*Acta Botanica Brasilica*
doi: 10.1590/0102-33062019abb0399

# Effect of fire under the soils on the organization of communities of three remnants of Amazonian savannas

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Received: December 12, 2019
Accepted: May 29, 2020

**ABSTRACT**

Areas of cerrado (Brazilian savanna) in the Amazon have been poorly studied from the perspective of fire impacts on environmental sustainability, especially with regard to disturbances to soil and vegetation structure. This study aimed to analyze the influence of edaphic variables and fire together on the composition and structure of tree and shrub vegetation of three cerrado remnants in the Amazon. Eight plots were systematically installed in burned and unburned environments in each remnant. Data were submitted to floristic diversity, similarity, and diametric and altimetric structural assessments. Phytosociological parameters were obtained and submitted to Principal Component Analysis (PCA) and Canonical Correspondence Analysis (CCA). A total of 808 individuals (34 species, 30 genera, and 21 families) were recorded. The CCA indicated that the distribution of species is influenced by edaphic factors, as confirmed by the strong direct correlation of tree and shrub species with the reduced nutrition and high acidity of the soils common in the analyzed remnants. Our results support the hypothesis that fire plays a relevant role in structuring vegetation since it contributed to good indicators of soil properties and caused changes in the composition of woody species.

**Keywords:** amazon savannas, PCA, CCA, soil properties, phytosociological analysis

## Introduction

The cerrado *sensu stricto* is a savanna that occupies a large part of Central Brazil. It possesses 10 % to 60 % woody cover with trees that reach up to seven meters in height (Ribeiro & Walter 2008). There are many areas of cerrado inserted in high-biomass forest vegetation of the Amazon, which are referred to as "Amazonian savannas". These savannas occur in discontinuous areas in the Brazilian states of Rondônia, Roraima, Amazonas, Pará, Mato Grosso and Amapá (Mendonça *et al*. 2008). They jointly possess low floristic richness compared to the cerrado areas of the Brazilian Central plateau, although they demonstrate peculiar floristic elements and unique levels of endemism (Costa-Neto 2014).

Cerrado represents the second largest phytophysiognomy in the state of Amapá, covering an area of ~ 9,861.89 km$^2$ or ~ 7.2 % of the State (ZEE 2008). Compared to other areas of Amazonian savanna, those of Amapá possess very similar physiognomies to those found in the Brazilian Central plateau, consisting of a mosaic of different forest types and having a connection with the savannas of the Guiana Plateau (Costa-Neto *et al*. 2017; Mustin *et al*. 2017). Despite their biological importance, the savannas of Amapá have been the focus of few studies regarding the effects of fire on soil

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and the impacts of these two factors on native vegetation, questions that have aroused the interest of the scientific community.

The interest in studying these savanna formations is based on environmental concerns, such as the conversion of woody vegetation for activities associated with agriculture and livestock production, which has reduced local biodiversity in recent decades. The lack of public policies related to protecting this natural heritage in the Amazon is alarming, and is particularly worrisome in Amapá because the state's savannas are under increasing threat due to pressure from activities such as large-scale agriculture (Silva 2016; Carvalho & Mustin 2017), and are now considered the "final frontier" of soybean plantations in Brazil (Silva 2016; Hilário *et al*. 2017).

The occurrence of a plant species in a given natural environment presupposes the existence of adaptations for survival. The ecological niche of a species can be determined by the physical and chemical parameters of the environment where it occurs (Gotelli 2007). In this context, studies that seek to analyze the structural correlation between plant community and environmental factors are essential from the viewpoints of both management and forest conservation. Such studies can help to elucidate the processes involved in maintaining Amazonian savannas, which are still poorly understood. They also provide support for further studies of forest dynamics and especially for the evaluation and recovery of degraded areas with native species (Braga *et al*. 2015).

Despite the existence of many studies on community structure, dynamics and composition for various biological groups in Brazilian savannas, knowledge about the structure and composition of Amazonian savanna vegetation still requires further research, considering that studies in these areas are incipient (Costa-Neto 2014). In this context, floristic and phytosociological studies make it possible to assess the biological diversity and structural patterns of communities, and are even more important when describing patterns in areas that suffer some type of disorder, whether natural or anthropogenic.

Among the factors that influence the formation of a landscape, soil plays a fundamental role by providing mechanical support and essential nutrients for plant establishment and development (Silva *et al*. 2015). Therefore, it is understood that edaphic heterogeneities along environmental gradients determine variation in the composition and phytosociological structure of forest communities (Abreu *et al*. 2012). Thus, there is a need for research aimed at identifying the relationships between soil and vegetation, particularly in the savanna areas of Amapá and concerning the influence of fire since its actions in these areas remain unknown.

Community ecology studies that seek to investigate the responses of plant species to soil contribute to understanding local and regional biodiversity (Finger & Oestrich-Filho 2014). Associating the soil-plant relationship with the actions fire may reveal interesting aspects of the structure and landscape of ecosystems because such an association can help explain the dynamics of forest communities in response to the environment in case of fire, and also indicate species that are resilient to changes in the availability of soil nutrients (Haridasan 1992; Barbosa & Fearnside 2005).

Fire is a source of disturbance in the Cerrado biome and generally determines vegetation structure and composition, with the potential for quite expressive change in species composition depending on the frequency and intensity of disturbances (Lopes *et al*. 2009). Considering the premise that both fire and the physical-chemical attributes of the soil influence savanna plant communities and, thus, cause changes to the landscape, this study aimed to clarify how these two environmental factors act jointly on the floristic structure and composition of savanna remnants in the state of Amapá. To the best of our knowledge, there has been no study to date that has quantified the effects of edaphic attributes and fire on savanna vegetation concurrently. Canonical correspondence analysis (CCA), principal components analysis (PCA) and redundancy analysis (RDA) may help clarify these complex associations (Abreu *et al*. 2012).

Seeking to expand the understanding of the ecological patterns and processes involved in structuring communities, we hypothesized that, at a local geographical scale, soil properties and fire together can alter the floristic structure and composition of savanna remnants in the Northern Amazon of Brazil. Specifically, we aimed to answer the following questions: (1) What effects does fire have on the structure and composition of the woody plant community of the investigated savanna remnants? (2) Are changes in structure and composition along the spatial gradient associated with changes in soil attributes due to fire? (3) What is the degree of floristic similarity among remnants considering fire disturbance?

# Materials and methods

## Study area

The study was carried out in three remnants of cerrado *sensu stricto* (~ 20, 13 and 40 ha) in the urban perimeter of the municipality of Macapá, located in the southeast region of the state of Amapá, Brazil. The municipality fits the Amw' climatic type according to the Köppen classification, with a rainy season from November to June and a dry season from July to October (ZEE 2008). The average temperature is around 25 ºC, with a maximum of 32 ºC and a minimum of 22 ºC, while the average annual rainfall for the region is 2,284 mm (ZEE 2008). The remnants possess aluminous-type Latosol soil with sandy-clayey, sandy, clay-silt and conglomerate sediments distributed among smooth and undulating relief (Rodrigues *et al.* 2000).

The three studied remnants have the same phytophysiognomy of cerrado *sensu stricto* vegetation. The remnants, identified here as A1 (0°04'30.39" N, 51°06'21.74" W), A2 (0°01'13.91" N, 51°10'01.18" W) and A3 (0°01'56.20" N, 51°6'1.70" W), are under pressure from rapid urban growth in their surroundings and are widely used for agricultural activities, which partly explains their susceptibility to fire almost always resulting from human interventions (Hilário *et al*. 2017). The remnants also experience seasonal fires, specifically during the Amazonian summer.

Due to the "dry" vegetation along with the Amazonian summer, these areas of Amapá savanna are susceptible to fire outbreaks, which are caused by increased heat or the human factor. Indeed, this was observed for the studied remnants, but more associated with the human factor, such as itinerant agriculture (i.e., actions of cutting and burning vegetation). As the studied remnants are small, the intensity of fires was not so significant while the duration, three to six hours, varied among them.

## *Vegetation sampling*

To characterize the vegetation in more detail, a phytosociological survey was carried out in burned (T1) and unburned (T2) environments of each of the three savanna remnants (Fig. S1 in supplementary material), following the methodology described by Felfili *et al*. (2005). Data were collected in October 2017. The T1 and T2 environments in each fragment are separated by a road (interconnecting the studied perimeter with adjacent urban areas), which functions as a firebreak by preventing the passage of fire. It is important to emphasize that T1 environments were subjected to fire in August 2016 with a recurrence in August 2017.

A grid of eight equidistant (18 m) 7 x 50 m (350 $m^2$) plots (sampling units) was systematically inserted in each T1 and T2 environment of the three remnants for a total of 0.56 ha for each remnant (Fig. 1), and a grand total of 1.68 ha of inventoried area. Floristic and phytosociological surveys were undertaken in all plots with all tree and shrub individuals with minimum stem diameters ≥ 5 cm at 30 cm above soil level ($DB_{30}$) being identified to the species level, according to the protocol of Felfili *et al*. (2005). The circumference of each living shrub and tree was measured at 30 cm above soil level while their total height was measured with a telescopic rod (~ 5 m) with the help of experienced field crews.

