



Original Paper

Revealing floristic and structural variation in regenerating areas in the *Cerrado-Caatinga* transition: an analysis across seres

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Abstract

In the savanna-seasonally dry tropical forest ecotone in Northeastern Brazil, we studied variations in flora and structure within old growth and two sites in secondary succession (10 and 25 years). We sampled 2,127 trees and shrubs with a diameter at ground level of 3 cm or more, excluding cacti, palm trees, and vines. Old growth contained 478 plants from 29 species, the 25-year site had 819 plants from 27 species, and the 10-year site had 829 plants from 25 species, totaling 38 species across the sites. Regarding the regenerating stratum, we found 2,776 individuals, with the largest and smallest number of individuals for 10 and 25 years regeneration, respectively. Rarefaction and Jackknife richness showed greater tree richness in old growth, whereas 10 and 25 years regeneration presented similar richness estimates; furthermore, the highest richness in the regenerating stratum was observed in 10 years and the lowest in old growth. Our results reveal that changes in composition are caused by species replacement, demonstrating that even in areas deforested for traditional agriculture, turnover causes significant changes in composition and results in the requirement of a long time for reestablishment, similar to the old growth.

Key words: arid environments, species richness, succession, turnover, woody plants.

Resumo

Em uma área de ecótono entre a savana e a floresta tropical sazonalmente seca no Nordeste do Brasil, estudamos variações na flora e na estrutura em áreas com estágio de sucessão avançada e em dois locais em sucessão secundária (10 e 25 anos). Amostramos 2.127 árvores e arbustos com um diâmetro ao nível do solo de 3 cm ou mais, excluindo cactos, palmeiras e trepadeiras. A vegetação antiga continha 478 plantas de 29 espécies, o local de 25 anos tinha 819 plantas de 27 espécies, e o local de 10 anos tinha 829 plantas de 25 espécies, totalizando 38 espécies nos locais. Em relação ao estrato regenerante, encontramos 2.776 indivíduos, com maior e menor número de indivíduos para 10 e 25 anos de regeneração, respectivamente. Rarefação e riqueza de Jackknife mostraram maior riqueza de árvores em crescimento antigo, enquanto 10 e 25 anos de sucessão secundária apresentaram estimativas de riqueza semelhantes; além disso, a maior riqueza no estrato regenerante foi observada em 10 anos de sucessão secundária e a menor em crescimento antigo. Nossos resultados revelam que as mudanças na composição são causadas pela substituição de espécies, demonstrando que mesmo em áreas desmatadas para agricultura tradicional, o *turnover* causa mudanças significativas na composição e resulta na exigência de um longo tempo para restabelecimento, semelhante ao crescimento antigo.

Palavras-chave: ambientes áridos, riqueza de espécies, sucessão, *turnover*, plantas lenhosas.

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Introduction

In Northeastern Brazil, the *Cerrado-Caatinga* ecotone covers vast areas, with transition between savannas and seasonally dry tropical forests and woodlands, where the most notable ecotones are the ecotonal belts between the *Caatinga* and the *Cerrado* phytogeographic domain (Moro *et al.* 2016). The ecotones can be defined as areas that connect different biological communities, being a transition zone that has species characteristic of each community and, consequently, is intermediate in terms of environmental conditions, representing areas of ecological tension in the territorial extensions where two or more plant domains coexist (Moro & Milan 2016). Ecotones often appear along ecological gradients, these are created because of spatial shifts in elevation, climate, soil, and many other ecological factors (Erdős 2011; Kark 2013). Ecotones are more than just a boundary or an edge; the idea of an ecotone indicates the presence of active interaction between two or more ecosystems, with features that are not present in either of the neighboring ecosystems (Rahman *et al.* 2021).

The transition between such vegetation types Savanna (*Cerrado*) and SDTFW (*Caatinga*) occupies vast areas in such as in Piauí sState, where 37% of its territorial area is covered by seasonally dry tropical forest and woodland (SDTFW), 33% by savanna, 19% by savanna-SDTFW transition, and the rest of the territory corresponds to other vegetation types with lower expression in the state (Farias & Castro 2004; Macedo *et al.* 2019). The ecotone concept arose from community ecology to indicate a change in structure and composition of plant communities, but its use was then generalized to broader spatial scales such as landscapes and biomes (Risser 1995; Ferro & Morrone 2014).

The *Cerrado* domain has been identified as one of the richest and most threatened in the world (Felfili *et al.* 2004), and its main vegetation type, the *Cerrado* Savanna, is one of the remarkable ecosystems of South America originally covering millions of hectares (Overbeck *et al.* 2022; Fiaschi & Pirani 2009; Ab'Saber 2003). The *Cerrado* is considered one of the world's biodiversity hotspots due to the great biological richness, high proportion of endemic species and high human threat, due deforestation for agriculture (Myers *et al.* 2000; Maracahipes-Santos *et al.* 2017). The Brazilian savanna covers approximately 2 million kilometers, representing 23% of the country's land

surface (Ratter *et al.* 1997; Abreu & Durigan 2011; Overbeck *et al.* 2022), with two main strata: the woody, which includes larger trees and shrubs, and the subshrub and grass strata (Rizzini 1992; Madonsela *et al.* 2018; Vieira *et al.* 2019). Across the *Cerrado* domain, vegetation is very variable, ranging from grassland areas and sites with sparse cover of shrubs and small trees to areas with an almost closed forest physiognomy with a 12–15 m tall canopy (Ratter & Dargie 1992; Ratter *et al.* 1997; Ribeiro & Walter 2008). One hectare of *Cerrado* can include 80 to 90 woody species, distributed in diverse families, among which Fabaceae and Myrtaceae are among the most richly represented and dominant components (Rossatto 2014). Piauí has a territorial area of 251,617 km², of which 132,721 km² is represented by the *Cerrado* biome (IBGE 2019).

The phytophysiognomy and flora of the seasonally dry tropical forest and woodland that is regionally called *Caatinga*, are quite varied, presenting both a shrubby and arboreal pattern and reaching a forest physiognomy in many places, or a shrubland in other places. While the structure of the woody component varies from open and dense shrub to arboreal, the herbaceous component is mostly composed of therophytes, with short-lived annual plants (Moro *et al.* 2016; Queiroz *et al.* 2015). This makes the ecology of *Caatinga* different from, the savanna vegetation, where the herbaceous layer is perennial. The flora of *Caatinga* is represented by approximately 3.347 species, of which at least 526 are endemic, with a high proportion of herbaceous species observed, although this component is commonly neglected in studies carried out on this vegetation (Queiroz *et al.* 2015; Lima *et al.* 2019; Fernandes *et al.* 2020). Seasonally dry tropical forests and woodlands have received attention from researchers in recent decades, as they have begun to reveal higher levels of species richness and endemism than previously expected (Moro *et al.* 2015).

Species richness, uniformity, and various other measures of abundance and rarity are essential components of biological diversity, but the number of species present in a location (alpha diversity) is the easiest biodiversity variable to quantify; therefore, it has been used as a measure of the relative conservation value between different areas (Bock *et al.* 2007; Silva *et al.* 2013). Changes in the vegetation structure of tropical savannas often occur due to fires, human activities, and climate change (Gonçalves *et al.* 2021). Some of

these changes along the scale have been observed, such as changes in tree density and floristic diversity, causing negative impacts on ecosystem functioning and the benefits it provides (Sambuichi 1991; Fiedler *et al.* 2004; Madonsela *et al.* 2018). These processes can lead to primary or secondary succession, depending on whether these changes and disturbances alter the substrate and floristic composition of the site (Neto *et al.* 2017).

Understanding the patterns of plant species diversity is of great importance in determining conservation strategies (Henneron *et al.* 2019). This can be explained by the alpha diversity that describes the species diversity at a local scale, by the gamma diversity or regional diversity, which is the total number of species observed in all habitats, and by beta diversity that is used on a landscape or regional scale to compare the variation in species composition between communities (Nogueira *et al.* 2008; Zhang *et al.* 2015; Li *et al.* 2019; Soares *et al.* 2020). Understanding the mechanisms that drive alpha and beta diversities is important for regional biodiversity studies (Koleff *et al.* 2003). Beta diversity is used to measure the variation in species composition; in the narrowest sense, it is the ratio between gamma and alpha diversity (Whittaker 1960; Baselga & Orme 2012).

