific habitat (Siddig *et al*. 2016). However, due to Fabaceae's adaptations to restrictive environments, it is possible that its assemblages are not restricted by the soil, as with other species. In addition, there is a scarcity of studies including the edaphic component. Thus, it is still unknown if the soil leads the distribution of Fabaceae in the Chaco (Mazzarino *et al*. 1991; Alvarez & Lavado 1998; Bueno *et al*. 2017). With the increasing advance in agriculture and the absence of conservation units, Chaco is one of the most threatened vegetation types in Brazil (Silva *et al*. 2009). Understanding the relationships between Fabaceae and edaphic characteristics is crucial to explain its high rate of endemism (Prado & Gibbs 1993; Lima *et al*. 2015) and the high species richness (Nunes 2006; Alves & Sartori 2009). Besides, understanding the floristic patterns of Chaco communities might shed some light on the functioning of not only the different ecological processes acting in this environment, but its association with neotropical dry vegetation species at different scales and how it is structured (Webb *et al*. 2002).

Here, we evaluated the influence of edaphic component and Fabaceae assemblages on the floristic patterns of Chaco communities. More specifically, our objectives were i) to evaluate the floristic consistency of the wooded and forested Chaco; ii) to quantify the explained variation of the environmental and spatial variables combined; iii) to evaluate the importance of Fabaceae assemblages in each community and iv) to identify potential indicator species for vegetation types. We hypothesized that there are two types of consistent vegetation, differentiated by spatial and environmental factors and that a fraction of the spatial components would be explained by the percentage of Fabaceae presence, especially in environments whose soil is a restrictive factor. In this way, we expected to identify species of Fabaceae as more related to the wooded Chaco. Considering the importance of environmental variables and spatially structured ecological factors on the distribution of woody species, this study will contribute to understanding Chaco ecology and the role of species of Fabaceae on seasonal environment communities.

Materials and methods

Study area

The 800,000 km^2 phytogeographical domain of the Chaco covers Argentina, Bolivia, Paraguay and Brazil (Hueck 1972), and can be divided into dry (500 to 700 mm) and wet (over 1200 mm) sectors, according to its average annual precipitation (Brasil 1982). The studied area is located in the wet sector, and has an Aw type climate classification (Alvares *et al*. 2013), *i.e.* rainy summers and dry winters. In Brazil, it is divided into four vegetation types (forested, wooded, woody park and grassy–woody) according to its vegetation stature, floristic composition and soil characteristics (IBGE 2012). We focused on wooded and forested Chaco at Porto Murtinho, Mato Grosso do Sul, Brazil (Figs. 1, 2) since they are non–monodominant vegetation types and are highly threatened environments (Silva *et al*. 2009).

Wooded Chaco is described as a thorny forest, as the plants are predominantly spinescent. Its 3–15 m high trees, usually without canopies, form the higher shrub–arboreal stratum. The continuous and representative grassy–woody species, such as cacti and bromeliads, form dense agglomerates that compose the lower stratum (Fig. 2A-B) (UNESCO 1973).

On the other hand, forested Chaco is classified as a montane tropical or subtropical semi–deciduous forest with 20 m high trees, vines, and thickened shrubs, whose trunks are highly branched, spiny, or aculeate (UNESCO 1973). Succulent species occur in the sub–forest while discontinuous grassy–shrub species with a small proportion of herbaceous vegetation and xerophyte epiphytes are usually found in the lower stratum (Fig. 2C-D). Forested Chaco soils have eutrophic characteristics and a representative litter; thus, its soil is usually more fertile, presenting higher nutrient concentration than wooded Chaco soils (Nunes 2006).

Data sampling

We selected an area from the wooded Chaco and another from the forested Chaco. In each vegetation type, we randomized 50 land plots (10 x 20 m). We sampled all woody individuals with ≥ 1 m height and ≥ 3 cm trunk diameter at ground level. All botanical material was incorporated into the Jardim Botânico do Rio de Janeiro and the Universidade Federal do Mato Grosso do Sul herbaria. In each land plot, we randomly collected one soil sample at 20 cm depth. The soil analysis was carried out at the Laboratorio de Fertilidade do Solo of the Universidade Federal de São Carlos – Araras *campus*, São Paulo. The analyses included the measurements of pH, potential acidity (H + Al), cation exchange capacity (CEC) and sum of bases (SB), organic matter content (OM), base saturation (V %), macro– (Mg, Na, K, and P) and micronutrient (Al, Mn, Fe, Cu, Zn, S, B) contents. The procedures for soil analysis followed Classen (1997).

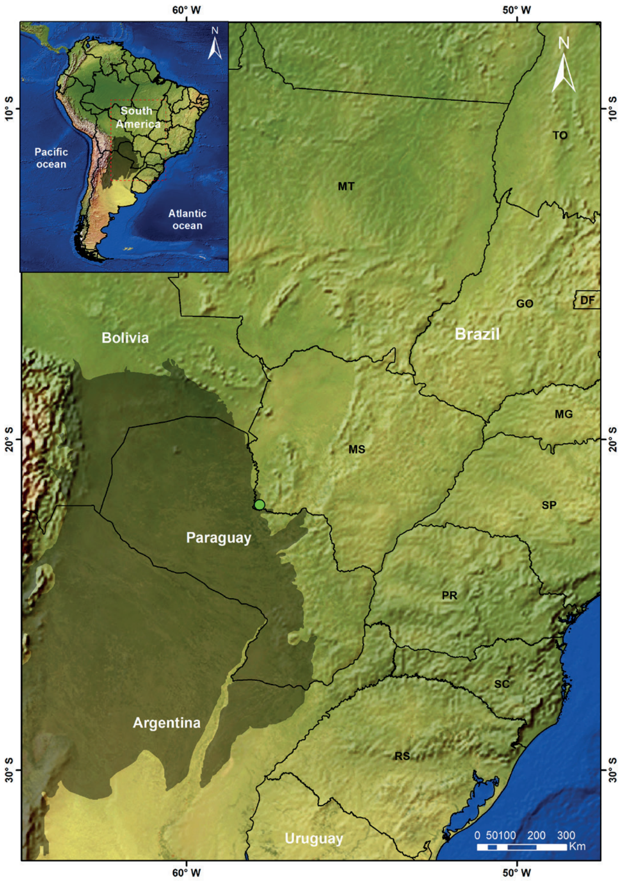

Figure 1. Geographic distribution of the study area in the boundaries of Porto Murtinho, Mato Grosso do Sul, Brazil, evidenced by a green circle. The black shaded area represents the Chaco domain and its distribution in South America. Abbreviations correspond to Brazilian states: DF – Distrito Federal, GO – Goiás, MG – Minas Gerais, MS – Mato Grosso do Sul, MT – Mato Grosso, PR – Paraná, RS – Rio Grande do Sul, SC – Santa Catarina, SP – São Paulo, TO – Tocantins. Chaco boundary is based on ecoregion boundaries (.shp) of Olson *et al*. (2001).