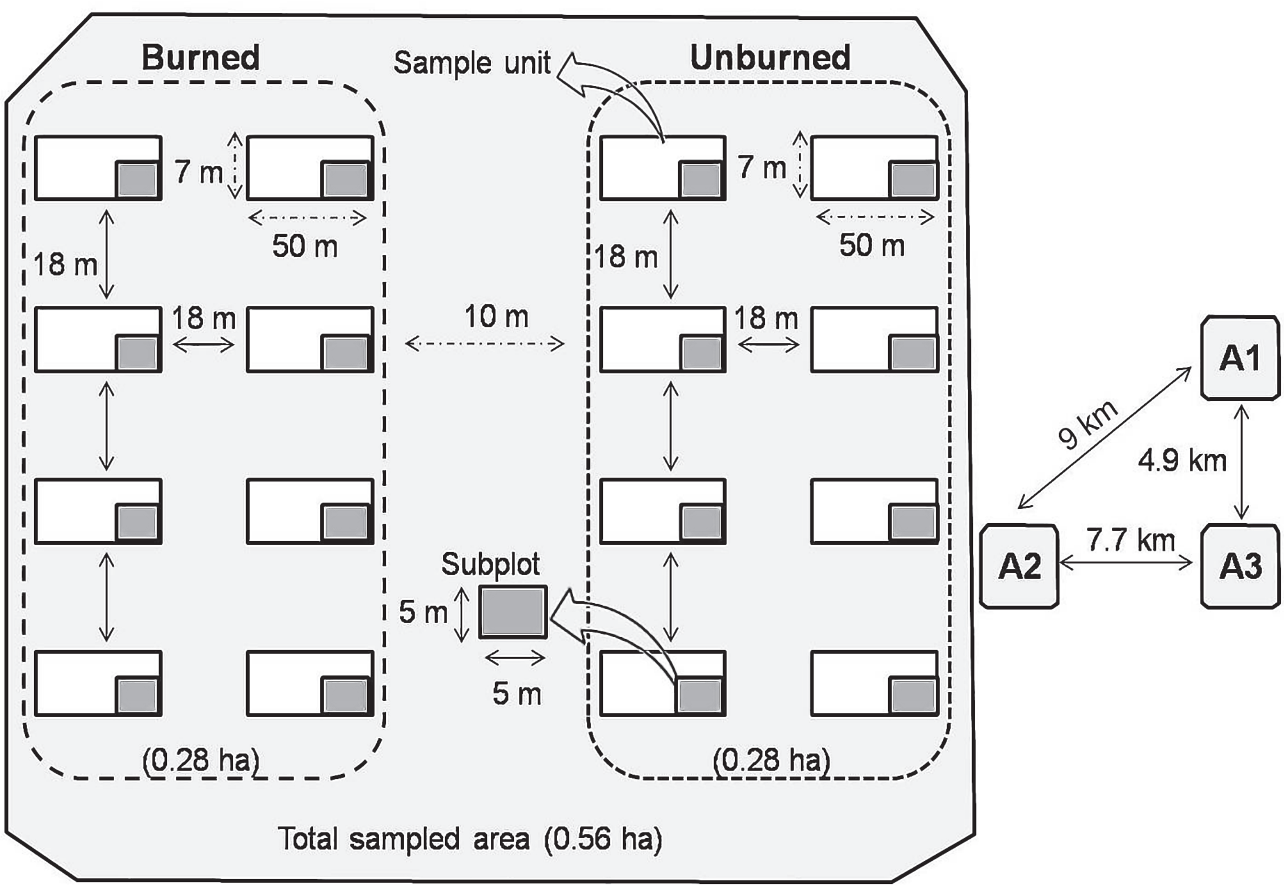


**Figure 1.** Plots (sampling units) used for the study of adult tree and shrub species and natural regeneration in savanna remnants of the state of Amapá, Brazil.

A 5 x 5 m subplot was established in each of the 48 plots used for the floristic survey of the adult stratum for a total of 48 subplots for sampling the regeneration stratum (Fig. 1). The criteria for the inclusion of individuals were height (h) 0.30 m < h ≤ 1 m and diameter 2.5 cm ≤ $DB_{30}$ < 5 cm. The plants were previously identified in the field with the help of specialists, respecting classical standards of taxonomy, while fertile botanical material was collected for those species not identified *in loco*, which was then herborized and deposited in the didactic collection of plants at the Universidade do Estado do Amapá (UEAP), following the scientific names of Flora do Brasil 2020 em construção (2018) and Angiosperm Phylogeny Group (APG IV 2016). Synonyms and the spelling of the names of taxa were updated by consulting the species index of the Royal Botanic Garden and the Missouri Botanical Garden database, available at <http://legacy.tropicos.org/Home.aspx>.

## Soil collection and analysis

Soil samples for physical-chemical analysis were systematically collected in only 36 of the 48 total plots of the remnants since they are geographically close to one another. Therefore, soil samples were collected in 12 of the 16 sample plots of each remnant, with six in T1 and six in T2. The samples were obtained from the 0–20 cm layer using a Dutch auger, with each sample being composed of eight subsamples obtained by way of zigzag displacement, according to the protocol of Donagema *et al*. (2011).

Granulometric analysis was performed using 0.1 mol $L^{-1}$ NaOH as a chemical dispersant and shaking with an apparatus at 50 rpm for 16 hours. The coarse and fine sand contents were then separated by wet sieving using a mesh sizes of 0.2 mm and 0.053 mm, respectively, thereby obtaining the total sand fraction. Clay fractions were determined by the pipette method and the silt fraction calculated as the difference between the total sand and clay fractions, as suggested by Camargo *et al*. (2009).

The following constituents were determined by chemical analysis: organic matter (OM), hydrogenionic potential (pH in $H_2O$), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), potential acidity (H + Al) and aluminum (Al). The concentrations of Ca, Mg and exchangeable Al were determined by AAS (Atomic Absorption Spectrometry) after extraction with one mol $L^{-1}$ KCl at a ratio of 1:20. Exchangeable K and Na were extracted with $Mehlich^{-1}$ solution and determined by flame photometry. Phosphorus was extracted with 0.05 mol $L^{-1}$ HCl and 0.025 mol $L^{-1}$ $H_2SO_4$ ($Mehlich^{-1}$) and determined by ascorbic acid colorimetry (Donagema *et al*. 2011). Potential acidity was determined by titration with 0.025 mol $L^{-1}$ NaOH of the extraction of 0.5 mol $L^{-1}$ calcium acetate at pH 7.0. The values for these elements were used to calculate sum-of-bases (SB), cation exchange capacity (CEC) and base saturation percentage (V).

## Floristics and community structure

The characteristics of the horizontal structure of the forest communities in the T1 and T2 environments of each remnant (A1, A2 and A3) were determined from the following phytosociological parameters: absolute (AD) and relative (RD) densities, absolute (AF) and relative (RF) frequencies, absolute (ADo) and relative (RDo) dominance, coverage value (CV) and importance value (IV). These parameters were calculated using the Fitopac 2.1 program (Shepherd 2010). The distribution of individuals was analyzed by diametric and height classes, with the division of these classes following the Spiegel formula as cited by Felfili & Fagg (2007).

Floristic characterization of the remnants was based on inventorying the species composition of the adult and woody regenerating strata, highlighting the following community parameters: richness (S, number of species numers), diversity (H', Shannon index, natural logarithm basis) and evenness (J', Pielou's species evenness index) (Magurran 1988). Floristic similarity among remnants was assessed by the Sørensen similarity index (Sij), which evaluates floristic similarity based on species common among remnants, as described by Mueller-Dombois & Ellemberg (1974).

## Statistical analysis

We first performed an exploratory data analysis to investigate the characteristics of the dendrometric variables of vegetation. This procedure avoids substantial errors, since a partial analysis makes it possible to diagnose inappropriate data and reveals normality and outliers by the graphic box-plot technique (Ruppert 2011).

We then constructed three data matrices for analyzing the interactions between species and soil attributes, as follows: (1) a vegetation matrix with the values of species density per plot (based on the union of data about the abundance of individuals in both the adult and regeneration strata, that is, considering the sum of the values found in both strata for each remnant); (2) an edaphic matrix with soil analysis data; and (3) a spatial matrix with the geographical coordinates of the center of each plot, which all three matrices were analyzed by canonical correspondence analysis (CCA) (Ter Braak 1987).

The edaphic matrix initially consisted of the following soil 12 variables: pH, OM, P, K, molar ratios ($Ca^{+}$ + $Mg^{2+}$), H + Al, $Al^{3+}$, SB, CEC, and total sand, silt and clay fractions. The dataset was reduced after applying linear combinations by means of principal component analysis (PCA), in which we selected attributes with very high correlations (> 70 %) with the first ordination axis of the PCA. This procedure helped eliminate variables with low correlations and significance, resulting in the selection of nine principal edaphic variables (pH, OM, P, K, H + Al, CEC, clay, silt and total sand).

We then performed a second PCA to correlate these edaphic variables with the plots of the sampled communities. Thus, we aimed to group plots with soils with similar attributes. We carried out a hierarchical classification of plots. (sample units) to group them according to average values for the physicochemical properties of the soil, adopting the agglomerative hierarchical clustering technique with "Unweighted Pair Group Method with Arithmetic Mean" (UPGMA) as described by Ruokolainen & Tuomisto (1998). Differences in soil attributes between burned and unburned environments were tested for significance by one-way ANOVA, followed by post-hoc corrected two tail T-test assuming equal variances ($P < 0.05$), using R software version 3.4.0 (R Development Core Team 2016).

Canonical correspondence analysis was used to assesses correlations between species distributions among plots and the environment (Ter Braak 1987). In this case, a primary matrix of species was built using the most abundant species in the three remnants (n ≥ 10 individuals; total of 14 species) and a secondary matrix of the variables selected by the PCA, according to the procedure used by Mendonça *et al.* (2017). Abundance was adopted as a criterion to eliminate rare or low abundance species from the analysis since they could generate redundancies among variables (Ter Braak 1987). Values of the species abundance matrix were transformed by their natural logarithm ($x = \ln(y + 1)$) in order to standardize the data and enable comparisons between variables with very high values (Ter Braak & Smilauer 2002).

A Monte Carlo test, with 999 permutations at 5 % probability, was used to evaluate the significance of species-environment relationships with the ordination axes generated by the CCA using the vegan package in R software version 3.4.0 (R Development Core Team 2016), as indicated by Borcard *et al.* (2011). In this approach, the CCA enables a direct ordination of the gradient and attempts to explain species distributions in relation to the main components of the PCA, which in turn is a representation of environmental variables (Ter Braak 1987).

Methods of variation partitioning were applied to complement direct ordination gradient from the CCA (Økland & Elilertsen 1994), including spatial vectors of all plots with the respective geographic coordinates. Following Eisenlohr (2014), variance partitioning was performed of the explanation provided by: [a] only spatial components; [b] the spatially structured fraction of these variables; [c] a group of soil physicochemical variables including pH, OM, P, K, CEC, clay, silt and sands; and [d] factors not measured.