Beta diversity emerges from two distinct processes, turnover and nestedness (Baselga 2010; Piroozi *et al.* 2018; Magurran *et al.* 2019). Turnover refers to the replacement of some species by others, which can be explained by dispersal processes, either simultaneously or historically (Barton *et al.* 2013; Piroozi *et al.* 2018). Thus, a high species turnover rate is expected, where conditions are very different between two neighboring localities (Soares *et al.* 2020). Nestedness, however, is responsible for differences in composition, occurring when no species is replaced from one location to another (Piroozi *et al.* 2018). Analyzing the floristic and structural composition, as well as working on aspects of diversity in areas with different stages of natural regeneration, will provide information on the dynamics of plant species between areas and how they are distributed in these environments (Silva *et al.* 2002; Vasconcelos *et al.* 2017). Furthermore, provide further understanding on how succession is the process of vegetation recovery following disturbance (Clements 1916; Chang & Turner 2019; Prach & Walker 2011).

The present study aimed to investigate changes in the structure and composition of species in the tree/shrub community and in the regenerating

stratum in areas of conserved vegetation and secondary succession in the savanna–SDTFW transition, in the extreme south of the state of Piauí, Northeastern Brazil. We hypothesized that there would be differences in structure (basal area, height), abundance, richness of tree and shrub species, and species composition in regenerating strata between areas of conserved vegetation and secondary succession. Additionally, we expect that changes in species composition among the areas will be determined by turnover. Evaluation of floristic and structural variation upon succession may improve our understanding of succession, and also help practitioners in restoring sites or predicting the future vegetation of disturbed sites (Vítovcová *et al.* 2021).

Material and Methods

Study area

The study area is located in the chapadas region, in the municipality of Corrente, south of Piauí state, at coordinates 10°31'16,5"S 45°11'24,51"W. The municipality whose area of 3,521 km², is located in Northeastern Brazil, comprises a mosaic of savanna and seasonally dry tropical forest (Fig. 1), subdeciduous broadleaved forest. This is an ecotonal area influenced by the Amazon, *Cerrado*, and *Caatinga* phytogeographical domains (Andrade *et al.* 2019). The region has a tropical climate (type Aw based on the Köppen system; Alvares *et al.* 2013), characterized by rainy summers and dry winters, with a rainy season from December to May, 1,035 mm of annual rainfall, and 23 °C to 39 °C of temperature (Aguiar & Gomes 2004).

Data collection

This study was conducted at two vegetation fragments (10°31'48.05"S–45°11'44.29"W, 10°21'37.99"S–45°11'15.62"W) respectively, with different stages of secondary succession, as well as at an old growth site with no record of previous deforestation. Thus, in each fragment, we established plots in three sites: a site without know deforestation in the last decades, which we termed old growth plot (Fig. 2a–b); a deforested site, in which fire was used for cleaning and subsequent agricultural planting, which has been in regeneration for 10 years, which we termed secondary succession 10 years regeneration (Fig. 2c–d); and a deforested site, in which fire was used for cleaning and subsequent agricultural

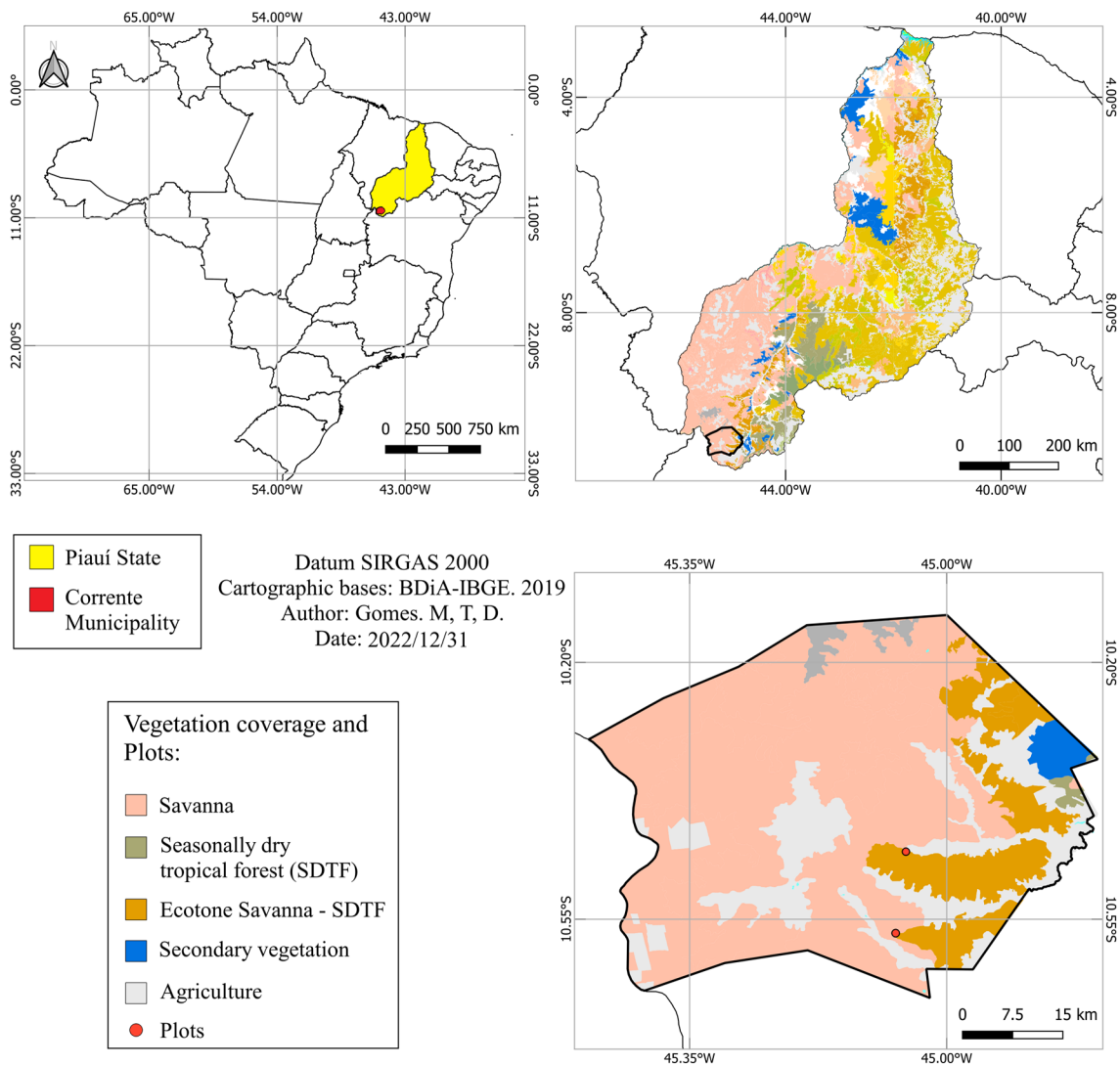


Figure 1 – Location of the study areas and vegetation coverage in the Piauí state, Brazil.

planting, which has been in regeneration for 25 years, which we termed secondary succession 25 years regeneration (Fig. 2e-f). A total of six plots were established for this study, that is, three plots in each fragment.

Plots with dimensions of 50×50 m were adopted and subsequently subdivided into subplots of 10×10 m, totaling 25 subplots. Two 50×50 m plots were implanted in each successional stage, totaling six 50×50 m plots and a total sample area of 1.5 hectares (0.5 ha per successional stage). We sampled living and dead arboreal and shrub individuals in the three plots with a diameter at ground height (DGH) ≥ 3 cm (Lemos & Rodal 2002). Cacti and palm trees did not occur in the

plots, however, climbing plants were excluded from the samples. The following information was obtained for each individual measured: species, DGH of the stem and tillers (when present) and total height of each individual. For each 50×50 m plot, 10 subplots were randomly selected for sampling the regenerating stratum, totaling 20 subplots in each regeneration stage. For the survey of the regenerating stratum, woody species were surveyed, and the researchers adopted as a criterion plant with a height of less than 1 m and above 50 cm, and perimeter at ground height (DGH) < 3 cm.