Floristic consistency patterns

In order to analyze the differences between plots and among vegetation types in terms of species composition, we employed NMDS (Non-metric multidimensional scaling) multivariate analysis with three dimensions (k = 3) (McCune & Grace 2002), and utilized the Bray Curtis coefficient as a measure of similarity, in the '*vegan*' package (Oksanen et al. 2016) of R statistical environment program (R Development Core Team 2017). Then we used permutational multivariate analysis of variance (PERMANOVA, 9999 permutations) to determine differences in species composition by using the '*adonis*' routine in the package '*vegan*'.

Variation partitioning

We investigated the relationships between species distribution and environmental variables through redundancy analysis (RDA) (Dray *et al*. 2012; Legendre & Legendre 2012). In order to perform it, we used the packages '*spacemakeR*' (Dray 2010), '*packfor*' (Dray *et al*. 2009), '*vegan*' (Oksanen *et al*. 2016) and '*spdep*' (Bivand 2013). Initially, singleton species were excluded (Lepš & Šmilauer 2003), and Hellinger transformation was applied to the presence/absence data. We then standardized the environmental variables by adjusting them to the standard deviation (Legendre & Gallagher 2001), and excluded the collinear variables to maintain only those with a variance inflation factor (VIF) greater than ten (Quinn & Keough 2002). Finally, we used successive RDAs to select the environmental and spatial variables while checking if the respective global models were significant (Blanchet *et al*. 2008).

To select the spatial variables, we used the best Moran eigenvector maps (MEMs) based on the algorithm that kept the subset of spatial variables with the highest adjustment - Adjusted R^2 (Borcard *et al*. 2011; Legendre & Legendre 2012). MEMs are useful as they represent the spatial structure of the sampling units at multiple spatial scales without considering environmental variation (Borcard *et al*. 1992; Legendre *et al*. 2002; Borcard *et al*. 2004). We then divided the variance by separating the environmental effect from the spatial effect, and from the shared fraction between

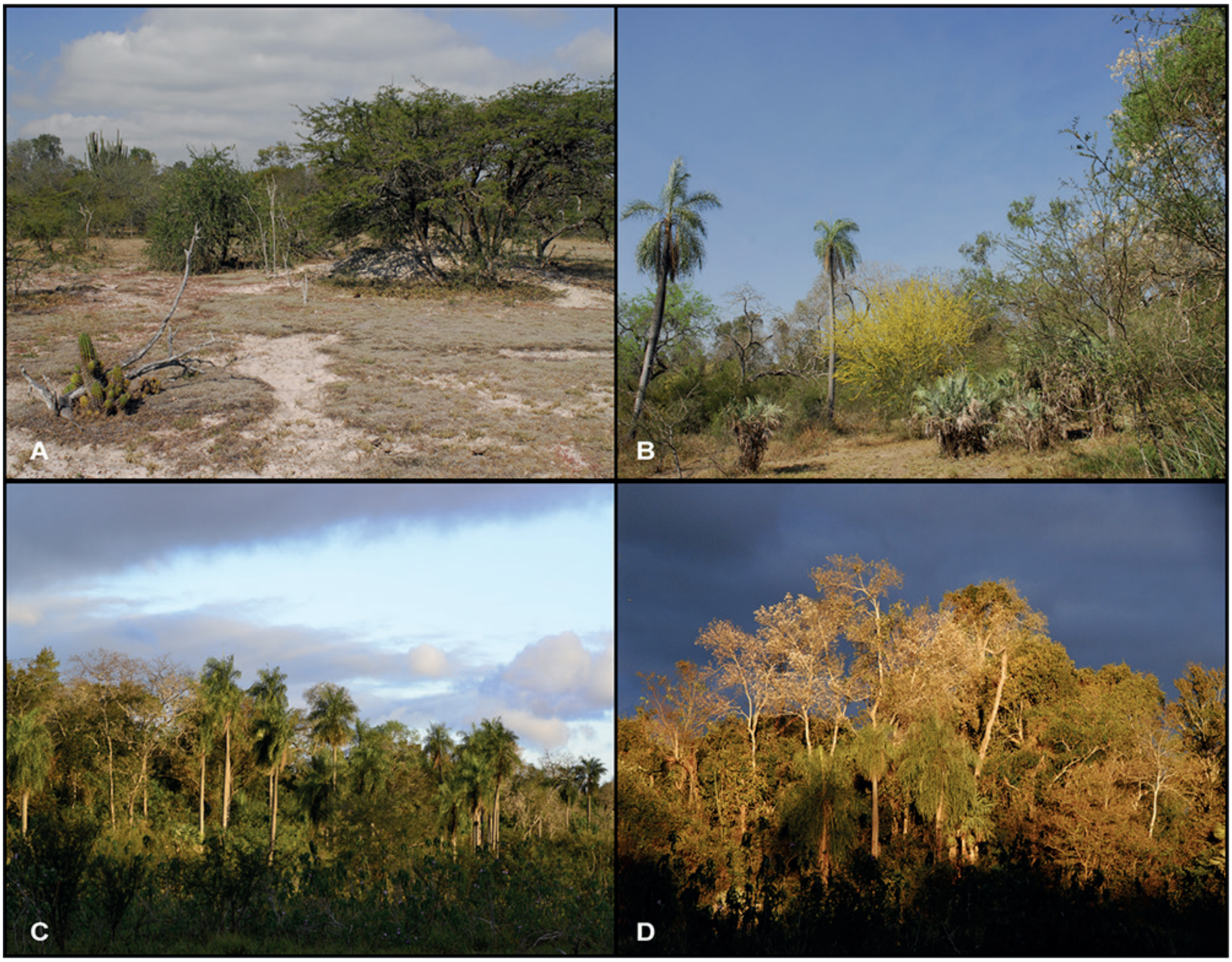

Figure 2. Vegetation types of the Chaco samples at Porto Murtinho, Mato Grosso do Sul, Brazil. **A** and **B** wooded Chaco; **C** and **D** forested Chaco. Photo: Paulo Robson de Souza.

them. Each 'pure' fraction was tested by ANOVA based on permutation (Peres-Neto *et al*. 2006). For this purpose, a test available in the analysis of partial redundancy (partial RDA) was associated to the species composition. Finally, we obtained the standardized coefficients for each selected variable. This procedure was performed in communities containing all species and Fabaceae communities separately.

Fabaceae-soil effect

To verify the representativeness of Fabaceae in vegetation types we evaluated the difference in Fabaceae richness between wooded and forested Chaco and the percentage of presence of species of Fabaceae in the land plots. To classify the soil of each vegetation type, we used soil fertility analysis based on two main criteria: base saturation higher than 50 % (eutrophic) and base saturation lower than 50 % (dystrophic). To verify whether the Fabaceae percentage presence and the base saturation influence the studied Chaco phytophysiognomies, generalized linear mixed models (GLM Mixed) were performed. In these models, the phytophysiognomy was used as a random variable to avoid effects of spatial autocorrelation between the results. For this analysis, we verified the data distribution type by means of the '*Ftdistrplus*' package (Delignette-Muller & Dutang 2015). The family used for richness analysis was binomial.

