Floristic composition, diversity and edaphic effects in two rocky savanna communities in the Amazon and Cerrado, Brazil

Composição florística, diversidade e efeitos edáficos em duas comunidades de savanas rochosas na Amazônia e Cerrado, Brasil

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ABSTRACT

Despite the uniqueness and reach of the flora from natural savannas in the Brazilian Amazon, and the existence of studies on its origin and diversity, there are no local studies associating floristic patterns with soil properties in savanna enclaves in the Amazon region of the state of Mato Grosso. Floristic composition and diversity were compared between a woody community from a rocky savanna inselberg in a transition region (RTS) between the two largest South American biomes (Cerrado-Amazon), and an enclave of rocky savanna in the Amazon (RAS), and the effects of soil properties were investigated. Floristic comparisons were also made between the two studied communities and two other rocky savanna communities near the Cerrado-Amazon transition. The flora and physical and chemical soil properties in twenty-five 20 × 20 m subplots (1 ha) in each community were sampled and georeferenced. An evident floristic distinction was found between the two studied communities, with low similarity values and a high number of indicator species. The observed and estimated richness and Rényi diversity profiles indicated lower species diversity in RAS than in RTS. Soils were found to be lithic, poorly drained, dystrophic, alic, extremely acidic, sandy and nutrient poor. Species composition and abundance was associated with soil properties in both communities. The clear difference in species composition and diversity between RTS and RAS seem to be shaped by soil properties, geographic isolation and floristic influence from the Cerrado and the Amazon. These results broaden the knowledge regarding the composition and diversity of woody plants of savannas in Amazonian enclaves and Cerrado inselbergs, and provide an important set of floristic and edaphic descriptors for the phytogeography of rocky savannas.

Keywords: Amazonian savanna; Inselbergs; Phytogeography; Cerrado-Amazonian Forest transition
RESUMO

Apesar da singularidade e extensão da flora de savanas naturais na Amazônia brasileira, e da existência de trabalhos sobre sua origem e diversidade, não há estudos locais que associam padrões florísticos com propriedades do solo em enclaves de cerrado na região amazônica no estado de Mato Grosso. Comparamos a composição florística e a diversidade entre uma comunidade lenhosa de um *inselberg* de savana rochosa em uma região de transição (STR) entre os dois maiores biomas sul-americanos (Cerrado-Amazônia) e um enclave de savana rochosa na Amazônia (SAR) e investigamos os efeitos das propriedades do solo. Além disso, comparamos as duas comunidades estudadas com outras duas comunidades de savanas rochosas próximas da transição Cerrado-Amazônia. A flora e as propriedades físicas e químicas do solo de vinte e cinco subparcelas de 20 × 20 m (1 ha), em cada comunidade foram amostradas e georreferenciadas. Uma evidente distinção florística foi encontrada entre as duas comunidades estudadas, com baixos valores de similaridade e um número elevado de espécies indicadoras. A riqueza observada e estimada e os perfis de diversidade de Rényi indicaram menor diversidade de espécies na SAR do que na STR. Os solos são litólicos, pouco drenados, distróficos, állicos, extremamente ácidos, arenosos e pobres em nutrientes em ambas as comunidades. A composição e a abundância de espécies foram associadas às propriedades do solo. A clara diferença na composição e diversidade entre STR e SAR parecem ser moldadas pelas propriedades do solo, isolamento geográfico e influências florísticas do Cerrado e Amazônia. Esses resultados ampliam o conhecimento sobre a composição e diversidade de plantas lenhosas de savanas em enclaves da Amazônia e *inselbergs* do Cerrado e fornecem um importante conjunto de descritores florísticos e edáficos para a fitogeografia de savanas rochosas.

**Palavras-chave:** Savanas amazônicas; *Inselbergs*; Fitogeografia; Transição Cerrado-Floresta Amazônica

1 INTRODUCTION

A major challenge in ecological studies is to understand the roles of the environment and geographic isolation on the assemblage of isolated plant communities in the landscape. Soil properties, geographical distance and floristic influence from neighboring communities play important roles in determining plant species distributions and diversity in Neotropical savannas (ABADIA *et al*., 2018; ROCHA; NETO, 2019). Neotropical inselbergs are patches of isolated habitats with rocky outcrops and different ecological conditions and vegetation from the surrounding landscape (POREMBSKI; SILVEIRA; FIEDLER, 2016). In turn, enclaves are patches of vegetation representative of ecosystems belonging to phytogeographic provinces totally distinct from those within which they are embedded and are characterized by specific and unique floral elements (RATTER; BRIDGEWATER; RIBEIRO, 2003; ROCHA; NETO, 2019).
In the Cerrado biome, inselbergs of rocky savanna vegetation, locally called *Cerrado Rupestre*, are generally surrounded by fields and savannas on deep soil (PINTO; LENZA; PINTO, 2009). In the Amazon Basin, enclaves of savanna-type vegetation, known as Amazonian savannas, are characterized by their distinct species composition, structure, and ecology in comparison with savanna formations of the Cerrado of the Central Brazilian Plateau and other regions of South America, due to their affinities with adjacent tropical forest systems (RATTER; BRIDGEWATER; RIBEIRO, 2003; ROCHA; NETO, 2019). Thus, comparisons between Cerrado inselbergs and Amazonian enclaves provide a good opportunity to evaluate the effect of isolation, and the edaphic and floristic influence on species composition and diversity in these savannas.

