

Seasonally dry tropical forest temporal patterns are marked by floristic stability and structural changes

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ABSTRACT

Background: Seasonally Dry Tropical Forests (SDTF) are recognized by their great biological diversity, but little is known about their temporal patterns, which may be crucial in a changing world. Here we aimed to characterize the SDTF dynamic patterns in floristic and structural changes, and also to evaluate shifts in dynamic rates and structural attributes such as richness, number of trees and biomass. Our hypothesis is that SDTF tree communities have their dynamic characterized by temporal fluctuations related to an instability pattern, in according to the already found for others tropical forests. For this we used a data of 42 400 m² plots in three fragments in the Brazilian Arboreal Caatinga, measured in 2005, 2010 and 2015. We evaluated temporal changes in richness, species composition, trees density, biomass and rates of tree mortality and recruitment; and also rates of biomass gain and loss.

Results: We found a pattern of floristic composition stability, but with changes in structure and dynamics. There was a tree density decrease driven by constant mortality and by recruitment decrease, and biomass increase due to decrease in biomass loss and to increase in biomass gain. The biomass increase was main related to a small set of dominant species that are the most representative in the community dynamics.

Conclusion: SDTF dynamics are related to stability in species composition, but with structural changes towards higher biomass stocks. The results are main related to community dynamics and to SDTF attributes such as climatic seasonality that drives the local ecological processes.

Keywords: Biomass increase; Caatinga Domain; communities stability; ecological dominance

HIGHLIGHTS

Seasonally dry tropical forests dynamic is marked by relative stability and tree increase.
Local temporal changes occurred towards trees density decrease and biomass increase.
Tree communities in tropical dry forests were not related to short-time floristic changes.
The biomass increase occurred by indicator species due to its competitive advantage.

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INTRODUCTION

Tropical forests are dynamic systems that present continuous variations at both species population and individual levels throughout space and time (Roitman *et al.*, 2016; McDowell *et al.*, 2020). These ecological processes may be related to environmental conditions and resource availability or/and to stochasticity and unpredictable events, in which different ecosystems present different specific importance of each one (Cadotte and Tucker, 2017; McDowell *et al.*, 2020). In seasonally dry tropical forests (SDTF) ecosystems, the tree communities' ecological patterns are broad related to climatic seasonality (DRYFLOR, 2016; Pennington *et al.*, 2018; Maia *et al.*, 2020). These vegetation types occur at sites with annual mean rainfall less than 1,800 mm and in which three or more months receive less than 100 mm, with approximately 80-90% of the annual precipitation distributed irregularly and unpredictably within the rainy season (DRYFLOR, 2016; Pennington *et al.*, 2018).

Due to its great climatic seasonality, ecological processes of growth and recruitment of tree individuals in SDTF occur predominant during the rainy season or after erratic rains occurring in the dry season, when more resources are available and the chance of establishment increases (Pennington *et al.*, 2009; Maestre *et al.*, 2016; Allen *et al.*, 2017). However, variations in climatic variables such as rainfall amount and temperature may occur between years and thus induce changes in ecological processes and consequently in the tree communities demographic rates and biomass (Toledo *et al.*, 2011; Niu *et al.*, 2014; Allen *et al.*, 2017; McDowell *et al.*, 2020).

These variations can also occur as changes in the timing of wet or dry seasons that may influence the stability of SDTF tree communities, since structured ecological patterns and process are affected (Maestre *et al.*, 2016; Allen *et al.*, 2017). The tree communities stability has been defined as the absence of large temporal fluctuations in attributes such as floristic composition, diversity (species richness and equability), demographic patterns and total biomass (Lehman and Tilman, 2000; Donohue *et al.*, 2016; McDowell *et al.*, 2020). Such fluctuations are naturally expected in ecological communities and are commonly responses to natural factors, such as climatic seasonality, and or/also to anthropic disturbances that may destabilize it and determine the forest successional dynamics and its structural development (Lewis *et al.*, 2009; Swanson *et al.*, 2011; Donohue *et al.*, 2016; Swenson *et al.*, 2020).