Fertile plant specimens were collected in expeditions carried out between November

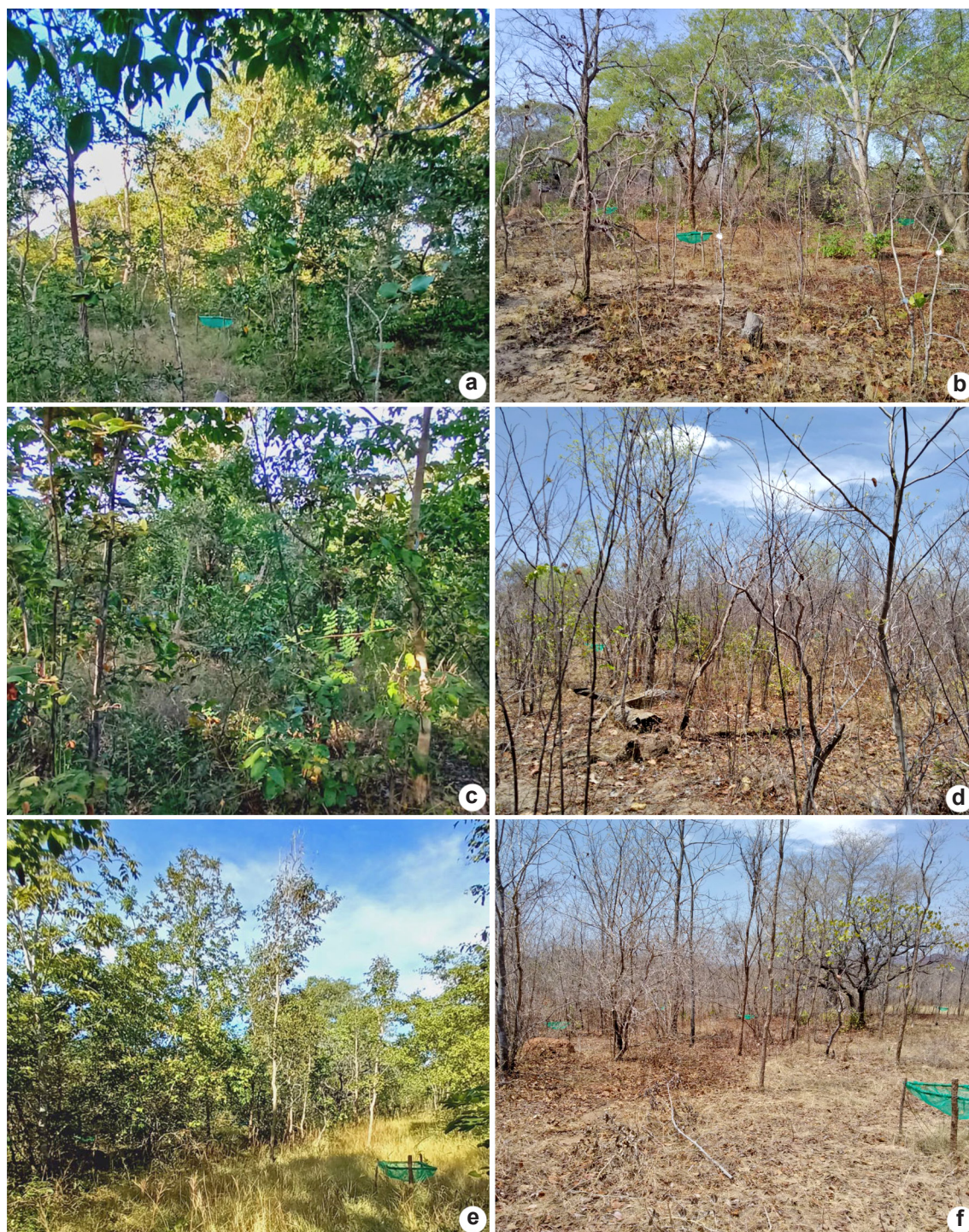


Figure 2 – Study areas during dry and rainy season, September and March, Chapadas Region, Piauí – a-b. old growth; c-d. 10 years regeneration; e-f. 25 years regeneration.

2020 and December 2021, and identification was carried out with the help of specialized literature such as Rodal *et al.* (1998), Lemos (2004), Moro *et al.* (2011), Soares Neto *et al.* (2014), Souza & Lorenzi (2019), specialists and specialized taxonomic databases, such as Flora do Brasil (2020). Family circumscriptions followed the classification proposed by APG IV (2016). Appropriate herborization techniques followed (Fidalgo & Bononi (1984) and herbarium samples were deposited at the HUEFS (Universidade Estadual de Feira de Santana herbarium). Duplicates, when available, were also deposited at the HUEFS herbarium for posterior donation to other herbaria.

Data analysis

ANOVA and Tukey's test were used to verify differences in the average basal area of the three seres, both for the arboreal and regenerating strata. For these analyses we used the value of $p < 0.05$ (Callegari-Jacques 2004). For the analysis of the ANOVA, we considered each subplot as a sampling unit. To understand the consequence of regeneration for species richness for both the adult and regenerating strata, we used rarefaction. The rarefaction curve is an intuitive way to compare sampling richness with different numbers of individuals (Gotelli & Ellison 2011). A rarefaction curve was elaborated with 999 permutations to compare the richness of sampled areas (Magurran 2004). An abundance matrix was used to calculate the Jackknife I estimator with 999 permutations to verify whether the observed richness was close to the estimated values for the surveyed areas (Magurran 2004; Gotelli & Ellison 2011).

By analyzing the abundances of the species, a ranking of the relative abundances was performed for all areas. In the graphical representation, the species abundance ranks are presented along the horizontal axis in ascending order of relative abundance. The abundance rank is commonly used to infer which species abundance model best describes a community (Magurran 2013; Gotelli & Ellison 2011).

Non-metric multidimensional scaling (NMDS) (Felfilli *et al.* 2011; Gotelli & Ellison 2011; Legendre & Legendre 2012) was used to order the areas based on the assumption that the species composition of areas with different regeneration times had distinct communities. A matrix of abundance of species was used to calculate a distance matrix using the Bray

Curtis index. The representation of ordination in portraying the actual distribution of species was verified by PERMANOVA with 999 permutations (Felfilli *et al.* 2011). To assess which areas presented significant differences in species composition, an a posteriori test was performed using the "pairwise.perm.amanova" function of the "RVAideMemoire" package (Hervé 2018).

To check whether the difference in species composition during succession is explained by nestedness or turnover, we used *beta.multi* and *parwise* functions of the *betapart* package (Baselga & Orme 2012) in R. Initially, we used the *beta.multi* function with the presence-absence matrix to calculate a dissimilarity matrix using the Sørensen index to obtain a measure of total dissimilarity and, later, the values of the turnover and nestedness components. The *beta.pair* function calculates the same three dissimilarity metrics as the previous function using the Sørensen index. Instead of returning three unique values, as in the *beta.multi* function, the *beta.pair* generates three dissimilarity matrices (total dissimilarity, turnover component, and nestedness). The generated dissimilarity matrices can be submitted to the construction of a cluster, which is selected as the component that best explains the diversity between areas (Baselga & Orme 2012).

Results

In total, we sampled 2.127 individual trees with $DGH \geq 3\text{cm}$ distributed across 18 families and 38 species in all six $50 \times 50\text{ m}$ plots ($150 \times 10 \times 10\text{ m}$ subplots). In the old growth site, we sampled 478 individuals, belonging to 17 families and 29 species. For the secondary succession plots with 10 years of regeneration, secondary succession, we sampled 829 individuals, 13 families, and 25 species. In the secondary succession area with 25 years under regeneration, we sampled 819 individuals, 12 families, and 27 species. *Eugenia dysenterica* (Mart.) DC. was the most abundant species in old growth and 25 years regeneration. In the area with 10 years of regeneration, we obtained greater abundance for *Combretum leprosum* Mart. (Tab. 1).