Isolated enclaves of Amazonian savanna are found in the Brazilian states, where they grow on distinct substrates, which are generally acidic and dystrophic (RATTER; BRIDGEWATER; RIBEIRO, 2003). Studies on plant communities from Amazonian savannas located on deep soils indicate that species richness and diversity are lower than for communities typically found in savannas of the Cerrado (RATTER; BRIDGEWATER; RIBEIRO, 2003; ROCHA; NETO, 2019). However, no data are available for Amazonian savanna enclaves on litholic soils. In contrast, woody or shrubby-arboreal savanna communities associated with rocky outcrops in the Cerrado biome have been amply studied in recent years (ABADIA et al., 2018). These authors showed the richness in savannas on rocky outcrops is similar to that found in adjacent savannas on deep soils. In general, these results suggest that the assemblage of woody communities is different between the rocky amazonian savanna enclaves and the Cerrado rocky savanna inselbergs.

Thus, this study aimed to increase knowledge regarding the processes that support biological diversity by comparing species composition and diversity, and investigating the influence of soil properties on floristic patterns, of two savanna woody communities: a savanna inselberg in a transition region between the Cerrado and Amazon, and an enclave of rocky savanna in the Amazon. The two studied floristic communities were also compared with two other communities of rocky cerrado near the Cerrado-Amazon transition.
2 MATERIAL AND METHODS

2.1 Study area

Three biomes occur in the state of Mato Grosso: Amazon, Cerrado and Pantanal (Figure 1). Here, we studied and compared the flora and the soil of two isolated woody communities (including monocots and lianas) found on rocky outcrops and separated by 520 km one each other (Figure 1). The first community (Figure 1a) is located near the banks of the Teles Pires River in a Permanent Preservation Area of the Colíder Hydroelectric Plant reservoir, in the municipality of Nova Canaã do Norte, Mato Grosso. This community grows on arenitic origin rocks of and is surrounded by dense and open Submontane Ombrophilous Forests, and on the other side by swamp bushes. Thus, this community is referred here as rocky amazonian savanna (RAS), in order to distinguish it from the other savannas that grow on deep soils scattered and isolated in the Amazon. The local climate is warm and humid equatorial (Am), according to the classification of Köppen, with temperatures ranging from 20ºC to 29ºC, and the mean annual temperature exceeding 27ºC (ALVARES et al., 2013). Total annual rainfall can reach 3,100 mm with two well-defined seasons: a rainy season from October to April, and a dry season from May to September (ALVARES et al., 2013). The region is composed of a variety of different geological units, with the topography ranging from flat or gently sloping plains to very steep mountainous terrain (BERNASCONI et al., 2009). A variety of soils can also be found in the region, although three types are predominant: red-yellow clays, litholicneosols, and red-yellow latosols (BERNASCONI et al., 2009). The second community (Figure 1b), referred here as rocky transition savanna (RTS), is located in a legal reserve, in a private property in the municipality of Ribeirão Cascalheira at the northwest border of the transition between the Cerrado and the Amazon. This community is surrounded by savanna and transitional forest both growing on deep soils, dystrophic or mesotrophic (RATTER; BRIDGEWATER; RIBEIRO, 2003). The climate of the region is rainy tropical savanna (Aw), according to the
classification of Köppen, with rainy summers and dry winters, temperatures ranging from 17°C to 26°C, a mean annual temperature exceeding 24°C, and annual rainfall ranging from 1,900 to 2,500 mm, characterized by a well-defined rainy season, from October and April, and a cooler, dry season between May and September (ALVARES et al., 2013). Both communities are well preserved, once they are located in preservation areas, and during this study, we did not notice recent signal of fire, cattle presence and logging.

Figure 1 – Location of sampling sites and arrangement of plots and subplots in a rocky amazonian savanna in Nova Canaã do Norte - RAS (a) and in a rocky transition savanna in Ribeirão Cascalheira - RTS (b) in the state of Mato Grosso, Brazil

Source: Authors (2021)

In where: Grids on the right show the sampling design and the soil sampling sites (●).
2.2 Data collection

A 1-hectare plot was delimited in each community, although the shape of the plots differed (Figure 1). A 100 m × 100 m plot was established in RAS, which was divided into 25 subplots of 20 m × 20 m. Since the rocky outcrop of RTS is very narrow, making it impossible to demarcate a 100 m × 100 m square plot as in RAS, an irregular-shaped plot divided into 25 subplots of 20 m × 20 m, was established. All live woody plants (including shrubs, trees, and lianas) with a basal diameter of at least 5 cm at 30 cm above the ground (Bd$_{30\,cm}$; MORO; MARTINS, 2011) were identified within each subplot.

Species were identified in the field when possible, while specimens were collected for further analysis in the laboratory based on specific literature, consultation with taxonomic experts, and comparisons with specimens of the Southern Amazonia Herbarium (HERBAM), in the municipality of Alta Floresta (UNEMAT) and the Herbarium NX, in the municipality of Nova Xavantina, both in the state of Mato Grosso, Brazil. Taxonomic classification of the specimens was based on APG IV (ANGIOSPERM PHYLOGENY GROUP, 2016), while species names were based on data available from the Flora do Brasil website (JARDIM BOTÂNICO DO RIO DE JANEIRO, 2019).