These tree community temporal changes in trees density, biomass, richness and floristic composition, should be considered differently across the temporal scales (Donohue *et al.*, 2016; McDowell *et al.*, 2020). Thus, while changes in structural variables such as density and biomass can be observed in short time-scale (Phillips and Lewis, 2014; Prado-Junior *et al.*, 2016), changes in composition are more subtle (Esquivel-Muelbert *et al.*, 2017; Feeley *et al.*, 2020). In this context the long-term monitoring of communities is a main issue for scientific efforts, since allows to understand the complexity of ecological processes, to

evaluate the tree communities stability, and also to design future scenarios for the ecosystems functioning (Bello *et al.*, 2020; McDowell *et al.*, 2020).

However, there is still a lack of investigations about temporal changes of seasonally dry tropical forests functionality. These forests have historically received less attention from the scientific community (Pennington *et al.*, 2009; Sunderland *et al.*, 2015), and the most studies are focused on the floristic and structural characterization in a space approach (Albuquerque *et al.*, 2012; DRYFLOR, 2016; Souza *et al.*, 2019; Maia *et al.*, 2020). Therefore, studies that analyze the tree communities dynamic in SDTF are scarce (Albuquerque *et al.*, 2012; Reis *et al.*, 2017), instead of other vegetation types such as the Rain Forests that have been had monitoring for decades (Lewis *et al.*, 2009; Phillips and Lewis, 2014; Brien *et al.*, 2015; Meyer *et al.*, 2015; Roitman *et al.*, 2016; Santos *et al.*, 2018; Sullivan *et al.*, 2020).

Thus, here we aimed to characterize the seasonally dry tropical forests temporal patterns by monitoring three fragments (42 plots) for 10 years. For this we evaluated whether the tree community attributes of individuals density, biomass, species richness and floristic composition varied throughout the evaluated period. We start from the hypothesis that the SDTF tree communities present its dynamic patterns characterized by temporal fluctuations that configure an instability pattern, since these patterns have been observed for other tropical forests.

MATERIAL AND METHODS

Study area

The studied areas are three fragments of seasonally dry tropical forest located in the southern limit of the Brazilian Caatinga domain, in Juvenília (14°26'04"S; 44°10'67"W), north of the Minas Gerais state, Brazil (Fig. 1). The climate in the region is classified as Köppen Aw/As (tropical dry winter) with average temperature of 24.6 °C and average annual rainfall of 868 mm, distributed in two contrasting periods (Santos *et al.*, 2012). The relief is flat in the three fragments and the altitude average is 450 m. The landscape is characterized by degraded pastures and abandoned areas in initial stage of regeneration. The vegetation in the studied fragments are classified as Arboreal Caatinga, characterized as a forest type of up to 20 m where most of the species are deciduous during the dry season (Santos *et al.*, 2012). This issue was addressed in Santos *et al.* (2012), in which this vegetation type was recognized as the arboreal expression of the Caatinga Domain flora.

Data collection

We made three forest inventories in the fragments in 2005, 2010 and 2015. In 2005, we systematically allocate 42 sampling units of 400 m² (20x20m) distributed among the fragments, 20 in fragment 1 (Vale Verde), 12 in fragment 2 (Lapinha) and 10 in fragment 3 (Poço da Jia). Within each sample unit we measured and identified at the

