

Tree community dynamics in the cerrado (2002-2016): A case of biome shift

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ABSTRACT

The cerrado is the result of profound structural changes from open Cerrado vegetation, associated with the absence of certain disturbances, such as wild fires. Little is known about these changes in the long term, both in species composition and structure after canopy closure, hindering predictions regarding the community trajectory. Cerrado is positioned along the higher biomass extreme in the Cerrado phytophysionomic gradient. This study is based on the changes recorded over a 14 yr period, in 256 plots totaling 10.24 ha of sampling area, in a cerrado located inside a conservation unit, protected from fire for at least 60 years in the state of São Paulo, Brazil. The changes in the community structure and species composition were assessed. We investigated if the changes are related to tree community structure or to biological attributes of the species, especially by their habitat preference (savanna specialists vs. generalists of forest species). Despite the long period without disturbance and the dystrophic soils, we found tree basal area still increasing and the largest trees still growing. On the other hand, tree density is decreasing over time, and 54% of trees recorded in the first survey had died 14 years later. Community diversity had only a slight increase over time, due to a small gain in species richness. Forest and generalist species presented higher increments in basal area and faster growth compared to the rare savanna specialists still alive in the community. We also verified that larger trees grow slightly faster than smaller trees. Although these changes point to an increase in competition, mortality was not correlated with tree basal area, and seemed to happen more randomly at community level. However, mortality and recruitment were not random at species level. We detected increase in abundance of forest and generalist species, which are shade tolerant. The lowest recruitment rates and highest mortality rates were associated with typical open Cerrado species (savanna specialists), that tend to disappear over time, consolidating the biome shift from savanna to forest. The contribution of cerrado to the conservation of Cerrado endemic tree species, therefore, is poor and tends to decrease over time.

1. Introduction

Characterizing changes in different types of vegetation over time is a fundamental step towards understanding their functioning and predicting ecosystem trajectories through changing anthropogenic or environmental factors. In old-growth forests, studies have shown that structure and growth are relatively stable, with balanced tree

recruitment and mortality and stable species composition (Terborgh et al., 1996). Thus, the tree community tends to change very little over time in its structure and composition if climatic conditions remain stable. On the other hand, in savannas, which are ecosystems modulated and maintained by a natural disturbance regime, the concept of “old-growth” is not based on structural stability over time at the community scale (Veldman et al., 2015). The suppression of disturbances in

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savannas generally leads to woody consolidation, unless some strong environmental constraint prevents the growth of trees. This densification process has been observed in different savannas around the world (Stevens et al., 2017), and may culminate in “biome shift” in vast regions in which forest and savanna are alternative stable states, maintained by different disturbance regimes in similar environmental conditions (Bond et al., 2005; Hirota et al., 2011; Staver et al., 2011).

The process of woody encroachment in savannas has been little studied at the community level and in the long term. In West Africa, the study by Menaut et al. (1990) stands out, who found a replacement trend of endemic savanna species by shade-tolerant forest species. In the Cerrado, which represents the savanna biome in Brazil, the study of the dynamics of tree communities has recently acquired moderate progress (Lima et al., 2009; Elias et al., 2019; Rios et al., 2019; Rodrigues-Souza et al., 2015), pointing out temporal changes similar to those observed by Menaut et al. (1990). However, studies on open physiognomies predominate, and little is known about the tree communities in the cerrado (Franczak et al., 2011; Flake et al., 2021; Flake et al., 2022). The cerrado (woodland savanna) can be defined as a vegetation with continuous tree stratum, where forest and generalist species mix with endemic species of the Cerrado, the savanna specialists (Walter et al., 2015). The cerrado occupies the extremity with the highest biomass within the spectrum of the so called “Cerrado phytophysionomies”. Due to the absence of a grassy ground layer, it is often questioned whether the cerrado can be considered a savanna phytophysionomy, or if it fits better as a forest phytophysionomy or if it would be a distinct vegetation type. Although old studies associated cerrado with high nutrients availability (Goodland and Pollard, 1973; Lopes and Cox, 1977), it has not been confirmed by recent studies which found similar structure and biomass in either dystrophic or mesotrophic soils (e.g. Rodrigues, Araujo, 2013). In addition, the relationship between nutrient availability and vegetation structure in the Cerrado has not been confirmed by other studies (Ruggiero et al., 2002), while a trend has been observed towards higher biomass in soils with higher clay content, that is, with greater soil water holding capacity. Among these studies are Elias et al., 2019 in Mato Grosso and, in the cerrados of São Paulo, this has been confirmed by Toppa (2004) and Assis et al. (2011), the latter carried out in the same conservation unit as the present study – Estação Ecológica de Assis.

What is also known from studies dealing with temporal changes in Cerrado vegetation is that, by reducing the frequency of burning, there is an increase in the basal area, a reduction in the herb-shrub layer (Pinheiro and Durigan, 2009; Roitman et al., 2008; Silvério et al., 2013; Almeida et al., 2014; Cordeiro et al., 2020) and change in the composition of functional groups (Flake et al., 2021), which may have drastic consequences for the long-term conservation of plant species. Differences in mortality and growth rates between species as the basal area of the community increases result in favoring some species and disfavoring others (Flake et al., 2022), so that the composition of species in the cerrado is considerably different from the composition of the open physiognomies of the Cerrado (Pinheiro and Durigan, 2012). In addition to temporal changes being differentiated between species in the cerrado (Mariano et al., 2019; Flake et al., 2022), studies have also shown that mortality rates vary between size classes and according to the density and basal area of tree communities (Oliveira and Felfili, 2008).

Although studies already carried out have demonstrated the existence of woody encroachment along the physiognomic gradient of the Cerrado through suppression of disturbances, there are still gaps in knowledge about the dynamics of tree communities that are undisturbed for an effectively long period and, supposedly, could have reached a stable condition compatible with environmental constraints. The present study was carried out in a stretch of cerrado that reached complete canopy closure more than 20 years ago, at the end of a tree encroachment process that has lasted more than six decades. We seek to clarify the following questions:

- 1) After the canopy closure achieved with long-term protection against disturbance, would the cerrado have reached a stable condition in terms of composition and structure?
- 2) If there is no stability, what are the directions of change?
- 3) Can the community have its dynamics explained by its own attributes?
- 4) Is there a pattern in the changes related to the species that form the community?

We start from the premise that if there were no changes in the structure (density, basal area and distribution of size classes) and no difference in mortality and recruitment between species over 14 years without disturbance, it can be considered that the cerrado reached stability. If it is not stable, we expect that light restriction resulting from the woody encroachment is still disfavoring the savanna specialists, as observed in previous studies.

2. Material and methods

2.1. Study area

The study was carried out at Assis Ecological Station, Assis municipality, state of São Paulo, Brazil. The study area is a set of 256 permanent plots (20 × 20 m each), totalling a continuous area of 10.24 ha (Fig. 1), conceived in the early 2000 s for community dynamics studies. The southeastern, southwestern, northeastern and northwestern corners of the study area have the following pairs of decimal geographical coordinates, respectively: 22.59581° S, 50.37824° W; 22.59525° S, 50.37507° W; 22.59240° S, 50.37561° W and 22.59295° S, 50.37862° W. The altitude within the plot ranges from 550 to 575 m above sea level, with an average slope of 7%. The region's climate is characterized by Köppen's Cfa (Alvares et al., 2013), humid subtropical with hot summer, with average annual precipitation of 1421.5 mm, concentrated in summer and average annual temperature of 21.8°C, with sporadic frosts. The soils at Assis Ecological Station are dystrophic, with less than 10% base saturation, being alic, sandy (less than 20% clay) and deep (Assis et al., 2011).

The study area was part of a cattle farm, and a common management practice for livestock in the Cerrado was to burn the native vegetation every two years to renovate the pasture (Dias et al., 2006). In 1992, the conservation unit was created, with conservation goals and part of the area slowly recovered, currently covering 1760.64 ha. The northeastern-most part of the reserve has its borders with the seasonal semideciduous forest, that, differently from the open surrounding cerrado formations, has low sprouting capability. The absence of fire can already be felt in the canopy closure of the northernmost parts of the area (Conciani et al., 2021; Durigan and Ratter, 2006; Rodrigues and Ivanuskas, 2006). In that northeastern-most face, a denser vegetation prevails, resembling a semideciduous seasonal forest. However, it is a forest-type of Cerrado vegetation, which has undergone woody encroachment (Pinheiro and Durigan, 2009) and biomass increase due to fire suppression.