We sampled 2.776 individual from the regenerating stratum with $DGH \leq 3\text{ cm}$ in the 60 randomly selected $10 \times 10\text{ m}$ subplots. These were, distributed in 38 species across 16 families. In the old growth, we sampled 724 individuals, 24

Table 1 – Families, species, number of individuals and basal area for each specie in the tree stratum for old growth, 10 years regeneration and 25 years regeneration, Chapadas region, Piauí. (N - Individuals number; BA - Basal area m²; Sample HUEFS - Herbarium sample number).

Families/Species	Sample HUEFS	Old Growth		10 years		25 years	
		N	BA	N	BA	N	BA
ANACARDIACEAE							
<i>Anacardium occidentale</i> L.	259187	12	0.64	1	0.05	16	0.47
<i>Astronium fraxinifolium</i> Schott	259171	12	0.22	16	0.3	27	0.32
<i>Astronium urundeuva</i> (M. Allemão) Engl.	259169	1	0.45	162	1.94	35	0.26
ANNONACEAE							
<i>Annona leptopetala</i> (R.E.Fr.) H.Rainer	259180	-	-	-	-	1	0.01
<i>Xylopia aromatica</i> (Lam.) Mart.	259184	1	0.01	4	0.01	6	0.06
APOCYNACEAE							
<i>Aspidosperma tomentosum</i> Mart. & Zucc.	259166	7	0.13	5	0.01	8	0.02
BIGNONIACEAE							
<i>Handroanthus ochraceus</i> (Cham.) Mattos	-	1	0.01	-	-	1	0.01
<i>Handroanthus serratifolius</i> (Vahl) S.Grose	-	2	0.07	1	0.03	2	0.02
<i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook.f. ex S.Moore	259188	-	-	3	0.01	-	-
BIXACEAE							
<i>Cochlospermum regium</i> (Mart. ex Schrank) Pilg.	-	2	0.01	-	-	-	-
BORAGINACEAE							
<i>Cordia glabrata</i> (Mart.) A.DC.	259170	1	0.09	3	0.01	-	-
COMBRETACEAE							
<i>Combretum leprosum</i> Mart.	259182	16	0.7	270	2.09	39	0.16
<i>Terminalia argentea</i> Mart. & Zucc.	259177	2	0.02	1	0.01	8	0.05
<i>Terminalia fagifolia</i> Mart.	259173	24	0.7	6	0.38	31	0.27
DILLENIACEAE							
<i>Curatella americana</i> L.	259165	-	-	17	0.08	6	0.02
ERYTHROXYLACEAE							
<i>Erythroxylum</i> sp	-	1	0.01	-	-	-	-
FABACEAE							
<i>Acacia</i> sp	-	2	0.01	-	-	2	0.04
<i>Andira cujabensis</i> Benth.	259175	-	-	-	-	1	0.01
<i>Andira fraxinifolia</i> Benth.	-	2	0.05	8	0.04	3	0.02
<i>Bauhinia acreana</i> Harms	259172	22	0.05	1	0.01	61	0.19
<i>Libidibia ferrea</i> (Mart. ex Tul.) L.P.Queiroz	-	-	-	1	0.01	-	-
<i>Hymenaea courbaril</i> L.	-	1	0.01	2	0.03	6	0.02
<i>Hymenaea stigonocarpa</i> Mart. ex Hayne	259168	1	0.01	-	-	-	-
<i>Machaerium opacum</i> Vogel	-	6	0.12	2	0.01	-	-
<i>Senegalia tenuifolia</i> (L.) Britton & Rose	-	-	-	1	0.01	-	-
<i>Pterodon pubescens</i> (Benth.) Benth.	-	2	0.01	-	-	1	0.01

Families/Species	Sample HUEFS	Old Growth		10 years		25 years	
		N	BA	N	BA	N	BA
<i>Tachigali aurea</i> Tul.	-	2	0.03	12	0.12	3	0.01
<i>Stryphnodendron adstringens</i> (Mart.) Coville	259192	1	0.15	-	-	3	0.09
<i>Tachigali rubiginosa</i> (Mart. ex Tul.) Oliveira-Filho	-	-	-	-	-	8	0.05
LYTHRACEAE							
<i>Lafoensia pacari</i> A.St.-Hil.	-	1	0.01	-	-	2	0.01
MALVACEAE							
<i>Guazuma ulmifolia</i> Lam.	259183	-	-	4	0.04	-	-
MORACEAE							
<i>Brosimum gaudichaudii</i> Trécul	-	-	-	-	-	8	0.13
MYRTACEAE							
<i>Eugenia dysenterica</i> (Mart.) DC.	259190	265	2.93	225	0.84	446	1.77
RUBIACEAE							
<i>Tocoyena formosa</i> (Cham. & Schltld.) K.Schum.	259179	20	0.09	-	-	-	-
SAPINDACEAE							
<i>Magonia pubescens</i> A.St.-Hil.	-	12	1.64	-	-	17	0.07
SIMAROUBACEAE							
<i>Simarouba versicolor</i> A.St.-Hil.	259167	4	0.37	1	0.01	-	-
VOCHYSIACEAE							
<i>Callisthene fasciculata</i> Mart.	259164	-	-	68	0.4	-	-
<i>Qualea grandiflora</i> Mart.	259191	41	0.47	3	0.01	56	0.31

species and 14 families. For the plots with 10 years under regeneration, we sampled 1.386 individuals, 31 species and 13 families. In the plots with 25 years under regeneration, we sampled 666 individuals, 27 species and 14 families (Tab. 2).

The Jackknife I richness estimator estimated 40 ± 2 species for all six component plots summed. The highest value was for individual areas was in the old growth plot, while the secondary succession plots presented similar richness estimates. For the regenerated stratum, the total estimated richness was 39 ± 2 for the total dataset of all plots. The highest richness value estimate was obtained from the secondary succession plots with 10 years under regeneration, and the lowest from the old growth plot (Tab. 3).

Regarding the structure of vegetation, old growth plots had the largest basal area (and presumably the highest biomass), followed by 25 years regeneration. The plots in the 10 years regeneration site had the smallest basal area (and presumably less biomass). In the regenerating

stratum, the 10 years regeneration showed the largest basal area and number of individuals, reflecting a large number of smaller trees. We found a statistically significant difference in mean basal area per 10×10 subplot when compared with old growth and 10 years regeneration ($Df=57$, $F=10.22$, $p<0,001$) (Fig. 3a). For the adult tree stratum we found differences in mean basal area (Fig. 3b), with the larger mean for old growth and the less mean basal area for 10 years regeneration ($Df=147$, $F=9.19$, $p<0,001$).

We verified differences in the mean of abundance in the regenerating stratum (Fig. 4a), with the larger mean for 10 years and old growth and the less mean abundance area for 25 years regeneration ($Df=57$, $F=7.607$, $p=0,001$). In the tree stratum, only old growth showed less mean when compared with old growth and 25 years and 10 years regeneration ($Df=147$, $F=16.04$, $p<0,001$) (Fig. 4b).

In the regenerating stratum, the 10 years regeneration and old growth showed a difference

Table 2 – Families, species, number of individuals and basal area for each specie in the regenerant stratum for areas old growth, 10 years regeneration and 25 years regeneration, Chapadas region, Piauí. (N - Individuals number; BA - Basal area m²; Sample HUEFS - Herbarium sample number).