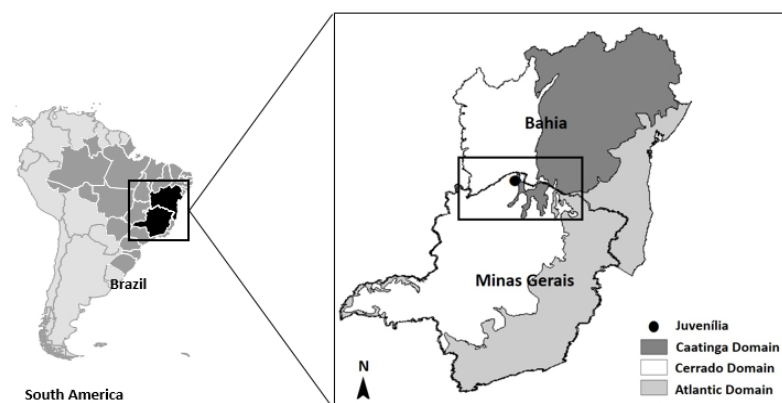


Fig. 1 Location of study areas (Juvenilia) in the state of Minas Gerais, Brazil and South America, and in relation to the Brazilian phytogeographic domains.

species level all arboreal individuals with circumference at breast height (CBH) ≥ 10 cm. Individuals with more than one stem were included when the sum of squares root of their circumferences reached the inclusion criterion. The botanical identification followed the APG IV (ANGIOSPERM PHYLOGENY GROUP – APG, 2016) and was carried out in the field by specialists. In the following forest inventories (2010 and 2015), all individuals found in previous inventories were measured again, in addition to measure the individuals who met the criterion (recruits) and count the dead individuals in the period between measurements.

Data analysis

Initially we evaluated whether the density (tree. ha^{-1}), biomass (ton/ha), biomass per individual (ton) and species richness varied significantly between the years of measurement. To test it we used generalized linear generalized models (GLMM), using each of the attributes cited as response variable, the years of measurement as a fixed explanatory variable. Next, we evaluated the communities' temporal trend for tree mortality and recruitment; biomass gain and loss; and in relation to temporal species substitution. For this, we calculated the annual rates of Mortality (M) and Recruitment (R) of individuals, Gain (G) and Loss (P) of biomass (Sheil *et al.*, 2000) and temporal beta diversity for the intervals between inventories (2005-2010 and 2010-2015). Here we also used GLMM with the dynamic variables as response variable and the interval of measurement as explanatory variable.

For all analysis, we used "plot" and "fragment" as random factors to deal with the repeated measures at the same plot and the fragments, in order to control the spatial autocorrelation found in models residuals. For density and richness, we used the Poisson family with "log" link function, while for the other variables we used the Gaussian family and the "identity" link function. When necessary, we performed transformations on the response variables in order to achieve the variance homogeneity and residuals normality. All selected models were absent of spatial autocorrelation.

The biomass values were obtained for each tree using the Pantropical equation of Chave *et al.* (2014), through the Biomass package (Rejou-Mechaine *et al.*, 2017),

that is broadly used to obtain the above-ground biomass (AGB) using data of diameter, species wood density and an E measure of restrictiveness. All analyzes were performed in the R Studio version 3.3.1 program, using the packages vegan, betapart, lme4, MuMin, lmerTest and ncf.

RESULTS

The Seasonally Dry Tropical Forest communities were floristically stable, but with significant temporal changes in structure and dynamics. Tree density ($\text{ind}.\text{ha}^{-1}$) decreased significantly from 1,606.5 trees. ha^{-1} in 2005 to 1,480.4 trees. ha^{-1} in 2015 (est=-0.03; $p=0.0028$) (Fig. 2a), while the total biomass increased significantly from 104.5 ton. ha^{-1} in 2005 to 122.1 ton. ha^{-1} in 2015 (est=0.07; $p<0.01$) (Fig. 2a) and the biomass per tree increased significantly from 0.065 ton in 2005 to 0.082 ton in 2015 (est=0.02; $p<0.01$) (Fig. 2b). We thus have a scenario of the expected temporal changes in community structure, in which the fragment space in occupied by less trees and that the remaining trees has their mean biomass value increased.