The maps of the permanent plots with the chronology of the woody encroachment (Fig. 1), shows cerrado (woodland savanna) expanding over time at the cost of open vegetation types, occupying the whole area by the time of the first inventory. The area occupied by the different vegetation types within the study area was quantified by aerial photos from the years 1962 (1:25,000), 1984 (1:35,000), 1994 (1:25,000) and images with high spatial resolution of 2006, from the “QuickBird” satellite (QB). The QB images, panchromatic and multispectral, were merged using the “Gram-Schmidt” method, available in the ENVI 4.3 application (Research Systems Inc. RSI, 2006). To orthorectify the QB image, the rational function model described by Tao and Hu (2001) was used. Digital aerial photos from each year were mosaicked using the “Image Registration and Mosaicking” (REGEMMY) application (Fedorov et al., 2003). An Affine transformation was applied for this task, using

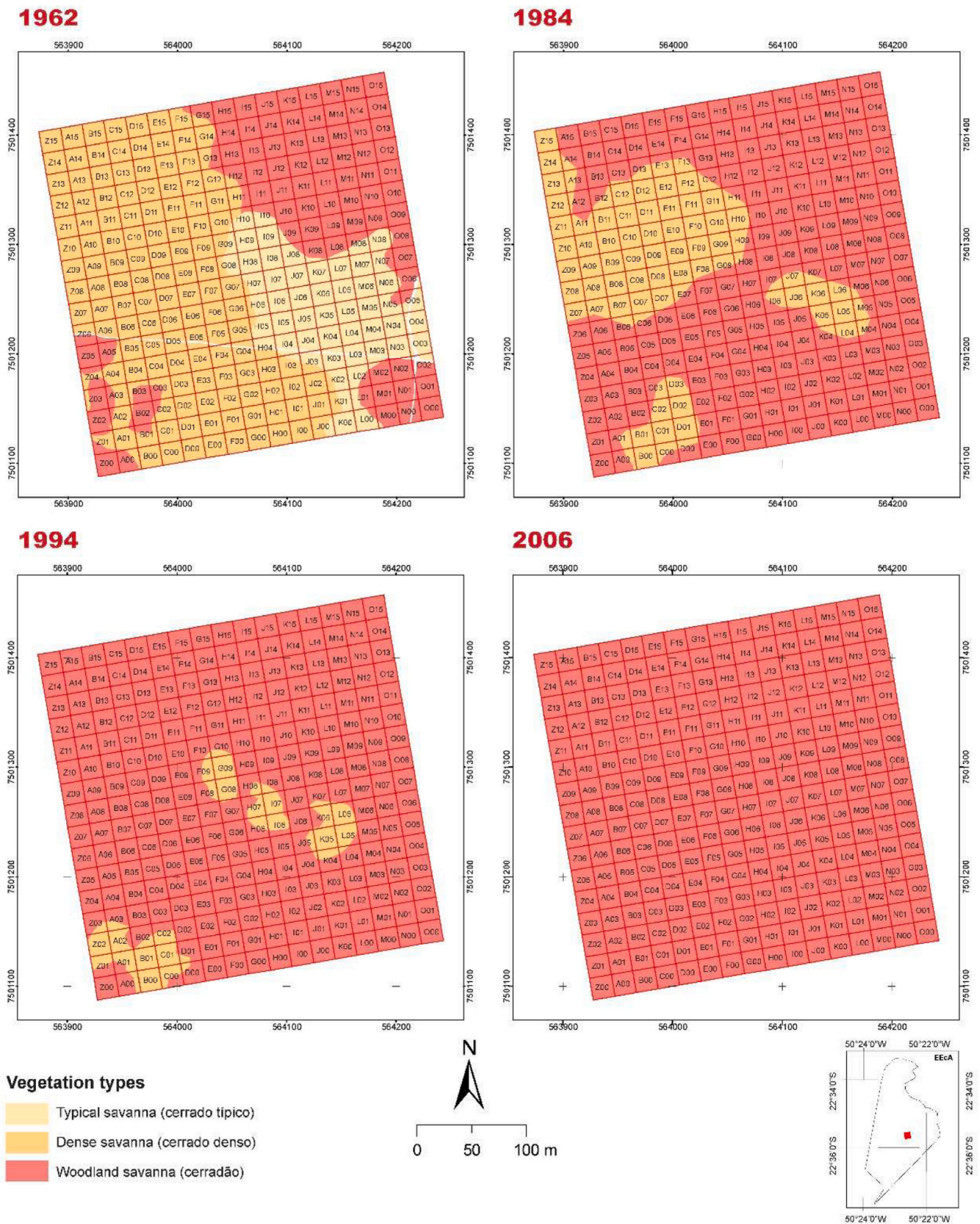


Fig. 1. Temporal changes (1962 – 2006) in the proportion between vegetation types in the study area of 10.24 ha of cerradão, located in the center of the Ecological Station of Assis (EECA), in the period 1962–2006, after complete suppression of fire. The red grid divides the study area in 256 plots (20 × 20 m), with their respective codes.

only the central part of the aerial photos. Subsequently, each mosaic was georeferenced, based on the “QuickBird” image.

2.2. Data collection

Data used in this study corresponds to the first survey of the tree community within the permanent plots, in the year of 2002, and to the survey carried out in the year of 2016, a 14-year interval. In each of the 256 plots, each tree with circumference at breast height (CBH) from 15 cm received an aluminum tag, fixed at the largest stem. CBH of each trunk was measured and the species registered. CBH data were used to calculate the basal area of each plot, and to obtain total basal area of each species. Since the first survey, plant material was collected in each occasion to identify the individuals sampled. For each species, at least one plant material was incorporated into the herbarium of the Escola Superior de Agricultura “Luiz de Queiroz”/USP (ESA). For identification, appropriate literature was used, supported by comparison with exsiccates existing in herbaria or consultation with specialists. Updated nomenclature followed the Brazilian Flora 2020 database (Flora do Brasil 2020). Species were classified as savanna specialists (shade-intolerant, typical of open vegetation types) or not (forest species and generalists). For this categorization, we followed a previous study in the same region (Flake et al., 2021). These authors carefully checked the occurrence of the species sampled with all records for São Paulo state in the speciesLink virtual herbarium database (CRIA, 2020). Species were assigned as ‘savanna specialists’ if at least 66% of the locality records were from savanna vegetation, and ‘forest specialists’ if at least 66% were from forest vegetation, with the remainder assigned as ‘generalists’ (Flake et al., 2021). In our study, because we aimed to address to what extent shade-tolerant trees (forest specialists or generalists) have colonized and could be dominating the studied vegetation, we merged them in a single category in some analyses, in contrast to the ‘savanna specialists’, which are associated to open vegetation types.

2.3. Changes in plant community structure

The CBH was used to obtain the basal area of each tree, by summing up the sectional areas of all stems in case of multiple stems. These values were used to calculate the basal area of each plot (sum of basal areas of all trees within a plot, converted in $m^2 ha^{-1}$), and also to obtain the total basal area of each species (sum of basal areas of all individuals of a particular species in the whole study area, converted in $m^2 ha^{-1}$ (Durigan et al., 2003).

To verify if the vegetation is stable in its structure, we compared the mean values for basal area (converted in $m^2 ha^{-1}$) and density (converted in $ind. ha^{-1}$) between surveys (2002 vs. 2016) in the 256 plots. To detect these differences, a Wilcoxon’s t test with 5% significance and 255 degrees of freedom was performed, using packages ggpubr (Kassambara, 2023), dplyr (Wickham et al., 2023) and PairedData (Champely, 2018). We also constructed a histogram based on the frequencies of basal area changes over 14 years, to illustrate the range of basal area change across all plots.