Partial redundancy analysis (RDA) was used to determine the proportion of the variance in the vegetation composition data that is attributable to soil properties and spatial location of each plot (Peres-Neto & Legendre 2010). This analysis used the packages 'vegan', 'adespatial' and 'spdep' of the R statistical environment (R Development Core Team 2016). Variation partitioning by RDA was performed to find the relative contributions of soil properties. For this reason, both simple term effects ([a] and [c]) and conditional term effects [b] were included in determining which parameters were most likely responsible for floristic-structural variation.

## Results

### *Vegetation composition, structure and diversity*

We can observe the implications about the studied vegetation structure data revealed a slightly homogeneous structural behavior between T1 and T2 environments (Fig. 2). The narrow standard deviation (arrow segment) around the mean (black point) confirms the low dispersion of the data set; however, some atypical values (*outliers*) still appeared

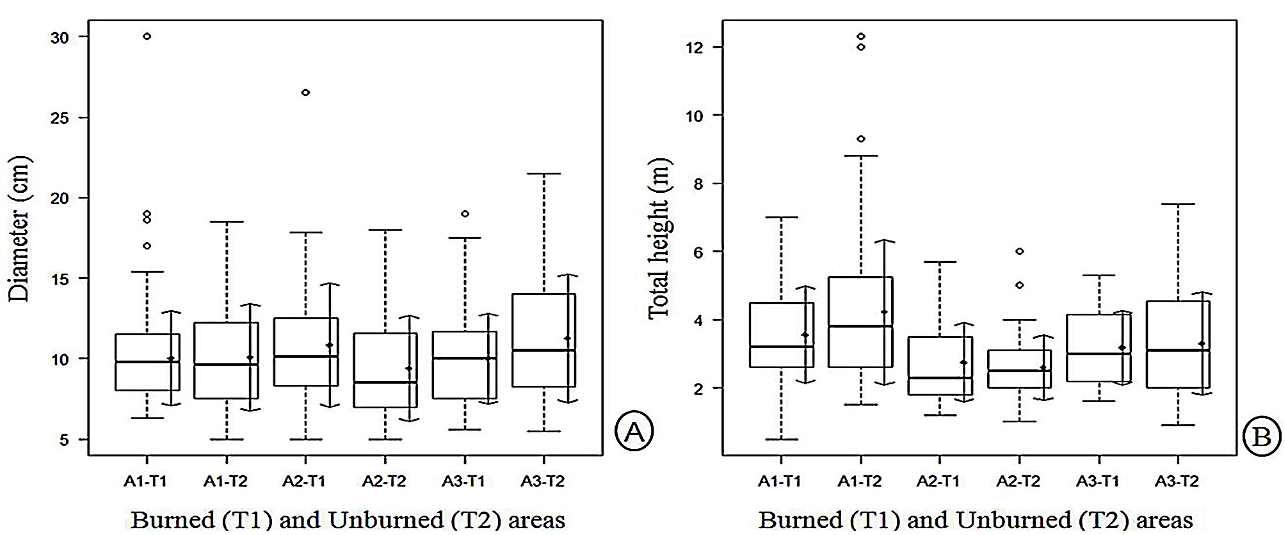


**Figure 2.** Box-plot of the variables diameter (**A**) and total height (**B**) of plant species inventoried in burned (T1) and unburned (T2) environments of the studied savanna remnants. Black dost (●) represent mean values while dots (○) indicate potential *outliers* for the data set of the dendrometric variables.

(Fig. 2), as this discrepancy is a function of the number of differentiated plants in each evaluated plot, since it is a common characteristic of this vegetation.

The diameter of plants ranged from 5 cm to 30 cm (Fig. 2A). The majority of the forest community species were distributed in diameter classes between 7 and 14 cm (50 %, interquartile range), considering both burned (T1) and unburned (T2) environments in the studied savanna remnants. The highest frequency of heights per species is similarly in the range of 2 m to 5.7 m in both environments (Fig. 2B).

Of all the individual plants sampled (1.68 ha) in the inventory, 808 were adult and regenerating individuals with a basal area (BA) of 16.24 $m^2$ (Tab. 1). These individuals were distributed across 21 botanical families, 30 genera and 34 species. The richest families in the survey were Myrtaceae (4 species), followed by Dilleniaceae (3), Fabaceae (3), Rubiaceae (3), Anacardiaceae (2), Bignoniaceae (2), Hypericaceae (2) and Malpighiacaeae (2), which together represented 61.76 % of the recorded species. The remaining 13 families had only one species each and accounted for the remaining 38.24 %.

The number of individuals in the adult stratum was higher in T2 (unburned) environments than in T1 (burned) environments. The regenerating stratum had an inverse relationship, with a higher number of individuals in T1 than in T2, with the exception of A2 (Tab. 1). Basal areas of the trees in T1 and T2 of each sampled fragment suggest marked differences among the three forest remnants, with BA for T2 being higher than for T1 (Tab. 1).

In general, A1 had the highest floristic richness (Tab. 1). There was minimum difference in the number of species (S) recorded for both adult and regenerating strata between plots in T1 and T2 in the three remnants since the adult stratum in T2 environments had a higher species richness than the adult stratum in T1 environments, except in A3 where the number of species was equal.

Diversity for the adult stratum was low, ranging from H' = 1.15 nats $ind^{-1}$ for A2-T1) to H' = 1.86 nats $ind^{-1}$ for A1-T2 (Tab. 1). Moreover, H' values for the regenerating stratum were substantially higher, suggesting significant floristic heterogeneity of vegetation cover. Similarly, species evenness (J') was better for the regenerating stratum than for the adult stratum. On the other hand, species evenness (J') revealed a uniform distribution of the number of individuals per species in both T1 and T2 environments (Tab. 1).

The phytosociological analysis indicated no significant differences in species composition among remnants (Tab. S1 in supplementary material). This is because the three remnants had the same floristic composition of the adult tree stratum of T1 and T2 (Tab. 2), which was also true for the regenerating stratum (Tab. 3).

It was observed that 21 % of all the species occurred in all three remnants. The most important of these, due to their concomitant occurrence in the adult and regenerating stratum strata, were *Salvertia convallariodora*, *Byrsonima crassifolia*, *Curatella americana*, *Palicourea rigida*, *Ouratea hexasperma*, *Annona paludosa* and *Casearia sylvestris* (Tabs. 2, 3). These seven species were responsible for more than half (> 150 %) of the cumulative importance value (IV) for each of the T1 and T2 environments of the three analyzed remnants.

The species *Byrsonima crassifolia* and *Salvertia convallariodora* had greater IV in the T1 and T2 environments (Tab. 2), and consequently greater phytosociological importance in the woody community. For the regenerating stratum, the species *Byrsonima coccolobifolia*, *Myrcia fallax*, *Myrcia splendens*, *Protium heptaphyllum*, *Pterogyne nitens*, *Tapirira guianensis* and *Zanthoxylum rhoifolium* were only recorded in A1 (Tab. 3). However, five species had moderate frequencies in the regeneration stratum of the three remnants, namely *Casearia sylvestris*, *Curatella americana*, *Erythroxylum suberosum*, *Palicourea rigida* and *Salvertia convallariodora* (Tab. 3).

The Sørensen similarity index (Sij) indicated a moderate degree of similarity in the floristic diversity of A1 and A3 (Sij = 51.42 %; with nine species in common) and of A2 and A3 (Sij = 70.58 %; with 12 species in common). On the other hand, the low degree of similarity between the A1

**Table 1.** Results for structural parameters of adult and regenerating vegetation of cerrado *sensu stricto* inventoried in burned (T1) and unburned (T2) environments of savanna remnants of the state of Amapá, Brazil.

| Tree stratum | Structural parameters | Area (1) | | Area (2) | | Area (3) | |
|---|---|---|---|---|---|---|---|
| | | T1 | T2 | T1 | T2 | T1 | T2 |
| **Adult** | N | 91.00 | 173.00 | 38.00 | 92.00 | 44.00 | 68.00 |
| | BA | 2.87 | 5.29 | 1.68 | 2.55 | 1.75 | 2.10 |
| | S | 10.0 | 12 | 6.0 | 10.0 | 6.00 | 6.00 |
| | H' | 1.44 | 1.86 | 1.15 | 1.38 | 1.22 | 1.38 |
| | J' | 0.67 | 0.78 | 0.60 | 0.65 | 0.65 | 0.71 |
| **Regenerant** | N | 62.00 | 56.00 | 43.00 | 49.00 | 47.00 | 45.00 |
| | S | 16.00 | 17.00 | 15.00 | 14.00 | 14.00 | 11.00 |
| | H' | 2.65 | 2.70 | 3.32 | 2.56 | 2.41 | 2.37 |
| | J' | 0.92 | 0.92 | 0.95 | 0.90 | 0.88 | 0.90 |

N: total number of individuals/0.28ha; BA: basal area ($m^2$/0.28ha); S: number of species; H': Shannon-Wiener diversity index; J': Pielou equability index.