We collected three soil samples from each subplot at a depth of 0-20 cm. One sample was collected at the center of each subplot and the other two were collected close to the opposite vertices. These samples were homogenized to form a single composite sample representing each subplot for analysis (Figure 1). The physical-chemical soils properties analyzed were potassium (K), sulfur (S), copper (Cu), saturation by aluminum (Sat. Al), sand, phosphorus (P), calcium (Ca), boron (B), iron (Fe), zinc (Zn), sodium (Na), base saturation (Sat. Base), silt, magnesium (Mg), aluminum (Al), potential acidity (H + Al), organic matter, manganese (Mn), cation exchange capacity (CEC), pH and clay, according to Santos et al. (2018).
2.3 Data analysis

Species richness was compared between communities using rarefaction with 1,000 randomizations and sampling standardized by the number of individuals (GOTELLI; COLWELL, 2001). This method is used to compare communities sampled with different sampling efforts (GOTELLI; COLWELL, 2001; MAGURRAN, 2011). We used diversity profiles based on the Rényi exponential series to compare species diversity of the two communities (TÓTHMÉRÉSZ, 1995). We performed these analyses in the PAST software (Paleontological S Tatistics), version 2.15.

Principal Coordinates Analysis (PCoA) using the Bray–Curtis dissimilarity index was used to evaluate whether the two communities (RTS and RAS) formed distinct groups based on species composition and abundance (LEGENDRE; LEGENDRE, 2012). The significance of the groups formed by the PCoA was tested using ANOSIM with Bonferroni correction (CLARKE; WARWICK, 1994). These analyses were run in the vegan package (OKSANEN et al., 2018) of the R statistical programming environment, version 3.4.4 (R CORE TEAM, 2018). Density and the Importance Value Index (IV) were calculated for each species of the two communities (MUELLER-DOMBOIS; ELLENBERG, 1974), which were then compared using the ten species with the highest IV scores. This analysis was run using FITOPAC 2.1.2 software (SHEPHERD, 2009). An Indicator Species Analysis (ISA) was performed with a Monte Carlo test to evaluate the significance of each species as an indicator of each community (DUFRÊNE; LEGENDRE, 1997). This analysis was performed with PC-ORD software version 6.07 (MCCUNE; MEFFORD, 2011).

The species composition of the two studied communities was compared with that of two others rocky Cerrado communities located near the southern border of the Amazon biome using Sørensen's qualitative index (CS) (BROWER; ZAR, 1984) and
Morisita’s quantitative index ($I_m$) (MAGURRAN, 2011). Both indices were calculated using the PAST (Paleontological S Tatistics) software, version 2.15. One of these communities was located in the municipality of Nova Xavantina, state of Mato Grosso (see GOMES et al., 2011) while the other was in the municipality of Piranhas, state of Goiás (see ABREU et al., 2012). These sites are located 200 km and 395 km south, respectively, from RTS. Since RTS is located at the southern extreme of the transition between the Amazon and the Cerrado (see Figure 1 and geographical coordinates in Table 1), we considered the two additional sites to represent a gradient of distance from the Amazon biome.

Table 1 – Geographic characteristics for the compared savanna communities on rocky outcrops in the states of Mato Grosso and Goiás, Brazil

| Codes | Locality                  | Latitude (S)  | Longitude (W) | Altitude (m) |
|-------|----------------------------|---------------|---------------|--------------|
| RTS   | RibeirãoCascalheira – MT *| 13º 00'09.8"  | 51º 45'12.5"  | 403          |
| RAS   | Nova Canaã do Norte – MT *| 10º 53'98.7"  | 55º 46'68.7"  | 437          |
| RNS   | Nova Xavantina – MT #      | 14º 41'00"    | 52º 20'00"    | 346          |
| RPS   | Piranhas – GO ▲            | 16º 26'55"    | 51º 53'58"    | 810          |

Source: Authors (2021)

In where: RTS = rocky transition savanna in Ribeirão Cascalheira; RAS = rocky amazonian savanna in Nova Canaã do Norte; RNS = rocky savanna in Nova Xavantina; RPS = rocky savanna in Piranhas; *Present study; *Gomes et al. (2011); ▲Abreu et al. (2012).

Edaphic variables were pre-selected using the Variance Inflation Factor (VIF) < 10. Following this analysis, 13 out of 21 edaphic variables were selected for further analysis (see Table 4). Redundancy Analysis – RDA (LEGENDRE; BORCARD; ROBERST, 2012) was used to test the association between edaphic variables and floristic composition of the communities. Finally, the significance of the communities was tested using a Monte Carlo permutation test with 999 permutations. All these analyses were performed in R environment, using the usdm package for VIF (NAIMI et al., 2014), and the vegan package for RDA (OKSANEN et al., 2018).
3 RESULTS

A total of 1,560 woody plants of 86 species were recorded (796 at RTS and 764 at RAS), of which only 13 species (15.1%) were common to both communities, 51 only in RTS (59.3%) and 22 only in RAS (25.6%). The number of species recorded in RTS (n = 64) was considerably greater than the number recorded in RAS (n = 35) (Table 2).