Families/Species	Sample HUEFS	Old Growth		10 years		25 years	
		N	AB	N	AB	N	AB
ANACARDIACEAE							
<i>Astronium fraxinifolium</i> Schott	259171	8	0.02	8	0.01	1	0.001
<i>Astronium urundeuva</i> (M.Allemão) Engl	259169	20	0.02	104	0.1	268	0.23
ANNONACEAE							
<i>Annona acutiflora</i> Mart.	259180	-	-	1	0.001	-	-
<i>Annona coriacea</i> Mart.	259185	-	-	4	0.001	1	0.001
<i>Annona crassiflora</i> Mart.	-	-	-	16	0.001	-	-
<i>Xylopia aromatica</i> (Lam.) Mart.	259184	3	0.01	-	-	-	-
APOCYNACEAE							
<i>Aspidosperma macrocarpon</i> Mart. & Zucc.	259181	-	-	10	0.001	12	0.01
<i>Aspidosperma pyriforme</i> Mart. & Zucc	-	1	0.01	21	0.02	5	0.01
BIGNONIACEAE							
<i>Handroanthus ochraceus</i> (Cham.) Mattos	-	-	-	10	0.01	5	0.001
<i>Handroanthus serratifolius</i> (Vahl) S.Grose	-	1	0.01	1	0.001	-	-
<i>Jacaranda brasiliana</i> (Lam.) Pers.	259189	-	-	4	0.01	1	0.001
<i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook.f. ex S.Moore	259188	-	-	-	-	1	0.001
BIXACEAE							
<i>Cochlospermum regium</i> (Mart. ex Schrank) Pilg.	-	-	-	1	0.001	-	-
BORAGINACEAE							
<i>Cordia glabrata</i> (Mart.) A.DC.	259170	1	0.01	-	-	9	0.001
COMBRETACEAE							
<i>Combretum leprosum</i> Mart.	259182	73	0.08	129	0.07	42	0.04
<i>Terminalia argentea</i> Mart. & Zucc.	259177	2	0.01	2	0.001	4	0.01
<i>Terminalia fagifolia</i> Mart.	259173	47	0.05	6	-	-	-
ERYTHROXYLACEAE							
<i>Erythroxylum</i> sp.	-	-	-	2	0.001	3	0.001
FABACEAE							
<i>Bauhinia acreana</i> Harms	259172	399	0.3	345	0.29	157	0.15
<i>Hymenaea courbaril</i> L.	-	10	0.03	8	0.01	4	0.001
<i>Machaerium opacum</i> Vogt	-	10	0.01	15	0.01	11	0.01
<i>Senegalia tenuifolia</i> (L.) Britton & Rose	-	2	0.01	3	0.001	1	0.001
<i>Pterodon emarginatus</i> Vogel	-	2	0.01	3	0.001	-	-
<i>Stryphnodendron adstringens</i> (Mart.) Coville	259192	3	0.01	-	-	-	-
<i>Tachigali aurea</i> Tul.	-	-	-	1	0.001	-	-
LYTHRACEAE							
<i>Lafoensia pacari</i> A.St.-Hil.	-	6	0.01	-	-	1	0.001

Families/Species	Sample HUEFS	Old Growth		10 years		25 years	
		N	AB	N	AB	N	AB
MALVACEAE							
<i>Gossypium</i> sp.	-	3	0.01	-	-	2	0.001
<i>Guazuma ulmifolia</i> Lam.	259183	1	0.01	-	-	6	0.001
MORACEAE							
<i>Brosimum gaudichaudii</i> Trécul	-	1	0.01	5	0.01	-	-
MYRTACEAE							
<i>Eugenia dysenterica</i> (Mart.) DC	259190	36	0.03	524	0.85	94	0.11
<i>Myrtus communis</i> L.	259176	-	-	49	0.02	1	0.001
<i>Psidium</i> sp.	-	64	0.08	6	0.01	7	0.01
RUBIACEAE							
<i>Tocoyena formosa</i> (Cham. & Schldl.) K.Schum.	259179	11	0.01	23	0.03	4	0.001
<i>Rudgea</i> sp.	-	-	-	9	0.01	12	0.01
SAPINDACEAE							
<i>Magonia pubescens</i> A.St.-Hil.	-	4	0.01	12	0.02	2	0.001
VOCHYSIACEAE							
<i>Callisthene fasciculata</i> Mart.	259164	-	-	1	0.001	5	0.01
<i>Qualea grandiflora</i> Mart.	259191	16	0.02	57	0.06	7	0.01

Table 3 – Quantitative descriptors for the arboreal and regenerating stratum for old growth, 10 years regeneration and 25 years regeneration, Chapadas region, Piauí.

Stratum	Plots	N	Basal area	Richness	Jackknife I	Chao I
Tree	Old growth	478	4.18	29	39±3	37±7
	10 years	829	2.20	25	32±2	33±8
	25 years	819	3.20	27	32±2	33±7
Regenerating	Old growth	724	0.07	24	29±3	27±3
	10 years	1.386	0.31	31	38±3	46±9
	25 years	666	0.13	27	35±4	36±5

in means richness when compared with 25 years regeneration (Df=57, F=7.521, p=0,001) (Fig. 5a). For the tree stratum we found differences in mean richness (Fig. 5b), with the larger mean for 25 years and 10 years regeneration and the less mean old growth (Df=147, F=3.205, p=0,043).

We verified the relationship between tree richness and the number of individuals sampled using the rarefaction curve for each area of the tree stratum. The old growth fragment showed the highest ascending richness, showing that

the richness for a given number of sampled individuals was higher in this area than in the regenerating plots. On the other hand, considering the extrapolation of the curves, all areas presented asymptotic curves (Fig. 6a). In the regenerating stratum, the same relationship between number of species and number of individuals sampled was verified; however, considering the interpolation and extrapolation intervals, we found greater richness for the areas at 10 and 25 years in regeneration (Fig. 6b).

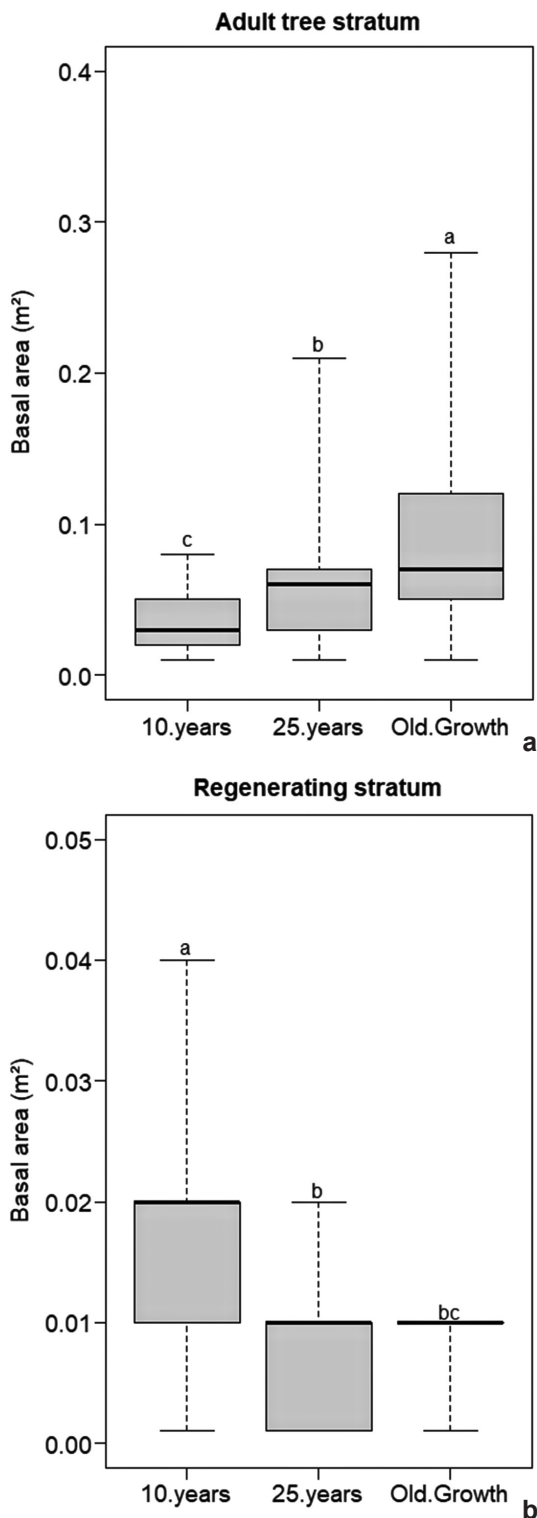


Figure 3 – Basal area for the adult tree stratum (a) regenerating stratum (b) for 10 years regeneration, 25 years regeneration and old growth, Chapadas region, Piauí.