Indicator species

Finally, an analysis of indicator species provided a set of species that were significantly associated with the vegetation types. It yielded an indicator value (IV), where a higher IV percentage leads to a greater affinity to a given species within a given vegetation type. We considered as indicator species those with IV greater than 10. This analysis was performed using the package '*labdsv*' (Roberts 2016), based on the method proposed by Dufrêne & Legendre (1997). All analysis was performed using R statistical environment (R Development Core Team 2017).

Results

Floristic consistency patterns

We observed a consistent vegetation distribution pattern along the edaphic gradient. NMDS results showed a floristic differentiation between forested and wooded Chaco (Fig. 3A). This pattern remained when Fabaceae assemblages were evaluated separately (Fig 3B). In the NMDS axis ordination, the first axis shows the distinction between vegetation types associated with copper, pH, boron, sulphur and aluminium for all community, and copper and pH for the Fabaceae assemblage only. There was a small overlap along the first

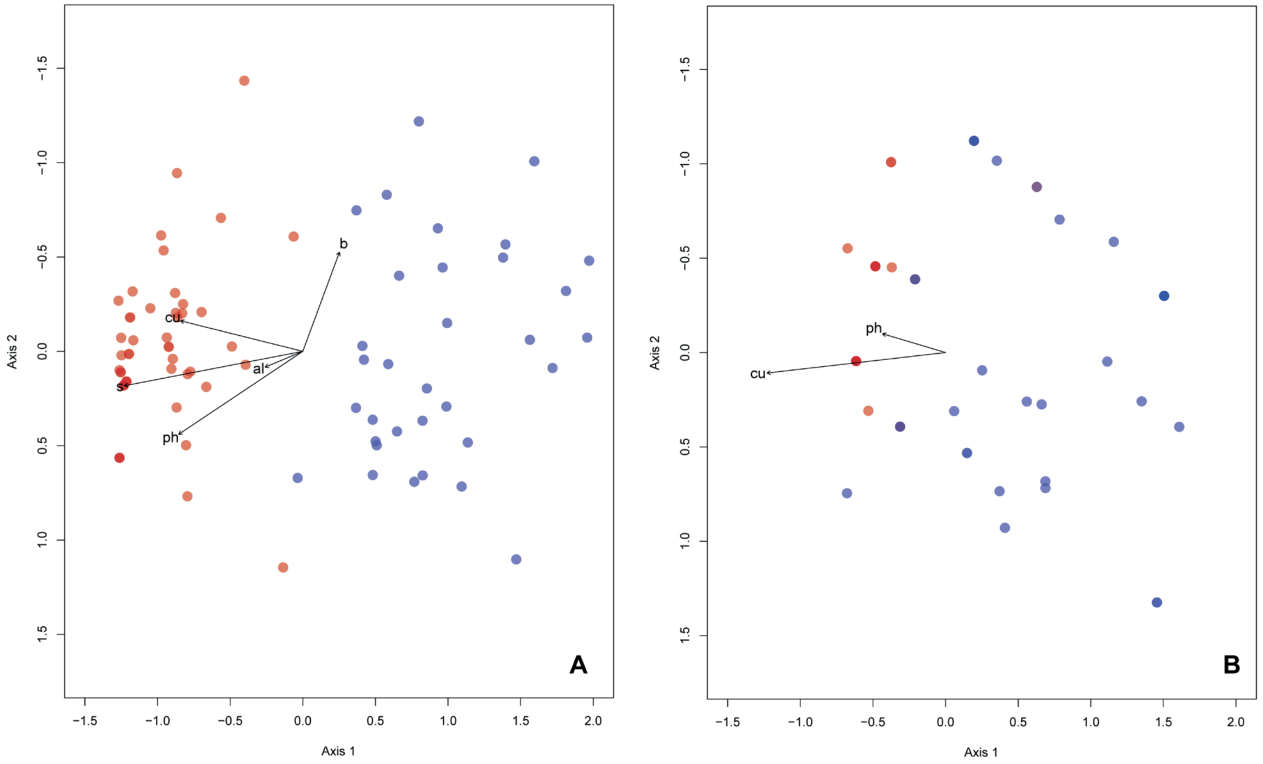

Figure 3. Non–metric multidimensional scaling analysis (NMDS) used the distribution data of 75 species related to the most significant components of the edaphic gradient (B = boron, Cu = copper, S = sulfur and Al = aluminium). Red circles represent forested Chaco and blue ones, wooded Chaco. **A)** Full set of woody individuals present in the two communities. **B)** assemblages of species of Fabaceae.

axis (from left to right in Fig. 3). The second axis represented the least variation among the vegetation types. Community composition was significantly different among forested and wooded Chaco (PERMANOVA: F = 44.822; $p < 0.001$), presented as two groups on the first axis.

Variation partitioning

Considering the whole community analysis, the variation explained by the spatially structured environment was higher among the fractions in the variance partition scheme (19 %). When considered separately, the environmental factor explained 4 % ($p < 0.05$) while the undetermined fraction was 72 %. On the other hand, when considering only Fabaceae assemblages on analysis, the results were similar: the variation explained by the spatially structured environment (12 %) was the most important one (See Tab. 1). To observe the variation of the edaphic components on the communities, the significant variables of each variable set and the NMDS results were overlapped. This shows the influence of the proximity of the land plots on the analysed environmental variables and the species composition (Fig. 4).

Table 1. Selected environmental variables, rated by the explanation of variation in species composition (R^2 and F values) in the woody community and Fabaceae assemblages of Chaco, Porto Murtinho, Mato Grosso do Sul, Brazil. $p < 0.05$ in all cases. Cu = copper (mg/dm^3), pH (Ca CI^2), B = boron (mg/dm^3), S = sulfur (mg/dm3), Al = aluminium (mmolc/dm^3).