Table 2 – Floristic list and phytosociological parameters of woody species sampled in two savanna communities on rocky outcrops in the state of Mato Grosso, Brazil

| Codes | Species | Families | AD RTS | IV RAS | AD RAS | IV RTS |
|-------|---------|----------|--------|--------|--------|--------|
| Vatmac | *Vatairea macrocarpa* (Benth.) Ducke | Fabaceae | 63 | 2 | 25.56 | 1.36 |
| Quapar | *Qualea parviflora* Mart. | Vochysiaceae | 89 | 6 | 25.44 | 3.86 |
| Xylaro | *Xylopia aromatica* (Lam.) Mart. | Annonaceae | 70 | 1 | 21.64 | 0.59 |
| Myrsp. | *Myrcia* sp. | Myrtaceae | 63 | 6 | 19.48 | 3.39 |
| Davell | *Davilla elliptica* A. St.-Hil. | Dilleniaceae | 66 | - | 19.20 | - |
| Anaocc | *Anacardium occidentale* L. | Anacardiaceae | 34 | 19 | 16.57 | 11.34 |
| Ptepub | *Pterodon pubescens* (Benth.) Benth. | Fabaceae | 18 | - | 12.20 | - |
| Salcon | *Salvertia convallariodora* A. St.-Hil. | Vochysiaceae | 18 | - | 9.69 | - |
| Ferell | *Ferdinandusa elliptica* (Pohl) Pohl | Rubiaceae | 23 | - | 9.87 | - |
| Byrpac | *Byrsonima pachyphylla* A. Juss. | Malpighiaceae | 20 | - | 8.52 | - |
| Emmnit | *Emmotum nitens* (Benth.) Miers | Icacinaceae | 16 | 11 | 7.71 | 5.17 |
| Curame | *Curatella americana* L. | Dilleniaceae | 23 | - | 7.59 | - |
| Byrcoc | *Byrsonima coccobolifolia* Kunth | Malpighiaceae | 19 | - | 7.42 | - |
| Pouram | *Pouteria ramiflora* (Mart.) Radlk. | Sapotaceae | 14 | - | 7.24 | - |
| Hirgla | *Hirtella glandulosa* Spreng. | Chrysobalanaceae | 17 | - | 7.56 | - |
| Ourhex | *Ouratea hexasperma* (A.St.-Hil.) Baill. | Ochnaceae | 18 | - | 6.31 | - |
| Consub | *Connarus suberosus* Planch. | Connaraceae | 18 | - | 6.07 | - |
| Myrmul | *Myrica multiflora* (Lam.) DC. | Myrtaceae | 23 | - | 5.75 | - |
| Kiecor | *Kielmeyera coriacea* Mart. & Zucc. | Calophyllaceae | 14 | - | 5.25 | - |
| Mapgui | *Maprounea guianensis* Aubl. | Euphorbiaceae | 14 | 34 | 4.84 | 15.14 |
| Guagra | *Guapira graciliflora* (Mart. ex Schmidt) Lundell | Nyctaginaceae | 9 | - | 3.89 | - |
| Hetbyr | *Heteropterys byrsonimifolia* A. Juss. | Malpighiaceae | 11 | - | 3.82 | - |
| Myrvar | *Myrica variabilis* DC. | Myrtaceae | 11 | - | 3.61 | - |
| Ferdsp | *Ferdinandusa sp.* | Rubiaceae | 9 | - | 3.42 | - |
| Andcuj | *Andira cujabensis* Benth. | Fabaceae | 5 | 11 | 3.32 | 6.81 |

To be continued ...
Table 1 – Continuation

| Codes | Species | Families | AD RTS | AD RAS | IV RTS | IV RAS |
|-------|---------|----------|--------|--------|--------|--------|
| Roumon | *Roupala montana* Aubl. | Proteaceae | 11 | - | 3.29 | - |
| Aspmac | *Aspidosperma macrocarpon* Mart. ♦ | Apocynaceae | 6 | 2 | 3.25 | 1.52 |
| Chakap | *Chaunochiton kappleri* (Sagot ex Engl.) Ducke * # | Olacaceae | 8 | - | 3.23 | - |
| Fricin | *Fridericia cinnamomea* (DC.) L. G. Lohmann ♦ | Bignoniaceae | 6 | 1 | 2.40 | 0.59 |
| Vocru | *Vochysia rufa* Mart. ♦ | Vochysiaceae | 5 | 2 | 2.20 | 1.57 |
| Hymsti | *Hymenaea stigonocarpa* Mart. ex Hayne | Fabaceae | 6 | - | 2.04 | - |
| Strpse | *Strychnos pseudoquina* A. St. -Hil. | Loganiaceae | 2 | - | 1.96 | - |
| Eriga | *Eriothea gracilipes* (K. Schum.) A. Robyns | Malvaceae | 4 | - | 1.95 | - |
| Myrsp. | *Myrcia sp.* | Myrtaceae | 5 | - | 1.77 | - |
| Salcra | *Salacia crassifolia* (Mart. ex Schult.) G. Don | Celastraceae | 3 | - | 1.65 | - |
| Mezcra | *Mezilaurus cassiniae* (Meisn.) Taub. ex Mez | Lauraceae | 3 | - | 1.64 | - |
| Himart | *Himatanthus articulatus* (Vall) Woodson | Apocynaceae | 4 | - | 1.58 | - |
| Bowvir | *Bowdichia virgilioides* Kunth | Fabaceae | 3 | - | 1.49 | - |
| Eugpun | *Eugenia punicifolia* (Kunth) DC. | Myrtaceae | 3 | - | 1.42 | - |
| Lepdas | *Leptolobium dasycarpum* Vogel. | Fabaceae | 3 | - | 1.40 | - |
| Erysub | *Erythroxylum suberosum* A. St. -Hil. | Erythroxylaceae | 3 | - | 1.34 | - |
| Buctom | *Terminalia corrugata* (Ducke) Gere & Boatwr. | Combretaceae | 3 | - | 1.33 | - |
| Rouind | *Rourea induta* Planch. | Connaraceae | 3 | - | 1.30 | - |
| Tacaur | *Tachigali aurea* Tul. | Fabaceae | 2 | - | 1.22 | - |
| Mouell | *Mouriri elliptica* Mart. | Melastomataceae | 3 | - | 1.12 | - |
| Carbra | *Caryocar brasiliense* Cambess. | Caryocaraceae | 1 | - | 1.11 | - |
| Tapgui | *Topirira guianensis* Aubl. * | Anacardiaceae | 2 | - | 1.07 | - |
| Euggem | *Eugenia gummiflora* O. Berg | Myrtaceae | 3 | - | 1.02 | - |
| Carcal | *Cardiopteryx calophyllum* Schltldl. * | Annonaceae | 2 | - | 0.95 | - |
| Plaret | *Plathymenia reticulata* Benth. | Fabaceae | 2 | - | 0.92 | - |
| Hanser | *Handroanthus serratifolius* (Vahl) S. Grose | Bignoniaceae | 2 | - | 0.91 | - |
| Micven | *Micropholis venulosa* (Mart. & Eichler) Pierre * | Sapotaceae | 1 | - | 0.65 | - |
| Lafpac | *Lafoensia pacari* A. St. -Hil. | Lythraceae | 1 | - | 0.60 | - |
| Dioser | *Diospyros sericea* A. DC. | Ebenaceae | 1 | - | 0.51 | - |
| Moupus | *Mouriri pusa* Gardner ♦ | Melastomataceae | 1 | 1 | 0.51 | 0.63 |