We found tree mortality was stable in about 1.4 $\%.\text{year}^{-1}$ (est=0.01; $p=0.36$) (Fig. 3a), while tree recruitment has declined significantly over time from 2.6 to 1.6 $\%.\text{year}^{-1}$ (est=-0.01; $p=0.01$) (Fig. 3a). Biomass loss decreased significantly over time from 4.5 to 1.6 $\%.\text{year}^{-1}$ (est=-0.92; $p=0.01$) (Fig. 3b), while the gain increased, but not significantly (est=0.01; $p=0.36$) (Fig. 3b). In this context, the biomass increase is main related to the size increase of remaining trees, since recruitment is not increasing over time. Although we found structural temporal changes, the community species composition was stable, since species richness (est=-0.01; $p=0.78$) (Fig. 4a) and the species substitution (est=-0.01; $p=0.65$) (Fig. 4b) did not change significantly over time. This result indicates a temporally stable composition in the community, and that temporal changes may had occurred just through punctual changes in the representativity of species already established.

This trend of biomass increment is related to a set of 11 dominant species that are between the 10 first species with high increment between 2005 or 2010 or between 2010 and 2015 (Tab. 1). The first 10 species with the highest increment represent 75.73 % of the total value between

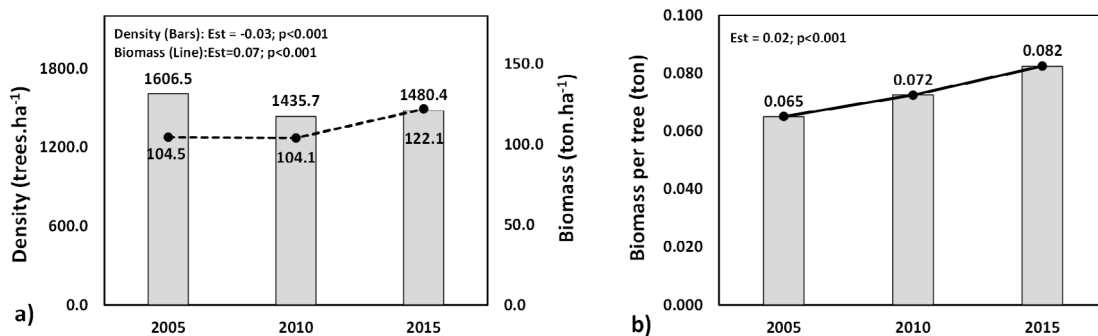


Fig. 2 A: Total of tree density (tree.ha⁻¹) (bars - left axis) and Biomass (ton.ha⁻¹) (black line – right axis) for the three years of measurement; B: Biomass per stem (ton) (bars and black line) for the three years of measurement for the studied seasonally dry tropical forests in Juvenília, Minas Gerais, Brazil. The number on the bars in the fig. a refers to the tree density, while the numbers inside de bars refers to the biomass in each year. The “Est” and “p” refers respectively to values of Estimate and p-value in the generalized linear mixed models for each response variable considered.

2005 and 2010 and 70.45 % between 2010 and 2015 (Fig. 5; Tab. 1), while the remaining increment is represented by 82 species in the first interval and by 80 species in the second, demonstrating an uneven growth pattern in biomass between species. Only 1 species present among the 10 in the first interval is not included in the 10 of the second interval, alternating in the 11th position with the species that occupied this position previously. Thus, the forest increment can be represented by a set of 11 species that only change in the increment rank positions.

DISCUSSION

The seasonally dry tropical forests (SDTF) communities temporal patterns was characterized by floristic stability and significant temporal changes in structure and dynamic. However, the SDTF communities are changing towards more stable stages by the biomass increase and also by the stability of mortality, richness and species substitution over time. These results are probably related to the main SDTF characteristics and to its component species. These forests present ecological processes and evolutionary history directly associated with climatic seasonality, which is

its main restrictive factor (Pennington et al., 2009; DRYFLOR, 2016; Pennington et al., 2018).

The plants in SDTF commonly present adaptations such as stem photosynthesis and reserves tissues that allow the maintenance of growth in initial stages of drought and/or less severe drought, and other adaptations as deciduousness and resprout that ensure the survival in rainfall absence (Dupuy et al., 2012; Santos et al., 2014; Corlett et al., 2016; Tettela-Rangel et al., 2017; Souza et al., 2019). By increasing the individuals survival, theses adaptations may avoid the mortality of species and consequently reduce the occurrence of large biomass losses (Sheil et al., 2000; Maestre et al., 2016; McDowell et al., 2020).