	Variables	R^2 Adj.	AIC.	F	p val
Community	Cu	0.15653	43.975	19.0012	0.002
	pH	0.20211	48.445	6.4841	0.002
	B	0.22011	49.718	3.1921	0.002
	S	0.23016	50.037	2.2272	0.026
	Al	0.23602	49.846	1.7139	0.046
Fabaceae	Cu	0.10168	59.240	11.9788	0.002
	pH	0.12582	60.936	3.6515	0.004

Fabaceae-soil effect

In this study, we recorded 75 woody species. The forested Chaco presented a higher richness (66) when compared to its counterpart (26). Fabaceae was the family with the largest number of species in both communities. This family was present in 84 % of the plots, and its occurrence was higher in the wooded (98 % of the plots) than in the forested Chaco (70 %). Soils were eutrophic in forested Chaco (V% > 50 %) and dystrophic in wooded Chaco (V % < 50 %). By checking the influence of presence percentages of Fabaceae species and the most representative soil variable (V %), we observed that both factors influenced the structure of the forested and wooded Chaco (Tab. 2)

Indicator species

We found 37 indicator species ($p \leq 0.05$, indicator value – IV ≥ 10), see Table S1, in material supplementary. The highest number of indicator species (30) was observed in environments where soil is more fertile (*i.e.* forested Chaco). Among them, the only species of Fabaceae was *Libidibia paraguariensis* (D. Parodi) GP Lewis (IV = 15, p = 0.011). The better potential indicators were Euphorbiaceae species: *Gymnanthes descolor* (Spreng.) Müll.Arg. (IV = 83, p = 0.001) and *Adelia membranifolia* (Müll. Arg.) Chodat & Hassl. (IV = 56, p = 0.001). In environments where soil fertility is a restrictive factor (*i.e.* wooded Chaco), seven species were considered indicators, among them, three were species of Fabaceae: *Prosopis rubriflora* (IV = 87, p = 0.001), *Parkinsonia praecox* (IV = 60, p = 0.001) and *Mimosa hexandra* (IV = 22, p = 0.038). These three species represented 51 % of the sampled individuals in this vegetation type.

Discussion

This is the first study that assessed the influence of the edaphic components and the importance of the representativeness of Fabaceae on the structuring of floristic patterns in Chaco woody communities. The results confirm our hypothesis and show that the interaction between soil types with species of Fabaceae indeed has an effect on structuring of communities, through the establishment of species of Fabaceae in more restrictive soils. The main evidences that support this statement are i) the floristic structuring in two consistent communities; ii) the association between environmental and spatial factors; iii) the influence of Fabaceae and soil fertility percentages; and iv) the greater potential of species of Fabaceae as indicators for wooded Chaco. These aspects suggest that, despite the recognized contribution of Fabaceae to communities in seasonal and restrictive environments, such as Chaco, the more restrictive the conditions, the more its adaptive contribution becomes evident. This fact highlights the role of the interaction between soil and species of Fabaceae on the structuring of ecological communities.

The variation of copper and pH in soil was one of the main responsible for the structuring of Chaco communities. Copper is essential for various plant activities

Table 2. Results of the generalized linear model considering the percentage of species of Fabaceae and soil base saturation (V %) as the most important variables on structuring the forested and wooded Chaco, in Porto Murtinho, Mato Grosso do Sul, Brazil.

Variables		Estimate	Standard Error	Z Value	Pr(>|z|)
Forested and Wooded Chaco	(Intercept)	10.8232	6.4630	1.675	0.0940
	Fabaceae %	-0.1034	0.1232	-0.840	0.4012
	V %	-0.4298	0.2135	-2.013	0.0441

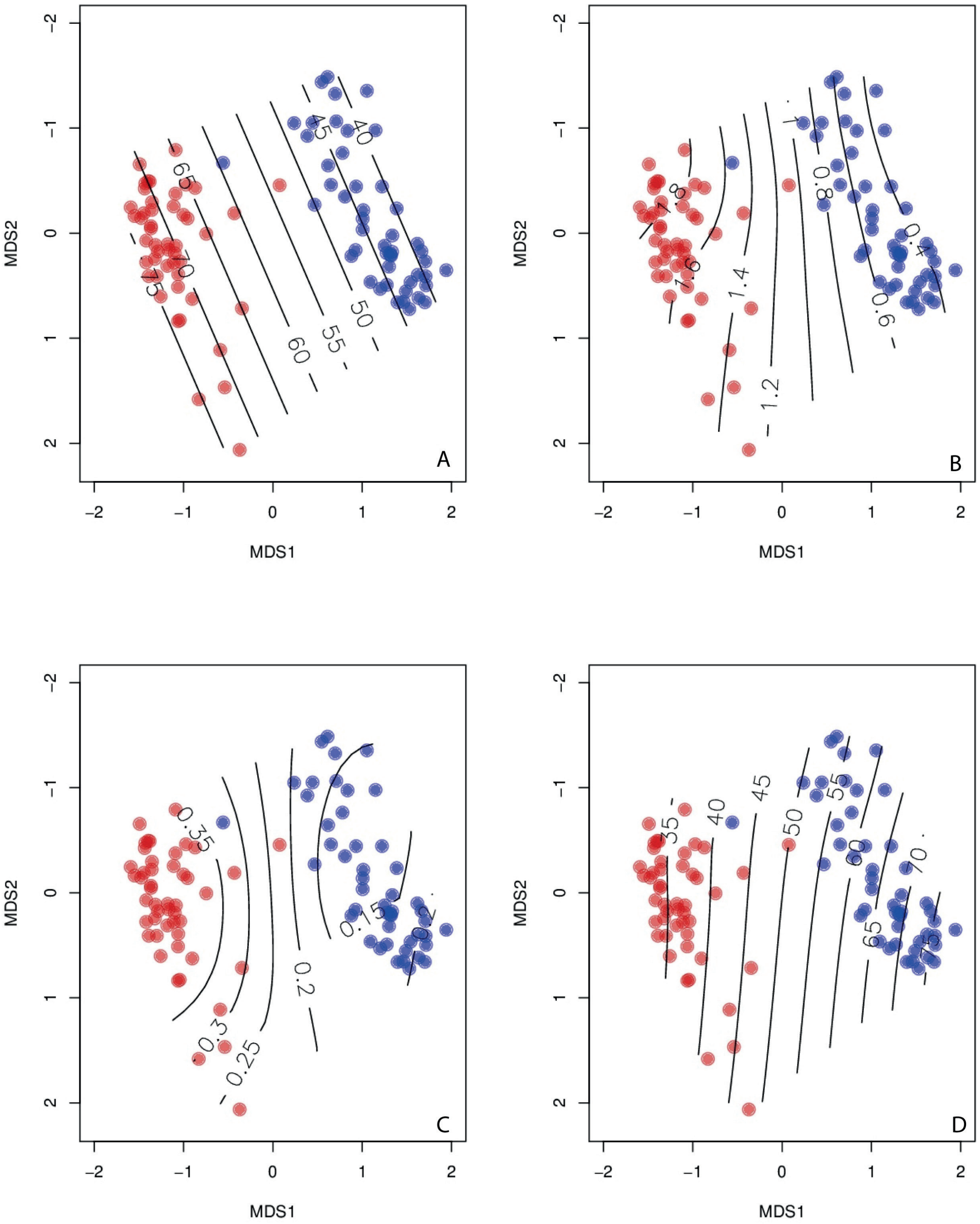

Figure 4. Spatialization of the scores of the sample units along axes 1 and 2 of the Environmental and Spatial Redundancy Analysis (RDAs), for the vegetation of Chaco, Porto Murtinho - Mato Grosso do Sul. **A)** Cu = copper (mg/dm^3), **B)** pH (Ca CI^2), **C)** B = boron (mg/dm^3) and **D)** S = sulfur (mg/dm^3). Red circles represent forested Chaco and blue ones wooded Chaco.

and for symbiotic nitrogen fixation (Marschner 1995), which reflects particularly on the nodulation capacity of species of Fabaceae. The dynamics of copper in the soil is strongly influenced by pH (Harter 1983; Hoog *et al*. 1993; Temminghoff *et al*. 1997). The acidic pH determines a greater absorption of the metal, and the alkaline pH favours its retention (McBride 1994). However, plants obtain copper more efficiently in alkaline soils (Pegoraro *et al*. 2006; Cornu *et al*. 2007). In the case of Chaco, both phytophysiognomies are inserted in predominantly acidic soils. However, in the wooded Chaco there are land plots where the pH is less acidic than in the forested plots. These land plots present a greater representation of species of Fabaceae. This aspect is an indication that in this phytophysiognomy, Fabaceae individuals are more prone to nodulations than in the phytophysiognomy of forested Chaco.