To be continued ...
Table 1 – Continuation

| Codes  | Species                          | Families            | AD     | IV     |
|--------|----------------------------------|---------------------|--------|--------|
|        |                                  |                     | RTS    | RAS    | RTS    | RAS    |
| Licbla | *Licania blackii* Prance         | Chrysobalanaceae    | 1      | 0.50   | -      | -      |
| Hanspe | *Hancornia speciosa* Gomes ♦     | Apocynaceae         | 1      | 0.48   | 0.67   | -      |
| Vissp  | *Vismia* sp.                     | Hypericaceae        | 1      | 0.47   | -      | -      |
| Aspmul | *Aspidosperma multiflorum* A. DC | Apocynaceae         | 1      | 0.46   | -      | -      |
| Agobra | *Agonandra brasiliensis* Miers ex Benth. & Hook. f. | Opiliaceae | 1      | 0.45   | -      | -      |
| Andver | *Andira vermifuga* (Mart.) Benth. | Fabaceae            | 1      | 0.44   | -      | -      |
| Anncor | *Annona coriacea* Mart.          | Annonaceae          | 1      | 0.43   | -      | -      |
| Corell | *Cordiera elliptica* (Cham.) Kuntze | Rubiaceae         | 1      | 0.43   | -      | -      |
| Micalb | *Miconia albicans* (Sw.) Triana  | Melastomataceae     | 1      | 0.43   | -      | -      |
| Kierub | *Kielmeyera rubriflora* Cambess. ▲† | Calophyllaceae      | -      | 163    | -      | 50.76  |
| Parcac | *Parkia cachimboensis* H. C. Hopkins ▲*† | Fabaceae            | -      | 126    | -      | 45.35  |
| Macrad | *Macairea radula* (Bonpl.) DC. ▲*† | Melastomataceae     | -      | 94     | -      | 26.93  |
| Alcdis | *Alchornea discolor* Poepp. ▲*† | Euphorbiaceae       | -      | 59     | -      | 23.37  |
| Norgui | *Norantea guianensis* Aubl. ▲**† | Marcgraviaceae      | -      | 59     | -      | 22.46  |
| Simver | *Simarouba versicolor* A. St.-Hil. ▲† | Simaroubaceae       | -      | 38     | -      | 13.53  |
| Pagthy | *Pagamea cf. thrysiflora* Spruce ex Benth. ▲† | Rubiaceae           | -      | 25     | -      | 11.71  |
| Dacmic | *Dacryodes microcarpa* Cuatrec. ▲† | Burseraceae         | -      | 22     | -      | 10.93  |
| Byrcra | *Byronima crassifolia* (L.) Kunth. † | Malpighiaceae       | -      | 11     | -      | 6.47   |
| Myrcit | *Myrcia cf. citrifolia* (Aubl.) Urb. † | Myrtaceae           | -      | 12     | -      | 5.54   |
| Chadum | *Chamaecrista dumalis* (Hoehne) H.S. Irwin & Barneby. † | Fabaceae            | -      | 12     | -      | 5.13   |
| Tacsub | *Tachigali subvelutina* (Benth.) Oliveira-Filho | Fabaceae           | -      | 5      | -      | 4.34   |
| Chrsp  | *Chrysophyllum* sp.              | Sapotaceae          | -      | 11     | -      | 4.09   |
| Ficmat | *Ficus cf. mathewsii* (Miq.) Miq. † | Moraceae            | -      | 9      | -      | 4.03   |
| Bredsp | *Bredemeyera* sp.               | Polygalaceae        | -      | 5      | -      | 2.60   |
| Licape | *Leptobalanus apetalus* (E. Mey.) Sothers & Prance | Chrysobalanaceae | -      | 4      | -      | 2.33   |
| Humbal | *Humiria balsamifera* (Aubl.) J.St.-Hil. * | Humiriaceae        | -      | 2      | -      | 2.02   |
| Cybful | *Cybianthus cf. fulvopulverulentus* (Mez) G. Agostini | Primulaceae       | -      | 3      | -      | 1.83   |
| Ferchl | *Ferdinandusa cf. chlorantha* (Wedd.) Standl. * | Rubiaceae          | -      | 3      | -      | 1.82   |
| Vochae | *Vochysia haenkeana* Mart.       | Vochysiaceae        | -      | 2      | -      | 0.88   |