**Table 2.** Number of individuals (N) and importance value (IV) per species in burned (T1) and unburned (T2) environments of savanna remnants of the state of Amapá, Brazil.

| Species | N | | | | | | IV | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | T1 | | | T2 | | | T1 | | | T2 | | |
| | A1 | A2 | A3 | A1 | A2 | A3 | A1 | A2 | A3 | A1 | A2 | A3 |
| *Byrsonima crassifolia* (L) Kunth. | 33 | 14 | 13 | 60 | 41 | 28 | 91.32 | 101.22 | 113.31 | 84.52 | 110.23 | 100.52 |
| *Salvertia convallariodora* A. St.-Hil. | 19 | 19 | 11 | 77 | 34 | 27 | 55.53 | 131.74 | 71.87 | 119.13 | 108.36 | 120.77 |
| *Curatella americana* L. | 4 | 1 | 16 | 10 | 2 | 9 | 13.39 | 11.02 | 81.04 | 25.31 | 12.42 | 56.42 |
| *Palicourea rigida* Kunth. | 1 | 1 | 1 | 3 | 5 | – | 4.96 | 9.04 | 8.63 | 8.68 | 16.48 | – |
| *Byrsonima coccolobifolia* Kunth. | 5 | – | – | – | – | – | 20.3 | – | – | – | – | – |
| *Himatanthus sucuuba* (Spruce ex Müll. Arg.) Woodson | 13 | 1 | – | 5 | – | – | 55.01 | 10.96 | – | 15.56 | – | – |
| *Vismia cayennensis* (Jacq.) Pers. | 2 | – | – | – | – | – | 9.7 | – | – | – | – | – |
| *Ouratea hexasperma* (A. St.-Hil.) Baill. | 1 | – | – | 4 | 1 | 1 | 6.08 | – | – | 6.48 | 8.45 | 7.14 |
| *Tabebuia aurea* (Manso) Benth. & Hook.f. | 2 | – | – | – | – | – | 5.96 | – | – | – | – | – |
| *Annona paludosa* Aubl. | 1 | – | – | 1 | 1 | 2 | 5.41 | – | – | 3.82 | 9.2 | 8.83 |
| *Platypodium elegans* Vogel | 9 | – | – | – | – | – | 27.4 | – | – | – | – | – |
| *Vismia guianensis* (Aubl.) Choisy | 1 | – | – | – | – | – | 4.96 | – | – | – | – | – |
| *Aegiphila verticillata* Vell. H | – | 2 | – | – | 1 | 1 | – | 36.02 | – | – | 6.39 | 6.31 |
| *Tocoyena formosa* (Cham. & Schltdl.) | – | – | 1 | – | – | – | – | – | 7.71 | – | – | – |
| *Tabebuia caraiba* (Mart.) | – | – | 2 | – | – | – | – | – | 17.43 | – | – | – |
| *Guettarda angelica* Mart. ex Mull. Arg | – | – | – | 7 | – | – | – | – | – | 18.72 | – | – |
| *Byrsonima coccolobifolia* Kunth. | – | – | – | 5 | – | – | – | – | – | 14.02 | – | – |
| *Vismia cayennensis* (Jacq.) Pers. | – | – | – | 1 | – | – | – | – | – | 3.76 | – | – |
| *Acacia mangium* Willd. | – | – | – | – | 4 | – | – | – | – | – | 13.85 | – |
| *Anacardium occidentale* L. | – | – | – | – | 2 | – | – | – | – | – | 8.71 | – |
| *Mimosa caesalpiniifolia* Benth. | – | – | – | – | 1 | – | – | – | – | – | 5.91 | – |
| **Total** | **91** | **38** | **44** | **173** | **92** | **68** | **300** | **300** | **300** | **300** | **300** | **300** |

**Table 3.** Number of individuals (N) per species, with the assignment of codes to their respective scientific names, of the regenerating stratum of burned T1 and unburned T2 environments of savanna remnants of the state of Amapá, Brazil.

| Code | Species | Area (1) | Area (2) | Area (3) | Area (1) | Area (2) | Area (3) |
|---|---|---|---|---|---|---|---|
| | | T1 (N) | T1 (N) | T1 (N) | T2 (N) | T2 (N) | T2 (N) |
| Ac man | *Acacia mangium* Wild. | – | 1.0 | – | – | 3.0 | – |
| Ae ev | *Aegiphila verticillata* Vell. H. | – | 7.0 | 3.0 | – | 6.0 | 4.0 |
| An occ | *Anacardium occidentale* L. | – | 1.0 | – | – | – | – |
| An pa | *Annona paludosa* Aubl. | 3.0 | – | 3.0 | – | 1.0 | 1.0 |
| Br gau | *Brosimum gaudichaudii* Trec. | – | – | 2.0 | – | – | – |
| By co | *Byrsonima coccolobifolia* Kunth | 4.0 | – | – | 3.0 | – | – |
| By cra | *Byrsonima crassifolia* (L.) Kunth | 8.0 | 4.0 | 8.0 | – | – | – |
| Ca sy | *Casearia sylvestris* Sw. | 8.0 | 6.0 | 8.0 | 8.0 | 6.0 | 6.0 |
| Cu ame | *Curatella americana* L. | 5.0 | 2.0 | 1.0 | 2.0 | 4.0 | 4.0 |
| Do den | *Doliocarpus dentatus* (Aubl.) Standl. | – | – | – | – | 2.0 | – |
| Er sub | *Erythroxylum suberosum* A. St.-Hil. | 2.0 | 1.0 | 4.0 | 1.0 | 1.0 | 6.0 |
| Eu pun | *Eugenia punicifolia* (Kunth) DC | – | – | 1.0 | – | – | – |
| Hi suc | *Himatanthus sucuuba* (Spruce ex Müll. Arg.) Woodson | 2.0 | 3.0 | – | 2.0 | 1.0 | – |
| Myr fa | *Myrcia fallax* (Rich.) DC. | 3.0 | – | – | 4.0 | – | – |
| Myr sp | *Myrcia splendens* (Sw.) DC. | 2.0 | – | – | 1.0 | – | – |
| Ou hex | *Ouratea hexasperma* (A. St.-Hil.) Baill. | 4.0 | 1.0 | 2.0 | 2.0 | 3.0 | – |
| Pa rig | *Palicourea rigida* Kunth. | 6.0 | 5.0 | 2.0 | 1.0 | 7.0 | 6.0 |
| Pl el | *Platypodium elegans* Vogel | 1.0 | – | 1.0 | 5.0 | – | 1.0 |
| Pr hep | *Protium heptaphyllum* (Aubl.) Marchand | – | – | – | 1.0 | – | – |
| Psi gua | *Psidium guajava* L. | – | 1.0 | 1.0 | – | – | 5.0 |
| Pt nit | *Pterogyne nitens* Tul. | – | – | – | 2.0 | – | – |
| Rou mo | *Roupala montana* Aubl. | – | – | – | – | 1.0 | – |
| Sa con | *Salvertia convallariodora* A. St.-Hil. | 7.0 | 6.0 | 8.0 | 4.0 | 7.0 | 6.0 |
| Sa glan | *Sapium glandulosum* (L.) Morong | – | – | – | – | 1.0 | – |
| Tab car | *Tabebuia caraiba* (Mart.) | – | 1.0 | 1.0 | – | – | 3.0 |
| Tap gui | *Tapirira guianensis* Aubl. | 1.0 | – | – | 5.0 | – | – |
| To for | *Tocoyena formosa* (Cham. & Schltdl.) | – | 2.0 | 2.0 | – | 4.0 | 3.0 |
| Vi cay | *Vismia cayennensis* (Jacq.) Pers. | – | – | – | 6.0 | – | – |
| Vi gui | *Vismia guianensis* (Aubl.) Choisy | 5.0 | 2.0 | – | 8.0 | 2.0 | – |
| Zan rho | *Zanthoxylum rhoifolium* Lam. | 1.0 | – | – | 1.0 | – | – |

and A2 (Sij = 48.78 %) indicates that they do not belong to the same plant community, even though they have ten species in common.

Regarding horizontal structure, the diameter of plants in T2 environments followed the expected pattern for native vegetation (an inverted-"J"), with a greater number of individuals in smaller-size classes and decreasingly fewer in increasing size classes (Fig. 3A). However, among T1 environments this tendency was only observed for A1-T1.

The analysis of diametric structure revealed that more than half (79 %) of all individuals inventoried in all environments blonged in the first three diameter classes, which comprises individuals between 5 cm and 15 cm (Fig. 3A), with few woody plants (2 %) with $DB_{30}$ > 20 cm. The maximum diameter measured in T1 environments was 30 cm for an individual of *Salvertia convallariodora*, while for T1 environments it was 21.5 cm for an individual of *Byrsonima crassifolia*.

Analysis of each T1 and T2 environment per fragment in isolation revealed that the frequencies of individuals per diametric classes were higher in T2 than T1 (Fig. 3A). There was a greater frequency of individuals with $DB_{30}$ < 10 cm in T2 environments (Fig. 3A), with significant percentages of 72.42 %, 57.51 % and 67.18 % for A1-T2, A2-T2 and A3-T2 respectively, while areas A1-T1, A2-T1 and A3-T1 had 68.18 %, 69.75 % and 55.54 %, respectively.

Height revealed a positive asymmetric class distribution (Fig. 3B), with the highest frequency of individuals (67.2 %) being in the initial classes between 2.17 m and 4.85 m, and only eight with Ht > 7.5 m. The average height for A1-T2 was 4.21 m, with a maximum of 12 m and a minimum of 1.8 m, revealing a distribution tending towards uniformity and a greater concentration of individuals (59.3 %) between 2.25 m and 3.65 m, including 13 of *Salvertia convallariodora* and *Byrsonima crassifolia* having Ht > 6 m. However, in A1-T1 the average height was 3.55 m, with a maximum of 7.3 m and minimum of 1.5 m. The mean height for A2- was