2.4. Richness, diversity and community similarity

We compared the total number of species, diversity and evenness between the two surveys. We used Estimate-S, version 9.1.0 (Colwell, 2013). We calculated the Shannon index (H'), that gives more weight to rare species and considers random sampling (Magurran, 1988). Evenness was calculated by the Pielou index (as the quotient of Shannon diversity and maximum diversity, this last one calculated as the natural log of the species number for each survey). To check if the permanent plot system conceived by the experiment has sampled a number of species close to the complete set, we calculated Chao 1 using data from the first survey. Chao 1 was calculated with lower and upper bonds with a 95% confidence interval. We used Chao 1 since not only incidence, but

also abundance data were present. Statistical significance for H' values obtained in the two sampling occasions was calculated through Hutcheson’s t test (Magurran, 1988), implemented through ecolTest R package (Salinas and Ramirez-Delgado, 2021).

2.5. Tree community dynamics

Dynamic rates were calculated considering the exponential model proposed by Sheil, May (1996). Mortality and recruitment rates were calculated for the entire community, for individual plots and for each species, in this case only for those with more than ten individuals sampled.

The equations for mortality and recruitment were:

$$M = [1 - \{[(N0 - m)/N0]^{(1/t)}\}] * 100 \text{ and.}$$

$$R = [1 - (1 - r/Nt)^{(1/t)}] * 100.$$

Where:

M = annual mortality rate.

R = annual recruitment rate.

N0 = number of individuals in the initial survey.

Nt = Number of individuals in the final survey.

m = number of dead individuals spanning the survey interval.

t = time spanning the survey interval.

r = number of recruits.

To verify if the mortality rates depend on initial basal area of the plots, we used a simple linear regression, with the basal area of the plots as the predictor variable.

We used an association chi-squared test in search of patterns of change in species composition, according to their habitat preference (savanna specialists associated to open savanna, and forest specialists + generalists associated to dense and continuous canopy). For this, we constructed a chi-squared table with the two surveys as rows and the number of individuals of each species with more than 10 individuals in the first survey in the columns. Species were classified as losers (significant loss in number of individuals between sampling occasions) or winners (significant gain in number of individuals), then proceeding to calculate the expected frequencies and the chi-squared statistics, with a 5% confidence interval. We used this analysis to see if there is a change in the composition of species, since with the increase in density, specialist savanna species tend to disappear (Flake et al., 2021).

2.6. Tree growth

For each tree that was sampled on both occasions, we calculated the annual increment in stem diameter by dividing the difference between the final and the first sampling occasion by 14 years. From the circumference at breast height (CBH), we obtained the diameter at breast height (DBH) or the equivalent diameter (Dg), which is a hypothetical single diameter calculated for multi-stemmed trees using the formula $Dg = \sqrt{(4g/\pi)}$, where g is the summed basal area of all individual stems.

To verify if the annual increment in stem diameter depended on tree size, we used the initial diameter as the independent variable. For this analysis, we used the modules scipy, pandas and matplotlib for python programming language (Van Rossum, Drake, 1995) in jupyter-lab to calculate regression parameters (r^2), the p-value. For this analysis, 5000 individuals were randomly taken from the community. The individuals that had negative increment were excluded from the analysis since they correspond to individuals that lost stems due to advanced age, injuries or diseases (had one or more stems died).

We also calculated the mean annual increment in diameter separately for savanna specialists or not (generalists and forest species), searching for a pattern related to the preferential habitat of the species. For this analysis, we obtained mean and standard deviation values for each species group, then performed a Student’s t-test with 5% significance to compare the mean values. The mean annual growth in stem

diameter was calculated based on the equivalent diameter of multi-stemmed individuals.

When not specified, all analyses were performed using R software Version 4.2.2 (R Development Core Team, 2022). For the inference procedures we set $\alpha = 0.05$.

3. Results

3.1. Changes in community structure

Over 14 years, the studied community had gain in basal area and reduction in density. Of the sampled trees in 2002 in the whole area, 54.3% were dead in 2016. No individuals died between surveys for 23% of the species. At the other extreme, for 17.5% of the species, all individuals initially sampled died, though not all these species disappeared from the community, given that there was recruitment for some of them. The mean basal area increased from $19.3 \text{ m}^2 \text{ ha}^{-1}$ to $22.3 \text{ m}^2 \text{ ha}^{-1}$ (Wilcoxon's $t = -14.53$, $df = 249$, $p < 0.001$), with an average gain of $0.21 \text{ m}^2 \text{ ha}^{-1}$ in basal area per year. For most plots (214) there was an increase in basal area over 14 years, with values around $2.5 \text{ m}^2 \text{ ha}^{-1}$ being the more frequent (Fig. 2). Density decreased (Wilcoxon's $t = 4.90$, $df = 249$, $p < 0.001$), from 1955 ind ha^{-1} to 1906 ind ha^{-1} , which corresponds to an average of -2.52% over 14 years (0.18% less density per year).

Distribution of individuals in size classes in both surveys (Fig. 3) showed decrease in the number of trees from 4.7 to 15 cm DBH (less 556 trees in the whole area), and increase in all size classes above 15 cm DBH over 14 years. The increase related to the initial survey was larger the larger the DBH, with trees above 25 cm DBH more than doubling.

3.2. Changes in richness, diversity and composition

In 14 years, tree species richness increased from 123 to 133 in the study area as a whole, a gain of 0.7 species per year. From the species recorded in the first survey, 17 were not recorded 14 years later, and 27 species entered the community in the period. The net gain in number of genera was null, as four genera disappeared from the community and four genera entered the community. There was change at family level only due to the inclusion of Lacistemaceae in 2016, represented by *Lacistema hasslerianum*. This species is a shade tolerant treelet which, despite abundant and certainly existing in 2002, only in the last survey reached the inclusion criteria, with four individuals surpassing 4.7 cm DBH. The community richness estimated by Chao 1 was 158 species,

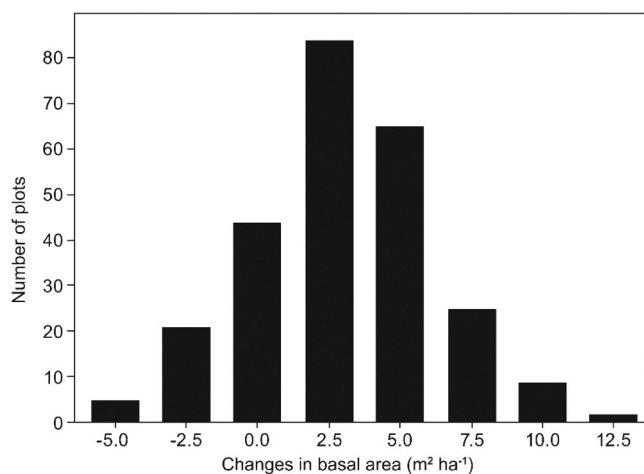


Fig. 2. Frequency distribution of changes in basal area of the cerradão tree community (Assis, São Paulo state) over 14 years (2002–2016), in 256 plots (400 m^2 each). In the X-axis, tickmarks correspond to the class midpoint ($\text{m}^2 \text{ ha}^{-1}$).

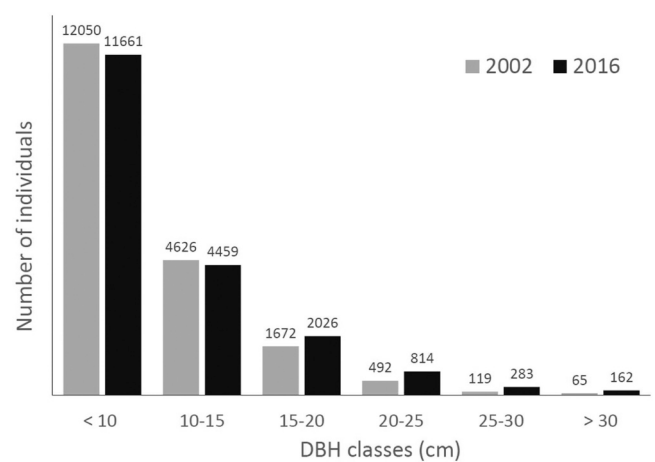


Fig. 3. Distribution of all individuals sampled in 10.24 ha of cerradão (woodland savanna, Assis, São Paulo State) among diameter classes in the initial survey (2002) and 14 years later (2016).

with lower and upper bounds of 136 and 218 species, with a 95% confidence interval (standard deviation 19 species). Changes in species populations (number of individuals and dominance represented by basal area) are shown in Table 1.