Another aspect that suggests a greater likelihood of nodulation in the wooded Chaco is that in environment where there is a greater nutrient recycle (*e.g.* forested Chaco), many species of Fabaceae, which are considered as fixatives, may not present nodulation. It occurs because such species assimilate soil nitrogen more easily than via biological fixation (Dobereiner 1984), as there are costs involved in the production of their nodules. In addition, arboreal individuals in disturbed areas may show nodulations more frequently and abundantly than in preserved areas (Sylvester-Bradley *et al*. 1980). In restrictive environments, Fabaceae that present nodule formation benefits other species by facilitation (Bertness & Callaway 1994; Brooker *et al*. 2008; Kikvidze *et al*. 2011). It is recognized that nitrogen deficiency in the soil strongly affects the ecosystem, as species of Fabaceae can intensify its nodule production and, as a result, they can present a large distribution (Dobereiner 1984; Dobereiner & Campello 1977).

Many monodominant species have associations with fungi and bacteria (McGuire 2008) that provide competitive advantages (Peh *et al*. 2011). In the wooded Chaco, some species of Fabaceae are found in high abundance (*e. g. P. rubriflora*, *P. praecox* and *M. hexandra* - Baptista *et al*. 2016). *Prosopis* and *Mimosa* are among the most diverse genera of the Chaco (Morales *et al*. 2019), with *P. rubriflora* being considered an indicative species of the Domain (Pott & Pott 1994; Oliveira-Filho *et al*. 2006). These species are nodulatory (Burkart 1976) and are often found in clusters interspersed with other species (Lima 2012), which suggests that it can act as a nursing plant. Studying the effect of nursery plants in areas with poor soils, Gómez-Aparicio *et al*. (2005) observed that individuals that grew under fixative species of Fabaceae showed greater survival and growth than individuals associated with other nurse plants. This aspect can be decisive for the structuring of a community (Cavieres & Badano 2009).

The explanation values for the spatially structured environmental factors may reflect the importance of soil for the Fabaceae assemblage. Pure fractions of spatial structures are important to explain the assemblage of the plant community in tropical forests (Svenning & Skov 2004; Eisenlohr *et al*. 2013; Punchi-Manage *et al*. 2014). However, we did not identify significant contribution from the pure effects of the spatial structure. Since the environmental changes are in a small scale, we believe that such fact is likely related to a greater relevance of processes based on niches on the assemblage of the community (Nettesheim *et al*. 2019). This is because edaphic factors are generally structured on locals where the distribution of some species change to keep up with this structure (Peres-Neto & Legendre 2010; Vleminckx *et al*. 2017). For instance, three species of Fabaceae co-occurred on the vegetation types (*Bauhinia hagenbeckii*, *Parapiptadenia rigida* and *Enterolobium contortisiliquum*). When occurred in the wooded Chaco, *B. hagenbeckii* and *P. rigida* were associated with areas where the soil is more fertile, like the one found in forested Chaco.

Regarding the group of potential indicator species, only seven species were identified in the wooded Chaco, three of which belonging to Fabaceae. In contrast, in the forested Chaco, only one species of Fabaceae (*L. paraguariensis*) was considered indicative among the 30 highest IV. The importance of Fabaceae for Chaco has been well described previously, with groups of species associated with specific vegetations (Lima *et al*. 2017). Here, we present an evident contribution focused on areas with more restrictive conditions edaphic. Within the same biome, species may have very different preferences for climatic and edaphic conditions (Swaine 1996; Condit *et al*. 2013). In addition, the lack of overlap between species with a higher IV among phytophysiognomies reinforces the hypothesis that there is a floristic difference between communities. This aspect demonstrates that species of Fabaceae can play an important role especially on communities inserted in environments that are more restrictive.

The study site is an interesting meeting place of Chaquenian *sensu stricto* and mesotrophic type forest floristic elements (Prado *et al*. 1992; Prado 1993). For example, in the sampled communities from forested Chaco, the main indicator species (Tab. S1in material supplementary) belong to Amazonian lineage (*e. g. Bignonia corymbosa*, *Eugenia subterminalis*, *Machaonia brasiliensis*, *Neea hermaphrodita*), or to Seasonally Dry Tropical Forest lineage (*e. g. Myracrodruon urundeuva*, *Calycophyllum multiflorum*, *Handroanthus heptaphyllus*), coexisting with a few characteristic Chaquenian species. Besides, the sampled communities from wooded Chaco seems to be more related to Chaquenian *sensu stricto* scrublands. Thus, the results of this paper support the differentiation of Chaquenian-related communities (growing in restrictive soils and Fabaceae-dominated), from another complex such as the "Transitional Belt" communities with Amazonian, SDTF's and Chaquenian mixed elements.

Although the study was concentrated in a single area of the Brazilian Chaco, it is likely that the observed pattern might be true for other Neotropical communities. The main evidences that support this generalization are (i) the differentiation of assemblages according to the soil type; (ii) the greater explanation of the spatially structured environmental fraction; and (iii) the greater association of species of Fabaceae with restrictive environments. Such aspects suggest that the typical Fabaceae assemblages from Chaco can play a major role in structuring the vegetation, especially in the Porto Murtinho region, where the natural areas are strongly affected by agriculture and cattle raising. Therefore, our study provides indications of an important contribution of Fabaceae to the structuring of the ecological community. Nevertheless, it shows its close relationship with seasonal environments, especially in areas where soil is a restrictive factor.

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References

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G. 2013. Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22: 711-728.

Alvarez R, Lavado RS. 1998. Climate, organic matter and clay content relationships in the Pampa and Chaco soils, Argentina. Geoderma 83: 127-141.

Alves FDM, Sartori ÂLB. 2009. Caesalpinioideae (Leguminosae) de um remanescente de Chaco em Porto Murtinho, Mato Grosso do Sul, Brasil. Rodriguésia 60: 531-550.

Assunção VA. 2016. Fatores bióticos, abióticos e evolutivos que afetam a ocorrência e distribuição de espécies lenhosas no Chaco. PhD Thesis, Jardim Botânico do Rio de Janeiro, Rio de Janeiro.