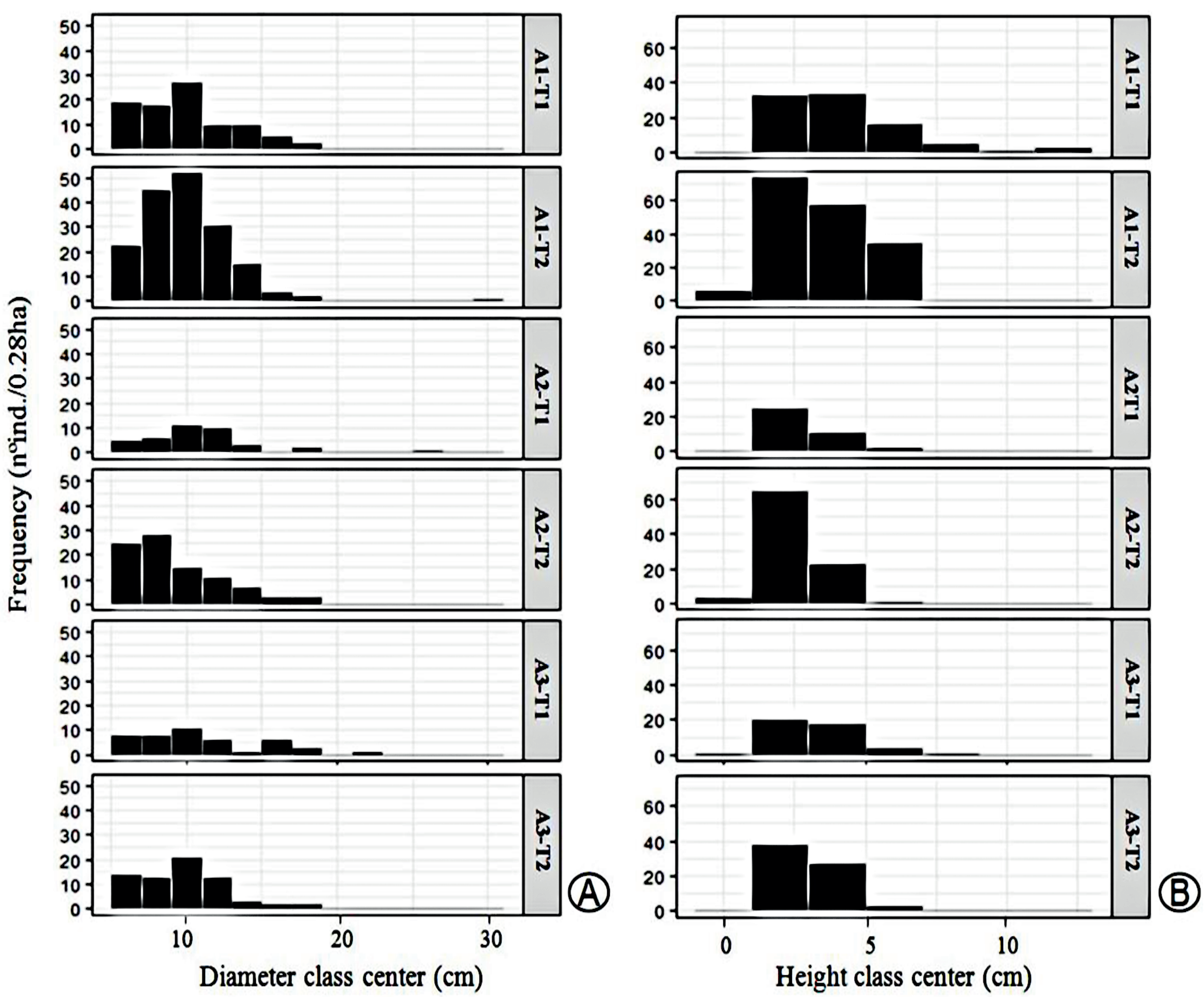


**Figure 3.** Frequency of individuals by diameter (**A**) and height (**B**) class recorded in the burned (T1) and unburned (T2) environments of the three studied savanna remnants in the state of Amapá, Brazil.

2.74 m, with a maximum of 5.7 m and a minimum of 1.2 m, demonstrating a positive asymmetrical distribution (Fig. 3B), with a greater abundance of individuals (79.4 %) being concentrated between 1.54 m and 2.24 m, that is, in the first altimetric classes. The species that dominated this vertical stratum were *Salvertia convallariodora*, *Byrsonima crassifolia* and *Curatella americana*, with all three having seven individuals recorded. These species also dominated the vertical stratum of A2-T2, with eight individuals for each being distributed between height classes.

In T2 environments, only 36 individuals of nine species had heights between 10 m and 17 m, namely: *Byrsonima crassifolia* (11 individuals), *Salvertia convallariodora* (9), *Himatanthus sucuuba* (6), *Curatella americana* (2), *Vismia cayennensis* (2), *Platypodium elegans* (2), *Ouratea hexasperma* (1), *Byrsonima coccolobifolia* (1), and *Annona paludosa* (1). In T1 environments, however, most species had individuals with heights of less than 7.5 m, with the exception of the *Byrsonima crassifolia*, which had two individuals with heights above 10 m in A1-T1.

## *Edaphic variables and species distribution*

The three studied remnants had soils with low nutrients, high acidity (pH < 6.0) and low saturation percentage by bases (V), demonstrating that the physical-chemical attributes of T1 and T2 environments are relatively homogeneous, although with significantly different concentrations (P < 0.05) for some attributes (pH, OM, P, K, and H+Al), with the highest mineral concentrations in T1 areas (Tab. 4).

The highest P and K concentrations were detected in T1 environments, with mean values ranging from 2.87 to 3.20 mg $dm^{-3}$ and 1.06 to 1.26 mg $dm^{-3}$, respectively (Tab. 4). In general, Ca + Mg levels varied from low to moderate in T1 and T2 environments, respectively. Potential acidity (H + Al) was significantly higher in T1, while OM content was higher in T2, with low V both T1 and T2 (Tab. 4). The granulometric analysis indicated that the soil has a predominantly clayey-loam texture according to classification by Donagema *et al.* (2011), with greater clay contents in T2 environments and the highest fractions of total sand in T1.

PCA ordination of the sampled plots according to the soil physical-chemical attributes evidenced three very distinct groups among the fragments (Fig. 4A), and the variance percentages explained by the PCA axes were 51.50, 32.50 and 15.85 % for axis 1, 2 and 3 respectively (Fig. 4B).The barycenter of each grouping is presented in the plots (Fig. 4C), and the distributions of soil properties (components of greater influence according to the PCA) are represented by vectors which indicate the direction of increasing values for each.

By diagnosis of the linear combination of the set of 12 variables (pH, OM, P, K, $Ca^{+}$ + $Mg^{2+}$, H + Al, $Al^{3+}$, SB, CEC, total sand, silt and clay), the PCA determined which of the combinations are responsible for most of the variability in the data. In this case, six variables presented values > 1.0 (clay, silt, total sand, OM, CEC and P), which together accounted for 99.98 % of the variability of the original data, which includes soil texture and the concentrations of these three chemical attributes. In general, axis one was associated with soil chemical variables, while axis 2 reflected physical variables.

The first two axes of the PCA explained 83.80 % of the variation, with the first axis, explaining 51.30 %, being influenced by the clay variable, which had a negative eigenvalue (-0.86), and P, which had a positive eigenvalue (0.77). The second axis, which explained 32.50 %, was influenced by silt, with a negative eigenvalue (-0.84), and by the OM, with a positive eigenvalue (0.78). Despite the low importance of the third axis (16 %), it revealed a significant positive score for OM, P and sand, and a high negative score for silt.

The hierarchical classification formed three groups. Group 1 is mostly composed of the majority of A2 plots (Fig. 4A), which includes plots 7 to 12 of T1 and 25 to 30 of T2. Group 3 is formed by a majority of A1 plots, which includes plots

**Table 4.** Physical and chemical properties of soil in burned (T1) and unburned (T2) environments of savanna remnants of the state of Amapá, Brazil. Values for plots are means and their standard deviations, followed by T-test result.

| Soil attributes | A1 | | *P* | A2 | | *P* | A3 | | *P* |
|---|---|---|---|---|---|---|---|---|---|
| | T1 | T2 | | T1 | T2 | | T1 | T2 | |
| pH ($H_2O$) | 5.50 ± 0.16 a | 4.97 ± 0.24 b | **0.017** | 5.48 ± 0.27 a | 4.95 ± 0.10 b | **0.011** | 5.23 ± 0.23 a | 5.03 ± 0.26 b | **0.031** |
| OM ($g.kg^{-1}$) | 17.82 ± 2.27 a | 15.72 ± 3.83 b | **0.042** | 19.13 ± 3.31 a | 17.04 ± 4.24 b | **0.023** | 24.28 ± 7.42 a | 18.09 ± 5.08 b | **0.001** |
| P ($mg.dm^{-3}$) | 2.87 ± 0.66 a | 2.11 ± 0.87 b | **0.001** | 3.20 ± 0.52 a | 2.12 ± 0.49 b | **0.041** | 3.09 ± 0.75 a | 1.84 ± 0.77 b | **0.022** |
| K ($cmolc.dm^{-3}$) | 1.06 ± 0.06 a | 0.73 ± 0.01 b | **0.003** | 1.26 ± 0.06 a | 0.54 ± 0.01 b | **0.011** | 1.16 ± 0.04 a | 0.89 ± 0.02 b | **0.022** |
| Ca + Mg ($cmolc.dm^{-3}$) | 1.60 ± 0.68 a | 1.05 ± 0.24 a | 0.204 | 1.73 ± 0.52 a | 1.40 ± 0.12 a | 0.396 | 1.89 ± 0.16 a | 1.44 ± 0.29 a | 0.447 |
| Al ($cmolc.dm^{-3}$) | 0.45 ± 0.19 a | 1.03 ± 0.14 a | 0.064 | 1.10 ± 0.34 a | 1.24 ± 0.36 a | 0.186 | 1.09 ± 0.31 a | 1.29 ± 0.44 a | 0.143 |
| H + Al ($cmolc.dm^{-3}$) | 6.07 ± 0.43 a | 6.92 ± 0.46 b | **0.013** | 6.02 ± 0.77 a | 6.87 ± 1.18 b | **0.002** | 5.65 ± 1.19 a | 6.86 ± 1.34 b | **0.010** |
| BS ($cmolc.dm^{-3}$) | 1.90 ± 0.70 a | 0.77 ± 0.27 a | 0.225 | 1.28 ± 0.57 a | 0.48 ± 0.10 a | 0.288 | 1.60 ± 0.19 a | 0.46 ± 0.30 a | 0.434 |
| CEC ($cmolc.dm^{-3}$) | 8.77 ± 1.45 a | 7.26 ± 1.33 b | **0.001** | 7.62 ± 0.80 a | 6.87 ± 0.59 b | **0.012** | 7.21 ± 0.59 a | 6.24 ± 0.95 b | **0.003** |
| Clay ($das.kg^{-1}$) | 38.63 ± 4.05 a | 40.34 ± 2.38 a | 0.136 | 35.62 ± 6.33 a | 37.65 ± 6.53 a | 0.162 | 31.22 ± 14.79 a | 35.54 ± 13.23 a | 0.272 |
| Sand ($das.kg^{-1}$) | 41.97 ± 3.18 a | 40.29 ± 3.30 a | 0.085 | 36.60 ± 9.56 a | 31.99 ± 9.32 a | 0.413 | 37.92 ± 10.06 a | 33.51 ± 9.39 a | 0.343 |
| Silt ($das.kg^{-1}$) | 19.63 ± 2.64 a | 20.87 ± 6.58 a | 0.353 | 32.88 ± 8.61 a | 30.99 ± 10.17 a | 0.068 | 27.87 ± 9.22 a | 25.16 ± 9.46 a | 0.264 |

Values on the same line followed by different letters differ by the T-test by 5%. Significant p-values (< 0.05) are highlighted in bold.