To be continued ...
Table 1 – Conclusion

| Codes | Species                                 | Families       | AD RTS | AD RAS | IV RTS | IV RAS |
|-------|-----------------------------------------|----------------|--------|--------|--------|--------|
| Mancae | *Manihot caerulescens* Pohl             | Euphorbiaceae  | -      | 1      | -      | 0.61   |
| Eryang | *Erythroxylum cf. anguifugum* Mart.     | Erythroxylaceae| -      | 1      | -      | 0.60   |
| Total  |                                         |                | 796    | 764    | 300    | 300    |

Source: Authors (2021)

In where: RTS = rocky transition savanna in Ribeirão Cascalheira; RAS = rocky amazonian savanna in Nova Canaã do Norte; AD = Absolute Density (number of individuals per ha$^{-1}$) and IV = relative Importance Value; ■ = highest IV in RTS; ▲ = highest IV in RAS; * = species typical of forest formations; ** = rocky cerrado specialist species; ♦ = species common to both RTS and RAS; # = indicator species of RTS; and † = indicator species of RAS.

Rarefaction curves (Figure 2A) confirmed the differences between the two communities, once estimated richness was higher in RST. Also, diversity profiles indicated greater diversity for RTS, regardless of the diversity index used (Figure 2B).

Figure 2 – Species rarefaction curves (A) and species diversity profiles in the Rényi exponential series (B) for the studied savanna communities on rocky outcrops in the state of Mato Grosso, Brazil

Source: Authors (2021)

In where: RTS = rocky transition savanna in Ribeirão Cascalheira; RAS = rocky amazonian savanna in Nova Canaã do Norte.
The two communities differed in species composition, with the PCoA forming two distinct groups (Figure 3), which were confirmed by ANOSIM ($R = 0.97$, $p = 0.001$). The contrast in the composition of the two communities was further reinforced by comparing the ten most important species for community structure (IV) in each community, with only *Anacardium occidentale* occurring on both lists (Table 2).

Figure 3 – Principal Coordinates Analysis of the composition and abundance of woody species studied in two savanna communities on rocky outcrops in the state of Mato Grosso, Brazil

Similarity in species composition of the two communities was also low, both qualitatively (Sørensen’s index - CS = 0.26) and quantitatively (Morisita’s index - $I_M$).
= 0.05). The similarity between RAS and the two other rocky savanna formations adjacent to the Cerrado-Amazon transition was consistently lower than that found between these formations and RTS (Table 3). The Indicator Species Analysis identified 22 indicator species (34.4% of total) for RTS and 13 indicator species (37.1% of total) for RAS (Monte Carlo: \( p < 0.001 \); Table 2). The other two rocky savanna communities located in the vicinity of the Cerrado-Amazon transition zone (Table 1: GOMES et al., 2011; ABREU et al., 2012) had greater species richness and were more diverse than RAS, but were quite similar to RTS for both parameters. Considering both Sørensen’s index and Morisita’s index, the two rocky savanna communities were more similar to RTS than to RAS (Table 3).

Table 3 – Matrix of Sørensen and Morisita similarity indices for compared savanna communities on rocky outcrops in the states of Mato Grosso and Goiás, Brazil

| Morisita’s index (I_M) | Sørensen’s index (CS) |
|------------------------|-----------------------|
|                        | RTS* | RAS* | RNS* | RPS ▲ |
| RTS*                   | 1    | 0.26 | 0.49 | 0.35 |
| RAS*                   | 0.05 | 1    | 0.15 | 0.12 |
| RNS*                   | 0.52 | 0.15 | 1    | 0.60 |
| RPS ▲                  | 0.45 | 0.15 | 0.57 | 1    |

Source: Authors (2021)

In where: RTS = rocky transition savanna in Ribeirão Cascalheira; RAS = rocky amazonian savanna in Nova Canaã do Norte; RNS = rocky savanna in Nova Xavantina; RPS = rocky savanna in Piranhas; * Present study; # Gomes et al. (2011); ▲ Abreu et al. (2012).