Baldeck CA, KE Harms, JB Yavitt, *et al*. 2013. Soil resources and topography shape local tree community structure in tropical forests. Proceedings of the Royal Society B: Biological Sciences 280: 20122532. doi: 10.1098/rspb.2012.2532

Baptista MSP, Assunção VA, Mansano VF, Sartori ALB. 2016. Distinção Taxonômica e Heterogeneidade do Solo no Chaco. Scientific Electronic Archives 9: 54-56.

Baptista MSP, Assunção VA, Seleme EP, Sartori ALB. 2017. Estrutura populacional de *Albizia niopoides* (Benth.) Burkart e *Mimosa hexandra* Micheli (Fabaceae) em Chaco brasileiro. Boletim do Museu Paraense Emílio Goeldi, Ciências Naturais 12: 169-176.

Barberis IM, Lewis JP, Batista WB. 2005. Heterogeneidad estructural de los bosques de la Cuña Boscosa de Santa Fe en distintas escalas espaciales. La heterogeneidad de la vegetación de los agroecosistemas: un homenaje a Rolando JC León, 43-58. https://www.researchgate.net/profile/William_Batista/publication/266074255_Heterogeneidad_estructural_de_los_bosques_de_la_Cuna_Boscosa_de_Santa_Fe_en_distintas_escalas_espaciales/links/555f380c08ae8c0cab2fbe24.pdf.

Beierkuhnlein C, Jentsch A. 2005. Ecological importance of species diversity: A review on the ecological implications of species diversity in plant communities. In: Henry RJ. (ed.) Plant diversity and evolution: genotypic and phenotypic variation in higher plants. Wallingford, CAB International Publishing. p. 249-285.

Benkman CW. 2013. Biotic interaction strength and the intensity of selection. Ecology Letters 16: 1054-1060.

Bertness MD, Callaway R. 1994. Positive interactions in communities. Trends in Ecology & Evolution 9: 191-193.

Bivand R. 2013. Package 'spdep': spatial dependence: weighting schemes, statistics and models. R package version 0.5-56. http://ftp.auckland.ac.nz/software/CRAN/src/contrib/Descriptions/spdep.html. 23 Feb. 2019.

Blamey FPC, Robinson NJ, Asher CJ. 1992. Interspecific differences in aluminium tolerance in relation to root cation-exchange capacity. Plant Soil 146: 77-82.

Blanchet FG, Legendre P, Borcard D. 2008. Forward selection of explanatory variables. Ecology 89: 2623-2632.

Borcard D, Gillet F, Legendre P. 2011. Spatial analysis of ecological data. In: Borcard D, Gillet F, Legendre P. (eds.) Numerical ecology with R. New York, Springer. p. 227-292.

Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85: 1826-1832.

Borcard D, Legendre P, Drapeau P. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.

Brasil. 1982. Projeto RADAMBRASIL. Levantamento de recursos naturais. Folha SF 21 Campo Grande: geologia, geomorfologia, pedologia, vegetação e uso potencial da terra. Rio de Janeiro, RADAMBRASIL, Ministério do Meio Ambiente.

Brooker RW, Maestre FT, Callaway RM, *et al*. 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology 96: 18-34.

Brunbjerg AK, Ejrnas R, Svenning JC. 2012. Species sorting dominates plant metacommunity structure in coastal dunes. Acta Oecologica 39: 33-42.

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.

Burkart A. 1976. A monograph of the genus *Prosopis* (Leguminosae subfam. Mimosoideae). Journal of the Arnold Arboretum 57: 450-525.

Cavieres LA, Badano EI. 2009. Do facilitative interactions increase species richness at the entire community level?. Journal of Ecology 97: 1181-1191.

Chase JM. 2014. Spatial scale resolves the niche versus neutral theory debate. Journal of Vegetation Science 25: 319-322.

Chase MW, Christenhusz MJM, Fay MF, *et al*. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181: 1-20.

Classen ME. 1997. Manual de métodos de análise de solo. 2nd. edn. Rio de Janeiro, Brazil, Embrapa Solos-Documentos (INFOTECA-E).

Condit R, Engelbrecht BM, Pino D, Pérez R, Turner BL. 2013. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. Proceedings of the National Academy of Sciences 110: 5064-5068.

Cornu JY, Staunton S, Hinsinger P. 2007. Copper concentration in plants and in the rhizosphere as influenced by the iron status of tomato (*Lycopersicon esculentum* L.). Plant and Soil 292: 63-77.

Cottenie K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8: 1175-1182.

Crews TE. 1999. The presence of nitrogen fixing legumes in terrestrial communities: Evolutionary vs ecological considerations. In: Townsend AR. (ed.) New Perspectives on Nitrogen Cycling in the Temperate and Tropical Americas. Dordrecht, Springer Science & Business Media. p. 233-246.

Delignette-Muller ML, Dutang C. 2015. fitdistrplus: An R package for fitting distributions. Journal of Statistical Software 64: 1-34.

Dludlu MN, Chimphango SB, Stirton CH, Muasya AM. 2017. Distinct edaphic habitats are occupied by discrete legume assemblages with unique indicator species in the Cape Peninsula of South Africa. Jornal of Plant Ecology 11: 632-644.

Dobereiner J, Campello AB. 1977. Importance of legumes and their contribution to tropical agriculture. In: Hardy RWF, GibsonAH. (eds.) A Treatise on Dinitrogen Fixation Section IV: Agronomy and Ecology. New York, NY, USA, John Wiley. p. 191-220.

Dobereiner J. 1984. Nodulação e fixação de nitrogênio em leguminosas florestais. Pesquisa Agropecuária Brasileira 19: 83-90.

Dray S, Legendre P, Blanchet FG. 2009. Packfor: Forward Selection with Permutation (Canoco p. 46) (R package version 0.0-7/r58). https://r-forge.r-project.org/projects/sedar/. 27 Feb. 2019.

Dray S, Pélissier R, Couteron P *et al*. 2012. Community ecology in the age of multivariate multiscale spatial analysis. Ecological Monographs 82: 257-275.

Dray S. 2010. SpacemakeR: spatial modelling. R package version 0.0-5. https://r-forge.r-project.org/projects/sedar/. 27 Feb. 2019.

Dufrêne M, Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366.

Eisenlohr PV, Alves LF, Bernacci LC, *et al*. 2013. Disturbances, elevation, topography and spatial proximity drive vegetation patterns along an altitudinal gradient of a top biodiversity hotspot. Biodiversity and Conservation 22: 2767-2783.

Ellison AM, Bank MS, Clinton BD, *et al*. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3: 479-486.

Gentry AH. 1995. Diversity and floristic composition of Neotropical dry forests. In: Bullock SH, Mooney HA, Medina E. (eds.) Seasonally dry tropical forests. Cambridge, UK, Cambridge University Press. p.146-194.

Gómez-Aparicio L, Gómez JM, Zamora R, Boettinger JL. 2005. Canopy *vs*. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. Journal of Vegetation Science 16: 191-198.