1 to 6 of T1 and 19 to 24 of T2, demonstrating a degree of similarity with Group (2). Plots 5 and 6 of A1-T2 formed the isolated Group 2 (Fig. 4A), as demonstrated by axis one of the PCA, which is positively associated with the highest P, K, OM, sand, CEC and pH values, and negatively associated with silt, H + Al and clay; a similar behavior to A3 and most of A1. In general, most T2 plots, located in the lower left of the diagram (Fig. 4C), were related to higher concentrations of H + Al and silt. The plots of T1, located in the upper right of the diagram (Fig. 4C), were related to higher concentrations of P and K and moderate OM concentrations.

The results of the CCA of the found eigenvalues are considered high (> 0.5), which suggests a substantial refinement by the PCA that summed the soil attributes for axes one and two of the CCA (Tab. 5). The three axes explained a total of 85.62 % of the accumulated variation, with 41.21 % for axis 1, 36.77 % for axis 2 and 7.64 % for axis three. This high explanation indicates positive correlations between components (PCs) and species, and was also confirmed by high species-environment correlations (> 60 %) for the three axes.

The Monte Carlo permutation test was significant at 5 % probability, indicating that species abundance and environmental variables are correlated with the first and second ordination axes (Tab. 5). According to the CCA ordination diagram (Fig. 5), the species *Casearia sylvestris* (Ca sy), *Curatella americana* (Cu ame) and *Erythroxylum suberosum* (Er sub) were strongly associated with levels of total sand, OM, P, and CEC on axis one. This axis was strongly positively associated with PC1 and PC3, and negatively associated with PC2. The majority of plots in the third quadrant (lower right of the ordination diagram) belong to T1 environments, suggesting that the highest correlations between the three species and the chemical attributes are located in these environments.

The ordination of species by CCA indicates that *Byrsonima coccolobifolia* (By co), *Himatanthus sucuuba* (Hi suc) and *Platypodium elegans* (Pl el) are abundant in more acidic soils with silty texture and high potential acidity (Fig. 5). The highest concentrations of these species were in plots 19, 20 and 21 of A1-T2, whose pH values were lower (more acidic) than in T1 (Fig. 4C).

**Table 5.** Results of the Canonical Correspondence Analysis (CCA) of principal components (PC) representing the physical-chemical properties of soil.

| Variables | Axis 1 | Axis 2 | Axis 3 |
|---|---|---|---|
| Eigenvalue | 0.5132 | 0.5028 | 0.08015 |
| Percentage of explained variance | 41.21 | 36.77 | 7.645 |
| Percentage of cumulative variance | 41.21 | 77.98 | 85.625 |
| Species-environment correlation | 0.775 | 0.728 | 0.672 |
| Significance of the correlation (Monte Carlo test) | 0.01 | 0.01 | 0.02 |
| **Correlations of the internal variables** | | | |
| PC1 | 0.4136 | 0.8091 | 0.00801 |
| PC2 | -0.5021 | -0.2986 | -0.07088 |
| PC3 | 0.3298 | -0.5230 | -0.23496 |

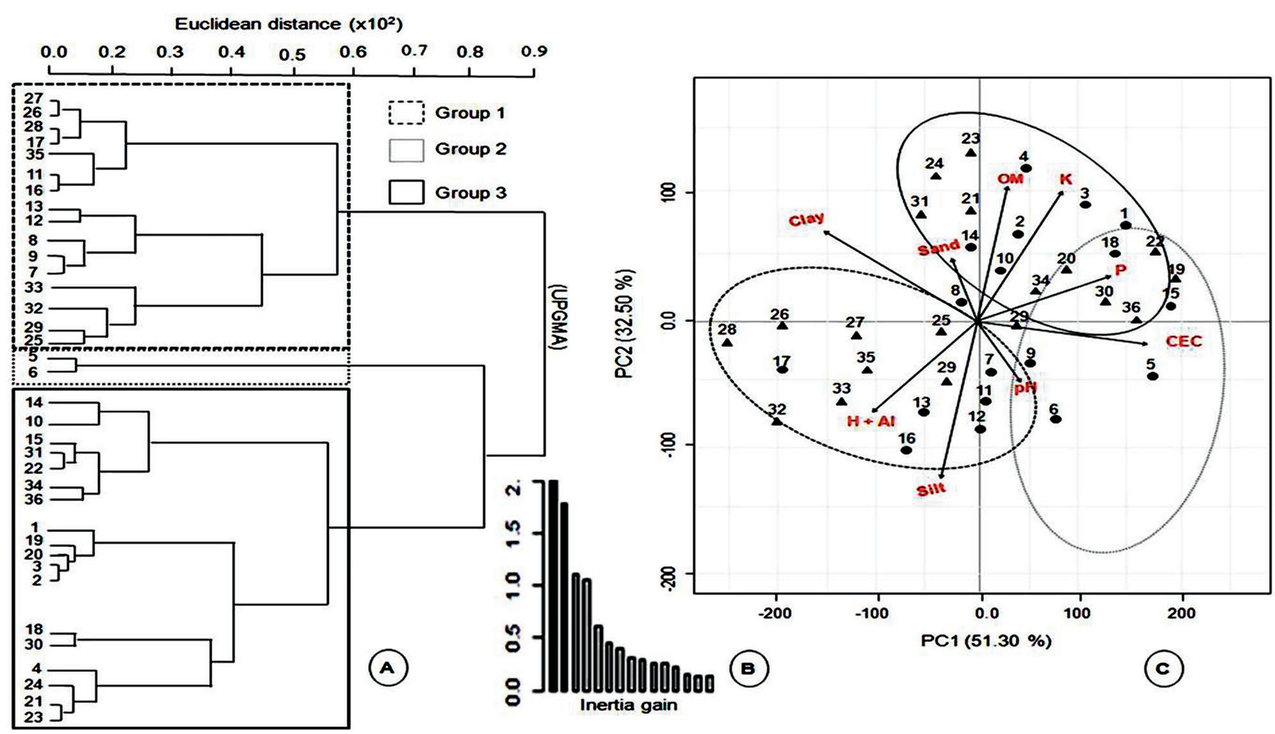


**Figure 4.** Results of PCA between soil properties of the plots of burned (●) and unburned (▲) environments of the three studied savanna remnants. (**A**) Hierarchical classification of the first factorial axes. (**B**) Values for the factorial axes. (**C**) Result of the analysis of chemical properties and the barycenter of the groups formed.

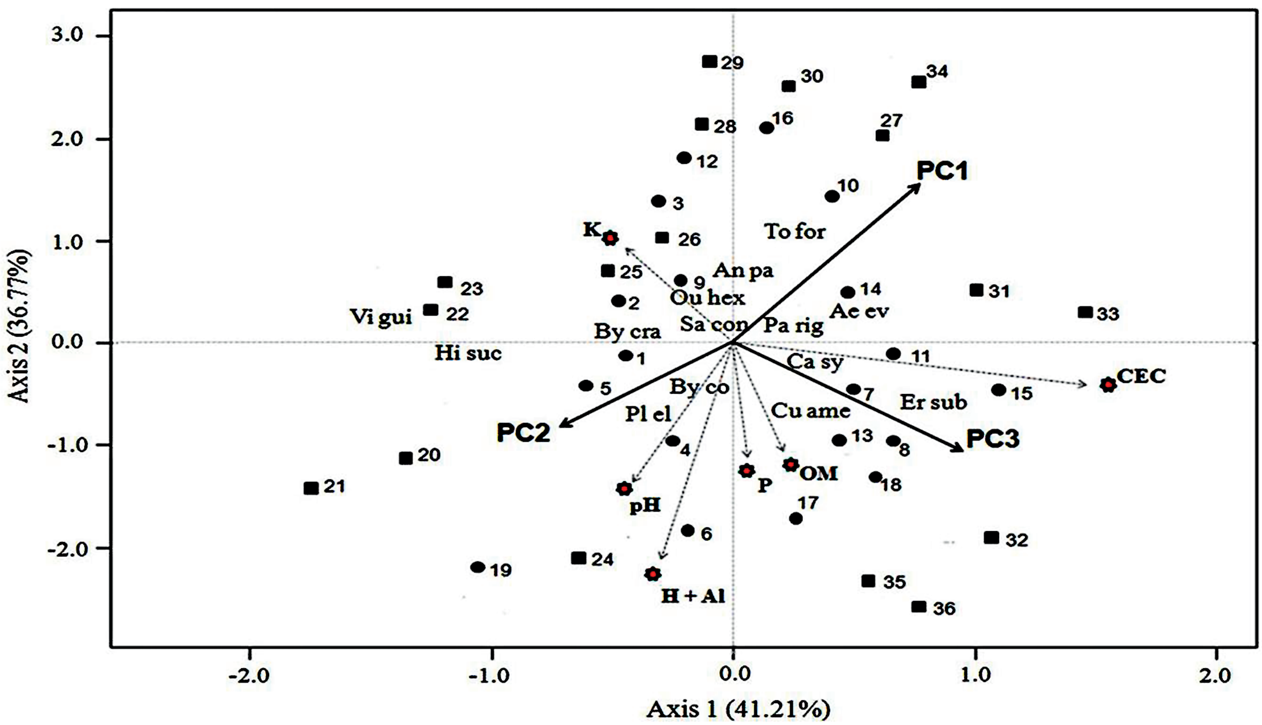


**Figure 5.** Ordination diagram for Canonical Correspondence Analysis (CCA) of axes 1 and 2 based on principal components of scores of edaphic variables and absolute plant densities on plots of burned (●) and unburned (■) environments of savanna remnants of the state of Amapá, Brazil.

Still considering the CCA, there was a set of more distributed species in soils with higher K and clay texture, such as, *Byrsonima crassifolia* (By cra), *Salvertia convallariodora* (Sa con), *Ouratea hexasperma* (Ou hex), *Annona padulosa* (An pa), *Palicourea rigida* (Pa rig), *Tocoyena formosa* (To for), *Aegiphila verticillata* (Ae ve) and *Vismia guianensis* (Vi gui) (Fig. 5). These species were distributed along the environmental gradient in the majority of A2-T2 plots and some A1-T1 plots, indicating intermediate values of association with the physical-chemical soil properties in these remnants.