Hutcheson's t test showed a significant difference in Shannon index between surveys ($t = -6.44$; $df = 39679$; $p = 1.189 \times 10^{-10}$), with a 2.57% increase, with the index changing from 3.22 to 3.30. Pielou's evenness was stable around 0.67, showing that the community remains dominated by few species.

The association chi-squared test indicated that the community composition is changing significantly, as the proportion of forest and generalist species is increasing more than expected by chance and the proportion of savanna specialists is decreasing ($\chi^2 = 740.56$, $p < 0.05$, $df = 1$).

3.3. Mortality and recruitment

The annual rates obtained for the whole community in the study area were 2.68% for mortality and 2.55% for recruitment. There was no significant correlation between the mortality rate per plot and the basal area of the plot ($R^2 = 0.01$; $p > 0.05$). Among the 61 species with more than ten individuals recorded in the first survey (Table 2), the average annual mortality was 11.6% for savanna specialists and 2.5% for generalists and forest species. Average annual recruitment was 2.8% among savanna specialists and 3.7% among forest and generalist species. Most species (85%) had a mortality rate lower than 5% per year. Among these, only one every five was a savanna specialist. Among the species with annual mortality being 5% or higher, 66% were savanna specialists.

3.4. Tree growth

The community mean annual growth in stem diameter was $1.23 \text{ mm year}^{-1}$. Though the linear regression between the annual increment in stem diameter and the equivalent diameter (Fig. 4) was weak ($r^2 = 0.0657$, $\beta = 0.0863$), it was significant ($p < 0.001$). This finding indicates that larger trees tend to grow a little faster than the smaller trees.

The Student t -test revealed that the mean annual increment in stem diameter was significantly lower ($t = 156.77$, $df = 5038$, $\alpha = 0.05$) for savanna specialists ($0.66 \text{ mm year}^{-1}$, $sd = 1.55 \text{ mm year}^{-1}$) in comparison to the other species (generalists or forest species, which grew $1.37 \text{ mm year}^{-1}$, $sd = 2.00 \text{ mm year}^{-1}$).

Table 1

Number of individuals sampled in the whole area and basal area ($m^2 ha^{-1}$) for each species (alphabetical order) at the initial (2002) and final survey (2016) in 10.24 ha of cerrado (woodland savanna), in Assis, state of São Paulo. Values obtained for the whole area. SS: Savanna specialist (yes or no). NI: initial number. NF: final number. CN: Change in number of individuals over time. Species within the ten highest gains in the basal area are presented in bold.

Species	SS	NI	NF	CN	BA initial ($m^2 ha^{-1}$)	BA final ($m^2 ha^{-1}$)	Change in BA ($m^2 ha^{-1}$)
<i>Actinostemon klotzschii</i> (Didr.) Pax	No	3	4	1	0.0014	0.0017	0.0003
<i>Amaioua intermedia</i> Mart. ex Schult. & Schult.f.	No	342	504	162	0.1467	0.2805	0.1338
<i>Anadenanthera peregrina</i> (L.) Speg.	No	6	5	-1	0.0246	0.0233	-0.0013
<i>Annona crassiflora</i> Mart.	Yes	14	3	-11	0.0172	0.004	-0.0132
<i>Aspidosperma tomentosum</i> Mart.	Yes	1	1	0	0.0002	0.0003	0.0001
<i>Bauhinia brevipes</i> Vogel	Yes	1	1	0	0.0002	0.0002	0
<i>Bowdichia virgilioides</i> Kunth	Yes	28	22	-6	0.0339	0.0430	0.0091
<i>Brosimum gaudichaudii</i> Trécul.	Yes	1	3	2	0.0004	0.0017	0.0013
<i>Byrsonima affinis</i> A. Juss.	Yes	4	3	-1	0.0074	0.0015	-0.0059
<i>Byrsonima coccolobifolia</i> Kunth	Yes	1	0	-1	0.0007	0.0000	-0.0007
<i>Byrsonima crassifolia</i> (L.) Kunth	Yes	1	2	1	0.0010	0.0042	0.0032
<i>Byrsonima laxiflora</i> Griseb.	No	282	437	155	0.1979	0.5497	0.3519
<i>Cabralea canjerana</i> (Vell.) Mart.	No	5	4	-1	0.0053	0.0047	-0.0006
<i>Calophyllum brasiliense</i> Cambess.	No	1	1	0	0.0005	0.0011	0.0006
<i>Caryocar brasiliense</i> Cambess.	Yes	3	4	1	0.0015	0.0038	0.0023
<i>Casearia decandra</i> Jacq.	No	2	4	2	0.0003	0.0015	0.0012
<i>Casearia lasiophylla</i> Eichler	No	1	1	0	0.0002	0.0015	0.0013
<i>Casearia sylvestris</i> Sw.	No	28	29	1	0.0105	0.0149	0.0044
<i>Clethra scabra</i> Pers.	No	26	24	-2	0.0384	0.0479	0.0095
<i>Copaifera langsdorffii</i> Desf.	No	3900	3776	-124	4.5626	6.8290	2.2664
<i>Couepia grandiflora</i> (Mart. & Zucc.) Benth. ex Hook.f.	Yes	3	1	-2	0.0026	0.0011	-0.0015
<i>Coussarea hydrangeifolia</i> (Benth.) Müll. Arg.	No	1	1	0	0.0003	0.0006	0.0003
<i>Croton floribundus</i> Spreng.	No	103	105	2	0.0880	0.1621	0.0741
<i>Cupania tenuivalvis</i> Radlk.	No	1	6	5	0.0032	0.0020	-0.0012
<i>Dalbergia miscolobium</i> Benth.	Yes	5	5	0	0.0208	0.0240	0.0032
<i>Daphnopsis fasciculata</i> (Meisn.) Nevlng.	No	192	328	136	0.0927	0.1553	0.0626
<i>Dendropanax cuneatus</i> (DC.) Decne. & Planch.	No	0	2	2	0	0.0008	0.0008
<i>Didymopanax vinosum</i> (Cham. & Schltdl.) Marchal	Yes	1	0	-1	0.0002	0	-0.0002
<i>Dimorphandra mollis</i> Benth.	Yes	1	1	0	0.0047	0.0067	0.0020
<i>Duguetia lanceolata</i> A.St.-Hil.	No	5	4	-1	0.0056	0.0066	0.0010
<i>Endlicheria paniculata</i> (Spreng.) J.F.Macbr.	No	4	0	-4	0.0046	0	-0.0046
<i>Enterolobium gummiferum</i> (Mart.) J.F.Macbr.	Yes	2	0	-2	0.0013	0	-0.0013
<i>Eriotheca gracilipes</i> (K.Schum.) A.Robyns	Yes	9	3	-6	0.0073	0.0024	-0.0049
<i>Erythroxylum cuneifolium</i> (Mart.) O.E.Schulz.	No	2	1	-1	0.0003	0.0003	-0.0001
<i>Erythroxylum deciduum</i> A. St.-Hil.	No	20	12	-8	0.0073	0.0050	-0.0023
<i>Eugenia aurata</i> O. Berg.	Yes	34	24	-10	0.0167	0.0119	-0.0048
<i>Eugenia cerasiflora</i> Miq.	No	0	1	1	0	0.0006	0.0006
<i>Eugenia florida</i> DC.	No	2	1	-1	0.0007	0.0006	-0.0001
<i>Eugenia myrcianthes</i> Nied.	Yes	1	3	2	0.0002	0.0008	0.0006
<i>Eugenia pluriflora</i> DC.	No	15	21	6	0.0064	0.0084	0.0020
<i>Eugenia repanda</i> O. Berg.	No	0	1	1	0	0.0010	0.0010
<i>Eugenia sparsiflora</i> DC.	No	0	1	1	0	0.0001	0.0001
<i>Faramea montevidensis</i> (Cham. & Schltdl.) DC.	No	249	633	384	0.1039	0.3379	0.2340
<i>Ficus eximia</i> Schott.	No	4	0	-4	0.0031	0	-0.0031
<i>Ficus guaranitica</i> Chodat.	No	1	3	2	0.0017	0.0034	0.0024
<i>Guapira graciliflora</i> (Mart. ex Schmidt) Lundell.	Yes	19	11	-8	0.0237	0.0200	-0.0037
<i>Guapira hirsuta</i> (Choisy) Lundell.	No	5	7	2	0.0036	0.0040	0.0004
<i>Guapira noxia</i> (Netto) Lundell.	Yes	12	6	-6	0.0234	0.0113	-0.0121
<i>Guapira opposita</i> (Vell.) Reitz.	No	15	10	-5	0.0087	0.0026	-0.0061
<i>Handroanthus ochraceus</i> (Cham.) Mattos.	Yes	2	0	-2	0.0010	0	-0.0010
<i>Ilex brasiliensis</i> Loes.	No	2	1	-1	0.0005	0.0001	-0.0004
<i>Ilex paraguariensis</i> A.St.-Hil.	No	33	60	27	0.0150	0.0249	0.0099
<i>Ixora brevifolia</i> Benth.	No	45	94	49	0.0186	0.0596	0.0410
<i>Lacistema hasslerianum</i> Chodat.	No	0	4	4	0	0.0008	0.0008
<i>Lafoesnia pacari</i> A.St.-Hil.	Yes	30	24	-6	0.0235	0.0218	-0.0017
<i>Leptolobium elegans</i> (Benth.) Yakovlev	Yes	80	20	-60	0.0433	0.0160	-0.0273
<i>Licania humilis</i> Cham. & Schltdl.	Yes	3	1	-2	0.0031	0.0001	-0.0030
<i>Lithraea molleoides</i> (Vell.) Engl.	No	0	1	1	0	0.0021	0.0021
<i>Luehea divaricata</i> Mart.	No	0	1	1	0	0.0002	0.0002
<i>Luehea grandiflora</i> Mart.	No	13	11	-2	0.0064	0.0043	-0.0021
<i>Mabea fistulifera</i> Emmerich	No	1	2	1	0.0017	0.0023	0.0006
<i>Machaerium acutifolium</i> Vogel	Yes	971	580	-391	0.9212	0.7309	-0.1903
<i>Machaerium brasiliense</i> Vogel	No	157	129	-28	0.1855	0.2231	0.0375
<i>Maprounea guianensis</i> Aubl.	No	123	288	165	0.0672	0.2687	0.2015
<i>Matayba elaeagnoides</i> Radlk.	No	77	81	4	0.0424	0.0542	0.0118
<i>Miconia ligustroides</i> Naud.	No	129	140	11	0.0629	0.0862	0.0233
<i>Miconia sellowiana</i> Naud.	No	30	29	-1	0.0132	0.0178	0.0046
<i>Mollinedia widgrenii</i> A. DC.	No	3	1	-2	0.0010	0.0006	-0.0004
<i>Monteverdia gonoclada</i> (Mart.) Biral	No	42	37	-5	0.0189	0.0240	0.0051
<i>Moquiniastrum polymorphum</i> (Less.) G.Sancho.	No	198	130	-68	0.4610	0.4130	-0.0481