Soils of the two communities were identified as Litholic Neosols that are poorly drained, dystrophic, alic, extremely acidic and sandy, and with low nutrient concentrations (Table 4).
Table 4 – Physical-chemical properties of the soil of the studied savanna communities on rocky outcrops in the state of Mato Grosso, Brazil

| Variables          | VIF | RTS Mean | RTS SD | RTS Median | RAS Mean | RAS SD | RAS Median |
|--------------------|-----|----------|--------|------------|----------|--------|------------|
| K (mg/dm³)         | 2.57| 0.08     | 0.03   | 0.07       | 0.09     | 0.05   | 0.07       |
| S (mg/dm³)         | 3.43| 2.48     | 1.09   | 2.00       | 4.98     | 2.08   | 5.00       |
| Cu (mg/dm³)        | 1.45| 0.78     | 0.40   | 0.80       | 0.52     | 0.22   | 0.60       |
| Sat. Al %          | 7.40| 55.35    | 10.00  | 56.82      | 78.00    | 9.03   | 81.08      |
| Sand %             | 4.98| 85.60    | 1.68   | 86.00      | 88.48    | 1.12   | 89.00      |
| P (mg/dm³)         | 2.40| 2.44     | 1.56   | 2.10       | 4.17     | 4.76   | 2.70       |
| Ca (cmolc/dm³)     | 2.78| 0.23     | 0.05   | 0.20       | 0.39     | 0.33   | 0.20       |
| B (mg/dm³)         | 1.20| 0.22     | 0.05   | 0.23       | 0.21     | 0.04   | 0.23       |
| Fe (mg/dm³)        | 3.22| 110.52   | 44.70  | 105.00     | 22.36    | 11.36  | 18.50      |
| Zn (mg/dm³)        | 3.75| 0.67     | 0.63   | 0.30       | 1.81     | 2.22   | 0.90       |
| Na (cmolc/dm³)     | 1.65| 13.72    | 1.37   | 14.00      | 15.12    | 1.24   | 15.00      |
| Sat. Base %        | 6.74| 13.29    | 4.58   | 13.05      | 4.50     | 1.44   | 4.55       |
| Silt %             | 3.17| 4.44     | 0.50   | 4.00       | 4.56     | 0.71   | 4.00       |
| Mg (mg/dm³)        | >10 | 0.13     | 0.05   | 0.10       | 0.19     | 0.14   | 0.10       |
| Al (cmolc/dm³)     | >10 | 0.57     | 0.17   | 0.50       | 2.22     | 0.72   | 2.30       |
| H+Al (cmolc/dm³)   | >10 | 3.58     | 1.11   | 3.50       | 15.48    | 7.64   | 13.90      |
| Organic matter (g/dm³) | >10 | 1.90 | 0.51 | 1.80 | 7.92 | 4.84 | 6.80 |
| Mn (mg/dm³)        | >10 | 1.14     | 1.12   | 0.80       | 7.42     | 7.40   | 4.20       |
| CEC                | >10 | 4.08     | 1.09   | 3.93       | 16.22    | 8.06   | 14.33      |
| pH                 | >10 | 3.82     | 0.18   | 3.90       | 2.98     | 0.22   | 3.00       |
| Clay %             | >10 | 9.96     | 1.21   | 10.00      | 6.96     | 0.61   | 7.00       |

Source: Authors (2021)

In where: RTS = rocky transition savanna in Ribeirão Cascalheira; RAS = rocky amazonian savanna in Nova Canaã do Norte; Sat. Al % = aluminum saturation; Sat. Base = base saturation; CEC = cation exchange capacity; SD = Standard Deviation; VIF = Variance Inflation Factor.

The first two axes of the RDA explained 66.9% and 6.1% variation, respectively, in the species composition and environment (Figure 4; $F_{(13, 36)} = 2.47, p = 0.001$). The first axis indicated associations of floristic composition with both chemical variables (e.g., higher Base Saturation and Iron content in RTS and higher Aluminum Saturation and Sulfur content in RAS) and particle size variables (e.g., sandier soils in RAS).
Figure 4 – Redundancy Analysis of the composition and abundance of the woody species and soil physical and-chemical properties for the studied savanna communities on rocky outcrops in the state of Mato Grosso, Brazil

4 DISCUSSIONS

One important finding of the present study was the low species richness and diversity of RAS (n=35), which were not only lower than those of RTS (n=64), but also lower than those of the other Cerrado savanna communities. From 61 to 84 species have been recorded in rocky cerrado communities in the state of Goiás (SANTOS; PINTO; LENZA, 2012), while 71 have been recorded in the state of Mato Grosso (GOMES et al., 2011). All of these values are similar to that recorded for RTS in the
present study, but higher than the number recorded for RAS. Amazonian savannas typically have lower species richness than savanna formations of the Cerrado (RATTER; BRIDGEWATER; RIBEIRO, 2003; ROCHA; NETO, 2019). It is possible that humidity, geographical isolation, edaphic properties, and in particular, higher concentrations of sand, may be influencing the distinction of the floristic component, once sandy areas usually have fewer species and only two species are predominantly covering more than 50% of the shrub stratum. Indeed, our RAS results are in accordance with this information due to the higher representativeness of *Kielmeyera rubriflora* and *Parkia cachimboensis*, regarding density and importance value (IV) (ROCHA; NETO, 2019).

The limited similarity in species composition between the two studied sites RTS and RAS, in both qualitative (Sørensen= 0.26) and quantitative terms (Morisita = 0.05), is among the lowest recorded between woody communities in the Cerrado savanna. Values of Sørensen’s index for comparisons of rocky cerrado savannas in Brazil ranged from 0.25 to 0.42 (PINTO; LENZA; PINTO, 2009). Comparing ten rocky savanna communities in the state of Goiás, Santos, Pinto and Lenza (2012) recorded values for this index ranging from 0.18 to 0.71, while scores for Czekanowski’s quantitative index ranged from 0.06 to 0.50. Gomes *et al.* (2011) reported high values for both Sørensen’s (0.75) and Morisita’s (0.73) indices in a comparative study of typical and rocky cerrado in Mato Grosso. The comparisons made with two other sites, representing rocky cerrado in the proximity of the Amazon-Cerrado transition zone (GOMES *et al.*, 2011; ABREU *et al.*, 2012) also revealed much greater similarity with RTS than with RAS. These results combined with the high number of indicator species for each community (about a third of the species are indicators for one or the other of the two communities) suggest that RAS is quite distinct from the rocky savannas in both the transition zone and on the Central Brazilian Plateau.