### *RDA variation partitioning*

In summary, soil properties had greater influence on the species composition of T1 and T2 plots ([c] 27.20 %; $R^2aj$ = 0.623) than did the distance between plots ([a] 5.10 %; $R^2aj$ = 0.514), as determined by RDA variance partitioning. The fraction explained by the interaction between environment and space was also greater ([b] 24.10 %) than the fraction explained by only average [a] distance between plots; the unexplained fraction was moderate ([d] 43.6 %). As demonstrated by RDA, the effect of the interaction between fire and soil attributes was responsible for changes in macronutrient concentrations (P and K) and for a slight increase in pH, which contributed to the change in floristic structure and composition of T1 in relation to T2 in the three studied remnants, corroborating previous analyses (Figs. 4C, 5; Tabs. 3, 4).

## Discussion

### *Vegetation composition, structure and diversity*

The exploratory analysis of dendrometric variables showed little variation through the box-plot (Fig. 2A-B), with low dispersion in the dataset as indicated by the standard deviations. This suggests that the three remnants have the same physiognomic structure, even though the vegetation experienced the effects of fire. The mean and median values suggest asymmetry in the data distribution for diameter ($DB_{30}$) and total height (Ht) by remnant. Corroborating these results, comparative studies on the woody flora of cerrado *sensu stricto* (Aquino *et al*. 2007; Lopes *et al*. 2009; Pereira *et al*. 2016) recorded low variation in diameter and height in cerrado fragments with fire.

The number of species, genera and botanical families sampled only in the arboreal-shrub stratum (1.68 ha) are within the range previously reported for Amapá savannas (Costa-Neto 2014). Moreover, the number of families recorded (24) is close to the average of 22 to 36 recorded for cerrado *sensu stricto* vegetation in other regions of Brazil (Felfili & Fagg 2007; Magnusson *et al*. 2008; Lopes *et al*. 2009; Martins 2014; Pereira *et al*. 2016), but only based on sampling of the woody component with $DB_{30}$ > 5 cm. According to Bridgewater *et al*. (2004), cerrado flora is commonly composed of a small group of families, although at the species level this flora is quite diversified.

The species *Eugenia punicifolia*, *Myrcia fallax*, *Myrcia splendens* and *Psidium guajava* contributed to the greater richness demonstrated by Myrtaceae; *Curatella americana*, *Doliocarpus dentatus* and *Tetracera breyniana* contributed to greater richness for Dilleniaceae; and *Acacia mangium*, *Platypodium elegans* and *Pterogyne nitens* contributed to greater richness of Fabaceae. These findings corroborate Magnusson *et al*. (2008), who found greater floristic richness attributed to these three families when analyzing the floristic composition of 3.75 ha of savanna in the municipality of Santarém in the state of Pará. This result confirms that these families, together with Vochysiaceae, Malpighiaceae and Rubiaceae, are represented in most of the phytosociological and botanical studies in environments of the Cerrado biome in Brazil (Ratter *et al*. 2003; Fiedler *et al*. 2004; Ribeiro *et al*. 2012).

From the 1960s to 1970s, native vegetation of the cerrado of Amapá was converted into plantations of the exotic pioneer species *Acacia mangium* and *Pinus* sp., while in the last three decades to the present day it was converted into large-scale production of *Eucalyptus* sp. (Costa-Neto 2014). This history helps to explain records of some exotic species in the survey, such as eight adult and regenerating individuals of *Acacia mangium* found in A2.

The frequent burning regimes observed annually in the vegetation in all three remnants during the study period indicate that the fire produced a deleterious effect on the structure of the adult woody community. This observation explains the low number of individuals (N) and basal area (BA) in burned compared to unburned environments (Tab. 1), which is common for cerrado areas since fires directly affect the survival, growth and reproduction of plants. In addition, fire has been cited as being responsible for the exclusion of some species that are susceptible to this disturbance and for reducing the number of individuals in the community, leading to a progressive simplification of floristic composition and forest structure over time (Fiedler *et al*. 2004; Líbano & Felfili 2006; Higgins *et al*. 2007; Hoffmann *et al*. 2009).

The lower floristic richness and moderate ecological dominance found in the burned plots are reflected in lower diversity indexes and average species evenness values (Tab. 1). This moderate ecological dominance, found in both burned and unburned environments, is largely due to the high abundances of *Salvertia convallariodora*, *Byrsonima crassifolia* and *Curatella americana*, which contribute to the significant uniformity in the distribution of the number of individuals in the adult and regenerating strata.

Thus, it is possible to affirm that the fire regime favored the germination and sprouting of these three species in the same way as it did for *Casearia sylvestris*, *Erythroxylum suberosum*, *Palicourea rigida* and *Aegiphila verticillata*. This affirmation is based on the expressive number of individuals of these species found in regeneration (0.30 m ≤ height < 1 m) compared to the low number in the adult stratum (Tab. 1).

In general, the ecological dominance by some species is influenced by extreme environmental conditions, such as the low nutrient availability in the soil, hydric stress caused by lack of water and high acidity common to savanna vegetation (Ashton 1990), which has led species to evolve adaptive survival mechanisms. In these terms, the expressive dominance presented by *Salvertia convallariodora* can be explained by the typical ecological behavior of species of the family Vochysiaceae, namely a good capacity to accumulate aluminum, which provides an advantage for successful growth in cerrado soils (Haridasan & Araújo 1988).

Annual burnings increase the dominance of small individuals, as indicated by the species evenness values (J'), which corroborates Higgins *et al*. (2007). The hypothesis that a fire regime favors germination and sprouting of these species in savanna vegetation is reinforced by Ribeiro *et al*. (2012), who showed that the post-fire pattern of regrowth in the cerrado is closely associated with the frequency of fires and the size of individuals, with greater regrowth occurring in the base of individuals belonging to smaller size classes than in the base of individuals of larger size classes. This regrowth tendency was observed in the present study with some species regenerating from gems at ground level, corroborating the studies of Hoffmann (1996), Hoffmann & Moreira (2002) and Miranda *et al*. (2003).

The low floristic heterogeneity among A1, A2 and A3, as indicated by the phytosociological analysis (Tabs. S1 in supplementary material, 2) and the Sørensen similarity index, indicates that all three remnants maintained the same common species in the adult stratum even though disturbances occurred to their vegetative structure, with A2 and A3 having more similar species compositions. The difference between A1 and the other remnants can be explained by the fact that this area had eight species that did not occur in the other remnants (*i.e.*, *Guettarda angelica*, *Byrsonima coccolobifolia*, *Vismia cayennensis*, *Tabebuia aurea*, *Myrcia fallax*, *Myrcia splendens*, *Tapirira guianensis* and *Zanthoxylum rhoifolium*; tabs. 2, 3).

A significant degree of floristic similarity among the remnants was expected since they belong to the same phytophysiognomy and are geographically close to each other, which reinforces the premise that adjacent areas are highly likely to contain similar groups of species coexisting in different regions. This idea is based on the Neutrality Theory of Hubbell (2001), which explains that similarity in species composition of communities decreases with increasing geographical distance between them, independent of environmental differences, with the reduction being due to spatial dispersion limitations.

Because they had higher importance values (IV) in the communities of the three studied savanna remnants, *Salvertia convallariodora*, *Byrsonima crassifolia* and *Curatella americana* contributed to the ecological balance of the vegetation structure since they demonstrated a greater probability of environmental restoration due to the high frequency of individuals in the adult stratum of burned areas. This interpretation was confirmed by the high abundance of these species also in the regenerating component after the effect of fire in the evaluated areas (Tab. 3), suggesting they possess aspects of resilience that are lacking in species that are more sensitive to fire. This observation is consistent with Hoffmann *et al*. (2009), who analyzed transitional savanna-forest vegetation and concluded that the number of plants and the size of individuals, as well as the intrinsic characteristics of each species, are fundamental parameters in determining the type of vegetation that can better survive fire, and consequently contribute to stabilizing and maintaining flora.

The greater abundance of individuals recorded in the regeneration stratum of the burned environments of the present study (151) compared to that of the unburned areas (149) (Tab. 3) suggests that although the fire caused a change in the structural stability of the remnants, it also contributed to increasing the number of individuals in vegetation because the effect of burning likely promoted dormancy breakage of some seeds present in the soil. This indicates a greater potential for regrowth of certain plants after fire, mainly *Salvertia convallariodora* and *Curatella americana* because these species were observed to be quite resistant to the disturbance of fire.

Some studies on the effects of fire on seed banks of savanna species (Oliveira-Filho & Ratter 2002; Williams *et al*. 2005) demonstrated a significant increase in soil seed quantity in forest communities and in the regeneration of burned vegetation one year after the effects of fire. Thus, the results of these studies corroborate the premise that fire may have contributed to increasing the natural regeneration on the burned areas of the savanna remnants studied. Nevertheless, future studies should be carried out, mainly on the effects of fire on the seed bank, to reach more consistent conclusions about this paradigm.

The inverted-"J" diametric distribution for the unburned environments of the three studied remnants indicates that the woody community is young and has a good level of regeneration, since this is an expected pattern for native forests (Cabacinha & Castro 2010; Pereira *et al*. 2016). The intensity and duration of fires, as well as human land use, are factors that explain the changes observed in the diametric structure of the vegetation in the burned environments of A2 and A3 (Fig. 3A-B).

By virtue of the three remnants being located near the urban perimeter, they are frequently used for agricultural activities (*i.e.*, plantations of fruit and grain species), which has caused them to be hotspots for fires each year. Thus, the history of anthropic action in these areas is a factor that contributes the most to explaining the alteration in the diametric structure of the remnants.

The low number of species with $DB_{30} > 20$ cm in the burned areas indicates that larger individuals suffered mortality from the fire regime, due to the death of tree shoots, as observed by Hoffmann & Moreira (2002), resulting in a change in community structure as evidenced by the reduced BA ($m^2\ ha^{-0.56}$) values of 2.47, 0.87, 0.45 for A1, A2 and A3, respectively (Tab. 1). The reduced basal area observed for the burned areas corroborates Lopes *et al*. (2009), who recorded a loss of 3.14 $m^2\ ha^{-1}$ of woody vegetation of cerrado *sensu stricto* submitted to fire in the municipality of Caldas Novas in the state of Goiás, Brazil.