The significant decrease in recruitment may have occurred because of two non-exclusive hypotheses. The first one is related to the dry season intensification, since the germination in these forests is a markedly seasonal process occurring during the rainy season (Morton et al., 2011; Silveira et al., 2016). As result, a shorter rainy season could reduce the several species germination and a longer dry season could lead individuals to death before their establishment, resulting consequently in lower recruitment rates (Silveira et al., 2016). The second one refers to the

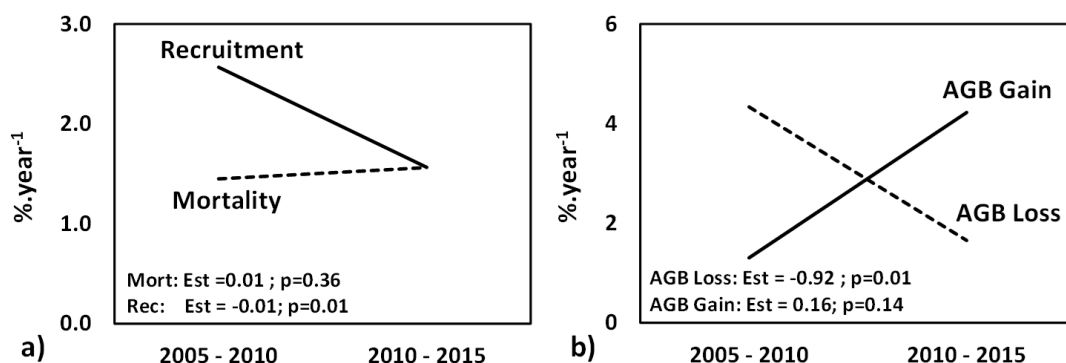


Fig. 3 Annual Taxes of individuals Recruitment and Mortality (%/year) for the two intervals between years of measurement (a); Annual Taxes of Biomass (AGB) Gain and Loss (%/year) for the two intervals between years of measurement for the studied seasonally dry tropical forests in Juvenília, Minas Gerais, Brazil (b). The “Est” and “p” refers respectively to values of Estimate and p-value in the generalized linear mixed models for each response variable considered.

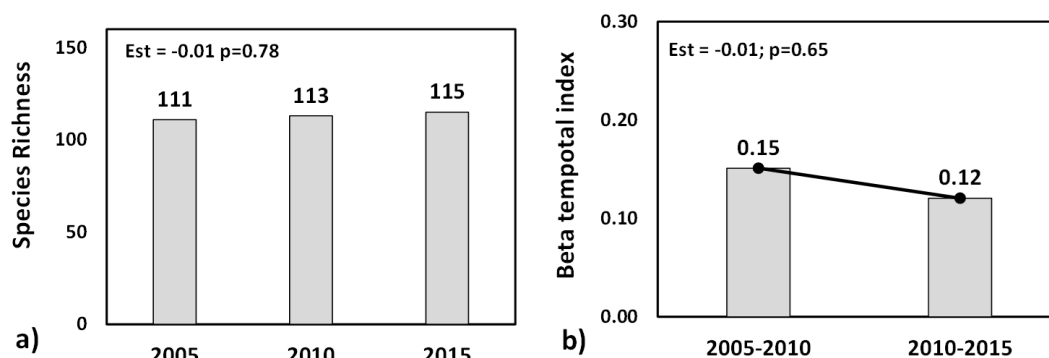


Fig. 4 Total species richness for the three years of measurement (a); Temporal Beta diversity (temporal species substitution) (Bars and black line) for the two intervals between years of measurement for the studied seasonally dry tropical forests in Juvenília, Minas Gerais, Brazil (b). The “Est” and “p” refers respectively to values of Estimate and p-value in the generalized linear mixed models for each response variable considered.

community changes towards temporal stability, which result in biomass increase and consequently in a greater ground coverage and occupation that may reduce the space for the recruitment of new individuals (Lebrija-Trejos *et al.*, 2010; McDowell *et al.*, 2020).