(continued on next page)

Table 1 (continued)

Species	SS	NI	NF	CN	BA initial (m ² ha ⁻¹)	BA final (m ² ha ⁻¹)	Change in BA (m ² ha ⁻¹)
<i>Myrcia bella</i> Cambess.	Yes	23	13	-10	0.0120	0.0067	-0.0053
<i>Myrcia glomerata</i> (Cambess.) G.P.Burton & E.Lucas	No	0	1	1	0	0.0003	0.0003
<i>Myrcia guianensis</i> (Aubl.) DC.	Yes	723	649	-74	0.2610	0.2563	-0.0046
<i>Myrcia fenzliana</i> O.Berg.	No	5	6	1	0.0032	0.0043	0.0011
<i>Myrcia multiflora</i> (Lam.) DC.	No	744	1039	295	0.2891	0.4408	0.1516
<i>Myrcia neochusiiifolia</i> A.R.Lourenço & E.Lucas	No	2	2	0	0.0063	0.0092	0.0029
<i>Myrcia</i> sp.	No	27	10	-17	0.0160	0.0030	-0.0130
<i>Myrcia splendens</i> (Sw.) DC.	No	220	270	50	0.1027	0.0914	-0.0113
<i>Myrcia tomentosa</i> (Aubl.) DC.	Yes	20	25	5	0.0045	0.0075	0.0030
<i>Myrcia venulosa</i> DC.	Yes	294	226	-68	0.0964	0.1882	0.0918
<i>Myrciaria floribunda</i> (H. West ex Willd.) O. Berg.	No	4	11	7	0.0012	0.0032	0.0020
<i>Myrsine ferruginea</i> (Ruiz & Pav.) Spreng.	No	2	29	27	0.0005	0.0106	0.0101
<i>Myrsine gardneriana</i> A. DC.	No	0	8	8	0	0.0020	0.0020
<i>Myrsine lancifolia</i> Mart.	No	241	325	84	0.0990	0.1881	0.0891
<i>Myrsine umbellata</i> Mart.	No	836	672	-164	0.2961	0.2948	-0.0013
<i>Nectandra cuspidata</i> Nees & Mart.	No	400	614	214	0.2377	0.4253	0.1876
<i>Nectandra oppositifolia</i> Nees	No	1	0	-1	0.0016	0	-0.0016
<i>Ocotea corymbosa</i> (Meisn.) Mez	No	1503	964	-539	1.7497	1.6488	-0.1009
<i>Ocotea</i> sp.	No	1	2	1	0.0017	0.0007	-0.001
<i>Ocotea velloziana</i> (Meisn.) Mez.	No	3	3	0	0.0016	0.0020	0.0004
<i>Ormosia arborea</i> (Vell.) Harms.	No	32	34	2	0.0296	0.0376	0.0080
<i>Ouratea spectabilis</i> (Mart ex Engl.) Engl.	Yes	24	0	-24	0.0199	0	-0.0199
<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	No	495	497	2	0.6115	0.7559	0.1444
<i>Persea willdenovii</i> Kosterm.	No	192	190	-2	0.4746	0.7962	0.3216
<i>Piptocarpha axillaris</i> (Less.) Baker.	No	76	64	-12	0.0536	0.0757	0.0221
<i>Plathymenia reticulata</i> Benth.	Yes	7	6	-1	0.0046	0.0043	-0.0003
<i>Platypodium elegans</i> Vogel	No	116	85	-26	0.2349	0.1864	-0.0485
<i>Plenckia populnea</i> Reissek	Yes	6	1	-5	0.0050	0.0002	-0.0048
<i>Pouteria ramiflora</i> (Mart.) Radlk.	No	122	144	22	0.1321	0.2629	0.1308
<i>Protium heptaphyllum</i> (Aubl.) Marchand	No	433	489	56	0.3142	0.5122	0.1980
<i>Prunus myrtifolia</i> (L.) Urb.	No	13	11	-2	0.0049	0.0067	0.0018
<i>Pseudolmedia laevigata</i> Trécul	No	4	5	1	0.0011	0.0027	0.0016
<i>Psidium</i> sp.	No	3	1	-2	0.0007	0.0003	-0.0004
<i>Psychotria velloziana</i> Benth.	No	0	1	1	0	0.0001	0.0001
<i>Qualea cordata</i> Spreng.	Yes	410	311	-99	0.2422	0.2225	-0.0197
<i>Qualea grandiflora</i> Mart.	Yes	57	41	-16	0.0740	0.0638	-0.0102
<i>Qualea multiflora</i> Mart.	Yes	1	0	-1	0.0006	0	-0.0006
<i>Qualea parviflora</i> Mart.	Yes	1	1	0	0.0072	0.0084	0.0012
<i>Roupala montana</i> Aubl.	Yes	19	13	-6	0.0088	0.0055	-0.0033
<i>Senegalia polyphylla</i> (DC.) Britton.	No	3	2	-1	0.0007	0.0014	0.0007
<i>Siparuna guianensis</i> Aubl.	No	223	691	468	0.0607	0.2333	0.1726
<i>Sorocea bonplandii</i> (Baill.) Burger, Lanj. & Boer.	No	1	2	1	0.0003	0.0005	0.0002
<i>Strychnos brasiliensis</i> (Spreng.) Mart.	No	4	0	-4	0.0012	0	-0.0012
<i>Strychnos pseudoquina</i> A.St.-Hil.	Yes	1	0	-1	0.0006	0	-0.0006
<i>Stryphnodendron rotundifolium</i> Mart.	Yes	7	2	-5	0.0047	0.0029	-0.0018
<i>Styrax camporum</i> Pohl	No	23	19	-4	0.0088	0.0124	0.0036
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	No	266	283	17	0.2569	0.3461	0.0892
<i>Symplocos pubescens</i> Klotzsch ex Benth.	No	15	9	-6	0.0073	0.0113	0.0040
<i>Symplocos revoluta</i> A. DC.	No	777	1069	292	1.0529	1.9674	0.9145
<i>Symplocos tenuifolia</i> Brand.	No	60	57	-3	0.0536	0.1252	0.0716
<i>Tabebuia</i> sp.	No	16	11	-5	0.0111	0.0091	-0.0020
<i>Tabernaemontana catharinensis</i> A.DC.	No	0	1	1	0	0.0003	0.0003
<i>Tapirira guianensis</i> Aubl.	No	879	376	-503	0.9253	0.4738	-0.4515
<i>Terminalia glabrescens</i> Mart.	No	176	206	30	0.1635	0.2012	0.0377
<i>Tibouchina stenocarpa</i> (DC.) Cogn.	No	1	1	0	0.0002	0.0007	0.0005
<i>Trichilia pallida</i> Sw.	No	6	7	1	0.0020	0.0033	0.0013
<i>Vochysia tucanorum</i> Mart.	No	1892	535	-1357	2.5804	0.8069	-1.7734
<i>Xylopia aromatica</i> (Lam.) Mart.	Yes	1571	1636	65	0.5501	0.9324	0.3823
<i>Xylopia brasiliensis</i> Spreng.	No	0	7	7	0	0.0052	0.0052
<i>Xylopia</i> sp.	No	0	2	2	0	0.0015	0.0015
<i>Zanthoxylum rhoifolium</i> Lam.	No	4	9	5	0.0012	0.0050	0.0038
<i>Zeyheria tuberculosa</i> (Vell.) Bureau ex Verl.	No	0	2	2	0.0000	0.0007	0.0007