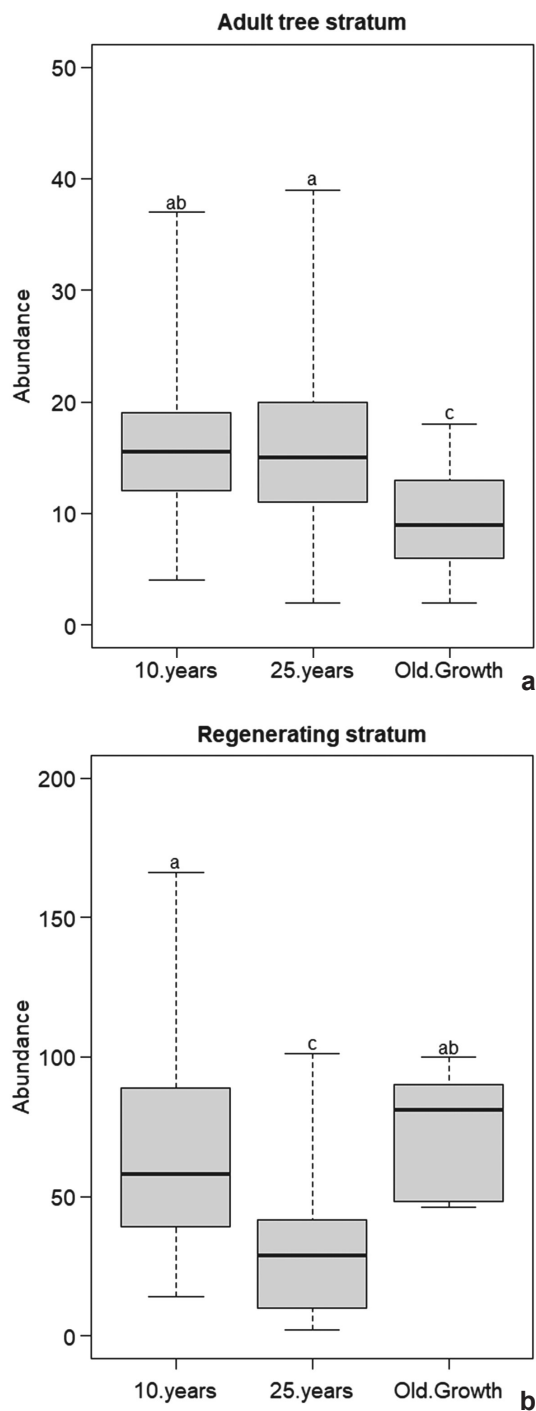


Figure 4 – Abundance for the adult tree stratum (a) regenerating stratum (b) for 10 years regeneration, 25 years regeneration and old growth, Chapadas region, Piauí.

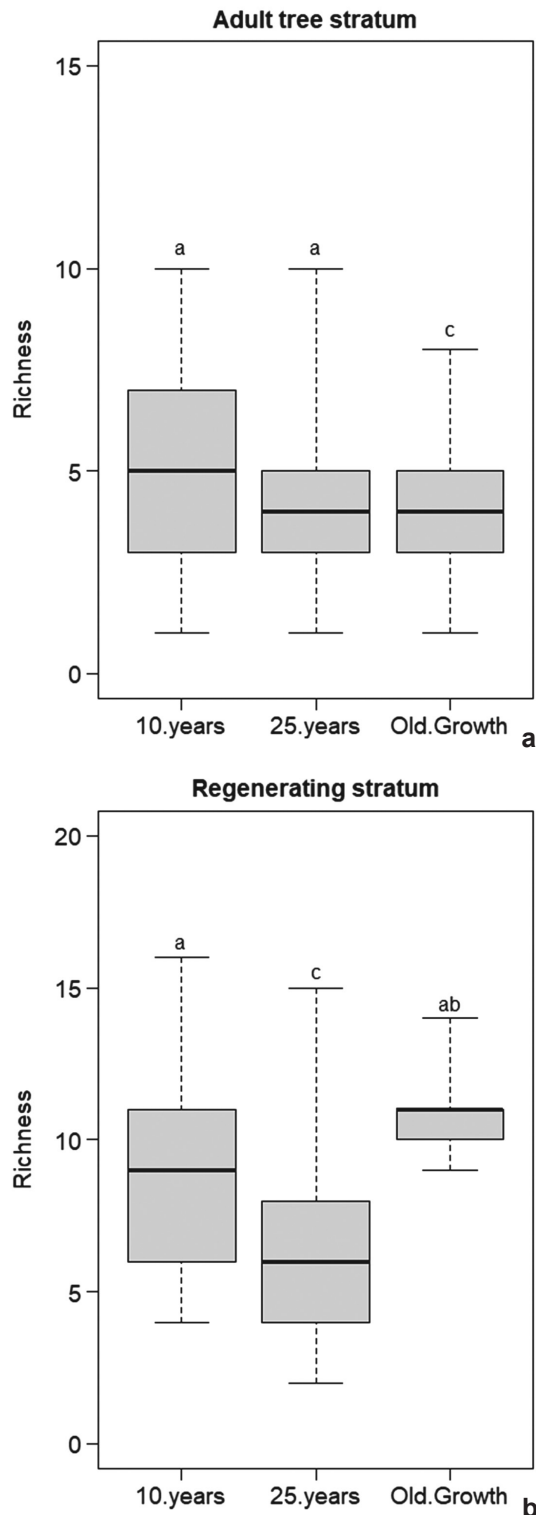


Figure 5 – Richness for the adult tree stratum (a) regenerating stratum (b) for 10 years regeneration, 25 years regeneration and old growth, Chapadas region, Piauí.

Both the tree strata (Fig. 7a) and regenerating strata (Fig. 7b) exhibited few species, representing more than 50% of the relative abundance, with the other species represented by a few individuals. *Eugenia dysenterica* represented 55.4% of the total relative abundance in the tree stratum during old growth. For secondary succession (10 years regeneration), *Combretum leprosum* (33.1%) and *Eugenia dysenterica* (27.5%), together accounted for 60.6% of the relative abundance. Finally, in the secondary succession (25 years regeneration), *Eugenia dysenterica* accounted for 54.4% of the total relative abundance (Fig. 7a). *Bauhinia acreana* represented 55.11% of the total relative abundance in the regenerating stratum for old growth. Secondary succession (10 years), *Eugenia dysenterica* (38%) and *Bauhinia acreana* (25%), together accounted for 63% of the total relative abundance. During secondary succession (25 years), *Astronium urundeuva* accounted for 40.2% of the total relative abundance (Fig. 7b).

The NMDS showed differences in species composition between the three areas, both in the tree (Fig. 8a) and regenerating strata (Fig. 8b). For the tree stratum, stress was 0.263 a moderate quality ordination, but Permanova showed that the difference in species composition was significant, although NMDS does not present a clear separation of areas. For the regenerated stratum, the ordination stress was 0.222 a moderate quality ordination. Permanova showed that the order of sampling units for the regenerating stratum was also significant ($p=0.001$).

The NMDS showed differences in species composition between the two strata for the three areas. The stresses for the old growth, 10 and 25 years regeneration (secondary succession) were 0.176 (Fig. 9a), 0.200 (Fig. 9b), and 0.184 (Fig. 9c), respectively. Permanova showed that the difference in the species composition between the two strata was significant ($p=0.001$).