A change in the height distribution of species was found within the remnants due to the effects of fire in burned environments (Fig. 3A-B). The frequency of fire probably influenced the horizontal and vertical growth of plants resulting in trees in the smallest size classes. The data of the present study confirmed this tendency, since woody communities affected by fire had shorter plants with smaller diameters. This finding can be interpreted as a response by plants to post-fire disturbances, because resilient trees develop morphological adaptive mechanisms to remain in post-fire vegetation, mainly related to the processes of regrowth in the lower and upper portion of the stem depending on the intrinsic characteristics of each species, as reported by Hoffmann & Solbrig (2003) and Ribeiro *et al*. (2012).

The species *Salvertia convallariodora*, *Byrsonima crassifolia* and *Curatella americana* were dominant in both strata, with a greater number of plants in the range 1.5 m < Ht < 6 m. These data are in accordance with Magnusson *et al*. (2008), who also reported these three species as having dominant canopy coverage in an Amazon savanna in the municipality of Santarém, state of Pará, Brazil. According to Gomes *et al*. (2004), from an environmental point of view, the explanation for this dominance is associated with the responses of the different ecological niches they hold in the vegetation, and connected to responses to biotic and abiotic factors that interact in the environment, as well as to the intrinsic ecological behavior of each species and of the successional group to which they belong.

The remnants studied here exhibited a relatively high degree of floristic diversity, as evidenced by the Sørensen index. However, despite having similar species compositions, the vegetation structure of the fragments differed significantly, as evidenced by the phytosociological analysis of the burned and unburned areas (Tab. S1 in supplementary material, 2). This finding can be explained by the stability of the environment potentially being influenced by the greater intensity of disturbances in burned areas (Lopes *et al*. 2009).

### *Edaphic variables and species distribution*

The low fertility and high acidity of the soil of the remnants was expected as Latosol soils predominate in the Brazilian Cerrado. In geomorphological terms this means this group possesses an accentuated weathering process due to the effects of dissection and leveling by successive erosion cycles; their sediment is dated from the Paleozoic and Mesozoic (Lopes 1983). This gives the soils great limitations for cultivation because of their low natural fertility (Carneiro *et al*. 2009) and high leaching of macronutrients in vegetation with spaced structure and species adapted to these nutritional limitations.

Fire had small positive effects on the soil chemical attributes of the studied remnants, as evidenced by increased OM and P contents, which contributed to maintaining limited variation in pH values (Tab. 4). Similar results have been reported by several researchers (Ramos & Rosa 1996; Roscoe *et al*. 2000; Rheinheimer *et al*. 2003; Knicker *et al*. 2006). The ash from burning organic matter has high concentrations of nutrients such as K, P and Ca (Redin *et al*. 2011) and if these elements remain in the soil, their concentrations increase, and they can become available to plants.

This tendency for increased OM and P after fire is explained by Knicker (2007) and Galang *et al*. (2010) as the consequence of the accumulation of ash, which has high concentrations of P, K, N, Ca and Mg, on the soil surface. In these terms, we can affirm that there was increased CEC values with increased OM in the burned environments (Tab. 4), which is evidenced by the influence that OM has on the chemical, physical and biological characteristics of soils, being one of the main properties considered in evaluating soil quality (Souza & Alves 2003; Dick *et al*. 2008).

Frequent burning at short intervals may cause nutritional impoverishment of the soil surface layer, resulting in greater losses in quality since fires accelerate the mineralization of OM and, consequently, release nutrients such as N, K and P into the soil solution, leaving them susceptible to loss by percolation and volatilization (Knicker *et al*. 2007; Dick *et al*. 2008). In the case of the present study, the small losses found for most of the chemical attributes of the soil can be explained by the varying frequency of burnings throughout one year.

Added to this is the traditional practice in the Amazon to cut and burn native vegetation to clear areas (e.g. itinerant agriculture) for sowing. This practice may also help to explain the previously mentioned variation in soil attributes observed in the present study. In general, the behaviors of exchangeable acidity ($Al^{3+}$) and potential acidity (H + Al) for the three remnants are compatible with soil pH values. On the other hand, the distributions of bases K, $Ca^{+}$ + $Mg^{2+}$ in the 0–20 cm surface layer reflect their association with OM levels (Tab. 4).

The contents of Al and potential acidity (H + Al) were lower in the burned environment. A similar result was found by Iwata *et al*. (2012), who evidenced that the burning has a tendency to decrease Al levels due to the release of exchangeable cations (Ca, Mg and K) in ash that neutralize the acidity of the soil. Thus, considering the there was a change in the contents of K and Ca + Mg, and there were low levels of Al and H + Al, in the burned environments, it can be said that burning affected this attribute of the soil.

Clay and total sand contents were greater than silt levels in all soil samples, which justifies the classification here of the soil as in the clayey-loam textural class. These results corroborate those of Coutinho (1990) and Fontana *et al*. (2016), who found that the soils with more clayey textures enable the formation of favorable conditions for developing forest physiognomies, mainly due to greater potential for humidity retention.

The ordination pattern of the plots produced by PCA (Fig. 4C), together with the results of the T-test analysis of the physical and chemical attributes of the soil (Tab. 4), and of the ordination data of the species of the woody community generated by the CCA (Tab. 5), indicate associations between structural patterns found in the burned and unburned phytophysiognomies and soil properties.

This finding can be explained by the direct correlation between tree-shrub species and the reduced nutritional values and the high acidity common of soils in the analyzed savanna remnants. It is also explained by the preference revealed by certain species (*Casearia sylvestris*, *Curatella americana* and *Erythroxylum suberosum*) (Fig. 5) for sites with moderate OM, P and CEC, meaning greater adaptations of post-fire vegetation to regions with increased ash content. This indicates that different species have different responses to the same edaphic parameter at a local scale, considering that areas of all three remnants were subjected to the same effects of the fire in terms of duration and period of recurrence.

The eigenvalues of the CCA are considered high compared to other studies in Amazonian savannas (Miranda *et al*. 2003; Costa-Neto 2014; Pessoa 2014), as well as in cerrado *sensu stricto* in different regions of Brazil (Martins 2014; Neri *et al*. 2012). This analysis clearly separated the three groups of plots with strong correlations for PC1, PC2 and PC3, representing the scores of edaphic variables that differentiated the studied fragments. In this way, it can be affirmed that fire altered the properties of the investigated soils and, consequently, OM, P and CEC contents, with these being the most important attributes in explaining structural variation of species in the environmental gradient of burned areas.

Therefore, it can be suggested that there is vegetation associated with the edaphic characteristics of the investigate burned and unburned environments because the soils of the three fragments, although having low fertility and acidic pH, had different contents of some elements and different textures, which dictated modifications in species composition and structure. In addition, species that are more predisposed to developing in clayey and more acidic soils (such as those evidenced in this study) can be recommended for use in environmental recovery programs.

From the ecological point of view, this result shows that lower fertility selects species with low nutritional requirements (Braga *et al*. 2015), which explains the distancing of species from the center of the ordination diagram because they have less requirements in relation to the selected environmental variables (Fig. 5). These data suggest that, in practice, it is necessary to adopt conservation interventions for soils that have suffered degrading activities in order to form a conservation proposal of the savanna remnants of Amapá.

### *RDA variation partitioning*

The results of the RDA analysis confirmed the observation that the physical-chemical properties of the soils better explained the structural differences observed in the vegetation of burned and unburned areas than did the distances between them. This, therefore, reinforces the hypothesis that fire influenced the soil properties and, consequently, influenced floristic and structural differences between burned and unburned areas. This hypothesis was also supported by the PCA, which demonstrated a relationship between burned plots and sandy soils with high levels of OM, P and K, while unburned plots were more associated with finer soil textures (more clay and silt), low base saturation and high aluminum saturation.

It was evident that the physical-chemical attributes of the soil were the factors most responsible for variation in floristic composition, corroborating the CCA results. The influence of spatial proximity in the patterns reported here cannot be disregarded. Although edaphic factors were been found to be very important in the explanation of floristic variation, the fraction explained purely by space [a] was significant as well, suggesting that even on a small scale (geographically close areas), there may be significant changes in floristic structure and composition. These results corroborate Costa-Neto (2014), who found that, even with the low latitudinal variation of the savanna remnants in Amapá, there is slight changes in species composition, and that latitude, together with average rainfall, were indicated as the factors that also contribute to explaining the distribution of species along the environmental gradient.

The moderate unexplained fraction ([d] = 43.60 %) of floristic variation can be attributed to undetermined residuals related to variables that were not included in the present analyses. In his regard, attention is drawn to the distributions of the investigated species since they are not restricted only to the evaluated scale, as well as other factors of positive interactions not studied in this work that can also influence species abundance (*e.g.* herbivory and invasion of exotic plants), since these factors are generally independent of soil type (Nano & Clarke 2010).

Therefore, we can infer that edaphic (physical-chemical attributes) factors are crucial, in association with biotic interactions (including anthropogenic effects, such as burned areas) in explaining the types, and distributions of, Amazon savanna vegetation. The knowledge about the effects of fire on the woody vegetation of the savanna remnants of Amapá synthesized in this study suggests that burning regimes result in more open physiognomies as a consequence of changes in recruitment and favoring the regrowth of vegetation, as well as negative responses in the horizontal structure of vegetation. This work showed a strong direct correlation between tree-shrub species and reduced nutrition and high acidity of common soils of the analyzed savanna remnants, as well as a preference of certain species, such as *Casearia sylvestris*, *Curatella americana* and *Erythroxylum suberosum*, for areas with moderate contents of chemical elements.

The peculiarities of the floristic structure and composition of burned and unburned areas were confirmed by ordination analyses (CCA) that separated the three remnants consistently and significantly according to edaphic variables, thus corroborating our hypothesis that soil properties and fire together significantly influence differences in floristic structure and composition of savanna remnants at the local geographical scale studied.

The information acquired here about the floristics, phytosociology and ecology of this ecosystem is extremely vital to the preparation of proposals for the recovery of areas that suffered fire disturbances since the maintenance of part of the remnants in this region is directly related to the level of knowledge of the dynamics of the processes that govern the soil-plant relationship.

## Acknowledgements

We thank the Forest Conservation Research Group of the Universidade do Estado do Amapá (UEAP) for support in obtaining data, as well as logistic support for performing the study.

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