4. Discussion

We addressed the changes in the tree community of a cerrado remnant growing on dystrophic soil and located in the southern limit of the Cerrado biome (savanna) in southeastern Brazil, in a transition zone to the Atlantic Forest. The study area has been protected against any form of disturbance for about six decades, over which the open savanna turned into cerrado (Pinheiro and Durigan, 2009). The vegetation had already reached complete canopy closure when monitoring of the

community dynamics began in 2002, which lead to the expectation of tree community stability. However, we found still substantial increase in basal area and in the number of large trees during the 14-yr period, showing no structural stabilization. Neither the species forming the community nor their relative abundance were stable. All changes are driving the tree community attributes to those of forest vegetation. Similar transformation from savanna to forest has already been observed by Passos et al. (2018) in the Cerrado-Amazônia transition. On-the-ground evidence that savanna woody encroachment is a

Table 2

Mortality and recruitment rates of tree species populations with 10 or more live individuals in the first survey in the cerrado (woodland savanna), Assis, state of São Paulo, between 2002 and 2016, in alphabetical order. SS: savanna specialist (Yes or No); N0: number individuals in the first survey; Nt: number of individuals in the final survey; r: number of recruits; R: annualized recruitment rate. m: number of dead individuals. M: annualized mortality rate.

Species	SS	N0 (2002)	r	R (%)	Nt (2016)	M (%)
<i>Amaioua intermedia</i>	No	342	191	4.47	28	0.60
<i>Annona crassiflora</i>	Yes	14	0	0.00	11	10.41
<i>Bowdichia virgilioides</i>	Yes	28	1	0.33	7	2.03
<i>Byrsonima laxiflora</i>	No	282	223	4.97	52	1.44
<i>Casearia sylvestris</i>	No	28	6	1.64	6	1.70
<i>Clethra scabra</i>	No	26	2	0.62	4	1.18
<i>Copaifera langsdorffii</i>	No	3900	247	0.48	334	0.63
<i>Croton floribundus</i>	No	103	23	1.75	21	1.61
<i>Daphnopsis fasciculata</i>	No	192	244	9.27	88	4.28
<i>Erythroxylum deciduum</i>	No	20	4	2.85	11	5.54
<i>Eugenia aurata</i>	Yes	34	12	4.83	16	4.44
<i>Eugenia pluriflora</i>	No	15	8	3.37	1	0.49
<i>Faramea montevidensis</i>	No	249	405	7.03	16	0.47
<i>Guapira graciliflora</i>	Yes	19	3	2.25	10	5.19
<i>Guapira opposita</i>	No	16	4	3.58	9	6.33
<i>Ilex paraguariensis</i>	No	39	33	5.54	8	1.96
<i>Ixora brevifolia</i>	No	45	52	5.59	1	0.16
<i>Lafoesia pacari</i>	Yes	30	4	1.29	10	2.85
<i>Leptobium elegans</i>	Yes	80	5	2.03	65	11.26
<i>Machaerium acutifolium</i>	No	971	76	1.00	413	3.87
<i>Machaerium brasiliense</i>	No	157	14	0.82	37	1.90
<i>Maprounea guianensis</i>	No	183	123	3.90	18	1.12
<i>Matayba elaeagnoides</i>	No	77	19	1.89	13	1.31
<i>Miconia ligustroides</i>	No	129	49	3.03	37	2.38
<i>Miconia sellowiana</i>	No	30	27	17.39	22	9.00
<i>Moquiniastrum polymorphum</i>	No	198	13	0.75	79	3.57
<i>Monteverdia gonoclada</i>	No	42	8	1.73	11	2.14
<i>Myrcia bella</i>	Yes	23	5	3.41	13	5.77
<i>Myrcia guianensis</i>	No	723	162	2.03	231	2.71
<i>Myrcia multiflora</i>	No	744	342	2.81	88	0.89
<i>Myrcia sp.</i>	Yes	27	6	6.34	19	8.32
<i>Myrcia splendens</i>	No	220	135	4.83	74	2.88
<i>Myrcia tomentosa</i>	No	20	9	3.14	4	1.58
<i>Myrcia venulosa</i>	No	294	67	2.48	114	3.44
<i>Myrsine lancifolia</i>	No	241	137	3.83	34	1.08
<i>Myrsine umbellata</i>	No	836	303	4.19	400	4.54
<i>Nectandra cuspidata</i>	No	400	396	7.13	139	3.00
<i>Ocotea corymbosa</i>	No	1503	74	0.57	580	3.42
<i>Ormosia arborea</i>	No	32	0	0.00	3	0.70
<i>Ouratea spectabilis</i>	Yes	24	5	0.00	24	100
<i>Pera glabrata</i>	No	493	68	1.05	66	1.02
<i>Persea willdenovii</i>	No	192	9	0.35	14	0.53
<i>Piptocarpha axillaris</i>	No	76	32	4.83	37	4.65
<i>Platypodium elegans</i>	No	116	8	0.70	40	2.97
<i>Pouteria ramiflora</i>	No	122	21	1.12	3	0.17
<i>Protium heptaphyllum</i>	No	433	103	1.68	49	0.85
<i>Qualea cordata</i>	Yes	410	80	2.11	133	2.76
<i>Qualea grandiflora</i>	Yes	57	3	0.54	17	2.49
<i>Roupala montana</i>	Yes	19	11	12.51	13	7.90
<i>Siparuna guianensis</i>	No	223	595	13.15	79	3.07
<i>Styrax camporum</i>	No	23	5	2.16	8	3.00
<i>Styrax sp.</i>	Yes	20	15	1.88	2	0.74
<i>Syagrus romanzoffiana</i>	No	266	66	14.52	40	1.15
<i>Symplocos pubescens</i>	Yes	15	8	2.94	13	13.40
<i>Symplocos revoluta</i>	No	777	365	5.99	57	0.54
<i>Symplocos tenuifolia</i>	Yes	60	33	0.00	29	4.60
<i>Tabebuia sp.</i>	No	16	0	1.46	11	2.64
<i>Tapirira guianensis</i>	No	879	70	2.53	549	6.75
<i>Terminalia glabrescens</i>	No	176	62	0.83	33	1.47
<i>Vochysia tucanorum</i>	No	1892	59	5.46	1379	8.90
<i>Xylopia aromatica</i>	Yes	1571	891	4.47	651	3.74