Harter RD. 1983. Effect of soil pH on adsorption of lead, copper, zinc and nickel. Soil Science Society of America Journal 47: 47-51.

Hoog DS, McLaren RG, Swift RS. 1993. Desorption of copper from New Zealand soils. Soil Science Society of America Journal 57:361-366.

Hooper DU, Chapin FS, Ewel JJ, *et al*. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75: 3-35.

Hubbell SP. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Priceton, USA, Princeton University Press.

Hueck K. 1972. As regiões de matas do Chaco e áreas marginais. In: Azevedo JCA, Anjos CV, Gomes LC, Lyra Filho R, Moraes RB, Paraense WL, Fonseca EN. (eds.) As florestas da América do Sul: ecologia, composição e importância econômica. São Paulo, Editora Polígono. p. 240-275.

Hutchinson GE. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? The American Naturalist 93: 145-159.

IBGE. 2012. Manual técnico da vegetação brasileira: sistema fitogeográfico, inventário das formações florestais e campestres, técnicas e manejo de coleções botânicas, procedimentos para mapeamentos. 2nd. edn. Rio de Janeiro, Brazil, IBGE (Instituto Brasileiro de Geografia e Estatística).

John R, Dalling JW, Harms KE, *et al*. 2007. Soil nutrients influence spatial distributions of tropical tree species. Proceedings of the National Academy of Sciences 104: 864-869.

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. In: Samson FB, Knopf FL. (eds.) Ecosystem management. New York, Springer. p. 130-147.

Khan MASA, Grant K, Beierkuhnlein C, Kreyling J, Jentsch A. 2014. Climatic extremes lead to species-specific legume facilitation in an experimental temperate grassland. Plant and Soil 379: 161-175.

Kikvidze Z, Michalet R, Brooker RW, *et al*. 2011. Climatic drivers of plant-plant interactions and diversity in alpine communities. Alpine Botany 121: 63-70.

Küchenmeister F, Küchenmeister K, Wrage N, Kayser M, Isselstein J. 2012. Yield and yield stability in mixtures of productive grassland species: does species number or functional group composition matter? Grassland Science 58: 94-100

Lavin M, Schrire BP, Lewis G, *et al*. 2004. Metacommunity process rather than continental tectonic history better explains geographically structured phylogenies in legumes. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 359: 1509-1522.

Legendre P, Dale MR, Fortin MJ, Gurevitch J, Hohn M, Myers D. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 25: 601-615.

Legendre P, Gallagher ED. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271-280.

Legendre P, Legendre L. 2012. Numerical ecology. Vol II. Amsterdam, Elsevier.

Legendre P, Mi X, Ren H, *et al*. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90: 663-674.

Lepš J, Šmilauer P. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge, Cambridge University Press.

Lewis GP. 2005. Acacieae. In: Lewis G, Schrire B, Mackinder B, Lock M. (eds.) Legumes of the world. London, Kew, Royal Botanic Gardens Kew. p. 187-191.

Lima JR, Santos ND, Tozzi AM, Mansano VF. 2017. Using legumes as indicators in the seasonally dry vegetation types in South America. Ecological Indicators 73: 708-715.

Lima JR, Tozzi AM, Mansano VF. 2015. A checklist of woody Leguminosae in the South American Corridor of Dry Vegetation. Phytotaxa 207: 1-38.

Lima TE. 2012. Perturbação ambiental em remanescentes de Chaco e mecanismos de defesa em leguminosas. MSc Thesis, Universidade Federal de Mato Grosso do Sul, Campo Grande.

Maia VA, Souza CR, Santos RM. 2019. Species tolerance degree to soil conditions shaping plant communities. Folia Geobotanica, 1-12.

Marquard E, Weigelt A, Temperton VM, *et al*. 2009. Plant species richness and functional composition drive overyielding in a six-year grassland experiment. Ecology 90: 3290-3302.

Marschner H. 1995. Mineral nutrition of higher plants. 2nd. edn. London, Academic Press London, Elsevier.

Martinelli LA, Piccolo MC, Townsend AR, *et al*. 1999. Nitrogen stable isotopic composition of leaves and soil: tropical versus temperate forests. Biogeochemistry 46: 45-65.

Mazzarino MJ, Oliva L, Abril A, Acosta M. 1991. Factors affecting nitrogen dynamics in a semiarid woodland (Dry Chaco, Argentina). Plant Soil 138: 85-98.

McBride MB. 1994. Environmental chemistry of soils. In: McBride MB. (ed.) Oxidatio-Reduction Reations. New York, Oxford, Oxford University Press. p. 240-273.

McCune B, Grace JB. 2002. Analysis of ecological communities. Vol. 28. Oregon, U.S.A, Gleneden Beach, OR: MjM software design..

McGuire KL. 2008. Ectomycorrhizal associations function to maintain tropical monodominance. In: Siddiqui ZA, Futai K. (eds.) Mycorrhizae: Sustainable Agriculture and Forestry. Dordrecht, New Delhi, Springer. p. 287-302.

McLean EO, Adams D, Franklin RE. 1956. Cation Exchange Capacities of Plant Roots as Related to Their Nitrogen Contents 1. Soil Science Society of America Journal 20: 345-347.

McPeek MA. 2017. The ecological dynamics of natural selection: traits and the coevolution of community structure. The American Naturalist 189: 91-117.

Meira-Neto JAA, Tolentino GS, Silva MCNAD, *et al*. 2017. Functional antagonism between nitrogen-fixing leguminous trees and calcicole-drought-tolerant trees in the Cerrado. Acta Botanica Brasilica 31: 11-18.

Morales M, Oakley L, Sartori AL, *et al*. 2019. Diversity and conservation of legumes in the Gran Chaco and biogeograpical inferences. PLOS ONE 14: e0220151. doi: 10.1371/journal.pone.0220151

Morrison ML. 2009. Restoring Wildlife: Ecological Concepts and Practical Applications. Washington, DC, Island Press.

Myers JA, Chase JM, Jiménez I, *et al*. 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assemblage. Ecology Letters 16: 151-157.

Nettesheim FC, Garbin ML, Pereira MG, Araujo DSDD. 2019. Local environmental controls of Atlantic Forest tree community assemblage on a coastal continental island in southeastern Brazil. Acta Botanica Brasilica 33: 88-96.

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.

Neves DM, Dexter KG, Pennington RT, *et al*. 2017. Dissecting a biodiversity hotspot: The importance of environmentally marginal habitats in the Atlantic Forest Domain of South America. Diversity and Distributions 23: 898-909.

Nunes GP. 2006. Estudo florístico de formações chaquenhas brasileiras e caracterização estrutural de um remanescente de Chaco de Porto Murtinho, MS, Brasil. MSc Thesis, Universidade Federal de Mato Grosso do Sul, Campo Grande.

Oksanen J, Blanchet FG, Kindt R, *et al*. 2016. vegan: community ecology package. https://cran.r-project.org/web/packages/vegan/index.html. 26 Feb. 2019.