The tree communities biomass is determined by three processes: biomass gain by tree recruitment, biomass growth of surviving trees and loss of biomass due to mortality, and this last tends to be the major determinant of biomass change (Brienen *et al.*, 2015; Rozendaal and Chazdon, 2015; Prado-Júnior *et al.*, 2016; McDowell *et al.*, 2020). Thus, with reduced recruitment and mortality stability, the biomass increase was conditioned by the growth of surviving trees, mainly between dominant species that increase both its total and per individual biomass. This result is demonstrated by the biomass increase related to the increment of few dominant species that account for more than 70% of the total increment in the two intervals.

This result may be related to the biomass ratio hypothesis proposed by Grime (1998), that predicts that ecosystem processes are driven by the (traits of the) most abundant species in community (van der Sande *et al.*, 2017). In dry forests, these dominant species often are related to conservative characteristics such as high wood density and

lower specific leaf area, that commonly is associated to less hydraulic failure and to transpiration reducing (Poorter and Bongers, 2006; Pineda-García *et al.*, 2013; Prado-Junior *et al.*, 2016). By resisting to dry conditions, these species may have their success improved in drought-stressed systems and hence increase their high productivity and biomass storage, and consequently the seasonally dry tropical forests productivity and biomass as a whole (Prado-Junior *et al.*, 2016; van der Sande *et al.*, 2017).

Furthermore, all these high-incremental species are described as SDTF characteristic species (Prado and Gibbs, 1993; Santos *et al.*, 2012; Mogni *et al.*, 2015; DRYFLOR, 2016) with some of them occurring widely in different nuclei, such as *Myracrodruon urundeuva* Allemão, *Anadenanthera colubrina* (Vell.) Brenan, *Tabebuia impetiginosa* (Mart. ex DC.) Stand., *Commiphora leptophloeos* (Mart.) Gillett and *Schinopsis brasiliensis* Engl. (Prado and Gibbs, 1993; Caetano *et al.*, 2008; Pennington *et al.*, 2009; Mogni *et al.*, 2015; DRYFLOR, 2016). These species can be considered as the most efficient in exploring the available resources, and its wide occurrence can be an indication of ecological plasticity, since the several nuclei present important environmental differences (Pennington *et al.*, 2009; DRYFLOR, 2016; Pennington *et al.*, 2018).

Tab. 1 Most representative species in Biomass increment with their respective values in ton and percentual (%) in relation to the community as a whole, for the two intervals between forest inventories for the studied Seasonally Dry Tropical Forests in Juvenília, Minas Gerais, Brazil.

Species	Inc 05-10 (ton)	%	Inc 10-15 (ton)	%
<i>Anadenanthera colubrina</i> (Vell.) Brenan	4.01	14.19	2.97	12.24
<i>Caesalpinia microphylla</i> Mart.	0.29	1.01	1.06	4.36
<i>Commiphora leptophloeos</i> (Mart.) Gillett	0.94	3.32	1.24	5.10
<i>Handroanthus ochraceus</i> (Cham.) Mattos	2.38	8.41	1.56	6.44
<i>Handroanthus spongiosus</i> (Rizzini) S.Grose	1.50	5.31	1.73	7.11
<i>Myracrodruon urundeuva</i> Allemão	5.38	19.00	3.76	15.49
<i>Piptadenia gonoacantha</i> (Mart.) J.F. Macbr.	1.25	4.41	1.12	4.61
<i>Poincianella pluviosa</i> (DC.) L.P.Queiroz	1.06	3.74	1.07	4.41
<i>Pseudopiptadenia leptostachya</i> (Benth.) Rauschert	1.87	6.62	1.68	6.90
<i>Schinopsis brasiliensis</i> Engl.	1.15	4.05	0.92	3.79
<i>Tabebuia impetiginosa</i> (Mart.ex DC.) Stand.	1.89	6.69	0.96	3.93