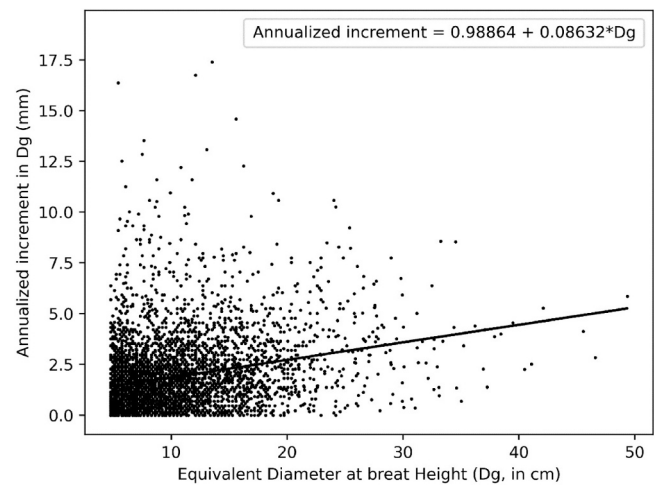


Fig. 4. Linear regression between the annualized increment in stem diameter and the equivalent diameter at breast height (Dg) for the tree community of the cerrado (Assis, state of São Paulo).

widespread phenomenon has been recently provided (Stevens et al., 2017), and it was demonstrated at large scale for South-American savannas by remote sensing (Rosan et al., 2019). Although the maximum biomass that a savanna can reach across the woody encroachment process is still unpredictable and likely vary among sites, the trend of increase triggered by suppression of disturbances is undeniable. In the case of our study, no environmental limitation seems to constrain the biome shift, which is favoured also by the surrounding sources of forest species propagules, in a transitional region between the Cerrado and the Atlantic Forest.

4.1. Structural changes towards tropical forest

The first evidence that a biome shift is ongoing was the 15.5% increase in tree basal area over 14 years (1.11% annually), a finding that is consistent with the mean rate for South American savannas that are passing through a canopy closure process, according to Stevens et al. (2017), that is, 1.04% per year. The increment in basal area was, on average, 0.21 m² ha⁻¹ yr⁻¹, lower than the increment being registered in other areas of Cerrado. Among these studies, Oliveira et al. (2014) found an increment of 0.45 m² ha⁻¹ yr⁻¹, Mews et al. (2011) found 0.55 m² ha⁻¹ yr⁻¹, Rodrigues-Souza et al. (2015) found increments between 0.48 and 0.55 m² ha⁻¹ yr⁻¹ in the cerrado and Honda and Durigan (2016) found 0.41 – 0.95 m² ha⁻¹ yr⁻¹ across the physiognomic gradient. In our plots, basal area in 2016 reached the mean value of 22.3 m² ha⁻¹, positioning itself between the values obtained at 1.30 m aboveground for cerrado and seasonal forest in all of Brazil (21.2 m² ha⁻¹ and 23.4 m² ha⁻¹, respectively, according to Walter et al. (2015).

The increment in basal area, which is lower than that observed in other studies, suggests that the tree biomass may be stabilizing according to the local soil and climate conditions (Van Breugel et al., 2006), following the expected asymptotic curve for tropical forests in secondary succession (Guariguata and Ostertag, 2001). Another change towards forest attributes was the reduction in overall density (2.5% lower after 14 years) and the increase in density of large trees (142% increase in trees with DBH greater than 25 cm), unlike what has been observed in the dynamics of tree communities in the cerrado *stricto sensu* (Aquino et al., 2007; Mews et al., 2011) and also in cerrado. Most dynamic studies in cerrado areas have found an increase in density over time (Oliveira et al., 2014; Rodrigues-Souza et al., 2015) and the authors consider that these communities are under construction (“growth phase”), that is, still in the process of consolidation. Passos et al. (2018), however, detected a reduction in the density of the cerrado, as well as in the present study, a trend towards a forest structure, of a lower density

of larger trees.

Density reduction as basal area increases is usually observed in tropical forests in advanced stages of secondary succession (Richards, 1996). In fact, in the studies by Oliveira et al. (2014) and Rodrigues-Souza et al. (2015), both comparing the dynamics of forests and cerrado, forest communities showed a reduction in density and an increase in basal area. The community dynamics analyzed in this study, therefore, corresponds to what is expected for changes over time in the structure of tropical forests. On average, for the whole Cerrado biome, the density of trees with DBH > 5 cm in the cerrado is 1587 ind ha⁻¹, while in the patches of semideciduous forest it is 1307 ind ha⁻¹ (Walter et al., 2015). If the studied cerrado is turning into a forest with no typical savanna species, the reduction in density until equaling the average of the surrounding forests is expected.

4.2. Stability, diversity, composition and change

The small differences between surveys in the total number of species recorded in the whole community, values of Shannon index and evenness show that the dynamic processes did not cause relevant quantitative changes in diversity, as has been observed in studies of Cerrado vegetation dynamics in other locations (Mews et al., 2011; Rodrigues-Souza et al., 2015). However, the quantitative changes were large, with many species showing substantial population increase (recruitment greater than mortality) and many other species showing a reduction in their populations (mortality greater than recruitment). Some species disappeared from the community, but in these cases the populations were already small in the initial survey, as has been observed in other studies in the Cerrado (Felfili et al., 2000; Hoffmann and Moreira, 2002; Libano and Felfili, 2006; Mews et al., 2011; Almeida et al., 2014).

When population changes were analyzed based on the preferential habitat of the species (if savanna, forest or either), savanna specialists showed to be already rare since the first survey, with generalist or forest species dominating the community. The difference in the proportion of the two groups increased over the 14 years, due to the much higher mortality and lower recruitment of savanna specialists in comparison to the other species. The lost species were mainly those that preferentially occur in open Cerrado vegetation, as observed in other studies of cerrado dynamics (Rodrigues-Souza et al., 2015; Passos et al., 2018). On the other hand, none of the species that appeared in the community after the initial survey were savanna specialists. Among the Cerrado endemic species that disappeared are *Enterolobium gummiferum*, *Ouatea spectabilis* and *Qualea multiflora*. *Eriotheca gracilipes* showed a drastic decrease in the number of individuals, with only three remaining, and *Plenckia populnea* also had only three individuals left in the end. *Qualea cordata* was the only savanna specialist maintaining a high number of individuals in the community, but the population has slowly decreased (from 410 to 311 individuals in 14 years), with annual recruitment of 2.1%, lower than the mortality rate of 2.8%, which is slightly higher than the community average. *Bowdichia virgilioides* tends also to disappear, even slowly. Of the 28 individuals in the first survey, only 7 died, implying a relatively low mortality of only 2.0% per year, which is below the average, but the species presented only one recruit. From the species preferentially occurring in forest vegetation in the study region (Durigan et al., 2004; Flake et al., 2021), some with small initial populations lost all individuals, such as *Endlicheria paniculata* (4 individuals) and *Nectandra oppositifolia* (one individual), likely constrained by environmental limitations. Others, such as *Croton floribundus* and *Trichilia palida* presented stable populations.