The beta diversity analysis for the tree stratum between successional stages showed that turnover was 0.95 and nestedness was 0.10. Beta diversity analysis for the regenerating stratum showed that the change in species composition was also influenced more by the turnover (0.88) than by nestedness (0.05). For the tree stratum, the species present exclusively in old growth were: *Cochlospermum regium* (Mart. ex Schrank) Pilg., *Tocoyena formosa* (Cham. & Schltdl.) K. Schum.,

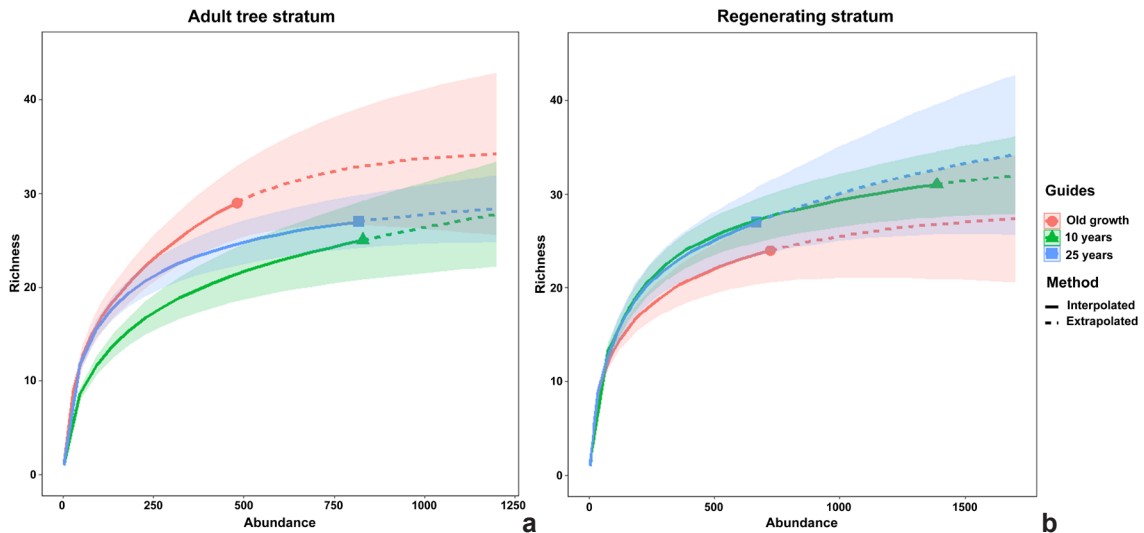


Figure 6 – Rarefaction curve for the tree (a) and regenerating stratum (b) for old growth, 10 years regeneration and 25 years regeneration, Chapadas region, Piauí.

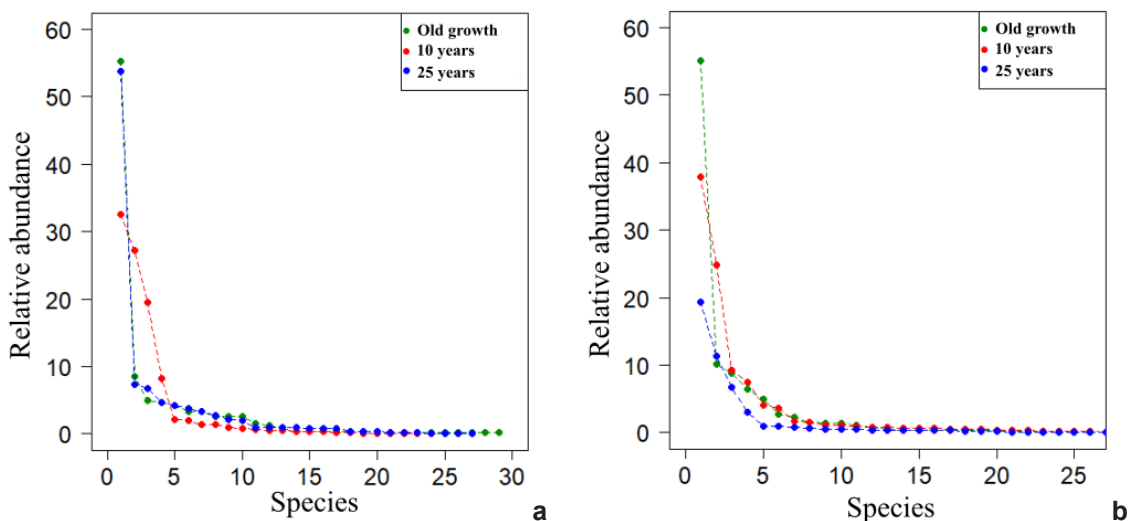


Figure 7 – Rank of relative abundances of species for the tree (a) and regenerating stratum (b) for old growth, 10 years regeneration and 25 years regeneration, Chapadas region, Piauí.

Erythroxylum sp, *Hymenaea stigonocarpa* Mart. ex Hayne. In 10 years regeneration *Callisthene fasciculata* Mart., *Guazuma ulmifolia* Lam., *Tabebuia aurea* (Silva Manso) Benth. & Hook.f. ex S.Moore, *Libidibia ferrea* (Mart. ex Tul.) L.P. Queiroz and *Mimosa* sp. Finally, in 25 years regeneration: *Brosimum gaudichaudii* Trécul, *Tachigali rubiginosa* (Mart. ex Tul.) Oliveira-

Filho, *Annona leptopetala* (R.E.Fr.) H.Rainer And *Andira cujabensis* Benth. (Fig. 10a).

For the regenerating stratum, the species present exclusively in old growth were: *Xylopia aromatica* (Lam.) Mart, *Stryphnodendron adstringens* (Mart.) Coville. To 10 years regeneration were *Cochlospermum regium* (Mart. ex Schrank) Pilg., *Tachigali aurea* Tul., *Annona*

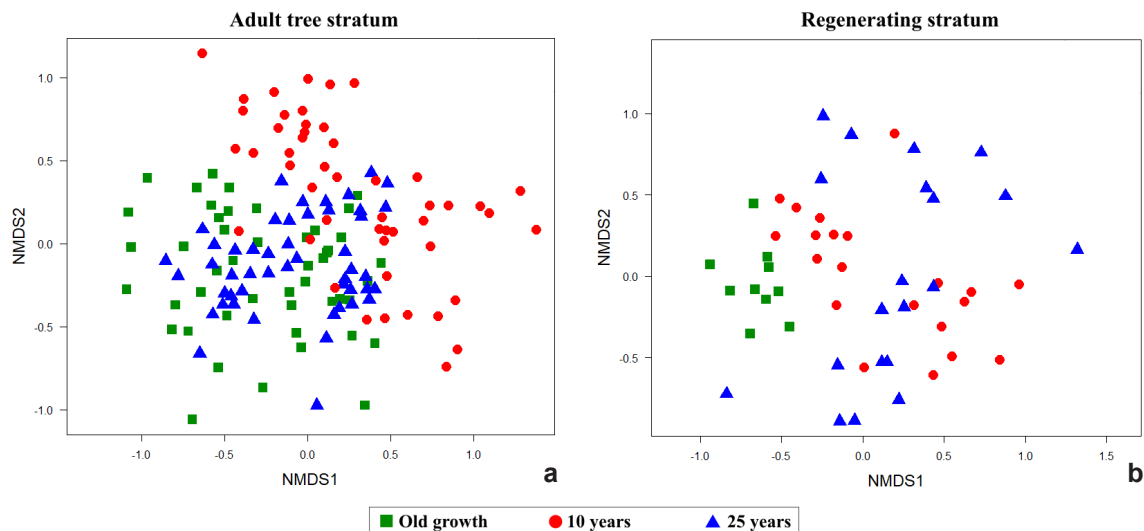


Figure 8 – Ordination for the tree (a) and regenerating stratum (b) for old growth, 10 years regeneration and 25 years regeneration, Chapadas region, Piauí.

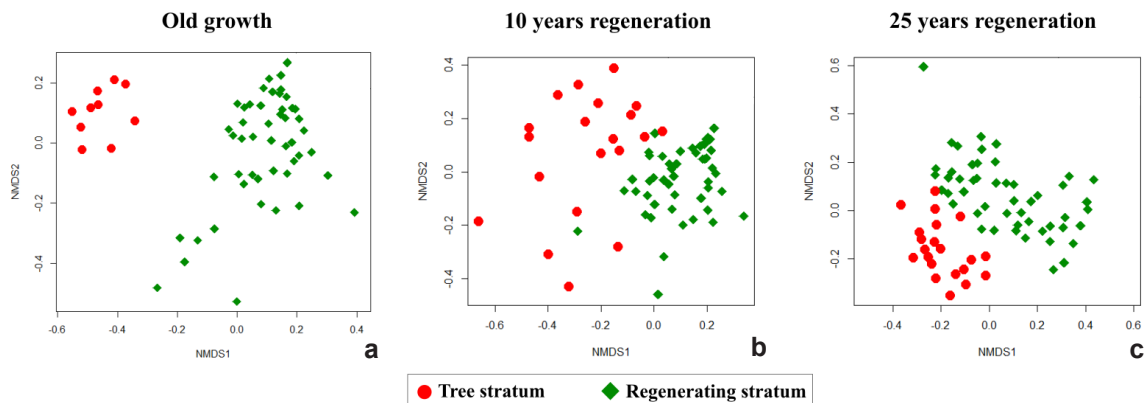


Figure 9 – Ordination of species from the tree and regenerating stratum for three areas, Chapadas region, Piauí – a. old growth; b. 10 years regeneration c. 25 years regeneration.

crassiflora Mart. And *Annona acutiflora* Mart. In the area with 25 years of regeneration, only the species *Tabebuia aurea* (Silva Manso) Benth. & Hook.f. ex S. Moore was exclusively present. (Fig. 10b).