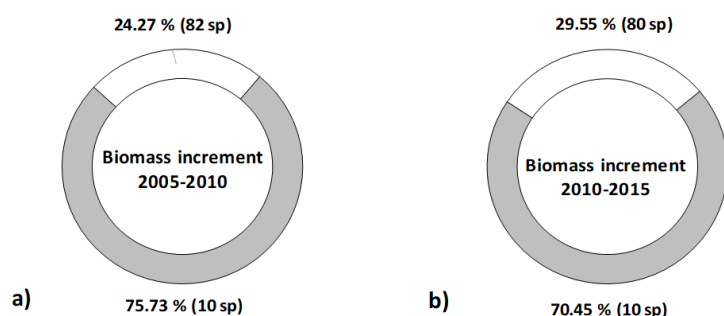


Fig. 5 Representation of the percentage increment and its related number of species for the first interval (2005-2010) (a) and for the second interval (2010-2015) (b) between measurements for the studied seasonally dry tropical forests in Juvenília, Minas Gerais.

The stability in richness and species composition over time found is related to the mainly restrictive SDTF environmental characteristics, such as the marked climatic seasonality, high temperatures and high light intensity. These harsh conditions select species that present functional characteristics that allow to resist to its conditions (Cadotte and Tucker, 2017; Tetetla-Rangel *et al.*, 2017), and that tend to establish and persist in environments which they are already well adapted (Ackerly, 2003; Donohue *et al.*, 2016; Cadotte and Tucker, 2017; Swenson *et al.*, 2020).

In this context, since species in harsh ecosystems such as the SDTF tend to present a great ecological specialization by habitat, along the forest dynamic the dead individuals tend to be replaced by members of their own species (Connell and Slatyer, 1997; Swenson *et al.*, 2020). This process is one of the most important diversity maintenance mechanisms (Connell and Slatyer, 1977; Chesson *et al.*, 2018), since they improve the communities local diversity (alpha), endemism and beta diversity (DRYFLOR, 2016). Besides this, the stability in species composition may also be associated with the sites good state of preservation, since disturbances is an important driver of changes in natural communities (Cavalcanti *et al.*, 2009; Swanson *et al.*, 2011; McDowell *et al.*, 2020).

The SDTF were historically neglected by the scientific community, with still incipient knowledge about its ecological patterns (Allen *et al.*, 2017; Sunderland *et al.*, 2015). For example, while for Rainforest studies with more than 20 years are common (Lewis *et al.*, 2009; Phillips and Lewis, 2014; Esquivel-Muelbert *et al.*, 2017; Sullivan *et al.*, 2020), the present study represents with 10 years of monitoring one of the largest periods already registered for Seasonally Dry Tropical Forest. The construction and improvement of this knowledge is urgent considering the importance of these forests for biodiversity and ecosystem services provision, and to their conservation current state by the intense land conversion and the low insertion in Conservation Units (Sunderland *et al.*, 2015; DRYFLOR, 2016; Maestre *et al.*, 2016).

CONCLUSION

The Seasonally Dry Tropical Forests temporal patterns are associated to different trends in relation to other vegetation types by presenting floristic stability and changes to more stable stages, with crescent increment of a set of important SDTF species. These responses are driven

by the main ecological environmental factors present in this vegetation type, such as the climatic seasonality, that is extremely important also in contexts of environmental changes in macro and local scale, such as from climate changes and logging.

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AUTHORSHIP CONTRIBUTION

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Funding: CRS, RMS

Database: CRS, ABMS, VAM, PAC, GGPP, NCAF, PFS, POG, RMS

Processing: JDM, PFS, CRS, ABMS, VAM, RMS

Analysis: CRS, VAM RMS

Writing: PFS, CRS, ABMS, VAM, GGPP, NCAF, PAC, RMS

Review: CRS, ABMS, VAM, GGPP, NCAF, PAC, PFS, POG, RMS

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