The species that were recorded in the community on both surveys formed three groups: species whose populations remained practically stable, species whose populations increased significantly and species that suffered significant population losses. When the three groups were analyzed according to the frequency of species relative to preferred habitat, we found populations of generalist and forest species tending to

increase, while savanna specialists are undergoing population reduction. From the relative density of 23.5% in 2002, these species corresponded to only 19.5% of the trees in the community 14 years later and the reason behind the reduction in number not being so high is because these species take longer to die. However, the low number of recruits of these species points out that savanna species will, sooner or later, be extinguished from the community. Other studies point out that the low light intensity inside the cerrado is the main factor driving this change in the composition of the community and seedling mortality (Franczak et al., 2011; Osunkjoya et al., 1992).

When the basal area is analyzed per species, it is noted that the shade-tolerant generalist *Copaifera langsdorffii*, one of the largest trees in the community, was the species with the highest basal area, both in the first and last surveys. For this species, the increase in basal area was 49.8% in 14 years. Among other species that stood out in basal area are *Vochysia tucanorum*, *Xylopia aromatica*, *Ocotea corymbosa* and *Symplocos revoluta*. Some of these dominant species also showed high rates of increase in basal area, such as *S. revoluta* and *X. aromatica*, with 86.9% and 69.5% increase, respectively. Other species showed decrease in basal area, such as *V. tucanorum* (68.7% less) and *Machaerium acutifolium* (20.7% less). Some species stood out with significant increases in basal area and there was great variation between species. *Maprounea guianensis*, a common tree in the seasonal semideciduous forest (Ramos et al., 2015; Souza et al., 2019), stood out with basal area increasing in 299.9%. Other species, however, had inexpressive changes in basal area, such as *Myrcia guianensis* and *Myrsine umbellata*, with losses of 1.8% and 0.8%, respectively.

In general, the species with the greatest gain in basal area were also the most frequent and dominant in the community. Among the highest densities, *C. langsdorffii* stood out, once again. However, some species with gain in basal area had a net loss of individuals, with the increase in basal area resulting from the increase in stem diameter of the remaining individuals. *C. langsdorffii* presented a net loss of 124 individuals, and *Persea wildenowii*, with lost only two, but the basal area of this species increased in 67.8%. Some species lost a high number of individuals, but their basal areas were relatively stable. For example, *Ocotea corymbosa*, had a net loss of 539 individuals, but the basal area decreased in only 5.8%. This finding is interpreted as the loss of small individuals from the understory, as there was a loss of 661 individuals for this species, much higher than the number of recruits (74). Some species, such as *V. tucanorum* and *X. aromatica*, despite the marked mortality and loss in basal area, remain among the dominant species in the community. The high mortality for these species did not affect their basal area since only small trees died.

4.3. Community dynamics is primarily driven by asymmetric competition

The considerable increase in density of trees in the upper size classes, the decrease in density of the lower size classes, associated with a little faster diameter growth for larger trees are all results compatible with asymmetric competition, characterized by slow growth or death of smaller individuals in the dispute for resources, especially light (Weiner, 1990; Van Breugel et al., 2006).

Besides tree size as a major force driving the community dynamics, however, we cannot disregard functional drivers behind the huge differences in the temporal changes between species populations. Differences exist among species in their ability to survive competition, especially for soil water and light. The shaded environment of the cerrado contributes to potentiate the environmental stress suffered by the smaller individuals, such as abnormal drought events. The greatest losses in number of individuals were for the species *Tapirira guianensis*, *V. tucanorum* and *X. aromatica*. These species behave, across the encroachment, similarly to pioneers in a classical forest succession, despite not presenting the expected pioneers' traits, such as the formation of seed bank or intolerance to shade (Swaine and Whitmore, 1988). Studies addressing community dynamics or ecophysiology with these

species indicate that, although they prefer relatively sunny environments, they are relatively tolerant to shade and their decrease in number is expected in more advanced stages of canopy closure. Under drought conditions, however, when there is a great loss of photosynthetic capacity, high mortality and loss of basal area of shaded individuals have been observed for these species (Ronquim et al., 2013). Because these species prefer relatively sunny environments, decrease in their populations is expected in more advanced stages of canopy closure. A study addressing gallery forest dynamics in Cerrado region (Lopes and Schiavini, 2007) revealed that *T. guianensis* was one of the species with greater losses over time in basal area and number of individuals, as in the present study.

The absence of relationship between mortality and basal area is likely a consequence of other factors influencing mortality, such as the level of shade, which is directly related to the functional composition of the stand. Competition for soil water, which is expected to be high in the cerrado (Honda and Durigan, 2016), could be critical under extreme drought, differently affecting the species in the community. It is also possible that basal area did not yet reach levels so high as to influence mortality. According to Kennard (2002), it takes longer to recover the basal area than to recover the canopy cover. This author found, in the recovery of seasonal forest 75% of the canopy cover recovered in eight years, while to reach the same percentage, the basal area required estimated 24 years. Thus, in the studied cerrado, our data show that growth in basal area is still possible, while the canopy cover is likely stabilized and, therefore, the functional groups are already defined by the shading level.

The reduction in density, and recruitment lower than mortality may further be a consequence of a change in the regeneration pattern, with a trend towards regeneration via seed production, in what was previously a pattern through the production of stem sprouts, which dominates in Cerrado vegetation disturbed by fire (Hoffmann and Moreira, 2002).

Phenology may also be taking its role in influencing the recruitment rates in the community. Seed production cycles differ among species, with some species surpassing a year in their seed production cycles and others having annual seed production cycles, which may have an effect on recruitment. Two species in the studied cerrado – *C. langsdorffii* and *X. aromatica* – have different seed production cycles, the first one taking longer than a year (Pedroni et al., 2002) and the latter having annual production cycles (Almeida et al., 1998). As expected, *C. langsdorffii* had a low annual recruitment rate, considering the fact that, initially, there were 3900 individuals present. In the case of *X. aromatica*, despite the high mortality (3.95% per year) the species presented a high number of recruits (891). This species is also known to be capable of frequent vegetative resprouting, which favors its recruitment (Gimenez, 2005). These opposite patterns are probably found in other species registered during this survey and should be responsible for the patterns of recruitment found. No matter which are the causes of reduction in density, mortality or recruitment, the reduction in density and gain in basal area are responsible for change in values of these variables, that put the community studied in close proximity to the nearby seasonal forests.

5. Conclusions

Even after a long time since the complete closure of the canopies and six decades without the occurrence of disturbances, the cerrado has not reached structural stability, heading towards a structural convergence (density and basal area) with the seasonal forests (Atlantic Forest) in the region. The relationships found between the structural attributes of the community and its dynamics differ from those found for open Cerrado physiognomies, indicating that even the dynamic drivers follow valid rules for forests.

Changes in community composition, both qualitative (species) and quantitative (abundance) point to the gradual disappearance of typical cerrado species through lack of light, while shade-tolerant generalist

and forest species grow faster and increase their dominance. Per definition, cerrado is a forest vegetation composed of tree species endemic to the Cerrado mixed with generalist and forest species. A small proportion of savanna specialists still remain in the community. However, these species tend to disappear, since they are not leaving descendants, consolidating the biome shift resulting from the suppression of disturbances where savanna and forest are considered alternative stable states. After six decades without disturbance, the tract of cerrado studied has contributed to enlarge the remaining habitat for forest species, while providing a negligible contribution to the conservation of typical Cerrado biodiversity.

CRedit authorship contribution statement

Durigan Giselda: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Validation, Writing – review & editing. **Stucchi Boschi Raquel:** Formal analysis. **Ivanauskas Natália Macedo:** Data curation, Funding acquisition, Methodology, Project administration, Resources. **Rodrigues Ricardo Ribeiro:** Data curation, Funding acquisition, Methodology, Project administration, Resources. **Santos Francisco Ferreira de Miranda:** Formal analysis, Software, Writing – original draft.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ricardo Ribeiro Rodrigues reports financial support was provided by Fundação de Amparo à Pesquisa do Estado de São Paulo.

Data Availability

Data will be made available on request.

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