Oliveira-Filho AT, Jarenkow JA, Rodal MN. 2006. Floristic relationships of seasonally dry forests of eastern South America based on tree species distribution patterns. In: Pennington RT, Lewis GP, Ratter JA. (eds). Neotropical savannas and seasonally dry forests: plant diversity, biogeography and conservation. Oxford, Francis CRC Press. p. 59-192.

Olson DM, Dinerstein E, Wikramanayake ED, *et al*. 2001. Terrestrial Ecoregions of the World: A New Map of Life on EarthA new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience 51: 933-938.

Pegoraro RF, Silva IRD, Novais RF, Mendonça EDS, Gebrim FDO, Moreira FF. 2006. Fluxo difusivo e biodisponibilidade de zinco, cobre, ferro e manganês no solo: influência da calagem, textura do solo e resíduos vegetais. Revista Brasileira de Ciência do Solo 30: 859-868.

Peh KSH, Sonké B, Lloyd J, Quesada CA, Lewis SL. 2011. Soil does not explain monodominance in a Central African tropical forest. PLOS ONE 6: e16996. doi: 10.1371/journal.pone.0016996

Pennington RT, Lavin M, Prado DE, Pendry CA, Pell SK, Butterworth CA. 2004. Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 359: 515-538.

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

Peres-Neto PR, Legendre P, Dray S, Borcard D. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87: 2614-2625.

Peres-Neto PR, Legendre P. 2010. Estimating and controlling for spatial structure in the study of ecological communities. Global Ecology and Biogeography 19: 174-184.

Perry GL, Miller BP, Lamont BB, Enright NJ. 2017. Community-level spatial structure supports a model of stochastic geometry in species-rich shrublands. Oikos 126: 833-842.

Pott A, Pott VJ. 1994. Plantas do Pantanal. Corumba, EMBRAPA-Centro de Pesquisa Agropecuária do Pantanal, EMBRAPA-Serviço de Produção de Informação.

Poulsen AD, Balslev H. 1991. Abundance and cover of ground herbs in an Amazonian rain forest. Journal of Vegetation Science 2: 315-322.

Prado DE, Gibbs PE, Pott A, Pott VJ. 1992. The chaco-transition in southern Mato-Grosso, Brazil. In: Furley PA; Proctor J; Ratter JA. (eds.) Nature and dynamics of forest-savanna boundaries. Vol. 5. London, Chapman & Hall. p. 451-470.

Prado DE, Gibbs PE. 1993. Patterns of species distributions in the dry seasonal forests of South America. Annals of the Missouri Botanical Garden 80: 902-927.

Prado DE. 1993. What is the Gran Chaco vegetation in South America? II: A redefinition. Contribution to the study of the flora and vegetation of the Chaco. VII. Candollea 48: 615-629.

Punchi-Manage R, Wiegand T, Wiegand K, Getzin S, Gunatilleke CS, Gunatilleke IN. 2014. Effect of spatial processes and topography on structuring species assemblages in a Sri Lankan dipterocarp forest. Ecology 95: 376-386.

Quinn GP, Keough MJ. 2002. Experimental design and data analysis for biologists. Cambridge, Cambridge University Press.

R Development Core Team. 2017. R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing 55: 275-86.

Roberts DW. 2016. Package "labdsv" R Package. https://cran.r-project.org/web/packages/labdsv/index.html. 27 Feb. 2019.

Roscher C, Schumacher J, Gubsch M, *et al*. 2012. Using plant functional traits to explain diversity-productivity relationships. PLOS ONE 7: e36760. doi: 10.1371/journal.pone.0036760

Sartori ALB. 2012. The Brazilian Chaco. Glalia 4: 11-18.

Siddig AA, Ellison AM, Ochs A, Villar-Leeman C, Lau MK. 2016. How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. Ecological Indicators 60: 223-230.

Silva J, Rocha F, Silva T. 2010. Determinação da CTC radicular de gramíneas e leguminosas forrageiras. Enciclopédia Biosfera 6: 1-7.

Silva MP, Mauro RDA, Abdon M, Silva J. 2009. Estado de conservação do Chaco (Savana Estépica) brasileiro. In: Simpósio Nacional Cerrado, 9th. edn. Simpósio Internacional Savanas Tropicais, 2nd. edn. Planaltina. Menções honrosas. Planaltina, DF, Embrapa Informática Agropecuária-Artigo em anais de congresso (ALICE), Embrapa Cerrados. p. 166-169.

Spehn EM, Scherer-Lorenzen M, Schmid B, *et al*. 2002. The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. Oikos 98: 205-218.

Sprent JI. 2007. Evolving ideas of legume evolution and diversity: a taxonomic perspective on the occurrence of nodulation. New Phytologist 174: 11-25.

Svenning JC, Skov F. 2004. Limited filling of the potential range in European tree species. Ecology Letters 7: 565-573.

Swaine MD. 1996. Rainfall and soil fertility as factors limiting forest species distributions in Ghana. Journal of Ecology 84: 419-428.

Sylvester-Bradley R, Oliveira LA, Podestá-Filho JA, John TS. 1980. Nodulation of legumes, nitrogenase activity of roots and occurrence of nitrogen-fixing *Azospirillum* ssp. in representative soils of central Amazonia. Agro-Ecosystems 6: 249-266.

Temminghoff EJ, Zee SEV, Haan FA. 1997. Copper mobility in a copper-contaminated sandy soil as affected by pH and solid and dissolved organic matter. Environmental Science & Technology 31: 1109-1115.

Temperton VM, Mwangi PN, Scherer-Lorenzen M, Schmid B, Buchmann N. 2007. Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. Oecologia 151:190-205

Tuomisto H, Ruokolainen K, Kalliola R, Linna A, Danjoy W, Rodriguez Z. 1995. Dissecting amazonian biodiversity. Science-New York Then Washington 269: 63-63.

UNESCO. 1973. International Classification and Mapping of Vegetation. United Nations Educational, Scientific and Cultural Organization, Paris, France. Ecology and Conservation 6: 1-102.

Vleminckx J, Doucet JL, Morin-Rivat J, *et al*. 2017. The influence of spatially structured soil properties on tree community assemblages at a landscape scale in the tropical forests of southern Cameroon. Journal of Ecology 105: 354-366.

Wang X, Hao Z, Ye J, Zhang J, Li B, Yao X. 2008. Spatial pattern of diversity in an old-growth temperate forest in Northeastern China. Acta Oecologica 33: 345-354.

Wang X, Wiegand T, Kraft NJ, *et al*. 2016. Stochastic dilution effects weaken deterministic effects of niche-based processes in species rich forests. Ecology 97: 347-360.

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33: 475-505.

Yang WQ, Goulart BL. 2000. Mycorrhizal infection reduces shortterm aluminum uptake and increases root cation exchange capacity of highbush blueberry plants. HortScience 35: 1083-1086.

Young KR, León B. 1989. Pteridophyte species diversity in the central Peruvian Amazon: importance of edaphic specialization. Brittonia 41: 388-395.