Discussion

Our results support the initial hypotheses of this study. We found differences in the structure, abundance, and richness of trees and shrubs, and regenerating strata between the three areas. These changes in species composition among areas were

determined mainly by turnover. We found greater species richness of the tree stratum in old growth, many species represented by a few individuals, and differences in species composition between the three areas. For the regenerating stratum, we verified similarities in species richness and the contribution of species richness represented by low-abundance species. With this, we show that even in deforested areas for traditional agriculture, as in the secondary succession plots (10 and 25 years regeneration), there were significant changes in species composition when compared with non

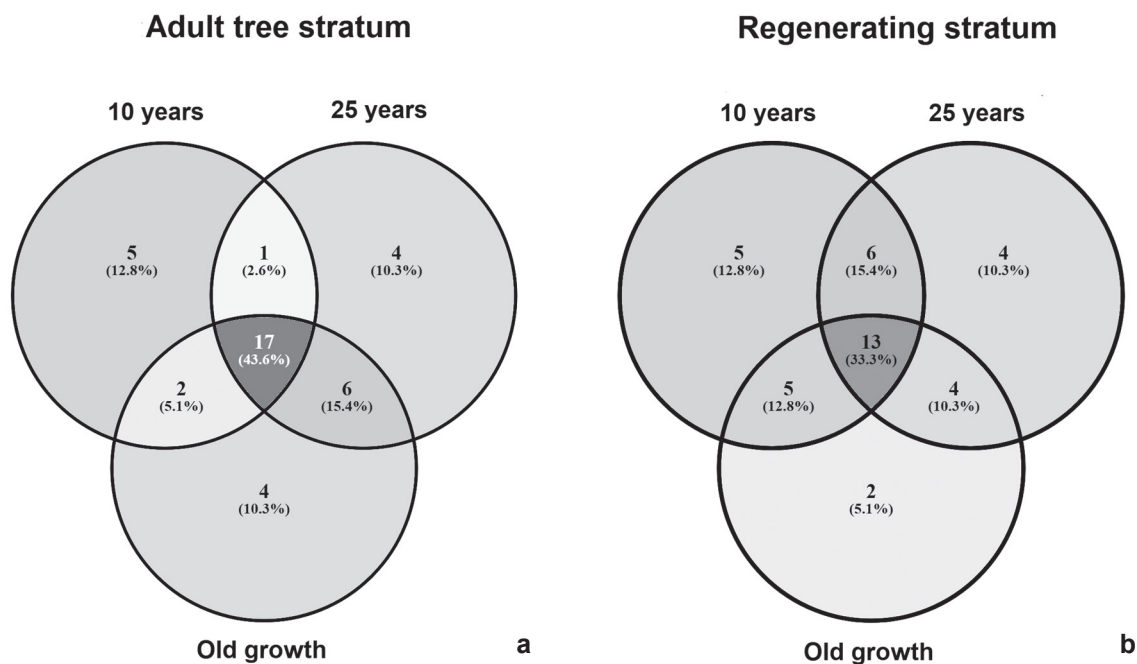


Figure 10 – Venn diagram for the tree (a) and regenerating stratum (b) for old growth, 10 years regeneration and 25 years regeneration, Chapadas region, Piauí.

disturbed sites, which can take a relatively long time for the reestablishment of communities, similar to the old growth.

According to Gotelli & Colwell (2001), as ecological disturbances reduce the abundance of species, it was expected, in some cases, that the disturbance would decrease the density of species, as there would be fewer individuals present to be sampled after a disturbance. However, the ranking of species abundance showed that the increase in community richness in the studied areas was influenced by the equability of species abundance (Magurran 2004). The prevalence of rare species in the presence of a few high-abundance species shows the importance of rare species in increasing local richness (alpha diversity) (Magurran 2004; Gotelli & Colwell 2011). We highlight the importance of rare species for increasing richness in areas that are undergoing natural regeneration processes and the dominant species for the contribution of population density, which in the *Cerrado* rarely exceeds 100 woody species per hectare (Felfili *et al.* 2004; Spera *et al.* 2005). Recent studies suggest that species of late succession of old growth can be replaced by pioneer species (with rapid growth), where pioneer species may become dominant in areas

that have undergone anthropogenic disturbances (Villa *et al.* 2019; Villa *et al.* 2020).

The most representative families in terms of the number of individuals were Fabaceae, Combretaceae, and Myrtaceae, which were also found in floristic and phytosociological studies in ecological transition areas (Farias & Castro 2004; Silva *et al.* 2015; Macedo *et al.* 2019). Studies performed in the *Caatinga* by Moro *et al.* (2014) found similar results, where the Fabaceae family was the most representative. Legumes are often featured prominently in *Caatinga* inventories (Machado *et al.* 2012; Costa *et al.* 2015). We found few species with high abundance of individuals and with high dominance, shown in the abundance rank and floristic list, considering that the *Cerrado* has a low number of species, where few abundant or rare species participate in the occupation of space (Andrade *et al.* 2002; Assunção & Felfili 2004). This result also agrees with what was found in research carried out in the *Caatinga*, where the Fabaceae family presented a higher value of importance as a result of the large number of individuals, when compared to less abundant species (Rodal *et al.* 2008; Guedes 2012). Abundance patterns are quite variable for species and families in general; that

is, the abundance of individuals is not always proportional to the number of species, as few species can be represented by large populations, or a single species can be very abundant in the community (Araújo *et al.* 2009). The species abundance values for the studied areas may indicate progress in the regeneration process.

Similarity analysis and beta diversity were influenced by turnover, reinforcing the idea that this change in species composition between areas is caused by species replacement, which can be explained by different stages of regeneration. The difference in species found can be justified by the succession time and changes in the structure of these communities due to agricultural activities, which can change soil and niche conditions and limit the occupation of late species in these communities leading to changes in species composition (Moutinho 2011; Chang & Turner 2019). Beta diversity was more affected by turnover than by nestedness in ecosystems with high diversity and environmental heterogeneity, suggesting that the history of disturbance or colonization is most responsible for community structuring (Soares *et al.* 2020).

For the three studied areas, we observed differences in species composition between the tree and regenerating strata, which indicates the entry of propagules in the areas, contributing to an increase in diversity, thus being important in the structuring of communities, as the regenerating strata will initiate ecological succession until tree species settle in the area. This process of replacing species over time commonly occurs in areas that are undergoing ecological succession, causing changes in species composition and reflecting the functionality of the community (Silva *et al.* 2012). Thus, ecological succession can be used to describe vegetation change processes at various scales such as temporal or spatial post-disruption events (Silva *et al.* 2012; Chang & Turner 2019). Thus, during this process, changes occur in a community over time, and because of disturbances, species can be removed (Moutinho 2011; Chun & Lee 2019). Despite the presence of old growth species in secondary communities, it is assumed that the total recovery of the composition of the old communities takes centuries, and that although these secondary communities have a high conservation value in human-modified context, but, in the short term, they do not replace old growth communities that are home to many old growth species (Rozendaal *et al.* 2019).

We note that the old-growth and secondary communities present differences in the richness estimates, which may be a response to disturbance and successional time. The richness in these areas was influenced by the equity of abundances of species with fewer individuals, both for trees and shrubs, and for the regenerating stratum. We emphasize that the predominant species contribute to the density and the rare ones to the increase in richness. Differences in species composition may reflect both the successional stage and the effect of the disturbance that areas were subjected to, which was corroborated by the partitioning of beta diversity, showing that turnover was more prevalent for diversity.

Open Access

In accordance with Open Science communication practices, the authors inform that all raw data generated by this study can be accessed in our supplementary data at <<http://doi.org/10.6084/m9.figshare.21830283>>.

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