The present study also documented a clear difference in species composition between Amazonian savannas and cerrado *sensu stricto*. This finding is consistent with what has been reported for communities of these vegetation types located on
deep soils with no rocky substrate (RATTER; BRIDGEWATER; RIBEIRO, 2003), although the present study is the first to systematically compare communities associated with rocky outcrops. On a broader scale, Amazonian savannas appear to be more similar to each another than to Cerrado savanna formations (RATTER; BRIDGEWATER; RIBEIRO, 2003). Amazonian savannas located in the southern Amazon Basin — Humaitá and Alter do Chão — have a greater affinity, in terms of species composition, for Cerrado savannas of central Brazil than for savannas in the northern Amazonian Basin in the states of Amapá and Roraima (RATTER; BRIDGEWATER; RIBEIRO, 2003). The unique characteristic of Amazonian savannas, rocky or otherwise, appear to be more accentuated in communities located in the central portion of the basin (i.e., RAS), and much less evident in savannas located within or adjacent to the Amazon-Cerrado transition zone (i.e., RTS).

Other studies of savannas on rocky outcrops (referred to as *rupestrian fields* by many authors) reported that closer areas have greater floristic similarity than more distant areas with the same lithology, and attributed this difference to edaphoclimatic factors, geographic distance and the number of microhabitats existing in outcrops (MESSIAS et al., 2012). Thus, geographical distance seems to promote floristic dissimilarity between savannas located in the interior of the Amazon and those near or in the transition between the Cerrado and the Amazon. In addition, the low similarity between the rocky transition savanna (RTS) and rocky amazonian savanna (RAS) indicates high beta diversity conditioned by the occurrence of environmental heterogeneity due to chemical and physical variation in the soil (MESSIAS et al., 2012).

Despite the similarities between the two study areas in terms of their elevation and underlying substrate, the marked distinctions in their species composition support the classification of RAS as an amazonian savanna due to the presence of woody species typical of both biomes, Cerrado (e.g., *Kielmeyera rubriflora*) and Amazon, such as *Parkia cachimboensis*, *Alchornea discolor*, *Pagamea* cf. *Thrysiflora* and *Dacryodes microcarpa*, which were present at high densities and structurally important (high IV
values) in RAS. These four species were not recorded by Santos, Pinto and Lenza (2012) in a broader study on ten rocky cerrado communities, nor at any location studied in Mato Grosso (GOMES et al., 2011; ABADIA et al., 2018). *Parkia cachimboensis* is found in isolated enclaves of savanna in the Brazilian Amazon Basin, and is thus considered typical of savanna enclaves (ZAPPI et al., 2011), as confirmed in the present study. *Norantea guianensis* is considered a specialist species that is found exclusively in rocky cerrado of central Brazil (ABADIA et al., 2018). The occurrence of this species in the rocky Amazonian savanna of the present study expands its known distribution to include the interior of the Amazon and confirms its occurrence in rocky habitats in the Amazon.

The evident floristic distinction between RTS and RAS was also determined by soil properties, since the first axis of the Redundancy Analysis, using only local edaphic variables, explained about two thirds of the floristic variation between the two communities. This first axis indicated associations of floristic composition with both chemical (e.g., Base Saturation and Iron in RTS - Aluminum Saturation and Sulfur in RAS) and particle size (e.g., Sand in RAS) variables. In communities from cerrado sensu stricto, the physical and chemical properties of the soil may contribute to distinctions in species composition between different sites, even when they are located within the same local area (ABREU et al., 2012; ABADIA et al., 2018). Thus, it can be concluded that the differences in species composition found here between the two study sites can also be explained, in part, by local edaphic conditions.

### 5 CONCLUSIONS

The present study revealed an evident floristic distinction between the two studied communities, reflected in low values of similarity and high numbers of indicator species for each community. Species richness and diversity were shown to be low in the enclave of rocky amazonian savanna (RAS) compared to the rocky transition savanna (RTS). From the floristic point of view, the cerrado enclave in the
Amazon has species in common to both the Cerrado and the Amazon. The few species shared between the areas, and typical of the Cerrado biome in RAS (e.g., *Kielmeyera rubriflora*), can be considered historical remnants of vegetation that were widely distributed in the past when climatic conditions were drier and more favorable to the cerrado vegetation. This study demonstrated that the soils of the two communities lack nutrients, and that soil characteristics are associated with floristic differences. This study also suggests the effect of distance and geographic isolation, as well as the influence of the adjacent flora in the landscape on the richness and composition of species in natural fragments of rocky savannas located in the Amazon, in Cerrado and in the transition zone between them. However, we suggest conducting new studies including other environmental parameters and with a larger number of sites, particularly in the scattered rocky savannas in the Amazon, where there are still few studies. Thus, the environmental, spatial, and floristic effects suggested in the present study, can be evaluated on a larger geographical scale. Such efforts would increase the knowledge about the savanna flora of the Amazon, the transition inselbergs, and the factors that determine the occurrence of savanna formations on rocky outcrops in this ecologically complex region between the Cerrado and Amazon biomes.

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